DIVERSITY AND ABUNDANCE OF DUNG BEETLES ACROSS DIFFERENT LAND USE TYPES AND THEIR ROLE IN SOIL FERTILITY IMPROVEMENT IN KENYA

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DECLARATION

This thesis is my original work and has not been presented for academic award in any other academic institution.

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DEDICATION

I dedicate this work to my late Dad, Charles Gachunu. Your advice and prayers shaped my academic life. May your soul rest in eternal peace.

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LIST OF ABBREVIATIONS

AEZ – Agro-Ecological Zones

C – Carbon

K - Potassium

LSD – Least significant difference

LH3 – Lower highland zone 3

LUT – Land Utilization Types

N – Nitrogen

P – Phosphorus

P – Probability

RDA – Redundancy analysis

S.E.D – Standard error of means

SSA – Sub-Saharan Africa

SOC – Soil organic carbon

TN – total nitrogen

TOC – Total organic carbon

UM3 – Upper midland zone 3

LARMAT – Department of Land Resource Management and Agricultural Technology

NICHE – Netherlands Initiative for Capacity Building in Higher Education

UoE – University of Eldoret

ABSTRACT

Dung beetles are crucial in livestock systems due to their contribution to dung removal, nutrients cycling and sustainable pasture production. There are limited studies to elucidate biodiversity and species-specific contribution of dung beetles to ecosystem services in Kenya. This study aimed at evaluating abundance of soil macrofauna and soil chemical properties across selected land-use types (LUTs), effect of LUTs and seasons on abundance and diversity of dung beetles and finally assessing effect of dung beetle species and dung type on dung removal and chemical quality of relocated dung balls. This information would be critical for conservation and utilization of dung beetles in the study sites. A survey on soil macrofauna was done using eight monoliths per each of the selected LUTs in Kabete and Chepkoilel sites located in Kiambu and Uasin Gishu Counties, respectively. Sampling of dung beetles was done using 10 cattle-dung baited pitfall traps per each LUT. Role of dung beetles on soil fertility was conducted through a terrarium experiment comprising of six treatments arranged in completely randomized design (CRD). Redundancy analysis (RDA) was carried out to correlate soil chemical properties with abundance of macrofauna. Analysis of variance (ANOVA) was undertaken to determine the effect of LUTs and season on the abundance and diversity of dung beetles. Abundance of termites, earthworms, ants, beetles and millipedes differed significantly across LUTs ($p < 0.05$) in both sites. Termites, beetles, spiders and centipedes were positively correlated with total N, organic C, pH, available P and exchangeable K along axis 2 in Kabete soils. All macrofauna groups were positively correlated with organic C, total N and pH, but negatively with exchangeable K and available P along axis 2 in Chepkoilel soils. Land use type and Season significantly affected the abundance and diversity of coprophagous beetles ($p < 0.001$). They were significantly higher during the wet season and in LUTs under frequent gazing influence. Grazed pasturelands in Kabete and Chepkoilel had significantly highest abundance of dung beetles of 27.3 and 18.5, respectively ($p < 0.001$). In Kabete, grazed and non-grazed pasturelands had the highest species richness of 6.2 and 6.5, respectively ($p < 0.001$) while in Chepkoilel, it was significantly highest in grazed pasturelands, wattle plantation and mixed woodland (4.9, 4.4 and 4.3, respectively) at $p < 0.001$. Type of animal fecal material and species of coprophagous beetle significantly influenced the amount and rate of dung removal ($p < 0.001$). *Euoniticellus triangulatu*s removed cattle dung at significantly faster rate of 13.04 g g^{-1} day^{-1} compared to *Milichus picticollis* which buried dung at the rate of 1.4 g g^{-1} day^{-1}($p < 0.001$). Relocated dung balls contained significantly lesser amounts of N, C, K and P than the original dung at $p \leq 0.001$. *E. triangulatus* is more efficient in relocating animal dung with significantly higher contents of N, P and K than *M. picticollis* ($p < 0.001$). In conclusion, *E. triangulatus* should be introduced into grazed pasturelands to enhance pasture production and dung removal.

CHAPTER ONE

1.0 INTRODUCTION

1.1 Background information

Dung beetles, also referred to as coprophagous beetles, belong to the taxonomic order Coleoptera, mainly from the Scarabaenae and Aphodiinae subfamilies of the Scarabaeidae family. The adults have specialized mouth parts for feeding on the liquid part of animal excreta. They dominate tropical ecosystems where they feed mainly on dung from large herbivores (Nichols *et al*., 2008; Sewak, 2009; Campos and Hernandez, 2013; Hanski and Camberfort, 2014).

Dung beetles are grouped into three functional guilds (rollers/telecoprids, dwellers/endocoprids and tunnelers/paracoprids) which determine extent of ecosystem services on their habitat (Nichols *et al*., 2008). Dwellers burrow into fresh dung, feed and breed within it without creating nests. Tunnelers create tunnels directly below the dung pats where they burry dung and use it for brooding and the rollers create a ball of dung that they roll and burry away from the dung pat (Nichols *et al*., 2008; Hanski and Camberfort, 2014). Dung beetles contribute to nutrients cycling and redistribution thus enhances soil aeration and porosity, seed dispersal, breakdown of animal excreta and suppress livestock parasites (Brown *et al*., 2010). Through their activities, dung beetles improve productivity of grazed pasturelands (Nichols *et al*., 2008; Arnaudin, 2012). Thus, introduction of aggressive and versatile species, especially the tunnelers into grazed pasturelands, would ensure sustainability in pasture production and enhanced food security. For these reasons, there is need to undertake species-specific research on the quantitative contribution of dung beetles (especially the tunnelers) to soil fertility and productivity of grazed pastures.

Dung beetles are good indicators of environmental changes that arise from anthropogenic disturbances because they inhabit a wide range of habitats such as forests and pasturelands

(Kessler *et al*., 2011; Braga *et al*., 2013; Barnes *et al*., 2014; Shahabuddin *et al*., 2014). Similarly, community attributes such as diversity and abundance can be inventorized using standard methods (Larsen and Forsyth, 2005; Van-de-Mello *et al*., 2011). Utilization of dung beetles species as bio-indicators is hinged on their specificity and fidelity with types of habitats and their contribution to ecological services such as improving the soil chemical, physical and biological properties such as soil organic carbon, total nitrogen (N) and available phosphorus(P) (Keino *et al*., 2015; Shahabuddin *et al*., 2014; Njoroge *et al*., 2018). Studies have been conducted on numerous attributes of dung beetles across various regions such as USA (Meaghan, 2007; Evans, 2016; Wagner, 2016), Nigeria (Barnes *et al*., 2014), Brazil (Andrade *et al*., 2011; Braga *et al*., 2013, Campos and Hernandez, 2013; Silva and Hernandez, 2015), France (Tixier *et al*., 2015), Indonesia (Shahabuddin *et al*., 2014) and Malaysia (Goh, 2014). However only a few of these studies such as Braga *et al*. (2013) have focused on community attributes across land use types (LUTs).

1.2 Statement of the problem and justification of study

Research elucidating the community attributes of dung beetles across LUTs as well as their role in nutrient cycling is limited in Kenya. Lack of such information limits the understanding of the diversity of dung beetles, their contribution to soil fertility and carbon sequestration. This also limits development of appropriate technologies for utilization of dung beetles especially in compost production, soil fertility improvement and as indicator of status of land resource.

Utilization of efficient dung beetles in dung relocation can reduce soil erosion by increasing water infiltration rates, improve soil fertility through nutrients cycling and carbon sequestration, reduce waste on pasturelands and mitigate greenhouse gases and nitrogen losses thus improving the quantity and quality of pastures (Bertone *at al*., 2006; Shahabuddin *et al*., 2008; Brown *et al*., 2010; Nervo *et al*., 2014; Slade *et al*., 2016).

Quantitative research on the contribution of coprophagous beetles to ecosystem services is necessary, especially with the current global demand to promote sustainable production systems and reducing emission of greenhouse gases for enhanced food security. However, such studies have been neglected within the sub-Saharan Africa (SSA) region. The lack of such critical information limits our understanding on the actual contribution of dung beetles in various ecosystems, their utilization as biological indicators of soil quality (Doran and Zeiss, 2000) and environmental changes across LUT gradients (Shahabuddin *et al*., 2014) especially in the SSA. Sub-Saharan Africa is dominated by soil degradation caused by human induced disturbances such as overgrazing, deforestation and over cultivation without replenishment of nutrients and organic matter (Sanginga and Woomer, 2009; Tully *et al*., 2015).

Thus, elucidating species-specific contribution of dung beetles to soil fertility, their abundance and diversity as affected by LUTs would contribute toward their conservation in agricultural systems.

1.3 Broad objective

To evaluate the abundance and diversity of dung beetles across different land use types and their role in soil fertility improvement in Kabete and Chepkoilel soils.

1.4 Specific objectives

1. To determine (a) soil chemical properties and abundance of soil macrofauna groups across land use types, (b) the correlation of soil macrofauna groups with soil chemical properties.
2. To determine the effect of different land use types and seasons on diversity and abundance of dung beetles.
3. To evaluate the effect of selected species of dung beetles and animal fecal materials on dung burial and chemical composition of buried dung balls.

1.5 Hypotheses

1) Abundance of soil macrofauna groups is similar across land use types and is not correlated with soil chemical parameters.
2) Land use types have no effect on the abundance and diversity of dung beetles.
3) Species and type of animal fecal material have no effect on the rate of dung burial and chemical composition of dung balls.

CHAPTER TWO

2.0 LITERATURE REVIEW

2.1 Soil macrofauna diversity and their roles in ecosystem services

Soil macrofauna refers to organisms visible to the naked eyes. Majority of these organisms have their body width equal to or more than 2 mm (Brown *et al*., 2001) and are part of soil arthropods which represent about 85 % of the total soil fauna (Bagyaraj *et al*., 2016). They dominate the upper 0 - 20 cm layer of the soil (Marchao *et al*., 2009). They have been classified into anecic, endogeic and epigeic depending on their location in the soil (Lavelle *et al*., 1994).

Soil macrofauna are very diverse and include but not limited to termites (Isopteran), centipedes (Chilopoda), earwigs (Dermaptera), crickets (Orthoptera), snails and slugs (Ara), scorpions (Scorpiones), true bugs and cicads (Hemiptera), millipedes (Diplopoda), ants (Hymenoptera), spiders (Arachnida), beetles (Coleoptera), earthworms (Oligochaeta), pot-worms (Oligochaeta), moth larvae (Lepidoptera), fly larvae (Lepidoptera), ant-lions, cockroaches (Blattodea), mermithid nematode (Mermithida), diplura (Diplura) and silver-fishes (Zygentoma) (Brown *et al*., 2001; Marchao *et al*., 2009; Bagyaraj *et al*., 2016).

Soil macrofauna contribute to various ecosystem services such as improvement of soil structure besides aeration, mixing of organic residue into the soil, decomposition of organic residue, mineralization of nutrients, and control of pathogens (Lavelle *et al*., 1994; Ruiz *et al*., 2008; Bagyaraj *et al*., 2016).Termites in particular, play critical role not only in decomposition of litter and dung materials, but also of materials high in lignin content such as wood (Freymann *et al*., 2008; Bagyaraj *et al*., 2016).

Based on the above ecological functions, soil macrofauna can be classified into soil engineers, chemical engineers and biological regulators (Bagyaraj *et al*., 2016). For a long time, ants, termites and earthworms are key soil engineers due to their contribution to decomposition of organic matter (by direct feeding, mixing and burial), improvement of soil structure as well as aeration (Ayuke, 2010; Bottinelli *et al*., 2015; Hirmas and Cooper, 2016). However, other macrofauna such as dung beetles could equally be classified as soil engineers besides being biological regulators, since they control dung flies and contribute to soil aeration and decomposition of animal fecal materials (Brown *et al*., 2010; Nervo *et al*., 2014). Such soil macrofauna contribute to the resilience of the soil ecosystem against degradation by improving the soil structure, porosity and organic carbon (Stork and Eggleton, 1992; Swift and Bignell, 2001; Bhadauria and Saxena, 2010; Cullinery, 2013). Hence, they contribute directly and indirectly to a sustainable ecosystem where animals and other organisms satisfactorily meet their food resources requirements.

Several factors affect the diversity, abundance and activities of soil macrofauna. These include land use practices (Lavelle *et al*., 1994; Barros *et al*., 2002; Siqueira *et al*., 2014), soil moisture (Jiang *et al*., 2015; Walmsey and Cerda, 2017), soil pollution such as heavy metals (Nahmani and Lavelle, 2002), fertilization (Jiang *et al*., 2015), litter quality (Warren and Zou, 2002; Marchao *et al*., 2009; Sayad *et al*., 2012), vegetation cover and composition (Kamau *et al*., 2017), and soil management practices such as addition of organic matter and conservation tillage (Brown *et al*., 2001; Marchao *etal*., 2009; Ayuke, 2010; Mutema *et al*., 2013;Manyanga *et al*., 2014; Walmsey and Cerda, 2017).

Complementarity of soil macrofauna in accelerating decomposition of mammalian dung resources is critical in maximizing the above ecological services (Lee and Wall, 2006; Bagyaraj *et al*., 2016). In addition, they are essential bio-indicators of soil health. Enumerating their abundance and diversity is important in understanding the likelihood of such complementarity, their utilization as bio-indicators and developing management plans for their conservation. This study enumerated the abundance of soil macrofauna (other than dung beetles) across several LUTs and its correlation to soil chemical properties.

2.2 Ecology of dung beetles

Dung beetles can be classified based on their utilization of dung resources or time of their activities. Generally, they are classified into rollers, dwellers and tunnelers depending on how they use the fiber part of the invertebrate dung for breeding (Nichols *et al*., 2008; Hanski and Camberfort, 2014). Rollers and tunnelers burry the brooding balls into the soil where they lay eggs that hatch into larvae. The dwellers feed and breed within the dung pat. However, despite these nesting behaviors, all adult dung beetles are attracted to fresh animal dung by its smell and they feed fluid part. The larvae chew the dung in their natal brood balls using their biting jaws even though, they use symbionts to obtain nutrients from the dung (Scholtz *et al*., 2009; Byrne *et al*., 2013; Hanski and Camberfort, 2014).

Dwellers mainly comprise of Aphodiinae subfamily, *Aphodius* genus, which are relatively small in size, being less than 10 mm in length. They burrow into fresh dung, feed and breed within it without creating nests. Competition for food is high among the dwellers since they feed on the dung *in situ* (Lee and Wall, 2006; Hanski and Camberfort, 2014). However, in some literature, a few of the Aphodiinae species such as *Aphodius sp*. and *Aphodius quadratus* Reiche have been classified as paracoprids (Yamada *et al*., 2007; Shahabuddin *et al*., 2008).

Tunnelers form majority of the dung beetles (Gardner *et al*., 2008; Campos and Hernandez, 2013). They create nests directly below the dung pats and in the process, relocate the animal excreta into the nests, using the fiber part of it to create brooding balls where they lay eggs inside. Although some feed directly from the dung pat, others feed on dung relocated to the nests. The larvae, by being enclosed in the brood balls within the nests, are protected from adverse weather conditions and competition for resources. However, adults compete for food and space. The sizes of tunnelers range from about 13 mm to < 10 mm (Hanski and

Camberfort, 2014). Plate 1 and 2 shows *Onthophagus taurus* and *Aphodius lividus,* which are tunneler species.

Plate 1: *Onthophagus taurus* (Source: Double and Dalton, 2003)

Plate 2: *Aphodius lividus* (Source: Double and Dalton, 2003)

Finally, rollers create a ball of dung that they roll and burry away from the dung pat. They are usually large being > 10 mm in length. Relocating the dung balls away from the dung pat reduces competition for space and food with other beetles (Hanski and Camberfort, 2014). Some of the rollers are from Coprinae subfamily, Sisyphus genus and Scarabaenae subfamily (Sewak, 2009).

All the above functional groups undergo four growth stages. These are egg, larval, pupate and adult. Larvae of rollers and tunnelers spend their entire lifespan in the soil system (Scholtz *et al*., 2009).

2.3 Factors influencing diversity and abundance of dung beetles

Abundance and diversity of coprophagous beetles is influenced by soil moisture, land use types, soil moisture, seasons, availability of dung resources and habitat disturbances (Andrade *et al*., 2011; Braga *et al*., 2013; Shahabuddin *et al*., 2014; Wagner, 2016).

Preference of dung beetles to specific habitats depends on the species type since different species have specific microclimate requirements (Barbero *et al*., 1999). Some species prefer cooler and shaded habitats (Shahabuddin *et al*., 2014). This is partly attributed to animal dung remaining moist for a longer period compared to open grounds, less light intensity, lower temperatures and higher humidity in such habitats (Escobar, 2004; Horgan, 2005). Undisturbed and closed habitats such as primary forests have significantly higher abundance as compared to agricultural fields and pasturelands which are open, under the influence of man and livestock and exposed to higher light intensity (Escobar, 2004; Braga *et al*., 2013). However, some species such as *Onthophagus trituber* and *Onthophagus limbatus* prefer unshaded and warmer habitats (Shahabuddin *et al*., 2014). Riparian reserves have been found to have significantly higher diversity, abundance and functional group richness of dung beetles than oil palm plantation (Gray *et al*., 2014).Dry grassland has been reported to favour high species richness with increasing dung density (Treitler *et al*., 2017). Escobar (2004) reported high abundance of nocturnal tunnelers in primary and secondary forests, and more tunnelers in pastureland and cropland.

Habitat disturbances affect assemblage of dung beetles, especially the large ones (> 10 mm) (Escobar, 2004). Disturbances include cultivation of cereals, cash crops or pasture and tree planting or grazing (Martello *et al*., 2016; Wagner, 2016). Habitat loss exposes dung beetles to unfavorable conditions such as increased temperatures and light intensity which could affect the abundance of nocturnal species (Escobar, 2004). Pastureland has been observed to have higher abundance of dung beetles than eucalyptus and sugar cane plantation (Martello *et al*., 2016).

Dung resources and its moisture content strongly influence the abundance of dung beetles. Animal fecal materials are the main feed material for both adult and larvae. In addition, it is used in brooding by the tunnelers and rollers (Hanski and Camberfort, 2014; Wagner, 2016). The animal dung must be moist for it to attract more dung beetles (Errouissi *et al*., 2004; Horgan, 2005). However, high accumulation of donkey and horse fecal materials in pastures reduces the abundance and diversity of coprophagous beetles. High temperatures in the dung-pad negatively affect dwellers (Treitler *et al*., 2017). Despite this, dung beetles exhibit strong preference for the type of dung, with majority preferring herbivore to carnivorous dung (Barbero *et al*., 1999) and omnivorous to carnivorous dung (Whipple, 2011). This notwithstanding, some dung beetles can feed on carrion such as millipedes (Krell, 2004).

Precipitation strongly influences the abundance and diversity of dung beetles (Liberal *et al*., 2011). Wet seasons have higher abundance and diversity compared to the dry one as shown by Andrade *et al*. (2011), Liberal *et al*. (2011) and Novais *et al*. (2016). Most adult dung beetles emerge at the beginning of the wet season in synchronization between their life cycle and the environmental conditions as affected by seasons (Novais *et al*., 2016). High solar radiation and soil moisture stress which characterizes the dry season limits growth and development of coprophagous beetles by affecting availability of dung resources.

The larval stage of dung beetles is intolerant to waterlogged soil (Osberg *et al*., 1994). Water content above 20 % has indeed been reported to cause high larval mortality rate of the larvae (Brussaard and Slager, 1986).

Sampling time influence the capture of either nocturnal or diurnal dung beetles. To capture only diurnal dung beetles, the traps have to be set up at dawn and sampling done at dusk (Andresen, 2002). Thus to ensure that both nocturnal and diurnal dung beetles are captured, it is necessary to expose the baited pitfall traps to both day and night conditions before collection(Hernandez, 2002).

2.4 Ecosystem functions and services of dung beetles

Depletion of soil organic carbon and deficiency of N and P are among the main factors bedeviling crop and pasture production in SSA including Kenya (Sanginga and Woomer, 2009; Keino *et al*., 2015; Njoroge *et al*., 2018).

Dung beetles contribute to nutrients cycling by enhancing animal dung decomposition both directly and indirectly. Among the soil nutrients so far reported to improve due to dung beetle activities include phosphorus, calcium, magnesium, potassium and nitrogen (Bertone *et al*., 2006; Yamada *et al*., 2007; Shahabuddin *et al*., 2008). However, Arnaudin (2012) did not find any significant contribution of dung beetles (*Onthophagus taurus*) to the above nutrients. This could have been contributed partly by the choice of species besides the type of dung used in the experiment (Alpaca dung). Bertone *et al*. (2006) reported *Onthophagus gazella* being superior to *Onthophagus taurus* in improving the soil nutrients. Yamada *et al*. (2007) reported an increased amount of N, but no conclusive contribution of dung beetles to soil available P and K.

Depletion of soil carbon causes loss of ecosystem resilience resulting to land degradation (Fairhurst, 2012; Feller *et al*., 2012). Dung beetles could contribute to improvement of soil organic carbon in grazed pastureland by burying dung. Unfortunately, despite the postulation of scarab beetle larvae improving SOC (Feller *et al*., 2012), there is no quantitative scientific evidence to support this. Their contribution to this soil chemical aspect is paramount in enhancing resilience of grazed pasturelands to degradation.

Quality of the animal dung affects rate of their decomposition and subsequent nutrients release. Organic materials containing C:N ratio of < 16 or 2.5 % N have been found to promote above two processes (Fairhurst, 2012). Thus, despite the dung beetles relocating animal dung regardless of its quality, the latter will determine how fast decomposition process and hence nutrients release will take.

Tunneling (tunnelers and rollers) coprophagous beetles contribute to soil aeration and porosity through burrowing into the soil as they relocate dung (Nichols *et al*., 2008; Brown *et al*., 2010). This is beneficial since it improves production of pastures and decomposition of organic matter through enhanced aeration (Bang*et al*., 2005). Tunnelers by virtue of being the most abundant dung beetles and their burrowing behavior (Yamada *et al*., 2007; Campos and Hernandez, 2013; Hanski and Camberfort, 2014), contribute more to nutrients cycling, soil aeration and porosity compared to the dwellers and rollers (Nichols *et al*., 2008).

In most studies highlighted above, the ecological contribution of coprophagous beetles to soil chemical properties were determined in controlled environments such as greenhouse (Shahabuddin *et al*., 2008) and laboratory (Bertone *et al*., 2006).

Dung beetles compete with pestiferous flies such as *H. irritans irritans* for dung resources reducing their abundance. Controlling the population of these flies is economically important since they reduce livestock productivity and quality of hide (Nichols *et al*., 2008; Sewak, 2009). However, other factors linked to land use influence the populations of detritus-feeding insects (Braga *et al*., 2012). Unfortunately, they may also serve as intermediate hosts for numerous dung-borne parasites of domestic animals such as nematodes and worms. They have been identified as intermediate hosts of *Ascarops strongylina* and *Gongylonema verrucosum* worms which are swine parasites and *Streptopharagus pigmentatus* and *Physocephalus sexalatus* (a nematode parasite). Some of these parasites such as *Physocephalus sexalatus* reduce the efficiency of dung beetles in burying animal dung (Nichols *et al*., 2008; Boze, 2012; Boze and Moore, 2014).

Finally, coprophagous beetles contribute to secondary seed dispersal during relocation of dung. This is mainly contributed by tunnelers and rollers when relocating animal fecal materials containing seeds either into the soil or away from the dung pat (Nichols *et al*., 2008; Braga *et al*., 2013). However, these studies on coprophagous beetles as secondary seed dispersal agents are based on simulations.

The contribution of dung beetles to above the ecological functions is a function of their body size, abundance, moisture content and type of the dung, nesting behavior/functional role, biomass and diversity (Nichols *et al.*, 2008; Shahabuddin *et al.*, 2008; Campos and Hernandez, 2013; Barnes *et al*., 2014; Nervo *et al*., 2014; Tixier *et al*., 2015).

The body size of dung beetles has stronger effects on dung burial, the precursor to nutrients cycling, than biomass. Larger beetles (> 10 mm) such as *Copris Saundersi* contribute more to nutrients cycling than the smaller species (< 10 mm) such as *Onthophagus limbatus* and *Aphodius sp* (Nichols *et al*., 2008; Shahabuddin *et al*., 2008).

The abundance of the beetles either small or large ones influence the amount of dung buried (Yamada *et al*., 2007; Braga *et al*., 2013; Tixier *et al*., 2015). Generally, the higher the abundance of large beetles (> 10 mm), the greater their contribution to dung burial, decomposition and hence soil fertility improvement (Braga *et al*., 2013). Unfortunately, such large beetles are sensitive to perturbations and hence proper conservation measures should be addressed to ensure their critical ecological benefits are not lost (Nervo *et al*., 2014).

Versatile and robust dung beetles could be introduced into grazed pasturelands or utilized in composting animal dung. This is critical in addressing the issues of nutrients depletion and loss of ecosystem resilience by enhancing decomposition of cattle dung. They do not require intense care during rearing besides being tolerant to adverse conditions. Thus, they offer a cheaper alternative to earthworms which require to be raised in vermiculture beds before introduction into agricultural systems (Sanginga and Woomer, 2009).

2.4.1 Quantification of the roles of dung beetles in nutrients cycling, dung removal and decomposition

The amount of dung removed, decomposed or nutrients added into the soil by dung beetles is dependent on their functional guilds (Nichols *et al*., 2008). Only tunnelers and rollers contribute to dung removal/burial. They make dung brooding balls which are buried into the soil. This mechanism makes quantification of dung beetles (rollers and tunnelers) effects on soil fertility unique from other soil macrofauna. Dwellers, although may contribute to decomposition of animal dung, they do not contribute to dung burial. The amount of dung removed through dung beetles activities could be quantified using the "*weight loss*" method used by Shahabuddin *et al*. (2008) and Braga *et al*. (2013).

2.5 Characterization of soils and animal dung

Soil samples must be sampled and prepared appropriately before analysis. During preparation, contamination between samples must be controlled by cleaning apparatus and equipment using ethanol and clean cotton wool. Particle sizes are critical in any analytical procedure. When analyzing soil samples for N and OC content, particles of ≤ 0.25 mm sieve are required to increase the surface area for chemical oxidation. On the other hand, particles of ≤ 2 mm are required when analyzing for available P, texture, cations and pH. Dung balls are ground and sieved through ≤ 0.25 mm sieve before analyzing for their nutrients content (Okalebo *et al*., 2002).

2.6 Opportunities for utilization of dung beetles

Ecological services of coprophagous beetles could be exploited in various circumstances. Robust and aggressive species could be introduced into grazed pasturelands to enhance sustainable pasture production (Bang *et al*., 2005; Yamada *et al*., 2007; Arnaudin, 2012) and improving their resilience against degradation, bio-indicators of anthropogenic activities and soil quality (Shahabuddin *et al*., 2014), control of dung borne parasites (Sewak, 2009), control of greenhouse gases emission from grazed pasturelands (Slade *et al*., 2016), composting of animal dung and finally in incorporation of slurry into the soil.

In order to realize this, there is need to enumerate the diversity and abundance of coprophagous beetles across different land use types, agro ecological zones and seasons (Doran and Zeiss, 2000; Pankihurst *et al*., 1997; Kessler *et al*., 2011; Shahabuddin *et al*., 2014; Muhaimin *et al*., 2015), besides species-specific contributions to soil total N, organic carbon and available P.

In Brazil, *Euoniticellus intermedius* is more effective in translocating dung into the soil than the native dung beetles. It is postulated that this species has a robust immune system due to its microbe-rich habitat (Khanyile *et al*., 2008).

2.7 Other macrofauna colonizing animal dung

The ecological services offered by the dung beetles could also be mediated by other macrofauna that feed on cattle dung. Some of these organisms include non-dung beetles, flies, termites and mites among others (Freymann *et al*., 2008; Scholtz *et al*., 2009; O'Hea *et al*., 2010). Termites have been indicated as most efficient macrofauna in the dry regions in facilitating degradation of organic matter especially the woody materials (Nichols *et al*., 2008). The macrofauna increase competition for the fresh dung resources. However, upon drying of dung, some macrofauna such as termites could take prominence in degrading the resource due to their diverse mode of feeding dependent on their functional guilds (Genet *et al*., 2001; Freymann *et al*., 2008; Jones, 1990).

2.8 Protocol for sampling dung beetles

Three methods are available for sampling dung beetles. These include baited pitfall traps, dung pat simulation and unbaited flight intercept traps (Larsen and Forsyth, 2005; Krell, 2007; Andrade *et al*., 2011). Baited pitfall traps are the most famous traps. Several baits have been used such as fresh dung from herbivores, omnivorous animals such as human beings, chimpanzees, and pigs to carrion and rotten fruits (Braga *et al*., 2013; Shahabuddin *et al*., 2014; Tissiani *et al*., 2014; Silva and Hernandez, 2015; Wagner, 2016).

Despite human feces being recommended as the most attractive bait (Silva and Hernandez, 2015; Correa *et al*., 2016), fresh cattle dung have been used efficiently in attracting dung beetles (Meaghan, 2007; Shahabuddin *et al*., 2014). In Brazil, human excreta have been reported to be more efficient, than cattle dung and carrion, in capturing generalist dung beetles (Correa *et al*., 2016). Fresh cattle dung is more hygienic and convenient to handle besides being readily available compared to human feces when required in large quantities. The latter needs to be suspended in a net over the pitfall trap containing a liquid such as detergent, which might be laborious when dealing with many traps and hence increase the survey cost. Use of detergent in the collection-traps, does not enable collection of live beetles. Use of untreated human excreta exposes human beings to bacterial, viral, helminth and protozoa infections. Bacterial and viral infections may lead to outbreak of diarrhea, typhoid and cholera (WHO, 2016). On the other side, carrion produces foul smell as they decompose which reduces their efficiency (Flechtmann *et al*., 2009).

The attractiveness of fecal matter from pigs, human beings and cattle can last for 48 h which reduces the frequencies of replacing the bait (Flechtmann *et al*., 2009; Silva and Hernandez, 2015). Amount of bait should be uniform across all the traps. This is because bait size affects the number of individual dung beetles and species captured (Andresen, 2002). Several bait sizes have been used depending on bait type. For example, 20 to 25 g of fresh human fecal bait have been used in several researches (Larsen and Forsyth, 2005; Braga *et al*., 2013; Silva and Hernandez, 2015) while cattle dung has ranged from 5 – 50 g (Andresen, 2002; Shahabuddin *et al*., 2014). However, the bait size used depends on the evaporation rates in the study area and its moisture content.

Various trap spacing has been recommended to avoid trap interferences. These range from 25 m to 50 m for areas with 500 m length (Larsen and Forsyth, 2005), to 100 m for areas with 1000 m length (Silva and Hernandez, 2015). Despite this, a distance of 30 m seems to be the best compromise for areas measuring ≤ 500 m in length (Larsen and Forsyth, 2005; Barragan *et al*., 2014). Finally, on the sampling interval, 24 and 48 h have been used widely in sampling dung beetles (Larsen and Forsyth, 2005; Campos and Hernandez, 2013; Barragan *et al*., 2014; Silva and Hernandez, 2015). However, sampling interval of 24 h is recommended since it improves the efficiency of the traps by reducing confounding effects due to loss of bait attractiveness caused by moisture loss (Braga *et al*., 2013). In case the temperatures are high, rebaiting after 48 h is necessary to retain its attractiveness. Total sampling duration per each sampling session varies from 48 h to 14 days. However, 4 days are sufficient (Larsen and Forsyth, 2005; Braga *et al*., 2013; Barnes *et al*., 2014; Wagner, 2016).

Use of traps installed into the ground and a sampling interval of 24 h ensures both nocturnal and diurnal dung beetles are captured and hence effects due to sampling time is eliminated (Andresen, 2002). Such traps are prone to effects of flooding and rainfall which reduces its efficiency. A baited trap that is suspended above the ground with a rain guard above it could offer a solution to this shortcoming of ordinary traps (Silva and Hernandez, 2015).

2.9 Existing information gaps in dung beetles studies

Several information gaps exist on the ecological importance and sampling protocol of dung beetles. These include;

1. Information on the abundance, diversity and functional guilds of coprophagous beetles in sub-Saharan Africa is very scanty.
2. Quantitative scientific evidence supporting the effect of coprophagous beetles to soil processes and carbon sequestration which are key determinant of resilience to degradation is missing.
3. *In-situ* scientific evidence of species-specific dung beetle contribution to N and P, main nutrients hindering crop and pasture productivity in SSA zone (Njoroge *et al*., 2017; Njoroge *et al*., 2018) is missing.

4. Species-specific data on the contribution of coprophagous beetles in mitigating emission of greenhouse gases from grazed pasturelands is missing.
5. There is need for more conclusive evidence on the contribution of coprophagous beetles in perpetuating and controlling livestock dung-borne parasites (worms and nematodes) (Boze, 2012; Boze and Moore, 2014).
6. Finally, there is no single standard sampling protocol for dung beetles. This hinders comparison of abundance and diversity data across regions and countries (Larsen and Forsyth, 2005; Silva and Hernandez, 2015).

CHAPTER THREE

3.0 MATERIALS AND METHODS

3.1 Description of the study site

This study was conducted at the University of Eldoret (Chepkoilel site) and at the College of Agriculture and Veterinary Services, University of Nairobi (Kabete site). Chepkoilel site is located at latitude 0° 34´ N and longitude 35° 18´ E. The area is at 2141 m above sea level. It is under Lower Highland zone 3 (LH3) with an annual temperature range of 15.1 – 17.9°C. Annual rainfall range from 900 to 1100 mm and the main soil type is Rhodic Ferralsols (Jaetzold and Schmidt, 1983; WRB, 2015). Kabete site is located at latitude 1° 14´ S and longitude 36° 44´ E at an elevation of about 1828 m above sea level. It falls under agro-ecological zone LH3 with a mean annual rainfall of 1061 mm and an annual mean temperature of 17.8 °C. July is usually the driest month recording a monthly mean rainfall of 17.6 mm while August is the wettest receiving about 242.3 mm. Generally, January is the hottest month while June is the coldest recording 19.4 and 15.6 °C, respectively. The main soil type is Eutric Nitisol (WRB, 2015).

These two sites were chosen because they are high potential areas, receiving more than 850 mm annual rainfall (FAO, 2011). In addition, they contribute significantly to the dairy sector hence the need to maximize pasture production per unit area while preventing soil degradation. Sampling of soil macrofauna was conducted in December 2016 and June 2017 for Kabete and Chepkoilel sites, respectively. Sampling for dung beetles was distributed over three months in each site. For Kabete, it was carried out in January, April and June 2017. In Chepkoilel, it was conducted in January, March and May 2017.

In Kabete, long rain season started in March and ended in May, recording the highest reading of 176.8 mm in April. June recorded the least monthly rainfall of 0.6 mm and lowest mean monthly temperature of 16.2 °C. Since only the month of April received >60 mm of rainfall (Figure 1), January, April and June 2017 could be classified as dry, wet and cold dry seasons, respectively (Peel *et al.*, 2007). In Chepkoilel, long rains occurred in April and May 2017. Thus, December 2016 to March 2017 represented a dry season with monthly rainfall ranging from 3.8 – 53.4 mm while May was a wet period. The highest (19.5 °C) and lowest (17.4 °C) mean monthly temperature was recorded in April and June, respectively (Figure 2).

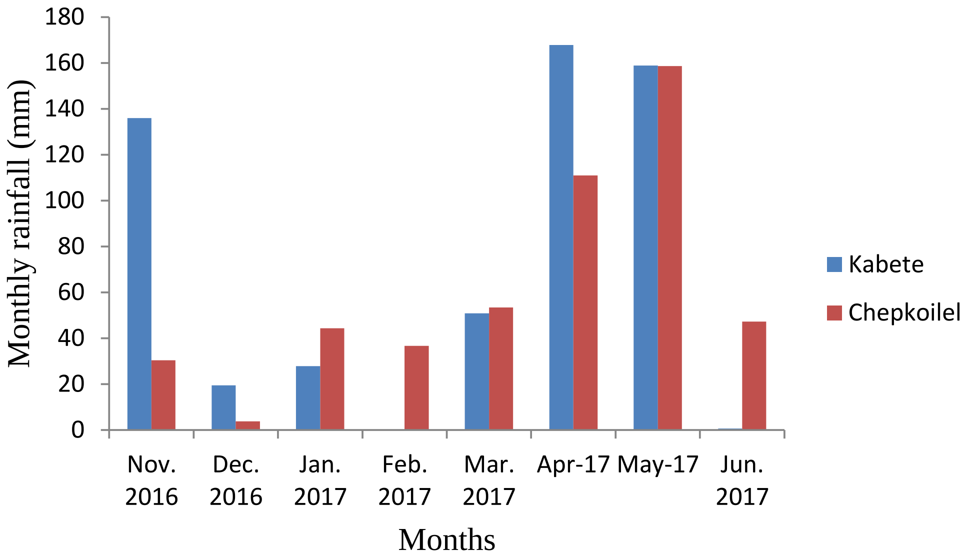

Figure 1: Monthly rainfall in Kabete and Chepkoilel

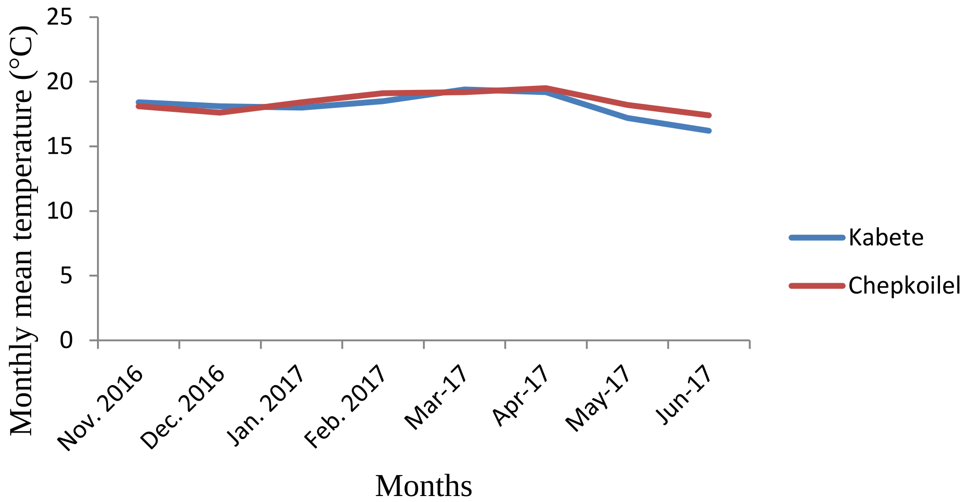

Figure 2: Monthly mean air temperature

3.2 Study designs and data collection

In Chepkoilel site, soil macrofauna and dung beetles were sampled across five LUTs namely; wattle plantation (WP), grazed pastureland (GP), eucalyptus plantation (EP), wetland (W) and mixed woodland plantation (MWP). Wattle plantation (WP) was located between two grazed pasturelands, one of which was burnt in March 2017. The GP was under cattle grazing during the first and third sampling period only. The EP was located between two farms under previous cropping of maize and canola. In the month of February, calves were left to graze on the grass under the trees. Decaying and fresh human excreta was observed during all the sampling periods. The wetland was under cattle grazing. The MW comprised of a mixture of several tree species and grass cover. It was under occasional cattle grazing and human excreta were observed on the lower parts.

In Kabete, soil macrofauna were sampled across five LUTs which included; non-grazed pastureland (NGP), eucalyptus plantation (EP), maize plantation (M), coffee plantation (CP) and grazed pasturelands (GP). Dung beetles were sampled in all LUTs except in maize plantation where a 300 m transect could not fit. NGP was under hay production. The EP had under-storey vegetation comprised of *Lantana camara* during the January sampling. However, prior to the second sampling, the entire under-storey was cleared through burning. Decaying and fresh human excreta was observed during all sampling seasons. The coffee plantation had a few blackjack during both sampling periods. Similarly to the eucalyptus, decaying and fresh human excreta were observed. The vegetation in the grazed pastureland comprised mainly of grass and *Lantana camara*. It had been under occasional cattle grazing prior to both sampling periods. Maize plantation comprised of pure stand of maize crop aged about 10 weeks. The field was treated with Di-ammonium Phosphate (DAP) fertilizer.

Plate 3: Cattle grazing in the pastureland of Kabete

3.2.1 Monolith sampling protocol

Eight monoliths measuring 0.25 by 0.25 by 0.30 m were used in sampling soil macrofauna per each of LUTs indicated in section 3.2. The monoliths were spaced at 10 m from each other along the line transect (Anderson and Ingram, 1993; Swift and Bignell, 2001). The excavated soil was put on plastic trays and soil macrofauna were handpicked. All macrofauna were immediately placed in sealed vials containing 75 % ethanol. After the sampling exercise, earthworms were transferred into separate vials containing 4 % formaldehyde for preservation while the rest were preserved in fresh 75 % ethanol. Identification was done to taxonomic units (orders), that is, earthworms, termites, millipedes, centipedes, spiders and ants (Brown *et al*., 2001; Kamau *et al*., 2017).

From each monolith, a soil sub-sample was collected, labeled and taken to the laboratory for analysis of soil pH, total nitrogen, organic carbon, available phosphorus and exchangeable potassium as described in section 3.6.

3.2.2 Pitfall traps

Line transects measuring about 300 m were randomly established per each LUT perpendicular to the wind direction. Within each transect, 10 baited pitfall traps were laid at equal distance of 30 m. This was preferred since none of the LUTs measured at least 500 m in length ideal to install traps at 50 m inter-distance. This spacing was also ideal in avoiding trap interferences (Barragan *et al*., 2014; Larsen and Forsyth, 2005). The plastic pitfall traps had a diameter of 13 cm and depth of 9 cm similar to those used by Silva and Hernandez (2015). All the pit-fall traps were inserted into the soil as shown in Plate 2.

Plate 4: Baited pitfall trap used in sampling dung beetles

Fresh cow dung (100 ± 5 g) was used as bait. This was preferably used in this study unlike the recommended fresh human feces (Braga *et al*., 2013; Silva and Hernandez, 2015), since it is equally efficient in attracting coprophagous beetles (Bayartogtokh and Otgonjargal, 2009; Slachta *et al*., 2009) and was readily available in both sites.

Collection of beetle was carried out at an interval of 24 h ± 30 min for 4 days (Larsen and Forsyth, 2005; Braga *et al*., 2013). Baits were replaced immediately after collecting beetles for the second time (after 48 h) to maintain their attractiveness (Braga *et al*., 2013). The captured dung beetles were put in plastic bottles, labeled and taken for identification and enumeration. Species identification was done using several taxonomic keys to the species level (Jessop, 1986; Gordon and Barbero, 2008; Chandra and Gupta, 2013) and later confirmed at the Department of Invertebrate Zoology of the National Museum of Kenya, Nairobi.

3.2.3 Terrarium experiment

A terrarium is closed environment used to grow plants or rear macrofauna. It mimics a natural ecosystem and thus it has been utilized in several experiments evaluating ecosystem functions or services of soil macrofauna (Eisenhauer *et al*., 2010; Astor, 2014).

A terrarium experiment was carried out to evaluate the effect of selected species of dung beetles on dung removal and quality of the dung balls (one of the biogenic structures produced by dung beetles). All terrariums were made up of clear plastic containers of 5 L which were covered with a net at the top to allow maximum aeration. This was placed in the greenhouse. This experiment was conducted in Chepkoilel farm (described in section 3.1). Since the terrarium experiment was conducted controlled environment, there was no need to replicate in Kabete site.

3.2.4 Treatments, coding and experimental designs

The dung beetles used in the terrarium experiment were collected in January 2018 from the grazed-grassland and mixed woodland both located at the Chepkoilel site (Bertone *et al*., 2006; Yamada *et al*., 2007; Brown *et al*., 2010; Arnaudin, 2012; Nervo *et al*., 2014).

The experiment comprised of eight treatments (Table 1). All the species were tunnelers belonging to different genus with body sizes < 10 mm long. Besides genus and functional guild, abundance of the species in grazed pasturelands was also considered during selection.Two types of animal dung were used: cattle and pig representing herbivorous and omnivorous dung, respectively.

All the treatments contained four individuals of the respective species and were replicated four times. The dung beetles were starved for 24 hours before introducing them into the terrarium. The terrarium contained 1500 g soil sieved through 5 mm mesh. Respective dung type weighing 150 ± 1 g was placed on soil in each terrarium before introduction of the beetles. The coding and experimental layout was as described in table 3.1 and 3.2.

Table 3.1: Treatment coding

Serial No.	Dung beetle species	Dung type	Treatment code
1	*Euoniticellus triangulatus*	Cattle	EC
2	*Milichus pictollis*	Cattle	MC
3	*Onthophagus sugillatus*	Cattle	OC
4	*Euoniticellus triangulatus*	Pig	EP
5	*Milichus pictollis*	Pig	MP
6	*Onthophagus sugillatus*	Pig	OP
7	None (Control)	Pig	C1
8	None (Control)	Cattle	C2

Key: The first letter in the treatment coding represents the species of dung beetles (E, M and O) while the second represents the dung type (C and P). Control was denoted by letter C.

Table 3.2: Experimental layout in the greenhouse

REP 1	**REP 2**	**REP 3**	**REP 4**
EC	MP	C2	OC
MC	OP	OP	C1
OC	MC	EC	MP
EP	C2	MP	EC
MP	EC	C1	OP
OP	C1	EP	C2
C1	OC	MC	EP
C2	EP	OC	MC

Key: For symbols refer to table 1.

Treatments in the terrarium experiment were arranged in a completely randomized design (CRD).

3.3 Data collection

The abundance of macrofauna (individual m^{-2}) was calculated using equation 1 adopted from Kamau *et al*. (2017).

$$Macrofauna\ abundance\ (no.per\ m^2) = \frac{n}{0.0625}\ \times 1\ m^2 \ldots\ldots\ldots\ldots \text{Eq. 1}$$

where n is the total numbers of each macrofauna taxonomic group obtained in a monolith measuring 0.25 by 0.25 m (0.0625 m^2) as described in section 3.2.

Relative abundance was calculated using equation 2.

$$Relatve\ abundance\ \% = \frac{Total\ abundance\ of\ each\ group\ per\ LUT}{total\ macrofauna\ abundance\ per\ LUT} \times 100\ \% \ldots\ldots\ldots\ldots \text{Eq. 2}$$

Data collection on abundance and diversity of dung beetle were carried out. Diversity was calculated using species richness and Shannon-wiener index (*H*'). *H*' was preferred over other diversity index because both abundant and rare dung beetle species are equally important (Morris et al., 2014). The *H*' index was calculated using equation 3.

$$H' = \Sigma piInpi \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{Eq. 3}$$

Where *H*' is the Shannon-Wiener index and *pi* was the proportion of individuals of each species belonging to the i^{th} species of the total number of individual beetles (Magurran, 1988; Nolan and Callahan, 2006).

Species richness and diversity index were done at trap level since functions influenced by the two attributes takes place at the point of dung pat manipulation (Braga *et al*., 2013).

The amount of dung removed was assumed to be equivalent to the weight (mg) of the dung ball buried into the soil after 7 days from the time of exposing the dung beetles to the cattle and pig dung. The exposure period is critical and this ranges from 24 h to nine days depending on the prevailing weather conditions (Yamada *et al*., 2007; Shahabuddin *et al*., 2008; Arnaudin, 2012; Braga *et al*., 2013).

Soil particles on the dung balls were brushed off using soft brush. Dung balls were oven-dried at 70° C for 48 hours and weighed using analytical balance to 0.0001 g precision. The beetles were killed by suffocation method and dried at 70° C for 48 h. The amount of dung relocated was determined according to equation 4 which was an improvement of "weight loss" method used by Shahabuddin *et al*. (2008) and Braga *et al*. (2013). This method takes into consideration the biomass of the dung beetles (Yamada *et al*., 2007).

$$Y = \frac{k-r}{m} \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{Eq. 4}$$

Where y is the amount of dung removed in g dung/mg of dung beetle; **k** is the dry mass of dung exposed to the dung beetles; **r** is the mean mass of the dry dung not exposed to dung beetles and **m** is the total biomass of the dung beetles in the terrarium.

The rate of dung relocation was carried out as illustrated in equation 5.

$$R = \frac{m}{7\ days \times dung\ beetle\ dry\ biomass} \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{Eq. 5}$$

where by y referred to the rate of cattle dung removal by dung beetles in g $g^{-1}day^{-1}$ dung beetle and m was weight of dung balls relocated within 7 days.

In quantifying the effects of dung beetles on soil nutrients, a soil sample could be sampled exclusively adjacent to the dung pad (Yamada *et al*., 2007; Shahabuddin *et al*., 2008) for nutrients analysis. However, a more accurate method would be to analyze the nutrients content of the relocated dung balls only. Hence, dung balls were ground using a pestle and mortar, sieved through <0.25 mm sieve (60 mesh) and analyzed for total P, total N, exchangeable K and organic C as described in section 3.6.

3.4 Laboratory analysis of soil and dung ball samples

Samples for determination of available P (Olsen P) and pH were sieved through 2 mm mesh. The remaining sample was sieved using 0.25 mm mesh and analyzed for organic C, total P and N. All procedures were based on standard protocols described in Okalebo *et al.* (2002).

a) Analysis of soil available P

Soil available P was determined using the Olsen method (Olsen *et al.*, 1954). The air dried samples were sieved using the 2 mm mesh and 2.5 g weighed into a 150 ml polythene shaking bottle. To each sample, 50 ml of 0.5 M sodium bicarbonate was added. They were shaken using mechanical shaker for 30 min and filtered through Whatman No. 42 filter paper. The filtrates were collected and 10 ml pipetted into respective 50 ml conical flasks before adding 10 ml of ascorbic acid to each and two blanks. Distilled water was used to fill the conical flask to the 50 ml mark. The contents were shaken well and the absorbance of the solution determined at 880 nm using a spectrophotometer (Milton Roy Company Spectronic 1001). P concentration was calculated in P mg kg^{-1}as described in equation 6.

$$\mathrm{P}(mg\ kg^{-1}) = \frac{(a-b)\times v\times f\times 1000}{1000\ \times w} \text{ ... ...Eq. 6}$$

whereby; *a* was the concentration of P in the sample, *b* the concentration of P in the blank, *v* the volume of the extracting solution (50 ml), *f* is the dilution factor and *w* was the weight of the sample (2.5 g).

b) Determination of soil pH

Soil pH was determined in the ratio of 2.5:1 water to soil (Okalebo *et al.*, 2002). 20 g of soil was weighed into labeled 150 ml bottles. To each, 50 ml of distilled water was added and stirred for 30 min. The samples were left to settle for 10 min and shaken again for 2 min. The pH of each soil suspensions was determined using pH meter (Metrohm 632 pH-meter) and recorded.

c) Analysis of total organic carbon (TOC)

Organic carbon was determined using the modified Walkley-Black method as described by Okalebo *et al*. (2002). Sulphuric acid (10 ml) and aqueous potassium dichromate (20 ml) were used to oxidize soil organic carbon. The residue potassium dichromate was titrated against ferrous ammonium sulphate. TOC was then calculated using equation 7.

$$TOC = \frac{(vol.blank - vol.sample)\times 0.3 \times N \times 100}{weight\ of\ the\ sample \times 77} \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{Eq. 7}$$

Where; N was actual normality of $FeSO_4$ given by 10/vol. blank, vol. sample was volume of the $FeSO_4$ used to titrate the sample (15.6 ml), vol. blank is the volume of $FeSO_4$ used to titrate the blank (20.8 ml).

d) Analysis of total nitrogen (TN)

TN was determined using Kjedahl method which is based on wet oxidation of soil samples using sulphuric acid (Parkinson and Allen, 1975). This was calculated using equation 8.

$$\%\, TN = \frac{(V\ sample - V\ blank)\times 14\ g \times V\ extracted}{weight\ of\ sample \times 1000 \times V\ distilled} \times 100 \ldots\ldots\ldots\ldots \text{Eq. 8}$$

Where; V is volume of H_2SO_4 used in titrating the samples, V extracted and distilled was 50 and 10 ml, respectively.

e) Analysis of exchangeable potassium (K)

Potassium was extracted using excess 1 M ammonium acetate (NH_4OAc) solution to ensure maximum exchange occurs between NH_4 and K occupying the exchange sites (Okalebo *et al*., 2002). 5 g of air dried soil (< 2 mm) was weighed into clean plastic bottle with a stopper and 100 ml of NH_4OAc solution (pH 7) added. The contents was shaken for 30 minutes and filtered through No. 42 Whatman paper. The amount of potassium in the extract was determined by flame photometry and calculated according to equation 9.

$$K\ mg/kg = \frac{(a-b)\times v\times f}{w} \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{Eq. 9}$$

where a = concentration of K in the sample extract; b = concentration analyte in the blank extract; v = volume of the extract solution; w = weight of the soil sample; f = dilution factor.

3.5 Data analysis

Data on abundance of dung beetles and soil macrofauna were checked for normality using Shapiro-Wilk test (*W*-test) (Royston, 1995) using Statistics package for Social Sciences (SPSS 20) software. Data on abundance of dung beetles and soil macrofauna was transformed using square-root and log-transformation, respectively before analysis of variance. These two were chosen because soil macrofauna data was highly skewed while that of dung beetles was less skewed. Two-way analysis of variance (ANOVA) was conducted to determine the effects of season and LUT on dung beetle abundance and diversity as well as effects of species and dung type on amount and chemical quality of buried dung balls. On the other hand, one-way ANOVA was done to determine the differences in soil chemical parameters and abundance of soil macrofauna across LUTs. Treatment differences were evaluated using least significant difference (LSD) at5 % level of significance. Transformed data was only used to obtain the *p* value and least significant difference (LSD). All ANOVA and LSD analysis were conducted using Genstat 14th edition software.

Finally, Pearson correlation coefficient (r) was done to determine the correlation of air temperature and rainfall with abundance of dung beetles using Microsoft excel.

Soil chemical parameters were standardized by transforming them into the same units before analysis so that each variable received equal weight besides making the canonical coefficients comparable (Leps and Smilauer, 2003). A preliminary detrended correspondence analysis (DCA) was carried out to determine the length of the axis. Since the first axis was less than 4 (2.3 and 2.4 for Kabete and Chepkoilel, respectively), redundancy analysis (RDA) was undertaken to establish the relationship between abundance of soil macrofauna and soil chemical properties using vegan package of R software (Oksanen *et al*., 2015).

CHAPTER FOUR

4.0 RESULTS

4.1 soil chemical properties and macrofauna abundance across land use types

4.1.0 Soil chemical properties across land use types

Soils in all LUTs in Kabete were strongly acidic (ranging from 4.9 to 5.6). Soil organic carbon and total nitrogen were high, > 3 % and > 0.25 %, respectively, with exception of soils under coffee plantation where the two were in moderate levels. Soil exchangeable K was in high concentrations ranging from 360.9 under Eucalyptus trees to 413.7 mg K/kg soil in non-grazed pastureland. All the soil chemical parameters (pH, OC, TN, P and K) differed significantly across LUTs ($p \leq 0.05$). Soils under eucalyptus plantation had significantly higher levels of OC. Soils under eucalyptus and non-grazed pastureland had significantly higher levels of TN ($p \leq 0.001$). Soil available P was significantly higher in soils under maize plantation (Table 4.1).

At Chepkoilel, soils from all LUTS were very strongly acidic, with high levels of exchangeable K (> 300 mg K/kg soil) and available P (> 10 mg P/kg soil). Except the soils under Eucalyptus plantation and wetland, soil organic C and total N were in moderate concentrations in all LUTs. All the soil chemical parameters (pH, OC, TN, P and K) differed significantly across LUTs ($p \leq 0.05$). Soils under eucalyptus plantation and wetland had significantly higher levels of OC. Soil TN and available P was significantly higher in soils under wetland and mixed woodland, respectively ($p \leq 0.001$) (Table 4.1).

Table 4.1: Soil chemical properties from different land use types at Kabete and Chepkoilel

Site	Land use types	pH (water)	% O.C	%TN	mg P/kg	mg K/kg soil
Kabete	Eucalyptus plantation	5.2b	3.65 a	0.32 ab	14.11 b	360.9 c
	Coffee plantation	4.9 c	2.87 c	0.24 c	14.68 b	389.8 bc
	Non-grazed pastureland	5.3 ab	3.14 bc	0.35 a	9.57 b	413.7 ab
	Maize	5.6 a	2.53 d	0.25 c	25.07 a	444.3 a
	Grazed pastureland	5.4 ab	3.25 b	0.27 bc	11.53 b	401.0 abc
	Means	5.3	3.09	0.29	14.99	401.90
	LSD	0.28	0.374	0.054	6.683	51.90
	P	≤0.001	≤0.001	≤0.004	≤0.001	≤0.037
Chepkoilel	Eucalyptus plantation	4.54 bc	3.17 a	0.26 b	34.84 b	632.90 a
	Wattle plantation	4.35 c	1.54 c	0.17 c	39.01 b	388.60 b
	Mixed woodland	4.81 ab	2.28 b	0.20 bc	55.76 a	567.00 a
	Wetland	4.95 a	3.61 a	0.39 a	36.59 b	615.80 a
	Grazed pastureland	4.50 c	1.73 bc	0.15 c	37.08 b	347.00 b
	Means	4.63	2.46	0.23	40.7	510.30
	LSD	0.268	0.573	0.070	14.86	92.73
	P	≤0.001	≤0.001	≤0.001	≤0.04	≤0.001

Means across columns followed by the same letter are not significantly different at $p \leq 0.05$.

4.1.1 Effect of LUTs on abundance of soil macrofauna in Kabete and Chepkoilel soils

Soil macrofauna included termites, ants, earthworms, millipedes, centipedes, spiders and beetles. In Kabete soils, termites were the dominant groups with a relative abundance of 46.1 followed by ants at 21.3 %. Except spiders, other soil macrofauna groups differed significantly across LUTs. Earthworms were significantly more abundant in soils under coffee and maize plantation ($p \leq 0.001$). Beetles were significantly more abundant in the grazed pastureland while termites dominated coffee plantation, grazed and non-grazed pasturelands at $p \leq 0.001$ (Table 4.2).

Table 4.2: Abundance of macrofauna (no. per m^2) in soils from Kabete

	Land use types							
Macrofauana groups	GP	NGP	C	E	M	R (%)	P value	LSD
Earthworms	148 bc	82 d	438 a	110 cd	296 ab	18.4	≤0.001	0.32
Termites	368 ab	1130 a	1032 ab	118 bc	42 c	46.1	≤0.001	0.63
Ants	180 ab	486 a	310 a	2 b	262 ab	21.3	≤0.022	0.64
Beetles	214 a	86 b	78 bc	36 bc	66 c	8.2	≤0.001	0.36
Millipedes	8 b	84 a	34 b	22 b	0 b	2.5	≤0.002	0.28
Centipedes	14 b	32 b	0 b	78 a	40 b	2.8	≤0.008	0.30
Spiders	4 a	10 a	14 a	6 a	4 a	0.7	≤0.57	0.11

Key: GP – grazed pastureland, M – maize plantation, W – wetland, NGP – non-grazed pastureland, E – eucalyptus plantation, C – coffee plantation, and R – relative abundance. Means across the rows followed by the same letter are not significantly different at $p \leq 0.05$

In Chepkoilel soils, termites were the dominant macrofauna group with a relative abundance of 68.2 %. The abundance of earthworms, termites, ants and millipedes differed significantly across LUTs at $p \leq 0.05$. Abundance of termites was significantly higher in soils under grazed pastureland ($p \leq 0.001$), whereas earthworms dominated the wetland and mixed woodland (Table 4.3).

Table 4.3: Abundance of macrofauna (no. per m^2) in soils from Chepkoilel

	Land use types							
Macrofauna groups	GP	WP	W	MW	E	R (%)	P value	LSD
Earthworms	6 bc	0 c	30 a	20 ab	8 c	3.6	≤0.004	0.64
Termites	910 a	8 c	0 c	72 bc	194 b	68.2	≤0.001	0.83
Ants	110 a	2 b	0 b	218 a	2 b	19.1	≤0.001	0.68
Beetles	38 a	20 a	40 a	6 a	6 a	6.3	≤0.053	0.75
Millipedes	0 b	0 b	8 ab	18 a	4 ab	1.7	≤0.044	0.54
Centipedes	2 a	0 a	0 a	0 a	0 a	0.1	≤0.421	0.19
Spiders	2 a	0 a	8 a	2 a	2 a	0.8	≤0.292	0.46

Key: GP – grazed pastureland, MW – mixed woodland, W – wetland, E – eucalyptus plantation, WP – wattle plantation and R – relative abundance. Means across the rows followed by the same letter are not significantly different at $p \leq 0.05$.

4.1.2 Correlation of macrofauna abundance with soil chemical properties in Kabete and Chepkoilel soils

In Kabete, axis 1 and 2 explained 42 % of the observed variations of soil macrofauna abundance in Kabete soils and soil macrofauna responded differently towards soil chemical properties. Centipedes were strongly and positively correlated with organic C but negatively with exchangeable K and total N along axis 1. However, termites, beetles and spiders were positively correlated with organic C, total N, available P, exchangeable K and pH along axis 2 (Fig. 3).

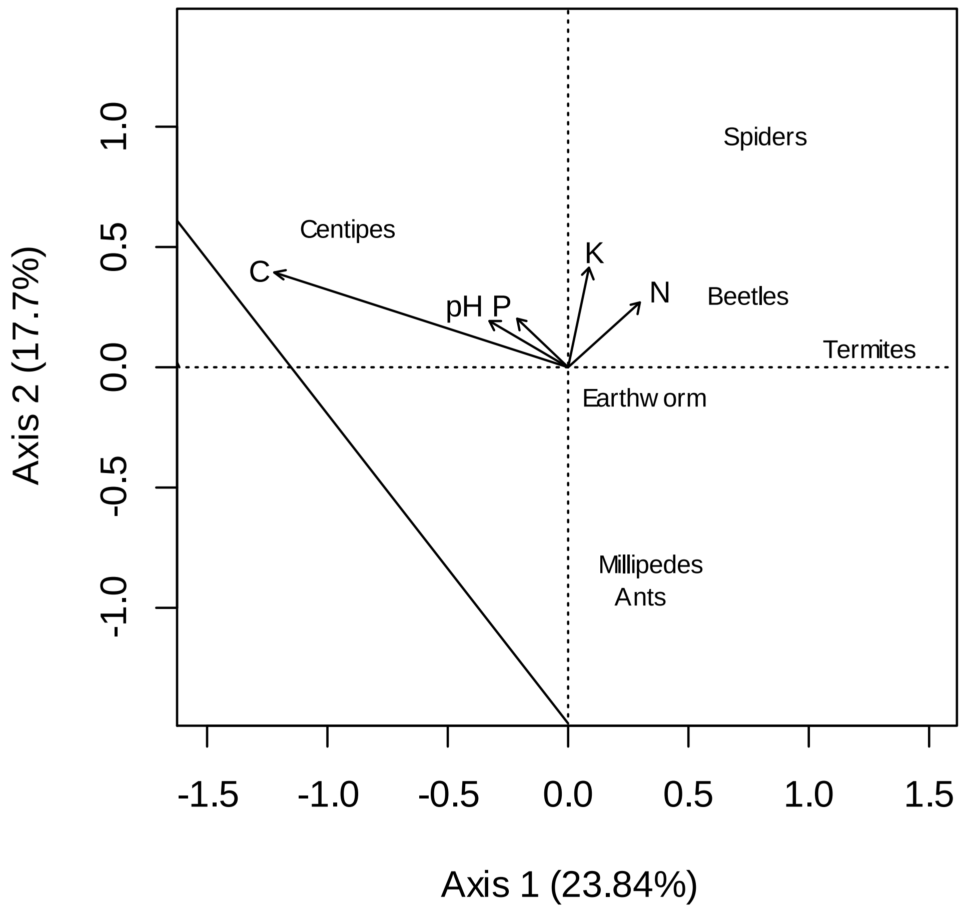

Figure 3: RDA biplot showing correlation of soil macrofauna with soil chemical parameters in Kabete soils

Key: Centipes = Centipedes

In Chepkoilel, the two axes explained 49 % of the observed variations in abundance of soil macrofauna. Earthworms, millipedes and spiders were positively correlated with exchangeable K, available P, total N and pH along axis 1 whereas all the macrofauna groups were positively correlated with organic C, total N and pH, but negatively with exchangeable K and available P along and axis 2 (Fig. 4).

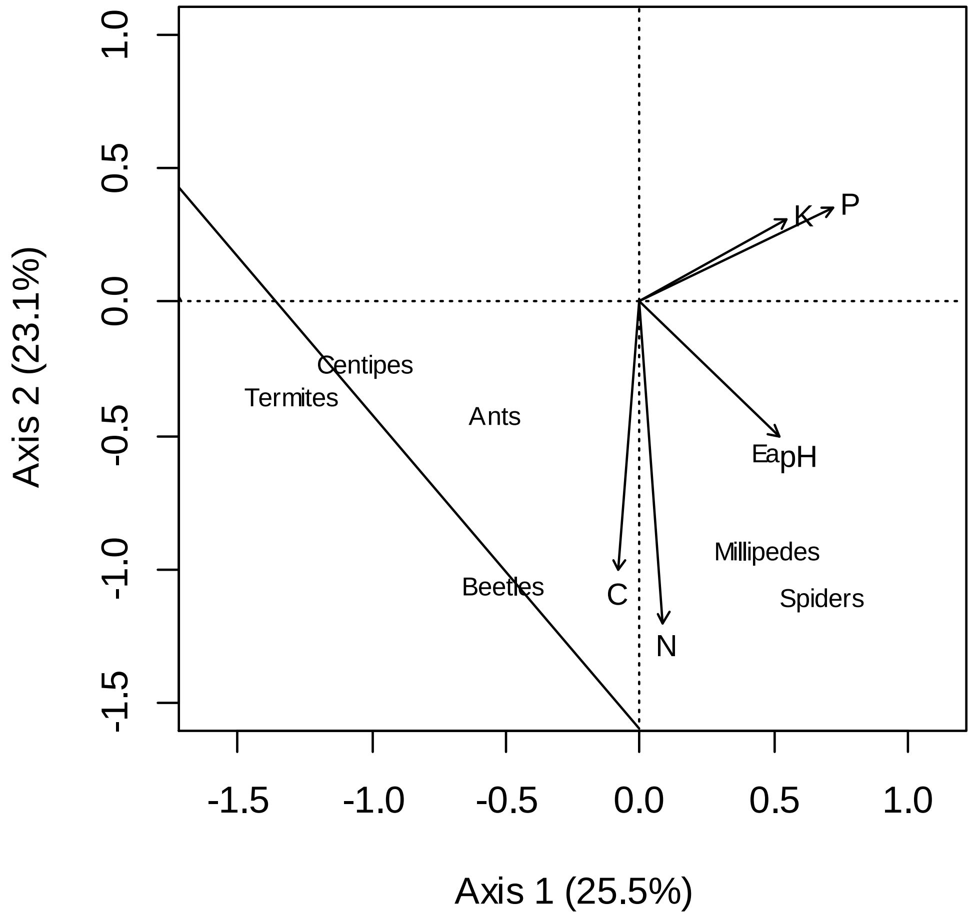

Figure 4: RDA biplot showing correlation between soil macrofauna groups and soil chemical parameters in Chepkoilel soils.

Key: Ea. = Earthworms and Centipes = Centipedes

4.2 Species abundance and distribution of dung beetles in Kabete and Chepkoilel soils

In Kabete soils, 336 dung beetles, comprising of 15 species from 10 genera, were collected in January 2017 during the dry season, across all the LUTs. The major genera were Calocolobopterus, Euoniticellus, and Onthophagus. *Colocolobopterus prinicpalis* Harold and

Euoniticellus triangulatus Harold were the most dominant species. *Liatongus militaris* Casteinau was only observed in coffee plantation whereas *Onthophagus fuscidorsis* D. Orbigny and *Onitis parvulus* Fabricius were present in the eucalyptus plantation. Several species were only observed in the grazed pastureland which included *Caccobius obtusus* Fahraeus, *Euoniticellus africanus* Gillet and *Caccobius sp.* Ratzeburg (Table 4.4).

In the cold dry season of June 2017, 610 individual dung beetles were collected, comprising of 11 species from five genera. *Onthophagus semiasper* Orbigny and *Aphodius heynei* Pic were the most dominant species with a relative abundance of 48.4 and 24.9, respectively. *Milichus picticollis* was identified for the first time during this study in Kabete from the grazed and non-grazed pasturelands under this study. *Onitis sulcipennis* Felsche was only identified in grazed pastureland and eucalyptus plantation (Table 4.4).

During the wet season (April 2017), a total of 581 dung beetles, comprising of 20 species from 9 genera, were collected across all the LUTs. The major genera were Onthophagus, Aphodius and Catharsius. *Onthophagus sugillatus* Klug, *Aphodius prodromus* Brahmand *Catharsius tricornutus* Bertone were the most dominant species in decreasing order of their relative abundance. The wet season had more species under Eucalyptus and coffee plantations. *Sisyphus barbarosa* Wiedemann, a roller dung beetle, was only collected during the wet season. More large (> 10 mm) dung beetles (Cartharsius, Onitis and Copris genus) were present during the wet season only (Table 4.4).

Table 4.4: Species abundance of dung beetles across land use types and seasons in Kabete soils

LUTs	GP			NGP			C			E			R		
Seasons	D	W	CD	D	W	CD	D	W	CD	D	W	CD	D	W	CD
Species															
Onthophagus sugillatus Klug, 1855	22	52	0	1	33	0	1	42	0	0	0	0	7.1	21.9	0
Onthophagus fuscidorsis D. Orbigny, 1902	4	0	0	0	0	0	1	0	0	2	0	0	2.1	0	0
Onitis parvulus Balthasar, 1963	1	0	0	0	0	0	0	0	0	7	0	0	2.4	0	0
Calocolobopterus principalis Harold, 1861	95	0	0	19	0	0	0	0	0	0	0	0	33.9	0	0
Eunniticellus triangulatus Harold, 1873	35	13	6	51	12	14	0	1	1	0	2	1	25.6	4.8	3.6
Caccobius obtusus Fahraeus, 1857	2	3	0	0	4	0	0	2	0	0	0	0	0.6	1.5	0
Onthophagus miricornis D. Orbigny, 1902	7	0	0	4	0	0	0	0	0	0	0	0	3.3	0	0
Aphodius heynei Pic, 1907	28	0	100	0	0	47	3	0	0	0	0	5	9.2	0	24.9
Onthophagus rufonotus Gagne, 1997	12	5	2	6	3	0	0	0	0	0	0	0	5.4	1.4	0.3
Onthophagus semiasper D. Orbigny, 1902	5	0	195	12	0	90	3	0	9	0	0	1	6.0	0	48.4
Euoniticellus africanus Harold, 1873	1	0	0	0	0	0	0	0	0	0	0	0	0.3	0	0
Oniticellus planatus Castelnau, 1840	1	0	0	1	0	0	0	0	0	0	0	0	0.6	0	0
Drepanocerus kirbyi Kirby, 1828	6	0	0	4	0	0	0	0	0	0	0	0	3.0	0	0
Liatongus militaris Casteinau, 1840	0	0	0	0	0	0	1	0	0	0	0	0	0.3	0	0
Onitis sulcipennis Felsche, 1907	0	2	3	0	2	0	0	0	0	0	5	17	0	1.6	0
Cartharsius tricornutus Deeger, 1778	0	11	0	0	21	0	0	14	0	0	20	0	0	11.4	0
Aphodius prodromus Brahm, 1790	0	56	47	0	16	0	0	1	0	0	1	1	0	12.9	7.9
O. sp. 1 Latreille, 1802	0	36	0	0	25	0	0	0	0	0	2	0	0	10.8	0
Caccobius sp. Ratzeburg, 1852	1	0	0	0	0	0	0	0	0	0	0	0	0.3	0	0
Onthophagus sp. 2	0	13	0	0	14	0	0	0	0	0	0	0	0	4.6	0
Copris amyntor, Klug, 1885	0	13	0	0	10	0	0	1	0	0	0	0	0	4.2	0
Aphodius sp Hellwig 1798	0	26	0	3	2	0	2	9	0	1	6	0	0	7.4	1.0
Aphodius angustatus Mulsant, 1842	0	0	0	0	8	0	0	1	0	0	1	0	0	1.7	0
Onthophagus fraticornis Harold 1873	0	0	13	0	0	15	0	0	0	0	0	0	0	0	4.6
Milichus picticollis Gerstaecker 1871	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0.7
Onthophagus fimetarius Roth 1851	0	0	3	0	0	6	0	0	0	0	0	1	0	0	1.6
Aphodius sp. 2 Hellwig 1798	0	0	21	0	0	1	0	0	0	0	0	1	0	0	3.8
Sisyphus barbarosa Wiedmann 1823	0	2	0	0	0	0	0	0	0	0	0	0	0	0.3	0
Copris harrisi Waterhouse 1891	0	13	0	0	5	0	0	1	0	0	1	0	0	3.4	0
Catharsius neptunus Kolbe, 1893	0	3	0	0	7	0	0	0	0	0	0	0	0	1.7	0
Drepanocerus abbyssinicus Roth 1851	0	0	0	0	24	0	0	2	0	0	1	0	0	4.6	0
Cartharsius sespstris Waterhouse, 1888	0	3	0	0	4	0	0	9	0	0	10	0	0	4.5	0
Caccobius convexifrons Raffray, 1877	0	5	0	0	1	0	0	0	0	0	1	0	0	1.2	0

Key: GP – grazed pastureland, NGP- non grazed pastureland, C – coffee plantation, E – eucalyptus plantation and R – relative abundance in %, D – dry season, W – wet season, CD – cold dry season

In Chepkoilel soils, a total of 538 dung beetles, comprising of 18 species from 8 genera, were collected during the dry season (January 2017) across all the LUTs. The major genera were Euoniticellus, Onthophagus and Milichus in decreasing order. *Euoniticellus triangulatus* Harold, *Onthophagus raffrayi* Harold and *Milichus picticollis* Gerstaecker were the most dominant species in decreasing order. *Sisyphus barbarosa* Wiedemann was only identified in grazed pastureland while *O. astrofasciatus* Orbiny, *Onitis arrowi* Reiche and *Caccobius convexifrons* Raffray were only present in the wattle plantation (Table 4.5).

During the dry season (March 2017), there was a drop in total abundance from 538 to 461. Species decreased from 18 to 13. *Onthophagus filicornis* Harold was the dominant species with relative abundance of 40.8 % and was present across all LUTs. *Sisyphus Barbarosa* Wiedemann, *Liatongus militaris* Casteinau and *O. miricornis* Orbiny were only present in the grazed pastureland. Abundance in the grazed pastureland decreased from 260 to 73 (Table 4.5).

During the wet season (May 2017), individual dung beetles increased from 447 to 873. *Onthophagus gazella* Fabricius, *Milichus picticollis* Gerstaecker, *Onthophagus Sagittarius* Fabricius and *Euoniticellus triangulatus* Harold were the dominant species in decreasing order. Surprisingly, *Milichus picticollis* Gerstaecker and *Sisyphus barbarosa* Wiedemann which were seen to have high preference for mixed woodland and grazed pastureland, respectively were found in other LUTS. *Milichus picticollis* Gerstaecker was observed in Eucalyptus and Wetland LUTs. Some species such as *Onthophagus gazellas*, *Onthophagus Sagittarius* Fabricius and *Aphodius ictericus* Laicharting were present across all LUTs and Onthophagus and Euoniticellus were the dominant genera (Table 4.5).

Table 4.5: Species abundance of dung beetles across land use types and seasons in Chepkoilel soils

Land use types (LUTs)	GP			S			MW			WP			E			R (%)		
Seasons	D	D	W	D	D	W	D	D	W	D	D	W	D	D	W	D	D	W
Species																		
Onthophagus raffrayi Harold, 1886	2	0	0	20	0	0	14	0	0	61	0	0	7	0	0	19.3	0	0
Euniticellus triangulatus Harold, 1873	222	24	60	0	3	2	4	7	8	0	0	0	2	1	0	42.4	7.6	8.0
Sisyphus Barbarossa Wiedemann, 1823	31	8	36	0	0	1	0	0	0	0	0	0	0	0	0	5.8	1.7	4.2
Onthophagus bidens Olivier, 1789	1	0	0	1	0	0	1	0	0	8	0	0	0	0	0	2.0	0	0
Drepanocerus abyssinicus Pinna, 1979	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0.6	0	0
Onthophagus rufonotus Gagne, 1997	2	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0.7	0	0
Aphodius ardens Harold, 1886	0	0	0	13	0	0	6	0	0	3	0	0	5	0	0	5.0	0	0
Onthophagus fimetarius Roth, 1851	0	4	0	3	2	0	5	2	0	15	7	0	1	2	0	4.5	3.7	0
Milichus picticollis Gerstaecker, 1871	0	5	0	0	7	0	61	41	80	23	9	30	2	3	30	16.0	14.1	16.0
Onthophagus fraticornis Harold, 1873	0	1	4	0	1	4	1	2	0	0	0	0	0	0	0	0.2	0.9	0.9
O. lamellliger Gerstaecker,1871	1	0	0	1	0	0	3	0	0	2	0	0	0	0	0	1.3	0	0
O. gazellas Fabricius, 1787	0	0	100	1	0	58	1	0	94	0	0	26	0	0	39	0.4	0	36.3
Caccobius sp. Ratzeburg, 1852	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0.6	0	0
Caccobius obtusus Fahraeus, 1857	0	12	0	1	0	0	0	15	0	0	31	0	0	1	0	0.2	12.8	0
O. filicornis Harold, 1873	0	4	0	1	9	0	0	42	0	0	89	0	0	44	0	0.2	40.8	0
O. atrofasciatus D. Orbigny, 1905	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0.2	0	0
Caccobius convexifrons Raffray, 1877	0	0	4	0	0	0	0	0	1	3	0	2	0	0	2	0.6	0	1.0
Onitis arrowi Reiche, 1884	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0.2	0	0
O. negriventris D. Orbiny, 1905	0	2	4	0	7	2	0	6	0	0	20	0	0	8	0	0	9.3	0.7
O. semiasper D. Orbiny, 1905	0	5	0	0	4	0	0	2	0	0	5	0	0	2	0	0	3.9	0
Liatongus militaris Casteinau 1840	0	7	7	0	0	0	0	0	0	0	0	0	0	0	0	0	1.5	0.8
O. miricornis D. Orbigny, 1902	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0
Copris amyntor Klug, 1855	0	0	3	0	2	0	0	1	2	0	0	0	0	0	0	0	0.7	0.6
Copris harrisi Waterhouse, 1891	0	0	4	0	0	0	0	0	4	0	0	3	0	0	0	0	0	1.3
Aphodius angustatus Mulsant, 1842	0	0	0	0	1		0	11	0	0	1	0	0	0	0	0	2.8	0
Aphodius obliterates Panzer, 1823	0	0	0	0	0	1	0	0	19	0	0	46	0	0	3	0	0	7.9
O. Sagittarius Fabricius	0	0	51	0	0	9	0	0	18	0	0	3	0	0	4	0	0	9.7
Catharsius neptunus Kolbe, 1893	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0.2
Catharsius pithecius Fabricius, 1775	0	0	8	0	0	0	0	0	2	0	0	1	0	0	1	0	0	1.4
Onthophagus marginalis Gebler, 1817	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0.3
Aphodius rufipes Linnaeus, 1758	0	0	6	0	0	0	0	0	27	0	0	2	0	0	0	0	0	4.0
Onitis sulcipennis Felsche, 1907	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0.2
Aphodius ictericus Laicharting, 1781	0	0	9	0	0	4	0	0	15	0	0	3	0	0	6	0	0	4.2
O. ludio Boucomont	0	0	0	0	0	0	0	0	0	0	0	1	0	0	5	0	0	0.7
O. nuchicornis Linnaeus, 1758	0	0	2	0	0	0	0	0	3	0	0	3	0	0	1	0	0	1.0
Aphodius podromus Brahm, 1790	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3

Key: GP – grazed pastureland, W – wattle plantation, MW – mixed woodland, S – wetland and E – eucalyptus plantation, R – relative abundance, D – dry season, W – wet

4.2.1 Abundance of dung beetles in Kabete soils as influenced by land use types and seasonality

Land use type and season had significant effects on the abundance of dung beetles ($p \leq 0.001$). Grazed pastureland had significantly higher abundance than the other LUTs of 29. Eucalyptus and coffee plantations had the lowest abundance of dung beetles recording 3 and 4, respectively. The interaction between LUTs and season had significant effect on the abundance of dung beetles ($p \leq 0.001$). There was a gradual increase in the abundance of dung beetles from dry, through wet to the cold seasons, with exception of Eucalyptus and coffee LUT whereby it decreased during the cold season. The dry season (January 2017) had the least abundance (8), while the wet and cold seasons had significantly highest abundance of 15 and 16, respectively (Table 4.6).

Table 4.6: Effects of land use types and seasonality on the abundance (individuals per trap) of dung beetles in Kabete soils

	Season			
Land use types	Dry (January 2017)	Wet (April 2017)	Cold dry (June 2017)	Means
Grazed pastureland	22	26	40	29 a
Non-grazed pastureland	10	19	21	17 b
Coffee plantation	1	8	1	4 c
Eucalyptus plantation	1	5	3	3 c
Means	9 b	15 a	16 a	
LSD (season)	0.44	$p \leq 0.001$		
LSD (LUTs)	0.51	$p \leq 0.001$		
LSD (season*LUTs	0.88	$p \leq 0.001$		

Means across rows or columns followed by the same letter are not significantly different at $p \leq 0.05$.

4.2.2 Effect of land use types and seasons on the abundance of dung beetles in Chepkoilel soils

Land use type and season had significant effect on the abundance of dung beetles ($p \leq 0.001$). Grazed pastureland and mixed woodland had significantly higher abundance (21 and 17, respectively) than the other LUTs. Eucalyptus plantation and wetland had the lowest abundance of 6 and 5, respectively. There was a significant interaction effect of LUT and season on the abundance of dung beetles ($p \leq 0.001$). The wet season had significantly higher abundance (17) compared to the dry seasons (11 and 9) (Table 4.7).

Table 4.7: Effect of land use types and season on the abundance (individuals per trap) of dung beetles in Chepkoilel soils

	Seasons			
Land use types	Dry (January 2017)	Dry (March 2017)	Wet (May 2017)	Means
Eucalyptus	2	6	9	6 c
Wetland	4	4	8	5 c
Wattle plantation	12	16	12	14 b
Mixed woodland	10	13	27	17 ab
Grazed pastureland	26	7	31	21 a
Means	11 b	9 b	17 a	
LSD (season)	0.50	$p \leq 0.001$		
LSD (LUTs)	0.65	$p \leq 0.001$		
LSD (season*LUTs)	1.12	$p \leq 0.001$		

Means across rows or columns followed by the same letter are not significantly different at $p \leq 0.05$.

4.2.3 Effect of seasonality and land use types on dung beetle diversity in Kabete soils

Season and LUT had significant effects on the diversity of dung beetles at $p \leq 0.001$ (Table 10 and11). Species richness was significantly highest in non-grazed pastureland (6.4) but lowest in coffee and eucalyptus plantations during the dry season at $p \leq 0.001$. Both grazed and non-grazed pasturelands had significantly higher species richness during the wet season

(9.1 and 8.1, respectively) at $p \leq 0.001$ (Table 4.8). The wet season (April 2017 had significantly higher species richness compared to the dry (January 2017) and cold dry (June 2017) seasons.

Table 4.8: Effects of land use types and season on species richness (S) of dung beetles in Kabete soils

	Seasons			
LUTs	Dry (January 2017)	Wet (April 2017)	Cold dry (June 2017)	Means
Grazed pastureland	3.8	9.1	5.8	6.2 a
Non-grazed pastureland	6.4	8.1	4.9	6.5 a
Coffee plantation	0.7	3.4	0.80	1.6 b
Eucalyptus plantation	0.6	2.6	1.1	1.4 b
Means	2.9 b	5.8 a	3.15 b	
LSD (season) 0.624	$p \leq 0.001$			
LSD (LUTs) 0.721	$p \leq 0.001$			
LSD (season*LUTs) 1.248	$p \leq 0.001$			

Means across rows or columns followed by the same letter are not significantly different $p \leq 0.05$.

Diversity (*H'*) of dung beetles differed significantly between LUTs and seasons ($p < 0.001$). Soils under grazed and non-grazed pasturelands had the highest diversity while those in the coffee and eucalyptus plantations had the lowest. However, this differed significantly between grazed and non-grazed pasturelands during the dry season (January) at $p < 0.001$. The diversity of dung beetles was significantly higher during the wet season and lowest during both dry and cold dry seasons (Table 4.9).

Table 4.9: Effects of land use types and season on species diversity (*H*') of dung beetles in Kabete soils

	Seasons			
LUTs	Dry (January 2017)	Wet (April 2017)	Cold dry (June 2017)	Means
Grazed pastureland	1.1	1.9	1.2	1.4 a
Non-grazed pastureland	1.5	1.8	1.3	1.5 a
Coffee plantation	0.1	1.0	0.0	0.4 b
Eucalyptus plantation	0.0	0.7	0.2	0.3 b
Means	0.7 b	1.4 a	0.7 b	
LSD (season) 0.16	$p \leq 0.001$			
LSD (LUTs) 0.18	$p \leq 0.001$			
LSD (season*LUTs) 0.31	$p \leq 0.028$			

Means across rows or columns followed by the same letter are not significantly different at $p \leq 0.05$.

4.2.4 Effect of LUTs and season on dung beetle species richness and diversity in Chepkoilel soils

LUTs and season had significant effects on the species richness and diversity of dung beetles at $p \leq 0.001$ (Table 11and12). Grazed pastureland, mixed woodland and wattle plantations had significantly higher species richness of 4.9, 4.3 and 4.4, respectively, than wetland (2.5) and eucalyptus plantation (2.2). The wet season had significantly higher species richness than both dry seasons at $p \leq 0.001$. During the dry season, mixed woodland and wattle plantation had the highest species richness of 3.0 and 4.3, respectively (Table 4.10).

Species diversity differed significantly across LUTs and seasons at $p \leq 0.001$. Grazed pastureland had the highest (1.70) diversity while wetland and eucalyptus plantation had the lowest diversity of 0.6 and 0.8, respectively during the wet (May 2017) season. However, during the dry season (March 2017), grazed pastureland, wattle plantation and mixed woodland had the highest diversity of 1.3, 1.2 and 1.2, respectively (Table 4.11).

Table 4.10: Effect of land use types and season on species richness of dung beetles in Chepkoilel soils

	Seasons			
LUT	Dry (January 2017)	Dry (March 2017)	Wet (May 2017)	Means
Grazed pastureland	2.3	4.5	8.0	4.9 a
Wattle plantation	4.3	4.5	4.5	4.4 a
Mixed woodland	3.0	4.7	5.3	4.3 a
Wetland	2.3	2.7	2.5	2.5 b
Eucalyptus plantation	1.3	2.5	2.9	2.2 b
Means	2.6 c	3.8 b	4.6 a	
LSD (seasons) 0.689	$p \leq 0.001$			
LSD (LUTs) 0.89	$p \leq 0.001$			
LSD (seasons*LUTs) 1.54	$p \leq 0.001$			

Means across rows or columns followed by the same letter are not significantly different at $p \leq 0.05$.

Table 4.11: Effect of land use types and season on species diversity (H') of dung beetles in Chepkoilel soils

	Seasons			
LUT	Dry (January 2017)	Dry (March 2017)	Wet (May 2017)	Means
Grazed pastureland	0.4	1.3	1.7	1.1 a
Wattle plantation	1.2	1.2	1.2	1.2 a
Mixed woodland	0.8	1.2	1.2	1.1 a
Wetland	0.6	0.8	0.6	0.7 b
Eucalyptus plantation	0.4	0.7	0.8	0.6 b
Means	0.6 b	1.0 a	1.1a	
LSD (season) 0.17	$p \leq 0.001$			
LSD (LUTs) 0.219	$p \leq 0.001$			
LSD (season*LUTs) 0.38	$p \leq 0.001$			

Means across rows or columns followed by the same letter are not significantly different at $p \leq 0.05$.

4.2.5 Correlation coefficient of abundance, richness and diversity of dung beetles with rainfall and air temperature

The rainfall and air temperature data used for this analysis is shown in Fig. 1 and 2. Species richness, diversity index and abundance of dung beetles showed a strong positive correlation with rainfall amounts. However, in Kabete the correlation between abundance with rainfall and air temperature was very weak. In both sites, abundance of dung beetles was negatively correlated with air temperature (Table 4.12).

Table 4.12: Pearson correlations (r) co-efficient values

Site	Parameters	Rainfall	Temperature
Chepkoilel	Richness	0.86	-0.11
	Diversity	0.67	0.20
	Abundance	0.97	-0.78
Kabete	Richness	0.97	0.75
	Diversity	0.99	0.80
	Abundance	0.19	-0.30

4.3 Effect of selected dung beetle species and type of animal fecal material on the amount and rate of dung removal

Dung and species types significantly affected the amount of dung relocated and rate of removal ($p \leq 0.001$). *E. triangulatus* removed significantly larger amounts of cattle dung than *M. picticollis*. Pig dung was only relocated by *E. triangulatus*, and the amounts relocated were significantly less than cattle dung. *O. sugillatus* did not relocate any type of dung (Table 4.13). Cattle dung was removed at significantly faster rate than pig (7.36 > 1.22 g g^{-1} day^{-1}). In addition, *E. triangulatus* buried dung at significantly faster rate than *M. picticollis* (8.35> 4.53 g $g^{-1}day^{-1}$). *E. triangulatus* removed cattle dung at significantly faster rate than *M. picticollis* (13.04 > 9.05 g $g^{-1}day^{-}1$) (Table 4.13).

Table 4.13: Effect of selected dung beetle species and type of animal fecal material on the amount and rate of dung removal

Parameters	Species	Type of dung		Mean
		Cattle	Pig	
Amount of dung removal	*E. triangulatus*	3.2	0.9	2.0 a
	O. sugillatus	0.0	0.0	0.0 c
	M. picticollis	1.5	0.0	0.8 b
	Mean	1.6 a	0.3 b	
	LSD (species)	0.16	$p \leq 0.001$	
	LSD (dung type)	0.13	$p \leq 0.001$	
	LSD (species*dung type)	0.23	$p \leq 0.001$	
Rate of dung removal	*E. triangulatus*	13.4	3.7	8.4 a
	O. sugillatus	0.0	0.0	0.0 c
	M. picticollis	9.1	0.0	4.5 b
	Mean	7.4 a	1.2 b	
	LSD (species)	0.808	$p \leq 0.001$	
	LSD (dung type)	0.660	$p \leq 0.001$	
	LSD (species*dung type)	1.143	$p \leq 0.001$	

Means across the rows followed by the same letter are not significantly different at $p \leq 0.05$.

4.3.1 Effect of selected dung beetle species and type of animal fecal material on nutrients content of buried dung balls

Species and type of animal fecal material significantly affected the chemical composition of dung balls ($p \leq 0.001$).Fecal materials from pig had significantly higher contents of OC and K than that from cattle ($p \leq 0.001$) (Table 4.14). In addition, it had significantly higher C/N than that from cattle ($p \leq 0.001$) (Table 4.14).

M. picticollis relocated cattle fecal materials only. Dung balls relocated by *E. triangulates* and *M. picticollis* species had significantly lower contents of TN, OC, P and K than the original cattle and pig fecal materials (controls) (Table 4.14).However, dung balls processed by *E. triangulates* from cattle fecal materials contained significantly lower contents of P and K, but with higher C/N ratio than those relocated by *M. picticollis* ($p \leq 0.001$) (Table 4.14). Interaction between species and type of fecal material had significant effect on the TN, OC, P, K and C/N contents of relocated dung balls at $p \leq 0.001$ (Table 4.14).

Table 4.14: Effect of species of dung beetles and type of animal fecal material on the chemical composition of dung balls

Chemical constituent	Species	Type of dung		Mean
		Cattle dung	Pig dung	
%TN	*E. triangulatus*	1.5	1.9	1.7 b
	M. picticollis	1.2	0.0	0.6 c
	Control	2.0	2.6	2.3 a
	Mean	1.6 a	1.5 a	
	LSD (species)	0.301	$p \leq 0.001$	
	LSD (type of dung)	0.245	$p \leq 0.590$	
	LSD (species*type of dung)	0.425	$p \leq 0.001$	
%OC	*E. triangulatus*	16.6	18.6	17.6 b
	M. picticollis	16.0	0.0	8.0 c
	Control	19.6	20.5	20.1 a
	Mean	17.4 a	13.2 b	
	LSD (species)	1.16	$p \leq 0.001$	
	LSD (type of dung)	0.94	$p \leq 0.001$	
	LSD (species*type of dung)	1.64	$p \leq 0.001$	
P mg/kg	*E. triangulatus*	3100.0	3936.0	3518.0 b
	M. picticollis	4629.0	0.0	2314.0 c
	Control	5551.0	8813.0	7182.0 a
	Mean	4427.0 a	4250.0 a	
	LSD (species)	299.0	$p \leq 0.001$	
	LSD (type of dung)	244.1	$p \leq 0.145$	
	LSD (species*type of dung)	422.8	$p \leq 0.001$	
K mg/kg	*E. triangulatus*	3218.0	3047.0	3132.0 b
	M. picticollis	3676.0	0.0	1838.0 c
	Control	6064.0	6480.0	6272.0 a
	Mean	4319.0 a	3176.0 b	
	LSD (species)	500.20	$p \leq 0.001$	
	LSD (type of dung)	408.40	$p \leq 0.001$	
	LSD (species*type of dung)	707.30	$p \leq 0.001$	
C/N	*E. triangulatus*	11.8	9.7	10.7 a
	M. picticollis	14.1	0.0	7.1 c
	Control	9.7	8.0	8.8 b
	Mean	11.9 a	5.9 b	
	LSD (species)	1.76	$p \leq 0.001$	
	LSD (type of dung)	1.44	$p \leq 0.001$	
	LSD (species*type of dung)	2.49	$p \leq 0.001$	

Means across the rows followed by the same letter are not significantly different at $p \leq 0.05$.

CHAPTER FIVE

5.0 DISCUSSION

5.1 Abundance of soil macrofauna and their correlation with soil chemical properties

5.1.1 Influence of land use types on abundance of soil macrofauna in Kabete and Chepkoilel soils

In the two study sites, termites, ants, beetles and earthworms were the dominant groups. These are among the key soil ecosystem engineers, which contribute to decomposition of organic matter (through fragmentation, mixing and burial), improvement of soil structure and aeration (Nervo *et al*., 2014; Bottinelli *et al*., 2015; Hirmas and Cooper, 2016). This concurs with previous studies (Lavelle *et al*., 1994; Karanja *et al*., 2009; Mutema *et al*., 2013; Kamau *et al*., 2017). Karanja *et al*. (2009) found ants and termites to be dominating in Taita Hills benchmark site constituting 36% and 22%, respectively of the total macrofauna. Similarly, Mutema *et al*. (2013) found out termites, ants, beetles and centipedes to be the dominant fauna groups under reduced tillage upon incorporation of crop residues in Zimbabwe.

Abundance of soil macrofauna, except spiders, was significantly impacted by land use types contrary to findings by Karanja *et al*., (2009), who noted insignificant impact of land use systems on the abundance of soil macrofauna in Taita Hills. High abundance of earthworms in coffee plantation, maize plantation, mixed woodland and wetland could be attributed to the high levels of soil OC, TN, exchangeable K and available P in these land use types. Besides, high moisture in the wetland and tillage (practiced in maize and coffee plantation) could have resulted in high abundance of earthworms in those LUTs as also observed by Walmsey and Cerda (2017).

Soils from grazed pasturelands recorded high abundance of beetles which could have been due to high availability of cattle dung which is a key feed resource to coprophagous beetles such as dung beetles and this corroborates the findings of Campos and Hernandez (2013) and Rodrigues *et al*. (2013).

Finally, soils from LUTs namely grazed pasturelands, non-grazed pasturelands, coffee plantation and mixed woodland which recorded high abundance of ants and termites had high surface litter composed of cattle fecal materials, leaves and branches which could have positively impacted on their population as also demonstrated by Freymann *et al.* (2008) and Manyanga *et al*. (2014). Termites feed on materials with varying quality from branches which are rich in lignin to grass that have low C/N ratio. On the other hand, ants feed on leaves, animal fecal materials among other feed materials (Freymann *et al*., 2008; Bagyaraj *et al*., 2016; Kumar, 2017).

5.1.2 Correlation between the abundance of soil macrofauna with soil chemical properties

Soil pH and soil nutrients notably; OC, TN, exchangeable K and available P influenced the abundance of major soil macrofauna groups such as earthworms, beetles, centipedes, millipedes and spiders. However, this differed across sites and macrofauna groups concurring with other studies (Karanja *et al*., 2009; Ayuke, 2010; Mbau, 2012; Kamau *et al*., 2017).Organic carbon provides energy to soil macrofauna while nitrogen and phosphorus is used in formation of new cells and amino acids. Soil pH affects the habitat conditions for the macrofauna especially earthworms. Decrease in pH negatively affects the population of such macrofauna.

Similarly to this study, Ayuke (2010) and Karanja *et al*. (2009) found positive correlation between most fauna groups with organic C, total N and soil pH. In addition, Kamau *et al*., (2017) reported strong correlation of soil available P with earthworms and millipedes.

However, Mbau (2012) reported negative correlation between fauna groups with organic C and total N.

The analyzed chemical parameters highlighted the importance of soil characteristics by explaining about 42 and 49 % of the total variations in abundance of soil macrofauna in Kabete and Chepkoilel soils, respectively. The unexplained variants in the abundance of soil macrofauna groups could be due to effect of land use practices, soil moisture, vegetation cover and composition, litter quality, fertilization and other soil exchangeable cations (Ayuke, 2010; Mbau, 2012; Sayad *et al*., 2012; Siqueira *et al*., 2014; Jiang *et al*., 2015; Kamau *et al*., 2017; Walmsey and Cerda, 2017). Mbau (2012), reported a correlation between abundance of earthworms, beetles, termites, centipedes and cockroaches with soil calcium and magnesium contents. Kamau e*t al*. (2017), reported a strong positive correlation between soil macrofauna abundance with litter quality (especially contents of lignin and polyphenols; C/N ratio). Some macrofauna groups such as earthworms were highly influenced by soil moisture content (Walmsey and Cerda, 2017) which could explain their high abundance in soils under wetland LUT of Chepkoilel.

5.2 Influence of land use types and seasonality on abundance and diversity of dung beetles in Kabete and Chepkoilel soils

Land use types significantly impacted on the abundance and diversity of dung beetles. Although present across all LUTs, dung beetles were dominant in soils from land use types under grazing influence; namely mixed woodland, grazed and non-grazed pasturelands due high availability of cattle fecal materials as also observed by Rodrigues *et al*. (2013). Animal fecal materials constitute their main feed and brooding material (Campos and Hernandez, 2013).These results concur with findings by Braga *et al*. (2013), Rodrigues *et al*. (2013), Imura *et al*. (2014), Martello *et al*. (2016) and De Farias and Hernandez (2017) who reported high abundance in LUTs under grazing influence.

Presence of dung beetles across all the LUTs in the two sites confirmed their potency as efficient and relatively cost effective indicators of environmental changes caused by anthropogenic disturbances (Kessler *et al*., 2011; Shahabuddin *et al*., 2014). Higher abundance of tunnelers reported in this study (Onthophagus, Milichus, Copris and Catharsius genera) compared to rollers (Sisyphus genus) and dwellers (most of Aphodius genus) concurs with findings by Campos and Hernandez, (2013), Hanski and Camberfort (2014) and Yamada *et al*. (2007). Based on their abundance and diverse functional groups, it is construed that dung beetles contributes significantly to ecosystem ecological services especially in the mixed woodland, grazed and non-grazed pasturelands as reported by Braga *et al*. (2013).

Land use types with grass vegetation or the combination of grass and well established tree canopy such as mixed woodland, grazed and non-grazed pasturelands promoted high diversity of dung beetles by influencing cattle grazing, a source of animal fecal materials and creating a cool micro-climate favorable to many dung beetle species as observed by Escobar (2004) and Horgan (2005). This agrees with Jameson (1989) who reported similar diversities of dung beetles in both grazed and un-grazed pasturelands.

Some species of dung beetles such as *Milichus picticollis*, *Sisyphus barbarosa*, and *Euoniticellus triangulatus* exhibited high specificity to LUTs. *Milichus picticollis* preferred the cool environments under mixed woodland since it is a nocturnal beetle. The diurnal species such as *Onthophagus sugillatus* and *Euoniticellus triangulatus* preferred open warm environments such as grazed pasturelands corroborating the findings of Escobar (2004). Roller species (*Sisyphus barbarosa*) were dominant during the dry season under grazed pasturelands because high temperatures facilitate formation and rolling of dung balls according to Hanski and Camberfort (2014).

Precipitation influenced positively the abundance and diversity of dung beetles evident by the strong positive correlation between rainfall amount and species richness and diversity indices in both Kabete and Chepkoilel soils. This could be explained by the effect of precipitation on rapid growth of vegetation cover that creates cool micro-climate favouring more dung beetle species, availability of animal droppings as influenced by grass vegetation, and finally loose soils during wet seasons facilitating brooding of dung beetles as observed by Hanski and Camberfort (2014), Novais *et al*. (2016) and Escobar (2004).These findings concurred with Andrade *et al*. (2011), Liberal *et al*. (2011) and Novais *et al*. (2016) who reported significantly higher species abundance and diversity of dung beetles during wet seasons than dry one. However, Liberal *et al*. (2011) reported higher abundance at the onset of wet season probably due to emergence of adult dung beetles for most species at the onset of rains (Novais *et al*., 2016).

Finally, large tunneler species were abundant during the wet season due to their sensitivity to dry conditions as reported by Escobar (2004) and Nervo *et al*. (2014).In addition, dry weather limit availability of animal droppings, due to inhibited grass growth, which is unfavorable to large dung beetles which need more fecal materials during brooding as observed by Braga *et al*. (2013). Most large beetles have been reported to hibernate deep into the soils and emerge at the onset of rains (Novais *et al*., 2016).

5.3 Effect of selected dung beetle species and type of animal fecal material on the chemical composition, amount and rate of dung removal

Cattle dung was relocated by both *M. picticollis* and *E. triangulates* while pig dung was only relocated by the latter due to preference of dung resources as reported by other studies (Barbero *et al*., 1999; Whipple, 2011), where dung beetles prefer herbivorous dung to that from omnivores. In terms of dung relocation, *E. intermedius* was found to be more effective than other species concurring with the findings by Khanyile *et al.* (2008) where they were more effective than the native dung beetles in Brazil.

In this study, *E. intermedius* was found in open grasslands indicating its adaptation to adverse conditions compared to *M. picticollis* which was only found in cool environments such as mixed woodland. Failure of *O. sugillatus species* to relocate dung could be explained by stress induced by changing their habitats which hindered mating hence preventing dung relocation as observed by Hanski and Camberfort (2014). Other species of Onthophagus genus have been reported to relocate cattle dung (Bertone *et al*., 2006; Shahabuddin *et al*., 2008).

The amounts of N, P and K in cattle dung was significantly lower than in pig dung which agrees with Gbenou *et al*. (2017). The nutrient levels in cattle dung was similar to those reported by Gichangi *et al.* (2006). The chemical quality of animal dung vary widely based on quality of feeds and manure management (Gbenou *et al*., 2017).

Dung beetles assimilated nutrients contained in the liquid part of the dung during the relocation of dung and processing of dung balls as observed by Hanski and Camberfort (2014). This may have reduced the nutrients content in the dung balls. However, the dung beetles contributed significantly to nutrients cycling and carbon sequestration concurring with the findings of Bertone *et al*. (2006). Both *E. triangulatus* and *M. picticollis* were equally effective in relocating dung of low C/N ratio besides considerable amounts of organic C, K, total N and P. This is critical in mitigating emission of methane from grazed pasturelands as well as nitrogen loss through volatilization (Huerta *et al*., 2013; Slade *et al*., 2016). The dung balls had a C/N ratio of < 16 necessary for fast decomposition (Fairhurst, 2012). Hence, relocated dung could undergo quick decomposition releasing essential nutrients thus contributing to sustainable pasture production (Yamada *et al*., 2007; Arnaudin, 2012; Huerta *et al*., 2013).

Given the environmental preference of *E. triangulatus* and *M. picticollis* across LUTs, the former could be best utilized in open grazed pasturelands while the latter in cool silvipastoral systems.

CHAPTER SIX

6.0 CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

The following conclusions were made;

1. Termites, earthworms, ants and beetles were the most dominant groups across all LUTs and sites. Soil macrofauna groups reacted differently to soil chemical parameters. Generally, termites, beetles, spiders and centipedes were positively correlated to total N, OC, exchangeable K and pH.
2. Land use type and season significantly affected the abundance and diversity of dung beetles. They were significantly higher in LUTs under frequent gazing influence and during the wet season. The nocturnal *M. picticollis* preferred cool environments while the roller *S. barbarosa* and tunneler *E. triangulatus* both present in grazed pasturelands.
3. Type of animal fecal material and species of coprophagous beetle affect significantly the amount and rate of dung removal. Relocated dung balls contained significantly lesser amounts of N, P, K and OC than the original dung. *E. triangulates* relocates cattle dung at significantly higher amounts and at a faster rate than *M. picticollis*. *E. triangulatus* and *M. picticollis* were both efficient in forming dung balls from cattle dung of similar chemical composition and quality with an exception of phosphorus contents.

6.2 Recommendations

1. *E. triangulatus* could be reared and purposely introduced into grazed pasturelands to enhance dung removal and nutrients cycling.
2. Further investigations on the effect of *M. picticollis* and *E. triangulatus* on dung relocation and nutrients cycling should be conducted under their natural conditions. This should comprise of more species which are tunnelers and rollers.
3. The effect of *E. triangulatus* on reducing emission of greenhouse gases from grazed pasturelands should be investigated to quantify its economic contribution in grazed pasturelands.

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APPENDICES

Appendix 1: ANOVA table showing effects of LUTs on abundance of soil macrofauna in Kabete and Chepkoilel soils

Ants	Kabete	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
		LUT	4	5.1340	1.2835	3.27	0.022
		Residual	35	13.7393	0.3926		
		Total	39	18.8733			
	Chepkoilel	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
		LUT	4	19.0476	4.7619	10.50	<.001
		Residual	35	15.8752	0.4536		
		Total	39	34.9228			
Termites	Kabete	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
		LUT	4	8.7516	2.1879	5.67	0.001
		Residual	35	13.4984	0.3857		
		Total	39	22.2499			
		Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
		LUT	4	40.2077	10.0519	14.89	<.001
		Residual	35	23.6200	0.6749		
		Total	39	63.8277			
Beetles	Kabete	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
		LUT	4	3.6435	0.9109	7.09	<.001
		Residual	35	4.4941	0.1284		
		Total	39	8.1376			
	Chepkoile	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
		LUT	4	5.7213	1.4303	2.59	0.053
		Residual	35	19.2947	0.5513		
		Total	39	25.0160			
Earthworms	Kabete	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
		LUT	4	3.0660	0.7665	7.60	<.001
		Residual	35	3.5307	0.1009		
		Total	39	6.5966			
	Chepkoilel	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.

		LUT	4	7.4413	1.8603	4.74	0.004
		Residual	35	13.7294	0.3923		
		Total	39	21.1706			
Centipedes	Kabete	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
		LUT	4	1.45367	0.36342	4.09	0.008
		Residual	35	3.10983	0.08885		
		Total	39	4.56350			
		Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
		LUT	4	0.14499	0.03625	1.00	0.421
		Residual	35	1.26867	0.03625		
		Total	39	1.41366			
Millipedes	Kabete	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
		LUT	4	1.62142	0.40536	5.27	0.002
		Residual	35	2.69068	0.07688		
		Total	39	4.31210			
	Chepkoilel	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
		LUT	4	3.0448	0.7612	2.73	0.044
		Residual	35	9.7415	0.2783		
		Total	39	12.7863			
Spiders	Kabete	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
		LUT	4	0.03415	0.00854	0.75	0.565
		Residual	35	0.39838	0.01138		
		Total	39	0.43252			
	Chepkoilel	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
		LUT	4	1.0421	0.2605	1.29	0.292
		Residual	35	7.0570	0.2016		
		Total	39	8.0991			

Appendix 2: ANOVA table showing effects of LUTs and seasonality on abundance of dung beetles in Kabete and Chepkoilel soils

Site	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
Kabete	LUT	3	313.6419	104.5473	107.03	<.001
	Season	2	34.7897	17.3949	17.81	<.001
	LUT*season	6	25.1338	4.1890	4.29	<.001
	Residual	108	105.4969	0.9768		
	Total	119	479.0623			
Chepkoilel	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
	LUT	4	129.099	32.275	19.98	<.001
	Season	2	34.610	17.305	10.71	<.001
	LUT*season	8	52.868	6.609	4.09	<.001
	Residual	135	218.116	1.616		
	Total	149	434.693			

Appendix 3: ANOVA table showing effects of LUTs and seasonality on species richness of dung beetles in Kabete soils

Site	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
Kabete	LUT	3	697.425	232.475	117.27	<.001
	Season	2	208.717	104.358	52.64	<.001
	LUT*season	6	54.350	9.058	4.57	<.001
	Residual	108	214.100	1.982		
	Total	119	1174.592			
Chepkoilel	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
	LUT	4	181.507	45.377	14.94	<.001
	Season	2	100.653	50.327	16.57	<.001
	LUT*season	8	108.013	13.502	4.44	<.001
	Residual	135	410.100	3.038		
	Total	149	800.273			

Appendix 4: ANOVA table showing effects of LUTs and seasonality on diversity of dung beetles in Kabete soils

Site	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
Kabete	LUT	3	38.4360	12.8120	103.28	<.001
	Season	2	11.7887	5.8943	47.52	<.001
	LUT*season	6	1.8345	0.3058	2.46	0.028
	Residual	108	13.3974	0.1241		
	Total	119	65.4567			
Chepkoilel	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
	LUT	4	9.2764	2.3191	12.57	<.001
	Season	2	5.2134	2.6067	14.13	<.001
	LUT*season	8	6.2384	0.7798	4.23	<.001
	Residual	135	24.9121	0.1845		
	Total	149	45.6404			

Appendix 5: ANOVA table showing effect of LUTs on soil chemical parameter content in Kabete

Soil chemical parameter	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
Soil N%	LUT	4	0.064948	0.016237	5.77	0.001
	Residual	35	0.098450	0.002813		
	Total	39	0.163398			
OC	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
	LUT	4	5.7213	1.4303	10.52	<.001
	Residual	35	4.7590	0.1360		
	Total	39	10.4803			
K	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
	LUT	4	30085	7521.	2.88	0.037
	Residual	35	91492.	2614		
	Total	39	121577			
P	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
	LUT	4	1150.58	287.65	6.64	<.001
	Residual	35	1517.22	43.35		
	Total	39	2667.80			
pH	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
	LUT	4	2.39017	0.59754	7.60	<.001
	Residual	35	2.75336	0.07867		
	Total	39	5.14353			

Appendix 6: ANOVA table showing effect of LUTs on Soil chemical property in Chepkoilel

Soil chemical Property	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
%N	LUT	4	0.286525	0.071631	15.01	<.001
	Residual	35	0.167013	0.004772		
	Total	39	0.453538			
OC	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
	LUT	4	26.0170	6.5043	20.43	<.001
	Residual	35	11.1426	0.3184		
	Total	39	37.1596			
K	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
	LUT	4	566940.	141735.	16.98	<.001
	Residual	35	292098.	8346.		
	Total	39	859038			
P	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
	LUT	4	2351.2	587.8	2.74	0.044
	Residual	35	7498.3	214.2		
	Total	39	9849.5			
pH	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
	LUT	4	1.87905	0.46976	0.06965	<.001
	Residual	35	2.43775	0.06965		
	Total	39	4.31680			

Appendix 7: ANOVA table showing effect of dung type and species of dung beetle on dung removal

Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
Species	2	16.70407	8.35204	345.86	<.001
Type of dung	1	9.51300	9.51300	393.94	
Species*Type of dung	2	5.36101	2.68050	111.00	
Residual	18	0.43467	0.02415		
Total	23	32.01276			

Appendix 8: ANOVA table showing effect of dung type and species of dung beetle on rate of dung removal

Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
Species	2	279.5433	139.7717	236.08	<.001
Type of dung	1	226.4433	226.4433	382.48	<.001
Species*Type of dung	2	113.3305	56.6653	95.71	<.001
Residual	18	10.6568	0.5920		
Total	23	629.9739			

Appendix 9: ANOVA table showing effect of dung type and species of dung beetles on chemical composition of dung balls

Chemical parameters	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
TN	Species	2	12.38182	6.19091	75.57	<.001
	Type of dung	1	0.02470	0.02470	0.30	0.590
	Species _ type of dung	2	3.55601	1.77800	21.70	<.001
	Residual	18	1.47463	0.08192		
	Total	23	17.43716			
K	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
	Species	2	83173717	41586858	183.44	<.001
	Type of dung	1	7847841	7847841	34.62	<.001
	Species _ type of dung	2	19586798	9793399	43.20	<.001
	Residual	18	4080617	226701		
	Total	23	114688972.			
OC	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
	Species	2	648.310	324.155	267.48	<.001
	Type of dung	1	114.844	114.844	94.76	<.001
	Species _ type of dung	2	406.334	203.167	167.64	<.001
	Residual	18	21.814	1.212		
	Total	23	1191.302			
C/N	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
	Species	2	54.560	27.280	9.69	0.001
	Type of dung	1	213.806	213.806	75.93	<.001
	Species _ type of dung	2	198.690	99.345	35.28	<.001
	Residual	18	50.682	2.816		
	Total	23	517.738			
P	Source of variation	d.f.	s.s	m.s	v.r.	F.pr.
	Species	2	102846353	51423176	634.79	<.001
	Type of dung	1	188151	188151	2.32	0.145
	Species _ type of dung	2	65339911	32669955	403.29	<.001
	Residual	18	1458140	81008		
	Total	23	169832555			