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Impact of land use on assemblages of carabid beetles (Coleoptera: Carabidae) in Zambia

Dissertation

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Marburg an der Lahn, December 2014

Donald Chungu

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1 General introduction

Biodiversity in Africa

Africa harbors diverse habitats ranging from tropical rainforests to deserts: The continent includes some of the driest deserts (e.g. Sahara and Kalahari deserts), largest tropical rainforests (e.g. Ituri forest) and highest mountains in the world (e.g. Kilimanjaro mountain; UNEP 2002). Based on these habitat diversity and historical reasons (Heywood 1995; Oba 2014), Africa possesses a unique flora and fauna with even large genetic breaks within the continent (see Cape Flora) and between the main land and the adjacent islands like Madagascar (Myers 1990; Goldblatt 1997). Of the 25 global biodiversity hotspots, a total of five are found in Africa (Koppler et al. 2002).

Tropical forests are the most diverse and the most ecologically complex of all terrestrial ecosystems, probably sustain over one-third of all species (Raven 1980; Wilson 1992) and play a disproportionately large role in global carbon and energy cycles (Detwiler 1988; Le Quere et al. 2014). Due to their heterogeneity, greater variety of microhabitats, a greater range of microclimates and increased resource spectrum, tropical forests accommodate a rich diversity of invertebrates as well as vertebrates (Huston 1993; Townsend et al. 2008). It has been estimated that tropical forests in Africa cover 520 million hectares and constitutes more than 17% of the world’s forests stretching from western Africa through central to southern Africa (Achard et al. 2002; Klopper et al. 2002). Recent evidence suggests that the earth is undergoing a period of substantial decreases in biodiversity and mass extinction of species (Myers & Knoll 2001; Butchart et al. 2010; Uchida & Ushimaru 2014), which threaten ecosystem processes and therefore also ecosystem services (Heywood 1995; Bihn et al. 2010) and the welfare of humans (Balmford & Bond 2005). Due to population explosion and urbanization, tropical forests have been extensively modified and are shrinking at an unprecedented rate (Matson et al. 1997). As a consequence, Africa had lost 39 million hectares of tropical forest during the 1980s and another 10 million hectares by 1995 (UNEP 2002), and the continent's large and diverse biological heritage has been exposed to greater risk. Most studies on biodiversity loss have focused on mammals (Dirzo & Raven 2003; Gonzalez 2013), birds (Gregory et al. 2005; de Lima et al. 2013; Boyer & Jetz 2014) and plants (Wood et al. 2013; Newbold et al. 2014). However, the decline and extinction rates of insects, which comprise the majority of terrestrial biodiversity, are inadequately quantified and poorly understood, especially so in Africa (Dunn 2005; Thomas 2005; Runge et al. 2014).

Land use change and species assemblages

The major drivers underlying the potential loss of biodiversity are land use change and climate change (Fig. 1.1; Sala et al. 2000; Thomas et al. 2004; Foley et al. 2005). Climate change is already affecting species distributions and traits around the world (Thomas et al. 2004; Zeuss et al. 2014) and is projected to have considerable further impacts this century (Gitay et al 2002; Thomas et al. 2004). Nevertheless, land use change remains to be the dominant driver of biodiversity loss over the next century (Souza et al. 2014; Riordan & Rundel 2014). For instance in Europe, land use change has been identified as the principle driver of butterfly declines (Asher et al. 2001; Van Dyck et al. 2009) and population decrease in birds (Gregory et al. 2005).

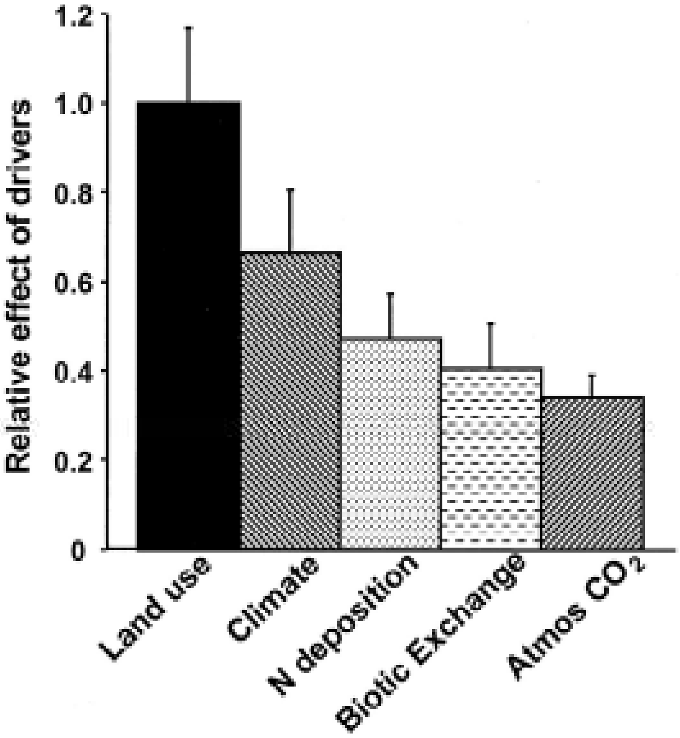

Fig. 1.1: *Major biodiversity threats; land use and climate change are the dominant threats to biodiversity. Source: Sala et al. (2000).*

Agriculture is a dominant and socioeconomically important land use in Africa and elsewhere (Heywood 1995; Halada et al. 2011). However, agricultural expansion generally reduces habitat area, quality and heterogeneity through the interlinked impacts of increased agrochemical use, changes in tillage or grazing practices and is widely recognized as a major driver of biodiversity decline (Benton et al. 2003; Tscharntke et al. 2012). Another form of land use that is increasingly becoming a common feature in many African countries are plantations of non-native tree species and is regarded as a strategy to alleviate the critical shortages of fuel-wood and timber (Evans & Turnbull 2004). Plantation forestry often creates artificially homogenous forests with one or few tree species with individuals of the same size and age. Homogeneous forests have relatively few available niches and have been reported to support fewer species (Stephens & Wagner 2007; Bremer & Farley 2010). These plantations are also characterized by special silvicultural treatments, use of fire and chemicals and constant soil cultivation (Evans & Turnbull 2004; Chungu et al. 2010) which may also threaten native biodiversity (Heywood 1995; Tscharntke et al. 2012). Although plantations can be managed to maximize species diversity in some cases (Pawson et al. 2008; Brockerhoff et al. 2008), they are unlikely to attain the biodiversity levels of natural forest (Sloan et al. 2014) and should not be regarded as an alternative to natural forests but rather as complementary to them (Heywood 1995).

Beside its influence on species richness, land use change is often suggested as the source of variation in species assemblages at both local and regional scales (Huston 1993; Myers & Knoll 2001; Adams 2010), and has contributed significantly to the decline of sensitive species including carabid beetles in many parts of the world (Brooks et al. 2002; Kotze & O’Hara 2003; Vanbergen et al. 2010). Carabid beetles are widely distributed, are taxonomically well known, with relatively stable systematics, and their ecology has been widely studied (Lövei & Sunderland 1996; Homburg et al. 2014). Carabid beetles are especially important in five major different ways. (i) Experimental evidence suggests that carabid beetles may potentially serve as keystone indicators (Kotze et al. 2011). (ii) Carabids are sensitive to anthropogenic induced conditions, such as pesticide use in agro-ecosystems or contamination of soils by heavy metals (Menalled et al. 2007; Butovsky 2011). (iii) Carabid assemblages host numerous species that are characteristic of particular habitat types or successional stages, which makes them promising bioindicators (Lövei & Sunderland 1996). (iv) Carabids may function as early-warning signalers, as suggested by recent studies linking climate and carabid distributions (Gómez et al. 2014; Pozsgai & Littlewood 2014). (v) Carabids reflect natural and human-caused disturbances and management (Lövei & Sunderland 1996).

Current theory, e.g. the habitat templet theory (Townsend et al. 1997), predicts that abiotic factors act like filters, sorting organisms with unique trait combinations appropriate for specific habitat conditions (Keddy 1992; Statzner et al. 2004; Berg et al. 2010). Consistent with this theory, land use change is likely to affect the assemblage of species in communities. Body size is one of the most fundamental properties of an organism and correlates with host range, metabolism and extinction risk (Blackburn & Gaston 1994; Brändle et al. 2000; Woodward et al. 2005). Body size has been used to quantify energy transfer, biogeochemical cycling in ecosystems and division of resources within a community (White et al. 2007; Yvon-Durocher & Allen 2012). Therefore, body size has been reported to vary between carabid species inhabiting different forms of land use (Zygmunt et al. 2006;

Lagisz 2008). Body size variation among species has resulted in the development of an important hypothesis commonly referred to as "body size hypothesis", which predicts that body size should decrease in disturbed ecosystems (Gray's 1989; Blake et al. 1994).

Pollution and species assemblages

Africa is richly endowed with mineral and fossil fuel resources. Globally, the continent currently accounts for about 70% of the diamond, 60% of the gold and 20% of the copper (Nriagu 1992). In many countries, mining operations rely on pollution prone technologies and the controls on the discharge of pollutants from African mines and smelters are lax and emission guidelines are often ignored (Wilson et al. 2002; Kukenova & Monteiro 2008). The net result is that the air, water, soils, plants and animals near the mining centers of Africa tend to be severely contaminated with heavy metals (Nriagu 1992). As a consequence, effects of mines and smelters on the surrounding natural environment are enormous (Dudka & Adriano 1997; Deikumah et al. 2014).

Air pollution as well as eutrophication is important in affecting species assemblages in natural environments. Numerous studies have generally demonstrated changes in insects performance at elevated levels of air pollution (Coviella & Trumble 1999; Seinfeld & Pandis 2012) and particularly elevated concentration of CO_2 has been reported to favor some parasitoid families but limit populations of sucking insects (Hillstrom & Lindroth 2008). Furthermore, eutrophication, i.e. increased soil and water fertility caused by unintended nutrient inputs from fossil fuel combustion and agriculture (Smith et al. 1999), is altering the plant composition and vegetation structure of many habitats, often in conjunction with other drivers such as management intensity and climate change (Hartley & Mitchell 2005). Biodiversity of plant and insect populations (e.g. butterflies) have been shown to correlate negatively with nitrogen input (Stevens et al. 2010; Wallisdevries & Van Swaay 2006).

In addition, contamination of the natural environment with various heavy metals is a long lasting problem (Nriagu 1992). Heavy metals accumulate in litter and soil due to their high affinity for organic substances and clay particles (Brändle et al. 2001; Walker 2012). Although many metals are essential for the biochemistry and physiology of organisms (e.g. iron, copper and zinc), all become toxic when the required levels are greatly exceeded (Clement & Rohr 2009). Other metals, such as mercury, plutonium and lead, often called xenobiotic metals, are not used by organisms in any biochemical process and can become highly toxic even at low concentrations (Clement & Rohr 2009). Both groups of metals are by-products of human industry (Walker 2012) and often are found in such high concentrations that they reach toxic levels in some ecosystem components leading to disturbance in their proper functioning (Clement & Rohr 2009). Such negative effects of metal pollution may lead to stressed ecosystems and may reduce richness of soil-dwelling organisms, including many species of invertebrates (Walker 2012). For example in carabid species, high metal concentrations have been reported to decrease survival probability (Sousa 1984), increase mortality (Mozdzer et al. 2003), and decrease fecundity and body mass (Kramarz 2000).

The study area

All field work for this dissertation was carried out in the Copperbelt and North-western provinces of Zambia. This region is dominated by Miombo woodland which covers 53% of the country (Chidumayo 1997) and is economically important for the supply of timber, poles, firewood and charcoal (Chidumayo 1997). Miombo is regarded as a vegetation type that has been maintained by man through a long history of cutting, cultivation and frequent dry season fires over the last 55,000 years (Lawton 1978). The 20th century witnessed the intensification of land use activities as a result of increasing human and livestock populations. More than 7% of this region has been converted into monoculture plantations of non-native tree species including eucalyptus and pine (Chidumayo 1997). Agricultural activities have continued to add huge pressure on native forest resources and have become one of the most important land use type in the area. Further, mining is a major activity not only in the region but also contribute significantly to the economic activities in Zambia. As a consequence, the region consists of different land use types resulting in heterogeneous landscape (Fig. 1.2).

Fig. 1.2: *Land use types in Zambia; (a) Natural forests, (b) Eucalyptus plantations, (c) Pine plantations, (d) Mining, and (e, f) Agriculture fields. [Photos (a)-(c) and (e), by D. Chungu; Photo (d) was obtained from www.funtrivia.com and photo (f) from www.fao.org]*

Dissertation outline and objectives

The primary objective of this dissertation is to broaden the understanding of species response to land use change in the tropical landscape. I used carabid species (Coleoptera: Carabidae) as model organisms and analyzed their response to changes in the environmental variables due to anthropogenic pressure in Zambia. As stated earlier, carabid beetles were ideal for this study due to their sensitivity to anthropogenic induced conditions, habitat destruction and their importance as pollution indicators (Lövei & Sunderland 1996; Gómez et al. 2014). The basis for the studies presented here forms the intensive sampling of carabids in 50 study sites consisting of 250 plots in native tropical forests, eucalyptus plantations, pine plantations and agriculture fields across a 14,000 km^2 landscape (Fig. 1.3).

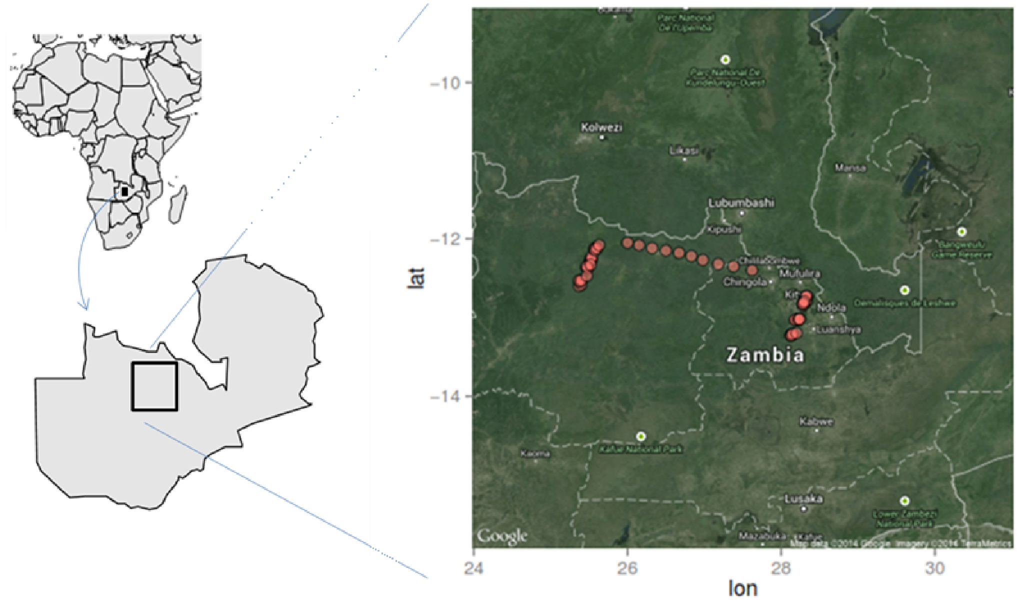

Fig. 1.3*: Location of study sites in the Copperbelt and North-western region in Zambia. Study sites are shown in red circles. Maps were sourced from Google Earth and generated in R*

I collected more than 23,000 carabids consisting of 47 species and approximately 66,000 other insects belonging to 940 species from 5 insect orders, which with the help of specialists I sorted and identified to either species level or morphospecies. Consistent with this sampling, my dissertation is composed of three major chapters (2, 3 & 4). They are framed by a general introduction in chapter 1 as well as a summary and recommendations in chapter 5. The three main chapters are structured like publications in scientific journal starting with an abstract, followed by an introduction, material and methods, results, and discussion and conclusions. They can therefore be read as independent units which may lead to redundancy in some of the contents. Part of this dissertation has been published as a poster (Appendix A.1) and other parts are in preparation for submission to journals.

In **chapter 2**, I report on the implications of introducing non-native plantations by focusing on richness and abundance of insects in general and carabids in particular between native forests and non-native plantations. For this purpose, I used 30 study sites from the 50 shown in Fig. 1.3 consisting of 150 plots in native broadleaved forests, eucalyptus and pine plantations. The results are based on a collection of 14,930 individuals consisting of 42 species of carabids, as well as a total of 66,114 other insects belonging to 940 species from 5 insect orders. In this chapter, I examined consequences of replacing native forests with non-native plantations by answering the following questions; (i) Does species richness of carabid beetles decrease from native forests to plantations of non-native tree species? (ii) What factors modulate differential species composition of carabid beetles between native and non-native forests? Results in this chapter showed that replacing native forests with non-native plantations decrease richness and change the species composition of carabid beetles and other insect taxa.

The aim of **chapter 3** was to evaluate body size of carabids between forest ecosystem and agriculture ecosystem in Zambia. I used 20 study sites comprising 100 plots. Results were based on 13,672 individuals of 38 carabid species of which 1,257 individuals were used for body size measurements to test the hypothesis that agriculture ecosystems reduce body size of carabids. Phylogenetic relatedness of species was taken into consideration when making statistical inference. Specifically in this study, I addressed the following questions. (i) What is the relationship between body size and abundance in forest ecosystem and agriculture ecosystem? (ii) Does body size of carabids decrease from forests to agricultural systems? This chapter revealed that carabids in agriculture ecosystems were significantly smaller than carabids in native forests.

The aim of **chapter 4** was to investigate the response of carabids to pollution and to evaluate their suitability as indicators for copper or lead contamination. I used 10 study sites consisting 50 plots, each study site at every 20 km from the emission source along a 200 km pollution gradient for sampling of carabids, ants and soil. I focused on the abundance patterns of carabid populations and concentrations of heavy metals (copper and lead) in six most dominant carabids as well as ants along this gradient to address the following questions: (i) Does abundance and species richness decrease or increase along the pollution gradient? (ii) Does heavy metal concentration in carabids correlate with contamination in the soil? (iii) Between carabids and ants, which insect group is a better indicator of Cu and Pb contaminations? I observed that abundance and richness increased with distance from the mine. The fact that copper mining in Zambia is a major economic activity, chapter 4 of this dissertation forms the most important study as it provides crucial information for the pollution monitoring efforts in the region.

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2 Plantations of non-native trees decrease richness and change composition of carabid assemblages in Zambia

With Roland Brandl

Abstract

Plantations of non-native tree species are becoming a common feature in the tropics in order to sustain an increasing demand for wood and wood products. These plantations, unfortunately, are replacing native forests in many developing countries leading to biodiversity loss. The aim of this study was to determine consequences of replacing native forests with non-native plantations on carabid assemblages. Using pitfall trapping, 14,930 individuals consisting of 42 species were sampled. Abundance significantly decreased ($b = 5.36$, $z = 4.19$, $p < 0.001$) from mixed broadleaved forests 6,862 (712 ± 163), to pine plantations, 3,724 (439 ± 65). Species richness also decreased from mixed broadleaved forests (29 species, 8.1 ± 1.3) to pine plantations (7 species, 3.8 ± 0.6) and correlated with ground cover ($r = 0.86$, $p < 0.001$) and with litter ($r = 0.93$, $p < 0.01$). Indicator species comprised 45% and 10% of the carabid species sampled in mixed broadleaved forests and pine plantations respectively. Species composition considerably differed between forest types (ANOSIM $R = 0.257$; $p < 0.001$). This study suggests that introductions of non-native plantations to replace native forests negatively affect species composition, and therefore, underscores the importance of sustainable management of native forests in order to protect biodiversity.

Keywords: Ground beetles, habitat disturbance, afforestation, landscape heterogeneity, species composition

Introduction

Native forests are rich in biodiversity (Mittermeier et al. 1999; Balmford et al. 2001; Kamelarczyk & Gamborg 2014). However, forest cover is decreasing dramatically in developing countries for agricultural production and the demand for wood and wood products (Achard et al. 2002; Brink et al. 2014). In Zambia, native forests are also under severe pressure and decrease annually by 2.4% (Chidumayo 1989; FAO 2007; Chungu et al. 2010) and deforestation has been identified as one of the main environmental problems facing the country (Anon. 1985). In order to counter deforestation the Zambian government has initiated afforestation programs through its Forestry Department (Environmental Council of Zambia 2003). Although more than 50,000 ha have been planted with trees, more than 90% of these plantations have replaced native trees with mostly fast growing, non-native tree species, particularly species of pines and to the lesser extent members of the genus *Eucalyptus* (Chidumayo 1997; Sekeli 1998; Chungu et al. 2010).

The structure and functions of forests varies between forest types due to differences in tree species composition, which influences for example the plant cover of the forest floor as well as the structural and chemical features of the litter (Binkley & Giardina 1998; Oijen et al. 2005; Rice et al. 2004). Such variations in the characteristics of the forest floor have a considerable impact on the abundance, richness and species composition of assemblages of ground dwelling arthropods

(Reich et al. 2005). These insects do not only depend on the structure of the forest as a habitat but in turn also modify ecosystem processes leading to complex interactions between the environment and species assemblages (Didham et al. 1996; Digel et al. 2014).

In forests, beetles are abundant and diverse groups of ground dwelling arthropods (Loyttyniemi 1980). Together with other soil invertebrates they depend on the structure and composition of the forest floor as habitat (Payer & Harrison 2003; Digel et al. 2014) but also affect the physical and chemical properties of soils, and influence almost every level of the decomposition cascade (Huston 1993). They directly modify decomposition processes by feeding on organic matter and indirectly by influencing microbial communities (Huston 1993; Fonseca & Ganade 2001). Furthermore, several beetle lineages are predators of other soil animals and are therefore important components in the food-webs (Booij & den Nijs 1992). Because of these functions, epigaeic beetles are good bioindicators (Rainio & Niemelä 2003; Bates et al. 2006). Ground beetles are especially sensitive to changes in structural and chemical properties of the forest floor (Clark et al. 1997; Woodcock et al. 2003; Wang et al. 2014) and are known to react sensitively to changes from native forests to plantations of non-native species (Samways et al. 1996, Finch 2005).

Despite their significant role in the ecosystem, ecological studies of ground-dwelling beetles are rather scarce in southern hemisphere, particularly in Africa (Samways et al. 1996; Magagula 2003; Padayachi et al. 2014). The majority of studies focus on beetles in northern hemisphere where the taxonomy and ecology of this group of beetles is well-known (Thiele 1977; Atlegrim et al. 1997; Fahy & Gormally 1998; Jukes et al. 2001; Woodcock et al. 2003; Wang et al. 2014). In this study, we explore consequences of plantations with non-native tree species on the assemblages of carabid beetles. Specifically, we address the following questions: (i) Does species richness of carabid beetles decrease from native forests to plantations of non-native tree species? (ii) What factors modulate species composition of carabid beetles between native and non-native forests? By answering these questions we hope to contribute to the awareness of local authorities for the conservation of native forests.

Materials and Methods

Study area and sampling

The study was conducted from May 2013 to January 2014 in a landscape stretching from Copperbelt province (Kitwe; 12°41′S–13°21′S, 28°23′E–28°07′E; 1,170–1,286 m a.s.l) to North-western province (Solwezi; 12°02′S–12°43′S, 26°38′E–26°20′E; 1,293–1,390 m a.s.l), Zambia. This region covering around 14,000 km^2 was originally dominated by native broadleaved forests commonly referred to as Miombo woodlands, which are an important component of the Zambezian phytoregion with *Julbernadia, Brachystegia, Isoberlinia, Parinari* and *Marquesia* as dominant tree species (Chidumayo 1997).

In the mid of the 20th century, considerable portion of these forests particularly in the Copperbelt province were cleared and replaced with non-native species of pines and eucalyptus in the quest to establish industrial plantations for the production of wood and wood products (Sekeli 1998). These non-native plantations continue to expand (Chungu et al. 2010). The study area belongs to the summer rainfall (November–April) tropical climate zone and features seasonal differences with an annual temperature range from 3 to 31°C and a rainfall range from 1,200 to 1,500 mm. There is no significant variation in topography, soils and climatic conditions across the study area (Chidumayo 1997).

Sampling was conducted in native forests and non-native plantations. Native forests were mixed stands of broadleaved species that included *Julbernadia paniculata, Albizia adianthifolia, Brachystegia spiciformis, Isorbelinia angolensis* and *Marquesia macroura* while non-native plantations were mainly pure stands of either pine or eucalyptus. Two transects, 70 km long and 200km apart, each passing through both forest types, were established. We established 30 (30 m x 30 m) study sites in total, 10 in each forest type i.e. mixed broadleaved, eucalyptus and pine plantations along the transects. Each study site was sub divided into 5 (10 m x 10 m) plots resulting in 150 plots, in which we recorded habitat characteristics (Table 2.1).

Table 2.1: Means and standard deviations for habitat characteristics in native forests and non-native plantations

Habitat characteristics	Native forests	Non-native plantations		(t-test, p)
	Mixed broadleaved $n = 10$	Eucalyptus $n = 10$	Pine $n = 10$	
Plant richness	8.02 ± 0.5	4.01 ± 0.2	3.40 ± 0.6	**0.000**
Canopy cover	12.3 ± 2.4	31.8 ± 4.5	11.6 ± 2.8	**0.000**
Ground cover	41.6 ± 3.5	28.1 ± 6.2	11.4 ± 3.9	**0.000**
Litter	44.0 ± 3.9	21.9 ± 4.4	15.1 ± 2.6	**0.000**
Soil pH	4.5 ± 0.02	4.6 ± 0.04	4.6 ± 0.01	**0.000**

To estimate plant richness within plots, all individuals of trees and shrubs were counted and identified (Palgrave 1977; Storrs 1995). Canopy cover was estimated by eye as percentage area occupied by the vertical projection of tree crowns (Jennings et al. 1999). Ground cover was quantified as percentage ground that was not bare (Higgins et al. 2014). Canopy and ground cover were estimated to the nearest 5%. Litter was recorded as percentage depth of the pitfall height (10 cm in our case; Delgado et al. 2013) that included undecomposed plant residues and the humus soil horizon. Recording of ground cover, canopy cover and litter was based on averages of visual assessments taken from three different points within each plot. Soil pH was measured using a field pH meter by inserting its electrodes directly into the soil (HI 99121, Hanna Instruments, Denver, U.S.A).

Pitfall trapping was used to sample carabid beetles. This method is fast, inexpensive, and relatively unbiased for obtaining data on species abundance and diversity (Digweed et al. 1995). In each study site we used 5 traps each in the middle of the 10 m x 10 m plot. Each pitfall trap consisted of two stacked plastic cups (diameter: 9 cm; height: 10 cm) buried in the ground so that top rim was flat with soil surface. Two cups were used to enable top cup containing the sample be removed easily and replaced again after each collection. Traps were half-filled with 50% glycol and a few drops of ordinary unscented liquid detergent to reduce surface tension. Each trap was covered with a metal roof (12 cm x 12 cm) to protect from rain, litter-fall and disturbance by animals. Traps were emptied and refilled once a week.

All samples collected from each pitfall trap were taken to laboratory for sorting and identification. Identification of carabids, most of them to species level and few to morphospecies, was based on available published information (Thiele 1977; Lindroth 1974; Scholt 1985; Luff & Duff 2001; Werner 2003, 2007; Kirschenhofer 2008; Lassalle 2010; Valaini 2011; Assmann et al. 2011; Facchini 2011, 2012; Hamburg et al. 2014). In all cases, identification was confirmed or corrected by appropriate specialists, and the voucher specimens were deposited at Division of Entomology Research, Forestry Department, and at School of Natural Resources, Copperbelt University, Kitwe, Zambia. We also sorted the other groups of insects and identified them to morphospecies. For further analyses all individuals of each trap were pooled.

Statistical analysis

We examined the effect of replacing native forests with non-native plantations by comparing abundance and species richness of major groups of epigaeic arthropods and particularly carabid assemblages with linear mixed-effects models (Quinn & Keough 2002; Nieuwenhuis et al. 2012) using the *lme4* package (Bates et al. 2012) in R version 3.0.3 (R Development Core Team 2014). We included plant richness, canopy cover, ground cover, litter, forest types, soil pH and as a three level factor the three forest types as explanatory variables. Transects and plots within transects were treated as random factors.

In order to test whether abundance had an effect on species richness, we re-ran the analysis for richness and included abundance among the fixed factors. Following Quinn & Keough (2002); abundance data were *log* transformed, litter, ground cover and canopy cover were *arcsin* transformed and, soil pH and richness data were *sqrt* transformed, to approach a normal distribution and to stabilize error variance. To define species preferences between forest types, we applied multilevel pattern analysis, implemented in *indicspecies* package (Dufrêne & Legendre 1997).

Compositional dissimilarities within and between forest types was evaluated with an analysis of similarity (ANOSIM) based on Braye-Curtis dissimilarity index to test whether there is a difference in assemblage between native forests and non-native plantations. To detect how carabid assemblage was associated with forest types, we used redundancy analysis (RDA) (Jongman et al. 1995) implemented in *vegan* package (Oksanen et al. 2007). We visualized species composition between native forests and non-native plantations using a biplot.

Results

We collected a total of 66,114 insects belonging to 940 species from 5 insect orders. In all forest types the majority (72 %) of these were Coleoptera (Fig. 2.1). Richness in Coleoptera in native forests was significantly higher than in eucalyptus or pine plantations but did not differ in Hymenoptera, Isoptera, Lepidoptera or Orthoptera between forest types (Fig. 2.1; Table 2.2).

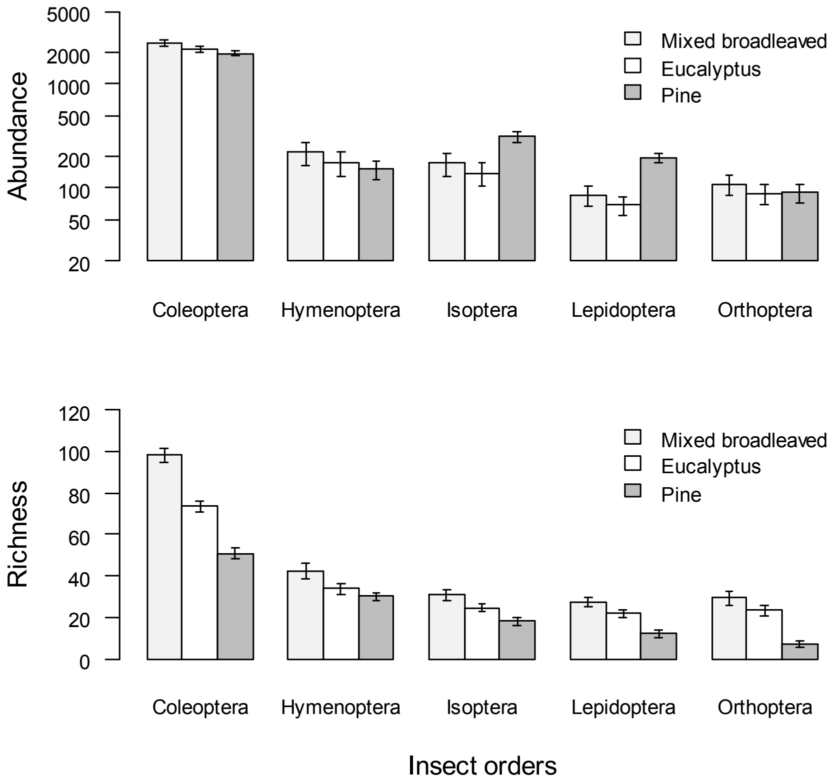

Fig. 2.1: *Abundance and richness for insect assemblages in mixed broadleaved forests, eucalyptus and pine plantations. Abundance is plotted on log scale. Error bars indicate the standard deviation.*

Table 2.2: Linear mixed-effects model for the relationships between abundance and richness with habitat characteristics for all insects observed in native forests and non-native plantations

	Abundance			Richness		
	Estimate	SE	*z* value	Estimate	SE	*z* value
Model	6.240	3.910	1.695*	2.30	1.170	1.956*
Abundance (log)				0.380	0.035	11.13***
Litter	0.000044	0.017	0.0030	0.0013	0.0062	0.149
Ground cover	0.0027	0.013	0.202	-0.0011	0.0041	-0.274
Canopy cover	-0.068	0.0302	-2.255*	0.012	0.0087	1.341
Plant richness	0.081	0.170	0.490	-0.016	0.049	-0.339
Soil pH	-0.170	0.780	-0.219	-0.150	0.230	-0.656
Eucalyptus	1.540	1.201	1.278	-0.440	0.350	-1.254
Pine	1.160	1.006	1.158	-0.990	0.302	-3.271***

*significant at $p < 0.05$; ***significant at $p < 0.001$

We collected 14,930 individuals of carabids consisting of 42 species. Regardless of the habitat characteristics, abundance varied significantly between forest types ($b = 5.36$, $z = 4.19$, $p < 0.001$; Table 2.3), and decreased from mixed broadleaved forests, 6,862 (712 ± 163), to pine plantations, 3,724 (439 ± 65; Fig. 2.2). There was a strong link between abundance and richness across plots (Table 2.3).

Table 2.3: Linear mixed-effects model for the relationships between abundance and richness with habitat characteristics for carabid species observed in native forests and non-native plantations

	Abundance			Richness		
	Estimate	SE	*z* value	Estimate	SE	z value
Model	5.362	1.279	4.193***	-0.9184	0.7001	-1.312
Abundance (log)				0.1003	0.04272	2.348*
Litter	0.000671	0.00587	0.114	0.00856	0.00314	2.732**
Ground cover	-0.00144	0.00450	-0.319	0.01302	0.00237	5.502***
Canopy cover	-0.00720	0.01008	-0.715	-0.00486	0.00521	-0.934
Plant richness	0.00129	0.0544	0.0240	0.0196	0.0281	0.698
Soil pH	-0.0775	0.257	-0.302	-0.00859	0.133	-0.0650
Eucalyptus	-0.493	0.384	-1.284	0.3457	0.199	1.730
Pine	-1.420	0.318	-4.473***	0.3251	0.176	1.848

*significant at $p < 0.05$; **significant at $p < 0.01$; ***significant at $p < 0.001$

Carabid richness also decreased from mixed broadleaved forests (29 species, 8.1 ± 1.3) to pine plantations (7 species, 3.8 ± 0.6; Fig. 2.2) and was correlated with ground cover ($r = 0.86$, $p < 0.001$) and with litter ($r = 0.93$, $p < 0.01$) (Table 2.3).

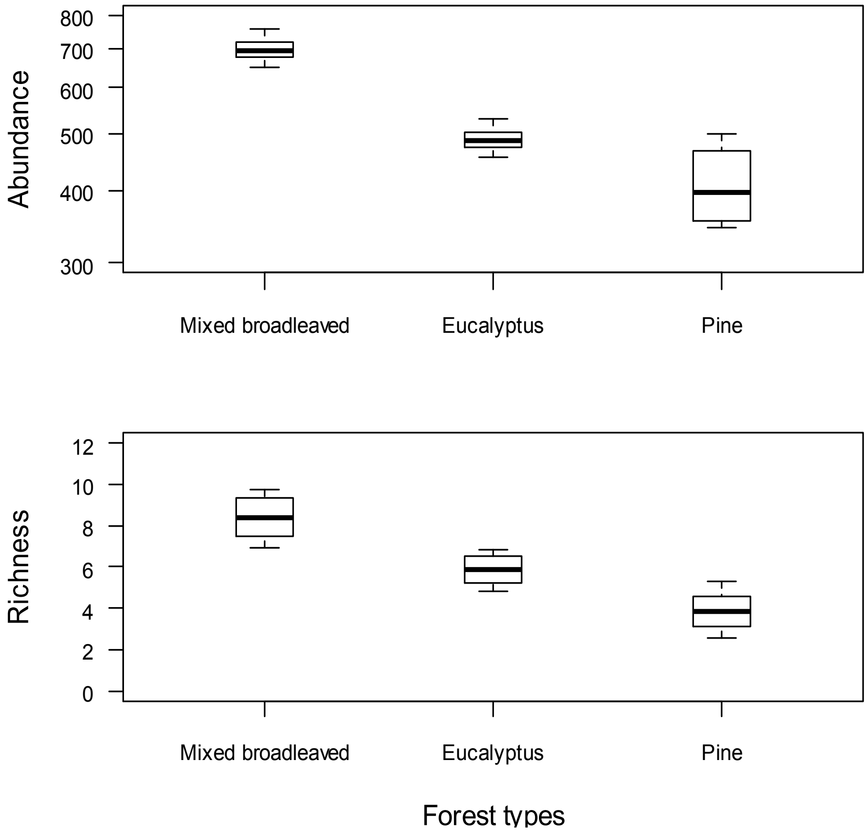

***Fig. 2.2**: Abundance and richness for carabid assemblages in mixed broadleaved forests, eucalyptus and pine plantations. Abundance is plotted on a log scale*

Our data on species preference revealed that *Epigraphodes congoensis, T. muata* and *Procletus* sp had a strong affinity with native forests, *Lobodontus* sp with eucalyptus plantations while *P. singularis* was associated with pine plantations (Appendix B.1). Number of species specific to a single forest type (indicator species) ranged from 19 in mixed broadleaved to 4 in pine plantations (Appendix B.1). These comprise 45% and 10% of the carabid species sampled in mixed broadleaved forests and pine plantations respectively. Of these indicators, 3 species (*E. congoensis, T. muata* and *Procletus* sp) were found exclusively in mixed broadleaved forests and 1 species (*P. singularis*) was found only in pine plantations (Appendix B.1). There was some overlap in the species composition particularly between native forests and eucalyptus plantations. *Tefflus* sp and *Hylopaussus sebakuanus* occurred in all forest types.

Analysis of Similarity (ANOSIM) showed that overall difference in species composition between forest types was significant (ANOSIM $R = 0.257$; $p < 0.001$). Redundancy analysis also revealed distinct pattern in species composition between forest types (Fig. 2.3). The first three components accounted for 79% of the variability in the dataset. There was a distinct gradient of plant richness, litter and ground cover along the first component increasing from pine plantations to mixed broadleaved forests (Fig. 2.3; 37% of total variance). The second component distinguished between pine and eucalyptus plantations (26% and 16% of the variance respectively) and was associated with increasing pH and canopy cover.

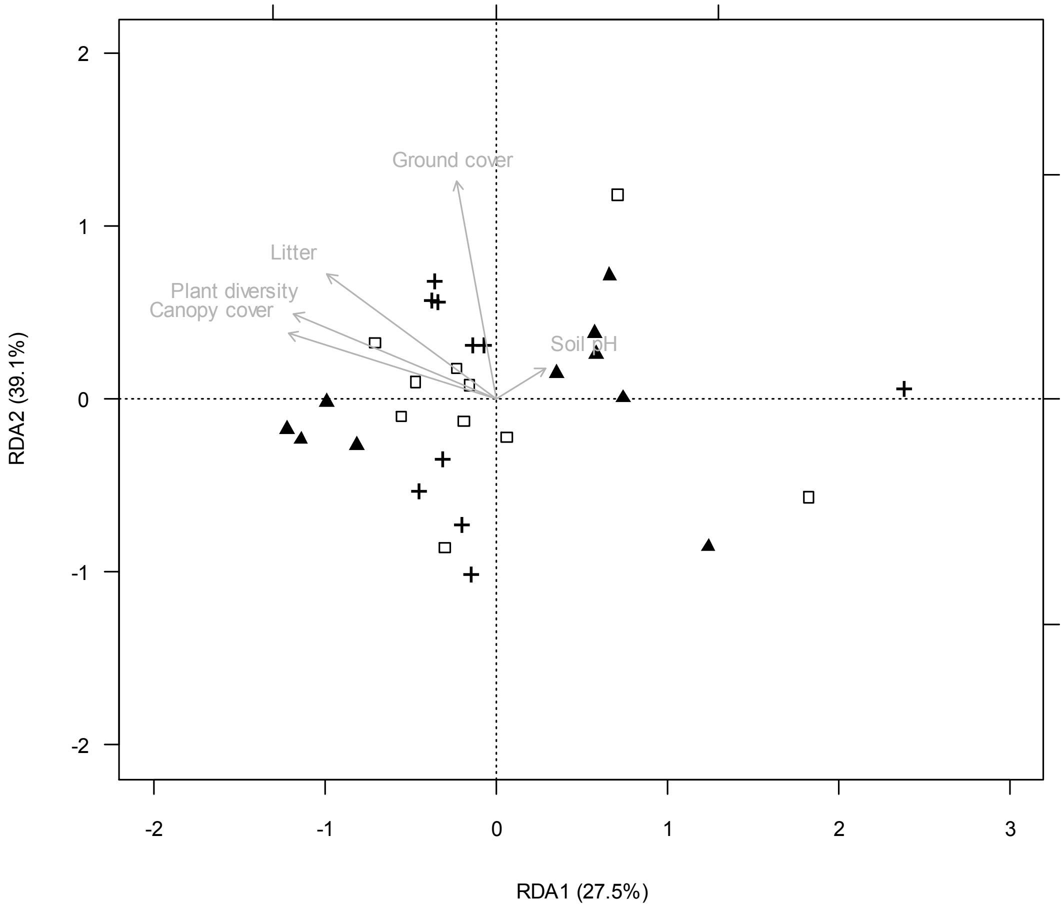

***Fig. 2.3**: Relationship between species composition of carabid beetles and habitat characteristics. Different forest types are represented by different symbols i.e. square symbols = native forests (mixed broadleaved), plus symbols = eucalyptus plantations, and triangle symbols = pine plantations. (ANOSIM R = 0.257, p < 0.001)*

Discussion

Overall, changes in ground dwelling insect communities in our study followed the differences in forest types. Composition of carabid communities decreased in richness from native forest to pine plantations and the assemblages of the pine plantations were characterized by a distinct assemblage of carabids (Figs. 2.1 & 2.2). In addition to compositional changes, species exclusive to a single habitat were significantly more in native forests than in pine plantations (Appendix B.1, suggesting a decrease in indicator species when portion of native forests were transformed into non-native plantations. Relative abundance in our study showed that species constituting less than 0.05% of the total abundance were only associated with native forests and were absent in pine plantations (Appendix B.1), which suggests that rare species are vulnerable to the introduction of non-native plantations. Our data also support the observation that when non-native plantations are established in degraded landscapes where native forests are rare, these forests play an important role in sustaining biodiversity (Brockerhoff et al. 2008; Pawson et al. 2008; for carabids see Berndt et al. 2008).

Our results also revealed that species richness significantly correlated with litter and ground cover (Table 2.3), suggesting that litter and ground cover rather than canopy cover, plant richness or soil pH were more important for modulating richness of carabid species. Decrease in species richness is generally more pronounced when native broadleaved ecosystems are transformed to pine plantations (Fig 2.3a, b; Fahy & Gormally 1998; Bonham et al. 2002; Jung et al. 2012). Tree species in the native broadleaved forests and in the non-native pine plantations differed considerably in their litter quantity (Table 2.1) and probably quality, and are likely to influence properties of soil environment and associated communities of soil invertebrates including carabid beetles (Thiele 1977; Bicknell et al. 2014; Li et al. 2014). In fact, some groups of carabid beetles particularly phytophagous individuals preferentially feed on certain types of litter (Zimmer et al. 1996; Sklodowski 2013). Phytophagous carabids, therefore, are directly limited by the quality and quantity of litter which serves as food substrate in addition to its role as a habitat (Millan-Pena et al. 2003; Niemelä, et al. 2002; Niwa & Peck 2002; Holliday 1992). Consequences of replacing native forests with non-native plantations are, thus, clearly predictable (Finch 2005; Huber & Baumgarten 2005; Latty et al. 2006; Oliver et al. 2014; Pakeman & Stockan 2014).

Obviously, the introduction of non-native plantations to replace native forests leads to habitat loss, and can modify quality and quantity of prey (Guillemain et al. 1997; Bonham et al. 2002). Litter under pine plantations is usually formed by undecomposed needle layer that can provide only a little shelter for large predatory carabids (Berg et al. 1993; Bonham et al. 2002). Furthermore, we have shown that the abundance and richness of carabids decreased in pine plantations where litter is proportionately low compared to native forests. Thus, it is likely that part of the trophic base for at least some of the carabids was probably affected. Pine plantations maintained populations of very few probably generalist species while more species, likely to be specialists that require microclimate and litter characteristics specific to native forests were rare or missing.

In addition, non-native plantations are usually characterized by soil cultivation and prescribed burning (Evans & Turnbull 2004). These silvicultural practices often reduce availability of microhabitats which are important in promoting species diversity (Holliday 1992; Townsend et al. 2008; Adams 2010). Silvicultural practices in non-native plantations also tend to simplify stand structure

(Bonham et al. 2002) and litter decomposition may be slowed down and soil properties altered (Riley & Browne 2011). These habitat changes may increase vulnerability of ground beetles (Miñarro & Dapena 2003; Bicknell et al. 2014). Decrease of carabid abundance and richness in non-native plantations in the current study is likely to be associated with changes in ecosystem properties triggered by silvicultural practices. This decrease of species richness from native forest to non-native plantations is consistent with several published studies (Bonham et al. 2002; Finch 2005; Vanbergen et al. 2005; Packeman & Stokan 2014).

Native forests in our study did not frequently experience silvicultural treatments, fire or soil cultivation and were generally free from direct anthropogenic intervention for more than 50 years (Chidumayo 1989; Chungu et al. 2010). This stability in native forests allows for the development of habitat complexity (Clark et al. 1997; Fonseca & Ganade 2001) through higher plant richness, increase in ground cover and gradual accumulation of litter in various decomposition classes (Townsend et al. 2008; Adams 2010). A more complex environment increases available microhabitat, food and shelter, which may lead to increased species richness of carabids and other ground beetles (Lys et al. 1994; Purvis & Fadl 2002; Vanbergen et al. 2010). Stability and diversity of environmental conditions in native forests is especially important for the occurrence of a number of specialist carabid species that tend to be affected by forestry practices (Symstad et al. 2000; Magagula 2003; Halme & Niemelia 1993; Bettacchioli et al. 2012), particularly the introduction of non-native plantations. In our study, a large proportion of richness in the native forests was characterized by habitat specific species which were either rare or missing in non-native plantations (Appendix B.1). Although information about ecology of these species is scant, we suspect this group of species tends to be constrained to natural undisturbed ecosystems and could be considered as indicator species.

Conclusions

Results of this study underline the implications of converting native forests to non-native plantations on carabid biodiversity. Carabid assemblages in native forests were species rich, and converting native forests decrease biodiversity. Decrease in carabid richness may be used as an indicator for biodiversity loss when native forests are being converted to non-native plantations. Species in non-native plantations had a different species composition and a considerably lower species richness which decreased with litter, ground cover and plant richness. The only beetle species able to maintain viable populations in these altered ecosystems were probably habitat generalists. The adverse effects of replacing native forests with non-native plantations or the use of non-native trees as a surrogate for afforestation underscore the importance of native forest management if forest biodiversity is one of the management priorities.

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3 Agriculture ecosystems reduce body size of carabid species

With Roland Brandl

Abstract

Estimates on biodiversity loss due to agriculture expansion have primary focused on species abundance or richness data and other aspects of biodiversity loss linked to ecological and morphological traits remain poorly understood. The aim of this study was to assess body size of carabid beetles as a consequence of converting native forests to agriculture fields. Using pitfall trapping, 1,257 individuals consisting of 38 species were sampled in forest ecosystem and agroecosystem in Zambia and assessed for body size. Body length within species decreased from forest ecosystem to agroecosystem ($t = 3.58$, $p < 0.001$), the pattern was the same for wing length ($t = 4.11$, $p < 0.001$) and body mass ($t = 3.72$, $p < 0.001$). Using phylogenetic filtered data, generally, body length decreased from forest ecosystem to agroecosystem ($b = -0.26$, $t = -5.29$, $p < 0.001$). In agroecosystem, body length decreased with increasing abundance ($r = -0.59$, $p < 0.01$), but in forest ecosystem, body length increased with abundance ($r = 0.64$, $p < 0.01$). Differential habitat structure and species specialization are probably the main causes of body size decrease in agroecosystem. Our study provides evidence that agriculture ecosystems reduce body size of carabid species which may probably lead to loss of ecological traits in species assemblages.

Keywords: Ground beetles, morphological traits, habitat disturbance, body length, body mass

Introduction

Agricultural expansion, driven largely by population growth, is by far, the leading land-use change (Tilman et al. 2001; Grau et al. 2005) leading to biodiversity loss (Joseph-Wright & Muller-Landau 2006; Laurance 2007). Evidence of biodiversity loss due to agriculture expansion is well documented but most studies have primarily focused on abundance or richness to document biodiversity loss (Heywood 1995; Turner 1996; Ellsbury et al. 1998; Laurance 2007; Vanbergen et al. 2010). As a consequence, critical and equally important components of biodiversity, such as the loss of ecological traits have received little attention in the literature (Hanihara et al. 2003; Flynn et al. 2009; Dorazio & Connor 2014).

General hypotheses regarding changes in morphological traits as a result of habitat loss has been developed. One such hypothesis is referred to as "body size hypothesis", which predicts that body size should decrease in disturbed ecosystems (Gray's 1989; Blake et al. 1994), and several studies have tested and confirmed this hypothesis (Niemelä et al. 2002; Rusch et al. 2014). Body size is one of the most fundamental properties of an organism and correlates with many other physiological and ecological traits (Peters 1986; Blackburn & Gaston 1994; Brändle et al. 2000; Woodward et al. 2005). Furthermore, body size has been used to quantify energy transfer, biogeochemical cycling in ecosystems and division of resources within a community (Peterson et al. 1998; White et al. 2007; Yvon-Durocher & Allen 2012).

The importance of body size and its link to abundance has been widely recognized in insect populations (Blackburn et al. 1993; Siemann et al. 1996; Gaston & Lawton 1988; Chown & Gaston 2010; Wray et al. 2014). Evidence from studies on regional and global scale suggests that body size negatively correlates with abundance (Quinn et al. 1997; Ernest 2005; Gaston & Blackburn 2008). But, few studies have compared body size in insect populations between habitats. For instance, Steffan-Dewenter & Tscharntke (2000) studied body size in butterflies between natural forest and planted habitat and found that smaller butterflies dominated planted habitats. Cunning & Murray (2007) observed that beetles in eucalyptus plantations were larger than beetles in remnants of natural forests. Gobbi et al. (2003) did not find a significant difference in body size among carabid populations in meadows with different management regimes. But, these studies did not incorporate phylogenetic relatedness between species or corrected body size with abundance. It is not clear whether the differences in body size between habitats were caused by variation in abundance or phylogenetic differences between species. Coexisting species may be more closely related than expected by chance if environmental features of a given habitat filter certain traits that are shared by closely related species (Cornwell et al. 2006; Duarte, 2011). In addition, coexisting species may be more distantly related than expected by chance if species tend to competitively exclude their closest relatives (Mayfield et al. 2010). In fact, species interact based on their phenotypic differences or similarities and this phenotypic variation is generated through evolutionary history (Agrawal 2001; Thompson 2014). It is, therefore, important to incorporate phylogenetic relationships into the study of species assemblages so as to control non-independence in data caused by phylogenetic patterns (Harvey & Pagel 1991; Gaston & Blackburn 2008).

The aim of our study was to assess body length of carabids between forest ecosystem and agriculture ecosystem in Zambia. Since morphology is linked to phylogeny of species (Felsenstein 1985), we analyzed our data in two phases. Firstly, we used mean body length of species as independent data points. Secondly, we applied a technique to remove phylogenetic information among species and used the data to detect the effect of ecosystem and abundance on body size. This was done to test the hypothesis that agriculture ecosystems reduce body size of carabids. Specifically in this study, we addressed the following questions. (i) What is the relationship between body size and abundance in forest ecosystem and agriculture ecosystem? (ii) Does body size of carabids increase or decrease between ecosystems? Our results may be used to develop predictions regarding species morphological responses to land use modification for biological resource management.

Materials and Methods

Study area and sampling

The study was conducted from May 2013 to January 2014 in a landscape stretching from Copperbelt province (Kitwe; 12°41′S–13°21′S, 28°23′E–28°07′E; 1,170–1,286 m a.s.l) to North-western province (Solwezi; 12°02′S–12°43′S, 26°38′E–26°20′E; 1,293–1,390 m a.s.l), Zambia. This region covering around 14,000 km^2 was originally dominated by native forests commonly referred to as Miombo woodlands, which are an important component of the Zambezian phytoregion with *Julbernadia, Brachystegia, Isoberlinia, Parinari* and *Marquesia* as dominant tree species (Chidumayo 1989). Since the mid of 1900, these forests, however, have suffered intense exploitation and a considerable portion of them particularly in the Copperbelt province has been converted to agriculture fields. These farmlands have continued to expand (Angelsen & Kaimowitz 2001). The resulting landscape mosaic consists of *forest ecosystem* and *agroecosystem.* The study area belongs to the summer rainfall (November–April) tropical climate zone and features seasonal differences with an annual temperature range from 3 to 31°C and a rainfall range from 1,200 to 1,500 mm. There is no significant variation in topography, soils and climatic conditions in the study area (Chidumayo 1989).

Sampling was conducted in native forests and agriculture fields. Native forests were mixed stands of broadleaved species that included *Julbernadia* *paniculata, Albizia adianthifolia, Brachystegia spiciformis, Isorbelinia angolensis* and *Marquesia macroura* while agriculture fields were mainly farmlands of maize, millet, potatoes, groundnuts and cassava (Adams 2003). Two transects, 70 km apart, each passing through forests and farmlands, were run. We established 20 (30 m x 30 m) study sites in total, 10 in native forests and 10 in the farmlands along transects. Each study site was sub divided into 5 (10 m x 10 m) plots resulting in 100 plots.

Pitfall trapping was used to sample carabid beetles. This method is fast, inexpensive, and relatively unbiased for obtaining data on species diversity and abundance distributions (Digweed et al. 1995). In each study site we used 5 traps each in the middle of the 10 m x 10 m plot. Each pitfall trap consisted of two stacked plastic cups (diameter: 9 cm; height: 10 cm) buried in the ground so that top rim was flat with soil surface. Two cups were used to enable top cup containing the sample be removed easily and replaced again after each collection. Traps were half-filled with 50% glycol and a few drops of ordinary unscented liquid detergent to reduce surface tension. Each trap was covered with a metal roof (12 cm x 12 cm) to protect from rain, litter-fall and disturbance by animals. Traps were emptied and refilled once a week. All samples collected from each pitfall trap were taken to laboratory for sorting and identification. Identification of carabids, most of them to species level and few to morphospecies, was based on available published information (Thiele 1977; Lindroth 1974; Scholt 1985; Luff & Duff 2001; Werner 2003, 2007; Kirschenhofer 2008; Lassalle 2010; Valaini 2011; Assmann et al. 2011; Facchini 2011, 2012). In all cases, identification was confirmed or corrected by appropriate specialists, and the voucher carabid specimens were deposited at Division of Entomology Research, Forestry Department, and at School of Natural Resources, Copperbelt University, Kitwe, Zambia. For further analyses all individuals of each trap were pooled.

For every species from the pitfall traps, we selected 5 males and 5 live females for morphological measurements. For species with less than 10 specimens, all individuals were measured. Morphological traits measured were body length, wing length and body mass. *Body length* is generally considered to be one of the most important attributes of an organism because it correlates strongly with many physiological, ecological and life-history traits (Brown 1995). Specifically, the body length of an organism determines the quantity and quality of resources consumed (Peters 1986), and may indicate the type of habitat an organism inhibits. Body length was measured from the frons to the apex of the abdomen. Ovipositors, mandibles, wings, spines and antennae extending beyond these points were not included in the total length measurement. Longer wings allow for faster flight and more efficient locomotion and foraging (Gutierrez & Menéndez 1997). *Wing length* was taken as a length of elytra i.e. distance from apex to upper limit of scutellum. Body length and wing length were measured to the nearest 0.01 mm, using a stereomicroscope fitted with an ocular micrometer x64 (SMZ 1270, Tokyo, Japan) for smaller specimens, and a Vernier caliper for most specimens. To measure *body mass,* specimens were dried at 70 ^{o}C in a drying oven for 48 hours, allowed to cool then weighed to the nearest 0.001 g on an electronic balance (NFB 224, Heman, China).

Statistical analysis

Mean body length, wing length and body mass were computed per species for each ecosystem. Pearson's correlations were used to detect relationships between traits. Because of strong dependence of wing length and body mass on body length (Brown 1995), further analyses were based on body length and abundance only. That distribution of body length in insect populations is skewed and highly modal (Brown 1995; Cotgreave 1993; White et al. 2007), we determined body length distributions of individuals per ecosystem, irrespective of species. Body length classes may yield information on how resources are divided across body sizes in each ecosystem (White et al. 2007). To test the effect of agriculture ecosystem on body length, we analyzed our data in two ways i.e. (1) using mean body length of species as independent data points, and (2) using data after filtering phylogenetic information among species.

(1) Trait measurement weighted with abundance provides more discriminatory power regarding habitat imposed differences than solely looking at species mean values (Nash et al. 2013). We, therefore, considered the value for each species as a measurement of the mean multiplied by number of individuals for that species and divided by total abundance in a plot. Significant differences in body length between ecosystems were tested using a simple *t*-test for within species

(species common to both ecosystems) and for between species (species that were restricted to one ecosystem). Furthermore, multivariate analysis of species composition in relation to body size (body length and body mass) was conducted using *vegan* package. Redundancy analysis (RDA) was used to assess the relationship between body size and species composition of carabids in agriculture fields and natural forests.

(2) Since morphological traits within species are associated with phylogenetic relatedness (Felsenstein 1985; Harvey & Pagel 1991), these traits should then exhibit correlations across phylogenetic history. Closely related species tend to be more similar morphologically and ecologically than would be expected by chance alone (Harvey & Pagel 1991). Therefore, we incorporated phylogenetic information in the analysis. This approach relies on a phylogenetic tree of the considered. A resolved phylogenetic tree for African carabids, however, is not available. Based on a method by Paradis (2013) in which species were arranged according to subfamily, tribe, genus and species, we reconstructed the phylogeny of carabids by maximum likelihood method implemented in *ape* package (Paradis et al. 2004). We used this tree as a surrogate of the true, though, only partially resolved phylogeny in our further analyses.

Removing phylogenetic information among species was accomplished in two stages. Firstly, using Pagel's lambda (λ), we detected whether our data sets contained phylogenetic signal (if $\lambda = 0$, indicate no signal; if $\lambda < 0.5$, indicate low signal; and if $\lambda > 0.5$, indicate high signal; Pagel 1999). Phylogenetic signal is recognized when closely related species tend to be more similar to one another than expected by chance (Pagel 1999; Revell 2010). Secondly, we corrected data for the phylogenetic relatedness of species (i.e. removing phylogenetic information) by generating phylogenetically independent contrasts (Felsenstein 1985), and analyzed these data with a generalized least squares model (GLS) using residual maximum likelihood criterion implemented in *nlme* and *ape* packages (Pinheiro 2014; Paradis 2014). Statistical analyses were performed in R version 3.0.3 (R Development Core Team 2014).

Results

Our analyses were based on 13,358 individuals of 38 carabid species in total. Out of these, 1,257 individuals consisting of 25 species in forest ecosystem (563 individuals) and 27 species in agroecosystem (694 individuals) were assessed for body length, wing length and biomass.

Mean body length in forest ecosystem for the smallest carabid (6.09 ± 0.33 mm; *Stenidia angusta*) was almost eight times smaller than that of the largest carabid (48.6 ± 2.29 mm; *Tefflus muata*) (Appendix C.1). While in agroecosystem, the mean body length of the smallest carabid (4.83 ± 0.06 mm; *Cicindela compressicornis*) was more than eight times than that of the largest carabid (39.5 ± 3.05 mm; *Tefflus muata*) (Appendix C.2). Body length within species significantly reduced from forest ecosystem to agroecosystem ($t = 3.58$, $p < 0.001$; Fig 3.1), the pattern was the same for wing length ($t = 4.11$, $p < 0.001$) and body mass ($t = 3.72$, $p < 0.001$; Fig 3.1). Female species in both ecosystems were slightly larger than male species but the difference was not significant. Wing length and body mass were highly correlated with body length in forest ecosystem (wing length, $r = 0.99$; body mass, $r = 0.92$) and in agroecosystem (wing length, $r = 0.97$; body mass, $r = 0.93$).

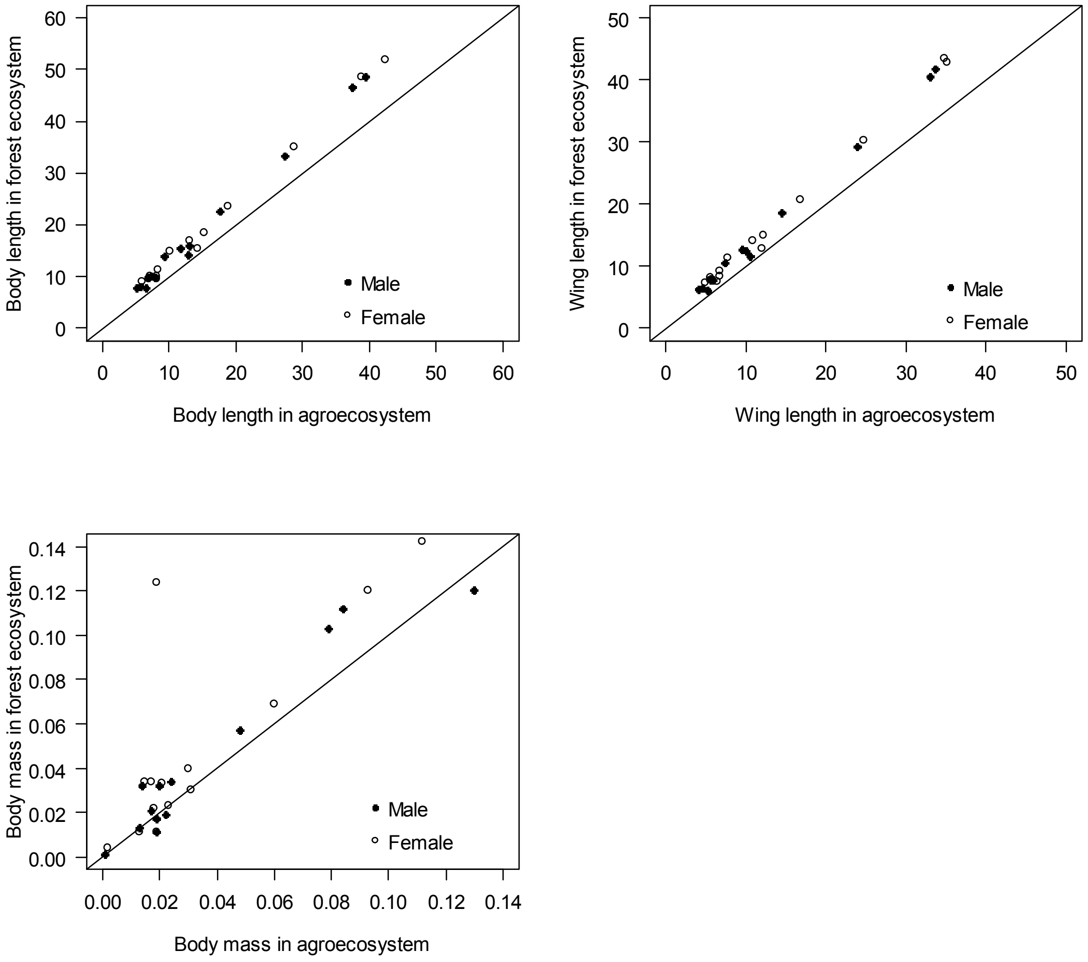

Fig. 3.1: *Relationship between forest ecosystem and agroecosystem of body length (mm), wing length (mm) and body mass (g) for carabid species common to both ecosystems. The regression line is symmetric around the origin*

RDA revealed that the composition of carabid assemblages were significantly different between agriculture fields and natural forests ($F = 7.3$, $p < 0.01$, permutation number = 999; Fig 3.2). The assemblage of agriculture fields was composed of smaller carabid species than that of natural forests (Fig 3.2).

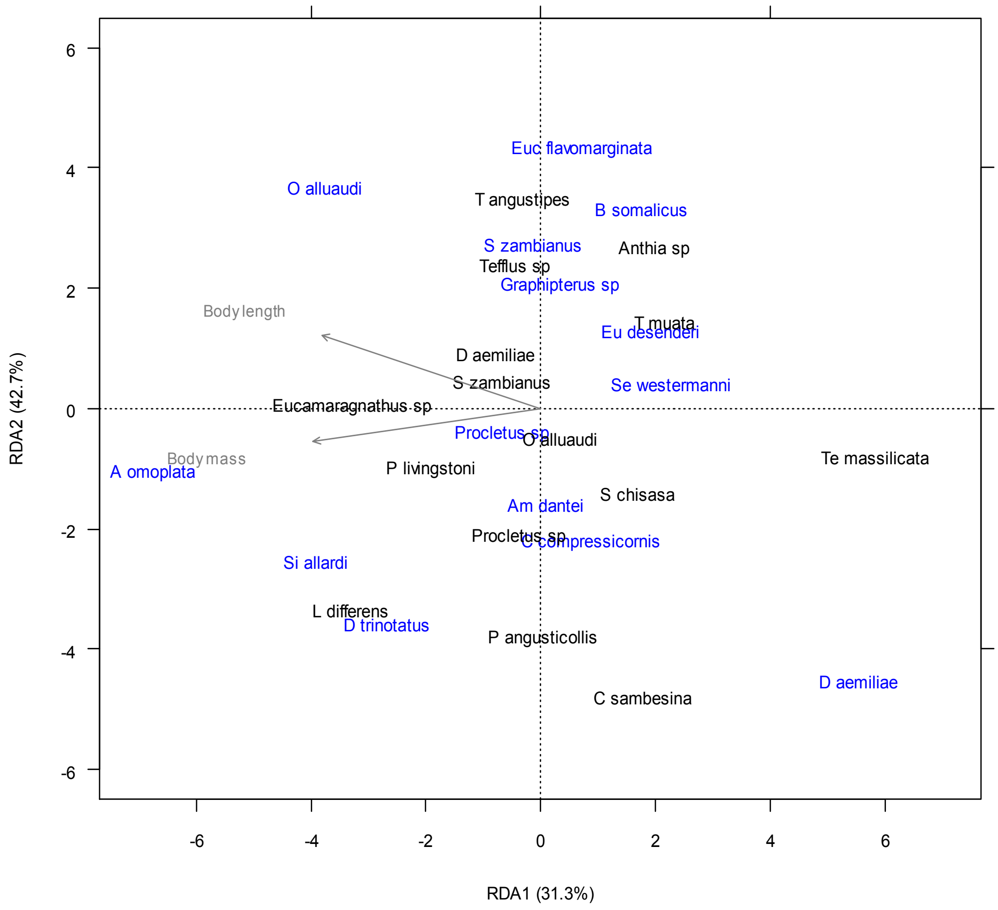

Fig. 3.2*: Redundancy analysis (RDA) biplot for carabid species recorded in agriculture fields (blue text) and natural forests (black text). Smaller carabid species dominated the agriculture fields than natural forests*

Partially resolved phylogenetic tree showed relatedness of species in both ecosystems (Fig 3.3) leading to considerable amount of phylogenetic signal in body length ($\lambda = 0.7$) and abundance ($\lambda = 0.9$) data ($p < 0.001$, Table 3.1). After filtering phylogenetic relatedness between species, generalized linear squares analysis showed a decrease in body length from forest ecosystem to agroecosystem (*b* = -0.26, *t* = -5.29, *p* < 0.001, Table 3.1).

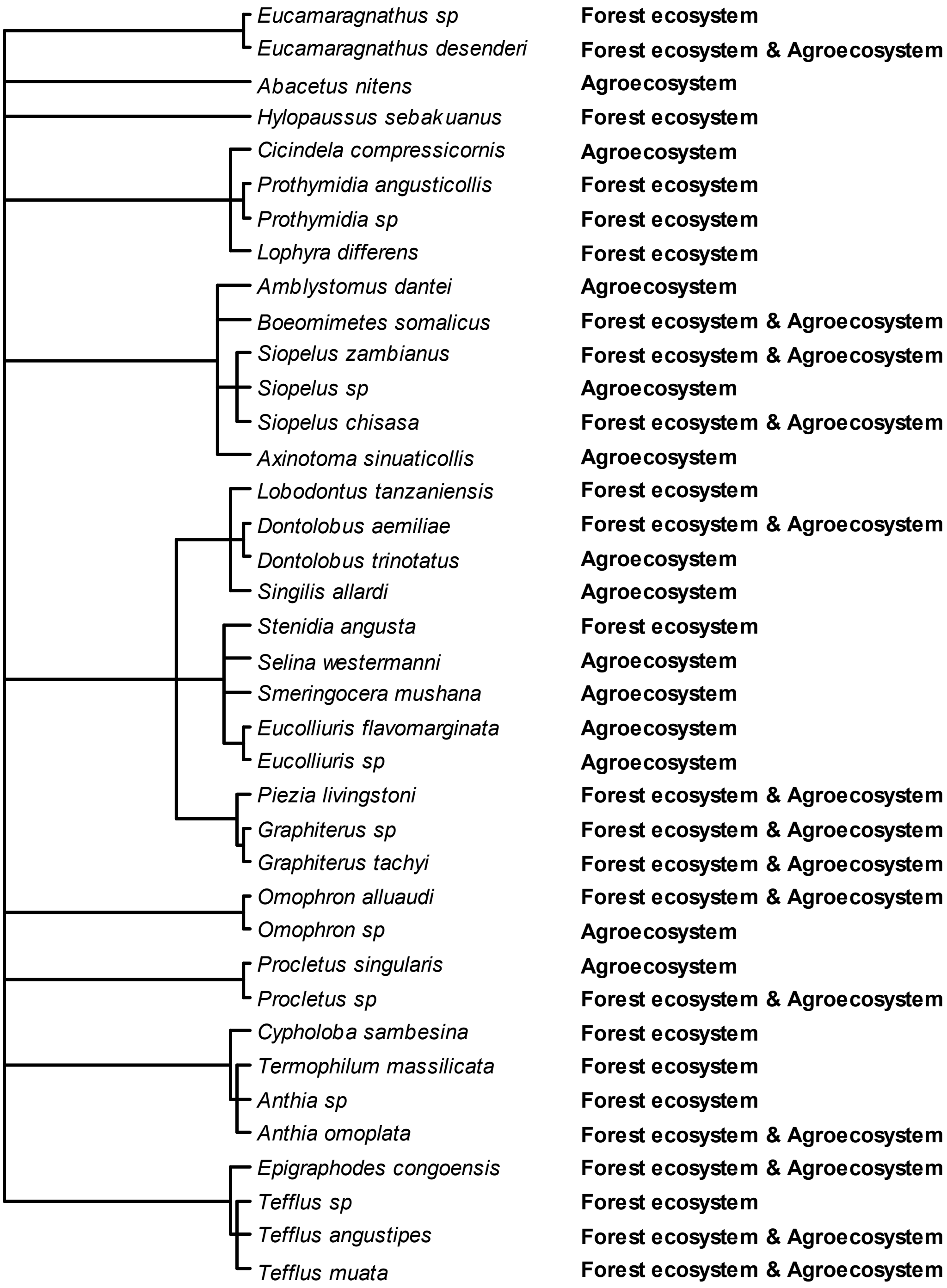

Fig 3.3*: Species relatedness. On the left: a partially reconstructed phylogeny of 38 carabid species. On the right: habitats where each species was present*

Table 3.1: Generalized Least Squares regression of body length as a function of abundance and ecosystem using data without phylogenetic information for 38 species of carabids. An independent, maximum-likelihood estimate of λ – a phylogenetic signal strength between species phylogeny and species traits (body length and abundance), is also given

Coefficients	Estimate	SE	t value	p^*
Intercept	3.456	21.16	0.163	0.8710
Abundance	0.159	0.037	4.317	**0.0001**
Ecosystem	22.50	5.450	4.105	**0.0002**
Abundance x Ecosystem	-0.255	0.048	-5.292	**0.0000**

Phylogenetic signal		
Species traits	λ	p^*
Body length	0.699	**0.001**
Abundance	0.913	**0.000**

*Values in bold indicate significance at $p < 0.001$

There was a positive correlation between body length and abundance in forest ecosystem ($r = 0.64$, $p < 0.01$, $n = 25$; Fig. 3.4), suggesting that body length increased with abundance. But in agroecosystem, we found a negative correlation ($r = -0.59$, $p < 0.01$, $n = 27$; Fig. 3.4), suggesting a decrease in body length with increasing abundance.

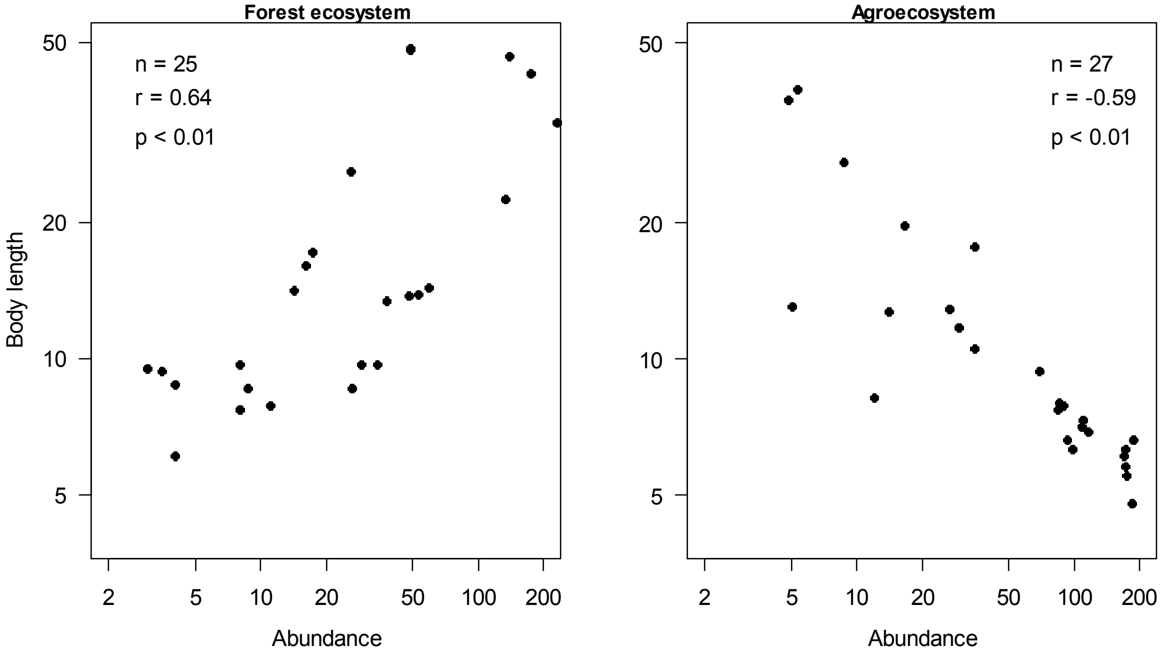

***Fig. 3.4**: Relationship between body length (mm) and abundance of carabid species in forest ecosystem and agroecosystem. Each point represents mean value for each species. Body length and abundance data are on log scales*

Furthermore, body length range for dominant species in forest ecosystem was > 30 ≤ 40 mm or above 40 mm but in agroecosystem was either > 10 ≤ 20 mm or > 20 ≥ 30 mm (Fig. 3.5), suggesting that agroecosystem was dominated by smaller species while forest ecosystem with larger species.

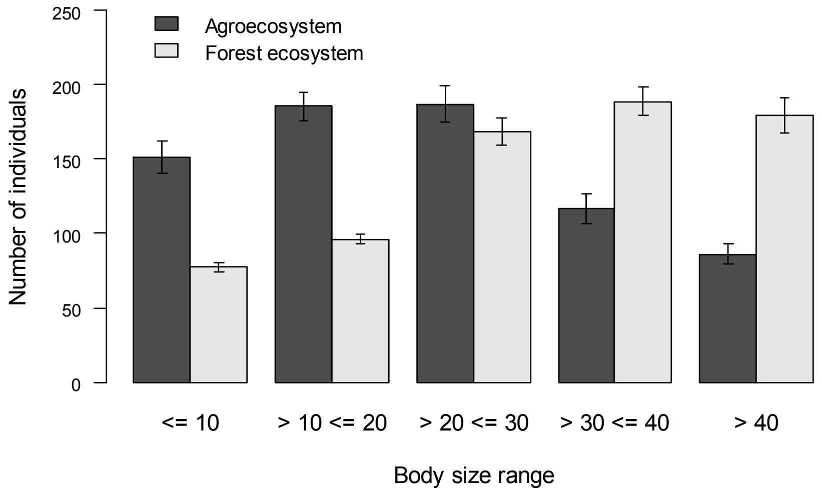

Fig. 3.5: *Body length range (mm) for individuals in agroecosystem and forest ecosystem regardless of species. Error bars represent standard deviation*

Discussion

Our results showed that carabids in the agroecosystem environment were smaller on average than those in forest ecosystem; this was true for within and between species. Body length for carabids in agroecosystem decreased with increasing abundance but in forest ecosystem carabids increased body length with abundance. After filtering phylogenetic relatedness between species, our data revealed that body length decreased from forest ecosystem to agroecosystem, which suggests that differences in habitat stricture between ecosystems might be the primary factor driving this pattern. Our data also support the observation that body length correlates with other morphological traits including wing length and body mass (Peters 1983; Woodward et al. 2005; Chown & Gaston 2010).

Agroecosystem in our study was characterized by frequent cultivation of land, use of fire and reduced vegetation cover (Adams 2003; Haggblade & Tembo 2003; Ngoma et al. 2014). Such disturbed habitats support smaller carabids (Šustek 1987; Holliday 1991; Blake et al. 1994; Magura et al. 2002), that are capable of flying and poses higher dispersal ability (Den Boer 1970; Duelli et al. 1990; Brigić et al. 2014). Species inhabiting habitats with persistence disturbance can only maintain high populations, if they possess high dispersal ability (Townsend et al. 2008; Pedley & Dolman 2014; Cardarelli & Bogliani 2014). As a consequence, smaller carabids in our study dominated the agroecosystem environment where similar disturbance was relatively high. The outcome of this study also supports the body size hypothesis, which suggests that the mean body size of the species decreases in disturbed habitats (Gray's 1989; Blake et al. 1994; Magura et al. 2004; Cunningham & Murray 2007).

It is also argued that larger carabids predominantly breed between summer and winter and their larvae require a longer period in undisturbed condition and of stable resource supply (Blake et al. 1994; Butterfield 1997; Magura et al. 2002). Seasonal crop production, frequent land cultivation and use of fire, usually associated with agriculture fields, may not provide stable supply of resources and may not guarantee undisturbed condition. This may partly explain why agroecosystem in our study did not support larger carabids. Blake et al. (1994) observed body size to increase with litter and organic matter in carabid assemblages. In fact, agroecosystem environments are reported to have relatively low percentage of litter (Arslan et al. 2014; Ngoma et al. 2014) compared to forest ecosystem (Chungu & Brandl *unpublished*). As a consequence, smaller carabids were more supported in agroecosystem than in forest ecosystem.

Several studies have shown strong correlations between prey abundance and carabid abundance (Guillemain et al. 1997; Menalled et al. 1999). Agricultural fields are usually characterized with high abundance of aphids (Minja et al. 1999; Atangana et al. 2014) which are important components in the diet of predatory carabids (Hengeveled 1979; Lovei & Sunderland 1996; Swaminathan 2014). Due to the constraints posed by body size on metabolisms and digestion, smaller organisms require lower rates of food consumption per individual but higher-quality diet than larger relatives (Bommarco 1998; Jørgensen & Lövei 1999; Bilde & Toft 1994; Rusch et al. 2014). Food supplies such as earthworms, corn earworms, various seeds and aphids are among the most preferred in the high-quality diet of carabids (Eubanks & Denno 2000; Fawki & Toft 2005). Such a menu is primarily provided in agriculture fields (Menalled et al. 1999; Fawki & Toft 2005; Mitchell et al. 2014). We suspect that high abundance of smaller carabids observed in agroecosystem, could have been driven by the presence of abundant and high-quality prey.

Empirical studies have shown that species of small size are dietary specialists because they use only a subset of foods that can be consumed by their larger relatives (Hengeveld 1979; Niemelä & Kotze 2009). It is probable that small species specialize on a variety of foods; as a consequence, subdivision of resources may play a major role in stimulating high abundance of species. This may be the case with agroecosystem environment in our study where carabids were not only smaller but abundant too. Despite their requirements for high-quality food, smaller species tend to maintain population densities that are high or higher than those in their large relatives (Siemann et al. 1996). Much of the specialization of small species is actually for habitat type rather than for food type as such (Townsend et al. 2008; Brouat et al. 2004; Peyras et al. 2013). But, constraints on the diet can cause species to be restricted to habitats where certain kinds of foods are abundant and can be harvested economically and with low risk of predation (Thiele 1977; Rosenzweig 1981; Morris 2011; Bertoncelj & Dolman 2013). This may suggest why some of the species were restricted only to either forest ecosystem or agroecosystem.

Conclusions

In conclusion, loss of biodiversity due to clearing of forests for agricultural expansion is well known, but, other aspects of biodiversity loss linked to morphological traits remain poorly understood. For example, body size variation across habitats has not been thoroughly documented in carabids. By incorporating abundance data and phylogenetic information between species, our study has made a first attempt to document the effect of agriculture ecosystem on body size in carabid assemblages. Carabids were smaller in agriculture ecosystem than in forest ecosystem. Body length decreased with increasing abundance in agriculture ecosystem but increased with abundance in forest ecosystem, suggesting that the general negative relationship between body size and abundance at the global scale may not hold at the local scale because mechanisms acting at the local scale might possibly differ from those acting at the regional or global scale. Differential variation in habitat structure, prey abundance and species specialization were plausible explanations in reduced body length observed in agroecosystem, however, we recommend further experiments to test how these mechanisms at the local scale affect body size in agricultural ecosystems and other habitats.

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4 Heavy metal concentrations in carabids reveal differential response of species to contamination along a Cu-Pb pollution gradient in Zambia

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Abstract

Areas in close proximity to the smelters and mines are highly polluted with heavy metals and xenobiotic chemicals, which usually exceed permissible limits. However, it is not clear how carabids inhibiting such environments respond to heavy metal contaminations. Using pitfall trapping along a 200 km pollution gradient in Zambia, we collected 8,134 carabid beetles consisting of 29 species and assessed metal concentrations in the body. Abundance for some species increased while for other species decreased with increasing distance from the mine. Copper and lead contaminations in the soil decreased with distance from the mining site (Cu: r =-0.92; and Pb: r = -0.88, $p < 0.001$). Cu concentration in carabids generally increased with Cu contamination (b = 0.91, t = 20.12, $p < 0.001$) but patterns of Cu concentration varied considerably between species. Concentrations in some species increased with contamination while in other species metal concentration did not significantly vary along the pollution gradient. In contrats, Cu and Pb concentrations in ants always increased with contaminations. Inconsistence in abundance patterns and Cu concentrations between species along the pollution gradient suggests that using abundance in carabids as an index of pollution could be misleading and that carabids in general may not reliably indicate Cu contaminations in polluted environments.

Keywords: Pollution gradient; Environmental pollution; Copper mining; Pollution indicators

Introduction

Mineral exploration in Zambia started during the 1920s and resulted in the discovery and development of several mines (Fleischer et al. 1976; Brooks et al. 1978; McGowan et al. 2003). The province of Copperbelt has been a place of intensive mining activities since then. Both, open pits and underground mines exist in the province with washing plants and smelters, generating substantial mine waste (Dudka & Andriano 1997; Pettersson & Ingri 2001; Ntengwe 2005). When the world prices of copper fell, the capital available to maintain and update mining technology declined and production deteriorated. In response, Zambia embarked on the options for privatization in early 1990s (Craig 2001; Kríbek et al. 2010). With privatization of mines, and the recent industrial development of fast-growing economies in Asia (Northey et al. 2014), production of copper and other minerals have increased drastically. Zambia is nowadays with the Democratic Republic of Congo the number one producer of copper in Africa (Mikesell 2013; Northey et al. 2014).

Mining operations in Zambia, however, rely on pollution prone technology and the controls on the discharge of pollutants from the mines and smelters are lax (Nriagu 1992; Tembo et al. 2006). The emissions as well as wind-blown dust from mine tailings and smelter dumps are usually the main sources of pollution (Ettler et al. 2011; Tembo et al. 2006). Although robust measures have been undertaken to control emissions in Zambia, areas in close proximity to the smelters and mines remain highly polluted with heavy metals and other xenobiotic chemicals (Ettler et al. 2012). In forest ecosystems, close to the mine works, the substantial contamination of heavy metals occurs in the litter layer (Martin et al. 1982; Laskowski & Berg 1993). Considerable amount of heavy metal particles in dust deposits on leaves is also conveyed to the soil by rainfall and shedding of leaves (Haiyan & Stuanes 2003). As a consequence, organisms inhabiting the forest floor are often exposed to a high contamination with heavy metals (Hopkin 1989; Talarico et al. 2014; Santorufo et al. 2014).

Carabids are mostly confined to the ground and thereby exposed to heavy metal contamination in polluted sites. Evidence from laboratory experiments shows a decrease in survival probability of carabids in environments contaminated with heavy metals (Stone et al. 2001; Maryanski et al. 2002; Mozdzer et al. 2003). Decreased body mass, reduced fecundity, and increased developmental time have also been reported in carabid populations exposed to metal contamination (Bayley et al. 1995; Šustek 1994; Kramarz 2000; Lagisz et al. 2002). Thus, pollution has a profound effect on beetle individuals and may therefore also affect abundance, population dynamics and composition of assemblages.

Although the effect of heavy metal contamination on carabids in the laboratory is well documented (Skalski et al. 2010; Lagisz et al. 2002; Mozdzer et al. 2003), their response to pollution in the field is far from clear (Gongalsky et al. 2004; Belskaya & Zinoviev 2007; Kiovula 2011; Cui et al. 2014). For instance, Skalski et al. (2010) found abundance and richness to decrease with increasing metal pollution. In contrast, several studies observed no correlation between richness and metal contamination along a pollution gradient despite high concentrations of xenobiotic chemical (Read et al. 1987; Lock et al. 2001). Babin-Fenske & Anand (2011) reported a complex pattern of response to heavy metal contamination across carabid species, where some species increased but other species did not change in abundance near the emission source.

Many studies have primarily endorsed the utility of carabids as pollution indicators (Ermakov 2004; Gongalsky et al. 2004; Belskaya & Zinoview 2007; Martinson & Raupp 2013; but see Koivula 2011). Contrasting responses to contamination among species, however, may put into question the general utility of carabids as pollution indicators. We examined carabid species along the 200 km heavy metal pollution gradient in Zambia. We focused on abundance patterns and the Cu and Pb concentrations in the six most dominant species. Additionally, along the same pollution gradient, we investigated also the six most dominant species of ants i.e. *Acanthognathus* sp., *Camponotus* sp.1, *Camponotus* sp.2, *Cephalores* sp., *Formica* sp.1 and *Formica* sp.2. Similar to carabids, most ants live on the ground and ants may also be affected by xenobiotic chemicals. Specifically we address the following questions: (1) Does abundance and richness of carabids increase along the Cu-Pb pollution gradient? (2) Does heavy metal concentration in carabids correlate with contamination in the soil, and is there variation between species? (3) Comparing carabids and ants, we assessed which insect group is a better indicator of Cu or Pb contaminations?

Materials and Methods

Study site and sampling

The study was conducted from May 2013 to January 2014 in the Copperbelt region stretching from Chingola (12°24′S, 27°37′E; 1311 m a.sl) to Solwezi (12°03′S, 26°00′E; 1429 m a.s.l), Zambia. Copperbelt region belongs to the summer rainfall (November–April) tropical climate zone and features seasonal differences with an annual temperature range from 3 to 31°C and a rainfall range from 1,200 to 1,500 mm. There is no significant variation in topography, soils and climatic conditions in the region (Chidumayo 1997). Chingola is a place of intensive mining activities since 1920s and based on heavy metal contaminations, copper has been reported as a dominant soil contaminant in the area (Ettler et al. 2012). We established a 200 km transect from Chingola to Solwezi and placed 10 study sites (30 m x 30 m) each at every 20 km along this transect for carabids, ants and soil sampling. All study sites were located in the same forest type of native tree species with similar soil characteristics and forest structure.

Each study site was sub divided into five 10 m x 10 m plots (see also Chungu & Brandl *unpublished*). We installed one pitfall trap in every plot (n = 50) for the collection of carabids and ants in May 2013 and trapping continued until January 2014. Traps were emptied and refilled once a week. Carabids were identified to species level and ants to morphospecies. Voucher specimens were deposited at Division of Entomology Research, Forestry Department, and at School of Natural

Resources, Copperbelt University, Kitwe, Zambia (Chungu & Brandl *unpublished*). We also randomly collected five soil samples from each study site. We sieved through a 1 mm mesh and stored the material at room temperature for heavy metal analysis. Soil samples from each study site were pooled.

Heavy metal determination

We selected five adult individuals from the pitfall traps for each of the six most dominant carabids and ants for heavy metal analysis following the method of van Straalen & van Wensem (1986) as well as Stone et al. (2002). The six species of carabids were *Anthia omoplata, Epigraphodes congoensis, Procletus* sp., *Siopelus chisasa, Tefflus muata* and *Tefflus* sp., and are known to be associated with native forests in the region (Chungu & Brandl *unpublished*). Species of ants included *Acanthognathus* sp., *Camponotus* sp.1, *Camponotus* sp.2, *Cephalores* sp., *Formica* sp.1 and *Formica* sp.2. Insects for metal analysis were stored at −70 °C until heavy metal content was determined. Soils and insects were dried at 105 °C, weighed and digested in 1 ml of nitric acid. Concentrations of copper and lead were analyzed with flame atomic absorption spectrometer (AAS, Perkin Elmer Analyst 200, Perkin Elmer Corporation, Norwalk, CT, USA).

Statistical analysis

To determine the significance of metal contamination in influencing abundance patterns of carabid species, we performed redundancy analysis and permutation test implemented in *vegan* package (Oksanen et al. 2007). To test the relationship between metal contamination in the soil and metal concentration in animals, we analyzed data using multiple regression models. Copper concentration in animals was expressed as a function of Cu contamination in the soil, animal species and study sites. Cu contamination in the soil and animal species were treated as fixed factors, and study sites as random factors in the model. The analysis was repeated with Pb and with ants. Carabid species used as fixed factors in the model were arranged as follows; *A. omoplata, E. congoensis, Procletus* sp., *S. chisasa, T. muata* and *Tefflus* sp. While species of ants were; *Acanthognathus* sp., *Camponotus* sp.1, *Camponotus* sp.2, *Cephalores* sp., *Formica* sp.1 and *Formica* sp.2. Assumptions of an ordinary least-squares regression are that the standard error of the error term is constant over all values of the response and, that explanatory variables and all estimates provide equally precise information (Quinn & Keough 2002). To improve the information quality of the data, heavy metal values were *log* transformed. Relationships between carabid abundance, richness, metal concentrations and soil contaminations were determined with Pearson correlations. All statistical analyses were performed with the software R version 3.0.3 (R Development Core Team 2014).

Results

We collected in the pitfall traps a total of 8,134 carabid beetles representing 29 species. Redundancy analysis showed differential abundance patterns between species in the contaminated environment (Fig 4.1). The effect of Pb contamination on the abundance of carabids was significant ($F = 2.6$, $p < 0.01$) while that of Cu was highly significant ($F = 4.2$, $p < 0.001$; Fig 4.1). Overall, abundance and richness increased with distance from the mining site (abundance: $r = 0.90$, $p < 0.001$; richness: $r = 0.85$; $p < 0.01$; Fig. 4.2). However for the six selected species, abundance patterns along the transect varied significantly between species (Fig 4.1). For instance, abundance for *A. omoplata* decreased from 99 (17.1 ± 3.2) at the 20 km site to 5 (1.5 ± 0.1) at 200 km site, and the trend was similar for *Tefflus* sp. But abundance for *E. congoensis* increased from 12 (3.1 ± 0.9) at 20 km site to 222 (45.6 ± 3.7) at 200 km site. A similar pattern was found for *S. chisasa, T. muata* and *Procletus* sp. (Appendix D.1).

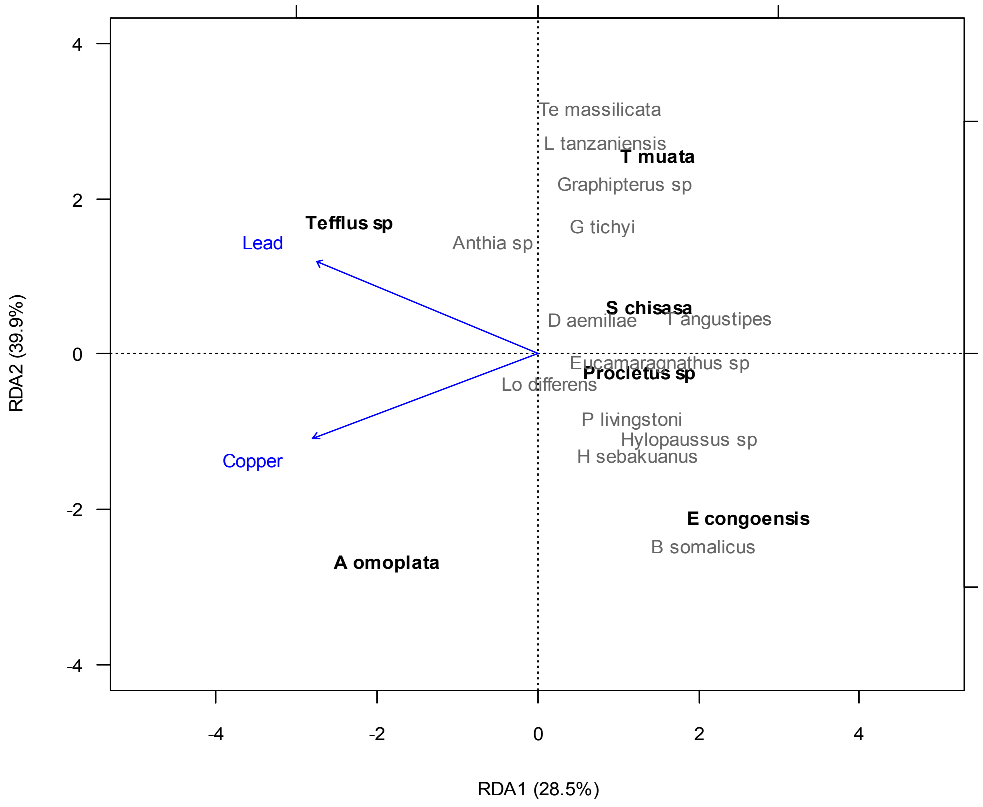

Fig 4.1: *Relationship between species abundance of carabids and metal contamination. Species used for metal analysis are in bold*

Copper contaminations in the soil ranged from 1090 ± 327.1 ppm at 20 km site to 69.57 ± 16.01 ppm at 200 km site, and lead contaminations ranged from 98.9 ± 22.8 ppm to 42.3 ± 10.4 ppm (Fig 4.2). These values exceed permissible limits set by WHO (Cu, 30 ppm and Pb, 35 ppm; WHO 1996). Heavy metal contaminations in the soil decreased with distance from the mining site (Cu: r =-0.92; and Pb: r = -0.88, $p < 0.001$, Fig 4.2). However, particularly the decrease of the Pb-concentration was not linear.

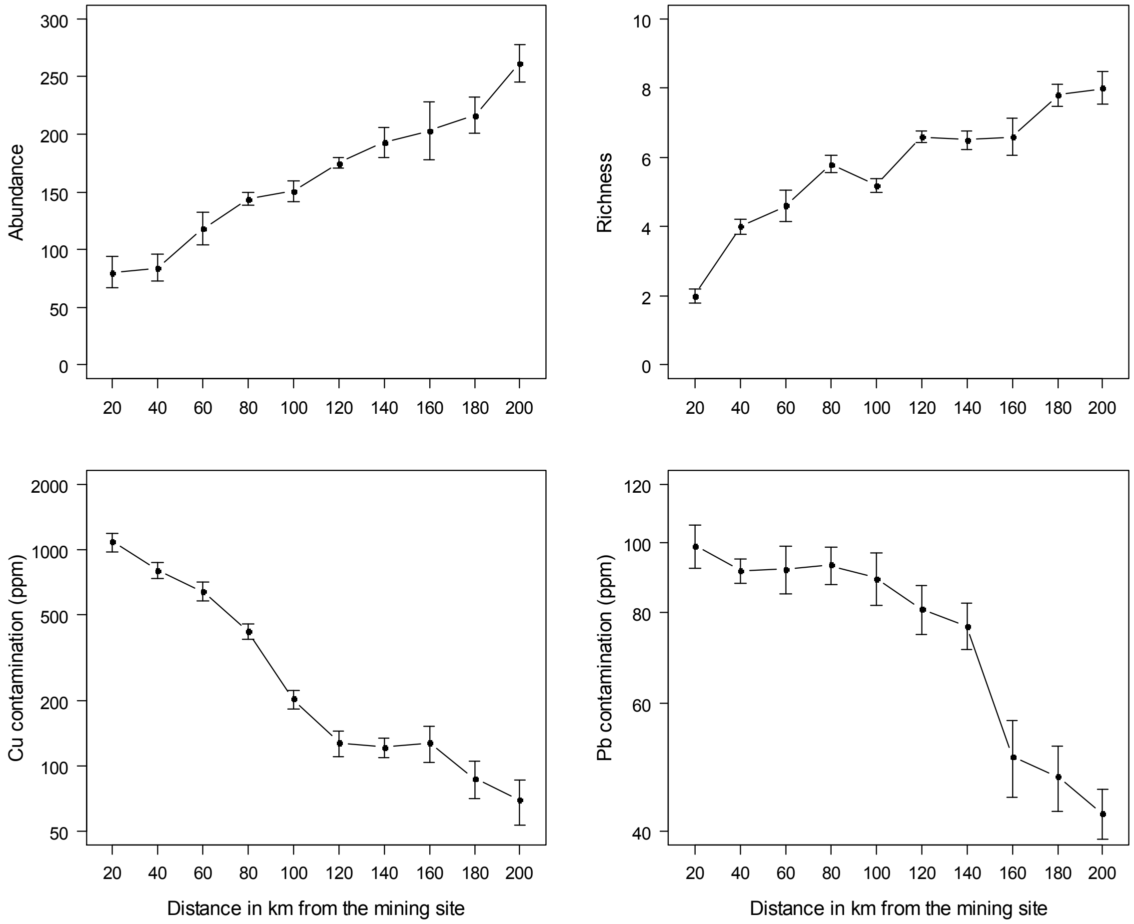

Fig. 4.2*: Patterns of means of the pooled samples for abundance, richness, Cu and Pb contaminations along the distance in km from the mining site. Cu and Pb contamination are drawn on log scale. Error bars represent standard error of the mean*

Copper concentrations in carabids ranged from 0.22 ppm to 23.6 ppm and lead concentrations from 1.13 ppm to 43.5 ppm. Regression analyses revealed that Cu concentration in carabid species increased with Cu contamination in the soil ($b = 0.91$, $t = 20.12$, $p < 0.001$; Table 4.1) along the metal pollution gradient. However, Cu concentration varied considerably between species and the interactions between contamination and species were highly significant (Table 4.1). For example, Cu concentrations in *E. congoensis* decreased from 19.7 ± 1.8 ppm at 20 km site to 14.1 ± 1.5 ppm at 200 km site, but in *T. muata* and *S. chisasa* Cu concentrations did not vary between 20 km and 200 km sites (Fig 4.3). Although Pb contaminations in the soil were different between sites, concentrations of this metal in carabids did not significantly vary between species except for *Tefflus* sp and the interactions between contaminations and species were not significant in all species along the metal pollution gradient (Table 4.1).

Table 4.1: Linear regression model for the effect of heavy metal contamination on metal concentrations in carabids

	Copper			Lead		
Coefficients	Estimate	SE	*t* value	Estimate	SE	*t*-value
Intercept	-4.169	0.249	-16.72***	-4.745	0.727	-6.529***
Contamination in the soil	0.908	0.045	20.12***	1.640	0.169	9.688***
Epigraphodes congoensis	6.113	0.352	17.35***	-0.776	1.028	-0.755
Procletus sp	2.865	0.352	8.13****	-1.119	1.028	-1.089
Siopelus chisasa	3.944	0.352	11.19***	-0.536	1.028	-0.521
Tefflus muata	6.074	0.352	17.24***	-0.203	1.028	-0.198
Tefflus sp	4.769	0.352	13.53***	2.507	1.028	2.439*
Contamination x *E. congoensis*	-0.760	0.064	-11.92***	0.120	0.024	0.500
Contamination x *Procletus* sp	-0.555	0.064	-8.71***	0.187	0.024	0.780
Contamination x *S. chisasa*	-0.662	0.064	-10.37***	0.098	0.024	0.410
Contamination x *T. muata*	-0.880	0.064	-13.79***	0.014	0.024	0.060
Contamination x *Tefflus* sp	-0.726	0.064	-11.37***	-0.426	0.024	-1.777

*significant at $p < 0.05$; ***significant at $p < 0.001$

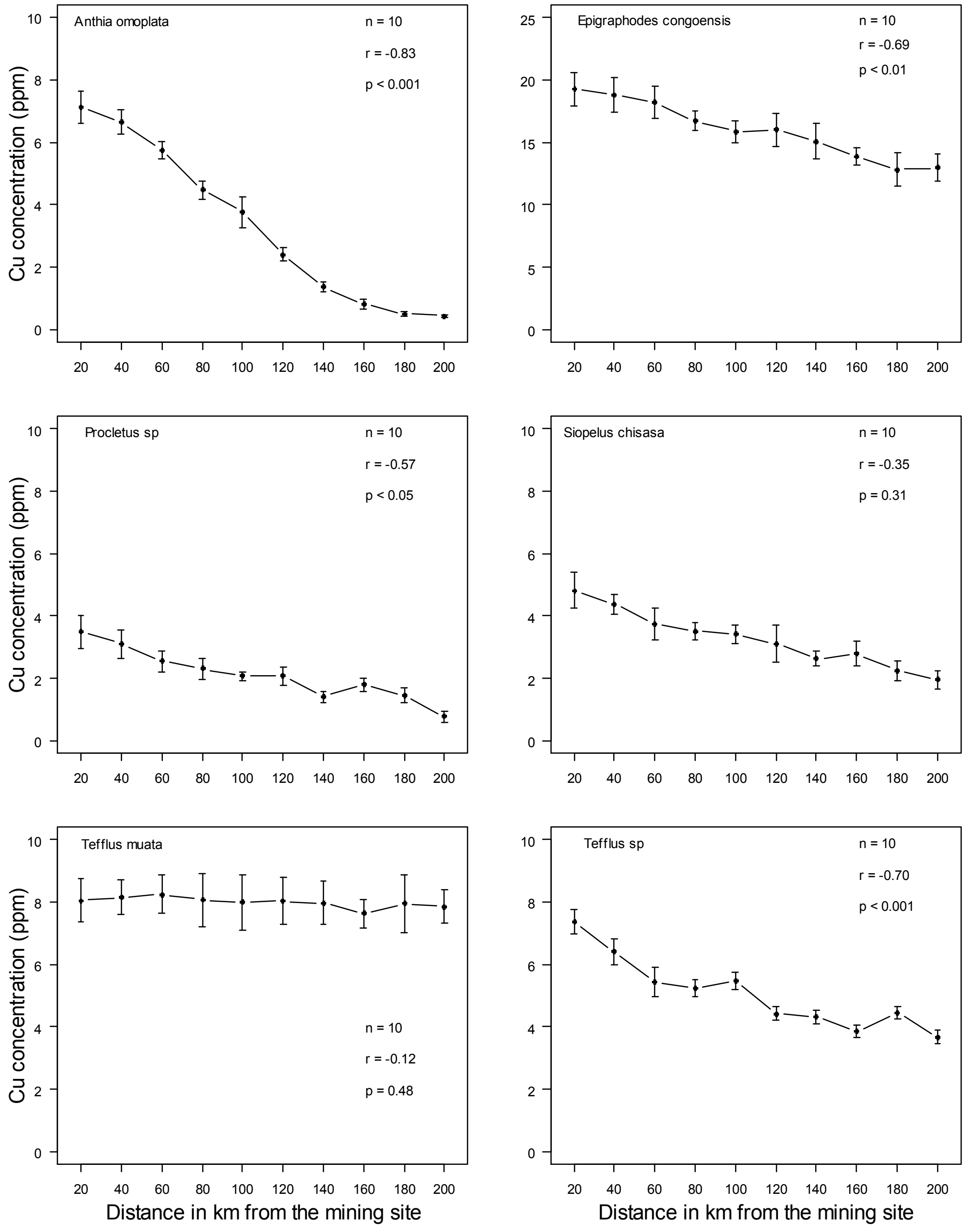

Fig. 4.3: Mean Cu concentrations across five individuals in carabid species along the distance from the mine

Cu concentrations in ants ranged from 0.084 ppm to 32.3 ppm and Pb concentrations from 5.05 ppm to 37.6 ppm (Appendix D.2). Regression analyses consistently showed that Cu concentrations in ants increased with Cu contaminations in the soil ($b = 0.43$, $t = 6.76$, $p < 0.001$; Table 4.2; Appendix D.3). Neither of the interactions between species and Cu contamination were significant except for *Formica* sp1 and *Cephalores* sp (Table 4.2). We did not detect any significant differences in Pb concentrations between species (Table 4.2), suggesting a uniform response to heavy metal pollution between ant species.

Table 4.2: Linear regression model for the effect of heavy metal contamination on metal concentrations in ants

	Copper			Lead		
Coefficients	Estimate	SE	*t* value	Estimate	SE	*t*-value
Intercept	0.361	0.353	1.026	-1.268	0.502	-2.525*
Contamination in the soil	0.431	0.064	6.756***	0.924	0.117	7.896***
Camponotus sp1	-0.739	0.498	-1.482	0.692	0.710	0.975
Camponotus sp2	-0.650	0.498	-1.305	-0.191	0.710	-0.269
Cephalores sp	-1.608	0.498	-3.225**	-0.917	0.710	-1.292
Formica sp1	-2.845	0.498	-5.708***	1.390	0.710	1.957
Formica sp2	0.349	0.498	0.772	0.478	0.710	0.674
Contamination x *Camponotus* sp1	0.084	0.090	0.928	-0.185	0.165	-1.120
Contamination x *Camponotus* sp2	0.089	0.090	0.981	-0.015	0.165	-0.091
Contamination x *Cephalores* sp	0.221	0.090	2.451*	0.213	0.165	1.286
Contamination x *Formica* sp1	0.411	0.090	4.557***	-0.308	0.165	-1.862
Contamination x *Formica* sp2	-0.053	0.090	-0.585	-0.074	0.165	-0.450

*significant at $p < 0.05$; **significant at $p < 0.01$; ***significant at $p < 0.001$

Discussion

Our results indicate that abundance and richness of carabid assemblages change with the contamination of sites. Total abundance and richness generally increased with distance from the metal pollution source. But, abundance in some carabid beetles, *A. omoplata* and *Tefflus* sp., decreased with increasing distance from the metal pollution source. To our knowledge, this is the first case that suggests that abundance increases in Cu or Pb contaminated environments. However, there was no correlation between abundance and Cu concentrations in carabids along the pollution gradient (Appendix D.4). Carabid species that benefit from higher contaminations are usually generalists with a broad ecological niche (Bengtsson & Rundgren 1984; Skalski &

Pośpiech 2006). Therefore, an explanation for this unusual pattern is that these generalists are able to increase in abundance with the decrease of abundance in other species due competitive release (Azevedo et al. 2012; Miraldo & Hanski 2014).

As carabid beetles are in most cases second order consumers, they are at least potentially exposed to contaminations of metals in their diet (Lindqvist et al. 1995; Kramarz 1999) and some heavy metals may enrich along the food chain (Peralta-Videa et al. 2009; Abreu et al. 2014). Thus, we expected elevated metal concentrations in carabids living in contaminated environment compared to those in less polluted sites. However, we found a significant variation in Cu concentrations between species across sites. Regarding individual carabid species, Cu concentrations in most species decreased with metal contaminations. But Cu concentrations in individuals of *T. muata* and *S. chisasa* did not follow site contaminations. In contrast, in ants all species consistently followed site contamination. This suggests that ants are possibly better indicators of Cu pollution than carabids.

Concentrations of Pb in carabids and ants appeared to increase with Pb contaminations in our study. This is consistent with other studies where elevated concentrations of Pb have been reported in ground beetles dwelling in Pb polluted environments (Hopkin 1989; Rabitsch 1995). Due to the fact that xenobiotic metals such as Pb are not efficiently regulated in invertebrates (Kramarz 1999), it is not surprising that our study detected an increase in Pb concentrations in carabids and ants with increasing Pb contaminations in the soil. Overall, all species of carabids and ants showed an increase in Pb concentrations with increased Pb contaminations, but

Cu concentration patterns varied between species in the current investigation. However, it is important to recognize that the level of metal concentration depends on specific carabid species and not on carabids in general.

Carabids are known to regulate the concentration of metals in their organs (Lagisz & Lawskowski 2008; Janssen et al. 1991; Lagisz et al. 2005) and different abilities in regulatory mechanisms between species (Maryanski et al. 2002; Jelaska et al. 2007; Arini et al. 2014), could potentially lead to differences in metal concentrations. Despite dwelling in the same habitat, carabids were found to contain lower Cu or Pb concentrations than ants. However, this finding is not new and has been previously reported in many studies (Rabitsch 1995; Eeva et al. 2004; Stone et al. 2002; Sorvari et al. 2007). In fact, Cu concentrations above 50 ppm in the body are known to be toxic to carabids (Bengtsson & Tranvik 1989). However, much higher concentrations of Cu and Pb have been reported in ants (*Formica* species) (Bengtsson & Rundgren 1984). Distinct feeding preferences between carabids and ants as well as metal regulatory mechanisms specific to each taxonomic group (Langan et al. 2004; White et al. 2009; Rasib & Ashraf 2014), might be plausible explanation for variation in metal concentrations we observed in animals.

Conclusions

Copper and lead contaminations in the soil decreased with increasing distance from the mining site. Differential abundance patterns in carabid species along a metal pollution gradient revealed that the effect of pollution on carabids is not universal.

Copper concentrations in most carabids increased with Cu contaminations in the soil, but in some species, Cu contaminations decreased with increasing contaminations. This variation could have been driven by differences in detoxification abilities or differences in feeding preferences between species. Metal concentrations in ants, however, correlated with metal contaminations in the soil for all species, suggesting that ants are better indicators of Cu or Pb pollution in the environment than carabids. Differential response to metal pollution between carabid species suggests that only carabids should be cautiously utilized as pollution indicators. The continuous build-up of metal concentrations may have long-term consequences for insect populations, thus it would seem reasonable to press ahead with attempts to reduce the emissions of metals to the environment.

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5 Summary

The major threat underlying the potential loss of biodiversity is land use change. Land use change is driven by agriculture expansion, plantation establishment and mining in Zambia. Understanding the impact of these drivers of land use change on biodiversity is important to attain sustainable management of biological resources. The main objective of my dissertation was to broaden the understanding of the response of species assemblages to land use change in a tropical landscape. I used carabid species (Coleoptera: Carabidae) as model organisms and analyzed their response along gradients of anthropogenic pressure. For this purpose, I based my study in 14,000 km^2 landscape consisting of natural forests, non-native plantations, agriculture fields and mining activities and I sampled carabid species across 50 study sites, each consisting of 5 plots.

Clearing of native forests for the introduction of non-native plantations leads to biodiversity loss. I found that richness for arthropods and particularly carabids decreased from native forests to non-native plantations. This decrease was particularly pronounced when native broadleaved forests were transformed to pine plantations. Of course non-native plantations influence properties of the soil. However, after considering such differences in litter and soil pH the plantations were still species poor compared to native forests. Overall, the results showed clearly that converting native forests decrease biodiversity in epigeic invertebrates.

Agricultural expansion is by far the leading land-use change associated with forest loss which in turn alters assemblages of species. By incorporating abundance data and phylogenetic information between species, I made an attempt to document the effect of agriculture ecosystem on body size in carabid assemblages. I discovered that carabid species were smaller in agriculture ecosystem than in forest ecosystem. Body length decreased with increasing abundance in agriculture ecosystem but in forest ecosystem I observed that abundance of species increased with body length. This observation, suggests that, the general negative correlation between body size and abundance that is widely reported in the literature may not hold at the local scale.

Furthermore, areas in close proximity to the smelters and mines are highly polluted with heavy metals and xenobiotic chemicals, which usually exceed permissible limits. I observed that the assemblages of carabid beetles living in metal contaminated environment differ in composition compared with those beetles inhabiting less polluted sites. Abundance and richness in carabids increased with distance from the metal pollution source. But, abundance in some carabid beetles decreased with increasing distance from the metal pollution source. Regarding individual carabid species, I observed that copper concentrations in most species decreased with copper contaminations along the pollution gradient. But copper concentrations in some carabid species showed not always a clear positive correlation to the contamination of the environment. In contrast, Cu and Pb concentrations in ants correlated with contaminations along the pollution gradient and all investigated ant species consistently followed this pattern.

Overall, my results provide evidence that land use change leads to biodiversity loss and changes in the composition of assemblages. The adverse effects of replacing native forests with non-native plantations underscore the importance of conserving native forests in order to protect biodiversity. Clearing natural forests for agriculture, influences assemblages in relation to morphological traits of species. My observation revealed that species occurring in agricultural fields were on average smaller than the species occurring in natural forests. Furthermore, inconsistence abundance patterns in carabid species inhabiting contaminated environment might imply that using abundance as an index of pollution could be misleading. My findings also revealed that ants are possibly better indicators of Cu pollution than carabids. The continuous build-up of metal concentrations may have long-term consequences for insect populations, thus it would seem reasonable to press ahead with attempts to reduce the emissions of metals into the environment.

Outlook and future research options

My dissertation supports the observation that land use change is an important form of global pressure affecting biodiversity. Certainly, this dissertation provides answers only to some questions that rise in the context of human forest modification and many more questions still remain to be investigated further regarding the effects of anthropogenic impact on biodiversity.

Introduction of non-native plantations is usually regarded as a surrogate for afforestation in Zambia but when this practice is done to replace native forests could lead to biodiversity loss. In fact, it has been established elsewhere that biodiversity is enhanced when plantations are established in previously degraded lands (Pawson et al. 2008; Brockerhoff et al. 2008). This dissertation revealed that replacing native forests with plantations of non-native trees (pine and eucalyptus) decreases richness and changes assemblages of carabid beetles. In order to fully understand the impact of replacing native forests with non-native plantations, further research is required. For example, investigating genetic diversity within and between species will deepen our understanding of biodiversity loss. In this regard, I will carry out genetic analyses using mitochondria and nuclear DNA of common carabid species in native forests and compare with their genetic diversity in non-native plantations. Changes in species richness or genetic diversity may have far reaching implications at the ecosystem scale and open further ecological questions that may relate to functional diversity. I will examine changes in species functional types by assessing those species sharing similar functioning at the organismic level between forest types. In this context, data on richness of various functional groups such as predators, herbivores and detritivores may provide deeper understanding on species responses when native forests are replaced with non-native plantations and may also provide additional insight on the pros and cons of plantations in the biodiversity conservation framework.

My dissertation has further shown that the response of carabid beetles to pollution is not consistent across species in the natural environment. Due to the fact that there could be many environmental variables affecting responses of animals to pollution, further research is required in order to pinpoint specific factors that may influence this inconsistence in carabid species. I will, therefore, carry out laboratory feeding experiments in which carabid species are fed with food contaminated with different quantities of Cu, Pb or other important heavy metals present in the Zambian environment. After feeding carabid beetles for at least one generation, I will then assess changes in body mass, fecundity and sex ratio of species. This will provide additional answers to questions on how species respond to specific contaminations in Zambia.

6 Zusammenfassung

Veränderte Landnutzung ist eine der wichtigsten Gefährdungsursachen für den potentiellen Verlust von Biodiversität. In Zambia sind es vor allem die Ausweitung der landwirtschaftlichen Anbauflächen, die Etablierung von Forsten sowie der Bergbau. Um die biologischen Ressourcen nachhaltig sichern zu können ist es daher wichtig den Einfluss veränderter Landnutzung auf die Biodiversität zu verstehen. Die Hauptaufgabe meiner Dissertation war es, den Kenntnisstand des Einflusses von veränderter Landnutzung auf die Zusammensetzung von Artengemeinschaften in einer tropischen Landschaft zu erweitern. Als Modelorganismen wählte ich Laufkäfer und analysierte die Veränderung der Käfergemeinschaften entlang eines anthropogenen Störungsgradienten. Das Untersuchungsgebiet erstreckte sich über 14 000 km^2 und beinhaltete gebietstypische Wälder, Forste, landwirtschaftlich genutzte Flächen und Bergbauflächen. Insgesamt habe ich 50 Untersuchungsflächen, die jeweils nochmals in 5 Teilflächen unterteilt waren, untersucht.

Die Abholzung von gebietstypischen Wäldern zugunsten von Forsten mit gebietsfremden Arten führen zu einem Verlust von Biodiversität. Der Artenreichtum von Arthropoden, vor allem von Laufkäfern, nahm von gebietstypischen Wäldern zu Forsten mit gebietsfremden Arten hin ab, vor allem wenn heimischer Laubwald in Kiefernforste überführt wurde. Der Anbau von gebietsfremden Forstbäumen beeinflusst auch die Böden. Nichtsdestoweniger waren nachdem der Einfluss von Bodenstreu und Boden pH-Werten berücksichtigt wurde, die Forste deutlich artenärmer als die heimischen Wälder. Zusammenfassend lässt sich damit sagen, dass die Überführung von heimischen Wäldern in Forste mit gebietsfremden Arten die Biodiversität von bodenbewohenden Arthropoden verringert.

Die Ausweitung von landwirtschaftlich genutzten Flächen durch die Abholzung von Wäldern ist eine der bedeutendsten Landnutzungsveränderungen. Dadurch werden auch die ansässigen Artengemeinschaften verändert. Unter der Berücksichtigung von Häufigkeit und der stammesgeschichtlichen Zusammenhänge der Arten habe ich den Effekt der landwirtschaftlichen Nutzung auf die Körpergrößenverteilung von Laufkäfergemeinschaften untersucht. Im Mittel waren die Körpergrößen der Arten der landwirtschaftlich genutzten Flächen im Vergleich zu Arten der Wälder kleiner. Die Körperlänge in den lanwirtschaftlich genutzten Flächen nahm mit zunehmender Häufigkeit der Arten ab, wogegen in Wäldern die Häufigkeit mit zunehmender Körpergröße anstieg. Das bedeutet, dass der in vielen Studien berichtete negative Zusammenhang zwischen Körpergröße und Häufigkeit auf der lokalen Skala nicht zutreffen muss.

Flächen in der Nähe der Bergbaugebiete und der Hüttenwerke sind stark mit Schwermetallen und Chemikalien belastet die gewöhnlich die zugelassenen Grenzen überschreiten. Ich fand heraus, dass sich die Artengemeinschaften der Käfer der belasteten Gebiete von denen weniger belasteter Flächen unterscheiden.

Die Artenvielfalt und die Häufigkeit der Laufkäferarten nahmen mit zunehmender Entfernung von der Emissionsquelle zu. Allerdings nahm von einigen Laufkäferarten die Häufigkeit mit zunehmender Entfernung von der Emissionsquelle ab. Bei einigen Laufkäferarten nahm die Kupferkonzentration der Käfer entsprechend der Abnahme der Kupferkonzentrationen entlang des Verschmutzungsgradienten ab. Allerdings gab es nicht immer einen positiven Zusammenhang zwischen der Kupferkonzentration in den Arten und der Kupferbelastung der Umgebung. Bei allen Ameisenarten waren hingegen die Kupfer- und Bleikonzentrationen immer mit der Verschmutzung der Umgebung korreliert.

Die Ergebnisse meiner Studie unterstützen den Befund, dass Veränderungen in der Landnutzung zu einem Rückgang der Artenvielfalt und zu einer Veränderung der Artenzusammensetzung führen. Der nachteilige Effekt der Überführung von gebietstypischen Wäldern in Forste mit gebietsfremden Arten unterstreicht die Bedeutung des Schutzes von heimischen Wäldern für den Erhalt von Biodiversität. Die Abholzung von Wäldern und deren Umwandlung in landwirtschaftlich genutzte Flächen beeinflusst die morphologischen Merkmale der Arten. Meine Untersuchungen zeigen, dass die Arten der landwirtschaftlich genutzten Flächen im Mittel kleiner sind als die Arten der gebietstypischen Wälder. Die inkonsistenten Ergebnisse hinsichtlich des Zusammenhangs zwischen Verschmutzungsgrad und Häufigkeit legen nahe, dass Häufigkeit als ein Maß für den Verschmutzungsgrad zu falschen Einschätzungen führen kann. Ameisen scheinen bessere Indikatoren für Kupferverschmutzung zu sein als Laufkäfer. Der fortschreitende Anstieg der Metallkonzentrationen könnte Langzeit-Effekte auf die Insektenpopulationen haben. Es ist daher angebracht die Emissionen von Metallen in die Umwelt zu reduzieren.

Zukünftige Forschungsmöglichkeitenoptions

Meine Dissertation unterstützt den Befund, dass veränderte Landnutzung einen wichtigen Einfluss auf die globale Biodiversität hat. Die Arbeit kann aber sicherlich nur Antworten zu einigen der aufgeworfenen Fragen im Kontext der Modifizierung von Wäldern durch den Menschen geben. Es verbleiben daher noch viele offene Fragen die untersucht werden müssen.

Die Etablierung von Forsten mit gebietsfremden Arten wird gewöhnlich als Maßnahme zur Wiederbewaldung betrachtet. Wenn dadurch aber gebietstypische Wälder in Forste umgewandelt werden, kann es zu einem Verlust von Biodiversität kommen. Es hat sich gezeigt, dass Aufforstungen auf degradierten Flächen die Biodiversität erhöhen kann (Pawson et al. 2008; Brockerhoff et al. 2008). Diese Dissertation zeigt, dass die Umwandlung von gebietstypischen Wäldern in Forste mit nicht-heimischen Arten (Kiefern und Eukalyptus) die Artenvielfalt von Laufkäfern verringert und die Artenzusammensetzung von Laufkäfern verändert. Um die Zusammenhänge genau zu verstehen sind allerdings noch weitere Studien notwendig.

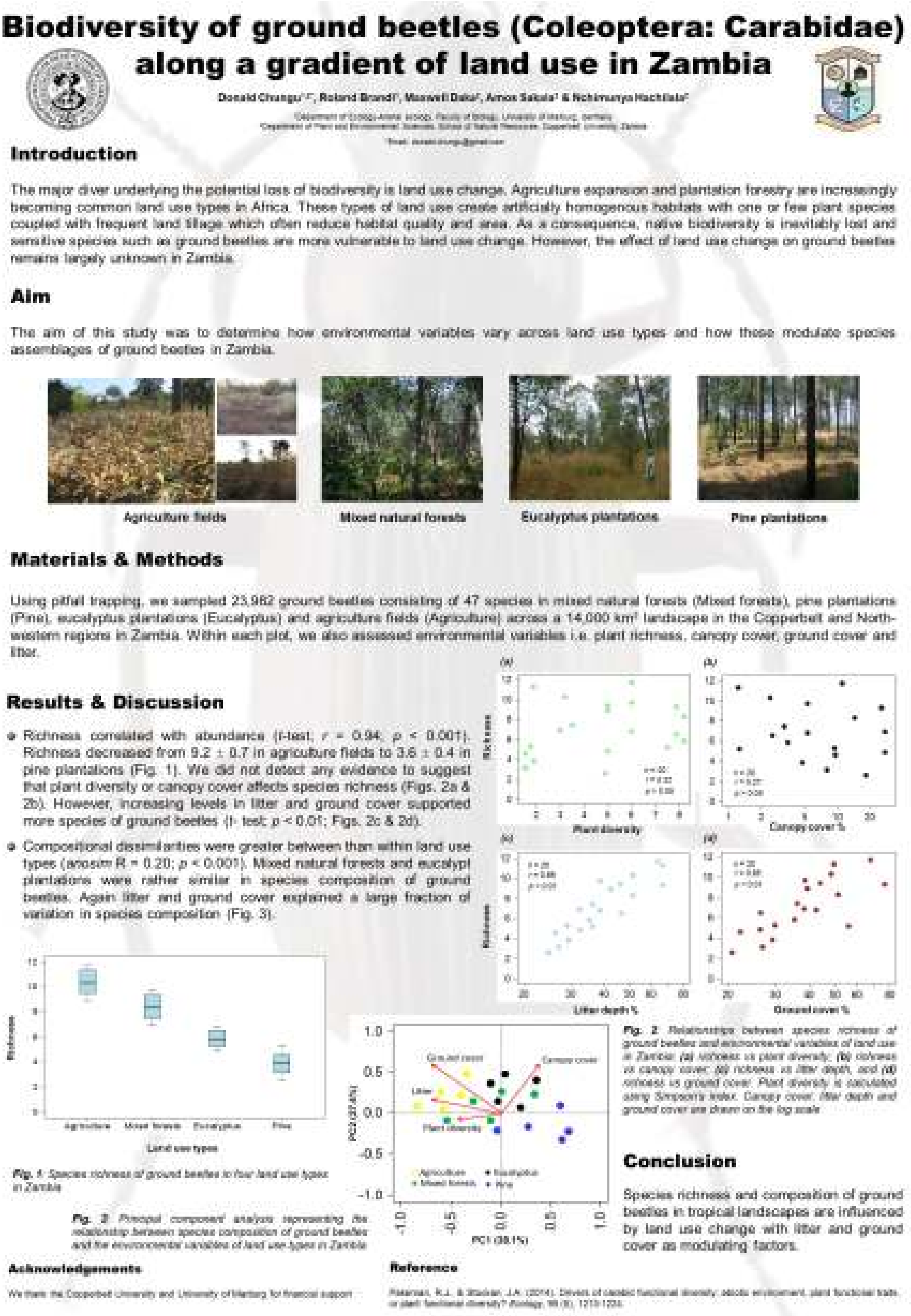
Zum Beispiel können Untersuchungen zur genetischen Diversität innerhalb und zwischen Arten unser Verständnis des Verlusts von Biodiversität verbessern. Ich möchte daher in künftigen Studien mitochondriale und nukleäre DNA häufiger Laufkäfer Arten zwischen gebietstypischen Wäldern und Forsten mit gebietsfremden Bäumen vergleichen. Veränderungen in der Artenvielfalt und der genetischen Vielfalt können zu ökosytemaren Veränderungen führen und neue Fragen in Richtung funktioneller Diversität aufwerfen. Ich möchte daher die Veränderung von funktionellen Typen zwischen verschiedenen Waldtypen vergleichen. In diesem Kontext sollen der Artenreichtum von verschiedenen funktionellen Gruppen wie Räuber, Herbivore und Zersetzter untersucht werden. Dadurch könnte man eventuell zu einer besseren Einschätzung der Auswirkung der Umwandlung von heimischen Wäldern in Forste mit gebietsfremden Arten kommen. Außerdem könnte das Für und Wider von Forsten im Zusammenhang mit den Rahmenbedingungen des Schutzes der Biodiversität besser verstanden werden.

Meine Dissertation zeigt zudem, dass Laufkäfer nicht einheitlich auf Umweltverschmutzungen reagieren. Da viele andere Umweltfaktoren den Einfluss von Umweltverschmutzung auf Laufkäfer beeinflussen können, ist zusätzliche Forschungsbedarf der die Bedeutung der einzelnen Faktoren genauer beleuchtet unumgänglich. Ich möchte daher in Laboruntersuchungen Fütterungsexperimente mit unterschiedlichen Mengen von Kupfer und Blei sowie anderen Schwermetallen die in den Lebensräumen in Sambia vorkommen durchführen. Nach einer Generationsfolge möchte ich dann die Veränderungen der Körpergröße, Fertilität und des Geschlechterverhältnis der Laufkäferarten vergleichen. Diese Untersuchen werden dann weitere Antworten auf die Frage wie Laufkäfer auf spezische Kontamination in Sambia reagieren unterbreiten

7 Appendices

Appendices

Appendix A.1: Poster presented at the 62nd Annual Meeting of the Entomological Society of America, November 16-18, 2014, Portland, Oregon, USA



Biodiversity of ground beetles (Coleoptera: Carabidae) along a gradient of land use in Zambia

Donald Chungu, Roland Brandl, Maxwell Dalu, Amos Sakala & Nchimunya Hachilala

Introduction

The major diver underlying the potential loss of biodiversity is land use change. Agriculture expansion and plantation forestry are increasingly becoming common land use types in Africa. These types of land use create artificially homogenous habitats with one or few plant species coupled with frequent land tillage which often reduce habital quality and area. As a consequence, native biodiversity is inevitably lost and sensitive species such as ground beetles are more vulnerable to land use change. However, the effect of land use change on ground beetles remains largely unknown in Zambia.

Aim

The aim of this study was to determine how environmental variables vary across land use types and how these modulate species assemblages of ground beetles in Zambia.

Agriculture fields

Mixed natural forests

Eucalyptus plantations

Pine plantations

Materials & Methods

Using pitfall trapping, we sampled 23,982 ground beetles consisting of 47 species in mixed natural forests (Mixed forests), pine plantations (Pine), eucalyptus plantations (Eucalyptus) and agriculture fields (Agriculture) across a 14,000 km² landscape in the Copperbelt and North-western regions in Zambia. Within each plot, we also assessed environmental variables i.e. plant richness, canopy cover, ground cover and litter.

Results & Discussion

- Richness correlated with abundance (t-test; r = 0.94; p < 0.001). Richness decreased from 9.2 ± 0.7 in agriculture fields to 3.6 ± 0.4 in pine plantations (Fig. 1). We did not detect any evidence to suggest that plant diversity or canopy cover affects species richness (Figs. 2a & 2b). However, increasing levels in litter and ground cover supported more species of ground beetles (t- test; p < 0.01; Figs. 2c & 2d).
- Compositional dissimilarities were greater between than within land use types (anosim R = 0.20; p < 0.001). Mixed natural forests and eucalypt plantations were rather similar in species composition of ground beetles. Again litter and ground cover explained a large fraction of variation in species composition (Fig. 3).

Fig. 1: *Species richness of ground beetles in four land use types in Zambia*

Fig. 2: *Relationships between species richness of ground beetles and environmental variables of land use in Zambia: (a) richness vs plant diversity, (b) richness vs canopy cover, (c) richness vs litter depth, and (d) richness vs ground cover. Plant diversity is calculated using Simpson's index. Canopy cover, litter depth and ground cover are drawn on the log scale*

Fig. 3: *Principal component analysis representing the relationship between species composition of ground beetles and the environmental variables of land use types in Zambia*

Conclusion

Species richness and composition of ground beetles in tropical landscapes are influenced by land use change with litter and ground cover as modulating factors.

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Reference

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Appendix B.1: Relative abundance and probabilities of occurrence (indicator values) for 42 carabid species in native forests and non-native plantations. Probabilities or indicator values in bold face are for species that are exclusive to each forest type and are identified as indicator species in this study

Rank	Species	Relative abundance %	Native forests	Non-native plantations		*p*
			Mixed broadleaved	Eucalyptus	Pine	
			$n = 10$	$n = 10$	$n = 10$	
1	*Tefflus* sp	30.7	1.00	1.00	1.00	na
2	*Anthia omoplata*	16.9	0.98	0.97		0.001***
3	*Epigraphodes congoensis*	10.3	**1.00**			0.001***
4	*Siopelus chisasa*	8.04	1.00	1.00		0.001***
5	*Tefflus angustipes*	7.1			0.78	0.002**
6	*Procletus singularis*	6.9			**1.00**	0.001***
7	*Lobodontus* sp	4.4		**1.00**		0.001***
8	*Tefflus muata*	3.2	**1.00**			0.001***
9	*Hylopaussus sebakuanus*	2.3	1.00	1.00	1.00	na
10	*Procletus* sp	2.6	**1.00**			0.001***
11	*Omophron alluaudi*	1.4	0.92	0.92		0.001**
12	*Lobodontus tanzaniensis*	1.3	0.84			0.001**
13	*Dontolobus aemiliae*	1.2	0.78			0.001**
14	*Anthia* sp	1.2	0.89			0.001**
15	*Stenidia angusta*	0.40		0.84		0.001**
16	*Eucamaragnathus sp*	0.40		0.69		0.005**
17	*Boeomimetes somalicus*	0.37	0.77	0.78		0.006**
18	*Bennigsenium hauseranum*	0.33	0.67	0.67		0.052
19	*Amblystomus dantei*	0.31		0.77		0.001***
20	*Graphipterus tichyi*	0.25	0.78			0.002**

21	*Siopelus* sp	0.22	0.84			0.001**
22	*Abacetus nitens*	0.21		0.55		0.091
23	*Tefflus angustipes*	0.20	0.62	0.61		0.180
24	*Eucamaragnathus desenderi*	0.18	0.63			0.021*
25	*Eucolliuris* sp	0.12		0.77		0.002**
26	*Piezia* sp	0.12	0.50	0.50		0.335
27	*Cymbionotum namwala*	0.09		0.59		0.067
28	*Omophron* sp	0.09	0.78			0.002**
29	*Eucolliuris flavomarginata*	0.08			0.55	0.083
30	*Axinotoma sinuaticollis*	0.08			0.55	0.092
31	*Graphipterus* sp	0.07	0.59		0.59	0.117
32	*Cicindela compressicornis*	0.07		0.70		0.015*
33	*Selina westermanni*	0.06		0.63		0.023*
34	*Siopelus zambianus*	0.05	0.63			0.023*
35	*Siopelus* sp1	0.04	0.63			0.020*
36	*Termophilum massilicata*	0.02	0.55			0.086
37	*Lophyra differens*	0.02	0.55			0.103
38	*Prothymidia angusticollis*	0.01	0.45			0.337
39	*Prothymidia* sp	0.01	0.45			0.314
40	*Piezia livingstoni*	0.006	0.45			0.314
41	*Smeringocera mashuna*	0.004	0.45			0.330
42	*Cypholoba sambesina*	0.002	0.32			0.100
	Number of species		*29*	*18*	*7*	
	Number of indicator species		*19*	*9*	*4*	

Appendix C.1: Means with standard deviations for body length, wing length and body mass of carabid species in natural forest ecosystem

Body size ranking	Species	Body length (mm)		Wing length (mm)		Body mass (g)	
		Male	*Female*	*Male*	*Female*	*Male*	*Female*
1	*Tefflus muata*	48.6 ± 2.29	51.8 ± 1.76	40.4 ± 1.15	42.9 ± 1.76	0.120 ± 0.001	0.142 ± 0.012
2	*Tefflus* sp	48.2 ± 1.78	49.4 ± 1.63	40.3 ± 1.36	41.9 ± 1.53	0.113 ± 0.010	0.180 ± 0.011
3	*Tefflus angustipes*	46.6 ± 0.41	48.5 ± 1.82	41.8 ± 0.37	43.5 ± 1.63	0.112 ± 0.002	0.120 ± 0.011
4	*Termophilum massilicata*	42.6 ± 2.51	44.7 ± 1.79	38.2 ± 1.11	39.9 ± 1.42	0.166 ± 0.011	0.181 ± 0.010
5	*Anthia omoplata*	33.3 ± 1.80	35.1 ± 1.54	29.3 ± 1.72	30.2 ± 1.18	0.103 ± 0.001	0.124 ± 0.013
6	*Anthia* sp	25.9 ± 1.10	28.8 ± 0.87	23.4 ± 0.77	26.3 ± 1.43	0.054 ± 0.003	0.058 ± 0.004
7	*Procletus* sp	22.6 ± 0.44	23.6 ± 1.39	18.6 ± 0.57	20.8 ± 1.56	0.057 ± 0.004	0.069 ± 0.004
8	*Cypholoba sambesina*	17.2 ± 1.05	17.5 ± 0.93	12.9 ± 0.81	13.2 ± 0.56	0.049 ± 0.003	0.057 ± 0.003
9	*Omophron alluaudi*	16.0 ± 0.30	18.5 ± 0.72	12.3 ± 0.50	14.9 ± 0.89	0.013 ± 0.001	0.011 ± 0.001
10	*Graphipterus* sp	15.4 ± 0.61	17.0 ± 0.03	12.6 ± 0.22	14.1 ± 0.01	0.021 ± 0.002	0.030 ± 0.001
11	*Lophyra differens*	15.1 ± 0.11	15.8 ± 0.48	12.2 ± 0.09	12.8 ± 0.39	0.018 ± 0.001	0.025 ± 0.002
12	*Hylopaussus sebakuanus*	14.4 ± 0.67	16.6 ± 0.53	11.7 ± 0.70	13.3 ± 0.57	0.034 ± 0.001	0.033 ± 0.013
13	*Graphipterus tichyi*	14.1 ± 0.45	15.5 ± 0.59	11.6 ± 0.45	12.9 ± 0.42	0.034 ± 0.003	0.022 ± 0.002
14	*Epigraphodes congoensis*	13.8 ± 0.91	14.9 ± 0.34	10.5 ± 0.26	11.3 ± 0.33	0.032 ± 0.012	0.034 ± 0.010
15	*Lobodontus tanzaniensis*	13.4 ± 0.76	15.0 ± 0.64	11.0 ± 0.59	12.7 ± 1.21	0.029 ± 0.002	0.041 ± 0.004
16	*Prothymidia* sp	10.7 ± 0.74	11.7 ± 0.42	7.25 ± 0.52	8.57 ± 0.39	0.021 ± 0.001	0.033 ± 0.003
17	*Siopelus chisasa*	9.94 ± 0.45	11.2 ± 1.72	7.66 ± 0.34	9.15 ± 0.79	0.034 ± 0.001	0.040 ± 0.010
18	*Dontolobus aemiliae*	9.76 ± 0.23	10.1 ± 0.30	7.89 ± 0.19	8.17 ± 0.25	0.019 ± 0.002	0.023 ± 0.002
19	*Piezia livingstoni*	9.71 ± 0.14	10.1 ± 0.80	7.67 ± 0.38	8.41 ± 0.69	0.011 ± 0.001	0.011 ± 0.001
20	*Prothymidia angusticollis*	8.89 ± 0.42	9.15 ± 0.38	6.82 ± 0.54	7.22 ± 0.30	0.022 ± 0.001	0.031 ± 0.002
21	*Eucamaragnathus sp*	8.57 ± 0.99	10.2 ± 0.68	6.89 ± 0.83	8.43 ± 0.95	0.003 ± 0.001	0.002 ± 0.001
22	*Boeomimetes somalicus*	7.98 ± 0.54	9.65 ± 0.43	6.39 ± 0.43	7.74 ± 0.38	0.032 ± 0.004	0.034 ± 0.001
23	*Siopelus zambianus*	7.77 ± 0.09	9.43 ± 0.52	6.05 ± 0.07	7.64 ± 0.42	0.017 ± 0.002	0.033 ± 0.004
24	*Eucamaragnathus desenderi*	7.72 ± 0.39	8.91 ± 0.81	6.22 ± 0.32	7.26 ± 0.75	0.001 ± 0.001	0.004 ± 0.001
25	*Stenidia angusta*	6.09 ± 0.33	5.89 ± 0.44	4.12 ± 0.26	4.94 ± 0.93	0.012 ± 0.001	0.013 ± 0.001

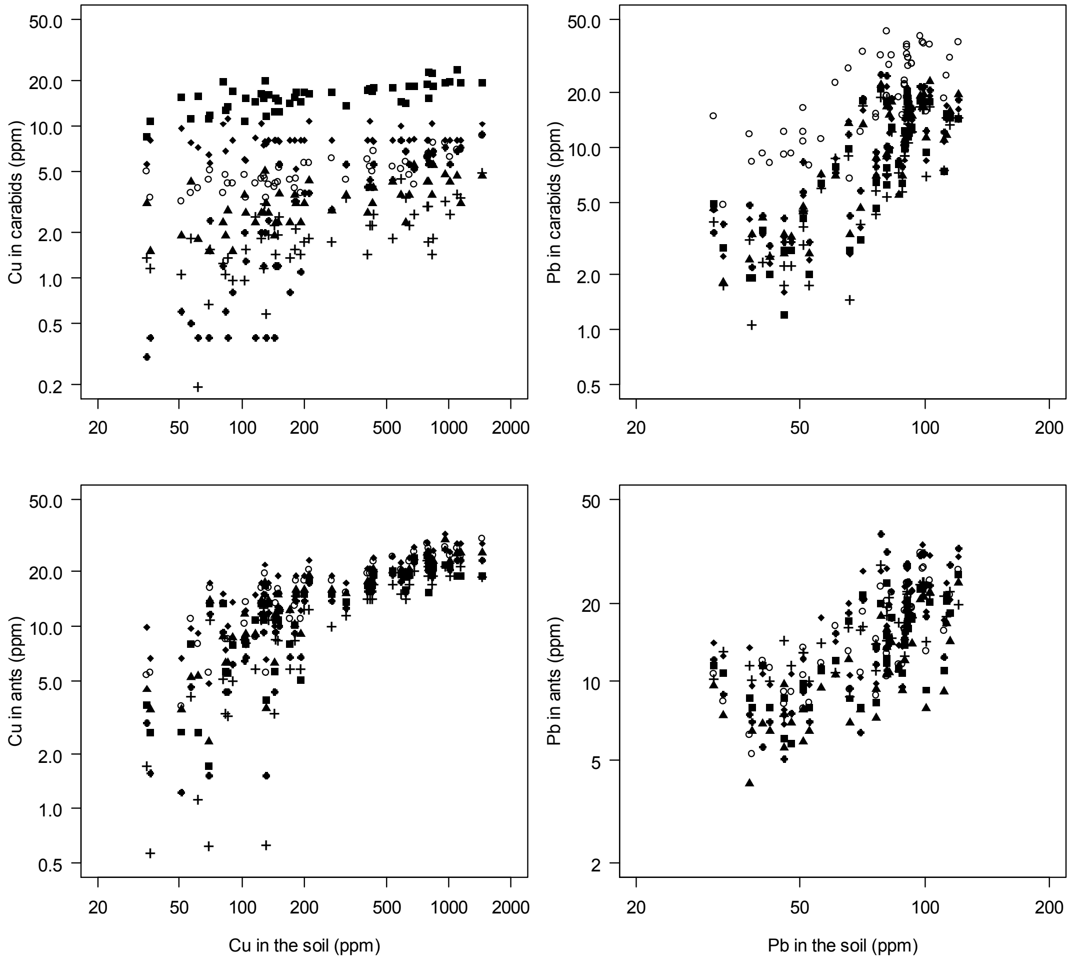
Appendix C.2: Means with standard deviations for body length, wing length and body mass of carabid species in agricultural ecosystem

Body size ranking	Species	Body length (mm)		Wing length (mm)		Body mass (g)	
		Male	*Female*	*Male*	*Female*	*Male*	*Female*
1	*Tefflus muata*	39.5 ± 3.05	42.3 ± 2.91	33.0 ± 2.01	35.1 ± 1.95	0.103 ± 0.001	0.112 ± 0.010
2	*Tefflus angustipes*	37.4 ± 3.11	38.9 ± 1.74	33.6 ± 1.29	34.9 ± 1.74	0.084 ± 0.011	0.093 ± 0.004
3	*Anthia omoplata*	27.3 ± 2.63	28.8 ± 2.25	23.9 ± 1.14	24.7 ± 2.11	0.079 ± 0.002	0.091 ± 0.002
4	*Procletus singularis*	19.7 ± 0.95	20.9 ± 1.86	16.9 ± 0.92	18.1 ± 0.77	0.033 ± 0.004	0.033 ± 0.003
5	*Procletus* sp	17.7 ± 0.41	18.8 ± 0.37	14.6 ± 0.14	16.9 ± 0.21	0.048 ± 0.004	0.060 ± 0.005
6	*Omophron alluaudi*	13.1 ± 1.10	15.2 ± 0.83	10.1 ± 0.11	12.2 ± 0.09	0.013 ± 0.002	0.013 ± 0.010
7	*Graphipterus tichyi*	12.9 ± 0.39	14.3 ± 0.21	10.6 ± 0.2	12.0 ± 0.14	0.024 ± 0.002	0.018 ± 0.002
8	*Axinotoma sinuaticollis*	12.7 ± 0.58	13.5 ± 0.49	9.99 ± 0.13	10.6 ± 0.15	0.011 ± 0.001	0.020 ± 0.002
9	*Graphipterus* sp	11.7 ± 0.24	13.0 ± 0.12	9.60 ± 0.07	10.9± 0.07	0.017 ± 0.002	0.031 ± 0.001
10	*Omophron* sp	10.5 ± 0.17	12.2 ± 0.34	7.93 ± 0.03	9.52 ± 0.06	0.016 ± 0.003	0.011 ± 0.002
11	*Epigraphodes congoensis*	9.38 ± 0.24	10.1 ± 0.55	7.42 ± 0.13	7.72 ± 0.18	0.020 ± 0.001	0.017 ± 0.002
12	*Eucolliuris* sp	8.46 ± 0.74	10.5± 0.33	6.16 ± 0.05	7.81 ± 0.04	0.002 ± 0.001	0.014 ± 0.001
13	*Siopelus* sp	8.28 ± 0.61	9.33 ± 0.57	6.28 ± 0.5	6.77 ± 0.04	0.002 ± 0.010	0.003 ± 0.010
14	*Singilis allardi*	8.13 ± 0.94	8.73 ± 0.86	6.39 ± 0.02	6.61 ± 0.2	0.031 ± 0.001	0.021 ± 0.002
15	*Piezia livingstoni*	7.92 ± 0.11	8.17 ± 0.08	6.01 ± 0.07	6.78 ± 0.04	0.019 ± 0.002	0.019 ± 0.002
16	*Eucolliuris flavomarginata*	7.91 ± 0.37	9.53 ± 0.42	5.76 ± 0.02	6.82 ± 0.03	0.002 ± 0.001	0.002 ± 0.001
17	*Siopelus chisasa*	7.40 ± 0.54	8.33 ± 0.73	5.71 ± 0.05	6.83 ± 0.04	0.024 ± 0.003	0.030 ± 0.002
18	*Abacetus nitens*	7.03 ± 0.14	7.44 ± 0.13	5.60 ± 0.03	5.29 ± 0.5	0.001 ± 0.001	0.002 ± 0.001
19	*Smeringocera mashuna*	6.97 ± 0.16	7.19 ± 0.20	5.29 ± 0.11	5.97 ± 0.08	0.010 ± 0.002	0.022 ± 0.010
20	*Dontolobus aemiliae*	6.87 ± 0.42	7.11 ± 0.17	5.55 ± 0.05	5.74 ± 0.02	0.022 ± 0.010	0.023 ± 0.010
21	*Siopelus zambianus*	6.64 ± 0.05	8.20 ± 0.05	5.30 ± 0.05	6.54 ± 0.37	0.019 ± 0.011	0.021 ± 0.002
22	*Amblystomus dantei*	6.58 ± 0.43	8.05 ± 0.22	4.80 ± 0.05	5.87 ± 0.06	0.003 ± 0.010	0.004 ± 0.010
23	*Selina westermanni*	6.32 ± 0.04	7.07 ± 0.11	5.71 ± 0.04	5.10 ± 0.02	0.021 ± 0.002	0.021 ± 0.003
24	*Dontolobus trinotatus*	6.11 ± 0.08	8.95 ± 0.22	4.74 ± 0.07	5.09 ± 0.09	0.028 ± 0.01	0.026 ± 0.002
25	*Boeomimetes somalicus*	5.77 ± 0.09	6.95 ± 0.75	4.65 ± 0.01	5.59 ± 0.03	0.014 ± 0.002	0.015 ± 0.002
26	*Eucamaragnathus desenderi*	5.18 ± 0.05	5.94 ± 0.07	4.17 ± 0.01	4.85 ± 0.01	0.001 ± 0.001	0.002 ± 0.001
27	*Cicindela compressicornis*	4.83 ± 0.06	5.48 ± 0.09	3.78± 0.01	4.29 ± 0.02	0.011 ± 0.001	0.011 ± 0.001

Appendix D.1: Abundance for six most dominant carabid species along the distance from the mining site Chingola to Solwezi, Zambia. Means and standard deviations for the abundance observed for each species are shown in brackets. GPS coordinates and altitudes for the location of study sites are also given

Distance from the mine (km)	GPS location	Altitude (m)	Carabid species					
			Anthia omoplata	*Epigraphodes congoensis*	*Procletus* sp	*Siopelus chisasa*	*Tefflus muata*	*Tefflus* sp
20	12°24′S, 27°37′E	1311	99 (17.1 ± 3.2)	12 (3.1 ± 0.9)	2 (0.5 ± 0.1)	7 (1.6 ± 0.01	3 (0.5 ± 0.02)	202 (39.5 ± 2.7)
40	12°21′S, 27°23′E	1283	91 (19 ± 4.1)	10 (2.7 ± 0.8)	5 (1.3 ± 0.1	16 (3.2 ± 0.1)	5 (0.9 ± 0.01)	177 (35.6 ± 3.9)
60	12°19′S, 27°11′E	1332	68 (11.6 ± 2.7)	17 (3.3 ± 1.1)	11 (2.6 ± 0.3)	19 (4.0 ± 0.3)	13 (2.5 ± 0.5)	159 (30.3 ± 3.1
80	12°16′S, 26°59′E	1345	51 (9 ± 1.5)	29 (5.5 ± 1.0)	13 (3.1 ± 0.2)	26 (4.9 ± 0.5)	21 (3.8 ± 0.7)	124 (25.1 ± 2.6)
100	12°13′S, 26°50′E	1323	32 (7.2 ± 1.9)	62 (13.4 ± 2.4)	19 (3.7 ± 0.1)	43 (8.8 ± 0.9)	36 (7.5 ± 0.4)	89 (17.4 ± 2.2
120	12°11′S, 26°40′E	1329	15 (4 ± 0.6)	84 (16.2 ± 1.8)	23 (4.9 ± 0.5)	49 (9.5 ± 1.2)	45 (8.7 ± 0.9)	86 (17.5 ± 1.8)
140	12°09′S, 26°30′E	1388	10 (2.4 ± 0.3)	109 (21.3 ± 2.5)	30 (6.5 ± 0.7)	47 (9.6 ± 0.8)	47 (9.2 ± 0.2)	51 (10.4 ± 1.6)
160	12°07′S, 26°19′E	1441	11 (2.1 ± 0.3)	115 (22.4 ± 3.9)	35 (8.0 ± 0.6)	63 (12.4 ± 1.5)	54 (10.1 ± 1.0)	38 (8.3 ± 1.5)
180	12°05′S, 26°09′E	1460	8 (1.9 ± 0.4)	163 (31.4 ± 3.1)	47 (9.1 ± 0.9)	75 (14.8 ± 1.7)	60 (11.7 ± 0.8)	19 (3.6 ± 0.9)
200	12°03′S, 26°00′E	1429	5 (1.5 ± 0.1)	222 (45.6 ± 3.7)	55 (10.7 ± 0.5)	81 (16.3 ± 1.2)	68 (13.2 ± 1.4)	19 (3.4 ± 0.7)

Appendix D.2: Relationships between metal concentrations in animals and metal contaminations in the soil along the pollution gradient. Different symbols represent different species for carabids and ants. Note that metal concentrations and contaminations are plotted on *log* scales



Appendix D.3: Means and correlations for Cu concentrations and abundance of six dominant carabid species along the distance from the mine in Zambia

Species	Abundance		Cu concentration (ppm)	
	Mean	Correlation	Mean	Correlation
Anthia omoplata	39	-0.94	3.3	-0.85
Epigraphodes congoensis	82.3	0.95	15.9	-0.69
Procletus sp	24	0.65	2.1	-0.57
Siopelus chisasa	42.6	0.98	3.3	-0.35
Tefflus muata	35.2	0.95	7.9	--0.12
Tefflus sp	96.4	-0.98	5.1	-0.70

Appendix D.4: Means and stand deviations of Cu and Pb metals in soils, carabids and ants along a pollution gradient. Range for each mean value is in italics

Distance from the mine (km)	Contaminations in soils (*n* = 30)		Concentrations in carabids (*n* = 60)		Concentrations in ants (*n* = 60)	
	Cu (ppm)	Pb (ppm)	Cu (ppm)	Pb (ppm)	Cu (ppm)	Pb (ppm)
20	1090.6 ± 327.11	98.9 ± 22.8	8.35 ± 0.96	21.9 ± 3.86	24.2 ± 5.16	26.3 ± 5.06
	800.30 - 1137.90	*78.33 - 120.6*	*1.83 - 23.6*	*14.4 - 40.5*	*15.27 - 32.31*	*17.7 – 37.6*
40	806.66 ± 105.41	91.3 ± 11.9	7.91 ± 1.13	22.0 ± 4.61	22.6 ± 4.94	23.2 ± 5.88
	586.81 - 1015.7	*80.91 - 102.9*	*1.90 - 22.8*	*15.2 - 43.5*	*15.5 - 29.1*	*15.9 - 31.4*
60	641.31 ± 124.13	91.9 ± 16.6	7.32 ± 0.75	18.06 ± 2.78	20.7 ± 4.47	20.6 ± 4.62
	431.34 - 829.10	*71.13 - 115.1*	*1.56 - 22.1*	*10.90 - 33.7*	*14.56 - 27.41*	*14.2 - 27.9*
80	421.26 ± 63.81	93.2 ± 10.5	6.71 ± 1.48	16.52 ± 4.11	17.5 ± 3.19	18.1 ± 2.77
	320.9 - 534.2	*82.20 - 113.2*	*1.52 - 18.3*	*9.72 - 31.8*	*11.85 - 24.16*	*10.79 - 23.8*
100	204.03 ± 49.20	89.2 ± 20.2	6.42 ± 2.17	12.70 ± 2.84	15.7 ± 3.08	15.5 ± 2.64
	152.4 - 271.4	*65.64 - 111.6*	*1.84 - 16.8*	*7.40 - 26.9*	*10.1 - 23.1*	*9.12 - 23.0*
120	128.0 ± 24.33	80.8 ± 17.4	6.02 ± 0.98	10.3 ± 2.43	14.0 ± 4.53	13.5 ± 4.07
	70.51 - 180.7	*60.81 - 100.8*	*1.54 - 20.1*	*5.51 - 22.7*	*8.62 - 21.9*	*7.89 - 18.5*
140	121.7 ± 34.11	76.7 ± 14.8	5.46 ± 1.14	8.20 ± 1.92	11.6 ± 4.76	11.9 ± 2.22
	81.6 - 150.2	*56.3 - 88.3*	*1.03 - 19.6*	*4.43 - 18.9*	*5.34 - 18.9*	*7.22 - 17.5*
160	128.5 ± 18.64	50.7 ± 15.1	5.12 ± 1.62	6.01 ± 1.31	8.86 ± 2.50	10.4 ± 2.91
	56.81 - 192.5	*30.9 - 69.9*	*0.42 - 15.2*	*3.09 - 16.3*	*4.22 - 14.8*	*5.88 - 16.2*
180	87.38 ± 14.25	47.5 ± 11.5	4.90 ± 1.11	4.14 ± 1.07	6.42 ± 1.85	9.08 ± 3.22
	34.62 - 143.2	*37.6 - 65.9*	*0.31 - 16.9*	*1.52 - 11.8*	*1.77 - 13.7*	*4.49 - 14.71*
200	69.57 ± 16.01	42.3 ± 10.4	4.60 ± 0.99	3.34 ± 0.07	3.52 ± 0.98	8.30 ± 1.73
	35.93 - 130.4	*38.3 - 52.6*	*0.22 - 15.7*	*1.13 - 12.2*	*0.084 - 9.22*	*5.05 - 13.3*

8 Curriculum vitae

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ACADEMIC AND PROFESSION BACKGROUND

2012-to date:	Pursuing Ph.D study at Philipps-University Marburg, Germany
2007-2009:	Obtained **M.Sc. degree** in Plant Pathology at the University of Pretoria, South Africa. Thesis title: *Pathogens associated with plantation tree diseases in Zambia.*
2004-2006:	Obtained **B.Sc. degree** in Forestry at the Copperbelt University, Zambia. Thesis title: *Bark removal for medicinal use predisposes indigenous forest trees to wood degradation in Zambia*
1993-1997:	Obtained **Grade 12 certificate** at Mufulira High School, Zambia.

WORK EXPERIENCE

2009-to date:	Lecturer at the Copperbelt University, Zambia
2008-2009:	Practical demonstrator for undergraduate students, University of Pretoria, South Africa.
2007-2008:	Member of plant disease diagnostic clinic, University of Pretoria, South Africa.
2005-2006:	Lecturer at Zambia Forestry College.
2002-2008:	Extension assistant in the Ministry of Environment and Natural Resources-Forestry Department, Zambia.

AWARDS AND SCHOLARSHIPS

2012-2014: Sponsorship provided by the Staff development fellowship of the Copperbelt University and the University of Marburg to pursue PhD study at the University of Marburg, Germany

2007-2009: Scholarship provided by National Research Foundation of RSA to pursue Masters' degree at University of Pretoria, South Africa.

2004-2006: Sponsorship provided by the Ministry of Environment & Natural Resources of Zambia to pursue Bachelor's degree at Copperbelt University.

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