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THE SCARABAEIDAE DUNG BEETLES OF THE ABERDARE NATIONAL PARK, REPUBLIC OF KENYA: ECOSYSTEM SERVICES AND FACTORS AFFECTING DIVERSITY AND ABUNDANCE.

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A thesis submitted in partial fulfilment of the

Requirements of the Manchester Metropolitan

University for the degree of Doctor of Philosophy

June 2018

DEDICATION

I dedicate this thesis to my Grandmothers, who each in their own way inspired me to succeed and follow my dreams.

ACKNOWLEDGMENTS

This thesis would not have been possible without the help of numerous friends and colleagues both in the UK and in Kenya. Darren Mann at the Oxford University Museum of Natural History kindly spent hours and in some cases, days, helping me understand the intricacies of East African dung beetle identification. Much of this project would be rendered impossible without his help and support throughout the years. I will miss our late-night discussions, and dung beetle genitalia extractions accompanied by super strong coffee, cherry tobacco and Peruvian panpipe music. I can only hope that in some small way I can continue to inspire the next generation of dung beetle ecologists with the same enthusiasm and patience that Darren has shown me.

Thanks must also go to my friends and colleagues at the National Museums Kenya in Nairobi who ensured my export permits were issued every year without delay. Special thanks must go to Reuban Mwajuma who provided me with a trustworthy field vehicle and in one instance drove all night with a spare part, then turned back around to Nairobi before daybreak to make sure I could continue fieldwork without delay. Asante Reuban!

My supervisors Martin Jones, Ed Harris, and Phil Wheater have helped and encouraged me along this sometimes rocky journey to completion. I thank them all for their dedication and for seeing the potential in me, which at times I must admit was only apparent to them. Dr Liz Price, Dr Neil Cresswell, and Professor Stuart Marsden provided much of the financial support for the final years of this project. I thank you all for your benevolence and hope you can see your investments were worthwhile. This PhD has taught me many things but has reinforced in me the belief that the world is run on the small acts of kindness we commit daily.

Lastly, I wish to thank and apologize to my friends and family who tolerated my extended periods of absence when I was off conducting fieldwork in Kenya, too busy with work in the UK, or mentally absent but in the same room, dreaming of dung beetles. The future starts here.

DECLARATION

This dissertation is the result of my own work and includes nothing, which is the outcome of work done in collaboration except where specifically indicated in the text. It has not been previously submitted, in part or whole, to any university of institution for any degree, diploma, or other qualification.

Signed:______Roisin Stanbrook____

Date:_______11th May 2018____

PUBLICATIONS ASSOCIATED WITH THIS THESIS

Roggero, A., Stanbrook, R., Josso, J-F., Barbero, E., Palestrini C (2017) Phylogenetic relationships of Epidrepanus within the subtribe Drepanocerina (Coleoptera: Scarabaeidae: Scarabaeinae: Oniticellini), with the description of two new species. *Zootaxa,* 4320 (1), 1-24.

Stanbrook, R., Raisin, C., Vulinec, K. (2017) Observations on the Tunneling Behavior and Seed Dispersal Efficacy of *Copris nubilosus* (Kohlmann) (Coleoptera: Scarabaeinae: Coprini). *The Coleopterists Bulletin* 74 (1), 1-4.

Stanbrook, R. (2018) Assessing the nutrient status of forest elephants in the Aberdares NP, Kenya. *Pachyderm 59:19-25.*

Manuscripts in review

Chapter 4: Stanbrook, R., Wafula, G.W., Jones, M.J., Harris, W.E. 'Experimental estimate of soil nutrient exchange in an Afrotropical high elevation forest: the role of dung beetle community complexity' *Acta Oeceologica*

Manuscripts in preparation

Stanbrook, R., Josso, J-F. Descriptions of two new Kenyan dung beetles (Coleoptera: Scarabaeinae) and notes on their distribution. *Catharsius La Revue*

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Abstract

Dung beetles are a species group highly lauded for their sensitivity to land use change and their ecosystem service provision. There are few studies of the dung beetle communities found in Afromontane forests despite the fact these forests form part of a global hotspot of biodiversity. I sampled the dung beetle community in six habitats across an altitudinal gradient in the Aberdare National Park in central Kenya using standardised trapping methods.

This study provides insight on the distribution, diversity and abundance of dung beetles and sheds new light on how dung beetle abundance and distribution respond to biotic and abiotic changes in Afromontane ecosystems. It has also identified that fluctuations in abundance occur in accordance with both elevation and habitat variability. The interspecific response sensitivity to even slight modifications in habitat type has facilitated the identification of eight potential ecological indicator species and showed that gradients in their population response (abundance) reflect overall preference for open vegetation or closed canopy forests within the Aberdare National Park.

Due to their biogeographical history and specialisms the dung beetles of the Aberdare National Park may be particularly negatively affected by temperature increases associated with global warming for two reasons. Firstly, 50% of the variation in dung beetle species richness is attributable to mammal abundance, the presence of herbivores plus the distance between sampling points; and secondly, there is both intra- and interspecific variation in elevational placement and habitat preference of species and individuals.

The results of this study have important conservation implications. This study underscores the importance of conserving as much habitat heterogeneity in mountain ecosystems as possible. Differences in dung beetle diversity and species richness between habitat types are manifest and

the high turnover of species between altitude bands means that all locations within the ANP should be afforded equal protection.

1 Introduction

1.1 BACKGROUND

Invertebrates constitute the bulk of known macrodiversity on Earth and dominate virtually every ecosystem in terms of species richness, animal biomass, and critical ecological functions (Gerlach et al., 2013). Dung beetles in particular are a discernible component of the insect fauna found in Afrotropical forests (Krell et al., 2003; Banks et al., 2010). Dung beetles use dung produced by vertebrates, particularly mammals and occasionally that of birds and reptiles (Davis, 1998) as food and as a substrate for oviposition (Klemperer, 1979; Estrada et al., 1998). The presence of a diversity of dung-producing mammals has effects on the relative abundance and diversity of dung beetles (Wardle and Bardgett, 2004; Filgueiras et al., 2009; Enari et al., 2013). Resources can be extremely patchy both spatially and temporally leading to resource partitioning and competition between co-occurring species. Thus, partitioning and intra- and interspecies competition plays a major role in structuring dung beetle communities (Horgan and Fuentes, 2005).

Based on their nesting strategies, African dung beetles are divided *sensu lato* into three functional groups; rollers (telecoprid nesters), tunnelers (paracoprid nesters) and dwellers (endocoprid nesters) (Doube, 1990). Telecoprids form balls from a dung pat which are rolled away often with a male and female cooperating. A tunnel is dug and the relocated dung is buried for use in both feeding and breeding. Tunnelers create underground chambers at various depths beneath pats and construct complex nests using dung from the pat. Dwellers breed in the dung pat itself. This functional stratification allows dung beetles to minimize the intense competition for limited food and space and also to protect the food from adverse environmental conditions (Klemperer, 1983; Ilka Hanski and Cambefort, 1991).

The importance of different community traits in ecosystem function has garnered increasing interest in recent years because of growing alarm over altered species abundance and diversity patterns under anthropogenic change (Cardinale et al., 2012). There is increasing concern about the conservation of dung beetles which are threatened by habitat change, the reduction of dung resources and an increasing use of anthelminthic veterinary medicine to treat cattle (Nichols et al., 2007; Sutton et al., 2014; Bogoni et al., 2016a). Dung beetles are deemed an ecologically important taxon due to their ability to relocate nutrient-rich dung underground as part of their breeding process (Spector, 2006; Nichols et al., 2008; Nichols, 2013; Manning et al., 2016). This behaviour plays a crucial role in (i) soil nutrient cycling; (Bang et al., 2007; Yamada et al., 2007; Menéndez et al., 2016); (ii) secondary seed dispersal (Vullnec, 2002; Griffiths et al., 2015; Stanbrook et al., 2017) and (iii) parasite suppression (Beynon et al., 2012; Nichols and Gómez, 2014). Dung beetles are known to contain stenotopic species, which display strong associations with habitat and/or dung type. This high fidelity to certain dung types and habitat types has recently given rise to literature describing dung beetles as bioindicators for assessing sustainability within tropical forests (Slade et al., 2011; Korasaki et al., 2013; Bicknell et al., 2014a)

1.1.1 Functional Guilds

Dung beetles are characterized according to the way they use and disrupt dung. Scarabaeid dung beetles have been separated, on the basis of their dung relocation behaviour *senso lato*, into four primary groups (Hanski and Cambefort, 1991). A competitive hierarchy based on the ability to compete for ephemeral and patchy dung resources secondarily divides dung beetles into one of seven functional groups (see Table 1-1). Dung beetle body size is one important determinant of their capacity to compete for dung and is used to divide groups of species with similar habits into separate functional groups. Larger and more competitive species are able to relocate greater amounts of dung faster and further from the original dung source than smaller less able species (Gregory et al., 2015).

Table 1-1 Classification and description of functional guilds *sensu* Doube (1990) and the effect of each functional group on dung removal

Functional Guild	Description	Effect on Dung Removal
FGI	Large telecoprids >400 mg dry weight	Complete and rapid dung removal
FGII	Small telecoprids <400 mg dry weight	Complete dung removal within 24 h
FGIII	Fast burying paracoprids	Complete dung removal over several days
FGIV	Larger slow burying paracoprids > 10 mg dry weight	Complete burial (some species); complete shredding of pad with little or no burial (other species)
FGV	Smaller slow burying paracoprids <I0 mg dry weight	Shredding of dung pad with little or no burial
FGVI	Kleptocoprids	Shredding of dung
FGVII	Endocoprids	Unknown

1.1.2 Effects of climate change on Afrotropical insects

The high species richness and diversity found in tropical montane habitats are often related to three main factors; (1) an effect of climatic and geological history on biotic evolution; (2) the various environmental impacts on species adaptation mechanisms; and 3) the continuous dispersal of fauna and flora over time. Climatic changes during the Pleistocene Epoch, the time when a number of glacial periods occurred and when climates were very cold and wet, interrupted by warm, dry periods, allowed the formation of refuges (Fjeldsa and Lovett, 1997), which not only served as shelters for a rich diversity of species, but as sources for dispersion to neighbouring areas as warming of the climate allowed species to propagate. In East Africa these refuges are now mostly relegated to the forest archipelago of mountains dotted from southern Tanzania to the Bale mountains in Ethiopia to the Usambaras in Tanzania. (Hedburg, 1969). Altitudinal differences within mountains have also made for very varied climates, promoting the diversification of groups of species, adapted to different environments. The wide diversity of climates combined with local differences owing to geomorphological, edaphic and plant cover features have given rise to a range of microclimates which help generate a wide range of specific niches (Coe, 1969).

Insect biota living on mountains have long been overlooked in terms of their importance and for their ability to act as an early warning indicator for the effects of climatic change on other animals (Hodkinson, 2005). Mountain environments are threatened with change worldwide due to climate change. The Eastern African Afromontane forest is getting increased attention in conservation studies (Loader et al., 2014) because of its high endemicity levels and shrinking geographic distribution, yet few studies have evaluated the implications of mountain living on dung beetle populations. East Africa is thought to be particularly affected by the future effects of climate change. It is predicted that the average temperature for East Africa will increase by approximately 3.2 °C by 2080 and heat waves and warm spells will increase (IPCC, 2007). Such temperature increases will affect the suitability of certain agricultural crops, creating the need to introduce other crop types leading to decreased agricultural yields. These temperature increases will also reduce the remaining montane glaciers in East Africa – which have already shown more than 80% decline since the 1990s (EAC et al., 2016). Precipitation rates will also change. The IPCC (2014) notes that changes in precipitation will greatly affect the climate in Africa. East Africa will become wetter, both during the 'long' and 'short' rainy seasons. Future scenarios predict that the current trend towards a drier climate will reverse, but as there is a 15% increase in annual precipitation projected for 2080-2099 compared to 1980-1999, the risk of flooding will increase dramatically. These effects will alter African biodiversity, as species struggle to adapt to changing conditions (Laurance et al., 2011) leading to shifts in the geographical distributions of species and ecosystems. For example, the deciduous and semi-deciduous closed canopy forests such as those found in the Aberdare National Park are predicted to be particularly susceptible to the effects of precipitation change (Hély et al., 2006).

1.1.3 Dung Beetles in African Tropical Forests

In contrast to the usual pattern of high species richness and high abundance found in dung beetle communities in African savannas, forest dung beetles are less species rich (Cambefort and Hanski, 1991). Afrotropical forest dung beetles are of special interest because of the species richness of Afrotropical mammalian fauna. A special element of interest is the presence of essentially two kinds of dung beetles in African forests: (1) the species using the relatively small droppings of omnivorous mammals, and (2) species exploiting the large droppings of the elephant and other large herbivores. The first set of species are widespread and well represented elsewhere in the tropics, but the second set of species are characteristic to Africa only. Most of the information on African forest dung beetles comes from West Africa from Cote d'Ivore and Gabon, from sites situated in the Guinean- Congolese forests (Cambefort and Hanski, 1991). The only previous study to have assessed dung beetles diversity in East African forests occurred in Bundongo forests blocks in 2009 (Nyeko, 2009) and briefly in Kenya and Tanzania in 1975 (Davis and Dewhurst, 1993). Dung beetles from tropical forests tend to be relatively smaller (Klein, 1989) than those found in savannahs and other types of open vegetation and are more likely to be paracoprids (Lopes et al., 2011) rather than have a telecoprid nesting strategy. These differences are thought to have arisen from narrow niche requirements associated with canopy cover, tree density, soil type and the extent and density of vegetation found on the ground (Hanski and Cambefort, 1991).

1.1.4 Dung beetle response to Habitat Change

A recent global meta-analysis (Nichols et al., 2007) of 26 studies of dung beetle community responses to tropical forest modification and fragmentation showed that dung beetle species richness, abundance, and biomass undergo a gradual decline across a modification gradient from intact tropical forest to clear-cut areas, and as forest fragments became smaller and/or more isolated. Dung beetle communities are very sensitive to changes in abundance of food resources, microclimatic variables and soil characteristics (Hanski et al., 1979; Ilkka Hanski and Cambefort, 1991; Osberg et al., 1994; Pryke et al., 2013). Changes in community organization of dung beetles include alterations in species richness, composition, abundance and guild structure. The physical structure of habitats can be an important determining factor in the composition and distribution of dung beetle assemblages (Davis and Sutton, 1998) with a complete species turnover observed across a natural ecotone spanning as little as 100m (Spector and Ayzama, 2003). Consequently, dung beetles are a useful indicator group because they reflect structural differences between biotope types (Carpio et al., 2009; Nichols et al., 2013). From savannahs to tropical forests, dung beetles are highly habitat specific and there are distinct communities of beetles associated with forests, edges and pasture habitats. Although some species can utilize more than a single habitat type, certain species may never be found outside their preferred habitat (Scheffler, 2005).

In contrast to the well documented data on the composition, community structure and habitat preference of dung beetle communities from forests and montane Neotropical regions (Escobar et al., 2006; Braga et al., 2013; Campos and Hernández, 2015) there are few studies of the dung beetle communities of Afrotropical forests despite the fact that they form part of a global hotspot of biodiversity (Myers et al., 2000; CEPF, 2012). Rainforests and Afromontane forests are the most threatened ecotype in Africa due to extensive clear cutting or selective logging, and pressures associated with conversion to agricultural use (European Commission, 2015). Even if forests are not completely lost, reduction in overall size and fragmentation is associated with wildlife loss and consequential reduction in the diversity of available dung types. Dung beetle communities are strongly influenced by dung types and they may change in relation to the availability of different dung types (Andresen and Laurance, 2007; Tshikae et al., 2008). Many dung beetles are stenotopic (Horgan 2007; Horgan 2009) and preferably select coarse fibred dung of non-ruminants, while others prefer the more fluid and fine dung of ruminants, or the odoriferous dung of omnivores (Davis, 1994; Davis, Scholtz, et al., 2002; Holter, 2016)(Davis 1994; Davis 2002; Holter et al. 2002; Krell et al. 2003). The dung of elephants has been demonstrated to be the preferred resource for several African dung beetle species (Davis et al., 2008; Davis and Scholtz, 2010) and it has therefore been used as the bait type for this study.

Elevation and habitat type are often important factors influencing insect communities (Romero-alcaraz and Avila, 2000). Altitudinal variation is believed to be a main factor determining the organization of dung beetle communities in upland areas (Davis et al., 1999; Celi et al., 2004; Herzog et al., 2013). It is generally accepted that species diversity and richness decline with increasing altitude (Wolda, 1987). Numerous studies have attempted to describe the patterns of biodiversity along elevation gradients (Hodkinson, 2005; McCain and Grytnes, 2010; Verdú, 2011) (McCain & Grytnes 2010; Hodkinson 2005; Verdú et al. 2011). However, there is no general pattern of diversity (Rahbek, 1995), and results vary with mountain range and with organism group. This disparate response may be due to different scales and scope of the studies (Rahbek 1995, Escobar et al 2007, Herzog 2013), to different sampling methods (Wolda 1987), and the influence of a large number of variables acting at regional levels (Hodkinson 2005). These results highlight the importance of local studies on specific taxa.

1.2 STUDY AIM AND OBJECTIVES

General aim

To identify the factors affecting the diversity and abundance of Scarabaeidae dung beetles and assess their potential in ecosystem service provision in an Afrotropical forest.

Specific objectives

Given the limited data available on the factors affecting African montane dung beetles this thesis has four objectives; (1) to identify patterns in dung beetle diversity, abundance and distribution; (2) describe the potential for dung beetle ecosystem service provision within the context of dung burial and nutrient cycling; (3) establish the role mammal communities play in determining dung beetle communities and; (4) investigate the effect of altitude on dung beetle morphology.

1.3 THESIS STRUCTURE

In order to address the aims of this study on the diversity and abundance of Scarabaeidae dung beetles and assess their potential in ecosystem service provision, this thesis progresses as follows:

CHAPTER TWO:

This chapter further introduces the dung beetles of the Aberdare National Park (ANP) and their associated forest mammal fauna. This chapter also introduces the climate and geology of the ANP, outlines its unique geographical and environmental nature and its importance as a Protected Area for ecosystem services. I then outline the research approach, general methods and analytical techniques employed in this thesis.

CHAPTER THREE:

To address how habitat type affects dung beetle communities, the diversity and evenness of the dung beetle community within the Aberdare NP was assessed using diversity and dissimilarity matrices. In addition, Indicator analyses were performed to ascertain which beetles are indicators of habitat type, including forest or open vegetation specialist.

CHAPTER FOUR:

This chapter focuses attention on the beneficial effects of dung beetle mediated nutrient cycling in tropical forest ecosystem. Previous studies have assessed how species richness (Yoshihara and Sato, 2015b), abundance (Yamada et al., 2007) functional behaviour (Menéndez et al., 2016), and introduced dung beetle species (Bertone and Green, 2006) affect changes on soil macronutrient status. All these studies occurred within an agricultural context and concluded that dung beetle presence in some form, has a positive effect in enriching soil with macronutrients yet little experimental research is conducted on the nutrient cycling capacity of dung beetles in other types of ecosystem.

CHAPTER FIVE:

This chapter looks at morphological predictors of elevational distribution in *Onthophagus proteus*, a regionally endemic dung beetle. I report on the colour variation and morphology of *Onthophagus proteus* as predictors of its location on an elevation gradient using Conditional Inference Tree modelling. Factors determining intraspecific variation are examined and discussed within the context of sexual selection and the warming of montane environments due to climate change.

CHAPTER SIX:

Chapter Six examines the response of dung beetle species composition, abundance, species richness, and body size to mammalian, spatial and habitat predictors using variation partitioning (Legendre, 2008). The relative importance of mammal and environmental factors are evaluated in the context of dung beetle persistence in the face of mammal decline in tropical forests. Indicator analysis (CLAM) is used to assess the impact of elephant absence of Afromontane dung beetle communities and the repercussions of continuing large mammal decline on dung beetles in tropical areas.

CHAPTER SEVEN:

I summarise the key findings of Chapters 3-6 above, evaluating the major predictors of distribution, abundance of Afromontane forest dung beetles, and how these vary between taxa. Results are placed in a biogeographical perspective and in the context of the few other available studies from other African forest sites and in terms of ecosystem service provision potential. I discuss the intraspecific variation in *Onthophagus proteus* a regional endemic dung beetle. I also discuss the overall significance of environmental and anthropogenic factors for the persistence of dung beetle populations and identify conservation measures to help safeguard these irreplaceable species and communities.

2 CHAPTER 2: STUDY SITE AND GENERAL METHODS

2.1 INTRODUCTION

2.2 ABERDARE NATIONAL PARK

2.2.1 Geography, Topography and Rivers

The Aberdare National Park (ANP) belongs to the northern volcanic sub-region of the eastern Afromontane (EAM) biodiversity hotspot. The hotspot is well known for regional variation in vegetation, rainfall patterns, topography and high levels of endemism across its entire stretch (Taylor, 2015). The ANP lies to the east of the Gregory Rift Valley and is about 80km north of Nairobi and 17km from Nyeri town (0.4167° S, 36.9500° E). It is an elongated massif, running approximately north south, parallel to the direction of the Rift Valley, 60 km to the west of Mt. Kenya. The Aberdare Forest Reserve (AFR), a protected area, surrounds the Park.

The highest peaks are Oldonyo Lesatima (4001m) in the north and Il Kinangop (3906m) in the south (Figure 2-1). Between the two peaks is an extensive moorland region between 3300m and 3700m. Like many East African mountains, the Aberdare range was formed by volcanic activity during the Pleiocene and the elongate form of the range is a result of the lava spillage. As a result, the main peaks and ravines of the ANP run in almost straight lines linked by a series of ridges.

The Aberdare range is the source for at least three river systems: the Malewa, Ewaso Nyiro and Tana. The Malewa River flows south westwards and is responsible for 90% of the water discharged into Lake Naivasha in the Central Kenya rift valley (Gherardi, 2007) whose water level were described as critically low in recent years (Gross, 2006). The Tana river flows eastward from the mountain range. The Muringato, Chania and Ngobit Rivers are tributaries of the Kenya' largest river, the Tana, which traverses 1000 km before flowing into the Indian Ocean, while the Ewaso Ng'iro flows northwards into desert and recharges the Merti aquifer, which extends into neighbouring Somalia.

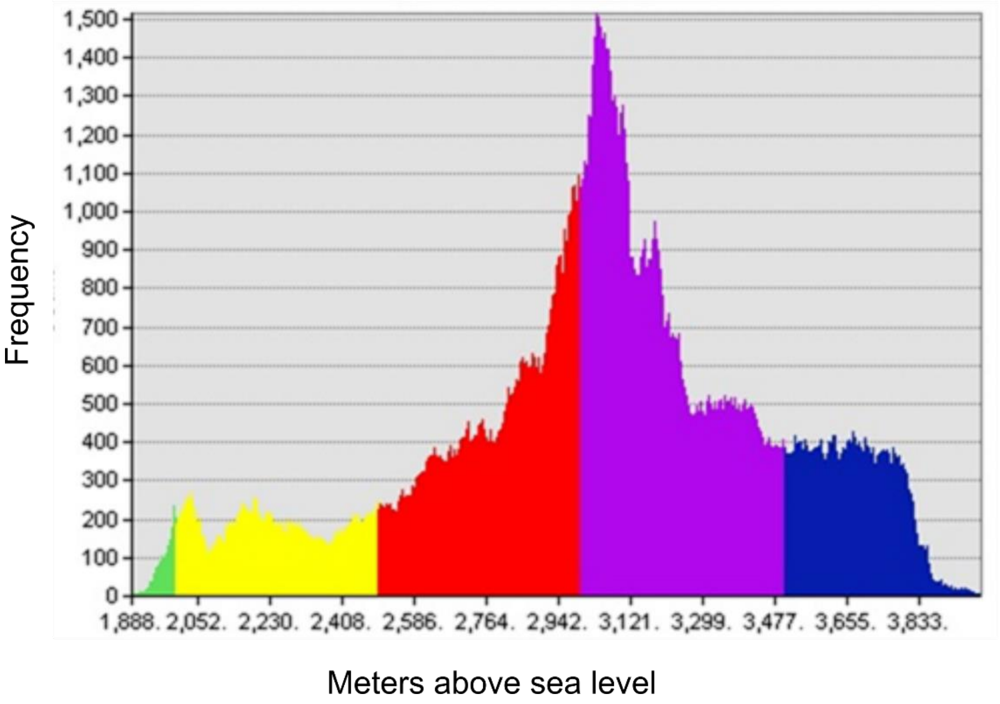


Figure 2-1 The distribution of elevation (m asl) within the boundary of the Aberdare NP. SRTM (Shuttle Radar Topographic Mission) data were obtained from a digital elevation model using a 30m resolution. The colours indicate different altitude bands separated into 500m intervals.

2.2.2 Vegetation

Topographic and edaphic elements modify the distribution of the seven main vegetation types (Bushland, *Juniperus* dominated forest, *Podocarpus* dominated forest *Hagenia* dominated forest, Bamboo and Ericaceous moorland) found within the park (Fig 2-2). The biotopes consist mainly of bamboo, high heath and moorland with large areas of open and closed canopy forest and bushland occurring particularly in the Salient sector that extends eastwards from the main peaks and drops to a level of 1800m (Table 2-1).

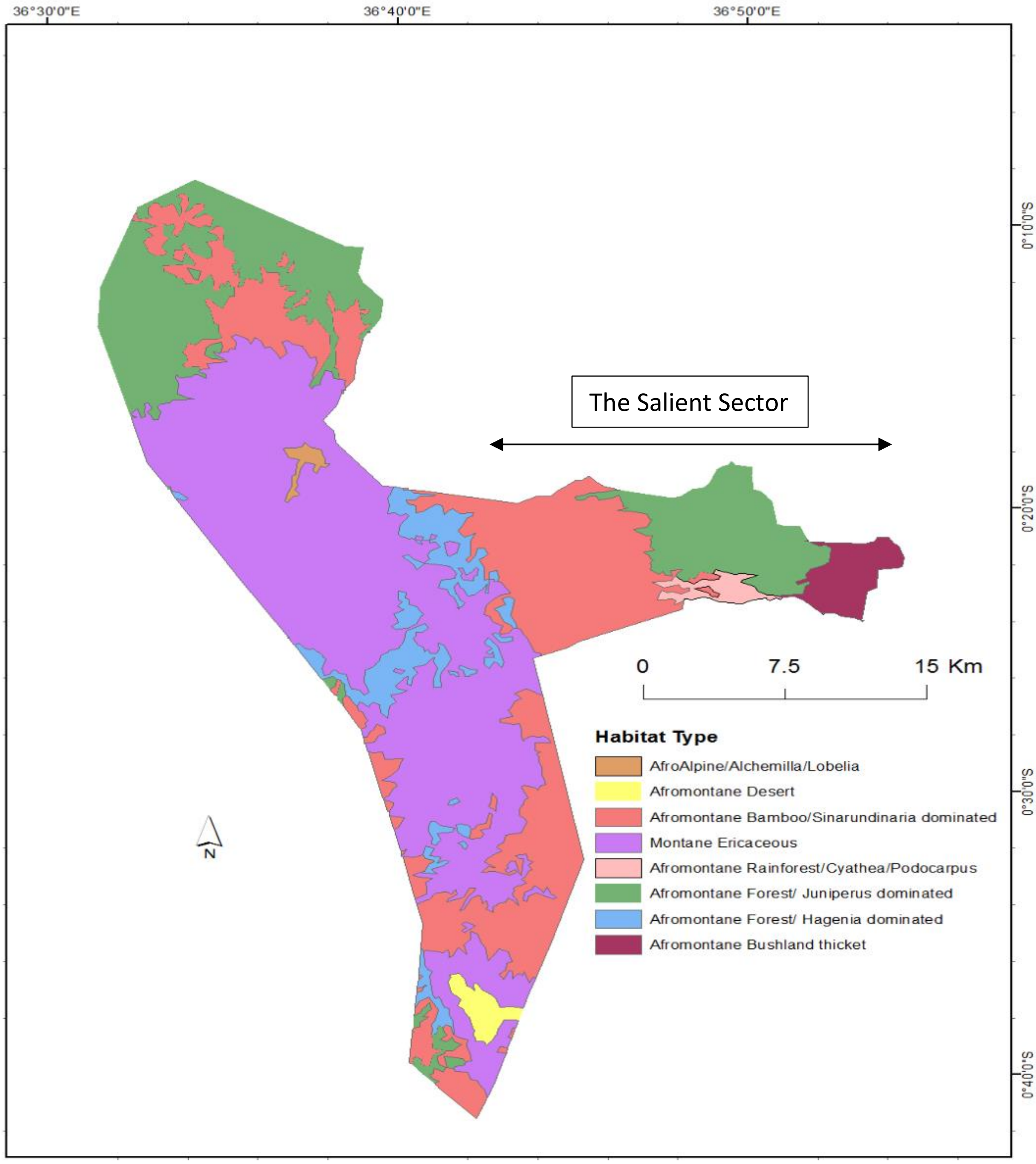


Figure 2-2 The distribution of habitat types found within the Aberdare NP. The map was created using Sentinel-2 data at 10m^2 resolution.

Figure 2-3 Examples of the six habitat types used in this study. (A) Bushland Thicket; (B) *Podocarpus* dominated forest; (C) *Juniperus* dominated forest; (D) *Hagenia* dominated forest; (E) Afrotropical Bamboo, and (F) Ericaceous moorland. Image F courtesy of Boniface Mwalimu.

Table 2-1 Features of the main habitats types within the Aberdare National Park, Kenya. This classification follows White et al., 1983

Name	Type	Altitude range (m) asl	Dominant plant species	Mean ground cover (%)	Mean canopy cover (%)
Bushland thicket	Bushland	1834-2200	*Croton macrostachyus, Chrysophyllum gorungosanum, Olea capensis*	91	63
Juniperus dominated	Forest	2275-2405	*Ekerbergia capensis Juniperus procera*	78	56
Podocarpus dominated	Forest	2416-3150	*Podocarpus spp, Nuxia congesta*	86	43
Hagenia dominated	Forest	3187-3600	*Hagenia abyssinica, Hypericum kenienses*	81	78
Bamboo	Forest	2706-3100	*Sinarundinaria alpine*	17	23
Montane Ericaceous	Tussock Moorland	3672-4001	*Erica arborea, Deschampsia flexuosa*	87	0

2.2.3 Ecosystem services

The Aberdare range is worth Ksh 55.8 billion (£403,000,000) in annual benefits to the Kenyan economy (Kenya Water Tower Agency, 2016) and the upper slopes of the mountain are valuable as a water catchment area. The Tana River provides the majority of hydro-electric power (HEP) generation in Kenya. The Tana and Ewaso Ng'iro rivers flow through arid and semi-arid areas in the north of Kenya. These two rivers also sustain various wetlands. One of these wetlands forms part of the Merti aquifer that is found between the lower reaches of both rivers (Luedeling et al., 2015) and provides essential groundwater. This ground water sustains communities of pastoralists who depend heavily upon its water supply in areas which are significantly drought prone.

The Aberdares are also the main source (90%) of the Nairobi municipal water supply (Mungai et al., 2011). Two dams, the Sasumua and Ruiru, provide Nairobi with water. The Sasumua Dam alone contributes approximately 12% of Nairobi's water supply (Mungai et al., 2011). In this regard, the Aberdare range sustains over 10 million people, including the inhabitants of the city and the people within the various catchment areas and demonstrates the importance of the Aberdare ecosystem as a 'water tower'.

While the slopes within the NP are steep and densely forested, the foothills have been cleared of forest and are intensively farmed. The area around the Park is densely populated as the eastern and north-eastern sides lie directly adjacent to land converted to agricultural use. Many local farmers and households live in small holdings adjacent to the NP and rely on year-round water supply from the mountains, and the stable climate and levels of rainfall locally influenced by the forested slopes. Large-scale commercial enterprises such as horticultural and coffee plantations are also heavily dependent on an almost constant supply of water.

2.2.4 Climate

Temperatures naturally follow an altitudinal gradient. Seasonally, temperatures rise to their peak in December/January, and fall to the lowest mean temperatures in June/July each year (Figure 2-4). The rainfall distribution is greatly influenced by movement of the Inter-tropical Convergence Zone – an area of low pressure created by the confluence of the North East and South East Trade Winds which moves North and South across the tropics. There are two rainy seasons: long rains from April to May, and short rains from

October to November (Ngecu & Ichang'i , 1999). The annual rainfall in the Aberdares ranges from 940 mm - 3220 mm^{-1}, and is maximal in the southeast with an average of 2500mm per annum (Schmitt, 1992a) as the ranges face the rain bearing winds. The north and north-western slopes are the driest, about 700mm per annum being in the rain shadow. There is also a substantial mist effect (Gatano) above 1,500 m over the montane forest and upland heath communities during the months of July and August.

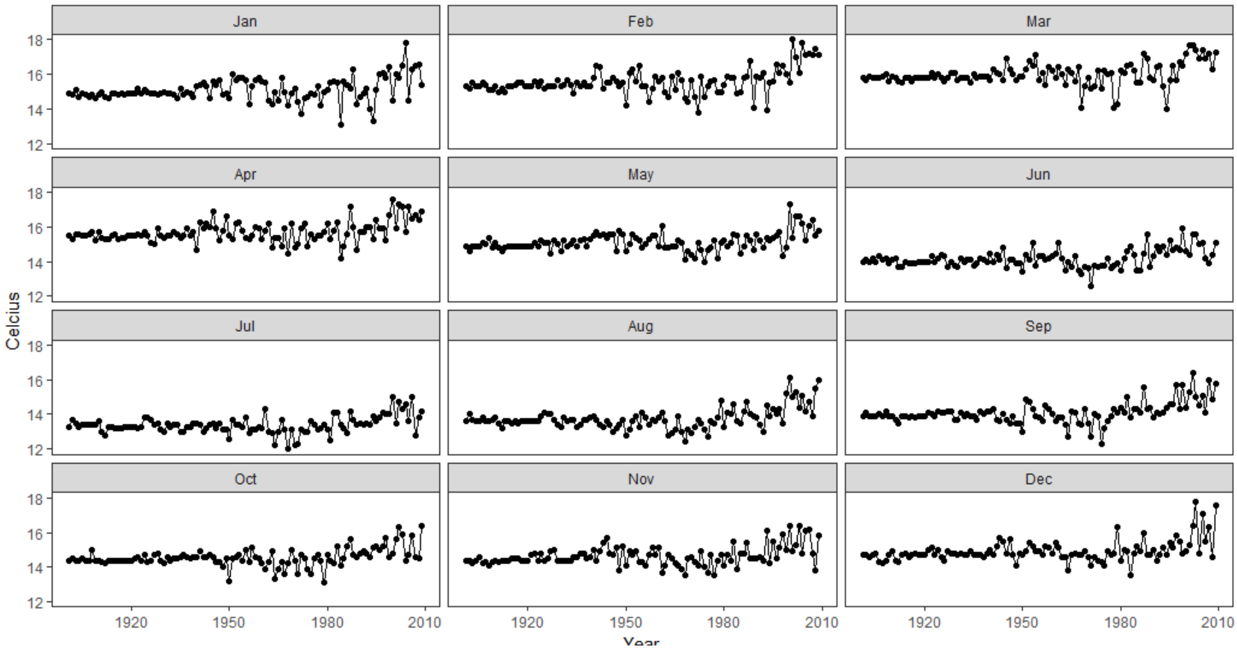


Figure 2-4 Climate data for the Aberdare National Park based on the NOAA monthly climate data (http://www.noaa.gov/) from 1909-2011.

2.2.5 Protected Area Status

The initial boundary containing the Aberdare forest was demarcated and gazetted in 1913 by the Kenya Land Commission and contained 947.7 km^2 of land protected by the Forest Department (Goldammer, 1992). Subsequently, the Aberdare range was divided into two protected areas; a National Park (NP), which was gazetted in 1950 (765.7 km^2), and a Forest Reserve (FR) gazetted in 1962 (182 km^2). The Aberdare NP is defined as a category II protected area by the IUCN (IUCN, 2012). Category II areas are typically large and conserve a functioning ecosystem that may allow tourist infrastructure but only in certain areas (http://www.iucn.org/). In 1988, a charity, Rhino Ark, proposed the fencing of the entire park boundary. The electric fencing commenced in 1989 and was completed in phases over a period of 21 years (Butynski, 1999) becoming at the time, the longest conservation barrier in the world (C.Wambani, *pers.comm*). Initially the fence was constructed to protect the Black rhino population within the park but poaching outstripped fence construction and rhino numbers within the park fell drastically between 1989 and 2009 when the fence was completed. However, the fence has minimized, and appears to have stopped, other illegal activities such as firewood collection and illegal logging and is now being heralded as saving and conserving a whole, much valued ecosystem (Massey et al., 2014).

2.3 DUNG BEETLES OF THE ABERDARE NP

2.3.1 Study Species, Functional Guilds and Communities

STUDY SPECIES

One other previous study was undertaken in 1975 (Davis and Dewhurst, 1993) to describe the community of Scarabaeid dung beetles resident in the Aberdares (Figure 2-5). The study described 19 species in six locations at varying altitudes but was restricted mainly to the Salient sector of the NP (A.Davis, *pers.comm*). Dung beetles were collected with the permission of Kenya Wildlife Service under research permit number NACOSTI/P/15/0573/3206 and under affiliation with National Museums Kenya (NMK). Dung beetles were exported with Material Transfer Agreements from NMK in accordance with Kenyan law.

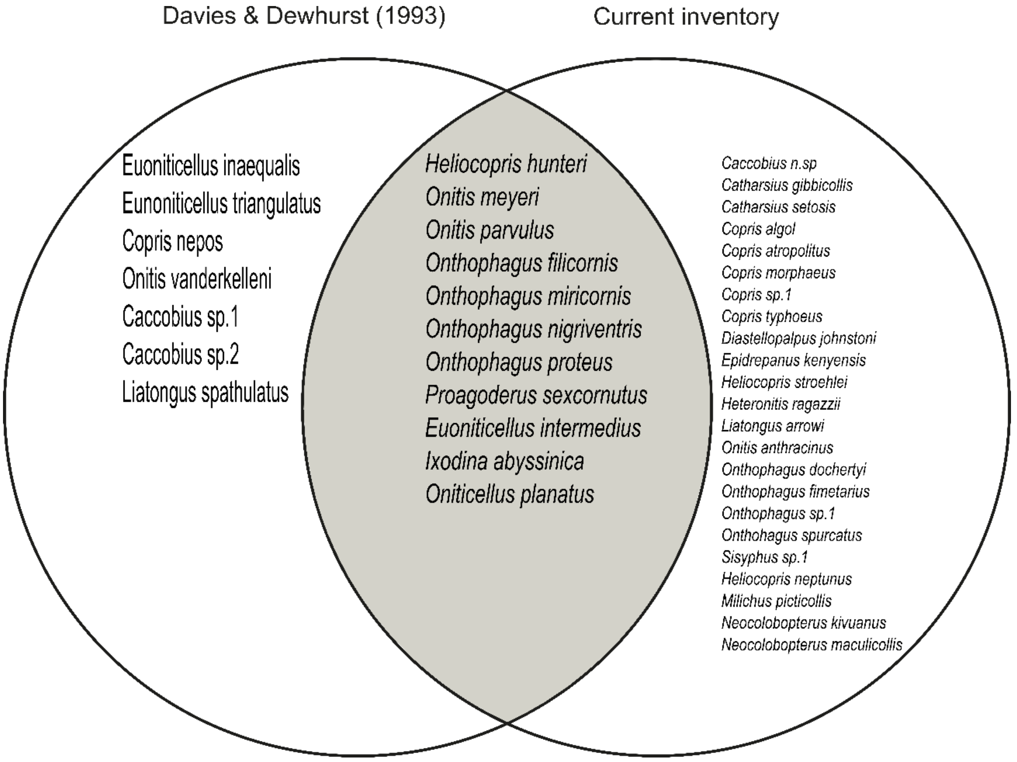


Figure 2-5 The species overlap between a study conducted in 1975 (Davis & Dewhurst, 1993), and dung beetle data collected between 2014-2016 as part of this thesis.

SPECIES ATTRIBUTES AND ECOSYSTEM FUNCTIONS

This study uses the definition of community proposed by Stroud et al., (2015) who defined a community as "a group of interacting species populations occurring together in space" as this definition acknowledges that direct interspecific interactions can give rise to important indirect consequences. Doube (1990) classified functional guilds based on traits associated with dung relocation behaviour. The functional guild classifications for dung beetles of the Aberdare NP are outlined in Table 2-2.

Table 2-2 The classification of Functional Guilds of dung beetles found in the Aberdare National Park *sensu* Doube (1990)

Dung Beetle Functional Guilds				
FGII	FGIII	FGIV	FGV	FGVII
Sisyphus sp.	*Heliocopris hunteri*	*Onitis anthracinus*	*Euoniticellus intermedius*	*Caccobius n.sp*

	Heliocopris neptunus	*Onitis meyeri*	*Liatongus arrowi*	*Epidrepanus kenyensis*
	Heliocopris stroehli	*Onitis parvvulus*	*Milichus picticollis*	*Ixodina abysinnicus*
	Hetronitis ragazzii	*Proagoderus sexcornutus*	*Neocolobopterus kivuanus*	
	Catharsius gibbicollis	*Copris atropolitus*	*Neocolobopterus sengelensis*	
	Catharsius setostris gp	*Copris morphaeus*	*Oniticellus planatus*	
		Copris algol	*Onthophagus dochertyi*	
		Copris typhoeus	*Onthophagus filicornis*	
		Diastellopalpus johnsonii	*Onthophagus fimetarius*	
			Onthophagus miricornis	
			Onthophagus sp1	
			Onthophagus spurcatus	

2.4 MAMMALS OF THE ABERDARE NP

Though mammalian diversity is lower here than in other tropical hotspots, e.g the Usambara’s (Rovero et al., 2014).The forests of the Aberdare’s support important populations of many endemic and non-endemic mammalian species (Butynski, 1999) displaying different feeding habits, which gives rise to the coexistence of various dung beetle species. The African elephant, (*Loxodonta africana*), buffalo (*Syncerus caffer*), and many species of antelopes including the mountain bongo (*Tragelaphus eurycerus isaaci*) are the major mega-mammalian herbivores in the Aberdare forests (Massey et al., 2014).

2.5 STUDY DESIGN

Section 2.3 above describes the dung beetle diversity present within the Aberdare NP and the clines that exist in terms of altitude and habitat type. Twelve transects within six different habitat types (Figure 2-6) and five sites within five altitude bands were selected for the study. Each transect comprised eight baited pitfall traps each.

2.5.1 Transect Site Selection

Sites were selected using ArcMap in ArcGIS 10.4.0 and took into account differences in altitude, vegetation and distances from the nearest track within the NP. The majority of land area within the park falls within the 3,000-3500m range (Fig 2-1) and as such, transects sites were chosen to reflect both habitat type and elevation. In particular, transect sites were selected so that each altitudinal band contained a transect.

Table 2-3

Transect	Transect coordinates X Y	Mean Elevation (m asl)	Habitat Type	Sampling dates	Chapter (s)
Transect 1.1	36.89201 -0.3638791	1834-2185	Bushland Thicket	June-July 2014 June 2015 February 2016	3,4,5,6
Transect 1.2	36.88358 -0.3615264	1989-2200	Bushland Thicket	June-July 2014 June 2015 February 2016	3,5,6
Transect 2.1	36.79259 -0.3582319	2416-2579	Podocarpus dominated forest	June-July 2014 June 2015 February 2016	3,5,6
Transect 2.2	36.74835 -0.32845	2789-3150	Podocarpus dominated forest	June-July 2014 June 2015 February 2016	3,5,6
Transect 3.1	36.75775 -0.3430085	2275-2389	Juniperus dominated forest	June-July 2014 July 2015 February 2016	3,5,6
Transect 3.2	36.75775 -0.351714	2211-2405	Juniperus dominated forest	June-July 2014 July 2015	3,5,6

				February 2016	
Transect 4.1	36.77688 -0.3409337	2706-2989	Bamboo forest	June-July 2014 July 2015 February 2016	3,5,6
Transect 4.2	36.75826 -0.3342576	2814-3100	Bamboo forest	June-July 2014 August 2015 February 2016	3,5,6
Transect 5.1	36.6054 -0.208077	3187-3467	Hagenia dominated forest	June-July 2014 August 2015 February 2016	3,5,6
Transect 5.2	36.6145 -0.207283	3331-3600	Hagenia dominated forest	June-July 2014 August 2015 February 2016	3,5,6
Transect 6.1	36.54248 -0.23469	3672-3809	Montane Ericaceous	June-July 2014 August 2015 March 2016	3,5,6
Transect 6.2	36.60535 -0.20806	3781-3998	Montane Ericaceous	June-July 2014 August 2015 March 2016	3,5,6

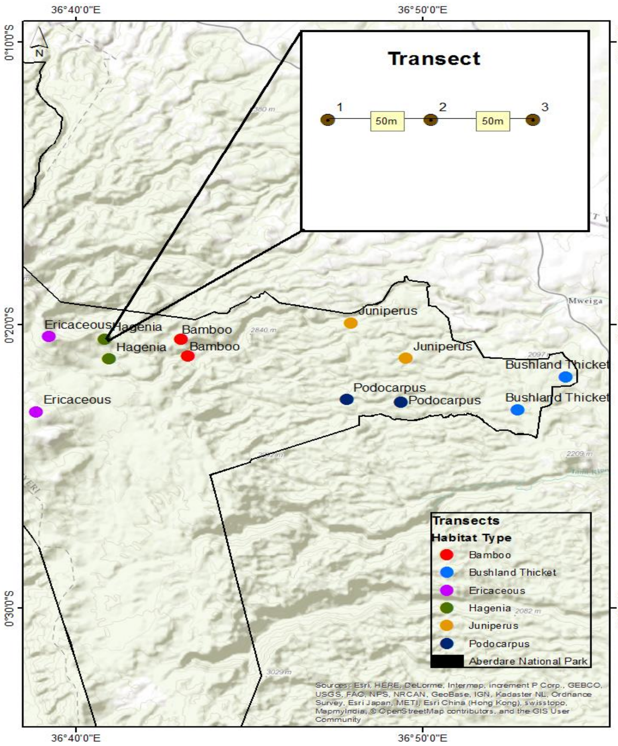


Figure 2-6 Map of the transect locations and example of how pitfall traps were distributed within each transect.

2.5.2 Study Timeframe

The study took place during a three-year period from June 2014 to March 2017 and makes the assumption that there were no significant changes to distribution or abundance of dung beetle and large mammal populations during this time. This assumption is supported *a posteriori* by the rangers and park management, author's local knowledge, and the fact that no major local perturbations or anthropogenic events occurred during the study period that may have caused significant differences in the study population.

2.6 DUNG BEETLE DATA

Sampling of dung beetles consisted of three methods; 1) hand collecting individual specimens from dung pats or pellets; 2) pitfall traps baited with dung of various mammal species; and 3) light trapping for nocturnal species.

2.6.1 Baited pit-fall trapping

Pitfall traps were the main method used to collect all the data on dung beetle distribution which are used for analysis in chapters 3-6. The pitfall traps were designed following (Krell, 2007) and consisted of eight 1 litre bowls placed flush with the ground with a bait net suspended 8cm over the bowl by a string loop. Traps were baited with 50g of elephant dung wrapped in fine gauge mesh netting which allowed dung volatiles to be emitted, while excluding dung beetles, and left for four days at each site. Traps were emptied and re-baited every 24 hours to provide a total sample of 32 samples per site and total of 384 collections for the whole study. Once collected, the dung beetles were transferred into a 70% Ethanol solution for preservation and identification. Dung beetles were identified with the help of Darren Mann using the following keys; Ferreira (1972), Cambefort (1984), D'Orbigny (1911), Zídek & Pokorný (2004) and Cambefort & Nguyen-Phung, (1996).

2.6.2 Light trapping

Light-trapping was undertaken during August 2015 and February 2016 at all sites over four consecutive nights between the hours of 7pm-9am to ensure a complete inventory for all species niches was achieved. Light-trapping was conducted using a Quantum™ 368 UVA black-light tube operated from a 12-volt battery.

2.6.3 Manual Collecting

Searching for dung beetles by hand occurred within the 10m radius around each baited pit fall trap. The origin of the dung was identified and recorded to mammal species. A collapsible spade was used to remove dung from the soil surface, and any dung beetles on the dung-soil interface were removed and preserved. Additionally, tunnels located directly beneath dung pats or pellets were excavated to remove dung beetles located beneath the soil surface.

2.7 MAMMAL DATA

2.7.1 Camera Traps

Two Bushnell™ NatureView camera traps were set up within a 50m radius of two pitfall trap per transect between June-August 2015 and during February and March 2016. The camera traps were the primary method of data collection to ascertain the abundance and distribution of mammals. Cameras were set at 140 cm above the ground to accommodate the height of most of the mammals suspected of being present within the sample site and to avoid camera loss by hyena (*Crocuta crocuta*). Cameras were set to record for 24 hours per day with a time delay for activation set at 30 seconds. This time delay was set to avoid multiple images of the same individual and the risk of false-positive image capturing. Camera traps were checked after nine days, the images were downloaded and the cameras reset in their original positions. Giving a sample size of 36 days in total (6th July-13th August 2015 and 12th -1st March 2016).

2.7.2 Dung and Signs

Discrete dung piles were recorded within a 20 m radius of each pitfall trap. The animal source and age of the dung was assessed visually using the dung degradation characteristics described by Barnes (1992) and were either identified and recorded in the field, or preserved for later identification. Because of the considerable variation and overlap in the dung size in the Aberdare forest community, antelope dung (Suni, red duiker, black fronted duiker, Bongo and Bushbuck) provided the greatest challenge in terms of dung identification to species level. Dung that could not be identified in-situ was measured, photographed and checked against available literature (Hesse, 1954, Kingdon, 1988). Where the identity of the animal was ambiguous, the dung was classified as “unknown”.

2.8 VEGETATION DATA

The following vegetation characteristics were recorded at each site; tree species richness, abundance, ground cover, and canopy cover around each trap. A modified version of the Standard International Forestry Resources and Institutions method for vegetation sampling (Ostrom, 2008) was used (Figure 2-7). Two concentric circles (1-m, and 10-m radius; see Figure 2.2) were established around each trap to record the aforementioned data. Tree seedlings and saplings (2.5–10 cm diameter) were counted in the 1 m radius circle, and mature trees (>10 cm diam.) in the 10 m-radius circle. Tree diameter at breast height (dbh) was measured at the standard 1.3 m height.

Ground vegetation and canopy cover were determined in the 1 m radius circles. Estimates of percentage ground cover were taken for herbs when individuals were impractical to count. This was done in each 1 m radius circle in each forest type, except in a few cases where traps were found removed or damaged. For each trap, the ground vegetation cover was visually scored on five scales as follows: (1) 0-5 percent of the total area of the 1 m radius circle; (2) 5–25 percent of the total area of the circle;(3) 25–50 percent of the total area of the circle; (4) 50–75 percent of the total area of the circle; and (5) >75 percent of the total area of the circle. Canopy cover was measured at three haphazardly selected points within the 1 m radius of every trap using a spherical densiometer.

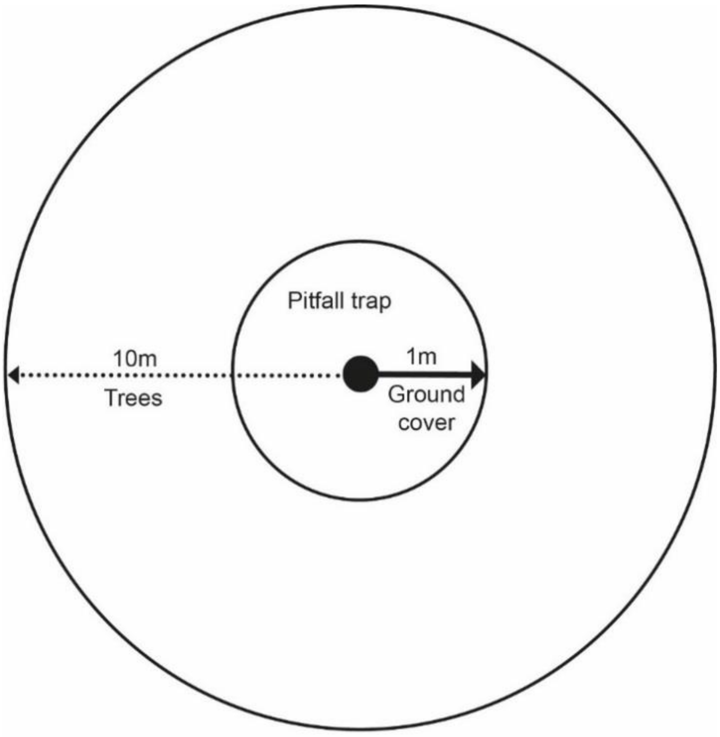


Figure 2-7 Schematic of vegetation sampling protocol, modified from Ostrom (2008).

2.9 DATA ANALYSIS AND MANAGEMENT

This section provides a brief overview of data processing and analysis techniques used; full details on statistical methodology are provided as appropriate in chapters 3-6.

2.10 STATISTICAL ANALYSIS

2.10.1 Timelapse2

The open source software Timelapse2 (Greenberg and Godin, 2015) was used for camera trap image classification and analysis. A standard template file (.tdb) was made in Microsoft Access to include the following information in Table 2-3. This information was used to generate a file in .csv format for use in R software (R Development Core Team, 2017)

Table 2-4 List and description of variables used in image analysis and classification of images taken by the camera traps.

Variable	Description
DateTime	Date and Time the image was taken
Species	Common Name as listed in the Catalogue of Life
N individuals	Number of individuals *per* image
Group Size	Number of individuals *per* group
Habitat	Habitat classification
TrapSite	Specific camera trap location

2.10.2 Spatial Analysis

The co-ordinates of the pitfall traps and the transects were recorded using Garmin™ GPS Map60Cx and downloaded and processed using open source software EasyGPS (TopoGrafix, version 5.53). The Geographical Information System software ArcGis™ (version 10.4.0) was used for spatial analysis, particularly in constructing vegetation classes and altitude bands (Chapter 3), and to produce the maps throughout this thesis. The open source Geographical Information System software Quantum GIS (QGIS, version 2.2.2-Valmiera; http://www.qgis.org/) was used for additional spatial analysis, particularly for generating site-specific transects using the Transectizer Plug-in (version 1.14;http://imasdemase.com).

3 The role of vegetation and altitude in shaping community structure of dung beetles in montane Afrotropical forest

Abstract

Afromontane forests are the most threatened ecotype in Africa due to extensive anthropogenic impacts associated with land use change and currently little is known about the dung beetle communities which reside within them. Comparisons of species richness, abundance and dominance of Scarabaeidae dung beetles were used to investigate the effect of habitat and elevation on the species composition of dung beetles. Over the study period of 94 trapping days, 8020 individuals of 34 species belonging to 5 tribes (Onthophagini, Canthonini, Coprini, Sisyphini, Oniti, Oniticellini) were recorded. All the indices measuring species richness and dominance showed significant differences between the six vegetation types and there was little overlap in the species collected at each site. Analysis using Bray-Curtis dendrograms illustrates dissimilarity between species composition between elevation bands. Increasing altitude did not decrease beetle diversity but abundance was found to decline with altitude. Indicator species for use in future management programs were identified for each vegetation type.

3.1 INTRODUCTION

Determining the causal factors for variation in the spatial distribution of biodiversity is a fundamental objective in conservation and ecology (Gaston 2000). One of the most widely documented of these patterns is the species–area relationship, and the relationship between local and regional richness - differences which are driven partly as a result of geological history and isolation (Parmentier et al., 2009). Another pattern is that of the gradients across space or environmental conditions (e.g. latitude, longitude, aridity and altitude). In tropical mountains, the refugia hypothesis (Fjeldsa and Lovett, 1997) suggests that differences in species diversity and occurrence between isolated patches is the result of allopatric speciation.

Changes in species distribution across environmental gradients may reflect habitat specialization by constituent species (Laurance et al., 2011) as limiters such as thermal tolerance and resource availability restrict niche space and determine the spatial extent of species distributions and successional patterns. One well-studied aspect of patterns in spatial biodiversity is the species turnover that occurs along altitudinal gradients, especially those which occur in montane tropical habitats (Lobo , 1997). These changes may arise over small spatial extents due to the close proximity of different habitats and, as a consequence, communities may differ dramatically in species composition over small distances, for example between valleys or mountain peaks (Jankowski et al., 2009).

Tropical montane forests constitute one of the biologically richest environments on earth (Aldrich et al., 1997) and often contain a large number of endemic species (Merckx et al., 2015). However, African montane (Afromontane) forests and their associated biota are poorly studied. This is important, because Afromontane habitats are noted to be important hotspots of terrestrial biodiversity (Mittermeier et al. 2011; CEPF 2012). Montane ecosystems are estimated to cover 7.4% (58 Mha) of Kenya’s terrestrial area and montane forests represent 57% (740,000 ha) of the country’s total forest type (Paron et al., 2013).

The majority of the studies in East African montane forests refer to vertebrates (Martin et al., 2015; Rovero et al., 2016; Stanley and Kihaule, 2016) and plants (Nyundo et al., 2006; Eisenring et al., 2016) and little is known of the arthropod diversity located in such habitats. Invertebrates constitute the bulk of known biodiversity on Earth and dominate virtually every terrestrial ecosystem in terms of species richness, animal biomass, and provision of ecosystem services (Samways, 2015). An understanding of the factors influencing invertebrate taxonomic richness and diversity at both local and regional scales is important for conserving biodiversity. Dung beetles are recognized to represent an important functional component of the animal fauna found in tropical forests (Krell-westerwalbesloh and Linsenmair, 2004; Banks et al., 2010) as they provide several key ecological functions such as seed dispersal, parasite suppression and dung removal (Nichols et al., 2008).

A number of factors are thought to influence the spatial pattern of dung beetle species occurrence as species may have their range restricted by lack of suitable habitat or the decline in quality of existing habitats. There are few studies describing dung beetles in montane regions globally, and their ecology and response to biotic and abiotic factors in African montane forests has seldom been analysed. The only study of dung beetle assemblages explicitly looking at dung beetles across an altitudinal gradient in African mountains is that by Davis et al. (1999) from the Drakensburg mountain range in South Africa.

It is generally accepted that in most invertebrate taxa, species diversity and richness generally decline with increasing altitude (Wolda 1987), although previous studies have found that Neotropical montane dung beetle biodiversity actually peaks at mid-elevations (Escobar et al., 2006; Lobo et al., 2007; Herzog et al., 2013; Nunes et al., 2016). These studies unravel both specific and general patterns that help explain the mechanisms driving the distribution of dung beetles along elevation gradients and with significant implications for biogeographic analysis and conservation priorities. Understanding these patterns is important as there is growing evidence that the effects of climate change are amplified with elevation (Mayor et al., 2017).

In this study, I investigate the factors influencing the spatial pattern of dung beetle biodiversity in Afromontane vegetation. I sampled dung beetles associated with six different habitats, characterized by differences in vegetation types, located along a altitudinal gradient. I tested the hypothesis that altitude and habitat type underpin the variation of dung beetle diversity and species composition. My objectives were: 1) to describe alpha diversity (α) at the habitat scale; 2) to assess beta diversity (β) between elevation bands; and 3) to assess gamma diversity (γ) for the whole mountain. I expected a decrease in species richness with increasing altitude but less species attenuation between habitat types. Additionally, I tested the hypothesis that different habitat types would have distinct species and so discrete assemblages from which indicator species can be described. I discuss the implications of my findings for future conservation planning and climate change monitoring within the ANP.

3.2 METHODS

3.2.1 Pitfall traps

Pitfall trapping was conducted with the methods described in section 2-4 on page 42.

3.2.2 Vegetation Data

Data collection was conducted with the methods described in section 2-8 on page 44. A habitat map using a (NDVI) Normalized Differentiated Vegetation Index and an elevation model of the Aberdare NP was created to ensure transects were placed within each available habitat type and within each elevation band (Figures 3-1; 3-2).

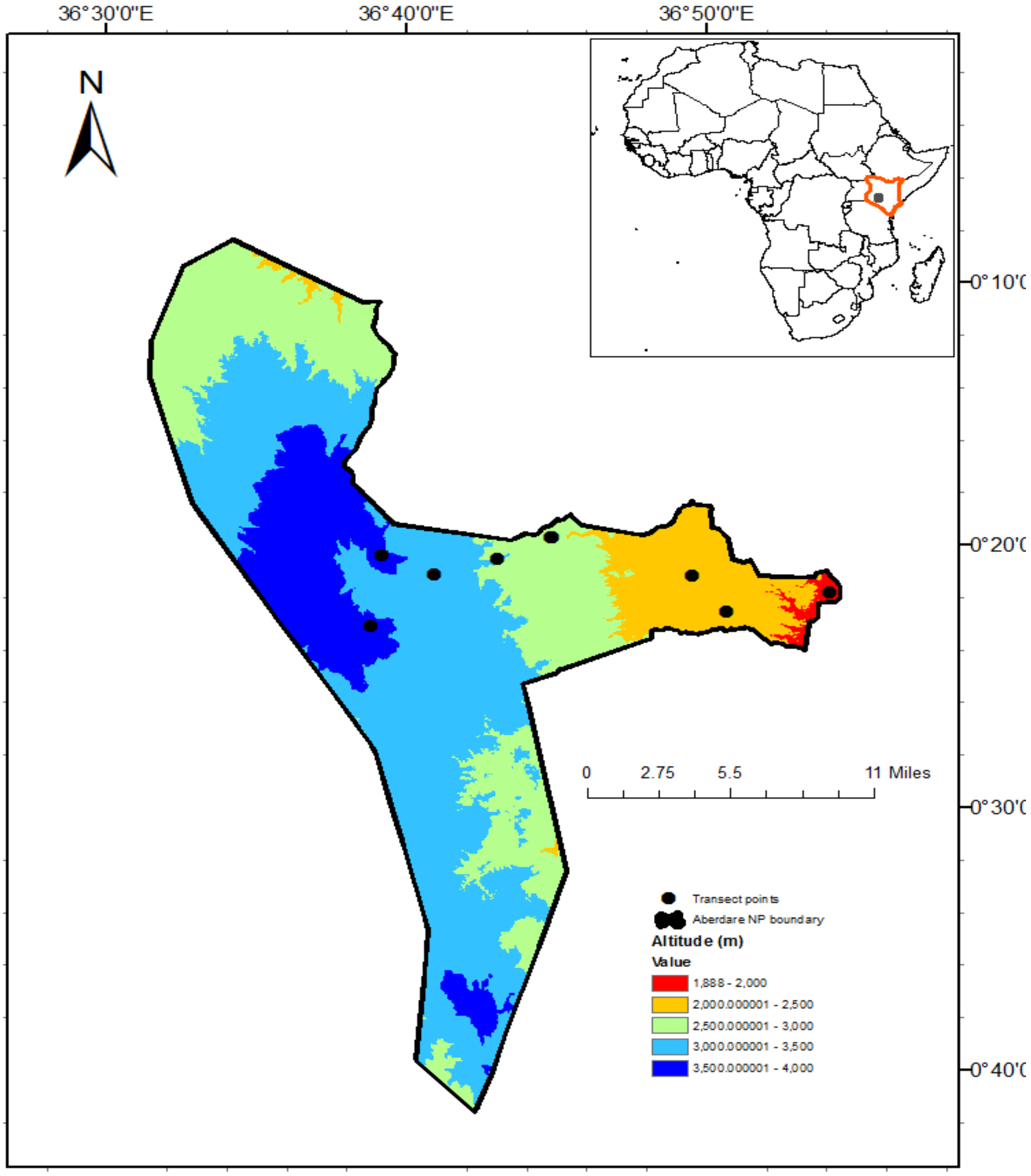


Figure 3-1 The study area showing the location of Aberdare National Park within Kenya shaded in grey, and the distribution of the altitudinal bands found within the Aberdare NP. SRTM data is jenked at 500m equidistant intervals to divide the Aberdare National Park into five elevation bands. Dots represent transect locations. Red band =B1, Orange band = B2, Green band =B3, Blue band = B4, Navy band =B5.

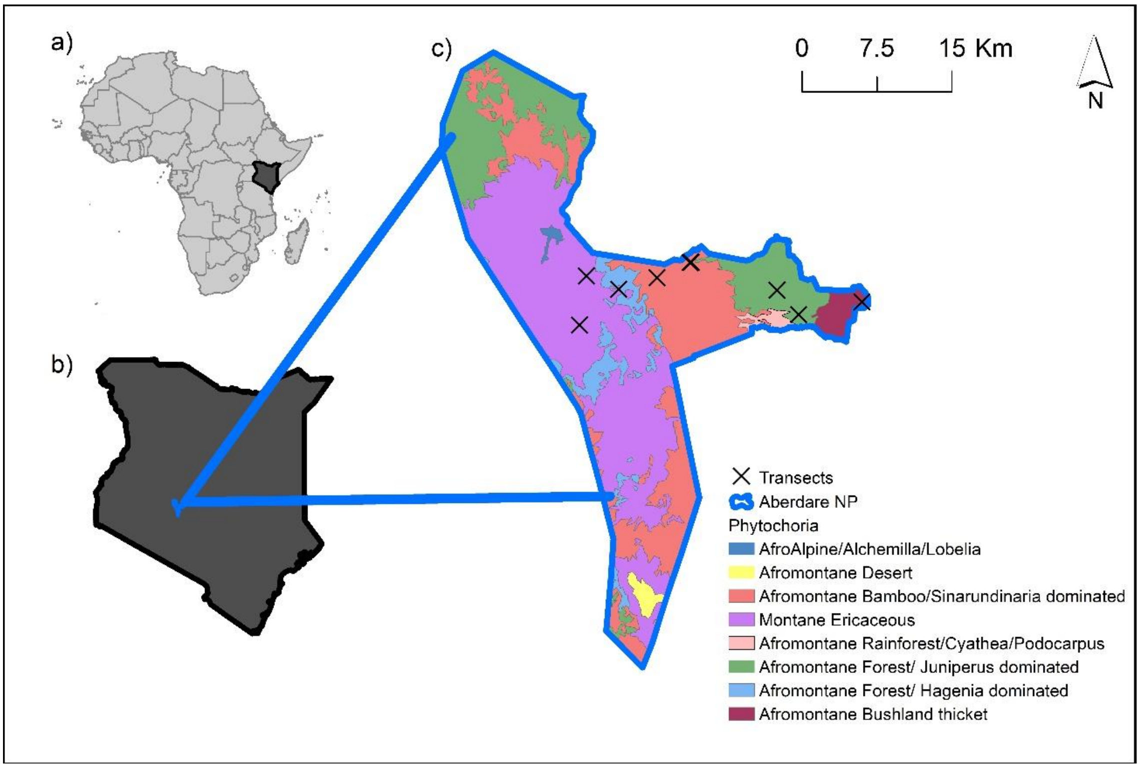


Figure 3-2 The location of the NP in Kenya (a,b) and (c) the locations of transects and the distribution of vegetation types found within the Aberdare NP. The map was created using Sentinel-2 data at $10m^2$ resolution to categorise land uses classes in ArcGis 10.4.1. 'X'represents transect locations

3.3 DATA ANALYSIS

Species richness was estimated for each vegetation type using the non-parametric estimators 'Chao1' (Chao, 1984). Chao1 gives an estimate of absolute number of species in an assemblage based on the number of rare species (singletons and doubletons) in a sample. A Chao1 estimate of species richness is recommended for inventory completeness values, completeness being the ratio between observed and estimated richness (Cao and Epifanio, 2010; Buddle et al., 2012).

Alpha diversity (α-diversity) is the biodiversity within an area, community or ecosystem, and is usually expressed as the species richness of the area. This can be measured by counting the number of taxa (distinct groups of organisms) within the ecosystem (e.g., families, genera, and species). Shannon index (H') was used to measure diversity; the index is increased either by having additional unique species, or by having greater species evenness. Pielou's J' provided the species evenness (based on the Shannon Index) that is the relative abundance or proportion of individuals among the species.

3.3.1 Species Richness, Diversity and Evenness in Habitat types

Beetles captured by all sampling methods were pooled by site for analysis. To test for differences in species richness, abundance and diversity between habitat types and altitude bands, I used a Kruskal Wallis test with Nemenyi tests for multiple comparisons (Zar, 2010). I used GLM with Poisson errors and the log link function with Habitat type and Altitude as factors. The χ^2 statistic was used to test for significant changes in deviance. I used a Mantel test to evaluate association patterns between distance matrices (Jankowski et al., 2009) using Bray-Curtis dissimilarities for dung beetle species composition, and Euclidean distance matrices for altitudinal distance, canopy cover and ground cover with 999 permutations.

Beta diversity is a measure of biodiversity that compares the species diversity between habitats or ecosystems along environmental gradients. This involves comparing the number of taxa that are unique to each class (e.g. habitat type). Thus, it is the rate of change in species composition across habitats or among communities. It gives a quantitative measure of diversity of communities that experience changing environments. Together with diversity within a habitat, β diversity gives overall diversity of an area (Ji et al., 2013). Beta diversity can then be partitioned into two components: dissimilarity due to species replacement and dissimilarity due to nestedness (Baselga, 2012). The former component relates to the replacement of some species by others from one site to the next, a concept that has been termed spatial turnover (Gaston & Blackburn, 2000). The latter component, nestedness, is a pattern characterized by the poorest site being a 'filtered' representation of the richest site. The Beta.SOR function within the R package Betapart (Baselga et al., 2013) was used to establish the percentage nestedness and turnover between altitude bands and between habitat types. Data were converted from relative abundance data into a presence/absence matrix for use with Sørensen's index. Data were further explored using the beta.core function which evaluates the differences in shared species richness between samples.

The Bray-Curtis similarity coefficient is expressed by:

$$C_N = 2jN/((Na + Nb))$$

where N_a = the total number of individuals in site A; N_b = the total number of individuals in site B; and 2jN = the sum of the lower of the two abundances for species found in both sites. The Bray-Curtis similarity coefficient is used to determine site similarities based on species abundances. It is widely employed in multivariate analysis of assemblage data. It reflects differences between samples due both to differing community composition and/or differing total abundance. Bray-Curtis cluster analysis (single link) was performed to identify the clustering of habitats into distinct groups. Hierarchical single link clustering takes the similarity matrix as the starting point and successively fuses the samples into groups and the groups into larger clusters, starting with the highest mutual similarities then gradually reducing the similarity level at which groups are formed resulting in a tree diagram or dendrogram plot.

I tested for normality and equal variance. Where data conformed to a normal distribution parametric tests were used, otherwise GLM's with appropriate error structure were used. I used R version 3.3.1 (R Development Core Team, 2017) to perform all statistical analyses. Mantel tests and calculations of Euclidean distances between altitude pairs were carried out using 'vegan' and 'ecodist' packages.

3.3.2 Indicator analysis

CLAM analysis (Multinomial Species Classification Method (Chazdon et al., 2011)) is a multinomial model which uses relative abundance of species in two distinguishable habitats. One advantage of CLAM is that the procedure explicitly considers a threshold for rarity, meaning that species that are too rare cannot be classified, and distinguishes species that are generalists from those that demonstrate specificity to one habitat type (Chazdon et al., 2011). An important parameter of the multinomial model is K, which refers to the cut-off point for classifying species according to their habitat type. CLAM was used to classify generalists and specialists into open and closed vegetation types by setting a specialization threshold of K = 0.667, *P* = <0.05 (Bicknell et al., 2014b). The model classifies species into one of four groups: (1) Generalist; (2) Habitat A specialist (specialist of open vegetation); (3) Habitat B specialist (specialist of closed canopy vegetation); and (4) too rare to classify with confidence.

Habitat associations of individual species and functional guilds were ascertained using Pearson Chi-squared residuals and plotted using the hclust function in the Vegan package to visualize positive and negative associations and split dung beetle species into community groups. To see which species were indicative of the six habitat types in the ANP, indicator species analysis in the form of association analysis was undertaken using Pearson residuals.

3.4 RESULTS

A total of 8020 individuals from 34 species belonging to 16 genera were captured at twelve locations and a 1.5 km altitudinal gradient over the study period of 94 trapping days. Eleven species from a previous study (Davis and Dewhurst, 1993) were recorded (Figure 2-4) plus a further 23 species, three of which were new records for Kenya; *Catharsius gibbicollis, Catharsius sesostris,* and *Hetronitis ragazzi*, and three which are new to science; *Caccobius* n.sp., *Onthophagus* n.sp., (both in prep) and *Epidrepanus kenyensis* (Roggero et al., 2017). Tunnelling dung beetles constituted the majority of species collected with 82% of the total versus 15% for dwellers and just 3% of rollers. The non-parametric estimates of total species richness was 43 species for Chao1, indicating that most of the species pool was collected (around 80%). The most abundant species across all habitats were, *Neocolobopterus kivuanus (*1362, 17%), *Onthophagus proteus (*935, 11.6%)*, Onthophagus sp 2*, *(*875, 10.9%), *Onthophagus spurcatus (*792, 9.8%)*, and Milichus picticollis (*587, 7.3%). These five species accounted for 57% of all individuals collected, demonstrating that habitats were dominated by a few abundant species. An overview of the dung beetle assemblages found in each habitat type is found in Table 3-1

Table 3-1 The number of Dung beetle species recorded *per* habitat type in Aberdare NP, Kenya.

Habitat Species	Bushland Thicket	Juniperus dominated Forest	Podocarpus dominated Forest	Hagenia dominated forest	Bamboo	Ericaceous grassland
Caccobius n.sp	30	173	67	15	1	0
Catharsius gibbicollis	1	2	0	1	0	0
Catharsius setosis gp	0	2	3	0	0	0
Copris algol	2	0	1	0	1	0
Copris atropolitus	21	30	25	22	0	0
Copris morphaeus	92	44	31	26	1	0
Copris Spp2	2	5	4	0	0	0
Copris typhoeus	22	19	21	13	0	0

Diastellopalpus johnstoni	7	4	2	0	0	0
Epidrepanus keniensis	1	4	0	0	0	0
Euoniticellus intermedius	54	116	45	77	11	0
Heliocopris hunteri	6	2	0	0	0	0
Heliocopris neptunus	3	1	0	0	0	0
Heliocopris stroehli	23	2	0	0	0	0
Hetronitis ragazzi	1	5	2	0	0	0
Ixodina abysinnicus	125	6	0	2	0	0
Liatongus arrowi	34	74	35	35	11	0

Milichus picticollis	52	444	89	0	0	2
Neocolobopterus kivuanus	232	287	259	379	173	32
Neocolobopterus macaucollis	20	103	46	11	5	0
Oniticellus planatus	63	105	39	3	8	0
Onitis anthracinus	15	30	37	0	1	0
Onitis meyeri	95	75	38	49	8	0
Onitis parvvulus	41	63	46	9	2	0
Onthophagis nigriventis	11	30	13	22	3	3
Onthophagus proteus	179	308	204	21	112	111
Onthophagus dochertyi	40	143	61	3	4	26

Onthophagus filicornis	67	46	0	51	51	29
Onthophagus fimetarius	4	22	8	0	9	1
Onthophagus miricornis	45	102	8	61	101	99
Onthophagus spp1	28	17	17	0	6	1
Onthophagus spp2	129	446	235	55	1	9
Onthophagus spurcatus	180	297	129	165	21	0
Proagoderus sexcornutus	40	3	9	3	0	0
Sisyphus sp1	5	0	0	0	0	0

3.4.1 Variation in dung beetle assemblages between habitats and altitude bands

Each habitat type was described in terms of its diversity, evenness, and estimated richness (Table 3-2). Significant positive correlations were found between mean ground cover and dung beetle abundance (rho = 0.40, df = 95, P =<0.001) and species richness (rho = 0.42, df = 95, P =<0.001). Significant negative correlations were found between mean canopy cover and dung beetle abundance (rho = -0.24, df = 95, P =<0.01) and species richness (rho = -0.23, df = 95, P =<0.05). The overall abundance of individuals, species richness and diversity between habitats did not differ significantly when altitude was also accounted for (Table 3-3).

Altitude was negatively correlated with dung beetle abundance, species richness, and diversity (abundance; R^2=-0.392, *P*=<0.001, richness; R^2=-0.779, *P*=<0.001, diversity R^2=-0.735, *P*=<0.001), and there were also significant differences abundance, species richness and diversity between altitude bands (Table 3-3, Figure 3-3). However, dung beetle abundance, species richness, and diversity did not significantly differ among habitat types (Table 3-4).

Table 3-2 Alpha, Beta and Gamma diversity, Simpsons (H'); Simpsons (λ) and Evenness (J') and Species Richness estimators for each habitat type in the Aberdare National Park, Kenya

Habitat type	Diversity			Evenness			Richness estimator
	γ	β	α	H'	λ	J'	Chao1†
Bushland				2.94	0.922	0.828	36.87
Thicket	32	1.63	21.43				
Juniper dominated forest	31	1.95	17.37	2.86	0.923	0.811	34.15
Podocarpus dominated forest	32	2.05	15.56	2.85	0.925	0.823	32.11
Bamboo	26	2.53	10.25	2.36	0.837	0.727	31.62

Hagenia dominated forest	26	2.63	9.87	2.20	0.833	0.677	26.93
Ericaceous grassland	19	3.14	5.56	2.00	0.808	0.68	22.75

†(Chao, 1984)

Table 3-3 Results of a generalised linear model assessing dung beetle community Richness(A); Abundance (B); and Shannon Index (C), at six habitats in the Aberdare National Park and five Altitude Bands (B1-B5).

(A)Richness

Source	Sum of Squares	DF	Mean Squares	F	P
Habitat	2609.39	3	652.35	35.56	0.083
Altitude Bands	126.02	4	42.01	2.290	<0.001
Habitat*Altitude Bands	3314.06	88	22.156	16.14	<0.001

(B) Abundance

Source	Sum of Squares	DF	Mean Squares	F	P
Habitat	19793	3	6598	0.180	0.909
Altitude Bands	619846	4	154962	4.229	<0.05
Habitat*Altitude Bands	119546	88	95214	2.291	<0.01

(C) Shannon (‘H)

Source	Sum of Squares	DF	Mean Squares	F	P
Habitat	0.9123	3	0.3041	2.1892	0.09
Altitude Bands	15.2140	4	3.8035	27.381	<0.001
Habitat*Altitude Bands	9.3184	88	1.9414	16.58	<0.001

Table 3-4 Dung beetle abundance, species richness and diversity recorded *per* Altitude band in Aberdare NP, Kenya.

Altitude Band	B1 1888-2000m	B2 2001-2500m	B3 2501-3000m	B4 3001-3500m	B5 3500-4000m
Species					
Caccobius n.sp	73	543	15	32	0
Catharsius gibbicollis	11	9	0	1	0
Catharsius setosis gp	5	7	0	0	0
Copris algol	6	152	6	8	13
Copris atropolitus	14	101	10	25	9
Copris morphaeus	19	189	10	33	1
Copris Spp2	18	99	13	50	1
Copris typhoeus	14	99	15	16	9
Diastellopalpus johnstoni	13	187	0	6	0
Epidrepanus keniensis n.sp	1	4	0	0	0
Euoniticellus intermedius	65	718	97	165	22
Heliocopris hunteri	31	24	0	0	0
Heliocopris neptunus	4	25	0	0	0
Heliocopris stroehli	9	31	0	0	0

Hetronitis ragazzi	0	5	0	0	0
Ixodina abysinnicus	16	66	2	3	0
Liatongus arrowi	38	185	13	10	0
Milichus picticollis	465	794	0	3	0
Neocolobopterus kivuanus	209	1450	51	1140	227
Neocolobopterus macaucollis	70	208	15	39	30
Oniticellus planatus	43	428	146	150	3
Onitis anthracinus	13	179	50	29	1
Onitis meyeri	28	77	28	8	0
Onitis parvvulus	33	213	6	20	4
Onthophagis nigriventis	9	92	8	19	5
Onthophagus proteus	72	422	77	40	2
Onthophagus dochertyi	22	235	50	154	86
Onthophagus filicornis	17	93	8	62	72
Onthophagus fimetarius	173	1096	193	703	43
Onthophagus miricornis	54	835	34	273	188
Onthophagus sp1	50	144	13	19	13

Onthophagus sp2	201	802	38	49	0
Onthophagus spurcatus	58	598	31	90	0
Proagoderus sexcornutus	23	43	0	3	0
Sisyphus sp1	4	1	0	0	0
Abundance	1881	10154	929	3150	727
Species Richness	33	34	24	26	18
Diversity (‘H)	2.69	2.64	2.71	2.19	1.54

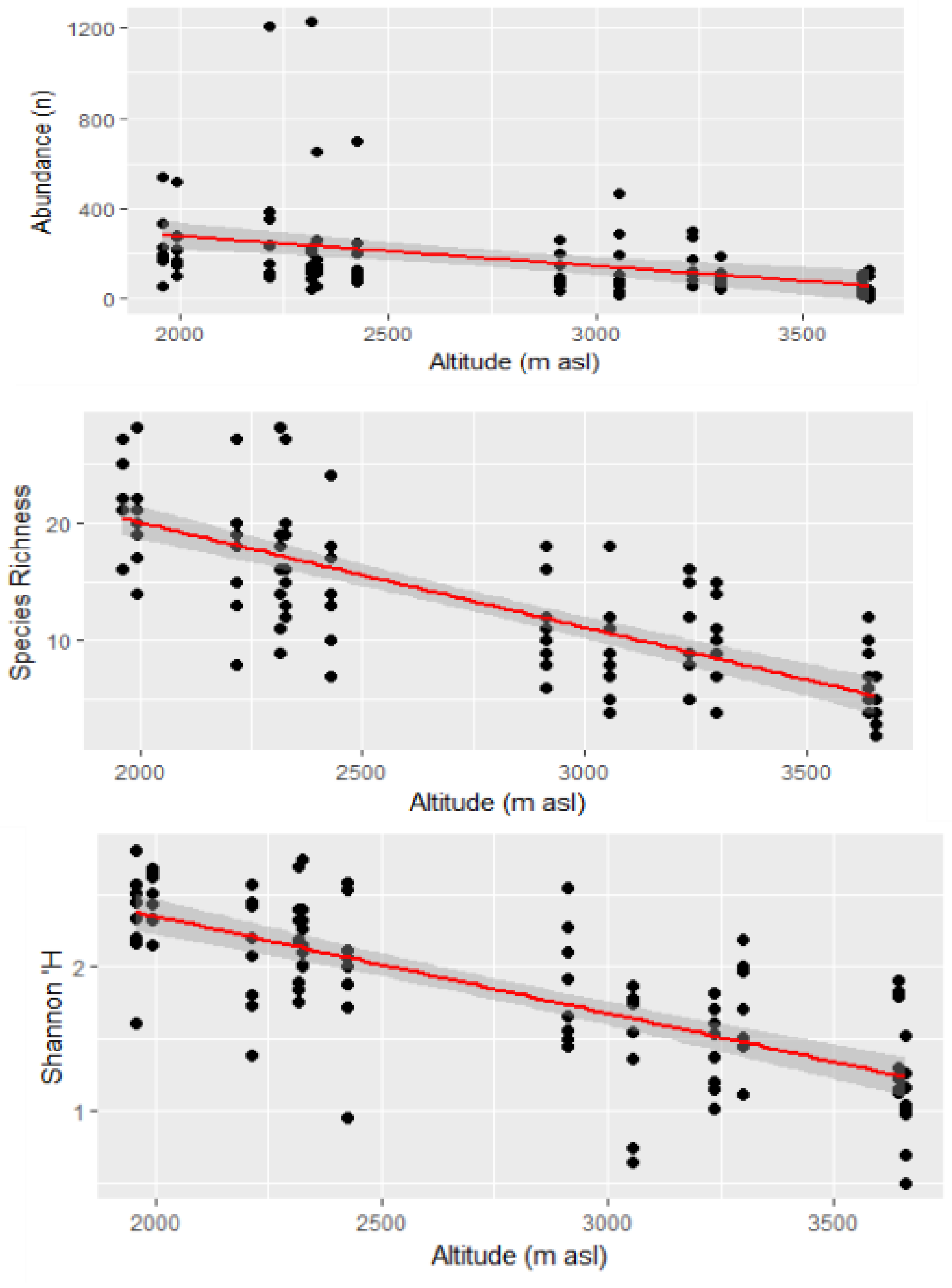


Figure 3-3 Altitude as a predictor of dung beetle (A) abundance, (B) richness and (C) diversity. The regression line is indicated in red, with the standard error of the mean plotted in grey.

3.4.2 Species composition and categories of habitat specificity

Of the 34-species found in this study, eight (23%) were judged as indicator species by the Pearson residuals in Chi squared tests of association - *Diastellopalpus johnsonii, Milichus picticollis, Neocolobopterus kivanus, Oniticellus planatus, Onitis anthracinus, Onitis meyeri, Onthophagus miricornis*, and *Onthophagus proteus*. Most habitats have more than one indicator species. The strongest positive associations for Bushland thicket is *Milichus picticollis,* followed by *Diastellopalpus johnsonii* and *Onitis meyeri* (Figure 3-4) all of which have also been indicated as either generalist or open vegetation specialists (Table 3-5). Bamboo habitat had four indicator species, with *Neocolobpterus kivunaus* belonging to the Aphodiine having the strongest positive association followed by *Oniticellus planatus, Onitis anthracinus,* and *Onthophagus miricornis. Onthophagus proteus* was positively associated with Ericaceous moorland along with *Neocolobpterus kivunaus*. Hagenia Forest had four indicator species but was most positively associated with *Onthophagus miricornis*. Two species were positively associated with Juniper forest the large tunneller *Onitis anthracinus* and *Milichus picticollis*, while Podocarpus dominated forest had associated two species; *Oniticellus planatus* and *Onitis anthracinus.*

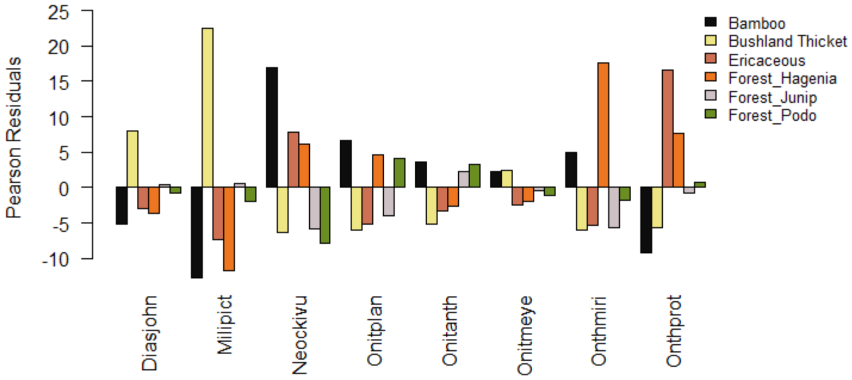


Figure 3-4 Indicator species for each habitat using Pearson residuals derived from Chi Squared test of association. Positive residuals relate to positive associations, negative residuals relate to negative associations. Diasjohn = *Diastellopalpus johnstonii;* Milipict = *Milichus picticollis; Neokivu =Neocolobopterus kivuanus; Onitplan =Oniticellus planatus; Onitanth= Onitis anthracinus; Onitmeyeri=Onitis meyeri; Onthmiri= Onthophagus miricornis; Onthprot=Onthophagus proteus*

CLAM analysis (Chazdon et al., 2011) further identified which species could be considered forest and open vegetation specialists. Dung beetles were classified as an indicator of a particular habitat type if ≥66% of their occurrences were within that habitat during the sample period. Fourteen species (41%) were classified as open vegetation specialists, ten species (32%) were classified as forest specialists and five species (15%) were found in both open and closed vegetation. Five species (*Epidrepanus kenyensis* n.sp, *Catharsisus gibbicollis, Catharsisus setostris*, *Heteronitis ragazzii*, and *Heliocopris stroehli*) were categorised as too rare to classify as either a generalist or specialist.

Table 3-5 The results of CLAM analysis which assigns specialist or generalist status on the proportion of individuals found in each vegetation type.

Generalist species	Open Vegetation species	Forest Specialist Species
Copris atropolitus	*Catharsius setostris*	*Caccobius sp*
Helicopris neptunus	*Copris morphaeus*	*Copris algol*
Ixodina abyssinica	*Copris pp2*	*Euoniticellus intermedius*
Onitis meyeri	*Copris typhoeus*	*Neocolobterus kivuanus*
Onitis parvulus	*Diastellopalpus johnstonii*	*Onitis planatus*
	Helicopris hunteri	*Onthophagus nigriventris*
	Liatongus arrowi	*Onthophagus dochertyi*
	Milichus picticollis	Onthophagus miricornis
	Neocolobopterus maculicollis	*Onthophagus spp2*
	Onthophagus filicornis	*Onthophagus spurcatus*

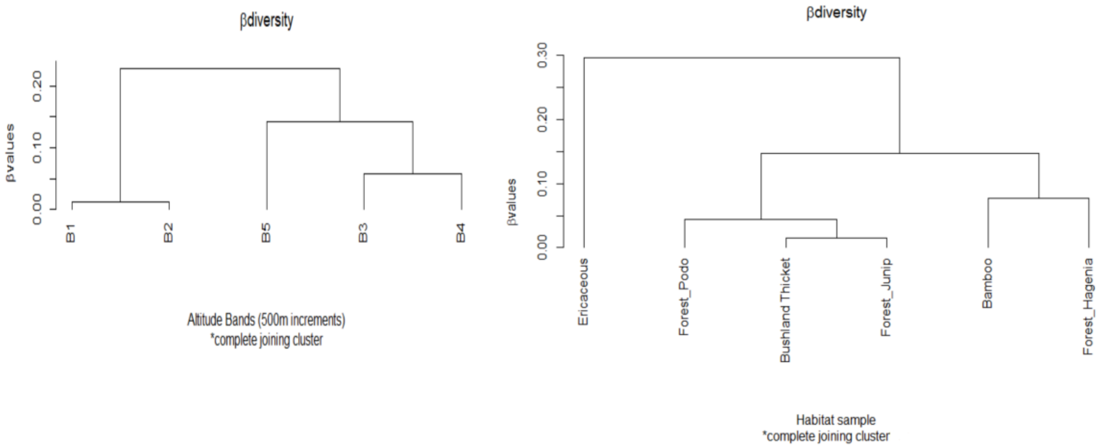
	Onthophagus proteus
	Onthophagus spp1
	Proagoderus sexcornutus
	Sisysphus spp1

3.4.3 Turnover and nestedness between habitat types and Altitude bands

Overall beta diversity (the effective number of distinct compositional units in the region (Tuomisto, 2010) was high between all habitats types showing very little species overlap (Table 3-2). The Bray-Curtis dendrogram in Figure 3-6 illustrates the differences in community composition between habitats and altitude bands by measuring the degree of community overlap between habitat types. The axis height of the dendrogram is β values per habitat type or altitude band. The scale ranges between zero (no overlap) and one (perfect overlap). The Bray Curtis index grouped the species communities in *Juniperus* and *Podocarpus* lowland forest types together along with bushland thicket demonstrating that there are more shared species between these three sites in comparison to the mid altitude *Hagenia* dominated forest and bamboo habitat types (Figure 3-8a). The upland Ericaceous moorland is the most dissimilar in terms of species composition between habitat types. The pattern is replicated with the analysis of dissimilarity between altitude bands with two branches separating bands above and below 2500m asl.

Analysis of β-diversity patterns revealed a significant positive correlation between dung beetle pairwise community dissimilarity (βSOR) and the Euclidean distance between sites (Mantel r^2 = 0.65, $P < 0.05$) demonstrating that variation in communities is strongly and significantly related to their spatial distance. β-diversity partitioning between altitude bands showed that effects were mostly due to species turnover, which accounted for 91% of total variation compared to 4% for nestedness. β-diversity partitioning between habitat types showed that effects were split between species turnover, which accounted for 64% of total variation and 87% for nestedness. This indicates that species replacement (turnover) is occurring at a much higher rate between altitude bands than between habitat types.

Figure 3-5 Dendrograms showing degree of dissimilarity in dung beetle beta diversity among (a) altitude bands and (b) habitats based on a cluster analysis of Bray-Curtis indices using abundance data. The height of the dendrogram is β values per habitat type or altitude band. The scale ranges between zero (no overlap) and one (perfect overlap).



3.5 DISCUSSION

This study addressed the effects of landscape heterogeneity and altitude on dung beetle communities by comparing community dissimilarity, species diversity and species abundance among sites that varied in habitat type and altitude. This study found no significant relationship between species richness and habitat type but a significant negative relationship between species richness and altitude showing that altitude is the main factor in shaping species composition in the ANP.

Variation in community structure between habitat types

Of the environmental factors measured in this study, the most important characteristic for determining community structure was mean canopy cover *per* habitat. This showed a decrease in dung beetle species richness with increasing cover but an increase in abundance in sites with increased canopy cover. The structure and complexity of forest canopies and understory vegetation can enact changes on local microclimatic conditions by causing changes in, levels of radiant heat (Jay-Robert et al., 1997), light intensity and air and soil temperature. Many forest dung beetles are extremely sensitive to light intensity (Davis et al., 2002) and as such may be restricted to either shaded or unshaded habitats. These differences may be related to the temperature requirements of developing larvae; Halffter and Matthews, (1966) suggested that some species can only develop in shady forest habitats, whereas others will thrive in the very warmest parts of sun-drenched pastures.

Two species captured in open vegetation were not found in *Juniperus, Hagenia* or *Podocarpus* dominated forests, (*Sisyphus sp1* and *Copris algol*), whilst one species, *Catharsius setotris* was found to be unique to forest vegetation. These three beetle species were found in low abundance (<8 individuals) and thus this is below the abundance threshold required by CLAM to conduct analysis. Of the 28 species used in CLAM, the majority of the dung beetles in the ANP are either restricted to closed canopy forest, or open vegetation that is located on the edges of forests and in glades, with few species inhabiting both (Table 3-5).

Distinct differences, such as the ones reported here, in beetle abundance and species richness in open habitats versus forested habitats have been found repeatedly throughout the Neotropics (Davis et al., 2001; Estrada and Coates-estrada, 2002; Vulinec, 2002). Half of the dung beetles which were found to be resident in forested habitats in the ANP belong to the same genus, *Onthophagus.* Onthophagine dung beetles are ubiquitous in all habitats in Afrotropical forests (Cambefort and Hanski, 1991) and therefore their presence in large numbers in forested habitats in the ANP was expected. Onthophagines are generally smaller bodied tunneller beetles that dig comparatively shallow nests and exist on a wide range of dung types (Davis et al., 2008). Over two thousand species of onthophagines are currently described and the genus is supposed to have diversified during the Oligocene, a diversification that coincided with the expansion of grasslands and the spread of mammals (Davis et al. 2002). Onthophagines were abundant in all habitats and across all elevations in the ANP up to 3800m asl. In South America, however, this genus is restricted to habitat types below 2000m asl, with few species found at higher altitude on mountains (Zunino and Halffter, 2007).

Additionally, and in contrast to the results of studies from the Neotropics (Pineda et al., 2005; Halffter et al., 2007; França et al., 2017), there was a higher number of species considered open vegetation specialists in comparison to forest specialists (Table 3-5). Interestingly, comparisons may be drawn to the similarity in composition between temperate European dung beetle communities and those of the ANP, as both have a greater association with open vegetation and have demonstrated decreases in species richness as vegetation cover increases. Additionally, the high proportion of tunnellers, the large number of individuals belonging to the genus Neocolobopterus in the Aphodiidae family, plus the paucity of roller species is more akin to a community found in a temperate ecosystem rather than an Afrotropical one. This undoubtedly is an altitudinal effect related to decreases in temperature and increases in rainfall found in mountainous areas. Similar findings in altitudinal replacement between the two main groups of dung beetles Aphodiini and Scarabaeinae (Lobo and Halffter, 2000), have been reported from the mountainous areas of the Neotropics and are similar to that which takes place along higher latitudes (Lobo, 2000). The cool-adapted species of Aphodiidae dominate the high altitude and species-poor temperate communities, while the warm-adapted Scarabaeinae species often dominate the low altitude and species-rich tropical communities (Escobar et al., 2005). The almost complete absence of roller species could be explained by their reproductive strategy, small body size (Hanski & Cambefort 1991) and inability to manoeuvre within densely forested habitats. The weak, but significant, correlation between beetle abundance and ground cover suggests that dung beetle distribution may be affected by another factor namely soil type, with the degree of vegetative cover being of lesser importance. However, as soil identification in each habitat type was not undertaken for this study, this cannot be clarified.

Six of the eight species indicated as having strong associations with the habitats studied are tunnelling dung beetles, with the remaining two, *Neocolopterus kivuanus* and *Oniticellus planatus* dweller species (Davis, 1989). All eight species adhere to Caro's (2010) criteria for ecological disturbance indicator species in that their inventory, life history, and population can form a measurable temporal response to environmental change (Siddig et al., 2016). *Onthophagus proteus* and *O. miricornis* are considered regional endemics with a distribution likely centred around the Aberdare and Mount Kenya National Parks (D'Orbigny, 1913). It is recommended that these dung beetles be used as an ecological disturbance indicator species group defined by (McGeoch, 2007) as "a species or group of species that demonstrates the effects of environmental change (such as habitat alteration and fragmentation and climate) on biota or biotic systems" to construct management plans and be informed by future shifts in habitat health in the ANP. However, very little is known about these species' dung preferences or dispersal ability and information on these traits would need to be collected to form part of future planning processes.

Turnover and Nestedness

Investigation of the patterns of dung beetle distribution clearly showed that the attenuation of dung beetle species richness at higher altitude bands is accompanied by species turnover, as species composition at low and high-altitude bands was largely different from that of mid-altitude bands. Numerous dung beetle species 'dropped out' with increasing elevation and were replaced by higher elevation specialists (e.g. *Onthophagus proteus* and species of the Neocolobopterus genera), resulting in little nestedness (4% of variation) but high turnover (91%) This type of high species compositional turnover along elevation gradients has been related to temperature and resource availability (Whittaker, 1956; MacArthur, 1972). High rates of turnover, as demonstrated here, have been documented for Central and South American montane ecosystems (Alvarado et al., 2014). The rate at which species are replaced on an altitudinal gradient is related to a number factors ranging from a landscape scale down to the availability of microhabitats along the gradient. The degree to which species turnover affects mountain species may also depend on the biogeographical history of the mountain (Lobo and Halffter, 2000; Escobar et al., 2005; Alvarado et al., 2014). The ANP forms part of the Aberdare range which when formed during the Miocene (23-11 mya) was an isolated uplift (Scoon, 2018a) and was almost entirely covered by savannah grassland (Pound et al., 2012). Mountain tops exhibit a filtered, less diverse set of species which are phylogenetically related to those inhabiting lower elevations (Lobo and Halffter, 2000). This may account for the high degree of nestedness between habitat types as species composition of the species-poor sites is a subset of the species-rich sites. However, this interpretation cannot be clarified until further work is undertaken on the dung beetle fauna of African montane habitats.

Conclusion

Research exclusively focused on diversity patterns on tropical mountains at elevations higher than 2500m asl is rare (Mastretta-Yanes et al., 2015) and rarer still for African mountains. This chapter is one of only a few known studies to specifically concentrate on the dung beetle fauna found in Afromontane vegetation and the compositional changes which occur along an altitudinal gradient. The results of my study have important conservation implications. This study underscores the importance of conserving as much habitat heterogeneity in mountain ecosystems as possible. The differences in dung beetle diversity and species richness between habitat types are manifest and the high turnover of species between altitude bands means that all locations within the ANP should be given the same level of protection.

Kohler and Maselli, (2012) refer to mountains as early warning systems as they may provide an indication of the changes that lowland ecosystems can expect in the future due to climate change. Changes in the distribution of biota between lowlands and mountains in response to climate change are already widely documented (Pounds et al., 1999; Menéndez and Gutiérrez, 2004; Gottfried et al., 2012) and the use of dung beetles as indicators of environmental changes due to climate change is now growing (Menendez et al., 2014; Birkett et al., 2017). The indicator species highlighted in this study could form a strong starting point for the instigation of a concerted management plan involving dung beetle distributional change in the ANP by Kenya Wildlife Services managers.

4 The role of Dung Beetle community complexity in soil nutrient exchange

Despite recognition of its importance, little is known about functional aspects of soil fauna. Here, I investigate the effect that different dung beetle functional groups have on macronutrient movement (N, P, K, and C) from dung into soil over 112-day period. I report a large overall effect where more macronutrients are moved into soil over time when beetles are present compared to a control treatment. I also report a large effect of beetle functional groupings on the amount of macronutrient movement, with larger dung beetles moving more nutrients over time. I provide the first experimental evidence that dung beetle body size directly influences macronutrient recycling and discuss the importance of dung beetle functional characteristics in maintaining soil fertility.

4.1 INTRODUCTION

There is universal recognition that soil nutrient recycling is fundamental to the maintenance of global ecosystem services. It has been suggested that soil be viewed as natural capital that contributes to the function of ecosystems by maintaining the bioavailability of nutrients and physical structure of the environment (de Groot et al., 2002; Dominati et al., 2010) , as well as contributing to human and ecological food security (Barrios, 2007). There is much evidence that soil contributes to the maintenance of biodiversity and stability, for example through the regulation of the microclimate and the control of pathogens (Altieri, 1999). However, while there is wide acknowledgement of the importance of soil systems in contributing to these environmental functions, soil arthropods have received relatively little research attention in comparison to microbes (Lavelle et al., 2006). Further, although the function and importance of dung in nutrient cycling is almost unstudied it is likely to have a critical role in soil environments because most herbivores use only a small proportion of the nutrients they ingest; in mammals, 60-99% of the ingested nutrients returned to the soil in the form of dung and urine (Williams and Haynes, 1990).

One important group in soil nutrient cycling is the paracoprid dung beetles (Nichols et al., 2008). Paracoprid dung beetles dig tunnels below dung in which they bury brood balls in specially constructed nests. Incidental nutrient cycling occurs when dung is mechanically relocated underground during nest building. This manipulation is thought to accelerate nutrient breakdown and incorporation of macronutrients, such as faecal nitrogen, directly into the soil (Gillard, 1967; Kakkar et al., 2008).

As outlined in section 2.10, dung beetles are classified into functional guilds based on traits such as body size, reproductive strategy, flight activity patterns and dung removal behaviour (Doube, 1990; Pincebourde, 2005). The functional diversity and guild structure of dung beetle communities has previously been shown to affect important ecosystem functions such as dung removal, seed dispersal and parasite suppression (Slade et al., 2007; Griffiths et al., 2016; Manning et al., 2016). Furthermore, the recycling of nutrients by dung beetles has been shown, experimentally, to increase pasture productivity through the incorporation of organic matter into substrates (Bang et al., 2005; Yoshihara and Sato, 2015). However, while some evidence exists to demonstrate that large dung beetles can function to remove greater quantities of dung from soil surfaces (Nervo et al., 2014), and that the presumed movement of the nutrients in dung affects primary productivity (e.g., Bertone et al., 2006; Menéndez et al., 2016) which contribute to ecosystem functioning (Slade et al., 2007, 2017; Dangles et al., 2012), the functional relationship between paracoprid dung beetle trait diversity (e.g. body size or nesting behaviour) and maintenance of soil nutrients due to nutrient recycling remain unclear.

I investigated the effect of functional variation in paracoprid dung beetles on soil macronutrient recycling in an equatorial African ecosystem. I focussed on the ecological effect on nutrient cycling in paracoprid tunnellers, as they comprise the most abundant functional dung beetle group (Davis et al., 2008) and have previously been shown to have a large role in dung removal

(Slade et al., 2007). My overall aim was to test whether there is a strong functional effect of dung beetle body size on the quantity of macronutrients passed from elephant (*Loxodonta africana*) dung into the soil. Specifically, my objectives were to 1) assess whether the transfer of nutrients from dung to soil is influenced by dung beetle body size, and 2) estimate the temporal effect of the dung beetles on dung to soil nutrient transfer. I discuss my findings in the context of the functional diversity of soil macrobiota and its implications for soil nutrient enrichment. Thus, providing a greater understanding of the linkages between functional diversity and the processes of nutrient cycling.

4.2 MATERIALS AND METHODS

4.2.1 Dung beetle classification

Dung beetles were collected using dung baited pitfall traps 24 hours before the start of the experiment, refer to section 2.6.2 for an overview of the technique. All captured individuals were identified to genus. Total body length (anterior clypeal sinuation to pygidium) was measured to the nearest millimetre using digital callipers, and live beetle mass was measured to the nearest gram. Dung beetles were classified into functional guilds using functional guild categories outlined in section 2.3.1, then assigned to one of three treatments (see Table 4-1): (1) small (body size range: >5mm to <15mm), (2) medium (>15mm to <25mm), or (3) large (>25mm). I also had a negative control treatment with no beetles. Each treatment contained an equal biomass of beetles (8.1 ± 0.04 grams), with the proportion of individual species approximately equal to the biomass which was found to be naturally represented in pit fall traps during previous sampling.

Table 4-1 Treatment, body size, and ordered proportionate composition of Genera used in each replicate.

TREATMENT	BODY SIZE (MM)	GENERA	TOTAL NUMBER OF INDIVIDUALS PER GENERA	PROPORTION IN TREATMENT (%)
Large	>25mm	*Heliocopris*	2	100
Medium	>15 mm <25	*Onitis*	*8*	*80*
		Diastellopalpus	*4*	*15*
		Copris	*6*	*5*
Small	>5 mm <15mm	*Onthophagus*	*16*	*70*
		Milichus	*22*	*10*
		Oniticellus	*6*	*12*
		Liatongus	*8*	*6*
		Euoniticellus	*12*	*1*
		Caccobius	*6*	*1*

Two replicates consisting of four treatments were used to assess macronutrient transfer. The experiment was set up at the edge of secondary forest adjacent to the Ark Gate entrance of the ANP. Each treatment consisted of a 40L (height: 50cm x diameter: 40cm) plastic bucket buried with the top lip placed flush with the soil surface. Excavated soil was sifted with a 2mm aperture to remove debris and macroinvertebrates and was then placed back into each bucket until it was completely filled with firmly packed soil. Freshly deposited elephant dung was collected by removing the top section of boli, leaving behind dung that was in contact with the ground to avoid soil contamination. Similarly, dung contaminated by urine was not used. Dung was shaped into hemispherical 1L pats and frozen for 20 hours to kill any macroinvertebrates present. Dung pats were defrosted at ambient temperature and placed on top of each soil-filled bucket and then the dung beetles for each treatment were released. A pyramidal structure made of wooden poles wrapped in 1.2mm gauge netting was placed above each bucket to prevent ingress or egress of dung beetles during the experiment. In the control treatment, a dung pat was placed but no beetles were released. The experiment began on the 28 April 2015 and ended after 112 days, as this timeframe covered the expected completed lifecycle for all species used in the experiment and allowed the action of both adult and larval dung beetles to be recorded.

Soil samples were collected by using a standard soil corer (2.5 x 10cm) with one core collected from under each pat at the start of the experiment (day 0) and subsequently at days 7, 14, 28, 56 and 112. Each soil sample was frozen at -20°C in preparation for transport and laboratory analysis. Dung samples from each time interval were dried for 24hrs at 70°C, then pulverized in a ceramic mortar to pass through a 2mm sieve and were analysed using the Mehlich-3 extraction procedure (Mehlich, 1984). I added five grams of dung to 20ml of 0.05 M HCl in 0.025 M $H2SO4$, and the filtrate was analysed by Inductively Coupled Plasma-atomic Emission Spectrometry (ICP-OES). Approximately 5g of dried and weighed soil were decarbonised with 1M solution of HCl before being analysed for total C and N concentrations through the LECO TruSpec analyser using the combustion (Dumas) method. Data were analysed using a linear mixed effects model with time and guild as a random effect and nutrient transfer (N, P,C,K) calculated as the amount of mg passed from dung into the soil. All analyses were completed using the nlme package (Pinheiro et al., 2017) in R software version 3.1.1. (R Core Team, 2016).

4.3 RESULTS

There was a highly significant difference between treatments for all tested macronutrients across the 112-day experimental period (all $P < 0.05$ for C, N, P and K, see Table 4- 2; Figure 4- 1). That is, the presence of beetles in the treatments increased nutrient uptake in the soil for all treatments, relative to passive leeching of nutrients from dung in the absence of beetles in the control treatment. Large-bodied beetles effected the greatest change in macronutrient status, enriching the soil on average by 44.51% for all macronutrients when the control at day 0 was compared with this group 112 days later. All functional groups had a significant effect on available

P transfer from dung into the soil. The available P content in each treatment increased rapidly from day 0 for all functional guilds but appeared to stabilise by day 56 of the study except for the largest beetles where it continued to increase (Figure 4-1d, bottom left panel).

When between treatment effects were analysed, the greatest effects were observed between the control (dung + no beetles) and the large body size functional guild (beetles with a body length >0.25mm; Table 4-2). Thus, large bodied beetles accounted for the greatest transfer of nutrients into the soil for all macronutrients I measured; Carbon (P=0.002); Inorganic Nitrogen (P=0.002); Potassium (P<0.001); Phosphorus (P<<0.001) over time (see Figure 4-1) with the largest overall effect being found for the transfer for exchangeable Potassium. The small-bodied functional guild showed the smallest effect for macronutrient transfer to the control; with significant effects for K (P=0.003) and P (P=0.01), but not for N or C (both P>0.05; see Figure 4-1 (a-b) and Table 4-2). The medium-bodied functional guild showed a moderate effect on soil macronutrient enrichment with significant effects for K (P=0.0008), P (P=0.003), and C (p=0.01), but no difference for N (P=0.08).

Table 4-2 Effect of macronutrient transfer between the control and functional guilds (based on beetle body size) and the effect of nutrient transfer over time Bold indicates a significant difference.

Treatment main effect			Treatment effect over time		Large		Medium		Small	
	F (df)	*P*	F (df	*P*	contrast	*P*	contrast	*P*	contrast	*P*
N	4.61 (3, 15)	**0.01**	8.31 (3, 39)	**0.001**	0.26	**0.002**	0.13	0.08	0.09	0.19
C	4.84 (3, 15)	**0.01**	10.16(3, 39	**0.01**	3.14	**0.002**	2.56	**0.01**	1.67	0.07
P	10.68 (3, 15)	**<0.001**	0.36 (3, 39)	**<0.05**	1.63	**<0.001**	1.21	**0.003**	0.75	**0.01**
K	14.17 (3, 15)	**<0.001**	21.76 (3, 39)	**<0.001**	118.72	**0.001**	92.54	**<0.001**	75.33	**0.01**

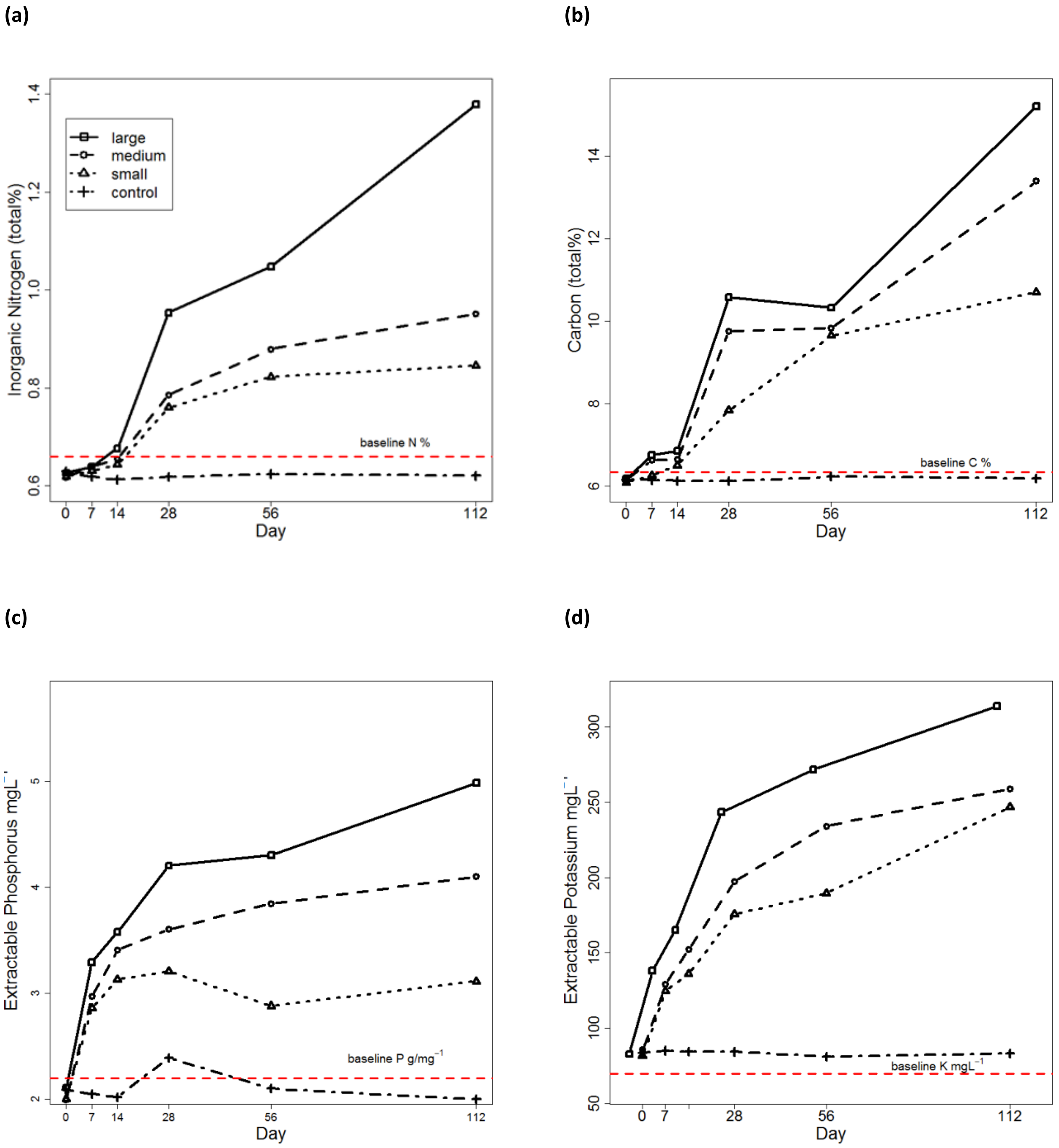


Figure 4-1 Changes in the soil nutrient contents (a) total Nitrogen; (b) total Carbon; (c) extractable Phosphorus; (d) extractable Potassium for 112 days The horizontal dashed lines are published evidence of the baseline bioavailable nutrients found in (Nicholson, 1976), a previous study in the same area and soil type as the current study.

4.4 DISCUSSION

My main finding was that body size in paracoprid dung beetles has a large and positive effect on the incorporation of macronutrients from dung into the soil and that this effect increases over time to a period of at least 112 days (Figure 4- 1(a-d). When the functional guilds I identified are ranked in order of their capacity to facilitate nutrient exchange, large beetles have the largest effect, followed by medium and small-bodied beetle groups, respectively. My results also suggest the movement process and rate from dung to soil differed *per* nutrient. Inorganic N content in the soil from all the treatments increased from day 14 for all treatments and tended to increase again from until day 56 where they tapered off. My results suggest that the inorganic N content in the soil only significantly increased due to the large-bodied functional guild. The transfer of readily available K content was much faster than those of other nutrients, irrespective of the dung beetle treatments. Hogg, (1981) reported that most K in dung is water soluble and that the contents of water soluble N and P in dung are relatively small. Therefore, the difference in movement of those nutrients from the dung to the soil is possibly explained by the difference in their water solubility.

The largest beetles in my experiment are in the genus *Heliocopris*, which contains species that are among the largest dung beetles in the world (Pokorný et al., 2009) and are known for their ability to relocate large quantities dung underground (Klemperer and Boulton, 1976; Kingston and Coe, 1977). *Heliocopris* tend to specialize on the dung of large herbivores such as elephant and rhino and occur at relatively low population density, most likely because of their large body size and the low density of their preferred dung (Davis, 2013b). However, their large body size is frequently cited as a trait that correlates significantly with increased extinction risk over ecological time scales. Indeed, several studies highlight declines in large-bodied dung beetles in the presence of habitat disturbance (Larsen et al., 2005; Gardner et al., 2007), and a concomitant decline with large herbivore density (Bogoni et al., 2016).

Slade et al. (2007) assessed dung beetle morphological traits in the context of ecosystem functioning and reported that the absence of large, nocturnal tunnellers yielded a 75% reduction in the quantity of dung removed from soil surfaces. Other studies investigating different aspects of functional diversity have established that single species may be more influential in terms of ecosystem services provision than overall species richness, and that these functionally important species may occur at different densities in an ecosystem (e.g. Larsen et al., 2005; Soliveres et al., 2016). These observations are congruent with my findings as my results suggest the largest dung beetles are, functionally, the most important in affecting soil nutrient transfer from dung, as they are more effective at burying larger quantities of dung and perturbing buried dung. However, these large dung beetles generally appear to be the least tolerant to habitat perturbation and other drivers of ecosystem change (Séguin et al., 2014) and (Díaz et al., 2013).This suggests a relationship between taxonomic diversity, functional diversity and a decline in ecosystem productivity (Cardinale et al., 2012; Hooper et al., 2012).

Soil nutrient depletion has been linked with declines in crop productivity in sub Saharan Africa, (Sanchez et al., 1997) and Kenya is particularly affected by falling agricultural productivity and diminishing food security, with 12 million people residing in areas with land degradation (Mulinge et al., 2016). Food webs may be linked across habitat boundaries and the biodiversity of one ecosystem, in this case a Protected Area, may influence the functional delivery of services to adjacent ecosystems such as the agriculturally important land described here. Depletion of soil nutrients has been indicated as the major cause of low yields in economically important crops. Historically, soil fertility depletion is the major biophysical cause of declining crop productivity and a fundamental root cause for declining food security on smallholder farms in central Kenya (Mugendi et al., 2007; Njeru et al., 2011).This may have an impact on a local scale and may indirectly affect the communities which surround the ANP. These effects may include less fodder for cattle, firewood for cooking, and less crop residues and cattle manure to recycle nutrients (Smaling et al., 1997). This study reinforces the functional importance of interspecific variation in dung beetle functional characteristics and highlights that loss of dung beetle diversity could negatively impact functional capacity in delivering macronutrients to soil. My study highlights the importance of safeguarding those species that are the most important for sustaining ecosystem function and ascertaining how sensitive they may be to ongoing anthropogenic activity.

5 Colouration and morphological clines of an Afromontane Dung Beetle along an altitudinal gradient

Abstract

High altitude insects are an ecologically specialised group and possess a suite of adaptions which allow persistence in the inhospitable conditions often associated with inhabiting mountain tops. Melanic individuals, or individuals containing high levels of eumelanin, possess several traits which increase resistance to solar radiation and desiccation, while aiding thermoregulation. The aim of this study was to identify phenotypic trait variation along an altitudinal gradient in a regionally endemic Afromontane dung beetle with enormous variation in colour and horn morphology. To understand the predictive relationship between dung beetle morphological traits and altitude I used nonparametric conditional inference trees. The results of this study suggest that colour polymorphism in *Onthophagus proteus* might be at least partly driven by environmental factors as there is significant differences between colour hues among altitude bands.

5.1 INTRODUCTION

The existence of discrete morphs as a response to environmentally cued factors regularly accounts for observations of intraspecific variation throughout the animal kingdom. Environmental factors commonly influence patterns of morphological variation within natural populations. The study of intraspecific variability along elevation gradients represent an appropriate natural experiment to understand the response of organisms to environmental changes that occur over short spatial distances (Körner, 2007). The study of these responses has serve as an opportunity to understand the response of species and communities to both climate change (Hodkinson, 2005) and the role of sexual selection (Pomfret and Knell, 2006; Valverde and Schielzeth, 2015).

Phenotypic plasticity can be defined as 'the ability of individual genotypes to produce different phenotypes when exposed to different environmental conditions' (Pigliucci et al., 2006). Examples of such polyphenism may commonly encompass several forms. These can include caste polyphenism seen in social insects, such as in ants (Trible and Kronauer, 2017), bees (Wheeler, 1986; Collins et al., 2017), and termites (Watanabe et al., 2014) and seasonal polyphenism occurring in butterflies and caterpillars (Brakefield, 1996). However, perhaps the most widely described phenotypic phenomena is alternative male morphologies observed in many arthropods, most notably the dung beetles belonging to the family Scarabaeidae (Moczek and Emlen, 1999; Emlen et al., 2005; Kishi et al., 2015).

The horns of horned dung beetles belonging to the genus *Onthophagus* are ideal characteristics for studying the origin and diversification of novel traits (Moczek, 2006). These horns take the role of weapons that are used by male dung beetles to mate-guard tunnel entrances where females are present (Knell, 2011). However, horn size is thought to have directly arisen from sexual selection through the extreme competition by males over access to a limited number of reproductive females and are considered an honest signal of sexual fitness making mate selection more efficient (Clifton et al., 2016).

High altitude insects are an ecologically specialised group (Mani, 1968) and possess a suite of adaptions which allow persistence in the inhospitable conditions often associated with inhabiting mountaintops. Melanism, 'the occurrence of variant(s) that is/are mostly or completely dark in pigmentation as intraspecific polymorphisms' (True, 2003), is a widespread phenomenon found in both arthropods and vertebrates and is often lauded as a textbook example of evolution in action. Melanic individuals, or individuals containing high levels of eumelanin, possess several traits which increase resistance to solar radiation and desiccation, while aiding thermoregulation. The thermal melanism hypothesis, (e.g. Watt, 1968; Kingsolver, 1987) posits that body colour is a significant factor affecting body temperature as darker coloured individuals can attain higher body temperatures than light coloured individuals when exposed to direct sunlight. Therefore, darker coloured individuals may be better adapted to cold regions as they can be active for longer periods while feeding, mating or during oviposition. This is especially pertinent for insects who live in mountainous tropical regions where the difference between atmospheric temperature and objects exposed to direct sunshine can be as great as 73° C (Mani, 1968). There is general evidence of a positive relationship between altitude and melanism (True, 2003; Clusella Trullas et al., 2007), however the range of studies in which this has been demonstrated is limited with very few studies investigating change along a continuous altitudinal gradient. Those that have, report a general relationship between altitude and colour at spatially separated sites (Guerrucci and Voisin, 1988) or compare the extremes of altitude (Rajpurohit et al. 2008; Karl et al. 2010).

Onthophagus proteus is a medium sized paracoprid Afrotropical dung beetle with a recorded distribution strictly limited to high elevation locations in Uganda (Nyeko, 2009), Tanzania and Kenya (Davis and Dewhurst, 1993). In Kenya, the known species distribution is restricted to Mt Kenya and Aberdare National Parks. This study found it is the most abundant Scarabaeine dung beetle between 2500-4000m asl in the ANP, and it has a wide ranging vertical distribution which spans from the lowland forest to the moorland in the uppermost region of the Park. This dung beetle was first described in D'Orbigny's (1913) '*Synopsis des Onthophagides d'Afrique*'. Its protean characteristics were evidently apparent as notes contained within the description define the elytral and pronotal colour as being "extremely variable". Three colour variants were originally described by D'Orbigny; pronotum bronze or green bronze, or pronotum bronze or dark brown, or body entirely black. However, no mention is given to other morphologic traits including body or horn size or any other combination of pronotal or elytral colouration.

Conditional inference trees (hereafter; CITs) is a methodology for examining the relationship between a single response variable and multiple potentially explanatory variables (Quinn et al., 2002; Zhang, 2016). They are widely used in engineering and medicine because they tend to be better at predicting known relationships from data than more commonly used methods, such as logistic and linear regression (Nagy et al., 2010). However, their full potential has yet to be realised in conservation and ecological disciplines. This is despite increasing awareness of the efficacy and robustness of machine learning in clarifying collinearity between factors which influence a population, and the knowledge that such factors may interact, have synergistic effects or partially negate one another in large datasets which may contain a mixture of continuous, ordinal or nominal measurements and where the data may be non-linear or non-normally distributed. Using CITs is advantageous when compared to linear regression because no modification needs to be applied when using non-Gaussian distributions to describe these sorts of data (Zuur et al., 2007) and they are able to detect relationships that are outside the boundaries of general or generalised linear/additive models (Debeljak and Džerosk, 2011; Johnstone et al., 2014). Another advantage of CITs model methods is that they form the first step toward a Random Forests analysis (Zhang, 2016). Random forests analysis is a predictive, model-averaging approach, where random bootstrapped samples of predictor variables are used to generate a 'forest' of models, and from this forest the relative importance of predictor variables can be calculated (Breiman, 2001). Random forests methods tend to outperform other modelling techniques such as generalised linear models and generalised additive models, for predicting actual species presence or absence (Lawler et al., 2006) Therefore, Random Forests analyses are being increasingly applied when exploring complex relationships in ecology (Cutler et al., 2007). Furthermore, CITs are a valuable tool because they produce decision trees which can be interpreted easily visually. By generating CIT models, clear decision paths can be used to determine the relative importance of predictors and their interactions. The predictive performance of each CIT was assessed using the ConfusionMatrix function in the Caret package (Kuhn et al., 2017) in R (R Development Core Team, 2017) which was used to construct a multiclass confusion matrix for each CIT.

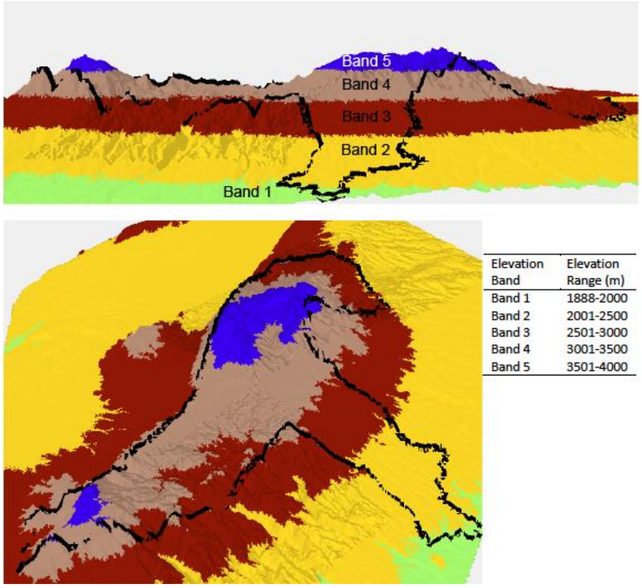
The aim of this study was to identify phenotypic trait variation along an altitudinal gradient in a regionally endemic Afromontane dung beetle with enormous variation in colour and horn morphology. It was hypothesized that beetles demonstrating a higher proportion of blue within a Red-Green-Blue model but at a decreased level of colour intensity could be found at higher elevation bands due to a higher quantity of eumelanin contained within exoskeletons which has naturally darker pigments and thermoregulatory benefits. Three models were used to explain the variance in morphology and colouration in *O. proteus*. The first model solely used colour hue, the second model used morphological traits including pronotal variables and elytral measurements to explain altitudinal location, and the final model used both colour and morphology combined. Bergmann's rule (Bergmann, 1847) states that individuals of a species/clade at higher altitudes or latitudes will be larger than those at lower elevations because larger body masses will suffer smaller losses of heat and larger animals have to produce less heat to increase body temperatures energy due to their more favourable relationship between body volume and surface area. I hypothesized that trait size in *O. proteus* would be positively correlated with elevational increase in accordance with Bergmann's Rule as diurnal dung beetles require high body temperatures as a requirement for flight (Caveney et al., 1995; Verdú et al., 2004), and maintain elevated body temperatures not only during flight, but also while manipulating dung for burial (Bartholomew and Heinrich, 1978). Cephalic horn size was also included as a morphological trait but was not thought to be positively correlated with altitude. Horn size in dung beetles is considered to be sexually selected trait (Moczek and Emlen, 1999; D. Emlen et al., 2005; J. Pomfret and Knell, 2006) and is thought to relate to reliable signal of male quality being indicative a male dung beetle's nutritional history and physiological condition in comparison to other traits.

5.2 METHODS

5.2.1 Transect locations and dung beetle collection

TRANSECT LOCATIONS

Shuttle Radar Topography Mission (SRTM) raster data at one arc second resolution (30m along the equator) were used to create a three-dimensional model of the Aberdare mountain range in ArcScene 10.4. Data were categorised along equal interval breaks of 500m to delineate elevation bands. Base height was adjusted from 0 to 3.28m, and the pixel value (*z* value) changed from 0 to 1 to provide a hillshade aspect. The data were then 'floated' (Bajjali, 2018) to create the elevation model. A polygon of the ANP boundary was overlaid on the model to enable to viewer to see which category of bands were found within the ANP. Transects were placed as central to the band as was logistically possible and were located in both open and closed canopy areas.



Elevation Band	Elevation Range (m)
Band 1	1888-2000
Band 2	2001-2500
Band 3	2501-3000
Band 4	3001-3500
Band 5	3501-4000

Figure 5-1 model of elevational bands in the Aberdare National Park (black boundary line) created using ArcScene 10.4 and STRM data at a 30m resolution.

DUNG BEETLE COLLECTIONS

Eight baited pitfall traps were placed in the ground 50 m apart along two transects in each altitude band and exposed for four days. Each trap comprised of a small plastic container (120 mm top diameter, 125 mm deep) with a plastic funnel (50 mm deep at apex) suspended from its inner rim, which prevented the escape of trapped beetles. The bait comprised 40g elephant dung contained within a net that was suspended directly above each trap and supported by two 25cm wooden sticks. Collected material was preserved in 70% alcohol and then dried for four hours at 50°C.

5.2.2 Study Species

Dung beetles from each elevation band were sorted into morphospecies and then according to sex by examining the ventral surface of the penultimate segment of the abdomen which is medially compressed in males, but equal in females. Dung beetles were further identified as belonging to *O.proteus* by the dissection of the male genitalia. The aedeagus was removed and heated in a 5% potassium hydroxide solution until internal structures were soft. The internal sac was drawn out by gently pulling the outer portion of the sac from the inside of the sclerotized capsule of the aedeagus (see Figure 6-1). Once the sac was completely clean, it was rinsed with 70% ethyl alcohol. The structures were prepared on microscope slides in liquid glycerine. Preparations on microscope slides were labelled with an individual number and the corresponding number of the preserved specimen.

Male genitalia have been widely used in Scarabaeinae systematics (Medina et al., 2013; Tarasov and Génier, 2015) as the process allows all of the scleral structures to be compared and analysed regarding their position and shape. These structures vary greatly among the groups, are species specific, and are widely used to identify beetle taxa to species level when other morphometric measurements will not suffice (Tarasov and Solodovnikov, 2011).

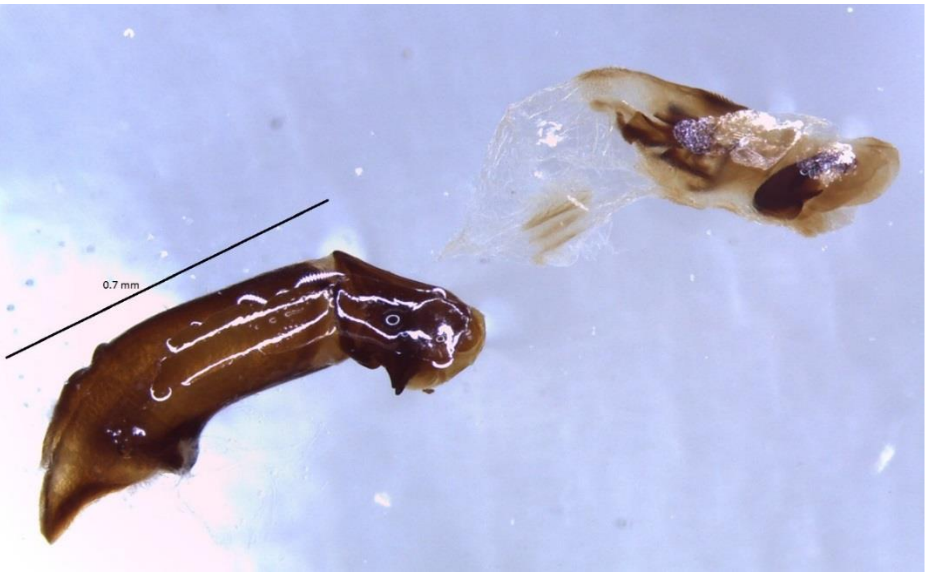


Figure 5-2 The adeagus of *Onthophagus proteus* with the sclerotized capsule exposed.

5.2.3 Measuring Colour Polymorphism

Dung beetles were first visually separated into six colour categories. Individuals categorised by pronotal colour then by elytron colour, resulting in a pseudonym for each colour morph. For example, ‘GrBr’ would describe an individual with a green pronotum, and brown elytron. The individuals with black elytron and pronotum were initially categorised as ‘BlkBlk’ but further analysis revealed the black hue was in fact a very dark ‘blue-black’ which was undistinguishable with the human eye see Figure 5-3.

RGB MODEL VALUES

Ninety-nine individuals (47 males and 52 females) belonging to *O. proteus* were photographed at 16x magnification with a Nikon D3100 (effective pixel count of 14.2 megapixels) which was attached to Leica M165C microscope. Each image was captured in .nef format (Nikon Electronic Format) to avoid image compression. Both the microscope and camera were placed inside a lightbox to control for fluctuating light conditions. A ForensiGraph™ grey and colour standard (http://www.forensigraph.co.uk) was included in each photograph to allow RGB calibrations to be derived for each image. Measurements of grey standards were taken by drawing a box over the area of interest on the grey colour standard, and then using the histogram function in ImageJ (Schneider et al., 2012) to determine the mean grey scale value and standard deviation for each channel (*sensu* Stevens et al., 2007). Six regions of interest (ROI); two pronotal and four elytral measurements, each measuring 2mm^2 were chosen to obtain RGB values for each individual, see Figure 5-4. These ROI were analysed using the RGB Measure plugin in Image J (Schneider et al., 2012) to obtain mean RGB pronotal and elytral values for each individual and expressed as a digital 8-bit per channel resulting in each component expressed as proportion of 255 bytes within the RGB triplet, see Table 5-1. Component values are stored as integer numbers in the range 0 to 255. If all the components are at zero, the result is black; if all are at maximum (255), the result is the most representable white. For example, if the following RGB colour model (R=0, G=0, B=255) was converted to a hexadecimal string the resulting colour would be a vivid royal blue, but if the same model with a blue component equalling 20 was used, the resulting colour would be much darker hue, appearing almost black to the human eye, (see Figure 5-3).

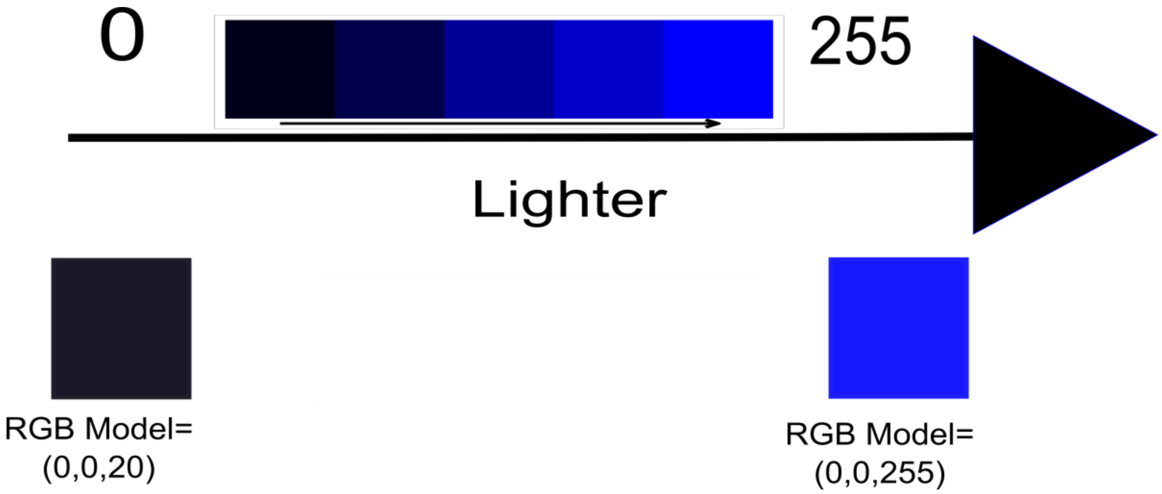


Figure 5-3 An example of when a component of an RGB models varies, the resulting hue will change. In this case, when the blue component of the model is increased it produces a lighter and more vivid colour blue.

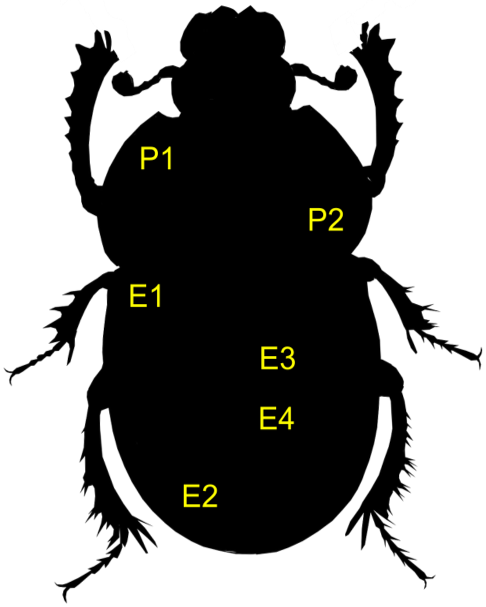


Figure 5-4 Locations of six body ROI from which I sampled dorsal colouration of *Onthophagus proteus*. P1-P2 are Pronotal measurements; E1-E4 are Elytral measurements.

Table 5-1 Description of the average values for each of the two regions measured used in the RGB models

Measurement description	Name
Mean Red value for Elytra	RGB_Ely_R
Mean Green value for Elytra	RGB_Ely_G
Mean Blue value for Elytra	RGB_Ely_B
Mean Red value for Pronotum	RGB_Pro_R
Mean Green value for Pronotum	RGB_Pro_G
Mean Blue value for Pronotum	RGB_Pro_B

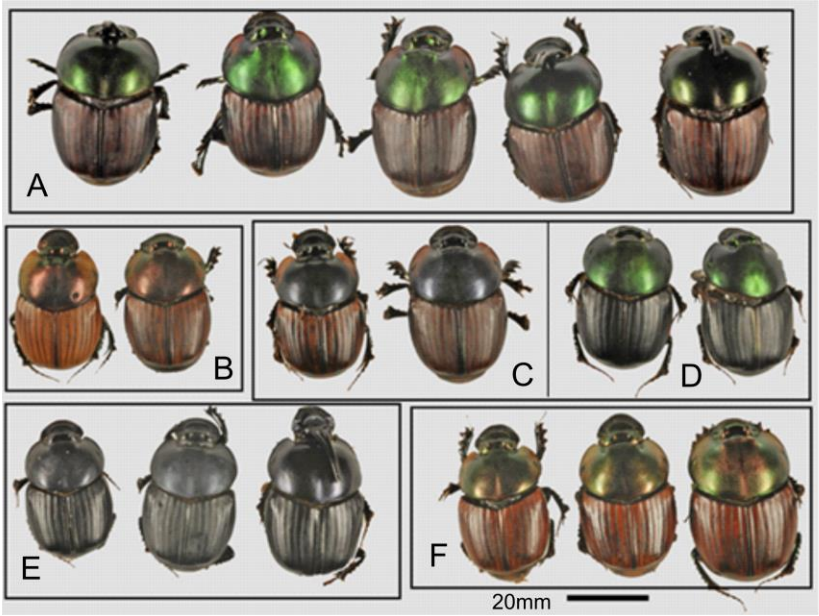


Figure 5-5 The interspecific variation of colour found within O. proteus (A) Green Pronotum, Brown Elytron (GrBr); (B) Brown Pronotum, Brown Elytron (BrBr);(C) Black Pronotum, Brown Elytron (BrBlk); (D) Green Pronotum, Black Elytron (GrBlk);(E) Black Pronotum (F) most prevalent colour morph

MEASURING BODY SIZE VARIATION

To ensure continuity within each image, and between individuals, dung beetles were orientated according to positions described in Hernández et al., (2011) who outlined optimal Cartesian coordinates such as the points of convergence of structures, the apices of processes or their corresponding endpoints to record dung beetle body size measurements. Eight trait measurements were taken using the line tool bar found in the AxioVision software package and recorded in micrometres (µm) *per* individual dung beetle. They are described in Table 5-2 below. I used three morphological traits; total body length, pronotal length and elytral length to describe differences between sexes and between colour morphs.

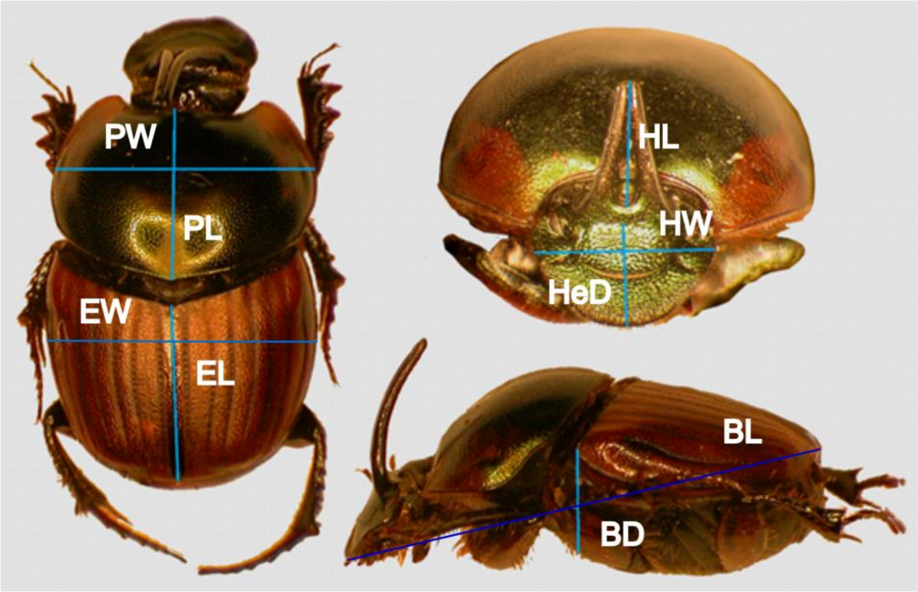


Figure 5-6 Approximate sample location of each morphometric trait within *Onthophagus proteus.*

Table 5-2 Description of each morphological trait used in the analysis.

Measurement	Measurement Description	Name
Head Width	Between the lateral basal margins of the genae	HW
Head Length	From the medial base to the medial apex of the head	HeD
Horn Length	From the medial base to the horn apex	HL
Pronotum Length	From the medial base to the medial apex of the pronotum	PL
Pronotum Width	Between the anterior lateral angles of the pronotum	PW
Elytra Length	From medial base to medial apex of elytra	EL
Elytra Width	Between anterior basal angles	EW
Body Depth	From the apical humeral callosity to the posterior of the mesothorax	BD

Body Length	From the medial base of the clypeus to the medial apex of the pygidium	BL

5.3 DATA ANALYSIS

I used non-parametric Kruskal Wallis tests with Bonferroni corrections to compare morphological traits within individuals between elevation bands. In addition, chi-squared tests of goodness of fit were performed to identify which dung beetle colour morphs appeared more frequently than average across all elevation bands.

Furthermore, I used Mann Whitney U tests with a Wilcoxon paired post-hoc tests to describe differences among males and females between elevation bands. Linear regression was used to assess the relationship between horn size and the level of red, green, and blue found in male pronotum and elytra.

5.3.1 Using conditional inference trees to predict altitudinal location of *Onthophagus proteus*

To understand the predictive relationship between dung beetle morphological traits and altitude I used nonparametric conditional inference trees using the “Ctree” function within “Party” package (Hothorn et al., 2006) in R (R Development Core Team, 2017). This method creates groups that are most different from each other based on the probability of being located within a particular altitude band. These inference trees first identify a binary split (cut off point) in the predictor variable or ‘root’ variable which creates subgroups or nodes (Zhang, 2016) . Above the first cut off, the regression relationship is stronger and below, the relationship is significantly less strong. Following the first binary split, the process is recursively repeated, creating multiple cut off points or nodes (Quinn and Keough, 2002; Zuur et al., 2007). The model when plotted, produces an inverted tree which shows the relative importance of different predictors and how they interact. Response variables for RGB values were averaged by individual for both the elytral and pronotal values.

5.4 RESULTS

5.4.1 Abundance of *Onthophagus proteus* across elevation bands

Onthophagus proteus was the most abundant Scarabaeidae dung beetle found within the ANP with 935 individuals trapped in June-August 2015 and February-March 2016. Unlike the other dung beetle species in the park there was no significant decline in abundance with an increasing elevation (r^2=0.009, p<0.34). *Onthophagus proteus* was the most abundant Scarabaeidae dung beetle found above 3500m asl. Two dung beetle species belonging to the Aphodiidae family, *Neocolobopterus kivuanus* and *Neocolobopterus maculicollis* were the most abundant dung beetles overall at elevations greater than 3000m asl.

5.4.2 Differences in morphological variables between elevation bands

Kruskal Wallis tests revealed that both horn length and pronotal width were found to be significantly different between altitude bands, (HL: w=27.281, df = 4, p=<0.001; PW: w= 2.9267, df = 4, p=0.05). Inspection of the group means using a Wilcoxon test with Bonferroni correction suggests horn length is significantly different in elevation bands four and five compared to horn length in elevation bands 1-3 (Fig 6-6). The median horn length for the groups in elevation bands four and five was greater compared to those in lower bands. There was also a difference (P<0.05) between pronotal width in elevation bands three and four. The median pronotal width for the group in band three was lower compared to those in band four. There was no evidence of a difference in pronotal width between other pairs.

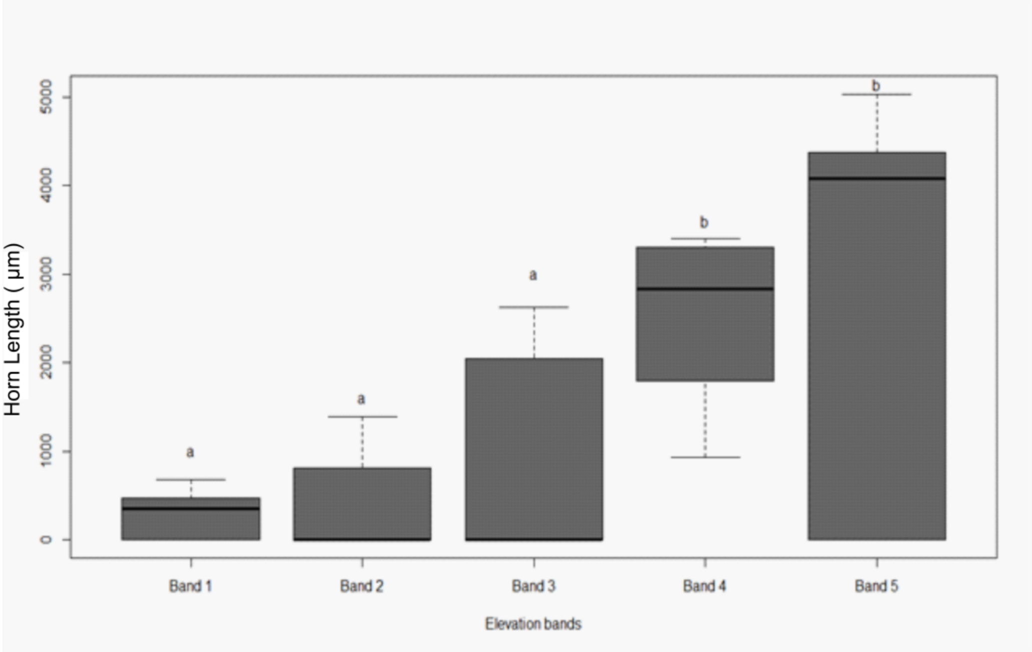


Figure 5-7 Comparison of horn length between elevation bands. Samples from lower elevations (Bands 1-3) are significantly different from upper elevations (Bands 4 and 5) in the Aberdare National Park. Boxplots show the median values as the dark horizontal lines; 25th and 75th percentiles as the top and bottom of the boxes. The dashed lines show the interquartile range. The letters indicate significant differences between bands.

Table 5-3 Differences in morphology of *Onthophagus proteus* across five altitudinal bands. N=99 individuals. Significant variation ascertained by implementing a Chi squared test is indicated in bold.

Morphological Traits		
	X^2	P
Head Length	1.51	0.82
Head Width	5.66	0.22
Horn Length†	27.28	**<0.001**
Pronotum Length	0.93	0.91
Pronotum Width	2.92	**0.05**
Elytron Length	2.61	0.62

Elytron Width	2.83	0.66
Body Length	0.99	0.90
Abdomen Length	1.26	0.86
Depth Max	2.55	0.63

† N=47 *

5.4.3 Sexual dimorphism between colour morphs on an altitudinal gradient

There were no significant differences in total body length or total elytral length between males and females of any colour morph (see Appendix 4). However, there was a significant difference in median pronotal length between males in the BrBr group and females in the BrBr group between elevation bands (Mann–Whitney U = 29, $P < 0.01$) with males having significantly longer pronotal discs.

5.4.4 Differences in horn length and blue component of Elytron

Horn length was a significant predictor of the average proportion of blue found in dung beetle elytra (r^2=0.55, df=45, p= <0.001), with males with bigger horns having a lower blue component which results in darker wings when compared with beetles with horns less than 3532 mm in length (Fig 5-9).

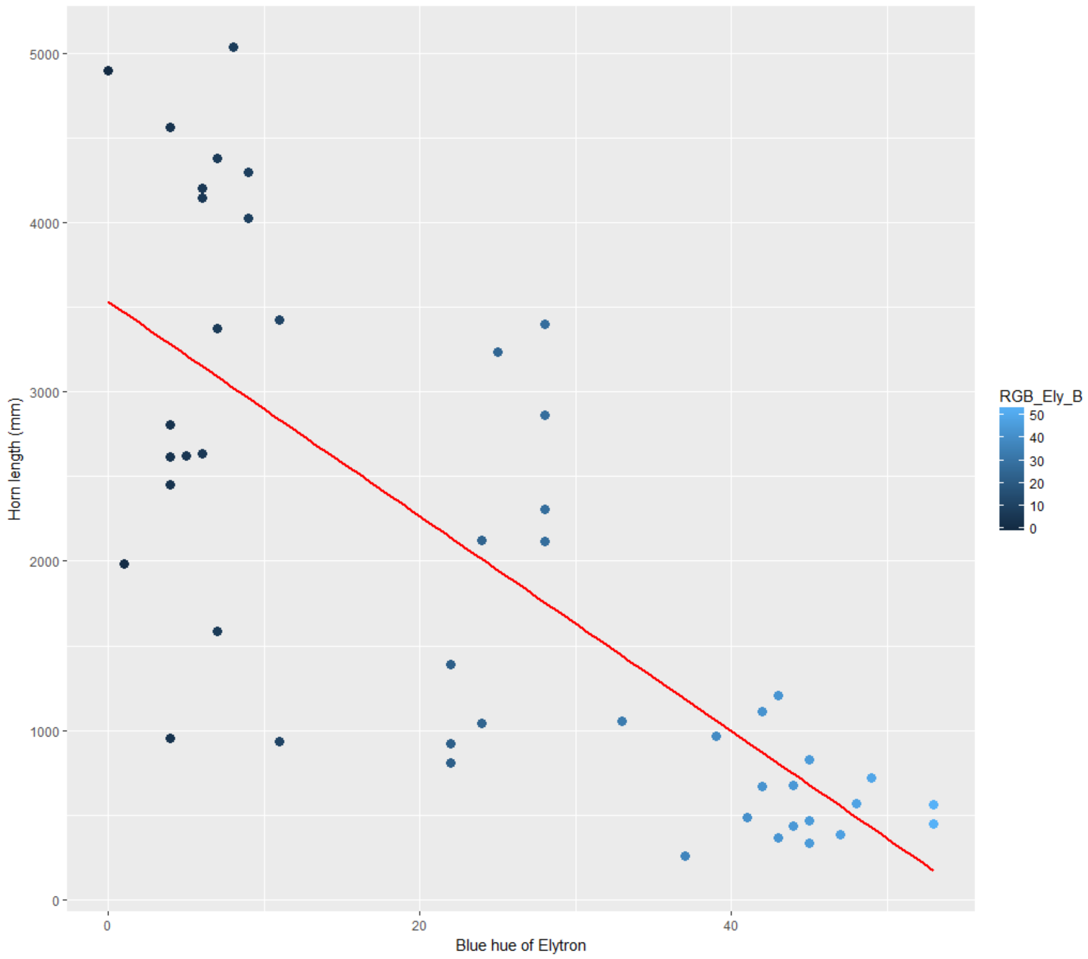


Figure 5-8 Horn length versus proportion of blue in male dung beetle elytra. Darker elytra are found in males with longer cepahlic horns.

5.4.5 Differences in colour morph frequency between altitudinal bands

I used Chi-squared tests of goodness of fit test to compare the frequencies of colour morphs between altitudinal bands. There was an association between beetle colour and elevational band (χ^2=131.42, df=16, P=<0.001), with a greater frequency of darker beetles found at higher altitudes compared with lower altitudes than expected by chance. When the residuals of the Chi squared test were extracted, the strongest positive association can be seen between the brown/green colour morphs (11.89% contribution) and elevation band 1 and between the brown/black (18.94% contribution) and the black/black (12.36% contribution) colour morphs in elevation band five. These cells contribute 43.19% to the total Chi-square score and therefore account for most of the difference between expected and observed values.

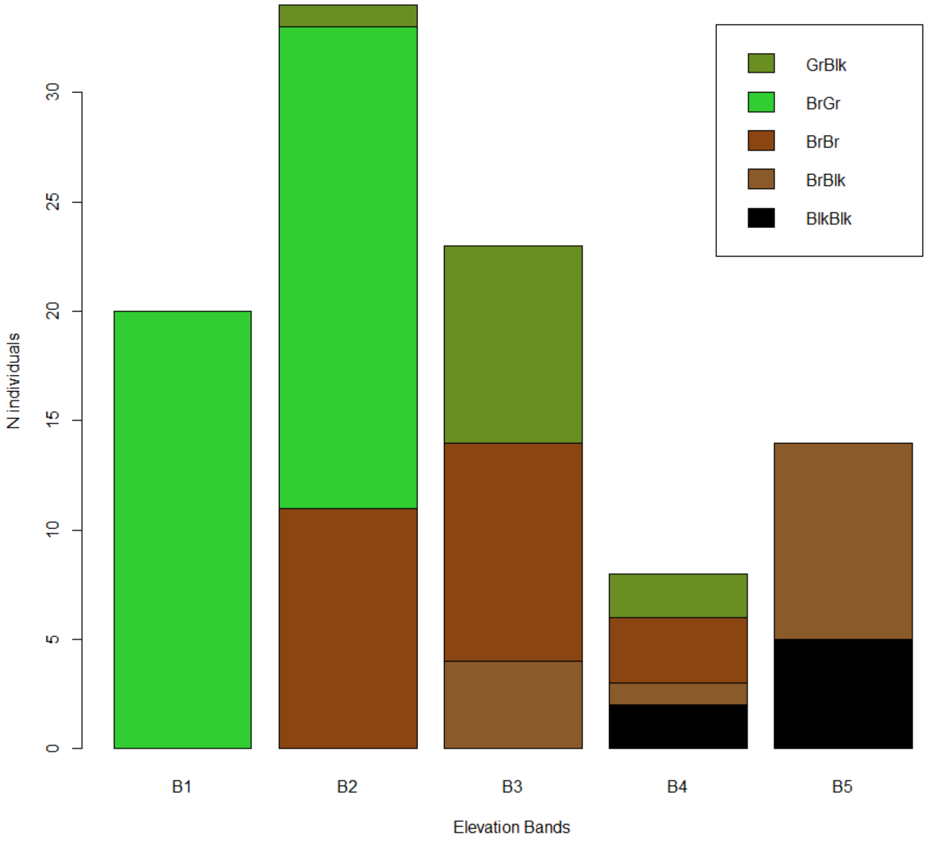


Figure 5-9 Number of individuals of *Onthophagus proteus per* colour group in each altitude band. GrBlk= Green Pronotum with Black Elytra; BrGr=Green Pronotum with Brown Elytra;BrBr= Brown Pronotum with Brown Elytra; BrBlk=Brown Pronotum with Black Elytra; BlkBlk= Black Pronotum with Black Elytra.

5.5 CONDITIONAL INFERENCE TREES

5.5.1 Predicting altitudinal placement based on RGB colour models

The algorithm using just colour predictors identified the strongest predictor as being the proportion of blue found in dung beetle Elytra which had statistical cut-off value of 11/255. Those beetles which have a lower proportion of blue, e.g. a darker body hue had a greater probability of being placed in the mid and upper elevation bands Figure 5-10 (A). Two other secondary nodes;

the proportion of green in the pronotum, and the proportion of red in the elytra partition the data into four terminal leaf nodes. A proportion of green in the pronotum greater than 24/255 explains a higher probability of an individual not being located in elevation band one. However, a proportion lower than 24/255 gives an individual a higher probability of being located in areas of 3000-4000m asl in the upper elevation bands. The proportion of red in the elytron splits the data into greater or fewer than 78/255. Those with a darker red (<78) are found in mid to high elevations and those with a lighter red (>78) are found in elevation bands one and two.

5.5.2 Predicting Altitudinal Placement based on Morphometric Measurements

Horn length was the only significant morphometric predictor in the suite of traits analysed. The decision tree illustrated in Figure 5-10 (B) demonstrates a clear demarcation between individuals with a horn length greater than 3396.2 µm and their probability of placement in the highest elevation band. If males have a horn length which is less than this cut off point but greater than 2618.42 µm they have a higher probability of being placed in the mid-elevations which constitute elevation bands three and four. Individuals who had a horn length less than the 2618 µm cut off point have a higher probability of being placed in the lower elevation bands particularly elevation band two.

5.5.3 Predicting altitudinal placement based on both Morphometric traits and colour models

The proportion of blue in dung beetle elytron was the best predictor of elevational placement using a combination of traits and colours. Individuals who scored below 11/255 and who had a less than 24/255 proportion on green in their pronotum were more likely to be found in higher elevation bands. For those individuals which had a proportion of Pronotal green greater than 24/255, the secondary node containing the predictive category horn length greater or less than 1983.37 µm was used to create to leaf nodes which describe the probability of being placed either mid elevation (bands two, three and four) or mid elevation and high elevation, bands 3 or five (Figure 10.5 (C).

Individuals that had a higher proportion of blue in their elytra were categorised by two further secondary nodes. The first node, horn length, partitioned those beetles with horn length greater than 1209.24 µm into a leaf nose which classified those beetles (n=7) as having a higher probability of being located at mid-elevations. The second node divided individual beetles into two leaf nodes based on the proportion of red in the elytra. Those beetles with a higher proportion of red were placed into bands one and two and those with a proportion of 78/255 or fewer into bands two and three.

5.5.4 Confusion Matrices and Predictive Power

. The overall accuracy and precision of each band *per* confusion matrix was computed and is displayed in Table 6-2. The CIT containing just the RGB values (model B) had the lowest overall accuracy 87.67% as it contained the highest number of false positives (FP) or "Type I errors" by incorrectly assigning three individuals from band four into band three and two individuals from band four into band five, in addition to two individuals from band five into band four. Model C, containing all morphometric and colour traits had an overall accuracy of 94.36% with just a single band, band four containing Type I errors, incorrectly predicting that two individuals from both bands three and five should be assigned to band four. Model A (all morphometric measurements) had the highest overall accuracy with 97.10% of individuals correctly placed in the true bands with a single individual incorrectly placed into band five instead of band four and one individual incorrectly placed in band four instead of band five. Overall, the models predicted dung beetle location in altitude bands very well as most errors occurred between neighbouring bands demonstrating a cline of variability between morphometric traits rather than distinct morphotypes.

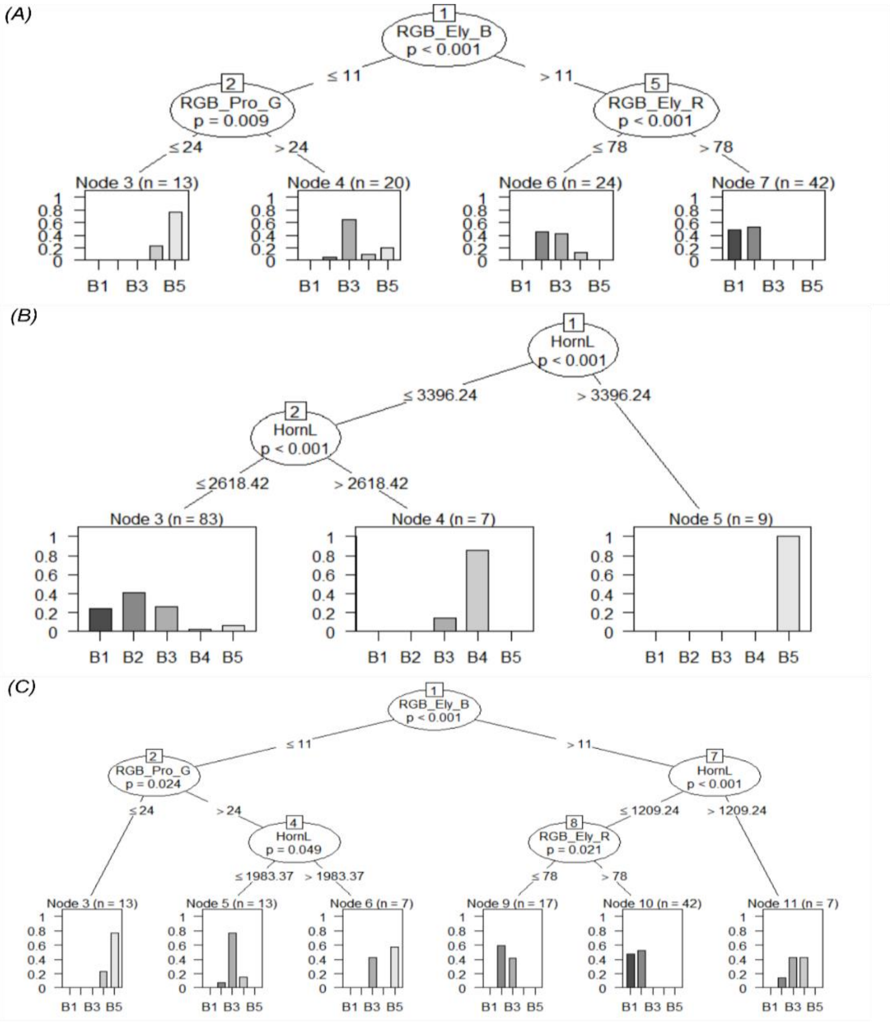
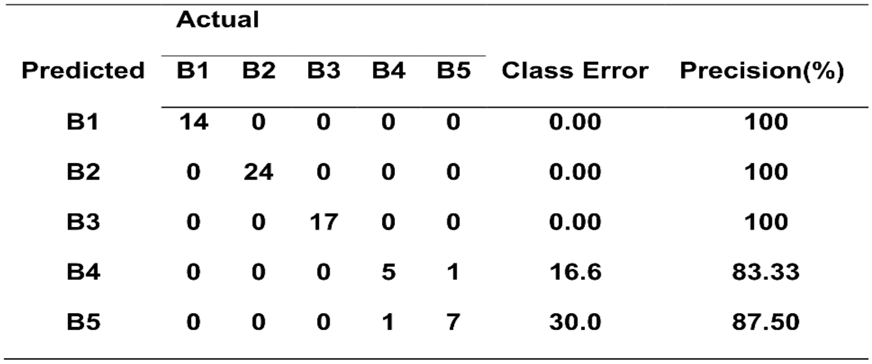


Figure 5-10 Examples of CITs for *Onthophagus proteus* morphometric models for elevational placement of individuals based on (A) proportion of RGB values in pronotum and elytron (RGB predictors only), (B) all morphometric measurements (all measurements included as predictors) and (C) morphometric measurements and RGB values (all variables). In the leaf nodes, bar charts visualise the probability of being located within a particular elevation band. The partition of objects from the training data set among the leaf nodes on the top of the diagram boxes (n). See Table 1 for variable names. All morphological measurements are in micrometres, all RGB values are a proportion of 255. P values indicate the significance of the binary split between predictors. The values between nodes indicate the cut off point for each binary split.

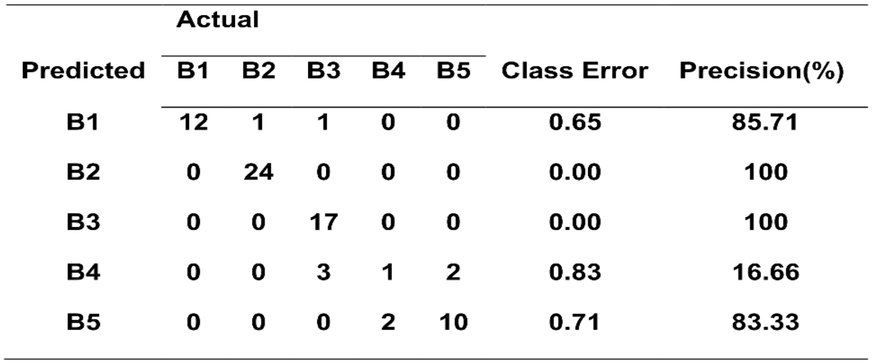
Table 5-4 Confusion matrices for CIT models; (A) RGB values only; (B) all morphometric measurements;(C) combination of all morphometric and RGB values

(A)



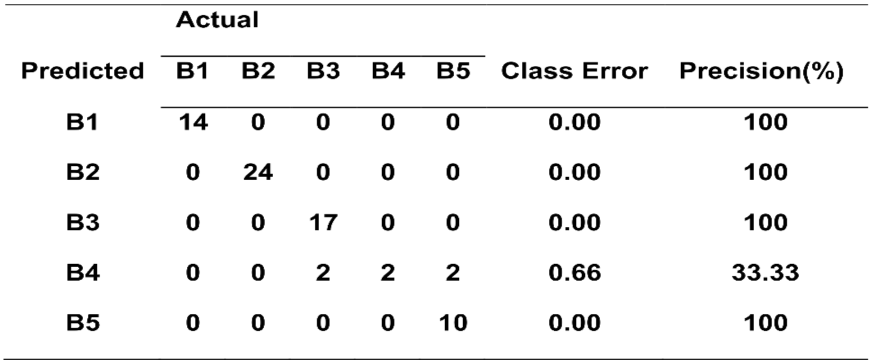
	Actual						
Predicted	**B1**	**B2**	**B3**	**B4**	**B5**	**Class Error**	**Precision(%)**
B1	14	0	0	0	0	0.00	100
B2	0	24	0	0	0	0.00	100
B3	0	0	17	0	0	0.00	100
B4	0	0	0	5	1	16.6	83.33
B5	0	0	0	1	7	30.0	87.50

(B)



	Actual						
Predicted	**B1**	**B2**	**B3**	**B4**	**B5**	**Class Error**	**Precision(%)**
B1	12	1	1	0	0	0.65	85.71
B2	0	24	0	0	0	0.00	100
B3	0	0	17	0	0	0.00	100
B4	0	0	3	1	2	0.83	16.66
B5	0	0	0	2	10	0.71	83.33

(C)



	Actual						
Predicted	**B1**	**B2**	**B3**	**B4**	**B5**	**Class Error**	**Precision(%)**
B1	14	0	0	0	0	0.00	100
B2	0	24	0	0	0	0.00	100
B3	0	0	17	0	0	0.00	100
B4	0	0	2	2	2	0.66	33.33
B5	0	0	0	0	10	0.00	100

5.6 DISCUSSION

Here I report altitudinal clines in morphological and colour traits from a single population of a regionally endemic dung beetle *O. proteus* from the Aberdare mountain range in central Kenya.

The results from the CITs indicate a combination of morphological traits and colour are a better classifier of elevational placement when compared with colour and morphological traits alone. Variability in horn length and proportion of both elytral blue and red, plus the proportion of pronotal green was effective in predicting elevational placement as these predictive factors when working in tandem produced stronger associations between all morphological traits and produced greater predictive power. Overfitting of data can occur when more variables are applied without any increase in predictive power.

Band Four was consistently contained the greatest number of Type I errors and had the lowest percentage precision in all models, but particularly in the models which included RGB values as predictor (Table 5-4). This may be partly due to the large area (295.6km^2) which this altitudinal band covers in the park, as the majority of the park lies between 3000-3500m asl (Figure 5-1). This band also contains the greatest variety of habitat types (*Hagenia* dominated forest, Bamboo forest, and Ericaeous moorland) and vegetation ecotones of any elevation band in the ANP. This diversity of habitat types may account for high variation in beetle colour, as positive natural selection applies pressure on the colour morph which benefits an organism's persistence in a particular habitat. The dispersal ability of *O. proteus* is unknown, however, a similar-sized dung beetle *Canthon luctuosus* which is also diurnal and lives in forest, was found have a maximal dispersal distance of 504.7m (Silva and Hernández, 2015). This indicates that it would be possible for *O. proteus* to disperse between adjacent altitude bands in search of food resources and potential mates.

Onthophagus proteus does not undergo any clinal change in overall body size with altitude. Body length, pronotum length and elytron length did not change either in males or in females for each colour morph, but horn length and pronotum width did vary across an altitudinal gradient with males with longer horns and wider pronotal discs more prevalent at higher altitudes see Appendix 4. I found that horn size was the best overall morphometric classifier of elevational placement and darker coloured (melanic) males had longer horns in comparison to males with lighter elytral hue. Furthermore, I observed that green and brown morphs (typicals), being widespread at lower altitudes, progressively disappear with increasing elevation. Simultaneously, brown and black morphs, which were typically rare in the lowlands, increased in frequency, with a particularly steep increase between elevation bands three and four (2,500 m and 3,500 m asl) and become dominant at high altitudes (Figure 5-9). This suggests that colour polymorphism might be at least partly driven by environmental factors as similar trend in colour polymorphism can be found in montane Chrysomelidae beetles (Mikhailov, 2008) and grasshoppers (Köhler et al., 2017) who display similar colour changes on an elevational cline.

Onthophagus proteus is the most abundant Scarabaeinae dung beetle within the park accounting for 11.6% of the total dung beetle abundance and has the widest elevational range of any sampled Scarabaeinae dung beetle within the ANP. Many species demonstrate this positive relationship between the altitudinal range over which species occur and elevation, and this relationship has been termed elevational Rapoport's rule (Stevens, 1992). One of the conditions of the elevational Rapoport's rule is based on 'the breadth of climatic conditions organisms experience along gradients' (Stevens, 1992) . The evolution of intraspecific polymorphic traits along elevational gradients may allow species to adapt under variable and often harsh climatic conditions often indicative of montane environments. These adaptions may occur as directional changes in morphological traits, such as wingspan reductions or enlargement (Hodkinson, 2005; Eweleit and Reinhold, 2014; McCulloch and Waters, 2018) or colour polymorphism which is considered an adaptive trait beneficial in aiding thermoregulation and decreasing ultra violet penetration (Schweiger and Beierkuhnlein, 2016).

Melanism is the occurrence of dark pigmentation and may manifest as intraspecific polymorphism or as variation between closely related species (True, 2003). The thermal melanism hypothesis (TMH) states that compared to light individuals, dark individuals are at an advantage under conditions of low temperature because they heat up faster at a given level of solar radiation (True, 2003). Thermal melanism has been widely studied in endothermic vertebrates (Clusella-Trullas et al., 2008; A. Schneider et al., 2012) but less so in ectotherms and particularly insects. Thermal tolerance is thought to be the determining factor in the altitudinal distribution of dung beetles (Gaston and Chown, 2008; Birkett et al., 2017). One of the assumptions of TMH is that melanism results in greater fitness in cold climates. The direct mechanisms by which melanic individuals gain fitness benefits by thermoregulation appear to differ between taxa. Melanic butterflies benefit from being able to fly for longer and further when compared with lighter individuals under cool temperatures and low intensity solar radiation (Roland, 1982; Guppy, 1986), but melanic ladybirds gain advantage by emerging earlier in spring time than typicals and consequently have increased mating success (Ueno et al., 1998). My results suggest that the variability in colour of *O. proteus* might be at least be partly driven by thermal melanism as an adaptive trait as there was a higher occurrence of darker hued individuals with increasing elevation and potentially increased ultra violet penetration. The Aberdare National Park has a peak elevation of 4001m asl and is situated almost directly on the equator. This equatorial location means that the ultra violet index for that particular area of Kenya can reach up to 14 at midday which is high when compared with upland areas at higher latitudes such as the UK which routinely maximally reach 8 (*http://www.who.int/uv/*). Traits which confer protection against increased UV penetration may be selected for in equatorial montane populations. Beetles in lower altitudes tend to display an array of bright colours that is thought to play a vital role as an anti-predatory strategy (Tan et al., 2017). For example, green and brown colouration provides excellent camouflage against the densely vegetated backgrounds that tend to be more prevalent in the lower altitudes of montane environments, and vegetation in general. This may explain the abundance of green and brown colour morphs across many invertebrate taxa.

Horn size in dung beetles is sexually dimorphic in many species (Moczek, 2002; Moczek and Nijhout, 2003). Both horned ‘major’ and hornless ‘minor’ male *Onthophagus* dung beetles rely on alternative reproductive tactics to gain access to females. Major males use their horns as weapons in male to male combat, whereas minor males, with smaller body and absent or reduced horn rely on sneaking behaviours to acquire mating opportunities (Moczek and Emlen, 2000). Cephalic and pronotal horns in male dung beetles are likely used as intraspecific signals between males as an indicator of health, size, and status by competing males, or by females as a reliable signal of genetic fitness (Searcy and Nowicki, 2005). These sexually selected traits are remarkably reliable signals of individual male quality because their growth is closely linked to nutritional history and the physiological condition of individuals in comparison to other morphological traits. These traits also tend to be more exaggerated and display ‘hyper-variability’ (Emlen et al., 2012) in comparison to other extremities, but are costly to produce (Cook, 1987; Emlen, 1997; Pomfret and Knell, 2006; Knell, 2011) and hamper the development of other morphological traits because of competition between traits for limited resources. Moreover, large structures such as exaggerated cephalic horns can limit the growth of other adjacent organs such as eyes (Nijhout and Emlen, 1998). The predicted costs of having exaggerated horn vary depending on the niche occupied by a species. For example, nocturnal dung beetles have larger eyes (Dacke, 2003) and any reduction of eye size would likely be more costly to night flyers than diurnal dung beetles. Furthermore, taxa using dung that is sparsely distributed may rely more heavily on wings which ensure efficient resource acquisition than taxa that use dung resources that are densely distributed, thus thoracic horns, which reduce relative wing size (Emlen, 2001), may be prohibitively costly to these taxa. Additionally, variation in trait size in Onthophagus dung beetles may be influenced by other factors, including maternal effects. Maternal effects have been shown to be widespread and to influence a large variety of traits, including sexually selected traits (Bernardo, 1996; Steiger, 2013) and be defined as the environmental influences on the phenotype of an individual that are due to the expression of genes in its mother (Wolf and Wade, 2009). Buzatto et al. (2012) explored the mechanism by which female dung beetles adaptively respond to perceived increased population density by preparing their male offspring for the level of sexual competition they will face as adults with larger horns. They discovered major male offspring of the same body size could have significantly larger horn if they were produced by females that experienced high population density than if they were produced by females that experienced low population density. Lloyd (1967) defined population density or ‘mean crowding’ as the number of conspecific male competitors a male may encounter *per* resource patch. He hypothesized that crowded species will experience more intraspecific competition for resources such as food and mates, and therefore reproductive skew and the strength of sexual selection will be greater. As previously mentioned, *O. proteus* is one of 19 species that occupy habitats above 3000m asl and it is the most abundant Scarabaenidae dung beetle at this elevation. This abundance may potentially explain the large variation in horn length at upper elevations in the ANP as female perception of increased population density resulted in major male offspring being produced with larger horns as described by Buzatto et al., (2012).

There is growing evidence that the rate of warming is amplified with elevation, meaning that high-mountain environments experience more rapid changes in temperature than environments at lower elevations (Mayor et al., 2017) with fauna occupying montane environments subjected to considerable fluctuations in available suitable habitats, and ill equipped with the traits required for persistence. This is particularly worrying for range restricted species and may leave them with an increased risk of extinction as they are unable to expand into other areas containing suitable habitat (e.g Sekercioglu et al., 2008; La Sorte & Jetz, 2010; McCain & Colwell, 2011).

Climatic gradients associated with elevation are frequently used as 'space-for-time' substitutions to infer potential trait responses to temporal climate change (Körner, 2007; Spehn et al., 2010). However, sites along a altitudinal gradient may differ in many factors, including temperature, soil types, precipitation and ultra violet radiation that have not been studied here. Therefore, 'space-for-time' approaches such this study will not directly translate into community responses to climate warming but may provide a valuable starting point for future studies that specifically test hypotheses produced by field observations.

6 ASSESSING THE PREDICTIVE POWER OF THE HABITAT STRUCTURE AND MAMMAL COMMUNITY IN SHAPING DUNG BEETLE COMMUNITIES

Abstract

Anthropogenic disturbance continues unabated and global animal populations are declining at an alarming rate with large-scale declines in wildlife populations are often particularly severe for animals with large body size. Many of these species provide important ecological functions such as arthropod suppression, seed dispersal, pollination, material and nutrient distribution and their extirpation can initiate cascading effects likely to instigate functional losses in the ecosystems that once harboured them. This study aims to clarify how much of the variation in dung beetle species' composition among sites is spatially structured and to determine how much of the variation can be explained by biotic variables including mammal abundance. Results indicate habitat structure and mammal abundance explained 22% of dung beetle abundance but less than 1% of species richness. The forest dung beetle communities in the ANP are fragile as they depend on both a high tree density, and a species rich mammalian fauna plus the synergy these parameters acting in concert to ensure continuing dung beetle persistence.

6.1 INTRODUCTION

Habitat fragmentation and the reduction in the extent of natural areas continues to threaten biodiversity (Cassano et al., 2014; Quinn et al., 2017). Vertebrates are known to be particularly affected (Pimm et al., 2014), and on average, global animal populations are roughly half the size they were during the 1970s (WWF, 2016). Defaunation, defined as the loss or depletion of animal species in an ecological community (Giacomini and Galetti, 2013; Dirzo et al., 2014) causes palpable modifications in community structure and composition, and in ecosystem functioning (Estes et al., 2011). The loss of these ecosystem services ranges from limiting the potential for seed dispersal (Kurten, 2013) to reducing the amount of carbon storage (Bello et al., 2015).

Human induced large-scale declines in wildlife populations are often particularly severe for animals with large body size (Cardillo et al., 2008; Galetti and Dirzo, 2013). Globally, large terrestrial mammals (bodyweight >3kg) are in drastic decline both within (Craigie et al., 2010) and outside protected areas (Harris et al. 2009). In Kenya, large mammals are at a third of their recorded abundance in the 1970s (Ogutu et al., 2011) and have undergone severe declines due to poaching, land use change and livestock incursion. Many of these species provide important ecological functions such as arthropod suppression, seed dispersal, pollination, material and nutrient distribution (Duffy et al., 2007) and their extirpation can initiate cascading effects likely to instigate functional losses in the ecosystems that once harboured them (Fleming et al., 2014). This may become particularly relevant in East Africa where the majority of the world's largest mammals now exist (Faurby and Svenning, 2015) and form the backbone of ecosystem service provision (Dobson, 2009).

Recently, studies have linked dung beetle species richness and abundance to co-declines in mammalian species richness (Nichols et al., 2009; Coggan, 2012; Culot et al., 2013; Bogoni et al., 2016). Many dung beetles belonging to the subfamily Scarabaeinae are obligate feeders of mammal dung, particularly herbivore dung (Holter, 2016). The availability and size of dung resources is especially important for nesting, as females, with or without the help of the male, must locate then bury, a quantity of dung sufficient to make one or more brood balls. The presence of large mammals therefore has the greatest influence on dung beetles through larval requirements (Hanski and Cambefort, 1991). In the case of large tunnelers, especially *Heliocopris* species, the quantity of dung resources required is very large (Kingston and Coe, 1977; Pokorný et al., 2009). Elephant dung specialists can occasionally use a substitute when elephants have disappeared, but then the individuals body size remains distinctly smaller (Hanski and Cambefort,

1991) demonstrating a directional selection in dung beetle body size when elephants are extirpated from a locality. Therefore, the presence and diversity of dung-producing mammals affects the relative abundance and diversity of dung beetles (Wardle and Bardgett, 2004; Enari et al., 2013; Bogoni et al., 2016). Dung beetles are also affected by habitat structure and other biotic variables. These are discussed in Chapter three of this thesis.

This chapter has three aims: (a) to elucidate how much of the variation in dung beetle species' composition among sites is spatially structured; (b) to determine, how much of the variation can be explained by biotic variables including mammal abundance; and (c) better understanding how the distribution and absence of elephants may directly and indirectly affect dung beetle communities which occur within Afromontane protected areas.

METHODS

In addition to the sites used to assess the effect of spatial and habitat structure on dung beetle community composition (see Figure 3-2), two further sites were chosen to model a gradient of defaunation (Figure 6-1). In addition to the sites used to assess the effect of spatial and habitat structure on dung beetle community composition (see Chapter Two), two further sites were chosen to model a gradient of defaunation. The Salient has been part of an important migration route for large herbivores. Elephants still try to find their way to Mt. Kenya, although their migration has now been prevented by an electric fence (Schmitt, 1992b). At the beginning of the long rains (mid-March) the elephants start to migrate from the higher areas of the Park to the Salient sector. They are stopped by the electric fence and are funnelled to the area around Treetops Lodge, where a large population of elephants builds up within the next two months. In 1998, a section of the National Park adjacent to the Treetops Lodge was completely enclosed by an electric fence located inside the existing electrified boundary (J. Mathenge, pers.comm). The fence was constructed to exclude elephant and buffalo and aims to protect the vegetation surrounding a nearby water hole from increasing elephant induced damage - because of a seasonally high concentration of elephants in a such restricted area, there has been significant destruction of forest around Treetops. The electric fence consists of six strands of electrified wire spaced so small mammals may enter and exit but large mammals may not.

6.1.1 Camera Trapping

I used camera trap data to identify the sites with varying elephant abundance and one site where elephant was absent. The camera traps collected a total of 66 independent occurrences of elephant within the three sites. Elephant abundance was then used to classify the sites into three categories; Elephant absent, Low abundance and High abundance.

Table 6-1 Treatment categories and relative abundance for determining dung beetle assemblages with increased elephant abundance

Site	Occurance	Relative abundance (n)	Area (km^2)	Habitat
1 (Elephant absent)	0	0	0.980	Grassland
2 (Low abundance)	8	28	0.013	Grassland
3 (high abundance)	58	196	0.141	Grassland

6.1.2 Data Analysis

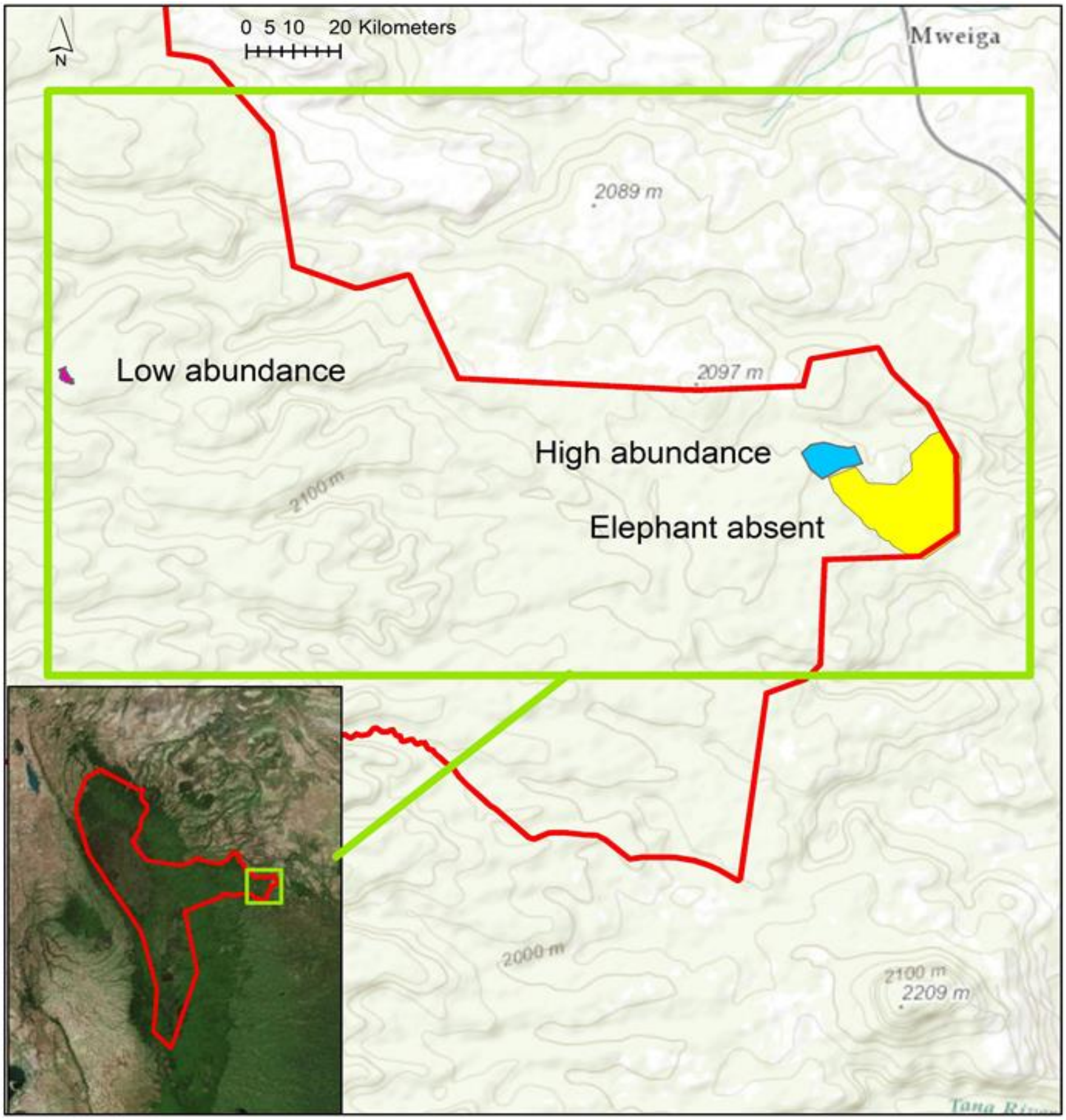


Figure 6-1 The area contained within the green rectangle are the locations of sites describing variation in elephant density. Elephant absent (yellow polygon) and the highest abundance site (blue polygon) are adjacent to each other at Treetops Lodge in the East salient area. The low abundance site (purple) is located in an open glade in the central salient sector.

Figure 6-2 A camera trap image taken in February 2016 showing elephant herds at the high abundance Treetops Lodge site.

Figure 6-3 Regenerating vegetation located inside the exclusion area. The partition fence which separates sites can be seen in the top right of the image.

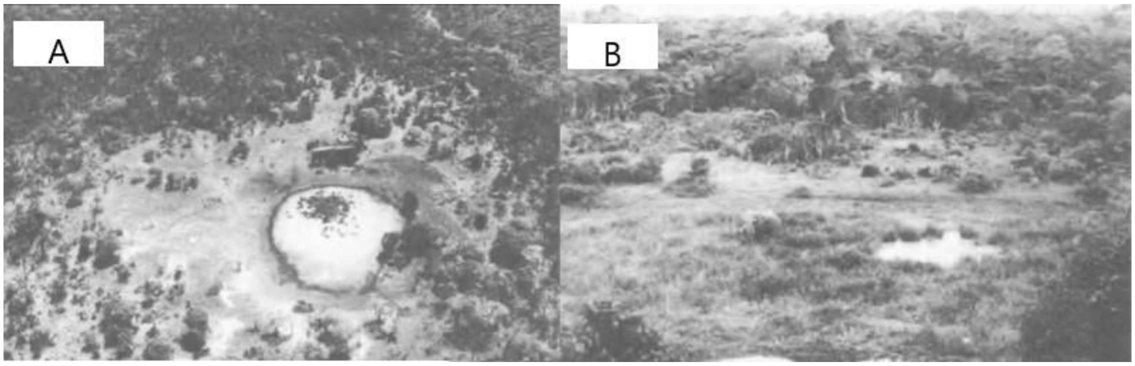


Figure 6-4 (A) Treetops site in 1959; (B) Treetops site in 1932. The vegetation surrounding the waterhole had been severely degraded by elephant congregating at the site. Images reproduced with the kind permission of Clifford Hastings and National Museums Kenya

6.1.3 Mammal Sampling with camera traps

Two Bushnell™ NatureView camera traps were set up within 20m of 2 pitfall traps per transect for a total of 18 days in 2015 (6th July- 13rd August) and 2016 (12th-29th February), yielding a total sample effort of 2640 trapping nights ($55_{NIGHT}X12_{TRANSECT}X4_{CTRAP}$) and 61, 230 images of which 56,578 were false positives and 4,652 were images containing extractable mammal data. Cameras were set at 140 cm above the ground to accommodate the height of most mammals suspected of being present within the sample site and to avoid camera loss by hyena (*Crocuta crocuta*). Cameras were set to record for 24 hours per day with a time delay for activation set at 30 seconds. Traps were checked and reset every four days.

6.1.4 Statistical analysis

I used total species richness, total abundance and mean body length (mean of 10 individuals *per* species) to describe dung beetle community attributes (Figure 6-2). Mammal community attributes were described using total species richness, total abundance and abundance of feeding guilds (Figure 6-3).

I conducted Principle Coordinate Analysis of Neighbourhood matrices (PCNM) using the distance matrix to determine the spatial heterogeneity of the dung beetle community data between sample sites (Borcard and Legendre, 2002). The PCNM functions were constructed using the ‘pcnm’ function from the R software ‘vegan’ library. I selected the positive PCNM vectors according to spatial autocorrelation acquired by the Moran index (Dray et al., 2006) using the ‘moran’ function in the R software ‘spdep’ library. PCNM represents spectral decomposition of the spatial relationships among the study sites. Multivariate variation partitioning (Borcard and Legendre, 1994; Blanchet et al., 2008) can be applied using PCNM variables as spatial or temporal descriptors and for this reason can be employed as predictors of spatial variation among sample sites.

I used variation partitioning via Redundancy Analysis (RDA) to assess the percentage contribution for each of my group predictor variables. Group one contained the mammal community predictors (Table 6-3), group two contained predictors relating to habitat structure (Table 6-4), and group three contained the linear spatial distance obtained from the PCNMs. These groups were then used to describe the variation in the dung beetle community composition, abundance and body size.

I used non-metric multidimensional scaling (NMDS) based on the Bray-Curtis distance metric to characterize the species composition in the three dung beetle communities in grassland habitats within the ANP (Figure 6-1). I examined whether elephant abundance explained the composition of the local communities in a three-dimensional ordination. NMDS is an unconstrained ordination method used for exploratory analyses of the relationships between species occurrences and environmental variables (Legendre and Legendre, 1998). NMDS places sites in ordination space in such a way that ordination distances correspond to differences in the similarity (sites placed closer together) or dissimilarity (sites placed further apart) in species composition (McCune et al. 2002). Ordination analysis was carried out with version 2.4-5 of the community ecology package vegan (Oksanen, 2015) and implemented in version 3.1.1 of R (R Development Core Team, 2017).To verify statistical differences between groups formed by the NMDS, an analysis of similarity (ANOSIM) was performed (Clarke and Warwick, 2001).

In order to best identify dung beetle species contributing most to the overall assemblage response to elephant presence, I undertook indicator species analyses using a recently developed classification method (CLAM: Chazdon et al., 2011)). The method was applied to assess the two extremes of elephant in high density (EP) and elephant absent (EA) sites.

CLAM is a multinomial model which uses pooled species abundance data from two distinct groups to classify species into four categories: (1) ‘Group A specialist’; (2) ‘Group B specialist’; (3) ‘Generalist’, and; (4) ‘Too rare to classify’ (Chazdon et al., 2011). Species are considered as specialists if ≥66% of their occurrences were within a specified group. The analysis was conducted in R (R Development Core Team, 2017) using the function ‘clamtest’ located in the vegan package (Oksanen, 2015). An important parameter of the multinomial model is K, which refers to the threshold for classifying species according to their habitat preference. I used a super-majority specialization threshold of K = 0.667, and p = 0.05 to classify which species were specialists or generalists to areas with and without the presence of elephants. The alpha value was set at p= 0.05 as suggested when the aim is to classify individual species (Chazdon et al., 2011) instead of all species.

6.2 RESULTS

6.2.1 Dung Beetles

I collected 8020 dung beetles from 34 different species (Appendix 2). The number of species *per* transect varied between nine and twenty-nine and ranged in abundance between 149 and 1511 individuals. Mean body size ranged between 2.72±1.14mm to 18.2±3.17mm (Table 6-2).

Table 6-2 Dung beetles variables *per* transect used in variance partitioning analysis to assess the effect of mammal, habitat and spatial factors.

Site	Habitat	Dung Beetle Species richness	Dung Beetle Abundance	Mean beetle body length (mm) ±SE
transect 1.1	Bushland thicket	22	816	8.22±2.39
transect 1.2	Bushland thicket	26	854	18.2±3.17
transect 2.1	Forest_Junip	29	1511	16.7±3.38
transect 2.2	Forest_Junip	28	1499	9.36±2.89
transect 3.1	Forest_Podo	22	650	10.3±7.16
transect 3.2	Forest_Podo	20	824	7.64±3.04
transect 4.1	Forest_Hagenia	10	426	6.98±1.09
transect 4.2	Forest_Hagenia	14	597	5.12±0.45
transect 5.1	Bamboo	11	289	4.32±1.78
transect 5.2	Bamboo	10	241	4.77±0.89
transect 6.1	Ericaceous	9	164	2.72±1.14
transect 6.2	Ericaceous	10	149	3.41±0.32

6.2.2 Mammal composition, habitat structure, spatial distance

6.2.2 MAMMAL COMMUNITY ATTRIBUTES

I recorded 2592 mammals from 26 species see (Appendix 1). Richness among the eleven sites varied from three to 26 species (Table 6-3). Total species richness included five carnivores (ranging from 1–4 per site), 14 omnivores (0–13 *per* site), and nine herbivores (1–11 *per* site). Abundance varied from 19 individuals in Ericaceous grassland to 903 individuals in Bushland thickets. All full list of the mammal species of the ANP can be found in Appendix 1.

Table 6-3 Mammal explanatory variables used in variance partitioning analysis.

				Abundance of Trophic Guild			
Site	Habitat	Mammal Species richness	Mammal Abundance	Mammal insectivore	Mammal herbivore	Mammal Omnivore	Mammal Carnivore
transect 1.1	Bushland thicket	18	903	1	8	5	4
transect 1.2	Bushland thicket	24	858	0	11	2	3
transect 2.1	Forest_Junip	26	91	0	9	13	2
transect 2.2	Forest_Junip	15	35	0	10	3	2
transect 3.1	Forest_Podo	16	92	0	6	7	3
transect 3.2	Forest_Podo	13	72	0	9	2	2
transect 4.1	Forest Hagenia	10	166	0	3	4	3

transect 4.2	Forest Hagenia	7	111	0	3	3	1
transect 5.1	Bamboo	9	116	0	2	5	2
transect 5.2	Bamboo	8	96	0	3	2	3
transect 6.1	Ericaceous	3	33	0	1	1	1
transect 6.2	Ericaceous	4	19	0	3	0	1

6.2.2.2 HABITAT STRUCTURE AND SPATIAL DISTANCE

Habitat structure varied among sites, particularly in the percentage of ground cover, and tree density. The measurement technique of these parameters are outlined in section 2.8. Other parameters with high variation were generally multicollinear with each other or with elevation. The average elevation of the study transects was 2800 meters above sea level (m.a.s.l.) (range 1850–3960m.a.s.l.). The linear distance between transects within a habitat type was at least 800 m, with a mean of 1500 m.

Table 6-4 Habitat explanatory variables used in variance partitioning analysis

Site	Habitat	Tree density m^2	Tree species richness	Mean DBH of all trees	Mean Ground cover %	Mean Canopy cover %
transect 1.1	Bushland thicket	0	0	0	0	9
transect 1.2	Bushland thicket	0.005	2	17.15	17	2
transect 2.1	Forest_Junip	0.082	2	14.85	24	100
transect 2.2	Forest_Junip	0.045	3	34.13	39	90
transect 3.1	Forest_Podo	0.047	5	21.1	20	100

transect 3.2	Forest_Podo	0.03	5	48.172	27	22
transect 4.1	Forest Hagenia	0.01	3	152.25	14	52
transect 4.2	Forest Hagenia	0.02	2	41.23	26	7
transect 5.1	Bamboo	0.025	1	64.51	16	40
transect 5.2	Bamboo	0.007	3	58.4	11	8
transect 6.1	Ericaceous	0	0	0	0	0
transect 6.2	Ericaceous	0	0	0	15	0

6.2.3 Ecological correlations between habitat structure, mammal composition and spatial distance in the use of variation partitioning

Variation Partitioning

Forward selection using complete community data varied according to response variable (dung beetle composition, species richness abundance, and body size). Tree density and percentage of ground cover and spatial vectors derived from PCNMs were the significant predictors of habitat and spatial variables, and abundance of herbivores and overall mammal abundance were the significant predictors of mammal community attributes. Variation partitioning using these significant predictors indicated that 17% of the total variation in dung beetle richness and abundance was explained by mammal composition (total abundance and herbivore abundance) whereas less than 1 percent was explained by the variation in mammal community attributes and habitat structure combined. Habitat structure and mammal abundance explained 22% of dung beetle abundance but less than 1% of species richness. Spatial distance explained 13% of the community composition (richness and abundance combined), 4% of dung beetle species richness and 3% of abundance. Half of the variation in dung beetle species richness was collectively explained by mammal composition and spatial distance. Mammals explained 15% of the variation in dung beetle body size, whereas spatial distance explained less than 1%, and both mammals and habitat complexity explained 19% (Fig 6-5)

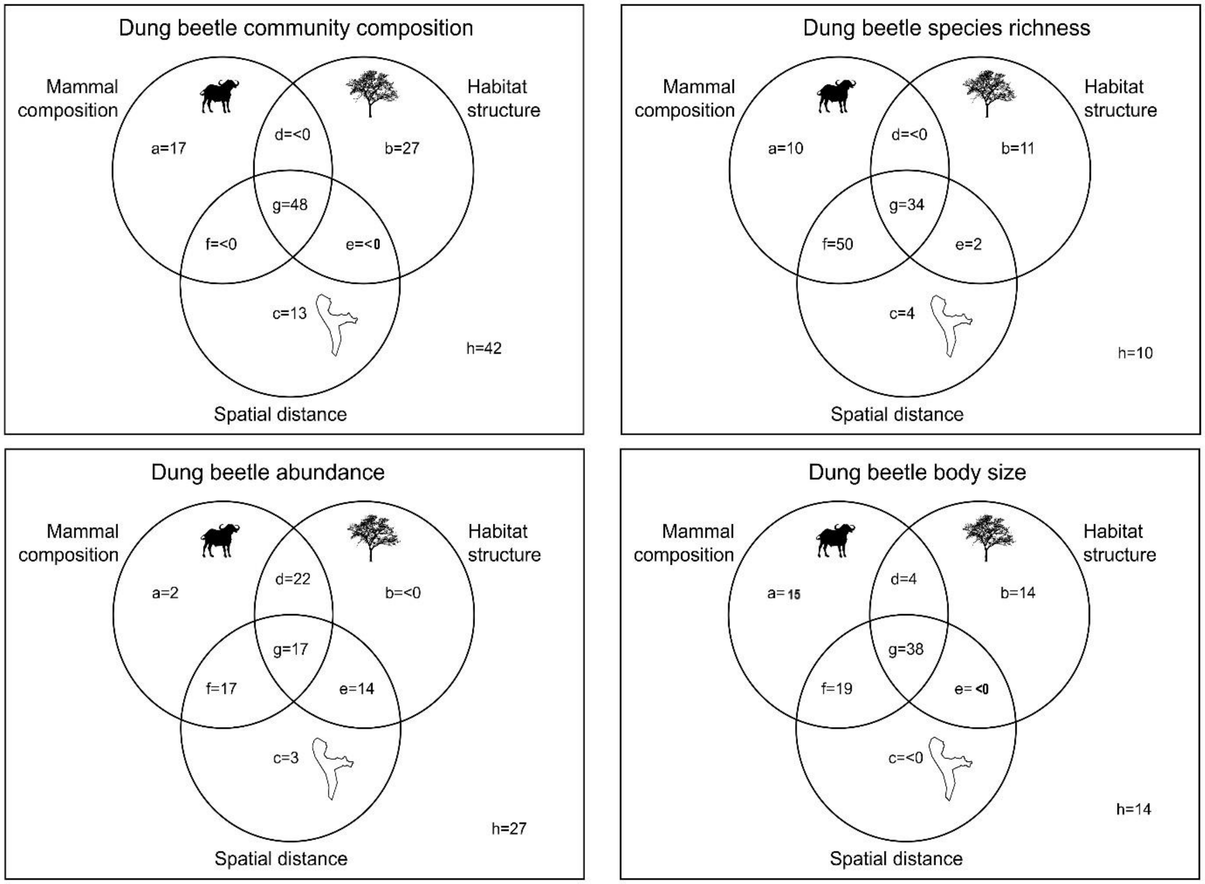


Figure 6-5 Variation partitioning analysis for eleven sites within Aberdare NP. Dung beetle community composition, species richness, abundance, and average body size were analysed in relation to the percentage explained by several biotic and abiotic predictors. *(a)* mammals; *(b)* habitat structure; (*c*) spatial distance; (*d*) mammals and habitat complexity; (*e*) habitat complexity and spatial distance; (*f*) mammals and habitat complexity; (*g*) all factors; (*h*) residuals

6.2.4 The effect of elephant abundance on dung beetle community composition?

The NMDS analysis revealed clear differences in dung beetle community composition (both richness and abundance) between the three sampling sites (Fig 6-6). Stress was low (0.19) indicating a high degree of fit. The distribution pattern of species composition was different for each sample site (ANOSIM R = 0.38, p<0.01), revealing a high turnover of species between areas.

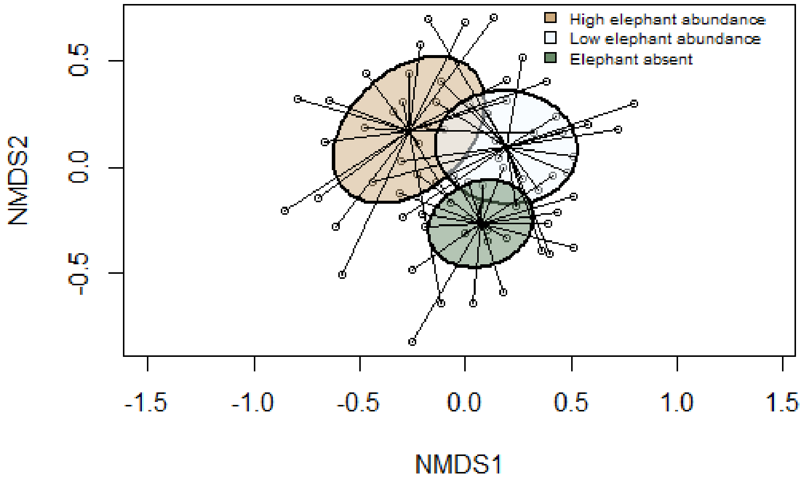


Figure 6-6 Non-metric multidimensional scaling (NMDS) ordination (stress =0.19) using the Bray-Curtis distance metric based on dung beetle community composition for the sites with high, low and absent elephant occurrence. Ellipses represent 95% Confidence Interval around the centroid and depict groupings. Circles are the ordinated data points representing individual species and are linked to the centroid of each respective site.

Indicator species analysis

A total of 1435 (34 species) dung beetles were observed in the elephant present (EP) sites compared with 1165 (30) in the elephant absent (EA) site; 20 out of 34 (58%) of species were shared between the two sites. Twelve species (35%) were too rare to classify as they fell within the minimum abundance for classification EA (9); EP (7); (p=0.05). The percentage of species with singleton or doubletons was 4 (9%) for EP treatment and 5 (13.8%) for the EA treatment. Four species, *Neocolobopterus kivuanus*, *Onitis meyeri*, *Diastellopalpus johnstoni* and *Heliocopris hunteri* were classified as specific to the sites where elephants were present. Twenty-five species (Appendix 1) were classified as generalists, and a single species *Onthophagus filicornis* was considered as a habitat specialist in areas where elephant was absent (Figure 6-6).

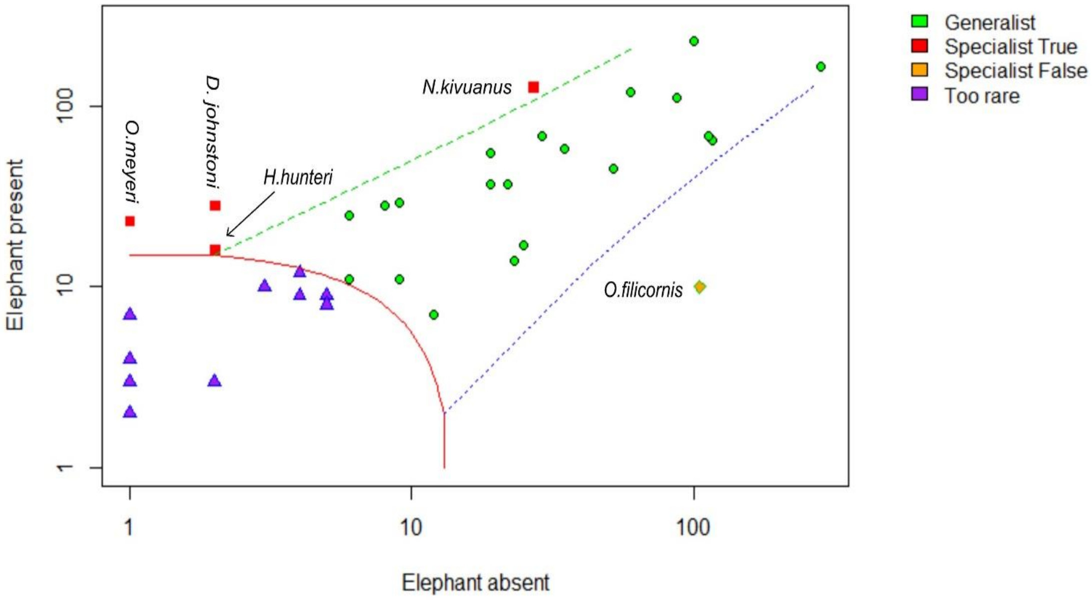


Figure 6-7. The classification of generalists and specialists found where there is high elephant density and where elephant are absent based on CLAM analysis. The x and y axes represent the log abundance of different dung beetle species in elephant present and absent samples respectively.

6.3 DISCUSSION

The main finding of this study highlights the importance of both mammals and habitat structure, acting separately or in concert, drive the variation in dung beetle communities in Afromontane forest. This study also emphasis the role of large herbivores, whose occurrence, even at low densities, can shape the structure of dung beetle assemblages. Comparison of these findings with those of other studies (Koike et al., 2014; Bogoni et al., 2016) confirms the significance of mammal abundance for dung beetle communities. My results demonstrate that the composition of Afromontane dung beetle communities, although partly affected by mammal composition are mostly driven by a contingent of factors related to habitat structure working in concert with mammal diversity and abundance. Generally, equilibrium in dung beetle abundance is complete when the surrounding habitat offers a high mammalian biomass (Andresen and Laurance, 2007; Barlow et al., 2007; Culot et al., 2013).

A quarter of the world's mammal population are threatened with extinction in the near future (WWF, 2016). Large mammals in particular are undergoing a heightened risk of extinction that has been brought about by human associated activities such poaching, illegal logging, climate change, and habitat fragmentation (Fa and Brown, 2009). African large mammals have lost 59% of their populations in the past 40 years including from within Protected Areas (Craigie et al., 2010). They often singularly represent the apex predator or largest herbivore in an ecosystem and are often crucial in structuring communities in ecosystems, which, in many cases may lack a functional equivalent (Brocardo et al., 2013; Jorge et al., 2013; Young et al., 2015). Therefore, large mammal extirpation or extinction can cause dramatic changes that induce cascading 'top down' effects that drive alterations at multiple trophic levels (Eklöf and Ebenman, 2006).

Elephant abundance and dung beetle community composition

One limitation of using elephant presence and absence data from a small sample size is the lack of replication between sites. There are several other factors such as the variation of microhabitats found within the grasslands, soil type and the presence or absence of other mammals which may have also influenced the dung beetle community composition. Nevertheless, elephant presence had a strong effect on the community composition of dung beetles (Figure 6-6). Overall, dung beetles were more abundant where elephant were present compared with the elephant absent treatment. Four dung beetles were indicated as specialists in the site where elephants had a high relative abundance. Three of the four dung beetle species (*Onitis meyeri*, *Diastellopalpus johnstoni*, and *Heliocopris hunteri*) are large paracoprids (32-48mm in length) which are capable of constructing nests up to 1m below the earth surface

(Klemperer and Boulton, 1976). *Onitis meyeri* was categorised as 'data deficient' by the IUCN in 2013 (Davis, 2013a). It is described as having a disjunct and restricted distribution limited to the ANP and Mt Kilimanjaro in Tanzania. The assessment also noted "some category of extinction risk would be justified" if data including "dung type… and specializations" became available. The data shown Figure 6-7 indicates that *O. meyeri* is an African elephant specialist and will be only present in sufficient numbers within east African high-altitude areas where sufficient dung resources are available. Currently, those areas are limited to four forested locations that have an elevation in excess of 2000m asl and are within the range for elephant defined by the IUCN; Mount Meru National Park, Tanzania; Mount Elgon National Park, Uganda; the ANP, Mount Kenya NP and Mt Kilimanjaro National Park, Tanzania. *Diastellopalpus johnstonii* has a distribution which is centred in high altitude Afromontane vegetation with records from upland locations in both east (Kenya, Tanzania, Rwanda, Burundi), and west Africa (Cameroon, Republic Democratic Congo) (Davis and Scholtz, 2010). Its dung preferences are unknown but most other species belonging to the genus are specialists of elephant dung.

Biotic and abiotic drivers of dung beetle communities

Body size is an important functional trait of species (Perkins et al. 2010, Reiss et al. 2010, 2011) as the variation in an organisms' body size can have pivotal consequences for the relationship between biodiversity and ecosystem functioning (Dangles et al., 2012). There are numerous reasons for this; (1) an individual's role reflects its weight dependent metabolic requirements, so size can be a useful proxy of the impact of a given species (or assemblage) on ecosystem functioning (Reiss et al., 2009); (2) species' who have similar body size should overlap in niche use (Kleynhans et al., 2011); and, (3) large species (Cardillo et al., 2005), are particularly vulnerable to many types of environmental alteration; including climate change (Kleynhans et al., 2011) habitat fragmentation (Crooks et al., 2017), land use changes (Karanth et al., 2010; Kiffner et al., 2015) or exploitation (Fa and Brown, 2009; Scholte, 2011).

The effects of species loss on the functioning of ecosystems has only recently begun to be widely discussed in the context of functional trait loss (e.g. Hillebrand et al., 2017). The effects of functional trait loss has been explored in dung beetle ecology mostly in the context of body size, dung burial and seed dispersal capability (Slade et al., 2007; Nervo et al., 2014; Manning et al., 2016).

In forests, the biological processes that maintain ecosystem functioning (such as nutrient recycling, pollination and secondary seed dispersal) are largely driven by insects (Didham et al., 1996) . Alarmingly, forest fragmentation-induced changes in abundance and species richness have been shown in many insect groups. The modification, fragmentation and loss of tropical forest habitat are reported to lead to high local extinction rates across forest restricted dung beetle communities (Nichols et al. 2007). An abundance of interconnected high-quality habitat is essential for both the maintenance of functioning ecosystems and the preservation of the mammals contained within them. Habitat quality directly affects mammal composition and abundance (Burkepile et al., 2013; Di Marco et al., 2014) in addition to dung beetle community structure (Campos and Hernández, 2013; Nichols, et al., 2013; França et al., 2017). My findings show that for Afromontane dung beetles, habitat structure is more important than mammal composition in shaping dung beetle communities but that it does not drive dung beetle abundance (Fig 6-2).

These results provide support for Halffter and Arellano (2002) who asserted that it is vegetation cover rather than dung supply that is more important for determining the structure and diversity of a forested dung beetle communities. The structure and integrity of forested habitats has been found to be the most important factor in dung beetle species richness in Neotropical dung beetle populations (Gardner et al., 2008; Carpio et al., 2009; Lopes et al., 2011; Campos and Hernández, 2013; Silva and Hernández, 2015). The structural loss of biomass and reductions in canopy cover negatively affect forest dependent species (Slade et al., 2011; França et al., 2017). Illegal logging is one of many factors that drives forest degradation and defaunation in many Afrotropical forests (Poulsen et al., 2013) and is responsible for the loss of large bodied species (Edwards et al., 2014). This functional loss has already demonstrated to lead to lower dung removal and seed dispersal rates in Neotropical forests (Santos-heredia et al., 2010; Braga et al., 2013) but the effects on Afrotropical forests remain largely less well understood. Historically, the ANP has suffered from illegal logging and from livestock incursion (Schmitt, 1992b). However, since the recent completion of the electric fence which surrounds the park, only a small fraction of illegal timber extraction now occurs (Butynski, 1999; Lambrechts et al., 2003; Mungai et al., 2011). As the majority of dung beetles in the ANP have a generalist feeding behaviour (Table 3 -5) they rely on a highly abundant and varied mammalian community to provide a stable and copious nutrient rich dung supply.

To summarise, the forest dung beetle communities in the ANP are fragile as they depend on both a high tree density, and a species rich mammalian fauna plus the synergy these parameters acting in concert to ensure continuing dung beetle persistence. It is clear there are distinct factors which drive the abundance, richness and distribution of dung beetles in the ANP. This study illuminates the importance of suitable habitat and a species rich and abundant mammal community in preserving healthy, speciose and functionally viable dung beetle populations. This study is one of very few studies which have assessed the biotic drivers of dung beetle communities and is one of just two from forested ecosystems. In terms of the ANP, it appears there are two conditions which promote the abundance of dung beetles: (1) plentiful supplies of dung resources provided by an abundant herbivore and mammal population and (2) alongside suitable habitat in the form of high tree density *per* m^2. The total number of mammal species does not explain all the variation in the number of dung beetle species, but dung beetle richness in the ANP is positively and highly significantly related to the number of large-bodied herbivores.

7 DISCUSSION

This final discussion chapter is composed of two parts. Firstly, I summarise the results chapters three to six by reviewing the predictors of dung beetle diversity and the contribution of dung beetles to ecosystem services in the ANP. In the second half of this chapter, I return to the local context of the Aberdare NP and review the implications of my findings for the practical protection of these important forests, and their dung beetle communities. I also propose directions for future research and conclude the thesis with a very brief overview of its main findings.

7.1 CHAPTER KEY FINDINGS

7.1.1 Chapter Three: The Role of Vegetation and Altitude in Shaping Community Structure of Dung Beetles In Montane Afrotropical Forest

The use of invertebrate diversity in conservation planning and management has lagged behind more charismatic and more widely appreciated taxa. One of the aims of this thesis was to construct a biodiversity assessment of the dung beetle population of the ANP. Monitoring biodiversity in protected areas (PAs) forms an integral component of assessing and enhancing the performance of management strategies. The monitoring and conservation of invertebrate fauna is also important in its own right, as a means of ensuring adequate protection of rare and threatened invertebrate species and communities (Samways 1993a). This study found 34 species of Scarabaenidae dung beetles within the ANP boundary. Species diversity and abundance declined with increasing altitude but betadiversity between habitat types remained high demonstrating the importance of maintaining habitat variation in management planning.

Key Findings:

1. dung beetle species richness declines montonically with altitude;
2. abundance declines sharply from elevation bands three (2500m asl) to band five (3500-4000m asl);

3. beta diversity and species turnover remains high between all habitat types.

7.1.2 Chapter Four: Experimental Estimate of Soil Nutrient Exchange In An Afrotropical High Elevation Forest: The Role Of Dung Beetle Community Complexity

This chapter had two objectives. Firstly, to assess whether the transfer of nutrients from dung to soil is influenced by dung beetle body size, and secondly to estimate the temporal effect of the dung beetles on dung to soil nutrient transfer. The results from this chapter include the first description and evidence of Afrotropical dung beetle mediated macronutrient transfer from dung into soil. The results support the theory that diverse multifunctional groups of species are necessary to provide optimum ecosystem functioning and the identification of interspecific traits is important in terms of conserving functionally relevant organisms (Gagic et al., 2015).

Key findings:

1. there was a highly significant difference between treatments for all tested macronutrients across the 112-day experimental period;
2. large-bodied beetles effected the greatest change in macronutrient status, enriching the soil by 26% over a 112 day time period;
3. the small-bodied beetles showed the smallest difference in macronutrient transfer in comparison to the control and did not have a significant effect on the quantity of Nitrogen transferred from dung into soil over the experimental time period;
4. the medium-bodied beetles showed a moderate effect on soil macronutrient enrichment with significant nutrient transfer effects for potassium, phosphorus and carbon but no significant difference in the amount of Nitrogen transferred versus the control.

7.1.3 Chapter Five: Colouration and morphological clines of an Afromontane Dung Beetle along an altitudinal gradient

In Chapter 5, morphometric and colour data in the form of RGB parameters were collated to predict the altitudinal association and intraspecific variability of an East African endemic dung beetle, *Onthophagus proteus*. This chapter used trait-based analysis via conditional inference trees to conduct a predictive estimate of a phenotypic response along an altitudinal cline. The thermal melanism hypothesis predicts that darker individuals living in cooler climates should have a distinct advantage over lighter individuals because of their greater heat capacity and warming rate. The results in this chapter are consistent with those of other studies which have found intraspecific colour variation on an elevation gradient in insects but highlights an underutilised methodology for discerning environmental and morphometric associations. Conditional inferences trees are the mainstay of machine learning methods which are often employed to parse large datasets. The use of machine learning algorithms to classify morphotypes based on images has begun to be explored in botany but has not yet been explored for use in other taxa. This chapter offers an initial step into using machine learning to classify images of one species into different phenotypes but it is not unforeseeable that in the future tools like these could be used to allocate unknown taxonomic units to genera or species.

Key findings:

1. horn length and pronotal width were found to be significantly different between altitudinal bands;
2. horn length was a significant predictor of the average proportion of blue found in dung beetle elytra with males with bigger horns having a lower blue component which results in darker wings;
3. there was an association between beetle colour and elevational band, with a greater frequency of darker beetles found at higher altitudes;
4. the strongest relative predictor using an RGB composite is the proportion of blue found in dung beetle elytron;

5. horn length was the only significant morphometric predictor of elevational placement in the suite of traits analysed.

7.1.4 Chapter Six: The Predictive Power of the Mammal Community and Habitat Structure in Shaping Dung Beetle Community Composition

Chapter six used a large, comprehensive dataset with mammalian and spatial variables to predict how dung beetle community composition is explained by spatial, biotic and abiotic factors in the Aberdare National Park. The aim of this chapter was to determine whether patterns in dung beetle species abundance, richness, and body size relate to mammal abundance, habitat variation, and spatial distance between sample sites. The results from the chapter have identified the drivers of dung beetle, abundance and species richness in Afromontane forest using spatial distance, mammal data and habitat parameters. The results from the analysis provide a strong inference on the importance of having abundant and species rich mammal fauna to provide abundant and diverse dung types and corroborates previous work (Bogoni et al., 2016).

Key findings:

1. Afromontane dung beetles rely more heavily on habitat and a combination of habitat and mammal abundance than mammal species richness alone;
2. the amount of bare ground and tree density are predictors of dung beetle abundance and species richness, number of habitats occupied, niche width and exotic forest and disturbed habitat abundance;
3. there are four dung beetle species which can be identified as elephant dung specialists - these species may be used in future management plans as indicators of elephant density in lowland Afromontane forests.

7.2 THE USE OF DUNG BEETLES FOR CONSERVATION PLANNING IN EAST AFRICAN MOUNTAINS

7.2.1 Conservation Planning

Data on species distributions are the basis of conservation planning, priority-setting, and management strategies at global to landscape scales (Margules and Pressey, 2000; Pressey et al., 2007). Much of conservation planning has been built around protecting areas which deliver ecosystem services or contain the greatest diversity, but is typically limited to the protection of mammals, plants or birds (e.g. Myers et al., 2000). This taxonomic bias is likely to continue, unless cost effective long term and consistent monitoring of other taxa including invertebrates is undertaken. Such monitoring programmes are unfortunately rare, but in the UK, the Butterfly Monitoring Survey, for example, has been monitoring the relative abundance of butterflies since the 1970s. This long term monitoring programme is now in a position to provide important information on the conservation maps to monitor changes in species distributions, regional Red List compilations on species conservation status, and transects that provide information on population trends (Dennis et al., 2016) The data now informs the Joint Nature Conservation Committee who use the twenty five of the most abundant butterfly species as indicators of habitat health in the UK Biodiversity Framework (Brereton and Roy, 2017).The framework, which has been set up to identify priorities for UK-level work for the Convention on Biological Diversity has been instrumental in forming policy and supporting nature restoration in the UK.

The data resulting from the current work can be used to monitor dung beetle populations to inform conservation and management actions within the ANP. Rohr et al. (2007) outline three steps to develop an invertebrate monitoring program; (1) characterising the community; (2) identifying surrogates for biodiversity; and (3) establishing efficient methods to monitor surrogates and any ecologically important or sensitive taxa. Much of this thesis has been focussed on meeting those targets to instigate a much-needed monitoring programme for the dung beetles of the Aberdare NP. This thesis has highlighted that fact that Afromontane dung beetles are abundant and have a complex set of requirements, but functionally rich dung beetle populations will only continue to persist in upland protected areas if they contain a mixture of suitable habitat types complete with an abundant and species rich mammalian fauna.

7.2.2 Indicator species

Simberloff, (1998) suggests conservation managers use indicators for two different reasons: (1) because their presence or fluctuations are believed to reflect those of other species in a community; and (2) because they are believed to reflect physical or chemical modifications in an environment. This thesis aimed to synthesize data relating to the identification of dung beetle species and diversity measures which could be used to track habitat modification and mammalian community change. Dung beetles are easily interpretable indicators of ecological change (Davis et al., 2004; Spector, 2006; Nichols et al., 2008; Audino et al., 2014).

Chapter 3 provides insight on the distribution, diversity and abundance of dung beetles and sheds new light on how dung beetle abundance and distribution respond to biotic and abiotic changes in Afromontane ecosystems. It has also identified that fluctuations in abundance occur in accordance with both elevation and habitat variability. The interspecific response sensitivity to even slight modifications in habitat type has facilitated the identification of eight potential ecological indicator species (Table 3-4) and showed that gradients in their population response (abundance) reflect overall preference for open vegetation or closed canopy forests with in the ANP.

This information may become especially important for future monitoring as it is predicted that areas in which Afromontane forest occur in Kenya are set to decline due to expansion and intensification of agriculture and deforestation (Eckert et al., 2017). Heavily modified habitats with little or no tree canopy cover have been shown to support species-poor dung beetle communities with high species turnover, dramatically reduced abundance and smaller body size compared to species found in intact forest types (Nichols et al., 2007). However, my results do not corroborate these findings as indicator species for closed canopy forest found by this study have a smaller average body size (6.21±3.51mm) compared to species found in open vegetation

(10.26±7.9mm). This is thought to be due to the comparatively high diversity and quantity of dung resources found in the open clearings, which in the ANP are likely to contain a water source, usually a waterhole. These clearings form patches of grassland which are kept open by animals, particularly large mammals such as elephant and herds of buffalo who physically modify the landscape by trampling and breaking vegetation (Blake and Inkamba-Nkulu, 2004). These clearings are often used as congregation sites for elephant herds who may occupy them overnight, leaving copious dung deposits behind which consequentially attracts a diverse community of dung beetles.

7.2.3 Is it important to have a high species diversity?

Most conservation and restoration management plans aim to protect and preserve the highest number of species possible within ecosystems. By protecting the maximum number of species, we hope not only to preserve taxa for their own sake but to preserve the functional trait and species niches which translate into ecosystem services that this diversity provides. Ecologically, a species is a collection of individuals with phenotypes and behavioural traits which determine their niche space and their interspecific interactions (McGill et al., 2006). Functional diversity (FD) represents the diversity of traits within a community but is deemed to symbolise the diversity of species' niches or functions (Tilman, 2001; Petchey and Gaston, 2006; Schleuter et al., 2010). As a representation of niches or functions, FD has been used to understand how species richness or diversity relates to ecosystem function (Petchey and Gaston, 2002; Laureto et al., 2015) and how diversity responds to environmental stress or disturbance (Tilman et al., 1997). More recently two alternative theories have emerged regarding the importance of diversity in facilitating optimum ecological processes. Firstly, according to the insurance hypothesis, biodiversity insures ecosystems against declines in their functioning because many species provide greater guarantees that some will maintain functioning even if others fail (Yachi and Loreau, 1999). Alternatively Winfree et al., (2015) posit that it is the variation in abundance in a few dominant species that drives ecosystem services and that because some species perform similar functions they are 'functionally redundant' and therefore interchangeable with little repercussion for the delivery on ecosystem processes and services.

The importance of functional diversity in dung beetles has been explored through the lens of ecosystem service provision (Slade et al., 2007, 2016; Griffiths et al., 2016; Manning et al., 2016) and habitat restoration (Barragán et al., 2011; Audino et al., 2014; Gómez-Cifuentes et al., 2017) and emphasizes the need to conserve functionally complete ecosystems to maintain full ecosystem functioning. In comparison to other montane studies the dung beetle species richness of the ANP with 34 species, is relatively low (Table 8-1). However, the functional diversity of the ANP dung beetle fauna can be considered high as five of the seven functional groups outlined by Doube, (1990) are present (Table 2-2).

Representatives of species from Functional Guilds; FGIII, FGIV FGV and FGVII were used to describe the importance of species richness and functional diversity of Afromontane paracoprid dung beetles on nutrient cycling and found a highly significant difference between body size and the quantity of macronutrients cycled from dung into soil. While studies support the theory that larger beetles do deliver greater ecosystem functioning in terms of dung removal (Nervo et al., 2014), seed dispersal (Andresen, 2005; Griffiths et al., 2015; Miloti et al., 2016), parasite suppression (Nichols and Gómez, 2014; Gregory et al., 2015) in comparison to smaller bodied beetles, it also illuminates the need to maintain and protect species-rich multifunctional groups of taxa. This is because all treatments which encompassed five separate genera used in the experimental design all had an effect on macronutrient transfer. Although there may be significant trait overlap within species of dung beetles in the ANP, especially in functional groups FGIV and FGV, until further research ascertains how interspecific interaction occurs between dung beetle species by sociochemical means or through niche competition we cannot prioritise conservation efforts solely towards one functional group.

Nichols et al., (2013) report that they found no consistent pattern of association between beetle nesting strategy (tunnelers, rollers or dwellers), responses to human presence or game mammal abundance. However, the same study suggests that Neotropical small-bodied beetle species are disproportionately more sensitive to human presence in upland forests; this is supported by Culot et al., (2013) who also reported that negative relationships between mammal abundance and dung beetle species richness were stronger for smaller-bodied beetles in Brazilian Atlantic rainforest. The results of Chapter Six are the first to outline the effects of mammal decline on Afrotropical montane dung beetles and strongly support the importance of having an abundant and species rich mammal fauna to provide abundant and diverse dung types. Mammal abundance and the number of herbivores present at each sample site accounted for 15% of the variation in dung beetle body size, this contrasts with the results of a similar study undertaken by Bogoni et al. (2016) who found that mammals explained 26% of the variation in dung beetle body size in Atlantic Forest. The difference in variation may be attributable to the higher level of resource specialisation found in African dung beetles (Tshikae et al., 2008; Holter, 2016) relative to those from the Neotropics (Bogoni et al., 2014) with a greater proportion relying on large mammal dung which is absent from Neotropical forests. This study also described four species of dung beetle that could be considered specialists of elephant dung they were more abundant in areas with greater elephant presence. Three of the four dung species (*Onitis meyeri, Diastellopalpus johnstoni, Heliocopris hunteri*) exhibit congruent traits; they are all large bodied (>30mm in length), paracoprid and thought to be nocturnal.

Table 7-1 Examples of other recent studies which have assessed species richness in montane ecosystems

Study	Location	Elevation Range m.a.s.l	Species Richness
This study	Aberdare NP, Kenya	1890-3912	34
Nunes et al.,2016	Espinhaço, Brazil	800-1400	56
Domínguez et al., 2015	Alamala, Ecuador	1100-1700	
Herzog et al., 2013*	Multiple localities, Boliva	0-3999	39
Alvardo et al., 2013	Sierra Los Tuxtlas, Mexico	200-1600	31
	Sierra de La Chinantla, Mexico	200-2600	40
Larsen, 2012	Andes, Peru	290-3450	16
Escobar et al., 2007	Cofre de Perote, Mexico	50-3000	40
	Chiles Volcano, Ecuador	50-3300	37
	Rio Cusiana, Colombia	450-2500	49

Lobo et., 2007	Rhodopes Mountains, Bulgaria	662-2016	48
Errouissi et al., 2004	Verdon Valley, France	1000-2000	48

*Study assessed the species richness of Phanaeine dung beetles only

7.2.4 Why are montane communities different and important?

Mountain peaks experience widely contrasting ecological conditions in comparison to their surrounding lowlands. In their comprehensive global study of altitudinal variation in dung beetle assemblages on different mountains, Lobo and Halffter (2000) proposed two separate biological processes to explain the conformation of montane biota, the patterns of species richness and variations in community composition. Firstly, vertical colonization defined as upland assemblages composed by species phylogenetically related with those inhabiting lowlands; and secondly, horizontal colonization defined as colonization of highland assemblages by lineages with a different evolutionary history and origin than those occupying lowlands. These processes as well as speciation are described as the drivers of mountain diversity (Lobo and Halffter, 2000b; Escobar et al., 2006; Arriaga-Jiménez et al., 2018). Additionally, mountain tops may act as refuges for flora and fauna that had expanded during glacial or cooler conditions and were left stranded as temperatures rose (Körner, 2007), consequentially mountain biota exhibit greater variation in species diversity when compared to that of lower elevations.

The relative effects of both horizontal and vertical colonisation depends on the orientation and location of the mountains, and on their degree of isolation and biogeographical history, as these characteristics greatly influence the refuge capacity and interconnectedness of mountain areas (Escobar et al., 2007). The Aberdare range lies on the edge of the Gregory rift, and was formed by regional orogenics in the form of volcanism in the Late Miocene Epoch (11.6 million to 5.3 million years ago, making it one of Africa's youngest mountain ranges (Scoon, 2018b). Fossil and pollen evidence suggests that lowland forest extended right across intertropical Africa to the east coast until the Langhian age of the mid-Miocene (23-11mya) but during the formation of the

Aberdare range, four million years later during the Tortonian age of the Late Miocene, vegetation had shifted from warm temperate forests to tropical savannahs and grasslands (Pound et al., 2012). This means that the initial vegetation which formed on the area that now includes the ANP consisted of open savannah grasslands and not the varied forest types resident today, with forested vegetation only returned to the ANP later in the Pleistocene (Feakins and Demenocal, 2010).

This biogeography is important in terms of ascertaining the how dung beetle colonisation occurred in the ANP. When the Aberdare mountain range was formed it was an isolated uplift, with its nearest neighbour being Mount Elgon, also newly formed, 350 km away (Scoon, 2018b). Mount Kenya, its current closest highland block was not formed until the Pliocene Epoch, two million years later (Scoon, 2018a). This makes it unlikely that horizontal colonisation occurred due to the source population of Mount Elgon being at a greater distance than dung beetle dispersal capabilities allow, meaning that dung beetles originally colonised the Aberdare range, vertically, from the lowlands upwards. Lobo and Halffter (2000) outline two criteria that govern vertical colonisation from lowlands: (1) vertically colonised mountain tops exhibit a filtered, less diverse set of species which are phylogenetically related to those inhabiting lower elevations; and (2) species richness decreases with increasing altitude as consequence of the environmental restrictions imposed on the fauna from warmer altitudes, especially in tropical regions (Janzen 1967). The most recent published dung beetle survey in the lowlands of the Aberdare range occurred at Mpala Ranch approximately 75 km away in 2002 (Gordon and Barbero, 2008). A comparison of the species found at Mpala and those in the ANP reveal some overlap with seven species present in both locations, accounting for 23.5% of the species present in the ANP (Table 7-2). These common species have an East African or Central West African distribution and are widespread in savannah habitat. With this in mind, and by meeting the criteria described above, it is likely that vertical colonisation of the Aberdare range occurred as there is a significant overlap between lowland species and those found in the ANP. Also, the ANP dung beetle fauna does exhibit a notable decrease in species richness with altitude dropping from 29 species found at ~2000m to just 19 residents at elevations greater 3500m asl (Table 3-2).

Table 7-2 Species common to both the Aberdare National Park and Mpala Wildlife Centre, Kenya

Species	Distribution*
Oniticellus planatus	D.R.C, Rwanda, Tanzania
Liatongus militaris	All of eastern Africa, from Sudan and Eritrea to central and southern Africa
Euoniticellus intermedius	Widely distributed in the entire Afrotropical Region
Ixodina abyssinicus	Widely distributed from Guinea to Ethiopia and Tanzania
Milichus picticollis	Eastern Africa, from Ethiopia to Tanzania and the D.R.C.
Onthophagus nigriventris	Somalia and Ethiopia to Tanzania
Onthophagus jugicola	Angola, D.R.C., and eastern Africa, from Ethiopia to Tanzania.
*According Gordon & Barbero (2008)	D.R.C (Democratic Republic Congo)

It is also likely that the dung beetle fauna of the ANP represent a Pleistocene refuge community with many of the species, especially those found in elevations greater than 2500m asl, having a recorded East and West central African distribution. The Pleistocene produced drastic changes in the distribution of vegetation in the Afrotropics (Mayr and O'Hara, 1986) due to periods of reduced rainfall which led to the temporary division of previously contiguous rainforests into forest islands separated by wide belts of grassland. Four of the dung beetle species (*Diastellopalpus johnstoni*, *Catharsius sestostris, Copris atropolitus*, and *Onthophagus fimetarius*) have records (Roskov et al., 2018) from highland blocks in both East (Kenya, Tanzania, Rwanda, Burundi) and West Africa (Cote D'Ivoire, Cameroon, Angola) and are widely separated by an intervening space of approximately 2000 km of 'unsuitable' lowland forest across Central Africa. According to the Catalogue of Life (Roskov et al., 2018) twelve of the species found in the ANP are regional endemics, having a distribution restricted to Kenya only, and of those six (*Copris morphaeus*, *Copris typhoeus*, *Onthophagus miricornus*, *Heliocopris stroehlei, Epidrepanus kenyensis* n. sp and *Onitis parvulus*) have a known range restricted to either the protected areas encompassing the Aberdare NP or these areas plus Mount Kenya National Parks.

Mountains are key environments for conservation of biodiversity during climatic change, providing refugia for species during postglacial cycles. Montane communities of dung beetles are important not only as historical and biographical reference points, and suppliers of values ecosystem services, but also as potential barometers of environmental change due to global warming. Global warming threatens montane dung beetle diversity by forcing species upslope, and reducing the space occupied by species specifically adapted to the cold or those that have limited thermal tolerance (Birkett et al., 2017). Any environmental change will cause local native populations to either adapt or migrate to avoid extirpation. Ectotherms are predicted to shift more rapidly in response to climate change than mammals (Paaijmans et al., 2013), due to having limited control of their body temperature compared to endothermic animals (Sheldon et al. 2011) and the unlinking of dung beetles and the food resources they depend upon may lead to declines and extinctions of Afromontane dung beetles in the future.

Due to their biogeographical history and specialisms the dung beetles of the ANP may be particularly negatively affected by temperature increases associated with global warming for two reasons. Firstly, as the results of chapter six outline, 50% of the variation in dung beetle species richness is attributable to mammal abundance, the presence of herbivores plus the distance between sampling points (Figure 6-3). Species richness may be negatively affected with any decline in mammal abundance and changes in abiotic parameters, notably in the predicted increase in temperatures, associated with global warming. Secondly, the results of chapters three and five indicate that there is both intra- and interspecific variation in elevational placement (Figure 5-10) and habitat preference (Table 3-5) of species and individuals. The upward shift in plant species, resulting in changes to habitat structure and even habitat loss is a well-documented occurrence in climate change literature (Thomas et al., 2004; Dirnböck et al., 2011); this will likely affect the dung beetle species in the ANP already at the extreme of their habitat range.

7.3 FUTURE WORK

This thesis has illustrated that there is a rich dung beetle fauna to conserve in the ANP and there are a number of avenues one may pursue to further develop the results presented here. Many of the dung beetle species caught in the forested areas ANP also reside in the open glades and grasslands which are interspersed throughout the lower regions of the park. Further studies may include sampling gradient encompassing open vegetation, at the forest edge, and deeper into the forest to determine whether the species captured are habitat specialists or generalists. However, there are few, namely *Onthophagus spurcatus*, *Onthophagus docheryti* and *Copris algol* which should be considered closed canopy forest specialists as the majority of individuals were found only in this habitat type. Results from a previous short study in 1974 (see Fig 2-4) (Davis and Dewhurst, 1993) indicate while there was significant overlap between dung beetles caught 40 years ago and the present day there were also seven species which were absent; *Euoniticellus inequalis, Euoniticellus triangulates*, *Copris nepos, Onitis vanderkellini*, two species of the genus *Caccobius* and *Liatongus spathulatus.* All of these species have climatic distributions centred around the wet highlands of East Africa (Davis and Dewhurst, 1993) and further work is urgently required to understand why these species are no longer detectable in the ANP.

7.3.1 IUCN Red List

As discussed in Chapter Three, 34 species of Scarabaeidae dung beetle were found to resident within the ANP. Only five of these; *Onthophagus nigriventris, Onthophagus jugicola, Onitis meyeri, Onitis parvulus* and *Copris morphaeus* have been assessed, categorised, and listed by the IUCN for inclusion in the Red List of Threatened Species (http://www.iucnredlist.org). Of these five, *O. meyeri*, *O. parvulus* and *C. morphaeus* are categorised as Data Deficient and two; *O. jugicola* and *O. nigriventris* are categorised as Least Concern. According to the assessments the biggest threat to their persistence may be the extensive clearance of forest on the lower slopes of the ANP for commercial tea and coffee plantations. However, these assessments do need updating (IUCN 2015) and the effective management and conservation of Afromontane dung beetles is impaired by the paucity of knowledge on their natural history. I suggest the 29 remaining species detailed in this PhD be assessed and added to the Red List to instigate the setting of conservation priorities and legislation.

Table 3-5 outlines which species were found predominantly in open vegetation or closed canopy forest in the ANP and categorises *O. meyeri,* and *O. parvulus* as habitat generalist*s,* meaning no clear trend was observed between the abundance of individuals found between open and closed forest habitat types. The results from my analysis also indicate that *C. morphaeus* may prove to be associated primarily with forest habitat, however these results contradict the those in the Red List assessment which describes most individuals being found in clearings adjacent to shaded vegetation. *C. morphaeus* has a very restricted known distribution limited to just the Aberdare mountain range, Mau escarpment and Mount Kenya National Park (MKNP) all which are in locations in excess of 2000m asl and although conversion to commercial cropland and agriculture is a potential threat at that altitude, extensive forest fires are known to increasingly occur in the upper regions of the ANP and MKNP where it is also present enhancing its potential extinction risk. Its restricted distribution and reliance on closed canopy forest in cool, wet mountain blocks makes this dung beetle likely to undergo increased extinction risk in the future. Based on the results of this work I recommend that this species should be reclassified from Data Deficient to Near Threatened on the basis of it being present few locations, its small range (its extent of occurrence is estimated at around 1,700 km^2), and continuing threats of habitat loss because of conversion to agriculture and naturally occurring wildfires. The two species categorised as Least Concern are thought to come from wide ranging populations across Africa and the middle east and are currently not believed to be under threat. Both are known to reside in open vegetation adjacent to montane forests in Africa and be reliant on herbivore dung, particularly cattle dung outside protected areas (Davis, 2015). However, more monitoring of dung beetle populations is urgently needed, as currently just 224 out of an estimated 7,500 species of sub Saharan Scarabaeidae dung beetle have been assessed for inclusion in the Red List by the IUCN. Those species which reside in mountain ranges should take priority, as the conversion of available habitats into commercial and agricultural small holdings plus the upland shifting of agriculture into forests is expected and often means it is montane species that are threatened with a loss of climate space when in some cases they are already at the edge of their range (Elsen and Tingley, 2015).

References

Aldrich, M., Billington, C., Edwards, M. and Laidlaw, R. (1997) 'Tropical montane cloud forests: an urgent priority for conservation.' *World Conservation Monitoring Centre*, 2(2) p. 17.

Altieri, M. A. (1999) 'The ecological role of biodiversity in agroecosystems.' *Agriculture, Ecosystems & Environment*, 74(1) pp. 19–31.

Alvarado, F., Escobar, F. and Montero-Muñoz, J. (2014) 'Diversity and biogeographical makeup of the dung beetle communities inhabiting two mountains in the Mexican Transition Zone.' *Organisms Diversity & Evolution*, 14(1) pp. 105–114.

Andresen, E. (2005) 'The Role of Dung Beetles as Secondary Seed Dispersers' pp. 331–349.

Andresen, E. and Laurance, S. G. W. (2007) 'Possible Indirect Effects of Mammal Hunting on Dung Beetle Assemblages in Panama.' *Biotropica*, 39(1) pp. 141–146.

Arriaga-Jiménez, A., Rös, M. and Halffter, G. (2018) 'High variability of dung beetle diversity patterns at four mountains of the Trans-Mexican Volcanic Belt.' *PeerJ*, 6 p. e4468.

Audino, L. D., Louzada, J. and Comita, L. (2014) 'Dung beetles as indicators of tropical forest restoration success: Is it possible to recover species and functional diversity?' *Biological Conservation*, 169 pp. 248–257.

Bajjali, W. (2018) '3-D Analysis.' *In ArcGIS for Environmental and Water Issues.* Cham: Springer Textbooks in Earth Sciences, Geography and Environment, pp. 297–314.

Bang, H. S., Lee, J.-H., Na, Y. E. and Wall, R. (2007) 'Reproduction of the dung beetle (Copris tripartitus) in the dung of cattle treated with cis-cypermethrin and chlorpyrifos.' *Applied Soil Ecology*, 35(3) pp. 546–552.

Bang, S. H., Lee, J. H., Oh, S. K., Young, E. N., Yong, S. J. and Won, H. K. (2005) 'Effects of paracoprid dung beetles (Coleoptera: Scarabaeidae) on the growth of pasture herbage and on the underlying soil.' *Applied Soil Ecology*, 29(2) pp. 165–171.

Banks, J. E., Jackson, C., Hannon, L. M., Thomas, C. M., Baya, A. and Njoroge, L. (2010) 'The cascading effects of elephant presence/absence on arthropods and an Afrotropical thrush in Arabuko-Sokoke Forest, Kenya.' *African Journal of Ecology*, 48(4) pp. 1030–1038.

Barlow, J., Gardner, T. a, Araujo, I. S., Avila-Pires, T. C., Bonaldo, a B., Costa, J. E., Esposito, M. C., Ferreira, L. V, Hawes, J., Hernandez, M. I. M., Hoogmoed, M. S., Leite, R. N., Lo-Man-Hung, N. F., Malcolm, J. R., Martins, M. B., Mestre, L. a M., Miranda-Santos, R., Nunes-Gutjahr, a L., Overal, W. L., Parry, L., Peters, S. L., Ribeiro-Junior, M. a, da Silva, M. N. F., da Silva Motta, C. and Peres, C. a (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(47) pp. 18555–60.

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

Barrios, E. (2007) 'Soil biota, ecosystem services and land productivity.' *Ecological Economics*, 64(2) pp. 269–285.

Bartholomew, G. a. and Heinrich, B. (1978) 'Endothermy in African Dung Beetles During Flight, Ball Making, and Ball Rolling.' *Journal of Experimental Biology*, 73(1) pp. 65–83.

Baselga, A. (2012) 'The relationship between species replacement, dissimilarity derived from nestedness, and nestedness.' *Global Ecology and Biogeography*, 21(12) pp. 1223–1232.

Baselga, A. A., Orme, D., Villeger, S., Bortoli, J. De, Leprieur, F. and Baselga, M. A. (2013) 'Package ' betapart ',' (1).

Bello, C., Galetti, M., Pizo, M. A., Magnago, L. F. S., Rocha, M. F., Lima, R. A. F., Peres, C. A., Ovaskainen, O. and Jordano, P. (2015) 'Defaunation affects carbon storage in tropical forests.' *Science Advances*, 1(11) pp. e1501105–e1501105.

Bergmann, C. (1847) 'Ueber die Verhältnisse der Wärmeökonomie der viere zu ihrer Grösse.' *Göttinger Studien*, 1 pp. 595–708.

Bernardo, J. (1996) 'Maternal Effects in Animal Ecology 1.' *Amer. Zool.*, 36(2) pp. 83–105.

Bertone, M. a., Green, J. T., Washburn, S. P., Poore, M. H. and Watson, D. W. (2006) 'The Contribution of Tunneling Dung Beetles to Pasture Soil Nutrition.' *Plant Health Progress*, (3).

Beynon, S. A., Peck, M., Mann, D. J. and Lewis, O. T. (2012) 'Consequences of alternative and conventional endoparasite control in cattle for dung-associated invertebrates and ecosystem functioning.' *Agriculture, Ecosystems & Environment*, 162 pp. 36–44.

Bicknell, J. E., Phelps, S. P., Davies, R. G., Mann, D. J., Struebig, M. J. and Davies, Z. G. (2014a) 'Dung beetles as indicators for rapid impact assessments: Evaluating best practice forestry in the neotropics.’ *Ecological Indicators*. Elsevier, 43, August, pp. 154–161.

Bicknell, J. E., Phelps, S. P., Davies, R. G., Mann, D. J., Struebig, M. J. and Davies, Z. G. (2014b) ‘Dung beetles as indicators for rapid impact assessments: Evaluating best practice forestry in the neotropics.’ *Ecological Indicators*. Elsevier Ltd, 43 pp. 154–161.

Birkett, A. J., Blackburn, G. A. and Menendez, R. (2017) ‘Linking species thermal tolerance to elevational range shifts in upland dung beetles.’ *Ecography*, 12 pp. 314–329.

Blake, S. and Inkamba-Nkulu, C. (2004) ‘Fruit, Minerals, and Forest Elephant Trails: Do All Roads Lead to Rome?’ *Biotropica*, 36(3) pp. 392–401.

Blanchet, F. G., Legendre, P. and Borcard, D. (2008) ‘Modelling directional spatial processes in ecological data.’ *Ecological Modelling*, 215(4) pp. 325–336.

Bogoni, J. A., Graipel, M. E., de Castilho, P. V., Fantacini, F. M., Kuhnen, V. V., Luiz, M. R., Maccarini, T. B., Marcon, C. B., de Souza Pimentel Teixeira, C., Tortato, M. A., Vaz-de-Mello, F. Z. and Hernández, M. I. M. (2016a) ‘Contributions of the mammal community, habitat structure, and spatial distance to dung beetle community structure.’ *Biodiversity and Conservation*, 25(9) pp. 1661–1675.

Bogoni, J. A., Graipel, M. E., de Castilho, P. V., Fantacini, F. M., Kuhnen, V. V., Luiz, M. R., Maccarini, T. B., Marcon, C. B., de Souza Pimentel Teixeira, C., Tortato, M. A., Vaz-de-Mello, F. Z. and Hernández, M. I. M. (2016b) ‘Contributions of the mammal community, habitat structure, and spatial distance to dung beetle community structure.’ *Biodiversity and Conservation*, 25(9) pp. 1661–1675.

Bogoni, J. A., Hern??ndez, M. I. M. and Preisser, E. (2014) ‘Attractiveness of Native Mammal’s feces of different trophic guilds to dung beetles (Coleoptera: Scarabaeinae).’ *Journal of Insect Science*.

Borcard, D. and Legendre, P. (1994) ‘Environmental control and spatial structure in ecological communities: an example using oribatid mites (Acari, Oribatei).’ *Environmental and Ecological Statistics*, 1(1) pp. 37–61.

Borcard, D. and Legendre, P. (2002) ‘All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices.’ *Ecological Modelling*, 153(1–2) pp. 51–68.

Braga, R. F., Korasaki, V., Andresen, E. and Louzada, J. (2013) ‘Dung Beetle Community and

Functions along a Habitat-Disturbance Gradient in the Amazon: A Rapid Assessment of Ecological Functions Associated to Biodiversity.' *PLoS ONE*, 8(2) p. e57786.

Brakefield, P. M. (1996) 'Seasonal polyphenism in butterflies and natural selection.' *Trends in Ecology & Evolution*, 11(96) pp. 275–277.

Breiman, L. (2001) 'Random forests.' *Machine Learning*, 45(1) pp. 5–32.

Brereton, T. M. and Roy, D. B. (2017) *UK Biodiversity Indicators 2017:Technical annex – Assessing change in England, Scotland and UK Butterfly Indicators*.

Brocardo, C. R., Zipparro, V. B., de Lima, R. a F., Guevara, R. and Galetti, M. (2013) 'No changes in seedling recruitment when terrestrial mammals are excluded in a partially defaunated Atlantic rainforest.' *Biological Conservation*. Elsevier Ltd, 163 pp. 107–114.

Buddle, C. M., Beguin, J., Bolduc, E., Mercado, A., Sackett, T. E., Selby, R. D., Varady-Szabo, H. and Zeran, R. M. (2012) 'The importance and use of taxon sampling curves for comparative biodiversity research with forest arthropod assemblages.' *The Canadian Entomologist*. Cambridge University Press, 137(01) pp. 120–127.

Burkepile, D. E., Burns, C. E., Tambling, C. J., Amendola, E., Buis, G. M., Govender, N., Nelson, V., Thompson, D. I., Zinn, A. D. and Smith, M. D. (2013) 'Habitat selection by large herbivores in a southern African savanna: The relative roles of bottom-up and top-down forces.' *Ecosphere*, 4(11) pp. 1–19.

Butynski, T. M. (1999) *Aberdares National Park and Aberdares Forest Reserves wildlife fence placement study and recommendations. Unpublished report.*

Buzatto, B. A., Tomkins, J. L. and Simmons, L. W. (2012) 'Maternal Effects on Male Weaponry: Female Dung Beetles Produce Major Sons With Longer Horns When They Perceive Higher Population Density.' *BMC Evolutionary Biology* pp. 1–12.

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

Campos, R. C. and Hernández, M. I. M. (2013) 'Dung beetle assemblages (Coleoptera , Scarabaeinae) in Atlantic forest fragments in southern Brazil,' 57(March) pp. 47–54.

Campos, R. C. and Hernández, M. I. M. (2015) 'Changes in the dynamics of functional groups in communities of dung beetles in Atlantic forest fragments adjacent to transgenic maize crops.' *Ecological Indicators*. Elsevier Ltd, 49 pp. 216–227.

Cao, Y. and Epifanio, J. (2010) ‘Quantifying the responses of macroinvertebrate assemblages to simulated stress: are more accurate similarity indices less useful?’ *Methods in Ecology and Evolution*, 1(4) pp. 380–388.

Cardillo, M., Mace, G. M., Gittleman, J. L., Jones, K. E., Bielby, J. and Purvis, A. (2008) ‘The predictability of extinction: biological and external correlates of decline in mammals.’ *Proceedings of the Royal Society of London B: Biological Sciences*, 275(1641).

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., Orme, C. D. L. and Purvis, A. (2005) ‘Multiple causes of high extinction risk in large mammal species.’ *Science (New York, N.Y.)*, 309(5738) pp. 1239–41.

Cardinale, B., Duffy, J., Gonzalez, A. and Hooper, D. (2012) ‘Biodiversity loss and its impact on humanity.’ *Nature*.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S. and Naeem, S. (2012) ‘Biodiversity loss and its impact on humanity.’ *Nature*, 486(7401) pp. 59–67.

Caro, T. (2010) *Conservation by proxy*.

Carpio, C., Donoso, D. a., Ramón, G. and Dangles, O. (2009) ‘Short term response of dung beetle communities to disturbance by road construction in the Ecuadorian Amazon.’ *Annales de la Société Entomologique de France*, 45(4) pp. 455–469.

Cassano, C. R., Barlow, J. and Pardini, R. (2014) ‘Forest loss or management intensification? Identifying causes of mammal decline in cacao agroforests.’ *Biological Conservation*. Elsevier Ltd, 169 pp. 14–22.

Caveney, S., Scholtz, C. H. and McIntyre, P. (1995) ‘Patterns of daily flight activity in onitine dung beetles (Scarabaeinae: Onitini).’ *Oecologia* pp. 444–452.

Celi, J., Terneus, E., Torres, J. and Ortega, M. (2004) ‘Dung Beetles (Coleoptera: Scarabaeinae) Diversity in an Altitudinal Gradient in the Cutucú Range, Morona Santiago, Ecuadorian Amazon.’ *Lyonia*, 7(December) pp. 37–52.

CEPF (2012) *Eastern Afromontane Biodiversity Hotspot*.

Chao, A. (1984) ‘On the Estimation of the Number of Classes in a Population.’ *Board of the*

Foundation of the Scandinavian Journal of Statistics, 11(4) pp. 265–270.

Chazdon, R. L., Chao, A., Colwell, R. K., Lin, S.-Y. Y., Norden, N., Letcher, S. G., Clark, D. B., Finegan, B., Arroya, P. J. and Arroyo, J. P. (2011) 'A novel statistical method for classifying habitat generalists and specialists generalists and specialists.' *Ecology*, 92(January) pp. 1332–1343.

Clarke, K. R. and Warwick, R. . (2001) *Change in marine communities: an approach to statistical analysis and interpretation*. *Primer-E*.

Clifton, S. M., Braun, R. I. and Abrams, D. M. (2016) 'Handicap principle implies emergence of dimorphic ornaments.' *Proceedings of the Royal Society B: Biological Sciences*, 283(1843) p. 20161970.

Clusella-Trullas, S., Terblanche, J. S., Blackburn, T. M. and Chown, S. L. (2008) 'Testing the thermal melanism hypothesis: A macrophysiological approach.' *Functional Ecology*, 22(2) pp. 232–238.

Clusella Trullas, S., van Wyk, J. H. and Spotila, J. R. (2007) 'Thermal melanism in ectotherms.' *Journal of Thermal Biology* pp. 235–245.

Coe, M. J. (1969) 'Microclimate and animal life in the equatorial mountains.' *Zoologica Africana*, 4(2) pp. 101–128.

Coggan, N. (2012) 'Are Native Dung Beetle Species Following Mammals in the Critical Weight Range towards Extinction ?' *Proceedings of the Linnean Society of New South Wales*, 134(August) pp. 5–9.

Collins, D. H., Mohorianu, I., Beckers, M., Moulton, V., Dalmay, T. and Bourke, A. F. G. (2017) 'MicroRNAs Associated with Caste Determination and Differentiation in a Primitively Eusocial Insect.' *Scientific Reports*. Nature Publishing Group, 7, March, p. 45674.

Cook, D. (1987) 'Sexual Selection in Dung Beetles I . A Multivariate Study of the Morphological Variation in Two Species of Onthophagus (Scarabaeidae : Onthophagini).'

Craigie, I. D., Baillie, J. E. M., Balmford, A., Carbone, C., Collen, B., Green, R. E. and Hutton, J. M. (2010) 'Large mammal population declines in Africa's protected areas.' *Biological Conservation*. Elsevier Ltd, 143(9) pp. 2221–2228.

Crooks, K. R., Burdett, C. L., Theobald, D. M., King, S. R. B., Di Marco, M., Rondinini, C. and Boitani, L. (2017) 'Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals.' *Proceedings of the National Academy of Sciences*, 114(29) pp. 7635–7640.

Culot, L., Bovy, E., Zagury Vaz-de-Mello, F., Guevara, R. and Galetti, M. (2013) 'Selective defaunation affects dung beetle communities in continuous Atlantic rainforest.' *Biological Conservation*. Elsevier Ltd, 163 pp. 79–89.

Cutler, D. R., Edwards, T. C., Beard, K. H., Cutler, A., Hess, K. T., Gibson, J. and Lawler, J. J. (2007) 'Random Forests for Classification in Ecology.' *Ecology*, 88(11) pp. 2783–2792.

D'Orbigny, H. (1913) 'Synopsis des Onthophagides D'Afrique.' *Annales de la Société Entomologique de France*, 82 pp. 1–743.

Dacke, M. (2003) 'Twilight orientation to polarised light in the crepuscular dung beetle Scarabaeus zambesianus.' *Journal of Experimental Biology*, 206(9) pp. 1535–1543.

Dangles, O., Carpio, C. and Woodward, G. (2012) 'Size-dependent species removal impairs ecosystem functioning in a large-scale tropical field experiment.' *Ecology*.

Davis, A. J. (1998) 'Dung beetle abundance and diversity in the Maliau Basin, Sabah, Malaysian Borneo.' *Malayan Nature Journal*, 52 p. 181–191 ST–Dung beetle abundance and diversity.

Davis, A. J., Holloway, J. D., Huijbregts, H., Krikken, J., Kirk-Spriggs, A. H. and Sutton, S. L. (2001) 'Dung beetles as indicators of change in the forests of northern Borneo.' *Journal of Applied Ecology*, 38(3) pp. 593–616.

Davis, A. J. and Sutton, S. L. (1998) 'The effects of rainforest canopy loss on arboreal; dung beetles in Borneo: implications for the measurement of biodiversity in derived tropical ecosystems.' *Diversity and Distributions*, 4 pp. 167–173.

Davis, A. L. ., Frolov, A. V and Scholtz, C. (2008) *The African Dung Beetle Genera*. Horn, K. (ed.). First Edit, Pretoria: Protea Brook House.

Davis, A. L. V. (1989) 'Nesting of Afrotropical Oniticellus (Coleoptera , Scarabaeidae) and its evolutionary trend from soil to dung.' *Ecological Entomology*, 14 pp. 11–21.

Davis, A. L. V. (1994) 'Compositional differences between dung beetle (Coleoptera: Scarabaeidae s. str.) assemblages in winter and summer rainfall climates.pdf.' *African Entomology*, 2(1) pp. 45–51.

Davis, A. L. V. (2013a) *Onitis meyeri*.

Davis, A. L. V. (2013b) *The Red List of Threatend Species: Heliocopris japetus*.

Davis, A. L. V. (2015) *Onthophagus jugicola*.

Davis, A. L. V., van Aarde, R. J., Scholtz, C. H. and Delport, J. H. (2002) 'Increasing representation of localized dung beetles across a chronosequence of regenerating vegetation and natural dune forest in South Africa.' *Global Ecology and Biogeography*, 11(3) pp. 191–209.

Davis, A. L. V. and Dewhurst, C. F. (1993) 'Climatic and biogeographical associations of Kenyan and northern Tanzanian dung beetles (Coleoptera: Scarabaeidae).' *African Journal of Ecology*, 31(4) pp. 290–305.

Davis, A. L. V. and Scholtz, C. H. (2010) 'Speciation and evolution of eco-climatic ranges in the intertropical African dung beetle genus, Diastellopalpus van Lansberge.' *Biological Journal of the Linnean Society*, 99(2) pp. 407–423.

Davis, A. L. V., Scholtz, C. H. and Chown, S. L. (1999) 'Species turnover, community boundaries and biogeographical composition of dung beetle assemblages across an altitudinal gradient in South Africa.' *Journal of Biogeography*, 26(5) pp. 1039–1055.

Davis, A. L. V., Scholtz, C. H. and Philips, T. K. (2002) 'Historical biogeography of scarabaeine dung beetles.' *Journal of Biogeography*, 29(9) pp. 1217–1256.

Davis, A. L. V and Dewhurst, C. F. (1993) 'Climatic and Biogepgraphical associations of Kenyan and Tanzanian dung beetles (Coleoptera: Scarabaeidae).' *African Journal of Ecology*, 31(4) pp. 290–305.

Davis, A. L. V, Scholtz, C. H., Dooley, P. W., Bham, N. and Kryger, U. (2004) 'Scarabaeine dung beetles as indicators of biodiversity , habitat transformation and pest control chemicals in agro-ecosystems,' (October) pp. 415–424.

Debeljak, M. and Džerosk, S. (2011) 'Decision Trees in Ecological Modelling.' *In* Jopp, F., Reuter, H., and Breckling, B. (eds) *Modelling Complex Ecological Dynamics: An Introduction into Ecological Modelling for Students, Teachers & Scientists*. Springer, pp. 1–387.

Dennis, E. B., Morgan, B. J. T., Freeman, S. N., Brereton, T. M. and Roy, D. B. (2016) 'A generalized abundance index for seasonal invertebrates.' *Biometrics*, 72(4) pp. 1305–1314.

Díaz, S., Purvis, A., Cornelissen, J. H. C., Mace, G. M., Donoghue, M. J., Ewers, R. M., Jordano, P. and Pearse, W. D. (2013) 'Functional traits, the phylogeny of function, and ecosystem service vulnerability.' *Ecology and Evolution*, 3(9) pp. 2958–2975.

Didham, R. K., Ghazoul, J., Stork, N. E. and Davis, A. J. (1996) 'Insects in fragmented forests: a functional approach.’ *Trends in Ecology & Evolution*, 11(6) pp. 255–260.

Dirnböck, T., Essl, F. and Rabitsch, W. (2011) ‘Disproportional risk for habitat loss of high-altitude endemic species under climate change.’ *Global Change Biology*, 17(2) pp. 990–996.

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B. and Collen, B. (2014) ‘Defaunation in the Anthropocene.’ *Science*, 345(6195) pp. 401–406.

Dobson, A. (2009) ‘Food-web structure and ecosystem services: insights from the Serengeti.’ *Philosophical Transactions of the Royal Society B: Biological Sciences*. London: The Royal Society, 364(1524) pp. 1665–1682.

Dominati, E., Patterson, M. and Mackay, A. (2010) ‘A framework for classifying and quantifying the natural capital and ecosystem services of soils.’ *Ecological Economics*. Elsevier B.V., 69(9) pp. 1858–1868.

Doube, B. M. (1990) ‘A functional classification for analysis of the structure of dung beetle assemblages.’ *Ecological Entomology*, 15 pp. 371–383.

Dray, S., Legendre, P. and Peres-Neto, P. R. (2006) ‘Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM).’ *Ecological Modelling*, 196(3–4) pp. 483–493.

Duffy, J. E., Cardinale, B. J., France, K. E., McIntyre, P. B., Thébault, E. and Loreau, M. (2007) ‘The functional role of biodiversity in ecosystems: Incorporating trophic complexity.’ *Ecology Letters* pp. 522–538.

EAC, UNEP and GRID-Arendal (2016) *Sustainable mountain development in East Africa in a changing climate*.

Eckert, S., Kiteme, B., Njuguna, E. and Zaehringer, J. G. (2017) ‘Agricultural expansion and intensification in the foothills of Mount Kenya: A landscape perspective.’ *Remote Sensing*, 9(8) pp. 1–20.

Edwards, F. a, Edwards, D. P., Sloan, S. and Hamer, K. C. (2014) ‘Sustainable management in crop monocultures: the impact of retaining forest on oil palm yield.’ *PloS one*, 9(3) p. e91695.

Eisenring, M., Beck, J., Agwanda, B., Kioko, E. and Curran, M. (2016) ‘Effects of habitat age and disturbance intensity on the biodiversity of three trophic levels in Central Kenya.’ *African Journal of Ecology*, 54(2) pp. 225–234.

Eklöf, A. and Ebenman, B. (2006) 'Species loss and secondary extinctions in simple and complex model communities.' *Journal of Animal Ecology*, 75(1) pp. 239–246.

Elsen, P. R. and Tingley, M. W. (2015) 'Global mountain topography and the fate of montane species under climate change.' *Nature Climate Change*. Nature Publishing Group, 5, May, p. 772.

Emlen, D. J. (1997) 'Alternative reproductive tactics and male-dimorphism in the horned beetle Onthophagus acuminatus (Coleoptera: Scarabaeidae).' *Behavioral Ecology and Sociobiology*, 41(5) pp. 335–341.

Emlen, D. J. (2001) 'Costs and the Diversification of Exaggerated Animal Structures,' 291(February) pp. 1534–1536.

Emlen, D. J., Hunt, J. and Simmons, L. W. (2005) 'Evolution of Sexual Dimorphism and Male Dimorphism in the Expression of Beetle Horns : Phylogenetic Evidence for Modularity , Evolutionary Lability , and Constraint,' 166(october).

Emlen, D. J., Warren, I. A., Johns, A., Dworkin, I. and Lavine, L. C. (2012) 'A mechanism of extreme growth and reliable signaling in sexually selected ornaments and weapons.' *Science*, 337(6096) pp. 860–864.

Emlen, D., Marangelo, J., Ball, B. and Cunningham, C. (2005) 'Diversity in the weapons of sexual selection: horn evolution in the beetle genus Onthophagus (Coleoptera: Scarabaeidae).' *Evolution*, 59(5) pp. 1060–1084.

Enari, H., Koike, S. and Sakamaki, H. (2013) 'Influences of different large mammalian fauna on dung beetle diversity in beech forests.' *Journal of insect science (Online)*, 13(54) p. 54.

Escobar, F., Halffter, G. and Arellano, L. (2007) 'From forest to pasture: An evaluation of the influence of environment and biogeography on the structure of dung beetle (Scarabaeinae) assemblages along three altitudinal gradients in the Neotropical region.' *Ecography*, 30(2) pp. 193–208.

Escobar, F., Lobo, J. M. and Halffter, G. (2005) 'Altitudinal variation of dung beetle (Scarabaeidae: Scarabaeinae) assemblages in the Colombian Andes.' *Global Ecology and Biogeography*, 14(4) pp. 327–337.

Escobar, F., Lobo, J. M. and Halffter, G. (2006) 'Assessing the origin of Neotropical mountain dung beetle assemblages (Scarabaeidae: Scarabaeinae): the comparative influence of vertical and horizontal colonization.' *Journal of Biogeography*, 33(10) pp. 1793–1803.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., Shurin, J. B., Sinclair, A. R. E., Soule, M. E., Virtanen, R. and Wardle, D. A. (2011) 'Trophic Downgrading of Planet Earth.' *Science*, 333(6040) pp. 301–306.

Estrada, A. and Coates-estrada, R. (2002) 'Dung beetles in continuous forest , forest fragments and in an agricultural mosaic habitat island at Los Tuxtlas , Mexico.'

Estrada, A., Coates-Estrada, R., Dadda, A. A. and Cammarano, P. (1998) 'Dung and carrion beetles in tropical rain forest fragments and agricultural habitats at Los Tuxtlas, Mexico.' *Journal of Tropical Ecology*, 14(5) pp. 577–593.

European Commission (2015) *Larger than elephants: Inputs for the design of an EU strategic approach to Wildlife Conservation in Africa*. *Government Report*.

Eweleit, L. and Reinhold, K. (2014) 'Body size and elevation: Do Bergmann's and Rensch's rule apply in the polytypic bushcricket Poecilimon veluchianus?' *Ecological Entomology*, 39(1) pp. 133–136.

Fa, J. and Brown, D. (2009) 'Impacts of hunting on mammals in African tropical moist forests: a review and synthesis.' *Mammal Review*, 39(4) pp. 231–264.

Faurby, S. and Svenning, J. C. (2015) 'Historic and prehistoric human-driven extinctions have reshaped global mammal diversity patterns.' *Diversity and Distributions*, 21(10) pp. 1155–1166.

Feakins, S. J. and Demenocal, P. B. (2010) 'Chapter four - Global and African Regional Climate during the Cenozoic.' *Cenozoic Mammals of Africa* pp. 45–56.

Filgueiras, B. K. C., Liberal, C. N., Aguiar, C. D. M., Hernández, M. I. M. and Iannuzzi, L. (2009) 'Attractivity of omnivore , carnivore and herbivore mammalian dung to Scarabaeinae (Coleoptera , Scarabaeidae) in a tropical Atlantic rainforest remnant,' 53(3) pp. 422–427.

Fjeldsa, J. and Lovett, J. C. (1997) 'Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres.' *Biodiversity and Conservation*, 6(3) pp. 325–346.

Fleming, P. A., Anderson, H., Prendergast, A. S., Bretz, M. R., Valentine, L. E. and Hardy, G. E. S.

(2014) ‘Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function?’ *Mammal Review*, 44(2) pp. 94–108.

França, F. M., Frazão, F. S., Korasaki, V., Louzada, J. and Barlow, J. (2017) ‘Identifying thresholds of logging intensity on dung beetle communities to improve the sustainable management of Amazonian tropical forests.’ *Biological Conservation*. Elsevier, 216(October) pp. 115–122.

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E. M., Steffan-dewenter, I., Emmerson, M., Potts, S. G., Tscharntke, T., Weisser, W. and Bommarco, R. (2015) ‘Functional identity and diversity of animals predict ecosystem functioning better than species-based indices.’

Galetti, M. and Dirzo, R. (2013) ‘Ecological and evolutionary consequences of living in a defaunated world.’ *Biological Conservation*. Elsevier Ltd, 163 pp. 1–6.

Gardner, T. A., Hernández, M. I. M., Barlow, J. and Peres, C. A. (2007) ‘Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles.’ *Journal of Applied Ecology*, 45(3) pp. 883–893.

Gardner, T. A., Hernández, M. I. M., Barlow, J. and Peres, C. A. (2008) ‘Understanding the biodiversity consequences of habitat change : the value of secondary and plantation forests for neotropical dung beetles.’ *Journal of Applied Ecology*, 45 pp. 883–893.

Gaston, K. J. and Chown, S. L. (2008) ‘Elevation and Climatic Tolerance : A Test Using Dung Beetles Elevation and climatic tolerance : a test using dung beetles,’ 86(3) pp. 584–590.

Gerlach, J., Samways, M. and Pryke, J. (2013) ‘Terrestrial invertebrates as bioindicators : an overview of available taxonomic groups’ pp. 831–850.

Gherardi, F. (2007) *Biological invaders in inland waters : profiles, distribution and threats*. Springer.

Giacomini, H. C. and Galetti, M. (2013) ‘An index for defaunation.’ *Biological Conservation*. Elsevier Ltd, 163 pp. 33–41.

Gillard, P. (1967) ‘Coprophagous Beetles in Pasture Ecosystems.’ *J_Aust_Inst_Agric_Sci_*, 33 pp. 30–34.

Goldammer, J. G. (Johann G. (1992) ‘Tropical forests in transition : ecology of natural and anthropogenic disturbance processes.’ *In*. Birkhäuser Verlag, p. 270.

Gómez-Cifuentes, A., Munevar, A., Gimenez, V. C., Gatti, M. G. and Zurita, G. A. (2017) ‘Influence of land use on the taxonomic and functional diversity of dung beetles (Coleoptera: Scarabaeinae) in the southern Atlantic forest of Argentina.’ *Journal of Insect Conservation*. Springer International Publishing, 0(0) p. 0.

Gordon, R. D. and Barbero, E. (2008) ‘Dung Beetles (Coleoptera : Scarabaeidae : Scarabaeinae) Of The Mpala Research Centre And Environs , Laikipia District , Kenya.’ *Journal of East African Natural History*, 97(2) pp. 135–164.

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J. L., Coldea, G., Dick, J., Erschbamer, B., Fernández Calzado, M. R., Kazakis, G., Krajči, J., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, D., Moiseev, P., Molau, U., Merzouki, A., Nagy, L., Nakhutsrishvili, G., Pedersen, B., Pelino, G., Puscas, M., Rossi, G., Stanisci, A., Theurillat, J.-P., Tomaselli, M., Villar, L., Vittoz, P., Vogiatzakis, I. and Grabherr, G. (2012) ‘Continent-wide response of mountain vegetation to climate change.’ *Nature Climate Change*. Nature Publishing Group, 2, January, p. 111.

Greenberg, S. and Godin, T. (2015) ‘A Tool Supporting the Extraction of Angling Effort Data from Remote Camera Images.’ *Fisheries*, 40(6) pp. 276–287.

Gregory, N., Gómez, A., Oliveira, T. M. F. d. S. and Nichols, E. (2015) ‘Big dung beetles dig deeper: Trait-based consequences for faecal parasite transmission.’ *International Journal for Parasitology*. Australian Society for Parasitology Inc., 45(2–3) pp. 101–105.

Griffiths, H. M., Bardgett, R. D., Louzada, J. and 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(1844) p. 20161634.

Griffiths, H. M., Louzada, J., Bardgett, R. D., Beiroz, W., França, F., Tregidgo, D. and Barlow, J. (2015) ‘Biodiversity and environmental context predict dung beetle mediated seed dispersal in a tropical forest field experiment.’ *Ecology*, 96(6) pp. 1607–1619.

de Groot, R. S., Wilson, M. A. and Boumans, R. M. . (2002) ‘A typology for the classification, description and valuation of ecosystem functions, goods and services.’ *Ecological Economics*, 41(3) pp. 393–408.

Gross, M. (2006) ‘Ebb tidings.’ *Current Biology*, 16(8) pp. 266–267.

Guerrucci, M. and Voisin, J.-F. (1988) ‘nfluence of a few environmental factors on the colour morphs of Chorthippus parallelus in the Massif Central France.’ *Bulletin de la Socie´te´ Zoologique de France*, 113 pp. 65–74.

Guppy, C. S. (1986) ‘The adaptive significance of alpine melanism in the butterfly Parnassius phoebus F. (Lepidoptera: Papilionidae).’ *Oecologia*, 70(2) pp. 205–213.

Halffter, G. and Matthews, E. . (1966) ‘The natural history of dung beetles of the subfamily Scarabaeinae.’ *Folia Entomologica Mexicana*, 12(14) pp. 1–312.

Halffter, G., Pineda, E., Arellano, L. and Escobar, F. (2007) ‘Instability of Copronecrophagous Beetle Assemblages (Coleoptera : Scarabaeinae) in a Mountainous Tropical Landscape of Mexico.’

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

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

Hanski, I., Ecology, A., Road, S. P. and Koskela, H. (1979) ‘Resource partitioning in six guilds of dung-inhabiting beetles (Coleoptera).’

Hedburg, O. (1969) ‘Evolution and speciation in a tropical high mountain flora.’ *Biological Journal of the Linnean Society*, 1(1–2) pp. 135–148.

Hély, C., Bremond, L., Alleaume, S., Smith, B., Sykes, M. T. and Guiot, J. (2006) ‘Sensitivity of African biomes to changes in the precipitation regime.’ *Global Ecology and Biogeography*, 15(3) pp. 258–270.

Hernández, M. I. M., Monteiro, L. and Favila, M. E. (2011) ‘The role of body size and shape in understanding competitive interactions within a community of Neotropical dung beetles.’ *Journal of insect science (Online)*, 11(FEBRUARY) p. 13.

Herzog, S. K., Hamel-Leigue, a. C., Larsen, T. H., Mann, D. J., Soria-Auza, R. W., Gill, B. D., Edmonds, W. D. and Spector, S. (2013) ‘Elevational Distribution and Conservation Biogeography of Phanaeine Dung Beetles (Coleoptera: Scarabaeinae) in Bolivia.’ *PLoS ONE*, 8(5) pp. 1–11.

Hesse, P. R. (1954) ‘The identification of the spoor and dung of East African mammals: Part I. The Antelopes.’ *The East African Natural History Society*, XXII.

Hillebrand, H., Blasius, B., Borer, E. T., Chase, J. M., Downing, J. A., Eriksson, B. K., Filstrup, C. T., Harpole, W. S., Hodapp, D., Larsen, S., Lewandowska, A. M., Seabloom, E. W., Van de Waal, D. B. and Ryabov, A. B. (2017) 'Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring.' *Journal of Applied Ecology*, (June 2017) pp. 169–184.

Hodkinson, I. D. (2005) 'Terrestrial insects along elevation gradients: species and community responses to altitude.' *Biological Reviews*, 80(03) p. 489.

Hogg, D. E. (1981) 'New Zealand Journal of Experimental Agriculture A lysimeter study of nutrient losses from urine and dung applications on pasture A lysimeter study of nutrient losses from urine and dung applications on pasture.' *New Zealand Journal of Experimental Agriculture N.Z. Journal of Experimental Agriculture*, 9(9) pp. 39–46.

Holter, P. (2016) 'Herbivore dung as food for dung beetles: elementary coprology for entomologists.' *Ecological Entomology*, 41(4) pp. 367–377.

Hooper, D., Adair, E., Cardinale, B. and Byrnes, J. (2012) 'A global synthesis reveals biodiversity loss as a major driver of ecosystem change.' *Nature*.

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

Hothorn, T., Hornik, K. and Zeileis, A. (2006) 'ctree: Conditional Inference Trees.' *Cran.At.R-Project.Org*, (Quinlan 1993).

http://www.iucnredlist.org (2017) *http://www.iucnredlist.org*. [Online] http://www.iucnredlist.org.

http://www.who.int/uv/intersunprogramme/activities/uv_index/en/index3.htmlTitle (n.d.). [Online] http://www.who.int/uv/intersunprogramme/activities/uv_index/en/index3.htmlTitle.

IPCC (2007) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*.

IPCC (2014) *IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change No Title*. Geneva.

IUCN (2012) 'Protected Areas Category VI.' *Global Protected Areas Programme*.

Jankowski, J. E., Ciecka, A. L., Meyer, N. Y. and Rabenold, K. N. (2009) ‘Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes.’ *Journal of Animal Ecology*, 78 pp. 315–327.

Jay-robert, P., Lobo, J. M. and Lumaret, J. (1997) ‘Altitudinal Turnover and Species Richness Variation in European Montane Dung Beetle Assemblages,’ 29(2) pp. 196–205.

Ji, Y., Ashton, L., Pedley, S. M., Edwards, D. P., Tang, Y., Nakamura, A., Kitching, R., Dolman, P. M., Woodcock, P., Edwards, F. a., Larsen, T. H., Hsu, W. W., Benedick, S., Hamer, K. C., Wilcove, D. S., Bruce, C., Wang, X., Levi, T., Lott, M., Emerson, B. C. and Yu, D. W. (2013) ‘Reliable, verifiable and efficient monitoring of biodiversity via metabarcoding.’ *Ecology Letters*, 16(10) pp. 1245–1257.

Johnstone, C. P., Lill, A. and Reina, R. D. (2014) ‘Habitat loss, fragmentation and degradation effects on small mammals: Analysis with conditional inference tree statistical modelling.’ *Biological Conservation*. Elsevier Ltd, 176 pp. 80–98.

Jorge, M. L. S. P., Galetti, M., Ribeiro, M. C. and Ferraz, K. M. P. M. B. (2013) ‘Mammal defaunation as surrogate of trophic cascades in a biodiversity hotspot.’ *Biological Conservation*. Elsevier Ltd, 163 pp. 49–57.

Kakkar, N., Singh, N. and Mittal, I. C. (2008) ‘Effect of habitat on the abundance and diversity of Scarabaeoid Dung beetle (Scarabaeidae) assemblages in India o o o,’ 32(4).

Karanth, K. K., Nichols, J. D., Karanth, K. U., Hines, J. E. and Christensen, N. L. (2010) ‘The shrinking ark: patterns of large mammal extinctions in India.’ *Proceedings of the Royal Society B: Biological Sciences*, 277(1690) pp. 1971–1979.

Kenya Water Tower Agency (2016) *Kenya Water Towers Agency (KWTA)*.

Kiffner, C., Wenner, C., Laviolet, A., Yeh, K. and Kioko, J. (2015) ‘From savannah to farmland: Effects of land-use on mammal communities in the Tarangire-Manyara ecosystem, Tanzania.’ *African Journal of Ecology*, 53(2) pp. 156–166.

Kingston, T. J. and Coe, M. (1977) ‘The biology of a giant dungbeetle (Heliocopris dilloni) (Coleoptera: Scarabaeidae).’ *Journal of Zoology*, 181(2) pp. 243–263.

Kishi, S., Takakura, K.-I. and Nishida, T. (2015) ‘Sexual shape dimorphism accelerated by male-male competition, but not prevented by sex-indiscriminate parental care in dung beetles (Scarabaeidae).’ *Ecology and evolution*. Wiley-Blackwell, 5(14) pp. 2754–61.

Klein, B. (1989) 'Effects of Forest Fragmentation on Dung and Carrion beetle communities in Central Amazonia.' *Ecology*, 70(6) pp. 1715–1725.

Klemperer, H. G. (1979) 'An analysis of the nesting behaviour of Geotrupes spiniger Marsham (Coleoptera, Scarabaeidae).' *Ecological Entomology*, 4(2) pp. 133–150.

Klemperer, H. G. (1983) 'Brood ball construction by the non-brooding Coprini Sulcophanaeus carnifex and Dichotomius torulosus (Coleoptera, Scarabaeidae).' *Ecological Entomology*, 8(1) pp. 61–68.

Klemperer, H. G. and Boulton, R. (1976) 'Brood burrow construction and brood care by Heliocopris japetus (Klug) and Heliocopris hamadryas (Fabricius) (Coleoptera, Scarabaeidae).' *Ecological Entomology*, 1(1) pp. 19–29.

Kleynhans, E. J., Jolles, A. E., Bos, M. R. E. and Olff, H. (2011) 'Resource partitioning along multiple niche dimensions in differently sized African savanna grazers.' *Oikos*, 120(4) pp. 591–600.

Knell, R. (2011) 'Male Contest Competition and the Evolution of Weapons.' *Ecology and Evolution of Dung Beetles* pp. 47–65.

Köhler, G., Samietz, J. and Schielzeth, H. (2017) 'Morphological and colour morph clines along an altitudinal gradient in the meadow grasshopper Pseudochorthippus parallelus.' *PLoS ONE*, 12(12) pp. 1–13.

Kohler, T. and Maselli, D. (2012) *Mountains and Climate Change*.

Koike, S., Soga, M., Nemoto, Y. and Kozakai, C. (2014) 'How are dung beetle species affected by deer population increases in a cool temperate forest ecosystem?' *Journal of Zoology*, 293(4) pp. 227–233.

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

Körner, C. (2007) 'The use of "altitude" in ecological research.' *Trends in Ecology and Evolution*, 22(11) pp. 569–574.

Krell-westerwalbesloh, S. and Linsenmair, K. E. (2004) 'Diel separation of Afrotropical dung beetle guilds — avoiding competition and neglecting resources (Coleoptera : Scarabaeoidea)' pp. 2225–2249.

Krell, F., Krell, F., Krell-westerwalbesloh, S., Krell-westerwalbesloh, S., Weiß, I., Weiß, I., Eggleton, P., Eggleton, P., Linsenmair, K. E. and Linsenmair, K. E. (2003) ‘Spatial separation of Afrotropical dung beetle guilds: a trade-off between competitive superiority and energetic constraints (Coleoptera: Scarabaeidae).’ *Ecography*, 26(July 2002) pp. 210–222.

Krell, F. T. (2007) *Dung Beetle Sampling Protocols*.

Kurten, E. L. (2013) ‘Cascading effects of contemporaneous defaunation on tropical forest communities.’ *Biological Conservation*. Elsevier Ltd, 163 pp. 22–32.

Lambrechts, C., Woodley, B., Church, C. and Gachanja, M. (2003) *Aerial survey of the destruction of the Aberdare Range forests*.

Larsen, T. H., Williams, N. M. and Kremen, C. (2005) ‘Extinction order and altered community structure rapidly disrupt ecosystem functioning.’ *Ecology Letters*, 8(5) pp. 538–547.

Laurance, W. F., Carolina Useche, D., Shoo, L. P., Herzog, S. K., Kessler, M., Escobar, F., Brehm, G., Axmacher, J. C., Chen, I. C., G??mez, L. A., Hietz, P., Fiedler, K., Pyrcz, T., Wolf, J., Merkord, C. L., Cardelus, C., Marshall, A. R., Ah-Peng, C., Aplet, G. H., del Coro Arizmendi, M., Baker, W. J., Barone, J., Br??hl, C. A., Bussmann, R. W., Cicuzza, D., Eilu, G., Favila, M. E., Hemp, A., Hemp, C., Homeier, J., Hurtado, J., Jankowski, J., Katt??n, G., Kluge, J., Kr??mer, T., Lees, D. C., Lehnert, M., Longino, J. T., Lovett, J., Martin, P. H., Patterson, B. D., Pearson, R. G., Peh, K. S. H., Richardson, B., Richardson, M., Samways, M. J., Senbeta, F., Smith, T. B., Utteridge, T. M. A., Watkins, J. E., Wilson, R., Williams, S. E. and Thomas, C. D. (2011) ‘Global warming, elevational ranges and the vulnerability of tropical biota.’ *Biological Conservation*. Elsevier Ltd, 144(1) pp. 548–557.

Laureto, L. M. O., Cianciaruso, M. V. and Samia, D. S. M. (2015) ‘Functional diversity: An overview of its history and applicability.’ *Natureza e Conservacao*. Associação Brasileira de Ciência Ecológica e Conservação, 13(2) pp. 112–116.

Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P. and Rossi, J.-P. (2006) ‘Soil invertebrates and ecosystem services.’ *European Journal of Soil Biology*, 42, November, pp. S3–S15.

Lawler, J. J., White, D., Neilson, R. P. and Blaustein, A. R. (2006) ‘Predicting climate-induced range shifts: Model differences and model reliability.’ *Global Change Biology*, 12(8) pp. 1568–1584.

Legendre, P. (2008) ‘Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis.’ *Journal of Plant Ecology*, 1(1) pp. 3–8.

Legendre, P. and Legendre, L. (1998) *Numerical ecolgy*. 2nd Editio, Amsterdam: Elesevier Science BV.

Lloyd, M. (1967) '`Mean Crowding'.' *Journal of Animal Ecology*, 36(1) pp. 1–30.

Loader, S. P., Sara Ceccarelli, F., Menegon, M., Howell, K. M., Kassahun, R., Mengistu, A. A., Saber, S. A., Gebresenbet, F., de Sá, R., Davenport, T. R. B., Larson, J. G., Müller, H., Wilkinson, M. and Gower, D. J. (2014) 'Persistence and stability of Eastern Afromontane forests: Evidence from brevicipitid frogs.' *Journal of Biogeography*, 41(9) pp. 1781–1792.

Lobo, J. M., Guéorguiev, B. and Chehlarov, E. (2007) 'Convergences and divergences between two European mountain dung beetle assemblages (Coleoptera , Scarabaeoidea),' 1 pp. 83–96.

Lobo, J. M. and Halffter, G. (2000a) 'Biogeographical and Ecological Factors Affecting the Altitudinal Variation of Mountainous Communities of Coprophagous Beetles (Coleoptera : Scarabaeoidea): a Comparative Study' pp. 115–126.

Lobo, J. M. and Halffter, G. (2000b) 'Biogeographical and Ecological Factors Affecting the Altitudinal Variation of Mountainous Communities of Coprophagous Beetles (Coleoptera: Scarabaeoidea): a Comparative Study.' *Annals of the Entomological Society of America*, 93 pp. 115–126.

Lobo, J. M. and Halffter, G. (2000) 'Biogeographical and Ecological Factors Affecting the Altitudinal Variation of Mountainous Communities of Coprophagous Beetles (Coleoptera: Scarabaeoidea): a Comparative Study.' *Annals of the Entomological Society of America*, 93(1) pp. 115–126.

Lobo J.M., S. I. & M.-P. F. (1997) 'Lobo J.M., Sanmartin I. & Martin-Piera F. 1997 Diversity and spatial turnover of Dung Beetle communities in a protected area of South Europe (Donana National Park, Huelva, Spain) Elytron 11:71-88.' *Europe*, (11) pp. 71–88.

Lopes, J., Korasaki, V., Catelli, L. L., Marçal, V. V. M. and Nunes, M. P. B. P. (2011) 'A comparison of dung beetle assemblage structure (Coleoptera : Scarabaeidae : Scarabaeinae) between an Atlantic forest fragment and adjacent abandoned pasture in Paraná , Brazil,' 28(1) pp. 72–79.

Luedeling, E., Oord, A. L., Kiteme, B., Ogalleh, S., Malesu, M., Shepherd, K. D. and De Leeuw, J. (2015) 'Fresh groundwater for Wajir -ex-ante assessment of uncertain benefits for multiple stakeholders in a water supply project in Northern Kenya.' *Frontiers in Environmental Science*.

Frontiers, 3, March, p. 16.

Mani, M. S. (1968) *Ecology and Biogepgraphy of High altitude insects. Series Entomologica*.

Manning, P., Slade, E. M., Beynon, S. A. and Lewis, O. T. (2016) 'Functionally rich dung beetle assemblages are required to provide multiple ecosystem services.' *Agriculture, Ecosystems and Environment*, 218(January) pp. 87–94.

Di Marco, M., Buchanan, G. M., Szantoi, Z., Holmgren, M., Grottolo Marasini, G., Gross, D., Tranquilli, S., Boitani, L. and Rondinini, C. (2014) 'Drivers of extinction risk in African mammals: the interplay of distribution state, human pressure, conservation response and species biology.' *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1643) pp. 20130198–20130198.

Margules, C. R. and Pressey, R. L. (2000) 'Systematic conservation planning.' *Nature*, 405(6783) pp. 243–253.

Martin, E. H., Cavada, N., Ndibalema, V. G. and Rovero, F. (2015) 'Modelling fine-scale habitat associations of medium-to-large forest mammals in the Udzungwa Mountains of Tanzania using camera trapping.' *Tropical Zoology*, 6975(March 2016) pp. 1–15.

Massey, A. L., King, A. a. and Foufopoulos, J. (2014) 'Fencing protected areas: A long-term assessment of the effects of reserve establishment and fencing on African mammalian diversity.' *Biological Conservation*. Elsevier Ltd, 176 pp. 162–171.

Mastretta-Yanes, A., Moreno-Letelier, A., Piñero, D., Jorgensen, T. H. and Emerson, B. C. (2015) 'Biodiversity in the Mexican highlands and the interaction of geology, geography and climate within the Trans-Mexican Volcanic Belt.' *Journal of Biogeography*, 42(9) pp. 1586–1600.

Max Kuhn Contributions from Jed Wing, A., Weston, S., Williams, A., Keefer, C., Engelhardt, A., Cooper, T., Mayer, Z., Benesty, M., Lescarbeau, R., Ziem, A., Scrucca, L., Tang, Y., Candan, C., Hunt, T. and Max Kuhn, M. (2017) 'Package "caret" Classification and Regression Training Description Misc functions for training and plotting classification and regression models.'

Mayor, J. R., Sanders, N. J., Classen, A. T., Bardgett, R. D., Clément, J.-C., Fajardo, A., Lavorel, S., Sundqvist, M. K., Bahn, M., Chisholm, C., Cieraad, E., Gedalof, Z., Grigulis, K., Kudo, G., Oberski, D. L. and Wardle, D. A. (2017) 'Elevation alters ecosystem properties across temperate treelines globally.' *Nature*. Macmillan Publishers Limited, part of Springer Nature. All rights reserved., 542(7639) pp. 91–95.

Mayr, E. and O’Hara, R. J. (1986) ‘The Biogeographic Evidence Supporting the Pleistocene Forest Refuge Hypothesis.’ *Evolution*, 40(1) p. 55.

McCain, C. M. and Grytnes, J.-A. (2010) ‘Elevational Gradients in Species Richness.’ *Encyclopedia of Life Sciences* pp. 1–10.

McCulloch, G. A. and Waters, J. M. (2018) ‘Does wing reduction influence the relationship between altitude and insect body size? A case study using New Zealand’s diverse stonefly fauna.’ *Ecology and Evolution*, 8(2) pp. 953–960.

Mcgeoch, M. A. (2007) ‘Insects and Bioindication:Theory and Progress.’ *In Insect conservation biology*, pp. 144–173.

McGill, B. J., Enquist, B. J., Weiher, E. and Westoby, M. (2006) ‘Rebuilding community ecology from functional traits.’ *Trends in Ecology and Evolution*, 21(4) pp. 178–185.

Medina, C. A., Molano, F. and Scholtz, C. H. (2013) ‘Morphology and terminology of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) male genitalia.’ *Zootaxa*, 3626 pp. 455–476.

Mehlich, A. (1984) ‘Communications in Soil Science and Plant Analysis Mehlich 3 soil test extractant : A modification of Mehlich 2 extractant.’ *Communications in Soil Science and Plant Analysis*, 15(12) pp. 37–41.

Menendez, R., Gonzalez-Megas, A., Jay-Robert, P. and Marquez-Ferrando, R. (2014) ‘Climate change and elevational range shifts: Evidence from dung beetles in two European mountain ranges.’ *Global Ecology and Biogeography*, 23 pp. 646–657.

Menéndez, R. and Gutiérrez, D. (2004) ‘Shifts in habitat associations of dung beetles in northern Spain : Climate change implications Shifts in habitat associations of dung beetles in northern Spain : Climate change implications 1.’ *Ecoscience*, 6860(August) pp. 329–337.

Menéndez, R., Webb, P. and Orwin, K. H. (2016a) ‘Complementarity of dung beetle species with different functional behaviours influence dung-soil carbon cycling.’ *Soil Biology and Biochemistry*, 92(October) pp. 142–148.

Merckx, V. S. F. T., Hendriks, K. P., Beentjes, K. K., Mennes, C. B., Becking, L. E., Peijnenburg, K. T. C. a., Afendy, A., Arumugam, N., de Boer, H., Biun, A., Buang, M. M., Chen, P.-P., Chung, A. Y. C., Dow, R., Feijen, F. a. a., Feijen, H., Soest, C. F., Geml, J., Geurts, R., Gravendeel, B., Hovenkamp, P., Imbun, P., Ipor, I., Janssens, S. B., Jocqué, M., Kappes, H., Khoo, E., Koomen, P., Lens, F., Majapun, R. J., Morgado, L. N., Neupane, S., Nieser, N., Pereira, J. T., Rahman, H., Sabran, S., Sawang, A., Schwallier, R. M., Shim, P.-S., Smit, H., Sol, N., Spait, M., Stech, M., Stokvis, F., Sugau, J. B., Suleiman, M., Sumail, S., Thomas, D. C., van Tol, J., Tuh, F. Y. Y., Yahya, B. E., Nais, J., Repin, R., Lakim, M. and Schilthuizen, M. (2015) 'Evolution of endemism on a young tropical mountain.' *Nature*.

Mikhailov, Y. E. (2008) 'Body colouration in the leaf beetle genera Oreina Chevrolat and CrositaMotschulsky and trends in its variation.' *In* Jolivet, P., Santiago-Blay, J., and Schmitt, M. (eds) *Research on Chrysomelidae*. Leidan: Brill, pp. 1–432.

Miloti??, T., Quid??, S., van Loo, T. and Hoffmann, M. (2016) 'Linking functional group richness and ecosystem functions of dung beetles: an experimental quantification.' *Oecologia* pp. 1–14.

Moczek, A. and Emlen, D. (2000) 'Male horn dimorphism in the scarab beetle, Onthophagus taurus: do alternative reproductive tactics favour alternative phenotypes?' *Animal behaviour* pp. 459–466.

Moczek, A. P. (2002) 'Allometric plasticity in a polyphenic beetle' pp. 58–67.

Moczek, A. P. (2006) 'Pupal Remodeling and the Development and Evolution of Sexual Dimorphism in Horned Beetles,' 168(6).

Moczek, A. P. and Emlen, D. J. (1999) 'Proximate determination of male horn dimorphism in the beetle Onthophagus taurus (Coleoptera : Scarabaeidae),' 12 pp. 27–37.

Moczek, A. P. and Nijhout, H. F. (2003) 'Rapid evolution of a polyphenic threshold,' 268 pp. 259–268.

Mugendi, D., Mucheru-Muna, M., Mugwe, J., Kung'u, J. and Bationo, A. (2007) 'Improving food production using "best bet" soil fertility technologies in the Central highlands of Kenya.' *Advances in Integrated Soil Fertility Management in Sub-Saharan Africa: Challenges and Opportunities*, (1996) pp. 345–351.

Mulinge, W., Gicheru, P., Murithi, F., Maingi, P., Kihiu, E., Kirui, O. K. and Mirzabaev, A. (2016) 'Economics of Land Degradation and Improvement in Kenya.' *In* Nkonya, E., Mirzabaev, A., and von Braun, J. (eds) *Economics of Land Degradation and Improvement -- A Global Assessment for Sustainable Development*. Cham: Springer International Publishing, pp. 471–498.

Mungai, D., Thuita, T. and Alfred, M. (2011) *Environmental, social and economic assessment of the fencing of the Aberdare Conservation Area*.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. and Kent, J. (2000) ‘Biodiversity hotspots for conservation priorities.’ *Nature*, 403(6772) pp. 853–8.

Naeem, S. and Wright, J. P. (2003) ‘Disentangling biodoversity effects on ecosystem functioning: deriving solutions to a seemingly insormountable problem.’ *Ecology Letters*, 6 pp. 567–579.

Nervo, B., Tocco, C., Caprio, E., Palestrini, C. and Rolando, A. (2014) ‘The Effects of Body Mass on Dung Removal Efficiency in Dung Beetles.’ *PLoS ONE*, 9(9) p. e107699.

Ngecu, W. M. and Ichang’i, D. W. (1999) ‘The environmental impact of landslides on the population living on the eastern footslopes of the Aberdare ranges in Kenya: A case study of Maringa Village landslide.’ *Environmental Geology*, 38(September) pp. 259–264.

Nichols, E., Gardner, T. A., Peres, C. A., Spector, S. and Scarabaeinae, T. (2009) ‘Co-declining mammals and dung beetles : an impending ecological cascade.’ *Oikos*, 118(November 2008) pp. 481–487.

Nichols, E. and Gómez, A. (2014) ‘Dung beetles and fecal helminth transmission: patterns, mechanisms and questions.’ *Parasitology*, 141(5) pp. 614–23.

Nichols, E., Larsen, T., Spector, S., Davis, A. L., Escobar, F., Favila, M. and Vulinec, K. (2007) ‘Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis.’ *Biological Conservation*, 137(1) pp. 1–19.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S. and Favila, M. E. (2008) ‘Ecological functions and ecosystem services provided by Scarabaeinae dung beetles.’ *Biological Conservation*, 141(6) pp. 1461–1474.

Nichols, E., Uriarte, M., Bunker, D. E., Favila, M. E., Slade, E. M., Vulinec, K., Larsen, T., Vaz-De-Mello, F. Z., Louzada, J., Naeem, S. and Spector, S. H. (2013) ‘Trait-dependent response of dung beetle populations to tropical forest conversion at local and regional scales.’ *Ecology*, 94(1) pp. 180–189.

Nichols, E., Uriarte, M., Peres, C. a., Louzada, J., Braga, R. F., Schiffler, G., Endo, W. and Spector, S. H. (2013) ‘Human-Induced Trophic Cascades along the Fecal Detritus Pathway.’ *PLoS ONE*, 8(10) p. e75819.

Nicholson, M. J. . (1976) *Soils and land Use On the Northern Foothills Of The Aberdare Range, Kenya*. University of Aberdeen.

Nijhout, H. F. and Emlen, D. J. (1998) 'Competition among body parts in the development and evolution of insect morphology.' *Proceedings of the National Academy of Sciences*, 95(7) pp. 3685–3689.

Njeru, P. N. M., Maina, I., Miruka, M., Amboga, J. S., Gitari, J., Rono, B., Mahasi, M. and Murithi, F. (2011) 'Soil fertility characterization of smallholder farms under group and individual management in central Kenya.' *African Crop Science Society*, 10(1986) pp. 621–624.

Nunes, C. A., Braga, R. F., Figueira, J. E. C., De Siqueira Neves, F. and Fernandes, G. W. (2016) 'Dung beetles along a tropical altitudinal gradient: Environmental filtering on taxonomic and functional diversity.' *PLoS ONE*, 11(6) pp. 1–16.

Nyeko, P. (2009) 'Dung Beetle Assemblages and Seasonality in Primary Forest and Forest Fragments on Agricultural Landscapes in Budongo , Uganda Published by : Association for Tropical Biology and Conservation All use subject to JSTOR Terms and Conditions on Agricultural La.' *Biotropica*, 41(4) pp. 476–484.

Nyundo, B. A., Mtui, A. and Kissaka, H. (2006) *An assessment of ecological and social-economic impacts caused by collection of deadwood, medicinal plants and cutting of grass for thatching in Udzungwa Mountains National Park*.

Ogutu, J. O., Owen-Smith, N., Piepho, H. P. and Said, M. Y. (2011) 'Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977-2009.' *Journal of Zoology*, 285(2) pp. 99–109.

Oksanen, J. (2015) 'Vegan: an introduction to ordination.' *Management*, 1 pp. 1–10.

Osberg, D. C., Doube, B. M. and Hanrahan, S. A. (1994) 'Habitat specificity in African dung beetles: the effect of soil type on the survival of dung beetle immatures (Coleoptera Scarabaeidae).' *Tropical Zoology*, 7(February 2015) pp. 1–10.

Ostrom, E. (2008) *International Forestry Resources and Institutions (IFRI)*.

Paaijmans, K. P., Heinig, R. L., Seliga, R. A., Blanford, J. I., Blanford, S., Murdock, C. C. and Thomas, M. B. (2013) 'Temperature variation makes ectotherms more sensitive to climate change.' *Global Change Biology*, 19(8) pp. 2373–2380.

Parmentier, I., Malhi, Y., Senterre, B., Whittaker, R. J., N., A. T. D., Alonso, A., Balinga, M. P. B., Bakayoko, A., Bongers, F., Chatelain, C., Comiskey, J. A., Cortay, R., Kamdem, M.-N. D., Doucet, J.-L., Gautier, L., Hawthorne, W. D., Issembe, Y. A., Kouamé, F. N., Kouka, L. A., Leal, M. E., Lejoly, J., Lewis, S. L., Nusbaumer, L., Parren, M. P. E., Peh, K. S. H., Phillips, O. L., Shell, D., Sonké, B., Sosef, M. S. M., Sunderland, T. C. H., Stropp, J., Steege, H. Ter, Swaine, M. D., Tchouto, M. G. P., Gemerden, B. S. van, Valkenburg, J. L. C. H. van and Wöll, H. (2009) 'The Odd Man Out? Might Climate Explain the Lower Tree α-Diversity of African Rain Forests Relative to Amazonian Rain Forests?' *Journal of Ecology*. British Ecological Society pp. 1058–1071.

Paron, P., Olago, D. O. and Omuto, C. T. (2013) *Kenya: A Natural Outlook: Developoments in Earth Surface Processes*. Shroder, J. . (ed.). 1st Editio, Oxford: Elsevier B.V.

Petchey, O. L. and Gaston, K. J. (2002) 'Functional diversity (FD), species richness and community composition.' *Ecology Letters*, 5 pp. 402–411.

Petchey, O. L. and Gaston, K. J. (2006) 'Functional diversity: Back to basics and looking forward.' *Ecology Letters*, 9(6) pp. 741–758.

Pigliucci, M., Murren, C. J. and Schlichting, C. D. (2006) 'Phenotypic plasticity and evolution by genetic assimilation.' *The Journal of experimental biology*. The Company of Biologists Ltd, 209(Pt 12) pp. 2362–7.

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M. and Sexton, J. O. (2014) 'The biodiversity of species and their rates of extinction, distribution, and protection.' *Science*, 344(6187).

Pincebourde, S. (2005) 'Diel flight activity and ecological segregation within an assemblage of tropical forest dung and carrion beetles Franc' pp. 21–30.

Pineda, E., Moreno, C., Escobar, F. and Halffter, G. (2005) 'Frog , Bat , and Dung Beetle Diversity in the Cloud Forest and Coffee Agroecosystems of Veracruz ,' 19(2) pp. 400–410.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S. and Van Willigen, B. (2017) 'nlme: Linear and Nonlinear Mixed Effects Models.' *R package 3rd edn.* pp. 1–336.

Pokorný, S., Zidek, J. and Werner, K. (2009) *Giant Dung Beetles of the Genus Heliocopris*. Hradec Králové, Czech Republic.: Taita Publishers.

Pomfret, J. C. and Knell, R. J. (2006) 'Immunity and the expression of a secondary sexual trait in a horned beetle,’ (February).

Pomfret, J. and Knell, R. (2006) ‘Sexual selection and horn allometry in the dung beetle Euoniticellus intermedius.’ *Animal Behaviour* pp. 567–576.

Poulsen, J. R., Clark, C. J. and Palmer, T. M. (2013) ‘Ecological erosion of an Afrotropical forest and potential consequences for tree recruitment and forest biomass.’ *Biological Conservation*. Elsevier Ltd, 163 pp. 122–130.

Pound, M. J., Haywood, A. M., Salzmann, U. and Riding, J. B. (2012) ‘Global vegetation dynamics and latitudinal temperature gradients during the Mid to Late Miocene (15.97-5.33Ma).’ *Earth-Science Reviews*. Elsevier B.V., 112(1–2) pp. 1–22.

Pounds, J. A., Fogden, M. P. L. and Campbell, J. H. (1999) ‘Biological response to climate change on a tropical mountain.’ *N*, 398(April) pp. 611–615.

Pressey, R. L., Cabeza, M., Watts, M. E., Cowling, R. M. and Wilson, K. A. (2007) ‘Conservation planning in a changing world.’ *Trends in Ecology and Evolution*, 22(11) pp. 583–592.

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

Quinn, G. P., Keough, M. J., Petraitis, P. S., Quinn, G. P. and Keough, M. J. (2002) *Experimental design and data analysis for biologists*. *Journal of Experimental Marine Biology and Ecology*.

Quinn, J. E., Awada, T., Trindade, F., Fulginiti, L. and Perrin, R. (2017) ‘Combining habitat loss and agricultural intensification improves our understanding of drivers of change in avian abundance in a North American cropland anthrome.’ *Ecology and Evolution*, 7(3) pp. 803–814.

R Core Team (2016) ‘R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.r-project.org/.’

R Development Core Team, R. (2017) ‘R: A Language and Environment for Statistical Computing.’ Team, R. D. C. (ed.) *R Foundation for Statistical Computing*. R Foundation for Statistical Computing (R Foundation for Statistical Computing) p. 409.

Rahbek, C. (1995) ‘The elevational gradient of species richness: a uniform pattern?’ *Ecography*, 18(2) pp. 200–205.

Reiss, J., Bridle, J. R., Montoya, J. M. and Woodward, G. (2009) ‘Emerging horizons in biodiversity and ecosystem functioning research.’ *Trends in Ecology and Evolution*, 24(9) pp. 505–514.

Roggero, A., Stanbrook, R., Josso, J., Barbero, E. and Palestrini, C. (2017) ‘Phylogenetic relationships of Epidrepanus within the subtribe Drepanocerina (Coleoptera: Scarabaeidae: Scarabaeinae: Oniticellini), with the description of two new species.’ *Zootaxa*, 4320(1) pp. 1–24.

Rohr, J. R., Mahan, C. G. and Kim, K. C. (2007) ‘Developing a monitoring program for invertebrates: Guidelines and a case study.’ *Conservation Biology*, 21(2) pp. 422–433.

Roland, J. (1982) ‘Melanism and diel activity of alpine Colias (Lepidoptera: Pieridae).’ *Oecologia*, 53(2) pp. 214–221.

Romero-alcaraz, E. and Avila, J. M. (2000) ‘Effect of Elevation and Type of Habitat on the Abundance and Diversity of Scarabaeoid Dung Beetle (Scarabaeoidea) Assemblages in a Mediterranean Area from Southern Iberian Peninsula.’ *Zoological Science*, 39(4) pp. 351–359.

Roskov, Y., L., A., T., O., D., N., N., B., P.M., K., T., B., R.E., D., W., D., A., D. W. and Nieukerken E. van, Z. J. (2018) *Catalogue of Life*.

Rovero, F., Owen, N., Jones, T., Canteri, E., Iemma, A. and Tattoni, C. (2016) ‘Camera trapping surveys of forest mammal communities in the Eastern Arc Mountains reveal generalized habitat and human disturbance responses.’ *Biodiversity and Conservation*. Springer Netherlands pp. 50–52.

Samways, M. J. (2015) ‘Future-proofing insect diversity.’ *Current Opinion in Insect Science*. Elsevier Inc, 12 pp. 71–78.

Sanchez, P. A., Shepherd, K. D., Soule, M. J., Place, F. M., Buresh, R. J., Izac, A. N., Mokwunye, A. U., Kwesiga, F. R., Ndiritu, C. G. and Woomer, P. L. (1997) ‘Soil Fertility Replenishment in Africa: An Investment in Natural Resource Capital Pedro.’ *Replenishing soil fertility in Africa*, (SSSA Special Publication 51) pp. 1–47.

Santos-heredia, C., Andresen, E., Diego, A. Z., Fiore, D. and Al, C. S. E. T. (2010) ‘Secondary seed dispersal by dung beetles in a Colombian rain forest : effects of dung type and defecation pattern on seed fate’ pp. 355–364.

Scheffler, P. Y. (2005) ‘Dung beetle (Coleoptera: Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia.’ *Journal of Tropical Ecology*, 21(1) pp. 9–19.

Schleuter, D., Daufresne, M., Massol, F. and Argillier, C. (2010) ‘User’s guide to functional diversity indices.’ *Ecological Monographs*, 80(3) pp. 448–469.

Schmitt, K. (1992a) ‘Anthropo-Zoogenic Impact on the Structure and Regeneration of a Submontane Forest in Kenya.’ *In* J.G. Goldammer (ed.) *Tropical Forests in Transition*. Birkhäuser Verlag.

Schmitt, K. (1992b) ‘Anthropo-Zoogenic Impact on the Structure and Regeneration of a Submontane Forest in Kenya BT - Tropical Forests in Transition: Ecology of Natural and Anthropogenic Disturbance Processes.’ *In* Goldammer, J. G. (ed.). Basel: Birkhäuser Basel, pp. 105–126.

Schneider, A., David, V. A., Johnson, W. E., O’Brien, S. J., Barsh, G. S., Menotti-Raymond, M. and Eizirik, E. (2012) ‘How the Leopard Hides Its Spots: ASIP Mutations and Melanism in Wild Cats.’ *PLoS ONE*, 7(12).

Schneider, C. A., Rasband, W. S. and Eliceiri, K. W. (2012) ‘NIH Image to ImageJ: 25 years of image analysis.’ *Nature Methods*, 9(7) pp. 671–675.

Schneider, C. A., Rasband, W. S. and Eliceiri, K. W. (2012) ‘NIH Image to ImageJ: 25 years of image analysis.’ *Nature Methods*. Nature Research, 9(7) pp. 671–675.

Scholte, P. (2011) ‘Towards understanding large mammal population declines in Africa’s protected areas: a West-Central African perspective.’ *Tropical Conservation Science*, 4(1) pp. 1–11.

Schweiger, A. H. and Beierkuhnlein, C. (2016) ‘Size dependency in colour patterns of Western Palearctic carabids.’ *Ecography*, 39(9) pp. 846–857.

Scoon, R. (2018a) ‘Aberdare and Mount Kenya National Parks.’ *In Geology of National Parks of Central/Southern Kenya and Northern Tanzania,*. Springer International Publishing, pp. 91–101.

Scoon, R. (2018b) ‘The Gregory Rift.’ *In Geology of National Parks of Central/Southern Kenya and Northern Tanzania,*. Springer International Publishing, pp. 39–57.

Searcy, W. A. and Nowicki, R. J. (2005) ‘The Evolution of Animal Communication Relaibility and Deception in Signaling Systems.’ *BioScience*, 56(6) pp. 533–537.

Séguin, A., Harvey, É., Archambault, P., Nozais, C., Gravel, D., Naeem, S., Poisot, T., Mouquet, N., Gravel, D., Hooper, D. U., Berlow, E. L., Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., West, G. B., Woodward, G., Raffaelli, D., Solan, M., Cardillo, M., Finke, D. L., Denno, R. F., Duffy, J. E., Petchey, O. L., Ives, A. R., Cardinale, B. J., Gross, K., Cardinale, B. J., Isbel, F., Harvey, É., Séguin, A., Nozais, C., Archambault, P., Gravel, D., Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Jr, F. T., Daufresne, M., Lengfellner, K., Sommer, U., Dossena, M., Holm-Hansen, O., Lorenzen, C. J., Holmes, R. W., Strickland, J. D. H., Belzile, C., Brugel, S., Nozais, C., Gratton, Y., Demers, S., Grasshoff, K., Ehrhardt, M. and Kremling, K. (2014) 'Body size as a predictor of species loss effect on ecosystem functioning.' *Scientific Reports*. Nature Publishing Group, 4, April, pp. 1537–1552.

Silva, P. G. da and Hernández, M. I. M. (2015) 'Spatial Patterns of Movement of Dung Beetle Species in a Tropical Forest Suggest a New Trap Spacing for Dung Beetle Biodiversity Studies.' *Plos One*, 10(5) p. e0126112.

Simberloff, D. (1998) 'Flagships, umbrellas, and keystones: Is single-species management passe in the landscape era?' *Biological Conservation*, 83(3) pp. 247–257.

Slade, E. M., Kirwan, L., Bell, T., Philipson, C., Lewis, O. T. and Roslin, T. (2017) 'The importance of species identity and interactions on multifunctionality depends on how ecosystem functions are valued.' *Ecology*.

Slade, E. M., Mann, D. J. and Lewis, O. T. (2011) 'Biodiversity and ecosystem function of tropical forest dung beetles under contrasting logging regimes.' *Biological Conservation*. Elsevier Ltd, 144(1) pp. 166–174.

Slade, E. M., Mann, D. J., Villanueva, J. F. and Lewis, O. T. (2007) 'Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest.' *Journal of Animal Ecology*, 76(6) pp. 1094–1104.

Slade, E. M., Roslin, T., Santalahti, M. and Bell, T. (2016) 'Disentangling the "brown world" faecal-detritus interaction web: Dung beetle effects on soil microbial properties.' *Oikos*, 125(5).

Soliveres, S., Van Der Plas, F., Manning, P., Prati, D., Gossner, M. M., Renner, S. C., Alt, F., Arndt, H., Baumgartner, V., Binkenstein, J., Birkhofer, K., Blaser, S., Blüthgen, N., Boch, S., Böhm, S., Börschig, C., Müller, J., Oelmann, Y., Overmann, J., Pašalić, E., Rillig, M. C., Schaefer, H. M., Schloter, M., Schmitt, B., Schöning, I., Schrumpf, M., Sikorski, J., Socher, S. A., Solly, E. F., Venter, P. C., Weiner, C. N., Weisser, W. W., Werner, M., Westphal, C., Wilcke, W., Wolters, V., Wubet, T., Wurst, S., Fischer, M. and Allan, E. (2016) 'Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality.' *Nature Publishing Group*, 536.

Spector, S. and Ayzama, S. (2003) ‘Rapid Turnover and Edge Effects in Dung Beetle Assemblages (Scarabaeidae) at a Bolivian Neotropical Forest-Savanna Ecotone1.’ *Biotropica*, 35(3) pp. 394–404.

Spector, S. H. (2006) ‘Scarabaeine Dung Beetles (Coleoptera: Scarabaeidae: Scarabaeinae): An Invertebrate Focal Taxon for Biodiversity Research and Conservation.’ *The Coleopterists Bulletin*, 5 pp. 71–83.

Spehn, E. M., Rudmann-Maurer, K., Körner, C. and D., M. (2010) ‘Mountain biodiversity and global change’ p. 59.

Stanbrook, R., Raisin, C. and Vulinec, K. (2017) ‘Observations on the tunneling behavior and seed dispersal efficacy of Copris nubilosus (Kohlmann) (Coleoptera: Scarabaeinae: Coprini).’ *Coleopterists Bulletin*, (December).

Stanley, W. T. and Kihaule, P. M. (2016) ‘Elevational distribution and ecology of small mammals on Tanzania’s second highest mountain.’ *PLoS ONE*, 11(9) pp. 1–15.

Steiger, S. (2013) ‘Bigger mothers are better mothers: disentangling size-related prenatal and postnatal maternal effects.’ *Proceedings of the Royal Society B: Biological Sciences*, 280(1766) pp. 20131225–20131225.

Stevens, G. C. (1992) ‘The Elevational Gradient in Altitudinal Range : An Extension of Rapoport ’ s Latitudinal Rule to Altitude Author (s): George C . Stevens Published by : The University of Chicago Press for The American Society of Naturalists Stable URL : http://www.jstor,’ 140(6) pp. 893–911.

Stevens, M., Párraga, C. A., Cuthill, I. C., Partridge, J. C. and Troscianko, T. S. (2007) ‘Using digital photography to study animal coloration.’ *Biological Journal of the Linnean Society*. Oxford University Press, 90(2) pp. 211–237.

Stroud, J. T., Bush, M. R., Ladd, M. C., Nowicki, R. J., Shantz, A. A. and Sweatman, J. (2015) ‘Is a community still a community? Reviewing definitions of key terms in community ecology.’ *Ecology and Evolution*, 5(21).

Sutton, G., Bennett, J. and Bateman, M. (2014) ‘Effects of ivermectin residues on dung invertebrate communities in a UK farmland habitat.’ Stewart, A. and Lobo, J. M. (eds) *Insect Conservation and Diversity*, 7(1) pp. 64–72.

Tan, E. J., Reid, C. A. M., Symonds, M. R. E., Jurado-Rivera, J. A. and Elgar, M. A. (2017) 'The Role of Life-History and Ecology in the Evolution of Color Patterns in Australian Chrysomeline Beetles.' *Frontiers in Ecology and Evolution*, 5(November) pp. 1–15.

Tarasov, S. and Génier, F. (2015) 'Innovative Bayesian and Parsimony Phylogeny of Dung Beetles (Coleoptera, Scarabaeidae, Scarabaeinae) Enhanced by Ontology-Based Partitioning of Morphological Characters.' Mans, B. J. (ed.) *PLOS ONE*. Public Library of Science, 10(3) p. e0116671.

Tarasov, S. I. and Solodovnikov, A. Y. (2011) 'Phylogenetic analyses reveal reliable morphological markers to classify mega-diversity in Onthophagini dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae).' *Cladistics*, 27(5) pp. 490–528.

Taylor, S. J. (2015) 'African biodiversity hotspots and other important conservation designations for unique areas which may include mountains African biodiversity hotspots and other important conservation designations for unique areas which may include mountains' pp. 1–18.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., De Siqueira, M. F., Grainger, A. and Hannah, L. (2004) 'Extinction risk from climate change.' *Nature CN - 4859*, 427(6970) pp. 145–148.

Tilman, D. (2001) 'Functional Diversity.' *Encyclopedia of Biodiversity* pp. 587–596.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. and Siemann, E. (1997) 'The influence of functional diversity and composition on ecosystem processes.' *Science*, 277(5330) pp. 1300–1302.

Trible, W. and Kronauer, D. J. C. (2017) 'Caste development and evolution in ants: it's all about size.' *The Journal of experimental biology*. The Company of Biologists Ltd, 220(Pt 1) pp. 53–62.

True, J. R. (2003) 'Insect melanism: the molecules matter.' *Trends in Ecology and Evolution*, 18(12) pp. 640–647.

Tshikae, B. P., Davis, A. L. V and Scholtz, C. H. (2008) 'Trophic Associations of a Dung Beetle Assemblage (Scarabaeidae : Scarabaeinae) in a Woodland Savanna of Botswana.'

Ueno, A. H., Sato, Y., Tsuchida, K., Ueno, H., Sato, Y. and Tsuchida, K. (1998) 'Colour-Associated Mating Success in a Polymorphic Ladybird Beetle , Harmonia axyridis Author (s): H . Ueno , Y . Sato , K . Tsuchida Published by : British Ecological Society Stable URL :

http://www.jstor.org/stable/2390462.’ *Functional Ecology*, 12(5) pp. 757–761.

Valverde, J. P. and Schielzeth, H. (2015) ‘What triggers colour change? Effects of background colour and temperature on the development of an alpine grasshopper.’ *BMC Evolutionary Biology*. BMC Evolutionary Biology, 15(1) p. 168.

Verdú, J. R. (2011) ‘Chill tolerance variability within and among populations in the dung beetle Canthon humectus hidalgoensis along an altitudinal gradient in the mexican semiarid high plateau.’ *Journal of Arid Environments*. Elsevier Ltd, 75(2) pp. 119–124.

Verdú, J. R., Díaz, A. and Galante, E. (2004) ‘Thermoregulatory strategies in two closely related sympatric Scarabaeus species (Coleoptera: Scarabaeinae).’ *Physiological Entomology*, 29 pp. 32–38.

Vulinec, K. (2002) ‘Dung Beetle Communities and Seed Dispersal in Primary Forest and Disturbed Land in Amazonia.’ *Biotropica*, 34(2) pp. 297–309.

Vullnec, K. (2002) ‘Dung Beetle Communities and Seed Dispersal in Primary Forest and Disturbed Land in Amazonia ’,’ 4 pp. 297–309.

Wardle, D. A. and Bardgett, R. D. (2004) ‘Human-induced changes in large herbivorous mammal density: the consequences for decomposers.’ *Frontiers in Ecology and the Environment*, 2(3) pp. 145–153.

Watanabe, D., Gotoh, H., Miura, T. and Maekawa, K. (2014) ‘Social interactions affecting caste development through physiological actions in termites.’ *Frontiers in physiology*. Frontiers Media SA, 5 p. 127.

Wheeler, D. E. (1986) ‘Developmental and Physiological Determinants of Caste in Social Hymenoptera: Evolutionary Implications.’ *The American Naturalist*, 128(1) pp. 13–34.

Williams, P. H. and Haynes, R. J. (1990) ‘Influence of improved pastures and grazing animals on nutrient cycling within New Zealand soils.’ *New Zealand Journal of Ecology*, 14 pp. 49–57.

Winfree, R., Fox, J. W., Williams, N. M., Reilly, J. R. and Cariveau, D. P. (2015) ‘Abundance of common species, not species richness, drives delivery of a real-world ecosystem service.’ *Ecology Letters*, 18(7) pp. 626–635.

Wolda, H. (1987) ‘Altitude, habitat and tropical insect diversity.’ *Biological Journal of the Linnean Society*, 30(4) pp. 313–323.

Wolf, J. B. and Wade, M. J. (2009) ‘What are maternal effects (and what are they not)?’ *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1520) pp. 1107–1115.

WWF (2016) *Living planet report: risk and resilience in a new era*. *WWF International*.

Yachi, S. and Loreau, M. (1999) ‘Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis.’ *Proceedings of the National Academy of Sciences*, 96(4) pp. 1463–1468.

Yamada, D., Imura, O., Shi, K. and Shibuya, T. (2007) ‘Effect of tunneler dung beetles on cattle dung decomposition, soil nutrients and herbage growth.’ *Grassland Science*, 53 pp. 121–129.

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

Young, H. S., Mccauley, D. J., Dirzo, R. and Goheen, J. R. (2015) ‘Context-dependent effects of large wildlife declines on small mammal communities in central Kenya.’ *Ecological Society of America*, 25(2) pp. 348–360.

Zar, J. . (2010) *Biostatistical Analysis*. 5th Editio.

Zhang, Z. (2016) ‘Decision tree modeling using R.’ *Annals of Translational Medicine*, 4(15) pp. 275–275.

Zunino, M. and Halffter, G. (2007) ‘The association of Onthophagus Latreille, 1802 beetles (Coleoptera: Scarabaeinae) with vertebrate burrows and caves.’ *Elytron (Barcelona)*, 21 pp. 17–55.

Zuur, A. F., Ieno, E. N. and Smith, G. M. (2007) *Analyzing Ecological Data*. *Methods*. Springer.

8 APPENDICES

Appendix 1: A list of the mammals and the habitats in which they were detected by camera trapping in the ANP

Species		Habitat Type					
Common Name	Binomial Name	Bamboo	Bushland/Shrub	Hagenia Forest	Juniper Forest	Erica	Montane
Aardvark	*Orycteropus afer*	0	2	0	0	0	0
African bush elephant	*Loxodonta africana*	3	106	5	12	1	0
Black rhino	*Diceros bicornis*	0	4	0	2	0	6
Bushbuck	*Tragelaphus sylvaticus*	0	19	1	0	0	0
Black fronted duiker	*Cephalophus nigrifrons*	10	59	91	26	6	9
Cape buffalo	*Syncerus caffer*	23	294	49	142	0	5
Cape hare	*Lepus capensis*	0	4	1	2	1	0
Colobus guereza		0	0	3	0	0	9
Common duiker	*Sylvicapra grimmia*	0	0	24	14	11	0
Common warthog	*Phacochoerus africanus*	0	57	3	39	0	0
Crested porcupine	*Hystrix cristata*	0	3	0	0	0	0
Defassa waterbuck	*Kobus ellipsiprymnus defassa*	0	26	2	9	1	0

Giant forest hog	*Hylchoerus meinertzhageni*	16	76	12	46	0	0
Harvey's Duiker	*Cephalophus herveyi*	20	4	0	1	0	0
Honey Badger	*Mellivora capensis*	0	1	0	0	0	0
Jackson's mongoose	*Bdeogale jacksoni*	0	1	0	0	0	0
Large-spotted genet	*Genetta maculata*	5	4	0	6	0	0
Leopard	*Panthera pardus*	0	4	1	9	0	0
Mountain bongo	*Tragelaphus eurycerus isaaci*	0	1	0	0	0	0
Olive baboon	*Papio anubis*	3	58	0	46	0	0
Rat	*Ratus*	0	0	0	0	0	0
Serval	*Leptailurus serval*	0	0	0	0	0	0
Slender Mongoose	*Galerella sanguinea*	0	4	5	0	0	0
Spotted hyena	*Crocuta crocuta*	2	161	8	39	0	0
Suni	*Neotragus moschatus*	45	22	13	15	0	2
Sykes' monkey	*Cercopithecus albogularis*	2	0	14	0	0	1
Tree hyrax	*Dendrohyrax arboreus*	0	0	0	0	0	0
White-tailed mongoose	*Ichneumia albicauda*	0	1	1	5	0	0

Zorilla	*Ictonyx striatus*	0	0	0	1	0	0

Appendix 2: A list of the dung beetles of the AnP and the habitats in which they were found.

Binomial Name	Bamboo	Bushland/ Shrub	Hagenia Forest	Juniper Forest	Podocarpus Forest	Ericaceous
Caccobius n.sp	1	2	15	173	67	0
Catharsius gibbicollis	0	106	1	2	0	0
Catharsius sestrostris	0	4	0	2	3	0
Copris atropolitus	0	19	0	0	1	0
Copris morphaeus	0	59	22	30	25	0
Copris algol	0	294	26	44	31	0
Copris typhoeus	0	4	0	5	4	0
Diastellopalpus johnstoni	0	0	13	19	21	0
Epidrepanus kenyensis	0	0	0	4	2	0
Euoniticellus intermedius	0	57	0	4	0	0
Heliocopris hunteri	0	3	77	116	45	0
Heliocopris neptunus	0	26	0	2	0	0
Heliocopris stroehli	0	76	0	1	0	0
Hetronitis ragazzii	0	4	0	2	0	0
Ixodina abysinnicus	0	1	0	5	2	0

Liatongus arrowi	0	1	2	6	0	0
Milichus picticollis	0	4	35	74	35	0
Neocolobopterus kivuanus	2	4	0	444	89	0
Neocolobopterus sengelensis	32	1	379	287	259	126
Oniticellus planatus	0	58	11	103	46	32
Onitis anthracinus	0	0	3	105	39	0
Onitis meyeri	0	0	0	30	37	0
Onitis parvulus	0	4	49	75	38	0
Onthophagis nigriventis	0	161	9	63	46	0
Onthophagus proteus	3	22	22	30	13	142
Onthophagus dohertyi	111	0	21	308	204	3
Onthophagus filicornis	26	0	3	143	61	111
Onthophagus fimetarius	29	1	51	46	0	26
Onthophagus miricornis	1	17	0	22	8	29
Onthophagus sp1	99	12	61	102	8	1
Onthophagus spurcatus	9	22	55	446	235	1
Proagoderus sexcornutus	0	0	165	297	129	9

Sisyphus sp.	0	5	0	0	0	0

Heliocopris stroehli

Heliocopris neptunus

Heliocopris
hunteri

Catharsius gibbicollis

Catharsius sesostris gp

Heteronitis ragazzii

Appendix 3

Diastellopalpus johnstoni

Copris algol

Copris morphaeus

Copris atropolitus

Copris typhoeus

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Onitis anthracinus

Onitis meyeri

Milichus picticollis

Ixodina abyssinica

Epidrepanus kenyensis n.sp

Liatongus arrowi

Euoniticellus intermedius

Oniticellus planatus

Proagoderus sexcornutus

Sisyphus sp.

Onthophagus fimetarius

Onthophagus dochertyi

Onthophagus miricornis

Onthophagus nigriventris

Onthophagus filicornis

Onthophagus sp.1

Onthophagus proteus

Caccobius n sp.

Onthophagus spurcatus

Appendix 4. Differences between colour morphs and morphometrics, sex and altitude band

ColourMorph	Sex	Total Body length mean ± SD (mm)					Total Pronotum length mean ± SD (mm)					Total Elytral length mean ± SD (mm)				
		Alt1	Alt2	Alt3	Alt4	Alt5	Alt1	Alt2	Alt3	Alt4	Alt5	Alt1	Alt2	Alt3	Alt4	Alt5
BrownGreen	Male	11728.5± 1527.5	9823.3 ±1109.7	-	-	-	3995.4± 442.5	3870.0± 271.9	-	-	-	4134.0± 397.8	3556.5± 647.8			
	Female	9499.5± 1417.5	10728.9± 1633.9	-	-	-	3604.4± 375.3	3832.8 ±468.9	-	-	-	3456.8± 620.4	3817.1± 596.9			
	Mann Whitney test	W=168 P=0.26					W= P=					W=171 P=0.29				
BrownBrown	Male	-	9442.4± NaN	11188.3± 1288.6	11852.1± 679.4	-		3679.5± 258.7	3663.8± 687.3	3554.0±			3937.2± 278.2	3654.5± 486.9	3953.6± 570.4	
	Female	-	10739.± 1288.3	10277.2± 1749.0	-	-		4255.1± 774.9	4794.3± 799.5	4258.9± 382.2			3841.7± 544.4			
	Mann Whitney test	W=58 P=0.45					W=29 P=0.01					W=55 P0.36				
GreenBlack	Male	-	-	12593.8± NaN	9056.5± 0.0	-			3973.630 NaN	3871.490 0.0000				4326.0± NaN	3637.2± 39.3	
	Female	-	11373.3± NaN	9754.5± 1568.4	-	-		4057.8± NaN	3513.264 585.1116				3413.500 ±NaN	3640.7± 567.0		
	Mann Whitney test	W=14 P=1					W=9 P=0.45					W=14 P=1				
BrownBlack	Male	-	-	12791.3± 1544.6	13058.8± 0.067	11957.8± 952.7			4384.9± 806.7	3842.9± NaN	4314.5± 511.5			4177.8± 658.3	3974.0± NaN	4207.7± 515.8