Norwegian University
of Life Sciences

Master’s Thesis 2016 60 ECTS
Department of Ecology and Natural Resource Management (INA)

Impact of Anthropogenic Forest Disturbance on Dung Beetle (Coleoptera, Scarabaeidae) Communities in Amani Nature Reserve, Tanzania

Maria Sæbjørnsen
Master of Science in Ecology

Acknowledgements

First of all, I would like to thank my supervisor Fred Midtgaard from the Department of Ecology and Natural Resource Management (INA) at the Norwegian University of Life Sciences (NMBU) for his guidance throughout this study. Furthermore, I am grateful for the help and feedback from Ronny Steen and Thrond Oddvar Haugen, and for their support in helping me understand the most difficult part of relevant statistics and analysis. I also want to thank the Department of Ecology and Natural Resource Management at NMBU, and the NMBU research fund for financial support for my fieldwork.

I also want to thank Ole Martin Bollandsås for teaching me how to use a GPS and a relascope in preparation for my fieldwork in Tanzania, and Ole Wiggo Røstad for feedback in the writing process. A huge thank you to my classmates and friends for their support with the statistical analysis and feedback in the writing process. A special mention to Hanna Kavli Lodberg- Holm for her help and advice throughout the writing process.

A special thanks to all the staff of Amani Nature Reserve, especially my field assistant and companion Aloyce for his kindness and help during my fieldwork.

Finally, I would like to thank my friends and family for their support, patience and encouragement during my studies.

Ås, 15 December 2016

____

Maria Sæbjørnsen

Abstract

Dung beetles (Coleoptera, Scarabaeidae) are important seed dispersers and are good indicators on environmental change and biodiversity in tropical forests. The diversity of dung beetles often decreases with forest disturbance and with reduction in canopy cover, as well as reduction of mammals. The aims of this study were to explore the dung beetle abundance, richness, diversity and evenness across three forest types: virgin forest, secondary forest and agroforest. The study area was located in Amani Nature Reserve. The reserve belongs to Eastern Arc Mountains in Tanzania, a biologically hotspot and threatened by increased agricultural use, population growth and forest disturbance. Dung beetles were sampled by using pitfall traps baited with pig- and cow dung. In total, 35 species were captured. Abundance was the only variable with significantly higher number of dung beetles in virgin forest. Composition of dung beetle species changed significantly in the different forest types. Large beetles were most abundant in virgin forest. The results indicate that virgin forest is important for conservation value. However, agroforest may have large value for overall conservation, because the species composition is highly different from closed canopy forest. The agroforest sites are located near preserved forests in Amani Nature Reserve, and can increase the heterogeneity of the general landscape.

Sammendrag

Gjødselbilller (Coleoptera, Scarabaeidae) er viktige frøspredere og gode indikatorer på habitatendringer og biodiversitet i tropisk skog. Diversiteten av gjødselbiller kan bli redusert ved økende habitatforstyrrelse og ved reduksjon av kronedekke, samt reduksjon av pattedyr. Målene ved denne studien var å undersøke endringer i antall arter, individer og diversitet i tre ulike skogshabitat: urskog, sekundærskog og agroskog. Studien ble utført i Amani Nature Reserve. Reservatet er lokalisert i Eastern Arc Mountains i Tanzania, en biologisk hotspot som er truet av økende aktivitet i landbruk, økende populasjonsvekst og skogbruk. Fallfeller med ku- og grisåte ble brukt til å fange gjødselbiller. Totalt ble det funnet 35 arter. Mengde av individer var den eneste variabelen som viste signifikant høyere antall av gjødselbiller i urskog. Sammensetningen av arter forandret seg signifikant mellom de ulike skogstypene. Resultatene fra denne studien viser viktigheten av å ivareta urskog. Agroskog er imidlertid også viktig for verneverdier, fordi artssammensetningen er ganske ulik fra urskog. Agroskog er lokalisert i nærheten av urskog i Amani Nature Reserve, og kan derfor være med på å øke heterogeniteten i landskapet.

Table of contents

1. Introduction

Tropical rainforests are the most diverse and species rich biomes on earth (Klein 1989). Rainforest biomes might be those that are subjected to most habitat destruction due to human land use (Lewis 2009), and this is happening at an alarming rate (Hall et al. 2011). Activities such as agriculture, timber production and other land- use changes have an enormous impact on the loss of species living in rainforests (Klein 1989). Forest modification and fragmentation can lead to decline in species richness and genetic variation (Klein 1989). Further, this can cause isolation in species communities, which also makes species vulnerable to stochastic changes in the environment (Soule & Simberloff 1986). For this reason, conservation is important for the survival of many species in rainforests, particularly in areas subjected to high human pressure (Daily 2001).

Due to deforestation, forest cover is disappearing at an increasing rate all over the tropical region, and almost one half of the closed-canopy rainforests have been converted to agroforests and plantations (Wright 2005). If a forest grows back as secondary forest, the tree composition is different from an old-growth forest (Wright 2005). As a result, there are generally fewer species in young secondary forests compared to virgin forests. Further, they have different species composition because of the secondary succession due to changing forest composition (Lugo & Helmer 2004). Animal species take in average 20-40 years to recolonize after heavy forest disturbance if source populations are close, and forest activities are low (Dunn 2004). According to a study by Gibson et al. (2011) conducted in several tropical forests throughout the tropical continents, primary forests are shrinking and cannot be replaced to maintain the same biodiversity, such as species richness only found in primary forests (Gibson et al. 2011). Degradation of forests may reduce important ecosystem services such as insect pollination and seed dispersal by insects (Foley et al. 2007). Tropical regions in general have smaller populations with a large percentage of specialist species compared to temperate regions and areas at higher latitudes (Collins & Sutton 2012). This can make tropical species more vulnerable and thus more exposed to local and functional extinction (Collins & Sutton 2012). Insects are among the species affected by deforestation and human modified habitats (Klein 1989). Species richness often declines with increased fragmentation, but the richness of insect species may also increase due to migration of species from outside the fragments (Didham 1997). As a result, the species composition of insects can change with increased forest modification (Didham 1997).

There are at least one million species of insects on earth, which cover over half of the world's described species (Groombridge et al. 1992). Further, there is a higher diversity of insect species living in the tropics compared to outside these areas. As stated by Groombridge et al. (1992), the high number of species can be an indicator on healthy ecosystems. Arthropod species represent about 56,4% described species on a global scale (Groombridge et al. 1992), and beetles (Coleoptera) is the largest insect group and covers 35% of the major groups of organisms in tropical areas (Groombridge et al. 1992).

Dung beetles contribute to the nutrient cycle, parasite suppression, pollination, secondary seed dispersal and bioturbation, and can therefore be used as indicators of healthy ecosystems (Scholtz et al. 2009). This is why the conservation of these species is important. Furthermore, the relocation of dung and seeds by dung beetles help to improve the regeneration of forest (Lewis 2009). Dung beetles are important secondary seed dispersers, especially in rainforests (Scholtz et al. 2009) because almost 90% of remaining seeds on the soil surface are eaten by seed predators living there. Dung beetles often get affected by changes in mammal communities because of their dependence on vertebrate dung (Nichols et al. 2007), and they can also be affected negatively by reduction in forest cover (Davis et al. 2008). Dung beetle diversity often decreases with increasing habitat disturbance, and species diversity is normally at a minimum in logged forest and plantations (Davis et al. 2001). Size of dung beetles varies in different forest types according to disturbance levels (Nichols et al. 2007), where large dung beetles are mostly found in continuous forest (Andresen 2003; Klein 1989). Large beetles can bury more seeds, which may lead to better secondary seed dispersal (Andresen 2002).

African rainforests and Afrotemperate forests are among the two most threatened ecosystems on the African continent. This is mostly due to anthropogenic activities such as logging practices and increasing agricultural use (Davis et al. 2008). East Usambara Mountains belong to The Eastern Arc Mountains which are located within Tanzania and Kenya. These mountains are home to a high species diversity and richness, which is why they have been defined as a biological hotspot (Doody et al. 2001). The largest percentage of all endemic species in East Africa can be found in The Eastern Arc Mountains. Compared to other large hot spot areas such as Madagascar and tropical Andes, endemic species in Eastern Arc are located in relatively small areas (Myers et al. 2000). According to Myers et al. (2000), there are about 1500 endemic plant species in East Usambara, in an area of 2000 km^2. Altogether, this gives us a 75:1 species-area ratio (75 species to 100 square kilometers) (Myers et al. 2000). The same area inhabits about 121 endemic vertebrate species. The highest species diversity in Tanzania, is located within the Eastern Arc Mountains (Newmark 2002).

According to Newmark (2002), many closed canopy forests have become open forest areas due to illegal collection of firewood in many areas in East Usambara. Forest cover in Eastern Arc Mountains has declined from 23,315 km^2 to 5,708 km^2 which represents a loss of 75, 5 % of the original forest cover (Conte 2004), a reduction of three quarters of the original size (Newmark 2002). Most of the reduction in these habitats, has occurred during the last 200 years (Newmark 2002). This has resulted in current fragmented forests (Newmark 2002). As a result of the loss of forest biomes, scientists estimate that about one quarter of all species can disappear during this century in Eastern Arc Mountains (Newmark 2002).

Amani Nature Reserve is found in the East Usambara Mountains, and supports a unique diversity, and is known for its high endemism (Doody et al. 2001). Studies indicate that Amani Nature Reserve and the Usambara Mountains in general, have been covered by intact forest before human settlement (Newmark 2002). In Amani Nature Reserve, mammal populations have been greatly reduced during the last decades, which have affected other species living there (Newmark 2002). Insect groups that dominate the forest floor in Amani Nature Reserve, are rove beetles (Staphylinidae), dried fruit beetles (Nitidulidae), ground beetles (Carabidae) and dung beetles (Scarabaeidae). Deforestation activities have resulted in loss of several endemic species in Amani Nature Reserve, and the extinction rate may increase in the coming years (Newmark 2002). By investigating the richness and diversity of dung beetles in Amani Nature Reserve, we can get an indication on the status regarding ecosystem health (Medina et al. 2002). This present study conducted in Amani Nature Reserve, used baited pit fall traps to compare dung beetle composition in three different forests; virgin forest, secondary forest and agroforest. This was done to investigate the effects of land-use changes on dung beetle communities, richness, diversity, abundance and evenness in Amani Nature Reserve. The main predictions for this study are:

1. Species richness, abundance, diversity and evenness will decrease in forests with increased human disturbance.

2. The dung beetle species composition will change between forests with different degree of human disturbance.

3. Dung beetles with large body size are less abundant in secondary forest and agroforest, compared to virgin forest.

4. Species composition of dung beetles is different according to dung type used in the pitfall traps.

2. Materials and methods

2.1 Study area

The current study was carried out in Amani Nature Reserve which is located in the isolated East Usambara Mountains. The East Usambara Mountains is a part of Eastern Arc Mountains that spans from the Taita Hills in Kenya to the Southern Highlands in Tanzania (Tropical Biology Association 2007) (fig.1). The Eastern Arc Mountains hold the largest amount of moist montane tropical forest in both Kenya and Tanzania (Newmark 2002).

The Amani Nature Reserve was established by East Usambara Management Program in 1977 (IUCN 2014), and has been protected under the Director of Forest and Beekeeping Division since the same year (WWF 2014). With an area of 83.8 km^2 (Doody et al. 2001), Amani Nature Reserve is the largest forest block in East Usambara Mountains (WWF 2014). In addition to Amani, there are 13 mountain blocks in the East Usambara Mountain chain (Pryke et al. 2013). Amani Nature Reserve is one of three nature reserves established in Eastern Arc Mountains (Lovett & Moyer 1992).

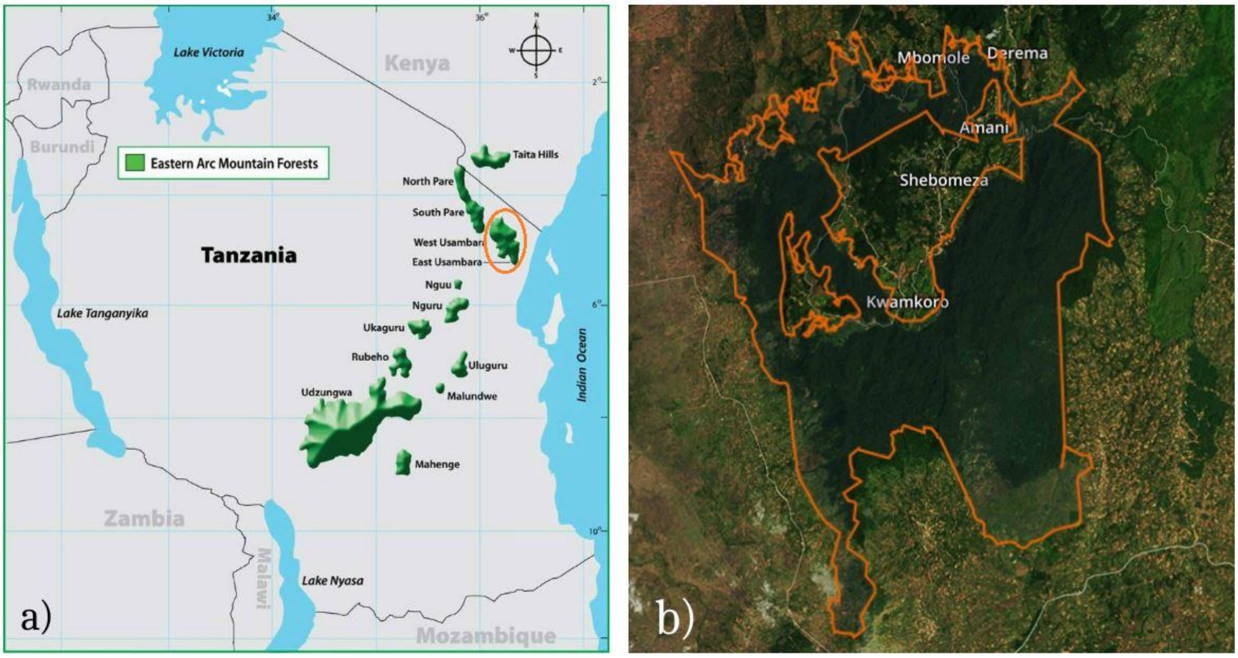


Figure 1: a) Map of Tanzania and the Eastern Arc Mountains, with East Usambara Mountains circled in orange (EAMCEF 2016), and b) satellite photo of Amani Nature Reserve (Protected Planet 2016).

The Eastern Arc Mountains have often been compared with The Galapagos Islands on account of high endemism (Myers et al. 2000). Amani Nature Reserve is biologically important, but experience pressure from increased human population and agriculture (Newmark & Senzota 2003). Due to the high endemism, many researchers look at Amani Nature Reserve as one of the most important forest areas in Africa (Tropical Biology Association 2007). Further, one of Amani Nature Reserve's main objective is to maintain the biodiversity of the undisturbed forests which will support a healthy ecosystem in these mountains (Ministry of Natural Resources and Tourism 2008). The richness of endemic species and the forests are unique, much due to the forest age and the moisture coming from the Indian Ocean (Doody et al. 2001). Additionally, the age of the forests has caused geographically separation between species, in form of "forest islands" (Tropical Biology Association 2007), and there are recorded approximately 3450 species in the Usambara Mountains (Tropical Biology Association 2007). According to Doody et al. (2001), there are 125 species in the reserve which are dependent on forest. The only connection Amani Nature Reserve has with other forest blocks is through the Derema corridor, a corridor on public land, which is not legally protected (Doody et al. 2001). In 2001, there were recorded 3450 vascular plant species in the Usambara Mountains, where about 860 species are endemic (Doody et al. 2001). The Usambara Mountain chain has more species diversity compared to any other area in East Africa. According to IUCN, it was registered seven endangered, and 26 vulnerable species in the reserve in 2001 (Doody et al. 2001).

Scientific research in Amani Nature Reserve started in the end of the 1890s, and in 1983, a small botanical garden was established. In the botanical garden, there has been done biological related research, which belongs to the Biological-Agricultural Institute of Amani (Schulman et al. 1998). The dominating crop in the reserve consists mostly of tea. Prior to the establishment of Amani Nature Reserve, Germans started logging activities in Amani in 1886 to make tea plantations. Most of the logging activities was ongoing until the middle of 1980s (Doody et al. 2001). Over 1 000 000km² are owned by East Usambara Tea Company according to WWF (2014), which include some areas of Amani Nature Reserve.

The secondary forests in Amani Nature Reserve is recognized by the presence of *Maesopsis eminii*, a tree species that were introduced by German colonists in the early 1900s. A large scale plantations happened in the 1960-70s (Binggeli & Hamilton 1993). *M. eminii* can act invasive, and replace open areas in forests with endemic species. Because of the introduction, *M. eminii* now cover large forest areas in Amani Nature Reserve. Secondary forests in the reserve can therefore be determined by the amount of this tree species (Binggeli & Hamilton 1993). The canopy cover of *M. eminii* makes it challenging for primary forest species to recover, which makes the species community different from what it used to be originally. Additionally, the species composition of the soil fauna is different in a *M. eminii* dominated forests compared to a natural old- growth forest (Binggeli & Hamilton 1993).

Even though Amani Nature Reserve is protected, the management in the Eastern Arc Mountains is weak (Burgess et al. 2003). Common challenges are illegal mining inside and outside of the reserve, introduction of invasive species, illegal timber harvesting, illegal harvesting of small animals and insects, and wildfires in lowland villages (Ministry of Natural Resources and Tourism 2008). In 1997 there were 20 villages located in the reserve, inhabited by more than 30 000 people. The population has increased since 1997, and the same applies for number of villages (Ministry of Natural Resources and Tourism 2008). According to earlier research, East Usambara has lost around 70% of its natural habitat, which has caused several species to be vulnerable to local extinction (Hall et al. 2009). According to Ministry of Natural Resources and Tourism (2008), Amani Nature Reserve is a threatened forest ecosystem due to the continuous reduction in the size of the reserve. Due to the rapid decline in size of Amani Nature Reserve and the high level of endemism, many researchers around the world express their concern about East Usambara and Amani Nature Reserve (Doody et al. 2001).

Climate

The highest peaks of rainfall in Amani Nature Reserve are during March and May, and between September and December (Doody et al. 2001). The time periods June- August, and January-March are dry seasons (Doody et al. 2001). Depending on the elevation, rainfall varies between 1200-2200mm /year. Due to differences in topography and climatic interactions, the mountain slopes on the east side of the mountains are wetter than the slopes on the west side (Doody et al. 2001). The temperature varies between 16.3°C – 24.1°C, depending on the season (Tropical Biology Association 2007).

2.2 Study species

In the Afrotropical region, the dung beetles belong to the subfamily Scarabaeinae (Coleoptera Scarabaeidae) (Scholtz et al. 2009). However, in temperate regions there are more species of the sister group of Scarabaeinae, Aphodiinae. But also the Geotrupidae group, a family related to Scarabaeidae (Scholtz et al. 2009).

Dung beetles are among insects that dominate the forest floor in Amani Nature Reserve (Doody et al. 2001). The Afrotropics are the most species rich dung beetle region in the world, with 105 known number of genera (Scholtz et al. 2009). Furthermore, dung beetles represent only around 5000 species in a global perspective, but Afrotropical dung beetles are the most species rich fauna. Even though the species differ from tropical to temperate regions, the morphology and behavior are similar (Scholtz et al. 2009).

Dung beetles are divided into the three functional groups tunnellers, rollers (fig.2) and dwellers based on their behavior (Davis et al. 2008), with both nocturnal and diurnal groups (Scholtz et al. 2009). Rollers usually create balls of dung for food or breeding, whereas tunnellers bury the dung, and dwellers live in the dung (Davis et al. 2008). According to Davis et al. (2008), roller species are commonly found in dry climate, in contrast to tunnellers where the majority prefer a moist climate. The African dung beetle species have a higher abundance and richness in moist and warm areas compared to cool and very wet or very dry conditions (Davis et al. 2008). According to Barkhouse and Ridsdill-Smith (1986), some dung beetle species made significantly more brood balls in soil with a high moisture level compared to dryer levels. Further, there are both specialists and non- specialists, where some species need one specific vegetation or soil type (Davis et al. 2008).

Dung beetles are important species in tropical forest and can be used as indicators for anthropogenic habitat change (Gardner et al. 2008). Because of the importance of the key roles in the ecosystem dung beetles have, it is especially important to conserve these species (Scholtz et al. 2009). Dung beetles contribute to nutrient cycling, help to suppress dung breeding pests and parasites, contribute as secondary seed dispersers (which can improve plant growth), pollination, and bioturbation (Scholtz et al. 2009). They contribute to all these roles by relocation of dung, and burying dung in the soil (Nichols et al. 2008). By being important secondary seed dispersers, they will have a positive effect on the seed predation rate (Estrada

& Coates-Estrada 1991), especially in rainforests (Scholtz et al. 2009) where almost 90% of remaining seeds on the soil surface are eaten by seed predators living there (Estrada & Coates-Estrada 1991). Therefore, the removal of dung and seeds by dung beetles help to improve the regeneration of forest (Lewis 2009).

Dung beetles may be affected by changes in mammal communities due to their dependence on vertebrate dung (Nichols et al. 2007). Moreover, activities can affect dung beetles in two ways, indirect and direct. Indirect is for instance a reduction in larger mammals and birds that produce dung, and direct is through deforestation and anthropogenic changes in habitats (Medina et al. 2002). In most cases, dung beetle abundance declines with increasing forest fragmentation, which also changes interactions between beetles and other organisms (Didham et al. 1996). Dung beetles are vulnerable to habitat change, and the species richness often declines from intact to modified forests (Nichols et al. 2007). A reduction in forest cover and a decrease in forest size, and also loss in mammals may change dung beetle composition, abundance and diversity (Nichols et al. 2008). Dung beetle species living in intact forests may be affected by the density of the canopy cover. This is because a higher canopy percentage can lead to increased moisture levels in the soil (Davis et al. 2008).

Figure 2: Roller species are rolling a piece of dung away from the source in Amani Nature Reserve. Picture taken by author (February 2016).

2.3 Data collection/ study design

This study was conducted with a baited pitfall trap survey during 8 weeks from January to March 2016. The study was done at an elevation varying between 840 and 1058 m.a.s.l.

Three different forest types were surveyed in this study; virgin forest, secondary forest which were logged the last time in the 1980's, and agroforest, logged the last time in the 1970's (fig.3). Five different forest sites were chosen for each forest type, which were chosen with help from local guide, and based on indicators and characteristics of the different forest types. After the introduction of the tree species *M. eminii* from the northwestern part of Tanzania and Central- and West Africa, it can often be found in forest gaps and along the edges as well (Newmark 2002). There was a large percent of *M. eminii* in all of the secondary forest sites. *M. eminii* was also found in primary forests, but in very small amounts, mostly located at the forest edge.

Virgin forest

All of the sites chosen in virgin forest in this study were undisturbed areas which have never been logged. In virgin forests, lianas and large old growth trees, were both used as an indication of no human interactions. All the virgin forest sites were used as control sites. The percentage of canopy covers differed from 70- 95% (table 1). Tree species that were mostly dominating in the virgin forest sites, were in most areas a mix between *Cephalosphaera usambarensis, Mesogyne insignis, Allanblackia stuhlmannii* and *Synsepalum cerasiferum.* The virgin forest plots consisted of V1P+V1C-V5C+V5P (appendix 1).

Secondary forest

In all the secondary forest sites used in this study, *M. eminii* was the most dominating tree species which was used as an indicator on previously logging history. Recently logged areas were not used. Furthermore, percentage of canopy covers differed from 55- 95% (table 1). The secondary forest plots consisted of S1P+S1C-S5C+S5P (appendix 1).

Agroforest

All the agroforest sites used in this study were areas that have originally been logged for agricultural use. The dominant tree species at these sites were a mix between different species of banana trees, *Eucalyptus Globu* (Eucalyptus), *Elettaria cardamomum* (cardamom), *Cinnamomum verum* (cinnamon), *Cedrela odorata* (Spanish cedar) and *M. eminii* (Maesopsis). All agroforests had reduced canopy covers (<60%) (table 1) compared to both virgin- and secondary forests. The agroforest plots consisted of S1P+S1C-S5C+S5P (appendix 1).

Figure 3: a) Virgin forest, b) secondary forests, c) agroforest, d) pitfall trap including bait used in this study in Amani Nature Reserve, Tanzania 2016.

The method used in this study consisted of 15 different trapping locations (five in virgin forest, five in secondary forest and five in agroforest as shown in fig.3). At each plot, two pitfall traps were placed with 10-15 meters apart, resulting in 30 traps in total (fig.4). Each trap location consisted of four- liter bucket, where one trap had cow dung as bait, and pig dung was used for the second trap. The dung was picked up at local farmers.

Salt (to prevent rotting) and soap (to break the surface tension) were added to the buckets. About 0,75L water with salt and soap was used in every pitfall trap. The dung was wrapped inside socks, which were attached on two sticks lying over the buckets (fig. 3 d). Furthermore, the bait was changed every 48 hours at the same time as harvesting. The water remained in the buckets until the third harvest. When the bait was changed, a hard substance (branch or stone) nearby was used to press odor out of the socks, which seemed to attract more beetles because of the stronger smell.

A bowl and a sieve were used in the field to collect the outcome in the traps. Every trap was harvested individually in large zip lock bags in the field, and were stored in smaller zip lock plastic bags back at the station containing local liquor (35%). Furthermore, the content from the same pitfall trap was collected in the same plastic bag with the name of the trap. For each harvest of the same trap, the beetles were collected in the same bag. In total, there were 30 bags with trap content, which means that each harvesting day did not get its own bag. The traps were divided by names: Virgin forest plot 1= V1P and V1C, secondary forest plot 1 = S1C and S1P, whereas agroforest plot 1 has the names A1P and A1C. The letters C and P describe the dung type (C = cow, P = pig). When the bait was changed, the socks with dung was brought back to the station where the dung was thrown away. The socks were washed to get rid of the dung smell, ready to be used again the next day. After placing the buckets in the holes that were made, the area around the bucket was made similar to the natural state. Back at the station, the dung beetles were put in alcohol with lab tweezer.

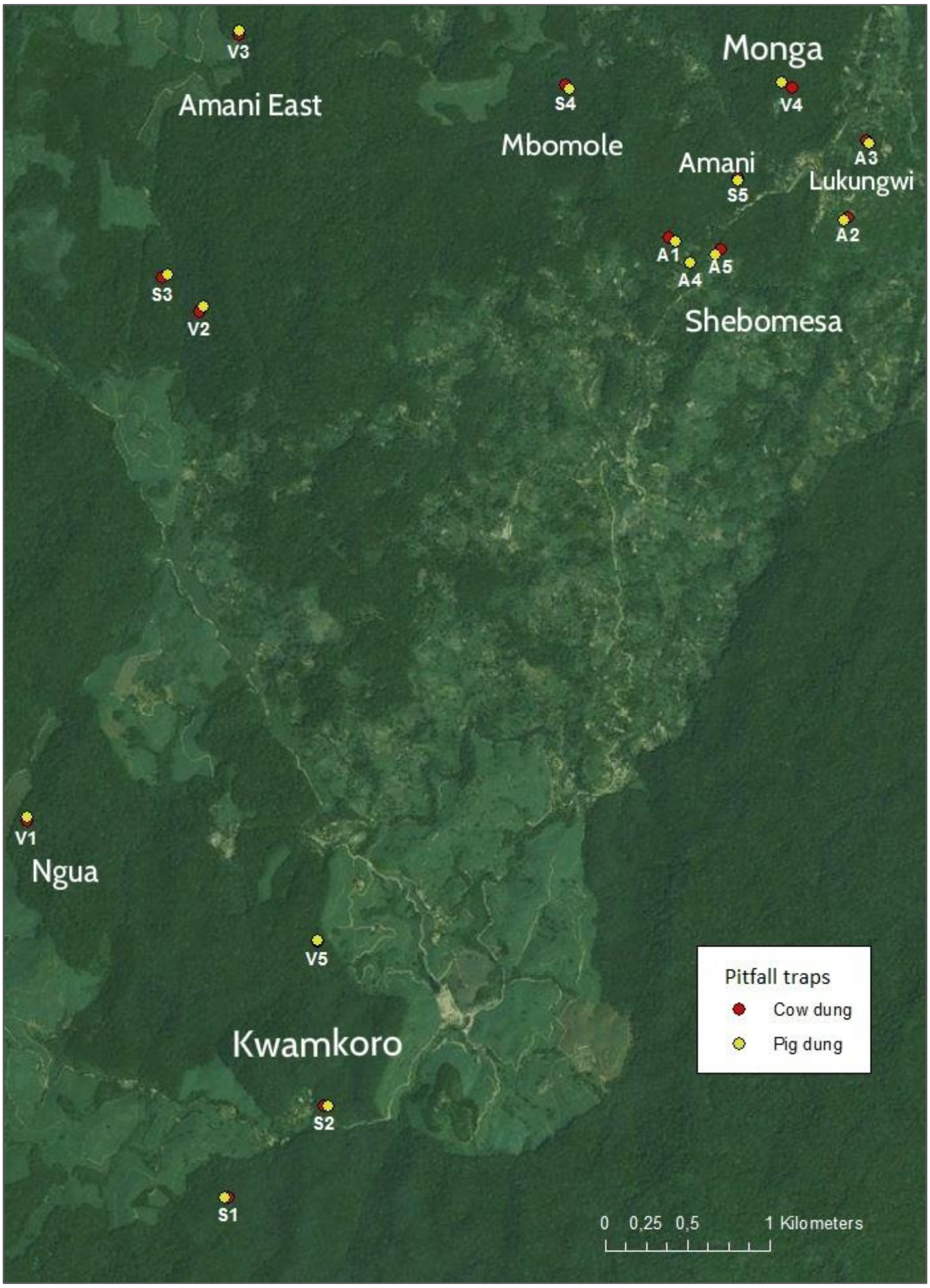


Figure 4: Location of the pitfall traps in Amani Nature Reserve (appendix 1).

2.4 Covariates

Different covariates at each plot were registered (table 1). Namely GPS coordinates, altitude, leaf litter %, canopy cover %, dominant tree species, and number of big trees by using a relascope. The relascope measured the density of the forests by measuring the tree diameter.

Table 1: Environmental variables registered at each plot. Canopy cover and leaf litter measured in percentage by eyesight. P and C are traps using pig and cow dung.

Forest type	Plot	Plot names	Canopy cover	Leaf Litter	Relascope
Virgin forest	1	V1P, V1C	90%, 80%	95%, 95%	68 m^2/ha,76 m^2/ha
Virgin forest	2	V2P, V2C	85%, 95%	95%, 95%	92 m^2/ha, 104 m^2/ha
Virgin forest	3	V3P, V3C	70%, 80%	75%, 95%	64 m^2/ha, 68 m^2/ha
Virgin forest	4	V4P, V4C	90%, 80%	95%, 95%	52 m^2/ha, 56 m^2/ha
Virgin forest	5	V5P, V5C	80%, 80%	90%, 90%	76 m^2/ha, 92 m^2/ha
Secondary forest	1	S1P, S1C	95%, 95%	90%, 92%	80 m^2/ha, 72 m^2/ha
Secondary forest	2	S2P, S2C	90%, 80%	95%, 75%	68 m^2/ha, 52 m^2/ha
Secondary forest	3	S3P, S3C	90%, 80%	95%, 95%	56 m^2/ha, 48 m^2/ha
Secondary forest	4	S4P, S4C	60%, 55%	70%, 70%	52 m^2/ha, 52 m^2/ha
Secondary forest	5	S5P, S5C	78%, 70%	65%, 80%	52 m^2/ha, 44 m^2/ha
Agroforest	1	A1P, A1C	40%, 35%	80%, 75%	36 m^2/ha, 32 m^2/ha
Agroforest	2	A2P, A2C	30%, 30%	70%, 70%	24 m^2/ha, 28 m^2/ha
Agroforest	3	A3P, A3C	50%, 30%	40%, 35%	24 m^2/ha, 24 m^2/ha
Agroforest	4	A4P, A4C	20%, 20%	50%, 45%	20 m^2/ha, 16 m^2/ha
Agroforest	5	A5P, A5C	40%, 60%	45%, 70%	32 m^2/ha, 28 m^2/ha

2.5 Morphospecies identification

After collecting the dung beetle specimens, all of the trap outcome was transported from Morogoro, Tanzania to the Norwegian University of Life Sciences (NMBU). After organizing the outcome from all the traps, only the dung beetles were put in new laboratory glass vials were ethanol (70%) was added. Other insect families such as crickets (Gryllidae), cockroaches (Blattodea), grasshoppers (Caelifera) and ants (Formicidae) were removed from the samplings. The dung beetles were dry-mounted (fig.5) at the entomology laboratory at NMBU, then counted and organized in groups, and later identified by morphospecies. The morphospecies identification is only based on external morphology. The length was measured for each morphospecies.

Figure 5: Dry-mounted dung beetles at the laboratory in insect shadow boxes after dividing the beetles into morphospecies at the Norwegian University of Life Sciences (NMBU). Photo taken by author (May 2016).

2.6 Statistical analysis

I used the statistical software RStudio, version 0.99.902 – © 2009-2016 RStudio, Inc. for statistical analyses.

To measure biodiversity, I used the reverse Simpson diversity index (1-D), and the Pielou's evenness index as an evenness measure. Simpson diversity index is a good measure when you have small sample sizes (Magurran 2013). I calculated the Simpson's diversity and Pielou's evenness for each trap. A Venn diagram was made to present the differences in species number in the different forest types, and species only found in each of the habitats. Species accumulation curves were made to look at the overall estimated species number both from every forest type, and for all the traps in total. They were also used as a validation for the methods used in this study. In this study, abundance is defined as number of individuals, and richness as number of species. Composition of species is defined as the combination of species in a forest type.

I used a generalized linear model (GLM) to look at the abundance of large dung beetle species (>15mm), in relation to forest type. I also tested significantly differences between the most common species captured in relation to forest type. A GLM model was also used to explore what variables were most important to predict abundance, richness, diversity and evenness. Dung type was not included as a variable in this GLM- model because I wanted to look at the overall capture of beetles from forest independent on dung- type when doing this test. Preference for dung type is tested later in the study. Due to a correlation between observed percentage of canopy cover and leaf litter, only canopy cover and forest type were included as explanatory variables in the models to look at the overall capture of beetles. I converted canopy cover to categorical variables, consisting low (< 33%), medium (33-66%) and high (> 66%). This was done because canopy cover was measured visually. All the models for each category were ranked with Akaike Information Criterion (AIC values). I used Poisson distribution for count data (abundance and species richness), and binomial distribution for diversity and evenness indexes. The models with the lowest AIC values were compared with AIC values from null- models, to see if forest type and canopy cover explained the model or not.

In order to explore effects of both environmental variables and forest types on species composition, I conducted ordination analyses (Fowler et al. 2013). A detrended correspondence analysis (DCA), a multivariate statistical analysis, was conducted to look at species composition using the VEGAN library in R. An unconstrained DCA was applied to decide whether to continue with a canonical correspondence analysis (CCA) or a principal component analysis (PCA). I continued with a principal component analysis (PCA) based on the eigenvalues. The eigenvalues are based on the sum of inertia, which accumulate the variance of the species (Oksanen 2015). The eigenvalues on the axes describe variation explained in the data. In association with the PCA, I did a permutation test to see if the factors included in the model had significantly different effects on the species composition. The greater the partial r-squared for each effect or model, the better the effect or model fits the data. The closer the angle of each line, the closer correlated are the species (Ieno & Zuur 2015). The DCA bi-plots used the arrows to describe species loadings. I chose to look at 10 of the species that had the largest response, with the most probability to find in one specific area. The strength of the gradient may often be seen through the arrows length.

I used a paired t-test and Wilcoxon signed rank test to look for significant differences in total abundance, richness and diversity between dung types. A t-test was used to test for statistical differences in normal distributed data (richness and abundance), whereas Wilcoxon signed ranked tests to test for non-normal data (diversity). Mean was calculated for normal distributed data, and median for non-normal data. GLM models were made to test significant differences in abundance between dung types for all forest types.

3. Results

3.1 Morphospecies analysis

3.1.1 Beetle sampling

During the eight weeks of fieldwork, a total of 4566 dung beetles were captured in the three forest types virgin forest, secondary forest and agroforest (table 2). Of the total number of individuals, 35 species were captured (appendix 9 and 10). Four species of the captured species did not belong to Scarabaeidae. Species FF belong to the superfamily Trogidae, BB belong to the subfamily Hydrophilidae, and species I + H belong to the subfamily Aphodiinae. Most species were captured in agroforest areas, but this area also had the lowest abundance (fig.6). Virgin forest had a greater overall species abundance, followed by secondary forest and agroforest. I captured 25 species in agroforest, but over half of these species was characterized by <6 individuals. Of the 35 species recorded, 8 were rollers and 22 non-rollers.

Table 2: Species richness and total abundance of beetles in virgin forest, secondary forest and agroforest in Amani Nature Reserve.

Forest type	Richness	Abundance
Virgin forest	22	2635
Secondary forest	14	1516
Agroforest	25	415

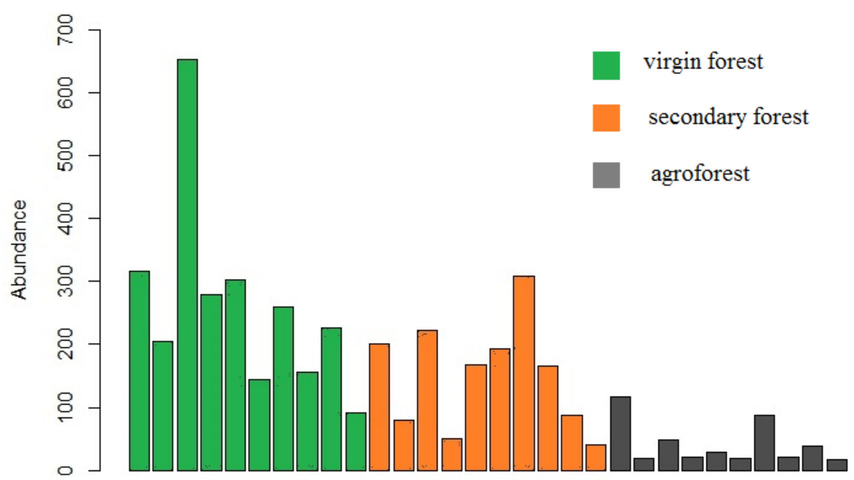


Figure 6: Number of individuals for each trap in virgin forest, secondary forest and agroforest in Amani Nature Reserve.

A species accumulation curve was made to look at the completeness of the sampling (fig.7). The accumulation curves were made for all traps in total, and separately by forest type (fig.8), and show the cumulative observed species richness. Figure 7 displays the number of species captured in all the 30 traps, distributed throughout all habitats, while figure 8 shows the number of species divided on 10 traps for each forest habitat. The number of species was still increasing after 30 traps as shown in figure 7. The accumulation of species in agroforest and virgin forest was still increasing after 10 traps as shown in figure 8.

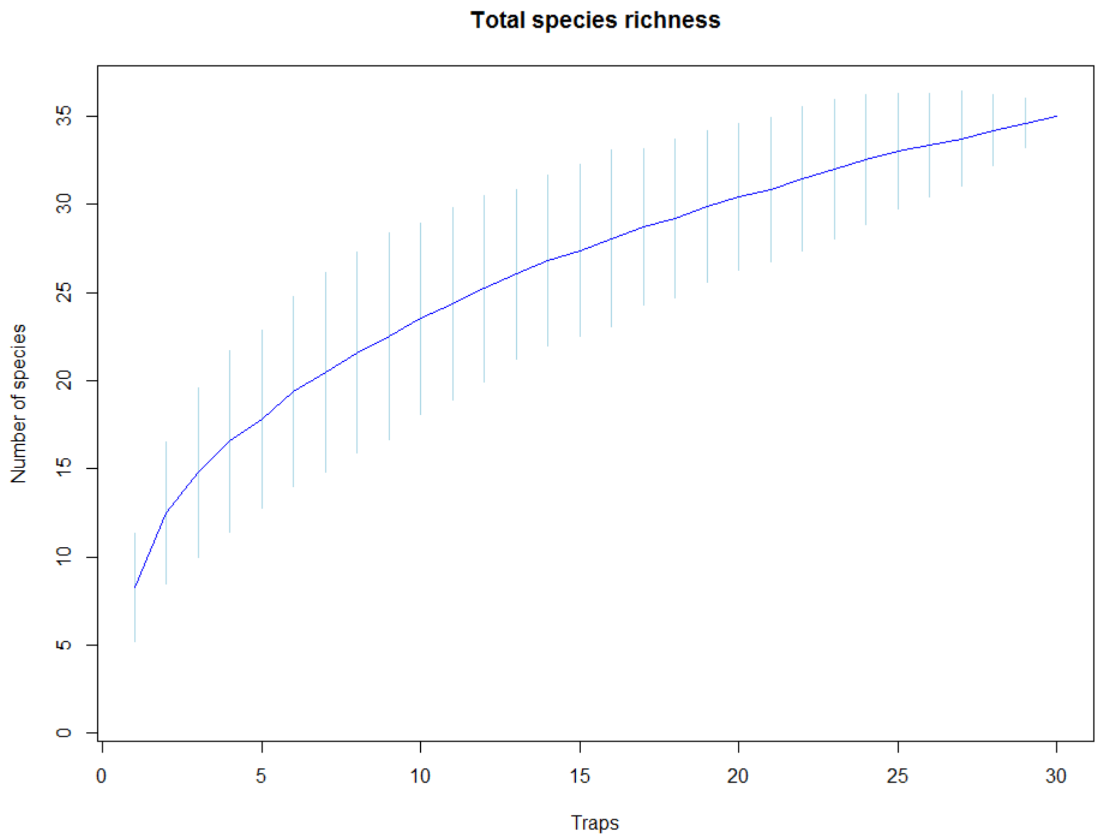


Figure 7: Species accumulation curve with 95% confidence interval from all the sampled traps of all forest types combined (±SE).

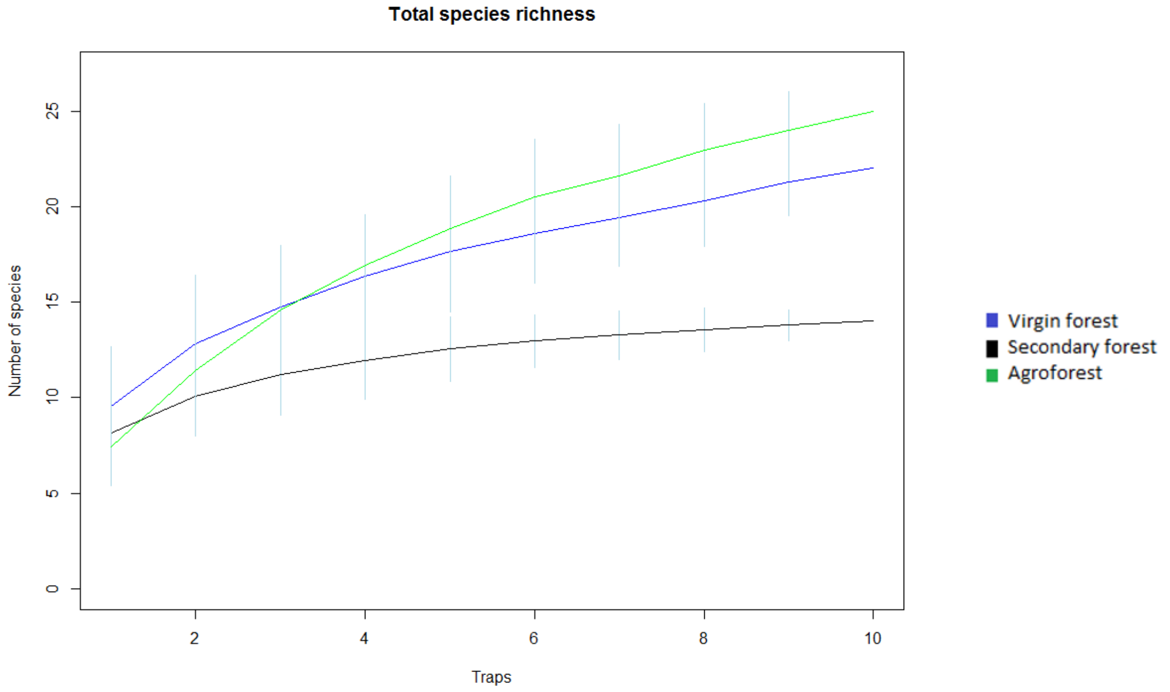


Figure 8: Species accumulation curve with 95% confidence interval, including virgin forest (±SE), secondary forest (±SE), and agroforest (±SE).

The most numerous species across all forest types were species J with 1998 individuals, followed by species CC with 639 individuals, and species G with 427 individuals (fig.9). Species I was also in high abundance, with 522 individuals, but as mentioned earlier, this species belongs to Aphodiinae. The abundance of all captured species is displayed in figure 9 and 10. Species J was the most abundant species in both virgin forest and secondary forest. While the most abundant species in agroforest was species M. In virgin forest, 1409 individuals were captured of species J, and 577 individuals from secondary forest. I captured 22 individuals of species M in agroforest.

Figure 9: Abundance of the most common captured species across all three forest types in this study.

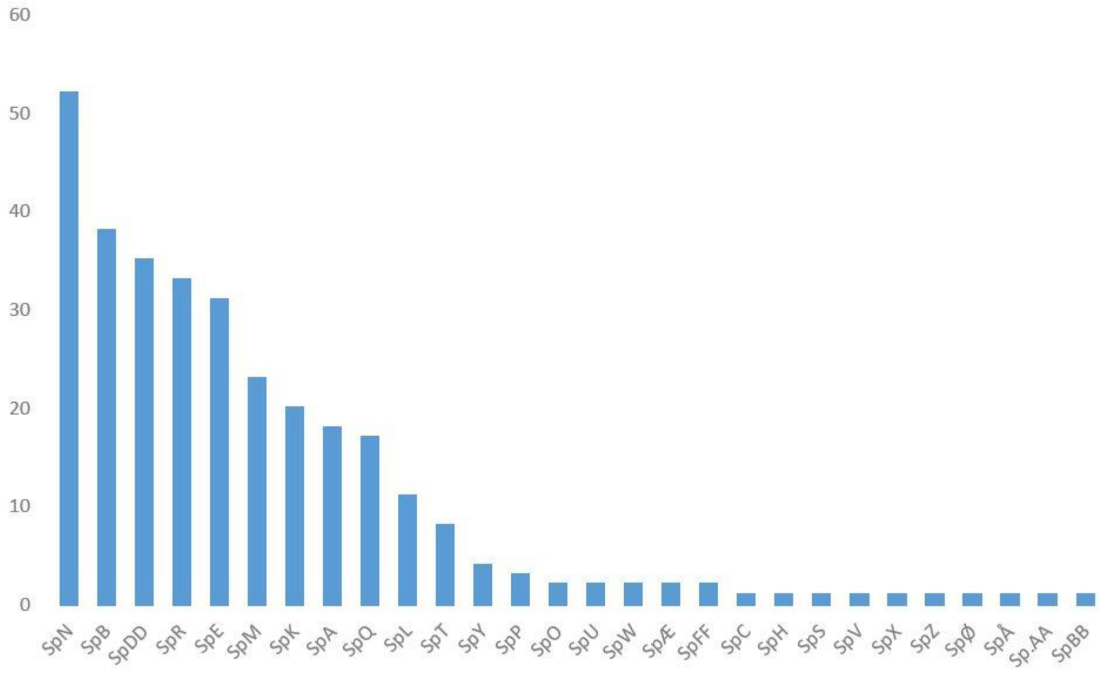


Figure 10: Abundance of the rest of the species captured across all forest types in this study, after the species displayed in figure 9.

Figure 11 a+ b, shows the distribution of species between virgin forest, secondary forest and agroforest. Only nine species were found in all forest types as shown in fig.11b. Figure 11a shows the total number of species in each forest type, whereas fig.11b shows the number of species found exclusively in each specific forest type. Out of the total 35 species I found in my samples, one species was only found in secondary forest, five in virgin forest, and 12 in agroforest. Four species were found both in secondary forest and virgin forest (fig 11b). Four species overlap both virgin forest and agroforest. I captured nine species that were found in all forest types. Even though 12 species were found exclusively in agroforest, a large percentage of the species had only one or <6 individuals in the samples.

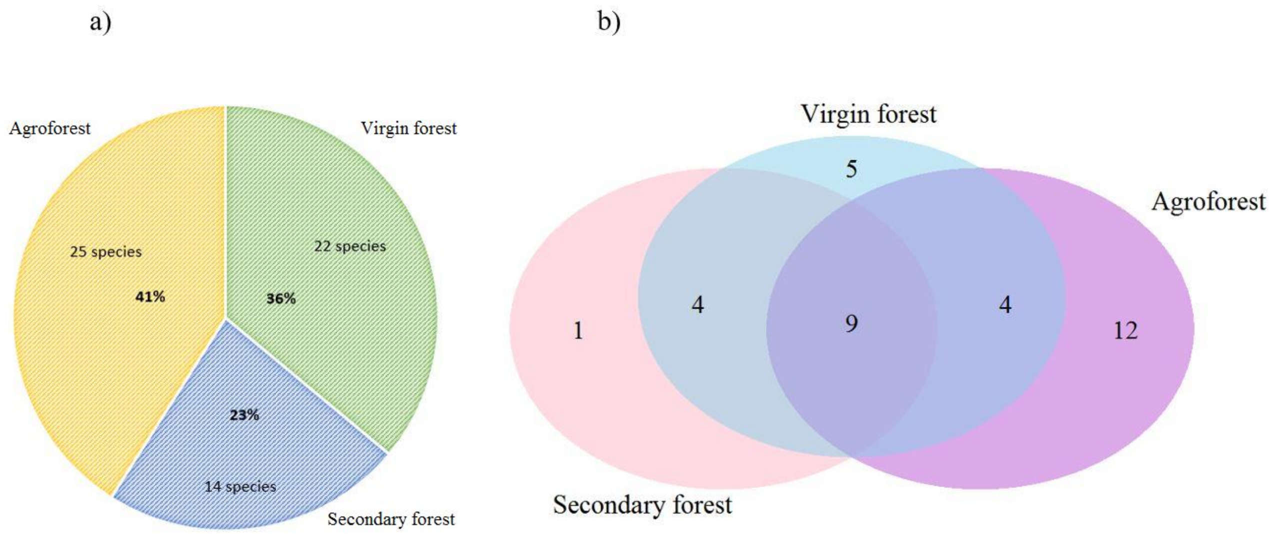


Figure 11: a) The percentage and number of species found in the different forest types. b) The distribution of the number of species which differs among the forest types. Pink= "Secondary forest", blue= "Virgin forest" and purple= "Agroforest". Only one species was found exclusively in secondary forest, five in virgin forest and 12 in agroforest. Four species were captured both in virgin forest and secondary forest, and the same number across agroforest and virgin forest. Nine species were captured in all forest habitats.

3.1.2 Distribution of the most common and largest species

The captured species with the largest size (10mm-33mm) were analyzed separately to look at the distribution between the forest types (appendix 2). The captured dung beetle species varied in size from 3.5-32.58mm. The abundance of the largest species (>10mm) was higher in virgin and secondary forests compared to agroforests figure 12. Species D, A, F, G were most abundant in virgin- and secondary forests, whereas species L, C and M were most abundant in agroforest. Based on morphology, species B, E, L, S, M are rollers, while D, C, A, K, F and G are tunnellers/ dwellers.

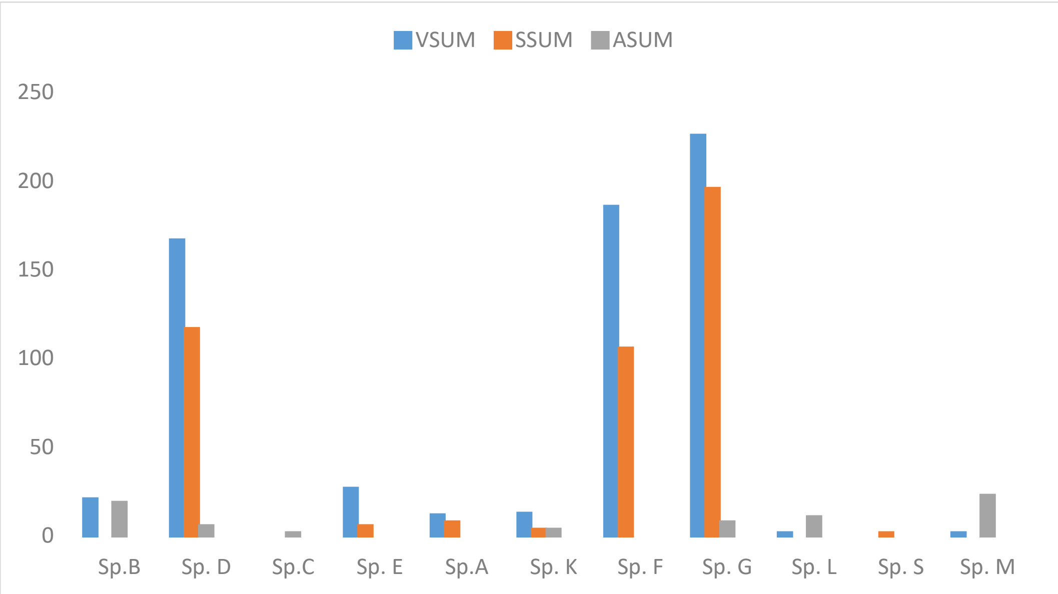


Figure 12: Distribution of species with largest body size (>10mm), where n=1145. Orange shows the number of individuals in secondary forest (n=432), blue in virgin forest (n=647), and grey in agroforest (n=66). VSUM= sum of individuals in virgin forest, SSUM= sum of individuals in secondary forest, and ASUM= sum of individuals in agroforest.

The distribution differed significantly in abundance between forest types and dung beetles >15mm (table 3). To analyze the abundance of all the largest species (>15mm) across forest types, GLM's were made for six species (table 3, table 4). I used the relevel function to make secondary forest as intercept, and the same result showed (appendix 3). There were no significant differences in species abundance of sp. A, sp. C and sp. B between the different forest types. Nevertheless, the last mentioned species were not captured in any of the agroforest sites, only in few numbers in virgin and secondary forest. The number of species D was significantly higher in secondary forest and virgin forest compared to agroforest. After using the releveling function in the GLM model, I also found a significantly lower number of the species in agroforest and secondary forest compared to agroforest. The number of species E was significantly lower in individuals in agroforest compared to virgin forest. Species K was significantly lower in abundance in secondary forest compared to virgin forest. The species that showed significant difference between forest types, were all significantly higher in abundance in virgin forest compared to secondary- and agroforest.

Table 3: Parameter estimates from GLM models of the six largest species (body size >15mm): Sp. A (n=18), Sp. B (n=38), Sp. C (n=1), Sp. D (n=287), Sp. E (n=31), Sp. K (n=20). Agroforest, secondary forest and virgin forest are used as response variables. Intercept is presented by the dummy variable "virgin forest" (V) for species E and K, and "agroforest" (A) for species A, B, C and D.

Species	**Variables**	**Estimate β**	**Std. Error**	**z**	**p- value**
Sp. A	Intercept (A)	-19.30	2980.96	-0.006	0.995
	Secondary forest	18.95	2980.96	0.006	0.995
	Virgin forest	19.40	2980.96	0.007	0.995
Sp. B	Intercept (A)	0.588	0.2357	2.494	0.013 *
	Secondary forest	-17.890	1096.633	-0.016	0.987
	Virgin forest	0.1054	0.3249	0.324	0.746
Sp. C	Intercept (A)	-2.303	1.000	-2.303	0.021 *
	Secondary forest	-19.000	8103.084	-0.002	0.998
	Virgin forest	-19.000	8103.084	-0.002	0.998
Sp. D	Intercept (A)	-0.693	0.447	-1.550	0.121
	Secondary forest	3.144	0.457	6.884	<0.001 ***
	Virgin forest	3.503	0.454	7.717	<0.001 ***
Sp. E	Intercept (V)	0.956	0.196	4.872	0.001 ***
	Secondary forest	19.258	1808.042	-0.011	0.992
	Agroforest	-1.649	0.488	-3.376	0.001 ***
Sp. K	Intercept (V)	0.182	0.289	0.632	0.528
	Secondary forest	-1.386	0.646	-2.148	0.032 *
	Agroforest	-0.876	0.532	-1.645	<0.001 ***

Table 4: Parameter estimates from the GLM model for total abundance for the six largest species (body size >15mm) across forest types (n=1145). “Agroforest”, “Secondary forest”, and “Virgin forest” are used as response variables. Intercept is presented by the dummy variable “Agroforest” (A).

Variables	Estimate β	Std. Error	z	p- value
Intercept (A)	4.190	0.123	34.04	< 0.001 ***
Secondary forest	1.879	0.132	14.22	< 0.001 ***
Virgin forest	2.283	0.129	17.67	< 0.001 ***

Five of the most common species were also analyzed between the three forest types, using GLM’s (table 5). Species F did only show significant difference between secondary forest and virgin forest, because of the zero values from agroforest. Species J, G, CC, and species D was significantly higher in virgin- and secondary forest than agroforest (table 5). There were significant differences between all the forest types, with lowest numbers in agroforest. I used the relevel function in R (appendix 5) to let all the variables be the intercept to look for significant differences with all forest types as intercept.

The five most frequently captured species, were species D, F, J, G, CC (appendix 4). Species I was also captured in a large number, but as mentioned earlier, the species belong to Aphodiinae. I found all these species in all forest types, but most of them in virgin and secondary forest. All of the traps did not contain all species. All the traps in virgin forest contained all the species, except one trap where I did not find species J (V4P). The same applies to secondary forest, where two traps (S3P and S5P) did not contain species CC and species F. In agroforest I only captured some individuals of species D, J, G and CC, except species F.

Table 5: Parameter estimates for GLM models for total abundance for the most common species across forest types, Sp. J (n=1998), Sp. G (n=427), Sp. CC (n=639), Sp. D (n=287) and Sp. F (n=290). "Agroforest", "Secondary forest", and "Virgin forest" are used as response variables. Intercept is presented by the dummy variable "Agroforest" (A).

Species	**Variables**	**Estimate β**	**Std. Error**	**z**	**p- value**
Sp. J	Intercept (A)	0.182	0.289	0.632	0.528
	Secondary forest	3.873	0.292	13.279	<0.001 ***
	Virgin forest	4.766	0.290	16.439	<0.001 ***
Sp. G	Intercept (A)	-0.357	0.378	-0.944	0.345
	Secondary forest	3.327	0.385	8.649	<0.001 ***
	Virgin forest	3.470	0.384	9.042	<0.001 ***
Sp. CC	Intercept (A)	0.588	0.236	2.494	0.013 *
	Secondary forest	2.783	0.243	11.458	<0.001 ***
	Virgin forest	2.909	0.242	12.017	<0.001 ***
Sp. D	Intercept (A)	-0.693	0.447	-1.550	0.121
	Secondary forest	3.144	0.457	6.884	<0.001 ***
	Virgin forest	3.503	0.454	7.717	<0.001 ***
Sp. F	Intercept (A)	-16.30	665.14	-0.025	0.980
	Secondary forest	18.65	665.14	0.028	0.978
	Virgin forest	19.22	665.14	0.029	0.977

3.2 Habitat analysis

The Simpson's diversity index (1-D) and Pielou's evenness index were calculated for each trap (appendix 6). When doing a habitat analysis, GLM's were used to test which variables that described abundance, diversity, evenness and richness the best. I included canopy cover: low (L), medium (M) and high (H). Leaf litter; high (H) and medium (M). Forest type; virgin forest (V), secondary forest (S) and agroforest (A) in the models. I found a correlation on 0.79 between canopy cover and leaf litter. Abundance was the only test that showed significant difference between the forest type and the environmental variables (canopy covers L, M, and H) as shown in table 6. I did not find any significant difference between richness, evenness and diversity and the forest types. Forest type A (agroforest) was automatically chosen as the dummy variable which represented the intercept (reference level) in the models.

A null- model for every GLM's except the abundance model presented a higher AIC when comparing the null- model with the GLM- model (appendix 7). This confirms that the variables explain the abundance. The variables may not have a significant impact on the diversity, richness and evenness, where the AIC value were lower than the null- models.

Table 6: Parameter estimates of the GLM model for overall abundance across forest types (n=4566), and the most important variable for abundance (canopy cover and forest type). "Agroforest", "Secondary forest", "Virgin forest" and Canopy cover (L=low, M=medium, H=high) are used as response variables. Intercept is presented by the dummy variable "Agroforest" and canopy cover H.

Variables	Estimate β	Std. Error	z	p- value
Intercept	3.081	0.085	36.08	< 0.001 ***
Secondary forest	1.790	0.080	22.49	< 0.001 ***
Virgin forest	2.493	0.088	28.47	< 0.001 ***
Canopy cover L	0.715	0.114	6.29	<0.001 ***
Canopy cover M	0.596	0.055	10.74	< 0.001 ***

When I found the best model which described abundance, I tested it for normality, and checked the residuals plot. The plots were nearly linear, which means that the data fits the model. I used the relevel function in R (table 7) to let all the variables be the intercept to see if all the variables in the model are significant to each other (i.e. each pair comparison), not only to the intercept variable. Both virgin- and secondary forest are significant to agroforest, but virgin and secondary forest are also significant to each other (table 7). The figure shows a reduction in abundance in forests with increasing habitat disturbance as displayed in figure 13.

Table 7: Difference in dung beetle abundance between all forest types, after checking all the combinations of variables as intercept.

Forest type			**p- value**
Agroforest (A)	vs.	Secondary forest (S)	<0.001***
Agroforest (A)	vs.	Virgin forest (V)	<0.001***
Secondary forest (S)	vs.	Virgin forest (V)	<0.001***

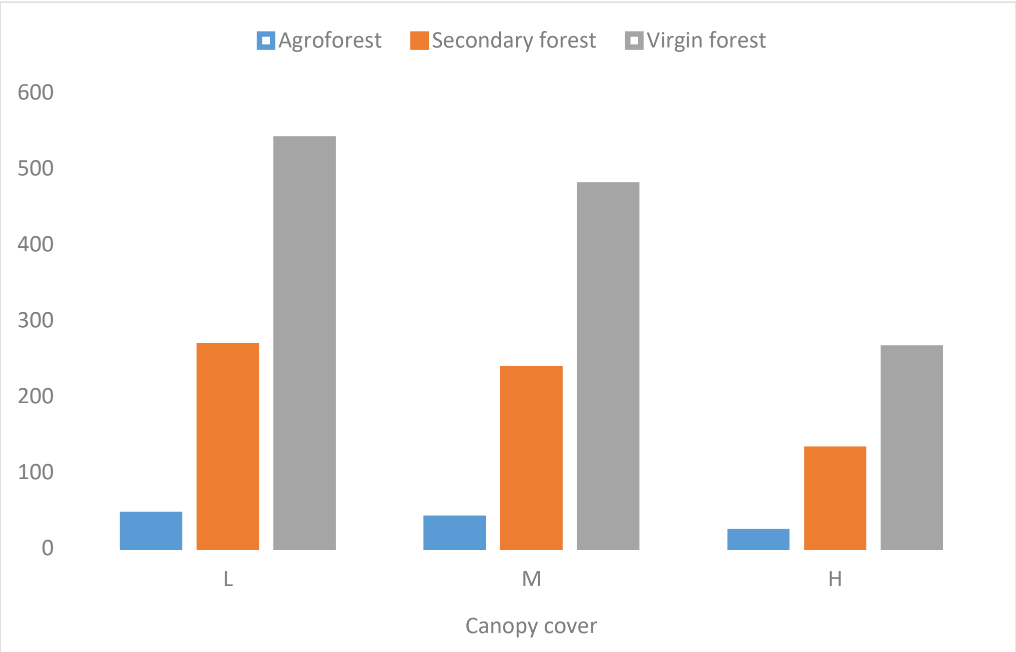


Figure 13: Total abundance (n=4566) divided between forest types (Blue= Agroforest, orange=Secondary forest, grey= Virgin forest), and canopy cover (L= low, M= medium, H= high.), calculated from the GLM model in table 6.

3.3 Dung type analysis

I used a paired t-test and a Wilcoxon signed rank test to test if there was significant difference between dung types for diversity, richness and abundance. A paired t-test was used for normal distributed data (abundance and richness), and Wilcoxon signed rank test for non-normal data (diversity). Mean was calculated for normal distributed data, whereas median for non-normal data. The difference in abundance, richness and diversity between pig and cow dung was tested for all forest types in total (table 8). There was a significant higher total abundance in pig dung compared to cow dung with $p<0.001$ (table 8). Total species richness showed no significant difference. The total diversity was also significantly higher in pig dung than cow dung. GLM models were made to test differences in abundance between dung types separately by forest type (table 9). The abundance was significantly higher in pig dung in all forest types as shown in table 9 ($p<0.001$).

Table 8: P-values based on a paired t-test (abundance and richness) and Wilcoxon signed ranked test (diversity) between pig- and cow dung in total (n=4566). Mean was calculated for abundance and richness, whereas median for diversity. Pig dung and cow dung are used as response variables.

Total	Pig vs. cow dung		p- value
Abundance	204.3	100.1 (mean)	0.0003***
Richness	8.7	7.9 (mean)	0.104
Diversity	0.29	0.26 (median)	0.023*

Table 9: Parameter estimates from GLM models for abundance captured in pig- and cow dung across forest types (n=4566). "Agroforest" (n=425), "Secondary forest" (n=1516) and "Virgin forest" (n= 2635) are used as response variables. Intercept is presented by the dummy variable "Cow dung".

Abundance	Variables	Estimate	Std. Error	z	p- value
Virgin forest	Cow dung (intercept)	5.166	0.034	152.90	<0.001 ***
	Pig dung	0.697	0.041	16.86	<0.001 ***
Secondary forest	Cow dung (intercept)	4.662	0.044	107.22	<0.001 ***
	Pig dung	0.624	0.054	11.57	<0.001 ***
Agroforest	Cow dung (intercept)	2.955	0.102	28.952	<0.001 ***
	Pig dung	0.967	0.124	7.801	<0.001 ***

3.4 Species composition

Because the axis length of the unconstrained DCA's PC1 was estimated to be 3.2 (close to 3) (appendix 8), I chose to continue the ordination analyses using a PCA approach, indicating that the response variables are mainly linearly distributed.

The arrows retrieved from the selected PCA describe the factor loadings of the 10 most responsive species. Species loading in different directions are negatively correlated, whereas species close to each other in the same direction are positively correlated. Larger arrows have higher loadings. I used canopy cover, dung type and forest type as effects in the model.

A permutation test was done to look at the combined effect for forest type, canopy cover and dung type. From the permutation test results (table 10) we can see that all predictors have a significant effect on species composition. As we can see from table 10, forest type explains 44% of the species composition data. The greater the r- squared, the better the model fits the data. The entire model explains 58% of the total variance as shown in table 11.

Table 10: Result from the permutation test. Partial R^2 and p-values explain variation from the PCA analysis in dung beetle communities based on the effects of "Forest type", "Dung type" and "Canopy cover". R^2 indicates how well the model fits the data. P-value shows statistical significance at 95% confidence level. Forest type is the best estimator of species composition, explaining 44% of the variance.

Effect	**R^2**	**p- value**
Forest type	0.438	0.001 ***
Dung type	0.228	0.004 **
Canopy cover	0.330	0.001 ***

Table 11: Partitioning of variance values from the PCA analysis. The inertia (total variance of the dataset), and proportion values in the model for canopy cover, dung type and forest type. The model explains 58% of the total variance from the PCA analysis.

	Inertia	**Proportion**
Total	19.947	1.000
Constrained	11.659	0.585
Unconstrained	8.288	0.416

In the following, I will look further into the nature of the fitted effects included in the PCA visualized as 90% centroids in the prediction figures. According to figure 14 a**,** agroforest has a different species composition compared to virgin- and secondary forest, which are correlated in similar species. The figure shows that species G, CC, J, F and D, are most commonly in virgin- and secondary forest, but not common in agroforest. Some individuals of agroforest species are also found in virgin forest, but in much lower abundance. The species composition is similar in virgin and secondary forest, but species G, CC, J, F and D show clear preference of virgin forest. This means that virgin forest as effect is most important for those species.

Figure 14a + b shows that virgin forest and secondary forest have similar patterns of species distribution, and show species similarity between canopy effect and forest type. Figure 14 a display that species G, J, CC, D and F are highly associated with virgin- and secondary forest, while species N is more associated with agroforest. It indicates a correlation between these species, and species G, species D and species CC are probably found in the same forest type. There is also more likely to find more individuals of species Q and E in virgin- and secondary forest. Also species E and Q is more likely to be found in virgin forest. Figure 14 b shows that the largest abundance of species G, J, CC, D and F was most likely to be found in medium- and high canopy cover. It is the same species (species G, J, CC, D and F) that were most likely to be found in high canopy cover and virgin forest. Figures 14a+b show similar patterns in species composition between different canopy densities and forest types. Fewer species are associated with low canopy cover, as well as agroforest as seen in the figures.

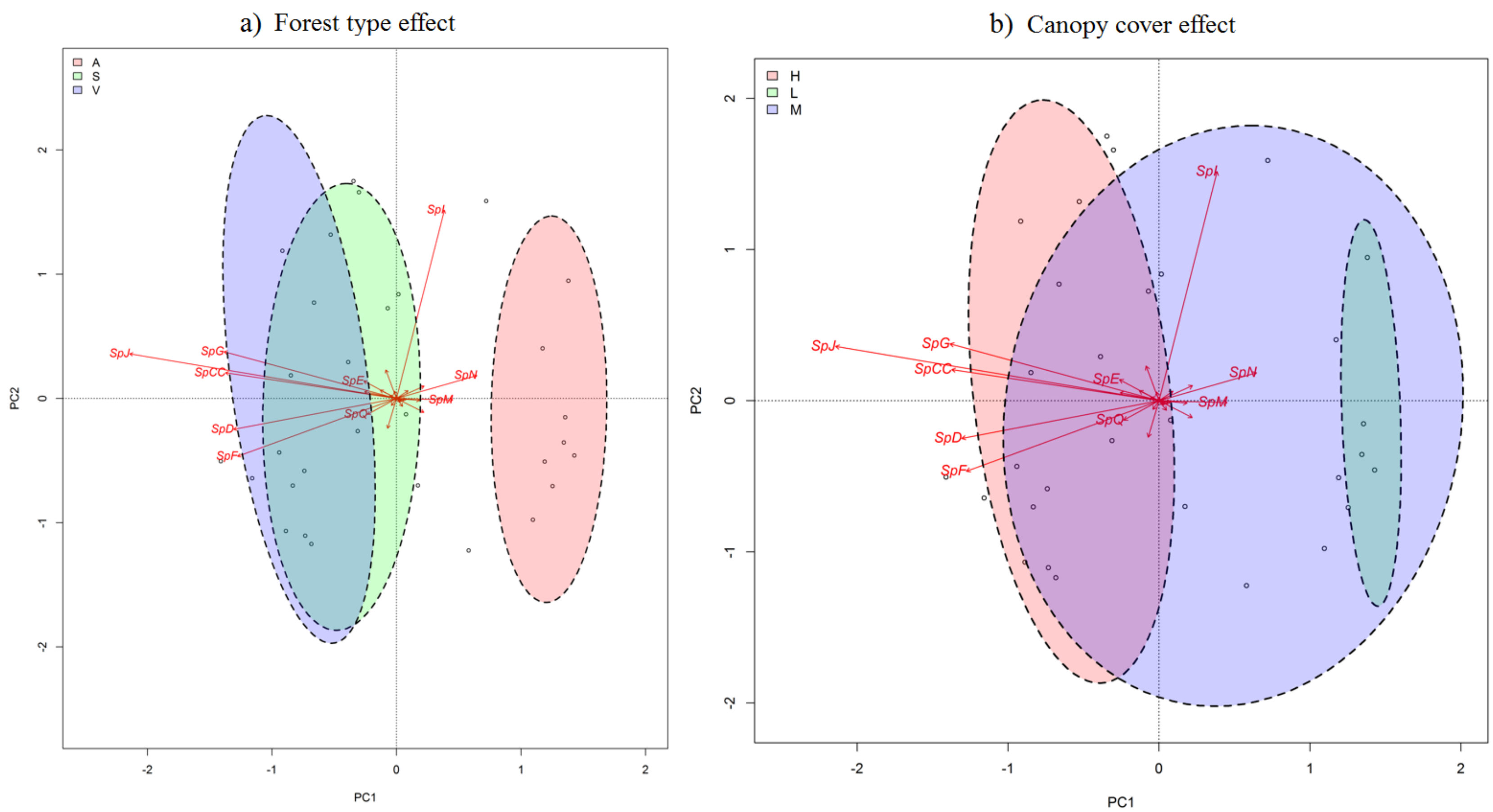


Figure 14: a) Biplot of the model presented in table 10. 90% centroids for the forest type effects (A= agroforest; S= secondary forest; V= virgin forest) as fitted in the model. The figure shows the effect on the species composition from forest type, the most important explanatory factor for species composition. b) 90% centroids for the canopy cover effects (H=high; M=medium; L=low) as fitted in the model presented in table 10. The figure shows the effect on the species composition from canopy cover. Only the ten most important species loadings are displayed in both figures.

Figure 15 shows that there are two species communities that prefer specific dung type, and they are negatively correlated. It shows obvious dung preferences between species G, J, CC, D and F and pig dung. The highest number of species where captured in traps with pig- dung, and there was a significant difference between the abundance captured in pig versus cow dung ($p<0.001$, table 8).

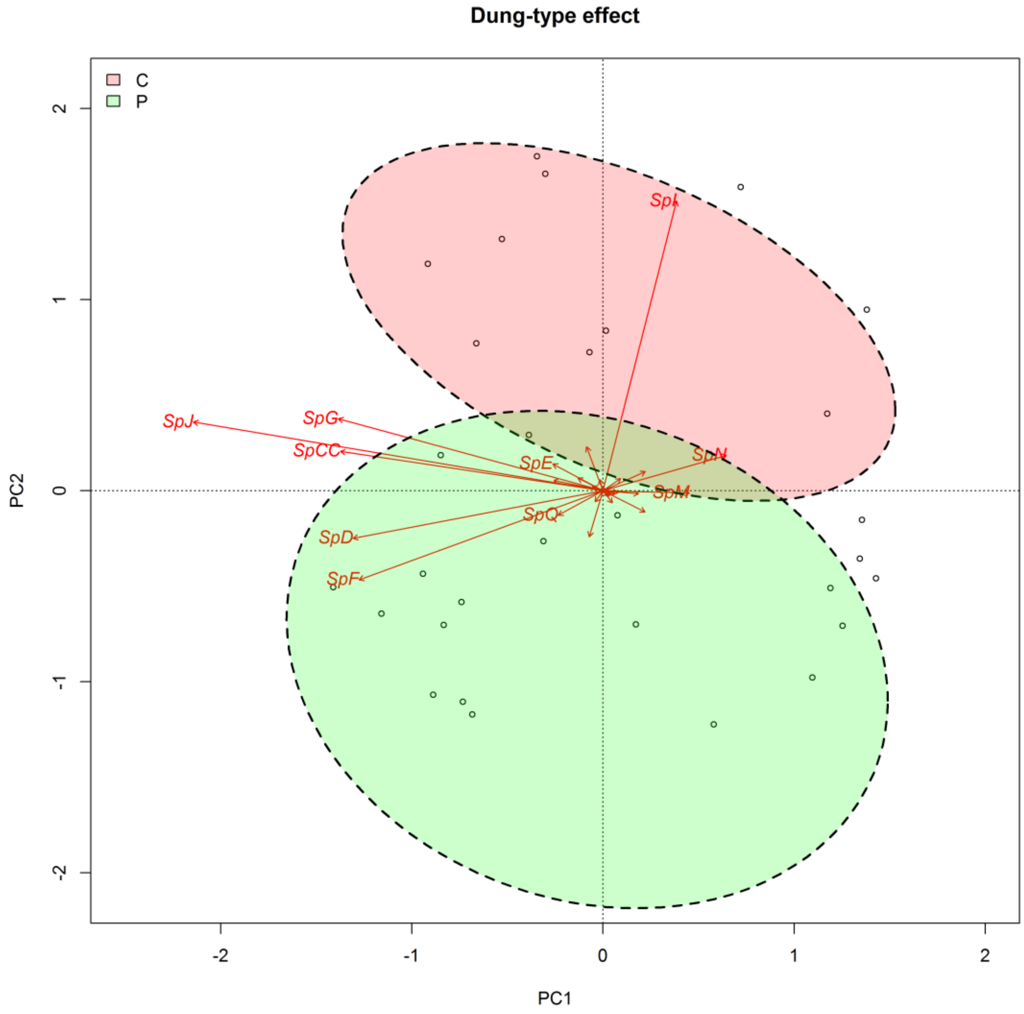


Figure 15: Biplot of the model presented in table 10. 90% centroids for the dung-type effects (P= pig; C= cow) as fitted in the model shows the effect on the species composition. Only the ten most important species loadings are displayed.

4. Discussion

4.1 Species richness, abundance, diversity and evenness in forests with different degree of disturbance

In total, 4566 individuals of dung beetles were captured, 2635 were captured in virgin forest, 1516 in secondary forest and 415 in agroforest. Abundance decreased significantly in forest types with more disturbance (secondary forest and agroforest), whereas richness, evenness and diversity did not show any significant difference across the three forest types. However, richness and evenness increased in the most disturbed habitat; agroforest. A higher dung beetle abundance was found in virgin forest, while evenness and richness were not higher in virgin forest as described in prediction number one.

Some dung beetle species were significantly more common in virgin forest than agroforest. Abundance was the only variable that was significantly different across all three forest types. Canopy cover and forest types were the best indicators that explained abundance of dung beetles in different forest types. This is supported by another study by Costa et al. (2013) that found a low dung beetle abundance in forests with a more open canopy. In a study done by Nichols et al. (2007), they found increasing abundance with increasing size in fragments. This could imply that more species could have inhabited agroforests in Amani Nature Reserve if the agroforest areas were larger. If the low abundance in agroforest compared to virgin- and secondary forests in this study represent an accurate estimation, the low abundance may cause reduced beetle activity (Kirk 1992). Further, this can have a negative impact on seed dispersal and soil fertility. Of all the most common species captured in this study, species were most abundant in secondary forest and virgin forest. Only secondary forest showed significantly lower individuals compared to virgin forest because of zero inflation in agroforest of species F. When primary forests gets fragmented, it may reduce insect species abundance, which again might cause species to be defined as functionally extinct due to the species rarity (Didham et al. 1996). This could be a possibility of the low abundance found in agroforest in Amani Nature Reserve. Low abundance in agroforests may be due to the presence of arid areas and a reduction in forest volume, but also the humidity and conditions inside a closed forest compared to sunny and dry areas like agroforest. All the agroforest sites in this study had small surface areas. On the other hand, agroforests may contain several niches due to alteration of the forests.

Diversity was higher in virgin forest, but the difference between forest types was non-significant. A significantly higher dung beetle diversity was found in primary forest compared to secondary forest in a study by Boonrotpong et al. (2004) in southern Thailand. In another study by Pryke et al. (2013), they found lower alpha-diversity in natural indigenous forests in South America. Further, there were recorded dung beetle species in pine plantation forests not found elsewhere in the study. Pine plantation was the habitat exposed to most human disturbance in the study by Pryke et al. (2013), which may show a similar pattern in Amani Nature Reserve where the number of species not found elsewhere, was highest in agroforest.

Out of the three forest types, agroforest showed the highest species richness followed by virgin forest. Only 14 species were captured in secondary forest. Some species of dung beetle were significantly more common in virgin forest than agroforest. Several other studies also found a reduction of dung beetle species in modified habitats compared to more pristine forests (Boonrotpong et al. 2004; Halffter & Arellano 2002; Nichols et al. 2007). The species richness in a disturbed area does not necessarily diminish (Costa et al. 2013; Halffter & Arellano 2002), because species from outside the forest may replace the dung beetles restricted to forest habitats (Halffter & Arellano 2002). Furthermore, species may eventually go functionally extinct or be replaced by other dung beetle species (Halffter & Arellano 2002). One possibility for the high number of species in agroforest in this study, might be a mix of generalist dung beetle species from habitats outside the study area. In addition, there could still be more species migrating to agroforests (Halffter & Arellano 2002). According to Lewis (2009), disturbed forests can have a larger number of species, even though it is normal to assume the opposite (Lewis 2009). This pattern may explain the high richness in agroforest but low abundance in Amani Nature Reserve. The results from this current study indicate that most species were only represented by very few individuals in agroforests. Over half of the species captured in agroforest in Amani Nature Reserve had only a few individuals or only one represented species. According to Lewis (2009), the low number of individuals can indicate a possible future local extinction, or at least a decline of species diversity and abundance with an increase of agroforestry fragments. This is largely because species in disturbed forests are rare and often specialists, endemic, or have arrived to the habitat from a small gene pool of small size (Lewis 2009). Klein (1989) found more rare species with few individuals in fragments in central Amazonia (Klein 1989). According to Kirk (1992), where dung beetle species are stenotopic (adaptable only to a narrow niche) to forests, increased disturbance might cause reduced species richness.

In a study by Nichols et al. (2007), they found a reduction in species richness with less tree cover. In addition, dung beetles with small size and less individuals per species were found in habitats with low percentage of canopy cover. Furthermore, this may lead to greater chance for species turnover (Nichols et al. 2007). A reduction in canopy cover and fragmented forest may be an explanation for the small dung beetle size and reduced abundance in agroforest in Amani Nature Reserve (Nichols et al. 2007). Additionally, species only captured in agroforest in Amani Nature Reserve were captured in low number in agroforests. Species only found in specific habitats may give biodiversity value (Pryke et al. 2013). Further, this study also indicates that habitats like agroforestry, may help dung beetle dispersal across forest types in a fragmented landscape (Pryke et al. 2013). Nevertheless, dung beetle composition does change in the agroforest sites compared to virgin- and secondary forest, as discussed later associated with prediction number two.

According to the species accumulation curves, they did not show accurate species richness estimation in virgin forest and agroforest. Species may still migrate into agroforest habitats. This can mean that more species could have been captured if more traps were added, and for a longer sampling period. Secondary forest managed to present a better estimation on the species richness. This may indicate that the number of species captured would probably not increase significantly with more traps. However, there could be a significantly higher species number with more traps in virgin forest and agroforest. It is important to take into consideration that due to a small dataset with great variety and zero inflation, it may be challenging to identify significant differences.

There were no significant differences in species evenness between forest types in this study. Nichols et al. (2007) however, found low evenness in highly modified habitats and small fragments because of the high abundance but low number of species. On the other hand, Barragán et al. (2011) found no difference in evenness between habitats with different degree of human interference. Both studies found higher species richness in larger fragments.

Changes in forests may cause decline in mammals and dung, that dung beetles depend on. Dung beetles depend on vertebrate dung, and a reduction in mammals can have a negative impact on the biodiversity of dung beetles. No data of animals were registered during the fieldwork. However, the reduction of mammals in Amani Nature Reserve in the last decades may have influenced dung beetle richness and abundance in agroforests (Newmark 2002; Spector 2006).

According to Estrada et al. (1998), there were more dung beetle species in closed canopy forests compared to forest fragments in Los Tuxtlas, Mexico. Further, this was most likely due to a reduction of the mammal population in the forest fragments. This is supported by another study done in Morogoro, Tanzania where the mammal population have decreased due to human population growth, deforestation and degradation of forests and woodlands (Nielsen 2007). This had a negative effect on dung beetle fauna, where both abundance and richness were reduced (Nielsen 2007). Small habitats that are isolated from larger fragments, may support a smaller community of mammals. This might have an influence on dung beetle communities (Estrada et al. 1998). Further, this may be one of the explanations of the differences in species composition found in Amani Nature Reserve. Viljanen et al. (2010) found that a reduction in mammals with a size larger than 10 kg had a negative effect on dung beetle richness in different regions throughout the tropics. Harvey et al. (2006) found a significantly higher number of mammals in intact forest compared to plantations and agroforestry in a study performed in Costa Rica. Further, the highest biodiversity of both dung beetles and mammals, were found in intact forests and on an intermediate level in agroforestry. Yet, the biodiversity was still higher in agroforestry compared to plantation forests (Harvey et al. 2006).

After heavy habitat disturbance, faunal species richness and communities may recover in 20-40 years if the source populations are nearby and the disturbance level is low (Dunn 2004). This may give a more accurate estimation of the species composition of dung beetles in relation to the composition of mammals in Amani Nature Reserve in secondary forest and agroforest, compared to forests that are recently logged or logged only a few years ago. In Amani Nature Reserve, secondary forest and agroforest are located near virgin forest.

Due to the change in diversity from natural forests to plantations, Pryke et al. (2013) highlights the importance of conservation not only for natural forest fragments, but also other forest patches such as agroforestry. Agroforestry may be important for conservation value as shown in a study by Harvey et al. (2006). As in Amani where agroforestry patches are included within the forest fragments, they may have great biodiversity value (Harvey et al. 2006). It is found that agroforestry as a habitat has less negative effect on mammal dung and dung beetle communities compared to plantations. Yet, dung beetles often get impacted on a higher level in agroforest than virgin forests (Harvey et al. 2006). The value of dung beetles in agroforest depends on the canopy cover, where agroforest with more canopy cover can support higher species richness than agroforests with low canopy cover (Bhagwat et al. 2008). Furthermore, agroforest may have large value for overall conservation, because the species composition can be highly different from forests with closed canopy cover, and specialist species in disturbed habitats are often few in numbers (Bhagwat et al. 2008).

4.2 Species composition in forests with different degree of human disturbance

As described in prediction number two, forest habitats with an increase in human disturbance may, not only cause a decrease in diversity and abundance, but also a change in species composition. Forest cover was the effect with largest impact on the dung beetle composition, then canopy cover followed by dung type. The species composition changed across the forest types, which might be caused by the differences in disturbance gradient. Species composition in agroforest was negatively correlated to the species composition in secondary forest and virgin forest. Virgin forest and secondary forest were closely correlated in species community. Low canopy cover was found in agroforest and high canopy cover in virgin forest. This result shows similar species composition based on forest type and canopy cover. A previous study by Aasland (2015) in Amani Nature Reserve, found two species from the genera *Sceliages* and *Sacrophorus,* assumed new species in the area. The species composition was found more evenly distributed in forests without any human disturbance, and a higher diversity was found in these forests (Aasland 2015). According to Davis et al. (2008), only two genera of dung beetles were found in Amani Nature Reserve in 2008 in a virgin forest which are endemic species to Eastern Africa.

According to Nichols et al. (2008), several studies show changes in dung beetle communities under large alterations in habitats. Wen habitats are disturbed, mammals are negatively affected both in temperate and tropical areas (Nichols et al. 2008). In East Usambara Mountains and Amani Nature Reserve, the mammal population has been greatly reduced the last decades (Newmark 2002). A study done in southern Thailand found that presence of native animals, structure of the forest and physical factors had an impact on beetle communities in primary- and secondary forest (Boonrotpong et al. 2004). A statement by Barbero et al. (1999); *"Patchy ecosystems characterized by open and wooded habitats and inhabited by several ungulate species can support the highest levels of dung beetle diversity",* might be used as a parallel to other species of mammals inhabiting Amani Nature Reserve. Even though there are no ungulate species in Amani Nature Reserve, the statement may show similar patterns to mammals.

As expected, species associated with virgin forest were highly correlated with forests with high percentage of canopy cover. Species composition differed between low and high percentage of canopy cover in this study. According to (Scholtz et al. 2009), dung beetle communities were similar in secondary and virgin forests, largely due to the similarity in forest cover in both forest types. A similar trend can be seen in the results from Amani Nature Reserve, where secondary- and virgin forest with high canopy cover have highly different species composition compared to agroforest with low canopy cover. Increased canopy cover can thus improve viable habitats for forest restricted dung beetle species. This is supported by another study that found changed local dung beetle species composition due to a reduction in canopy cover (Halffter & Arellano 2002). Further, they found more dung beetle species in less disturbed forests. According to Nichols et al. (2007), dung beetle communities was impacted negatively with major decrease in tree cover, or no tree cover at all. This caused a decline in dung beetle abundance (Nichols et al. 2007). They further concluded through different studies that dung beetle communities were reduced in richness and abundance in the majority of forest fragments compared to intact forest. In addition, areas with reduced forest cover lose more moisture (Davis et al. 2008) which can make beetle activity during day time shorter. Some dung beetles stay inactive in the soil during very dry conditions (Davis et al. 2008).

In fragmented landscapes, many factors have a role in the species community such as availability of dung, the time since disturbance and other vegetation changes (Nichols et al. 2007). Even though no rainfall measurements were registered during this fieldwork, or statistically tested, I could notice a difference in dung beetle abundance. After heavy rain in virgin- and secondary forest, a higher number of individuals than normal were captured. I did not notice any difference in agroforest. A minimum of beetles were collected at every agroforest trap during harvest. A previous study done in South Africa, found that environmental factors such as soil type and moisture most likely caused changes in grassland habitats. Further, these factors may cause the difference in dung beetle beta-diversity, and not the difference in the habitats itself (Pryke et al. 2013). According to a study done in central Amazonia, more dung beetle individuals were captured during the rainy season compared to the dry season (Andresen 2002). Different taxa have different resource requirements, where some dung beetle species are specialists in open and dry habitats with low soil moisture and higher levels of sunlight (Costa et al. 2013). This might apply for the species only captured in agroforest in Amani Nature Reserve. Because more individuals were captured in closed canopy forest, rainy conditions may have had an influence on the abundance found in closed canopy forest, with even more captured individuals with heavy rain. According to Davis et al. (2008), the beetle activity is normally affected by heavy rain, and is usually highest on days after these weather conditions. This applies for most of the dung beetle species as long as the temperature is relative warm (Davis et al. 2008). The temperature decrease in a slower rate in moist conditions compared to dry conditions (Davis et al. 2008).

As mentioned earlier, only eight species of rollers were captured where the majority of the individuals were captured in moist climate. According to Davis et al. 2008, the majority of roller species are most likely to be in majority in dry climate, whereas tunnellers often have a higher abundance in moist climate. This applies for all the species that are more abundant in virgin- and secondary forest in this study. Species A, D, F and species G that were in majority in virgin- and secondary forest, were all tunnellers or dwellers. Species L and species M were both rollers, and were found mostly in agroforest. Many roller species that prefer sunny areas, prefer agroforestry because closed canopy forests may act as barriers (Scholtz et al. 2009).

The production of brood balls was significantly higher in higher soil moisture levels (Barkhouse & Ridsdill-Smith 1986), which may show a similar pattern on the abundance in Amani Nature Reserve in closed-canopy forest, where the moisture level was high. Both secondary forest and virgin forest showed significantly higher abundance than agroforest. If brood ball production is increasing with moisture levels, it may be a possible explanation for the high dung beetle abundance in closed canopy forests. During pupation, the dung beetle will sometimes not continue emergence to the adult stage until the pupae has absorbed enough moisture from the soil after heavy rain (Hanski & Cambefort 2014).

4.3 Distribution of dung beetles with large body size

Dung beetle size in tropical areas commonly varies between 2.5-37mm depending on the species (Andresen & Feer 2004). This also applies for the dung beetles I collected in Amani Nature Reserve (3.5-33mm). As expected in prediction number three, beetles with larger body size were less abundant in agroforest. Species D was significantly more abundant in both virgin- and secondary forest compared to agroforest. Species E was significantly less abundant in agroforest compared to virgin forest, and species K was significantly less abundant in secondary forest compared to virgin forest. Species F was also one of the larger species, but due to no captured individuals in agroforest it did not show any significant difference. A study done by

Barragán et al. (2011) in central and southeastern Mexico, showed that the distribution of large beetles was negatively affected by habitat transformation because the species were depended on continuous forest (Barragán et al. 2011).

Loss of mammals may cause a poor dung beetle community which may affect the regeneration of the forest floor (Griffiths et al. 2016). Reduction in species higher up in the food chain can alter species interactions in a trophic cascade (Dyer & Letourneau 1999; McCann 2007). In dung beetle communities, exclusion of larger species can have an influence on the composition of plant species on the forest floor in a top-down effect (Griffiths et al. 2016). Large dung beetle species often bury more seeds, and can bury a larger amount of dung that may contain many seeds (Andresen 2002). Further, this may improve secondary seed dispersal of plants. An experimental study by Andresen (2003) show that far less seeds were buried with only small bodied dung beetle species present. Further, larger beetles bury seeds deeper in the soil compared to smaller dung beetles. Andresen (2003) found that with increasing habitat size in a central Amazonian rainforest, the mean dung beetle size also increased. Further, they found a decline in seed burial of three plants with reduction on the abundance in large bodied beetles. Since almost 90% of remaining seeds on the soil surface are eaten by seed predators living in tropical forests (Estrada & Coates-Estrada 1991), a large dung beetle abundance and diversity are important. Large dung beetles relocate seeds further away from the soil surface, which may reduce the precentage of seeds eaten by animals (Estrada & Coates-Estrada 1991). Because large dung beetle species often bury more seeds (Andresen 2002), this may have a positive impact on the soil and forest floor, by seed dispersal and nutrient cycling.

Large beetles were also found more commonly in continuous forest compared to fragments in central Amazonia (Andresen 2003; Klein 1989). Klein (1989) captured both more species and more individuals in continuous forest than in clear-cut areas and small fragments. A similar pattern might apply for species richness in virgin forest compared to agroforest in Amani Nature Reserve. Seed burial and removal of dung can happen to a greater extent in forests with a larger surface area compared to fragments (Andresen 2002). Amani Nature Reserve consists mostly of fragmented forest areas because of the large extent of logging prior to establishment of the reserve.

The reason why I did not find any significant differences between species B and C and all forest types, might be due to only one captured individual of species C in agroforest. No individuals of species B was found in secondary forest. Species A was not found in agroforest at all. These high values of zero inflation may have been affecting the results.

4.4 Species composition in different dung types

Dung beetles appeared to prefer pig dung over cow dung in Amani Nature Reserve, which were the two types of dung that were used. The abundance was significantly higher in pig dung compared to beetles captured with cow dung in overall abundance and diversity. The abundance was also significantly higher in pig dung compared to cow dung in all forest types. The species composition also changed from dung type as described in prediction four. Pig dung has a stronger smell than cow dung, which may be one reason why I found an increasing number of individuals captured in pig dung. If some species prefer a specific dung type rather than another, it would be possible to capture more individuals of beetles and species in Amani Nature Reserve if a preferred dung type was used. Previous studies have found that dung beetles were mostly attracted to carnivore dung, compared to herbivore dung (Whipple & Hoback 2012). Whipple and Hoback (2012) found that omnivore dung type was far more attractive than other bait types. This can be explained by the high nitrogen content and low fiber levels (Davis 1994). Davis (1994) found that 38 dung beetle species out of 39 were more attracted to pig dung. Since pigs are omnivores and cows are herbivores, these result may also show similar patterns as in Amani Nature Reserve.

According to Davis et al. (2008), deforestation results in wildlife loss which can affect diversity and composition of dung. In addition, this might have an influence on the composition of dung beetle species. Because dung beetles are attracted to different dung types, this may also have an effect on the beetle composition from Amani Nature Reserve (Barbero et al. 1999). In a study done in Bolivia by Kirk (1992), only cow dung was used as dung beetle bait. Further, he predicted that more beetles probably would have been captured if omnivore dung was used. In other words, a similar trend was found in this study where the abundance was significantly lower in cow dung compared to pig dung.

Dung beetles use dung for both egg laying and food, which makes dung important for sustaining a dung beetle community (Barbero et al. 1999). Since a different species composition of dung beetles was found in agroforest compared to virgin- and secondary forest, it might indicate a change of natural habitats. The introduction of cows in agroforests in Amani Nature Reserve might have an influence on the dung beetle community as well, as they are omnivores. Since a significantly higher abundance was found in pig dung in this current study, it might indicate a change in dung beetle communities if cows are continuing to dominate the agroforests. This can be supported by a study by Halffter and Arellano (2002), where dung beetle composition changed with cattle introduction in open areas in tropical forests in Veracruz, Mexico.

4.5 Importance of conservation

Decreasing diversity and abundance seems to follow a disturbance gradient, and alteration of forests seem to modify dung beetle communities as well as mammal populations, as found in a study by Harvey et al. (2006). However, several species were found only in agroforestry (Harvey et al. 2006). This can be supported by Pryke et al. (2013) who highlights the importance of conservation because it supports heterogeneity.

Amani Nature Reserve offers some of the last pristine forests in East Usambara Mountains, and primary forests are important to conserve species richness (Newmark 2002). However, agroforestry patches also have biodiversity value in fragmented landscapes (Pryke et al. 2013). As mentioned earlier, one of the main objectives for Amani Nature Reserve is to maintain the biodiversity by taking care of the undisturbed forests (Kremen et al. 1993). Further research on the dung beetle ecology in East Usambara and Amani Nature Reserve can have a positive effect on sustainable conservation management. Research on both intraspecific and interspecific competition between species is important, not only to study the number of individuals and species (McCann 2007). Because of the different habitats in Amani Nature Reserve, it is important to conserve habitats that have specialists, even if there are only few species. Small areas may maintain species with special ecosystem services, and specialist species may often not be found elsewhere (Rodrigues et al. 2013). Landscape heterogeneity allow some species to live in one habitat patch and other species in a different patch. This may be a possibility for the dung beetle species only captured in each forest type in Amani Nature Reserve. According to Pryke et al. (2013), a diversity of landscape patches and elements should be included in conservation planning due to the importance of heterogeneity.

This is one reason why it is important to conserve small geographical areas, and not only one habitat type with large surface are (Rodrigues et al. 2013).

According to Losey and Vaughan (2006), if 50% of the dung beetle density would disappear, 50% of the ecosystem services dung beetles provide can disappear as well. A reduction in mammals often affect the dung beetle communities and diversity because of reduction in vertebrate dung (Barbero et al. 1999). According to Barbero et al. (1999), conservation biologists should look at the degree of resilience applicable for dung beetle spices, and the factors they need to sustain a community. Common challenges for forest insects in a human influenced landscape is the forest cover that disappear (Warren & Key 1991), and the focus should therefore in many areas be for open areas which once had a larger radius in canopy cover, and mature old growth forest according to Warren & Key (1991).

Conservation corridors may benefit dung beetle communities in a fragmented landscape. Corridors makes it easier for mammals to stay in fragmented areas, where dung beetles will benefit from their dung (Hill 1997). According to Hill (1997), there is a question if corridors are efficient in a general context, and there should be done more research about the distribution and recolonizing of species when establishing a conservation corridor. Moreover, according to Kremen et al. (1993), especially arthropods which pollinate flowers and seed dispersing insects, should be a priority in management planning.

5. Conclusion

In conclusion, this study shows that two different species compositions of dung beetles are found based on forest type with different human disturbance level in Amani Nature Reserve. Virgin forest and secondary forest have many similar characteristics, and showed a similar species composition of dung beetles compared to agroforest. Furthermore, this indicates that species captured in this study, may prefer either agroforest or closed canopy forest. The differences in species composition and the number of individuals may be due to the reduction in mammals in Amani Nature Reserve during the last decades. Closed canopy forest soils have more moisture, which may affect dung beetle composition. This can support more beetles, and would thus improve viable habitat for forest restricted dung beetle species. Canopy cover and forest type may have been the main determining factors impacting dung beetle abundance and composition in this study. Species captured in virgin forest corresponded with high canopy cover. The same applied for secondary forest and agroforest with reduced levels of canopy cover. One might argue from this study together with other studies throughout the tropics looking at dung beetles and forest disturbance, that virgin forest is important for conservation value. This applies for forest restricted dung beetle species. However, agroforestry houses many species only found in that particular habitat, and 12 species were only captured in agroforest in this study. This underlines the importance of conservation of different habitat patches within a fragmented landscape, which adds to heterogeneity in the habitat. The agroforest sites are located near preserved fragments in Amani Nature Reserve, and can increase the heterogeneity of the general landscape.

6. References

Aasland, A. (2015). *Dung beetle (Scarabaeidae, Scarabaeinae) communities in mountain rain forests (Tanzania): A biodiversity survey from Amani Nature Reserve and Udzungwa Mountain National Park*. M.Sc. thesis. Ås: Norwegian University of Life Sciences, Department of Ecology and Natural Resource Management. 52 pp.

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

Andresen, E. (2003). Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. *Ecography*, 26 (1): 87-97.

Andresen, E. & Feer, F. (2004). The role of dung beetles as secondary seed dispersers and their effects on plant regeneration in tropical rainforests. In *Seed fate: predation, dispersal, and seedling establishment*, pp. 331-350. Cambridge, Massachusetts: CABI Publishing.

Barbero, E., Palestrini, C. & Rolando, A. (1999). Dung beetle conservation: effects of habitat and resource selection (Coleoptera: Scarabaeoidea). *Journal of Insect Conservation*, 3 (2): 75-84.

Barkhouse, J. & Ridsdill-Smith, T. J. (1986). Effect of soil moisture on brood ball production by Onthophagus binodis Thunberg and Euoniticellus intermedius (Reiche)(Coleoptera: Scarabaeinae). *Australian Journal of Entomology*, 25 (1): 75-78.

Barragán, F., Moreno, C. E., Escobar, F., Halffter, G. & Navarrete, D. (2011). Negative impacts of human land use on dung beetle functional diversity. *PLoS One*, 6 (3): 8.

Bhagwat, S. A., Willis, K. J., Birks, H. J. B. & Whittaker, R. J. (2008). Agroforestry: a refuge for tropical biodiversity? *Trends in ecology & evolution*, 23 (5): 261-267.

Binggeli, P. & Hamilton, A. C. (1993). Biological invasion by Maesopsis eminii in the East Usambara forests, Tanzania. *Opera Botanica*, 121: 229-235.

Boonrotpong, S., Sotthibandhu, S. & Pholpunthin, C. (2004). Species composition of dung beetles in the primary and secondary forests at Ton Nga Chang Wildlife Sanctuary. *Science Asia*, 30: 59-65.

Burgess, N. D., Butynski, T., Gordon, I., Luke, Q., Sumbi, P. & Watkin, J. (2003). Eastern Arc Mountains and coastal forests of Tanzania and Kenya: Biodiversity hotspots. *Ecosystem profile report prepared for Critical Ecosystem Partnership Fund*.

Collins, N. M. & Sutton, S. L. (2012). Insects and tropical forest conservation. In *The conservation of insects and their habitats*, pp. 405-422: Academic Press.

Conte, C. A. (2004). *Highland sanctuary: environmental history in Tanzania's Usambara Mountains*. Athens: Ohio University Press. 210 pp.

Costa, F. C., Pessoa, K. K. T., Liberal, C. N., Filgueiras, B. K. C., Salomão, R. P. & Iannuzzi, L. (2013). What is the importance of open habitat in a predominantly closed forest area to the dung beetle (Coleoptera, Scarabaeinae) assemblage? *Revista Brasileira de Entomologia*, 57 (3): 329-334.

Daily, G. C. (2001). Ecological forecasts. *Nature*, 411 (6835): 245-245.

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

Davis, A. L. V. (1994). Associations of Afrotropical Coleoptera (Scarabaeidae: Aphodiidae: Staphylinidae: Hydrophilidae: Histeridae) with dung and decaying matter: implications for selection of fly-control agents for Australia. *Journal of Natural History*, 28 (2): 383-399.

Davis, A. L. V., Frolov, A. V. & Scholtz, C. H. (2008). *The African dung beetle genera*. Pretoria: Protea Book House. 272 pp.

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

Didham, R. K. (1997). An overview of invertebrate responses to forest fragmentation. *Forests and insects*: 303-320.

Doody, K. Z., Howell, K. M. & Fanning, E. (2001). Amani Nature Reserve, A biodiversity survey. *East Usambara Conservation Area Management Programme, Technical Paper 52*. Tanga, Tanzania. 123 pp.

Dunn, R. R. (2004). Recovery of faunal communities during tropical forest regeneration. *Conservation Biology*, 18 (2): 302-309.

Dyer, L. A. & Letourneau, D. K. (1999). Trophic cascades in a complex terrestrial community. *Proceedings of the National Academy of Sciences*, 96 (9): 5072-5076.

EAMCEF. (2016). The Eastern Arc Mountains Conservation Endowment Fund. Available at: https://eamcef.wordpress.com/page/3/ (accessed: 23.08.2016).

Estrada, A. & Coates-Estrada, R. (1991). Howler monkeys (Alouatta palliata), dung beetles (Scarabaeidae) and seed dispersal: ecological interactions in the tropical rain forest of Los Tuxtlas, Mexico. *Journal of Tropical Ecology*, 7 (04): 459-474.

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

Foley, J. A., Asner, G. P., Costa, M. H., Coe, M. T., DeFries, R., Gibbs, H. K., Howard, E. A., Olson, S., Patz, J. & Ramankutty, N. (2007). Amazonia revealed: forest degradation and loss of ecosystem goods and services in the Amazon Basin. *Frontiers in Ecology and the Environment*, 5 (1): 25-32.

Fowler, J., Cohen, L. & Jarvis, P. (2013). *Practical statistics for field biology*. 2nd ed. Chichester: John Wiley & Sons. 259 pp.

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

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F. & Lovejoy, T. E. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478 (7369): 378-381.

Griffiths, H. M., Bardgett, R. D., Louzada, J. & Barlow, J. (2016). The value of trophic interactions for ecosystem function: dung beetle communities influence seed burial and seedling recruitment in tropical forests. *The Royal Society Publishing*.

Groombridge, B., Centre., W. C. M. & Museum., N. H. (1992). *Global biodiversity : status of the earth's living resources : a report*. London: Chapman & Hall. 585 pp.

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

Hall, J. M., Burgess, N. D., Lovett, J., Mbilinyi, B. & Gereau, R. E. (2009). Conservation implications of deforestation across an elevational gradient in the Eastern Arc Mountains, Tanzania. *Biological Conservation*, 142 (11): 2510-2521.

Hall, J. M., Gillespie, T. W. & Mwangoka, M. (2011). Comparison of agroforests and protected forests in the East Usambara Mountains, Tanzania. *Environmental management*, 48 (2): 237-247.

Hanski, I. & Cambefort, Y. (2014). Dung beetle population biology. In *Dung beetle ecology*

Princeton, New Jersey: Princeton University Press.

Harvey, C., Gonzalez, J. & Somarriba, E. (2006). Dung Beetle and Terrestrial Mammal Diversity in Forests, Indigenous Agroforestry Systems and Plantain Monocultures in Talamanca, Costa Rica. *Biodiversity & Conservation*, 15 (2): 555-585.

Hill, C. J. (1997). Conservation corridors and rainforest insects. *Forests and Insects*: 381-393.

Ieno, E. N. & Zuur, A. F. (2015). *A Beginner's Guide to Data Exploration and Visualisation with R*. Newburgh, United Kingdom: Highland Statistics Ltd. 174 pp.

IUCN. (2014). *Global appetite for resources pushing new species to the brink – IUCN Red List*: International Union for Conservation of Nature. Available at: http://www.iucn.org/?18621/Global-appetite-for-resources-pushing-new-species-to-the-brink--IUCN-Red-List (accessed: 08.12.14).

Kirk, A. A. (1992). Dung beetles (Coleoptera: Scarabaeidae) active in patchy forest and pasture habitats in Santa Cruz Province, Bolivia, during spring. *Folia Entomologica Mexicana*, 84: 45-54.

Klein, B. C. (1989). Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology*, 70 (6): 1715-1725.

Kremen, C., Colwell, R. K., Erwin, T. L., Murphy, D. D., Noss, R. F. & Sanjayan, M. A. (1993). Terrestrial arthropod assemblages: their use in conservation planning. *Conservation biology*, 7 (4): 796-808.

Lewis, O. T. (2009). Biodiversity change and ecosystem function in tropical forests. *Basic and Applied Ecology*, 10 (2): 97-102.

Losey, J. E. & Vaughan, M. (2006). The economic value of ecological services provided by insects. *Bioscience*, 56 (4): 311-323.

Lovett, J. C. & Moyer, D. C. (1992). A new nature reserve in the Eastern Arc mountains, Tanzania. *Oryx*, 26 (02): 115-118.

Lugo, A. E. & Helmer, E. (2004). Emerging forests on abandoned land: Puerto Rico's new forests. *Forest Ecology and Management*, 190 (2): 145-161.

Magurran, A. E. (2013). *Measuring biological diversity*: Wiley-Blackwell. 264 pp.

McCann, K. (2007). Protecting biostructure. *Nature*, 446 (7131): 29-29.

Medina, C. A., Escobar, F. & Kattan, G. H. (2002). Diversity and Habitat Use of Dung Beetles in a Restored Andean Landscape1. *Biotropica*, 34 (1): 181-187.

Ministry of Natural Resources and Tourism. (2008). *Executive Summary for Management of Amani Nature Reserve* Ministry of Natural Resources and Tourism, Tanzania Forestry and Beekeeping Division.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403 (6772): 853-858.

Newmark, W. D. (2002). *Conserving biodiversity in East African forests: a study of the Eastern Arc Mountains*, vol. 155. Germany: Springer Science & Business Media. 197 pp.

Newmark, W. D. & Senzota, R. B. M. (2003). Power to detect trends in ecological indicators in the East Usambara Mountains, Tanzania. *African Journal of Ecology*, 41 (4): 294-298.

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

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

Nielsen, S. T. (2007). Deforestation and biodiversity: effects of bushland cultivation on dung beetles in semi-arid Tanzania. *Biodiversity and Conservation*, 16 (10): 2753-2769.

Oksanen, J. (2015). *Multivariate analysis of ecological communities in R: vegan tutorial*. University Oulu, Finland. Available at: http://cc.oulu.fi/~jarioksa/opetus/metodi/vegantutor.pdf (accessed: 19.05).

Protected Planet. (2016). Available at: https://www.protectedplanet.net/ (accessed: 19.04).

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

Rodrigues, M. M., Uchoa, M. A. & Ide, S. (2013). Dung beetles (Coleoptera: Scarabaeoidea) in three landscapes in Mato Grosso do Sul, Brazil. *Brazilian Journal of Biology*, 73 (1): 211-220.

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

Schulman, L., Junikka, L., Mndolwa, A., Rajabu, I. & Lovett, J. (1998). *Trees of Amani Nature Reserve, NE Tanzania*. Tanzania: Ministry of Natural Resources and Tourism.

Soule, M. E. & Simberloff, D. (1986). What do genetics and ecology tell us about the design of nature reserves? *Biological conservation*, 35 (1): 19-40.

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

Tropical Biology Association. (2007). Amani Nature Reserve, an introduction.

Viljanen, H., Escobar, F. & Hanski, I. (2010). Low local but high beta diversity of tropical forest dung beetles in Madagascar. *Global Ecology and Biogeography*, 19 (6): 886-894.

Warren, M. S. & Key, R. S. (1991). Woodlands: past, present and potential for insects. *The conservation of insects and their habitats*: 155-211.

Whipple, S. D. & Hoback, W. W. (2012). A comparison of dung beetle (Coleoptera: Scarabaeidae) attraction to native and exotic mammal dung. *Environmental entomology*, 41 (2): 238-244.

Wright, S. J. (2005). Tropical forests in a changing environment. *Trends in ecology & evolution*, 20 (10): 553-560.

WWF. (2014). Amani Nature Reserve, tips for responsible tourism. *Amani Nature Reserve and East Usambara Mountains in Tanzania*. 31 pp.

Appendix 1

Appendix 1: GPS coordinates from every plot from Amani Nature Reserve, represented in map (figure 4). In the plot names, C= cow dung and P = pig dung.

Plot	Site name	GPS coordinates
VIP	Virgin forest	S 05*08.075' E 038*35.408'
VIC	Virgin forest	S 05*08.089' E 038*35.405'
V2P	Virgin forest	S 05*06.4061' E 038*35.981'
V2C	Virgin forest	S 05*06.422' E038*35.973'
V3P	Virgin forest	S 05*05.496' E038* 36.097'
V3C	Virgin forest	S 05*05.511' E 038*36.105'
V4P	Virgin forest	S 05*05.664' E 038*37.882'
V4C	Virgin forest	S 05*05.683' E038*37.903'
V5P	Virgin forest	S 05* 08.479' E 038*36.354'
V5C	Virgin forest	S 05*08.485' E 038*36.356'
S1P	Secondary forest	S 05*09.325' E 038*36.051'
S1C	Secondary forest	S 05*.09.322' E038*36.061'
S2P	Secondary forest	S 05*09.028' E038*36.388'
S2C	Secondary forest	S 05*09.028' E 038*36.378'
S3P	Secondary forest	S 05*06.294' E 038*35.862'
S3C	Secondary forest	S 05*06.308' E 038* 35.953'
S4P	Secondary forest	S 05*05.690' E 038*37.176'
S4C	Secondary forest	S 05*05.681'E 038*37.171'
S5P	Secondary forest	S 05*05.989' E 038*37.730'
S5C	Secondary forest	S 05*05.989' E 038*37.730'
A1P	Agroforest	S 05* 06.185' E038*37.524'
A1C	Agroforest	S 05* 06.179' E038*37.506'
A2P	Agroforest	S 05*06.123' E 038*38.084'
A2C	Agroforest	S 05*06.123' E 038*38.084'
A3P	Agroforest	S 05*05.866' E 038*38.164'
A3C	Agroforest	S 05*05.857' E 038*38.155'
A4P	Agroforest	S 05*06.265' E 038*37.579'
A4C	Agroforest	S 05*06.265' E 038*37.579'
A5P	Agroforest	S 05*06.229' E 038*37.661'
A5C	Agroforest	S 05*06.217' E 038*37.667'

Appendix 2

Appendix 2: Distribution of the large dung beetle species (>10mm) captured in Amani Nature Reserve.

Trap	Forest	SpB	SpD	SpE	SpG	SpC	SpA	SpK	SpF	SpL	SpM	SpS
V1P	V	20	20	0	18	0	3	2	7	0	0	0
V1C	V	0	9	0	10	0	5	3	45	0	1	0
V2P	V	0	39	4	73	0	0	2	12	0	0	0
V2C	V	0	34	0	9	0	1	0	74	0	0	0
V3P	V	0	21	4	53	0	0	3	15	0	0	0
V3C	V	0	13	0	7	0	1	0	15	0	0	0
V4P	V	0	9	18	24	0	0	1	0	1	0	0
V4C	V	0	17	0	12	0	0	0	12	0	0	0
V5P	V	0	1	0	15	0	0	1	3	0	0	0
V5C	V	0	3	0	4	0	1	0	2	0	0	0
S1P	S	0	11	0	19	0	0	0	5	0	0	0
S1C	S	0	4	0	7	0	1	1	14	0	0	0
S2P	S	0	2	0	18	0	2	1	1	0	0	0
S2C	S	0	2	0	1	0	0	0	5	0	0	1
S3P	S	0	31	0	65	0	1	0	4	0	0	0
S3C	S	0	14	0	19	0	0	0	31	0	0	0
S4P	S	0	15	1	41	0	2	0	14	0	0	0
S4C	S	0	26	0	6	0	1	1	29	0	0	0
S5P	S	0	3	3	13	0	0	0	0	0	0	0
S5C	S	0	8	1	6	0	0	0	2	0	0	0
A1P	A	0	1	0	5	0	0	0	0	4	5	0
A1C	A	0	4	0	1	0	0	0	0	0	3	0
A2P	A	6	0	0	0	0	0	0	0	2	2	0
A2C	A	4	0	0	0	0	0	0	0	0	0	0
A3P	A	7	0	0	0	0	0	1	0	0	0	0
A3C	A	1	0	0	0	0	0	0	0	2	4	0
A4P	A	0	0	0	0	0	0	2	0	0	2	0
A4C	A	0	0	0	0	1	0	0	0	2	2	0
A5P	A	0	0	0	1	0	0	2	0	0	1	0
A5C	A	0	0	0	0	0	0	0	0	0	3	0

Appendix 3

Appendix 3: Parameter estimates of GLM models of beetles with body size >15mm, after using the releveling function in R on the GLM models from table 3.

Species	Variables	Estimate β	Std. Error	z	p- value
Sp. A	Intercept (V)	0.095	0.302	0.316	0.752
	Agroforest	-19.398	2980.958	-0.007	0.995
	Secondary forest	-0.452	0.484	-0.935	0.350
Sp. B	Intercept (V)	0.693	0.224	3.100	0.002 **
	Agroforest	-0.105	0.325	-0.324	0.74572
	Secondary forest	-17.996	1096.633	-0.016	0.98691
Sp. C	Intercept (V)	-2.130e+01	8.103e+03	-0.003	0.100
	Agroforest	1.900e+01	8.103e+03	0.002	0.998
	Secondary forest	1.277e-12	1.146e+04	0.000	1.000
Sp. D	Intercept (V)	2.809	0.078	36.197	<0.001***
	Agroforest	-3.503	0.453	-7.717	<0.001 ***
	Secondary forest	-0.036	0.121	-2.962	0.003 **
Sp. E	Intercept (A)	-18.30	1808.04	-0.010	0.992
	Virgin forest	19.26	1808.04	0.011	0.992
	Secondary forest	17.61	1808.04	0.010	0.992
	Intercept (A)	-0.693	0.447	-1.550	0.121
Sp. K	Virgin forest	0.8756	0.532	1.645	0.100
	Secondary forest	-0.511	0.730	-0.699	0.484

Appendix 4

Appendix 4: Species number of the most common species captured in Amani Nature Reserve.

Trap	Forest	Dung type	SpD	SpF	SpJ	SpG	SpCC
V1P	V	P	20	7	200	18	33
V1C	V	C	9	45	71	10	58
V2P	V	P	39	12	467	73	54
V2C	V	C	34	74	141	9	17
V3P	V	P	21	15	136	53	39
V3C	V	C	13	15	78	7	23
V4P	V	P	9	0	122	24	31
V4C	V	C	17	12	59	12	45
V5P	V	P	1	3	98	15	22
V5C	V	C	3	2	37	4	8
S1P	S	P	11	5	104	19	45
S1C	S	C	4	14	37	7	10
S2P	S	P	2	1	87	18	38
S2C	S	C	2	5	24	1	12
S3P	S	P	31	4	57	65	0
S3C	S	C	14	31	59	19	68
S4P	S	P	15	14	106	41	65
S4C	S	C	26	29	59	6	34
S5P	S	P	3	0	28	13	19
S5C	S	C	8	2	16	6	0
A1P	A	P	1	0	6	5	7
A1C	A	C	4	0	5	1	2
A2P	A	P	0	0	0	0	0
A2C	A	C	0	0	0	0	3
A3P	A	P	0	0	0	0	1
A3C	A	C	0	0	0	0	0
A4P	A	P	0	0	0	0	1
A4C	A	C	0	0	0	0	1
A5P	A	P	0	0	1	1	1
A5C	A	C	0	0	0	0	2

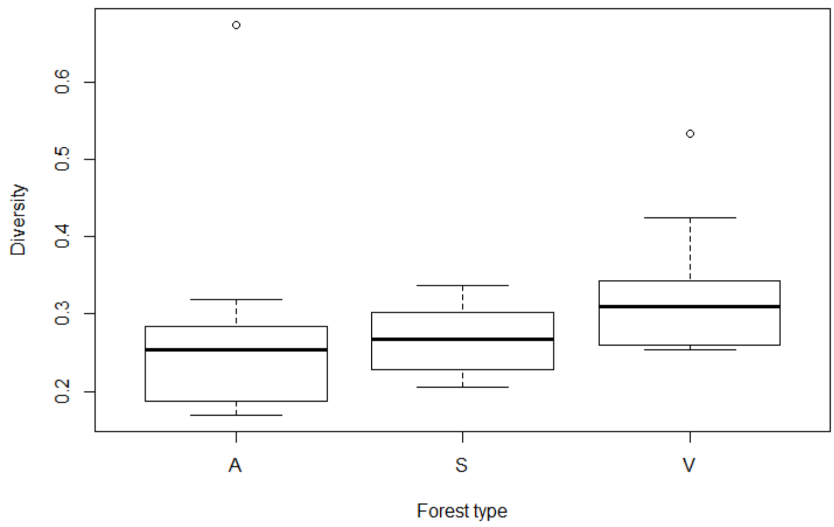
Appendix 5

Appendix 5: P-values after using the relevel function for the GLM models in table 5**,** of common dung beetle species abundance. It shows all the significant differences between species and forest types.

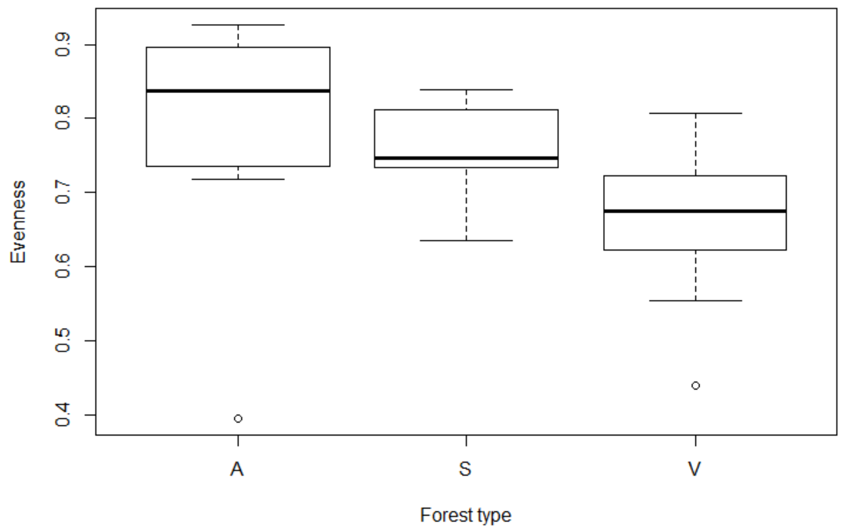
Species	**Forest type**	**p- value**
Sp. F	Virgin vs. secondary	p<0.001
Sp. J	Virgin forest vs. agroforest	p<0.001
	Virgin forest vs. secondary forest	p<0.001
	Secondary forest vs. agroforest	p<0.001
Sp. G	Agroforest vs. secondary forest	p<0.001
	Agroforest vs. virgin forest	p<0.001
Sp.CC	Agroforest vs. secondary forest	p<0.001
	Agroforest vs. virgin forest	p<0.001
Sp. D	Virgin forest vs. agroforest	p<0.001
	Secondary forest vs. agroforest	p<0.001
	Virgin forest vs. secondary forest	0.00306

Appendix 6

Values form calculated Simpson diversity index (D-1) and Pielou's evenness index.



Appendix 6a: Boxplot of the total Simpson diversity index for each forest type. A= agroforest, S= secondary forest, and V = virgin forest. The x- axis is forest type, and the y axis represents diversity.



Appendix 6b: Boxplot of the total Pielou's evenness index for each forest type. A= agroforest, S= secondary forest, and V = virgin forest. The x- axis is forest type, and the y axis represents evenness.

Appendix 6c: Values from calculated Simpson diversity index (D-1) and Pielou′s evenness index for each trap in Amani Nature Reserve.

Trap	Forest type	Diversity	Evenness
V1P	V	0.42399	0.5543638
V1C	V	0.2558631	0.6840070
V2P	V	0.5331154	0.4391942
V2C	V	0.3431122	0.6568878
V3P	V	0.259724	0.7221188
V3C	V	0.3417245	0.6902678
V4P	V	0.2704142	0.8073303
V4C	V	0.2541091	0.8073303
V5P	V	0.3248884	0.6226171
V5C	V	0.2951323	0.6672008
S1P	S	0.3367491	0.7079986
S1C	S	0.2796026	0.7360326
S2P	S	0.2948624	0.6353487
S2C	S	0.3025759	0.7481442
S3P	S	0.3030045	0.7441881
S3C	S	0.2559252	0.8395326
S4P	S	0.2177644	0.7486812
S4C	S	0.2285032	0.7334841
S5P	S	0.2058368	0.8385788
S5C	S	0.23875	0.8113946
A1P	A	0.3194536	0.7178530
A1C	A	0.1689751	0.9183525
A2P	A	0.2636401	0.7611046
A2C	A	0.2562358	0.8303775
A3P	A	0.2295918	0.8746047
A3C	A	0.1800554	0.8965085
A4P	A	0.6741974	0.3946705
A4C	A	0.2517007	0.8431821
A5P	A	0.2839335	0.7347180
A5C	A	0.1875	0.9269284

Appendix 7

Appendix 7: AIC values from GLM models made for abundance, richness, diversity and evenness between forest types. AIC values from GLM models are compared with AIC values from null models. Abundance is the only variable showing a lower AIC in the GLM model than the null model.

	GLM models AIC values	**null models AIC values**
Abundance	1449	3380
Richness	133.86	129.65
Diversity	33.47	26.31
Evenness	30.40	24.47

Appendix 8

Appendix 8: DCA values from Amani Nature Reserve (all plots included).

	DCA1	DCA2	DCA3	DCA4
Eigenvalues	0.4626	0.2592	0.1402	0.11663
Decorana values	0.5417	0.2683	0.1253	0.07767
Axis lengths	3.1798	2.6153	1.5774	1.33399

Appendix 9

Appendix 9: The total number of each species captured in each forest type in Amani Nature Reserve.

Species	Virgin forest	Secondary forest	Agroforest
Sp.A	11	7	0
Sp.B	20	0	18
Sp.C	0	0	1
Sp.D	166	116	5
Sp.E	26	5	0
Sp.F	185	105	0
Sp.G	225	195	7
Sp.H	0	0	1
Sp.I	156	181	185
Sp.J	1409	577	12
Sp.K	12	3	5
Sp.L	1	0	10
Sp.M	1	0	22
Sp.N	0	0	52
Sp.O	0	0	2
Sp.P	0	0	3
Sp.Q	17	0	0
Sp.R	14	7	12
Sp.S	0	1	0
Sp.T	0	0	8
Sp.U	0	0	2
Sp.V	0	0	1
Sp.W	1	1	0
Sp.X	0	0	1
Sp.Y	0	0	4
Sp.Z	1	0	0
Sp.Æ	1	0	1
Sp.Ø	0	0	1
Sp.Å	0	0	1
Sp.AA	1	0	0
Sp.BB	1	0	0
Sp.CC	330	291	18
Sp.DD	17	8	10
Sp.EE	38	19	33
Sp.FF	2	0	0
Total	**2635**	**1516**	**415**

Appendix 10

Collected morphospecies

Species A

FAMILY SCARABAEIDAE

Amount: 18

Length: 21mm

Found at plots: V1P, V1C, V2C, V3C, V5C, S1C, 2SP, S3P, S4P, S4C.

Ecology: Tunneller/ dweller only found in virgin- and secondary forest in both pig dung and cow dung.

Species B

FAMILY SCARABAEIDAE

Amount: 38

Length: 32.58mm

Found at plots: V1P, A2P, A2C, and A3C.

Ecology: The largest species found in this study, in both dung types. Because of its long hind legs, it is a rolling dung beetle. 20 individuals were found in the virgin forest plot.

Species C

FAMILY SCARABAEIDAE

Amount: 1

Length: 22.8mm

Found at plot: A4C.

Ecology: Only one individual of this dung beetle species was found in an agroforest plot. A tunneller/ dweller beetle because of the presence of horns. This beetle was found in the trap with cow dung.

Species D

FAMILY SCARABAEIDAE

Amount: 287

Length: 24.39mm

Found at plots: V1P, V1C, V2P, V2C, V3P, V3C, V4P, V4C, V5P, V5C, S1P, S1C, S2P, S2C, S3P, S3C, S4P, S4C, S5P, S5C, A1P and A1C.

Ecology: Tunneller/ dweller found in all virgin- and secondary forest plots, and in two agroforest plots. Captured both in pig and cow dung.

Species E

FAMILY SCARABAEIDAE

Amount: 31

Length: 21.49

Found at plots: V2P, V3P, V4P, S4P, S5P and S5C.

Ecology: A rolling dung beetle only found in virgin- and secondary forest. Most of them captured with pig dung.

Species F

FAMILY SCARABAEIDAE

Amount: 290
Length: 14.60mm
Found at plots: V1P, V1C, V2P, V2C, V3P, V3C, V4P, V4C, V5P, V5C, S1P, S1C, S2P, S2C, S3P, S3C, S4P, S4C and S5C.

Ecology: Tunneller/ dweller because of its horns. Only found in virgin- and secondary forest, in both pig and cow dung.

Species G

FAMILY SCARABAEIDAE

Amount: 427
Length: 14.08mm
Found at plots: V1P, V1C, V2P, V2C, V3P, V3C, V4P, V4C, V5P, V5C, S1P, S1C, S2P, S2C, S3P, S3C, S4P, S4C, S5P, S5C, A1P, A1C and A5P.

Ecology: Tunneller/ dweller because of its horns. Found in all forest types, but the majority was found in virgin- and secondary forest.

Species H

FAMILY APHODIINAE

Amount: 1

Length: 5.86mm

Found at plots: A3C.

Ecology: Subfamily of Scarabaeidae, where many species are dung beetles.

Species I

FAMILY APHODIINAE

Amount: 522

Length: 7.65mm

Found at plots: V1P, V1C, V2C, V4P, V5P, V5C, S1P, S1C, S2P, S2C, S3P, S3C, S4P, S4C, S5P, S5C, A1P, A1C, A2P, A2C, A3P, A3C, A4P, A4C, A5P and A5C.

Ecology: Subfamily of Scarabaeidae, where many species are dung beetles.

Species J

FAMILY SCARABAEIDAE

Amount: 1998

Length: 6.66mm

Found at plots: V1P, V1C, V2P, V2C, V3P, V3C, V4P, V4C, V5P, V5C, S1P, S1C, S2P, S2C, S3P, S3C, S4P, S4C, S5P, S5C, A1P, A1C and A5P.

Ecology: Tunneller/ dweller dung beetle found in all forest types, both with pig and cow dung. It was captured in every trap in virgin- and secondary forest. The largest abundance was found in virgin- and secondary forest.

Species K

FAMILY SCARABAEIDAE

Amount: 20

Length: 17mm

Found at plots: V1P, V1C, V2P, V2C, V3P, V4P, V5P, S1C, S4C, A3P and A5P.

Ecology: Tunneller/ dweller dung beetle because of horns. Captured in all forest types, in both pig and cow dung.

Species L

FAMILY SCARABAEIDAE

Amount: 11

Length: 10.72mm

Found at plots: V4P, A1P, A2P, A3C and A4C.

Ecology: A roller dung beetle because of its long hind legs. It was found in virgin forest and agroforest, but was captured mostly in agroforest.

Species M

FAMILY SCARABAEIDAE

Amount: 23

Length: 10mm

Found at plots: V1C, A1P, A1C, A2P, A3C, A4P, A4C, A5P and A5C.

Ecology: A roller dung beetle because of its long hind legs. It was found mostly in agroforest, except from one trap in virgin forest.

Species N

FAMILY SCARABAEIDAE

Amount: 52

Length: 5.63mm

Found at plots: A1P, A3C, A4P, A4C, A5P and A5C.

Ecology: Tunneller/ dweller dung beetle found only in agroforest, both in pig dung and cow dung.

Species O

FAMILY SCARABAEIDAE

Amount: 2

Length: 5.57mm

Found at plots: A1C and A2C.

Ecology: Roller dung beetle because of its long legs. Only found in agroforest traps with cow dung.

Species P

FAMILY SCARABAEIDAE

Amount: 3

Length: 4.59mm

Found at plots: A2P.

Ecology: Roller dung beetle only found in one agroforest trap with pig dung.

Species Q

FAMILY SCARABAEIDAE

Amount: 17

Length: 6.90mm

Found at plots: V1P, V2P, V3P and V3C**.**

Ecology: Roller dung beetle only found in virgin forest in traps with both cow and pig dung.

Species R

FAMILY SCARABAEIDAE

Amount: 33

Length: 7.07mm

Found at plots: V3P, V5P, S1P, S1C, S2P,

Ecology: Roller dung beetle because of its long hind legs. Captured only in virgin- and secondary forest, both in cow and pig dung.

Species S

FAMILY SCARABAEIDAE

Amount: 1

Length: 10.60mm

Found at plots: S2C.

Ecology: Only one individual of a tunneller/ dweller species found in one trap in secondary forest.

Species T

FAMILY SCARABAEIDAE

Amount: 8

Length: 3.77mm

Found at plots: A3C, A5P and A5C.

Ecology: Tunneller/ dweller species found only in agroforest.

Species U

FAMILY SCARABAEIDAE

Amount: 2

Length: 4.60mm

Found at plots: A4C.

Ecology: Tunneller/ dweller only found in agroforest in one plot with cow dung.

V

FAMILY SCARABAEIDAE

Amount: 1

Length: 4.80mm

Found at plots: A2P.

Ecology: Only one individual of a tunneller/ dweller species found in agroforest in one plot with pig dung.

Species W

FAMILY SCARABAEIDAE

Amount: 2

Length: 6.17mm

Found at plots: V4P and S5P.

Ecology: A tunneller/ dweller species found in only virgin- and secondary forest in pig dung.

Species X

FAMILY SCARABAEIDAE

Amount: 1

Length: 4.70mm

Found at plots: A2C.

Ecology: Only one individual of a tunneller/ dweller species found in only one agroforest trap with cow dung.

Species Y

FAMILY SCARABAEIDAE

Amount: 4

Length: 5.05mm

Found at plots: A4P.

Ecology: Tunneller/ dweller species only found in one trap with pig dung in agroforest.

Species Z

FAMILY SCARABAEIDAE

Amount: 1

Length: 8.23mm

Found at plots: V1P.

Ecology: Only one individual of a tunneller/ dweller species captured in virgin forest.

Species Æ

FAMILY SCARABAEIDAE

Amount: 2

Length: 4.90mm

Found at plots: V4C and A4P.

Ecology: Tunneller/ dweller species found in virgin forest and agroforest with both cow and pig dung.

Species Ø

FAMILY SCARABAEIDAE

Amount: 1

Length: 5.22mm

Found at plots: A2C.

Ecology: Tunneller/ dweller species only found in one trap with cow dung in agroforest.

Species Å

FAMILY SCARABAEIDAE

Amount: 1

Length: 7.34mm

Found at plots: A3C.

Ecology: Tunneller/ dweller species only found in one trap with cow dung in agroforest.

Species AA

FAMILY SCARABAEIDAE

Amount: 1

Length: 3.50mm

Found at plots: V5C.

Ecology: Tunneller/ dweller dung beetle only found in one trap with cow dung in virgin forest.

Species BB

HYDROPHILIDAE

Amount: 1

Length: 5.50mm

Found at plots: V5C.

Ecology: Belongs to the subfamily Hydrophiloidea.

Species CC

FAMILY SCARABAEIDAE

Amount: 639

Length: 9.76mm

Found at plots: V1P, V1C, V2P, V2C, V3P, V3C, V4P, V4C, V5P, V5C, S1P, S1C, S2P, S2C, S3C, S4P, S4C, S5P, A1P, A1C, A2C, A3P, A4P, A4C, A5P and A5C.

Ecology: Tunneller/ dweller dung beetle found in all forest types, and almost in every trap. The largest abundance was captured in virgin. And secondary forest.

Species DD

FAMILY SCARABAEIDAE

Amount: 35

Length: 4.31mm

Found at plots: V1P, V3P, V5P, V5C, V4C, V5C, A1C, A3P and A5C.

Ecology: Tunneller/ dweller dung beetle found in all forest types, both with pig and cow dung.

Species EE

FAMILY SCARABAEIDAE

Amount: 90

Length: 6.44mm

Found at plots: V1C, V2P, V3P, V3C, V4P, V4C, S3C, S4P, S4C, S5P, A1C, A2P, A2C, A3P and A5C.

Ecology: Tunneller/ dweller dung beetle found in all forest types, both with pig and cow dung.

SP. FF

FAMILY TROGIDAE

Amount: 2

Length: 7.31mm

Found at plots: V2P and V4P.

Ecology: Scavengers that belong to the superfamily Scarabaeoidea.

Norges miljø- og biovitenskapelig universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway