INFLUENCE OF ALTITUDINAL VARIATION ON THE ABUNDANCE AND DIVERSITY OF RIPARIAN GROUND BEETLES (COLEOPTERA, CARABIDAE) IN ULUGURU MOUNTAINS, TANZANIA

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By

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A Dissertation Submitted in Partial Fulfilment of the Requirements for the Degree of Master of Science (Biodiversity Conservation) of the University of Dar es Salaam

University of Dar es Salaam
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CERTIFICATION

The undersigned certify that he has read and hereby recommends for acceptance by the University of Dar es Salaam a dissertation titled: "***Influence of altitudinal variation on the abundance and diversity of riparian Ground Beetles (Coleoptera, Carabidae) in Uluguru Mountains, Tanzania***" in fulfillment of the requirements for the degree of Master of Science in Biodiversity Conservation of the University of Dar es Salaam.

BANyundo
....

Dr. B.A. Nyundo

(Supervisor)

Date: 23 November 2012

DECLARATION

AND

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I, **Justine Daudi Maganira**, hereby declare that this work is my own work except where acknowledged in the text. It has not been presented to any other University for a similar or any other degree award.

Signature ....

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This dissertation is dedicated to my beloved mother Bertha Daudi Maganira Bundara, whose love and care shaped my life and she has always inspired me to be my best.

ABSTRACT

Between May and June 2012 riparian carabid beetles diversity was studied along an altitudinal gradient and in response to vegetation cover in Uluguru Mountains, Tanzania. Riparian carabid beetle samples were collected by active searching on the ground, in leaf litter, under logs, stones and large debris along streams.

A total of 270 samples were collected. These yielded 3261 specimens of riparian carabid beetles belonging to 29 morphospecies. The data was used to calculate species diversity, species richness and abundance of the nine study sites at three altitudinal levels. Differences in diversity, species richness and abundance between altitudinal levels and sites were analysed statistically. Altitudinal variation in the abundance and species richness was investigated.

There were significant differences in the diversity of riparian carabid beetles between the three altitudinal levels with the highest diversity found at mid altitude. Pair-wise comparison of the three levels of altitude indicated a significant difference in diversity of riparian carabid species for all three pairs. Species richness increased from low to the mid altitudes, followed by a decrease in species richness towards higher altitudes. The results showed no significant statistical difference in abundance of riparian carabid beetles between forested and disturbed riparian areas. The study demonstrated that riparian beetle abundance and diversity were affected by altitude and human activities that depended on the intensity of land use.

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ABBREVIATIONS

a.s.l	above sea level
EAM	Eastern Arc Mountains (of Tanzania)
GPS	Global Positioning System
m	meters
n	Number of individual riparian carabid beetles
Pers. com.	Personal communication
Pers. obs.	Personal observation
UNR	Uluguru Nature Reserve

CHAPTER ONE

INTRODUCTION

1.1 General introduction

Beetles (order Coleoptera), are represented by some 350,000 known species (Lawrence *et al.*, 1999), but recent estimates suggest there are hundreds of thousands or even millions of undescribed species (Ødegaard, 2000). Beetles are not only rich in species, but also, extremely rich with respect to diversity in size, form, and ecological strategies. The need to document and understand patterns in species richness is important as threats to biodiversity escalate (Wilson, 1992). Beetle communities offer a very tractable study system, given their often clearly defined boundaries, restricted temporal activity period, and to a great extent well-studied taxonomy (Finn *et al.*, 1999).

1.2 Carabid beetle diversity and distribution

The family Carabidae, the ground beetles, are a large, cosmopolitan family of beetles, with more than 40,000 described species worldwide, classified into some 86 tribes (Erwin, 1985; Kromp, 1999). It is the largest adephagan family and one of the most speciose of beetle families. The suborder Adephaga is a relatively large group of specialized beetles that is morphologically defined by the presence of six abdominal ventrites, pygidial defense glands in the adult and liquid-feeding mouthparts in the larvae (Lawrence and Britton, 1991). They are well proportioned cursorial beetles with prominent mandibles and palps, long slender legs, striate elytra, and sets of punctures with tactile setae. Most have an antenna-cleaning organ and largely pubescent antennae (Lövei and Sunderland, 1996). They are distributed over broad geographic ranges and inhabit all major habitats, except the driest parts of deserts, the Antarctica and the open oceans (Thiele, 1977; Lövei and Sunderland, 1996).

Carabid beetles are holometabolous insects, generally reaching the adult stage in less than a year. Most carabid beetle species live for less than one year, reproducing only once; however, some species can survive for up to four years (Lövei and Sutherland, 1996). They vary in size from a few millimeters to over 4 centimeters. Most adults are brown or black, although a few are shiny metallic blue or green. The larvae are campodeiform, have well-developed legs, antennae, and mandibles, and bear fixed urogomphi (Crowson, 1981).

Carabid beetles are ecologically important as generalist invertebrate predators (Larsen *et al.*, 2003), with a few species being phytophagous or having specialized feeding preferences (Thiele, 1977; Lövei and Sutherland, 1996). The generalist predators feed on various insect larvae and eggs, Collembola, juvenile salamanders, earthworms, mollusks, spiders, centipedes, and isopods (Currie and Digweed, 1996; Vasconcelos *et al.*, 1996; Werner and Raffa, 2000).

The abundance, species richness, and attractive coloration of many species have made carabid beetle popular objects of study for both professional and amateur entomologists (Lövei and Sutherland, 1996). Although carabids beetles are present worldwide, with species richness highest in the tropical regions (Erwin, 1985), most research works have been done in the temperate regions of the Northern Hemisphere while surveys are scarcer in the Southern Hemisphere (New, 1998). Despite their high diversity and wide distribution, there are few published studies on the diversity of riparian carabid beetles (e.g. Hering, 1998; French *et al.*, 2001).

1.3 Distribution of carabid beetles along altitudinal gradient

Altitude is a variable that is frequently related to changes in the species richness and composition of assemblages (Huston, 1994). It has been documented that the altitude of sites is the main factor that influences the diversity and distribution of many organisms. It has been shown by various researchers that elevation has dramatic effects on species composition and population density in dung beetle (Hanski and Cambefort, 1991), copro-necrophagic beetle (Martin-Piera and Lobo, 1993), and butterfly (Gutierrez and Menendez, 1995) communities. Whereas the relationship between altitude and various insect groups, such as ants (Araújo and Fernandes, 2003), butterfly (Lien and Yuan, 2003), dung beetles (Lobo *et al.*, 2007; Escobar *et al.*, 2005) and wasps (Kumar *et al.*, 2008), have been extensively studied, riparian carabid beetles have remained poorly studied.

1.4 Carabid beetles in riparian environment

On a global scale river and stream banks have a specific terrestrial invertebrate fauna. This riparian element is to a large extent made up of arthropods, especially beetles of the Carabidae and Staphylinidae families (Andersen and Hanssen, 2005; Framenau *et al.*, 2002; Lott, 2003). Manderbach and Reich (1995) reported that the riparian fauna mainly consists of carnivorous arthropod species: Araneae, Staphylinidae, Formicidae, and Carabidae which in particular achieve high densities.

Close functional relationships between aquatic and terrestrial habitats are to be expected in riparian region characterized by frequent changes in the water table. Due to this functional relationship, riparian species have evolved special adaptations to survive floods and droughts (Siepe, 1989). In riparian ecosystems, carabid beetles link aquatic and terrestrial processes through predation receiving food from emerging stream insects (Paetzold and Tockner, 2005). Subfamilies of carabid beetles known to have some of the species occurring in the riparian environment include Bembidiinae, Brachininae, Harpalinae, Hexagoniinae, Lebiinae, Odacanthinae, Pentagonicinae, Pterostichinae, Scaritinae and Trechinae.

Worldwide, riparian areas are today more or less affected by human impact. As a result, the riparian fauna is generally vulnerable or threatened. Hence, for conservation purposes, several studies of riparian beetles have been performed in other parts of the world such as Central Europe, Great Britain and Scandinavia (e.g. Andersen and Hanssen, 1994; Manderbach and Reich 1995). Studies of this nature are scarce in the Afrotropical region. To ensure that the habitats of threatened or vulnerable species are appropriately managed, it is essential that their abundance, diversity and distribution are well known.

1.5 Influence of disturbance on carabid beetles

The concept of ecological disturbance was defined by Sousa (1984) as a ''discrete, punctuated killing, displacement or damaging of individuals that directly or indirectly creates an opportunity for new individuals to become established''. Either by killing individuals and/or by changing the environment to some degree, disturbance usually results in abrupt changes in community structure and can profoundly alter species composition. Therefore understanding the influence of human disturbance on biological diversity is critically important in guiding resource use and ecosystem management in a world with an increasing human population, diminishing natural resources, and impaired ecosystem functioning (Pogue *et al.*, 2008). Rising societal demands for resources along with existing natural disturbance regimes suggest that sustainable forest management will increasingly depend on better understanding the cumulative effects of natural and anthropogenic disturbances (Cobb *et al.*, 2007).

Although the Uluguru Mountain forests (Uluguru Nature Reserve, UNR) have long been known for their unique biodiversity and considered to be of top priority for the conservation of biodiversity in Africa, there has been an increasing rate of forest deterioration as a result of various socio-economic activities carried out within and around the forest. The climate of the area is not as favorable as it was in past years when forest cover was extensive and denser. A study by Pócs (1976) showed that the Eastern Arc Mountains, EAM, (Uluguru, Usambara, Uduzungwa) had already lost 73% of their original forest cover, while Uluguru alone had lost over an area of 527 km^2 (60%) of the vegetation cover. There has been a large loss of evergreen forest in the Uluguru Mountains since then. Field assessments of the current geographical extent of the remaining forest indicate that a little over 220 sq km remains. This is less than 40 % of the potential forest area (Burgess *et al.*, 2000). Most of the forest loss has been caused by change in land use from forest to subsistence farms with maize and various other crops. Evergreen forest on the Uluguru Mountains is now almost entirely confined to the 22 Forest Reserves on the Uluguru Mountains, managed centrally by the Tanzanian government. These forest reserves have been consolidated to form the Uluguru Nature Reserve (UNR).

There have been extensive surveys of birds (Svendsen and Hansen, 1995), mammals (Stanley *et al.,* 1998), reptiles (Doggart *et al.,* 2001), amphibians (Channing, 2000) and plants (Lovett, 1998, Munishi, 2007) and records for their endemism have been known in the Uluguru Mountains; however, such surveys for insects are rare.

As it has been the case in the tropics, forest decline is one of the most important environmental problems. Most of the species in the world live in the tropical forests and many of these are still unknown to science (May, 1992) because there have been less surveys in these forest. Thus most undescribed species might be lost even before being known to science. The present study therefore aims at investigating the altitudinal trend on the biodiversity of riparian carabid beetles in the Uluguru Mountains.

1.6 Statement of the research problem

The diversity of riparian carabid beetles in the Uluguru Mountains is unknown. This is because most of the researches have focused on forest floor (humicolous) carabid beetles. No attention has been paid on riparian carabid beetles despite the fact that these insects form an important component of the ecosystem as keystone generalist predators. This hinders scientific research into the ecology and basic biology of this vital group of insects. It also hinders the utilization of this group of beetles in biodiversity conservation and monitoring, and biological control of other organisms.

Many studies (e.g. Basilewsky, 1962, 1976; Channing, 2000; Doggart *et al.,* 2001; Evans and Anderson, 1993; Lovett, 1996, 1998; Munishi, 2007; Nummelin and Nshubemuki, 1998; Nyundo and Yarro, 2007; Stanley *et al.,* 1998; Svendsen and Hansen, 1995) have been conducted in the EAM investigating the influence of disturbance gradient and variation in habitat conditions on species diversity and distribution as part of efforts to understand their biodiversity and conservation measures. However studies involving invertebrates are rare and only few of these (Basilewsky, 1962, 1976; Nummelin and Nshubemuki, 1998) contain beetles from the Uluguru Mountains. In the present study, the influence of altitudinal variation on the abundance and diversity of riparian carabid beetles in the Uluguru Mountains was assessed. The impact of riparian vegetation cover on the fluctuations of the species abundance and diversity were also assessed.

1.7 Research objectives

The general objective of this study was to assess the diversity of riparian carabid beetles along altitudinal gradient in the Uluguru Mountains.

The following were the specific objectives:

(i) To compare the abundance and diversity of riparian carabid beetles at different altitudes in the Uluguru Mountains.

(ii) To determine the influence of vegetation cover on the abundance and diversity of riparian carabid beetles along altitudinal gradient in the Uluguru Mountains.

1.8 Significance of the study

This study provided baseline information on fauna composition, structure and diversity of riparian carabid beetles along an altitudinal gradient in Uluguru Mountains. The results may also be useful for further biological and ecological studies such as using the organisms in environmental monitoring of human influences on diversity and for proper biodiversity conservation strategies. The results of this study could also be used to gauge habitat destruction and other perturbations in the UNR and elsewhere.

1.9 Hypotheses

This study aimed at testing the following hypotheses.

i. High altitude has significantly lower species abundance and diversity of riparian carabid beetles than lower altitude.

ii. The abundance and diversity of riparian ground beetles are lower in open riparian habitat than forested riparian habitat in the Uluguru Mountains.

CHAPTER TWO

LITERATURE REVIEW

2.1 General introduction

Despite the fact that ground carabid beetles have been found to be very good bioindicators of habitat disturbance (Rainio and Niemelä, 2003) and hence used as indicators for riverine management to evaluate stream bank conditions (Van Looy *et al.*, 2005), most studies on ground beetles have been done in temperate forests and grasslands and few surveys have been done in tropical African forests (New, 1998). Most surveys concern tiger beetles (Cicindelidae) (Pearson and Cassola, 1992) or the beetle order in general (Lawton *et al.*, 1998) and are restricted to forest species, leaving riparian species unsurveyed. Information on the effect of riparian vegetation cover and the influence of altitudinal variation on the diversity of riparian carabid beetles is therefore missing in the Afrotropical region. Here the diversity and distribution of carabid beetles together with the factors affecting their diversity and distribution are reviewed.

2.2 Global distribution and diversity of carabid beetles

The family Carabidae, the ground beetles, contains more than 40,000 described species classified into some 86 tribes (Erwin, 1985). Different authors divide the family into different subfamilies; except for the tiger beetles (Pearson, 1988). Our ecological knowledge is scant concerning subfamilies outside the Carabinae (Lawrence and Britton, 1991).

The Family Carabidae has a world-wide distribution except only for the deserts (Erwin, 1985) and the continent of Antarctica (Noonan *et al.*, 1992), with species richness highest in the tropical regions (Erwin, 1985).While some species may be described as eurytopic, many individual species or genera show marked preferences for particular habitat or environmental conditions (Thiele, 1977). These preferences result in differences in the carabid beetle assemblages in different habitats. Through a series of taxon pulses, they have radiated to drier environments as well as higher latitudes and altitudes (Erwin, 1979). Several structural, physiological, and behavioural adaptations enabled carabid beetles to invade all major habitats, where at least some lineages have attained dominance; the only exception is deserts, where carabids are limited to streams and oases (Erwin, 1985). This distribution pattern suggests that humidity is a general limiting factor.

2.3 Factors influencing the distribution of carabid beetles

According to several studies (e.g. Thiele, 1977; van Huizen, 1977; Stork, 1990; Semida *et al.*, 2001), habitat and microhabitat distribution of ground beetles can be influenced by a number of factors including temperature or humidity extremes (Thiele, 1977), food conditions, presence and distribution of competitors (Stork, 1990), life history and season, (van Huizen, 1977) and altitude (Semida *et al.*, 2001). Some riparian ground beetles find their habitat by sensing volatile chemicals emitted by blue algae living in the same habitat (Evans, 1988). Biotic and abiotic factors such as soil moisture (Luff, 1996; Sroka and Finch, 2006), soil type (Thiele, 1977), heterogeneity of habitats (Epstein and Kulman, 1990), predation (Parmenter and MacMahon, 1988) and various disturbance regimes (Saunders *et al.*, 1991; Niemela, 1993; Davies and Margules, 1998; Carmona and Landis, 1999; Magura *et al.*, 2000; Saint-Germain, 2005; Ulyshen *et al.*, 2005; Phillips *et al.*, 2006; Cobb *et al.*, 2007; Balog *et al.*, 2012) are said to regulate carabid species abundance and diversity. However, there is high variation among species' sensitivities to these factors. In this review and for the matter of this study two factors influencing the distribution of carabid beetles, that is altitude and disturbance, are given priority.

2.3.1 Influence of altitude on carabid beetles

Species diversity and distribution vary in space. Begon *et al.* (1990) reported that some areas have more species and more individuals than others. Variation along altitudinal gradients common in other organisms such as birds (Rahbek, 1995; Acharya *et al.*, 2011) and plants (Bhattarai and Vetaas, 2003; Lovett *et al.*, 2006)) has also been documented in carabid beetles. The study of the Variation in plant species richness of different life forms along a subtropical elevation gradient in the Himalayas, east Nepal, indicated a mid-elevation peak in species (Bhattarai 2003). Lovett *et al.* (2006) described changes in woody vegetation in the Mwanihana forest, Udzungwa Mountains National Park, Tanzania, over an altitude range of 470–1700 m. In this study Lovett and others noted a linear trend of increasing stem density with altitude for variable-area plots. They also noted that species diversity is highest at high elevations and that there was no clear zonation of elevational vegetation types. Acharya *et al.* (2011) examined patterns of species richness, density and range size distribution of birds along a 4500 m elevational gradient in the Eastern Himalayan region, a biodiversity hotspot within the world's tallest mountains. This study in the

Eastern Himalaya indicates that species richness of birds is highest at intermediate elevations.

Several studies (Lawton *et al.*, 1987; Wolda, 1987; Fernandes and Price, 1988) have examined the distribution of insects along elevational gradients. Wolda (1987) collected insects with light-traps in Panama, and concluded that species richness declines with increasing elevation over a range of 100-2000 m. He noted that his results contrast with other studies such as Janzen *et al.* (1976) which have demonstrated maximum species richness at mid-elevations. The numbers of insects and species above intermediate elevations show a general decrease, and intermediate elevations appear to have the highest insect density (Janzen *et al.*, 1976). Unlike the results of other similar studies, the total number of species of bracken herbivores did not decline with altitude (Lawton *et al.*, 1987).

Semida *et al.* (2001) studied the diversity of beetles including forest carabid beetles in different habitats and along the altitudinal gradients in South Sinai, Egypt. In this study, altitude was positively correlated with beetle species diversity, and habitat heterogeneity played a role in influencing species diversity. Lobo *et al.* (2007) studied the variation with altitude in the composition of dung beetle assemblages and species richness in the Bulgarian Rhodopes Mountains in which it was reported that the rate of species richness decrease with altitude. The distribution of ground beetle assemblages along an elevation gradient in the Bieszczady National Park (East Carpathians) investigated by Skalski *et al.* (2011) showed the maximum at mid-elevation.

Other evidence of altitudinal gradients in species diversity and distribution can be found in studies that included a wide range of organisms for example insects in general (McCoy, 1990) and invertebrates (Miserendino, 2001).

Among scientists, there is a disagreement on how species richness varies with altitude. The number of species generally diminishes with increasing altitude (Greenslade, 1968; Rahbeck, 1995). On the other hand, there has been a view suggesting an initial increase in species richness, followed by a decrease in species richness (McCoy, 1990). More research works on the influence of altitude on the diversity and distribution of organisms including carabid beetles are needed to unfold this ambiguity.

Despite a number of studies of carabid beetles in the Afrotropical region, none dealt with altitudinal variation of riparian ground carabid beetles, although some contain fragmented information on the altitude (Basilewsky, 1962; Nyundo and Yarro, 2007). Basilewsky (1962) studied the differences in environmental requirements of mountain forest species of carabid beetles in which he suggested that mountain forest species have a narrower limit on environmental conditions, needing cold and humid conditions. Carabid beetles are known to have more or less narrow environmental variables (Thiele, 1977) which determine their distribution. Altitude is among the main environmental variables explaining invertebrate assemblage composition. The distribution and composition of carabid beetles influenced by altitude can be measured.

2.3.2 Impact of disturbance on carabid beetles

Various studies have been conducted as far as ground beetles and disturbance regimes are concerned, however most studies have been conducted on the influence of fragmentation (Saunders *et al.*, 1991; Davies and Margules, 1998), clear-cut harvesting (Niemela, 1993, Cobb *et al.*, 2007; Balog *et al.*, 2012), selective cutting (Ulyshen *et al.*, 2005), agriculture (Carmona and Landis, 1999; Magura *et al.*, 2000; Balog *et al.*, 2012), logging (Saint-Germain, 2005; Phillips *et al.*, 2006), wildfire and herbicide (Cobb *et al.*, 2007).

Fragmentation, and the associated loss of vegetation cover, is one of the greatest environmental problems all over the world, and it is one of the most important reasons for declining biodiversity (Pimm and Gilpin, 1989). It has been documented that habitat fragmentation reduces the amount of forested habitat available and this may lead to the decline of some species (Lenski, 1982).

Deforestation and consequent loss of forest species in tropical forest ecosystems have received considerable attention (Laurance and Bierregaard, 1997); however there have been few studies of riparian carabid beetle species. Since recent extinction rates are more than 100 times greater than background geological ones (Pimm, 1998), much of the tropical diversity is lost before it has been even discovered. Most of these studies reported decreased diversity and abundance of individuals. Ground beetle responses to both natural and anthropogenic disturbances differed strongly and suggested that, although some species appeared to benefit from the disturbance combinations, these effects were detrimental to others (Niemela, 1993; Cobb *et al.*, 2007; Balog *et al.*, 2012)

Ground beetles have been extensively studied as sensitive indicators of anthropogenic induced changes to the environment. Habitat disturbance can cause changes to various environmental variables resulting in an indirect impact to ground beetle species composition through alteration of the plant community (Beck, 2001). It has been documented that various disturbance regimes can alter a vegetation cover by removing a substantial portion of the plant community, creating a dramatically different habitat than existed prior to disturbance (Dennis *et al.*, 1997; Beck, 2001). In areas where a variety of disturbance regimes occur it is anticipated that the resulting plant communities would provide habitat for unique assemblages of ground beetles. In a study by Beck (2001), vegetation cover appeared to affect the type and size of ground beetles with larger ground beetles more prevalent in high vegetation cover and small bodied species in low vegetation cover.

In regions such as the temperate grasslands and forests in Europe, ground beetle species distributions have been found to be strongly correlated with different vegetation types and to changes in microhabitat due to disturbances (Luff, 1990; Dennis *et al.*, 1997). In this respect, they are often cited as environmental indicators, responding to particular changes in the environment before many other plant or animal species (Dufrene and Legendre, 1997). Ground beetles have shown significant responses to vegetation structure, plant species composition, and type of grazing regime (Dennis *et al.*, 1997). Ground beetle species richness is often representative of and correlate with species richness of other insect families therefore suggesting that they may be a surrogate for insect diversity within a given system (Oliver and Beattie, 1996).

The Uluguru Mountains are mostly inhabited by the Luguru people who depend on subsistence lifestyle and agriculture as their main economic activity. Many areas are used for food (maize, beans, cassava,, sweet potatoes, irish potatoes, sorghum, and vegetables) and cash crops (bananas, variety of fruits such a oranges mangoes, guava, coffee, sunflower seeds, coconuts, oil palm) production. Slash and burn and shifting cultivation, although not very common, are still practiced in some areas (Pers. com. Mr. Kiwanga, 2012). With time deforested areas in the Uluguru Mountains will lose their agricultural productivity due to great disturbance and are likely to be abandoned because of insufficient crop yield (Munishi *et al.*, 2007). The impact of disturbance on carabid beetles and other insects at large in the Uluguru Mountains need assessment.

CHAPTER THREE

MATERIALS AND METHODS

3.1 Study Area

This study was conducted in the Uluguru Mountains' riparian areas of the following streams: Zagila, Nyamigadu, Lung'angale (Kienzema Village in the high altitude zone), Mungula, Nola, Malongole (Bunduki Village in mid altitude zone), and Bigwa, Vituli and Lukuyu (Bigwa area in the low altitude zone). The low altitude zone ranged between 400 m and 1100 m a.s.l, mid altitude zone ranged between 1100 m and 1800 m a.s.l while high altitude zone ranged between 1800 m and 2500 m a.s.l.

The Uluguru range is in the central part of the Eastern Arc Mountains (EAM) (Figure 1). They form one of the component blocks of the EAM, an exceptionally rich area of biodiversity and endemicity under the direct climatic influence of the Indian Ocean (Lovett, 1998). The Uluguru Mountains forests lie immediately South of Morogoro town in Tanzania between latitude 7° and 8° S and longitude 37° - 38° E. It is approximately 180 Km from Dar es Salaam, the major business city of Tanzania. The mountains range from about 150 m a.s.l. on their south-eastern margin, and extend to 2630 m in altitude at their highest point, Kimhandu Peak. The description of the study site is also given in Table 1 and Figure 1.

3.1.1 Climate

The climate of Uluguru Mountains is oceanic with bimodal rainfall (short rains in October to December and long rains in March to May), peaking in April and

November. The annual rainfall is 2900–4000 mm on the eastern windward slopes and 1200–3100 mm on the western leeward slopes (Munishi *et al.*, 2007). The mean annual temperature is about 24.3° C (with a maximum of 26.5° C in December and a minimum of 21.1° C in July) (Lyamuya *et al.*, 1994).

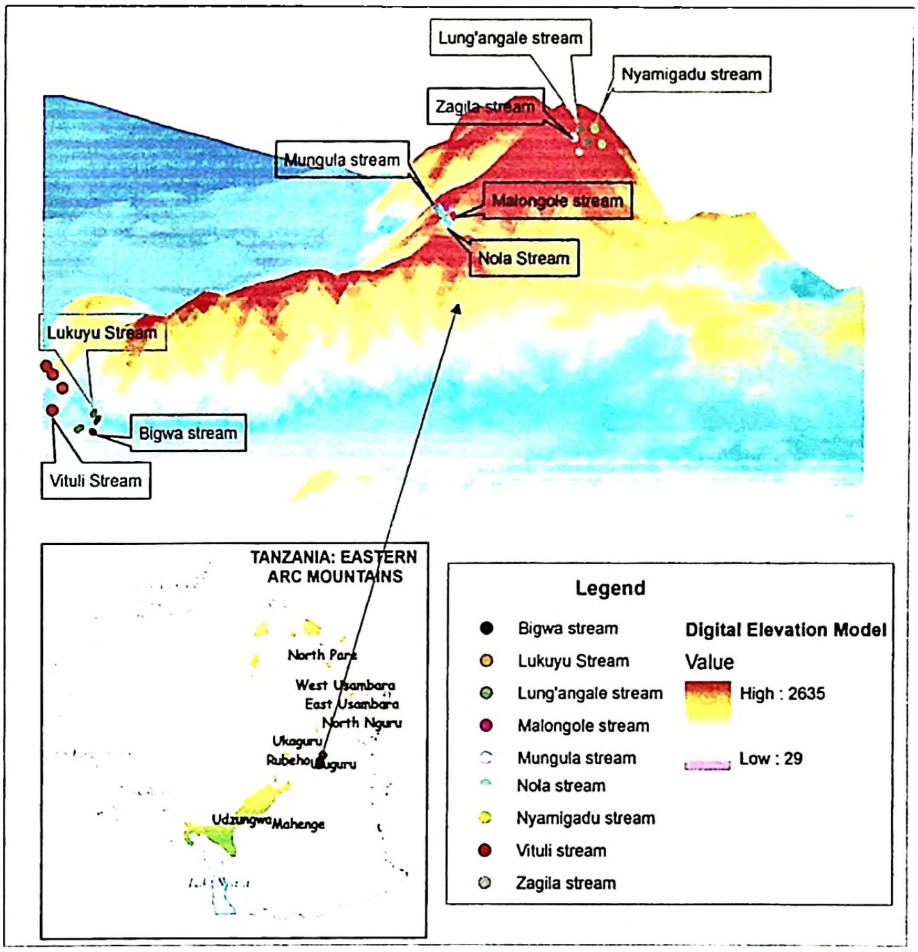

Figure 1: Map of Tanzania showing the EAM and the Uluguru Mountains' streams where carabid beetles were sampled.

Table 1: Description of the study sites

SITE	ST_{sb}	HABITAT	LEVEL	GPS READING		
ST1	ST1A	Forested	High	0345513		
				9213931	NR	NR
	ST1B	Disturbed	High	0345022		
				9213855	NR	NR
ST2	ST2A	Forested	High	0345671	0345574	
				9214503	9214509	NR
	ST2B	Disturbed	High	0345114		
				9214681	NR	NR
ST3	ST3A	Forested	High	0345232	0345304	0344560
				9212223	9212239	9212415
	ST3B	Disturbed	High	0344568	0344601	
				9212402	9212383	NR
ST4	ST4A	Forested	Mid	0348504	0348434	0348403
				9225694	9225595	9225631
	ST4B	Disturbed	Mid	0348205	0348256	0348275
				9225144	9225046	9225003
ST5	ST5A	Forested	Mid	0349205	0349130	0349284
				9224834	9224855	9224745
				0349320		
				9224694		
	ST5B	Disturbed	Mid	0349409	0349360	0349401
				9224193	9223888	9223764
ST6	ST6A	Forested	Mid	0350371	0350255	0350345
				9223716	9223667	9223703
	ST6B	Disturbed	Mid	0349971	0349938	0349845
				9223587	9223565	9223554
				0349824	0349721	
				9223527	9223523	
ST7	ST7A	Forested	Low	0360592	0360564	0360664
				9244626	9244618	9244606
	ST7B	Disturbed	Low	0360262	0360245	0360182
				9245101	9245136	9245279
ST8	ST8A	Forested	Low	0358947	0358971	0358994
				9245483	9245429	9245348
	ST8B	Disturbed	Low	0359130	0359166	035918
				9246301	9246493	9246520
ST9	ST9A	Forested	Low	0358494	0358497	0358482
				9245515	9245623	9245685
	ST9B	Disturbed	Low	0358277	0358256	0358173
				9246231	9246216	9246235

NR = GPS readings not recorded; ST_{sb} = Sub-site

Key for Table 1: ST1 = Lung'angale Stream, ST2 = Zagila Stream, ST3 = Nyamigadu Stream, ST4 = Malongole Stream, ST5 = Nola Stream, ST6 = Mungula Stream, ST7 = Vituli Stream, ST8 = Lukuyu Stream, ST9 = Bigwa Stream.

3.1.2 Geology, Soil and Water Catchment

The EAM, including the Uluguru Mountains bedrock is made up of Pre-Cambrian metamorphic rocks dominated by hornblende-pyroxine granulites with injections of granite and gneiss (Lovett, 1996; Munishi *et al.*, 2007). Soils are mostly sandy-loams or sandy-clay-loams (Lovett *et al.*, 2006)

Uluguru Mountains Forests are the major source of river flows supplying water to Morogoro, Pwani and Dar es Salaam regions of Tanzania. The forests provide fuels, maintenance of humid climate suitable for agriculture, secure stable and good water supply and the main source of water for the urban and industrial uses in Tanzania's major business city Dar es Salaam mainly through the Ruvu River. Similarly water from the Uluguru Mountains provides an opportunity for fishing and the water has been used for irrigation practices particularly for horticulture crops.

The value of the Catchment function of the Uluguru mountain forest has not been estimated in monetary terms (Nkombe, 2003). However, as most of the economic activities depend on water from this forest, the value must be billions of dollars over a ten-year period. However this is all jeopardized by the loss of the forest cover, woodlands and other trees from the mountain.

Nkombe (2003) document that although water from the Uluguru is relatively abundant, access to clean water is a serious problem in some areas. Even the supposedly clean and safe water is not protected and the springs are subject to sources of pollution and contamination. Water intakes are similarly contaminated due to farming and logging activities.

3.1.3 Vegetation

With the exception of rock out crops the mountain is entirely covered by moist submontane forest (canopy 30-50m tall). The number of the forest patches has also been quantified as one measure of fragmentation of the natural forest cover and according to literature an estimate of the loss has been estimated. On the average it is estimated that the Eastern arc mountains (Uluguru, Usambara, Uduzungwa) have already lost (73%) of their original forest cover, while Uluguru alone have lost sixty percent (60%) (Pócs, 1976). According to the data produced by Newmark, (1998) the Uluguru natural forest was 527 km^2. With 5 Km^2 of the forest patches and the closed forest was about 120 Km^2 and the total forest cover lost was about (60%). Other general information on the vegetation of the Uluguru Mountains forest, in which the study sites were located, is available from various sources (Lovett, 1996; 1998; Lovett *et al.*, 2006; Munishi *et al.*, 2007).

3.2. Data Collection

The sampling sites were established along streams with two types of habitat for each stream, that is, within the UNR (forested areas) and in cultivated or residential areas outside the UNR (disturbed area) (Plate 1, Plate 2 and Plate 3). Riparian carabid beetles were sampled at nine sampling sites (Appendix 1), ranging from 400 m a.s.l to 2200 m a.s.l within three altitudinal levels (High, Mid and Low). Sampling points ranged between three and five at each sampling site depending on the nature of the terrain of the riparian habitat/stream.

Collecting was conducted from 21st May 2012 to 1st June 2012. It involved active searching for the carabid beetles on the ground, in leaf litter and in other hiding places such as under logs, stones and large debris during the day. Moist leaf litter was scooped onto a piece of white cloth (1.0 m^2) and carabid beetles were caught using a "pootah" (aspirator) or just grabbed by fingers (Plate 4). Carabid beetles collected by each of the collectors (a laboratory artisan, local labourers and myself) for a period of one hour constituted one "sample" and were placed in one plastic vial or plastic bag which was then tied at its two ends. All collected carabid beetles were preserved in 75% ethanol. The geographical position and altitude of each site were recorded using a hand-held Global Positioning System (GPS) receiver (Garmin GPS 60) except where it was impossible such as under heavy canopy (Table 1).

Plate 1: High altitudinal level (The forested area in background and the disturbed riparian area in the foreground)

Plate 2: Mid altitudinal level (The forested area in background and the disturbed riparian area in the foreground)

Plate 3: High altitudinal level (The forested area in background/in the clouds and the disturbed/inhabited riparian area in the foreground)

Plate 4: The use of ''searching'' and "pootah" in sampling riparian carabid beetles

3.3 Laboratory activities

In the laboratory, the collected riparian carabid beetles in each sample were identified to the species level wherever possible; occasionally only subfamily or even generic designations were possible, but even though without a name, we are confident that each morphospecies represents a separate species. Identification of carabid beetles to subfamily was done according to identification keys by Basilewsky (1953), CSIRO (1991), White (1983) and other sourses. The identified morphospecies were given numbers, that is, Species 1, Species 2 and so on and the genus that was not known was labelled with a letter 'G' followed by a number (Appendix 3). Morphospecies is here used of Recognizable Taxonomic Unit (RTU) (CSIRO, 1991), meaning a morphologically recognizable entity, to which all morphologically similar specimens are assigned. Identification of species took place in June, 2012 in the Department of Zoology and Wildlife conservation at the University of Dar es Salaam by myself with the help of Dr. Bruno Alberto Nyundo who is a specialist in carabid beetle taxonomy. The identified species were mounted and pinned (for relatively larger specimens) and carding was done for smaller specimens (Plate 5). The rest of the specimens that were neither mounted nor pinned were placed in plastic vials with 75% ethanol alcohol and kept in the Department of Zoology and Wildlife at the University of Dar es Salaam for reference.

Plate 5: Identified morphospecies

3.4 Data analysis

Descriptive statistics were used to summarize and present data on the total number of species (species richness), diversity and abundance. The diversity of the riparian ground beetles was calculated using Shannon-Wiener index (Magurran, 1988). Statistical packages that were used in the analysis included the Species Diversity and Richness – 2.65 (Henderson and Seaby, 2001) and SYSTAT Version 10 (SPSS, 2000). The species diversity between pairs of different altitudinal levels was compared using special t-test (for comparing diversity indices) (Zar 1984; Barnett *et al.*, 2002). Kruskal-Wallis test was used to compare the abundance of beetles among sites.

CHAPTER FOUR

RESULTS

4.1 General results

In total, 3261 specimens belonging to twenty nine species from thirteen subfamilies were collected from the 270 samples at nine study sites. All specimens were collected at three levels of altitude in which each site included specimens from forested riparian area of the UNR and disturbed riparian area outside the UNR. The greatest number of the collected specimens occurred in forested riparian areas, whereas the least number of specimens were collected in disturbed riparian areas (farmland and residential areas) (Appendix 1 and Appendix 2). Individual riparian carabid beetles collected varied greatly with altitude, with the highest abundance found at low altitude, followed by high altitude and the least abundance found at mid altitude.

Among the twenty nine collected species, four species (Species 7 (Subfamily Omophroninae), Species 12 (Subfamily Odacanthinae), Species 13 (Subfamily Odacanthinae) and *Metagonum* sp.2) were represented by only one specimen (singletons), while the four most abundant species (*Trechodes* sp.1, Species 2 (Subfamily Bembidiinae), *Abacetus* sp.2 and *Trechodes babaulti*) were represented by more than 140 specimens each. Species richness varied between sites; species richness was higher at mid altitude and lower at both high and low altitude (Appendix 2 and Appendix 3).

4.2 Effect of altitude on the abundance of riparian carabid beetles

As depicted earlier, a total of 3261 individual riparian carabid beetles belonging to 29 species were caught throughout the study period. The contribution to the total number of individuals collected from the nine study sites at three different levels of altitude (Figure 2) showed that, low altitudinal level had the greatest abundance of individuals (n = 1988; 60.96% of the total), followed by high altitudinal level (n = 774; 23.74% of the total) and the least abundance of riparian carabid beetles was caught at mid altitudinal level (n = 499; 15.30% of the total). Kruskal-Wallis one-way analysis of variance showed a significant difference in abundance of riparian carabid beetles between the three altitudinal levels (Kruskal-Wallis H = 84.533, $p < 0.05$).

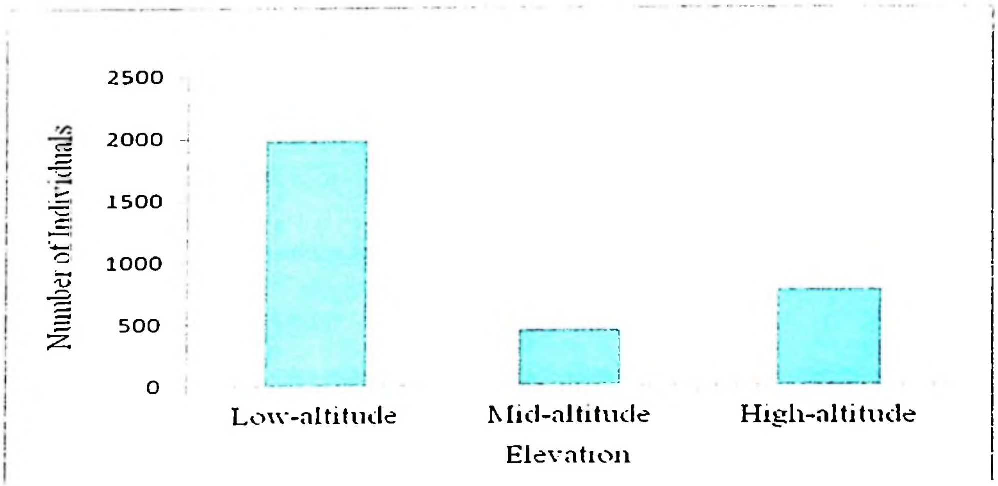

Figure 2: Abundance of carabid beetles with respect to levels of altitude in Uluguru Mountains.

Further analysis indicated that high abundance of riparian carabid beetles at low altitude was mostly due to only one site (ST9) which alone contributed 969 riparian carabid individuals accounting for 48.74% of the total individuals collected from that altitude (Figure 3). On the other hand, the two remaining low altitudinal level sites, ST7 and ST8, had relatively low abundance of individuals riparian carabid beetles (680 and 339 respectively) accounting for 34.21% and 17.05% respectively of the total individuals caught. Kruskal-Wallis analysis showed a significant difference in the number of specimens per sample between the three sites of the low altitudinal level (Kruskal-Wallis $H = 23.769$, $p < 0.05$). Although the mid altitudinal level gave the least abundance of carabid beetles, the analysis showed that ST4 contributed higher percent of individuals ($n = 333$; 66.73% of the total individuals at mid altitude) than the percentage contributed by ST9 at low altitudinal level. The other two mid altitudinal level sites (ST5 and ST6) contributed more or less the same number of individuals ($n = 85$; 17.03% and $n = 81$; 16.23% respectively) at mid altitude. The difference in abundance between mid altitude sites (ST4, ST5 and ST6) was statistically significant as shown by Kruskal-Wallis one-way analysis of variance (Kruskal-Wallis $H = 21.138$, $p < 0.05$). On the other hand, there was only a slight difference in abundance of carabid beetles for all three sites (ST1, ST2 and ST3) of high altitudinal level and their contribution ranged from a minimum of 28.55% at ST1 to a maximum of 36.69% at ST2. As indicated by the percentage contribution of specimens (see also Figure 3), at high altitudinal level sites there was no significant statistical difference in carabid beetles (Kruskal-Wallis $H = 4.580$, $p > 0.05$).

When the most abundant species, *Trechodes babaulti* (Subfamily Trechinae) was considered as an outlier (because it had extremely more individuals than the rest of the species) and removed from the sample, a mid altitude bulge pattern of abundance was obtained (Figure 4). In this case high altitude had the lowest abundance of carabid beetles (n = 273; 22.40%), followed by low altitude (n = 454; 37.24%) while mid altitude had the highest abundance (n = 492; 40.36%). After removing *Trechodes babaulti* from the sample, there was a significant statistical difference (Kruskal-Wallis H = 9.149, $p < 0.05$)

When nine most abundant species (with a total of more than fifty individuals from all the three altitude levels) were analysed, the results indicated a pattern (a pattern like that in Figure 2 above) in which the mid altitude had lower abundance (n = 420; 13.86% of the nine most abundant species) than both high (n = 705; 23.27% of the nine most abundant species) and low (n = 1905; 62.87% of the nine most abundant species) altitude. In this analysis low altitude again had the highest abundance compared to high altitude and there was a significant statistical difference in abundance (Kruskal-Wallis H = 83.029, $p < 0.05$) between the three levels of altitude for the nine most abundant species.

Furthermore the abundance of the five most abundant species at each altitudinal level (*Metagonum mboko*, Species 2 (Subfamily Bembidiinae), Species 5 (Subfamily Bembidiinae), *Trechodes babaulti* and *Tachys* sp.1 at high altitude; *Trechodes* sp.1, *Peryphus meruanus*, *Metagonum mboko*, Species 2 (Subfamily Bembidiinae) and Species 4 (Subfamily Bembidiinae) at mid altitude and *Trechodes* sp.1, Species 1 (Subfamily Bembidiinae), Species 5 (Subfamily Bembidiinae), *Abacetus* sp.2 and *Trechodes babaulti* at low altitude) indicated that low altitude had the highest abundance of carabid beetles (n = 1854; 62.53%), mid altitude had the least abundance (n = 390; 13.15%), while high altitude contributed 721 individuals (24.32%). Again, these were statistically significant (Kruskal-Wallis H = 84.977, $p < 0.05$)

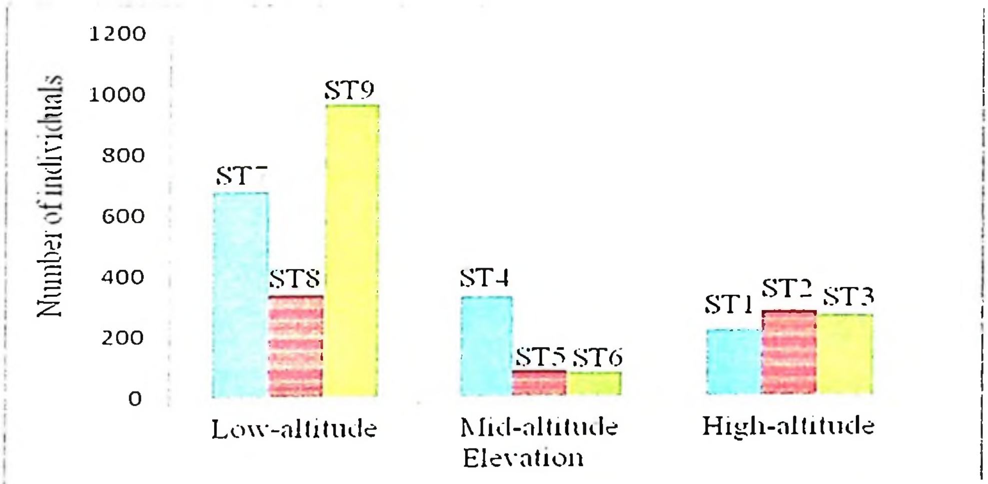

Figure 3: Comparison of beetle abundance in the nine sites (ST = Site) at three altitudinal levels.

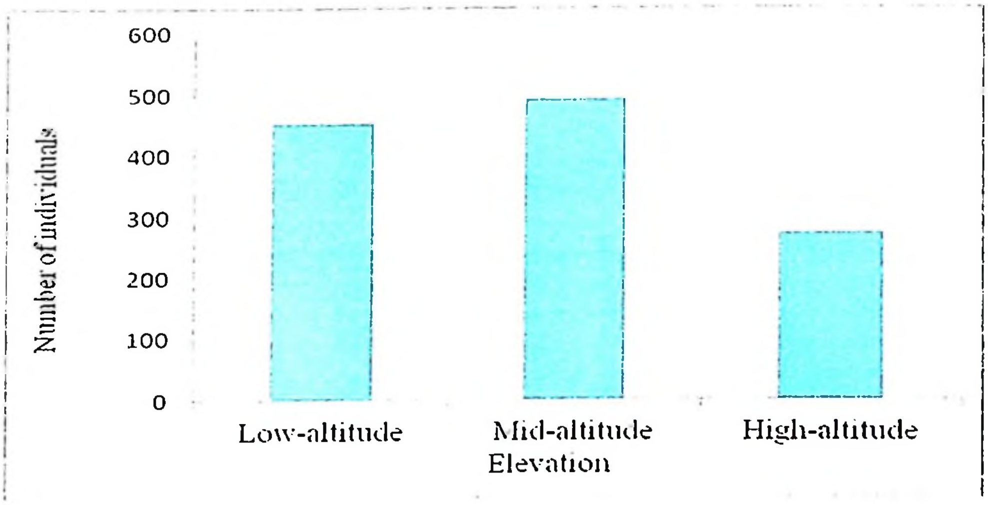

Figure 4: Abundance of carabid beetles with respect to levels of altitude when species 14 in considered as an outlier.

Individual carabid species appeared to be differently affected by altitude. Species 2 (Subfamily Bembidiinae) and *Metagonum mboko* increases in abundance as altitude increased. One species, *Abacetus* sp.2 decreased in abundance as altitude increased. Four species (Species 4 (Subfamily Bembidiinae), Species 8 (Subfamily Pterostichinae), *Trechodes* sp.1 and *Abacetus* sp.1) indicated a mid elevation hump, where as two species (Species 5 (Subfamily Bembidiinae) and *Trechodes babaulti*) showed a mid elevation trough (Appendix 2).

4.3 Effect of disturbance on the abundance of riparian carabid beetles

The contribution to the total number of individuals collected from the nine study sites was relatively high in streams passing through forested areas of the UNR (n = 1816; 55.69% of the total), while streams passing through the disturbed (farmland and residential areas) areas gave a relatively lower abundance (n = 1445; 44.31% of the total) (Figure 5).

A comparison of individual carabid beetles collected from forested riparian areas of the UNR and disturbed riparian areas using Mann-Whitney test showed no significant statistical difference (Mann-Whitney U = 7855.50, p = 0.05) in abundance.

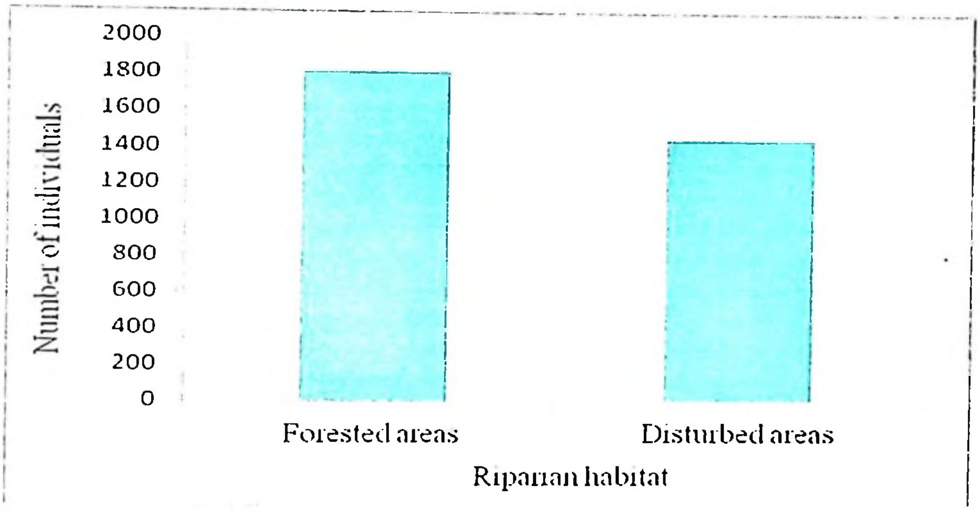

Figure 5: The abundance of riparian carabid beetles at two different levels of vegetation cover.

When analysis was carried out separately for each of the three altitudinal levels, the results of both low altitude and mid altitude showed no significant statistical difference between the disturbed and forested riparian areas (Figure 6). Disturbed riparian areas of the low altitude had slightly high number of riparian carabid individuals (n = 995; 50.05% of total individuals at low altitude) as compaired to the forested riparian areas (n = 993; 49.95% of total individuals at low altitude). The difference in abundance at low altitudinal level between disturbed and forested riparian areas was not statistically significant (Mann-Whitney U = 1029; $p > 0.05$). At both mid altitude and high altitude, the greatest abundance of riparian carabid beetles occurred in the forested areas (n = 293; 58.72% at mid altitude and n = 530; 68.48% at high altitude) whereas the disturbed riparian areas had the lowest abundance (n = 206; 41.28% at mid altitude and n = 244; 31.52% at high altitude). There was no significant statistical difference in abundance (Mann-Whitney U = 1086; $p > 0.05$) at mid altitude. On the other hand, disturbed riparian areas and forested riparian areas at high altitude showed a significant statistical difference (Mann-Whitney U = 417; $p < 0.05$) in riparian carabid beetle abundance.

Further analysis treated *Trechodes babaulti*, the most abundant species, as an outlier. The results indicated high abundance in forested riparian areas (n = 638; 52.34% of total individuals after removing *Trechodes babaulti*) and low abundance in disturbed riparian areas (n = 581; 47.66% of total individuals after removing *Trechodes babaulti*). There was a significant statistical difference (Mann-Whitney U = 10410.50, $p < 0.05$) in abundance between forested and disturbed riparian areas after removing *Trechodes babaulti* from the sample.

When nine most abundant species (with a total of more than fifty individuals from both disturbed and forested riparian habitat: that is *Trechodes* sp.1, *Peryphus meruanus*, Species 2 (Subfamily Bembidiinae), *Metagonum mboko*, Species 4 (Subfamily Bembidiinae), *Abacetus* sp.2, Species 11 (Subfamily Bembidiinae), Species 5 (Subfamily Bembidiinae) and *Trechodes babaulti*) were analysed, the results indicated that forested riparian habitat had high abundance of carabid beetles (n = 1726; 56.96% of the nine most abundant species) while disturbed riparian habitat had low abundance (n = 1304; 43.04% of the nine most abundant species). A comparison of these two habitats for the nine most abundant species using Mann-Whitney test showed a statistically significant difference in beetle abundance (Mann-Whitney U = 7457.00, $p < 0.05$). However, analysis of the most abundant species excluding *Trechodes babaulti* showed no significant statistical difference in abundance (Mann-Whitney U = 10055.500, $p > 0.05$) between forested and disturbed riparian areas.

Furthermore the abundance of the five most abundant species (including *Trechodes babaulti*) at each of the two habitats indicated that forested riparian habitat had the highest abundance of carabid beetles (n = 1585) while disturbed habitat gave the lowest abundance (n = 1205). These were statistically significant (Mann-Whitney U = 7559.00, $p < 0.05$).

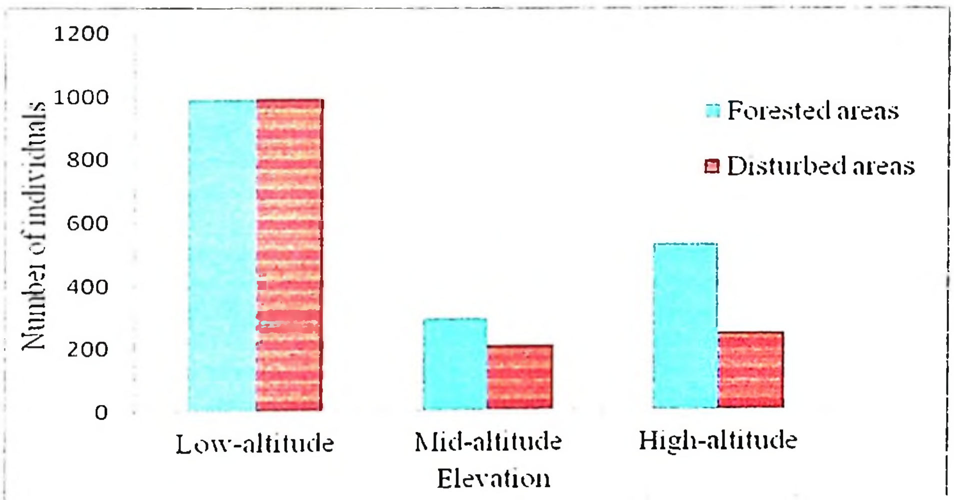

Figure 6: Comparison of individual riparian carabid beetle abundance at the three altitudinal levels between disturbed riparian areas and forested riparian areas.

Trechodes sp.1, *Peryphus meruanus*, Species 4 (Subfamily Bembidiinae), *Abacetus* sp.2 and *Trechodes babaulti* attained high abundance in the forested riparian habitat than in the disturbed habitat. On the other hand, *Metagonum mboko*, *Metagonum* sp.1, Species 2 (Subfamily Bembidiinae), *Crepidogaster* sp.1, Species 3 (Subfamily

Lebiinae), Species 5 (Subfamily Bembidiinae) *Abacetus* sp.1 and *Tachys* sp.1 had more individual in the disturbed habitat whereas the rest of the species had more or less the same number of individuals.

4.4 Effect of altitude on the diversity of riparian carabid beetles

The total number of species collected varied greatly with altitude, with the highest species richness (23 species) found at mid altitude and the least species richness (18 species) found at both high altitude and low altitude (Appendix 2 and Appendix 3).

There was a significant difference in diversity among the three levels of altitude in which the calculated Shannon-Wiener index of species diversity (H') for high, mid and low altitude levels were 1.3422, 2.1676 and 1.0370 respectively (see also Figure 7). The three levels of altitude were compared in pairs using special t – test and the result showed a significant difference in diversity of riparian carabid species for all three pairs (Table 2).

Table 2: Pair-wise comparison of carabid beetle species diversity at three altitudinal levels

ALTITUDE	H'	COMPARISON	DELTA	PROBABILITY
High altitude	1.3422	High & Mid altitude	0.825348	< 0.05
Mid altitude	2.1676	High & Low altitude	0.305237	< 0.05
Low altitude	1.0370	Mid & Low altitude	0.130590	< 0.05

Key: H' = Shannon-Wiener index of species diversity

There was a high level of site specificity for carabid beetle species collected (Appendix 2). About 27.57% (8 out of 29 species) of species were collected at only one altitudinal level (2 species at low, 3 species at mid and 3 species at high altitude), 41.38% (12 out of 29 species) of species were collected at two altitudinal levels (6 species at both low and mid altitude, 5 species at both high and mid altitude and 1 species at both high and low altitude) while only 31.03% (9 out of 29 species) of species were found at all three altitudinal levels (low, mid and high altitude). *Trechodes babaulti* was the most dominant species which comprised of 2042 individuals accounting for 62.62% of the total individual riparian carabid beetles collected. This species was most abundant at both; high and low altitudinal levels where it gave rise to 501 and 1534 individuals respectively and extremely few individuals (n = 7) at mid altitudinal level. In fact 75.34% of individuals were a contribution of only three species (*Trechodes* sp.1, Species 2 and *Trechodes babaulti*) where the rest of the species contributed only 24.66% of individuals among which four species (Species 7 (Subfamily Omophroninae), Species 12 (Subfamily Odacanthinae), Species 13 (Subfamily Odacanthinae) and *Metagonum* sp.2) had only one individual (singletons) (Appendix 2 and Appendix 3).

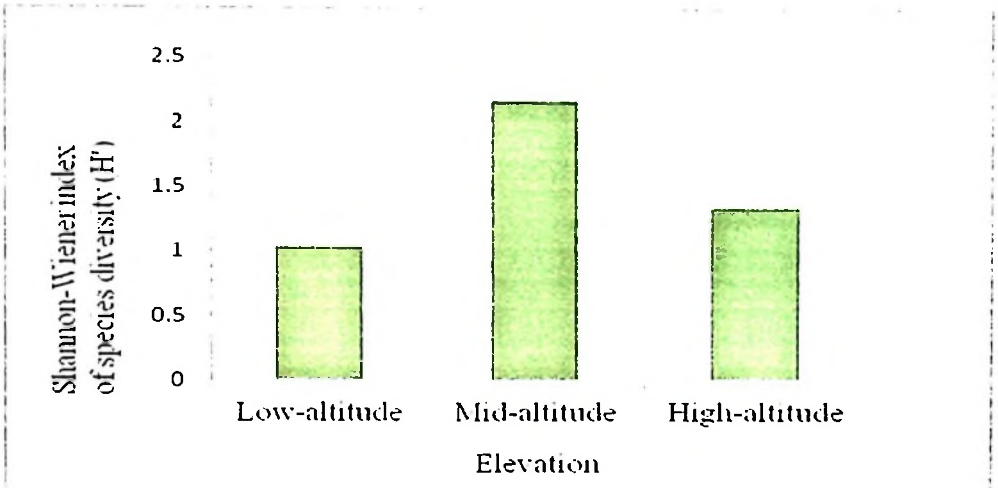

Figure 7: Diversity (Shannon-Wiener index H') at three levels of altitude

A total number of 13 species appeared to be rare, having less than 10 individuals each and their overall contribution to the total number of individuals collected was 1.59% (n = 53). There was no common rare species that occurred at all three altitudinal levels. Two (2) rare species were collected at low altitude only, while both high and mid altitude had 3 rare species each. Four (4) rare species where shared between high and mid altitude whereas one (1) rare species was shared between mid and low altitude (Appendix 2).

4.5 Effect of disturbance on the diversity of riparian carabid beetles

The disturbed riparian habitat yielded a slightly higher number of riparian carabid species (25 species) compared to the forested riparian habitat (24 species). Some species were exclusively found in disturbed riparian sites while others were exclusively found in the forested areas of the UNR. Among the 29 species caught, five species were only found in disturbed areas whereas four species were only found in the forested riparian areas of the UNR (Appendix 2).

Shannon-Wiener index of species diversity (H′) at the two habitat categories based on levels of disturbance were 1.6937 for disturbed riparian areas and 1.4794 for forested riparian areas of the UNR (Figure 8). Special t-test showed high statistical significant difference of species between disturbed riparian areas and forested riparian areas (Delta = 0.214289, $p < 0.05$).

Further analysis was carried out separately between disturbed and forested riparian areas for each of the three altitudinal levels (Figure 9). The results showed that all the three altitudinal levels had high diversity of riparian carabid beetles for disturbed riparian areas as compaired to the forested riparian areas. The results also indicated that among the three altitudinal levels the highest diversity was found at mid altitude for both disturbed and forested riparian areas (Figure 9).

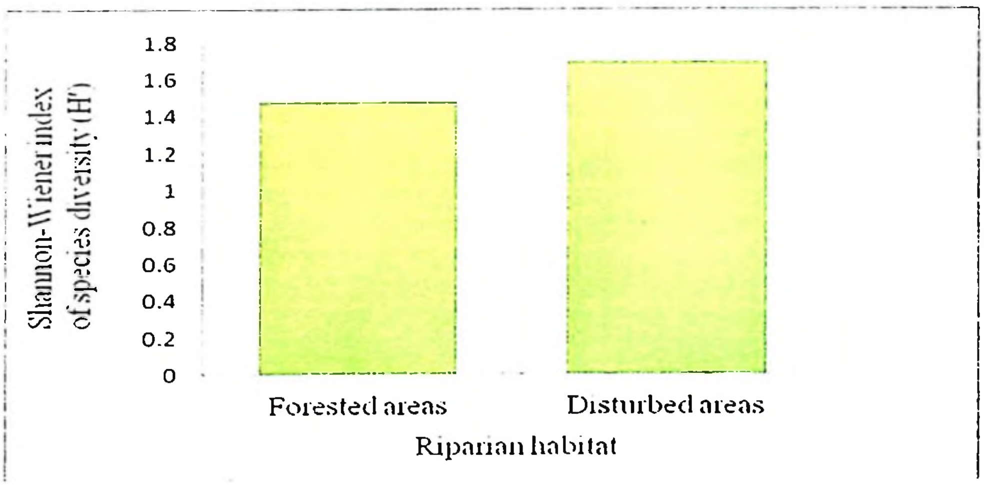

Figure 8: Diversity (Shannon-Wiener index H′) at two different levels of vegetation cover.

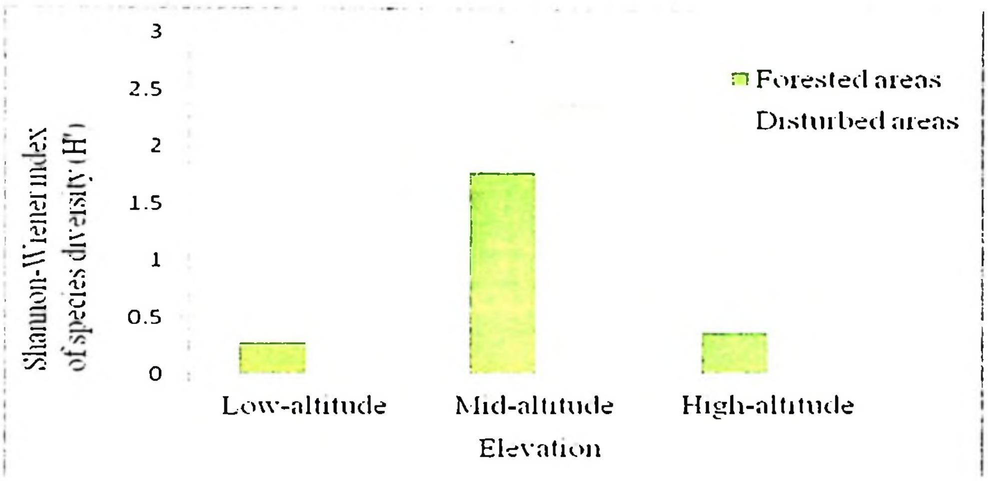

Figure 9: Comparison of riparian carabid beetle diversity at the three altitudinal levels between disturbed riparian areas and forested riparian areas.

CHAPTER FIVE

DISCUSSION AND CONCLUSIONS

5.1 Introductory remarks

The present work was the first biodiversity study of riparian carabid beetles along an altitudinal gradient in the Uluguru Mountains of Tanzania. This study has also for the first time employed active method (via hand searches) for insect sampling in the Uluguru Mountains. For approximately two weeks of collecting, 3261 individual riparian carabid beetles comprising of 29 species from thirteen subfamilies were collected. This is an indication that the Uluguru Mountains is very rich in carabid fauna and that the majority of species await discovery.

The objective of this study was to assess the diversity of riparian carabid beetles along altitudinal gradient in the Uluguru Mountains. This assessment involved active searching, a collection method necessary for complete inventory of carabid beetle biodiversity. This led to the second objective of the study which was to determine the influence of vegetation cover (disturbed and forested riparian) on the diversity of riparian carabid beetles along altitudinal gradient in the Uluguru Mountains. As far as the results of this study are concerned, the two objectives, to a great extent, have been met. In the following sections the results are interpreted and their implications to conservation of the UNR and the Uluguru Mountains in general, are discussed. Conclusions and recommendations are also given under this chapter.

5.2 Abundance of riparian carabid beetles

5.2.1 Effect of altitude on the abundance of riparian carabid beetles

In the present study, the abundance of individual riparian carabid beetles collected at the three altitudinal levels indicated that low altitudinal level had the highest abundance of individuals than high altitudinal level. These results are consistent and support the hypothesis that was formulated for this study. Similar results have also been obtained by other studies carried in the EAM, such as Nyundo and Yarro (2007). However there was no gradual decrease in abundance as altitude increased: mid altitude had extremely low abundance than high altitude resulting into a pattern forming a trough between low altitude and high altitude.

The high abundance of riparian carabid beetles at low altitude, as compared to the other two levels of altitude, may be explained by species composition at the three levels of altitude. Species are not equally abundant (Blackburn, 1999). Some areas have more species and more individuals than others (Begon *et al.*, 1990). At low altitude the dominant species belonging to the Subfamily Trechinae (*Trechodes babaulti*) attained very high densities. In total, 1534 individuals of the species, *Trechodes babaulti*, were collected from the low altitude sites. This species was also the most abundant species at high altitude giving a total of 501 individuals collected, however only 7 individuals were recorded at mid altitude. A virtual absence of *Trechodes babaulti* at mid altitude as compaired to both low and mid altitude may be one of the reasons for the observed low abundance of beetles at mid altitude. On the other hand, at mid altitude sites the dominant species (*Trechodes* sp.1: Trechinae) had lower abundance of 179 individuals as compared to the most abundant species

(*Trechodes babaulti*) at low altitude which had 1534 recorded individuals. *Trechodes* sp.1 (Trechinae), the dominant species at mid altitude, occurred also at low altitude with its individual abundance reduced to almost half and it also occurred at high altitude with only 3 individuals.

Alternative explanation for high abundance of riparian carabid beetles at low altitudinal level might be due to disturbance tolerance of *Trechodes babaulti* which also was abundant not only at low altitude forested riparian sites but also at low altitude disturbed riparian sites. Two out of three low altitude sites were sources of stones and gravels for building activities and the areas surrounding such riparian habitat were residential and cultivated farmland; however *Trechodes babaulti* attained high abundance, this might be indicating tolerance to disturbance. *Trechodes babaulti* also seemed to benefit from quick post-disturbance recovery and regeneration of low altitude riparian herbs. Post-disturbance regeneration of riparian herbs which seemed to be more pronounced at low altitude than at high and mid altitude may be due to differences in environmental temperature and humidity. Low altitude was relatively warm and dry than mid and high altitude, a condition which might have favored quick regeneration, hence availability of resources. Low abundance of carabid beetles at the mid altitude may also have been associated with the nature of the terrain (break in the terrain), stony surfaces and small amount of leaf litter which could not support high abundance of riparian beetles. There was also a possibility that disturbances had created habitat heterogeneity which might have supported high abundance of carabid beetles at low altitude.

The significant statistical difference in riparian carabid beetle abundance within mid and low altitude sites might be due to the condition of the current riparian vegetation cover; most low altitude sites were sources of stones and gravels, pronounced farming and residential areas. Within mid and high altitudinal sites out of the UNR were farms with short term crops such as maize, beans, peas and various kinds of vegetables. It was observed in mid altitude that farming activities included cultivating not only inside and around the riparian areas but also included removing all of the vegetation cover; only few areas remained with some weeds. Burning was also observed to be practiced at various phases of farming at low and mid altitude. The variation of the vegetation cover as a result of human activities might have caused the observed difference in abundance of riparian carabid beetles within sites of the low and mid altitude; however such activities seemed to have little effect on the variation of beetle abundance within sites of high altitude. High altitude sites had more or less the same riparian habitat situation hence might have led to similar microhabitats and food resources; this may explain the non-significant differences in beetle abundance within sites. The presence of *Trechodes babaulti* at high altitude sites (ST1, ST2 and ST3) in high and almost equal abundance may have buffered the differences in abundance as well. Within altitudinal levels, other factors also differed and they include slope, soil depth, vegetation cover, tree species, weeds and other factors.

The dynamics of insect abundance is a difficult and unsatisfactorily explained problem (Szujecki, 1987). Thiele (1977) and Erwin (1979) documented that carabid beetles, like most natural populations of invertebrates, have a patchy distribution. For this matter, Szujecki (1987) pointed out that there were decisive determining factors of insect abundance, which included parasites, physical agents (e.g. climate and soil) and trophic factors. In addition, there are intrinsic mechanisms on population increase and self regulation (Nyundo and Yarro, 2007). Some of these factors are directional while others act randomly, they can also act directly or indirectly. Therefore one or a combination of such abundance determining factors might act to influence the abundance of riparian carabid beetles along an altitudinal gradient. Undoubtedly, factors influencing species abundances with altitude are complex, and may differ both between species and along different altitudinal transects (Lawton *et al.*, 1987).

There are few studies on arthropod abundance from tropical Africa (e.g. Nummelin, 1989; Zilihona *et al.*, 1998; Davies, 1999). Most of these studies did not specifically address the variation of insect abundance along altitudinal variation and none of these studies dealt with the variation of riparian carabid beetles along altitudinal gradient. Instead, insect abundance was considered in some studies investigating other aspects of forest management such as the effect of river gorge impoundment (Zilihona *et al.*, 1998), the effect of burning, (Davies, 1999) and the impact of habitat heterogeneity (Semida *et al.*, 2001). All these studies produced results that showed no predictable pattern of abundance in space.

5.2.2 Effect of disturbance on the abundance of riparian carabid beetles

In the present study, there was no significant statistical difference in abundance between disturbed and forested riparian areas. The results in this study did not support the hypothesis that overall abundance of riparian ground beetles is lower in disturbed riparian habitat than forested riparian habitat. This may be explained by the abundance and distribution of *Trechodes babaulti* and its tolerance to disturbance. This species was the most abundant species at both low and high altitude and it occurred in high numbers in both disturbed and forested areas. *Trechodes babaulti* seems to have a wide distribution along altitudinal gradient (Bruno Alberto Nyundo, Pers. comm., 2012). It has also been found to occur in high abundance along streams passing through the University of Dar es Salaam, most of which contain polluted municipal effluent (Gasper Lugelelo, Pers. comm., 2012). The occurrence of *Trechodes babaulti* in such environments indicates high tolerance to disturbance. In the present study as shown by the analysis, *Trechodes babaulti* might have buffered the abundance of other beetles giving no significant differences between the two habitats. Lack of difference in overall carabid beetle abundance between disturbed and forested riparian areas may also be due to the fact that no matter the disturbances, the riparian areas seemed to remain with some vegetation (including various kinds of weeds) that may support high abundance of carabid beetles even in disturbed areas. The presence of water and vegetation may play part in attracting other invertebrates some of which are food resources for beetles.

There have been several studies (Howden and Nealis, 1975; Jennings *et al.*, 1986; Niemelä *et al.*, 1993; Spence *et al.*, 1996; Davis *et al.*, 2001; Koivula *et al.*, 2002; Boonrotpong *et al.*, 2004; Shahabuddin *et al.*, 2005; Masis and Marquis, 2007) supporting the previously formulated hypothesis. A study in Columbia Amazon documented that some community attributes such as abundance are negatively affected by athropogenic forest disturbance (Howden and Nealis, 1975). Similar results were also obtained in the research carried by Jennings *et al.* (1986), Niemelä *et al.* (1993) and Koivula *et al.* (2002) in which they all reported lower carabid beetle abundance in disturbed areas (clear-cut sites) compared to forested areas (mature forests). Spence *et al.* (1996) also reported higher carabid beetle abundance in intermediate aged boreal forests compaired to other areas with different levels of human mediated disturbance. Reduced abundance in other insect groups such as dung beetle as a result of timber harvesting has also been reported in Missouri Ozarks (Masis and Marquis, 2007). Other several researchers (Davis *et al.*, 2001; Boonrotpong *et al.*, 2004; Shahabuddin *et al.*, 2005) have documented lower dung beetle abundance in disturbed than undisturbed forest habitat.

On the other hand, Niemelä and Halme (1992) and Spence *et al.* (1996) reported that carabid beetles are often more numerous and more speciose in open habitats than in forests and that clear-cutting also had negative effects on the abundance of forest-specialist species.

Although some studies have shown an overall increase in the abundance of carabids following disturbance (Eryschov and Trophimova, 1984; Niemelä *et al.*, 1994; Thompson and Allen, 1993; Beaudry *et al.*, 1997; Heliola *et al.*, 2001; Warriner *et al.*, 2002), some studies have found no overall change in carabid abundance, they have identified significant effects at the species level (Atlegrim *et al.*, 1997) as well as differences in species composition between disturbed and undisturbed sites (Greenburg and Thomas, 1995; Butterfield, 1997; Werner and Raffa, 2000). As it has been documented, habitat specificity appears to determine the response of many carabids including riparian carabid beetles. The abundance of open-habitat species, for example, has been shown to increase in disturbed areas, while the number of forest-dwelling species often decreases or disappears following disturbance (Niemelä *et al.*, 1993).

In the present study, there might be several possible reasons for the observed significant differences in abundance at mid and high altitude sites and within forested riparian sites at the three altitudinal levels. Differences in abundance of carabid beetles observed in disturbed riparian areas of Uluguru Mountains might be due to the differences of extent and frequency of disturbance, for example, the disturbance at both high and mid altitude, was mostly due to clear-cutting for firewood, farming activities and utilizing the surrounding areas for residence. Farming activities involved clearing of the vegetation cover leaving such areas open. It has been reported that agricultural activities cause more-prominent changes to land and vegetation characteristics on smaller temporal scales and at a larger spatial scale than most natural processes (Jepsen *et al.*, 2005). In the present study, farmers used fire in the preparation of their farms and burned residuals after harvesting (Pers. obs.). The frequency of farming was up to twice a year and for high food crop yield and vegetables, farmers used in-organic fertilizers and insecticides (Julius Msimbe, Pers. comm., 2012). According to Herrn (2009) attempts of identifying biodiversity pattern should properly consider the extent and properties of disturbance as the driver of biodiversity. Although at low altitude most disturbed areas experienced farming activities, human habitation, extraction of stones and gravels for building purposes, there seems to be a quick regeneration of herbs and therefore availability of resources. One or a combination of these human induced disturbances might have affected carabid beetle assemblages and hence the observed difference in abundance within disturbed and forested riparian habitat sites. Various studies have demonstrated that beetle assemblages are sensitive to human activities (Purvis and Fadl, 2002; Klimaszewski, *et al.*, 2003).

5.3 Diversity of riparian carabid beetles

5.3.1 Effect of altitude on the diversity of riparian carabid beetles

In the present study, there were significant differences in the diversity indices (H') of carabid beetles between the three altitudinal levels with the highest diversity found at mid altitude. Pair-wise comparison of the three levels of altitude using special t – test indicated a significant difference in diversity of riparian carabid species for all three pairs. There was no difference between the numbers of species found at the low and high altitude. The results of the present study indicated high species richness at mid altitude than at both high and low altitude as above. Instead of lower riparian carabid beetle species richness at high altitude as expected, there was equal species richness at both high and mid altitude.

It has been documented that diversity is unevenly distributed over the surface of the earth (Herrn, 2009). The most conspicuous spatial pattern of species diversity is a latitudinal gradient of decreasing richness of species from equator to poles (Willig *et al.*, 2003). As far as species richness is concerned, another striking pattern of species diversity is an altitudinal diversity gradient (Lomolino, 2001). There are two opposing opinions among scientists with regard to the variation of species richness along altitudinal gradient. Generally, species diversity tends to decrease with increasing altitude (Greenslade, 1968; Rahbek, 1995; Brown and Lomolino, 1998). Nevertheless, several studies have documented a non-monotonic pattern of species richness (Rahbek, 1995; Bhattarai and Vetaas, 2003). However, a growing body of evidence suggests that, for a wide variety of taxa, mid elevation peaks in species richness are perhaps more general (McCoy, 1990; Rahbek, 1995; Rahbek, 2005). This pattern suggests an initial increase in species richness to the mid altitudes, followed by a decrease in species richness towards higher altitudes. In this view the maximum number of species is found at the middle forming a "hump-shaped" curve. There is also evidence of a mid altitudinal trough in species richness gradients along altitude (Peet, 1978; Nyundo and Yarro, 2007).

Results from the present study seem to support the views which suggest an increase in species richness to mid altitudes before falling off towards higher elevations. Such results form a mid altitude hump predicted by Rahbeck (1995, 1997). This unimodal mid altitudinal hump may be a result of two distinct communities of the same taxa which have a wide area of overlapping, resulting in the intermediate area having more species than the tails of the distribution simply because the area of intersection has species from both communities. In this study the intersection area of high altitude and low altitude carabid beetle communities seems to be at mid altitude, hence have more species of beetles. The mid altitude peak in species in this study may also be a result of human mediated disturbances. It was observed during the study that many areas of high and low altitude zones were heavily influenced by anthropogenic activities than mid altitude zone. This might have increasingly resulted into unfavorable environment for carabid beetles.

Studies of other groups of insects have also documented the same species richness pattern as in the present study. In the Philippines, a study of ants along an elevational gradient indicated that species richness picked at mid elevations and declined sharply with increasing altitude (Samson *et al.*, 1997). In a widespread survey of leaf litter ant diversity, Ward (2000) found that species richness peaked at mid elevations in the tropics but decreased continuously with elevation in temperate regions. In the study of dung beetles along an altitudinal gradient on the eastern slope of the eastern Cordillera, Colombian Andes, Escobar *et al.* (2005) reported a curvilinear relationship between altitude and species richness, with a peak in richness at mid elevations.

As for many other taxonomic groups, mid elevation peaks in species richness has been frequently documented for birds (Rahbek, 1995, 1997; McCain, 2009), small mammals (Graham, 1990; Patterson *et al.*, 1998; Heaney, 2001; McCain, 2004), herpetofauna (Hofer *et al.*, 1999; Fu, 2007), invertebrates (Olson, 1994; Sanders *et al.*, 2003), plants (Mmari and Mabula, 1996; Va`zquez and Givnish, 1998; Kessler, 2001; Oommen and Shanker, 2005; Kluge *et al.*, 2006; Grau *et al.*, 2007) and insects (McCoy, 1990; Olson, 1994; Brehm *et al.*, 2003), including dung beetles (Lobo and Halffter, 2000). It has been document in the Udzungwa Mountain National Park of the EAM that plant species richness increases with increasing altitude up to mid altitude and then species richness drops gradually towards high altitude (Mmari and

Mabula, 1996). Recently, in the Eastern Himalaya, a study by Acharya *et al.* (2011) indicated also that species richness of birds is highest at mid elevations along one of the most extensive elevational gradients in the world.

Various processes such as climate (Kluge *et al.*, 2006; McCain, 2007; Sanders *et al.*, 2007), productivity, habitat heterogeneity, interspecific interactions (Rosenzweig, 1992, 1995; Kattan and Franco, 2004; Whittaker, 2010) and evolutionary and historical processes (niche conservatism, isolation, speciation, endemism, and evolutionary diversification) (Heaney, 2001; Lomolino, 2001; Hawkins *et al.*, 2007; Machac *et al.*, 2011) and spatial factors including area and the mid-domain effect (Rahbek, 1997; Sanders, 2002; Colwell *et al.*, 2004; McCain, 2004) have been proposed to explain altitudinal distributions of species.

In the present study, the effect of area on the relationship between species richness and elevation was not considered, however it could also be an alternative explanation for the mid altitudinal hump. Areas often decrease with elevation because of generally steeper terrain toward the highest peaks (Rahbeck, 1995; Körner, 2000). This small area effect with increasing isolation of habitats at higher altitudes would result in lower number of species at the upper end of the gradient (Lomolino, 2001). As tops of mountains tend to be isolated, it is highly probable that species dispersal and exchange events will be lower there (Brown and Lomolino, 1998; Lomolino, 2001). If the mid altitude had a larger area compared to the high altitude and low altitude, species richness at mid altitude might be explained by its large area. The effect of area on the relationship between species richness and elevation needs to be tested in the future.

In addition to a significant change in species richness with altitude, the results of the present study indicated a high degree of altitudinal site specificity, suggesting preferences for specific altitudes for some riparian carabid beetle species. Some species were confined to a single altitudinal site. The physical extremes and abrupt changes in abiotic conditions, such as a decrease in temperature and partial pressure of respiratory gases as well as an increase in precipitation (Hodkinson, 2005), might have restricted carabid beetle communities to distinct altitudinal zones. These changes result in a decrease in resource diversity, reduced habitat area, increase in unfavourable environment, and decrease in primary productivity (McCoy, 1990).

One aspect of biodiversity is the variety of species. Two locations can have similar species richness and abundance, but still have a different species composition. The three altitudinal levels had different riparian carabid fauna composition. This can be seen clearly by considering the eight most abundant species at each altitudinal level making a total of 87.64% of all individual riparian carabid beetles (21.31% from high altitude, 10.91% from mid altitude and 55.41% from low altitude). In these dominant species, the low altitude shared one common species with the mid altitude (*Trechodes* sp.1) and two species with the high altitude (Species 5 (Subfamily Bembidiinae) and *Trechodes babaulti*), the high altitude and mid altitude shared one species (Species 2 (Subfamily Bembidiinae)) and there was no dominant species at all the three altitudinal levels.

5.3.2 Effect of disturbance on the diversity of riparian carabid beetles

In this study, the disturbed habitat had slightly higher species richness of riparian carabid beetles compared to the forested riparian habitat. There were significant differences in the diversity indices (H') of carabid beetles between the disturbed and forested riparian areas. The highest Shannon-Wiener index of species diversity (H') was recorded from the disturbed riparian areas, whereas the lowest diversity index was recorded from the forested riparian areas.

It has been documented that not all carabid beetle species decline following habitat disturbance and that species' response depends on its dispersal power and habitat preference (Niemela, 1993). Management practices seem to favor species preferring dry conditions (Blake *et al.*, 1996), and those that have high dispersal power (Rushton *et al.*, 1989). This might be due to the creation of more microhabitats following disturbance hence reducing competition among species. Various studies (Niemela, 1993; Balog *et al.*, 2012) done under different disturbance regimes gave results concurring with results of the present study. Niemela (1993) reported that although it affected carabid assemblages, logging did not have a negative effect on species richness, which increased after cutting. A more recent study carried out in Eastern Carpathians, Romania by Balog *et al.* (2012) showed that carabid communities react to landscape change induced by land use and the highest species diversity was found in clear-cut and willow. Species compositional variability was significantly reduced by human mediated disturbance combinations suggesting that multiple disturbances may lead to a simplification of the entire assemblage (Cobb *et* *al.*, 2007). From the cited examples, ground beetle response to human disturbance differed strongly, suggesting that, although some species may appear to benefit from such disturbance combinations, their effects are detrimental to others.

5.4 Conclusions and recommendations

5.4.1 Conclusions

5.4.1.1 A total of 3261 individuals represented by 29 species were collected from the three altitudinal levels in the Uluguru Mountains. From the evaluation of abundance and species richness, it appears that Uluguru Mountains is very rich carabid fauna.

5.4.1.2 The results of this study showed no significant statistical difference in abundance of riparian carabid beetles between disturbed and forested riparian habitat. Carabid beetle responses to anthropogenic disturbances differed strongly and suggested that, although some species appeared to benefit from the disturbance combinations, these effects were detrimental to others depending on various degrees and intensity of disturbance.

5.4.1.3 There is altitudinal variation in abundance and species richness of riparian carabid beetles in the Uluguru Mountains. There were significant differences in the diversity of riparian carabid beetles between the three altitudinal levels with the highest diversity found at mid altitude. Species richness increases to the mid altitudes, followed by a decrease in species richness towards higher altitudes.

5.4.2 Recommendations

5.4.2.1 Spatially, different parts of the Uluguru Mountains have different abundance and species richness of carabid beetles. Attempts to sample as many habitats as possible should be made in order to obtain a complete picture of the diversity of carabid beetles.

5.4.2.2 Main inventories should also be made during other times of the year in order to obtain a full picture in terms of species composition and assessing whether there are also seasonal variations.

5.4.2.3 There is altitudinal variation in abundance and species richness of carabid beetles in the Uluguru Mountains. As it has been done in this study, most studies on altitudinal diversity gradients are restricted to either low, mid or high altitude, in essence covering only a part of the gradient or on a smaller mountain with narrow altitudinal breadth. Data that span over the entire gradient or data from the highest elevations where life occurs, especially when the gradient itself is extensive, likely provide more opportunities for better understanding patterns of species richness.

5.4.2.4 For complete carabid beetle biodiversity inventory both active searching (during the day and night times) and pitfall trapping should be employed. Pitfall traps would collect night active ground carabid beetles as well.

5.4.2.5 Vegetation cover is one of the ubiquitous elements in the landscapes that act as driver of biodiversity; therefore attempts of identifying biodiversity pattern should properly consider the extent, frequency of occurrence and properties of disturbance regimes on the vegetation cover as the driver of biodiversity. There is a clear deficit of information on the role of vegetation cover as driver of diversity pattern at landscape level.

5.4.2.6 The present study has acknowledged the existence of a "taxonomic impediment" in Tanzania, and therefore fosters the need for establishment of taxonomic centers with the necessary infrastructure. Presently, identification is carried overseas under high costs. The purpose of this ''National Taxonomic Initiative'' should be to remove or reduce the taxonomic impediment, the shortage of trained taxonomists and curators, and the impact these deficiencies have on our ability to conserve, use and share the benefits of our biological diversity.

REFERENCES

Acharya, B.K., Sanders, N.J., Vijayan, L. and Chettri, B (2011), Elevational Gradients in Bird Diversity in the Eastern Himalaya: An Evaluation of Distribution Patterns and Their Underlying Mechanisms. *PLoS ONE* **6**(12), e29097.

Altegrim, O., Sjoeberg, K. and Ball, J.P (1997), Forestry effects on a boreal ground beetle community in spring: selective logging and clear-cutting compared. *Entomologica Fennica* **8**, 19–26.

Andersen, J. and Hanssen, O (1994), Invertebratfaunaen pa° elvebredder – et oversett element. 1. Biller (Coleoptera) ved Gaula i Sør-Trøndelag. *NINA Oppdragsmelding* **326**, 1–23.

Andersen, J. and Hanssen, O (2005), Riparian beetles, a unique, but vulnerable element in the fauna of Fennoscandia. *Biodiversity and Conservation*, **14**, 3497–3524.

Araújo, L.M. and Fernandes, G.W (2003), Altitudinal patterns in a tropical ant assemblage and variation in species richness between habitats. *Lundiana* **4**(2), 103-109.

Balog, A., Hartel, T., Máthé, I. and Urák, I (2012), Carabid assemblages along a land use gradient in a Carpathian Mountain landscape. *North-Western Journal Of Zoology* **8** (2), 215-222.

Barnett, A.A., Read, N., Scurlock, J., Low, C., Noris, H. and Shapley, R (2002), Ecology of Rodent communities in agricultural habitats in Sierra Leone: Cocoa groves as forest refugia. *Tropical ecology* **41**(2), 127-142.

Basilewsky, P (1962), Mission Zoologique de l'I.R.S.A.C. en Afrique orientale (P. Basilewsky et N. Leleup, 1957). LX. Coleoptera Carabidae. *Annales Musée Royal de l'Afrique Centrale, Tervuren,Série Octavo. Sciences Zoologiques* **107**, 48–337.

Basilewsky, P (1976), Mission entomologique du Musee royal de l'Afrique Centrale auxm Monts Uluguru, Tanzanie. 19. Coleoptera Carabidae. *Revue Zoologique Africaine* **90**, 671-722.

Basilewsky, P (1953). Carabidae (Coleoptera, Adephaga). *Exploration du Parc National de l'Upemba. Mission G.F. de Witte.* **10**, 1-152.

Beaudry, S., Duchesne, L.C. and Cote, B (1997), Short-term effects of three forestry practices on carabid assemblages in a jack pine forest. *Canadian Journal of Forest Research* **27**, 2065–2071.

Beck, H.H (2001), The effects of livestock grazing on vegetation and ground beetles (Coleoptera, Carabidae) in a semi-arid grassland. Master of Science, Thesis, Oklahoma State University, USA.

Begon, M., Harper, J.L. and Townsend, C.R (1990), *Ecology: Individuals, Populations and Communities*. Blackwell Scientific, Boston.

Bhattarai, K.R. and Vetaas, O.R (2003), Variation in plant species richness of different life forms along a subtropical elevation gradient in the Himalayas, east Nepal. *Global Ecology and Biogeography* **12**, 327-340.

Blackburn, T.M (1999), Density, survey area and the perfection (or otherwise) of ecologists. *Oikos* **85**, 570-573.

Blake, S., Foster, G.N., Fischer, G.E.J. and Ligertwood, G.L (1996), Effects of management practices on the ground beetle faunas of newly established wildflower meadows in southern Scotland. *Annales Zoologici Fennici* **33**, 139–147.

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

Brehm, G., Homeier, J. and Fiedler, K (2003), Beta diversity of geometrid moths (Lepidoptera: Geometridae) in an Andean montane rainforest. *Diversity and Distributions* **9**, 351–366.

Brown, J.H. and Lomolino, M.V (1998), *Biogeography*. 2nd ed. Sinauer Associates, Sunderlands, MA.

Burgess, N., Doggart, N. and Lovett, J (2000), The Uluguru Mountains of eastern Tanzania: are we loosing their globally significant biodiversity values? Wildlife Conservation Society of Tanzania, Uluguru Mountains Biodiversity Conservation Project.

Butterfield, J (1997), Carabid community succession during the forestry cycle in conifer plantations. *Ecography* **20**, 614–625.

Carmona, D.M. and Landis, D.A (1999), Influence of refuge and cover crops on seasonal activity density of ground beetles (Coleoptera: Carabidae) in field crops. *Environmental Entomology* **28**, 1145-1153.

Channing, A (2000), *Summary of the amphibians of the Uluguru Mountains*. WCST, Morogoro.

Cobb, T.P., Langor, D.W. and Spence, J.R (2007), Biodiversity and multiple disturbances: boreal forest ground beetle (Coleoptera: Carabidae) responses to wildfire, harvesting, and herbicide. *Canadian Journal of Forest Research* **37**(8), 1310-1323.

Colwell, R.K., Rahbek. C. and Gotelli, N.J (2004), The mid-domain effect and species richness patterns: what have we learned so far? *American Naturalist* **163**, E1–E23.

Crowson, R.A (1981), *The Biology of the Coleoptera.* Academic, London.

CSIRO (1991), *The Insects of Australia: a textbook for students and research workers. Second edition.* Melbourne University Press.

Currie, C.R. and Digweed, S.C (1996), Effect of substrate depth on predation of larval *Pterositchus adstrictus* eschscholtz by adults of *P. melanarius* (Illiger) (Coleoptera: Carabidae). *Coleopterists Bulletin* **50**, 291-296.

Davies, J.G (1999), Beetles (Coleoptera) of Mkomazi. In; Coe, M., McWilliam, N., Stone, G. and Packer, M. (eds.) *Mkomazi: The ecology, biodiversity and conservation of a Tanzania savanna.* Royal Geographical Society, London.

Davies, K.F. and Margules, C.R (1998), Effects of habitat fragmentation on carabid beetles: Experimental evidence. *Journal of Animal Ecology* **67**, 460-671

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

Dennis, P., Young, M.R., Howard, C.L. and Gordon, I.J (1997), The response of epigeal beetles (Col.: Carabidae, Staphylinidae) to varied grazing regimes on upland *Nardus stricta* grasslands. *Journal ofApplied Ecology* **34**, 433-443.

Doggart, N., Mohoro, B., Kiure, J., Perkin, A., Lovett, J. and Burgess, N.D (2001), Status and biodiversity values of the Uluguru Forest Reserves. WCST/DOF, Uluguru Mountains Biodiversity Conservation Project, Morogoro.

Dufrene, M. and Legendre, P (1997), Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs,* **67**(3), 345-366.

Epstein, M.E. and Kulman, H.M (1990), Habitat Distribution and Seasonal Occurrence of Carabid Beetles in East-central Minnesota. *American Midland Naturalist* **123,** 209-225.

Erwin, T.L (1979), Thoughts on the evolutionary history of ground beetles: hypotheses generated from comparative faunal analysis of lowland forest sites in temperate and tropical regions, In: Erwin, T.L., Ball, G.E., Whitehead, D.L., Halpern, A.L., (eds.) *Carabid Beetles: Their Evolution, Natural History and Classification.* Junk, The Hague, pp. 539-592.

Erwin, T.L (1985), The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. In: Ball, G.E. (ed.). *Taxonomy, Phylogeny and Zoogeography of Beetles and Ants* Junk, The Hague, pp. 437-472.

Eryschov, V.I. and Trophimova, O.L (1984), Changes in the population of ground beetles (Coleoptera, Carabidae) in a clearing in the mountain taiga of the Kuznetsky Alatau foothills. *Zoologicheskii Zhurnal, Moscow* **63,** 848–852.

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

Evans, T.D. and Anderson, Q.A (1993), Results of an ornithological survey in the Ukaguru and East Usambara mountains, Tanzania. *Scopus* **17**(1), 40-47.

Evans, W.G (1988), Chemically mediated habitat recognition in shore insects (Coleoptera: Carabidae; Hemiptera: Saldidae). *Journal of Chemical Ecology* **14,** 1441-1454.

Fernandes, G.W. and Price, P.W (1988), Biogeographical gradients in gallings pecies richness. *Oecologia* **76**, 161-167.

Finn, J.A., Gittings, T. and Giller P.S (1999), Spatial and temporal variation in species composition of dung beetle assemblages in Southern Ireland. *Ecological Entomology* **24**, 24-36.

Framenau, V.W., Manderbach, R. and Baehr, M (2002), Riparian gravel banks of upland and lowland rivers in Victoria (South-east Australia): arthropod community structure and life-history patterns along a longitudinal gradient. *Australian Journal of Zoology* **50**, 103–123.

French, B.W., Elliott, N.C., Berberet, R.C. and Burd, J.D (2001), Effects of Riparian and Grassland Habitats on Ground Beetle (Coleoptera: Carabidae) Assemblages in Adjacent Wheat Fields. *Environmental Entomology* **30**(2), 225-234

Fu, C., Wang, J., Pu, Z., Zhang, S., Chen, H. *et al.* (2007), Elevational gradients of diversity for lizards and snakes in the Hengduan Mountains, China. *Biodiversity Conservation* **16**, 707–726.

Graham. G.L (1990), Bats versus birds: comparisons among Peruvian Volant vertebrate faunas along an elevational gradient. *Journal of Biogeography* **17**, 657–668.

Grau, O., Grytnes, J.A. and Birks, H.J.B (2007), A comparison of altitudinal species richness patterns of bryophytes with other plant groups in Nepal, Central Himalaya. *Journal of Biogeography* **34**, 1907–1915.

Greenburg, C.G. and Thomas, M.C (1995), Effects of forest management on coleopteran assemblages in sand pine scrub. *Florida Entomologist* **78**, 271–285.

Greenslade, P.J.M (1968), Habitat and altitude distribution of Carabidae (Coleoptera) in Argyll, Scotland. *Transactions of the Royal entomological Society, London* **120**, 39-54.

Gutierrez, D. and Menendez, R (1995), Distribution and abundance of butterflies in a mountain area in the northern Iberian peninsula. *Ecography* **18**, 209-216.

Hanski, I. and Cambefort, Y (1991), *Dung beetle ecology*. Princeton University Press, Princeton, N.J.

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. and Soeller, S.A (2007), Climate, niche conservatism, and the global bird diversity gradient. *American Naturalist* **170**, S16–S27.

Heaney, L.R (2001), Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypothesis. *Global Ecology and Biogeography* **10**, 15–39.

Heliola, J., Koivula, M. and Niemelä, J. (2001), Distribution of carabid beetles (Coleoptera, Carabidae) across a boreal forest-clearcut ecotone. *Conservation Biology* **15**, 370–377.

Henderson, P.A. and Seaby, M.H (2001), Species diversity and richness, Version 2.65. PISCES Conservation Ltd IRC House, Pennington, UK. Statistical software package

Hering, D (1998), Riparian Beetles (Coleoptera) along a Small Stream in the Oregon Coast Range and Their Interactions with the Aquatic Environment. *Coleopterists Bulletin* **52**, 161-170

Herrn, D.W.D (2009), Plant Species and Functional Diversity along Altitudinal Gradients, Southwest Ethiopian Highlands. Dissertation. Universität Bayreuth

Hodkinson, I.D (2005), Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Review* **80**, 489–513.

Hofer, U., Bersier, L.F. and Borcard, D (1999), Spatial organization of a herpetofauna on an elevational gradient revealed by null model tests. *Ecology* **80**, 976–988.

Howden, H.F. and Nealis, V.G (1975), Effects of clearing in a tropical rain forest on the composition of the coprophagous scarab beetle fauna (Coleoptera). *Biotropica* **7**, 77-83.

Huston, M.A (1994), *Biology diversity: The coexistence of species on changing landscapes*. Cambridge University Press, Cambridge.

Janzen, D.H (1973), Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* **54**, 687-708.

Jennings, D.T., Houseweart, M.W. and Dunn, G.A (1986), Carabid beetles (Coleoptera: Carabidae) associated with strip clearcut and dense spruce-fir forests of Maine. *Coleopterists Bulletin* **40**, 251–263.

Jepsen, J.U., Topping, C.J., Odderskaer, P., and Andersen, P.N (2005), Evaluating consequences of land-use strategies on wildlife populations using multiple-species predictive scenarios. *Agriculture, Ecosystems and Environment* **105,** 581-594.

Kattan, G.H. and Franco, P (2004), Bird diversity along elevational gradients in the Andes of Colombia: area and mass effects. *Global Ecology and Biogeography* **13,** 451–458.

Kessler, M (2001), Patterns of diversity and range size of selected plan groups along an elevational transect in the Bolivian Andes. *Biodiversity and Conservation* **10,** 1897–1921.

Klimaszewski, J., Bernier-Cardou, M. and Germain, C (2003), The effects of forestry practices on the abundance of arthropods (Acarina, Araneae, Collembola, Coleoptera and Diptera). *Belgian Journal of Entomology* **5,** 103-116.

Kluge, J., Kessler, M. and Dunn, R.R (2006), What drives elevational patterns of diversity? A test of geometric constraints, climate, and species pool effects for pteridophytes on an elevational gradient in Costa Rica. *Global Ecology and Biogeography* **15,** 358–371.

Koivula, M., Kukkonen, J., Niemela, J (2002), Boreal carabid beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. *Biodiversity and Conservation* **11,** 1269–1288.

Körner, C (2000), Why are there global gradients in species richness? Mountains might hold the answer. *Trends in Ecology and Evolution* **15,** 513-514.

Kromp, B (1999), Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation aspects and enhancement. *Agriculture, Ecosystems and Environment* **74** (1–3), 187–228.

Kumar, A., Longino, J.T., Colwell, R.K. and O'Donnell, S (2008), Elevational Patterns of Diversity and Abundance of Eusocial Paper Wasps (Vespidae) in Costa Rica. *Biotropica* **10**, 1744-7429.

Larsen, K.J., Work, T.T. and Purrington, F.F (2003), Habitat use patterns by ground beetles (Coleoptera: Carabidae) of northeastern Iowa. *Pedobiologia* **11**, 288–299.

Laurance, W.F. and Bierregaard, R.O (1997), *Tropical forest remnants.* University of Chicago Press, Chicago, Illinois.

Lawrence, I.F. and Britton, E.B (1991), Coleoptera. In: The *Insects* of *Australia.* 2nd ed. Melbourne Univ. Press, Melbourne, pp. 543-683.

Lawrence, J.F., Hastings, A.M., Dallwitz, M.J., Paine, T.A. and Zurcher, E.J (1999), *Beetles of the World: A Key and Information System for Families and Subfamilies.* CD-ROM, Version 1.0 for MSWindows. CSIRO Publishing, Melbourne.

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M. *et al.* (1998), Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forests. *Nature* **391**, 72-76.

Lawton, J.H., MacGarvin, M. and Heads, P.A (1987), Effects of altitude on the abundance and species richness of insect herbivores on bracken. – *Journal of Animal Ecology* **56**, 147–160.

Lenski, R.E (1982), The impact of forest cutting on the diversity of ground beetles (Coleoptera: Carabidae) in the southern Appalachians. *Ecological Entomology* 7, 385–390.

Lien, V.V. and Yuan, D (2003), The differences of butterfly (Lepidoptera, Papilionoidea) communities in habitats with various degrees of disturbance and altitudes in tropical forests of Vietnam. *Biodiversity and Conservation* **12**, 1099–1111

Lobo, J.M. and Halffter, G (2000), Biogeographical and ecological factors affecting the altitudinal variation of mountainous communities of coprophagous beetles (Coleoptera, Scarabaeoidea): a comparative study. *Annals of the Entomological Society of America* **93**, 115–126.

Lobo, J.M., Chehlarov, E. and Guéorguiev, B (2007), Variation in dung beetle (Coleoptera: Scarabaeoidea) assemblages with altitude in the Bulgarian Rhodopes Mountains: A comparison. *European Journal of Entomology* **104**, 489–495.

Lomolino, M.V (2001), Elevation gradients in species density: historical and prospective views. *Global Ecology and Biogeography* **10**, 3-13.

Lott, D.A (2003), An annotated list of wetland ground beetles (Carabidae) and rove beetles (Staphylinidae) found in the British Isles including a literature review of their ecology. English Nature Research Reports.

Lövei, G.L. and Sunderland, K.D (1996), Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology* **41**, 231–256.

Lovett, J.C (1996), Elevational and latitudinal changes in tree associations and diversity in the Eastern Arc Mountains of Tanzania. *Journal of Tropical Ecology* **12**, 629–650.

Lovett, J.C (1998), Importance of the Eastern Arc mountains for vascular plants. *Journal of the East African Natural History Society* **87**, 59-74.

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

Luff, M.L (1996), Use of Carabids as environmental indicators in grasslands and cereals. *Annales Zoologici Fennici.* **35**, 185-195.

Luff, M.L (1990), Spatial and temporal stability of Carabid communities in a grass/arable mosaic. In N. Stork Ed. *The Role of Ground Beetles in Ecological and Environmental Studies.* Intercept, Andover, Hampshire.

Lyamuya, V.E., Noah, L.G., Kilasara, M., Kirenga, E.J. and Burgess, N.D (1994), Socio-economic and land-use factors affecting the degradation of the Uluguru mountains catchment in Morogoro region, Tanzania. Regional Natural Resources Office, Morogoro, and the Royal Society for the Protection of Birds, Sandy, UK.

Machac, A., Janda, M., Dunn, R.R. and Sanders, N.J (2011), Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity. *Ecography* **34**, 364–371.

Magura, T., Tothmeresz, B. and Bordan, Z.S (2000), Effects of nature management practice on carabid assemblages (Coleoptera: Carabidae) in a non-native plantation. *Biological Conservation* **93**, 95–102.

Magurran, A.E (1988), *Ecological Diversity and its Measuerement.* Chapman and Hall, London.

Manderbach, R. and Reich, M (1995), Auswirkungen groβer Qurbauwerke auf Laufkäferzönosen (Coleoptera, Carabidae) von Umlagerungsstrecken der Oberen Isar. *Archiv für Hydrobiologie, Supplement* **101**, 573-588.

Martin-Piera, F. and Lobo, J.M (1993), Altitudinal distribution patterns of copro-necrophage Scarabaeoidea in Veracruz, Mexico. *Coleopterist Bulletin* **47**, 321-334

Masis, A. and Marquis, R.J (2007), Dung Beetle (Coleoptera: Scarabaeoidea) Community Response to Clear-cutting in the Missouri Ozarks. *Journal of the Kansas Entomological Society* **80**, 146-155

May, R.M (1992), How many species inhabit the earth? *Scientific American* **267**, 42-48.

McCain, C.M (2004), The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *Journal of Biogeography* **31**, 19–31.

McCain, C.M (2007), Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography* **16**, 1–13.

McCain, C.M (2009), Global analysis of bird elevational diversity. *Global Ecology and Biogeography* **18**, 346–360.

McCoy, E.D (1990), The distribution of Insects along elevationla gradients. *Oikos* **58**, 313-322.

Miserendino, M.L (2001), Macroinvertebrate assemblages in Andean Patagonian rivers and streams: environmental relationships. *Hydrobiologia* **444**, 147-158.

Mmari, C. and Mabula, C (1996), A Botanical Survey in Kawemba, Kitemele and Kiranzi-Kitunguru Forest Reserves, Udzungwa Mountains, Tanzania. *A consultancy Report* submitted to HIMA- DANIDA, Iringa.

Munishi, P.K.T., Shear, T.H., Wentworth, T. and Temu, R.A.P.C (2007), Compositional gradients of plant communities in submontane rainforests of eastern Tanzania. *Journal of Tropical Forest Science* **19**(1), 35-45.

New, T.R (1998), The role of ground beetles (Coleoptera: Ground beetleae) in monitoring programmes in Australia. *Annales Zoologici Fennici* **35**, 163-171.

Newmark, W.D (1998), Forest area, fragmentation and loss in the Eastern Arc Mountains: Implications for the conservation of biological diversity. *Journal of East African Natural History* **87**, 29-36

Niemelä, J., Langor, D. and Spence, J.R (1993), Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. *Conservation Biology* 7, 551–557.

Niemela, J., Tukia, H. and Halme, E (1994), Patterns of carabid diversity in Finnish mature taiga. *Annales Zoologici Fennici* **31**, 123-129

Niemelä, J.and Halme, E (1992), Habitat associations of carabid beetles in fields and forests on the Åland Islands, SW Finland. *Ecography* **15**, 3–11.

Niemelä, J.K (1993), Mystery of the missing species: species-abundance distribution of boreal ground-beetles. *Annules Zoologici Fennici* **30**, 169–172.

Nkombe, P.M (2003), The Future of the Uluguru Mountain Forest, Tanzania. Unedited version of a paper submitted to the XII World Forestry Congress, Canada.

Noonan, G.R., Ball, G.E. and Stork, N.E (eds.) (1992), *The Biogeography of Ground Beetles of Mountains and Islands.* Intercept, Andover.

Nummelin, M. and Nshubemuki, L (1998), seasonality and structure of the arthropod community in a forested valley in the uluguru mountains, eastern tanzania In: Burgess,N.D., Nummelin, M., Fjeldså, J., Howell, K.M., Lukumbuzya,K. And Mhando,L.(Eds.) *Biodiversity and Conservation of the Eastern Arc Mountains of Tanzania and Kenya.* Special Issue: *Journal of East African Natural History.* **87**, 205 – 212.

Nummelin. M (1989), Seasonality and effects of forestry practices on forest floor arthropods in the Kibale Forest, Western Uganda. *Fauna Norvegica* **36**, 17-25

Nyundo, B.A. and Yarro, J.G (2007), Designing a biodiversity invertory for ground beetles (Coleoptera, Carabidae) in the udzungwa Mountains National Park. *Discovery and Innovation* **19** (Supplement 1), 61-68

Ødegaard, F (2000), How many species of arthropods? Erwin's estimate revised. *Biological Journal of the Linnean Society* **71**, 583–597.

Oliver, I. and Beattie, A.J (1996), Designing a cost-effective invertebrate survey: A test of methods for rapid assessment of biodiversity. *Ecological Applications* **6**(2), 594-607.

Olson, D.M (1994), The distribution of leaf litter invertebrates along a Neotropical altitudinal gradient. *Journal of Tropical Ecology* **10**, 129–150.

Oommen, M.A. and Shanker, K (2005), Elevational species richness patterns emerge from multiple local mechanisms in Himalayan woody plants. *Ecology* **86**, 3039–3047.

Paetzold, A. and Tockner, K (2005), Effects of riparian arthropod predation on the biomass and abundance of aquatic insect emergence. *Journal of the North American Benthological Society* **24**, 395-402.

Parmenter, R.R. and MacMahon, J.A (1988), Factors Influencing Species Composition and Population Sizes in a Ground Beetle Community (Carabidae): Predation by Rodents. *Oikos* **52**, 350-356.

Patterson, B.D., Stotz, D.F., Solari, S., Fitzpatrick, J.W., Pacheco, V (1998), Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *Journal of Biogeography* **25**, 593–607.

Pearson, D.L (1988), The biology of tiger beetles. *Annual Review of Entomology.* **33**, 12347

Pearson, D.L. and Cassola, F (1992), World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. *Conservation Biology* **6**, 376-391.

Peet, R.K (1978), Forest vegetation of colorado front range - patterns of species diversity. *Vegetation* **37**, 65-78.

Phillips, I.D., Cobb T.P., John R. Spence, J.R. and Brigham, R.M (2006), Salvage Logging, Edge Effects, and Carabid Beetles: Connections to Conservation and Sustainable Forest Management. *Environmental Entomology* **35**(4), 950-957

Pielou, E.C (1966), The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology* **13**, 131-144.

Pimm, S.L (1998), An assessment of the risk of extinction for the Cape Sable seasidesparrow. Unpublished report. Vero Beach and Homestead, Fla.: U.S. Fish and Wildlife Service and Everglades National Park.

Pimm, S.L. and Gilpin, M.E (1989), Theoretical issues in conservation biology. In: Roughgarden J., May R.M. and Lewin S.A. (eds), *Perspectives in Ecological Theory.* Princeton University Press, Princeton, New Jersey, pp. 287-305.

Pócs, T (1976), Vegetation mapping in the Uluguru Mountains (Tanzania, East Africa). *Boissera* **24,** 477-498.

Pogue, O., Clark, S. and Paulson, S (2008), Effects of human disturbance on ground beetle diversity. Department of Agriculture and Natural Resources, Berea, KY, 40404 (Unpublished report)

Purvis, G. and Fadl, A (2002), The influence of cropping rotations and soil cultivation practice on the population ecology of carabids (Coleoptera: Carabidae) in arable land. *Pedobiologia* **46,** 452-474.

Rahbek, C (1995), The elevational gradient of species richness - a uniform pattern? *Ecography* **18,** 200-205.

Rahbek, C (1997), The relationship among area, elevation and regional species richness in Neotropical birds. *American Naturalist* **149,** 875–902.

Rahbek, C (2005), The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters* **8,** 224-239.

Rainio, J. and Niemelä, J (2003), Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation* **12,** 487-506.

Rosenzweig, M.L (1992), Species diversity gradients: we know more and less than we thought. *Journal of Mammalogy* **73,** 715–730.

Rosenzweig, M.L (1995), *Species diversity in space and time*. Cambridge: Cambridge University Press.

Rushton, S.P., Luff, M.L. and Eyre, M.D (1989), Effect of pasture improvement and management on the ground beetle and spider communitites of upland grasslands. *Journal of Applied Ecology* **26**, 489–503.

Saint-Germain, M., Larrive´e, M. and Drapeau, P., Fahrig, L. and Buddle, C.M (2005), Short-term response of ground beetles (Coleoptera: Carabidae) to fire and logging in a spruce-dominated boreal landscape. *Forest Ecology and Management* **212**, 118–126

Samson, D.A., Rickhart, E.A. and Gonzalez, P.C (1997), Ant diversity and abundance along an elevational gradient in Philippines. *Biotropica* **29**, 349-363.

Sanders, N.J (2002), Elevational gradients in ant species richness: area, geometry, and Rapoport's Rule. *Ecography* **25**, 25–32.

Sanders, N.J., Lessard, J.P., Dunn, R.R. and Fitzpatrick, M.C (2007), Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography* **16**, 640–649.

Sanders, N.J., Moss, J. and Wagner, D (2003), Patterns of ant species richness along elevational gradients in an arid ecosystem. *Global Ecology and Biogeography* **12**, 77–100.

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

Semida, F.M., Abdel-Dayem, M.S., Zalat, S.M. and Gilbert, F.S (2001), Habitat heterogeneity, altitudinal gradients in relation to beetle diversity in South Sinai. *Egyptian Journal of Biology* **3**, 137-146.

Shahabuddin, G., Schulze, C.H. and Tscharntke, T (2005), Changes of dung beetle communities from rainforests towards agroforestry systems and annual cultures in Sulawesi. *Biodiversity and Conservation* **14**, 863-877.

Siepe, A (1989), Untersuchungen zur Besiedlung einer Auen-Catena am südlichen Oberrhein durch Laufkäfer (Coleoptera: Carabidae) unter besonderer Berücksichtigung der Einflüsse des Flutgeschehens. Dissertation, Universität Freiburg.

Skalski, T., Kędzior, R., Maciejowski, W. and Kacprzak, A (2011), Soil and habitat preferences of ground beetles (*Coleoptera, Carabidae*) in natural mountain landscape. *Baltic Journal of Coleopterology* **11**(2), 105-115.

Sousa, W.P (1984), The role of disturbance in natural communities. *Annual Reviewof Ecology and Systematics* **15**, 353–391.

Spence, J.R., Langor, D.W., Niemela, J.K., Carcamo, H.A. and Currie, C.R (1996), Northern forestry and carabids: the case for concern about old-growth species. *Annules Zoologici Fennici* **33**, 173–184.

SPSS (2000), SYSTAT Version 10. Statistical software Package

Sroka, K. and Finch, O.D (2006), Ground beetle diversity in ancient woodland remnants in north-western Germany (Coleoptera, Carabidae). *Journal of Insect Conservation* **10**, 335-350.

Stanley, W.T., Kihaule, P.M., Howell, K.M. and Hutterer, R (1998), Small mammals of the Eastern Arc Mountains, Tanzania. *Journal of the East African Natural History Society* **87**, 91-100.

Stork, N.E (ed.) (1990), *The Role* of *Ground Beetles in Ecological and Environmental Studies.* Andover: Intercept.

Svendsen, J.O. and Hansen, L.A (eds.) (1995), *Report on the Uluguru Biodiversity Survey 1993. Parts A and B.* Unpublished Report. Tanzania Forestry Research Institute, Royal Society for the Protection of Birds, Danish Centre for Tropical Biodiversity.

Szujecki, A (1987), *Ecology of Forest Insects.* Dr. W. Junk Publishers, Dordrecht, Boston and Lancaster.

Thiele, H.U (1977), *Carabid Beetles in Their Environments.* Springer-Verlag, Berlin.

Thompson, L.C. and Allen, R.T (1993), Site preparation affects ground beetles in a clear cut bottomland hardwood forest in southeastern Arkansas. In: Brissette J.C. (ed.), Proceedings of the Seventh Biennial Southern Silvicultural Research Conference, 1992 November 17–19, Mobile, AL. Gen. Tech. Rep. SO-93. U.S. Department of Agriculture, Forests Service, Southern Forest Experiment Station, New Orleans, LA, pp. 57–64.

Ulyshen, M.D., Hanula, J.L., Horn, S., Kilgo, J.C. and E. Moorman, C.E (2005), Herbivorous Insect Response to Group Selection Cutting in a South-eastern Bottomland Hardwood Forest. *Environmental Entomology* **34**(2), 395-402.

Va`zquez, G.J.A. and Givnish, T.J (1998), Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantla`n. *Journal of Ecology* **86**, 999–1020.

van Huizen, T.H.P (1977), The significance of flight activity in the life cycle of *Amam plebeja* Gyllh. (Coleoptera, Carabidae). *Oecologia* **29**, 27 - 41

Van Looy, K., Vanacker, S., Jochems, H. and Dufrêne, M (2005), Ground beetle habitat templets and riverbank integrity. *River Research and Applications* **21**(10), 1-14.

Vasconcelos, S.D., Williams, T., Hails, R.S. and Cory, J.S (1996), Prey selection and baculovirus dissemination by carabid predators of Lepidoptera. *Ecological Entomology* **21**, 98-104.

Ward, P.S (2000), Broad-scale patterns of diversity in leaf litter ant communities. *Ants: standard methods for measuring and monitoring biodiversity* (ed. D. Agosti, J.D. Majer, L.E. Alonso and T.R. Schultz), pp. 99–121. Smithsonian Institution Press, Washington, D.C.

Warriner, M.D., Nebeker, T.E., Leininger, T.D. and Meadows, J.S (2002), The effects of thinning on beetles (Coleoptera: Carabidae, Cerambycidae) in bottomland hardwood forests. In: Outcalt K.W. (ed.), Proceedings of the Eleventh Biennial Southern Silvicultural Research Conference, Gen. Tech. Rep. SRS-48. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp. 569–573.

Werner, S.M. and Raffa, K.F (2000), Effects of forest management practices on the diversity of ground-occurring beetles in mixed northern hardwood forests of the great lakes region. *Forest Ecology and Management* **139**, 135–155.

White, R.E (1983), *A Field Guide to the Beetles of North America*. Houghton Miifflin Co., Boston and New York.

Whittaker, R.J (2010), Meta-analyses and mega-mistakes: calling time on metaanalysis of the species richness–productivity relationship. *Ecology* **91**, 2522–2533.

Willig, M.R., Kaufman, D.M. and Stevens, R.D (2003), Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology Evolution and Systematics* **34**, 273-309.

Wilson, E.O (1992), *The diversity of life*. Harvard University Press, Cambridge, MA.

Wolda, H (1987), Altitude, habitat and tropical insect diversity. *Biological Journal of the Linnean Society* **30**, 313-323.

Zar, J.H (1984), *Biostatistical Analysis*. Second edition. Prentice Hall, Englewood Cliffs, NJ.

Zilihona, E.I. and Ntumi, C (1998), A comparison of Coleopteran diversity in the logged, unlogged and pine plantation in the Kibale forest, Western Uganda. Tropical Biology Association.

Zilihona, I., Heinonen, J. and Nummelin, M (1998), Arthropod diversity and abundance along the Kihansi gorge in the southern Udzungwa Mountains, Tanzania. *Journal of the East African Natural History* **87**, 233-240.

APPENDICES

Appendix 1: Carabid beetle abundance at different levels of altitude and habitat in Uluguru Mountains.

SITE	sSITE	HABITAT	ALT. BAND	LEVEL	ALTITUDE	N_{icol}
ST1	ST1A	Forested	1800-2500 m	High	2107	164
	ST1B	Disturbed	1800-2500 m	High	1889	57
ST2	ST2A	Forested	1800-2500 m	High	2054, 2068	205
	ST2B	Disturbed	1800-2500 m	High	1874	79
ST3	ST3A	Forested	1800-2500 m	High	1985, 1989	161
	ST3B	Disturbed	1800-2500 m	High	1828, 1830, 1833	108
ST4	ST4A	Forested	1100–1800 m	Mid	1752, 1774, 1798	226
	ST4B	Disturbed	1100–1800 m	Mid	1549, 1565, 1588	107
ST5	ST5A	Forested	1100–1800 m	Mid	1528, 1547, 1578, 1508	39
	ST5B	Disturbed	1100–1800 m	Mid	1320, 1345	46
ST6	ST6A	Forested	1100–1800 m	Mid	1442, 1449, 1467, 1473	28
	ST6B	Disturbed	1100–1800 m	Mid	1353, 1377, 1389, 1395, 1404	53
ST7	ST7A	Forested	400–1100 m	Low	642, 656, 665	469
	ST7B	Disturbed	400–1100 m	Low	561, 580, 597	211
ST8	ST8A	Forested	400 – 1100 m	Low	593, 612, 623	118
	ST8B	Disturbed	400 – 1100 m	Low	508, 511, 518	221
ST9	ST9A	Forested	400 – 1100 m	Low	584, 589, 597	406
	ST9B	Disturbed	400 – 1100 m	Low	517, 528, 589	563

Note: $N_{icol.}$ = Number of individuals collected, ALT. BAND = ALTITUDE BAND, ALTITUDE is measured in m a.s.l., sSITE = SUBSITE

Appendix 2: Detailed list of carabid beetles species at three altitudinal levels and two types of riparian habitat in Uluguru Mountains.

SPECIES	ALTITUDINAL LEVEL			RIPARIAN HABITAT	
	HIGH	MID	LOW	FORESTED	DISTURBED
Trechodes sp.1	3	179	80	176	86
Metagonum sp.1	1	8	0	1	8
Peryphus meruanus	0	74	6	61	19
Species 1	0	4	28	16	16
Metagonum mboko	44	34	6	33	51
Species 2	91	47	15	45	108
Crepidogaster sp.1	0	13	2	1	14
Species 3	0	9	0	0	9
Diatypus uluguruanus	0	3	0	0	3
Species 4	1	56	24	63	18
Abacetus sp.1	3	29	10	17	25
Species 5	59	9	67	39	96
Abacetus sp.2	6	10	126	91	51
Trechodes babaulti	501	7	1534	1178	864
Species 6	0	1	23	17	7
Thyreopterus sp.1	0	1	5	0	6
Tachys sp.1	26	0	9	4	31
Species 7	0	0	1	1	0
Species 8	5	2	4	6	5
Species 9	17	2	0	12	7
Species 10	3	2	0	2	3
Craspedophorus sp.1	2	2	0	2	2
Metagonum sp.2	1	0	0	0	1
Species 11	0	4	47	40	11
Species 12	0	0	1	1	0
Species 13	0	1	0	0	1
Species 14	3	0	0	3	0
Metagonum sp.3	4	0	0	4	0
Triaenogenius sp.1	4	2	0	3	3

Appendix 3: All carabid beetle species collected from the study sites

S/N	Subfamily	Genus	Species
1	Trechinae	*Trechodes*	*Trechodes* sp.1
2	Anchomeninae	*Metagonum*	*Metagonum* sp.1
3	Bembidiinae	*Peryphus*	*Peryphus meruanus*
4	Bembidiinae	G01	Species 1
5	Anchomeninae	*Metagonum*	*Metagonum mboko*
6	Bembidiinae	G02	Species 2
7	Brachininae	*Crepidogaster*	*Crepidogaster* sp.1
8	Lebiinae	G03	Species 3
9	Harpalinae	*Diatypus*	*Diatypus uluguruanus*
10	Bembidiinae	G04	Species 4
11	Pterostichinae	*Abacetus*	*Abacetus* sp.1
12	Bembidiinae	G05	Species 5
13	Pterostichinae	*Abacetus*	*Abacetus* sp.2
14	Trechinae	*Trechodes*	*Trechodes babaulti*
15	Scaritinae	G06	Species 6
16	Thyreopterinae	*Thyreopterus*	*Thyreopterus* sp.1
17	Bembidiinae	*Tachys*	*Tachys* sp.1
18	Omophroninae	G07	Species 7
19	Pterostichinae	G08	Species 8
20	Pterostichinae	G09	Species 9
21	Bembidiinae	G10	Species 10
22	Panagaeinae	*Craspedophorus*	*Craspedophorus* sp.1
23	Anchomeninae	*Metagonum*	*Metagonum* sp.2
24	Bembidiinae	G11	Species 11
25	Odacanthinae	G12	Species 12
26	Odacanthinae	G13	Species 13
27	Scaritinae	G14	Species 14
28	Anchomeninae	*Metagonum*	*Metagonum* sp.3
29	Helluoninae	*Triaenogenius*	*Triaenogenius* sp.1

Key: G01 to G014 = Unidentified Genus; Species 1 to Species 14 = Morphospecies