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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.

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Photo taken by author (September 2013)

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ABSTRACT

The family of ground beetles (Coleoptera, Carabidae) is one of the most species-rich coleopteran families. Ground beetles are good indicators of habitat disturbances, and could provide valuable information for sustainable management planning. Most studies are, however, restricted to temperate regions, even though tropical forests have the highest potential biodiversity loss. This study aimed to investigate effects of land-use change on the ground beetle communities in northeastern Tanzania. The study area was located in Amani Nature Reserve, a reserve that is situated in a biodiversity hotspot. The original tropical montane forest habitat in this reserve has been reduced due to historical logging activities. Currently, a few primary forest habitats coexist with several secondary forest habitats, plantation forests, and agroforestry land. Six sites, located in habitats with different disturbance degrees, were chosen: undisturbed forest, secondary forest that was moderately logged in the past, secondary forest that was heavily logged in the past, riverine secondary forest that was moderately logged in the past, an agroforestry habitat, and a recently logged part of the secondary forest that was heavily logged in the past. In total, 157 ground beetles, representing sixteen morphospecies, were collected during eight sampling weeks, using pitfall traps. The results of this study showed that all sampled sites had a significantly different ground beetle composition. An increasing ground beetle abundance was found with an increasing disturbance degree, while the species richness, species evenness, and the diversity decreased. The agroforestry site had a significant higher abundance compared to the undisturbed forest site, the moderately disturbed forest site, and the riverine forest site. The logging site had a significant higher abundance compared to the moderately disturbed, and the riverine forest site. No significant differences in observed species richness were found across the sampled sites.

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1. INTRODUCTION

Tropical forests contain world's highest biodiversity (Lewis 2009). These forests are situated in areas that also have the highest anthropogenic pressures on the local biodiversity, because human populations are growing and developing most rapidly in the tropical regions (Lewis 2009). This combination of high anthropogenic pressures and biodiversity levels indicates that tropical forests have the highest potential biodiversity loss, which will result in changes in ecosystem structures and functions (Lewis 2009). Approximately half the world's closed-canopy tropical forest areas are converted already to other uses (e.g. the logging of a natural forest for agricultural use) (Wright 2005). These changes in land-use cause a reduction and fragmentation of the natural forest habitat, resulting in an increased threat of species extinction (Debinski & Holt 2000) especially in tropical plant and animal communities since they usually have smaller populations compared to temperate regions (Connell 1978). Moreover, anthropogenic disturbances are qualitatively new disturbances to which organisms in tropical rainforests may not yet be adapted (Connell 1978). Therefore, human-caused disturbances may cause a decrease in diversity, even at intermediate levels (Connell 1978). The increasing human population in these tropical areas implies that threats to biodiversity will intensify, and that effective sustainable management will be necessary to protect the tropical biodiversity against disturbances (Hulme 2006). However, a disturbance in one place affects the entire ecosystem (i.e. both the structural habitat and the native and invasive species), and each ecosystem factor may respond differently to the disturbance (Zurlini et al. 2013). For this reason, effective sustainable management requires a detailed understanding of the complex relationships between disturbances and biodiversity (Hulme 2006).

The Eastern Arc Mountains, a mountain chain in Tanzania and Kenya that is part of a globally recognized biodiversity hotspot (Mittermeier et al. 2011), consists of thirteen separate mountain blocks (Burgess et al. 2007). The East Usambara Mountains constitutes one of those mountain blocks, situated in northeastern Tanzania. The Amani Nature Reserve is located in the East Usambara mountain block and encloses several villages and sub-villages (Frontier Tanzania 2001). Management plans allow the people living in these local villages to collect fuel wood twice a week from certain zones within the nature reserve (Frontier Tanzania 2001). Other anthropogenic disturbances that currently occur within the reserve are illegal activities such as pole and timber extraction, fires, gold mining, and poaching. In 1886, colonial Germans induced logging activities in this area to clear land for plantations (Frontier Tanzania 2001). A small medicinal garden was founded in the early 1890s in the Amani area

(Hamilton & Bensted-Smith 1989). This became the Amani Botanical Garden, in 1902, under German administration (Iversen 1991). After the First World War, British colonizers managed the Botanical Garden for agricultural research purposes until the research station closed in the early 1950s (Iversen 1991). Commercial logging activities continued at various intensities until the mid-1980s (Frontier Tanzania 2001). The Amani Botanical Garden originally consisted of several separate botanical gardens, spread over approximately 300 ha (Dawson et al. 2008). About 650 species were planted over a period of 30 years (Dawson et al. 2008). The majority were woody species introduced for potential commercial gain (Iversen 1991). Currently, about one third of these introduced species remains (Dawson et al. 2008) and has become either naturalized or invasive (Frontier Tanzania 2001). The historical disturbances of the Amani area are currently still visible in the tree species compositions of the different forests within the reserve. This creates the possibility to compare forest patches with different anthropogenic disturbance degrees with respect to the current biodiversity.

With an estimated number of one million described species, insects are by far the most diverse class of all living multicellular organisms (IUCN 2012). The total number of existing insects is not known and estimates vary widely from around two million (Nielsen & Mound 2000) to around eight million (Groombridge & Jenkins 2002) or even up to 30 million (Erwin 1982). Insects have a wide range of functional roles in tropical forest ecosystems which, according to Lewis (2009), implies that the insect diversity is of crucial importance for the functioning of these systems, and that insects are sensitive to land-use changes of these forests. Therefore, the study of insects is not only important because insects are the main contributors to the overall biodiversity of a given area, they are also often good indicators for disturbance of an ecosystem (Kremen et al. 1993). An increasing disturbance is predicted to cause a decrease in both abundance and species richness of the specialist species of the original habitat along the disturbance gradient (Gray 1989).

Approximately 40% of the estimated number of described insects belongs to the order of beetles (Coleoptera) (Hammond 1992), which is the world’s most species-rich order, constituting approximately 25% of all species on Earth described so far (Hunt et al. 2007). The family of ground beetles (Carabidae) is one of the most species-rich coleopteran families (Lövei 2008). According to Niemelä et al. (2000), ground beetles might serve as biodiversity indicators. Several studies have used ground beetles as indicator organisms for assessments of environmental pollution (e.g. Bednarska & Stachowicz 2013; Butovsky 2011), for habitat classification for nature protection (e.g. Luff et al. 1992), and for characterization of the soil-nutrient status (e.g. Sadej et al. 2012). Physical disturbances of the landscape may change the ground beetle microhabitat and influence their species composition. For example, a change in the physical structure and complexity of the soil (e.g. an increased layer of litter) can negatively influence the number of naturally occurring ground beetle individuals and species (Lövei 2008). This is because the naturally occurring species in that area are not adapted to a thick layer of deciduous litter which is slowing down the movement speed of walking beetles (Lövei 2008). Abrupt changes in light conditions (e.g. changes in canopy cover through logging) induce changes in soil, microclimate, and water conditions (Magura et al. 2002). These factors, in their turn, influence the spatial distribution of ground beetles (Guillemain et al. 1997). An increased trampling intensity will also change ground beetle species compositions (Kotze et al. 2012) with an increased abundance of generalist and “edge preferring” species (Lövei 2008). Several ground beetle species also play an important role in the natural control of agricultural pests (Kromp 1989). Agricultural land supports a species composition that is influenced by crop type, productivity and disturbance (Eyre et al. 2013). A study on the coleopteran diversity and abundance in different habitats near the Kihansi waterfall in the Udzungwa Mountains, another mountain block that is part of the Eastern Arc Mountains, in Tanzania (Zilihona & Nummelin 2001) showed that the family-level diversity of Coleoptera was highest in the spray zone of the waterfall, followed by the riverine and moist forest respectively. This indicates that habitats with an increased humidity seem to support higher beetle diversity.

Despite their contribution to the world’s number of species, biodiversity surveys rarely include insects, and even fewer include ground beetles. In addition, although the ground beetle diversity is highest in the tropics (Erwin 1982), most studies on ground beetles are performed in the northern hemisphere. A search on the Web of Science for publications with the term “carabid*” in their title resulted in 2180 publications published between 1990 and 2013 (search made by myself on 18 April 2014). Only 84 remaining when this was combined with the term “diversity” over the same period of time, with most of them concerning only one genus, and being performed in the northern hemisphere. Biological surveys all over the Eastern Arc Mountains contain only few data on insect species. The few insect surveys that have been conducted in the Amani Nature Reserve contain mainly information on butterflies (Frontier Tanzania 2001). Namwanda and Ngaboyamahina (2005) studied the diversity and abundance of Coleoptera families in the Amani Nature Reserve, but the family of ground beetles (Carabidae) has not been studied before. Carabidae identification keys are also mainly restricted to the northern hemisphere. Only a few keys to species within genera in limited areas in eastern Africa have been published (e.g. Belousov and Nyundo (2013); Bulirsch and

Magrini (2011)). Scattered information on some African genera and a few keys to species can be found in less recent works (e.g. Bänninger (1937); Basilewsky (1953); Basilewsky (1962); Burgeon (1937)), However, these works are less easily accessible, and the used classifications are sometimes outdated.

In the present study, I compared six forest habitats with different degrees of anthropogenic disturbance with respect to the ground beetle abundance, species richness, species evenness, diversity, and species composition. My overall objective was to investigate the effect of different degrees of land-use changes on the ground beetle species composition. The main predictions for this study were:

- THE CARABIDAE SPECIES COMPOSITION WILL DIFFER ACCORDING TO THE LEVEL OF LAND-USE CHANGE. Both the abundance and richness of the specialist species of the original tropical montane forest are expected to decrease with an increasing disturbance, while the abundances of a few opportunistic species are expected to increase.

- THE OVERALL CARABIDAE SPECIES RICHNESS WILL DECREASE WITH AN INCREASING DISTURBANCE. More forest specialist species are expected to disappear in proportion to new opportunistic species that could enter the disturbed habitat.

- THE OVERALL CARABIDAE ABUNDANCE WILL INCREASE WITH AN INCREASE IN DISTURBANCE. A higher proportion of opportunistic individuals are expected to enter the disturbed habitat compared to the number of forest specialist individuals that is expected to disappear.

- THE CARABIDAE SPECIES EVENNESS WILL DECREASE WITH AN INCREASING DISTURBANCE.
  A few opportunistic species are expected to have a much higher abundance, while several other species will only have low abundances.

- THE CARABIDAE DIVERSITY WILL DECREASE WITH AN INCREASING DISTURBANCE.
  With an expected decrease in species richness and evenness, also the diversity is expected to decrease with an increasing disturbance.

2. MATERIALS AND METHODS

2.1. STUDY AREA

The Amani Nature Reserve (ANR) is situated in the Muheza District (Tanga region) in northeastern Tanzania, between 5°14’10” – 5°04’30” S and 38°30’34” – 38°40’06” E (Fig. 1) (Frontier Tanzania 2001). This reserve is part of the East Usambara Mountains (EUM) which represents one of the thirteen mountain blocks that constitute the Eastern Arc Mountains (EAM) (Fig. 2) (Burgess et al. 2007). The EAM are a chain of mountains reaching from the Taita Hills in southern Kenya to the Mahenge massif in south-central Tanzania (Burgess et al. 2007). This mountain chain belongs to the Eastern Afromontane hotspot which is one of the 35 internationally recognized biodiversity hotspots because of high biodiversity values (Mittermeier et al. 2011).

Figure 1. Map of Tanzania. The red circle situates the study area, Amani Nature Reserve. (Downloaded from www.ezilon.com)

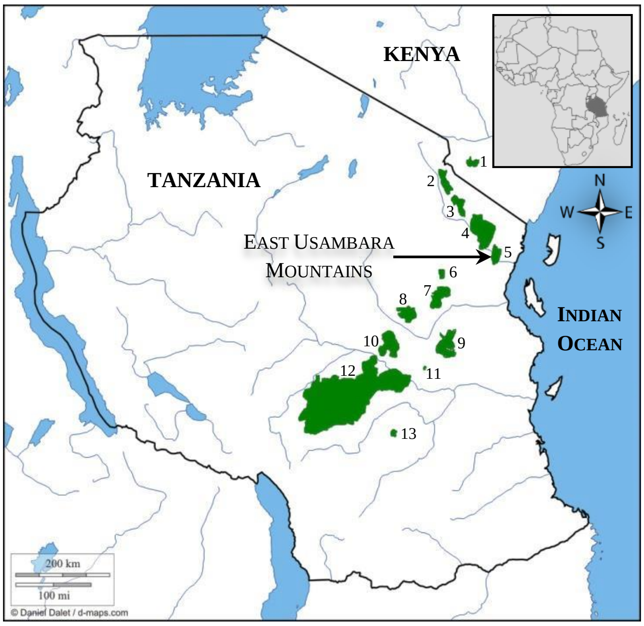

Figure 2. Map of Tanzania. The green patches represent the thirteen separated mountain blocks of the Eastern Arc Mountains mountain chain. Amani Nature Reserve is located in the southern part of the East Usambara Mountains mountain block. The thirteen mountain blocks are numbered from north to south: (1) Taita, (2) North Pare, (3) South Pare, (4) West Usambara, (5) East Usambara, (6) Nguu, (7) Nguru, (8) Ukaguru, (9) Uluguru, (10) Rubeho, (11) Malundwe, (12) Udzungwa, and (13) Mahenge. (Blank map downloaded fromwww.d-maps.com)

Gazetted in May 1997, ANR was the first nature reserve in Tanzania (Ministry of Natural Resources and Tourism 2006). UNEP et al. (2014) categorizes ANR as a Wilderness Area (i.e. Category Ib) according to the International Union for the Conservation of Nature (IUCN) Protected Area Management Categories. A Wilderness Area is defined as:

> *“Large area of unmodified or slightly modified land, and/or sea, retaining its natural character and influence, without permanent or significant habitation, which is protected and managed so as to preserve its natural condition.”* (Chape et al. 2003)

This categorization method is globally recognized and used as a framework within which countries can classify their protected areas (Chape et al. 2003). ANR is the only nature reserve in the EUM. The other, less protected areas are twelve forest reserves, four village forest reserves, and two private forests (EAMCEF 2013). Reasons for the high protection status of the ANR are its biodiversity, its size, the linkage of six former forest reserves, and the catchment for the Sigi River. Compared to other EUM forest reserves, the ANR has a high degree of (near-) endemism and an above average species richness for mammals, reptiles, amphibians, and butterflies (Frontier Tanzania 2001). At least 125 animal species in the reserve are dependent on primary forest (Frontier Tanzania 2001). Seven of them are endemic and 41 are near-endemic to the Usambara Mountains (Frontier Tanzania 2001). ANR contains at least 107 tree and shrub species that are dependent on primary forest (Frontier Tanzania 2001). Nineteen of them are endemic and 34 are near-endemic to the Usambara Mountains (Frontier Tanzania 2001). With an area of ca. 8350 ha, the ANR composes the largest forest block in the EUM and the largest forest block under unified management in the EAM (Frontier Tanzania 2001; Ministry of Natural Resources and Tourism 2006). The forests of the EUM are reduced to fragments within a matrix of agricultural land, the gazetted reserves provide almost the only available habitat for forest dependent species (Frontier Tanzania 2001). ANR is an assemblage of public land, 1068 ha of forest donated by the East Usambara Tea Company, and brings together six out of 24 separate former forest reserves (Amani Sigi, Amani East, Amani West, Kwamsambia, Kwamkoro and Mnyuzi) (Frontier Tanzania 2001; Ministry of Natural Resources and Tourism 2006). Linking together separate protection areas is a key part of conservation planning (Ministry of Natural Resources and Tourism 2006). More recently, ANR also got connected with other EUM forest blocks by the Derema Forest Corridor, which was newly gazetted in 2009 (Mtango & Kijazi 2011) on public land (Frontier

Tanzania 2001). ANR also encompasses the catchment for the Sigi River, which is the main catchment river of the EUM (Frontier Tanzania 2001).

ANR covers a continuous forest over a wide altitudinal range (ca. 190 m to ca. 1130 m above sea level) composed of lowland, submontane, and plantation forest (Frontier Tanzania 2001). The topography is characterized by a Y-shaped ridge, orientated from the southwest towards the north and northeast (Frontier Tanzania 2001). Although variable in time and intensity, most of central and northern Tanzania experiences a big rainy season during March and April, up to mid-May, and a smaller rainy season, with less rainfall, in late October and November, up to mid-December (Holmes 1995). ANR, however, is situated on a mountain where orographic lifting causes precipitation to occur throughout the year (Frontier Tanzania 2001). Nevertheless, there is still a bimodal regime noticeable with precipitation peaks from March to mid-May and from October to mid-December (Frontier Tanzania 2001; Holmes 1995). In ANR rainfall increases with altitude from 1200 mm annually in the foothills to over 2200 mm at higher altitudes (Frontier Tanzania 2001). The eastern side of the reserve is situated close to the Indian Ocean, causing the west-facing slopes of the mountains to be drier compared to the east-facing slopes (Frontier Tanzania 2001).

2.2. STUDY SPECIES

Ground beetles (Carabidae) are a large family of beetles (Coleoptera), that contains more than 40 000 described species (Lövei 2008). Ground beetles occur worldwide but their highest species richness is found in the tropics, where humidity seems to be the general limiting factor for their distribution (Lövei 2008). Most ground beetles are polyphagous feeders that consume both live prey and carrion (e.g. aphids, spiders, lepidopteran larvae and adults, mites, fly larvae, heteropterans, opilionids and collembola), and eat plant material (especially fruits and seeds) to complete their diet (Lövei 2008). Also both exclusively carnivorous and exclusively phytophagous species exist (Lövei 2008). Depending on species, ground beetles can consume up to 3½ times their own body weight per day (Trautner & Geigenmüller 1987). Although body length is species dependent, varying from a few millimeters to a few centimeters, their body structure and leg morphology are characteristically modified for running, digging, burrowing, climbing, or swimming (Lövei 2008). Many species have well-developed wings, while others have either completely lost the ability to fly or are dimorph (Lövei 2008). In temperate regions, most ground beetles live on or in the ground and some also climb plants (Trautner & Geigenmüller 1987), while in the tropics, a much larger proportion is canopy-dwelling (Erwin 1994). Although specific habitat requirements are species-dependent, ground beetle abundances generally increase with less variable and more favorable humidity and temperature conditions, more variable microsites, and more available habitat and prey (Lövei 2008). Ground beetles usually lay singular eggs, and the choice of the ovipositing site is species dependent (Lövei 2008). Eggs can be laid in the soil or in fissures (Lövei 2008), or even high above the ground on tree leaves (e.g. King (1919)). The typical ground beetle larva is campodeiform (i.e. flattened, elongated, and actively moving) (Crowson 1981). After completing several instar stages, the larva usually creates a specially constructed pupal chamber in the soil where it is more safe to pupate (Lövei 2008). In general, ground beetles complete their life cycle in less than one year, however, individual development can last up to four years under detrimental conditions (Lövei 2008).

2.3. CARABIDAE IDENTIFICATION

After collection, all ground beetle specimens were transported to the Royal Belgian Institute of Natural Sciences in Brussels (Belgium) where I dry-mounted the beetles. After mounting, I grouped the ground beetles according to morphospecies, and I tried to identify them until genus level. However, the ground beetles of Tanzania as well as of all eastern Africa and Africa in general, are poorly known and a key to Tanzania, or (eastern) African genera was not available. The specimens were therefore identified by using an identification key for European Carabids by Trautner and Geigenmüller (1987), and by comparing them to identified specimens in the collections of the Royal Museum for Central Africa in Tervuren (Belgium). Identification was only based on external morphology, not including genitalia. Each morphospecies belonged to a different genus.

2.4. STUDY DESIGN

The Carabidae were collected via pitfall trapping. The pitfall traps for this survey consisted of 200 ml plastic cups (7.0 cm x 9.5 cm), the opening inserted level with the surface level (Fig. 3). A transparent plexi lid (9.0 cm x 9.0 cm) was fixed at 4 cm above the opening of each trap to prevent rain water, falling leafs, and bigger animals from entering the cups, as well as to prevent animals from feeding on the trapped insects and on the salt water. Each trap was filled with 100 ml saturated salt solution as a preservative liquid, and some drops of detergent to minimize the surface tension.

For this study, ground beetles were sampled in six different sites (Table 1, Fig. 4). These sites were located in habitats that differed according to anthropogenic disturbance conditions. All habitats were originally tropical submontane forests. One site was located in an undisturbed primary forest habitat. Three other sites were located in secondary forest habitats that were either moderately or heavily logged in the past (ca. 120 years ago). The last two sites were located in open areas that were logged more recently and did not recover to forests. Both of these areas were logged for agroforestry use. One area was already a functional agroforestry area for more than 20 years at the time the samplings for this study started. The other area was logged more recently (January 2013), only eight months before the start of this study, and most of the logs were still present in this area.

Figure 3. Pitfall trap design. A 200 ml plastic cup, opening inserted level with the surface level. A transparent plexi lid was fixed above the opening by iron wires. © Hanne Geeraert

According to available area, each of the six sites contained either two or three sampling plots (Table 1). Appendix 1 presents the GPS-coordinates of each plot. Each plot contained twelve pitfall traps, arranged in a rectangular grid with three meters between the traps. During each sampling day the contents of the twelve traps were collected in one collection box and considered as one sample for that plot, since the twelve pitfalls in one plot influence each other. After collection, the trap contents were thoroughly checked for the presence of ground beetles. Ground beetles were taken out of the trap content and preserved in labeled boxes, ready to be transported afterwards. Pure ethanol (70% or more) was not available at site, all collected specimens were therefore preserved in gin (40%).

The sampling sites were surveyed during eight weeks from 27/09/2013 to 20/11/2013 (Appendix 2). This period should have covered the end of the drier season and part of the October – December rain season; however precipitation varied widely during this period without a clear pattern (see Table 9 in 3.6. Sample round-specific covariate).

Table 2 gives an overview of the dominant tree species that occurred in the sampled sites. The invasive tree species *Maesopsis eminii* is a well known introduced tree in the East Usambaras (Viisteensaari et al. 2000) and is relatively easily recognizable. This pioneer tree species is mainly dispersed by hornbills (Fig. 5) (Hall 1995). I used the relative number of *Maesopsis eminii* trees as an indicator for the historical disturbance conditions of the forest habitats, combined with information provided by local guides, to choose the six sites. The primary forest site had much less *Maesopsis eminii* trees (only occurring in natural gaps) compared to the secondary forest sites that were moderately and heavily logged in the past.

Figure 5. Picture of a Silvery-cheeked Hornbill (*Bycanistes brevis*) holding a *Maesopsis eminii* seed in his beak. Photo taken by author (November 2013).

Table 1. Habitat and disturbance description of the six different sampling sites with corresponding number of plots.

Site name	Plots	Habitat description	Disturbance level
‘Amani Primary Forest’ (AP)	3	Primary forest	Undisturbed
‘Kwamkoro Moderately Disturbed Forest’ (KM)	3	Secondary forest	Historically moderately logged
‘Kwamkoro Riverine Forest’ (KR)	3	Secondary forest, close to river/stream	Historically moderately logged
‘Mbomole Agroforestry Area’ (MA)	2	Agroforestry area	Recently heavily logged
‘Mbomole Heavily Disturbed Forest’ (MHD)	3	Secondary forest	Historically heavily logged
‘Mbomole Logging Area’ (ML)	2	Logged area	Recently heavily logged

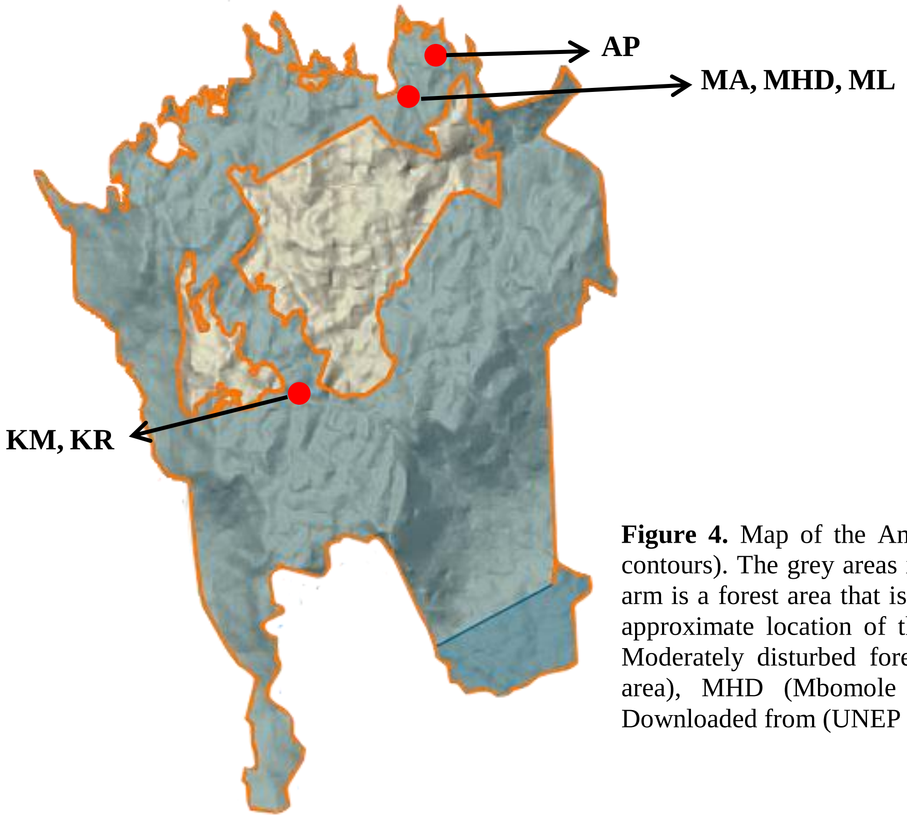

Figure 4. Map of the Amani Nature Reserve area (i.e. the light blue area within the orange contours). The grey areas in the center are tea plantations. The dark blue area in the lower right arm is a forest area that is not included in the Amani Nature Reserve. The red dots indicate the approximate location of the six different sites: AP (Amani Primary forest), KM (Kwamkoro Moderately disturbed forest), KR (Kwamkoro Riverine forest), MA (Mbomole Agroforestry area), MHD (Mbomole Heavily Disturbed forest), and ML (Mbomole Logging area). Downloaded from (UNEP et al. 2014).

Table 2. Overview of the dominant tree species occurring in the sampled sites.

Tree Species	**Status**	**Distribution**	**Reference**
Alchornea hirtella	Native	Widespread in Tropical Africa	Frontier Tanzania (2001)
Allanblackia stuhlmannii	Native (vulnerable)	Endemic to a few Tanzanian montane forests	Lovett and Clarke (1998a); Schulman et al. (1998)
Cephalosphaera usambarensis	Native (vulnerable)	Endemic to a few Tanzanian montane forests, and to the Shimba Hills in Kenya	Lovett and Clarke (1998b); Schulman et al. (1998)
Macaranga capensis	Native	Widespread in Tropical Africa	Frontier Tanzania (2001); Schulman et al. (1998)
Maesopsis eminii	Introduced	Naturalized in East Usambara	Schulman et al. (1998)
Mesogyne insignis	Native (near threatened)	Endemic to eastern Tanzania and the island of São Tomé	IUCN SSC East African Plants Red List Authority (2013); Schulman et al. (1998)
Parinari excelsa	Native	Widespread in Tropical Africa	Schulman et al. (1998)
Tabernaemontana stapfiana	Native	Widespread in Tropical Africa	Frontier Tanzania (2001); Schulman et al. (1998)

The ‘Amani Primary Forest’ site (from now referred to as ‘undisturbed forest site’) was an undisturbed forest. The very low density of *Maesopsis eminii* trees indicates that no logging has occurred in this forest in the past. This forest was dominated by native endemic tree species (e.g. *Allanblackia stuhlmannii*, *Cephalosphaera usambarensis*, and *Mesogyne insignis* (Table 2)).

The ‘Kwamkoro Moderately Disturbed Forest’ site (from now on referred to as ‘moderately disturbed forest site’) was a moderately disturbed forest that has been moderately logged in the past. This forest was dominated by a mix of native endemic tree species (e.g. *Allanblackia stuhlmannii*, and *Cephalosphaera usambarensis* (Table 2)) and native widespread tree species (e.g. *Alchornea hirtella, Macaranga capensis, Parinari excelsa*, and *Tabernaemontana stapfiana* (Table 2)). There were more *Maesopsis eminii* trees in this forest patch compared to the undisturbed forest patch, but they did not dominate.

The ‘Mbomole Heavily Disturbed Forest’ site (from now on referred to as ‘heavily disturbed forest site’) was situated in a heavily disturbed forest. This forest has been heavily logged in the past and contained the greatest amount of *Maesopsis eminii* trees (Table 2), compared to the previous two forest types. Parts of this forest have been logged in order to clear land for botanical garden plantations.

The ‘Kwamkoro Riverine Forest’ site (from now on referred to as ‘riverine forest site’) was located in the same secondary forest as the moderately disturbed forest site, but the plots were situated adjacent to a river or stream. As in the moderately disturbed forest site, the dominant tree composition in these plots consisted of a mix of endemic and widespread native tree species (e.g. *Cephalosphaera usambarensis*, *Allanblackia stuhlmannii*, and *Alchornea hirtella* (Table 2)). Introduced fern trees (Latin name unknown), which did not occur in the moderately disturbed forest site, were dominant as well.

The ‘Mbomole Agroforestry Area’ site (from now on referred to as ‘agroforestry site’) was an area that has been logged in order to use it as agroforestry land. The agroforestry site was fully functional during more than 20 years at the moment of this study. This was an open area dominated by a few invasive *Maesopsis eminii* trees and some cultivated cinnamon trees. Ferns and crops formed a relatively dense understory.

The ‘Mbomole Logging Area’ site (from now on referred to as ‘logging site’) was an area where legal logging occurred recently (January 2013), in order to use the land for agroforestry in the future. This was an open area that bordered the heavily disturbed forest site. The few trees that were standing in this area were mainly *Maesopsis eminii* trees.

2.5. COVARIATES

Notes on different environmental covariates were taken at each plot (Table 3). The altitude, the slope, the number of big logs laying in and within a distance of three meters of each plot, the number of big trees (i.e. trees with a trunk base wider than one meter in diameter) standing in and within a distance of three meters of each plot, the distance to roads or big paths, distances to habitat edges, and distances to a river or stream were taken into account as a way to standardize the plots as much as possible (Table 3). The plots were chosen at an altitude between 850 m and 1100 m above sea level, at least 100 m apart in air distance and at a distance of minimum 50 m in air distance from habitat edges. Steep slopes were avoided as much as possible, as were big logs and big standing trees. Following parameters were estimated in order to provide plot specific information: the stand basal area, the percentage of canopy openness, the dominant tree species, the percentage of ground vegetation, the soil texture and color, the percentage of soil surface covered by rocks and by leaf litter and small branches, and the percentage of bare soil (Table 3). Altitude and distances were measured by GPS (GPSmap 62s). The slope was estimated according to following categories: ‘flat’, ‘gentle’, or ‘steep’. All percentages were measured without special equipment and were estimated according to following categories: ‘< 10 %’, ‘10 – 30 %’, ‘30 – 50 %’, ‘50 – 80 %’, ‘> 80 %’. The stand basal areas were measured by use of a standard bottle-opener dendrometer. A basal area factor of 4 was chosen, and the sweep was taken while standing in the center of each plot. Tree species, soil texture and soil color were recorded as nominal variables.

Notes were also taken on the weather conditions every day. The amount of rain per sample round was considered as a sample specific covariate. Each day of the sampling period was given a level (0, 1, or 2) referring to the amount of rain that day (0 = no rain, 1 = a few short downpours, 2 = a whole day of rain).

After completing the fieldwork, the full body length (mandibles included) of each morphospecies was estimated based on pictures (taken at the same magnification) of the collected specimens. The size of each morphospecies was used as a morphospecies-specific covariate. Also the leg morphology, i.e. whether the front legs were adapted for burrowing (subfamily Scaritinae) or not, was used as a morphospecies-specific covariate in some analyses.

Table 3. Overview of the measured environmental covariates. Each covariate was measured either to standardize all plots or to provide plot specific information.

Environmental covariates	Function
Altitude	Plot standardization
Bare soil (%)	Plot specific information
Canopy openness (%)	Plot specific information
Distances to habitat edges	Plot standardization
Distances to river or stream	Plot standardization
Distances to roads or big paths	Plot standardization
Dominant tree species	Plot specific information
Ground vegetation (%)	Plot specific information
Number of big logs	Plot standardization
Number of big trees	Plot standardization
Slope	Plot standardization
Soil surface covered by leaf litter and small branches (%)	Plot specific information
Soil surface covered by rocks (%)	Plot specific information
Soil texture and color	Plot specific information
Stand basal area	Plot specific information

2.6. STATISTICAL ANALYSES

My obtained data are count data. One sample contained the number of Carabidae caught in all pitfall traps of one plot collected in one sample round. However, many samples did not contain any ground beetles, resulting in a zero-inflated dataset (Fig. 6). All analyses were done in the statistical program R, version 2.15.2. (R Core Team 2012). The level of significance for all analyses in this study was put at a value of 0.05.

To investigate the completeness of the sampling, I plotted a species accumulation curve (Colwell & Coddington 1994). Since all sites had a different observed ground beetle abundance, I plotted an individual-based rarefaction curve for each site which provided a direct comparison of the rarefied richness between the six sampled sites (Magurran 2004). I used the vegan package (Oksanen et al. 2013) to make both abovementioned plots. I also used this package to calculate the Simpson diversity indices and the Pielou’s evenness indices of each site. I chose the Simpson diversity index as a biodiversity measure, which was recommended by Magurran (2004) for small datasets which contain only a relatively small proportion of the real species richness.

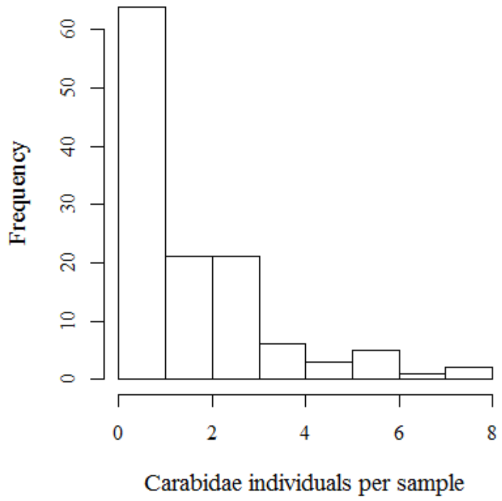

Figure 6. Frequency histogram of the adjusted dataset, showing zero-inflation. (For more info about the applied adjustments, see 3.1 Adjustments)

I performed different Kruskal-Wallis Rank Sum tests to investigate if there were significant differences in the observed abundance and the observed species richness between the different sites. When a significant difference across sites was found, I performed a multiple comparison test after the Kruskal-Wallis test, using the pgirmess package (Giraudoux 2013), to see which sites were significantly different.

A chi-squared test gave information on the distribution of the different morphospecies across the different sites. The overall outcome of this test showed that the observed genera were significantly differently (i.e. not randomly) distributed across the six sampled sites. As a next step, I explored the potential influences of selected covariates on this observed variation in morphospecies distribution. First I investigated the correlation between both observed abundance and observed species richness, and selected environmental covariates, selected morphospecies-specific covariates, and the amount of rainfall as a sample round-specific covariate. Then I tried to find the model that provided the best ecological explanation for the variation in observed abundance. The Poisson, binomial, and negative binomial distributions are commonly used to represent count data (Fowler et al. 1998). However, these models would be overdispersed because of the high frequency of zeros in my dataset. A zero-inflated model takes care of this overdispersion (Zuur et al. 2009). There are two types of zero-inflated models that could be used to analyze zero-inflated data: two-part models and mixture models

(Zuur et al. 2009). I chose to use a mixture model because this type of zero-inflated models makes a distinction between true and false zeros (Zuur et al. 2009). This distinction was necessary to make because, in this study, an observed zero could either be caused by a structural error (i.e. a true zero; a morphospecies was not observed because the habitat was not suitable) or by an observer error (i.e. a false zero; a morphospecies was present in the habitat, but was not observed) (Zuur et al. 2009). The zero-inflated Poisson model and the zero-inflated negative binomial model are two possible mixture models (Zuur et al. 2009). I chose to use the zero-inflated Poisson model because there is no overdispersion in my non-zero count data (Zuur et al. 2009). In a zero-inflated Poisson model, a binomial generalized linear model is used to model the probability of measuring a false zero (i.e. the probability of not catching any ground beetles while the habitat is suitable), and a Poisson generalized linear model is used to model the count process (Zuur et al. 2009). By manually creating different models, I explored which (combination) of main covariates (i.e. site, morphospecies, and sample round) provided the most supported model according to the Akaike Information Criterion (AIC). Zuur et al. (2009) recommended to compare this most supported zero-inflated Poisson model with the corresponding zero-inflated negative binomial model in a likelihood ratio test. The p-value of this test was not small enough to reject the null hypothesis (H0 = the variance structure of the Poisson generalized linear model does not differ from the variance structure of the negative binomial generalized linear model), which confirmed that the zero-inflated Poisson model was the appropriate model to use. In a next step, I replaced the main covariates by (combinations of) selected corresponding specific covariates, based on ecological thinking because too many combinations were possible to perform. I did this to investigate if a better explanation of the observed variation in abundance could be obtained. I used the pscl package (Zeileis et al. 2008) for the modelling, and the lmtest package (Zeileis & Hothorn 2002) to perform the likelihood ratio test.

3. RESULTS

A total of 157 ground beetles, representing sixteen morphospecies, was collected during the eight sample rounds (27/09/2013 – 20/11/2013) (see appendix 3 for the results per plot per site). Five morphospecies could not be identified until genus level, two of them were identified to subfamily level (*Harpalinae_X* and *Scaritinae_X*) and three morphospecies remained unidentified but belonged to three different genera (*Unknown_A*, *Unknown_B*, and *Unknown_C*). In total, 125 samples were taken. A species accumulation curve indicated that this sampling effort was sufficient to reliably reflect the real species richness of ground-dwelling Carabidae within the sampled area (Fig. 7).

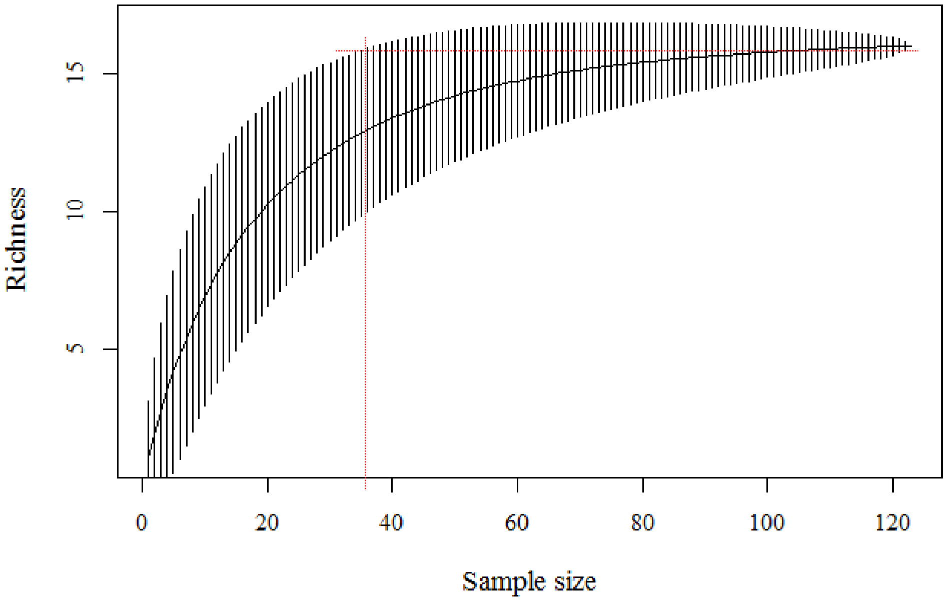

Figure 7. Species accumulation curve, showing the cumulative number of observed morphospecies as a function of the cumulative number of samples taken. The vertical lines show the 95% confidence intervals. The red dotted lines indicate the first confidence interval that overlaps with the last confidence interval. This implies that from ca. 35 samples onwards, there is no longer a significant increase obtained in the number of new observed morphospecies with an increased number of samples taken.

3.1. ADJUSTMENTS

Some adjustments had to be made to the original results in order to obtain a common sampling effort (see appendix 4 for the adjusted results per plot per site). The undisturbed forest site was sampled during 50 days while the other sites were sampled during 53 days. Adjusting the number of sampling days resulted in a total number of 22.26 instead of 21 observed ground beetles in the undisturbed forest site. The available surface area in both the agroforestry and the logging site did allow for only two instead of three plots. Adjusting the number of traps changed the total number from 37 to 55.5 ground beetle individuals in the agroforestry site and from 26 to 39 individuals in the logging site. As a last adjustment, the results for the first plot in the riverine forest site of sample rounds seven and eight were removed from the dataset, because too many traps were destroyed by rodents (probably giant pouched rats (*Cricetomys gambianus*)) during these sample rounds (see appendix 5). Adjusting the results for the number of traps of sample rounds seven and eight in the riverine forest site changed the total number of observed ground beetles from 11 to 13.5 individuals in this site. All together, these adjustments resulted in a total of 192.26 observed ground beetles, divided between sixteen different morphospecies, each morphospecies belonging to a different genus (Table 4). Unless it is stated that the originally observed abundances are used, all following analyses are based on the adjusted observed abundances.

3.2. MORPHOSPECIES ANALYSIS

The three most abundant morphospecies were *Harpalinae_X*, *Dyschiridium*, and *Galerita*, together comprising 51% of the total catch (Table 4). All *Harpalinae_X* individuals in this study were caught in one site only, while *Galerita* was the only morphospecies that was found in all sampled habitats (Table 4). *Tefflus* was the second most general morphospecies, found in all but one site (Table 4). Other than *Harpalinae_X*, also *Anaulacus*, *Apristus*, *Tachys* and *Unknown_B* were found in just one of the sampled habitats (Table 4).

Table 4. The subfamily and genus names of the sixteen morphospecies, with the corresponding adjusted number of observed individuals and their percentage of the adjusted overall total (192.26 Carabidae), and the number of sites in which the morphospecies were caught.

Subfamily	**Genus**	**No. of Carabidae**	**% of total Carabidae**	**No. of sites**
BRACHININAE	*Crepidogaster*	7	3.65	3
DRYPTINAE	*Galerita*	25.8	13.45	6
HARPALINAE	*Harpalinae_X*	40.5	21.12	1
LEBIINAE	*Anaulacus*	4.5	2.35	1
	Apristus	1.5	0.78	1
	Pentagonica	7.12	3.71	3
PANAGAEINAE	*Disphaericus*	3.5	1.83	3
	Dyschiridium	33.06	17.24	4
	Tefflus	17.56	9.16	5
SCARITINAE	*Mamboicus*	7.24	3.78	3
	Scaritinae_X	6.24	3.25	2
	Typhloscaris	8.12	4.23	2
TRECHINAE	*Tachys*	6.5	3.39	1
UNKNOWN	*Unknown_A*	3.5	1.83	3
UNKNOWN	*Unknown_B*	3	1.56	1
UNKNOWN	*Unknown_C*	17.12	8.93	3

The morphospecies *Harpalinae_X*, *Anaulacus*, *Apristus* and *Unknown_B* were only caught in the agroforestry site, while *Mamboicus*, *Pentagonica*, *Scaritinae_X*, and *Unknown_C* individuals were caught exclusively in the non-riverine forest sites. *Tachys* was the only morphospecies that was exclusive to the riverine forest site, and no morphospecies were exclusive to the logging site. The p-values in appendix 6 show that following morphospecies were significantly differently distributed across the six sampled sites: *Dyschiridium*, *Galerita*, *Harpalinae_X*, *Mamboicus*, *Scaritinae_X*, *Tachys*, *Tefflus*, *Typhloscaris*, and *Unknown_C* (Table 5).

Table 5. Overview of the observed abundance of the sixteen morphospecies (presented by their genus name), across the different sites. All values, larger than zero, are shown in bold. The morphospecies marked in red are significantly differently distributed across the different sites. All sites had a significantly different morphospecies composition.

Morphospecies / Site	Undisturbed forest	Moderately disturbed forest	Heavily disturbed forest	Riverine forest	Logging area	Agroforestry area
Anaulacus	0.00	0.00	0.00	0.00	0.00	**4.50**
Apristus	0.00	0.00	0.00	0.00	0.00	**1.50**
Crepidogaster	0.00	**1.00**	**3.00**	0.00	**3.00**	0.00
Disphaericus	0.00	**1.00**	0.00	**1.00**	**1.50**	0.00
Dyschiridium	**1.06**	**10.00**	**7.00**	0.00	**15.00**	0.00
Galerita	**5.30**	**2.00**	**10.00**	**4.00**	**1.50**	**3.00**
Harpalinae_X	0.00	0.00	0.00	0.00	0.00	**40.50**
Mamboicus	**4.24**	**2.00**	**1.00**	0.00	0.00	0.00
Pentagonica	**2.12**	0.00	**4.00**	**1.00**	0.00	0.00
Scaritinae_X	**4.24**	0.00	**2.00**	0.00	0.00	0.00
Tachys	0.00	0.00	0.00	**6.50**	0.00	0.00
Tefflus	**1.06**	0.00	**2.00**	**1.00**	**10.50**	**3.00**
Typhloscaris	**2.12**	0.00	0.00	0.00	**6.00**	0.00
Unknown_A	0.00	**1.00**	**1.00**	0.00	**1.50**	0.00
Unknown_B	0.00	0.00	0.00	0.00	0.00	**3.00**
Unknown_C	**2.12**	**1.00**	**14.00**	0.00	0.00	0.00

3.3. HABITAT ANALYSIS

Overall, most ground beetles were caught in the agroforestry site, and fewest were caught in the riverine forest site (Fig. 8). The site with the highest number of observed morphospecies was the heavily disturbed forest site, and the fewest different morphospecies were caught in the riverine forest site (Fig. 8). However, at an equal abundance of 13.5 ground beetles, the undisturbed forest site had the highest rarified species richness, and the agroforestry site had the lowest rarified richness (Fig. 8). The undisturbed forest site was the site with the highest Simpson diversity index and the second highest evenness (Fig. 9). The highest species evenness was found in the riverine forest site (Fig. 9). Figures A and B in appendix 7 present the diversity index and the species evenness for the six sampled sites, calculated based on the original results. The results were very similar to the results presented in figure 9, and the same trends were observed.

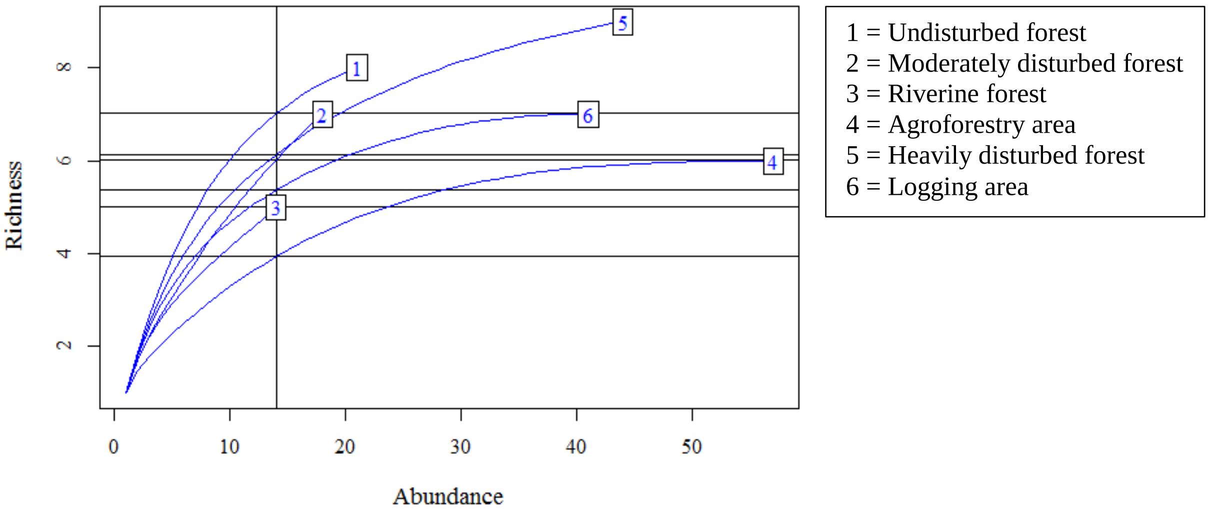

Figure 8. Individual-based rarefaction curves showing the rarified richness as a function of the observed ground beetle abundance. The rarified richness gives estimates for the richness at lower abundances, in this way the richness can be compared across the different sites. The site with the lowest observed ground beetle abundance is the riverine forest site. The horizontal lines indicate the rarified richness for each site at the same abundance as the observed abundance in the riverine forest site.

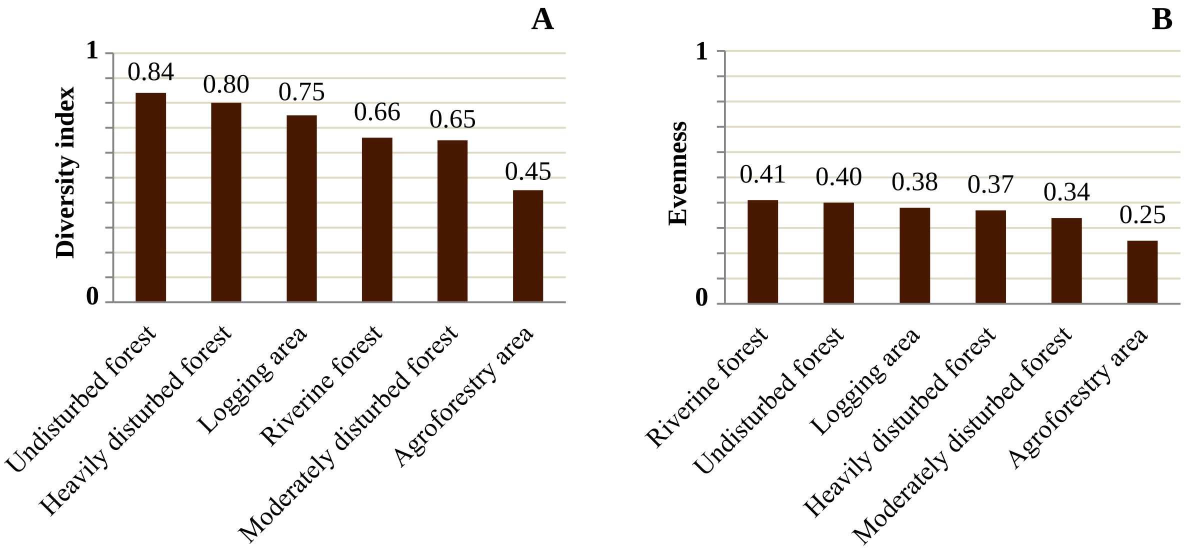

Figure 9. A) The Simpson diversity index per site. **B)** Species evenness per site.

The number of ground beetles caught was significantly different in the six sites (p-value = 1.208E^{-05}). The agroforestry site had a significantly higher observed abundance compared to the undisturbed forest site, the moderately disturbed forest site, and the riverine forest site. The logging site had a significantly higher observed abundance compared to the moderately disturbed forest site and the riverine forest site. There was no significant difference in observed morphospecies richness across the sites (p-value = 0.752) (Fig. 10).

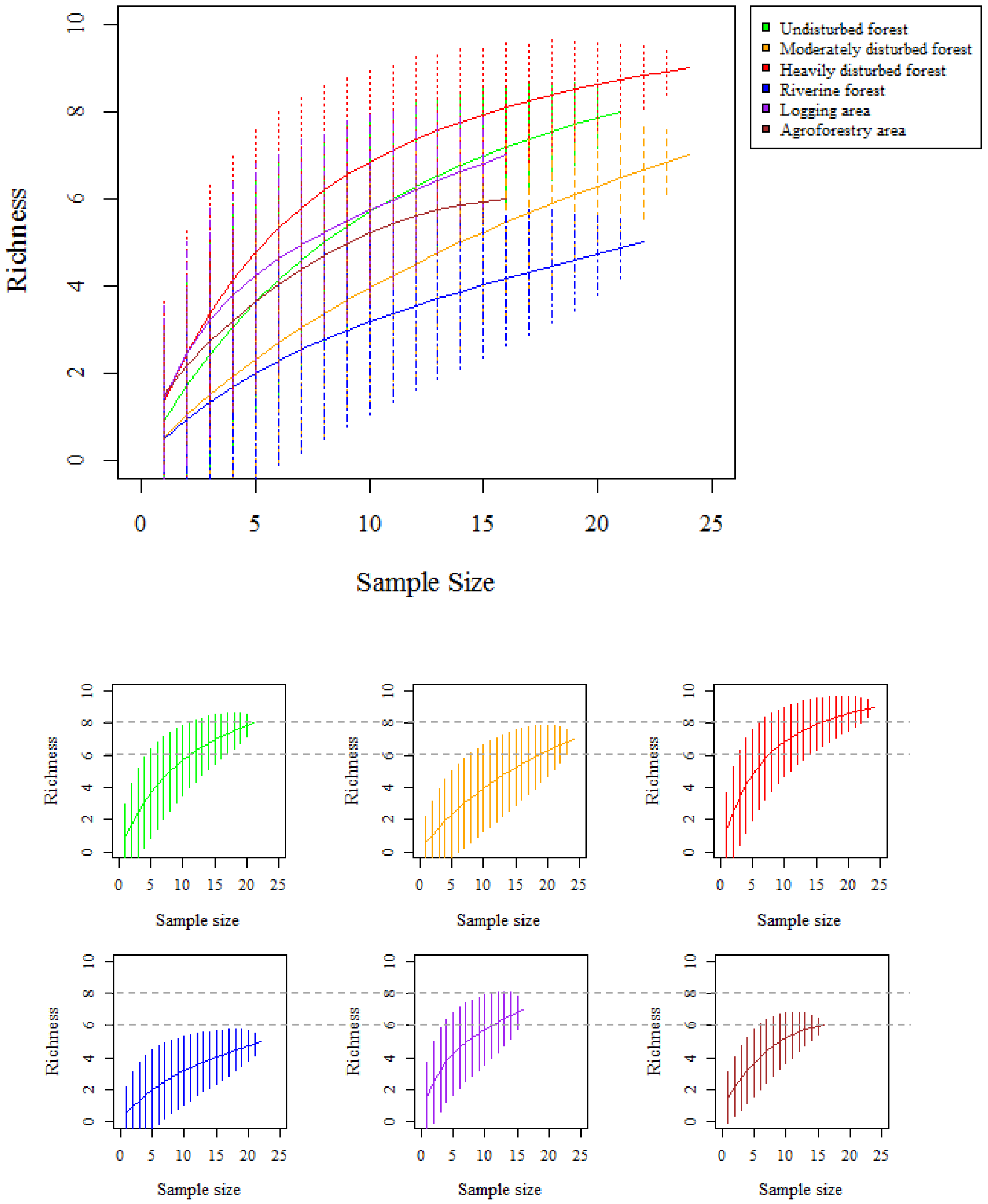

Figure 10. Species accumulation curves, showing the cumulative observed species richness per site as a function of the cumulative number of samples taken. Less samples were taken in the undisturbed forest site, the riverine forest site, the logging site, and the agroforestry site (see 3.1. Adjustments). The vertical lines represent the 95% confidence intervals. When the confidence intervals of one curve no longer overlap with the confidence intervals of another curve, then the cumulative observed richness between the corresponding sites is significantly different. Overall, the confidence intervals of all curves overlap to a large extend, and significant differences in species richness are only observed after a high number of samples were taken. Therefore, no significant difference was found in the overall observed species richness between the sites.

3.4. SITE-SPECIFIC COVARIATES

The results of the environmental covariates that were estimated in order to provide plot specific information are presented in appendix 8. Further analyses are based on a selection of environmental covariates consisting of those covariates that were most likely to have an effect on the ground beetles (Table 6). A correlation test showed that there is a relative strong correlation between the percentage of canopy openness, the percentage of ground vegetation, and the stand basal area (Table 7). Each of these three covariates showed a significant correlation with the observed ground beetle abundance (Fig. 11 A-C). The percentage of leaf litter and small branches covering the plot surface did not show a significant correlation with the observed ground beetle abundance (Fig. 11 D). There were strong trends showing a decreasing species richness with an increasing percentage of canopy openness (Fig. 12 A), and an increasing species richness with an increasing percentage of leaf litter and small branches covering the plot surface (Fig. 12 D), however both correlations were not significant. Also the percentage of ground vegetation in the plot and the stand basal area did not show a significant correlation with the observed species richness (Fig. 12 B-C).

Table 7. Correlation matrix for a selection of environmental covariates: the percentage of canopy openness above the plot, the stand basal area (m²/ha), the percentage of leaf litter and small branches covering the plot surface, and the percentage of ground vegetation covering the plot surface.

	Canopy openness	**Stand basal area**	**Leaf litter**	**Ground vegetation**
Canopy openness	1	-0.39	0.29	0.75
Stand basal area		1	-0.05	-0.34
Litter			1	0.14
Ground vegetation				1

Table 6. Estimates of the plot specific environmental covariates: Canopy openness = the percentage of canopy openness above the plot; SBA = the stand basal area; Leaf litter = the percentage of leaf litter and small branches covering the plot surface; Ground vegetation = the percentage of ground vegetation covering the plot surface.

Site	Plot	Canopy openness (%)	SBA (m^2/ha)	Leaf litter (%)	Ground vegetation (%)
Undisturbed forest	**1**	20	42	90	40
Undisturbed forest	**2**	20	50	75	20
Undisturbed forest	**3**	10	36	75	40
Moderately disturbed forest	**1**	10	38	90	20
Moderately disturbed forest	**2**	20	56	90	40
Moderately disturbed forest	**3**	40	56	90	40
Heavily disturbed forest	**1**	20	44	75	40
Heavily disturbed forest	**2**	10	84	75	40
Heavily disturbed forest	**3**	40	74	90	75
Riverine forest	**1**	20	58	75	40
Riverine forest	**2**	40	40	90	40
Riverine forest	**3**	20	36	40	40
Logging area	**1**	75	26	90	75
Logging area	**2**	90	14	90	75
Agroforestry area	**1**	90	18	90	90
Agroforestry area	**2**	90	26	75	90

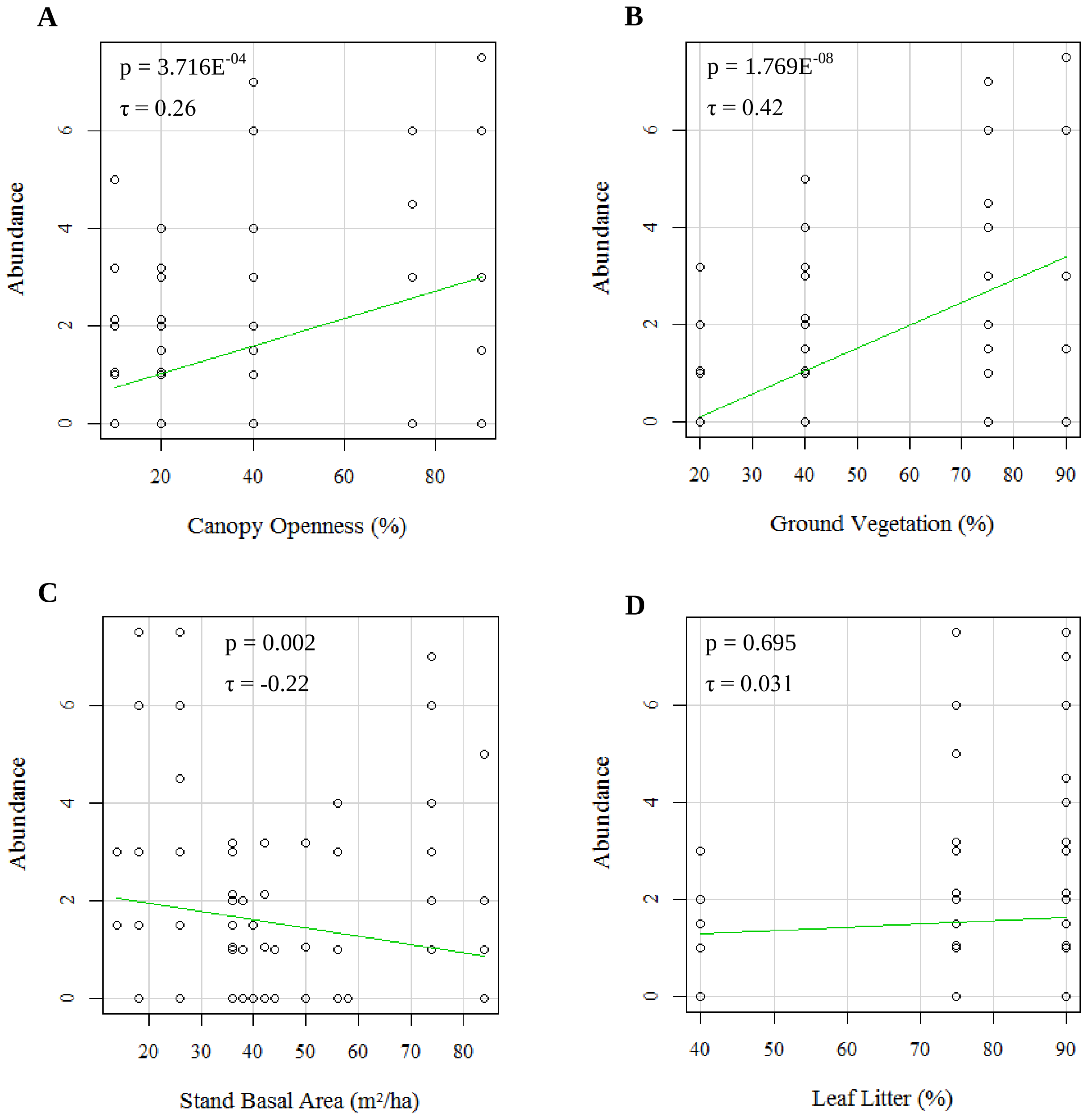

Figure 11. Correlation scatterplots for the observed number of ground beetles as a function of **A)** the percentage of canopy openness above the plot, **B)** the percentage of ground vegetation covering the plot surface, **C)** the stand basal area, and **D)** the percentage of leaf litter and small branches covering the plot surface. The p-value (p) and Kendall's rank correlation tau (τ) are given for each correlation. The green lines represent the regression lines.

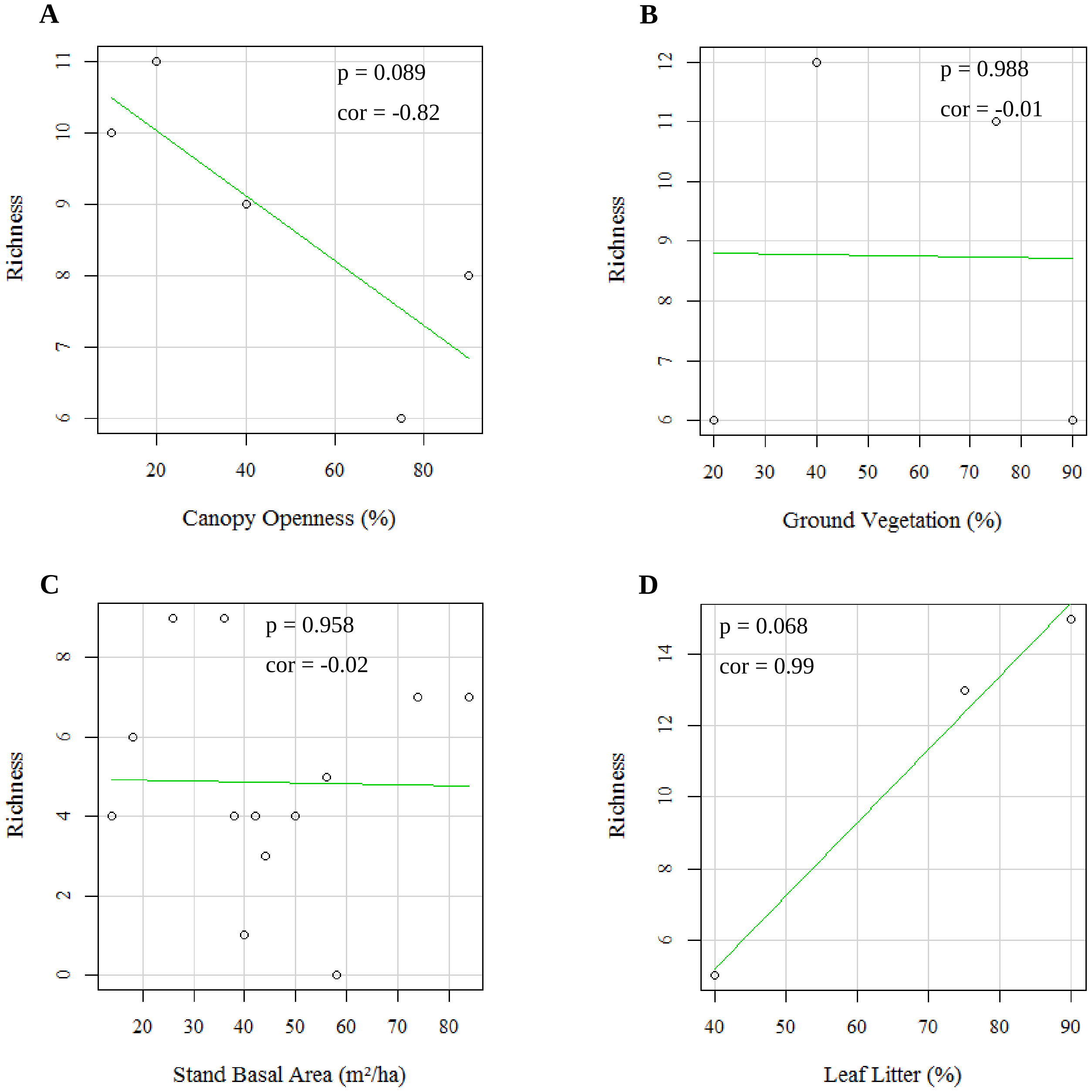

Figure 12. Correlation scatterplots for observed species richness as a function of **A)** the percentage of canopy openness above the plot, **B)** the percentage of ground vegetation covering the plot surface, **C)** the stand basal area, and **D)** the percentage of leaf litter and small branches covering the plot surface. The p-value (p) and the Pearson correlation coefficient (cor) are given for each correlation. The green lines represent the regression lines.

3.5. MORPHOSPECIES-SPECIFIC COVARIATES

The files in appendix 9 present specific information on each observed morphospecies. The two largest morphospecies in this study, *Galerita* and *Tefflus*, were the only morphospecies that were represented in closed-canopy sites as well as in the agroforestry site (Table 6). All forest sites together (i.e. the undisturbed, moderately disturbed, heavily disturbed, and riverine forest sites) embraced the largest range of sizes (Table 6). Morphospecies that were exclusive to the agroforestry site were all relatively small species, while the logging site only contained larger species (Table 6). However, there was no significant difference between the observed body sizes across the different sites (p-value = 1). Figure 13 shows a positive trend, however no significant correlation, between the sizes of the ground beetles and the observed abundances.

Table 6. The sixteen observed morphospecies (presented by their genus name), ordered according to indicative size (mm). The original total number of caught individuals is given for each morphospecies, along with the sites they were represented in. Forest sites = the undisturbed, moderately disturbed, heavily disturbed, and riverine forest sites.

Morphospecies	**Size (mm)**	**Abundance**	**Forest sites**	**Logging site**	**Agroforestry site**
Tefflus	34.0	13	✓	✓	✓
Galerita	29.0	23	✓	✓	✓
Mamboicus	25.0	7	✓	-	-
Typhloscaris	17.0	6	✓	✓	-
Disphaericus	14.0	3	✓	✓	-
Dyschiridium	10.0	28	✓	✓	-
Crepidogaster	9.5	6	✓	✓	-
Harpalinae_X	8.5	27	-	-	✓
Unknown_A	8.0	3	✓	✓	-
Anaulacus	7.5	3	-	-	✓
Unknown_B	7.5	2	-	-	✓
Unknown_C	7.5	17	✓	-	-
Pentagonica	5.0	7	✓	-	-
Apristus	4.0	1	-	-	✓
Tachys	3.0	5	✓	-	-
Scaritinae_X	2.5	6	✓	-	-
TOTAL		**157**			

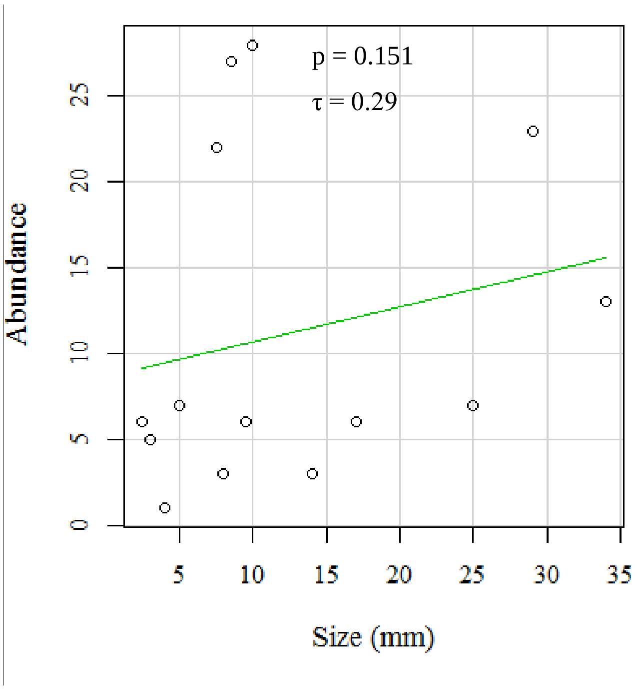

Figure 13. Correlation scatterplot for the observed abundance as a function of body size (mm). The p-value (p) and Kendall's rank correlation tau (τ) are presented in the figure. The green line represents the regression line.

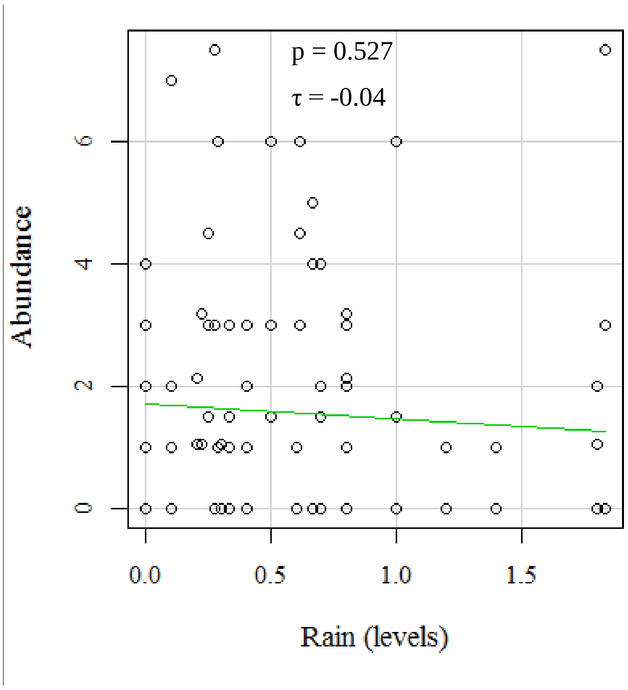

Figure 14. Correlation scatterplot for the observed abundance as a function of the amount of rainfall. The amount of rainfall was calculted based on following levels: 0 = no rain, 1 = short downpour, 2 = full day of rain (for more explanation, see 2.5. Covariates).The p-value (p) and Kendall's rank correlation tau (τ) are presented in the figure. The green line represents the regression line.

3.6. SAMPLE ROUND-SPECIFIC COVARIATE

The amount of rainfall was recorded as a sample round-specific covariate (Table 9). Figure 14 shows only a weak trend in the relationship between the amount of rainfall and the number of observed individuals.

Table 9. The average level of rain (based on the levels 0, 1, and 2 (see 2.5. Covariates)) and the adjusted observed Carabidae abundance per sample round.

Sample round	Rain	Abundance
1	0.20	19.00
2	1.68	17.56
3	1.00	18.12
4	0.50	24.80
5	0.19	26.56
6	0.31	10.50
7	0.69	39.80
8	0.28	35.92

3.7. ZERO-INFLATED POISSON REGRESSION

The model that provided the best ecological explanation for the variation in observed abundances in this study, according to the AIC values, was the model with the additive effect of the main covariates ‘sample round’ and ‘morphospecies’ on the count process, and the interaction effect of the main covariates ‘site’ and ‘morphospecies’ on the probability of measuring a false zero (i.e. the probability of not catching any ground beetles while the habitat is suitable) (Table 10). Replacing the main covariates by (combinations of) selected corresponding specific covariates, did not improve this model.

Table 10. Overview of the eight most supportive models according to the AIC values. The top model is the most supportive model, shown in bold. The degrees of freedom (df), and the difference in AIC values (Δ AIC) compared to the most supportive model are presented for each model.

Model	Count process	Catch process	df	Δ AIC
1	**sample round + morphospecies**	**site * morphospecies**	**119**	**0**
2	morphospecies	site * morphospecies	112	5.14
3	site + morphospecies + sample round	site * morphospecies	124	5.74
4	site + morphospecies	site * morphospecies	117	10.49
5	site + sample round	site * morphospecies	109	21.05
6	site	site * morphospecies	102	25.50
7	sample round	site * morphospecies	104	47.01
8	sample round * morphospecies	site * morphospecies	224	100.55

4. DISCUSSION

The results of this study followed the expected disturbance gradient. The ground beetle abundance increased with an increasing anthropogenic disturbance while the species richness, species evenness, and the diversity decreased. The observed abundance in this study was significantly different across the sampled sites, but no significant differences in observed species richness were found. According to zero-inflated Poisson models and corresponding AIC values, the probability of not catching any ground beetles in a suitable habitat (i.e. the probability of measuring a false zero) was dependent on the combined interaction of the specific site and morphospecies in consideration. This was expected because certain Carabidae species are habitat-specific and will not occur if the habitat is not suitable (i.e. a true zero). Given that a habitat is suitable (i.e. the probability of measuring a false zero is zero), then the observed abundance appeared to be influenced by an additive effect of the sample round and the morphospecies in consideration. The different sample rounds had different amounts of rainfall, as well as some minor differences in temperature, and other, unknown, habitat characteristics may have differed in time as well. Therefore, observed trap catches were indeed expected to differ according to the moment in time when the sampling occurred. These differences were, in addition, expected to be dependent on the morphospecies in consideration. The investigation of the individual sample round, site, and morphospecies covariates did not result in a better explanation of the observed variance in ground beetle abundance. Reasons for this could either be related to the measured covariates, indicating that maybe other parameters were responsible for the observed variance, or to the sample size of this study. After all, it is important to realize that my collected data, with many zeroes and low count numbers, was not large enough to show statistically significant results in all tests. It was, however, interesting to observe trends that supported the predictions of this study, even though most of the species were represented only by few individuals. The relative low original total number of ground beetles caught in this study (n = 157 Carabidae) corresponded with the numbers caught in similar studies (Maveety et al. 2011; Nyundo & Yarro 2007). Tropical communities in general are usually more diverse, and they have a higher degree of niche-specialization and smaller species populations compared to their temperate variants (Connell 1978). A large proportion of the tropical ground beetles are canopy-dwelling (Erwin 1994), meaning that only a smal proportion of the community will be ground-dwelling and available for sampling by pitfall trapping. The majority of tropical ground beetles are also confined to specific altitudinal zones (Hodkinson 2005), with a negative correlation between species richness and altitude (Maveety et al. 2011; Wolda 1987). This results in even more localized and lower occurrences. In addition, the effectiveness of pitfall trapping is also limited by the soil composition of tropical forests. The high level of non-decomposed organic material in the upper soil layers creates numerous interstitial spaces, limiting the catchability of ground-dwelling Carabidae because they may move under the actual soil surface and avoid the pitfall traps (Maveety et al. 2011).

The adjustments that were applied to the original data in this study, in order to obtain a common sampling effort caused an increase in the observed abundances while the observed species richness did not change. However, the results for the evenness and diversity indices did almost not differ when the calculations were based on the original data or the adjusted data. It is well known that species diversity (i.e. the integration of both species richness and species evenness) decreases along an increasing disturbance gradient, with significant declines found at higher disturbance levels (Gray 1989). All, or at least a large proportion of, the established habitat specialist species disappear when the natural habitat is heavily disturbed (Gray 1989). Proportionally fewer opportunist species enter the disturbed habitat, resulting in an overall reduced species richness (Gray 1989). Also the species evenness is reduced in heavily disturbed habitats with only a few individuals representing the remaining species that are specialists to the native habitat, and many individuals representing the few opportunistic species (Gray 1989). Consistent patterns are found in this present study as well as in other studies that are comparing the diversity of Carabidae in heavily disturbed areas and (semi-)natural forests (Fahy & Gormally 1998; Magura et al. 2003; Meng et al. 2012; Moraes et al. 2013; Uehara-Prado et al. 2009). Results from different studies are not consistent, however, on the response of the overall abundance of Carabidae to severe disturbances of (semi-)natural forest habitats. This disagreement seems related to the canopy structure of the disturbed areas in question. After a native deciduous forest in the North Hungarian Mountain Range was clear-cut, Magura et al. (2003) found an increased ground beetle abundance in the clear-felled area, even though the abundance of native forest specialist species was reduced significantly. This is because the loss of forest specialist individuals is exceeded by the abundance of opportunistic and open-canopy specialist species (Gray 1989). Also, da Silva et al. (2008) found higher ground beetle abundances in the most severely disturbed study area (agricultural land) compared to the native cork-oak forest in Portugal. However, after the clear-felled area was replanted with non-native spruce, Magura et al. (2003) observed a significant decrease in the abundance of these open-canopy specialists with an increasing canopy closure. The native forest specialist species did not return, not even after 50 years, resulting in a non-native tree plantation with a lower ground beetle abundance compared to the native forest (Magura et al. 2003). Also Moraes et al. (2013) observed a lower ground beetle abundance in a pine silviculture area compared to a native subtropical rainforest in southern Brazil. Meng et al. (2012) observed a significantly higher abundance in open-canopy rice field fallows in south-west China compared to a natural tropical rainforest as well as to rubber plantations.

As already indicated above, disturbances do not only affect the species richness and abundance, but also the specific species composition (Gray 1989). With an increasing disturbance of a natural forest, the original ground beetle community will decrease in forest dependent species, and increase in opportunistic and open-canopy specialist species (Gray 1989). A corresponding pattern was seen in the present study. Two morphospecies, *Tefflus* and *Galerita*, were found to be eurytopic in this study. They were not restricted to the natural forest habitat and appeared to be tolerant to disturbances. They were the only two ground beetle morphospecies that were represented in the forest sites as well as in the agroforestry site. This indicates that the forest-dependent species in this nature reserve would disappear if the forests were transformed to agroforestry land.

Ten morphospecies in this study were exclusive to forest sites and were not represented in the agroforestry site. Six of them appeared to be significant forest-dependent species. One of these six forest dependent morphospecies, *Tachys*, was found to be characteristic for the riverine-forest. Also Poddar (1996) found a *Tachys* species (*Tachys horni*) that was significantly associated with water in India, and it is also known that European *Tachys* species are waterside species, found beside running water (Harde 2000). The riverine forest site, in this present study, was included mainly to investigate the Carabidae diversity in this specific habitat, rather than to make comparisons according to disturbance degrees. The river in this forest site provided, however, only narrow riparian zones, giving only a small brim of habitat that was distinct from the overall forest habitat surrounding it. This could explain why the ground beetle abundance and the rarefied species richness were smaller in this site compared to the other forest sites. In a study by Magagula (2003), the ground beetle abundance was found to be significantly higher in a wide riparian border compared to other habitats in a fragmented agricultural landscape in Swaziland. This is in contrast with the results of the present study, showing a significantly lower abundance of ground beetles compared to the two open-canopy sites. This could possibly also be addressed to the small size of the riparian habitat in this study, possibly supporting only small populations of specialized Carabidae.

Four other morphospecies in the present study were exclusive to the agroforestry site. Due to the low abundances, only one morphospecies could, however, be considered as being characteristic to the open-canopy area: *Harpalinae_X*. This is consistent with the habitat preferences of the granivorous members of the Harpalinae subfamily. Ground beetle species belonging to the genus *Harpalus*, for example, eat both prey and seeds, they prefer dry and sandy habitats, and are therefore mainly found in open-canopy areas (Harde 2000). The logging area in this study did not have any morphospecies exclusive to it, and shared all species with at least one forest site. Except for the two eurytopic morphospecies (*Galerita* and *Tefflus*), no species that occurred in the logging site did also occur in the agroforestry site. This could be because the clear-felling in the logging site happened only eight months before the start of this study. It may be possible that the species present were still characteristic to the pre-logging state of this area (i.e. forest that was heavily logged in the past), because certain soil characteristics may have been still similar to the pre-logging state. The results from the logging site did indeed resemble more the heavily disturbed forest site compared to the agroforestry site, even though the logging site looked more like the agroforestry site in terms of canopy openness.

Also the mean size of species is thought to decrease along the disturbance gradient (Gray 1989). Magura et al. (2002) found a significantly higher number of small sized ground beetles, and also a significantly higher number of ground beetle individuals that were capable of flying, in a 5-year old spruce plantation compared to a native deciduous forest in northern Hungary. The number of medium and large sized ground beetles was significantly higher in the original forest (Magura et al. 2002). Also Blake et al. (1994), studying grassland, moorland, and woodland habitats in the UK, concluded that a smaller average body size was found with an increasing disturbance level. Corresponding trends were found in the present study, however, the observed sizes did not differ significantly across the sampled sites. Ground beetles belonging to the two most eurytopic morphospecies, *Galerita* and *Tefflus*, were the largest individuals in this study. Morphospecies that were exclusive to the agroforestry site were all relatively small, while the logging site contained only relatively large ground beetles. This result also reflects the higher similarity in species composition of the logging site to the forest sites, rather than to the agroforestry site. All forest sites together (i.e. the undisturbed, moderately disturbed, heavily disturbed, and riverine forest sites) embraced the largest range of sizes, with relatively more large-sized Carabidae compared to smaller ones. The correlation of flight capability and habitat was not tested in this study due to a lack of information on the flight capability of the observed morphospecies. A nonsignificant, positive trend was found between the body size and total abundance of ground beetles observed in this study. This could be explained by the fact that more forest sites were sampled in comparison to open-canopy sites. However, according to Greenslade (1964), body size and activity pattern of Carabidae may be positively correlated, implying that the probability of capture may also be positively correlated with an increasing body size. On the contrary, in habitats with a dense ground vegetation, the hinder of movement may be positively correlated with the size of ground beetles, which would suggest a negative correlation between body size and capture probability (Greenslade 1964). Another possible reason for the positive trend between observed abundance and body size, could be that small beetles may escape more easily out of the traps because it is expected that they can more easily climb on scratches in the plastic pitfall cups, or on small leafs and branches that could have ended up in the traps. However, Halsall and Wratten (1988) concluded that differences in capture rates between ground beetle species in pitfall traps are unrelated to body size or speed of movement.

In this nature reserve, logging activities severely reduced the stand basal area of both the agroforestry and the logging site. A reduced stand basal area was naturally significantly correlated with an increase in canopy openness and ground vegetation cover. All three of these environmental covariates were significantly correlated with the observed ground beetle abundances in this study. With a change in canopy tree species composition and structure, not only the ground vegetation will change, but also the leaf litter structure and composition, resulting in an altered compactness and pH of the soil (Magura et al. 2002). A change in canopy cover also results in a changed amount of local insolation, and consequently in an altered local temperature and humidity (Magura et al. 2002). These changed environmental factors, in their turn, influence the spatial distribution of the ground beetles by qualifying their feeding resources and microhabitats (Guillemain et al. 1997; Magura et al. 2002). An interesting result from this present study was that all observed morphospecies belonging to the Scaritinae subfamily (i.e. *Mamboicus*, *Scaritinae_X*, and *Typhloscaris*) were significantly associated with forest habitats (including the logging site). The front legs, as well as the head and mandibles of these morphospecies have important burrowing functions (Baehr 1979). Even though it is known that Scaritinae beetles occur in a wide variety of habitats, from humid forests to dry agricultural lands (Hogan 2012), it may be possible that they prefer forest habitats in this nature reserve. After all, digging could be a bigger challenge in the more compact soil of the agroforestry site, compared to the softer forest soils in this nature reserve (including the soil of the logging site). And since they are mainly generalist predators and scavengers (Hogan 2012) that are able to crush any available arthropod prey with their large mandibles (Forsythe 1991), it seems that they are not otherwise restricted to a specific habitat for their food resources.

Also the *Galerita* morphospecies appeared to prefer the forest habitats in this study. Even though this morphospecies was represented in all sampled sites, it was significantly overrepresented in the forest sites. This is in accordance with suggestions made on the habitat preferences of *Galerita* species in other studies. These suggestions included a preference for humid soil (Dajoz 2005; Pech & Graham 2013), and hiding possibilities in case of an open canopy (Forsythe 1991). The forest soils in the Amani Nature Reserve were overall much more humid compared to the soils of the open-canopy sites. This could explain why, in this study, *Galerita* seemed to have preferences for the forest sites. Along with the humidity, also other characteristics of the forest soils (e.g. soil pH) could be more suitable for prey species, possibly providing more feeding resources for the *Galerita* morphospecies compared to the open-canopy sites. The morphology of *Galerita* species is thought to be adapted to penetrate narrow fissures in order to reach their prey (Forsythe 1991). They are moderate runners that do not chase their prey for more than a few centimeters (Forsythe 1991). Certain *Galerita* species (e.g. *Galerita bicolor* (King 1919)) deposit their eggs on the under surface of specifically chosen trees leafs, which could also be a reason for this genus' preference for forest habitats. Furthermore, it is thought that all *Galerita* species are able to fly (Forsythe 1991) and at least some species are attracted to light (Dajoz 2005; Forsythe 1991).

In contrast with *Galerita*, *Tefflus*, the other generalist species in this study, seemed to prefer the open-canopy sites instead of the forest sites. This finding corresponds with a study by (Magagula 2003) where a *Tefflus* species (*Tefflus delagorguei*) was found to be a dominant species during an investigation of the ground beetle diversity in an agricultural landscape in Swaziland. *Tefflus* species are flightless and follow the activity patterns of land snails, particularly the giant land snails of the genus *Achatina* (Raut & Barker 2002), which are their main prey (Mawdsley et al. 2011). I observed the species *Achatina fulica* in both the forest sites and the open-canopy sites. This giant land snail species is invasive in Tanzania, and has a preference for plantation crops (Raut & Barker 2002). This suggests that the main abundance of this snail species, along with the *Tefflus* morphospecies, should be in the agroforestry site. However, *Tefflus* was significantly overrepresented in the logging site, not in the agroforestry site. Apparently there were more preferred plant types for *A. fulica* (e.g. seedlings) in the logging site compared to the agroforestry site and/or other, unknown factors are causing this. The presence of the *Tefflus* morphospecies in this nature reserve could, however, be important to improve the natural control of the invasive *A. fulica*, especially in agroforestry sites.

Both the moderately and heavily disturbed forest areas in this study recovered to fully grown secondary forests after the historical logging events. Therefore, the undisturbed, the moderately disturbed, and the heavily disturbed forest sites in this study had a similar canopy structure, but a different species composition of the canopy trees according to the historical disturbance degrees (i.e. more exotic tree species with an increasing degree of historical logging). The observed differences in ground beetle abundance, species richness, species evenness and diversity in these forest sites were in correspondence with the expected patterns along a disturbance gradient (Gray 1989). This could suggest that the effects of historical disturbances are still visible in the current ground-dwelling ground beetle communities in this nature reserve. However, the results were not significantly different between these forest sites. According to Gray (1989), it is indeed expected to see significant differences only at higher levels of disturbance. Also Wolda (1987) found, during a study in Panama, that an intermediate anthropogenic disturbance has little, if any, effect on insect diversity. This was, however, if the tree species richness remained relatively high (Wolda 1987). At high disturbance levels (i.e. pastures), Wolda (1987) found significant differences in insect diversity compared to undisturbed forests.

According to (Kremen et al. 1993), information on the diversity of terrestrial arthropods is a rich data source for conservation planning and management. Arthropod indicator species, such as ground beetles (Niemelä et al. 2000), have shorter life cycles, more rapid evolutionary rates, and are therefore responding more rapidly to environmental changes compared to vertebrate indicator species (Kremen et al. 1993). Further investigations on the ecology of Carabidae in the Eastern Arc Mountains could provide valuable information for sustainable management planning in this biodiversity hotspot.

4.1. SAMPLING METHOD

Pitfall trapping is a traditional and widely used method for sampling ground beetles (Greenslade 1964; Niemelä et al. 1990). Pitfalls generally represent a simple (in terms of setting and using) and cheap method to collect ground-dwelling invertebrates (Nyundo & Yarro 2007). However, the interpretation of pitfall trap catches is not as simple or straightforward since these data rarely reflect the correct relative abundances of the different occurring species (Desender & Maelfait 1986). There are numerous factors that influence the efficiency of the method, including:

- the trap design (i.e. materials, size, and shape of the traps) (e.g. Desender and Maelfait (1986); Spence and Niemelä (1994));
- the sampling effort (i.e. number of plots, number of traps, the sampling time) (e.g. Baars (1979); Vennila and Rajagopal (1999));
- the behavioral attributes of the target organisms (e.g. Desender and Maelfait (1986); Greenslade (1964); Spence and Niemelä (1994));
- the habitat features (i.e. both climatic conditions and structural conditions) (e.g. dense ground vegetation may impede movement and reduce catches (Greenslade 1964))
- the presence of defensive secretions and sexual pheromones of other individuals (i.e. either individuals of the same species, same family, or prey species) (Luff 1986).

The trap design used in this study was as recommended in the literature. The transparent plexi lid, fixed above the opening of each trap successfully prevented most of the rain water, falling leafs, and bigger animals from entering the cups. The heavy downpours, however, inevitably still caused soil runoff, together with leaf litter, to enter the traps. The lids did not fully succeed in preventing animals from feeding on the trapped insects and on the salt water. Some traps were damaged by rodents, probably giant pouched rats (*Cricetomys gambianus*), during the study. It remains unclear why the rats could be attracted to the traps. Each trap was filled with 100 ml saturated salt solution as a preservative liquid, and some drops of detergent to minimize the surface tension. Possible ways in which the trap design of this study could be improved are:

- The use of larger pitfall cups. The pitfall traps for this survey consisted of 200 ml plastic cups (7 cm x 9.5 cm). According to Mawdsley et al. (2011), smaller diameter pitfall traps (less than 10 cm diameter) could be less effective at trapping larger ground beetles such as adults of the *Tefflus* genus. Larger pitfall cups also can resist more rainfall, and soil and leaf litter runoff. In this way flooding of the traps will occur less often and the traps will have to be serviced less often, causing less disturbance to the sampled habitats.

- The use of an outer PVC pipe in which the pitfall cups are put. If PVC tubes are put in the ground, where the actual pitfall traps are supposed to come, and remain there for the entire duration of the study, the pitfall traps can be taken out and put back much more easily. In this way the traps will be placed in the exact same position after every service, and the disturbance of the sampling environment will be minimized.

In order to obtain a more complete sampling of the overall ground beetle diversity in this area, the sampling effort should be increased. The use of several plots within one site increased the overall sample size of each site in this study, and reduced the influence of local microhabitat variation between the sites. By increasing the number of plots, naturally the microhabitat parameters would vary between the plots and thus give a better overall representation of the habitat. The plots were chosen to be at least 100 m apart in air distance and to be at a distance of minimum 50 m in air distance from habitat edges. Even though this would not rule out pseudoreplication, it would still increase small scale local habitat parameter variation and thus increase the validity of the data. In order to increase the sampling effort, more sites could be sampled, and more independent replicas per site could be chosen. The sampling sites in this present study were surveyed during eight weeks from 27/09/2013 to 20/11/2013, a period which should have covered the end of the drier season and part of the October – December rainy season. However precipitation varied widely during this period without a clear pattern. Although climate is an unpredictable variable that is beyond our power to control, an increased sampling period could improve the chances of obtaining more clear seasonal patterns. Concerning the environmental covariates, more specialized equipment should be used in order to improve the accuracy of the measurements. The replacement, in the zero-inflated Poisson model, of the main covariates (i.e. site, sampling round, and morphospecies) by more specific covariates did not provide a better explanation for the observed variation in abundance and species richness in this study. Regardless the low power of the dataset, this could be because other covariates, which were not measured in this study, may have been responsible for this variation. Therefore, in addition to the environmental covariates I estimated in this study, the soil pH and soil moisture percentage could also be interesting to include. The accuracy of the morphospecies-specific covariate in this study could be improved by measuring the mean body size of the sampled morphospecies in real life instead of measurements based on pictures. Also the presence of wings could be an interesting covariate to take into account.

Originally a seventh site was sampled during this study: the settlement area where the head-quarters of the Amani Nature Reserve Conservation Centre was located. However, only eighteen traps (i.e. $1^{1/2}$ plots) could be put out in this site due to restrictions in available surface. Additionally, many traps were ‘destroyed’ by excessive soil runoff caused by the frequent downpours. At the end of this study, only one ground beetle morphospecies (*Orthotrichus* sp.) was caught in this site, while more morphospecies were visually observed. Adjusting this result for a common sampling effort would give an even worse representation of the ground beetle morphospecies composition in this habitat. For this reason, I decided to exclude this site.

It is important to know that pitfalls sample only the ground-dwelling part of the Carabidae community (Greenslade 1964). In order to obtain a more complete overview of the overall ground beetle diversity, methods such as hand searches, light trapping, and soil sampling should be used in addition to pitfall trapping (Maveety et al. 2011; Nyundo & Yarro 2007). In a study by Nyundo and Yarro (2007) in a tropical montane forest in the Udzungwa Mountains (which also constitute one of the thirteen mountain blocks of the Eastern Arc Mountains), a significantly higher ground beetle abundance and species richness resulted from hand searching on the ground compared to pitfall trapping. However, the pitfalls trapped several species that were not found during hand searches (Nyundo & Yarro 2007). Therefore, and because of its simplicity and cheapness, Nyundo and Yarro (2007) concluded that pitfall trapping should not be left out of ground beetle sampling protocols. Also in my study, more species and specimens could most likely have been collected if I had used a combination of active searching, light trapping, and baited traps, in addition to pitfall trapping. However, I think the passive pitfall traps may represent each habitat better because accidental occurrences are less likely. In my opinion, this could also be the reason why my results showed significant differences in ground beetle abundances in certain different habitats, even with the relatively small total number of specimens I caught.

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APPENDIX 1

Appendix 1. GPS-coordinates of each plot.

Site Name	**Plot**	**GPS Coordinates**	
		S	**E**
Amani Primary Forest	AP1	05°05.604’	038°37.845’
	AP2	05°05.602’	038°37.960’
	AP3	05°05.674’	038°37.959’
Kwamkoro Moderately Disturbed Forest	KM1	05°09.372’	038°36.030’
	KM2	05°09.466’	038°35.968’
	KM3	05°09.298’	038°36.076’
Mbomole Heavily Disturbed Forest	MHD1	05°05.981’	038°37.743’
	MHD2	05°06.089’	038°37.446’
	MHD3	05°05.904’	038°37.424’
Kwamkoro Riverine Forest	KR1	05°09.418’	038°36.161’
	KR2	05°09.472’	038°36.130’
	KR3	05°09.326’	038°36.192’
Mbomole Logging Area	ML1	05°06.184’	038°37.525’
	ML2	05°06.208’	038°37.509’
Mbomole Agroforestry Area	MA1	05°06.286’	038°37.471’
	MA2	05°06.239’	038°37.509’

APPENDIX 2

Appendix 2. Overview of the sampling period. The first traps were filled on 27/09/13, and the first collection took place 3 days later, on 30/09/13. The collections in the undisturbed forest site started one sample round later.

Round	Date	Site	Round	Date	Site
1	30/09/13	Moderately disturbed forest	**5**	25/10/13	Moderately disturbed forest
1	30/09/13	Riverine forest	**5**	25/10/13	Riverine forest
1	01/10/13	Heavily disturbed forest	**5**	26/10/13	Heavily disturbed forest
1	01/10/13	Logging area	**5**	26/10/13	Logging area
1	01/10/13	Agroforestry area	**5**	26/10/13	Agroforestry area
1	---	Undisturbed forest	**5**	27/10/13	Undisturbed forest
2	05/10/13	Moderately disturbed forest	**6**	30/10/13	Moderately disturbed forest
2	05/10/13	Riverine forest	**6**	30/10/13	Riverine forest
2	06/10/13	Heavily disturbed forest	**6**	31/10/13	Heavily disturbed forest
2	06/10/13	Logging area	**6**	31/10/13	Logging area
2	06/10/13	Agroforestry area	**6**	31/10/13	Agroforestry area
2	07/10/13	Undisturbed forest	**6**	01/11/13	Undisturbed forest
3	10/10/13	Moderately disturbed forest	**7**	09/11/13	Moderately disturbed forest
3	10/10/13	Riverine forest	**7**	09/11/13	Riverine forest
3	11/10/13	Heavily disturbed forest	**7**	11/11/13	Agroforestry area
3	11/10/13	Logging area	**7**	11/11/13	Undisturbed forest
3	11/10/13	Agroforestry area	**7**	12/11/13	Heavily disturbed forest
3	12/10/13	Undisturbed forest	**7**	12/11/13	Logging area
4	15/10/13	Moderately disturbed forest	**8**	18/11/13	Moderately disturbed forest
4	15/10/13	Riverine forest	**8**	18/11/13	Riverine forest
4	16/10/13	Heavily disturbed forest	**8**	19/11/13	Heavily disturbed forest
4	16/10/13	Logging area	**8**	19/11/13	Logging area
4	16/10/13	Agroforestry area	**8**	19/11/13	Agroforestry area
4	17/10/13	Undisturbed forest	**8**	20/11/13	Undisturbed forest

APPENDIX 3

Appendix 3. Original number of observed Carabidae per morphospecies (presented by their genus name) per plot. All forest sites contained three plots each. The agroforestry area and the logging area contained two plots each. A total of 157 Carabidae was caught during this study. The observed total ground beetle abundance per plot and per site are also given, as well as the observed total species richness per site, and the total number of Carabidae caught per morphospecies.

	Undisturbed forest			Moderately disturbed forest			Heavily disturbed forest			Riverine forest			Logging area		Agroforestry area		
Morphospecies / Plot	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**1**	**2**	**Total**
Anaulacus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	**3**
Apristus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	**1**
Crepidogaster	0	0	0	1	0	0	1	1	1	0	0	0	2	0	0	0	**6**
Disphaericus	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	**3**
Dyschiridium	0	0	1	0	8	2	0	5	2	0	0	0	4	6	0	0	**28**
Galerita	2	2	1	1	1	0	0	3	7	0	0	3	0	1	1	1	**23**
Harpalinae_X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	15	**27**
Mamboicus	0	1	3	1	0	1	0	0	1	0	0	0	0	0	0	0	**7**
Pentagonica	1	1	0	0	0	0	0	0	4	0	0	1	0	0	0	0	**7**
Scaritinae_X	1	0	3	0	0	0	0	1	1	0	0	0	0	0	0	0	**6**
Tachys	0	0	0	0	0	0	0	0	0	0	2	3	0	0	0	0	**5**
Tefflus	0	0	1	0	0	0	1	1	0	0	0	1	3	4	2	0	**13**
Typhloscaris	0	1	1	0	0	0	0	0	0	0	0	0	1	3	0	0	**6**
Unknown_A	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	**3**
Unknown_B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	**2**
Unknown_C	2	0	0	0	1	0	1	1	12	0	0	0	0	0	0	0	**17**
Total plot abundance	**6**	**5**	**10**	**4**	**10**	**4**	**3**	**13**	**28**	**0**	**2**	**9**	**12**	**14**	**19**	**18**	**157**
Total site abundance		**21**			**18**			**44**			**11**		**26**		**37**		
Species richness		**8**			**7**			**9**			**5**		**7**		6		

APPENDIX 4

Appendix 4. Adjusted number of observed Carabidae per morphospecies (presented by their genus name) per plot. All forest sites contained three plots each. The agroforestry area and the logging area contained two plots each. An adjusted total of 192.26 Carabidae was caught in this study. The observed total ground beetle abundance per plot and per site are also given, as well as the observed total species richness per site, and the total number of Carabidae caught per morphospecies.

	Undisturbed forest			Moderately disturbed forest			Heavily disturbed forest			Riverine forest			Logging area		Agroforestry area		
Morphospecies ⁄ Plot	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**1**	**2**	**Total**
Anaulacus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.50	3.00	**4.50**
Apristus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.50	0	**1.50**
Crepidogaster	0	0	0	1.00	0	0	1.00	1.00	1.00	0	0	0	3.00	0	0	0	**7.00**
Disphaericus	0	0	0	1.00	0	0	0	0	0	0	0	1.00	1.50	0	0	0	**3.50**
Dyschiridium	0	0	1.06	0	8.00	2.00	0	5.00	2.00	0	0	0	6.00	9.00	0	0	**33.06**
Galerita	2.12	2.12	1.06	1.00	1.00	0	0	3.00	7.00	0	0	4.00	0	1.50	1.50	1.50	**25.80**
Harpalinae_X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18.00	22.50	**40.50**
Mamboicus	0	1.06	3.18	1.00	0	1.00	0	0	1.00	0	0	0	0	0	0	0	**7.24**
Pentagonica	1.06	1.06	0	0	0	0	0	0	4.00	0	0	1.00	0	0	0	0	**7.12**
Scaritinae_X	1.06	0	3.18	0	0	0	0	1.00	1.00	0	0	0	0	0	0	0	**6.24**
Tachys	0	0	0	0	0	0	0	0	0	0	3.00	3.50	0	0	0	0	**6.50**
Tefflus	0	0	1.06	0	0	0	1.00	1.00	0	0	0	1.00	4.50	6.00	3.00	0	**17.56**
Typhloscaris	0	1.06	1.06	0	0	0	0	0	0	0	0	0	1.50	4.50	0	0	**8.12**
Unknown_A	0	0	0	0	0	1.00	0	1.00	0	0	0	0	1.50	0	0	0	**3.50**
Unknown_B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	**3.00**
Unknown_C	2.12	0	0	0	1.00	0	1.00	1.00	12.00	0	0	0	0	0	0	0	**17.12**
Total plot abundance	**6.36**	**5.30**	**10.60**	**4.00**	**10.00**	**4.00**	**3.00**	**13.00**	**28.00**	**0**	**3.00**	**10.50**	**18.00**	**21.00**	**28.50**	**27.00**	**192.26**
Total site abundance	**22.26**			**18.00**			**44.00**			**13.50**			**26**		**55.50**		
Species richness	**8**			**7**			**9**			**5**			**7**		**6**		

APPENDIX 5

Appendix 5. Overview of the number of destroyed traps per sample round in the riverine forest site (KR). Rodents (probably giant pouched rats) destroyed almost all traps in the first riverine forest plot during the sample rounds seven and eight. The total number of caught Carabidae per plot is also given.

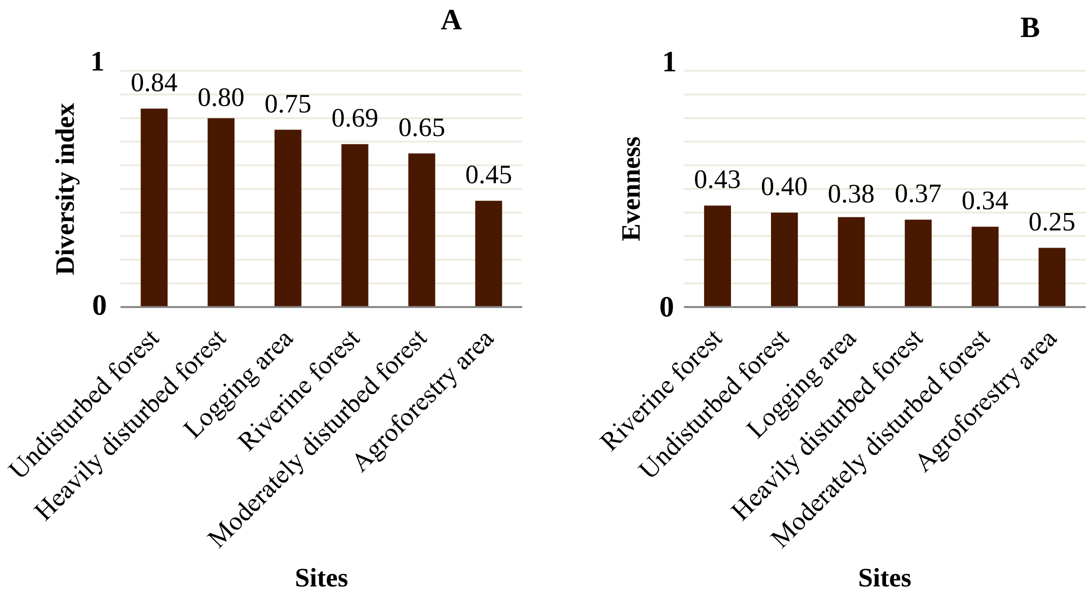
Sample round	Date	Plot	No. of Carabidae	No. of destroyed traps	Remarks
1_	30/09/2013	1_KR1	0	0	-
1_	30/09/2013	1_KR2	0	0	-
1_	30/09/2013	1_KR3	1	0	-
2_	5/10/2013	2_KR1	0	0	-
2_	5/10/2013	2_KR2	0	0	-
2_	5/10/2013	2_KR3	0	0	-
3_	10/10/2013	3_KR1	0	0	-
3_	10/10/2013	3_KR2	0	0	-
3_	10/10/2013	3_KR3	1	0	-
4_	15/10/2013	4_KR1	0	3	Destroyed by giant pouched rat
4_	15/10/2013	4_KR2	0	0	-
4_	15/10/2013	4_KR3	0	0	-
5_	25/10/2013	5_KR1	0	4	Destroyed by giant pouched rat
5_	25/10/2013	5_KR2	0	0	-
5_	25/10/2013	5_KR3	1	0	-
6_	30/10/2013	6_KR1	0	2	Filled with soil and leafs
6_	30/10/2013	6_KR2	1	0	-
6_	30/10/2013	6_KR3	3	0	-
7_	9/11/2013	7_KR1	0	11	Destroyed by giant pouched rat
7_	9/11/2013	7_KR2	1	1	Filled with soil and leafs
7_	9/11/2013	7_KR3	1	0	-
8_	18/11/2013	8_KR1	0	9	Destroyed by giant pouched rat
8_	18/11/2013	8_KR2	1	0	-
8_	18/11/2013	8_KR3	2	0	-

APPENDIX 6

Appendix 6. Output of the chi-squared test. The observed and expected counts of the different morphospecies (presented by their genus name) are given for each site, together with the corresponding chi-squared value (X^2), the degrees of freedom (df), and the p-value. Significant numbers are marked in red. The overall p-value of this chi-squared test is $< 2.2E^{-16}$, the overall X^2-value = 401.6671, and the overall degrees of freedom = 75.

Morphospecies	Undisturbed forest		Moderately disturbed forest		Heavily disturbed forest		Riverine forest		Logging area		Agroforestry area		X^2	df	p-value
	Obs	**Exp**	**Obs**	**Exp**	**Obs**	**Exp**	**Obs**	**Exp**	**Obs**	**Exp**	**Obs**	**Exp**			
Anaulacus	0.00	0.52	0.00	0.42	0.00	1.03	0.00	0.32	0.00	0.91	4.50	1.30	**11.09**	**15**	**0.050**
Apristus	0.00	0.17	0.00	0.14	0.00	0.34	0.00	0.11	0.00	0.30	1.50	0.43	**3.70**	**15**	**0.594**
Crepidogaster	0.00	0.81	1.00	0.66	3.00	1.60	0.00	0.49	3.00	1.42	0.00	2.02	**6.48**	**15**	**0.262**
Disphaericus	0.00	0.41	1.00	0.33	0.00	0.80	1.00	0.25	1.50	0.71	0.00	1.01	**6.79**	**15**	**0.237**
Dyschiridium	1.06	3.83	10.00	3.10	7.00	7.57	0.00	2.32	15.00	6.71	0.00	9.54	**39.57**	**15**	**$1.824E^{-07}$**
Galerita	5.30	2.99	2.00	2.42	10.00	5.90	4.00	1.81	1.50	5.23	3.00	7.45	**12.67**	**15**	**0.027**
Harpalinae_X	0.00	4.69	0.00	3.79	0.00	9.27	0.00	2.84	0.00	8.22	40.50	11.69	**99.80**	**15**	**$5.830E^{-20}$**
Mamboicus	4.24	0.84	2.00	0.68	1.00	1.66	0.00	0.51	0.00	1.47	0.00	2.09	**20.71**	**15**	**$9.184E^{-04}$**
Pentagonica	2.12	0.82	0.00	0.67	4.00	1.63	1.00	0.50	0.00	1.44	0.00	2.06	**10.15**	**15**	**0.071**
Scaritinae_X	4.24	0.72	0.00	0.58	2.00	1.43	0.00	0.44	0.00	1.27	0.00	1.80	**21.44**	**15**	**$6.675E^{-04}$**
Tachys	0.00	0.75	0.00	0.61	0.00	1.49	6.50	0.46	0.00	1.32	0.00	1.88	**86.07**	**15**	**$4.491E^{-17}$**
Tefflus	1.06	2.03	0.00	1.64	2.00	4.02	1.00	1.23	10.50	3.56	3.00	5.07	**17.53**	**15**	**0.004**
Typhloscaris	2.12	0.94	0.00	0.76	0.00	1.86	0.00	0.57	6.00	1.65	0.00	2.34	**18.52**	**15**	**0.002**
Unknown_A	0.00	0.41	1.00	0.33	1.00	0.80	0.00	0.25	1.50	0.71	0.00	1.01	**3.97**	**15**	**0.554**
Unknown_B	0.00	0.35	0.00	0.28	0.00	0.69	0.00	0.21	0.00	0.61	3.00	0.87	**7.39**	**15**	**0.193**
Unknown_C	2.12	1.98	1.00	1.60	14.00	3.92	0.00	1.20	0.00	3.47	0.00	4.94	**35.8**	**15**	**$1.043E^{-06}$**
X^2	**46.82**		**30.12**		**50.52**		**94.78**		**60.46**		**118.96**				
df	**5**		**5**		**5**		**5**		**5**		**5**				
p-value	**$3.935E^{-05}$**		**0.012**		**$9.887E^{-06}$**		**$1.261E^{-13}$**		**$2.098E^{-07}$**		**$3.012E^{-18}$**				

APPENDIX 7



Appendix 7. A) The Simpson diversity index per site, calculated based on the original results. **B)** Species evenness per site, calculated based on the original results.

APPENDIX 8

Appendix 8. Estimates of the plot specific environmental variables: the percentage of canopy openness above the plot, the stand basal area (SBA), the percentage of bare soil in the plot, the percentage of leaf litter and small branches covering the plot surface, the percentage of ground vegetation covering the plot surface, the percentage of rocks covering the plot surface, the soil texture, and the soil color.

Site	Plot	Canopy openness (%)	SBA (m^2/ha)	Bare soil (%)	Leaf litter (%)	Ground vegetation (%)	Rocks (%)	Soil texture	Soil color
Undisturbed forest	**1**	10-30	42	<10	>80	30-50	0	sandy loam	dark brown
Undisturbed forest	**2**	10-30	50	10-30	50-80	10-30	0	sandy loam	grey brown
Undisturbed forest	**3**	<10	36	10-30	50-80	30-50	0	sandy loam	red brown
Moderately disturbed forest	**1**	<10	38	<10	>80	10-30	0	sandy loam	red brown
Moderately disturbed forest	**2**	10-30	56	<10	>80	30-50	0	sandy loam	brown
Moderately disturbed forest	**3**	30-50	56	<10	>80	30-50	0	sandy loam	red brown
Heavily disturbed forest	**1**	10-30	44	10-30	50-80	30-50	0	sandy loam	brown
Heavily disturbed forest	**2**	<10	84	10-30	50-80	30-50	0	sandy loam	brown
Heavily disturbed forest	**3**	30-50	74	<10	>80	50-80	0	sandy loam	red brown
Riverine forest	**1**	10-30	58	10-30	50-80	30-50	0	loamy	grey brown
Riverine forest	**2**	30-50	40	<10	>80	30-50	<10	clay	grey brown
Riverine forest	**3**	10-30	36	50-80	30-50	30-50	<10	sandy clay	grey brown
Logging area	**1**	50-80	26	<10	>80	50-80	0	sandy loam	brown
Logging area	**2**	>80	14	<10	>80	50-80	0	sandy loam	brown
Agroforestry area	**1**	>80	18	<10	>80	>80	0	sandy loam	brown
Agroforestry area	**2**	>80	26	<10	50-80	>80	0	sandy loam	brown

APPENDIX 9

Collected morphospecies

Photo: dry-mounted Carabidae: *Tefflus* sp. (left) and *Galerita* sp. (right)
Photo taken by author (January 2014)

Crepidogaster BOHEMAN, 1848

FAMILY CARABIDAE

Subfamily	Brachininae BONELLI, 1810
Tribe	Crepidogastrini JEANNEL, 1949
Subtribe	-
Synonyms	-

Morphospecies information

Size (incl. mandibles)	9.5 mm
Observed altitude	950 - 1061 m above sea level
Original observed abundance per habitat	Moderately disturbed forest (n = 1) Heavily disturbed forest (n = 3) Logging area (n = 2)

Ecology of the genus

Species belonging to this genus tend to hide in both open- and closed-canopy areas and remain inactive during daytime (Deuve 2005; Eisner et al. 2001). At least a few species lack hind wings (Eisner et al. 2001). The morphospecies in this study seemed to prefer a forest habitat (including the logging site).

Galerita FABRICIUS, 1801

FAMILY CARABIDAE

Subfamily	Dryptinae BONELLI, 1810
Tribe	Galeritini LECONTE, 1853
Subtribe	Galeritina LACONTE, 1853
Synonyms	-

Morphospecies information

Size (incl. mandibles)	29 mm
Observed altitude	933 – 1061 m above sea level
Original observed abundance per habitat	Undisturbed forest (n = 5) Moderately disturbed forest (n = 2) Heavily disturbed forest (n = 10) Logging area (n = 1) Agroforestry area (n = 2) Riverine forest (n = 3)

Ecology of the genus

Galerita was found to be an eurytopic morphospecies in this study. This morphospecies was not restricted to the natural forest habitat and appeared to be tolerant to disturbances. Habitat preferences of *Galerita* species are suggested to be humid soil (Dajoz 2005; Pech & Graham 2013), and areas with hiding possibilities in case of an open canopy (Forsythe 1991). The forest soils in the Amani Nature Reserve were overall much more humid compared to the soils of the open-canopy sites. This could explain why, in this study, *Galerita* was significantly overrepresented in the forest habitats, even though it was represented in all six sites. It could also be possible that the forest sites contained more suitable prey for the *Galerita* morphospecies compared to the open-canopy sites. *Galerita* species are relatively large moderate runners that do not chase their prey for more than a few centimeters (Forsythe 1991). The narrow, shallow prothorax, the somewhat flattened head, and the relatively long constricted neck suggests that their morphology is adapted to penetrate narrow fissures in order to reach their prey (Forsythe 1991). Certain *Galerita* species (e.g. *Galerita bicolor* (King 1919)) deposit their eggs on the under surface of specifically chosen trees, which could also be a reason for this genus' preference for forest habitats. It is thought that all *Galerita* species are able to fly (Forsythe 1991) and at least some species are attracted to light (Dajoz 2005; Forsythe 1991).

Harpalinae_X BONELLI, 1810

FAMILY CARABIDAE

Subfamily	Harpalinae BONELLI, 1810
Tribe	Unknown
Subtribe	Unknown
Genus	Unknown

Morphospecies information

Size (incl. mandibles)	8.5 mm
Observed altitude	956 – 994 m above sea level
Original observed abundance per habitat	Agroforestry area (n = 27)

Ecology of the subfamily

The morphospecies that belonged to this subfamily (*Harpalinae_X*) was found to be a stenotopic species in this study. It was significantly abundant in the agroforestry site, and was not represented in any other site. This is consistent with the habitat preferences of the granivorous members of the Harpalinae subfamily. Ground beetle species belonging to the genus *Harpalus*, for example, eat both prey and seeds, they prefer dry and sandy habitats, and are therefore mainly found in open-canopy areas (Harde 2000). I could, however, not identify the genus of this morphospecies, which makes it hard to justify the results of this study based on literature. After all, the subfamily Harpalinae is the largest group of Carabidae, including about 19 000 species, expressing diverse lifestyles (Ober 2002).

Anaulacus MCLEAY, 1825

FAMILY CARABIDAE

Subfamily	Lebiinae BONELLI, 1810
Tribe	Cyclosomini LAPORTE , 1834
Subtribe	Masoreina CHAUDOIR, 1870
Synonyms	*Aephnidius* W.S. MACLEAY, 1825 *Macracanthus* CHAUDOIR, 1846

Morphospecies information

Size (incl. mandibles)	7.5 mm
Observed altitude	956 - 994 m above sea level
Original observed abundance per habitat	Agroforestry area (n = 3)

Ecology of the genus

The main habitat preference of Neotropical *Anaulacus* species is suggested to be tropical evergreen forest (Ball & Shpeley 2002). However, some also live in semi-tropical forests, in dry open-canopy areas, and in anthropogenic disturbed habitats such as mango plantations (Ball & Shpeley 2002). In this study, morphospecies belonging to this genus were only represented in the agroforestry site.

Apristus CHAUDOIR, 1846

FAMILY CARABIDAE

Subfamily	Lebiinae BONELLI, 1810
Tribe	Lebiini BONELLI, 1810
Subtribe	Lionychina JEANNEL, 1948
Synonyms	-

Morphospecies information

Size (incl. mandibles)	4 mm
Observed altitude	956 m above sea level
Original observed abundance per habitat	Agroforestry area (n = 1)

Ecology of the genus

Torres and Ruberson (2007) found an *Apristus* species (*Apristus latens*) in agricultural fields (cotton fields) in southern Georgia (USA), this species was a predominantly seed feeder. The only individual that was found in this study, belonging to this genus, was found in a similar open-canopy site, the agroforestry site.

Pentagonica SCHMIDT-GOBEL, 1846

FAMILY CARABIDAE

Subfamily	Lebiinae BONELLI, 1810
Tribe	Pentagonicini BATES, 1873
Subtribe	-
Synonyms	*Didetus* LECONTE, 1853 *Elliotia* NIETNER, 1856 *Rhombodera* REICHE, 1842 *Trichothorax* MONTROUZIER, 1860 *Wakefieldia* BRAUN, 1880 *Xenothorax* WOLLASTON, 1867

Morphospecies information

Size (incl. mandibles)	5 mm
Observed altitude	933 – 1061 m above sea level
Original observed abundance per habitat	Undisturbed forest (n = 2) Heavily disturbed forest (n = 4) Riverine forest (n = 1)

Ecology of the genus

Pentagonica flavipes individuals were collected on grasses at a saline lagoon in Mexico (Purrington et al. 1999). Also the morphospecies in this study seemed to prefer humid habitats. The *Pentagonica flavipes* individuals were collected by lighttrapping (Purrington et al. 1999), which could imply that at least this species may be night-active.

Tefflus LEACH, 1819

FAMILY CARABIDAE

Subfamily	Panagaeinae Bonelli, 1810
Tribe	Panagaeini BONELLI, 1810
Subtribe	-
Synonyms	*Archotefflus* KOLBE, 1903 *Mesotefflus* KOLBE, 1903 *Stictotefflus* KOLBE, 1903 *Heterotefflus* KOLBE, 1904 *Alexotefflus* BASILEWSKY, 1935

Morphospecies information

Size (incl. mandibles)	34 mm
Observed altitude	936 – 1043 m above sea level
Original observed abundance per habitat	Undisturbed forest (n = 1) Heavily disturbed forest (n = 2) Logging area (n = 7) Agroforestry area (n = 2) Riverine forest (n = 1)

Ecology of the genus

Tefflus was found to be an eurytopic morphospecies in this study. This morphospecies was not restricted to the natural forest habitat and appeared to be tolerant to disturbances. *Tefflus* species are flightless and follow the activity patterns of land snails, particularly the giant land snails of the genus *Achatina* (Raut & Barker 2002), which are their main prey (Mawdsley et al. 2011). I observed the *Achatina fulica* in both the forest sites and the open-canopy sites. This giant land snail species is invasive in Tanzania, and has a preference for plantation crops (Raut & Barker 2002). This suggests that the main abundance of this snail species, along with the *Tefflus* morphospecies, should be present in the agroforestry site. However, *Tefflus* was significantly overrepresented in the logging site, not in the agroforestry site. Apparently there were more preferred plant types (e.g. seedlings) in the logging site compared to the agroforestry site and/or other, unknown factors are causing this. The presence of the *Tefflus* morphospecies in the nature reserve could, however, be important to maximize the natural control of the invasive *Achatina fulica*, especially in agroforestry sites.

Disphaericus WATERHOUSE, 1841

FAMILY CARABIDAE

Subfamily	Panagaeinae BONELLI, 1810
Tribe	Peleciini CHAUDOIR, 1880
Subtribe	Peleciina sensu stricto
Synonyms	*Disphaericus* AGASSIZ, 1847 *Dispherícus* BASILEWSKY, 1953

Morphospecies information

Size (incl. mandibles)	14 mm
Observed altitude	964 – 1061 m above sea level
Original observed abundance per habitat	Moderately disturbed forest (n = 1) Logging area (n = 1) Riverine forest (n = 1)

Ecology of the genus

This genus is confined to, but varies widely within, the Afrotropical Region (Straneo & Ball 1989). These beetles are flightless and carnivorous, their main prey being millipedes (Straneo & Ball 1989). All species belonging to the tribe Peleciini are specialized millipedes predators (Straneo & Ball 1989). These ground beetles are able to run on the smooth dorsal surface of the millipedes thanks to adapted tarsomeres with adhesive setae (Straneo & Ball 1989). Also their mounthparts are adapted to predate on millipedes (Straneo & Ball 1989). Millipedes are known to prefer humid habitats, which is probably the reason why the *Disphaericus* morphospecies in this study were only found in forest sites (including the logging site).

Dyschiridium CHAUDOIR, 1861

FAMILY CARABIDAE

Subfamily	Panagaeinae BONELLI, 1810
Tribe	Peleciini CHAUDOIR, 1880
Subtribe	Peleciina sensu stricto
Synonyms	*Spanus* WESTWOOD, 1864

Morphospecies information

Size (incl. mandibles)	10 mm
Observed altitude	936 – 1061 m above sea level
Original observed abundance per habitat	Undisturbed forest (n = 1) Moderately disturbed forest (n = 10) Heavily disturbed forest (n = 7) Logging area (n = 10)

Ecology of the genus

This genus is only known from southern and eastern Africa in the Afrotropical Region (Straneo & Ball 1989). These beetles are flightless and carnivorous, their main prey being millipedes (Straneo & Ball 1989). All species belonging to the tribe Peleciini are specialized millipedes predators (Straneo & Ball 1989). These ground beetles are able to run on the smooth dorsal surface of the millipedes thanks to adapted tarsomeres with adhesive setae (Straneo & Ball 1989). Also their mounthparts are adapted to predate on millipedes (Straneo & Ball 1989). Millipedes are known to prefer humid habitats, which is probably the reason why the *Dyschiridium* morphospecies in this study were only found in forest sites (including the logging area).

Mamboicus BATES, 1886

FAMILY CARABIDAE

Subfamily	Scaritinae BONELLI, 1810
Tribe	Scaritini BONELLI, 1810
Subtribe	Scaritina BONEILI, 1810
Synonyms	*Chondressus* BATES, 1886 *Macrotelus* PERINGUEY, 1896

Morphospecies information

Size (incl. mandibles)	25 mm
Observed altitude	933 – 1061 m above sea level
Original observed abundance per habitat	Undisturbed forest (n = 4) Moderately disturbed forest (n = 2) Heavily disturbed forest (n = 1)

Ecology of the genus

Like all members of the subfamily Scaritinae, this morphospecies had a distinctive body shape that is adapted for burrowing (Hogan 2012). Not only the front legs, but also the head and mandibles have important burrowing functions (Baehr 1979). Scaritinae beetles are mainly generalist nocturnal predators and scavengers (Hogan 2012). Their large mandibles are adapted for crushing any available arthropod prey (Forsythe 1991). They occur in a wide variety of habitats, from humid forests to dry agricultural lands (Hogan 2012). Like the two other morphospecies in this study that belonged to the Scaritinae subfamily, this morphospecies was only represented in forest sites. This could imply that this morphospecies prefers the more humid forest soil above the dry agroforestry soil. Maybe because the forest soil is found to be more suitable for burrowing, or because more preferred prey is available. Species belonging to the tribe Scaritini (body size 8-70mm) are often flightless (Hogan 2012).

Typhloscaris KUNTZEN, 1914

FAMILY CARABIDAE

Subfamily	Scaritinae BONELLI, 1810
Tribe	Scaritini BONELLI, 1810
Subtribe	Scaritina BONELLI, 1810
Synonyms	-

Morphospecies information

Size (incl. mandibles)	17 mm
Observed altitude	933 – 994 m above sea level
Original observed abundance per habitat	Undisturbed forest (n = 2) Logging area (n = 4)

Ecology of the genus

Like all members of the subfamily Scaritinae, this morphospecies had a distinctive body shape that is adapted for burrowing (Hogan 2012). Not only the front legs, but also the head and mandibles have important burrowing functions (Baehr 1979). Scaritinae beetles are mainly generalist nocturnal predators and scavengers (Hogan 2012). Their large mandibles are adapted for crushing any available arthropod prey (Forsythe 1991). They occur in a wide variety of habitats, from humid forests to dry agricultural lands (Hogan 2012). Like the two other morphospecies in this study that belonged to the Scaritinae subfamily, this morphospecies was only represented in forest sites (including the logging site). This could imply that this morphospecies prefers the more humid forest soil above the dry agroforestry soil. Maybe because the forest soil is found to be more suitable for burrowing, or because more preferred prey is available. Species belonging to the tribe Scaritini (body size 8-70mm) are often flightless (Hogan 2012).

Scaritinae **BONELLI, 1810**

FAMILY CARABIDAE

Subfamily	Scaritinae BONELLI, 1810
Tribe	Unknown
Subtribe	Unknown
Genus	Unknown

Morphospecies information

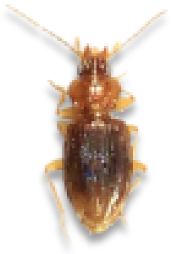
Size (incl. mandibles)	2.5 mm
Observed altitude	934 – 1061 m above sea level
Original observed abundance per habitat	Undisturbed forest (n = 4) Heavily disturbed forest (n = 2)

Ecology of the genus

Like all members of the subfamily Scaritinae, this morphospecies had a distinctive body shape that is adapted for burrowing (Hogan 2012). Not only the front legs, but also the head and mandibles have important burrowing functions (Baehr 1979). Scaritinae beetles are mainly generalist nocturnal predators and scavengers (Hogan 2012). Their large mandibles are adapted for crushing any available arthropod prey (Forsythe 1991). They occur in a wide variety of habitats, from humid forests to dry agricultural lands (Hogan 2012). Like the two other morphospecies in this study that belonged to the Scaritinae subfamily, this morphospecies was only represented in forest sites. This could imply that this morphospecies prefers the more humid forest soil above the dry agroforestry soil. Maybe because the forest soil is found to be more suitable for burrowing, or because more preferred prey is available. The subfamily Scaritinae is devided in four tribes. The tribe Scaritini contains larger beetles (8 – 70 mm) that are often flightless (Hogan 2012). The other three tribes contain smaller beetles (1.5 – 30 mm) which usually have fully functional wings (Hogan 2012).

Tachys DEJEAN, 1821

FAMILY CARABIDAE



Subfamily	Trechinae BONELLI, 1810
Tribe	Bembidiini STEPHENS, 1827
Subtribe	Tachyina MOTSCHULSKY, 1862
Synonyms	-

Morphospecies information

Size (incl. mandibles)	3 mm
Observed altitude	880 – 964 m above sea level
Original observed abundance per habitat	Riverine forest (n = 5)

Ecology of the genus

European *Tachys* species are waterside species, found beside running water (Harde 2000). The species *Tachys horni* is an intertidal species in India that predates on staphylinid beetles (Poddar 1996). Also in this study the *Tachys* morphospecies was significantly associated to water.

Unknown_A

FAMILY CARABIDAE

Subfamily	Unknown
Tribe	Unknown
Subtribe	Unknown
Genus	Unknown

Morphospecies information

Size (incl. mandibles)	8 mm
Observed altitude	964 – 1043 m above sea level
Original observed abundance per habitat	Moderately disturbed forest (n = 1) Heavily disturbed forest (n = 1) Logging area (n = 1)

Ecology of the genus

This morphospecies seemed to prefer a forest habitat in this study, including the logging site.

Unknown_B

FAMILY CARABIDAE

Subfamily	Unknown
Tribe	Unknown
Subtribe	Unknown
Genus	Unknown

Morphospecies information

Size (incl. mandibles)	7.5 mm
Observed altitude	956 m above sea level
Original observed abundance per habitat	Agroforestry area (n = 2)

Ecology of the genus

This morphospecies was only represent in the agroforestry site in this study.

Unknown_C

FAMILY CARABIDAE

Subfamily	Unknown
Tribe	Unknown
Subtribe	Unknown
Genus	Unknown

Morphospecies information

Size (incl. mandibles)	7.5 mm
Observed altitude	934 – 1061 m above sea level
Original observed abundance per habitat	Undisturbed forest (n = 2) Moderately disturbed forest (n = 1) Heavily disturbed forest (n = 14)

Ecology of the genus

This morphospecies was a forest-dependent species in this study.

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