Norwegian University of Life Sciences
Facultiy of Environmental Science and Technology
Department of Ecology and Natural Resource
Management (INA)

Master Thesis 2014
60 credits

Dung beetle (Scarabaeidae, Scarabaeinae) communities in mountain rain forests (Tanzania): A biodiversity survey from Amani Nature Reserve and Udzungwa Mountain National Park

Aadne Aasland

REGISTRATION FORM FOR SUBMISSION OF THESIS FOR A DEGREE

NORWEGIAN UNIVERSITY OF LIFE SCIENCES MDCCCLIX

Student name	Aadne Aasland		
Student no	976732	Due date:	15/05/2015

Main Supervisor	Fred Midtgaard
Department	Department of Ecology and Natural Resource Management (INA)
Name of co-authors if so	

The Department of Academic Affairs may need to contact you *before* your certificate is issued:
Please give the following contact information:

Mobile number	+4791817560
e-mail address	aadne.aasland@nmbu.no
Name and address your certificate is to be sent to	Aadne Aasland Åslandsvegen 418 4355 KVERNELAND NORWAY

Thesis	
English title	Dung beetle (Scarabaeidae, scarabaeinae) communities in mountain rain forests (Tanzania): A biodiversity survey from Amani Nature Reserve and Udzungwa Mountains National Park
Norwegian title (optional)	
Is your thesis confidential? If so, for how long?	

Declaration

I hereby declare that this assignment is written by me and

- is a result of my own work
- has not been used for another exam at another department/ university/ university college in Norway or another country.
- does not refer to/quote works of others without stating it both in the text and in the reference list
- does not refer to/quote previous writings of my own without stating it both in the text and in the reference list
- mentions explicitly all sources of information in the reference list.

I am aware of the fact that violation of these clauses is regarded as cheating and can result in annulment of the examination or paper. Cheating or attempted cheating can result in the expulsion of the examinee, in accordance with the University and College Act Chapter 4-7.

Signature	
Place/date	
Signature:	

Dung beetle (Scarabaeidae, scarabaeinae) communities in mountain rain forests (Tanzania): A biodiversity survey from Amani Nature Reserve and Udzungwa Mountain National Park

Aadne Aasland

ACKNOWLEDGEMENTS

First of all, I would like to thank my supervisor, Fred Midtgaard (professor at the Norwegian University of Life Sciences), for all his help prior to and during my fieldwork, and during the writing process. He has provided great support and very generous amounts of time. He was truly the best supervisor I could ever ask for.

A special thanks goes to Seif Madoffe (Professor at the Sokoine University of Agriculture in Morogoro, Tanzania) for his help during my fieldwork.

I would like to thank Beatrice Christopher Tarimo and Knut Arne Smeland for spending a lot of time to help me with my statistical analyses.

I would also like to thank Aloyce and Salim for their excellent guiding skills and field assistance.

Bård Aasland, Petter Lilleengen, Jan Tore Time and Espen Undheim deserves to be mentioned because of their feedback in my writing period.

The CCIAM program headed by Sokoine University of Agriculture (SUA), Morogoro, Tanzania, financially supported part of my field work. This thesis is part of the project on Carbon Mitigations headed by S. S. Madoffe (SUA) and F. Midtgaard (NMBU) under CCIAM. I am very grateful for the support from the project.

Lastly, I want to thank my family for their emotional and financial support. A special thanks goes to my father Arild Tore Aasland, who came to visit me in Tanzania during my fieldwork.

Ås, May 2015

Aadne Aasland

ABSTRACT

The African dung beetles (Scarabaeidae, Scarabeinae) is the most generic and species rich of the global faunas. Dung beetles are good indicators of biodiversity and habitat disturbances. This study aimed to investigate dung beetle communities in two different mountain rain forests in the eastern arc mountains, Tanzania. The study areas were located in Amani Nature Reserve and Udzungwa Mountains National Park. In Amani, the tropical forest habitat has been reduced due to historical logging activities. In this area, five habitats were chosen: undisturbed forest, secondary forest that was logged approximately 50 years ago, agroforestry habitat, riverine secondary forest that was moderately logged in the past and a secondary forest that was moderately logged in the past. Due to unforeseen problems regarding the research permit, the field work in Udzungwa was conducted outside the protected forest, different habitats were thus not used since all plots were essentially within the same habitat type. In total, 1376 dung beetles, representing 59 different morphospecies were collected, using pitfall traps with three types of bait; cow dung, pig dung and meat. In Amani, 352 specimens grouped in 18 different morphospecies were sampled, in Udzungwa, 1024 specimens grouped in 41 different morphospecies were sampled, and no common species were found between the two study areas. The body size distribution of the dung beetle assemblage were smaller in Udzungwa compared to Amani. This result was unexpected because of the larger diversity and size range of mammals in Udzungwa compared to Amani. The habitats in Udzungwa were different, however, from the Amani forest habitats, and the agricultural edges in Udzungwa may not represent the forest fauna. In Amani, the results from this study showed that the dung beetle composition were more evenly distributed in the undisturbed forest, this habitat also hosted the largest diversity of morphospecies. Results from Udzungwa showed significant differences in the dung beetle composition using different types of bait, where traps with pig dung constituted 74.7% of the total number of individuals in Udzungwa, with 16 morphospecies only occurring on this type of bait. In Amani, no significant differences in dung beetle composition were found between the type of bait used. Results from this study supported the use of dung beetles as bioindicator taxon for biodiversity and environmental changes and disturbances. Two assumed new species were found belonging to the genera *Sceliages* and *Sarophorus*.

TABLE OF CONTENTS

1. INTRODUCTION

Insects with their large diversity and biomass offer a wide range of functional roles in tropical forest ecosystems and are considered sensitive in responding to habitat changes (Lewis 2009).

Among the dung feeding organisms, the dung beetles (Scarabaeinae) are by far the most dominant (Davis et al. 2008a), with the highest diversity in tropical forests and savannas. Dung beetle communities are correlated with dung producing vertebrates and mammals (Hanski & Cambefort 1991).

Under natural conditions, an invertebrate dung community is hugely complex, consisting of thousands of individuals and hundreds of species, all depending on the same resource. The dung resource is highly desirable and nutritious. All types of dung are attractive to potential invertebrate dung colonizers, but different types of dung generally attract different groups of insects (Scholtz et al. 2009). Different types of dung may be used by dung beetles, but the majority feed on mammalian herbivore or omnivore dung. Just categorizing the dung based on those two groups is not sufficient. Grazing and browsing animals often produce very different dung types, adding a further complexity whether the herbivore is a ruminant producing a fine-textured dung, or a non-ruminant producing coarse dung. The dung may also be excreted in mass or in pellet-form and may be produced from high quality spring, or poor quality autumn graze, or something in between. All of these characteristics affect the dung insect communities colonizing the dung (Edwards 1991, Hanski & Cambefort 1991, Scholtz et al. 2009).

A typical dung community usually consists of dung feeders, many of which are beetles from the family Scarabaeidae, more specifically the subfamily Scarabaeinae (called true dung beetles) and, particularly in the northern hemisphere, Aphodiinae. The family Geotrupidae, common in e. g. Norway, is not found in Africa. The larvae of flies may also occur in large numbers and compete aggressively for the dung resource. Beetles of the families Histeridae and Staphylinidae will be feeding on mainly fly larvae, even though some may predate on dung beetle larvae as well. Ants are also usually present, waiting for the dung beetles to tunnel into the dung and open up passageways for them to access and feed on fly eggs and maggots (Hanski & Cambefort 1991, Scholtz et al. 2009).

Dung beetles locate the dung by smell and use the resource as food for oviposition and food for their offspring. The beetles consume or provide different fractions of the dung than their larvae. Adults usually filter out the nutritious liquid components consisting of tiny dung fragments, microbes and sloughed gut epithelial cells from the host animal, while the larvae feed on the larger fibrous fragments consisting mainly of cellulose. The adult dung beetles may also feed on rotting fruit or carrion (Estrada & Coetes-Estrada 1991, Hanski & Cambefort 1991, Holter et al. 2002, Nichols et al. 2008, Scholtz et al. 2009), or may even be specialist Milliped predators (Forgie et al. 2002, Forgie et al. 2003).

Some dung beetles may be attracted to carcasses of herbivores if the gut contents become exposed, and carrion-associated Histeridae may be found in dung or rotting vegetation (Villet 2011). Dung beetles rarely visits carrion, and those that do also visit feces (Krell et al. 2003a). According to Villet (2011) dung beetles are unlikely to breed in carrion unless it includes suitable gut contents. They also tend to visit carrion during the day (Braack 1981). Insects utilizing carcasses include those feeding directly from the substrates provided by the carrion resource and those feeding or parasitizing insects feeding on the carcass. Examples range from carrion beetles of the families Histeridae, Troxidae, Scarabaeidae, Dermestidae, Cleridae and Silphidae. The Dipteran families Phiophilidae, Sphaeroceridae, Chloropidae, Milichiidae, Muscidae and Calliphoridae may also visit the carrion resource. Some Lepidopterans like the true moths (Tineidae) may feed on dry carcasses or horn. Parasitic wasps of the families Pteromalidae and Diapriidae may parasite larvae in the dung. Different Formicidae and Arachnid mites may also forage in dung. The dung community show a clear predominance of the Coleoptera, and Diptera (Braack 1987).

Dung beetles have been used as indicator organisms for measuring biodiversity (Favila & Halffter 1997) and as indicators for environmental change and disturbance (Davis et al. 2001, Estrada et al. 1993, Newmark 1999). This is because of the strong relationship between dung producing mammals and dung beetles (Hanski & Cambefort 1991), and the fact that local distribution of dung beetles is strongly influenced by vegetation cover, soil type and the physical structure of the forest (Davis et al. 2001).

Dung beetles are considered ecologically important by providing some crucial ecosystem services. By burying the dung and carrion resource, they may enhance soil fertility by providing nutrients directly to the soil and preventing the loss of nitrogen through ammonia volatilization (Estrada et al. 1993, Gibbs & Stanton 2001, Hanski & Cambefort 1991, Nichols et al. 2008). Beetles with a burying behavior may also play a role in bioturbation by increasing the soil aeration and water porosity by their tunnelling activity and by moving earth upwards to the soil surface (Nichols et al. 2008).

By burying the dung and carrion resource, the beetles may control the abundance of detrivorous and necrophagous flies (Braack 1987, Nichols et al. 2008). African dung beetles have been introduced to Australia to control fly populations feeding on cattle dung (Scholtz et al. 2009). They may also act as secondary dispersal agents for seeds of many tropical trees, thus participating in the natural process of forest regeneration by transporting or burying the dung produced by e. g. howler monkeys feeding on fruits (Andresen 2003, Estrada & Coetes-Estrada 1991).

In this study, the dung beetles in Amani Nature Reserve and Udzungwa National Park were collected by using pitfall traps with bait. These two mountain forests are a part of the Eastern Arc Mountains (Figure 1), a chain of 14 mountain ranges located in East Africa. The two forests are located roughly 360km from each other. The main predictions for this study were:

- THE DUNG BEETLE SPECIES DIVERSITY AND ABUNDANCE WILL DIFFER BASED ON THE ABUNDANCE OF MAMMALS. A higher diversity of mammals is expected to be correlated with the diversity of dung beetles feeding on the dung or carrion resource.

- THE SIZE RANGE OF THE DUNG BEETLE COMMUNITY WILL BE BIGGER IN UDZUNGWA BECAUSE OF THE LARGER SIZE RANGE OF THE MAMMALS THERE COMPARED TO AMANI.

- THE ABUNDANCE AMONG DUNG BEETLE SPECIES WILL SHOW A MORE EVEN DISTRIBUTION IN UNDISTURBED FORESTS, COMPARED TO DISTURBED FORESTS. Specialized species will occur less frequently in disturbed habitats compared to generalist species.

- THE TYPE OF BAIT USED WILL AFFECT DUNG BEETLE COMPOSITION.

- ARE THE COMMUNITIES IN DIFFERENT FOREST TYPES SUFFICIENTLY DIFFERENT TO INDICATE THAT DUNG BEETLES COULD BE USEFUL AS BIOINDICATOR TAXON?

2. MATERIALS AND METHODS

2.1. STUDY AREA

The study was conducted in Amani Nature Reserve located in the East Usambara Mountains (Figure 1), northeastern Tanzania, and in Udzungwa Mountains National Park located in south-central Tanzania. Both areas are part of the "Eastern Arc Mountains" (EAM), a chain of mountains starting in southern Kenya through eastern Tanzania, with Udzungwa Mountains in the southern part. The EAM range up to 2635 meters in altitude and contains a diverse assemblage of habitats. The north-eastern and south-eastern parts consist mostly of continuous forest cover, while the more dry western and north-western parts support deciduous woodland at low elevations and evergreen forests at the higher elevations. For its size the EAM are considered the biologically richest area in Tanzania, and rank among the most important areas for conservation due to its high number of endemic or near-endemic species (Burgess et al. 2007, Newmark 1999). The mountain chain is considered one of the 35 global "hotspots" of biological diversity (Mittermeier et al. 2011).

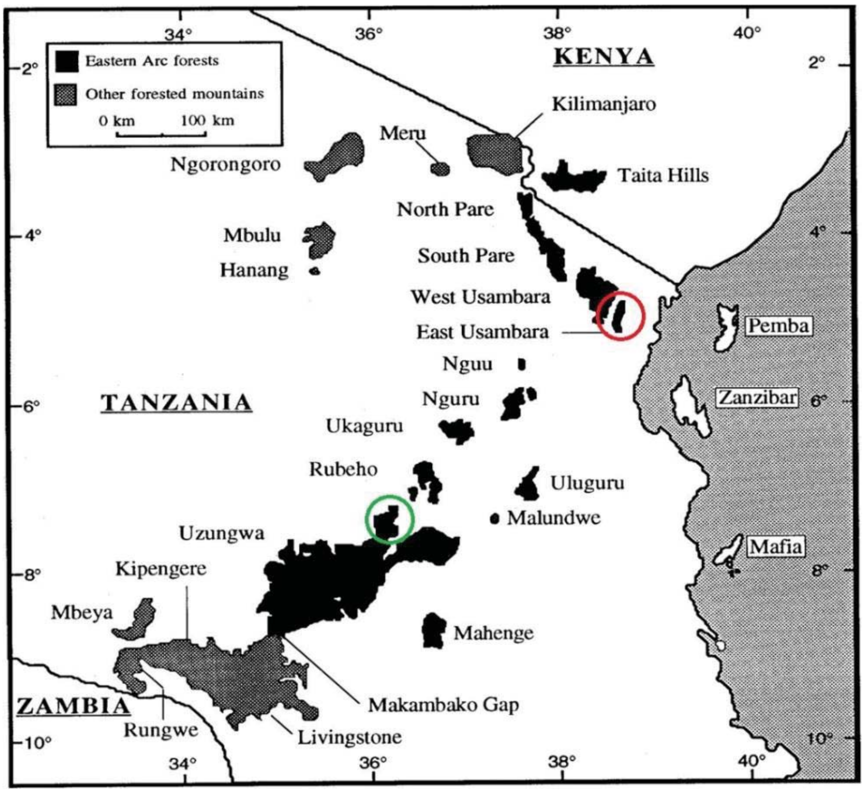


Figure 1. The forested areas of Eastern Arch Mountains, Amani Nature Reserve is in the red circle. Udzungwa Mountains National park is in the green circle (figure modified from Burgess et al. 2007).

Amani Nature Reserve (83 km^2) is the largest block of forest in the East Usambara Mountains, consisting of six former forest reserves (Amani Sigi, Amani East, Amani West, Kwamsambia, Kwamkoro and Mnyuzi). It is considered a good example of continuous forest, ranging from lowland to submontane forest. The rainfall distribution peaks between March and May and between September and December, with dry seasons occurring from June to August and January to March. Precipitation however, occurs in all seasons (Frontier Tanzania 2001). In terms of fauna, the reserve is home to seven endangered and 26 vulnerable species according to IUCN categories. The reserve has a high diversity of reptiles and amphibians and around 59 different species of mammals including bats. Among the mammals there are at least 24 species of small rodents, 16 species of bats, and some larger mammals, including 4 species of monkey (*Papio cynocephalus*, *Cercopithecus aethiops, Cercopithecus mitis, Rungwecebus kipunji*), bushbuck (*Tragelaphus sylvaticus*), 2 species of galago (*Otelemur crassicaudatus, Galagoides orinus*), porcupine (*Hysterix cristata*) and bush pig (*Potamochoerus larvatus*) (Burgess et al. 2007, Frontier Tanzania 2001, Miller 2013).

The Amani Nature reserve is not only important for its biodiversity. It also plays an important role in maintaining the hydrological cycle. Rainfall in Amani feeds the Sigi River which serves as a water source for local inhabitants as well as being a tributary to Pangani river supplying water for Tanga city (Frontier Tanzania 2001).

Human disturbances have been present on the East Usambara Mountains for at least 2000 years. The Germans started logging activities in Amani in 1886, mainly to clear land for coffee plantations. Due to poor coffee growing conditions they were replaced with tea plantations. Tea plantations are still present in a relative big part of the Amani area (6.5% of total area) (Frontier Tanzania 2001).

The area houses a botanical garden (Amani botanical garden) dating from 1893, where various researchers cultivated a total of 650 “useful plants” from all over the world in 1907. Since the 1960s the botanical garden has been poorly managed, enabling seedlings and saplings of some species to spread to neighboring forests. Many of the secondary forests in Amani Nature Reserve are thus consisting of both native and alien plant species (Dawson et al. 2008, Dawson et al. 2009, Frontier Tanzania 2001).

The Udzungwa Mountains (1900km^2) is a national park in the southern part of the EAM. The park contains large areas of mountain forest and grassland (Burgess et al. 2007). The area has an altitude between 200-2500 meters. The rain season in this area usually occurs between November and May, with a smaller season from November to December, and a bigger season between March and May (Lovett 1996, Lovett 2006). In terms of biodiversity, the area contains a higher number of dung producing species compared to Amani. Studies by Rovero & De Luca (2007) recorded 118 species of mammals belonging to 30 families. These include 26 species of carnivores, 25 species of rodents, 18 species of bats, 16 species of ungulates and 12 species of primates. The African elephant *Loxodonta africana* is also present in Udzungwa.

2.2. STUDY SPECIES

Dung beetles (Scarabaeinae), with roughly 5000 species worldwide, are considered a small group of insects; but the many different morphological, ecological and behavioral attributes makes them a unique and diverse group (Monaghan et al. 2007, Scholtz et al. 2009). The African dung beetle guild is considered the most generic and species rich of the global faunas, with 2141 different species among 105 genera in the Scarabaeinae alone (Scholtz et al. 2009).

Dung beetles locate the dung by smell and use the resource as food for oviposition and to feed their offspring. The dung resource does not only have a nutritional function, it serves also as the meeting place between male and female and appears to be the preferred location for mating. This happens either near the dung pile or in the chamber tunnelling species make in the soil. (Estrada & Coetes-Estrada 1991, Hanski & Cambefort 1991, Holter et al. 2002, Nichols et al. 2008, Scholtz et al. 2009).

The modern dung beetles appear to have radiated in response to increased occurrence of mammalian dung, so the high morphological diversity of dung beetles may be linked to radiation of mammals, an event that probably occurred sometime in either the Mesozoic or Cenozoic era (Davis et al. 2002, Scholtz et al. 2009). A generally accepted theory states that dung beetles probably evolved from detritus-feeding organisms, where the beetles mostly fed on microbe rich liquid (Hanski & Cambefort 1991, Scholtz et al. 2009). However, fossil dinosaur dung balls made by dung beetles have been found, so the association to dung has a long historical record (Scholtz et al. 2009). With the increasing availability of mammalian dung following the diversification of mammals, the ancestral dung beetles may have adapted and specialized in feeding on various dung resources in open savannas and grasslands. The modern dung beetles are considered the major consumers of fresh herbivore dung in tropical areas (Scholtz et al. 2009). According to Monaghan (2007) and Sole & Scholtz (2010), the subfamily Scarabaeinae probably originated from Africa.

The dung beetles most likely developed their dung burying behavior to avoid competition from flies or other dung-utilizing organisms, and to protect the dung resource from drying out and losing its nutritional value. By locating the dung quickly, and either rolling the dung away or burying it at site, they isolated the resource to fully utilize it without competition or waste (Scholtz et al. 2009).

There are three different functional groups of dung beetles: tunnellers, rollers and dwellers. The tunnellers burrow balls of dung where they find it, usually under the dung pile but sometimes near the pile. The rollers form the dung into round, compact balls of varying size and roll the dung away for hiding, normally followed by burying the dung. The dwellers occupy the dung at the same location it is found and live inside it. The amount of dung buried appears to depend on the size of female beetles. But other factors seems to be included, such as soil type, moisture and dung quality (Hanski & Cambefort 1991, Nichols et al. 2008). Regarding the morphological differences between the functional groups, the rollers generally have long hind legs. The rollers roll the dung ball with their back legs, rolling with their head down, making long legs preferred for this type of work. The tunnelling dung beetles have relatively shorter hind legs and the front legs are well adapted for digging. The presence of horns is common in the tunnelling dung beetles (Hanski & Cambefort 1991, Scholtz et al. 2009).

The dung ball used by rolling dung beetles may serve various roles: They may be rolled mainly to feed the rolling beetle (food ball), they may be rolled by a male to be shared with a female (nuptial ball), and they may be rolled to mainly serve as food for offspring (brood ball). Mostly larger dung beetles (>7.0-8.0 mm) appear to be the ones with a rolling behavior, where smaller beetles in some cases may be physically incapable in forming and rolling a dung ball (Scholtz et al. 2009). The rolling dung beetles appear to use the sun, moon and even the stars to move dung balls along straight paths away from competition (Dacke et al. 2013).

Tunnelling dung beetles appear to have some behavioral advantages compared to the rollers: the burial site is located closer to the dung resource, making it possible to collect more dung in a shorter time span. Because of the lower amount of energy spent transporting dung they may have more energy to produce offspring, and they are probably less likely to be exposed to predators due to less amount of time spent above the ground. Competition among tunnelling and dwelling species occurs more frequently, because both groups utilize the immediate area in and around the dung (Hanski & Cambefort 1991, Scholtz et al. 2009). Because of the larger legs of the rolling dung beetles, they appear to be worse suited for digging compared to the tunnelling beetles. An example here is the ball rolling species *Circellium bacchus*, which may use up to 24 hours to bury the dung resource following successful transportation (Scholtz et al. 2006, Scholtz et al. 2009). According to Hanski & Cambefort (1991), the faster a rolling dung beetle is able to roll the dung ball, the less adapted it will be to burying. Some rolling dung beetles like the Mauritian species *Neosisyphus spinipes* have such long hind legs that it leaves the ball at the surface or attaches it to a vegetation structure without burying it.

As mentioned, some dung beetles are armed with exoskeletal outgrowths (horns), mainly used as weapons. Since the tunnelling dung beetles generally appear to have horns, and rollers rarely do, this may suggest that fighting is more common near the opening of tunnels (Emlen & Philips 2006). The presence of horn structures may also serve a function in sexual selection, but horns may at times also be present on females. However, these horned females are mostly found in tribes with horned males, and their horn structures are smaller in size compared to the male horn structures (Emlen et al. 2005, Scholtz et al. 2009).

The tunnelling species *Onthophagus acuminatus* show a different type of reproductive behavior depending on the body size and the presence of horns. The female beetle is located in a chamber in a tunnel made by a male under the dung resource, protecting its brood while a big sized male with big horns protects the entrance of the tunnel to defend it against other potential mates. A proportion of the males in this species are smaller and have small horns. These males are not able to fight with the bigger males protecting the entrance of the tunnel. Instead they make a new tunnel from the side into the chamber to get in contact with the female beetle. In this, and some other species there can thus be a dimorphism in the appearance of the males (Emlen 1997).

Both the rollers and tunnellers feed on the same fractions of the dung. Large particles are filtered out by the mouthparts and the small particles are ingested, and this is understandable because the mouthparts of both functional groups are built similarly (Holter & Scholtz 2005).

The dung beetles have a well-developed brood care. Fewer offspring are produced each generation compared to other similarly sized insects with comparable underground life cycles. The offspring produced may range from one each year to about 100 each year (Scholtz et al. 2009). The dung beetle *Circellium bacchus* is an extreme example of low fecundity. The females produce between one to two eggs each year. This is one of the lowest fecundity rates recorded in insects (Scholtz et al. 2006).

Scholtz (2009) propose some obvious advantages for leaving the eggs and larvae inside a secure and hidden chamber with the food resource: Firstly, no further energy is expended by acquiring food after oviposition. Secondly, the larvae are less affected by environmental variables, because of relative small fluctuations in temperature and humidity. Lastly, competitors, predators or parasites are less likely to locate the larvae or the food resource. This brood care strategy appears to result in a low juvenile mortality (Scholtz et al. 2009).

Some dung beetles may be attracted to carcasses of herbivores if the gut contents become exposed (Villet 2011). Dung beetles visiting carrion occur rarely, and as previously mentioned, those that do also visit feces (Krell et al. 2003a). According to Villet (2011), dung beetles are unlikely to breed in carrion unless it includes suitable gut contents.

Deforestation, degradation and fragmentation are clearly reducing species diversity in tropical forests (Didham et al. 1998, Estrada et al. 1993, Fahrig 2003, Gibbs & Stanton 2001, Klein 1989, Primack 2012). Dung beetles are among the insect groups affected by fragmentation (Andresen 2003, Didham et al. 1998, Estrada et al. 1993, Feer & Pincebourde 2005, Klein 1989). Habitat fragmentation may cause a loss of species diversity in several different ways. It may limit dispersal between habitat fragments and may thus reduce the recolonization potential (Laurance et al. 2009), where some bird, mammal or insect species found inside a forest interior may not cross certain stretches of open area because of the danger of predation, or to avoid sunny, hot, noisy or dry environments (Ibarra-Macias et al. 2011). Smaller forest remnants may also harbor smaller populations of dung producing mammals and these populations may be prune to local extinction. This will of cause have effect on the dung beetles depending on dung from these mammals. The population gene pool may also be reduced (Klein 1989). Fragmented forests experience altered environmental conditions close to the edges called edge effects. Smaller remnants will have relatively more edge than they had before the size was reduced (Saunders et al. 1991).

Klein (1989) found different communities of dung beetles in forest fragments as compared to continuous forest in Amazon rain forest. The fragmented forest had lower species richness and sparser populations compared to the continuous forest, resulting in significantly lower decomposition rates of dung in the fragmented areas. Horgan (2005) found similar results in the rainforest of Peruvian Amazon, where their results indicated a higher richness and assemblage of dung beetles in the intact forests compared to fragmented areas.

The dung beetles are considered a useful group for ecological monitoring, with relative well known taxonomy and species rich assemblages. Most species are attracted to a universal dung bait, making a simple trap with bait an effective way of obtaining material (Davis 1996, Hanski & Cambefort 1991).

2.3. MORPHOSPECIES IDENTIFICATION

After collection, all beetle specimens were transported to NMBU (Norway) where they were glued to paper rectangles needled for easy handling. The beetles were given morphological codes based on clear morphological differences in legs, shape of body and antennae. These body parts are considered the most crucial parts for identification (Krell 2006, Scholtz et al. 2009). The presence/absence of horns was also used as a morphological trait. Classification based on horns should be done cautiously, since drastic differences in horn structure may at times occur on the same species of dung beetles, or between male and female beetles (Emlen et al. 2005, Scholtz et al. 2009).

Color variation between the beetles that were otherwise morphologically identical was not used to characterize them as new morphospecies. After all the beetles had been sorted and/or mounted, they were compared for morphological similarities for all plots. The morphospecies were also estimated to be either rollers or tunnellers/dwellers based on the presence/absence of horns, the length of hind legs, and how suitable the front legs appeared for digging. A differentiation between tunnellers and dwellers was not feasible because they may be very similar morphologically.

2.4. STUDY DESIGN

The beetles were collected using pitfall traps with bait (Figure 2). The traps consisted of five-liter buckets with 0.5 l water containing salt and some drops of detergent to minimize the surface tension. Socks filled with fresh dung or meat were tied to a stick and placed at the top of the bucket to act as bait. The bait was changed for every 48 hour trap period. The dung was wrapped in cloth material to allow dissemination of dung volatiles, so that the attracted beetles fell into the liquid mix. After placement of the bucket, the area around the trap was reorganized to look as natural as possible by reintroducing removed litter and removing leftover soil. Both omnivore pig dung, herbivore cow dung and rotting meat were used as bait in this study. The traps were emptied 48 hours later and placed in sealable plastic bags. After emptying all the traps, everything except the dung beetles were removed at the stations in Amani and Udzungwa respectively. The pitfall traps yielded a large number of ants, spiders, flies, grasshoppers and a smaller number of scorpions, butterflies and small rodents. The beetles were placed separately for each trap in plastic bags containing a local Tanzanian liquor (35% alcohol). This trapping method is suitable only for destructive sampling, where beetles, if not immobilized, may fly out of the trap. Possible predators may also be captured (Davis 1996).

Figure 2: The pitfall trap, including the bucket, the water including salt and detergent, and the sock filled with bait (in this case cow dung) tied to a stick. Photo taken by author.

The pitfall traps were placed at 8 different plot-sites in both Udzungwa Mountains National Park (UMNP) and in Amani Nature Reserve (ANR). Appendix 1 presents the GPS-coordinates of each plot-site. At each plot-site, both types of dung (cow and pig) as well as rotting meat were used as bait, with a few meters between each trap. Collected beetles were given a code depending on which trap they fell in and what kind of bait was used. For example, beetles collected at the first plot in Amani were given the code "A1C" if cow dung was used as bait, "A1P" if pig dung was used as bait or "A1M" if rotting meat was used as bait. If another plot location was used like, Plot 2 or 3, then the beetles collected using pig dung would be placed in a plastic container named "A2P" or "A3P". The collection process was repeated five times for each set of traps. Pictures were taken from all plots in both Amani and Udzungwa (Appendix 2).

In ANR, The same plot-sites that were used in a previous study (Geeraert 2014) were reused. The eight plot-sites were divided in two large areas, the first four plot-sites were located close to the Amani conservation center in a primary forest (plot-site 1 and 2), a secondary forest logged approximately 50 years ago (plot-site 3) and in a farmland located close to the secondary forest (plot-site 4). The final four plots-sites were located in the Kwamkoro area in a secondary, moderately disturbed forest. Plot-site 5 was placed close to a river in this secondary forest, while plot-sites 6, 7 and 8 were placed in various locations in the secondary forest. All plot-sites in Amani were 950-1000 meters over the sea level.

Maesopsis eminii is a pioneer tree species introduced in Amani Nature Reserve by the colonizing Germans in the early 1900s. The relative number of *Maesopsis eminii* may be used as an indicator for disturbance among different habitats in Amani, where for example the primary forest (undisturbed habitat) contains small numbers of the species compared to secondary forests that has been logged or disturbed in the past (Geeraert 2014). The species spreads easily as the relatively common hornbills (several species) disperse the tree species (Binggeli & Hamilton 1993, Hall 1995).

Primary Forest: Undisturbed habitat that represent plot-sites 1 and 2 (Appendix 2, pic 1, 2). Contains very low densities of *Maesopsis eminii* trees compared to all the other habitats (Geeraert 2014).

Secondary Forest Logged: Located in a heavily disturbed forest in Mbole, an area which has been heavily logged in the past (approximately 50 years ago according to local guides). Represents plot-site 3 (Appendix 2, pic 3). The forest has a large number of *Maesopsis eminii* trees, especially compared to the primary forest habitat (Geeraert 2014). From personal field observations, the seeds of *Maesopsis eminii* occurred in large numbers on the trail leading to the plot-site.

Farmland: The farmland habitat is a logged area currently being used as agroforestry land. Represents plot-site 4 (Appendix 2, pic 4). It is an open logged area dominated by *Maesopsis eminii* trees and cinnamon trees (Geeraert 2014).

Secondary Disturbed River: A moderately disturbed forest that has been logged in the past. Represents plot-site 5 (Appendix 2, pic 5), which is located about 5-10 meters from a river. *Maesopsis eminii* trees were more present in this forest compared to the undisturbed forest but did not dominate (Geeraert 2014).

Secondary Disturbed: Similar habitat to Secondary Disturbed River but not close to a river. Represents plot-site 6-8 (Appendix 2, pic 6-8).

The fieldwork done in Udzungwa Mountains, were not done inside the National park due to some unforeseen problems regarding the research permit. The plots were instead located as close as possible to the National Park forest area but outside the border (Appendix 2, pic 9-16), approximately 350 meters over sea level.

2.5. ENVIRONMENTAL VARIABLES

Some notes on different environmental variables were taken at each plot in both areas. These included: cover (%) and litter (%). Both these variables were estimated by eyesight. By standing over the trap and looking upwards, the amount of sunlight penetrating the cover vegetation was estimated. The cover (%) thus represents how much sunlight was blocked from the vegetation. The litter (%) was estimated by how much dead vegetation was located around the plot-site, this mostly included leaves and twigs. Cover (%) was estimated for each trap, litter (%) however was estimated for each plot-site, with the same approximation used for the three traps in a given plot.

Table 1. *Environmental variables in Amani Nature Reserve. Showing Cover (%) and Litter (%) for each plot. Plots with C = Cow, P = Pig, M = Meat.*

Plot	Cover (%)	Litter (%)
1C	85	95
1P	70	95
1M	77	95
2C	92	72
2P	37	72
2M	61	72
3C	84	76
3P	52	76
3M	92	76
4C	62	98
4P	33	98
4M	47	98
5C	93	52
5P	95	52
5M	91	52
6C	48	60
6P	87	60
6M	66	60
7C	69	94
7P	85	94
7M	89	94
8C	93	88
8P	90	88
8M	74	88

Table 2. *Environmental variables in Udzungwa Mountains National Park. Showing Cover (%) and Litter (%) for each plot. Plots with C = Cow, P = Pig, M = Meat.*

Plot	Cover (%)	Litter (%)
1C	0	20
1P	0	20
1M	0	20
2C	34	98
2P	22	98
2M	0	98
3C	5	64
3P	4	64
3M	0	64
4C	83	71
4P	64	71
4M	53	71
5C	76	67
5P	93	67
5M	67	67
6C	7	32
6P	3	32
6M	5	32
7C	26	92
7P	44	92
7M	43	92
8C	18	85
8P	39	85
8M	16	85

2.6. STATISTICAL ANALYSES

All analyses were done in the statistical program R, version 3.1.2 (R Core Team 2014).

A general linear model (GLM) was used to test for differences between types of bait and different plots. The dataset consisted of the number of morphospecies and the number of individuals for both Amani and Udzungwa.

The Shannon-Wiener Index (H') was used to compare the dung beetle communities between the habitats. This analysis is widely used to test for such differences (Davis 2000, Estrada & Coetes-Estrada 2002, Hanski 1983, Klein 1989)

A Detrended Correspondence Analysis (DCA) was used to show similarities in species composition and abundance (Durães et al. 2005). Plots with similar habitats were expected to be grouped closer together than plots in different habitats. Traps with the same type of bait were expected to be grouped closer together than traps with different types of bait.

A Canonical Correspondence Analysis (CCA) was also used to look for relationships among the dung beetle composition and abundance between plots. CCA is a multivariate analysis technique that mostly relates community composition to environmental variables. CCA used in combination with DCA may infer whether measured environmental variables are sufficient to explain variation in species data (Didham et al. 1998, Verdú et al. 2007, Ter Braak 1986).

3. RESULTS

A total of 1376 true dung beetles, representing 59 different morphospecies, were collected during the sample period for both sites. In Amani, 352 specimens grouped in 18 different morphospecies were sampled, in Udzungwa, 1024 specimens grouped in 41 different morphospecies were sampled. No common species were found between Amani and Udzungwa.

The traps containing rotting meat often got disturbed, probably by local dogs or bush rats, and the sock containing meat was at times removed from location. The transporting process unfortunately resulted in some damage to collected data (loss of head, limbs etc.), destroyed specimens were not used as viable data.

3.1. MORPHOSPECIES ANALYSIS

Some of the morphospecies occurred in larger numbers and on several different plot-sites. In Amani, eight morphospecies appeared to occur more often than other (Table 3, Figure 3). Morphospecies A1C-X1 represented close to 31% of the total number of specimens, followed by A2C-5 (18.75%). The eight morphospecies with highest occurrence (> 4.5 % of total) were found on all types of bait. Of the eight most common species, only morphospecies A1C-3 (8.81% of total) was solely found using dung bait. These eight species were generally present on many of the eight plot-sites, A2C-3 was present on five of the sites while the seven others were found between six to eight sites. The eight morphospecies A1C-1, A1C-2, A1C-3, A1P-3, A2C-3, A2C-5, A1C-X1 and A1C-X2 are for the purposes of this study, considered common species in Amani.

Table 3: Amani morphospecies with number of captured individuals, their percentage of the total number of individuals (352), number of plots (individual traps) the given morphospecies was found in, number of plot-sites and what kind of bait was used.

Species	No. of individuals	% of total	no. of plots	no. of sites	Bait
A1C-1	20	5.68	10	6	Cow, Pig, Meat
A1C-2	19	5.4	13	8	Cow, Pig, Meat
A1C-3	31	8.81	6	6	Cow, Pig
A1P-3	16	4.55	9	7	Cow, Pig, Meat
A1M-1	10	2.84	6	6	Meat
A1M-2	1	0.38	1	1	Meat
A2C-3	24	6.82	9	5	Cow, Pig, Meat
A2C-5	66	18.75	14	7	Cow, Pig, Meat
A2P-2	1	0.28	1	1	Pig
A2M-1	7	1.99	5	4	Pig, Meat
A3C-5	2	0.57	2	2	Cow
A4P-7	4	1.14	2	1	Cow, Pig
A5M-3	2	0.57	1	1	Meat
A7P-4	1	0.28	1	1	Pig
A1C-X1	109	30.97	20	8	Cow, Pig, Meat
A1C-X2	30	8.52	5	3	Cow, Pig, Meat
A1C-X3	2	0.57	1	1	Cow
A1C-X4	7	1.99	4	3	Cow, Pig

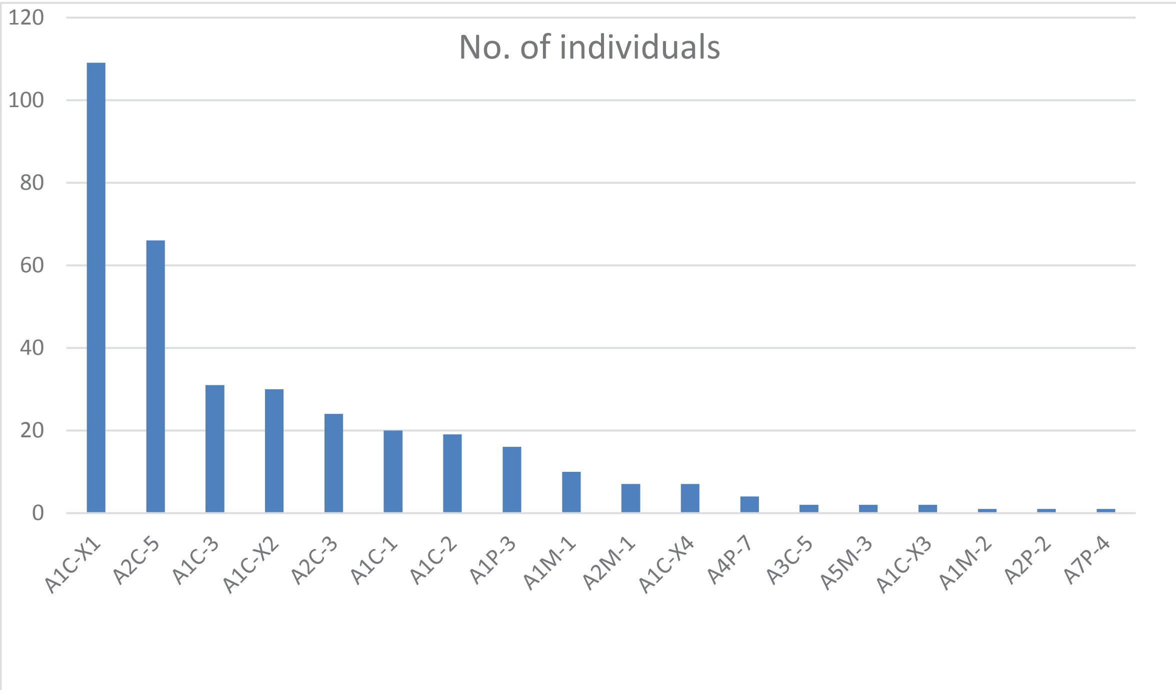


Figure 3: The abundance of captured beetles in Amani, from the largest to smallest number.

In Udzungwa five morphospecies appeared to be more common than others (Table 4, Figure 4). The three morphospecies with the highest abundance (U1P-6, U1M-3 and U2P-5) were located on seven to eight of the total sites (eight). Among these only U1M-3 were found on traps with meat as bait. Both U1P-6 and U2P-5 were only found using cow or pig dung. The abundance of different morphospecies appeared to be largely dominated by morphospecies U1P-6 representing 58.69% of total beetles from Udzungwa. This morphospecies and U2P-5 belong to the genus *Sisyphus*. The two Sisyphus spp. were clearly different but may include several closely related species.The morphospecies U1C-7 (Appendix 5) is most likely a member of the genus S*arophorus* (Frolov & Scholtz 2003).

Table 4: Udzungwa morphospecies with number of individuals captured, their percentage of the total number of individuals (1024), number of plots (individual traps) the given morphospecies was found, number of plot-sites and what kind of bait was used.

Species	No. of individuals	% of total	no. of plots	no. of sites	Bait
U1M-3	101	9.86	17	8	Cow, Pig, Meat
U1P-1	2	0.195	2	1	Cow, Pig
U1P-2	3	0.29	3	2	Cow, Pig
U1P-3	4	0.39	2	1	Cow, Pig
U1P-4-2	18	1.76	5	4	Pig, Meat
U1P-6	601	58.69	13	7	Cow, Pig
U1P-7	16	1.56	3	3	Pig
U1C-7	15	1.465	7	5	Cow, Pig, Meat
U1C-8	16	1.56	6	5	Cow, Pig
U1C-9	3	0.29	2	2	Cow, Pig
U2P-5	78	7.6	11	7	Cow, Pig
U3P-1	2	0.195	1	1	Pig
U3P-2	1	0.098	1	1	Pig
U3P-5(6)	4	0.39	3	2	Cow, Pig
U3P-7	3	0.29	3	3	Pig
U3C-2	11	1.07	2	2	Cow, Pig
U4C-1	2	1.195	2	1	Cow, Pig
U4P-1	1	0.098	1	1	Pig
U4P-8	1	0.098	1	1	Pig
U5C-5	1	0.098	1	1	Cow
U5P-3	18	1.76	5	4	Pig, Meat
U5P-4	1	0.098	1	1	Pig
U6C-2	21	2.05	4	3	Cow, Pig
U6C-5	1	0.098	1	1	Cow
U6P-1	1	0.098	1	1	Pig
U7P-4	4	0.39	2	1	Cow, Pig
U7C-1	1	0.098	1	1	Cow
U8P-1	1	0.098	1	1	Pig
U8P-3	1	0.098	1	1	Pig
U8P-4	2	0.195	1	1	Pig
U8P-13	1	0.098	1	1	Pig
U8P-14	1	0.098	1	1	Pig
U8P-15	1	0.098	1	1	Pig
U1C-X2	1	0.098	1	1	Cow
U1C-X3	5	0.488	3	3	Cow, Pig
U1P-X4	25	2.44	8	6	Cow, Pig, Meat
U1P-X5	33	3.22	4	2	Cow, Pig
U1P-X6	2	0.195	1	1	Pig
U2P-X3	11	1.07	4	4	Pig
U5P-X4	8	0.78	3	2	Cow, Pig, Meat
U8P-X6	2	0.195	1	1	Pig

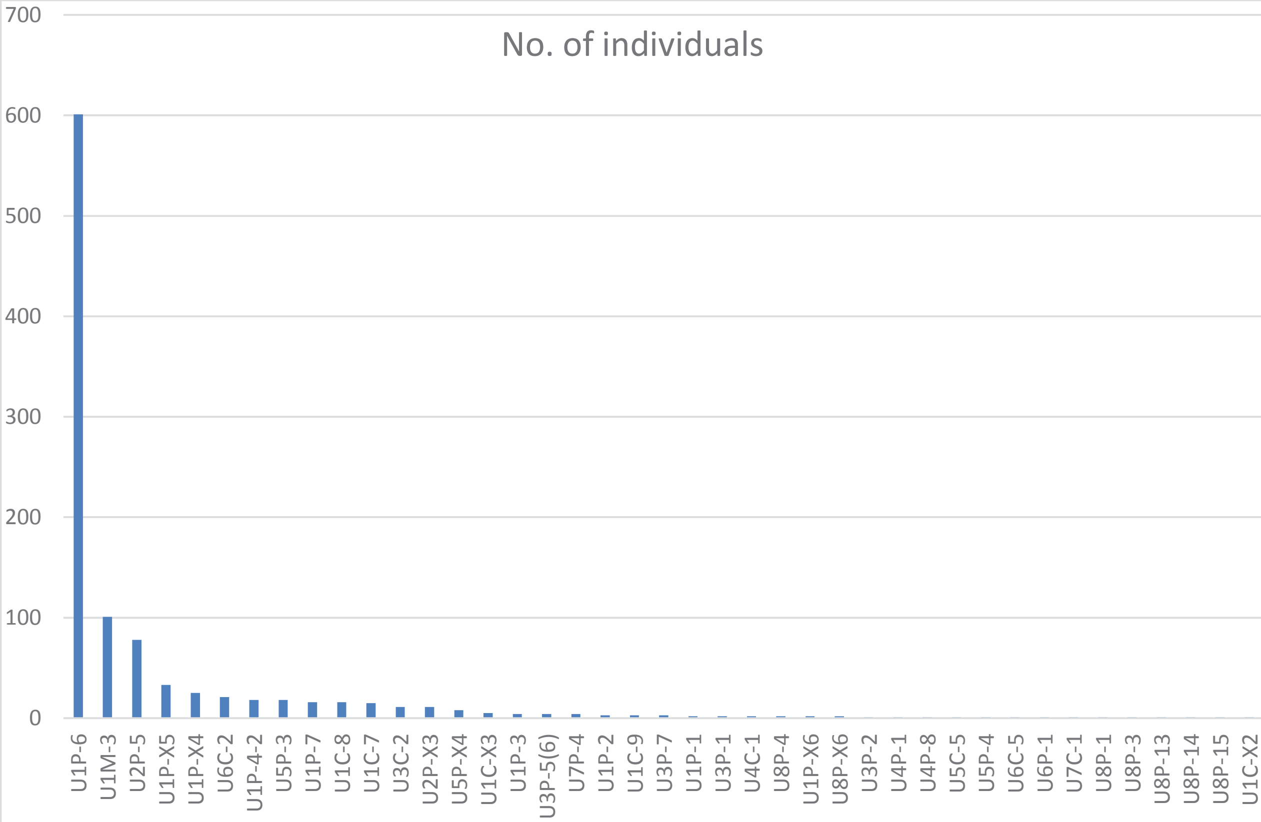


Figure 4: The abundance of captured beetles in Udzungwa, from largest number of specimens per morphospecies to the smallest.

Collected beetles from Amani on different types of bait (Table 5) showed more unique morphospecies on meat compared to both pig and cow dung. Approximately 16.7 % of the total number of different morphospecies in Amani were caught on traps with meat, 11.1% of the total number of morphospecies were unique for cow dung and 11.1 % for pig dung. Also, note that the number of morphospecies found at each type of bait appeared similar (12 on cow, 13 on pig and 11 on meat). The morphospecies A2P-2 (Appendix 5) which were unique for pig dung (Table 5), is most likely a member of the genus *Sceliages* (Forgie et al 2002, Forgie et al. 2003).

Table 5: Unique morphospecies found only on a specific type of bait in Amani. Number (Species) showed how many morphospecies were found on a given type of bait (modified from Table 3). Unique Code showed which morphospecies were unique with the number of individuals in brackets.

Bait	Unique	Number (Species)	Unique Code (Individuals)
Cow	2	12	A3C-5 (2), A1C-X3 (2)
Pig	2	13	A2P-2 (1), A7P-4 (1)
Meat	3	11	A1M-1 (10), A1M-2 (1), A5M-3 (2)

The collected material from Udzungwa (Table 6) appeared to show another story with zero unique species found on meat and only six different morphospecies appearing on these traps. Traps with pig captured 37 morphospecies, and traps with cow captured 22 morphospecies. Sixteen of the morphospecies found on pig dung were only found using this type of bait, this represents 39% of the total number of morphospecies in Udzungwa. Only 9.75 % of the total number of morphospecies were solely captured in traps with cow dung. Table 7 showed the number of specimens from Udzungwa that was present at traps with pig bait.

Table 6: Unique morphospecies found only on a specific type of bait in Udzungwa. Number (Species) showed how many morphospecies were found on a given type of bait (modified from Table 4). Unique Code showed which morphospecies were unique with the number of individuals in brackets.

Bait	Unique	Number (Species)	Unique Code (Individuals)
Cow	4	22	U5C-5 (1), U6C-5 (1), U7C-1 (1), U1C-X3 (1)
Pig	16	37	U1P-7 (16), U3P-1 (2), U3P-2 (1), U3P-7 (3),
			U4P-1 (1), U4P-8 (1), U5P-4 (1), U6P-1 (1),
			U8P-1 (1), U8P-3 (1), U8P-4 (2), U8P-13 (1),
			U8P- 14 (1), U8P-15 (1), U1P-X6 (2), U2P-X3 (11),
			U8P-X6 (2)
Meat	0	6	

Table 7: The number of captured dung beetles for each plot-site (P1-8) in Udzungwa. The first number is the number of specimens of a given morphospecies with any kind of bait. Numbers inside brackets and written in bold represent the number of specimens of the given morphospecies that were only found at traps with pig as bait.

Species	P1	P2	P3	P4	P5	P6	P7	P8
U1M-3	24 **(9)**	12 **(6)**	2 **(2)**	2 **(2)**	12 **(5)**	1 **(1)**	14 **(13)**	35 **(24)**
U1P-1	2 **(1)**							
U1P-2	2 **(1)**						1 **(1)**	
U1P-3	4 **(1)**							
U1P-4-2	4 **(3)**				4 **(4)**		1 **(1)**	9 **(9)**
U1P-6	38 **(28)**	58 **(49)**	1		37 **(20)**	9 **(4)**	91 **(76)**	364 **(279)**
U1P-7	1 **(1)**						13 **(13)**	2 **(2)**
U1C-7	2 **(1)**		2 **(2)**	1	9 **(7)**	2 **(1)**		
U1C-8	1	6 **(6)**		1 **(1)**	2 **(1)**		6 **(6)**	
U1C-9	1			2 **(2)**				
U2P-5	2 **(1)**	4 **(3)**	1 **(1)**	3 **(3)**	42 **(35)**		3 **(2)**	23 **(17)**
U3P-1			2 **(2)**					
U3P-2			1 **(1)**					
U3P-5(6)			2 **(2)**			2 **(1)**		
U3P-7			1 **(1)**		1 **(1)**			1 **(1)**
U3C-2		10 **(10)**	2					
U4C-1				2 **(1)**				
U4P-1				1 **(1)**				
U4P-8				1 **(1)**				
U5C-5					1			
U5P-3					2 **(2)**	6 **(5)**	2 **(2)**	8 **(8)**
U5P-4					1 **(1)**			
U6C-2						13 **(10)**	2 **(2)**	6 **(6)**
U6C-5						1		
U6P-1						1 **(1)**		
U7P-4							4 **(1)**	
U7C-1							1	
U8P-1								1 **(1)**
U8P-3								1 **(1)**
U8P-4								2 **(2)**
U8P-13								1 **(1)**
U8P-14								1 **(1)**
U8P-15								1 **(1)**
U1C-X2	1							
U1C-X3	3	1 **(1)**		1 **(1)**				
U1P-X4	8 **(3)**	1	1 **(1)**	1 **(1)**	13 **(10)**			1
U1P-X5	10 **(3)**				23 **(18)**			
U1P-X6	2 **(2)**							
U2P-X3		1 **(1)**			3 **(3)**		1 **(1)**	6 **(6)**
U5P-X4					1 **(1)**			7
U8P-X6								2 **(2)**

Most of the captured dung beetles were dark colored. In Amani, two morphospecies (A2M-1, A2C-5, Appendix 5) had a bright color pattern, and one morphospecies (A1C-2, Appendix 5) had a metallic color variation. In Udzungwa, six morphospecies (U1C-9, U4C-1, U5P-4, U7C-1, U7P-4, U8P-13, Appendix 5) had bright color patterns, and two morphospecies (U3P-1, U3P-2, Appendix 5) had a metallic color variation. Most of the bright colored morphospecies in both Amani and Udzungwa were dark with lighter-colored spots.

3.3. HABITAT ANALYSIS

Only captured material from Amani was included in habitat analysis. Material from Udzungwa was collected outside the forest border, with no clear differences in habitat type.

In terms of unique morphospecies (Table 9), most of the unique species (species only found in a given habitat) were located in the primary forest. This habitat also represents the highest diversity of morphospecies. All other habitats resulted in only one unique morphospecies. A Shannon-Wiener diversity index value was calculated for the communities in each of the habitats (Table 10). Primary forest habitat showed the highest value (2.57157) and the farmland habitat has the lowest value (1.239101). The secondary logged habitat had the second lowest value, while the secondary disturbed riverine forest plot (1.690678) had similar value to the secondary disturbed forest habitat (1.643884). The secondary disturbed riverine forest had a higher value than the secondary disturbed forest, even though the secondary disturbed forest had more morphospecies present (11 compared to eight). The reason for this was most likely that the abundance of the different morphospecies in the secondary disturbed riverine forest were more evenly matched in numbers compared to the other habitat (Table 8).

Table 8: Observed abundance of Amani morphospecies across different habitats. Values larger than zero, are shown in bold.

Species	Primary Forest	Secondary Logged	Farmland	Secondary Disturbed River	Secondary Disturbed
A1C-1	**5**	**2**	0	**2**	**14**
A1C-2	**5**	**4**	**4**	**1**	**2**
A1C-3	**6**	0	0	**3**	**22**
A1P-3	**11**	**1**	**1**	**1**	**2**
A1M-1	**5**	**2**	**1**	0	**2**
A1M-2	**1**	0	0	0	0
A2C-3	**3**	**11**	**4**	0	**6**
A2C-5	**3**	**17**	**3**	**6**	**35**
A2P-2	**1**	0	0	0	0
A2M-1	**1**	0	0	**4**	**2**
A3C-5	**1**	**1**	0	0	0
A4P-7	0	0	**4**	0	0
A5M-3	0	0	0	**2**	0
A7P-4	0	0	0	0	**1**
A1C-X1	**19**	**2**	**59**	**9**	**20**
A1C-X2	**4**	**1**	**25**	0	0
A1C-X3	**2**	0	0	0	0
A1C-X4	**6**	0	0	0	**1**

Table 9: Morphospecies found only in a specific habitat in Amani. Unique represents number of morphospecies only occurring in a given habitat, Number (Species) represents the number of morphospecies found at a given plot (modified from table 5). Unique Code showed which morphospecies were unique in the given habitat.

Habitat	Unique	Number (Species)	Unique Code
Primary Forest	3	15	A1M-2, A2P-2, A1C-X3
Secondary Logged	1	9	A3C-5
Farmland	1	8	A4P-7
Secondary Disturbed River	1	8	A5M-3
Secondary Disturbed	1	11	A7P-4

Table 10: Shannon Diversity values (H') for beetle communities in different habitats in Amani

Habitat	Shannon Value
Primary Forest	2.57157
Secondary Logged	1.538966
Farmland	1.239101
Secondary Disturbed River	1.690678
Secondary Disturbed	1.643884

The eight most commonly occurring morphospecies in Amani (A1C-1, A1C-2, A1C-3, A1P-3, A2C-3, A2C-5, A1C-X1 and A1C-X2) are among the 10 morphospecies most common in primary forest as well (Figure 5A). For the secondary logged forest (Figure 5B), merely three morphospecies were more frequent than the other observed beetles. These three species are among the eight most common morphospecies found in Amani. In the farmland habitat only two morphospecies (A1C-X1 and A1C-X2) occurred in large numbers (Figure 5C). These are both among the most common species found in Amani. The secondary disturbed riverine forest did not appear to host a large number of beetles (Figure 5D). The two highest numbered species (A1C-X1 and A2C-5) were both among the eight most common species in Amani. The last habitat, secondary disturbed forest (Figure 5E) showed the largest number of morphospecies A2C-5, A1C-3, A1C-X1 and A1C-1. All of these beetles were among the eight most common species found in Amani.

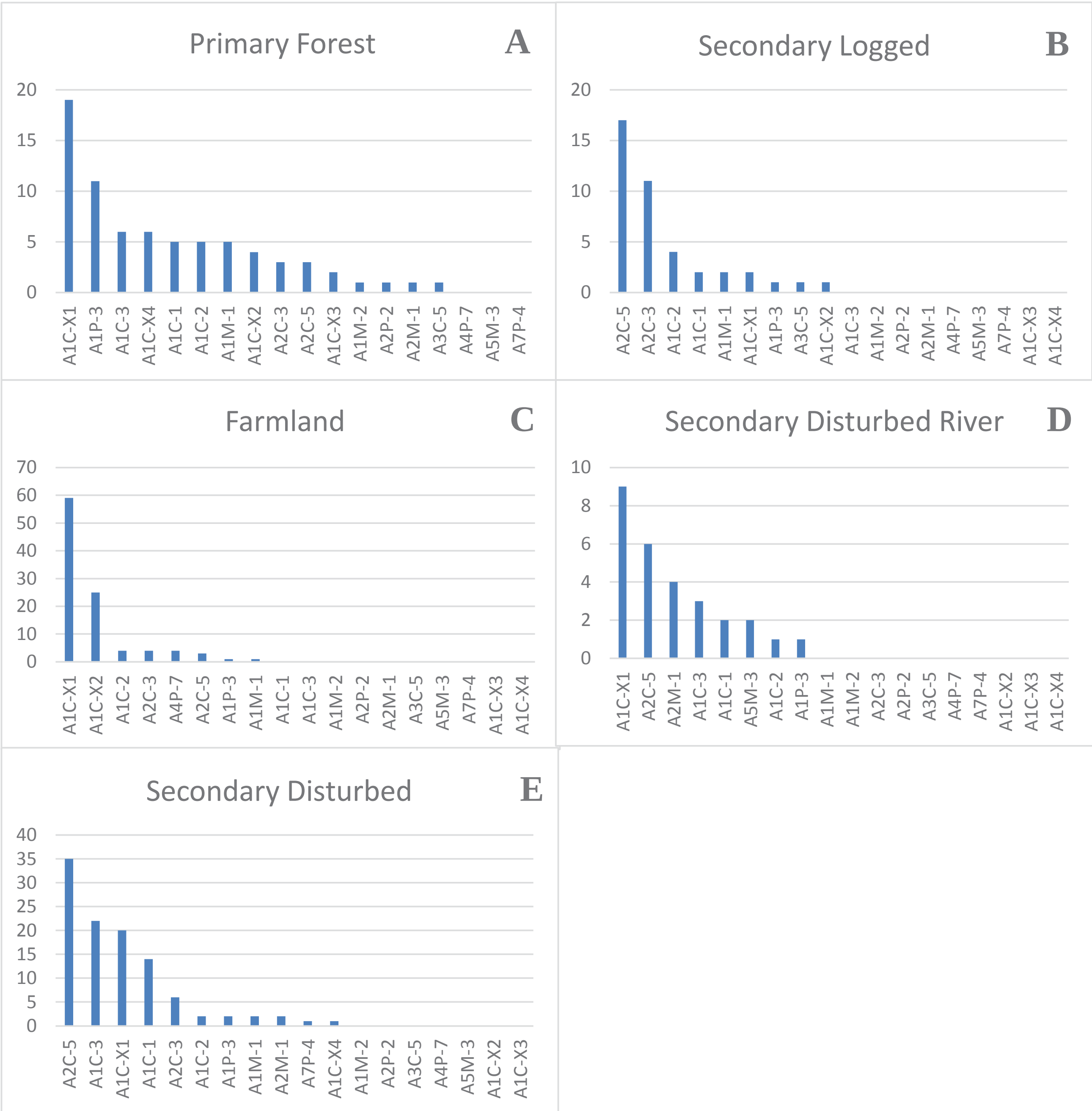


Figure 5 (A-E): The number of morphospecies between the different habitats in Amani. **A**: Primary Forest, **B**: Secondary Forest (Logged approximately 50 years ago), **C**: Farmland (Agroforestry), **D**: Secondary Disturbed Riverine Forest, **E**: Secondary Disturbed Forest. Figures modified from Table 5.

The largest number of individuals was found in the farmland and secondary disturbed forest (Figure 6). Even though the primary forest hosted the largest diversity of morphospecies, it came third in terms of number of individuals. As mentioned previously, the secondary disturbed riverine forest hosted a relatively small number of individuals, with only 28 specimens found. It is necessary to mention that the number of plot-sites used in each habitat was unevenly numbered. The primary forest habitat hosted two plot-sites and the Secondary Disturbed habitat hosted three. The last three habitats (Secondary Logged, Farmland and Secondary Disturbed River) only had one plot-site each (See Material and Methods).

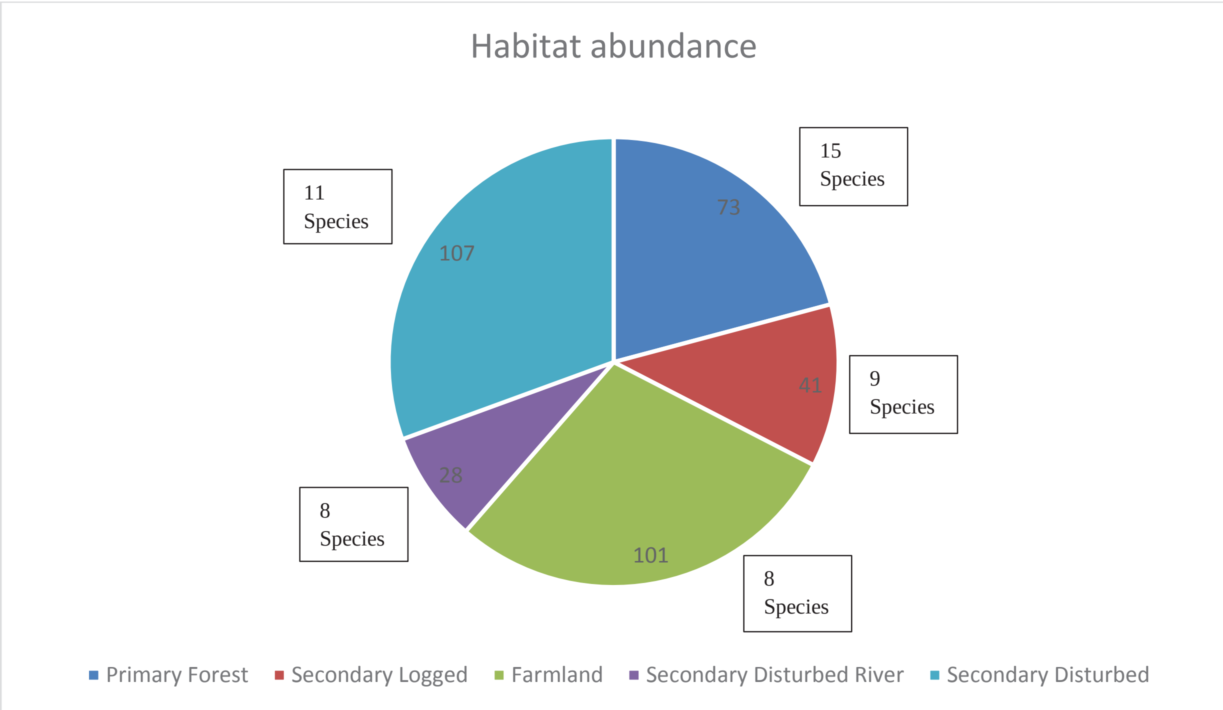


Figure 6: The number of individuals (colors in diagram) and morphospecies (numbers in rectangles) found in different habitats in Amani (modified from Table 8 and 9).

3.4. GENERAL LINEAR MODEL

A GLM analysis with number of morphospecies for both Amani and Udzungwa were made to test for significant differences between types of bait and differences between plots-sites. Distribution was set as Poisson. The intercept variable was set as plots with cow bait. Significant differences were found on meat as bait (p value < 0.001), and on pig (p value < 0.01).

I also made a GLM with plots from Amani and Udzungwa separately.

GLM with morphospecies from Amani showed no real significant values between different types of bait. Plots with cow dung were the intercept variable here as well. Plots with meat however were close to significant, with a P value of 0.101.

GLM with morphospecies from Udzungwa on the other hand showed significant differences between all types of bait. Different types of bait all had a P value < 0.001.

Another GLM was made with the number of individuals to test for significant differences between types of bait used.

The first GLM in this case, grouped together beetles from Amani and Udzungwa and showed very significant results for all types of bait (all P values < 0.001).

The GLM with the number of individuals from Amani showed a trend between the number of morphospecies on cow and pig (p value = 0.0915), where pig dung yielded a larger number of individuals.

GLM from number of individuals from Udzungwa on the other hand showed significance in differences between all types of bait and between different plot-sites (p values < 0.001).

3.5. ORDINATION

A Detrended Correspondence Analysis (DCA) was used to show similarities in species composition and abundance. Wartenberg et al. (1987) recommends a cautious interpretation of the DCA ordination.

Figure 7 showed some interesting placements of plot-sites in Amani. Number 6, 7 and 8 are all grouped very closely, these plots were all in the Kwamkoro disturbed forest and appeared to suggest some relation among the three sites in terms of diversity and abundance of dung beetles. Plot-site 5 was not far away from the three other Disturbed forest sites, it was located in the same forest but closer to a river. Plot-site 1 and 2 were both located in the same forest (Primary Forest habitat), but in this ordination there seemed to be no relationship between the two plots. Figure 8 did not show any clear placements of plot-sites.

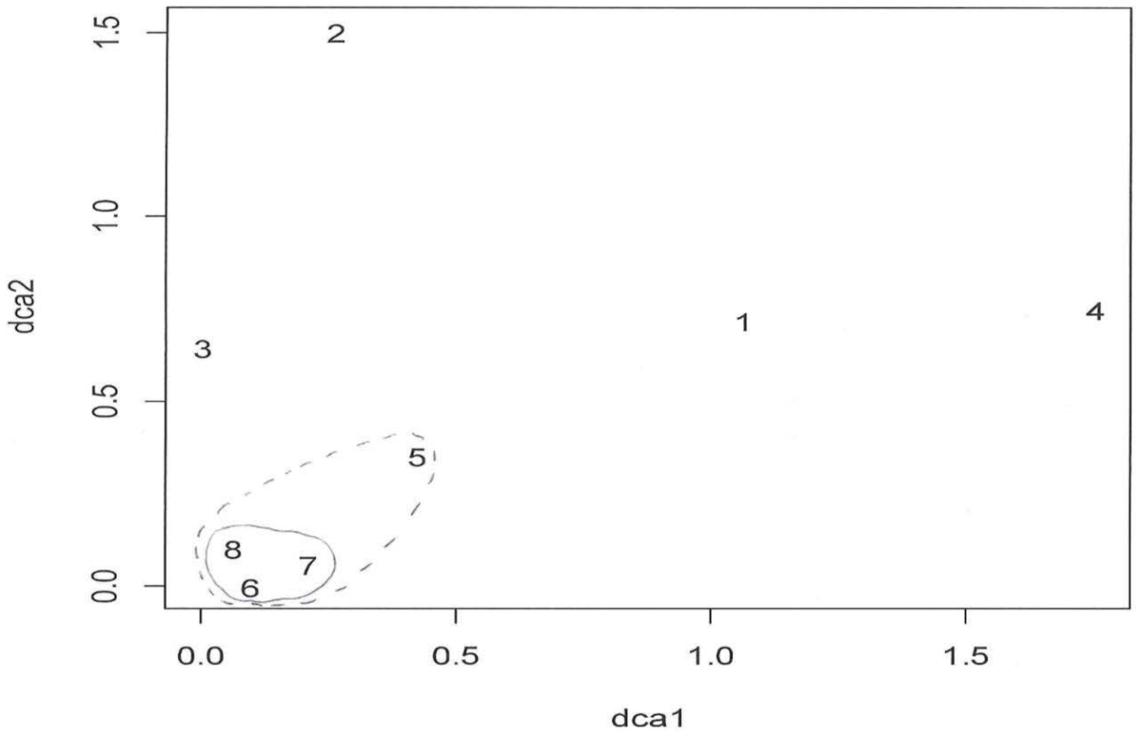


Figure 7: DCA plot based on species diversity and abundance in Amani. Numbers represents the eight different plot-sites in Amani. Circled plots are further discussed in the text.

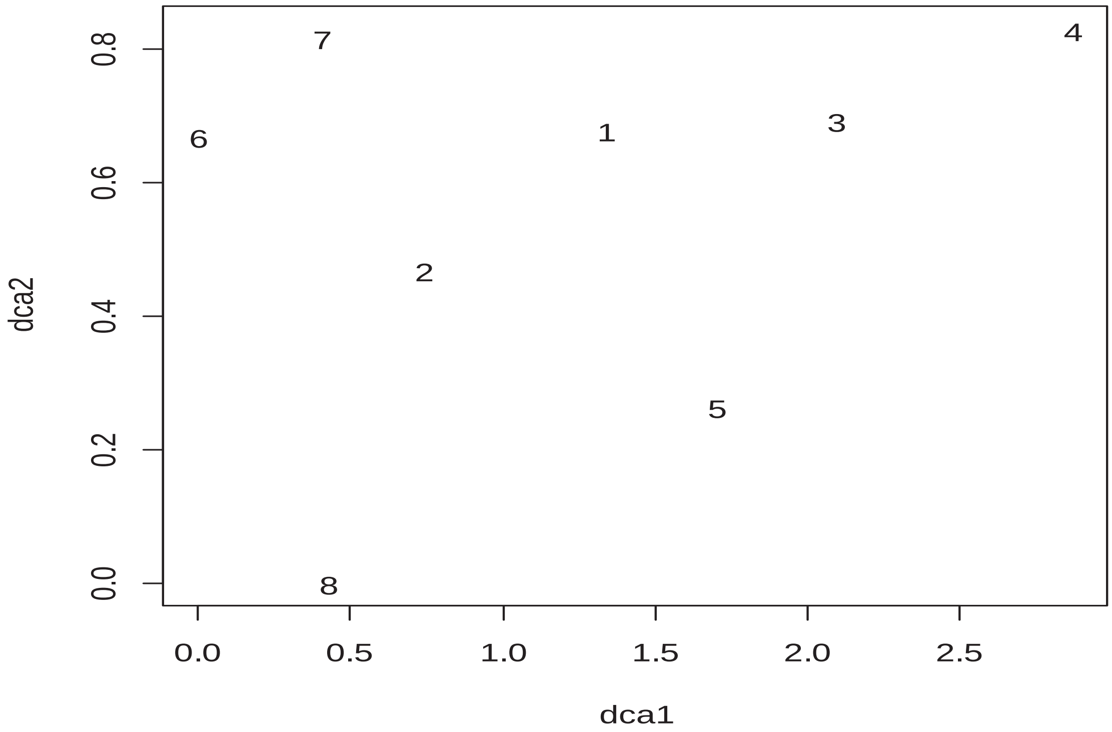


Figure 8: DCA plot based on species diversity and abundance in Udzungwa. Numbers represents the eight different plot-sites in Udzungwa.

Figure 9 showed differences between abundance and diversity of collected dung beetles between different plot-sites and type of bait used. DCA value 1 and 2 were used due to their higher values (Appendix 3-1). All plots with meat (green) appear to be grouped in the middle and right part of the ordination. The abundance and diversity of captured beetles with meat as bait consequently appeared to show some similarities. Plot 4 pig and plot 4 cow were also located close to plots with meat. Plot 4 represent the farmland habitat, where captured material from meat and pig appear similar. Plot 4 pig hosted a larger diversity of beetles than meat (seven compared to four). The most abundant dung beetle for both plots was however the same morphospecies, and the same two species as mentioned previously from Figure 5C.

Plot 1 and 2 with cow as bait were grouped relatively close together, the same cannot be said for plot 1 and 2 with pig bait. The fact that the plots from the primary forest habitat with cow as bait appeared similar may still be relevant, and at least it showed some similarities between sampled morphospecies from this habitat.

Most of the plots with pig and cow dung from Kwamkoro Disturbed forest (plot 5-8) are located on the left, middle part of the ordination. Many of the plots in Kwamkore, both for pig (plot 5,6,7) and cow (plot 5,7,8) appear grouped together. The remaining two plots for this habitat (plot 8 pig and plot 6 cow) were not placed very far away from the others in the DCA plot (Fig. 9). This grouping appeared similar to Figure 7, and may offer support in similarities for the Kwamkoro disturbed forest habitat. Note also that plot 3 pig, a plot in the secondary logged habitat, was located close to the other habitats with secondary forest. Even though the plots were placed far from each other in the DCA (Fig. 9), the forests may appear similar to the inhabiting dung beetles. This trend of relatively close grouping, however, was not apparent for the other plots in the secondary logged forest, where plot 3 cow and plot 3 meat were grouped distant from each other in the DCA. It should, however, be mentioned that of these three plots from the secondary logged habitat, the plot with meat only captured two morphospecies, while the plot with pig captured six different species and the plot with cow captured five different species. Four of the five morphospecies found on plot 3 cow were also found at plot 3 pig. Plot 3 cow hosted the morphospecies (A3C-5), which appeared to be a rare beetle only found at one other plot (plot 2 cow).

Plot 2 pig was located far away from all the other plots. It should be mentioned that this plot hosted a unique large beetle only found at this plot (A2P-2, Appendix 5) and may because of this one morphospecies be located far away from other plots.

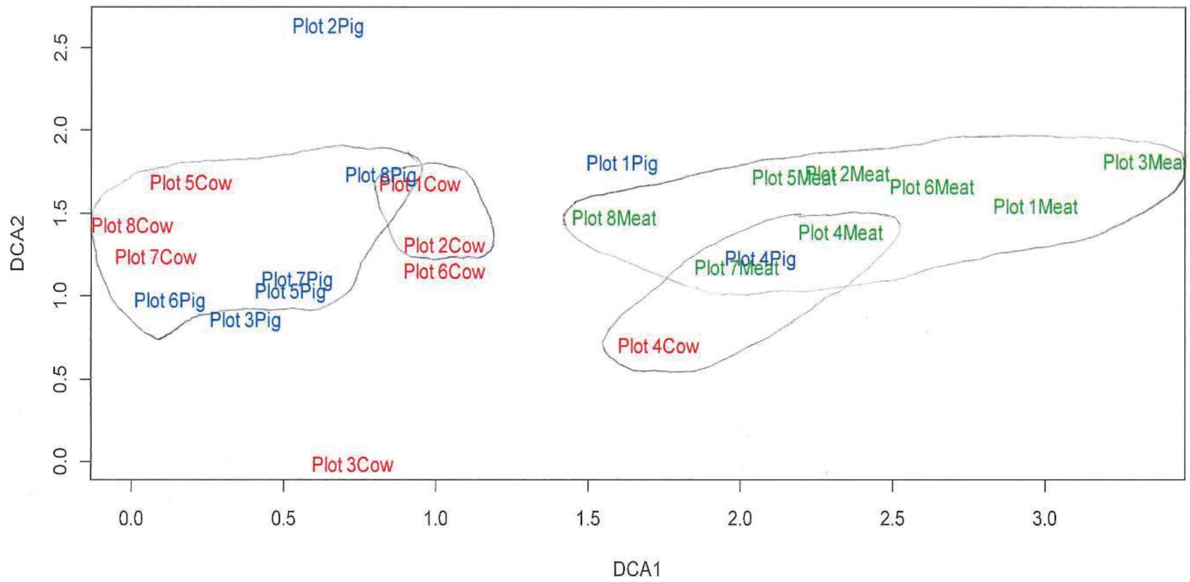


Figure 9: DCA plot (DCA1 and DCA2) with bait in Amani based on species abundance and diversity. Red are plots with cow bait, Green is meat, blue is pig. Circled plots are further discussed in the text.

Plot 4 cow dominates and skewers the ordination if included (Appendix 3-3). According to Hill & Gauch (1980), the only way to cope with extreme outliers is to remove them, because these extremes may result in a badly estimated gap. In plot 4 cow only one morphospecies was found. This beetle was unique only for plot-site 4, with plot 4 pig being the only other plot where this beetle occurred, possibly explaining the extreme value. Plot 7 meat and plot 3 meat were not included in these ordinations, because they failed to capture any dung beetles due to removal of the bait, probably by dogs.

Figure 10 showed the same ordination without plot 4 cow, DCA value 1 and 2 were used due to their higher values (Appendix 3-4). This figure did not appear to show clear grouping of plots like Figure 9 does. One thing to note about this figure was the grouping of plot-site 6. All the plots here, regardless of what type of bait used, were grouped together. This plot-site was different from the other Udzungwa plots because it was located furthest away from the forest. Plot 7 and 8 with pig and cow were grouped relatively close together. These plots were both located close to an inhabited village. Plot 7 and 8, especially the traps with pig as bait, were the most successful plots in terms of number of individuals and diversity of morphospecies. Six of the 16 unique morphospecies only found on pig bait in Udzungwa (Table 6) were found exclusively on plot 8 pig.

Plot 8 meat was located away from all the other plots, and it should be mentioned that this was the only "semi-successful" plot using meat as bait in Udzungwa, were it hosted 13 individual beetles from three different morphospecies. All other plots with meat in Udzungwa hosted between zero to two individuals.

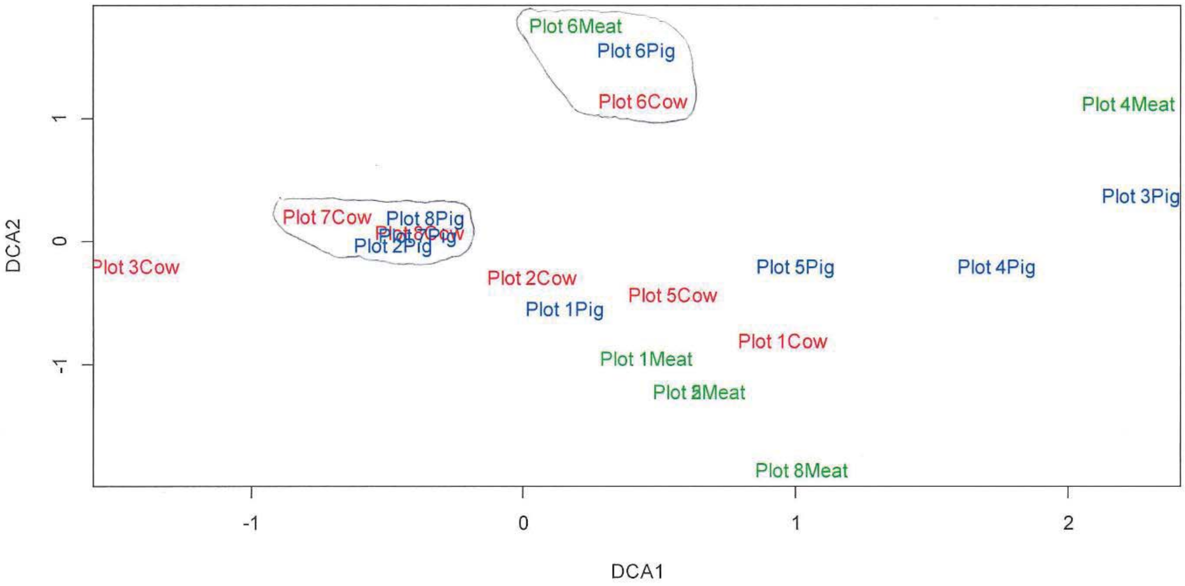


Figure 10: DCA plot (DCA 1 and DCA 2) with bait in Udzungwa based on species abundance and diversity (plot 4 cow not included). Red are plots with cow bait, Blue is pig, green is meat. Circled plots are further discussed in the text.

3.6. ENVIRONMENTAL ORDINATION

To test if measured environmental variables (Table 1, Table 2) may help explain variation in species data, two CCA plots (Appendix 4-3, 4-6) were made in addition to the DCA plots (Appendix 4-2, 4-5). The environmental data was first tested for correlation (Appendix 4-1, 4-4) and because of relatively low values they were not considered correlated.

In Amani (Appendix 4-2, 4-3) the environmental vectors pointed in similar directions and appear to overlap with some plots. In Udzungwa (Appendix 4-5, 4-6) the environmental vectors pointed in opposite directions but some of the plots appear to overlap. The CCA from

Udzungwa (Appendix 4-6) did not appear to give sufficient information, since most of the plots were all located in the same area. Because some overlap occured, the environmental vectors may help explain some of the variation in species data for the ordinations (Didham et al. 1998, Verdú et al. 2007), especially in Amani.

4. DISCUSSION

The diversity and abundance of dung beetles were higher in Udzungwa (1024 individuals with 41 morphospecies) compared to Amani (352 individuals with 18 morphospecies). This result was expected because of the larger diversity of mammals being present in Udzungwa, giving support to the first prediction of this study. However, the plots in Udzungwa were at a lower altitude (approximately 350 m. a. s. l.) compared to Amani (950-1000 m. a. s. l.). For most animal and plant groups there is generally a decline in species numbers with increasing altitude (Lovett 2006). In addition, since the plots in Udzungwa were located on agricultural land on the border of the National Park and not inside the forest (like in Amani), this may have affected the species composition.

No common species were found between Amani and Udzungwa. The habitats in the two study areas were as previously mentioned, very different. Additionally, the environmental variables between Amani (Table 1) and Udzungwa (Table 2) showed large differences, especially in the forest cover percentage.

Data collected in Udzungwa generally consisted of medium to small sized morphospecies, with the largest dung beetle being 16 mm in length (U8P-1, Appendix 5). This species was only captured once (Table 4), and was thus one of the rarest beetles found in Udzungwa (Figure 4). In Amani, larger beetles were more common, especially the morphospecies A1C-1 (Appendix 5) which was up to 23 mm in length. This species was among the most common morphospecies found in Amani (Figure 3). Results from this study do not give support for the second prediction. This may be related to plot-sites at Udzungwa being located outside the protected forest, where the number of mammals may have been lower. Large dung beetles were personally observed while hiking in the protected forest in Udzungwa on elephant dung. Unfortunately, none of these larger beetles were captured outside the national park.

Bernon (1981) found between 742 to 1585 beetles occurring at fresh cattle dung after 24 hours in Central South Africa. The recorded data consisted of 161 species belonging to Scarabaeinae, Aphodiinae, Hydrophilidae, Staphylinidae and Histeridae. As previously mentioned, all beetles not representing Scarabaeinae were removed from the dataset. Among these beetles were members of the genera Aphodiinae, Hydrophilidae, Cucuidae, Troxidae, Histerdiae, Staphylinidae and Tenebrionidae. Except for Cucuidae, all of these naturally occur in dung.

As stated previously, the morphospecies U1C-7 (Appendix 5) was most likely a member of the genus *Sarophorus* (Frolov & Scholtz 2003), which is the most recent revision of this genus. The morphological traits from the collected morphospecies U1C-7 appears to be a new species compared to the six species described in the revision. Members of this genus feed on old dung and carrion remains, which may indicate feeding on detritus. The morphospecies A2P-2 (Appendix 5) which was unique for pig dung (Table 5), was most likely a member of the genus *Sceliages* (Forgie et al 2002, Forgie et al. 2003), which is the most recent revision of this African genus. The members of this genus feed and breed exclusively on millipedes (Forgie et al. 2003). The morphological traits from the collected morphospecies A2P-2 points to this being a new undescribed species. These morphospecies may thus be previously undiscovered species.

Different types of bait and how it is related to dung beetle composition:

Dung beetles from Udzungwa appeared to prefer pig dung compared to all other types of bait. 37 of the 41 morphospecies found in Udzungwa were captured using pig dung, representing 74.7% of the total number of beetles (756 of 1024) (Table 7), with 16 morphospecies only being found on pig (Table 6). 22 morphospecies were captured using cow dung, with four morphospecies only occurring in traps with cow dung.

The large number of beetles found on pig dung in Udzungwa may possibly be connected to the presence of human villages and farms located relatively close to the trapping areas. Humans and pigs are both omnivores and may thus produce similar dung.

Results from the GLM supported strong statistical differences between captured beetles on different kinds of bait in Udzungwa. The p values were lower than 0.001 in the models for both abundance and diversity on all three bait types. Differences in Amani were not as clear. In terms of abundance there was a trend for differences between number of individuals on pig and cow (p value = 0.0915) with 141 beetles captured using pig dung and 114 using cow dung. Figure 9 however, showed that the abundance and diversity of morphospecies in Amani appear to be different for traps with meat. This trend was not present in Figure 10 (Udzungwa), even though the GLM showed statistical differences between meat bait and all types of dung in Udzungwa.

Dung beetles feeding on carrion are generally considered uncommon in Africa, mainly because of competition from large vertebrate scavengers. The carrion resource also tends to be available in a short timespan (Scholtz et al. 2009). Some Scarabaeinae may feed on carrion however, especially if the gut contents are exposed and if the carrion is of large size, like for example buffalo and elephant carcasses (Braack 1987). Why beetles from Amani appeared to accept the meat resource (Table 5) was unclear. Plots with meat in Udzungwa were disturbed more (probably by dogs locating the resource) compared to Amani. Traps at site 3 and 7 with meat as bait captured no true dung beetles. At plot-site 7, the meat resource was absent from the trap at all harvesting times. Disturbances to meat traps also occurred in Amani but not nearly as much as in Udzungwa. No scavenging animals inhabit Amani (Frontier Tanzania 2001, Rickart 1999), with the exception of local dogs. And thus dung beetles utilizing the meat resource appeared to have little competition among large vertebrates.

The results from this study, especially from Udzungwa, support the fourth prediction. Pig dung clearly caught the biggest diversity and abundance of dung beetles (37 of 41 morphospecies), while the meat resource attracted a very small number of morphospecies (6 of 41). As previously mentioned, more beetles were captured using pig dung in Amani (141 individuals) compared to cow dung (114 individuals) and meat (97 individuals). Species diversity between types of bait in Amani (Table 5) dit not appear to show clear differences. In Amani, 12 morphospecies were collected using cow dung, 13 using pig dung and 11 using meat. In terms of unique morphospecies, two species were captured only on cow dung, two species only on pig dung and three unique morphospecies only caught on meat. The results from Amani (Table 5) were thus, not as clear compared to Udzungwa (Table 6).

Functional groups and morphological differences among dung beetles:

The traps were operating for 48 hour periods and this hopefully resulted in the capture of both diurnal and nocturnal dung beetles. By day in a savannah ecosystem, rollers and kleptoparasites dominate the dung resource, while the tunnelling and dwelling beetles dominate at night (Krell et al. 2003b, Scholtz et al. 2009). According to Krell (2003b) this pattern occurs because the rollers are competitively superior, but when night arrives they disappear from site, making the resource available for the competitively inferior dwellers and tunnellers.

Based on morphological differences, the morphospecies were estimated to be either rollers or tunnellers/dwellers. In Amani the morphospecies A4P-7 and A2P-2 (Appendix 5) were considered rolling dung beetles mostly because of large hind legs and absence of horns. All other morphospecies were considered tunnellers or dwellers. These two rolling dung beetles in Amani represent 1.42 % (Table 3) of the captured morphospecies. In Udzungwa the morphospecies U1P-6, U1P-7, U2P-5 and U3P-1 (Appendix 5) were considered rolling dung beetles based on the same traits as previously mentioned. These five morphospecies constitute 68.045 % (Table 4) of the total number of individuals.

The U1P-6 morphospecies, together with A4P-7 and U2P-5 (Appendix 5), belong to the genus *Sisyphus*. A large number of species within this genus are very similar in appearance, making the taxonomy confusing (Davis et al. 2008a). No recent revision has been made. The morphospecies called U1P-6 - which was caught in 601 individuals, and U2P-5 with 78 specimens were most likely a combination of different species.

This difference in numbers of rolling dung beetle individuals between Amani and Udzungwa is noteworthy, and may be partly explained by the differences between habitats in the two areas. By having all the plot-sites inside the forest, the cover percentage in Amani (Table 1) had higher values compared to Udzungwa (Table 2), with the mean cover percentage in Amani being 73.83% compared to 29.25% in Udzungwa. The process of forming and rolling a dung ball has a high energetic cost for the rolling dung beetles. In savannas during the day, the beetles may be optimized by external heat in open areas when the sun is present (Bartholomew & Heinrich 1978, Scholtz et al. 2009). Heat and surface temperature are also crucial for flight initiation by some dung beetles (Houston and McIntyre 1985). This may affect the composition of dung beetles in forests, where the tree cover may prevent sunlight from entering the ground level. Additionally, the forest may function as a barrier for rollers, possibly giving a competitive edge to dung beetles without the rolling behavior (Bartholomew & Heinrich 1978, Scholtz et al. 2009). The rolling dung beetle A4P-7 was only caught in the Farmland habitat in Amani, a more open habitat compared to the other sites due to farmland activities. Digging activities may possibly be easier in forested areas, because the soil may be more wet and soft due to cover vegetation.

Most dung beetles across all functional groups are black or dark colored. The colors possibly serve as camouflage on the dung or soil, which gives them some cryptic protection against predators. The dark color may also have a role in gathering ectothermal heat from sunlight to boost energy activity (Scholtz et al. 2009). Dung beetles may have different colors, from brown, yellow to metallic variants of green and blue. Most of these brightly colored species are diurnal (Scholtz et al. 2009). Bright colors may also be relevant in terms of sexual selection (Scholtz et al. 2009). In Amani, two morphospecies (A2M-1, A2C-5, Appendix 5) had a bright color pattern, and one morphospecies (A1C-2, Appendix 5) had a metallic color. In Udzungwa, six morphospecies (U1C-9, U4C-1, U5P-4, U7C-1, U7P-4, U8P-13, Appendix 5) had a bright color pattern, and two morphospecies (U3P-1, U3P-2, Appendix 5) had a metallic color. Colors may vary within some species as well. Davis et al. (2008b) tried to explain color morphing in the species *Gymnopleurus humanus*. Both genetic and climatic explanations were proposed, but no clear conclusion could be made. There was however, a strong correlation between environmental factors and color variation in the field. As previously mentioned, color variation was not used to identify different morphospecies, if the individuals were otherwise morphologically identical.

Disturbed habitats and its consequences for dung beetle communities:

As stated previously, habitat analysis from Udzungwa was not included because all plot-sites were essentially within the same habitat type. This decision appear to be supported in Figure 8, where all the plot-site numbers were placed differently.

The disturbed or logged forest sites, as well as the farmland in Amani, showed generally a lower number of morphospecies compared to the undisturbed primary forest (Table 8 and 9). The Shannon-Wiener diversity index (Table 10) was higher for the undisturbed Primary Forest, were all the disturbed habitats showed a lower value. These results correspond with a study from Thailand comparing the dung beetle composition between a primary forest and a secondary forest. The study observed the species composition to be significantly higher in the primary forest compared to the secondary forest (Boonrotpong et al. 2004).

The farmland habitat may be considered a degraded habitat, where most of the large vegetation had been removed (Appendix 2, picture 4). In this study, the morphospecies A1C-1 (Appendix 5) was captured in all habitats except the farmland habitat (Table 8). This beetle was among the largest in size (20-23mm).

The farmland habitat also had the lowest Shannon Diversity Value (Table 10) and had two small species representing most of the captured material (Figure 5C). All other habitats showed a more even distribution of different morphospecies (Figure 5), with Figure 5A (Primary Forest) consisting of the most evenly distributed beetles. Dung beetle abundance was still large in the Farmland habitat (Figure 6) even though only one of the eight plot-sites was located in this habitat, as mentioned, most of these 101 beetles were of the morphospecies A1C-X1 (59) and A1C-X2 (25). This result may suggest that degraded habitats mostly affect the number of species and not necessarily the number of individuals (Andresen 2003, Boonrotpong et al. 2014). However, dung beetle abundance have been shown in some studies to be lower in degraded and secondary forests compared to undisturbed forest (Estrada & Coetes-Estrada 2002, Horgan 2005, Klein 1989).

As stated previously, the three habitats (Secondary Logged, Farmland and Secondary Disturbed River) in Amani only had one plot-site each. This fact may help to explain the small number of individuals found at the Secondary Logged and Secondary Disturbed River habitat (Figure 6), as well as the large number of individuals found in the Secondary Disturbed habitat (three plot-sites).

The habitats with more than one plot-site (Primary Forest, Secondary Disturbed) showed different similarities in number of species and number of individuals in the ordination analysis (Figure 7). As mentioned, plot-site 6-8 (Secondary Disturbed) showed a similar distribution, while plot-site 1 and 2 (Primary Forest) does not. The reason for this result remains unclear.

A study from Madagascar showed how an annual deforestation rate of 1.4-2.0% since 1953 appears to have played a role in the extinction of 43% of the endemic forest-dwelling dung beetle species (Hanski et al. 2007). The author associated this decline with the fragmentation pressure on lemurs, one of the most important dung producers in Madagascar. Other studies showed that the diversity, composition and abundance of dung beetles appear to be positively related to the size of forest fragments (Feer & Hingrat 2005).

In this study the intact forest remnants were isolated pockets of forest in a “sea” of secondary forest. One might expect the small forest remnants to have fewer species than the surrounding secondary forest, but the data showed the opposite. A reason for this could be that degradation is a more powerful process in this context than fragmentation, or that the intact forest species do not perceive the secondary forest “sea” surrounding their habitat as an inhospitable environment. In addition, the relatively few dung producers in Amani may not distinguish strongly between the two forest types.

The results mentioned above lend support to the third prediction.

Dung beetles as bioindicator taxon:

Ecosystem services are the functions certain organisms provide in an ecosystem that directly benefit human society (De Groot et al. 2002). Dung beetles are ecologically important by burying the dung and carrion resource in addition to increasing the rate of soil nutrient cycling and the soil turnover rate (Estrada et al. 1993, Gibbs & Stanton 2001, Hanski & Cambefort 1991, Vulinec 2000). Dung burial prevents the loss of nitrogen through ammonia volatilization, which enhances the soil fertility by increasing the amount of available nitrogen for uptake by plants. The dung beetles with a tunnelling behavior may also play a role in bioturbation, when they increase the soil aeration and water porosity by moving large quantities of earth to the surface (Hanski & Cambefort 1991, Nichols et al. 2008).

Adult and larval dung beetles may serve to control the abundance of blood-feeding and detrivorous flies, as well as dung-dispersed nematodes and protozoa. These processes may have implications for livestock, wildlife and human health (Byford et al. 1992, Horgan 2005, Nichols et al. 2008). Beetle activity elevates fly mortality by various factors: firstly, the brood ball production constitutes resource competition with fly larvae. Secondly, feeding dung beetles may lead to damage of fly eggs and larvae. Lastly, the dung beetle disturbance may lead to a microclimate inside the dung, which may act unfavorable for fly eggs or larvae (Scholtz et al. 2009).

The beetles may also act as secondary seed dispersal agents for many tropical trees by transporting or burying the dung produced by fruit eating animals. In tropical forests up to 90% of excreted seeds left on the soil surface appear to be eaten by seed predators. Dung beetles burying excreted seeds may greatly decrease seed mortality (Andresen 2002, Andresen 2003, Estrada & Coetes-Estrada 1991, Shepherd & Chapman 1998). Some of these plants may be important resources for fruit eating animals and may present habitats for other organisms. Seed dispersal by dung beetles may therefore be linked to the integrity of the entire ecosystem (Estrada & Coetes-Estrada 1991, Scholtz et al. 2009, Shepherd & Chapman 1998).

In some cases dung beetles may act as pollinators. This is the case for the plant families *Lowiaceae* and *Araceae.* Both these plant families have decay-scented flowers, which act as an attractant to some dung beetles (Nichols et al. 2008, Scholtz et al 2009). In the case of the plant family *Lowiaceae*, the plants do not produce any nectar or other kind of reward for the pollinating dung beetles. It appears that the beetles are simply attracted to the "dung-like" smell of the decaying flowers and thus arrive at the site looking for dung. This is called "deception pollination" where the beetles get no reward for pollination (Sakai & Inoue 1999).

Dung beetles may even serve as a tourist or wildlife attraction, where many wildlife enthusiasts may be fascinated by the rolling behavior of dung beetles in the African savannas (Scholtz et al. 2009).

Losey & Vaughan (2006) tried to estimate an economical value of the services dung beetles provide for cattle farms in USA. They estimated a value of 380 million dollars each year based on forage fouling, nitrogen volatilization, reducing parasitism and pest flies; factors that are all relevant to dung burial. However, it is difficult to accurately estimate the value of these services, but they may be useful to give an estimate of the importance of conservation (Losey and Vaughan 2006, Scholtz et al. 2009).

Invertebrates represent the highest known biodiversity on earth and dominate close to every ecosystem in terms of species richness, biomass and ecological functions (Spector 2006). Dung beetles have been proposed as bioindicators for environmental change and disturbances (Andresen 2005, Favila & Halffter 1997, Davis et al. 2001, Newmark 1999, Spector 2006).

Favila & Halffter (1997) propose six guidelines for correct selection of indicator organisms:

> **1:** "The group should be compromised of a rich guild and be well defined in the type of community which one wishes to evaluate biodiversity. The guild should also have an importance in the structure and/or functioning of the ecosystem chosen".

The true dung beetles are well represented in tropical areas with a large number of both individuals and species (Favilla & Halfter 1997, Hanski & Cambefort 1991, Nichols et al. 2007), and as previously mentioned, they provide some key ecosystem services.

> **2:** "There must be sufficient information available on the natural history and taxonomy of the proposed group to allow for both identification and ecological interpretation of the results obtained".

The biology, behavior and ecology of the true dung beetles have been well studied (Davis et al. 2008a, Hanski & Cambefort 1991, Scholtz et al. 2009).

> **3:** "The organisms of the indicator group must be easy to capture with standardized methods to make it possible for repeated experiments".

Using pitfall traps with bait, the dung beetles are easy to capture in pretty much any given area (Hanski & Cambefort 1991, Scholtz et al. 2009).

4: "The indicator group collection method must not jeopardize the conservation of the given group".

The dung beetles are, as already stated, very numerous in both individuals and species (Favila & Halffter 1997) so the collection of species probably does not have a large negative impact on the conservation of the species.

5: "Capture data must provide enough ecological information to determine the composition and structure of the guild and its interaction with the rest of the community".

6: "The indicator group must not only provide information about the intact community, but also serve to measure decreases in biodiversity resulting from different causes like anthropogenic disturbance and environmental change".

Dung beetle communities are correlated with dung producing vertebrates and mammals (Hanski & Cambefort 1991), as well as being particularly vulnerable to habitat changes like deforestation and fragmentation (Feer & Hingrat 2005, Feer & Pincebourde 2005, Hanski & Cambefort 1991, Hanski et al. 2007, Horgan 2005, Klein 1989, Tscharntke et al. 2002).

Results from this study support the use of dung beetles as bioindicator organisms for environmental change, disturbance and biodiversity. As previously mentioned, a higher diversity of dung producing mammals in Udzungwa compared to Amani, appears to be correlated with the larger abundance and diversity of dung beetles captured in Udzungwa compared to Amani. In Udzungwa, some morphospecies only occurred on a single type of bait (Table 6), with 16 unique morphospecies (39 % of total number of morphospecies in Udzungwa) on pig dung and four unique morphospecies (9 % of total number of morphospecies in Udzungwa) occurring only on cow dung. This result was also found in Amani (Table 5), with two unique morphospecies (11.1 % of total number of morphospecies in Amani) only occurring on cow dung (11.1 % of total number of morphospecies in Amani), two unique morphospecies only captured using pig dung and three unique morphospecies (16.7 % of total number of morphospecies in Amani) only occurring on meat. This suggests that a higher diversity of dung producing animals may be important to certain specialized dung beetles. It is possible, that more types of dung used for beetle collection may result in a larger diversity of collected dung beetles. It thus seems that dung beetles may be possible bioindicators for mammal biodiversity. The different dung beetle communities in different habitats in Amani also suggest a more even distribution of dung beetles in undisturbed forest, compared to disturbed and degraded habitats (Table 9, Figure 6). These results indicate that dung beetles may be possible bioindicators for environmental change and disturbance. The fifth and final prediction for this study is thus supported.

REFERENCES

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. (2005). Effects of Season and Vegetation Type on Community Organization of Dung Beetles in a Tropical Dry Forest1. *Biotropica*, *37*(2), 291-300.

Bartholomew, G. A., & Heinrich, B. (1978). Endothermy in African dung beetles during flight, ball making, and ball rolling. *The Journal of Experimental Biology*, *73*(1), 65-83.

Bernon, G. (1981). *Species Abundance and Diversity of the Coleoptera Component of a South African Cow Dung Community and Associated Insect Predators* (Doctoral dissertation, Bowling Green University).

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.

Braack, L.E. O. (1981). Visitation Patterns of Principal Species of the Insect-Complex at Carcasses in the Kruger National Park. *Koedoe*, *24*, 33-49.

Braack, L. E. O. (1987). Community dynamics of carrion-attendant arthropods in tropical african woodland. *Oecologia*, *72*, 402-409.

Burgess, N. D., Butynski, T. M., Cordeiro, N. J., Doggart, N. H., Fjeldså, J., Howell, K. M., ... & Stuart, S. N. (2007). The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological conservation*, *134*(2), 209-231.

Byford, R. L., Craig, M. E., & Crosby, B. L. (1992). Ectoparasites and Their Cattle Production'. *J. Anim. Sci*, *70*, 597-602.

Dacke, M., Baird, E., Byrne, M., Scholtz, C. H., & Warrant, E. J. (2013). Dung beetles use the milky way for orientation. *Current Biology*, *23*(4), 298-300.

Davis, A. L. (1996). Methods for the inventory and ecological monitoring of dung beetles, butterflies and termites in the East Usambaras. *Ecological Monitoring for Biodiversity in the East Usambaras, from 8-13 July, 1996*, 38.

Davis, A. J. (2000). Does reduced-impact logging help preserve biodiversity in tropical rainforests? A case study from Borneo using dung beetles (Coleoptera: Scarabaeoidea) as indicators. *Environmental Entomology*, *29*(3), 467-475.

Davis, A. J., Hollow, J. D., Huijbregts, H., Krikken, J., Spriggs, A. H. K., & Sutton, S. L. (2001). Dung beetles as indicators of change in forest of northern Borneo. Journal of *Applied Ecology*, *38*, 593-616.

Davis, A. L., Scholtz, C. H., & Philips, T. K. (2002). Historical biogeography of scarabaeine dung beetles. *Journal of Biogeography*, *29*(9), 1217-1256.

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

Davis, A. L., Brink, D. J., Scholtz, C. H., Prinsloo, L. C., & Deschodt, C. M. (2008b). Functional implications of temperature-correlated colour polymorphism in an iridescent, scarabaeine dung beetle. *Ecological Entomology*, *33*(6), 771-779.

Dawson, W., Mndolwa, A. S., Burslem, D. F., & Hulme, P. E. (2008). Assessing the risks of plant invasions arising from collections in tropical botanical gardens. *Biodiversity and Conservation*, *17*(8), 1979-1995.

Dawson, W., Burslem, D. F., & Hulme, P. E. (2009). Herbivory is related to taxonomic isolation, but not to invasiveness of tropical alien plants. *Diversity and Distributions*, *15*(1), 141-147.

De Groot, R. S., Wilson, M. A., & Boumans, R. M. (2002). A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological economics*, *41*(3), 393-408.

Didham, R. K., Hammond, P. M., Lawton, J. H., Eggleton, P., & Stork, N. E. (1998). Beetle species responses to tropical forest fragmentation. *Ecological Monographs*, *68*(3), 295-323.

Durães, R., Martins, W. P., & Vaz-de-Mellos, F. Z. (2005). Dung beetle (Coleoptera: Scarabaeidae) assemblages across a natural forest-cerrado ecotone in Minas Gerais, Brazil. *Neotropical Entomology*, *34*(5), 721-731.

Edwards, P. B. (1991). Seasonal Variation in the Dung of African Grazing Mammals, and its Consequences for Copgophagous Insects. *Functional Ecology*, *5*, 617-628.

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

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

Emlen, D. J., & Keith Philips, T. (2006). Phylogenetic evidence for an association between tunnelling behavior and the evolution of horns in dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *The Coleopterists Bulletin*,*60*(sp5), 47-56.

Estrada, A., & Coetes-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(4)*, 459-474.

Estrada, A., Estrada, R., Dadda, A. A., & Cammarano, P. (1993). Dung and Carrion Beetles in Tropical Rain Forest Fragments and Agricultural Habitats at Los Tuxtlas Mexico. *Journal of Tropical Ecology, 14(5)*, 577-593.

Estrada, A., & Coates-Estrada, R. (2002). Dung beetles in continuous forest, forest fragments and in an agricultural mosaic habitat island at Los Tuxtlas, Mexico. *Biodiversity & Conservation*, *11*(11), 1903-1918.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual review of ecology, evolution, and systematics*, 487-515.

Favila, M. E., & Halffter, G. (1997). The use of indicator groups for measuring biodiversity as related to community structure and function. *Acta Zool. Mex.*, 72, 1-25.

Feer, F., & Hingrat, Y. (2005). Effects of forest fragmentation on a dung beetle community in French Guiana. *Conservation Biology*, *19*(4), 1103-1112.

Feer, F., & Pincebourde, S. (2005). Diel flight activity and ecological segregation within an assemblage of tropical forest dung and carrion beetles.*Journal of Tropical Ecology*, *21*(01), 21-30.

Forgie, S. A., Grebennikov, V. V., & Scholtz, C. H. (2002). Revision of Sceliages Westwood, a millipede-eating genus of southern African dung beetles (Coleoptera: Scarabaeidae). *Invertebrate Systematics*, *16*(6), 931-955.

Forgie, S. A. (2003). *Phylogeny of the Scarabaeini (Coleoptera: Scarabaeidae)*(Doctoral dissertation, University of Pretoria Pretoria).

Frolov, A. V., & Scholtz, C. H. (2003). Revision of the Afrotropical dung beetle genus Sarophorus Erichson (Coleoptera: Scarabaeidae). *African entomology*,*11*(2), p-183.

Frontier Tanzania (2001). Technical Paper 52 Amani Nature Reserve A biodiversity survey.

Geeraert, Lore (2014) Effects of anthropogenic disturbances on ground beetle (Coleoptera, Carabidae) communities in Afromontane forests: a comparison between habitats with different levels of disturbance in Amani Nature Reserve, Tanzania. Master thesis, NMBU.

Gibbs, J.P., & Stanton, E. J. (2001). Habitat Fragmentation and Arthropod Community Change: Carrion Beetles Phoretic Mites and Flies. *Ecological Applications*, *11*(1), 79-85.

Hall, J. B. (1995). *Maesopsis eminii and its status in the East Usambara Mountains*. Finnish Forest and Park Service.

Hanski, I. (1983). *Distributional ecology and abundance of dung and carrion-feeding beetles (Scarabaeidae) in tropical rain forests in Sarawak, Borneo*. Finnish Zoological Publ. Board.

Hanski, I., & Cambefort, Y. (1991). *Dung beetle ecology*. Princeton: Princeton University Press.

Hanski, I., Koivulehto, H., Cameron, A., & Rahagalala, P. (2007). Deforestation and apparent extinctions of endemic forest beetles in Madagascar. *Biology Letters*, *3*(3), 344-347.

Hill, M. O., & Gauch Jr, H. G. (1980). Detrended correspondence analysis: an improved ordination technique. *Vegetatio*, *42*(1-3), 47-58.

Holter, P., Scholtz, C. H., & Wardhaugh, K. G. (2002). Dung Feeding in adult scarabaeines (tunnellers and endocoprids): even large dung beetles eat small particles. *Ecological Entomology*, *27*, 169-176.

Holter, P., & Scholtz, C. H. (2005). Are ball-rolling (Scarabaeini, Gymnopleurini, Sisyphini) and tunnelling scarabaeine dung beetles equally choosy about the size of ingested dung particles?. *Ecological Entomology*, *30*(6), 700-705.

Horgan, F. G. (2005). Effects of deforestation on diversity, biomass and function of dung beetles on the eastern slopes of the Peruvian Andes. *Forest Ecology and Management*, *216*(1), 117-133.

Houston, W. W., & McIntyre, P. (1985). The daily onset of flight in the crepuscular dung beetle Onitis alexis. *Entomologia experimentalis et applicata*,*39*(3), 223-232.

Ibarra-Macias, A., Robinson, W. D., & Gaines, M. S. (2011). Experimental evaluation of bird movements in a fragmented Neotropical landscape. *Biological Conservation*, *144*(2), 703-712.

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

Krell, F. T., Korb, J., & Walter, P. (2003a). The beetle fauna of hyana latrines: coprocenoses consisting of necrophagous beetles (Coleoptera Trogidae Scarabaeidae). *Tropical Zoology*, *16*, 145-152.

Krell, F. T., Krell-Westerwalbesloh, S., Weiß, I., Eggleton, P., & Linsenmair, K. E. (2003b). Spatial separation of Afrotropical dung beetle guilds: a trade-off between competitive superiority and energetic constraints (Coleoptera: Scarabaeidae). *Ecography*, *26*(2), 210-222.

Krell, F. T. (2006). Fossil record and evolution of Scarabaeoidea (Coleoptera: Polyphaga). *The Coleopterists Bulletin*, *60*(sp5), 120-143.

Laurance, W. F., Goosem, M., & Laurance, S. G. (2009). Impacts of roads and linear clearings on tropical forests. *Trends in Ecology & Evolution*, *24*(12), 659-669.

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. (1996). Elevational and latitudinal changes in tree associations and diversity in the Eastern Arc mountains of Tanzania. *Journal of Tropical Ecology*, *12*(05), 629-650.

Lovett, J. C., Marshall, A. R., & Carr, J. (2006). Changes in tropical forest vegetation along an altitudinal gradient in the Udzungwa Mountains National Park, Tanzania. *African Journal of Ecology, 44*(4), 478-490.

Miller, K. J. (2013). Establishing the Derema Corridor in the East Usambara Mountains, Tanzania: A Study of Intentions versus Realities.

Mittermeier, R. A., Turner, W. R., Larsen, F. W., Brooks, T. M., & Gascon, C. (2011). Global biodiversity conservation: the critical role of hotspots. In*Biodiversity hotspots* (pp. 3-22). Springer Berlin Heidelberg.

Monaghan, M. T., Inward, D. J., Hunt, T., & Vogler, A. P. (2007). A molecular phylogenetic analysis of the Scarabaeinae (dung beetles). *Molecular phylogenetics and evolution, 45*(2), 674-692.

Newmark, W. D. (1999). Ecological monitoring: its importance for the conservation of biological diversity in the Eastern Arc forests. *Ecological Monitoring for Biodiversity in the East Usambaras, from 8-13 July, 1996*, 5.

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.

Primack, R. B. 2012. *A Primer of Conservation Biology*. Sinaer Associates, Inc., Sunderland, U.S.A. 363 pp.

R Core Team. (2014). R: *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rovero, F., & De Luca, D. W. (2007). Checklist of mammals of the Udzungwa Mountains of Tanzania, *mammalia, 71*(1/2). doi: 10.1515/mamm.2007.015

Rickart, Eric (1999). Techniques for Long-Term Monitoring of Key Mammal Groups in the East Usambaras, Tanzania. *Ecological Monitoring for Biodiversity in the East Usambaras, from 8-13 July, 1996*, 5.

Sakai, S., & Inoue, T. (1999). A new pollination system: dung-beetle pollination discovered in Orchidantha inouei (Lowiaceae, Zingiberales) in Sarawak, Malaysia. *American Journal of Botany, 86*(1), 56-61.

Saunders, D. A., Hobbs, R. J., & Margules, C. R. (1991). Biological consequences of ecosystem fragmentation: a review. *Conservation biology,5*(1), 18-32.

Scholtz, C. H., Cole, K. S., Tukker, R., & Kryger, U. (2006). Biology and ecology of Circellium bacchus (Fabricius 1781)(Coleoptera Scarabaeidae), a South African dung beetle of conservation concern. *Tropical Zoology*, *19*(2), 185-207.

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

Shepherd, V. E., & Chapman, C. A. (1998). Dung beetles as secondary seed dispersers: impact on seed predation and germination. *Journal of Tropical Ecology*, *14*(02), 199-215.

Sole, C. L., & Scholtz, C. H. (2010). Did dung beetles arise in Africa? A phylogenetic hypothesis based on five gene regions. *Molecular Phylogenetics and Evolution*, *56*(2), 631-641.

Spector, S. (2006). Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. *The coleopterists bulletin*, *60*(sp5), 71-83.

Ter Braak, C. J. (1986). Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, *67*(5), 1167-1179.

Tscharntke, T., Steffan-Dewenter, I., Kruess, A., & Thies, C. (2002). Characteristics of insect populations on habitat fragments: a mini review.*Ecological research*, *17*(2), 229-239.

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

Villet, M. H. (2011). African Carrion Ecosystems and Their Insect Communities in Relation to Forensic Entomology *Pest Technology*: Global Science Books.

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

Wartenberg, D., Ferson, S., & Rohlf, F. J. (1987). Putting things in order: a critique of detrended correspondence analysis. *American Naturalist*, 434-448.

APPENDIX 1

APPENDIX 1A

GPS coordinates for Amani, plot represents the plot-site.

Plot	GPS
1	S 05o 05.605' E 038o37.847'
2	S 05o 05.67' E 038o37.951'
3	S 05o 05.984' E 038o37.740'
4	S 05o 06.185' E 038o37.524'
5	S 05o 09.327 E 038o 36.209'
6	S 05o 09.277 E 038o36.108'
7	S 05o 09.369 E 038o 36.024'
8	S 05o 09.457 E 038o 35.968'

APPENDIX 1B

GPS coordinates for Udzungwa, plot represents the plot-site.

Plot	GPS
1	S 07o 49.891' E 036o 53.488'
2	S 07o 49.947' E 036o 53.437'
3	S 07o 50.550' E 036o 53.267'
4	S 07o 50.664' E 036o 53.147'
5	S 07o 50.722' E 036o 53.165'
6	S 07o 50.833' E 036o 53.282'
7	S 07o 51.517' E 036o 53.387'
8	S 07o 51.574' E 036o 53.298'

APPENDIX 2

Plot-sites pictures, all photographs taken by author.

Picture 1. Plot-site 1, ANR, located in a primary forest

Picture 2. Plot-site 2, ANR, located in a primary forest

Picture 3. Plot-site 3, ANR, located in a secondary forest last cut ca. 50 years ago

Picture 4. Plot-site 4, ANR, located at a farmland area for spices, regular cutting occur.

Picture 5. Plot-site 5, ANR, Kwamkoro secondary forest close to a river

Picture 6. Plot-site 6, ANR, at a secondary forest site Kwamkoro

Picture 7. Plot-site 7, ANR, at a secondary forest site Kwamkoro

Picture 8. Plot-site 8, ANR, at a secondary forest site Kwamkoro

Picture 9. Plot-site 1, Udzungwa

Picture 10. Plot-site 2, Udzungwa

Picture 11. Plot-site 3, Udzungwa

Picture 12. Plot-site 4, Udzungwa

Picture 13. Plot-site 5, Udzungwa

Picture 14. Plot-site 6 Udzungwa,

Picture 15. Plot-site 7, Udzungwa

Picture 16. Plot-site 8, Udzungwa

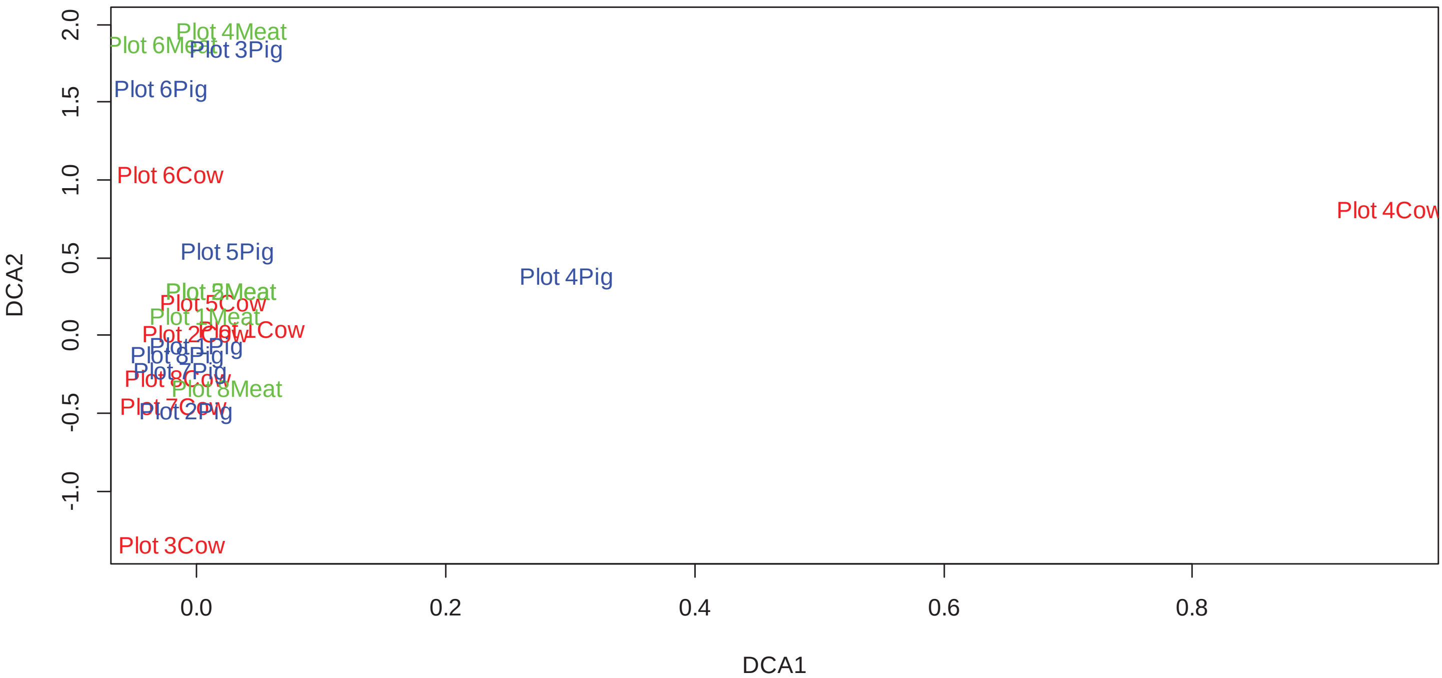
APPENDIX 3

APPENDIX 3-1: The various DCA values for Amani.

DCA Values	DCA1	DCA2	DCA3	DCA4
Eigenvalues	0.6184	0.3063	0.3133	0.14696
Decorana values	0.637	0.2956	0.2152	0.07128
Axis lengths	3.3268	2.6357	1.7513	1.68516

APPENDIX 3-2: The various DCA values for Udzungwa (all plots included).

DCA Values	DCA1	DCA2	DCA3	DCA4
Eigenvalues	0.5295	0.3561	0.2347	0.22067
Decorana values	0.5808	0.4322	0.2606	0.08845
Axis lengths	0.9873	3.3108	2.8491	3.54102



APPENDIX 3-3: DCA plots (DCA 1 and DCA 2) with bait in Udzungwa based on species abundance and diversity. Red are plots with cow bait, Blue is pig, green is meat.

APPENDIX 3-4: The various DCA values for Udzungwa, Plot 4 cow not included.

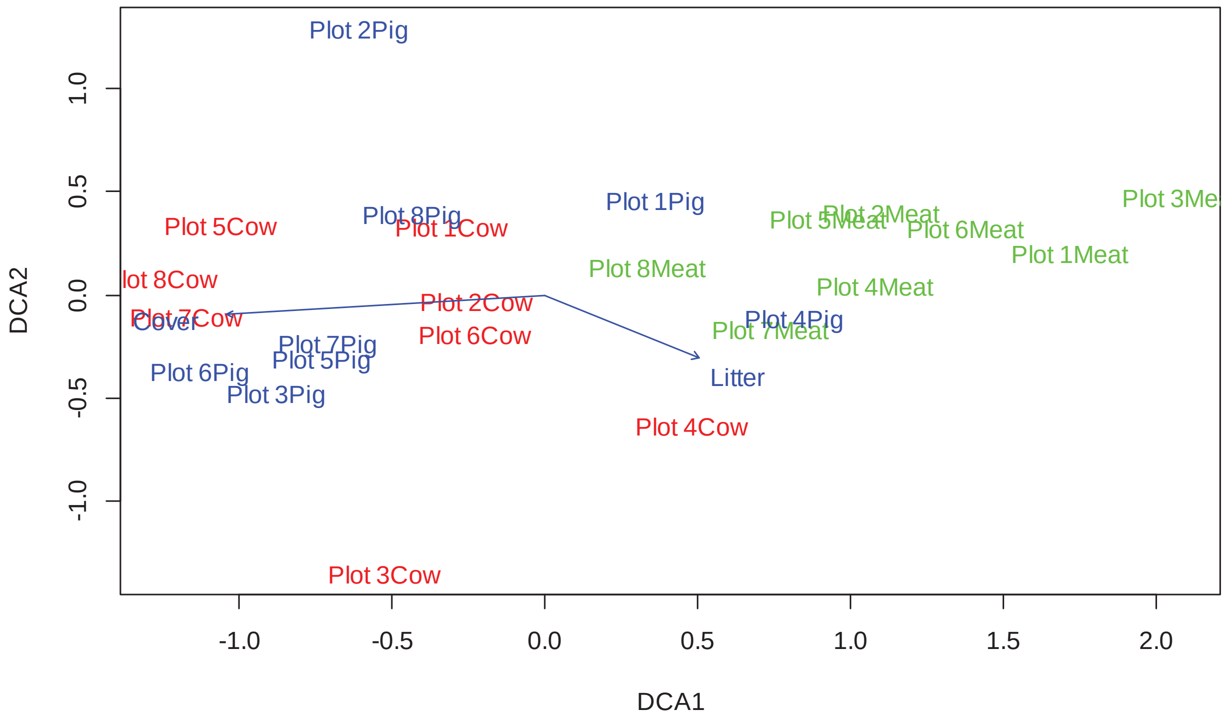
DCA Values	DCA1	DCA2	DCA3	DCA4
Eigenvalues	0.4403	0.2889	0.14595	0.19741
Decorana values	0.4651	0.2985	0.09123	0.04856
Axis lengths	3.6966	3.616	1.61374	2.0407

APPENDIX 4

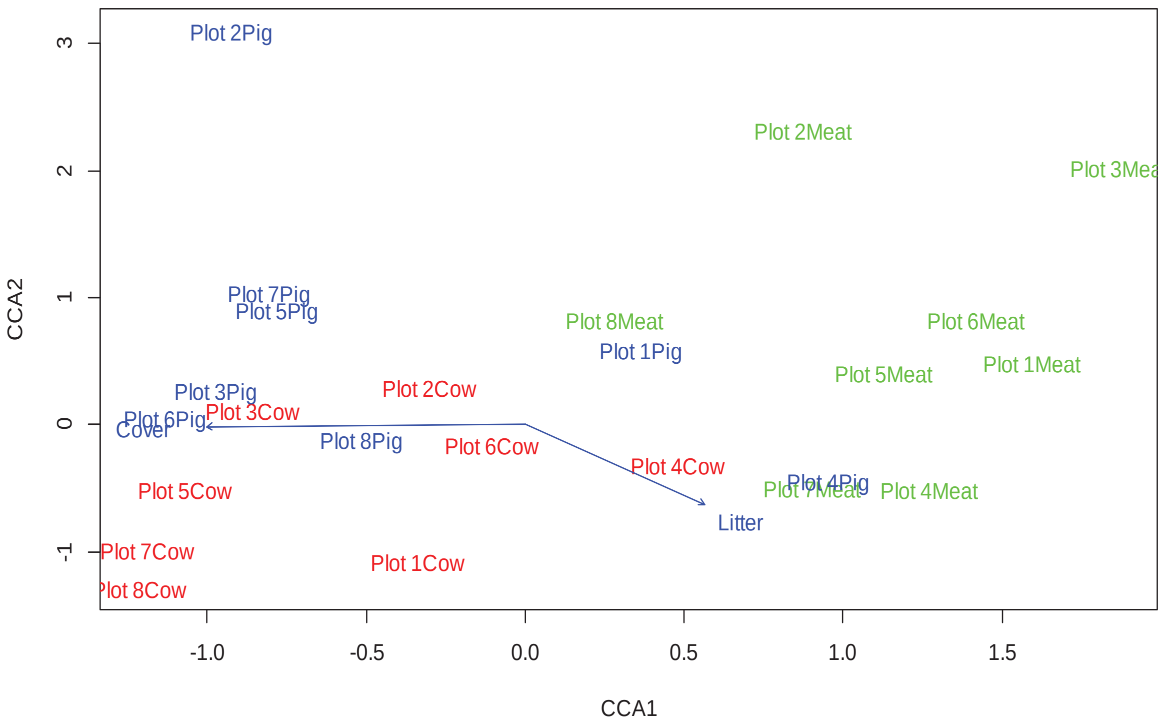
APPENDIX 4-1: Correlation data from environmental data in Amani (code source: http://www.highstat.com/Book2/HighstatLibV6.R)

Cover	1.227682
Litter	1.456699

All values are relatively low (under 1.5) and are thus not considered correlated



APPENDIX 4-2: DCA plots (DCA1 and DCA2) with bait in Amani based on species abundance and diversity. Red are plots with cow bait, Green is meat, blue is pig, including the environmental data as vectors to represent how environmental data possibly may correlate with the ordination.

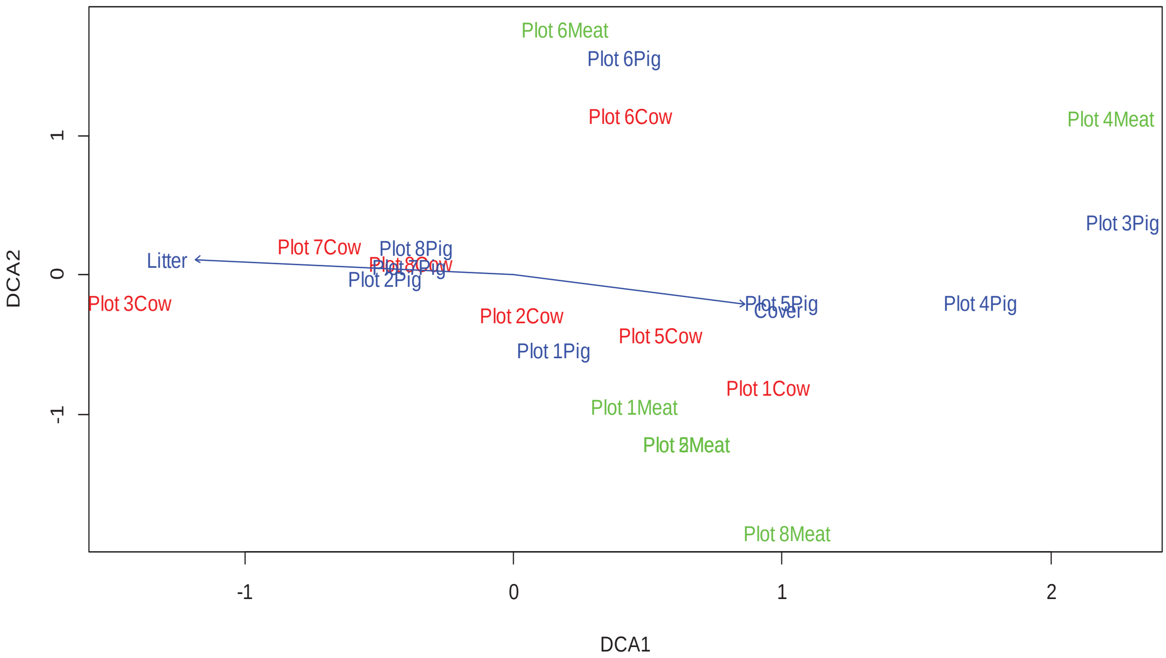


APPENDIX 4-3: CCA plots (CCA1 and CCA2) with bait in Amani based on species abundance and diversity. Red are plots with cow bait, Green is meat, blue is pig, including the environmental data as vectors to represent how environmental data possibly may correlate with the ordination.

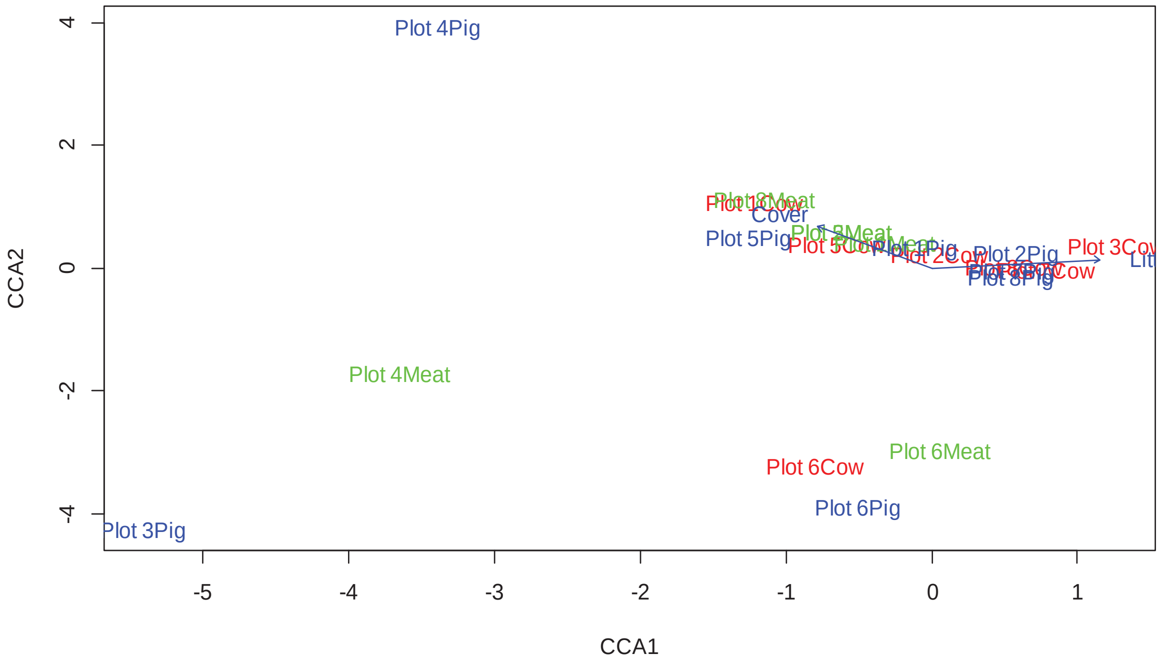
APPENDIX 4-4: Correlation data from environmental data in Udzungwa (code source: http://www.highstat.com/Book2/HighstatLibV6.R)

Cover	1.822957
Litter	2.603140

All values are still relatively low (under 2.61) and are thus not considered correlated.



APPENDIX 4-5: DCA plots (DCA1 and DCA2) with bait in Udzungwa based on species abundance and diversity. Red are plots with cow bait, Green is meat, blue is pig, including the environmental data as vectors to represent how environmental data possibly may correlate with the ordination.



APPENDIX 4-6: CCA plots (CCA1 and CCA2) with bait in Udzungwa based on species abundance and diversity. Red are plots with cow bait, Green is meat, blue is pig, including the environmental data as vectors to represent how environmental data possibly may correlate with the ordination.

APPENDIX 5

Pictures of most collected morphospecies (>=4mm). Smaller morphospecies ("X" present in morphological code) were not glued to a piece of paper, and are thus not photographed.

AMANI MORPHOSPECIES:

A1C-1

Amount: 20

Length: 20-23 mm

Found at plots: A1C, A1P, A2P, A3C, A3P, A5C, A7C, A8P

Ecology: Tunnelling/dwelling dung beetle due to the presence of horns and strong front legs suited for digging. Among the biggest of the collected morphospecies. Only found on different types of dung in all habitats except Farmland.

A1C-2

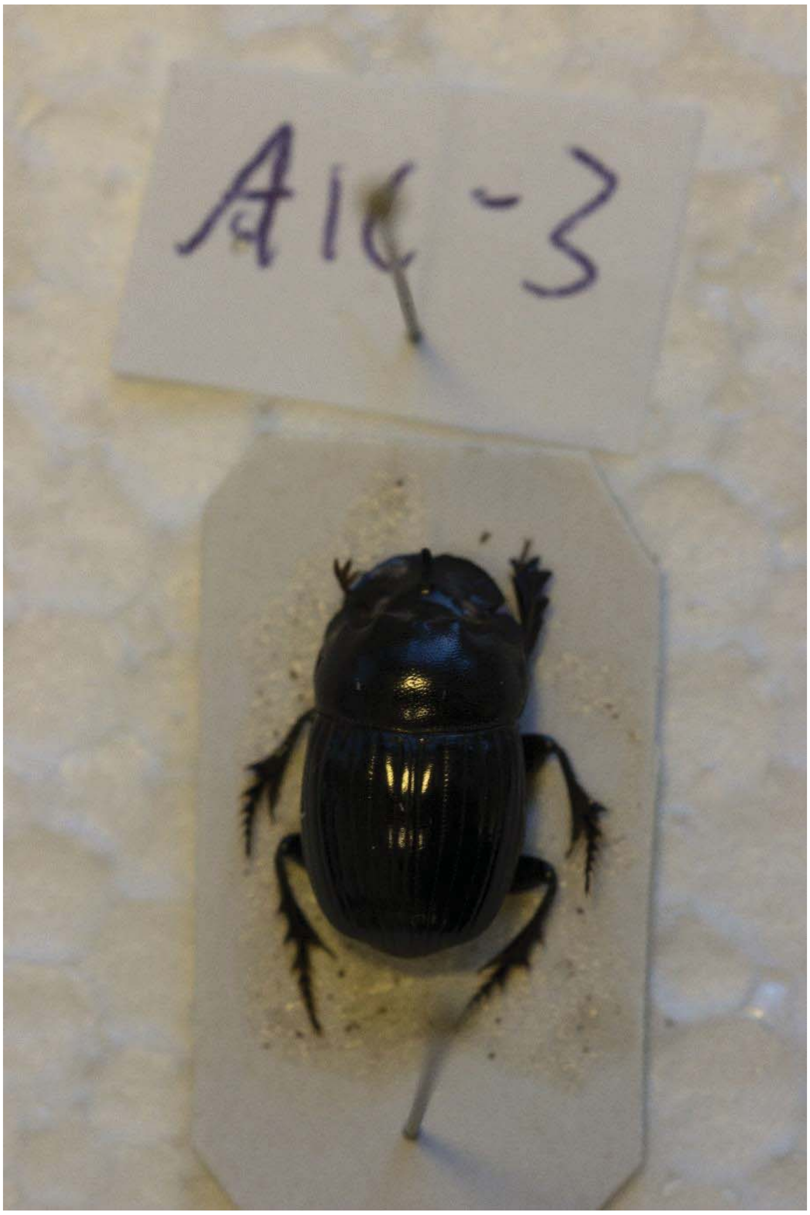
Amount: 19

Length: 10-15 mm

Found at plots: A1C, A1P, A2C, A2P, A3C, A3P, A4P, A4C, A4M, A5P, A6P, A7P, A8M

Ecology: Tunnelling/dwelling dung beetle found on both dung and meat in all habitats in Amani.

A1C-3



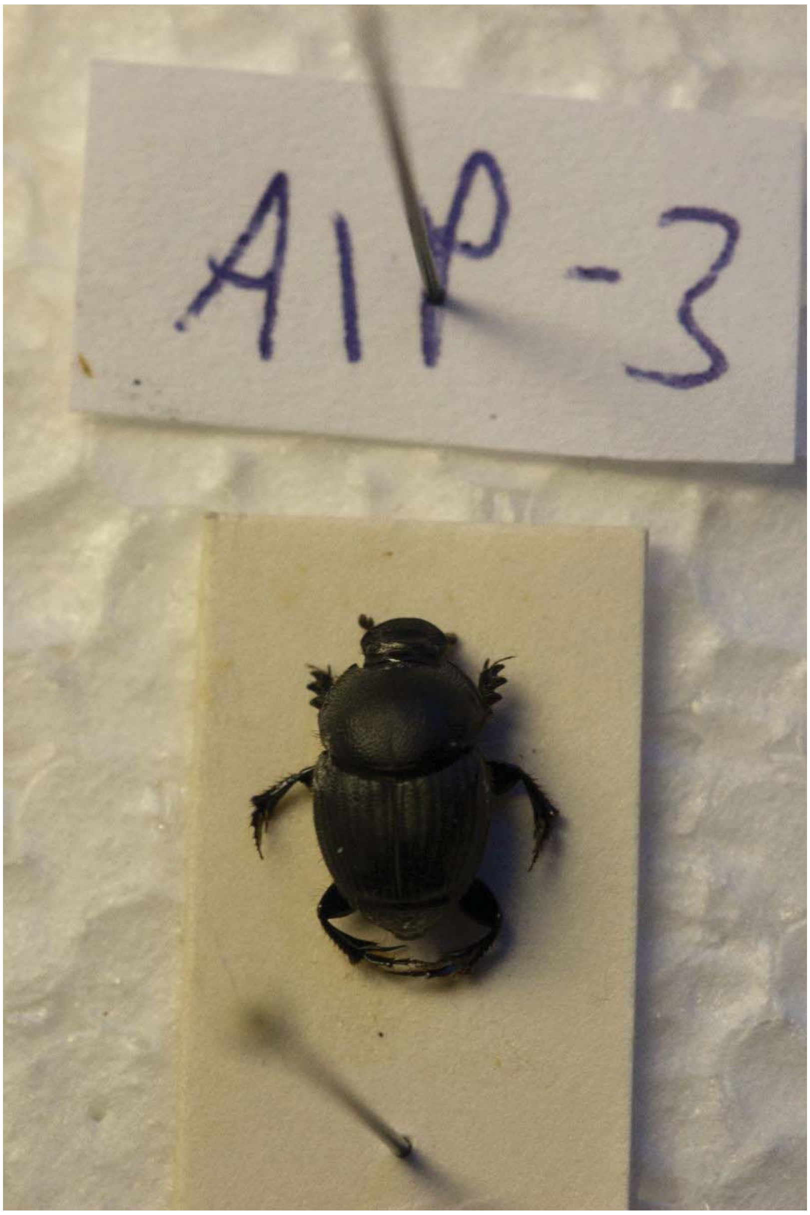
Amount: 31

Length: 12-14 mm

Found at plots: A1C, A2C, A5C, A6P, A7C, A8C,

Ecology: Tunnelling/dwelling dung beetle, only found on dung. Appears to prefer the dung of cows but are also observed on pig. Found in primary forest and the secondary disturbed forest sites in Kwamkoro.

A1P-3



Amount: 16

Length: 6-9 mm

Found at plots: A1P, A2C, A2P, A2M, A3P, A4P, A5C, A7P

Ecology: Tunnelling/dwelling dung beetle found at all habitats on both dung and meat. Appears to prefer dung because only one specimen was caught on a trap using meat.

A1M-1

Amount: 10

Length: 6-8 mm

Found at plots: A1M, A2M, A3M, A4M, A6M, A8M

Ecology: Tunnelling/dwelling dung beetle, only found on meat. Found on all habitats except secondary disturbed riverine forest.

A1M-2

Amount: 1

Length: 10 mm

Found at plot: A1M

Ecology: Tunnelling/dwelling dung beetle, only caught once in the primary forest on meat.

A2C-3

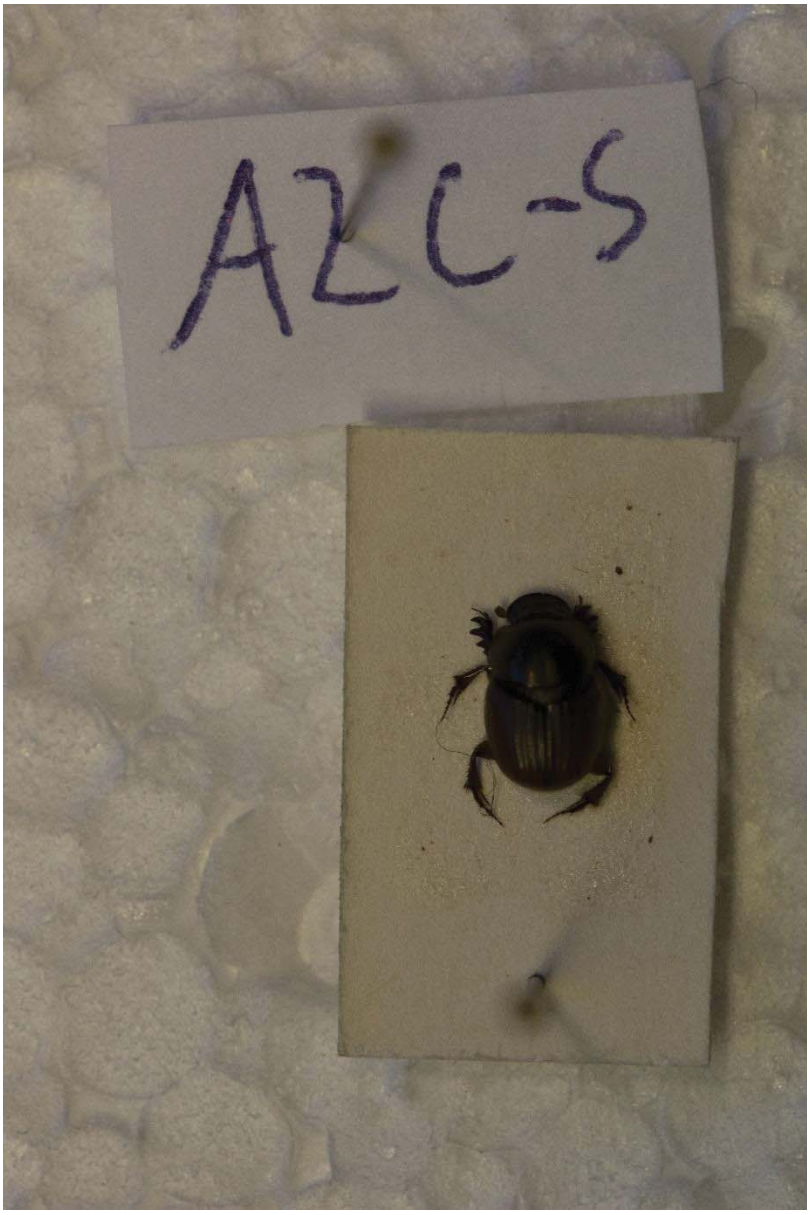
Amount: 24

Length: 7-10 mm

Found at plot: A2C, A2M, A3C, A3P, A4P, A4C, A7C, A7M, A8C

Ecology: Tunnelling/dwelling dung beetle found on all habits except secondary disturbed riverine forest. Found on both dung and meat bait.

A2C-5



Number: 66

Length: 5-7mm

Found at plot: A2C, A2P, A3C, A3P, A4P, A5C, A5P, A6C, A6P, A7C, A7P, A8P, A8C, A8M

Ecology: Tunnelling/dwelling dung beetle found at all habitats with both dung and meat as bait. Only one beetle was caught on meat so it appears to prefer dung.

A2P-2

Number: 1

Length: 21 mm

Found at plot: A2P

Ecology: One of the two largest dung beetles observed in the study. A rolling dung beetle due to the presence of long hind legs. Only one individual was caught in this study in the primary forest with pig dung as bait. This beetle is most likely a member of the genus *Sceliages* (Forgie et al 2002, Forgie et al. 2003). Many of the members in this genus feeds and breeds exclusively on millipedes. Assumed to be a new, undescribed species.

A2M-1

Amount: 7

Length: 9-13 mm

Found at plot: A2M, A5P, A5M, A7P, A8M

Ecology: Tunnelling/dwelling dung beetle found in primary forest and secondary disturbed forest (including secondary disturbed riverine forest). Only caught using pig dung and meat.

A3C-5

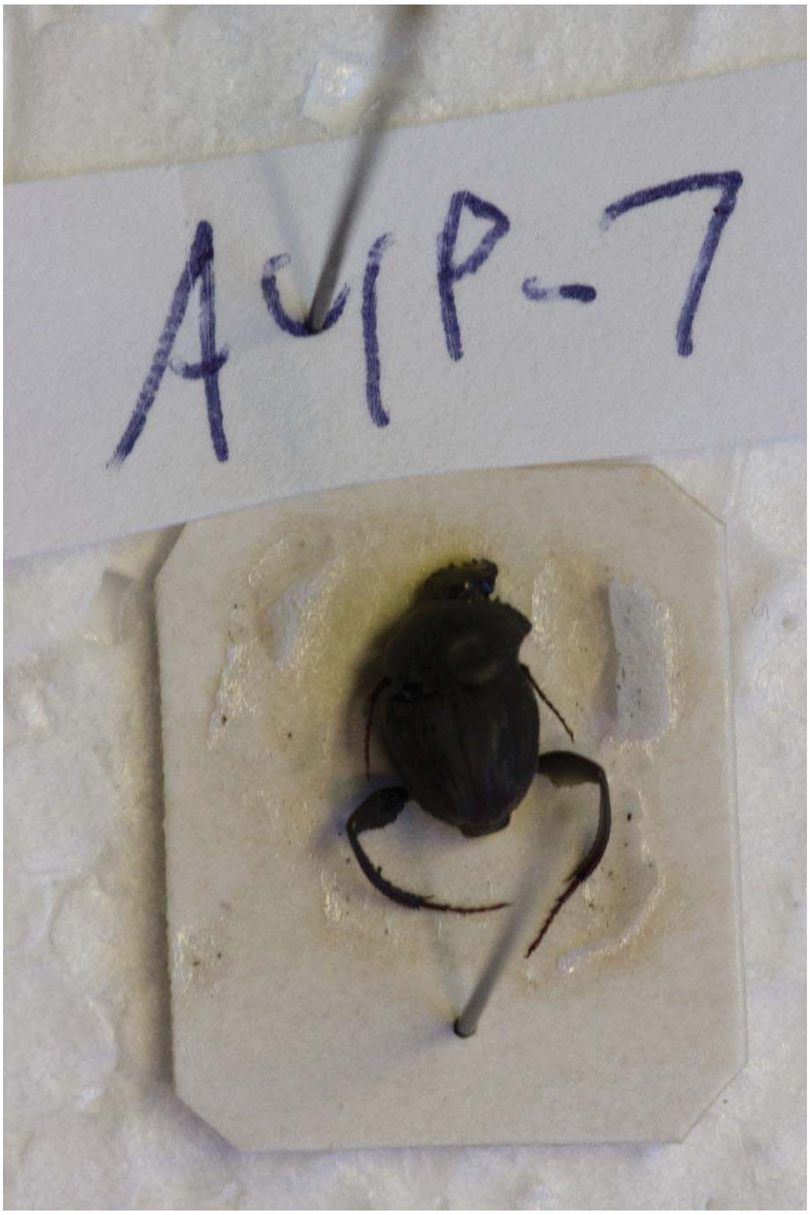
Amount: 2

Length: 5mm

Found at plot: A2C, A3C

Ecology: Tunnelling/dwelling dung beetle, only found on cow dung in the primary forest and the secondary logged forest.

A4P-7



Amount: 4

Length: 6-7 mm

Found at plot: A4P, A4C

Ecology: Rolling dung beetle (long hind legs) of the genus *Sisyphus*. Caught only in farmland on dung.

A5M-3

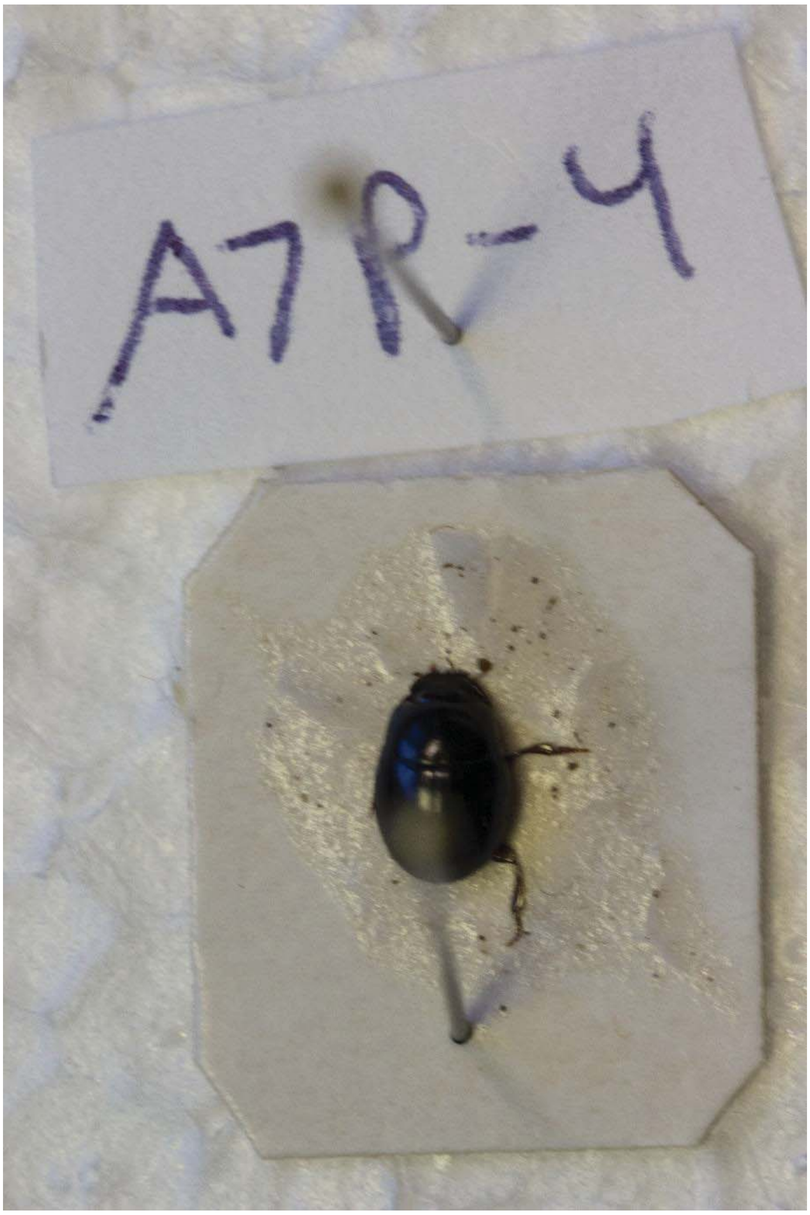
Amount: 2

Length: 4mm

Found at plot: A5M

Ecology: Tunnelling/dwelling dung beetle, only found on secondary disturbed riverine forest on meat

A7P-4



Amount: 1

Length: 5mm

Found at plot: A7P

Ecology: Tunnelling/dwelling dung beetle, only found on the secondary disturbed forest on pig dung.

UDZUNGWA MORPHOSPECIES:

U1M-3

Amount: 101

Length: 6-8mm

Found at plot: U1M, U1P, U1C, U2M, U2P, U2C, U3P, U4P, U5M, U5C, U5P, U6P, U7P, U7C, U8M, U8C, U8P

Ecology: Tunnelling/dwelling dung beetle found on all plot-sites in Udzungwa on both meat and dung.

U1P-1

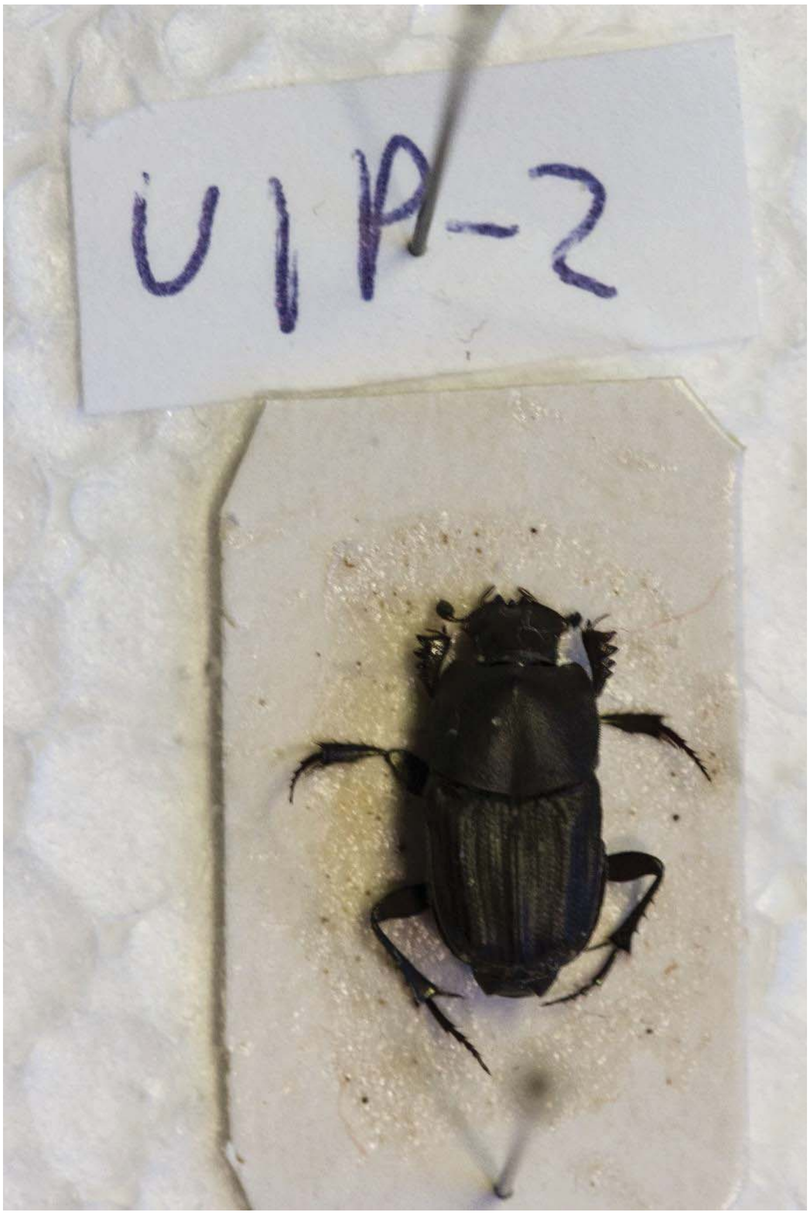
Amount: 2

Length: 14 mm

Found at plot: U1P, U1C

Ecology: Tunnelling/dwelling dung beetle, only found on plot-site 1 on cow and pig dung.

U1P-2



Amount: 3

Length: 10-11 mm

Found at plot: U1P, U1C, U7P

Ecology: Tunnelling/dwelling dung beetle, only found on plot-site 1 and 7 on dung.

U1P-3

Amount: 4

Length: 10 mm

Found at plot: U1P, U1C

Ecology: Tunnelling/dwelling dung beetle, only found on plot-site 1 on dung.

U1P-4-2

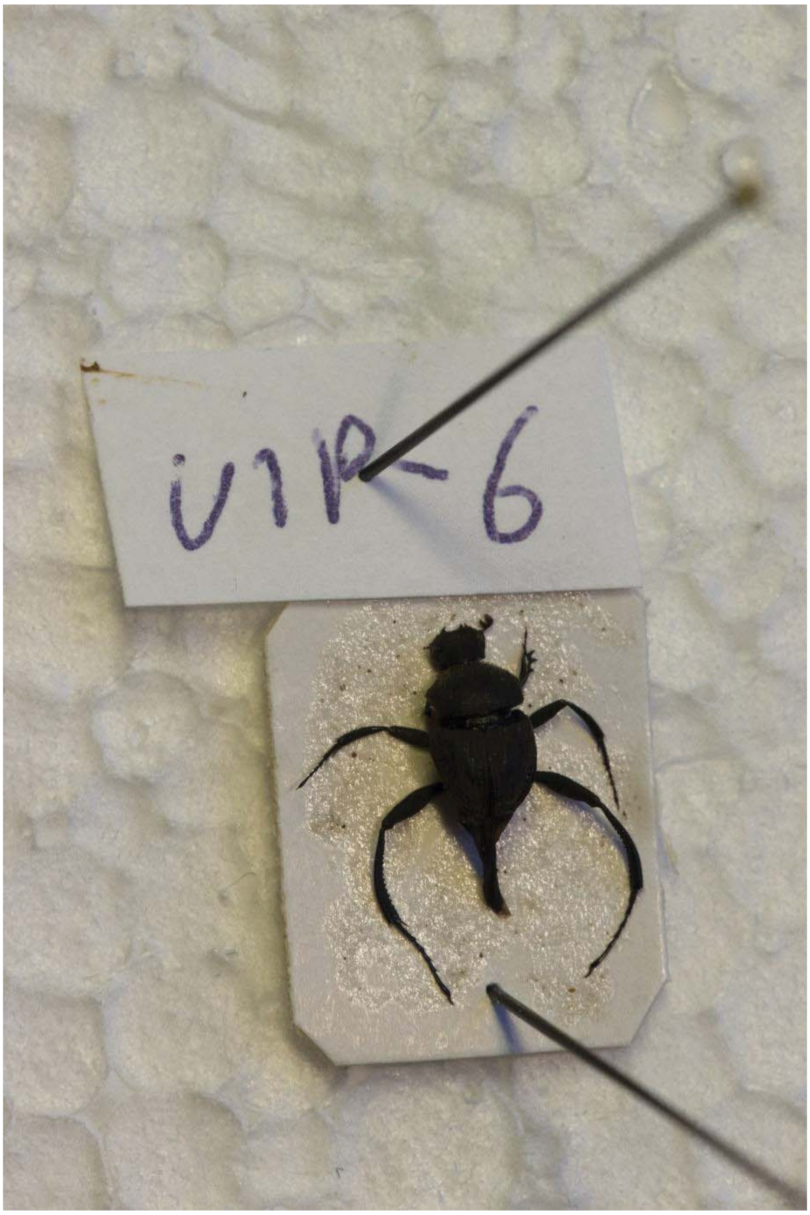
Amount: 18

Length: 7-9 mm

Found at plot: U1M, U1P, U5P, U7P, U8P

Ecology: Tunnelling/dwelling dung beetle found at 4 of the 8 plot-sites in Udzungwa. Only one individual caught in a trap with meat. All other 17 individuals were caught on pig dung.

U1P-6



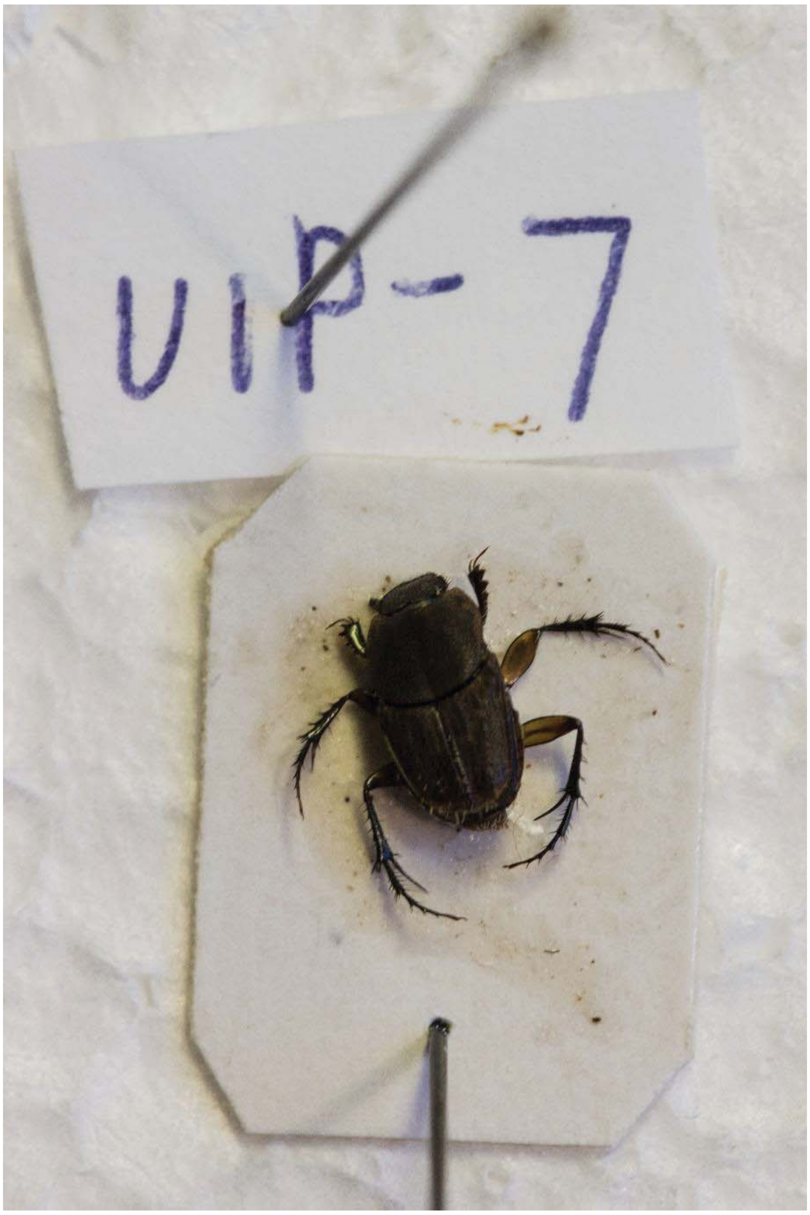
Amount: 601

Length: 5-7mm

Found at plot: U1P, U1C, U2P, U2C, U3C, U5C, U5P, U6C, U6P, U7P, U7C, U8C, U8P

Ecology: Rolling dung beetle of the genus *Sisyphus*, found on all plot-sites except plot-site 4 on cow and pig dung. All of the 601 collected morphospecies are from this tribe but many of them are most likely different species, they are considered as one morphospecies due to taxonomic difficulties for this tribe (see Discussion: Functional groups and morphological differences among dung beetles). I distinguish between two clearly different morphospecies (or groups) of this genus from Udzungwa.

U1P-7



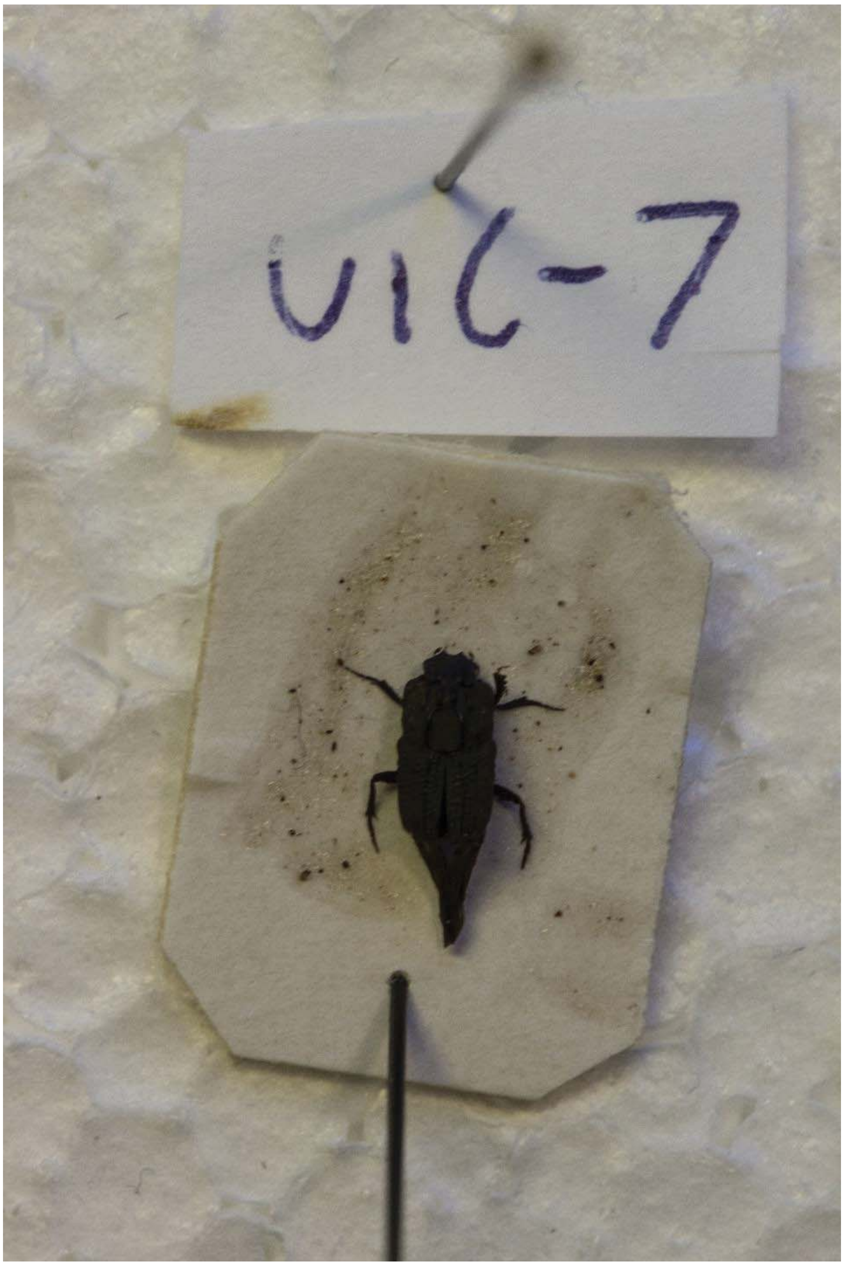
Amount: 16

Length: 7mm

Found at plot: U1P, U7P, U8P

Ecology: Rolling dung beetle (presence of long hind legs). Only found in traps with pig dung.

U1C-7



Amount: 15

Length: 5mm

Found at plot: U5P, U1C, U3P, U4M, U5C, U6C, U6P

Ecology: Tunnelling/dwelling dung beetle found on five of the eight plot-sites in Udzungwa. Caught on all types of bait but only one individual caught on meat, so it appears to prefer dung over meat. This morphospecies has been identified as belonging to the genus *Sarophorus*. There is a recent revision of all species in this genus (Frolov & Scholtz 2003), but the species found in this study appears to be an undescribed new species. Assumed to be a new, undescribed species. Members of this genus feed on old dung and carrion remains, which may indicate feeding on detritus (Frolov & Scholtz 2003).

U1C-8

Amount: 16

Length: 5mm

Found at plot: U1C, U2P, U4P, U5C, U5P, U7P

Ecology: Tunnelling/dwelling dung beetle found only on dung at five of the plot-sites.

U1C-9

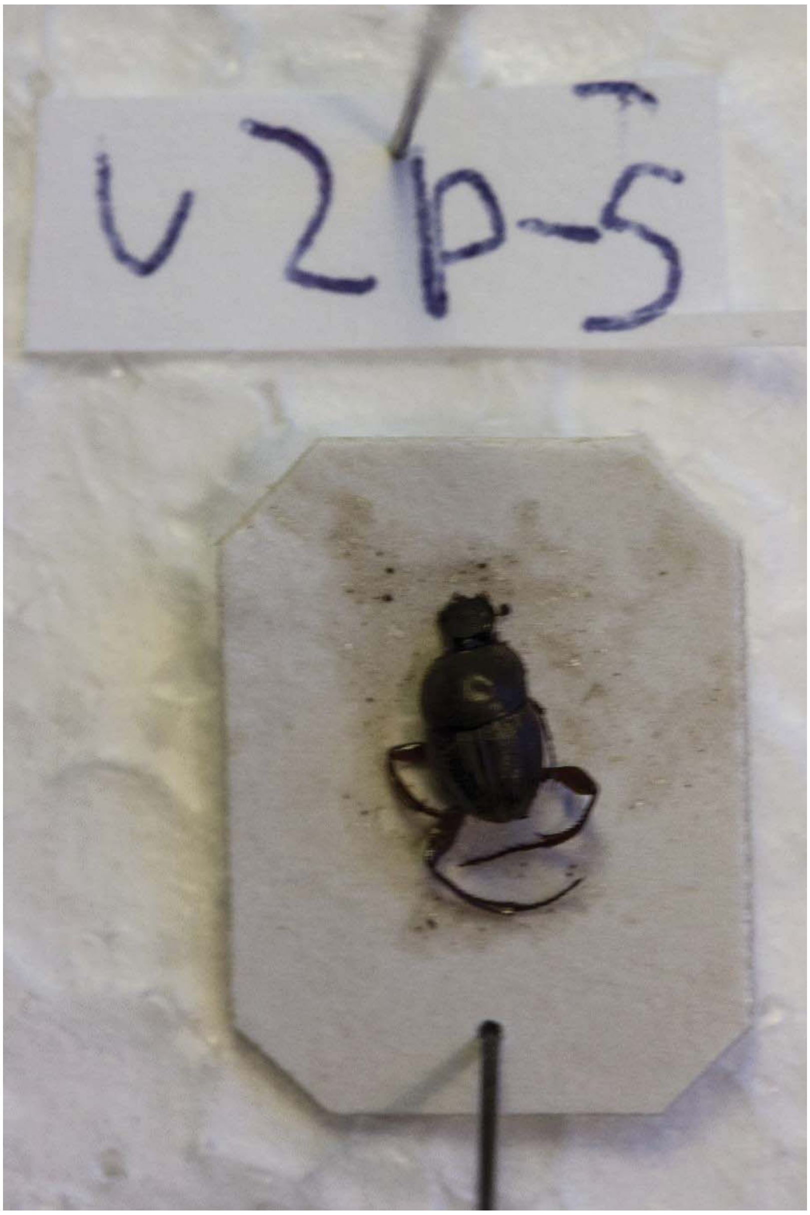
Amount: 3

Length: 5mm

Found at plot: U1C, U4P

Ecology: Tunnelling/dwelling dung beetle, only found on two of the eight plot-sites on dung.

U2P-5



Amount: 78

Length: 5-7mm

Found at plot: U1C, U1P-U2P, U2C, U3P, U4P, U5C, U5P, U7C, U7P, U8C, U8P

Ecology: Rolling dung beetle of the genus *Sisyphus* found at all plot-sites except plot-site 6 on cow and Pig dung. All of the 78 collected morphospecies are from this tribe but some of them may be different species, they are considered as one morphospecies due to taxonomic difficulties for this tribe (see Discussion: Morphospecies analysis). I distinguish between two clearly different morphospecies (or groups) of this genus from Udzungwa.

U3P-1

Amount: 2

Length: 12mm

Found at plot: U3P

Ecology: Rolling dung beetle, only found at plot-site 3 on traps with pig dung.

U3P-2

Amount: 1

Length: 7mm

Found at plot: U3P

Ecology: Tunnelling/dwelling dung beetle, only found on plot-site 3 with pig dung as bait.

U3P-5

Amount: 4

Length: 6-7mm

Found at plot: U3P, U6C, U6P

Ecology: Tunnelling/dwelling dung beetle, only found on dung on two of the eight plot-sites.

U3P-7

Amount: 3

Length: 5-7mm

Found at plot. U3P, U5P, U8P

Ecology: Tunnelling/dwelling dung beetle found on three of the eight plot-sites only on pig dung.

U3C-2

Amount: 11

Length: 6-7mm

Found at plot: U2P, U3C

Ecology: Tunnelling/dwelling dung beetle found on two of the eight plot-sites on dung.

U4C-1

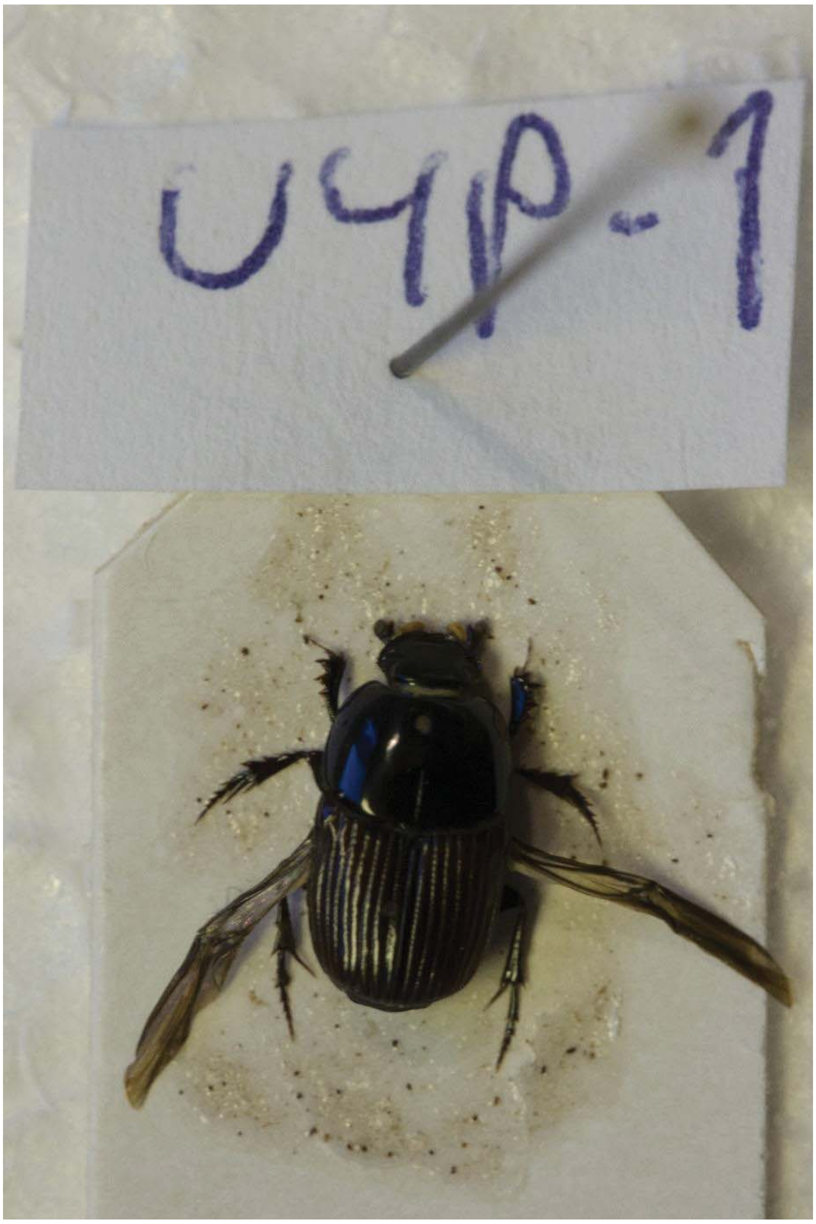
Amount: 2

Length: 7mm

Found at plot: U4C, U4P

Ecology: Tunnelling/dwelling dung beetle, only found at plot-site 4 on dung. The only true dung beetle found on plot U4C.

U4P-1



Amount: 1

Length: 8mm

Found at plot: U4P

Ecology: Tunnelling/dwelling dung beetle, only found on plot-site 4 with pig dung as bait.

U4P-8

Amount: 1

Length: 5mm

Found at plot: U4P

Ecology: Tunnelling/dwelling dung beetle, only found on plot-site 4 with pig dung as bait.

U5C-5

Amount: 1

Length: 6mm

Found at plot: U5C

Ecology: Tunnelling/dwelling dung beetle, only found on plot-site 5 on cow dung.

U5P-3

Amount: 18

Length: 6-8mm

Found at plot: U5P, U6M, U6P, U7P, U8P

Ecology: Tunnelling/dwelling dung beetle found at plot-site 5-8 on pig dung and meat. Only one individual caught in traps with meat so it appears to prefer dung over meat.

U5P-4

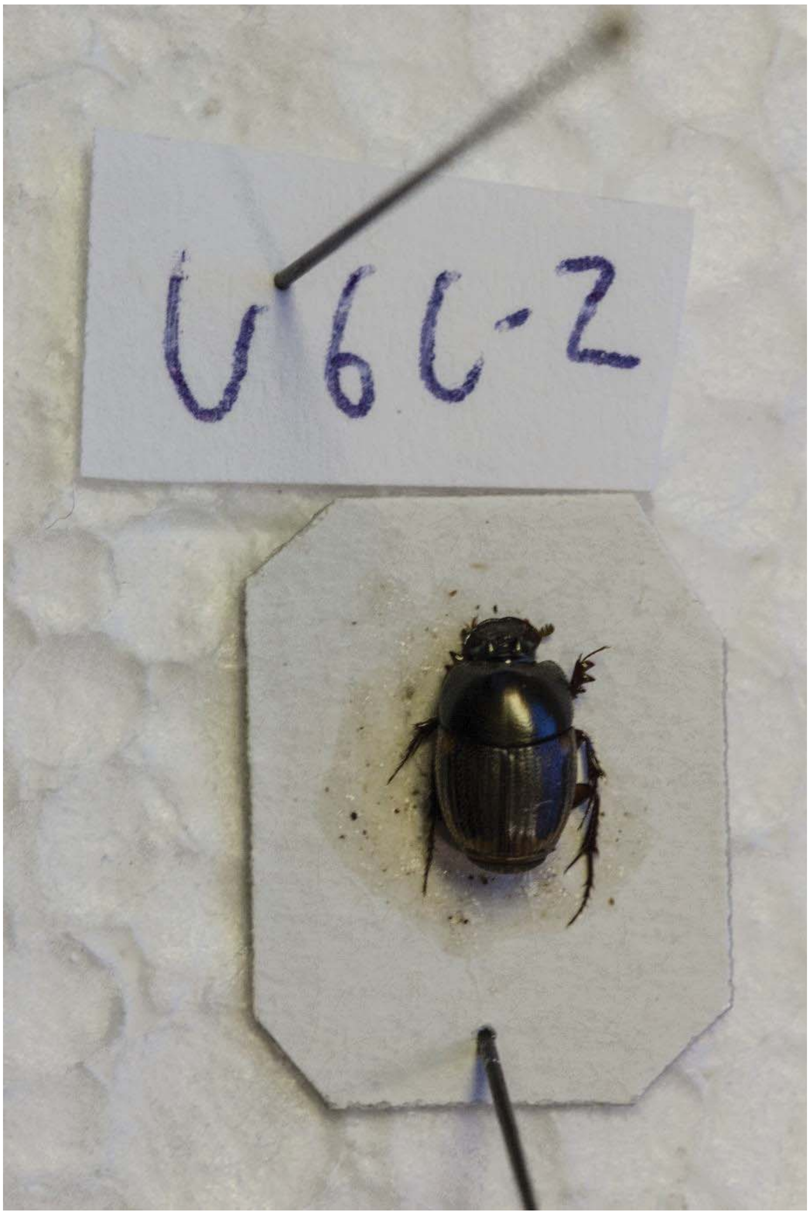
Amount: 1

Length: 8mm

Found at plot: U5P

Ecology: Tunnelling/dwelling dung beetle, only found at plot-site 5 using pig dung.

U6C-2



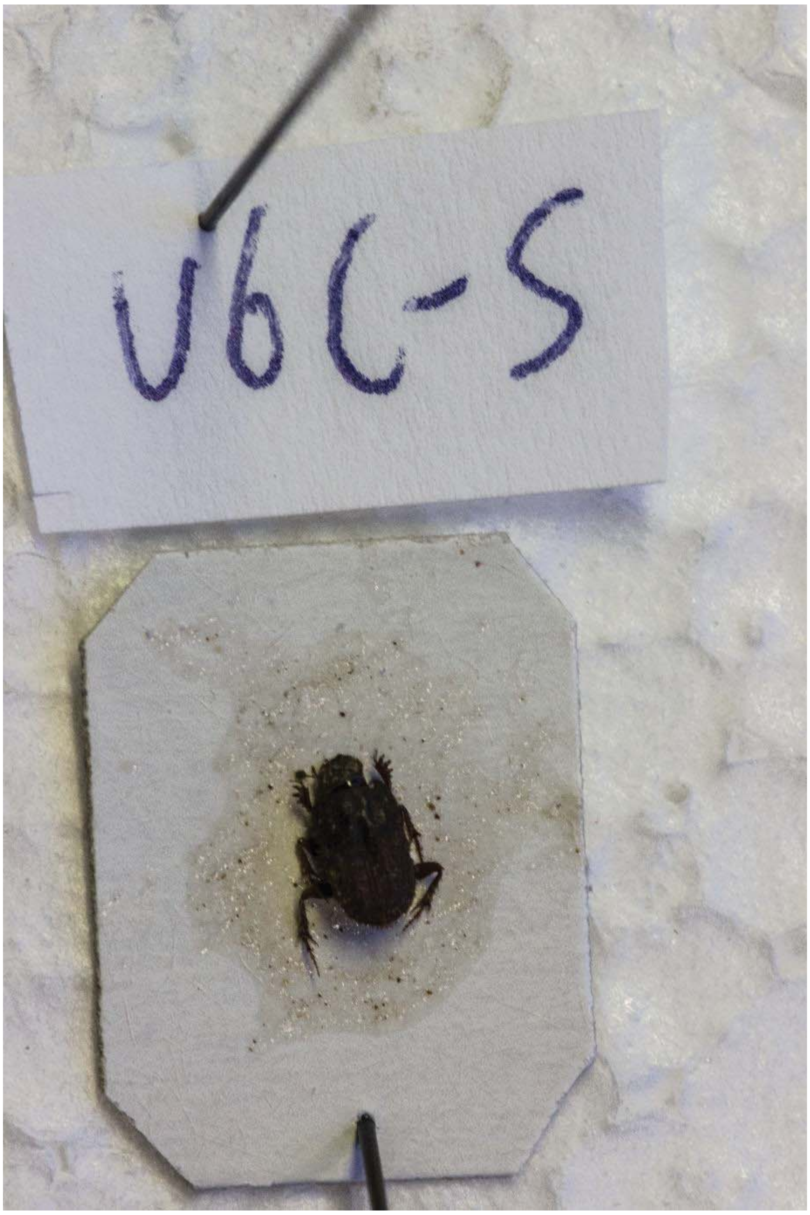
Amount: 21

Length: 6-7mm

Found at plot: U6C, U6P, U7P, U8P

Ecology: Tunnelling/dwelling dung beetle found on three of the eight plot sites on dung. Three individuals caught on the trap with cow (U6C) while the remaining 18 individuals were found in pig dung traps.

U6C-5



Amount: 1

Length: 5mm

Found at plot: U6C

Ecology: Tunnelling/dwelling dung beetle, only found on plot-site 6 using cow dung.

U6P-1

Amount: 1

Length: 9mm

Found at plot: U6P

Ecology: Tunnelling dung beetle, only found on plot-site 6 on pig dung.

U7P-4

Amount: 4

Length: 8-9mm

Found at plot: U7P, U7C

Ecology: Tunnelling/dwelling dung beetle, only found at plot-site 7 on dung.

U7C-1

Amount: 1

Length: 9mm

Found at plot: U7C

Ecology: Tunnelling/dwelling dung beetle, only found on plot-site 7 on cow dung.

U8P-1

Amount: 1

Length: 16mm

Found at plot: U8P

Ecology: Tunnelling/dwelling dung beetle, only found at plot-site 8 on pig dung. The only semi-large dung beetle collected close to the forest border in Udzungwa.

U8P-3

Amount: 1

Length: 7mm

Found at plot: U8P

Ecology: Tunnelling/dwelling dung beetle, only found on plot-site 8 on pig dung.

U8P-4

Amount: 2

Length: 6mm

Found at plot: U8P

Ecology: Tunnelling/dwelling dung beetle, only found on plot-site 8 on pig-dung.

U8P-13

Amount: 1

Length: 4mm

Found at plot: U8P

Ecology: Tunnelling/dwelling dung beetle, only found on plot-site 8 on pig-dung.

U8P-14

Amount: 1

Length: 4mm

Found at plot: U8P

Ecology: Tunnelling/dwelling dung beetle, only found on plot-site 8 on pig-dung.

U8P-15

Amount: 1

Length: 4mm

Found at plot: U8P

Ecology: Tunnelling/dwelling dung beetle, only found on plot-site 8 on pig-dung.

Norwegian University
of Life Sciences

Postboks 5003
NO-1432 Ås, Norway
+47 67 23 00 00
www.nmbu.no