Insect diversity patterns along environmental gradients in the temperate forests of Northern China

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This thesis is submitted for the degree of PhD in Ecology

March 2014

I, Yi Zou, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Zouyi

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13 March 2014

Acknowledgements

Foremost, I would like to express my sincerely appreciation to my lovely supervisor, Dr. Jan Axmacher, who has fully supported me in a number of ways during my study. Jan's encouragement and guidance enabled me to develop my research ability and in-depth understanding of this subject, and allowed me to start my career as a research scientist. I also would like to thank my second supervisor Dr. Simon Lewis, for his full support in my upgrade and his insightful comments on this thesis. I also want to thank my two thesis examiners, Dr. Helene Burningham and Professor Simon Leather, for their constructive comments.

I am grateful for the support from Professor Weiguo Sang from the Institute of Botany, Chinese Academy of Sciences, who offered advice and also financial support and a variety of other resources for this research. I would not have been able to complete my research without help from him and his group members. In this respect, I particularly want to thank Dr Fan Bai, Dr Shunzhong Wang, Dr Haifeng Liu and Mr Wenchao Li for providing data and helping me to complete vegetation surveys during my research.

I also thank Professor Zhenrong Yu and Dr Yunhui Liu and their group members from the China Agricultural University. They provided valuable assistance in my insect specimen preparation. I have spent a very good and productive time while working with their team members, particularly with Mr Meichun Duan.

Professor Hongbin Liang, Dr Hongliang Shi and Mr Ye Liu from the Institute of Botany, Chinese Academy of Sciences kindly helped me with the sorting and identification of ground beetles. Professor Dayong Xue and Dr Hongxiang Han helped me with the identification of geometrid moths.

Many thanks to Mr Haicheng Zhou from the Changbaishan Nature Reserve Management Centre for his great support during the field work. My sincerest thanks also go to the members of the Changbaishan Academy of Sciences and the Changbaishan Natural Museum for their great assistance. I furthermore sincerely thank the staff of the Changbaishan Forest Ecosystem Research Station and the Beijing Forest Ecosystem Research Station for their hospitality. In addition, I greatly appreciate the help with my fieldwork from Eleanor Warren-Thomas, Chao Long, Min Liu, Xiasai Zhou, Furen Han, Lijia Dong, Xuenan Yao, Mengjie Yang, Xiaoliang Zhang and Ya Qin.

My final warmest thanks go to my wife, who has always been my joy and given me the greatest support. Thank you for spending those difficult times with me! I thank my new-born beloved daughter bringing greatest joy and a great source of inspiration.

Abstract

Insects, which represent the most species-rich taxa, are extremely important ecosystem components. The diversity patterns of insects have, however, been widely ignored in biodiversity research. In my thesis, I aim to establish a basic understanding of the diversity patterns of insect assemblages in the temperate forest and forest plantation ecosystems of Northern China, and to investigate how these patterns correlate with vegetation and environmental conditions. The study aims to give further insights into the insect diversity status and measures to conserve or even enhance their diversity in the large secondary and plantation forests which have been and are currently established throughout northern China.

The study focuses on two distinct insect taxa: ground beetles (Coleoptera: Carabidae) and geometrid moths (Lepidoptera: Geometridae). In the main study area located within the Changbaishan Natural Reserve (CNR) in Jilin Province, 4844 individuals (47 species) of ground beetle and 9285 individuals (155 species) of geometrid moth were sampled. In addition, 1488 ground beetles (24 species) and 2047 geometrid moths (165 species) were sampled in the secondary and plantation forest area at Dongling Mountain (DLM) in Beijing.

A first important result of this work is that the α-diversity of both ground beetle and geometrid moth assemblages decreased significantly with increasing elevation at CNR. My results also show that the relationships between phyto-diversity and the diversity of insects are weak and furthermore likely to be driven by underlying environmental factors. The significant changes which have recently occurred in the plant species composition at CNR chiefly related to changes in the climatic conditions suggest that insect species are also under high pressure in this area. Finally, this study suggests that in the temperate religions of Northern China, secondary and plantation forests can potentially harbour high levels of insect α-diversity compared with mature, more pristine forests.

Abbreviations

ACE	Abundance-based Coverage Estimator
AIC	Akaike information criterion
BF	birch forest
BFERS	Beijing Forest Ecosystem Research Station
BSP	Bashang Plateau
CBD	Convention on Biological Diversity
CCDB	Canadian Centre for DNA Barcoding
CCFP	Conversion of Cropland to Forest Programme
CNESS	chord-normalized expected species shared
CNR	Changbaishan Natural Reserve
DLM	Dongling Mountain
FPC	family-based principal component
FTP	Fast-Growing and High-Yielding Timber Base Construction Programme in Key Areas
HD	herb density
HH	herb Shannon diversity
IB-CAS	Institute of Botany, Chinese Academy of Sciences
ICE	Incidence-based Coverage Estimator
IDH	intermediate disturbance hypothesis
IISE	International Institute for Species Exploration
IndVal	indicator value
IUCN	International Union for Conservation of Nature
IV	importance value
IZ-CAS	Institute of Zoology, Chinese Academy of Sciences
KPF	Korea Pine Forest
LDG	latitudinal diversity gradient
MCBF	mixed coniferous and broad-leaved forest

MCF	mixed coniferous forest
MDE	mid-domain effect
MDS	multidimensional scaling
MLR	multiple linear regression
MM	Michaelis–Menten estimator
NFPP	Natural Forest Protection Programme
NMDS	non-metric multidimensional scaling
PC	Principal Component
PCA	Principal Components Analysis
RDA	Redundancy analysis
SCP	Sand Control Programme
SD	shrub density
SH	shrub Shannon diversity
SHE	species richness, Shannon diversity index and evenness
SKFP	Six Key Forestry Programmes
SMCF	sub-alpine mixed coniferous forest
SPC	species-based principal component
TD	tree density
TH	tree Shannon diversity
TYSDP	Yangtze River Basin' Shelterbelt Development Programme
WNDP	Wildlife Conservation and Nature Reserves Development Programme

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Chapter 1. Introduction

1.1. <u>Biodiversity</u>

1.1.1. What is biodiversity?

Biodiversity is defined by the Convention on Biological Diversity (CBD) ((http://www.cbd.int/convention/articles)) as "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems." The term 'biodiversity' was originated form the conference of 'National Forum on Biological Diversity' in 1986 organized by the National Research Council (Wilson, 1988). Generally, biodiversity includes three distinct levels, genetic diversity, species diversity and ecosystem diversity (Hooper et al., 2005; Larsson, 2001). Some studies include landscape diversity as a further distinct level of biodiversity (Fu & Chen, 1996; Romme & Knight, 1982), while others consider landscape diversity within the concept of ecosystem diversity at large geographical scales (Lapin & Barnes, 1995).

Genetic diversity refers to the overall genetic information from all individuals of a species or population. Genetic distinctiveness is also seen as a basis for species diversity. Genetic diversity within a species is dependent upon diversity among species, and vice versa (Lankau & Strauss, 2007; Tisdell, 2003; Vellend & Geber, 2005). Quantitative traits of genetic diversity are measured as the genetic variance or the total phenotypic variance within a population lead by individual genetic differences (Falconer et al., 1996). Genetic diversity is maintained by four factors: mutation, drift, selection and migration (Vellend & Geber, 2005). From an ecosystem perspective, a species will have greater resilience to environmental change if its populations have a wider genetic variation (Luck et al., 2003). For example, Ehlers et al. (2008) revealed that the density of eelgrass (*Zostera marina* L.) is negatively correlated with climate warming, but positively correlated with genotypic diversity, indicating that species genetic diversity enhances the resistance to temperature stress. The economic and ecological value of a species also relates to its distinct genetic composition (Notter, 1999; Rajora, 1999). A species' extinction risk increases with the depression of inbreeding, the loss of genetic diversity and the accumulation of mutations (Frankham, 2005). A good example is the monoculture in agriculture attributed to selective breeding, resulting in crop species with a low suppression to disease. To maintain crop genetic diversity is key to enhance crop disease suppression as well as to secure an overall sustainable crop production (Skamnioti & Gurr, 2009; Zhu et al., 2000).

Species diversity is the diversity at species level, based on the distribution patterns of species and their spatial-temporal variations. Species diversity can be studied from taxonomic, phylogenetic and biogeographic perspectives. The issue of species definitions has been confused due to a variety of species concepts existing in the literature. These vary from biological, ecological, evolutionary and phylogenetic to phonetic approaches (see reviews by De Queiroz, 2007). Without a generally agreeddefinition of the term 'species', the concept of 'species richness' has also been strongly debated (De Queiroz, 2007; Gaston & Spicer, 2009; Ricotta, 2005). Nonetheless, species richness in practice is still treated as the fundamental element or currency of biodiversity (Gaston & Spicer, 2009). The diversity status of rare, endangered and endemic species is a key indicator in measuring biodiversity conservation outcomes. Whittaker (1960) distinguished species diversity at three levels: α-diversity as species richness within a sampling plot, community or habitat; β-diversity as species compositional heterogeneity amongst plots or habitats and γ-diversity as the total species diversity over a larger geographic area. While Whittaker (1960) did not give a very specific definition of β-diversity, Cody (1975) defined β-diversity as turnover of species along environmental gradients or between habitats, focussing also on shifts in abundance patterns. More recently, Tuomisto (2010) defined the 'true beta diversity' as being "obtained when the total effective number of species in a dataset (true gamma diversity γ) is multiplicatively partitioned into the effective number of species per compositionally distinct virtual sampling unit (true alpha diversity α) and the effective number of such compositional units" (Tuomisto, 2010, pp. 2). α-diversity and β-diversity can generally be described by a variety of diversity indices (see more details in following section).

Ecosystem diversity refers to the diversity of habitats, communities and ecological processes in the biosphere (McNeely et al., 1990). Globally, ecosystem can be classified into two key categories, terrestrial and aquatic. Aquatic ecosystems are further separated into marine and freshwater ecosystems, resulting in three essential global ecosystem types. Each ecosystem contains several sub-ecosystems. For example, terrestrial ecosystems can be separated into forest, desert or grassland ecosystems. Forest ecosystems are again separated for example into tropical, temperate and taiga forests; these ecosystems can again be divided into smaller ecosystem units. Nonetheless, ecosystem classifications, particular for small units, are not widely agreed by scientists (Carranza et al., 2008; Pojar et al., 1987; Rankin et al., 2012; Rowe & Rowe, 1996). Habitat diversity is the foundation of community and ecosystem diversities, which comprises the variety of physical environmental factors such as topography and climatic conditions. Community diversity refers to differences in the biological composition and ecosystem dynamics. Community and habitat form complex functional units, ecosystems. Ecological processes cause temporal and spatial changes in composition, structure and function of ecosystem, as well as in the interactions between biological components and the environments.

1.1.2. Biodiversity and human well-being

Biodiversity is the basis for human survival (Millennium Ecosystem Assessment, 2005). Most species are part of natural ecosystems that provide a wide range of ecosystem processes and conditions to sustain human life (Chivian & Bernstein, 2008). Broadly, the value of biodiversity provided for humans can be divided into use value and non-use value. The use value can again be categorized as direct-use value and indirect-use value (Gaston & Spicer, 2009).

Food is the most obvious direct-use value that biodiversity provides in support of human life. Other direct-use values include (but are not limited to) medicine, industrial materials, biological control and cultural value. Sustainable production of biological resources is particularly important for people living in economically poorly developed areas (Becker & Ostrom, 1995; Brown et al., 1987). It is estimated that about 80% of the world's population rely on plant medicine either in part or entirely for primary health care (Farnsworth & Soejarto, 1991). In China, many plants are highly valued in Tradition Chinese Medicine (TCM), such as Fleeceflower Root (*Polygonum multiflorum* Haraldson), Ginseng (*Panax ginseng* Meyer) and Notoginseng (*Panax notoginseng* Chen & Chow). In addition, some raw biological materials will have a higher value after being processed through industrial production, such as timber, animal furs, antlers, honey, natural rubber and dyes. As already mentioned above, biological control is another direct-use value that has already partly been used as alternative for chemical pesticides. Biodiversity in pest control not only comprises the direct agricultural or forest pest control by natural enemies (e.g. Karp et al., 2013; Thomson & Hoffmann, 2010; Wilby & Thomas, 2002), but also refers to the fact that an increase of diversity per se, from both genetic diversity, species diversity and ecological diversity levels, can enhance crops' resistance against pests (Bianchi et al., 2006; Harwood et al., 2009; Skamnioti & Gurr, 2009; Veres et al., 2013). Finally, from a cultural aspect, biodiversity is also valuable for tourism (Appiah-Opoku, 2011), education (Kassas, 2002) and scientific studies (Diaz & Duffy, 2006; Gaston & Spicer, 2009; Millennium Ecosystem Assessment, 2005).

As biodiversity is a core factor ensuring sustainability and productivity of many ecosystems, benefits from ecosystem services can be viewed as indirect-use value provided by biodiversity. Biodiversity can indirectly affect the provision of ecosystem services via influences on the nutrient and water cycles, soil formation and retention, crop pollination, disease and pollution control and climate regulation (Millennium

Ecosystem Assessment, 2005; Naeem et al., 1999). These services generally cannot be traded in the marketplace directly (Gaston & Spicer, 2009). Among these services, biodiversity providing for ecosystem functioning is one of the most important ones (see following sections). In an ecosystem context, many species of lesser direct importance for the direct production and consumption of resources used by humans are still vital in sustaining viable populations of key ecosystem service providers (Gaston & Spicer, 2009). For example, the decline in the species number and abundance of wild bees, which are important pollinators but generally are non-commercial species, will affect the crop yields and result in a direct economic loss (O'Toole, 1993).

1.1.3. Biodiversity and ecosystem functioning

Biodiversity has many components that can play important roles in sustaining the lives of organisms within ecosystems. Ecosystem functioning reflects the collective life activities of living organisms (e.g. nutrient and carbon cycling) and the effects of these activities (e.g. feeding, moving and growing) on their environment (Naeem et al., 1999). The importance of different biodiversity components, such as species richness, abundance, community structure and functional traits (where a functional trait is “the characteristics of an organism that are considered relevant to its response to the environment and/or its effects on ecosystem functioning”, see (Díaz & Cabido, 2001, pp.654)), varies in affecting specific ecosystem services. For example, the functional trait diversity often plays a more important role than species richness per se in an ecosystem’s biomass production, effective pollination, soil retention, climatic regulation, and in protecting against natural hazards such as environmental fluctuations (Diaz & Duffy, 2006).

The relationship between biodiversity (here mainly refers to species diversity) and ecosystem functioning has received increasing scientific interest in recent decades (Balvanera et al., 2006; Ehrlich & Wilson, 1991; Kremen, 2005; Zavaleta et al., 2010). The outcomes of experimental and theoretical biodiversity and ecosystem functioning studies have, however, led to a number of contested debates. The first one is the biodiversity-productivity debate. Classic model predict that the biodiversity – productivity relationship is ‘hump-shaped’, with species richness peaking at intermediate productivity level (Rosenzweig, 1992; Rosenzweig & Abramsky, 1993). This model has however been challenged. Probably the most influential model in the 1990s was proposed by Tilman et al. (1997) who predicted a general positive relationship between biodiversity and productivity. Tilman et al. (1997)’s first model, also called ‘niche differentiation’ model, stated that higher diversity in species or functional groups enhances the usage of resources due to the niche differentiation and facilitation, which results in an overall higher productivity (Naeem et al., 1994; Tilman et al., 1997). Tilman et al. (1997)’s second model, named ‘sampling effect’ model (or ‘selection probability effect’ (Huston, 1997) and ‘selection effect’ (Loreau, 2000), based on very similar concepts) predicted that high species diversity of a plot automatically increased the probability that one of the species contained was a highly productive species or a species providing growth-enhancing ecosystem services such as N-fixation, again resulting in positive biodiversity-productivity relationship (Huston, 1997; Loreau et al., 2001; Tilman et al., 1997; Wardle et al., 2000). This positive relationship attracted great interests because it seems to contrast natural observations, where typical highly productive ecosystems such as agro-ecosystems optimized for their yield usually contain only a very low species richness (Grime, 2006).

The empirical results of biodiversity-productivity studies are mixed, with relationship reported as ‘hump-shaped’ (Huston & DeAngelis, 1994; Waide et al., 1999), positive (Currie, 1991; Grace et al., 2007; Hector et al., 1999; Mittelbach et al., 2001), U-shaped and negative (see reviews by Waide et al., 1999) or completely missing (Adler et al., 2011). In addition, scale-dependent models (Bond & Chase, 2002) and experiments (Chase & Leibold, 2002) propose a ‘hump-shaped’ biodiversity-productivity relationship at a local scale and a linear increase relationship at a regional scale, while some scientists also argue that the observed relationship depends on the assembly sequence (Fukami & Morin, 2003). It should particular be noticed that a recent study of 48 plant communities on five continents undertaken by Adler et al. (2011) found that there was no clear relationship between diversity and productivity. They encouraged ecologists to focus on more sophisticated approaches rather than on a single, dominant pattern.

Another debate linking biodiversity and ecosystem functioning is the role of biodiversity in safeguarding ecosystem stability. Stability has a variety of meanings (Ives & Carpenter, 2007). For example, one definition refers that ecosystems have the ability of maintaining a stable state—returning to their pre-disturbance equilibrium after small perturbations or showing a general resilience and resistance to change (McCann, 2000). In biodiversity and ecosystem debates, it mainly refers to temporal stability, measured of the mean value divided by the standard deviation of production for a given time period (Tilman et al., 2006). In the 1950s, MacArthur (1955) and Elton (1958) proposed that the increase of species richness can enhance ecosystem stability. This theory was considered as one of the main ecological principals for the following 20 years (Hastings, 1986; McNaughton, 1988; Pimm, 1984). The positive relationship has been supported by a variety of experiments in the 1990s (De Grandpre & Bergeron, 1997; Frank & McNaughton, 1991; Tilman & Downing, 1994; Tilman et al., 1996), including in microcosms (McGrady-Steed et al., 1997; Naeem & Li, 1997). A few hypotheses have been proposed to explain mechanisms of a positive biodiversity-stability relationship. As a species-diverse ecosystem has a higher likelihood to contain species that confer resilience to changes in that ecosystem, a higher diversity of a system could be buffered against the loss of species, a trend termed 'insurance effect' (Naeem & Li, 1997; Yachi & Loreau, 1999). As the definition of ecosystem stability *per se* is multifaceted and not generally agreed, there is no unique theory supporting a general trend for increased biodiversity to enhance the stability in all ecosystems (Ives & Carpenter, 2007). If stability refers to species level, the increase of diversity will reduce the stability. This is not difficult to understand because the increase of diversity will result in a reduction of the population size of individual species, while a smaller population size increases the risks for entire populations of species to go locally extinct (Cleland, 2011).

The entire ecosystem forms a complex web in which the abundances of most species on earth are interdependent. The extinction of a species may trigger a domino-effect that causes a wide range of impacts (Hintz & Garvey, 2012). Changes in diversity at higher trophic levels can lead to significant alternation for the ecosystem functioning because the diversity of predators can strengthen the food web complexity (Crooks & Soulé, 1999; Finke & Denno, 2004; Snyder et al., 2006). In many conservation strategies, apex predators often serve as an umbrella species, namely 'species whose conservation confers a protective umbrella to numerous co-occurring species' (Fleishman et al., 2000). The loss of these predators can have a particularly strong influence on ecosystem structure and functioning (Berger et al., 2001; Borrvall & Ebenman, 2006; Estes et al., 2011; Frank et al., 2005). The dramatically decreasing populations of sharks—the top predators in the ocean—for example leads to a dramatic increase of their prey such as cownose rays, subsequently leading to a significantly reduction of bay scallops and other shellfish (Baum et al., 2003). In China's Changbai Mountain area, the increasing number of wild boars leading to an increasing food source competition with other mammal species is partly believed to be due to the local extinction of the local top predators, Amur Tiger (*Panthera tigris altaica* Temminck) and Amur leopard (*Panthera pardus orientalis* Schlegel).

1.1.4. Global biodiversity and its distribution

Current knowledge of biodiversity is very incomplete and strongly biased. Estimates of global species numbers range between 3 and >100 million species, based on different estimation methods, taxonomic knowledge and differences in the consideration of prokaryotic species and viruses (Dirzo & Raven, 2003; May, 2010; Stork, 1993). Most recent studies by Mora et al. (2011) suggest 8.7 (±1.3SE) million seems a reasonable estimate for multi-cellular organisms (Costello et al., 2013; May, 2011; Scheffers et al., 2012). About 1.94 million of eukaryotic species had been described by 2010, and thousands of new species are described each year (IISE, 2012). This number is nonetheless likely to account for less than 10% of the total species once microbes are included. Among all described eukaryote species, more than half (1,023,430) are insects, 14.7% plants, 5.4% arachnids, 5.2% fungi and 3.3% invertebrates (Figure 1).

Figure 1 The number of described species (×1000) by 2010 (IISE, 2012)

A large proportion of global terrestrial species is concentrated in relatively small areas. Tropical rainforests for example are estimated to contain almost half of the world's species (Qian, 1993), with for example the Amazon basin alone containing more than 3,000 species of fish (Naeem et al., 1999). Williams et al. (1997) mapped the global terrestrial species distribution of families for plants, reptiles, amphibians and mammals, which showed a clear, consistent gradient of diversity in relation to latitude, with biodiversity generally increasing from the poles to the equator (see also Franklin, 2009). In marine ecosystems, species richness also shows a broad latitudinal gradient (Ormond et al., 1997), with an increase from the arctic to the tropics, and with the highest diversity recorded in coral reefs of tropical regions (Gray, 1997; Kendall & Aschan, 1993; Ormond et al., 1997). Hillebrand (2004)'s meta-analysis also showed a general increase in species richness towards the equator, with the trend at regional scales being stronger than at local scales.

The current decreasing trend of species richness with increasing latitude has been considered as the most common bio-geographical rule (Mora & Robertson, 2005; Willig et al., 2003), although it needs to be noticed that the latitudinal diversity gradient (LDG) was not unique in the earth's past (Sahney & Benton, 2008). Explanation of what determines the LDG has been considered as a key research theme in biology (Gaston, 2000). In general, species richness must be determined by dispersal (immigration), speciation and extinction (Condamine et al., 2012; Mittelbach et al., 2007; Wiens & Donoghue, 2004; Willig et al., 2003). There are three kinds of explanations of the latitudinal diversity gradient: the ecological hypothese, which focuses on species coexistence, dispersal and maintenance; the evolutionary hypothesis, which focuses on diversification rate; and the historical hypotheses focusing on the history of earth's tropical environments (Mittelbach et al., 2007).

One of the ecological explanations, which is also named the 'Rapoport rule', is that species in high latitudes suffer from harsh climatic conditions resulting in a broader tolerance range than in species at low latitudes, so that species at high latitudes have a wider ecological amplitude resulting in a wider dispersal range compared with tropical species that often occupy a very small ecological niche (Lyons & Willig, 2002; Rapoport, 1982; Stevens, 1989). Species in tropical region are therefore also more sensitive to environmental change than species in temperate and cold areas, and the spatial distributions of tropical species are generally more limited and heterogeneous (Lyons & Willig, 2002). Such heterogeneous species distribution pattern results in diverse habitats that forms a variety of abiotic conditions (Brose, 2001), which in turn enhance biodiversity. As local species diversity is governed by the combination between species extinction rates and species colonization rates (Brown & Kodric-Brown, 1977), an area of higher habitat heterogeneity, higher species immigration rates occur between neighbouring habitats (Brown & Kodric-Brown, 1977). Consequently, high habitat heterogeneity in tropical region results in a high diversity (Stevens, 1989). It has, however, been also argued that 'Rapoport's rule' is a local phenomenon which cannot explain the overall latitudinal gradients of biodiversity (Rohde, 1996). Rapoport's rule is very pronounced in the high latitude of the northern hemisphere, which is potentially due to the strong influence of the glacial periods on this region, with severe temperature fluctuations and changes in habitat conditions causing the differential extinction for species, resulting in a higher survival rate for those species with very wide tolerance ranges (Price et al., 1997; Rohde, 1996).

From the evolutionary aspect, there are several hypothesises to explain the LDG. The speciation rate hypothesis argues that tropical areas have a higher species richness due to the temperature-induced increased generation turnover and subsequent speciation rate (Rohde, 1992). The differences in temperature of different latitudinal areas lead not only to shorter generation times, but also to higher mutation rates and higher selection pressure in tropical areas, resulting in higher species richness (Rohde, 1992). Other explanations of higher speciation rates in the tropics include more opportunities for isolation due to large areas and in more opportunities of paratactic and sympatric speciation and genetic drift in the many small populations of species typically encountered in the tropics (see review in Mittelbach et al., 2007). In addition, the evolutionary hypothesises also includes the hypothesis of lower extinction rates in the tropics due to stable climatic conditions (see review in Mittelbach et al., 2007).

From a historical aspect, the time and area hypothesis suggests that, historically, areas in tropical climate are older and larger than other global areas, which allows more chances for species diversification in this area (see review in Mittelbach et al., 2007). This has been supported by several studies (e.g. Fine & Ree, 2006). For example, Fine and Ree (2006) found positive correlations between current tree diversity and time-integrated biome areas (as biome areas have been changing with the change of climate through time) for older time periods. Supporting evidence also includes the phylogenetic relationships between temperature and tropical species (Condamine et al., 2012; Jablonski et al., 2006). Nonetheless, the overall LDG are not possibly driven by a single explanatory factor, while to identify which mechanisms have greater influence than others is a key challenge for future research (Stevens, 2011).

In mountain ranges, environmental factors relating to altitude exert a dominant influence on species diversity, which change primarily in relation to changes in temperature and precipitation (Stevens, 1992). Four contrasting species diversity patterns for the altitudinal gradients of species have been proposed in reaction to increasing altitude: a continuous decline, a hump-shaped distribution with a distinct mid-elevation peak, a diversity plateau and an increase in diversity (García-López et al., 2011; McCain & Grytnes, 2010). Of these, a monotonic decrease and a hump-shaped distribution are most commonly observed. Both these patterns have been revealed in plants (Hamilton & Perrott, 1981; Kessler, 2001), vertebrates (Graham, 1983; Terborgh, 1977) and terrestrial arthropods (Beck & Chey, 2008; Goldsmith, 2007; McCoy, 1990; Pyrcz & Wojtusiak, 2002; Tykarski, 2006; Wolda, 1987).

A variety of different hypotheses have been proposed to explain the decreasing trend of species richness along altitudinal gradients. According to the Productivity Hypothesis, species richness is positively associated with overall ecosystem productivity (Chase & Leibold, 2002; Currie, 1991; Fargione et al., 2007; Mittelbach et al., 2001; Rahbek, 1995; Roy, 2001). This is often argued to lead to a continuous decrease in diversity with increasing elevation as temperature decreases (Orians, 1969; Terborgh, 1971), although evidence shows that productivity can also peak at mid-elevation (Rahbek, 1997). Alternatively, the harsher environmental conditions encountered at high elevation will, according to the Harsh Environment Hypothesis, led to a decrease in diversity. This relates to Rapoport's rule, which was originally proposed to explain the biodiversity increase from the pole towards the tropics (see statements above). The harsh climatic conditions species encounter at high latitudes, but also at high altitudes, require them to have broader tolerance ranges than species at low latitudes and altitudes. This in term will lead to wider species distribution ranges with increasing elevation and to higher species richness at low altitudes (Rapoport, 1982; Stevens, 1989, 1992). The Resource Diversity Hypothesis links increases in diversity to increases in the diversity of resources (Price, 1984), for example postulating increases in plant diversity to be associated with increases in herbivore diversity. Another commonly mentioned hypothesis in relation to altitudinal gradients is the Species-Area Hypothesis, relating a decrease in species richness with increasing elevation to the overall decrease in available area from the base to the top of mountains (Rosenzweig, 1995).

There are also a few hypotheses to explain the hump-shaped distribution. Water supply usually peaks at intermediate elevations (Rahbek, 1995), potentially resulting in a peak of productivity at the middle of the elevational range (Brown, 2001). Climatic models combining all climatic factors influencing species diversity such as rainfall and temperature, furthermore predict a maximum of species richness to occur at higher elevation on higher mountains than on shorter ones (McCain, 2005). This phenomenon is called ‘Massenerhebungseffekt’, which refers to the higher elevation of tree limits on higher than shorter mountain (Körner, 2012). The compression of vegetation distribution in smaller mountain then may affect the distribution of other species such as insects by providing food sources and suitable habitats (Van Balen & Nijman, 2004). The peaks of species richness would be amplified if the range with maximum combination effects of climatic factors located at the maximum-productivity area (Brown, 2001). A famous model that developed during the last decades to predict the hump-shaped distribution is the mid-domain effect (MDE) (Colwell & Lees, 2000; Colwell et al., 2004). The MDE model considers that species with random distribution are expected to overlap more near the centre of a bounded domain than the edge of the domain. According to this hypothesis, species richness along a geographic elevational gradient is expected to peak at the middle between the mountain base and the summit of the highest mountain. This ‘null model’ has, however, been criticized by many researchers (Dunn et al., 2007; Hawkins et al., 2005; McClain et al., 2007). One reason is that species are not possibly randomly distributed (McClain et al., 2007).

Each mountain range has its unique history, distinct geographic setting and is influenced by specific anthropogenic biotic and abiotic factors, and this can result in very unique, complex diversity distribution patterns (Axmacher & Fiedler, 2009; Axmacher et al., 2004a; Brehm et al., 2003b). Furthermore, different species and species groups show highly variable responses to environmental changes along altitudinal gradients (Axmacher et al., 2011; Kessler, 2001; Rahbek, 1995), rendering predictions based on patterns observed in well-known, species poor taxa which are commonly used in biodiversity studies, highly unreliable (Axmacher et al., 2011). In highly diverse insect groups, altitudinal diversity patterns can generally be linked to specific changes in environmental conditions (Axmacher et al., 2009; Axmacher et al., 2011; Beck et al., 2010; Brehm et al., 2007; Liu et al., 2006; Taboada et al., 2010). As these patterns are highly complex and currently not well understood, it is very important to establish and understand the underlying relationships for individual taxa, with research especially required for the most species-rich, highly under-studied insect taxa who contribute substantially towards the global species pool.

1.1.5. Threats to biodiversity

Global biodiversity is seriously under threat. Estimated species extinction rates are extremely high and many species are believed to have gone extinct before we even described them (Smith et al., 1993). Recent studies argue that this situation may have changed partly due to the increase of taxonomists - not only those who working in the field, but also those ‘fans’ of individual taxonomic groups in the general public (Costello et al., 2013). This trend could be nourished by species conservation receiving increasingly more publicity and becoming a greater general concern. Estimates suggest that from the 16th century until the end of 20th century, the mean annual species extinction rate is about 26 per million, while this number is estimated to reach 1000 per million in the 21st century, and if current forest loss rates continue, it could even reach 1500 per million by the end of the 21st century (Pimm et al., 2006). Despite the great number of estimated species extinctions, most estimates are based on well-known, species poor groups such as plants (Skole & Compton, 1993), mammals and birds (Thomas et al., 2004). According to the IUCN (International Union for Conservation of Nature) Red List (Baillie et al., 2004), between 12% and 52% of species in well-studied taxonomic groups such as mammals, birds and amphibians are threatened with extinction. These species are physiognomically and ecologically very different from the mega-diverse insect taxa such as beetles and moths, so that published estimated numbers are to be treated with great care (Dunn, 2005; Fonseca, 2009; Jocque et al., 2010). In addition, estimation based on the reversing of species-area relationship curves, which is widely used in estimating extinction rates, generally leads to overestimations (He & Hubbell, 2011).

Although species extinction is a natural process, it is general argued that human actions have greatly increased extinction rates (Brooks et al., 2006). Following the industrial revolution, the rapidly expanding human population and its economic activities have caused a dramatic loss in global biodiversity in the last two centuries, resulting from significant disturbances of ecosystems and land-use changes, which manifested themselves in deforestation, habitat degradation, desertification, deteriorating water quality and potentially intensification of natural disasters. The ongoing destruction of ecosystems threatens the diversity of remaining forest, grassland and agricultural habitats and the supply of clean water. Between 1950 and 1980, more land was converted for agricultural use than in the 150 years from 1700 to 1850, strongly affecting all forest types on earth. Between 1980 and 1995, a further ~180 M ha of forest were lost - mainly in developing countries (Millennium Ecosystem Assessment, 2005).

The resulting habitat destruction and fragmentation of pristine habitats are considered to be among the most important drivers of biodiversity loss (Debinski & Holt, 2000; Fahrig, 2003). Fragmentation leads to the reduction of habitat area, generating isolated populations, which can affect species' behaviours (Davies & Margules, 1998), genetic exchange between populations and subpopulations (Fahrig, 2003) and species interactions (Kruess, 2003; Kruess & Tscharntke, 1994) and ecological processes among populations (Zschokke et al., 2000). Many species face eventual local extinction if they are ill adapted to survival in fragmented habitat mosaics, a trend strongly affecting top predators, but also many habitat specialist species (Crooks, 2002; Fahrig, 1997; Haag et al., 2010; Riley et al., 2003).

The over-exploitation of natural resources is another key threat to biodiversity. Many large vertebrate species such as African Elephant (*Loxodonta cyclotis* Matschie and *Loxodonta africana* Blumenbach), Amur Tiger (*Panthera tigris altaica* Temminck) and Eurasian Brown Bear (*Ursus arctos arctos* Linnaeus) are under severe hunting pressure for the demands of traditional medicine, food and clothing. These large mammals play a crucial roles in ecosystems not only due to their significant interactions with the vegetation and their effects on energy flow and nutrient cycling (Botkin et al., 1978), but also as keystone species for researchers to understand overall ecosystem functioning (McNaughton et al., 1988). In addition, many valuable trees have also become endangered because of commercial over-exploitation. Wildlife extraction from tropical forests is estimated to be about 6 times greater than sustainable rates (Bennett, 2002), resulting in a dramatic pressure for tropical forest biodiversity. In Africa, the widespread overgrazing has led to widespread degradation and ecosystem change; in Southeast Asia and the Amazon region, half of drylands are becoming desertificated mainly due to overgrazing (Millennium Ecosystem Assessment, 2005). Between 4,000 and 10,000 medicinal plant species may furthermore be endangered due to unsustainable harvesting from the wild (Hamilton, 2003).

Local biodiversity is additionally threatened by the invasion of exotic species. Exotic plants compete for water, light, nutrients and space with native species, but in contrast to them, often live in an 'enemy-free space', as their traditional herbivore counterparts are missing. Some invasive plants furthermore secrete inhibiting allele-chemicals decreasing the fitness of native species, in turn affecting the ecosystem structure and functioning and eventually leading to the reduction or extinction of competing local species. One example of this is provided by the water hyacinth (*Eichhornia crassipes* Solms), which was first introduced from South America into China as a fodder plant in the early 1900s. A large coverage of water hyacinth that currently occurs on many Chinese lakes and slow-moving canals decreases sunlight and subsequently reduces underwater plants' photosynthesis leading to the reduction of water oxygen content. In Dianchi Lake, Yunnan province, 60% of the local, native species became extinct because of this spreading foreign weed (Chu et al., 2006).

Exotic predatory animals can expand rapidly if they are introduced to areas that were previously without natural predators occupying similar niches. An extreme example of negative impacts from alien animals is shown by the brown tree snake (*Boiga irregularis* Merrem), which was brought to American Guam accidentally during World War II. This island ecosystem previously lacked larger vertebrate predators. Brown tree snakes prey on birds, small mammals and lizards. As a result of their invasion, 10 of 13 bird species and 9 of 12 lizard species on American Guam have become extinct (Savidge, 1987). Although the rate of exotic species becoming invaders is only about 1‰ (Williamson & Fitter, 1996), a large number of species being taken into different areas intentionally or unintentionally every year still results in a number of successful invaders. China currently harbours 754 known invasive species (Database of Invasive Alien Spices in China, 2013), which have already had significant ecological, environmental and economical impacts (Axmacher & Sang, 2013; Yan et al., 2001).

Environmental pollution is also an important driver for biodiversity loss (Freedman, 1995; Lovett et al., 2009). Examples of environmental pollution for economic purposes include air pollution by automobile exhausts, oil spills and pollution by chemical products such as pesticide residue that deteriorates the living environment supporting the diversity of organisms. Environmental pollution can reduce the reproduction ability of plant species and change the long-term ecological status of dormancy and dispersal (Cox, 1992). Pollution has also caused an extensive decline of vertebrate species richness and abundance, with examples inducing amphibians (Jeliazkov et al., 2013), birds (Saha & Padhy, 2011), mammals (Sánchez-Chardi et al., 2007) and fish (Agostinho et al., 2007). The mega-diverse invertebrates are commonly used in the assessment of the pollution status such as for soil pollution (Eeva et al., 2010; Gongalsky et al., 2010; Santorufo et al., 2012), as a variety of invertebrate species have also shown a substantial decline due to pollution (Gongalsky et al., 2010; Gunnarsson, 1990; Moroń et al., 2012). Additionally, a few aquatic invertebrates are sensitive to pollution and hence can be used in the assessment of water quality (Brix et al., 2011; Emere & Nasiru, 2008; Kunz et al., 2010).

1.1.6. Biodiversity and climate change

The global climate has changed significantly during the 20th century. The average global air temperature near the Earth's surface rose by about 0.74ºC between 1906 and 2005 (IPCC, 2007). Simultaneously, precipitation increased by 0.5% - 1.0% per decade in middle and high latitude regions of the Northern Hemisphere, but decreased by 0.3% per decade in sub-tropical regions (IPCC, 2007). On a global level, climate change resulting in the change of temperature and precipitation is believed to be a key factor affecting future developments in biodiversity (Beck et al., 2011; Hawkins et al., 2003; Rahbek et al., 2007; Sala et al., 2000), with wide-ranging effects for vegetation structure and local species distribution patterns (Sang & Bai, 2009). Models predict that a large proportion of extant species will go extinct in the future if current climate change trends continue. Thomas et al. (2004)suggested that 15-52% of a sample of 1,103 animal and plant species will go extinct by 2050 under current change trends, although Harte et al. (2004) and others argue that these are overestimations, as predictions should also consider the specific topography, species migration patterns and adaptation abilities (Willis & Bhagwat, 2009).

Climate change can also induce a higher risk of natural disasters such as floods and droughts, which potentially increase extinction risks, while the relationship between biodiversity and climate change is mostly discussed from a more ‘inherent’ aspect: the biological response. All species have their specific biological niche (Hutchinson, 1957). Climate change can lead to the change of population sizes, distribution patterns, breeding time and migration behaviour. Only those individuals, populations or species with strong ability to adapt to the changing climate can have a high chance to survive (Bellard et al., 2012). When considering climate change effects on biodiversity, it also needs to be considered that species are not only passively exposed to climate change, but they are continuously adapting to environmental change through evolution, changing distribution areas and other specific adaptations (Franks et al., 2007; Guo et al., 2009).

Bellard et al. (2012) reviewed the biodiversity response to climate change from ‘spatial’, ‘temporal’ and ‘self’ aspects. The spatial response is mainly through dispersion, shifting species distributions to different areas. A meta-analysis estimated that the median rate that organisms have recently shifted to higher areas amounts to 11 m and to higher latitudes at a rate of 16.9 km per decade (Chen et al., 2011). Temporal shifts refer to species showing variations in certain periodicities (for example, daily or seasonal) because of climate changes. A good example is the response of plants to climate change by the change of their phenology and the increase of their resistance to temperature change, leading to the increase in their inter-specific competitive ability (Parmesan, 2006). The self response, which is also referred as *in situ* changes by Bellard et al. (2012), is the change of species to allow tolerance to wider ecological pressures such as drier or warmer conditions. A recent study by Quintero and Wiens (2013), however, predicted that rates of climatic niche evolution of terrestrial vertebrate species need to be 10,000 times faster in response to climate change during next 100 years than those species have had to adapt to in the past. Although Quintero and Wiens (2013)'s model is not the only prediction (for example Hoffmann & Sgrò, 2011), their results also indicate that *in situ* changes may not be an option for many species.

In the terrestrial biosphere, raising temperatures can accelerate carbon release rates more strongly than carbon absorption rates, which can cause an increase of atmospheric CO_2 concentrations (Cox et al., 2000).A recent study, however, found that the reduction of forest carbon stocks led by climate change is much less than expected and may even not occur at all (Huntingford et al., 2013). In addition, Lapola et al. (2009) indicate that the increase in atmospheric CO_2 concentrations and temperature can also enhance net primary productivity, while (Costanza et al., 2007) reported an increasing trend of a positive link between biodiversity and primary productivity with the increase of temperature. These intricate links again increase the difficulty of predicting biodiversity patterns under climate change. Overall, current evidence of species extinction caused by climate change is very limited (Lavergne et al., 2010), and estimations are very variable according to the study method used, taxonomic group studied as well as the spatial and temporal scale. Nonetheless, the potential biodiversity loss caused by climate change should still be highly concerning (Bellard et al., 2012).

1.2. Insect diversity[1]

1.2.1. Importance of insects

Insects are by far the most species-rich taxonomic group on Earth. To date, more than one million insect species have been described and many millions await discovery (IISE, 2012). Insects have high intellectual and economic value, supporting and providing livelihoods for numerous people. These range from the silk trade to

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[1] Part of this information has been published in Zou et al. (2011). In this paper, I was the main, lead author, with the other authors mainly commenting on the manuscript drafts I prepared and they edited some of the grammar, as well as making minor suggestions for additional aspects to be covered in the text.

beekeeping and the pollination of most of our fruit and other agricultural produce. The description of insects and their colourful body patterns have initiated prominent contributions to art, literature and culture, and they offer great educational tools (Pyle et al., 1981). In many regions, insects also form an important component of human diet and medicine. For instance, the Chinese fungal drug Dongchongxiacao (*Cordyceps sinensis* Berk) is the fruiting body of a parasitic fungus which develops inside the caterpillar of a ghost moth and has a very prominent role and long history in traditional Chinese medicine.

In addition to intellectual and economic value, insects are extremely important ecosystem components. They perform many key ecosystem functions, commonly relating to interactions with the vegetation. These interactions include herbivory and many mutualistic relationships such as pollination, seed dispersal and decomposition (Qin & Wang, 2001). Insect-plant interactions therefore have direct effects on ecosystem functioning, for example on the storage and cycling of carbon and nutrients, as well as strongly influencing succession and competition patterns in plant communities and overall food web interactions (Swank et al., 1981; Weisser & Siemann, 2004).

Another important application of insects is biological pest management. Insect predators are known to be more effective than many chemicals in controlling economically damaging insects (Dempster, 1968). Additionally, due to their conspicuousness and susceptibility to environmental factors, many insect taxa can also be used as bio-indicators (Choi, 2006; Kati et al., 2004). For example, butterfly population dynamics have been suggested as indicators of species richness in overall pollinators and of the structural and floristic diversity of habitats, as indicators of climate change and of landscape distinctiveness (Heath, 1981; Kremen, 1994; Pe'er & Settele, 2008; Pyle, 1976).

1.2.2. Implications of knowledge gaps relating to insect diversity

Due to the very limited knowledge base on the exact number of species of insects, their distribution and rarity, only a small number of species have been listed in regional and global red lists. It has been estimated that about 44,000 extinctions of insect species have occurred in the last 600 years, but only 70 such events have actually been documented (Dunn, 2005). Of an estimated 29,000 insect species endangered or threatened in North America alone, only 37 are included in regional red lists (Dunn, 2005; Redak, 2000). Factors such as habitat loss that result in the extinction of vertebrates can also lead to the extinction of insects, while insects may be going through unique extinction patterns in comparison to vertebrates and plants, such as extinctions of narrow habitat specialists and co-extinctions with their hosts (Dunn, 2005). According to some authors, the extinction of insects possibly exceeds vertebrates and plants (Fonseca, 2009; Jocque et al., 2010). Overall, the diversity of insects has received very little attention by researchers, due not least to constraints in time, energy, and funds available to thoroughly investigate mega-diverse insect taxa. The small body size, as well as the variability in colour patterns and size of insect species increases the difficulties with their identification and makes insect diversity studies more challenging than studies of vascular plants or vertebrate species. Additionally, the incomplete knowledge in entomological taxonomy increases the difficulties in studying insects.

Apart from the diversity and distribution patterns for insect taxa, relationships between insect assemblages and plant communities are another key topic requiring urgent research attention. As plants provide key habitat parameters for many insect species ranging from shelter to breeding sites, insect diversity can be affected by parameters of vegetation structure such as plant height, plant size or leave shape (Axmacher et al., 2004b; Haysom & Coulson, 1998; Lawton, 1983; Price & Wilson, 1979; Schuldt et al., 2012). Insect species richness often increases with an increase in vegetation height, with the highest diversity levels often recorded in full-grown forests (Haysom & Coulson, 1998; Pöyry et al., 2006; Price & Wilson, 1979; Treweek et al., 1997). This has been related to a greater resource availability in mature forest ecosystems (Lawton, 1983). In contrast, higher diversity has also been observed in open habitats as compared to closed forests, potentially in reaction to changes in the microclimatic conditions (Axmacher et al., 2004b, 2009).

Plant species richness and community composition affects the diversity of herbivore insects. According to the 'Resource Concentration Hypothesis' (Root, 1973), herbivores are more likely to find and remain on hosts in monocultures. Reduced plant diversity therefore increases the potential damage of the vegetation by pest species, while simultaneously reducing overall insect diversity. Supported by experiments, it has been predicted that herbivorous insect diversity is therefore generally positively correlated with the diversity of plant species (Beck et al., 2002; Chey et al., 1997; Ghazoul, 2002; Intachat et al., 1999; Lewinsohn & Roslin, 2008; Niemelä et al., 1996; Siemann, 1998; Tilman, 1986).

The increasing diversity in plants is also assumed to enhance the diversity of predatory insects (Root, 1973). Arthropod consumers are also known to be influenced by top-down control via the abundance of their natural enemies (Hairston et al., 1960; Russell, 1989; Walker & Jones, 2003). This control forms the basis of the "Enemies Hypothesis" (Root, 1973), which postulates that species-rich vegetation assemblages can provide more refuges and more stable prey availability for predators than plant species-poor assemblages, resulting in predators catching and feeding on prey more effectively, so that a higher diversity in the plant community is believed to support a higher diversity and abundance also of predatory species (Jactel et al., 2005; Russell, 1989).

The links between plant diversity and the diversity of insects is not always positive. Negative relationships have been reported in forest (Axmacher et al., 2004b; Cuevas-Reyes et al., 2003) and grassland ecosystems (Unsicker et al., 2006; Wardle et al., 1999) and in experiments (Kanaga et al., 2009). Other studies found no significant link between plant diversity and the diversity of herbivorous insects (Axmacher et al., 2009; Hawkins & Porter, 2003). The underlying patterns governing the links between phyto-diversity and the diversity of insects are still unclear, and more studies are urgently needed to investigate these links.

The relationship between insect diversity and temperature shifts is another topic that needs to be addressed. This question is also correlated with several core ecological issues such as insect altitudinal and latitudinal distribution patterns and their respective responses to overall climate change. Insect species richness and species composition are known to be particularly strongly affected by environmental factors such as temperature and precipitation (Axmacher et al., 2004b, 2009; Brehm et al., 2003b). Global climate change is accordingly predicted to strongly alter the distribution and also diversity patterns in insect communities. Many insect species are already observed to alter and extend their distribution ranges northwards in the northern hemisphere, while others have declined in population size in reaction to climatic changes (Asher et al., 2001; Hill et al., 1999; Masters & Clarke, 1998; Thomas et al., 2001; Thomas et al., 2006b; Warren et al., 2001). In other cases including the silver spotted skipper buttery (*Hesperia comma* Linnaeus) and Roesel's bush cricket (*Metrioptera roeselii* Hagenbach), population sizes have actually increased with increasing temperature (Thomas et al., 2001).

It is unsurprising that there is no unique response of different insect taxa to temperature. Nonetheless, while temperature can affect the life cycles, phenology and distribution of insects, responses of different taxa are not unique (Bale et al., 2002; Samways, 2005). For herbivore insects, temperature can also change their diversity and distribution patterns by altering the phenology of their host plants (Bale et al., 2002). Other indirect influences on herbivores include climate-change induced changes in predation pressure from birds or predatory insects, and through affecting mycorrhizal fungi and subsequently the secondary metabolism of plant species (Ayres & Lombardero, 2000; Bennett et al., 2006). These interactions are in turn likely to also result in alterations at higher trophic interactions, which increases the difficulty of predicting the diversity of predatory insects in response to temperature (Samways, 2005). Additionally, as many insects can move faster than plants in response to climate change, plant species from high latitudes are likely to meet new insect pests, which enhances the challenges of pest control (Samways, 2005). A good prediction of the response patterns of insect diversity to alterations in precipitation and particularly temperature is therefore urgently needed.

1.3. Insect taxa selected in this study

In this study, two insect groups have been selected – ground beetles (Coleoptera: Carabidae) and geometrid moths (Lepidoptera: Geometridae). These two groups were chiefly selected due to three reasons. Firstly, both taxa can be seen as strong bioindicators (see following). Secondly, the two families represent different trophic levels, with ground beetles chiefly representing predatory insects and geometrid moths a group of herbivores – disregarding the insectivorous geometrid caterpillars encountered on Hawaii (Montgomery, 1983). Thirdly, both groups have been studied previously by members of the UCL Department of Geography and the China Agricultural University in Northern China (Axmacher et al., 2011; Liu et al., 2010b, 2012), which offered not only a good basis for the identification of specimens, but also a baseline for comparison of diversity data (Chapter 7).

1.3.1. Carabidae

Carabids (ground beetles, Coleoptera: Carabidae) are one of the largest adephagan families and one of the most species-rich beetle families, containing more than 40,000 species in 34 subfamilies (Carabidae of the World, 2011; Lövei & Sunderland, 1996). Carabids are taxonomically and ecologically well-known. The distribution of carabids is influenced by a wide range of factors, including temperature, humidity, food availability, competitors' distribution, life history and seasonality, and most habitats are inhabited by a mixture of specialist and generalist species (Lövei & Sunderland, 1996; Rainio & Niemelä, 2003). The larva's survival rate is crucial in overall mortality because it is the most vulnerable life stage of carabids, resulting in a high selectivity of suitable habitat conditions by adult females when laying eggs (Lövei & Sunderland, 1996). Considering their wide geographical distribution and environmental sensitivity and also their cost-effective standardized sampling using pitfall traps, carabids are ideal bioindicators (Rainio & Niemelä, 2003). Their assemblages are a reflection of the state of their environment and environmental change (McGeoch, 1998). Carabids have been used as bioindicator in many ways such as in indicating the land management status and use (Blake et al., 1996; Desender et al., 1994; Liu et al., 2006), in environmental quality assessments (Eyre et al., 1996), to characterize degrees of urbanization (Niemelä *et al.* 2000), habitat fragmentation (Spence *et al.* 1996; Davies and Margules 1998), forest management (Niemelä, 1993), climate change (Ashworth, 1996) and overall biodiversity (Duelli & Obrist, 1998).

Most carabids are predators. A worldwide survey of literature on 1054 carabid species showed that 73.5% are purely carnivorous, consuming molluscs, worms, small insects and insect larvae; 8.1% are herbivores and 19.5% omnivorous (Larochelle, 1990). Larvae are more often strictly carnivorous and also more specialized in their food range than adults (Lövei & Sunderland, 1996). Carabids are therefore also an important group in biological pest control (Kromp, 1999). The body of the adults of carabids can be dark, matte, shiny, bright or metallic coloured, sometimes it is also pubescent. Their body size ranges from 1 to 60 mm; the elytra of most species are fused, especially in large ones, resulting in many species being unable to fly. Carabids have pronounced mandibles and palps, long slender legs and sets of punctures; their antennae are mostly large and pubescent with 11 segments (Figure 2). They generally reproduce once a year in temperate regions.

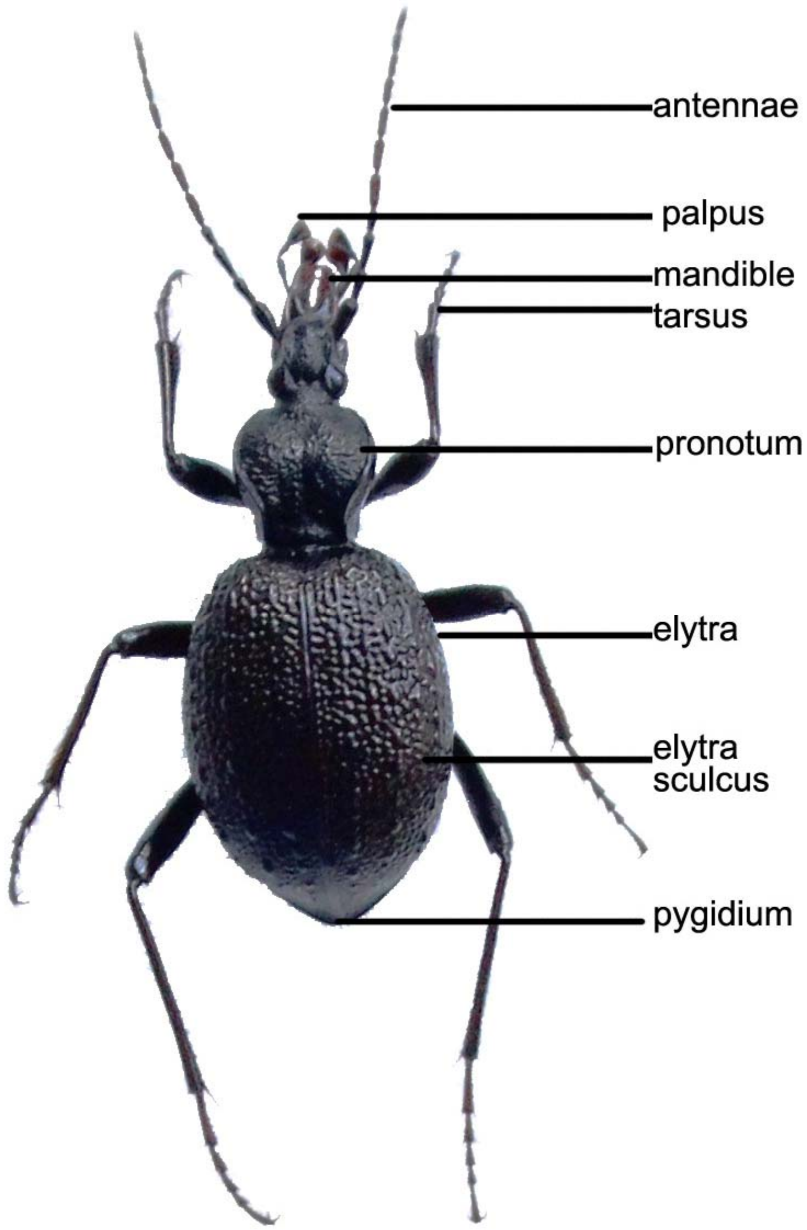

Figure 2 Photo of the carabid *Cychrus morawitzi* Gehin

1.3.2. Geometridae

Geometrid moths (Lepidoptera: Geometridae) are a second, highly species-rich insect family with more than 21,000 described species (Scoble, 1999). Similar to carabids, geometrid moths can also be used as bioindicators (Kati et al., 2004), as they are taxonomically well-known (Scoble, 1999), environmental sensitive (Holloway, 1985), readily surveyed on a wide range of light sources (Axmacher & Fiedler, 2004; Intachat & Woiwod, 1999; Muirhead-Thomson, 1991) and the wide caterpillars' food selection and the wide ecological amplitude occupied by members if this family leads to their widespread distribution, for example also at high latitudes and altitudes (Axmacher et al., 2009; Axmacher et al., 2004a; Robinson et al., 2010). The diversity pattern of geometrid moths has been studied in America (Brehm & Fiedler, 2003; Brehm et al., 2003a; Hilt et al., 2006), Southeast Asia (Beck et al., 2002; Willott, 1999), Australia (Kitching et al., 2000) and Africa (Axmacher et al., 2004a).

Caterpillars of geometrid moths are mainly phytophagous. Larvae of geometrids are widely feed on trees, shrubs or herbs, occasionally also on ferns (Scoble, 1992). Adult moths generally have functioning proboscis and feed on nectar (Han & Xue, 2011; Xue & Zhu, 1999). Their bodies are usually slender, and they have large and broad forewings, while females in some species are wingless and cannot fly. Many species hold their wings away from the body and flat against the substrate when at rest (Figure 3a), while some also close their wings vertically over their back when resting (Figure 3b). Their tympanal organs are located on the ventral side of the first segment of the tergum and are usually oval in form (Figure 4), which is one of the key identification traits of geometridae. Caterpillars' bodies are also slender and usually only have two pairs of prolegs on the sixth and tenth segments, leading to the special locomotion method of geometrid caterpillars: looping the end of the body to the front and then extending the body forward. In English, they are therefore also called loopers, and since their movement looks as if they are measuring the length of their path. In Chinese, they are called 'Chie', which means 'inch moth'.

Figure 3 Different resting positions of geometrid moths: (a) *Scopula limboundata* Haworth[1] and (b) *Plemyria georgii* Hulst[2]

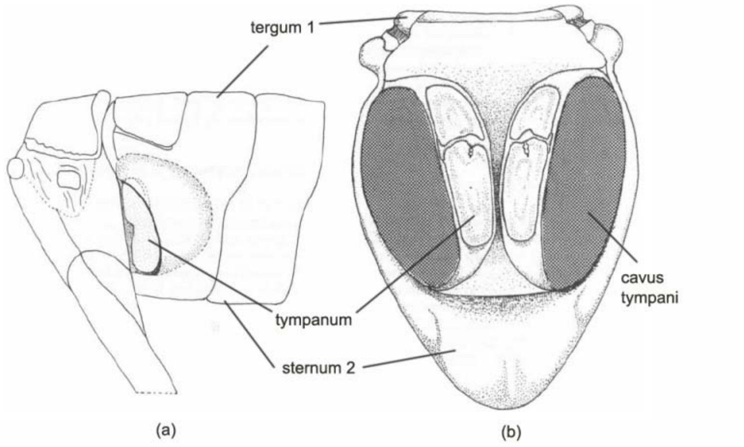

Figure 4 Lateral (a) and anterior (b) view of tympanal organs of geometrid moths (Cook & Scoble, 1992)

1.4. <u>China's temperate forests and their biodiversity</u>

1.4.1. China's temperate forests distribution

Long-term climatic patterns are the main drivers of forest distribution. Globally, there are four climatic zones along the latitudinal gradient with relatively stable air masses classified by Alissow (1954): the tropical, subtropical, temperate and polar zone. In

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[1] Image available from online source: http://bugguide.net/node/view/484393
[2] Image available from online source: http://bugguide.net/node/view/442828

China, according to the classical climate classification, there are nine climatic zones distinguishable: a cool temperate zone, a central temperate zone, a warm temperate zone, a northern sub-tropical zone, a central sub-tropical zone, a southern sub-tropical zone, a northern tropical zone, a central tropical zone and a southern tropical zone. Furthermore, the Qinghai-Tibet Plateau represents a separate climatic zone due to its distinct geographical and climatological conditions (Chen et al., 1997). The Pacific southeast monsoon and Indian Ocean southwest monsoon form the main sources of precipitation in China. Thus, the eastern and southern parts are humid and north-western parts are arid. Based on humidity levels, China can be divided chiefly from the southeast to the northwest into a humid zone, a sub-humid zone, a sub-arid zone, an arid zone and an extremely arid zone, with forests being mainly distributed in the humid and sub-humid zones (Chen et al., 1997). The vegetation clearly reflects this with its latitudinal distribution from north to south. In western China, the Qinghai-Tibet Plateau has a distinct local climate, leading to a clear and distinct vegetation zonation in this area. Overall, there are six main forest zones in China along the latitudinal gradient: a cool temperate coniferous forest zone, a temperate mixed coniferous and deciduous broad-leaved forest zone, a warm temperate deciduous broad-leaved forest zone, a subtropical evergreen broad-leaved forest zone, a tropical rainforest and monsoon rainforest zone and the forests of the Qinghai-Tibet Plateau (Figure 5). According to climatic conditions, China's temperate forests can be further subdivided into cool temperate deciduous coniferous forests, cool temperate evergreen coniferous forests, central temperate mixed coniferous and deciduous broad-leaved forests, warm temperate coniferous forests and warm temperate coniferous and deciduous broad-leaved mixed forests (Chen et al., 1997).

Nonetheless, cool temperate forests and warm temperate forests are usually combined. They harbour a range of conifer-dominated forests, including Dahurian Larch (*Larix gmelinii* Kuzen) forests, Olgan larch (*Larix olgensis* Henry) forests, Yezo spruce (*Picea jezoensis* Carr) forests, Korean Spruce (*Picea koraiensis* Nakai) forests, Manchurian Fir (*Abies nephrolepis* Maxim) forests and Korean Pine (*Pinus koraiensis*

Siebold et Zuccarini) forests. It should be pointed out that Scots Pine (*Pinus sylvestris var. mongolica* Litv) forests were widely distributed in China, but were cut largely during the 1930s. Remaining Scots Pine forests are mainly located at the mid-elevation (450 – 1000m) of the Daxing'an Mountain range. On the boundary between Inner Mongolia and Hebei province, there are also some afforested Scots Pine forests to resist desertification. Japanese Red Pine (*Pinus densiflora* Siebold et Zuccarini) forests are usually successions of deforestation of the Yezo spruce forests, spruce forests or Korean Pine and broad-leaved mixed forests. These are mainly located in the Changbai Mountain range, Jilin Province.

Figure 5 Simplified vegetation regionalization map of China, based on 'Vegetation Regionalization Map of China' by the Chinese Academic of Sciences (Zhang, 2007).

Coniferous forests in warm temperate areas are less abundant compared with cold and central temperate areas. These forests mainly include Chinese Red Pine (*Pinus tabuliformis* Carrière) forests and Chinese Arborvitae (*Platycladus orientalis* Franco) forests at low elevations, Japanese Red Pine forests, Chinese White Pine (*Pinus armandii* Franch) forests in mid-elevation, and Prince Rupprecht's Larch (*Larix principis-rupprechtii* Mayr) forests at high elevations (Chen, 1995). The representative forest types of deciduous broad-leaved forests in warm temperate areas are mixed forests composed of oak (*Quercus* spp.), lime (*Tilia* spp.), maple (*Acer* spp.) and Korean Hornbeam (*Carpinus turczaninowii* Hance), where deciduous trees dominate in the north and the proportion of evergreen trees increases with decreasing latitude.

1.4.2. Forest plantations in China

The loss of biodiversity due to deforestation has been of increasing global concern. Only 36% of the world's forest cover of 4 billion ha consists of primary forests, whereas 53% of the forest ecosystems are modified natural forests, 7% are semi-natural forests and 4% are plantation forests (FAO, 2006). Secondary and plantation forests are therefore becoming an increasingly important component of global forest cover (Bass, 2004; FAO, 2006; Liu et al., 2008).

Forest surveys show that China's forest cover was only 8% in 1949 after World War II and the Chinese Civil War (Chinese Ministry of Forestry, 1977), although this figure might be a slight underestimation (Zhang & Song, 2006). Forest cover reached 20.36% (195 million ha) in 2010 (Chinese State Forestry Bureau, 2011), and the increase can chiefly be attributed to active afforestation and reforestation. In fact, from 1949 to 2003, accumulated planted areas accounted to 241 million ha (Zhang & Song, 2006). Due to the combined impacts of afforestation, deforestation and reforestation, many afforested areas actually failed to reach the minimum requirement of being classified as forests, with only 37% of afforested areas eventually forming plantation forests (Zhang & Song, 2006). Nonetheless, China currently still harbours the world's largest plantation forest cover, totalling about 62 million ha (Chinese State Forestry Bureau, 2011). This represents about 31.8% of China's total forest cover.

Deforestation historically posed a serious threat for China's forest ecosystems, resulting in more than 200 plant species and 61% of large animal species suffering from local extinction since 1950 (Li & Zhao, 1995). Nonetheless, the resulting habitat degradation and a series of environmental issue changed past deforestation policies, and the central Chinese government has established a variety of large-scale ecological restoration programmes. The Six Key Forestry Programmes (SKFPs) in China cover more than 97% of China's counties and target 76 million ha for afforestation (Wang et al., 2007). These SKFPs are the Natural Forest Protection Programme (NFPP), the Conversion of Cropland to Forest Programme (CCFP) (also called the Grain for Green Project), the Sand Control Programmes for the Beijing and Tianjin area (SCP), the 'Three-North (north, northeast and northwest China) Shelterbelt Programme' and the 'Yangtze River Basin' Shelterbelt Development Programme (TYSDP), the Wildlife Conservation and Nature Reserves Development Programme (WNDP) and the Fast-Growing and High-Yielding Timber Base Construction Programme in Key Areas (FTP),.

The NFPP aims to fundamentally restore natural forest resources by the end of 2050, with most timber demands coming from plantation forests, and to establish a sustainable forestry industry system. According to the NFPP, logging in the middle and upper reaches of the Yangtze and Yellow Rivers is completely banned. The CCFP includes two aspects: transferring unsuitable farmland which mainly refers to land on slopes of more than 25° to forest, and establish plantations on barren, degraded land. The SCP and TYSDP both aim to prevent desertification via the establishment of forests in semi-arid areas. These programmes have reduced desertification from an annual increase of 3436 km^2 by 2000 to an annual reduction of 1283 km^2 in 2005 (Wang et al., 2007). The WNDP aims to protect endangered wildlife species, such as giant panda (*Ailuropoda melanoleuca* David), Yangtze alligator (*Alligator sinensis* Fauvel), golden monkey (*Rhinopithecus roxellana* Milne-Edwards) and chiru (*Pantholops hodgsoni* Abvel). China had established 363 national natural reserves and more than 2000 county or provincial level natural reserves by the end of 2012. The FTP was established to solve the short supply of timber in order to protect natural forest. Key plantation areas are located in regions with substantial annual precipitation on flat areas, including in the tropical and subtropical regions of Guangdong, Guangxi, Hainan and Fujian Province, but also in the northern subtropical Yangtze River region, the temperate region around the Yellow River region and the cool temperate northeast and Inner Mongolia region.

These large scales of plantations were partly motivated by the demands in timber and partly by concerns for biodiversity and other natural resources. Policy-makers believe that plantations benefit the environment, but plantation programmes still lack precise restoration objectives (Sayer et al., 2004). For example, reforestations of China's Three-North SDP play an important role in preventing sand storms and in retaining soil water, but they lack a clear strategy how to support further ecological issues such as biodiversity conservation, and some researchers even claim that they may destroy the entire regional ecosystem (Xu, 2011).

1.4.3. Plantation and secondary forest and biodiversity

Although it is believed that 'primary' forests are irreplaceable for sustaining biodiversity (Gibson et al., 2011), secondary and plantation forests play an increasingly important role in maintaining forest biodiversity (Barbaro et al., 2005). The overall contribution these forests make towards biodiversity conservation has been vigorously debated (Brockerhoff et al., 2008; Gibson et al., 2011; Hartley, 2002; Lawton et al., 1998; Sayer et al., 2004). It is impossible to assess the diversity status of all species in secondary and plantation forests, while to compare and even study a wide range of different taxa needs substantial time, manpower and economic resources. Consequently, a possible way to evaluate the role of secondary and plantation forests in supporting biodiversity is to find suitable bioindicator taxa (Larsson, 2001), with highly species-rich and habitat-sensitive insect taxa being ideal candidates (Maleque et al., 2009).

Plantation forests have been reported to host low insect biodiversity levels in comparison with mature forest ecosystems because of their generally more homogenous habitat composition (Fahy & Gormally, 1998; Maeto et al., 2002;

Makino et al., 2007). Some studies have however pointed out that plantations forests can provide important habitats for forest arthropod species (Barbaro et al., 2005; Brockerhoff et al., 2005; Felton et al., 2010). For example *Holcaspis brevicula* Butcher, a locally endangered ground beetle species, is currently restrictedly known from the plantation forests of *Pinus radiata* D. Don in New Zealand (Brockerhoff et al., 2005). Overall, results are incongruent for different insect taxa (Barlow et al., 2007a; Lawton et al., 1998; Meng et al., 2012; Schulze et al., 2004) and also strongly dependent on the tree species composition used in the plantations (Bremer & Farley, 2010; Coote et al., 2012).

Similar to forest plantations, the role of secondary forests in biodiversity conservation is also widely unclear. It has been argued that the increasing cover of secondary forests provides important refuges for species endangered by the declining old-growth forest cover particularly in tropical regions (Wright & Muller-Landau, 2006). According to the intermediate disturbance hypothesis (IDH) (Connell, 1978; Grime, 1973), the relationship between species richness and disturbance is hump-shaped, with diversity peaking at intermediate levels of, and age since, disturbance events. In relation to forest succession states, particularly older unmanaged secondary forests are hence hypothetically able to support high levels of diversity in plants and animals. Nontheless, whether secondary forest can maintain high levels of insect biodiversity is again being controversially debated (Barlow et al., 2007b; Bobo et al., 2006; Brook et al., 2006; Laurance, 2007; Schulze et al., 2004).

In temperate regions of Europe and North America, studies have already reviewed the biodiversity patterns of bioindicator taxa in primary forest (Chumak et al., 2005; Lövei & Sunderland, 1996), and some have explored the effect of plantation and secondary forests on biodiversity patterns (Elek et al., 2001; Maeto & Sato, 2004; Magura et al., 2002). In China as the world’s largest plantation forests country, very limited studies have been conducted concerning the biodiversity status of planted temperate forests. One of the most important reasons is that the understating of the biodiversity status in temperate primary forests is still widely lacking. Studying biodiversity patterns of important, diverse target taxa in China's primary forests is a first step which will be significantly meaningful for setting conservation objectives for forest restoration and afforestation projects.

1.5. The insects research gap in Northern China

China has a very rich insect fauna, and the study of insect diversity patterns in China has great value. Some estimates render insects in China to account for 10% of the total global species number (You, 1997), with Wu (1992) indicating an even bigger contribution. In addition to the high species diversity, there are many rare and endangered species in China. For example, the country harbours 120 species of Protura, the most primitive insect order, of the 400 species currently known (You, 1997). Compared with the extensive vegetation studies in China, very limited attention has been given to the country's species-rich insect communities, their conservation status, the likely influence of past and future climate change on these communities, and to the interactions between vegetation and insects.

Ecological models indicate that China's forest ecosystems are shifting northwards in response to global warming, and that the alpine forests are shrinking (Ni et al., 2000; Zhao et al., 2002). In northern China, particularly north of 33° latitude, forests ecosystem productivity reacts more sensitive to climate change than in southern China, so that forests in northern China provide ideal study objects to investigate forest ecosystem reactions to climate change (Yu et al., 2001). The main research area of this study is located in a mature temperate forest in northeast China—Changbaishan Natural Reserve (CNR). In temperate regions of northern China, ground beetles have chiefly been studied in grassland and agricultural ecosystems (for example, Duan et al., 2012; Liu et al., 2010b, 2006, 2012; Yu et al., 2007), with few studies investigating the diversity patterns of ground beetles in temperate mountain forests (Axmacher et al., 2011; Ji & Hu, 2007; Jiang, 2006; Yu et al., 2006a; Yu et al., 2002). Nearly all of these latter studies were based in secondary forests and forest plantations, while very little information has so far become available on insect assemblages from the last remaining pristine temperate forests of China. In comparison to ground beetles, geometrid moths have already been studied in Changbai Mountain in the past (Chen et al., 2007; Liu et al., 2007a). These studies, however, mainly focused on general fauna diversity and distribution surveys, and none of these investigations analysed how the diversity of geometrids is linked to vegetation and environmental factors. The authors also considered their studies to be premature and encouraged more detailed studies of geometrids at CNR (Chen et al., 2007).

1.6. Research aim and objectives

In this thesis, I aim to establish the diversity patterns of insect assemblages in CNR in relation to vegetation and environmental conditions, focussing on the distribution patterns of different insect taxa and functional groups at various spatial scales. The resulting patterns furthermore form the basis for an assessment into the effects of different environmental change scenarios on biodiversity patterns, as well as providing a baseline for biodiversity studies in the large-scale secondary and plantation forests in northern China. The following research questions hence will be addressed:

1) What are the elevational α-diversity patterns of different insect taxa and functional groups in CNR?
2) What is the insects' species turnover status in relation to elevation and associated climatic factors?
3) How does insect α-diversity relate to vegetation diversity and composition and prevailing environmental conditions?
4) What is the trend of historical and future diversity patterns of insects at the CNR?
5) How does insect diversity differ among primary, secondary and plantation forest in northern China?

In particular, the main hypotheses will be tested in the following chapters:

1) Insect diversity decreases monotonically with increasing elevation in CNR (Chapter 3);
2) A distinct altitudinal vegetation zonation exists at the CNR, and species turnover of insects will mirror this zonation (Chapter 3);
3) There is a significant, positive relationship between plant diversity and diversity of carabids and geometrids (Chapter 4);
4) The diversity of insects is significantly linked with changes in the composition of the vegetation (Chapter 5);
5) Statistic models indicate that insects will move to higher elevational levels due to changes in the climatic conditions (Chapter 5);
6) In Dongling Mountain, the secondary forest harbours a higher α-diversity of insects than more homogeneous plantation forests, while each forest habitat type harbors a distinctive insect species composition (Chapter 6);
7) When comparing primary, secondary and plantation forest on a wider geographical area, primary forest harbors the highest insect diversity, followed by secondary forest, while plantation forest has the lowest diversity level (Chapter 7).

Chapter 2. Methodology

2.1. Study area

The main study area is located at the Changbaishan Natural Reserve (CNR), Jilin Province, China (N 41°41' to 42°51' and E 127°43' to 128°16'). Changbaishan is a sleeping volcano with a peak of 2745m. The southern, North Korean side of the mountain has mostly been used for agricultural production, causing dramatic changes in the natural environment. The Northern sections of the mountain form part of CNR which was established in the 1960s. This reserve comprises an area of about 20,000 ha, forming one of the best-protected Chinese large-scale natural forested environments, and also one of the world's largest coherent temperate forest ecosystems. The area was classified as cool temperate moist forest based on Holdridge (1967)'s life zone system (see Cao & LI, 2008; Zhang, 1993). Forests with strong Korean pine (*Pinus koraiensis* Siebold et Zuccarini) components are widespread in this area. There are many valuable and endangered species of flora and fauna inhabit the CNR, such as Ginseng (*Panax ginseng* Meyer), Scots pine (*Pinus sylvestris var. mongolica* Litv) Japanese Yew (*Taxus cuspidate* Siebold & Zucc), *Chosenia arbutifolia* Skvortsov, while animals recorded in the vicinity of Changbai Mountain include the Amur tiger (*Panthera tigris* Linnaeus), sika deer (*Cervus nippon* Temminc), sable (*Martes zibellina* Linnaeus) and Imperial Eagle (*Aquila heliaca* Savigny). The abundant flora and fauna of the CNR does not only provide an important economical resource for local people, but also maintains a complex and stable set of ecosystems, as well as an excellent scientific research object.

Along the altitude gradient, a clear plant community zonation can be distinguished in Changbai Mountain (Bai et al., 2011; Chen et al., 1964; Sang & Bai, 2009; Xu et al., 2004; Zhao et al., 2004). There are four main forest zones, the mixed coniferous and broad-leaved forest zone (MCBF) from 700m to1100m, the mixed coniferous forest zone (MCF) between 1100m and 1500m, the sub-alpine mixed coniferous forest zone

(SMCF) between 1500m and 1800m and the birch forest zone (BF) distributed from 1800m to the forest boundary at 2100m. In this study, annual mean climatic data was only available from Songjang meteorological station (at 720m asl) that is located on the northern section of the natural reserve (42°25′N, 128°07′E). Hence, climatic condition in respective forest zones was according to researcher’s description.

The mixed coniferous and broad-leaved forests (MCBF) zone below 1100m

This forest type, which is widely distributed along the base of the mountain, can be divided into two parts: the secondary forest at 500m – 800m, which is dominated by broad-leaved trees but contains a few conifers, and the primary forest chiefly above 800m, which consists of a more even mixture of coniferous and broad-leaved tress (Chen et al., 1964). The annual average temperature is 3.4 °C and the annual precipitation amounts to 654mm (according to observations from Songjang meteorological station 1996 to 2006, see Sang & Bai, 2009). Soils are loams or sandy loams, representing brown or dark brown forest soils (Chen et al., 1964). The forest canopy height is 18-28m (Chen et al., 1964). The flora of the study area is extremely species-rich, containing more than 1100 plant species of more than 130 families and 480 genera (Cao & LI, 2008). The mixed tree layer including deciduous broad-leaved species and evergreen conifers is dominated by *Pinus koraiensis* Siebold et Zuccarini, *Acer mono* Maxim, *Quercus mongolica* Fisch. et Turcz, *Tilia amurensis* Rupr and *Ulmus davidiana* Planch. Shrubs include *Lonicera maximowiczii* Regel, *Spiraea* spp., *Acanthopanax senticosus* Maxim., *Corylus mandshurica* Maxim. et Rupr., and herbs are dominated by *Anemone* spp., *Carex* spp. *and Meehania urticifolia* Makino (Chen et al., 1964; Xu et al., 2004).

Figure 6 The mixed coniferous and broad-leaved forest in Changbai Mountain

The mixed coniferous forests (MCF) zone between 1100m and 1500m

Compared with the MCBF zone, the proportion of coniferous species increases and the density of broad-leaved trees decrease dramatically in their distribution in the MCF (Figure 7); the coverage of shrubs and herbs also significantly decreases (Xu et al., 2004). Transition from MCBF to MCF is not abrupt, with mixture forest at 1000-1100m. This area together with the sub-alpine mixed coniferous forest zone between 1500-1800m represents cold temperate forests with an annual average temperature below 2°C (Xu et al., 2004). Geological parent material is mainly composed of gravel and volcanic ash, leading to the formation of brown coniferous forest soils. The average forest canopy height is 16-24m. The MCF is mainly dominated by *Picea koraiensis* Nakai and *Larix olgensis* Henry, but also contains *Picea jezoensis* Carr. and *Abies nephrolepis* Maxim. The common shrub species at lower altitudes such as *Spiraea* spp. and *Acanthopanax senticosus* Maxim are rare, with the shrub layer mainly consisting of *Lonicera maximowiczii* Regel*, Rosa davurica* Pall. and *Euonymus verrucosus* Scop. Herbs are dominated by *Maianthemum dilatatum* Nelson & Macbr and a variety of *Carex* spp..

Figure 7 The mixed coniferous forest in Changbai Mountain

The sub-alpine mixed coniferous forest (SMCF) zone between 1500m and 1800m

This forest type (see Figure 8) experiences high precipitation and low evaporation levels. The average forest canopy height is about 20m (Chen et al., 1964). Transition between MCF to SMCF is again not abrupt. This forest is dominated by *Abies nephrolepis, Larix olgensis* and *Picea jezoensis*, forming a dark and wet environment under the canopy; it is also called “dark coniferous forest” (Yu et al., 2003). Shrubs and herbs are rare, chiefly composed of suppressed *Rosa acicularis* Lindl, *Ribes maximowiczianum* Kom*, Linnaea borealis* Linnaeus and *Pyrola renifolia* Maxim. Mosses are very well-developed, covering the whole ground and the tree trunks (Xu et al., 2004).

Figure 8 The sub-alpine mixed coniferous forest in Changbai Mountain

The birch forest (BF) zone between 1800m and 2100m

The BF zone (Figure 9) forms the upper forest boundary on Changbai Mountain. Abrupt transition occurs between SMCF and BF. This forest is dominated by *Betula ermanii* Cham*,* interspersed by *Alnus mandshurica* Hand.-Mazz. and *Sorbus dacica* Borbás at 1800m to 2100m. Annual temperature is very low, with high humidity levels and strong winds, which is unsuitable for the survival of tall trees. As a pioneer species, the birches are usually small with an average height of 8-12m, reducing further to only 5-6m at the upper forest boundary. In some lower areas between 1600m and 1650m that experience strong winds, birch forests also occur; birches can reach up to 14-16m in height at these lower elevations (Xu et al., 2004). Undergrowth shrubs are scarce and mostly dominated by *Rhododendron aureum* Georgi, with *Vaccinium uliginosum* Linnaeus and *Phyllodoce caerulea* Babington also noteworthy components. The herb layer is highly diverse with more than 90% of the coverage, including species such as *Aquilegia japonica* Nakai et Hara*, Campanula glomerata* Linnaeus*, Deyeuxia angustifolia* Kunth*, Petasites saxatilis* Toman and *Saussurea tenerifolia* Kitagawa (Xu et al., 2004).

Figure 9 The birch forest on Changbai Mountain

Tundra zone above 2100m

Forest disappears abruptly from BF to tundra zone. The annual average temperature in the tundra zone (Figure 10) is lower than -5°C and precipitation reaches about 1700mm with extremely strong wind. Low shrubs such as *Phyllodoce caerulea, Rhododendron redowskianum* Maxim.*, Rh. Parvifolium* Wahlenb*, Rh. chrysanthum, Salix rotundifolia* Trautv. and *Vaccinium uliginosum* dominate in this area. Some typical herbaceous mountain plants can also be found, such as *Kobresia* spp.*, Phleum alpinum* Linnaeus*,* and *Ptilagrostis mongholica* Griseb., mixed with high-elevation mosses and lichens (Xu et al., 2004).

Figure 10 The tundra zone in Changbai Mountain

Apart from the main study area at CNR, research was also conducted at a second study area, Dongling Mountain (DLM) (40°00’N, 115°26’E). This area is located in the Beijing Xiaolongmen Forest Park that belongs to the Taihang Mountain range that is about 110 km southwest of Beijing city centre near the boundary between Beijing and Hebei Province. The altitude of this area ranges from 800m to 2300m. It was originally dominated by Oak (*Quercus liaotungensis* Mayr), but was extensively deforested and partly re-forested with pine (*Pinus tabulaeformis* Carrière) and larch (*Larix principis-rupprechtii* Mayr) plantations in the 1960s (Yu et al., 2010). Natural regeneration also generated mixed conifers and broadleaved forest patches. It hence results in a fine forest mosaic within a relatively small geographical area formed of oak, pine, larch, birch (*Betula platyphylla* Suk. and *B. dahurica* Pall.) and mixed forests. Forests harbors canopy of 8-15 metres with a maximum of 20m (Yu et al., 2010). This area experiences a warm temperate and continental monsoon climate, with an annual mean temperature at 1100m of 4.8°C and an average annual precipitation of 612mm (Sang, 2004).

Results were furthermore used in comparisons with original data generated in collaborative research between members of the UCL Department of Geography and the China Agricultural University, who sampled carabids and geometrid moths in plantation forests on the Bashang Plateau (BSP) in 2006 and 2007. The BSP is located in the mountain ranges in Hebei Province between Beijing and Inner Mongolia, in the transition zone between the sub-humid monsoon climate and the semi-arid steppe climate (Zhao et al., 2005). The vegetation therefore falls within the boundary between the warm temperate deciduous broad-leaved forest zone and the temperate grassland zone (Zhang, 2007). In the past, the area has experienced severe land degradation due to overgrazing and forest transformations into cropland (Zhao et al., 2005). At the end of the 20th century, a wide range of forest plantations was established in this area under policies such as the "Grain for Green" Project and the "Sand Control Program" (Cao, 2011), with larch (*Larix principis-rupprechtii* Mayr) as the main plantation tree species. For comparisons with data from Changbai Mountain and Dongling Mountain, I used the secondary data, described below, from two forest plantation areas, Baiqi Village (41°3'N, 116°11'E) at the elevation of about 1400m asl and Shizigou Village (41°13'N, 115°23'E) at about 1650m asl, each containing 4 sampling plots. Apart from one site in Shizigou which is a poplar (*Populus tomentosa* Carr) plantation, all sites are larch plantations. The annual mean temperature at Baiqi is 4-6°C, with an average annual precipitation of 515mm, whereas the annual mean temperature at Shizigou is 2-4°C, with precipitation of less than 500mm (Wang, 2010).

2.2. Research design

The primary forest at CNR provides ideal conditions to study the biodiversity status of insects in a pristine environment. With plots established from the mountain base to its uppermost forest boundary, research in this area can provide general information of how insects are distributed along elevational gradients. As vegetation was surveyed both in 1960s and 2000s (see details in following) (Bai et al., 2011; Chen et al., 1964; Sang & Bai, 2009), it is also possible for me to investigate long-term vegetation changes in the study area and to model how these changes reflect the long-term change of insect biodiversity. The secondary and plantation forest mosaics at DLM, in addition, provide an opportunity to generate a basic overview of how insect diversity differs between different forest habitats, also providing a reference for comparisons with the primary forests in CNR. Details of the research design are introduced in the following paragraphs.

At the CNR, scientists of the Institute of Botany, Chinese Academy of Sciences (IB-CAS) established a set of 68 study plots in the research area and conducted detailed vegetation surveys (method of vegetation survey can be found in 2.5) and recording of a baseline of environmental parameters in 1963 (Chen et al., 1964). These initial surveys were repeated in 2006, when 60 plots were revisited by scientists from the IB-CAS to investigate vegetation changes over the last four decades in relation to climate and environmental change (Bai et al., 2011; Sang & Bai, 2009). I used these data sets to establish models describing the insect diversity patterns in relation to vegetation and environmental factors. This study used 27 plots that had been surveyed by IB-CAS, and which were located at the four main forest types. Plots were found according to the GPS location and the guidance from staff of the CNR Management Centre who also participated in the vegetation surveys of 2006. In addition, I selected three plots in a habitat strongly dominated by Korean pine (*Pinus koraiensis*) between 1000m and 1100m. This forest type was contained in the MCBF by previous studies (Chen et al., 1964), but here is referred to as Korea Pine Forest (KPF). In addition, one plot was added in the MCF forest. In the upper-most birch forest, 2 additional plots were also added resulting in 5 plots established in this forest. The 33 sampling plots investigated in this study were distributed across the five different forest zones with increasing elevation from 770m to 2000m as follows: 11 plots in MCBF, 3 plots in KPF, 6 plots in MCF, 8 plots in SMCF and 5 plots in BF (Figure 11, Table 1). The closest distance between two plots was 60m, which is regarded sufficient to avoid light influencing neighbouring sites (Truxa & Fiedler, 2012).

In DLM, the main sampling was conducted at areas surrounding at elevations ranging from 1100m to 1500m asl the Beijing Forest Ecosystem Research Station (BFERS) of the Chinese Academy of Sciences. In this study area, a total of 12 sampling plots were selected covering the typical secondary forest habitats types, with four plots each located in oak, mixed broad-leaf forests and birch forests, and 8 plots with four each located in pine and larch plantations, respectively (Figure 12b). In addition, 4 plots were located at an elevation of about 900m, and 12 plots were situated between 1450 and 1700 (Figure 12a). Apart from four plots at 1700m were in the birch forest, all additional plots were located in oak forest or oak woodland. In this area, I was also in charge of vegetation survey, but was helped with plant identification from botanists of IB-CAS (see also 2.5).

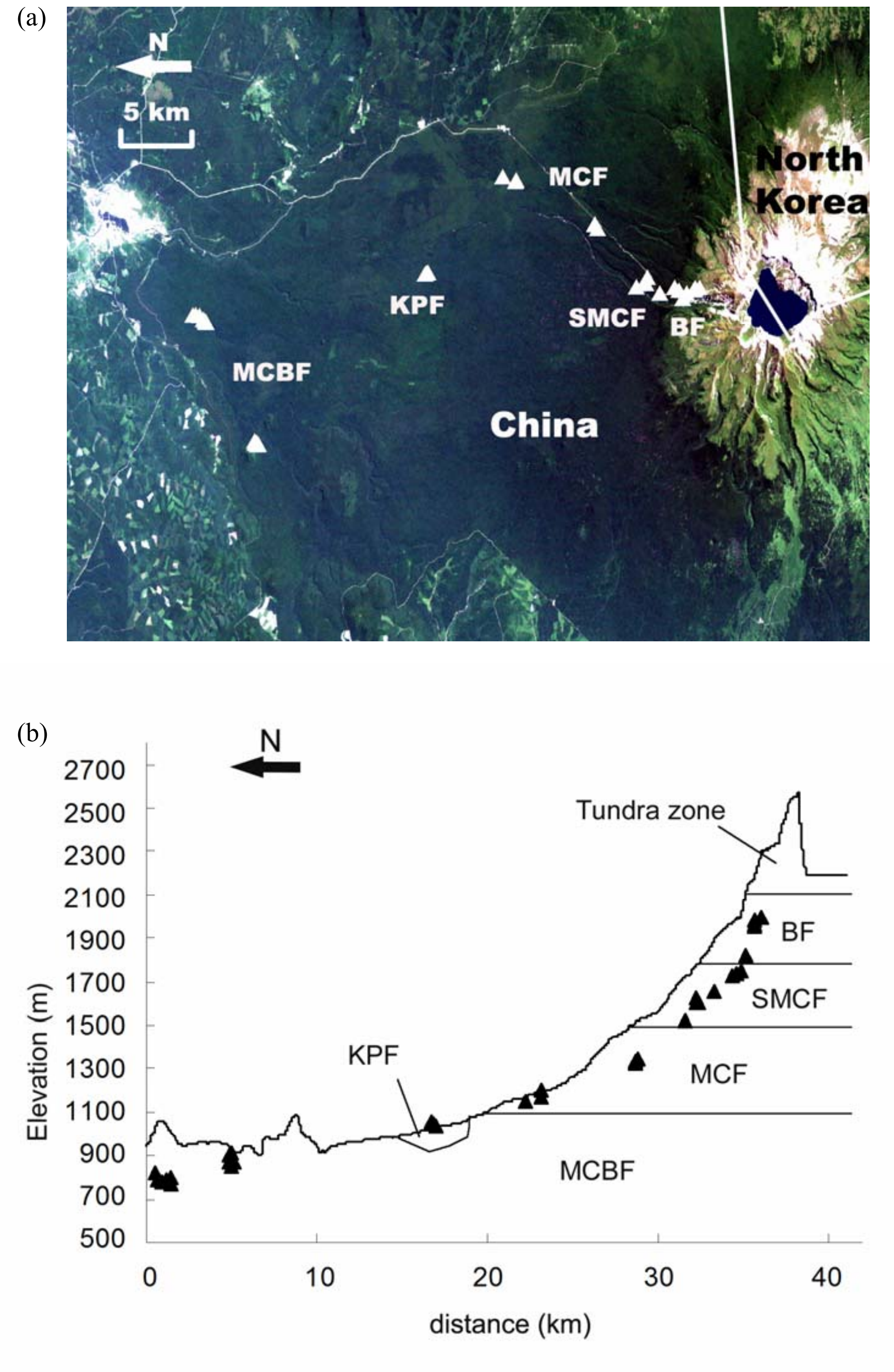

Figure 11 Satellite image of the study area at CNR with my sampling plots marked as white triangles (a) and schematic vertical cross-section of the study transect with distinct vegetation zones (b) (MCBF: mixed coniferous and broad-leaved forest; KPF: Korean Pine Forest; MCF: mixed coniferous forest; SMCF: sub-alpine mixed coniferous forest; BF: birch forest).

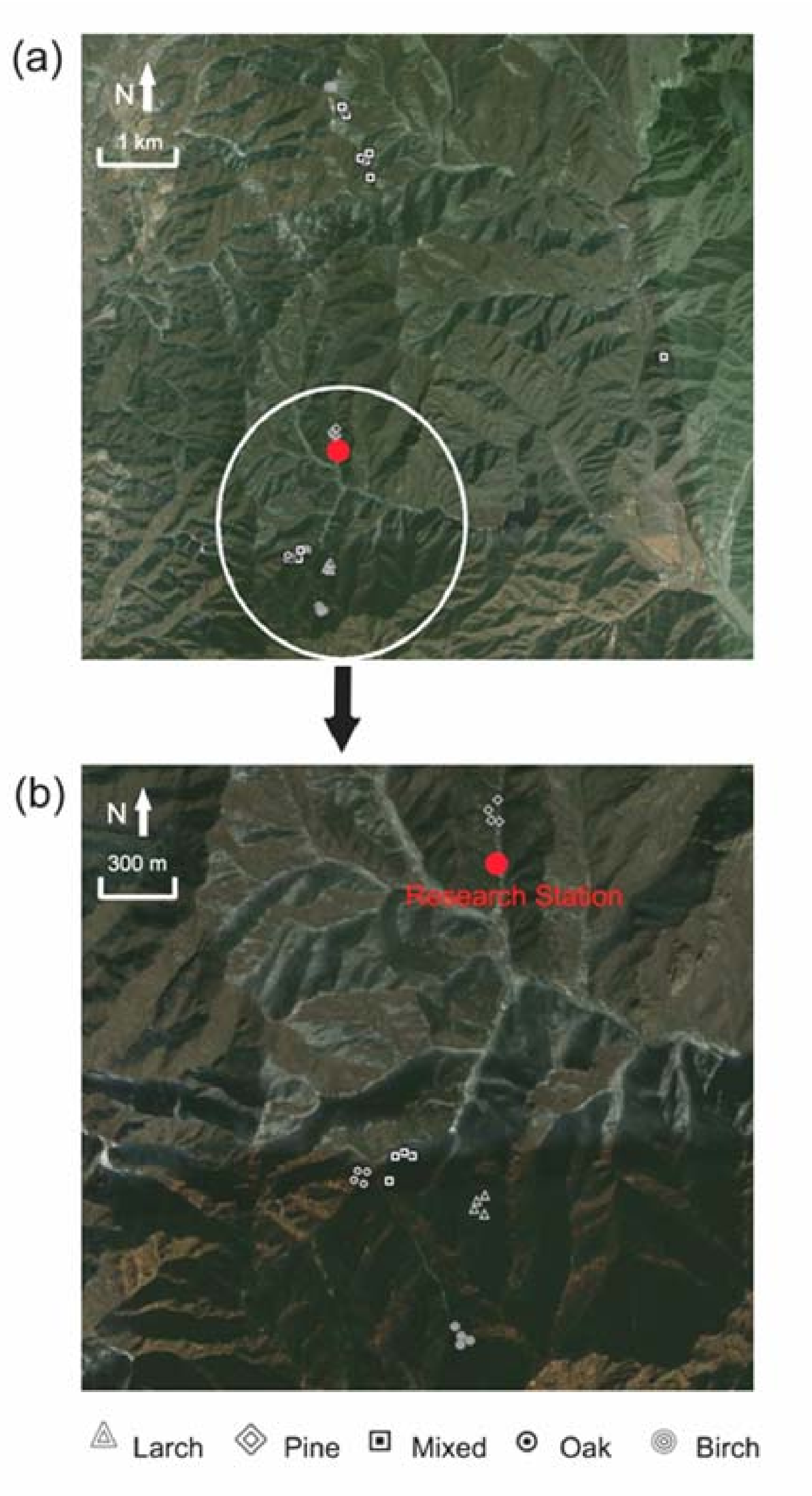

Figure 12 Satellite image of the study area at DLM; (a) shows all sampling plots and (b) shows the main sampling area

2.3. **Sampling plot design**

A total of 33 plots were selected in CNR; each study plot had a size of 20×20m^2 and was divided equally into four subplots. In the centre of each sub-plot, a pitfall trap was placed, and the light trap was located in the middle the study plot (Figure 13). Pitfall sampling was conducted on all plots, while light sampling was conducted on 25 of the 33 plots, excluding the most remote sites that were difficult and potentially dangerous to reach and work at night (Table 1). As the snow within the birch forest does not melt until mid-June and most of the forest areas are closed off due to fire precautions from late August, pitfall trap sampling was carried out from early July to early August in 2011, and from late June to late August in 2012, with empty-refill trap of ten days. Hence, typical autumnal carabids are potentially underrepresented in the samples. Nonetheless, the sampling period was standardized for the entire transect, so that this bias will have similar effects on all samples. Light trap sampling was carried out in July and August in 2011 and in June in 2012.

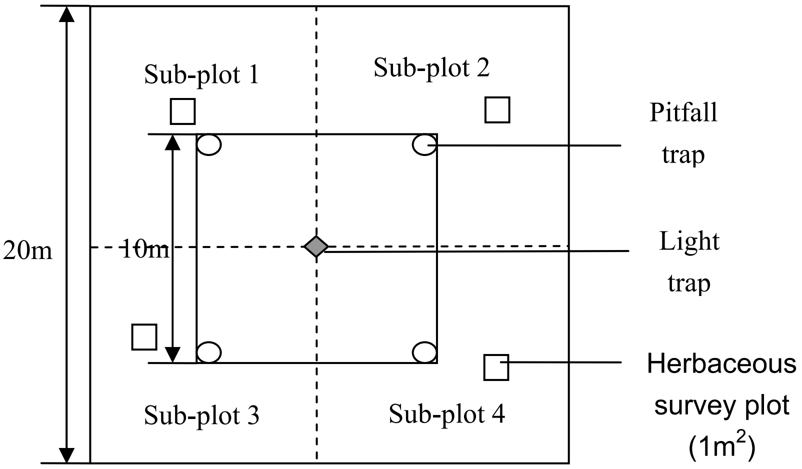

Figure 13 Sketch of the sampling design used in the CNR.

Table 1 Sampling methods and information of each plot in CNR, where "+" represents the use of a specific sampling method

Plot No.	**Forest types**	**Altitude (m)**	**Pitfall trap**	**Light trap**	**Window trap**
1	MCBF	770	+	-	-
2	MCBF	780	+	+	-
3	MCBF	790	+	+	-
4	MCBF	790	+	+	-
5	MCBF	800	+	-	-
6	MCBF	820	+	+	+
7	MCBF	850	+	+	-
8	MCBF	870	+	+	-
9	MCBF	870	+	+	-
10	MCBF	900	+	-	-
11	MCBF	910	+	+	+
12	KPF	1040	+	+	-
13	KPF	1050	+	+	+
14	KPF	1060	+	+	-
15	MCF	1150	+	+	+
16	MCF	1170	+	+	-
17	MCF	1200	+	+	-
18	MCF	1330	+	+	-
19	MCF	1340	+	+	-
20	MCF	1350	+	+	-
21	SMCF	1520	+	+	-
22	SMCF	1600	+	+	-
23	SMCF	1600	+	+	-
24	SMCF	1620	+	+	-
25	SMCF	1660	+	-	+
26	SMCF	1730	+	-	-
27	SMCF	1740	+	+	-
28	SMCF	1750	+	-	-
29	BF	1820	+	+	-
30	BF	1950	+	+	+
31	BF	2000	+	+	-
32	BF	1990	+	-	-
33	BF	1960	+	-	-

Study plots also measured 20×20m^2 in DLM, while two pitfall traps separated by a 2m distance of apart and a light trap were located in the middle of the plot (traps in some plots were not exactly in the middle due to terrain situation). Pitfall sampling was carried out on all plots, while light trapping was only conducted on the 20 plots in the main study area surrounding BFERS (Table 2). Carabids were sampled over ten weeks between June and August in 2011 for all plots, and over thirteen weeks between June and September in 2012 for the 20 main plots, again with ten days interval collecting and refilling traps; moths were sampled between June and August in 2011.

Table 2 Sampling methods and further information on vegetation type and altitude for each plot in DLM, where "+" represents the use of a specific sampling method

Plot No.	Plot info.	Forest types	Altitude (m)	Pitfall trap	Light trap
1	Main plot	Larch	1280	+	+
2	Main plot	Larch	1290	+	+
3	Main plot	Larch	1290	+	+
4	Main plot	Larch	1265	+	+
5	Main plot	Pine	1165	+	+
6	Main plot	Pine	1160	+	+
7	Main plot	Pine	1170	+	+
8	Main plot	Pine	1180	+	+
9	Main plot	Mixed	1220	+	+
10	Main plot	Mixed	1230	+	+
11	Main plot	Mixed	1220	+	+
12	Main plot	Mixed	1250	+	+
13	Main plot	Oak	1280	+	+
14	Main plot	Oak	1260	+	+
15	Main plot	Oak	1260	+	+
16	Main plot	Oak	1260	+	+
17	Main plot	Birch	1390	+	+
18	Main plot	Birch	1400	+	+
19	Main plot	Birch	1410	+	+
20	Main plot	Birch	1410	+	+
21	Additional Plot	Oak	905	+	-
22	Additional Plot	Oak	910	+	-
23	Additional Plot	Oak	930	+	-
24	Additional Plot	Oak	925	+	-
25	Additional Plot	Oak	1460	+	-
26	Additional Plot	Oak	1500	+	-
27	Additional Plot	Oak	1530	+	-
28	Additional Plot	Oak	1500	+	-
29	Additional Plot	Oak	1600	+	-
30	Additional Plot	Oak	1580	+	-
31	Additional Plot	Oak	1610	+	-
32	Additional Plot	Oak	1615	+	-
33	Additional Plot	Birch	1700	+	-
34	Additional Plot	Birch	1700	+	-
35	Additional Plot	Birch	1700	+	-
36	Additional Plot	Birch	1700	+	-

2.4. Sampling methods for carabids and geometrids[1]

2.4.1. *Pitfall trapping*

Surface-dwelling carabids can be sampled using cost-effective pitfall trapping. A pitfall trap consists of a container buried in the ground with its rim at surface level, and often with a roof above the trap to limit evaporation and dilution of the killing liquid in the container by rain water. The container can have different size, with materials also ranging from glass and plastic to metal (Greenslade, 1964; Luff, 1975; Oliver & Beattie, 1996). In sampling carabids, liquids to kill the samples and preserve them are commonly added to the container. These are usually covering the bottom of the container, ensuring that the specimens are easier to identify after prolonged sampling periods and limiting their chances to escape (Pekar, 2002). Solutions can be water, saturated salty water, diluted formaldehyde, ethylene glycol, benzoic acid and alcohol. In water-based solutions, a little detergent is often added to lower the surface tension and prevent samples from floating on the surface (Gullan & Cranston, 2005). The capture results of pitfall traps are affected by the design of the traps (Woodcock, 2005). For example, small traps are more efficient in catching small beetles (Luff, 1975); round traps catch more carabids than rectangular ones (Spence & Niemelä, 1994); glass traps are more capture-effective as compared to plastic and metal traps (Luff, 1975) and traps without covers are more effective than those with covers (Spence & Niemelä, 1994).

Pitfall trapping was the main sampling method used for the collection of carabids in this study. Plastic cups with an open diameter of 7.5cm and a volume of 250ml were used as pitfall traps. Although glass cups can potentially catch more specimens (Luff, 1975), plastic cups were selected because they are cost-effective, light and robust and hence easy to carry and extremely solid when buried in soil in forests for several

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[1] Part of this information has been published in Zou et al. (2012). In this paper, I was the main, lead author, with the other authors mainly commenting on the manuscript I had prepared and edited some of the grammar.

months. An aluminium roof of 10x10cm^2 was placed about 10cm above the cup (Figure 14). As the study area experiences high levels of precipitation during the sampling period, the roof was seen as essential to protect the killing solution from dilution by rain and litter contamination. Saturated salt-water solution, which is very cost-effective and minimizes attractant bias (Kotze et al., 2011), was used as the solution for killing and preserving specimens in the traps.

Figure 14 Pitfall trap with aluminium roof

2.4.2. Leaf litter collection

Leaf litter collecting is mainly used to sample microarthropods and small ground beetles. In this approach, the complete litter layer on top of the mineral soil is normally collected over a standardized area. Leaf litter arthropods can then be extracted with Berlese-Tullgren funnels (Crossley & Hoglund, 1962) or with litter-washing, where specimens appear on the water surface when litter is positioned in a water-filled tray (Spence & Niemelä, 1994). This is a very inexpensive method, but often relatively destructive as large amounts of litter are often required to sample sufficient numbers of specimens, which is also highly time consuming. Leaf litter washing requires dealing with the samples quickly to avoid the death of specimen. Leaf litter sampling can form a good composite technique with pitfall trapping, as specimen with small body size rarely appear in the latter (Olson, 1991; Spence & Niemelä, 1994). In this study, I collected 0.25x0.25m^2 leaf litter samples which were washed to sample small carabids, but for the first attempts based on 26 plots at DLM, only a single individual was found in all combined samples. In CNR, similarly, the first attempt from 9 plots with 0.25x0.25m^2 leave litter samples yielded not a single specimen. While an extension of the overall sample area might yield better results, the very low sample efficiency suggests that this method is very labour-intensive and was hence not followed through in the context of this study.

2.4.3. Window trapping

A window trap is a type of flight interception trap based on similar principles to a Malaise trap (Malaise, 1937). The construction of a window trap includes a pane of glass, perspex, silk or fine mesh which is considered invisible to the target arthropods. This pane or net is located in the centre of a suspected flight path as a barrier for arthropods using this path, and a container or gutter filled with liquid preservatives is placed beneath the net (Figure 15). Flying arthropods are collected once they fall into the preserving liquid after hitting the barrier. A roof is added on the top if the trap needs to resist rain.

Window trapping is an easily standardized, replicable sampling method and can capture large quantities of flying arthropods (Bouget et al., 2008). Small-scale diversity patterns are not always well reflected in samples from window traps, though, (Jonsson et al., 1986). The efficiency of window traps is also affected by the material of the barrier, with large beetles flying at high speed potentially bouncing off hard barriers without falling into the sampling containers below (Boiteau, 2000). The exact shape, silhouette and height of the barrier also has a strong influence on sampling efficiency (Bouget et al., 2008), as has the exact placement of the trap. Disadvantages of window traps include that they catch only flying arthropods; they are relatively expensive per unit especially in traps using hard barriers, can be easily damaged by high winds, have a relatively small flight interception area, and often suffer additional problems relating to the efficient installation and sample retrieval, and logistical problems can occur when sampling is to occur in the forest canopy (Bouget et al., 2008; Carrel, 2002; Gullan & Cranston, 2005; Peck & Davies, 1980).

In this study, window trapping was carried out using black silk mesh as the barrier. As the traps yielded extremely large amounts of beetles (more than 1000 individuals each time) but very low abundances of ground beetles (<<1% of the caught specimens), they were unsuitable for a robust analysis of carabids, and window trap results were not included in the analysis.

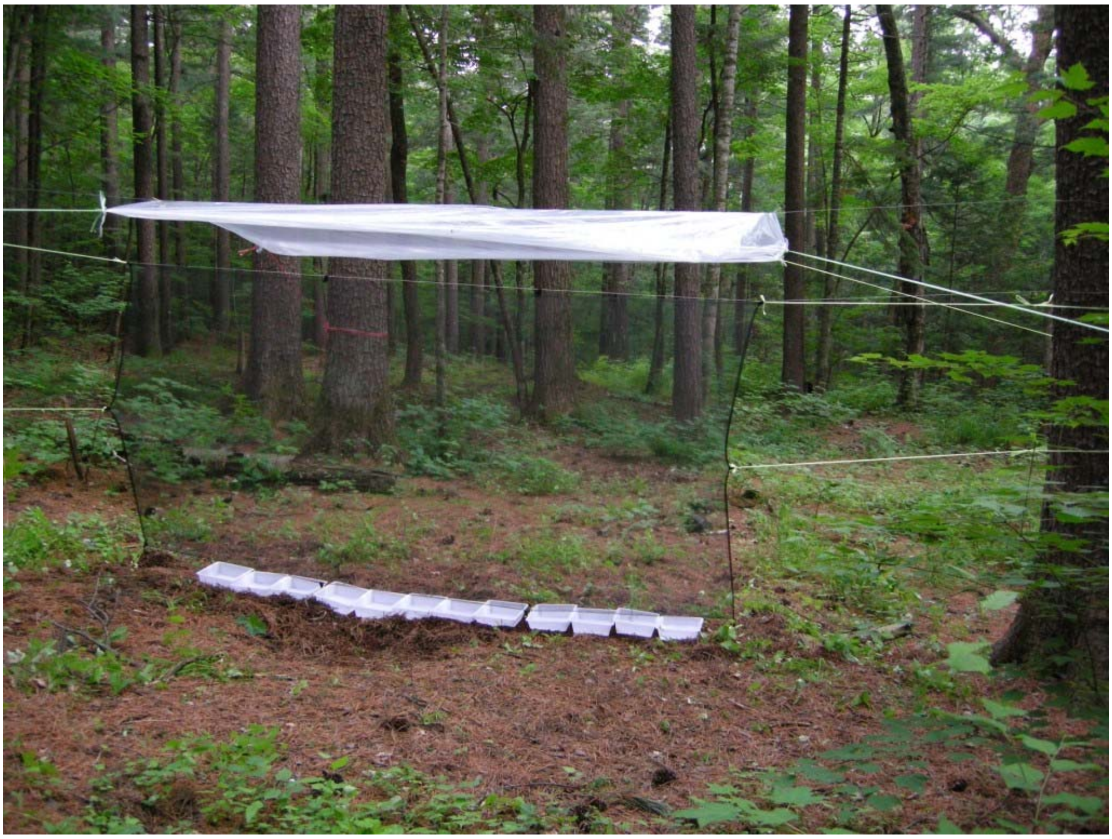

Figure 15 Window trap using black silk mesh of 1.5m x 3m with a plastic roof

2.4.4. Light trapping

The majority of moths are night-flying and are easily attracted by artificial light sources (Axmacher & Fiedler, 2004; Nag & Nath, 1991). Light traps are highly effective and can preserve specimens in relatively good condition, which is very important for sampling many of the relatively frail geometrid specimens. Light traps are often relatively expensive and not very robust sampling devices which can nonetheless collect large numbers of specimens (Basset et al., 1997; Liu et al., 2007b). Light sources vary greatly, ranging from gas lamps to mercury vapour lamps and fluorescent UV light tubes, and collection of samples can either be manual or automatically (Brehm & Axmacher, 2006). There are two basic types of light trapping devices: "light towers" or more basic devices such as white sheets spread behind light sources which are suitable for selective, manual collection, and automatic light traps. In the case of light towers, insects are collected in a jar equipped with a chemical to stun and kill the specimens after they land on the surface of the light tower.

Automatic light traps were used at both, CNR and DLM, while manual collections were additionally used as complementary to automatic light trapping in DLM. The light trap used in this study consisted of a 12V, 20W UV mercury light tube with a length of 60cm, a metal cover, three glass vanes and a collection box underneath containing the battery powering the device (Figure 16). Moths were attracted to the light, hit the glass vanes and then slipped through a metal funnel into the collection box. A plastic sheet was used to wrap up the trap when it was being carried through the forest to prevent damage from undergrowth. This plastic sheet was opened to the bottom of the trap during sampling, and the sheet was pulled around the trap again when sampling was completed, when moths staying on the outside of the trap and on this plastic sheet were also collected. A piece of chloroform-dipped tissue was dropped inside the trap to stun specimens.

Figure 16 Light trap used in this study.

2.5. Treatment and identification of insect specimens

All beetles were preserved in 75% alcohol after collecting and all ground beetles were subsequently pinned. Moths were kept in a -24°C freezer after collection before they were pinned. The main insect collections are kept in the Institute of Zoology, Chinese Academy of Sciences (IZ-CAS), Beijing, and identification of both, carabids and geometrids, was aided by the taxonomic experts from this institute. In addition, geometrids materials were also send to Canadian Centre for DNA Barcoding (CCDB) identification. As yet results from barcoding have not come out, all analysis was then based on identification results from IZ-CAS.

2.6. Vegetation survey

In CNR, raw vegetation data were obtained from IB-CAS, for the 27 plots that had previously been surveyed by the institute (Bai et al., 2011; Sang & Bai, 2009). Vegetation surveys for newly added plots were based on the same sampling methods used in the earlier sampling. Hence, all vegetation-related data in CNR in the following chapters refers to a combination of secondary data collected in 2006 and my own surveys. The new study plots were positioned at random locations. Plants were separated into three layers: tree layer or canopy layer including all trees with a height extending 2m; shrub layer including trees with a height between 0.4m and 2m and shrubs with a height extending 0.4m and the herb layer or understory/undergrowth layer, which included all woody plant species with the height of less than 0.4m and all herbaceous species. Species in tree and shrub layers were recorded in each of the four 10m×10 m sub-plots, while herbaceous species were recorded in four plots of $1m^2$ that were randomly located within the sub-plots (Figure 13). In CNR, the breast height of each tree specimen was measured and the abundance and average height of each shrub and herb species were recorded, with plant species identified by botanists from IB-CAS and the CNR management centre. At DLM, only the average % cover for each species was recorded, and plants were identified with the help of botanists from IB-CAS.

2.7. Data analysis

Fisher's α value was calculated measuring α-diversity of carabids and geometrids; several species richness estimators were used to analysis the sampling completeness. Chord-normalized expected species shared (CNESS) dissimilarity matrices was used for analysis the β-diversity of insects, and 'Jaccard' dissimilarity matrices was used for plants. Stepwise linear regression was used to analysis the relationship between plant variables and insect α-diversity. Multivariate analysis was used to investigate relationship between plant and insect compositions. Rarefactions were used to compare the diversity status among different forests and areas. Details of specific approaches to data analysis used to address the different research questions are outlined in each individual respective chapter (see chapters 3-7).

Chapter 3. Altitudinal diversity patterns of ground beetles and geometrid moth in the forests of Changbai Mountain[1]

Summary

This chapter focused on the α- and β-diversity patterns of ground beetles and geometrids at Changbai Mountain. Ground beetles were sampled on 33 plots and geometrid moths on 25 plots distributed across the five main distinct mature forest ecosystems occurring at altitudes between 700m and 2000m on Changbai Mountain. Pitfall trapping yielded a total of 4834 ground beetles representing 47 species, while light traps yielded 9285 geometrid moths representing 155 species. The abundance of both carabids and geometrids increased with increasing elevation while α-diversity decreased. For both taxa, no significant correlation was observed between the abundance of common species and their altitudinal distribution. Insect assemblages originating from the high elevation forest types formed a partly overlapping cluster, while assemblages at lower elevations were more strongly differentiated according to forest type, again a trend clearly apparent in both taxa. Results support the assumption that both carabids and geometrids are highly sensitive to climate change. The Korean pine-dominated forest, which has not previously been distinguished as a discrete forest type, showed a distinct species composition for both taxa, indicating its requirement of specific conservation attention.

3.1. Introduction

Species diversity and distribution patterns show clear altitudinal patterns (Brehm et al., 2007; Herzog et al., 2005; Lomolino, 2008; Rahbek, 1995, 2005). As altitudinal changes are closely linked to changes in a wide range of environmental parameters such as temperature and precipitation, species diversity patterns along elevational gradients may also provide important insights into the possible effects of climate

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[1] The main results have been published in Zou, et al., 2013b, where I was the lead author and did the analysis and wrote the main content.

change on biotic communities (Moritz et al., 2008; Parmesan, 2006; Wilson et al., 2007).

In general, along increasing altitude, four diversity patterns have been proposed: a continuous decline, a hump-shaped distribution with a distinct mid-elevation peak, a diversity plateau and a general increase in diversity (García-López et al., 2011; McCain & Grytnes, 2010). A monotonic decrease and a hump-shaped response are two most commonly observed patterns. A monotonic decrease can be explained by the Productivity Hypothesis (Chase & Leibold, 2002; Currie, 1991; Fargione et al., 2007; Mittelbach et al., 2001; Rahbek, 1995; Roy, 2001), the Harsh Environment Hypothesis (Rapoport, 1982; Stevens, 1989, 1992), the Resource Diversity Hypothesis (Price, 1984) and the Species-Area Hypothesis (Rosenzweig, 1995). Explanation of a hump-shaped distribution include climatic models combining temperature and precipitation (Brown, 2001; Rahbek, 1995) and the mid-domain effect (MDE) (Colwell & Lees, 2000; Colwell et al., 2004; Dunn et al., 2007; Hawkins et al., 2005; McClain et al., 2007). More details of the above-mentioned hypotheses can be found in Chapter 1.

Globally, the elevational distribution patterns of geometrid moth diversity has been studied in Southeast Asia (Beck & Chey, 2008), America (Brehm et al., 2003b), Africa (Axmacher et al., 2004a) and North China (Axmacher et al., 2011; Chen et al., 2007; Liu et al., 2007a). Results of these studies are mixed, with a monotone decrease (Chen et al., 2007; Liu et al., 2007a), hump-shaped distributions (Beck & Chey, 2008) and other, more complicated distribution patterns (Axmacher et al., 2004a; Axmacher et al., 2011; Brehm et al., 2003b) becoming evident. In comparison to primarily phytophagous insect groups whose distribution is partly restricted by the distribution of their potential host plant species (Warren et al., 2001), the distribution of predatory insects such as many ground beetle species is even more variable (Axmacher et al., 2011; Greenslade, 1968; Olson, 1994; Skalski et al., 2011). Nonetheless, the dispersal abilities of many ground beetle species is limited due to their lack of flight ability

(Lamoreux, 2004; Larochelle, 1990). Their elevational diversity patterns furthermore appear to be inconsistent, with also both a general decrease and mid-elevation-peaks in carabid species richness with increasing altitude being reported along elevational gradients (Greenslade, 1968; Skalski et al., 2011). Other studies support more complex patterns (Olson, 1994) or no significant changes in carabid α diversity in response to altitudinal changes (Axmacher et al., 2011).

Information on insect distribution patterns along elevational level in primary temperate forest is crucial in assessing how well the substantial reforested areas in temperate China serve in providing habitat for a proportion of China's highly diverse temperate insect taxa and their associated ecosystem services. The investigations into the diversity of ground beetles and geometrid moth of pristine forest ecosystems on Changbai Mountain allow unique insights in this respect. Given the very high levels of plant species richness in China's temperate forests (Chen et al., 1997; Chinese State Forestry Bureau, 2011; Qian & Ricklefs, 2000) and the associated habitat complexity, it is expected that both carabid and geometrid assemblages will be highly diverse in this area. The species richness plants on Changbai Mountain has previously been reported to decrease with increasing elevation (Hao & Yang, 2002) potentially in response to a general decrease in ambient temperature. It is therefore hypothesised that the diversity of these two taxa in these forests will also decrease with increasing elevation. Furthermore, species occupying a wide ecological niche often occur at high local abundance (Brown, 1984), and it was hypothesised accordingly that overall abundance and altitudinal range of individual species are positively correlated, with altitudinal generalists also being the most abundant species. The final postulation of this chapter is that the distinct altitudinal zonation of the vegetation in the Changbai Mountain forests is mirrored by parallel shifts in the insect species composition.

3.2. Method and data analysis

A total of 33 sampling plots were selected between 700m and 2000m at Changbaishan Natural Reserve (CNR) representing the five main forest types with increasing elevation: mixed coniferous and broad-leaved forest (MCBF) between 700m and 1000m, Korean Pine Forest (KPF) between 1000m-1100m, mixed coniferous forest (MCF) between 1100m and 1500m, sub-alpine mixed coniferous forest (SMCF) between 1500m and 1800m and birch forest (BF) between 1800m and 2000m. Carabids were sampled using pitfall traps at all sampling plots, while geometrids were sampled using light traps at a subset of 25 sampling plots. Pitfall trap sampling was carried out from early July to early August in 2011, and from late June to late August in 2012; light trap sampling was carried out in July and August in 2011 and in June in 2012. More details of study area and sampling design can be found in Chapter 2.

The abundance of all insect species for each plot over the entire sampling period were pooled to have large-enough sample sizes for robust statistical analyses as well as to avoid a strong influence of inter-annual variations on results. Elevational ranges for each species were established as the difference between the maximum and minimum elevations where the species was recorded. Only common species (i.e. ≥ 25 individuals) were considered for the analysis. Elevational ranges of rare species are subject to large uncertainty in range size.

Fisher's α (see Appendix 1, equation 5) was used as a measure of α-diversity, as this index is widely independent from sample size variations and has been commonly used in studies of insect α-diversity patterns (Axmacher et al., 2009; Axmacher et al., 2004b; Brehm et al., 2003b). To check the robustness of the Fisher's α patterns, rarefied species numbers (see Appendix 1, equation 1) (Hurlbert, 1971) were calculated as a further measure suitable to compare species richness for samples of highly variable sizes (Axmacher et al., 2004a; Axmacher et al., 2004b; Brehm et al., 2003b; Liu et al., 2012; Liu et al., 2006). In addition, the mean of the species richness estimators Abundance-based Coverage Estimator (ACE) (Appendix 1, equation) and Chao1 (see Appendix 1, equation 6) was used to estimate of the true species richness in each forest type. These two estimators were chosen because grain sizes vary in my samples, while both ACE and Chao1 are relatively independent from grain size

(Hortal et al., 2006). As sample sizes were too small for a meaningful calculation of diversity estimators generated for individual plots, only Fisher's α was used to analyse values of individual plots. In the analysis of abundance-elevation relationship, activity abundance was used. Due to differences in sampling intensity, activity abundance in this case refers to mean catches per trapping day (number of individuals/catching days) for both carabids and geometrids.

For the analysis of species turnover patterns between plots (β-diversity), chord-normalized expected species shared (CNESS) dissimilarity matrices (Trueblood et al., 1994) was calculated (see Appendix 1, equation 9). The CNESS matrices can be calculated for different sample sizes via changes of the sample size parameter m. The resulting matrix either puts a strong focus on dominant species when low numbers are selected (extreme: m=1) or on rarer species for large numbers of m. The matrix for m=1 as well as for m=number of individuals in the least well-sampled plot (m=47 for carabids and 87 for geometrids) as the largest common sample size were calculated. Non-metric multidimensional scaling (NMDS) of the CNESS matrices was subsequently used to visualize the species turnover patterns between different forest plots and types.

Species estimator richness was calculated using the software EstimateS (Colwell, 2013) and CNESS matrices were calculated by the programme COMPAH (Gallagher, 1998). All other calculations and statistics were carried out in R language (R Development Core Team, 2011) with the use of 'vegan' package (Oksanen et al., 2012).

3.3. Results

3.3.1. Species compositions

In total, 4834 ground beetles representing 47 species were caught (see Appendix 2) in summer of 2011 and 2012. Among the 47 species, 34 of them were identified to species level, which represented 91.2% of all sampled specimens. The remaining 13 morphospecies were all formally identified to genus level. The most dominant species in the study area belonged to the genera *Carabus* and *Pterostichus*, with *Pterostichus comorus* Jedlicka and *Carabus aurocinctus* Motschulsky contributing 18.7% and 18.6% of all individuals, respectively, *Pt. vladivostokensis* Lafer a further 10.2% and *Pt. orientalis* Motschulsky 10.0%. When comparing different forest types, there was a clear differentiation in regard to most common species for respect forest. *Pt. vladivostokensis* and *Pt. orientalis* dominated in the MCBF below 1000m, where these two species accounted for 27.1% and 21.7% of all individuals caught, respectively. *Pt. adstrictus* Eschscholtz dominated in the KPF between 1000m and 1100m, where it accounted for 34.7% of all individuals. Above 1100m, *C. venustus* Morawitz dominated in the MCF (18.7%), *C. aurocinctus* in the SMCF (37.5%) and *Pt. comorus* in the BF (38.1%).

The light traps yielded 9285 geometrid moths, of which 1072 specimens (11.5%) were badly damaged chiefly due to strong rains occurring during some sampling nights. These specimens had to be excluded from further analysis, while the remaining 8213 individuals were divided into 155 morphospecies, of which 85 species representing 6165 individuals (75% of all specimens) were identified to species level, with a further 32 species identified to genus and 38 to subfamily level (see Appendix 3). Ennominae and Larentiinae were the most abundant subfamilies, accounting for 56.2% and 41.6% of all individuals, respectively. Each forest type again differed in relation to dominant species, but with the most common species at individual forest being generally less pronounced than in the carabid assemblages: *Abraxas suspecta* Warren was dominant in MCBF (23.0%), *Hypomecis roboraria* Denis & Schiffermüller in KPF (14.4%), *Euchristophia cumulate* Christoph in MCF (17.3%), *Hydriomena impluviata* Denis & Schiffermüller in SMCF (18.7%) and *Venusia cambrica* Curtis in BF (27.6%) assemblages.

With the exception of KPF, all forest types contained at least two species of ground beetles that were not encountered in any of the other forest types. Furthermore, all forest types had at least 5 geometrid species that were not observed in other types. In particular, MCBF had 38 "unique" geometrid species that were not encountered in samples from other habitats, while this number in other forest types only ranged from 5 to 7 species.

For the subfamily composition of geometrid moths, individuals of Ennominae dominated most plots at lower elevations, while Larentiinae became increasingly dominant at altitudes above 1600m. Sterrhinae were restricted to elevations below 1100m (Figure 17a). With increasing elevation, the proportion of individuals in both Ennominae and Geometrinae decreased (Spearman rank correlation: r=-0.75, *P*<0.001, and r=-0.68, *P*<0.001), while the proportion of Larentiinae significantly increased (r=0.82, *P*<0.001). A similar trend is visible for the number of species (Figure 17b), although the patterns are much less pronounced. Again, both the proportion of species representing Ennominae and Geometrinae decreased with increasing elevation (r=-0.45, *P*=0.02, and r=-0.62, *P*=0.001), while the proportion contributed by species representing Larentiinae increased (r=0.73, *P*<0.001). Apart from one site at 1820m where Larentiinae species dominated, Ennominae dominated the species spectra on all plots.

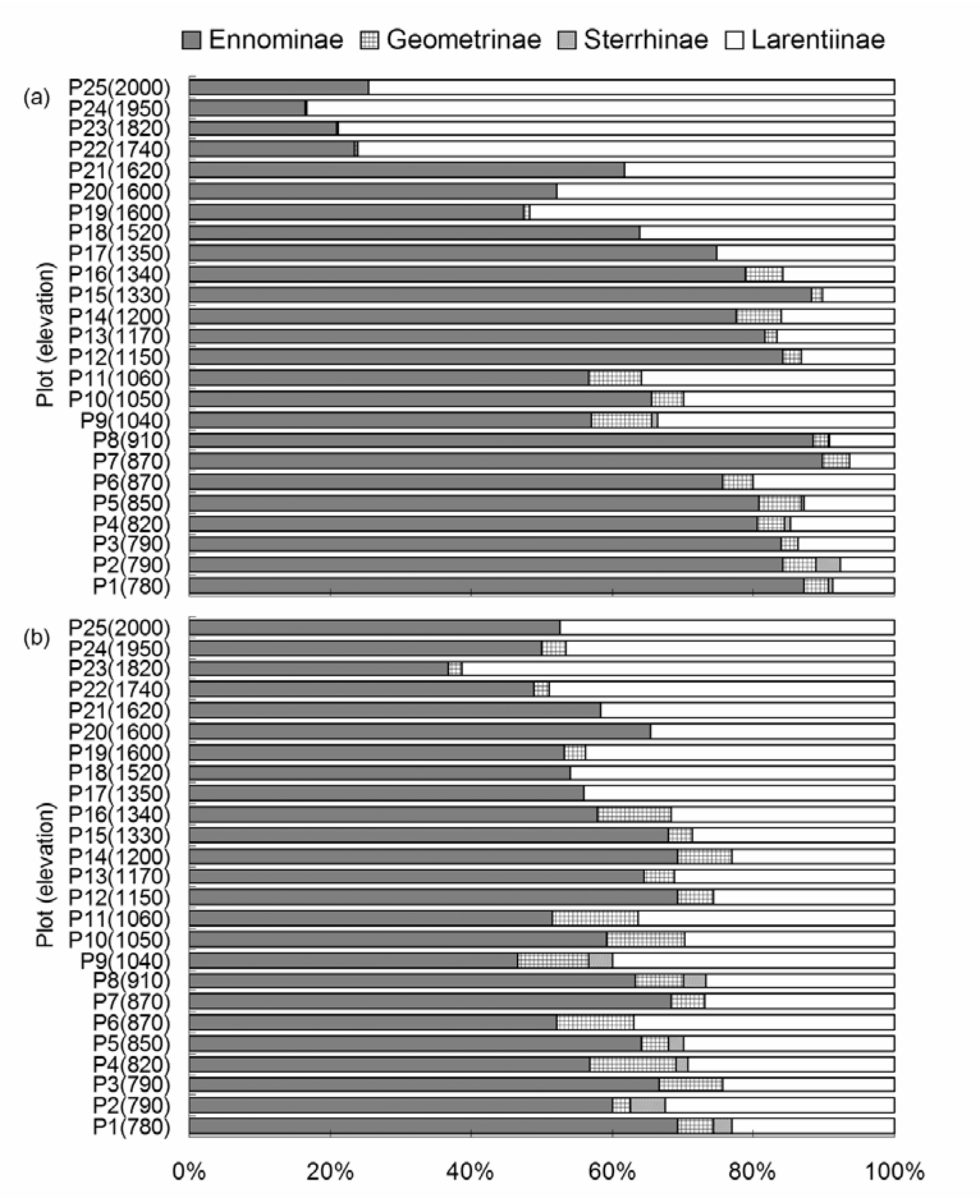

Figure 17 Subfamilies' proportion for geometrid moths of each sampling plot, plotted for the number of individuals (a) and the number of species (b)

3.3.2. Elevational distribution ranges

For carabids, the mean elevational range of the 17 species represented by more than 25 individuals each in this samples was 984m (SD=207.4m). Nonetheless, many of the common species had a much more limited distribution range, with 8 out of 17 species (47%) recorded over less than 1000m. *Carabus aurocinctus*, *C. seishinensis* Lapouge and *C. vietinghoffi* Adams were distributed over less than 700m. With one exception (480m in *Pterostichus* sp.1 for the shortest altitudinal range), all abundant *Pterostichus* spp. had relatively wide elevational distribution ranges exceeding 1100m, with three *Pt.* spp. encountered along the entire transect. No significant correlation was found between the overall abundance and the elevational distribution range of the common carabid species (Figure 18a). When the average distribution range of all common ground beetle species occurring at 100m elevational bands was investigated, the average distribution range increased initially, but then decreased again at higher elevations. It must nonetheless be taken into account that the elevational gradient only covered the section from the mountain base to 2000m, and it can be speculated that many of the species commonly encountered in the undergrowth of the light birch forest also extend further upwards into the tundra vegetation of the mountain, where both structure and composition of the herbaceous vegetation is very similar. Under the assumption that the distribution range of all species occurring in the uppermost birch forest plots extends well into the tundra zone, there is a clear linear trend of increasing distribution ranges throughout the transect (Pearson correlation: $r=0.95$, $p<0.001$, Figure 18b).

For geometrid moths, 46 species had more than 25 individuals in this sample and were hence treated as ‘common species’, with an average distribution range of 882m (SD=350m). A total of 21 out of the 46 species (45%) had the distribution range of less than 1000m. A weak positive relationship was observed between the abundance and the elevational range of common geometrid moths (Pearson correlation: $r=0.45$, $p=0.002$, Figure 18c). Again assuming an upwards extension of species occurring at the highest birch forest plots into the tundra zone, a highly significant positive linear trend was found between distribution range and an increase in elevation for geometrid moths ($r=0.97$, $p<0.001$, Figure 18d), reflecting the patterns observed in carabids.

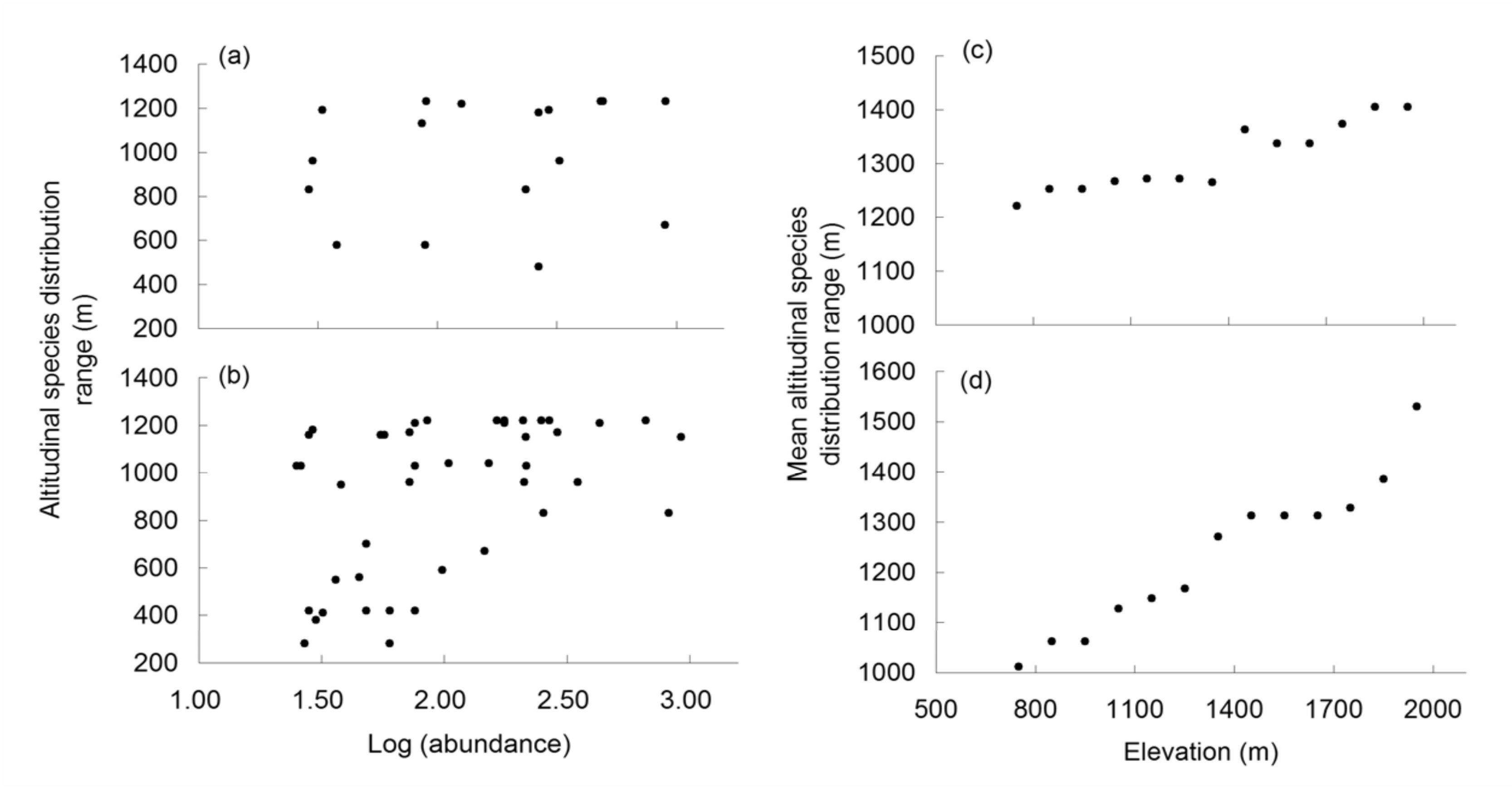

Figure 18 Comparison of mean altitudinal distribution ranges (m) of common species plotted against the log-transformed species abundance for carabid (a) and geometrid (b), and against changes in elevation for carabid (c) and geometrid (d) (Assumption for (c) and (d): species occurring at the uppermost open birch forest plots extend on average 500m into the alpine tundra vegetation).

3.3.3. Abundance and diversity change with increasing elevation

Fisher's α and rarefied species numbers for the largest common sample size (*n*=47 for carabids and *n*=87 for geometrids) were strongly correlated for both carabids and geometrid moths (Pearson correlation: r=0.92, *p*<0.001 for carabids and r=0.95, *p*<0.001 for geometrid moth), confirming the robustness and similarity of information content of these diversity measures. Accordingly, only Fisher's α was subsequently used to analyse the relationship between α-diversity and elevation. Along the entire elevational gradient, Fisher's α for both carabids (r=-0.53, *p*=0.002, see Figure 19a) and geometrids (r=-0.74, *p*<0.001, Figure 19b) strongly decreased with increasing elevation. The decrease was also observed in the two most common subfamilies, Ennominae and Larentiinae (Pearson correlation, r=-0.68, *P*<0.001, and r=-0.63, *P*<0.001, respectively, see Figure 19c and d).

The picture of activity abundance (number of individuals caught per sampling day) is different from α-diversity. Along the increasing elevation, the activity abundance of both ground beetles and geometrid moths increased significantly (,r=0.75, *p*<0.001, and r=0.52, *p*=0.008, see Figure 20)

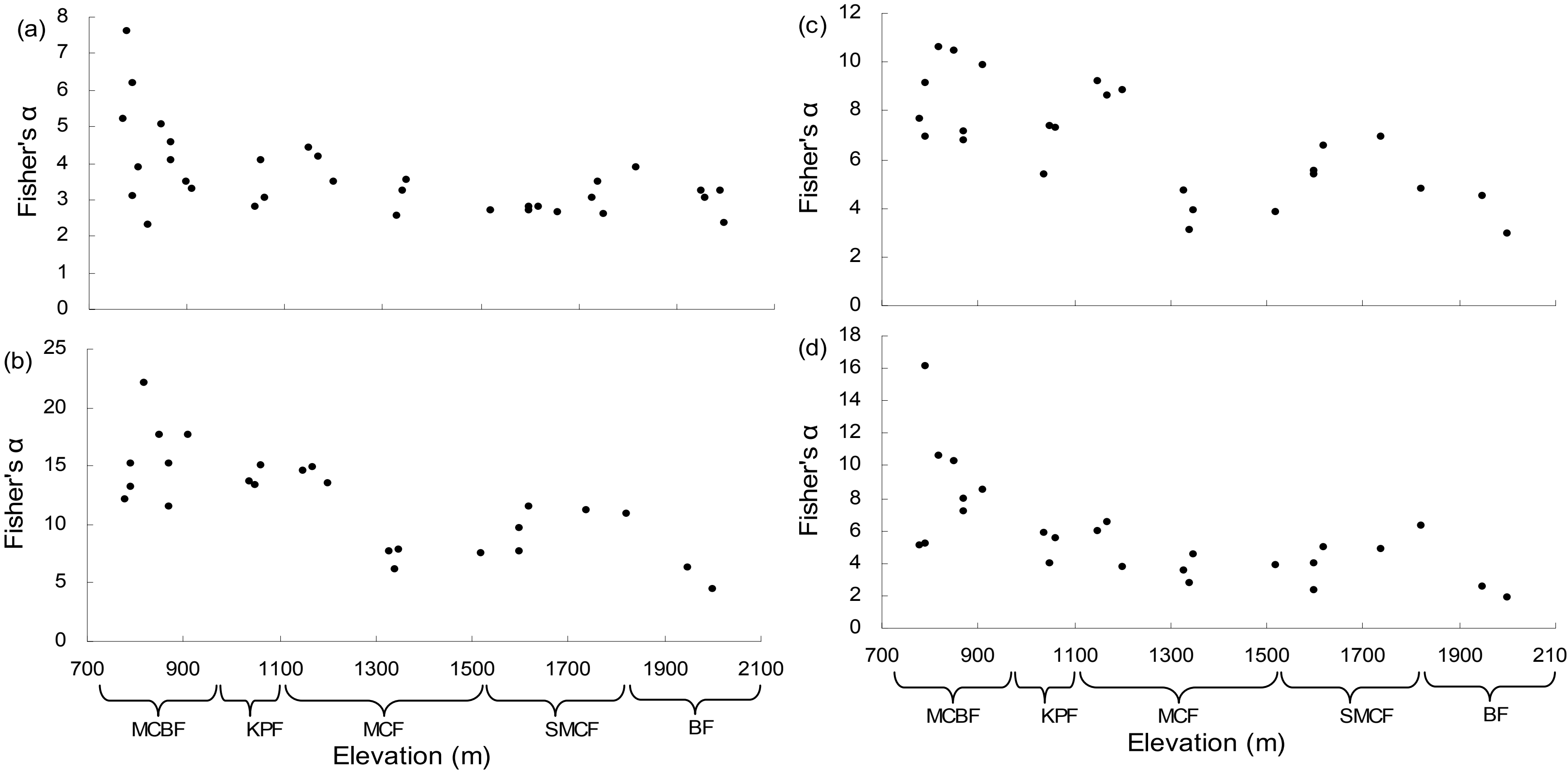

Figure 19 Changes in Fisher's α-diversity for carabids (a), geometrids (b), Ennominae (c) and Larentiinae (d) over an elevational gradient (MCBF: mixed coniferous and broad-leaved forest; KPF: Korean Pine Forest; MCF: mixed coniferous forest; SMCF: sub-alpine mixed coniferous forest; BF: birch forest).

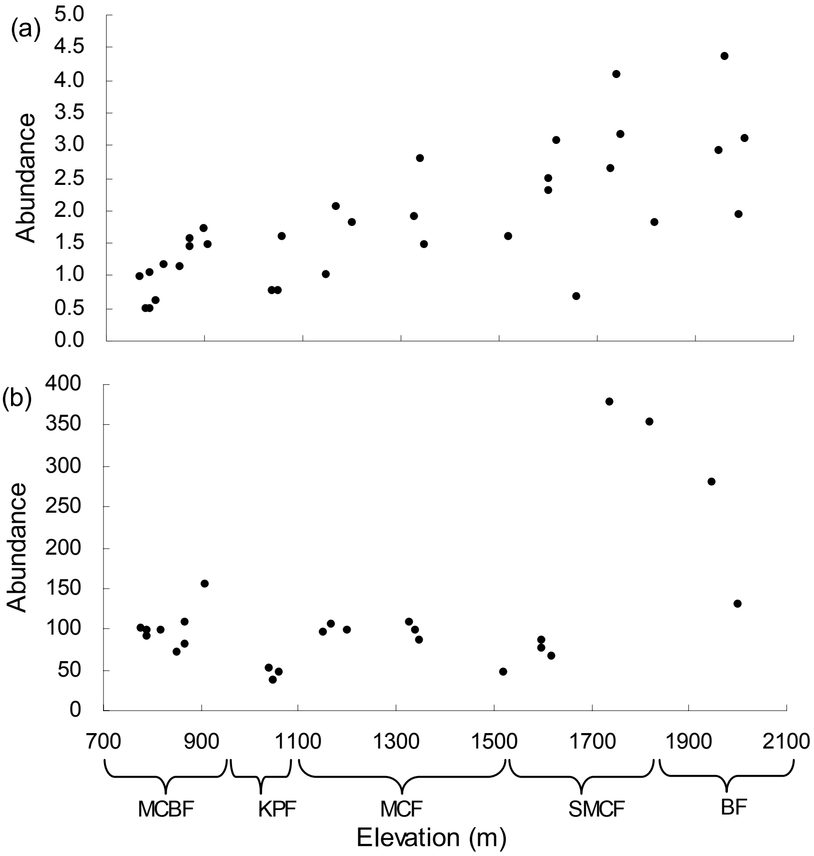

Figure 20 Changes in the activity abundance (number of individuals caught per sampling day) for carabids (a) and geometrids (b) with increasing elevation (MCBF: mixed coniferous and broad-leaved forest; KPF: Korean Pine Forest; MCF: mixed coniferous forest; SMCF: sub-alpine mixed coniferous forest; BF: birch forest)

3.3.4. Insects diversity in different forest types

Results based on the species richness estimators indicate that the mean sampling completeness of carabids in the five habitats was 87%, with an overall estimated species richness of 54 species in entire study area. In particular, samples already represent more than 85% of the expected species richness in all forests except for SMCF, where they contained 70% of the expected species (see Appendix 1). The estimated species richness is highest in the SMCF, followed closely by MCBF assemblages. MCF and BF harbour a distinctly lower diversity, while species assemblages in the KPF contain the lowest estimated species number. These trends are partly reflected in the rarefaction curves (Figure 21a), where MCF and BF species numbers appear to approach a species plateau, while no strong levelling off can be observed for MCBF and SMCF. Nonetheless, according to rarefaction results (n=771), MCBF is the most diverse forest type (27.7 spp.), while the remaining three forest types SMCF, BF and MCF all had similar rarefied species numbers (20.0-20.4 spp).

The overall sampling completeness for geometrids was 84%, with an overall estimated 185 species occurring in the sampling area. Sampling completeness in all forests exceeded 80% with the exception of BF with 77% (Appendix 3). According to the estimators, species richness was highest in MCBF, followed by MCF, SMCF and BF. Trends again were clearly consistent with rarefaction curves (Figure 21b). Excluding KPF due to the small sample size, rarefaction for the maximum common sample size (n=1327) of the remaining forest types showed highest species richness in the low elevation MCBF (95.9 spp.) and then decreased with the increase in elevation (76 spp. in MCF, 59.3 spp. in SMCF and 51.7 spp. in BF).

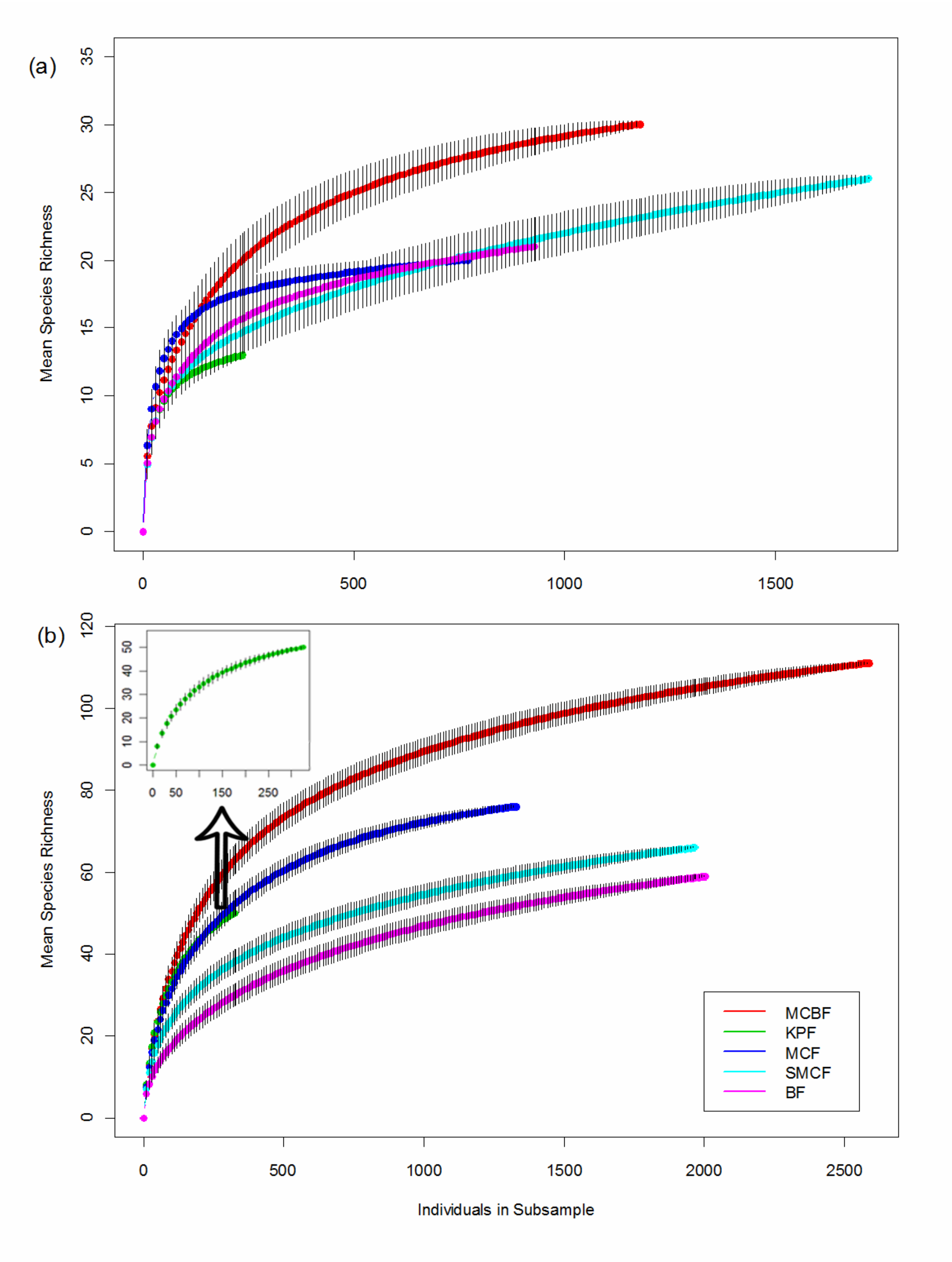

Figure 21 Rarefaction curves for pooled samples of different habitat types for (a) carabids and (b) geometrids (MCBF: mixed coniferous and broad-leaved forest; KPF: Korean Pine Forest; MCF: mixed coniferous forest; SMCF: sub-alpine mixed coniferous forest; BF: birch forest).

3.3.5. Species turnover

In NMDS ordination plots based on the turnover patterns in carabid assemblages for both the minimum m=1 (Figure 22a) and the maximum shared sample size m=47 (Figure 22b), plots at high elevations form a joined cluster. For m=1, this cluster contains the highest MCF as well as all SMCF and BF plots, whereas for larger sample sizes, there is a more distinct separation of the MCF plots from plots representing the other two forest types, while the overall cluster density also decreases. For the forest types at lower elevation, MCBF plots form a tight cluster, with KPF and lower elevation MCF plots located at intermediate positions. Overall, there appears to be a strong shift in the carabid species assemblages of MCF plots with increasing elevation, which can partly be related to the wide elevational range occupied by these forests. In all ordination plots, the 1st axis reflects primarily an increase in elevation (Pearson correlation: r=0.91 for m=1 and r=0.95 for m=47, p<0.001 in both cases).

For geometrid moths, NMDS ordination plots showed distinctive clusters between different forest types for both minimum (m=1) and maximum shared sample size (m=87), with KPF assemblages appearing more distinct from other forest type assemblages than in carabids (Figure 22). For both ordination diagrams, the 1st axis was again strongly correlated with an increase in elevation (Pearson correlation: r=0.95 for m=1 and r=0.89 for m=87, with both p<0.001).

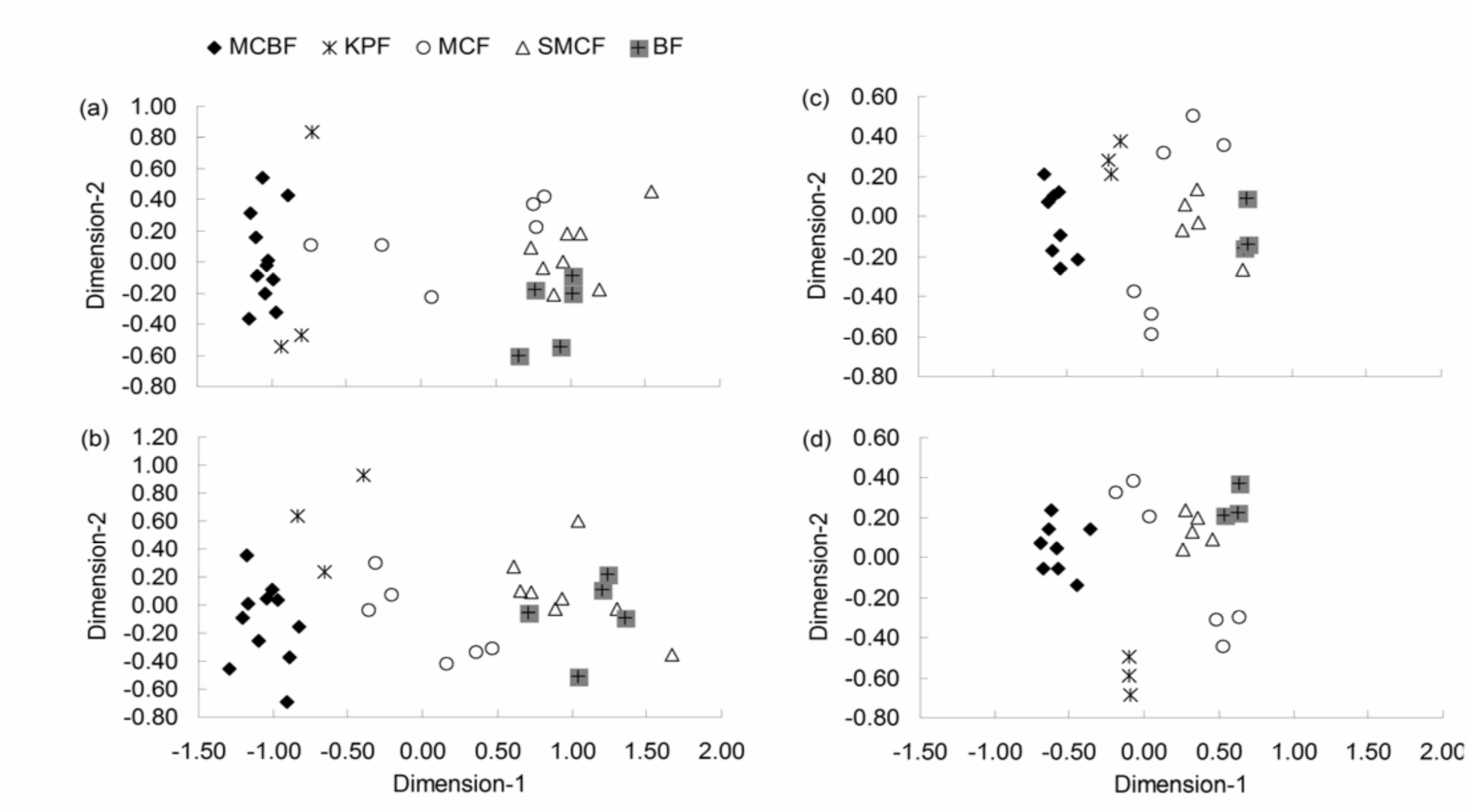

Figure 22 Non-metric two-dimensional scaling ordination plot based on the CNESS dissimilarity matrix between all sampling plots of carabids for a minimal sample size (m=1, stress=0.11) (a) and the maximum common sample size (m=47, stress=0.11) (b), and of geometrids for a minimal sample size (m=1, stress=0.12) (c) and the maximum common sample size (m=87, stress=0.11) (d)

3.4. **Discussion**

3.4.1. Overall diversity and species composition of carabids and geometrids

A total of 47 carabid species were observed, with estimated species richness for the entire study area of 54 species. This species richness in the Changbai Mountain forests is well within the range previously reported from China's Northern and North-eastern mountain ranges (Axmacher et al. (2011); Jiang, 2006; Yu et al., 2006b). Along an elevational transect ranging from 500m to 1650m in Hebei Province which comprised forest, grassland and agricultural habitats, Axmacher et al. (2011) recorded a total of 59 species, while 43 species were recorded in the secondary and plantation forests on Ziwu Mountain in the Gansu Province between elevations of 1100m and 1750m (Jiang, 2006). The species richness recorded in the Changbai Mountain area is also comparable with the species richness recorded from Chinese temperate forests in more southerly regions, with 46 species reported from Wolong Natural Reserve at elevations between 2200m and 2650m in Sichuan Province (Yu et al., 2006b), and from temperate forests in Europe, with 31 species recorded in the Başkonuş mountains in Turkey between 300m and 1780m (Avgın, 2006) and 21 species from the Eastern Carpathians between 910m and 1300m (Skalski et al., 2011).

For geometrid moths, the total of 155 species in my sample is the highest species number recorded in the study area to date, with Liu et al. (2007a) reporting 97 species and 2092 individuals in the inventory of geometrid moth species in CNR, while Chen et al. (2007) recorded 136 species and 3000 individuals when studying the elevational distribution of geometrid moths in the CNR. Both of these two previous studies also covered the entire altitudinal gradient from MCBF at about 700m to the tundra zone up to 2600m.

When compared with the results published by Chen (2007; Liu did not present a full species list), species similarity in sample composition is low. This is partly due to a large number of my morphospecies (70) that were not identified to species level. Nonetheless, the species number and also their exact identification will become clearer once results from DNA barcoding are reported back and fully analyzed. Another possible reason for the current low overlap in species names could be relating to the difference in sampling locations between our sampling sites and the associated differences in environmental conditions. Nonetheless, the heterogeneity in the geometrid species composition also reflects an overall remarkably high geometrid diversity in the CNR. In addition, my records of species richness are also comparable with other studies in Northern and North-eastern mountain ranges in China. For example, studies recorded only 110 species based on 14692 individuals collected between 500m and 1650m in the Bashang Plateau of Heibei Province (Axmacher et al., 2011), and 187 species in 1950 specimens collected between 600m and 3450m in the Baishuijiang Nature Reserve of Gansu Province (Yang et al., 2010).

As hypothesised, the composition of both carabid and geometrid assemblages varied strongly between different forest types. One mechanism to potentially explain the distinctive species composition of insects in different forest types would be that these two taxa are closely linked with changes in vegetation composition reflected by the forest types. Alternatively, the distinctive insect composition between different forests might reflect a simultaneous reaction in both insect taxa and the vegetation in response to the same environmental factors, precipitation and temperature. This would indicate that both carabids and geometrids are highly sensitive to climate change and might hence be suitable climate change indicator groups. In the subsequent Chapters 4 and 5, I will test further whether changing α-diversity and composition of carabids and geometrids in the research area are driven by core environmental factors or changes in the vegetation.

The observed decrease in Ennominae and increase in Larentiinae along the elevational gradient are consistent with other studies carried out in South America (Brehm, 2002) and Africa (Axmacher et al., 2004a). The increased proportion of Larentiinae with increased elevation reflects this subfamily's good adaptation to cooler and wetter environmental conditions in comparison to other geometrid subfamilies (Brehm, 2002; Holloway, 1987). In this study, members of the Sterrhinae did not occur above 1100m, which is again somewhat mirrored in findings by Axmacher et al. (2004a) who reported that no Sterrhinae were present above 2600m on the afrotropical Mt Kilimanjaro. This result indicates that Sterrhinae are likely to be strongly sensitive to the changes in climatic conditions.

3.4.2. α-diversity and species distribution with increasing elevation

In support of the original hypothesis, Fisher's α of both ground beetle and geometrid moth assemblages decreased with increasing elevation at CNR. The α-diversity pattern of ground beetles corresponded with the diversity changes observed for example by Greenslade (1968) in Scotland, although hump-shaped patterns with mid-elevation diversity peaks have also been regularly documented in studies from Europe's temperate region (Schuldt & Assmann, 2011; Skalski et al., 2011). Decrease trends were also observed for previous studies of geometrid (Chen et al., 2007) and noctuid (Liu et al., 2007a) moth assemblages in CNR. Furthermore, results are also consistent with the trends observed in the vegetation communities in CNR that showed a general decrease in species richness with increasing elevation (Hao & Yang, 2002).

It could be assumed that these patterns are an effect of increasingly extreme climatic conditions and annual climatic variations experienced on Changbai Mountain with increasing elevation. The respective Harsh Environment Hypothesis is supported by the observed significant linear increase in species' altitudinal ranges with increasing elevation. According to this hypothesis, species at high latitudes, but also high altitudes, experience harsh climatic conditions which require them to have broader overall tolerance ranges than species at low latitudes and altitudes, which in term also leads to wider distribution ranges with increasing elevation, and to a higher species richness at low altitudes (Rapoport, 1982; Stevens, 1989, 1992). This hypothesis is supported by the observed significant linear increase in species' altitudinal ranges with increasing elevation. In addition, the decrease in net primary productivity in the forest ecosystems at Changbai Mountain with increasing elevation (Sun et al., 2004) could arguably further reinforce a diversity decline.

The strong increase in carabids species' abundance with increasing altitude has similarly been reported from tropical forests (Olson, 1994). In fact, for both geometrids and carabids, the higher activity abundance at higher elevations is chiefly as a result of very high abundances in a few dominant species that appear particularly well adapted to the conditions at higher altitudes, such as *Hydriomena impluviata* (Geometridae: Larentiinae) and *Carabus aurocinctus* (Carabidae). The decrease in α-diversity with increasing elevation further supports these trends. One possible explanation for the increase in abundance but decrease in diversity along increasing elevation is the existence of evolutionary barriers due to lower temperature in higher elevation area leading to the presence of highly evolved successful high-elevation specialists, which due to lack of competition might occur at very high abundances. Lower temperature are also likely to reduce speciation rates (Rohde, 1992). For carabids, for example, the decrease in species and abundance of many warm-adapted species (and also other key predatory insect taxa such as ants (Olson, 1994)) results in a strong decrease in competition for prey, and could hence explain the strong increase of the few cold-adapted species.

3.4.3. Species composition and abundance-distribution relationships

Many studies have reported a positive correlation between abundance and altitudinal distribution ranges of species (Bock, 1987; Gaston & Lawton, 1988; Gotelli & Simberloff, 1987; Pollard et al., 1995). The mechanism of this positive abundance-distribution relationship is that generalist species as species able to exploit a wider range of resources tend to become widespread and more abundant than specialists (Brown, 1984). The lack of this trend in this study is not necessarily surprising. In fact, positive abundance-distribution relationships are commonly observed when the difference between sampled habitats (reference habitats) and their surrounding are small, while a lack of clear positive trends can occur when between-habitat differences are more pronounced (Schoener, 1987; Thomas & Mallorie, 1985). If the reference habitat differs distinctly from its surrounding regions, species generalists are also unlikely successfully spreading to other areas (Gaston & Lawton, 1990). It hence will result in a high abundance of species gathering in a relatively small area, and eventually leads to a negative abundance-distribution relationship (Gaston & Lawton, 1990). A lack of significant correlations might hence relate to differences between the survey plots and their wider environment is at an intermediate level, *id est* reference habitats are neither sufficiently different from the wider region to result in a negative relationship, nor sufficiently similar to lead to a positive trend (Gaston & Lawton, 1990).

The distinct zonation of the vegetation on Changbai Mountain (Bai et al., 2011; Chen et al., 1964; Sang & Bai, 2009; Xu et al., 2004; Zhao et al., 2004) is reflected in the occurrence of distinct insect assemblages. This is shown by the clear distinction of plots in relation to their dominant species, which mirrors the strong turnover in dominant species between forest types, a trend which becomes less pronounced for the highest elevation plots.

3.4.4. Potential threats to insect diversity at CNR

The similarity in both, beetle and moth assemblages, at the high elevation birch and conifer forest types may be surprising given the great dissimilarity in environmental conditions expected under these morphologically distinct different tree species. Nonetheless, a long-term vegetation study in this area (Bai et al., 2011) revealed that herbaceous plant species typically encountered in sub-alpine coniferous forests have increasingly started to colonize the birch forest above the current distribution limit of the coniferous forests in response to changing climatic conditions. The resulting increasing homogeneity in the ground vegetation could partly explain the similarity in insect assemblage compositions between these forest types.

The composition of rare species for both ground beetles and geometrid moths in SMCF and BF was distinctly more dissimilar than that of common species, while it is also true that rare species are more specialized to their respective habitats. The shrinking extent of typical birch forest plant communities at the upper forest boundary and the increasing colonization of the undergrowth of these forests by plant species formerly restricted to conifer forests could therefore put rare, specialised birch forest insects under increasing pressure and might even lead to their eventual local extinction, although further research is needed to establish if these species also occur above the current forest distribution line in the alpine tundra vegetation of Changbai Mountain. In response to global warming, insect species are likely to move upwards on mountain ranges (Chen et al., 2009). For geometrids in this case, warm-adaptive species such as Ennominae and Sterrhinae can move to higher elevations and possibly increase their overall distribution range. For insects adapted to cooler conditions such as many members of the Larentiinae, however, it is likely that they get under increasing pressure due to the restricted height and negative relationship between area and elevation on mountains, which is a particularly serious concern for upper-most forest specialists. A further analysis of links between insect and vegetation diversity patterns under climate change at CNR will be presented in Chapter 5.

Apart from the threats beetles face at the upper forest boundary, for both ground beetles and geometrid moths, low-elevation communities may also be under pressure. These investigations have revealed that assemblages for both these taxa particularly at the mixed broad-leaved and conifer forests are highly diverse in comparison to communities at higher-elevation forest types. Nonetheless, Bai et al. (2011) reported that particularly the forest tree composition in these forests is becoming increasingly homogenized again as a result of changes in the climatic conditions over the last four decades. Both beetles and geometrids have been likely going through the same pressure due to the same climate changes in the past decades.

Results also highlight the faunal distinctiveness of the KPF in the diversity patterns of its insect assemblages, particularly with reference to geometrid moths. While this forest is already of high conservation concern due to the Korean pine, a species of high conservation value (Wu, 1980), the distinct composition of beetle and moth assemblages inhabiting these forests indicates that the entire habitat is special and—not least due to its extreme rareness—requires particular conservation attention.

3.4.5. Synthesis

In general, the CNR area harbours a high diversity level of both carabid beetles and geometrid moths, which is comparable to other temperate forests in North China, as well as to forests in the temperate region of Europe. The α-diversity of both carabids and geometrids decreases significantly with an increase in elevation. This trend supports the Harsh Environment Hypothesis, which can also be used to explain the observed increase in species' altitudinal range with increasing altitude. Distinctive changes in species composition was observed with increasing elevation for both carabids and geometrids, which indicates that these taxa are highly sensitive to climate change. The distinctive Korean pine-dominated forest, which was included in other forest types in previous studies, harboured a distinct insect composition that in my view will require specific conservation attention in the future.

Chapter 4. Statistical models of the links between insect and plant diversity[1]

Summary

The "Resource Concentration Hypothesis" and the "Enemies Hypothesis" are two commonly mentioned hypotheses based on bottom-up and top-down control theories, respectively. These hypotheses have been analyzed using experiments and investigations of agricultural and grassland ecosystems, while evidence from more complex mature forest ecosystems is limited. In this chapter based on Changbai Mountain as study area, I investigated the relationship between the diversity of insects and the vegetation via the establishment of a series of statistical models. My results show that variables describing plant diversity were not commonly included in models predicting α-diversity patterns of carabids and geometrids. Elevation was the most important predictor of changes in both carabid abundance and α-diversity, as well as in the α-diversity of geometrid moths. This indicates that, along the entire elevational gradient, relationships observed between plant and insects diversity are mainly driven by the underlying changes in abiotic factors. Results from this chapter also highlight that traditional bottom-up and top-down control theories that are suitable in less species-rich ecosystems might play a less pronounced role in the complex mature temperate forest ecosystems in Northern China.

4.1. Introduction

Bottom-up and top-down controls are two theoretical concepts of how biotic forces can determine the distribution of organisms in an ecosystem (Power, 1992; Rzanny et al., 2012). Accordingly, Root (1973) suggested two possible hypotheses to explain plant-arthropod interactions based on bottom-up and top-down actions, respectively: the "Resource Concentration Hypothesis" and the "Enemies Hypothesis". According to the "Resource Concentration Hypothesis", specialized herbivore abundance and diversity decrease with an increase in plant diversity. Higher plant diversity usually results in the decrease of host plant density and limits host-detection of herbivores, leading to a lower herbivore abundance (Root, 1973). If strong bottom-up effects

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[1] The main results were published in Zou et al. (2013a). In this paper, I was the main, lead author, did the analysis and wrote the main content.

affect a species assemblage, the abundance and diversity of generalist herbivores, but also of organisms at higher trophic ranks will be directly affected by plant species richness via the food chain (Scherber et al., 2010). An increase in plant diversity will howlever possible enhance net primary productivity (Hooper et al., 2005; Tilman et al., 1996) (although this still is a controversial topic, see Chapter 1), which in turn provides more food resources for herbivorous arthropods, hence increasing the overall biomass of arthropod consumers (Borer et al., 2012; Hunter & Price, 1992).

A positive association between phytodiversity and both diversity and abundance of herbivorous arthropods has been found in a variety of ecological experiments (Borer et al., 2012; Mulder et al., 1999; Scherber et al., 2010; Scherber et al., 2006), in low-diversity grassland (Pearson & Dyer, 2006; Perner et al., 2003; Siemann et al., 1999) and in agriculture fields (Cook-Patton et al., 2011; Padmavathy & Poyyamoli, 2011). Nonetheless, reports of negative relationships between plant diversity and the diversity of arthropod taxa are also common, backed again with results from experiments (Andow, 1991), grassland ecosystems (Unsicker et al., 2006; Wardle et al., 1999) and agricultural landscapes (Axmacher et al., 2011). In complex forest ecosystems, a number of studies report a positive feedback between the diversity of plants and herbivorous insects (Novotny et al., 2012; Schuldt et al., 2010; Sobek et al., 2009a). Other studies nonetheless again report a lack of significant relationships (Axmacher et al., 2009; Hawkins & Porter, 2003) or even negative correlations (Axmacher et al., 2004b; Cuevas-Reyes et al., 2003).

As arthropod consumers are known to be influenced by their natural enemies, it forms the key bias of top-down control effects (Hairston et al., 1960; Russell, 1989; Walker & Jones, 2003). The “Enemies Hypothesis” is one of the common top-down control theories which postulates that vegetation diversity can provide more refuges for predators and more stable prey resources for them (Root, 1973). Higher plant diversity can therefore enhance the effectiveness of catching and the feeding rate for predators (Root, 1973). Consequently, the hypothesis also predicts a positive relationship between plant diversity and both the diversity and abundance of predatory species (Jactel et al., 2005; Russell, 1989).

For studies investigating links between the phytodiversity and the diversity and abundance of predatory arthropods, the Enemies Hypothesis has been supported by a range of experimental studies (Haddad et al., 2011; Moreira et al., 2012; Scherber et al., 2010; Wenninger & Inouye, 2008) and by studies in agricultural (Cook-Patton et al., 2011; Varchola & Dunn, 1999) and grassland (Jonsson et al., 2009) ecosystems with relatively low phytodiversity levels. It is predicted that top-down control of herbivores by natural enemies would be more predominant in year-round growing ecosystem than in an annual one due not least to the more consistent prey availability (Andow, 1991; Risch et al., 1983). The associated positive link between plant diversity and the diversity and abundance of predatory arthropods is therefore predicted to be stronger in natural forest ecosystems in comparison to annual grassland and agriculture fields (Andow, 1991). Nonetheless, very little research has been conducted to date into these links in the world's remaining mature forest ecosystems. The limited published data suggest that areas of high phytodiversity do not automatically support a high diversity in predatory arthropods (Schuldt et al., 2011). The underlying patterns are not yet well-understood, and more studies into the links between the vegetation and predatory arthropod taxa in natural forest ecosystems are urgently needed (Dinnage et al., 2012; Zhang & Adams, 2011).

The aim of this chapter is to use carabids and geometrid moths, with focus on carabids, as target groups to analyze the relationship between plant diversity and the diversity and abundance of species-rich arthropod taxa in CNR. The main objectives addressed in this chapter are 1) to test if positive links between ground beetle abundance and diversity and the diversity in plant species exist as predicted by the Enemies Hypothesis, 2) to test the whether the relationship between plant diversity and the diversity of geometrids moth is positive, and 3) to establish how environmental factors affect the observed links.

4.2. Sampling method and data analysis

This chapter is again based on the plots located at the Changbaishan Natural Reserve (CNR). As indicated in Chapter 2, 33 plots between altitudes of 700m and 2000m were selected on the mountain. Each study plot had a size of $20\times20m^2$ and was divided equally into four subplots. In the centre of each sub-plot, a pitfall trap was placed. A light trap was also placed in the middle of each $20\times20m^2$ plot on 25 of the plots. For the recording of the vegetation, all trees and shrubs were recorded in each of the resulting $100m^2$ sub-plots. Herbaceous species were recorded at four plots of

1m^2 that were randomly located within each of the sub-plots (see Figure 13). The number of individuals or % cover was recorded for each plant species in each layer. The breast height area was recorded for each tree specimen and the average height was recorded for each shrub and herb species. More details of vegetation survey and insect sampling method can be found in Chapter 2.

Carabid activity abundance of each plot was calculated as the overall number of sampled individuals divided by the total sampling period in days, resulting in a mean daily sampling rate for each plot. As the abundance of moths caught from light traps is sensitive to different sampling conditions such as microclimatic conditions (Choi, 2008; Intachat et al., 2001) and background illumination (Bowden & Church, 1973; McGeachie, 1989), and these conditions cannot be standardized, geometrid abundance data are considered unreliable for direct comparisons and were not included in the analysis. α-diversity of both carabids and geometrid was measured as Fisher's α (see Appendix 1, equation 5). Shannon diversity (see Appendix 1, equation 4) of the vegetation was calculated individually for each plant layer based on the importance value (IV) of each plant species to avoid the bias from simple abundance-based calculations (Lamont et al., 1977; Sang & Bai, 2009). The IV contains three aspects reflecting the relative contributions of each plant species towards each layer: relative abundance (*d*), relative frequency (*f*) and relative dominance (*h*). The IV for i^{th} species in j^{th} sample plot is calculated according to Formula 1.

$$IV_{i,j} = \frac{1}{3}\left(\frac{d_i}{\sum_1^S d_i} + \frac{\left(f_i / n \right)}{\sum_1^S \left(f_i / n \right)} + \frac{h_i}{\sum_1^S h_i} \right)$$

Formula 1 Importance value calculation, where *d* is the number of individuals, *f* is the number of subplots in which the species occurred, *n* is the total number of subplots in a sample plot (4 in this case), and *h* is the dbh for tree species and the height for shrub and herb species.

Modelling of plant-insect relationships was based on multiple linear regressions (MLR), where carabid activity abundance, α-diversity of carabids and geometrids were used as response variables, respectively. A series of stepwise linear regression analyses was performed to identify the most important independent variables. Stepwise regression was used with both forward selection for selection of variables contributing significantly (P = 0.05) towards the model and backward elimination to verify that variables made no significant contribution in the selection of new variables. Vegetation variables included the total number of plant species (PS), the Shannon diversity (H) for trees (TH), shrubs (SH) and herbs (HH), and the abundance density (D) for trees (TD), shrubs (SD) and herbs (HD), respectively. Modelling included all vegetation parameters as independent variables first and then added elevation as additional independent variable.

To account for the substantial forest vegetation changes with changing elevation, Principal Components Analysis (PCA) based on the presence-absence data of plant species was used to establish the existence of distinct sample clusters representing a relatively homogeneous vegetation composition and re-ran the linear regression models separately for different clusters.

All statistical analysis was carried out in R (R Development Core Team, 2011), using the packages ‘spaa’ (Zhang et al., 2010) to calculate the Shannon diversity index and ‘vegan’ (Oksanen et al., 2012) to carry out the PCA and to calculate Fisher’s α values.

4.3. Results

Total sampling results for carabids and geometrids are presented in Chapter 3. The overall average daily activity abundance of carabids for the entire study area was 1.83 individuals per plot. Additionally, the 33 plots where plant surveys were conducted contained a total of 178 plant species belonging to 128 genera and 58 families. The tree layer was comprised of 32 species belonging to 20 genera and 12 families; the shrub layer contained 43 species of 28 genera and 15 families and the herb layer comprised 112 species representing 88 genera and 43 families.

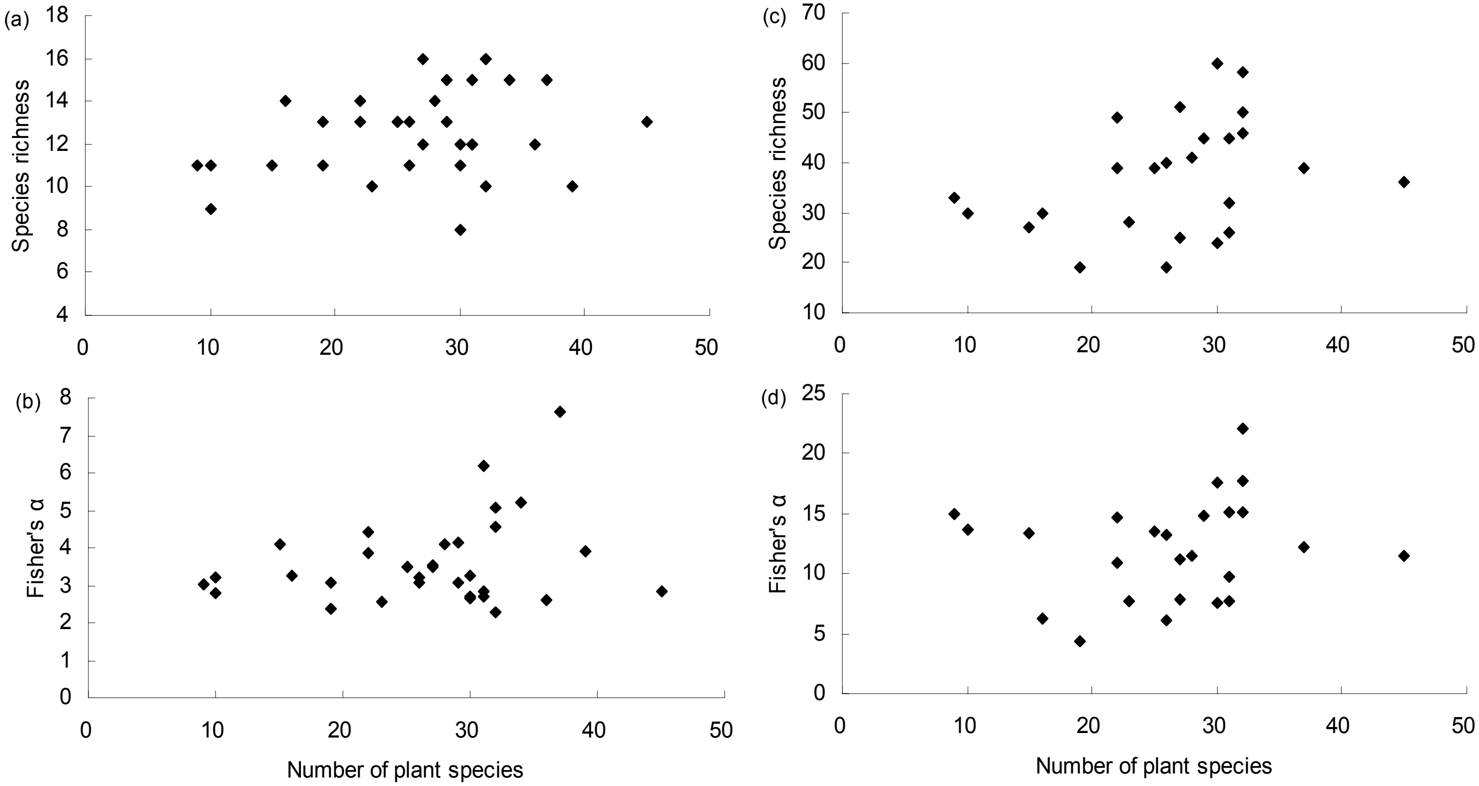

Figure 23 α-diversity and number of plant species of each sampling plot for carabids (a and b) and geometrids (c and d)

4.3.1. Insect-plant relationships

Total number of plant species (PS) neither correlated with species richness and Fisher's α-diversity of carabids nor geometrid moths (Pearson correlation: $P>0.05$, Figure 23). Stepwise regression entering all vegetation parameters produced two subsequent models predicting carabid activity abundance. The first model (adjusted $R^2=0.43$, $F_{1,31}=24.6$, $P<0.001$) included SH as significant negative ($\beta=-0.93$, $P<0.001$) predictor of carabid abundance, while the second model (adjusted $R^2=0.51$, $F_{2,30}=17.3$, $P<0.001$) additionally included HH as positively ($\beta=0.43$, $P=0.02$) affecting beetle abundance. The Akaike information criterion (AIC) slightly decreased from 79.4 to 75.3 between the models (Table 3, Models 1 and 2). The model predicting carabid α-diversity included SH as main predictor ($\beta=0.57$, $P=0.039$), which in this case was positively correlated with Fisher's α values. Overall, this model performed not good either (Table 3, Model 4, adjusted $R^2=0.10$, $F_{1,31}=4.7$, AIC=102.5). When elevation was entered as additional independent variable, MLR models for both, carabid activity abundance and α-diversity, only included this parameter as significant, with model fits markedly improved (AIC=71.7, adjusted $R^2=0.54$, $F_{1,31}=39.1$, beta=1.75, $P<0.001$ for beetle abundance, and AIC=96.3, adjusted $R^2=0.26$, $F_{1,31}=12.1$, beta=-1.45, $P=0.002$, for beetle α-diversity, Table 3 Models 3 and 5). Models therefore predict a linear increase in beetle abundance at a reduced diversity with increasing elevation.

When predicting the α-diversity of geometrid moths by vegetation parameters, stepwise regression also produced two models. The first model contained TD as the only predictor, with a negative beta value indicating a negative relationship between tree density and moth diversity (Table 3, Model 6, AIC=138.4, adjusted $R^2=0.28$, $F_{1,23}=10.5$, beta=-0.04, $P=0.004$), while the second model included both TD (beta=-0.04, $P=0.011$) and HD (beta=-0.01, $P=0.05$) as negative predictors (Table 3, Model 7, AIC=135.9, adjusted $R^2=0.38$, $F_{1,23}=8.2$, $P=0.002$). When adding elevation as additional independent variable, elevation again was the only significant predictor, with models indicating a linear decrease of α-diversity of geometrids with increasing elevation (Table 3, Model 8, AIC=128.0, adjusted $R^2=0.53$, $F_{1,23}=27.9$, $P<0.001$).

Table 3 Stepwise linear regression models using carabid activity abundance and Fisher’s α-diversity of both, carabids and geometrids, as dependent variables, respectively, and using vegetation parameters as independent variables (Model 1, 2, 4, 6 and 7), as well as models additionally including elevation (km) (ASL) as independent variable (Model 3, 5 and 8). (SH: Shannon diversity for shrubs; HH: Shannon diversity for herbs; TD: tree density; HD: herb density; ASL: elevation)

Dependent variable	Model No.	Adjusted R^2	F	Model P-value	Model AIC	Selected independent variable(s)	β	Std. Error of β	t	P-value
Carabid abundance	1	0.43	24.6	<0.001	79.4	SH	-0.93	0.186	-4.96	<0.001
	2	0.51	17.3	<0.001	75.3	SH	-0.90	0.173	-5.17	<0.001
						HH	0.43	0.174	2.45	0.02
	3	0.54	39.1	<0.001	71.7	ASL(km)	1.75	0.280	6.26	<0.001
Carabid α-diversity	4	0.1	4.7	0.039	102.5	SH	0.57	0.265	2.16	0.039
	5	0.26	12.1	0.002	96.3	ASL(km)	-1.42	0.530	-3.48	0.002
Geometrid α-diversity	6	0.28	10.5	0.004	138.4	TD	-0.04	0.013	-3.25	0.004
	7	0.38	8.2	0.002	135.9	TD	-0.04	0.013	-2.78	0.011
						HD	-0.01	0.003	-2.08	0.05
	8	0.53	27.9	<0.001	128.0	ASL(km)	-8.02	1.518	-5.28	<0.001

4.3.2. *Insect-plant relationship in the different vegetation types*

The ordination plot of the first two principle components (PCs) based on vegetation composition showed three distinctive clusters along the elevational gradient (Figure 24). I therefore separated the plots into the respective clusters, which chiefly coincided with the different forest zones. Nonetheless, sub-alpine mixed coniferous forest and birch forest were combined into a highest forest area and three plots within the mixed broad-leaved and coniferous forest between 1000m and 1100m were included in the mixed coniferous forest cluster. Accordingly, for pitfall traps, 11 plots represented the low-elevation zone below 1000m, 9 plots were located in a mid-elevation zone between 1000m and 1500m, and the remaining 13 plots represented the high-elevation zone above 1500m. As light trapping was only conducted on 25 of the 33 plots, geometrid moth samples were split into 8 plots in the low-elevation zone, 9 in the mid-elevation zone and 8 in the high-elevation zone.

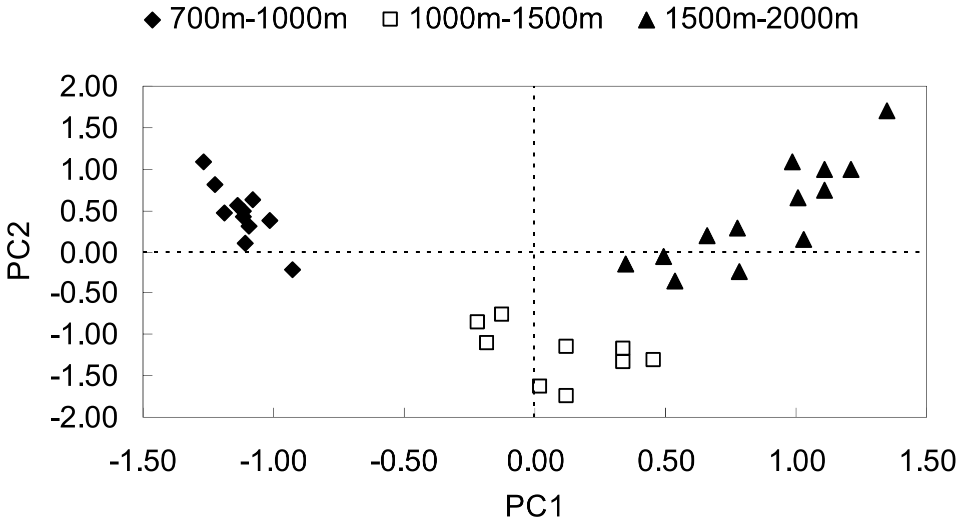

Figure 24 PCA ordination plot based on vegetation composition showing three distinct clusters (proportion variance explained for PC1=24% and for PC2=11%).

Below 1000m in the mixed coniferous and broad-leaved forest zone, the first model using vegetation parameters as independent variables indicated that carabid activity abundance was negatively associated with TH (β=-1.67, P=0.002) (Table 4, Model 9, AIC=5.4, adjusted R^2=0.62, $F_{2,8}$=17.4, P=0.002), while the second model additionally included a positive relationship with SD (β=0.01, P=0.012), with a highly significant overall model fit (Table 4, Model 10, AIC=-1.8, adjusted R^2=0.82, $F_{2,8}$=23.1, P<0.001). At the intermediate elevation forest area, only TD (β=0.002, P=0.011) was included in predicting carabid activity abundance (Table 4, Model 11, AIC=14.1, adjusted R^2=0.57, $F_{1,7}$=11.7, P=0.011). For the highest forest area, SH (β=-1.44, P<0.001) was the only independent variable included in the model (Table 4, Model 12, AIC=21.1, adjusted R^2=0.73, $F_{1,11}$=32.65, P<0.001).

None of the vegetation diversity variables was significantly linked with carabid α-diversity in any of the three distinct elevation zones. Nonetheless, carabid α-diversity was linked to the vegetation density parameters SD (β=-0.06, P=0.021) in the low elevation zone (Table 4, Model 13, AIC=21.8, adjusted R^2=0.40, $F_{1,11}$=7.74, P=0.021) and TD (β=-0.004, P=0.041) at high elevations (Table 4, Model 14, AIC=22.4, adjusted R^2=0.27, $F_{1,11}$=5.4, P=0.041). Neither herb diversity nor herb density appears to be linked with either activity abundance or α-diversity of carabids at any of the three elevation zones.

No vegetation variable was included in predicting α-diversity of geometrid moths at low and middle elevation zones. At the high elevation zone, TD was again the only predictor, being negatively correlated with geometrid diversity (Table 4, Model 15, AIC=34.5, adjusted R^2=0.64, $F_{1,6}$=10.8, P=0.017).

Table 4 Results of stepwise linear regressions for the three elevational zones using carabid activity abundance, carabid activity abundance, α-diversity of carabids and geometrids as dependent variables and vegetation parameters as independent variables (TH: Shannon diversity for trees; SH: Shannon diversity for shrubs: TD: the abundance density for trees; SD: the abundance density for shrubs; Low: low elevation zone of less than 1000m; Middle: intermediate elevation zone of 1000-1500m; High: high elevation zone of 1500-2000m)

Dependent variable	Elevation Zone	Model No.	Adjusted R^2	F	Model P-value	Model AIC	Selected independent variable(s)	β	Std. Error of β	t	P-value
Carabid abundance	Low	9	0.62	17.4	0.002	5.4	TH	-1.670	0.401	-4.17	0.002
		10	0.82	23.1	<0.001	-1.8	TH	-1.236	0.310	-3.99	0.004
							SD	0.012	0.004	3.24	0.012
	Middle	11	0.57	11.7	0.011	14.1	TD	0.012	0.003	3.41	0.011
	High	12	0.73	32.7	<0.001	21.1	SH	-1.435	0.251	-5.71	<0.001
Carabid α-diversity	Low	13	0.40	7.7	0.021	21.8	SD	-0.058	0.021	-2.78	0.021
	High	14	0.27	5.4	0.041	22.4	TD	-0.004	0.157	-2.32	0.041
Geometrid α-diversity	High	15	0.64	10.8	0.017	34.5	TD	-0.028	0.008	-3.28	0.017

4.4. <u>Discussion</u>

4.4.1. Plant diversity and insect diversity

Firstly, it is important to recognize that overall plant species richness did not act as a significant predictor of α-diversity in either of the two insect taxa; no plant diversity variable was included in predicting α-diversity of carabids and geometrids in separating vegetation types; and the only plant diversity variable, SH, which was included in predicting α-diversity of carabids for the entire area (Model 4), potentially reflects the same response in the diversity of plants and carabids to changing environmental conditions with increasing elevation. These results indicate that plant diversity poorly represents the diversity patterns of the species-rich arthropod assemblage in these forest ecosystems, adding further support to the caution urged for the use of plant-based biodiversity hotspots (Myers, 2003; Myers et al., 2000) in setting overall biodiversity conservation strategies (Axmacher et al., 2011).

The results further underline that elevation is the predominant driver of changes in both, carabid abundance and α-diversity, as well as in the α-diversity of geometrid moths. Shifting in elevation mainly associates changes in temperature and precipitation, indicating that these factors are more important in influencing the diversity of carabids and geometrids than plant diversity *per se*, which is also consistent with findings for previous studies that similarly revealed a closer link of insect diversity patterns with abiotic environmental factors rather than the vegetation in a wide range of geographical scales and areas (Axmacher et al., 2009; Condon et al., 2008; Hawkins & Porter, 2003; Rodríguez-Castañeda et al., 2010). Accordingly, it is believed that the observed relationships between vegetation variables and activity abundance of carabids and the α-diversity of both carabids and geometrids recorded for the entire elevational gradient are mainly driven by the underlying changes in abiotic factors.

4.4.2. Plant diversity and insect abundance

The observed, highly significant negative correlation between carabid activity abundance and the diversity of shrubs stands in direct contradiction to the Enemies Hypothesis, which predicts a positive relationship with carabid abundance. This observations also stands in contrast to many studies conducted in agricultural (Cook-Patton et al., 2011; Varchola & Dunn, 1999) and grassland ecosystems (Jonsson et al., 2009), which differ from my study site by their markedly lower overall phytodiversity. As species richness generally is higher in forests in comparison to most other terrestrial ecosystems, which results in a more complexity in food webs (Scherer-Lorenzen et al., 2005), traditional top-down control theories that are suitable in less species-rich ecosystems may overall be difficult to apply in forest ecosystem (Zhang & Adams, 2011).

Similar to this study, Koricheva et al. (2000) also reported a negative relationship between plant diversity and activity abundance of predatory arthropods in a grassland ecosystem. One of the explanations they present for this negative trend was a reduction in predator activity density with an increase in herb density, but this trend was not supported by my investigations. My results however are consistent with observations by Schuldt et al. (2011) who observed that activity abundance of spiders was also reduced in areas with an increased woody plant diversity in a natural forest at Zhejiang Province. Schuldt et al. (2008) and Vehviläinen et al. (2008) state that the abundance of predatory species depends more strongly on the presence of specific tree species rather than on overall tree diversity. The lack of validity of the Enemies Hypothesis for complex forest ecosystems might therefore relate to the multifaceted interactions between specific plant species, their herbivores and the predatory insect assemblages inhabiting these ecosystems (Heil, 2008; Zhang & Adams, 2011). Carabids are also likely to have individual preferences for specific plant species and specific functional groups which provide suitable micro-climatic conditions, shelter or even direct food resources for carabids or their key prey (Vehviläinen et al., 2008).

Although the role of specific tree or shrub species and their functional groups were not investigated here, high woody plant diversity might potentially reflect a reduction in the overall dominance of specific, favourable species.

Alternatively, Schuldt et al. (2011) also suggested that a high plant diversity can potentially support a higher density of herbivorous arthropods in natural forests, which might also result in a reduction of predators' overall foraging time and hence their recorded activity density. Higher plant diversity and the associated assumed increase in the abundance of herbivores can furthermore provide an increase in food sources and niches for competing predatory arthropod taxa such as spiders and ants, increasing the overall competition levels for prey and consequently reducing the overall abundance of carabids. Unfortunately, due to the inconsistent sampling efforts among different sites for light traps in catching geometrids mentioned above, it was not possible to test the actual density of geometrids for comparison. A variety of studies have nonetheless reported positive links between plant diversity and the biomass of herbivorous and detrivorous arthropods (Cook-Patton et al., 2011; Dyer et al., 2010; Gámez-Virués et al., 2010; Novotny et al., 2012; Schuldt et al., 2010; Sobek et al., 2009a; Spehn et al., 2000). These studies can potentially provide evidences of Schuldt et al. (2011)'s suggestion that more food resources are available for predator arthropods in higher plant diversity communities.

4.4.3. Plant density and insect diversity

Different mechanisms might explain the observed negative correlations between woody plant density and the α-diversity of carabid and geometrid communities at certain elevation zones. Many carabid species appear to prefer open-canopy areas in forests (Butterfield et al., 1995; Humphrey et al., 1999), where an increase in the woody plant density will hence likely result in the observed decrease of carabid diversity. For geometrid moths, where negative correlations between α-diversity and woody density were restricted to the high elevation zone with assemblages dominated by members of the Larentiinae, changes in the woody plant species composition might be a key driver (Riihimäki et al., 2005; Unsicker et al., 2006). It can be speculated that the dense crown cover affects undergrowth plant diversity and hence indirectly reduces host species diversity (Thompson & Price, 1977) particularly for Larentiinae species at high elevational area. Woody plant density can furthermore be associated with the concentration of available nectar in the flowering plants forming the forest undergrowth, their nutritional quality as hosts and the local microclimate (Price et al., 1980), so that the relationship between vegetation and the diversity of the insect communities requires further investigations.

4.4.4. Plant density and insect abundance

The reported positive relationship between carabid activity abundance and woody plant density at low and intermediate elevation forests potentially reflects a bottom-up effect: plots with a higher density in woody plants are likely to be more productive. High woody plant density can not only enhance shading and soil moisture levels and hence create favourable microhabitats for carabids and their larvae (Niemelä et al., 1992), but also producing more leaf litter, which can in term improve soil fertility and increase food availability for carabids (Koivula et al., 1999; Magura et al., 2005).

Finally, the results presented in this chapter showed that the density of herbaceous plants did not significantly influence carabid activity abundance nor their diversity, which stands in strong contrast to studies in grassland ecosystems that commonly record negative relationships between herbaceous plant density and carabid activity abundance (Greenslade, 1964; Melbourne, 1999; Thomas et al., 2006a). Pitfall traps have been widely used in surveys of ground-dwelling arthropods (Greenslade, 1964; Liu et al., 2012; Luff, 1975; Oliver & Beattie, 1996; Rainio & Niemelä, 2003; Spence & Niemelä, 1994) and can be considered as a standard method in ground beetle sampling (Rainio & Niemelä, 2003). Nonetheless, one of the main known pitfalls of pitfall trapping is the dependency of the sampling rate on both, the target population density and the individual specimen's activity (Gotelli & Colwell, 2001; Greenslade, 1964; Jansen & Metz, 1979; Mitchell, 1963). Factors affecting this activity need to be taken into consideration when comparing pitfall samples, and it has commonly been suggested that vegetation density particularly of herbaceous species needs to be considered in the respective data interpretation (Melbourne, 1999; Thomas et al., 2006a; Woodcock, 2005). The negative impact of this density in grassland ecosystems is believed to be due to a reduction in the ground beetle mobility caused directly by a dense herb layer (Melbourne, 1999; Thomas et al., 2006a). My results however strongly suggest that the density of this layer in the old-growth forests on Changbai Mountain is not high enough to significantly affect carabids' movements, supporting the argument that the influence of the density in understory vegetation can be neglected when studying forest carabid assemblages (Schuldt et al., 2011). Nonetheless, controlled capture-recapture experiments would be needed to strengthen this argument.

4.4.5. Synthesis

Overall, results in this chapter clearly indicate that, when studying the relationship between plant diversity and arthropods in forest ecosystems, neither predatory arthropod abundance and diversity patterns support traditional top-down control theories, nor does the herbivorous arthropod diversity support traditional bottom-up control theories. These hypotheses might be suitable for less species-rich ecosystems, only. To substantiate these conclusions and establish if these theories are generally unsuitable for high species-rich forest ecosystems, further, long-term monitoring of a wider range of predatory arthropod groups (e.g. spiders, ants and centipedes) and of further herbivorous insect taxa, with detailed monitoring techniques such as caterpillar collection and detailed leaf damage assessments. These should not only be conducted in temperate, but also in tropical and subtropical forests where the complexity of food-webs is even greater. Other temperate mature forests in Northeast China, such as Liangshui and Fenglin Natural Reserves in Heilongjiang Province, would nonetheless form ideal study areas to substantiate results from species-rich temperate forests. Studies in the last remaining highly diverse large mature temperate forest ecosystems in NE China would also allow a better understanding of the complex inter-linkages between arthropod taxa at the same and across different trophic levels, with particular foci on the role of the woody plant species composition on predator arthropod distribution patterns and on the mechanisms governing responses of herbivorous arthropods to changes in plant diversity and species composition.

Chapter 5. Implications of climate and vegetation change for spatial diversity patterns of insects

Summary

The lack of long-term monitoring of insect assemblages is a major challenge in predicting insect diversity changes in response to climate change. In Changbai Mountain, a series of vegetation surveys were conducted in 1963, and these surveys were repeated 43 years later in 2006. In this chapter, I investigated the relationship between plant species composition and the α-diversity of both carabids and geometrids as a basis to get a better understanding of the potential long-term α-diversity changes in the two insect taxa. Results from principal component analysis (PCA) identified a variety of plant families that were positively linked to the diversity of carabids and geometrids. Most of these plant families showed a decline in species richness since 1963. The analytical section of this chapter concludes with a basic model predicting the α-diversity of carabids and geometrids in relation to their temperature requirements since the 1960s, indicating a strong upward shift of insects in recent decades. Although this model is only basic, it still highlights the high potential risk of extinction for species specializing on the uppermost forest ecosystem.

5.1. Introduction

Global climate change resulting in changes of temperature and precipitation has been proposed as a key factor affecting biodiversity and species distribution patterns (Beck et al., 2011; Hawkins et al., 2003; Rahbek et al., 2007; Sala et al., 2000). To understand long-term diversity and distribution pattern of insects on distinct mountain ranges has significant value, as this can form the basis of tailored management to address and potentially reverse any adverse affects on a site’s biodiversity and might allow an extrapolation of trends also for the future. A major challenge for both the exploration of past and prediction of future insect species changes in response to climate change however is the lack of detailed historical data on insect diversity and distribution. Nonetheless, plant investigations are commonly conducted in China before the establishment of a natural reserve. A possible way to analysis the diversity changes in insect communities is therefore to establish the relationships between plant species composition and diversity and the diversity of insect taxa. Based on the detailed understanding of the plant-insect relationships gained in the process, the long-term changes in plant composition in combination with an understanding of relationships between insects and various climatic factors, it is possible to obtain strong indications of insect assemblages' changes in response to climate change.

Results from previous chapters have indicated that the link between insect alpha-diversity and the alpha-diversity of plants is overall weak. This does nonetheless not rule out that plant species composition may play an important role in determining insect diversity. This suggestion is supported by previous studies where insect-plant relationship often appear to be linked to specific plant species or functional groups (Jactel & Brockerhoff, 2007; Riihimäki et al., 2005; Schaffers et al., 2008; Unsicker et al., 2006; Vehviläinen et al., 2007, 2008; Wardle et al., 1999).

It appears obvious that herbivores are determined by particular host plant species rather than overall plant diversity (Sobek et al., 2009b). Predatory insects are also likely to display preferences for specific plant species and groups which provide favourable micro-climatic conditions or shelter (Vehviläinen et al., 2008), while these plant species also benefit from the predatory insects by saving resources in pest defence (Heil et al., 1997). Areas with high plant diversity might therefore not provide the specific habitat structures predators are adapted to for example in relation to their foraging behaviour, leading to a decline in predatory insects' predation efficiency (Riihimäki et al., 2005). Hence, abundance and diversity of predatory insects are also potentially more strongly influenced by specific plant species and functional groups rather than overall plant species richness (see reviews by Zhang & Adams, 2011).

At the Changbai Natural Reserve (CNR), a group of scientists from the Institute of

Botany, Chinese Academy of Sciences (IB-CAS) conducted a series of vegetation surveys in 1963 (Chen et al., 1964). Vegetation surveys were re-conducted in 2006 at the identical plots, again by scientists from IB-CAS (Bai et al., 2011; Sang & Bai, 2009) (see Chapter 2). These surveys were used as baseline to understand of how the vegetation composition changed during recent decades. The aim of this chapter is to provide some suggestions how insect assemblages have changed according to climate change, trying to explore how insect α-diversity relates to vegetation composition and environmental conditions; how these relationships differ between the trophic levels occupied by herbivorous geometrid moth and predominantly predatory ground beetles. Additionally, the chapter also aims to provide a general overview of shifts in vegetation composition between the two vegetation surveys of 1963 and 2006, and of how the long-term changes of climate and vegetation composition in CNR have therefore potentially affected the diversity and composition of these two insect taxa. The main hypotheses are that the vegetation composition is significantly linked with the diversity of insects, and that insects are generally expected to move to higher altitudes based on the predictions of the statistic model.

5.2. **Sampling plots and data analysis**

All carabid data from the 33 plots and geometrid data from 25 plots in CNR were included as a basis for the investigations conducted here (see general results in Chapter 3). As indicated in Chapter 2, of the 33 plots, 27 were surveyed twice: in 1963 by Chen et al. (1964) and in 2006 by Sang and Bai (2009). I selected 27 plots using plot descriptions, GPS locations and guidance from staff from CNR Management Centre who also participated in the vegetation survey in 2006. I added 6 additional plots, forming a total of 33 sampling plots. This part formed a basis for the analysis of the insect-plant relationships. The 27 plots also surveyed in 1963 were used to investigate the long-term changes in the vegetation composition at CNR. All vegetation surveys were based on the same approach; detailed survey method can be found in Chapter 2.

Principal Components Analysis (PCA) was use to condense vegetation data into principal components (PCs) reflecting the main gradients in the changes of the vegetation composition. Two different sets of PCs were created: the first PCA was based on the number of species in individual plant families (family-based principal components, FPCs); the second PCA was based on the importance value (see Formula 1, Chapter 4) for individual species (species-based principal components, SPCs). Fisher's α was used to represent α-diversity of carabids and geometrids. To model and predict the α-diversity of carabids and geometrids, multiple linear regression (MLR) analyses was performed to select the most important independent variables which contributed significantly towards the explained variance ($P<0.05$). In the MLR, independent variables first include FPCs and SPCs, respectively, before elevation was entered as an additional variable.

Redundancy analysis (RDA) was used to analyze insect species composition changes in relation to vegetation composition. Within RDA, stepwise regression was used entering plant principal components as independent variables, again differentiating between FPCs and SPCs. Stepwise regression was stopped based on the reduction of the Akaike information criterion (AIC) (Johnson & Omland, 2004; Pakeman & Stockan, 2013; Rushton et al., 2004). Meanwhile, whether individual selected predictor variable contributed significantly ($P<0.05$) towards the model in explaining insect diversity was also considered after the regression was stopped at a minimum AIC. If the AIC difference between a model entering all 'significant' variables and the model with minimum AIC was small (<1%), the former model was selected; otherwise, the minimum AIC model was selected as the final model.

Nonmetric Multidimensional Scaling (NMDS) based on the 'Jaccard' (Appendix 1, equation 8) similarity indices for the number of species of each plant family was used to observe the species turn-over in the vegetation composition between the two survey times (1963 and 2006). To observe the overall climate change in CNR over the past 50 years, climatic data from 1958 to 2006 was obtained from records of the Songjiang meteorological station (at 720m asl) that is located on the northern section of the natural reserve. Finally, a series of linear models was established to predict the α-diversity changes of carabids and geometrids over time.

5.3. Results

5.3.1. Vegetation principal components

The first PCA based on the number of species in each plant family generated a total of 32 components (FPCs), with the 5 principle components (FPC1 – FPC5) individually explaining more than 5% of the total variance and representing an accumulated 76.5% of the original variance (Table 5) being used in subsequent analysis. Aceraceae, Saxifragaceae, Caprifoliaceae, Pinaceae, Rosaceae, Liliaceae, Ranunculaceae and Compositae all had high loading (absolute value >0.5) on these components (Table 5). The first component (FPC1), which already explained 37.1% of the total variance, was highly positively correlated with altitude (Pearson correlation: r=0.85, P<0.001). It was also positively correlated with herb species richness (r=0.38, P=0.031) and negatively with woody species richness (r=-0.66, P<0.001). FPC2 representing 14.5% of the explained variance was significantly correlated with total plant species richness (r=0.72, P<0.001), woody species richness (r=0.43, P=0.013) and herb density (r=-0.53, P=0.002). FPC3 (variance explained=12.5%) correlated with woody species richness (r=-0.51, P=0.002), total plant species richness (r=-0.57, P=0.001) and shrub density (r=0.47, P=0.008) (see Table 6).

Table 5 Loading of plant families on FPCs with eigenvalue proportions high than 5% (PCA based on the number of species in each plant families; vegetation data from 33 plots of which 27 plots surveyed in 2006 and 6 in 2012), and number of species of each family observed from 2006 and 1963 from a total of 27 study plots ('*' refers to FPCs with absolute loading value higher than 0.5% for respective families; '**' refers to cases where less species were observed in 2006 than 1963 for respective families).

Plant Families	**FPC1**	**FPC2**	**FPC3**	**FPC4**	**FPC5**	**Number of species (2006)**	**Number of species (1963)**
Vitaceae	-0.01	-0.03	-0.02	-0.02	-0.01	1	0
Violaceae**	0.41	-0.12	-0.27	-0.04	-0.06	2	5
Valerianaceae	0.27	0.03	-0.07	0.02	-0.05	1	1
Urticaceae	-0.22	0.38	0.15	-0.10	0.03	4	1
Umbelliferae**	-0.07	0.25	0.17	0.07	0.02	4	7
Ulmaceae**	-0.34	0.41	-0.02	-0.06	0.10	3	4
Tiliaceae	-0.31	0.00	-0.17	0.14	0.26	2	1
Thelypteridaceae	0.26	-0.07	-0.13	-0.10	-0.06	2	2
Sinopteridaceae	-0.04	-0.02	-0.01	0.00	-0.01	1	0
Saxifragaceae	-1.11 *	0.86 *	-0.22	-0.40	-0.19	8	8
Salicaceae	0.02	-0.01	-0.12	0.06	-0.15	3	2
Rubiaceae	0.07	0.40	-0.25	-0.02	0.17	3	3
Rosaceae**	0.67 *	0.49	-0.41	-0.72 *	0.65 *	15	17
Rhamnaceae	-0.05	0.09	0.01	-0.06	0.08	1	1
Ranunculaceae**	1.25 *	0.97 *	-0.10	0.41	-0.23	15	18
Pyrolaceae**	0.15	-0.09	0.00	0.09	-0.06	2	3
Primulaceae**	0.02	-0.19	0.04	-0.05	0.00	1	2
Polypodiaceae	0.03	-0.01	0.00	-0.01	-0.02	1	0
Pinaceae	0.04	-0.61 *	-1.14 *	-0.10	-0.12	5	4
Phrymaceae	-0.09	-0.04	-0.06	0.09	0.05	1	1
Papaveraceae	-0.06	0.10	0.04	-0.02	0.01	1	1
Oxalidaceae	-0.22	-0.22	-0.26	0.04	0.06	1	1
Osmundaceae	-0.05	0.06	0.01	-0.08	-0.01	1	1
Orchidaceae**	0.14	0.01	-0.09	-0.02	-0.04	1	3
Onocleaceae?	-0.06	0.10	0.04	-0.02	0.01	1	0
Onocleaceae	-0.06	0.10	0.04	-0.02	0.01	1	1
Onagraceae	0.17	-0.25	-0.20	-0.17	-0.08	2	1
Oleaceae	-0.40	0.45	-0.02	-0.06	0.03	3	3
Lycopodiaceae	0.14	-0.03	-0.07	-0.07	0.03	2	2
Liliaceae**	1.08 *	0.22	-0.38	-0.26	0.18	9	14

Leguminosae**	-0.04	0.08	0.00	-0.04	0.06	1	4
Labiatae**	-0.34	0.42	0.08	-0.01	0.01	3	4
Juglandaceae	-0.02	0.04	0.01	0.01	0.01	1	0
Guttiferae?	0.07	0.03	-0.04	0.05	-0.04	1	0
Grossulariaceae	0.15	0.16	-0.13	-0.02	-0.17	1	1
Gramineae**	0.49	-0.04	0.17	-0.08	0.08	4	6
Geraniaceae**	0.25	0.03	0.09	0.02	-0.05	1	2
Fagaceae	-0.16	0.17	0.06	-0.05	-0.11	1	1
Ericaceae	0.27	-0.12	0.33	-0.20	0.19	3	2
Equisetaceae	-0.16	0.11	-0.01	-0.04	-0.15	2	2
Dryopteridaceae	0.16	0.09	-0.06	-0.03	0.00	3	2
Cyperaceae**	-0.36	0.38	0.13	-0.25	-0.34	7	8
Cupressaceae	0.01	-0.03	0.07	0.01	0.04	0	0
Cruciferae	-0.19	0.16	0.06	0.01	-0.14	1	1
Compositae**	1.77 *	0.23	-0.42	0.25	-0.32	9	10
Chenopodiaceae	0.03	0.00	0.07	0.03	-0.01	1	0
Celastraceae	-0.27	-0.05	-0.10	0.04	-0.02	2	2
Caprifoliaceae	-0.18	-0.28	-0.25	-0.78 *	-0.62 *	8	7
Campanulaceae	0.00	0.19	-0.05	0.10	0.01	1	1
Boraginaceae**	-0.07	0.42	-0.08	0.04	-0.12	2	3
Betulaceae**	0.04	0.22	0.09	-0.06	-0.08	3	4
Berberidaceae	-0.20	0.09	-0.15	0.05	0.05	2	2
Balsaminaceae	-0.19	0.24	0.01	0.03	0.08	1	1
Athyriaceae	0.03	0.03	-0.35	-0.07	0.15	3	3
Asteraceae**	0.09	-0.05	0.13	0.00	-0.04	1	3
Araliaceae	-0.13	0.25	0.07	0.03	-0.19	1	1
Araceae	-0.08	0.10	0.02	-0.07	0.00	1	1
Aceraceae	-1.3 *	0.23	-1.03 *	0.55 *	0.08	8	7
Aristolochiaceae	-	-	-	-	-	0	1
Asclepiadaceae	-	-	-	-	-	0	1
Caryophyllaceae	-	-	-	-	-	0	2
Chloranthaceae	-	-	-	-	-	0	1
Cupressaceae	-	-	-	-	-	0	1
Euphorbiaceae	-	-	-	-	-	0	1
Gentianaceae	-	-	-	-	-	0	1
Gracilariaceae	-	-	-	-	-	0	1
Paeoniaceae	-	-	-	-	-	0	1
Podophyllaceae	-	-	-	-	-	0	1
Polemoniaceae	-	-	-	-	-	0	1
Sapindacea	-	-	-	-	-	0	1
Thymelaeaceae	-	-	-	-	-	0	1
Proportion explained / total species number	**37.10%**	**14.50%**	**12.50%**	**7.20%**	**5.20%**	**169**	**199**

The second PCA, which was based on the importance value of individual plant species, also generated 32 components (SPCs), of which the first 4 principle components (SPC1–SPC4) individually explaining more than 5% of the total original variance and jointly accounted for 68.9% of the total variance. Species with high loading (>0.1) were primarily from the plant families Aceraceae, Betulaceae, Oleaceae, Pinaceae, Caprifoliaceae, Ericaceae, Grossulariaceae and Gramineae (Table 7). Trees and shrubs generally had higher loadings than herbaceous species. SPC1 representing 32.1% of the total variance and was positively correlated with altitude (Pearson correlation: $r=0.78$, $P<0.001$), but negatively correlated with tree species richness ($r=0.45$, $P=0.009$), woody species richness ($r=-0.70$, $P<0.001$) and total plant species richness ($r=0.39$, $P=0.024$). This component was also positively correlated with vegetation density of the respective layers (see Table 6). The second component (SPC2) explained 18.2% and was correlated with altitude ($r=-0.55$, $P<0.001$), herb species richness ($r=-0.42$, $P=0.017$) and shrub density ($r=0.42$, $P=0.019$). SPC3, which explained 37.1% of the total variance, mainly correlated with overall plant species richness ($r=-0.58$, $P<0.001$) (see Table 6).

Table 6 Pearson correlations between vegetation principle components and altitude and plant diversity/density factors (*: 0.01<P≤0.05, **: 0.001<P≤0.01, ***: P≤0.001).

PCs	Altitude (m)	Tree species richness	Shrub species richness	Herb species richness	Woody species richness	Total plant species richness	Tree density	Shrub density	Herb density
FPC1	0.85***	-0.46**	-	0.38*	-0.66***	-	-	-	-
FPC2	-	-	0.36*	-	0.43*	0.72**	-	-	-0.53**
FPC3	-	-	-	-	-0.51**	-0.57***	-	0.47**	-
FPC4	-	-	-	-	-	-	-	-	-0.60***
FPC5	-	-	-	-	-	-	-	-	-
SPC1	0.78***	-0.45**	-	-	-0.70***	-0.39*	0.36*	0.58***	0.40*
SPC2	-0.55***	-	-	-0.42*	-	-	-	0.42*	-
SPC3	-	-	-	-	-0.37*	-0.58***	-	-	-
SPC4	-	-	-	-	-	-	-	-	0.40*

Table 7 Loading of plant species on SPCs with eigenvalue proportions high than 5% (PCA based on the importance value of individual plant species; T: tree layer, S: shrub layer, H: herb layer); only species with absolute loading value higher than 0.1 were shown here

Vegetation layer	**Family**	**Species**	**SPC1**	**SPC2**	**SPC3**	**SPC4**
T	Aceraceae	*Acer mono*	-	0.12	-	-
T	Betulaceae	*Betula ermanii*	0.87	-	-	-
T	Oleaceae	*Syringa reticulata*	-	-	-0.11	-
T	Pinaceae	*Larix gmelini*	-	-0.15	-	0.21
T	Pinaceae	*Pinus koraiensis*	-0.21	0.23	0.18	-
S	Aceraceae	*Acer buergerianum*	-	0.10	0.25	-0.18
S	Betulaceae	*Corylus mandshurica*	-	0.11	-0.16	-
S	Caprifoliaceae	*Lonicera edulis*	-	-	0.10	0.24
S	Caprifoliaceae	*Lonicera maximowiczii*	-	-	-0.11	-
S	Celastraceae	*Euonymus pauciflorus*	-	-	0.14	-
S	Ericaceae	*Rhododendron chrysanthum*	0.60	-	-	-
S	Grossulariaceae	*Grossularia burejensis*	-	-0.61	-	-0.21
S	Pinaceae	*Abies nephrolepis*	-	-0.26	0.18	-
S	Pinaceae	*Picea jezoensis*	-	-0.26	-	-
S	Rosaceae	*Rosa marretii*	-	-	-	0.13
S	Saxifragaceae	*Philadelphus schrenkii*	-	-	-0.10	-
S	Saxifragaceae	*Philadelphus tenuifolius*	-	-	-0.12	-
H	Boraginaceae	*Brachybotrys paridiformis*	-	-	-0.12	-
H	Gramineae	*Calamagrostis angustifolia*	0.19	-	-	-
H	Liliaceae	*Maianthemum dilatatum*	-	-	-	0.11
H	Onagraceae	*Circaea alpina*	-	-	0.13	-
H	Oxalidaceae	*Oxalis acetosella*	-0.12	0.10	0.31	-
-	-	**Proportion explained**	**32.1%**	**18.2%**	**11.4%**	**6.9%**

5.3.2. *Models predicting insect α-diversity*

The MLR model based on a stepwise regression entering the plant family-based PCs only included FPC1. This PC was negatively correlated with the α-diversity of carabids (model AIC=99.1, adjusted R^2=0.19, $F_{1,31}$=8.6, β=-0.55, P=0.006). In predicting the α-diversity of geometrid moths, FPC1 (β=-2.55, P=0.001), FPC2 (β=1.83, p=0.008) and FPC4 (β=1.45, P=0.03) were all included in the model (AIC=131.4, adjusted R^2=0.50, $F_{3,21}$=8.8, P<0.001).

When SPCs were selected in the MLR, SPC2 was the only predictor included. This PC showed a weak positive correlation with the α-diversity of carabids (model AIC=104.6, adjusted R^2=0.12, $F_{1,31}$=2.5, β=0.39, P=0.026). Two MLR models were generated predicting the α-diversity of geometrid moths. The first model contained SPC1 as the only predictor. This PC was negatively correlated with the dependent variable (model AIC=138.8, adjusted R^2=0.27, β=-6.7, $F_{1,23}$=10.0, P=0.004). The second model (adjusted R^2=0.44, $F_{1,23}$=10.3, P=0.001) additionally included SPC2 as a positive (β=0.42, P=0.011) predictor, with the AIC reduced to 133.4.

When calculating predictive models containing core environmental parameters, elevation alone was a better predictor for the α-diversity of both carabids and geometrids than any of the vegetation-based principal components. Both the α-diversity of carabids and geometrids decreased highly significantly with increasing elevation, with the trends being stronger in geometrids. The detailed model results for the correlations between elevation and insect alpha-diversity had already been shown and discussed in Chapter 4 (see Table 3, model 5 for carabids and model 8 for geometrids).

5.3.3. *Insect species composition and vegetation*

The stepwise regression of the first RDA based on the species composition changes of carabids and entering family-based vegetation principle components (FPCs) as independent variables resulted in 2 components (FPC1 and FPC3) that significantly contributed to the model ($P<0.05$) with an AIC of 254.9. The AIC was only slightly higher than the model that contained three components (FPC1, FPC2 and FPC3, AIC = 254.4). The first two axes generated in the RDA accounted for an overall explained variance of 52%. The first axis was highly correlated with FPC1 (Pearson correlation: $r=0.89$, $P<0.001$), while the second axis was significantly correlated with FPC3 (Pearson correlation: $r=0.63$, $P<0.001$). Overall, FPC1 explained 46% of the original variance ($F_{1,31}=29.0$, $P=0.001$), while FPC3 only explained an additional 6% ($F_{1,30}=3.8$, $P=0.002$). Carabid species compositions at low elevational habitats (MCBF and KPF) formed a tight cluster, while species assemblages at higher elevation habitats did not group together (Figure 25a). Most of the 17 carabid species with more than 30 individuals in the samples were clustered towards the centre of the RDA plot, indicating that the distribution patterns of these species were not strongly influenced by plant compositions. Meanwhile, *Carabus aurocinctus* Motschulsky, *Pterostichus comorus* Jedlicka, *Pterostichus* sp.1 and *Carabus venustus* Morawitz were positively associated with increases in value of FPC1 (Figure 25b).

Similar to the results from carabids, stepwise regression of RDA based on geometrid moth distribution patterns resulted in the same two components (FPC1 and FPC3) showing significant contributions ($P<0.05$) to the resulting model, with an AIC of 242.3, which was also only very slightly larger than the AIC (241.6) for the model that included all five FPCs. The overall explanation of geometrid moth composition by these two components was 40%, where FPC1 contributed 26% ($F_{1,22}=9.6$, $P=0.001$) and FPC3 contributed 14% ($F_{1,22}=5.0$, $P=0.001$) to the overall variance, respectively. In addition, FPC1 was also significantly correlated with the first Axis (Pearson correlation: $R^2=0.62$, $P=0.001$), and FPC3 was significantly correlated with the second Axis (Pearson correlation: $r=0.6$, $P=0.002$). Geometrid moth assemblages at low elevational habitats were negatively associated with FPC1 (Figure 25c). Different forest types had strongly differentiated clusters, where KPF, MCF and SMCF were grouped adjacent to each other, while MCBF and BF communities appeared more heterogeneous (Figure 25c). Most common species of geometrid moth represented by more than 50 individuals in the samples were also grouped in the centre of the RDA plot. Of the remaining common species that had relatively high loadings on the ordination axes, most were positioned in the middle between FPC1 and FPC3, such as *Triphosa dubitata* Linnaeus, *Odontopera bidentata harutai* Inoue, *Xanthorhoe biriviata* Borhauson, *Venusia cambrica* Curtis and *Hydriomena impluviata* Denis & Schiffermüller, indicating that those species were somewhat influenced by environmental parameters underlying both FPC1 and FPC3 (Figure 25d).

Table 8 Species-abbreviations of carabids and geometrids for Figure 25 and Figure 26

Taxa	Species	Abbreviations
Carabids	*Carabus aurocinctus* Motschulsky	CarAur
	Pterostichus comorus Jedlicka	PteCom
	Pterostichus sp	PteSp
	Carabus venustus Morawitz	CarVen
	Pterostichus adstrictus Eschscholtz	PteAds
	Carabus seishinensis Lapouge	CarSei
Geometrids	*Venusia cambrica* Curtis	VenCam
	Hydriomena impluviata Denis & Schiffermüller	HydImp
	Abraxas suspecta Warren	AbrSus
	Xanthorhoe sp	XanSp
	Triphosa dubitata Linnaeus	TriDub
	Heterothera serraria Lienig	HetSer
	Odontopera bidentata Clerck	OdoBid
	Alcis sp	AlcSp
	Xanthorhoe biriviata Borhauson	XanBir
	Arichanna melanaria Butler	AriMel

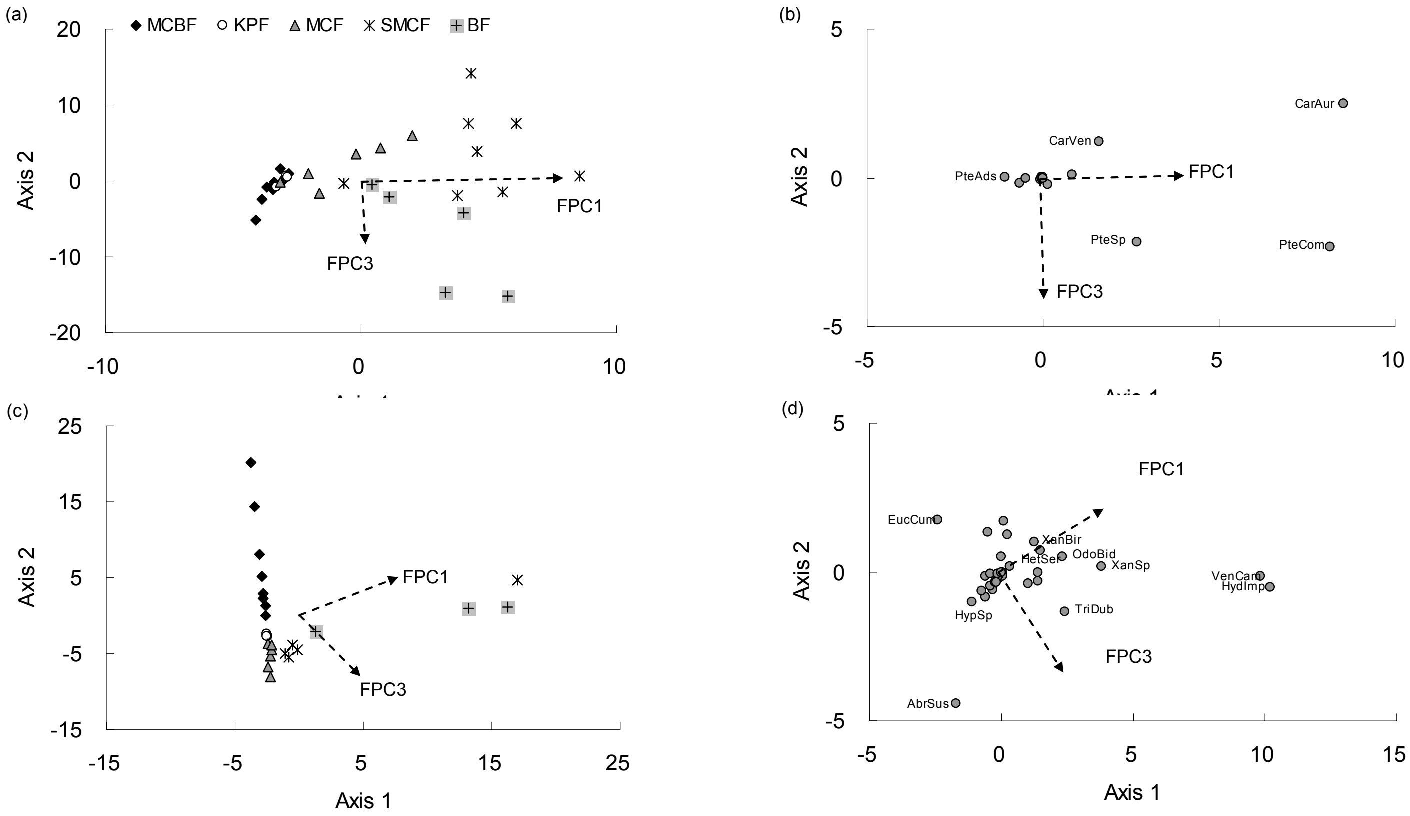

Figure 25 RDA ordination plots of the species distribution of ground beetles showing locations of study sites (a) and of common species (>30 individuals, b), and of geometrid moths again indicating the location of study sites (c) and common species (>50 individuals, d) on the ordination plots, where independent variables were selected from the FPCs (species abbreviations can be found in Table 8)

The second RDA stepwise regression based on the plant species-based principle components (SPCs) as independent variables also resulted in 2 components (SPC1 and SPC2) that significantly ($P<0.05$) contributed to the model. The AIC (249.9) of the finally selected model again was only slightly larger than the minimum AIC model (249.8) that contained three components (SPC1, SPC2 and SPC3). Thus, the model with two significant variables was selected. Again, two constrained axes were generated for the RDA ordination plot, where SPC1 ($F_{1,30}=14.4$, $P=0.001$) and SPC2 ($F_{1,30}=28.6$, $P=0.001$) contributed 50% and 9% towards the original variance. Pattern of carabid assemblages were very similar to the model from the first RDA, with assemblages originating from low elevational forest habitats again forming one dense cluster, while plots from higher elevational habitats were more dispersive (Figure 26a). Most common species grouped in the middle, and those species strongly influenced by the two SPCs were the same mentioned already above in the FPC-based models (Figure 26b).

In analysing species composition changes of geometrid moths, the overall diagram of the resulting second RDA using SPCs as independent variables was again similar to the RDA based on FPCs. Again, two significant components (SPC1 and SPC2) were included, with an overall explained variance of 40%, towards which SPC1 contributed 36% and SPC2 only contributed 4%. The AIC (242.1) of this model was very similar to the minimum AIC (241.9) model that additionally included component SPC3 which nonetheless did not contribute significantly ($P\geq0.05$) towards the explained variance. Sampling sites from low and middle ranges of the elevational gradient were again grouped together, while the higher elevation sites (BF) were more heterogeneous (Figure 26c). Common species of geometrids again strongly grouped in the middle of the ordination plots. For those species with relatively high loading on ordination axes, most were negatively associated with SPC2, but positively associated with SPC1 (Figure 26d).

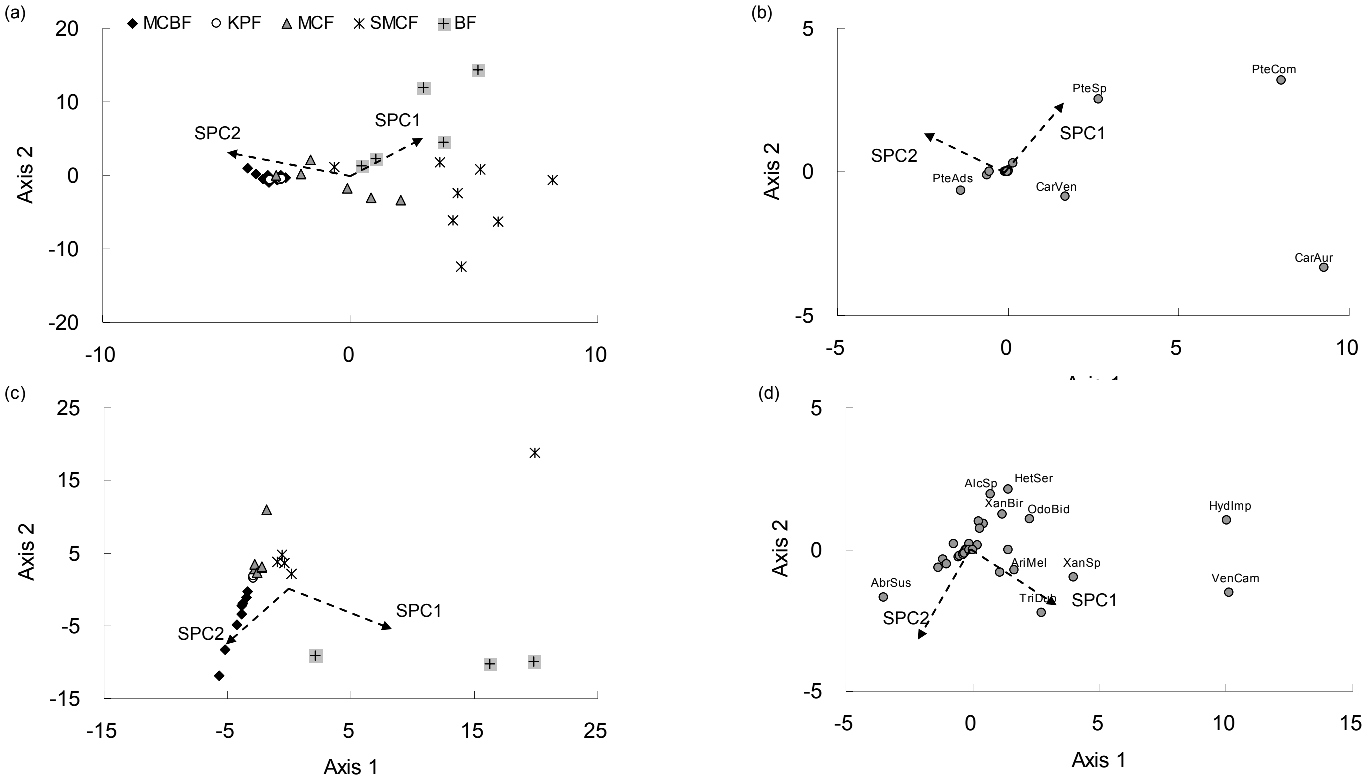

Figure 26 RDA of the species distribution of ground beetles focuses on study sites (a) and common species (>30 individuals, b), and geometrid moths focuses on study sites (c) and common species (>50 individuals, d), where independent variables were selected from the SPCs (species abbreviations can be found in Table 8)

5.3.4. Long term vegetation composition changes

In 1963, 199 plant species of 63 families were recorded on the 27 plots, and the same plots contained 169 plant species of 57 families in 2006. Seven of the 12 most species-rich families had fewer species observed in 2006 than 1963, with a total loss of 17 species. Number of plant species in the top 3 most species-rich plant families (Ranunculaceae, Rosaceae and Compositae) all had lower species numbers in the 2006 surveys compared with the 1963 surveys (Table 5).

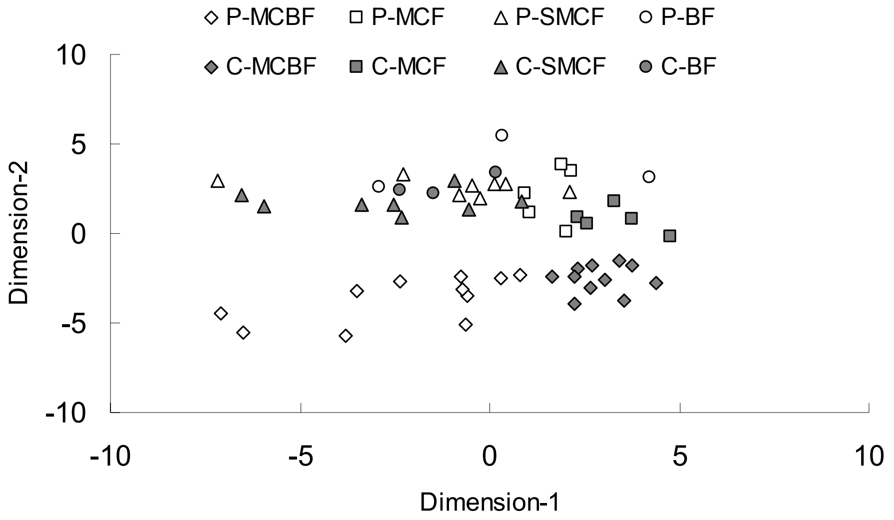

Figure 27 NMDS ordination plot based on 'Jaccard' similarity matrices of the comparison of vegetation family composition for different forest types (stress=0.09); symbols with the same shape refer to the same habitat, where white background refers to data from the past (P, surveyed in 1963) and grey background refers to current data (C, surveyed in 2006) (MCBF: mixed coniferous and broad-leaved forest; KPF: Korean Pine Forest; MCF: mixed coniferous forest; SMCF: sub-alpine mixed coniferous forest; BF: birch forest)

Results from the NMDS based on the plant family composition showed a shift in species composition between 1963 and 2006. In particular, vegetation composition of the low elevational forest types mixed coniferous and broad-leaved forest (MCBF) showed two distinctive, non-overlapping clusters for 1963 and 2006. The MCBF in 1963 also showed a greater heterogeneity than in 2006, reflecting a reduction in the β-diversity within this forest. The middle elevational forest types, mixed coniferous forest (MCF) and sub-alpine mixed coniferous forest (SMCF), on the contrary, showed a lower variation in plant species composition in 1963 than in 2006. Furthermore, the species composition of high elevation birch forests appears to resemble SMCF more closely in 2006 than in 1963 (Figure 27).

5.3.5. Long-term Climate change and insect diversity predictions

Long-term climatic data showed that annual mean temperature increased gradually over time since the 1950s (linear regression, R^2=0.5, $F_{1,47}$=47.2, β=0.035, P<0.001). No significant trend was observed for precipitation (Figure 28).

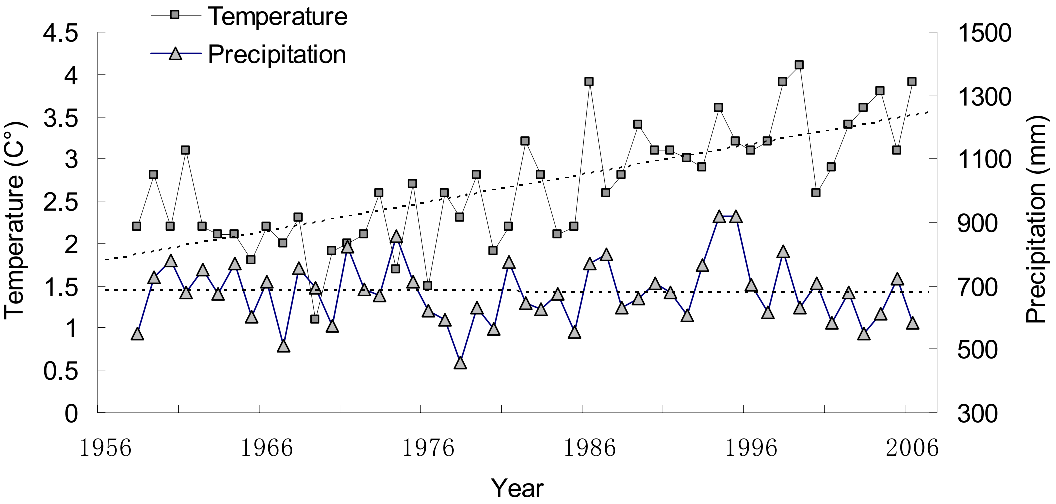

Figure 28 Changes in annual mean temperature and precipitation in CNR from 1958 to 2006 measured at Songjiang meteorological station (data from China Meteorological Data Sharing Service System, 2007)

Results from this chapter and Chapter 4 all indicated that elevation was the most significant factor in predicting α-diversity changes of both carabids and geometrids. Considering the main climatic factor correlated with elevation was temperature, a basic model based solely on temperature change already allows a first prediction of the trends of α-diversity in carabids and geometrids over time and with the changing elevation. According to Figure 28, the predicted annual mean temperature at the 720m where Songjiang meteorological station is located was 2.12°C in 1963 and 3.81°C in 2012. The predicted temperature change with increasing elevation was according to Bai et al. (2011)'s suggestion a decrease of 0.51°C with an increase of 100m in altitude. Hence, the temperature for year 'i' at altitude 'j' can be expressed by Formula 2, while the annual predicted mean temperatures for 2012 and 1963 can be seen in Table 9.

$$T_{i,j} = \beta_1 Y_i + \beta_2 (H_j - H_{base}) + C \text{, so } H_j = \frac{1}{\beta_2} T_{i,j} + (H_{\text{base}} - \frac{\beta_1 Y_i + C}{\beta_2})$$

Formula 2: Change of temperature with change of altitude, where '$T_{i,j}$' is the predicted temperature for year 'Y_i' and altitude 'H_i' ($700\text{m}<H_i<2600\text{m}$), '$H_{base}$' is the elevation of the reference area at 720m, 'β_1' is the annual temperature changing rate (0.0345°C/year), 'β_2' is the temperature change per unit altitude (-0.51°C/100m), and 'C' is a constant based on the temperature-year regression (-65.6).

In analyzing the relationship between elevation and α-diversity of carabids, using log transformed elevation as independent variable resulted in better model fits than using elevation directly, with the model AIC improved from 96.3 to 94.3, and with the adjusted R^2 improving from 0.26 to 0.30 ($P<0.001$ in both cases). Predicted temperature in 2012 was used to establish the relationship between temperature and α-diversity of carabids (Formula 3).

$$D_{car,i,j} = \beta_{car} \log\left[\frac{1}{\beta_2} T_{i,j} + (H_{base} - \frac{\beta_1 Y_{2012} + C}{\beta_2})\right] + C_{car} = \beta_{car} \log\left[\frac{\beta_1}{\beta_2}(Y_i - 2012) + H_{\text{j}}\right] + C_{car}$$

Formula 3: Predicting α-diversity of carabids ($D_{car,i,j}$) in year 'Y_i' and altitude 'H_i', where $\beta_{car}=-3.79$ and $C_{car}=15.04$.

For predicting α-diversity of geometrids, log transformed elevation did not improve the model fit; so that a direct linear regression model was established (Formula 4).

$$D_{\mathrm{geo},i,j} = \beta_{geo}\left\lfloor \beta_1 Y_i + \beta_2 (H_j - H_{base}) + C \right\rfloor + C_{geo}$$

Formula 4: Predicting α-diversity of geometrids ($D_{geo,i,j}$) in year 'Y_i' and altitude 'H_i', where β_{geo}=1.57 and C_{geo}=12.21.

Consequently, an overall predicted α-diversity of carabids and geometrids in each sampling plot in 1963 and 2050 can be found in Table 9. According to the model, temperature increased by about 1.7°C between 1963 and 2006. The model predicts an overall increase in α-diversity of insects at the elevational gradient in response to warming. As only one climate variable (temperature) was included, this basic model reflects the strength of species responses to temperature shifts according to their temperature requirements.

Table 9 Predicted Fisher’s α-diversity for carabids and geometrids in 1963 and 2050 (C.: carabid; G: Geometrid; α: Fisher’s α-diversity; Pre: predicted value; Obs: observed value)

		Pre.			Obs.	Pre.		Obs.	Pre.	
Plot No.	Alt (m)	2012 Temp (°C)	1963 Temp (°C)	2050 Temp (°C)	C. α	C. α (1963)	C. α (2050)	G. α	G. α(1963)	G. α(2050)
P1	770	3.55	1.86	4.86	5.23	3.51	4.77	-	15.14	19.85
P2	780	3.50	1.81	4.81	7.61	3.50	4.74	12.17	15.06	19.77
P3	790	3.45	1.76	4.76	3.09	3.48	4.71	13.23	14.97	19.69
P4	790	3.45	1.76	4.76	6.17	3.48	4.71	15.16	14.97	19.69
P5	800	3.40	1.71	4.71	3.89	3.47	4.68	-	14.89	19.61
P6	820	3.30	1.61	4.61	2.30	3.44	4.62	22.09	14.73	19.45
P7	850	3.15	1.45	4.46	5.07	3.40	4.53	17.71	14.49	19.21
P8	870	3.04	1.35	4.35	4.56	3.37	4.48	15.16	14.33	19.05
P9	870	3.04	1.35	4.35	4.08	3.37	4.48	11.46	14.33	19.05
P10	900	2.89	1.20	4.20	3.48	3.33	4.40	-	14.09	18.81
P11	910	2.84	1.15	4.15	3.27	3.31	4.37	17.58	14.01	18.73
P12	1040	2.18	0.49	3.49	2.78	3.15	4.07	13.62	12.97	17.69
P13	1050	2.13	0.43	3.44	4.10	3.14	4.05	13.41	12.89	17.61
P14	1060	2.07	0.38	3.39	3.02	3.13	4.03	15.03	12.81	17.53
P15	1150	1.62	-0.08	2.93	4.43	3.02	3.86	14.62	12.09	16.81
P16	1170	1.51	-0.18	2.82	4.15	3.00	3.82	14.82	11.93	16.65
P17	1200	1.36	-0.33	2.67	3.50	2.97	3.77	13.45	11.69	16.41
P18	1330	0.70	-0.99	2.01	2.57	2.83	3.55	7.64	10.65	15.36
P19	1340	0.65	-1.04	1.96	3.23	2.82	3.54	6.07	10.57	15.28
P20	1350	0.60	-1.10	1.91	3.53	2.81	3.52	7.83	10.49	15.20
P21	1520	-0.27	-1.96	1.04	2.71	2.66	3.29	7.58	9.12	13.84
P22	1600	-0.68	-2.37	0.63	2.82	2.59	3.18	9.70	8.48	13.20
P23	1600	-0.68	-2.37	0.63	2.71	2.59	3.18	7.68	8.48	13.20
P24	1620	-0.78	-2.47	0.53	2.82	2.57	3.16	11.47	8.32	13.04
P25	1660	-0.99	-2.68	0.33	2.64	2.54	3.11	-	8.00	12.72
P26	1730	-1.34	-3.03	-0.03	3.05	2.48	3.03	-	7.44	12.16
P27	1740	-1.39	-3.08	-0.08	3.50	2.47	3.02	11.15	7.36	12.08
P28	1750	-1.44	-3.14	-0.13	2.60	2.46	3.01	-	7.28	12.00
P29	1820	-1.80	-3.49	-0.49	3.85	2.41	2.93	10.95	6.72	11.44
P30	1950	-2.46	-4.16	-1.15	3.26	2.31	2.80	6.31	5.68	10.39
P31	2000	-2.72	-4.41	-1.41	2.38	2.28	2.76	4.38	5.28	9.99
P32	1990	-2.67	-4.36	-1.36	3.22	2.28	2.77	-	5.36	10.07
P33	1960	-2.52	-4.21	-1.20	3.05	2.31	2.79	-	5.60	10.31

5.4. Discussion

5.4.1. Vegetation composition and insect diversity

The responses in α-diversity and species composition of geometrid moths and ground beetles in relation to plant species composition and environmental parameters were similar, while the response magnitude was different. In models predicting insects' α-diversity based on the FPCs, both ground beetles and geometrid moths were negatively correlated with increases in FPC1. As Aceraceae, Saxifragaceae, Oleaceae, Cyperaceae and Ulmaceae all have high negative loadings on this component, the diversity of these families appears to be positively linked with the α-diversity of both insect taxa. In term of specific plant species, the positive correlation between SPC2 and α-diversity of both taxa indicates that those species with positive loading seems to be positively associated with the α-diversity of carabids and geometrids. These species include *Acer mono* Maxim, *A. buergerianum* Miq, *Corylus mandshurica* Maxim.et Rupr, *Pinus koraiensis* Siebold et Zuccarini and *Oxalis acetosella* Linnaeus. *P. koraiensis* and *O. acetosella* also appear positively associated with insect diversity via their negative association with SPC1.

As FPC1, SPC1 and SPC2 are however also highly correlated with elevation, it can be speculated that the relationship between the insect taxa and the aforementioned plant species and families are actually driven by their similar responses to changes in the same underlying abiotic factors such as temperature and precipitation, which are both significantly linked with changes in elevation. This assumption is strengthened when environmental parameter are added in the model, which resulted in elevation appearing as the best predictor, which has also been commonly reported by other studies (Axmacher et al., 2009; Brehm et al., 2007; Hawkins & Porter, 2003).

FPC1 and SPC1 were also the most important factors in explaining the variance of species turnover of insect assemblages, while the interactions were again more likely caused by the changes in the same environmental factors that resulted from the change in elevation. This finding is again in line with findings from Brehm et al. (2003a) and Rodríguez-Castañeda et al. (2010) in South America and from Axmacher et al. (2009) in Africa.

The overall elevational trends of the α-diversity of both geometrids and carabids were very similar – a linear decrease with an increase in elevation; but with a stronger trend in geometrid moths than in carabids. A possible reason of this difference might be due to the difference in dispersal ability for the two groups. Regional species diversity is determined by the combination of species immigration and extinction rate, while species dispersal ability can obviously influence species immigration (MacArthur, 1967). The higher dispersal ability of geometrids is an important factor potentially also determining the larger regional species richness in the moths in comparison to the ground beetles that are often unable to fly. Historically, in facing environmental fluctuations, geometrid species have better options to colonize other suitable habitat patches than ground beetles, resulting in more habitat generalists remaining in ground beetles as forest habitat specialists suffered when parts of the forests especially at lower elevations were logged (Shao et al., 1994). This pattern can also potentially explain that the species composition in different forests for ground beetles were less well distinguishable in comparison to geometrid moths.

The link between α-diversity of geometrid moths and both family-based and species-based plant composition was stronger than in carabids, which probably reflects bottom-up effects (Halaj & Wise, 2001; Kagata & Ohgushi, 2006; Randlkofer et al., 2010; Rzanny et al., 2012). Accordingly, the change of climate and plant species composition over the past half-century can be expected to have had a stronger impact on the α-diversity of geometrid moths than on ground beetles. RDA results, however, showed that vegetation principle components can explain a greater proportion of the species compositions of carabids in comparison to geometrid moths. The observed trends have also been reported by Voigt et al. (2003) who reported that species at different tropic levels have differing sensitivity in response to changes of core climatic factors, i.e. that species representing higher trophic level (here: carabids) have a higher sensitivity than species at lower trophic levels (here: geometrid moths). A possible explanation for this pattern is that carnivores are more active in their foraging and thus have higher metabolic rates than herbivores (Townsend & Hughes, 1981), resulting in carnivore ground beetles being more sensitive to resource and environmental changes than geometrids.

5.4.2. Long-term vegetation change and insect diversity

For the α-diversity of geometrid moths, the model results suggest positive links with the diversity of a number of plant families, including Ranunculaceae, Rosaceae, Compositae, Aceraceae and Saxifragaceae. Nonetheless, most of these families are not currently known to be important host plants for geometrid caterpillars, and the links between these plant families and the diversity of geometrid moth are therefore again likely to be due to the same response in moths and plants to environmental factors. Notwithstanding, these families could still be potentially used as indicators for the diversity of geometrids. Unfortunately, most of these plant families have decreased in species richness over the past half-century, indicating that geometrid moths may have also experienced decreases in diversity due to the climate changes occurring at CNR. In fact, apart from Ulmaceae and Betulaceae which lost one species from their local species pool according to the vegetation surveys, the remaining woody plant families are all still present, although partly with shifting abundances and distribution ranges. The main species loss for plants has occurred in the understory layer, as reported by Sang and Bai (2009).

In relation to the more subtle changes in the vegetation, there are distinctive shifts in the family-based plant compositions particularly at the lower elevation habitats MCBF. This indicates that species composition of insect taxa particularly in geometrids is likely to have changed significantly in these forests, too. These changes are most likely due to long-term climate change and particularly due to the increase in temperature. Climate change also results in a reduction in environmental heterogeneity at low elevation areas over time. Furthermore, as the undergrowth of the uppermost birch forest is becoming increasingly colonized by herbs previously restricted to the lower SMCF, it is likely that the respective moth species primarily restricted to the BF and its undergrowth will also come under increasing pressure (see also discussion in Chapter 3, and reports from Bai et al., 2011). The final model predicting α-diversity of carabids and geometrids reflects the pattern of species tracking temperature requirements and moving toward higher altitudes. The increasing temperature from 1963 to 2012 has as resulted in a theoretical upwards shift of temperature zones by about 400m, resulting in a high risk of extinction for species living in the uppermost forests. Meanwhile, the observed higher plant heterogeneity in 2006 compared with 1963 at middle elevations, which is probably partly due to human disturbances and especially the developing of roads with the development of tourism, could also pose further risks for insects. The increasing habitat heterogeneity resulting from forest fragmentations may prevent insects from successfully migrating to higher elevation habitats in the course of climate change (Noss, 2001).

5.4.3. Synthesis

Overall, given that links between the diversity and composition of plants and carabids and geometrids were weak and partly indirect, the long-term vegetation composition changes in CNR can only provide a first indication of the diversity changes of the insects. In order to get a more detailed view of how insects respond to climate change, long-term detailed insect monitoring is required. To predict insect diversity pattern in response to climate change more precisely, additional factors such as precipitation need to be included. Climatic data from more than one meteorological station are essential for such an approach, which nonetheless proves very difficult to obtain for the study region.

Chapter 6. Insect diversity patterns in secondary and plantation forests in central Northern China—a case study from Dongling Mountain, West Beijing

Summary

Secondary and plantation forests have become important components of the global forest cover, while it is unclear to what degree these forests contribute towards global biodiversity conservation. This question is particularly important for China, as China harbours the world's largest plantation forests. This chapter focused on the diversity of ground beetles and geometrid moths in the Dongling Mountain (DLM) range in Beijing, which contains a range of different secondary and plantation forests. Results showed that the overall α-diversity was high in this area compared with other temperate forest ecosystems in northern China. α-diversity was not significantly different between some of the plantation and secondary forest types, while species composition, particularly for carabids, differed distinctively between forest types. In this chapter, I also calculated species indicator values for carabids and geometrids in different forests. Results suggested that carabids species composition performs better than single carabid species, while single species are better indicators than species composition for geometrids moths.

6.1. <u>Introduction</u>

Harbouring the world's largest plantation forests (Chinese State Forestry Bureau, 2011; FAO, 2006), China's large-scale afforestation and reforestation programmes have been criticized of lacking clear conservation and habitat restoration objectives and may hence result in biodiversity degradation (Cao et al., 2010b; Sayer et al., 2004; Xu, 2011). In north China, nearly all primary temperate forests have been destroyed, resulting in a widespread cover of secondary forests and forest plantations. Nonetheless, not least due to the marked regeneration of native forest vegetation in the undergrowth of many forest plantations, logging beyond normal stand management has now been strictly banned even in most plantation forests (Wang et al., 2007), generating a number of extremely large-scale, well-protected plantation and secondary forest mosaics (Li, 2004). This development has been underpinned by a number of government programmes aimed at conserving reforestation and afforestation forests resources (see also Chapter 1).

The forest of Dongling Mountain (DLM), located in the Taihang Mountains in north-western Beijing, represents a typical mosaic of secondary forest and forest plantation ecosystems. The restored secondary forests and plantations of larch and pine forests about 50 years of age in this area harbour overall high levels of phytodiversity and a more complex structure than many similar representatives of these forest types (Huang & Chen, 1994; Jiang et al., 1994; Ma et al., 1995; Sang, 2004). Secondary and plantation forests are seen as instrumental in addressing a number of environmental issues like soil erosion and carbon sequestration. Nonetheless, their role in biodiversity conservation in DLM and elsewhere is widely unknown.

In spite of extensive vegetation studies conducted in the DLM area (Huang & Chen, 1994; Jiang et al., 1994; Liu et al., 2010a; Ma et al., 1995; Ren et al., 2006; Sang, 2004; Su et al., 2000; Su & Sang, 2004; Wang et al., 2000; Zhang et al., 2012), very little attention has been given to the species-rich insect groups. Within their limited study, Yu et al. (2010) proposed a lower species richness of ground-dwelling beetles in plantation forests of native pine than in oak-dominated secondary forests. The aim of this Chapter is to provide a basic overview of the species diversity of carabids and geometrids in the different forest types in DLM, to compare the α-diversity and species composition amongst the forests and to identify indicator species associated with individual forest types. The main hypotheses are that the secondary forest types (oak, mixed and birch forest) harbour a higher α-diversity of both insect taxa than larch and pine plantation forests, and that each forest type contains a distinctive insect species assemblage.

6.2. Sampling plots and data analysis

In DLM, a total of 36 sampling plots were selected. Of these, 20 plots were located near the Beijing Forest Ecosystem Research Station (BFERS) at elevations between 1100m and 1500m asl. At these plots pitfall trapping was carried out in the summers of 2011 and 2012, and light trapping in 2011. At the remaining 16 plots, pitfall trapping was limited to 2011 and did not yield enough specimens for further analysis (see also Chapter 2). The 20 main sampling plots were located at five distinct forest types with four plots each at plantation larch forest, plantation pine forests, secondary oak forests, mixed broad-leaf forests and birch forests. Each plot measured $20\times20\text{m}^2$, and two pitfall traps were set two metres apart in the centre of the plot. Light traps were located at the very centre of each plot where the topography allowed for this. In cases where the topography of the plots prevented the setting of traps in the plot centre, the equipment was moved to more level areas within the plot.

As the number of observed individuals sampled at individual plots was too small to calculate reliable α-diversity values (Hayek & Buzas, 2010) (11 plots for carabids and 5 plots for geometrids with number of individual less than 50), data for all plots representing the same forest type hence were pooled. To compare the α-diversity of carabids and geometrids among different forests, individual-based rarefaction was used (see Chapter1, equation 1).

The species indicator value (IndVal) (De Cáceres et al., 2010) was calculated to identify the most characteristic insect species of each forest type. This index is the combination of relative abundance and relative occurrence frequency of species in respective forest types (Formula 5), which has been widely used in identifying bioindicator species and taxa in ecology studies (Bachand et al., 2014; Brunet et al., 2011; Ding et al., 2011; Franssen et al., 2011; Hartmann et al., 2012; Keith et al., 2012; Schröder et al., 2013). The significance value of individual species was evaluated by Monte Carlo tests.

$$IndVal_{i,j} = \frac{\sum_{i \in C} a_i}{a} \times \frac{\sum_{i \in C} n_i}{\sum_{i \in C} N_i}$$

Formula 5: Indicator Value ‘$IndVal_{i,j}$’ for species ‘j’ in site group ‘i’, where ‘N_i’ is the number of sites belonging to the ‘i^{th}’ group, ‘n_i’ is the number of sites in the ‘i^{th}’ group where a species occurs, ‘a’ is the sum of abundance of the target species for all sites, and ‘a_i’ is the sum of abundances of that species in ‘i^{th}’ group

CNESS dissimilarity matrices (see Appendix 1, equation 9) were subsequently ran among the different forest types. NMDS ordination was used to visualize the resulting turnover patterns. Understory vegetation species were used to analysis species composition of plants because the tree cover is partly planted and hence not a very good representation of the site-specific environmental conditions. The plant species composition was analyzed using NMDS based on “Jaccard-Index” (see Appendix 1, equation 8) similarity matrices calculated using presence/absence data for the understory plant species. Mantel tests were used to analyse the correlation between species turnover of the two insect taxa and the vegetation.

CNESS results were calculated using the software COMPAH (Gallagher, 1998). All other calculations and statistics were computed in R (R Development Core Team, 2011), using the package ‘indicspecies’ (Cáceres & Legendre, 2009) to calculate species indicator values, the package ‘vegan’ (Oksanen et al., 2012) to carry out the NMDS analysis and the package ‘permute’ (Simpson, 2012) to carry out Monte Carlo permutation tests.

6.3. Results

In the main study area near the BFERS, vegetation surveys showed that the 20 study plots contained 24 mature tree species and 68 understory shrub and herb species. Pitfall traps caught 1488 ground beetles representing 24 species across the entire

DLM study area. As the additional area (see Chapter 2) was only sampled in 2011 and did not yield enough specimens for sufficient analysis, only samples from the main study area near the BFERS were used in the subsequent analysis. The 20 main sampling plots contained a total of 1191 carabid individuals representing 23 species (see Appendix 4). Among the five forests (pine, oak, mixed, larch and birch forests), the abundance of carabids was highest in birch forest where 413 individuals were sampled, followed by larch forests with 327 individuals, while the remaining three forests yielded very similar abundances of about 150 individuals, each. *Pterostichus acutidens* Fairmaire was the most abundant species for the main sampling area, accounting for 44.5% of all individuals caught. This species was dominant in mixed (57.0%), larch (63.6%) and birch (50.4%) forests, whereas the most dominant species in pine forest was *Carabus crassesculptus* Kraatz (40.7%) and *Carabus vladimirskyi* Dejean (42.0%) had the highest abundance in oak forest.

A total of 2047 geometrid moths were sampled in the five forest types, of which 105 specimens (5.1%) had to be discounted due to the substantial damage that obtained during sampling under very wet conditions, which prevented their secure identification. The remaining 1942 individuals were separated into 165 species representing the four families Ennominae (1309 individuals), Larentiinae (346 individuals), Sterrhinae (199 individuals) and Geometrinae (88 individuals) (Appendix 5). Overall, *Phanerothyris sinearia* Guenée was the most common species, accounting for 11.1% (215 individuals) of the total specimens. This species was dominant in pine (11.4%), mixed (25.3%) and larch (9.6%) forests. *Arichanna melanaria* Butler was the most abundant species in the birch forest (11.2%), and *Ctenognophos* sp. contributed the highest abundance in the oak forest samples (9.3%).

In term of all geometrid moths, automatic light traps recorded a total of 1238 individuals representing 140 species, while manual light tower allowed the catching of an additional 740 individuals representing 116 species. Subfamily compositions of both number of individuals and number of species were very similar for the two sampling techniques (Figure 29). Nonetheless, manual sampling yielded 25 species that were not recorded in the automatic sampling, while the light traps caught 49 species not recorded in the manual samples. Manual sampling resulting in 18 additional species in both larch and pine forest and 20 additional species in mixed forest, 10 in oak forest and 13 in birch forest when compared to the trap samples.

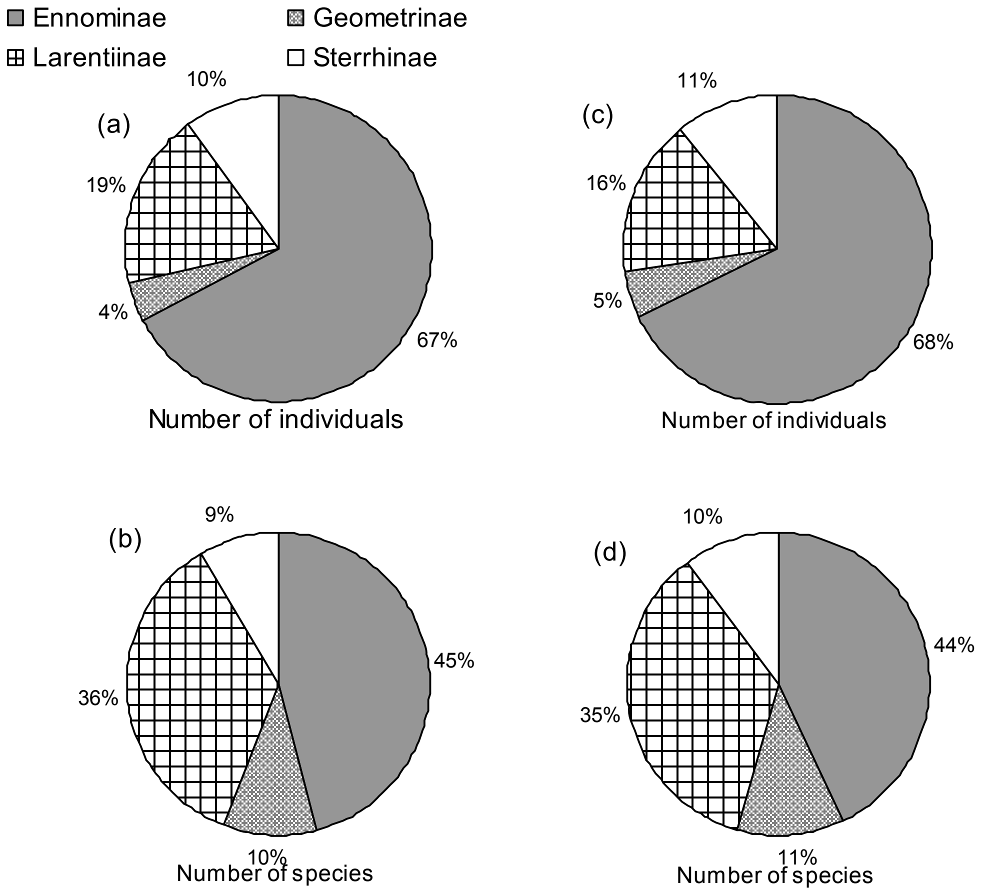

Figure 29 Subfamily composition for automatic sampling of number of individuals (a) and number of species (b) and for manual sampling of number of individuals (c) and number of species (d)

6.3.1. Comparison of α-diversity between different forests

The number of carabid species sampled was highest in mixed forest with 17 species, while pine and oak forests contained a recorded species richness of 16 and 14 species, respectively. Larch and birch samples had the joint lowest species richness with 13 species Rarefied species numbers were significantly higher for mixed, oak and pine forests, with the naturally regenerated mixed forest harbouring the highest beetle diversity, followed closely by oak forests and subsequently the pine plantations. Larch and birch forests had significantly lower rarefied species richness than the aforementioned three forest types (Figure 30).

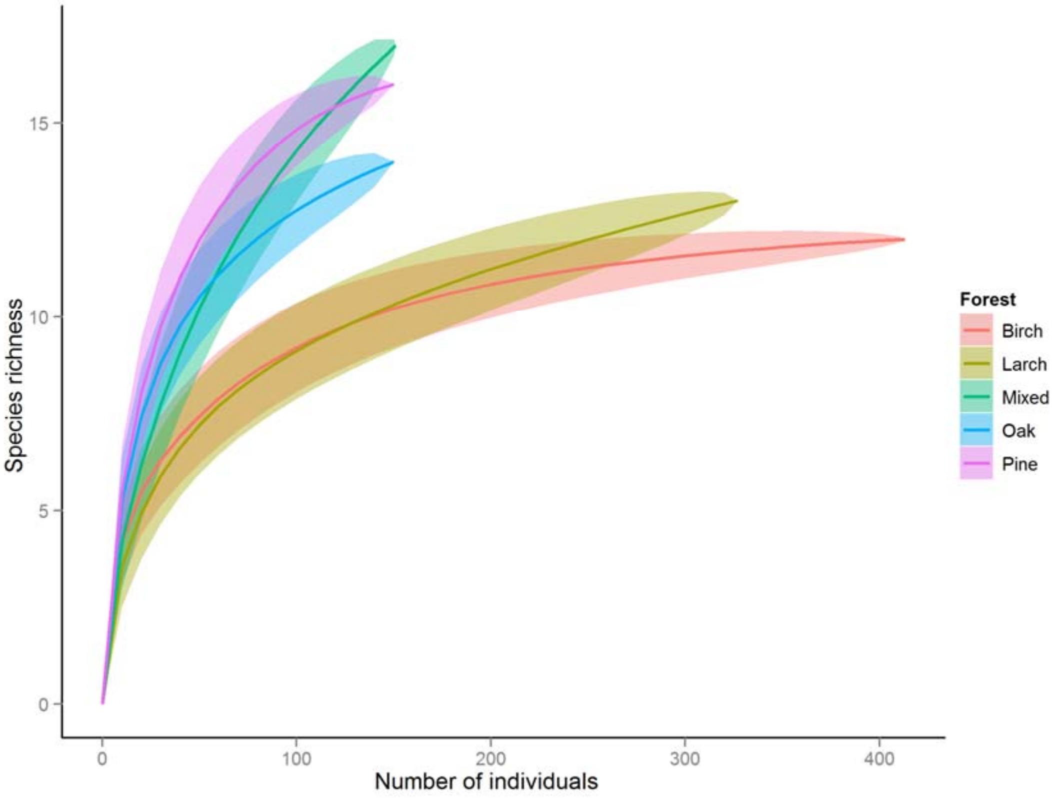

Figure 30 Rarefaction curves of carabids in different forest types (shaded areas represent 95% confidence intervals)

The sampled number of geometrid moth species was highest in pine forest (104 species) and lowest in birch (69 species), with the other three forests accounting for very similar recorded species richness values (79, 80 and 81 species for oak, mixed and larch forests, respectively). Rarefaction curves showed that oak forest had the highest rarefied number of species followed by pine plantations with a slightly lower rarefied species number, while birch forest accounted for the lowest number, with Larch and mixed forests harbouring similar, intermediate numbers of rarefied species

(Figure 31). Overall, rarefaction curves were closely aligned, with only relatively small differences observed between the five curves.

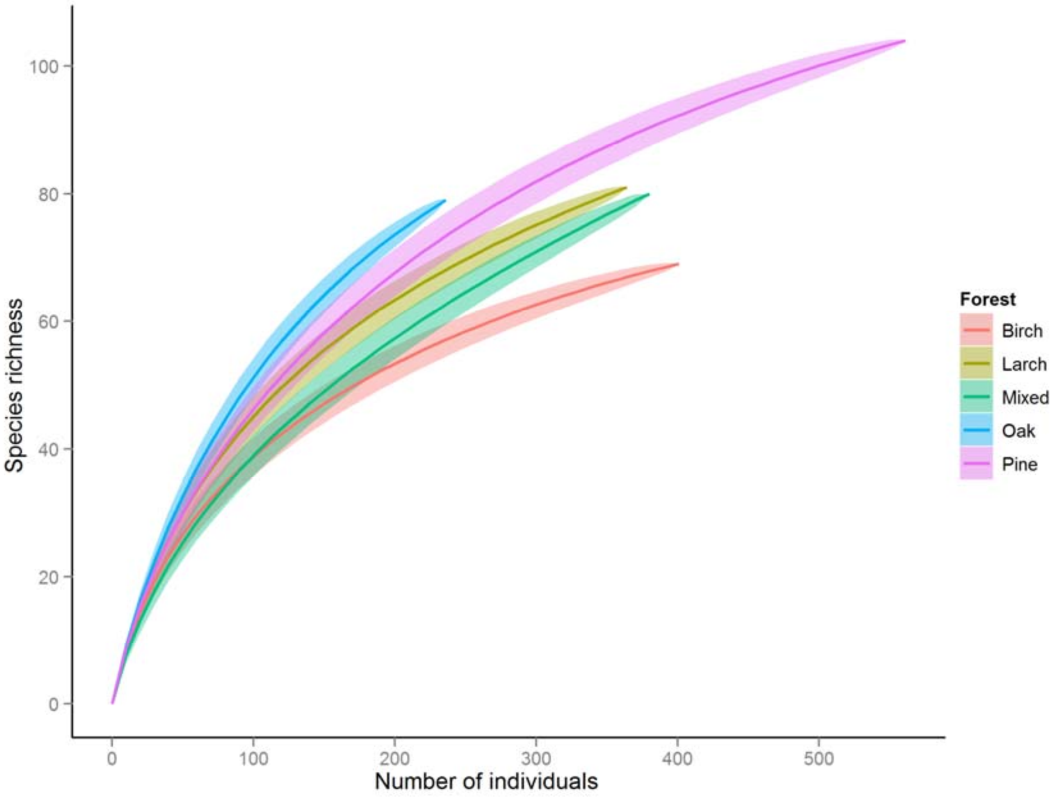

Figure 31 Rarefaction curves of geometrids in different forest types (shaded areas represent 95% confidence intervals)

6.3.2. Indicator species

No carabid species was found to be a good indicator of any single forest type. *Harpalus laevipes* Zetterstedt and *Carabus canaliculatus* Adams were good indicators for the combination of larch and birch forests, while *C. vladimirskyii* Dejean and *C. sui* Imura & Zhou were characteristic for both pine and oak forest (see Table 10). Ten geometrid moth species were characteristic of single forest types, with seven of these being indicators of pine forest (see Table 10), and *Horisme tersata* Denis et Schiffermüller was a good indicator species for the two plantation forests, stocked with either larch or pine.

Table 10 Significant indicator species for ground beetles and geometrid moths

Indicator species	Forest	IndVal	*P*
Ground beetles			
Harpalus laevipes	Larch+Birch	0.844	0.011
Carabus canaliculatus	Larch+Birch	0.824	0.025
Carabus vladimirskyi	Pine+Oak	0.973	0.001
Carabus sui	Pine+Oak	0.791	0.045
Pseudotaphoxnus mongolicus	Pine+Oak+Birch	0.904	0.049
Pterostichus acutidens	Larch+Pine+Oak+Brich	0.994	0.011
Geometrid Moths			
Larentiinae sp.4	Larch	0.853	0.011
Comibaena nigromacularia	Mixed	0.866	0.02
Selenia sordidaria	Mixed	0.816	0.002
Xenortholitha propinguata	Pine	0.941	0.014
Naxa seriaria	Pine	0.866	0.019
Thetidia albocostaria	Pine	0.866	0.011
Larentiinae sp.2	Pine	0.866	0.006
Larentiinae sp.1	Pine	0.853	0.013
Plagodis pulveraria	Pine	0.804	0.033
Ennominae sp.5	Pine	0.802	0.046
Horisme tersata	Larch+Pine	0.819	0.047
Arichanna melanaria	Pine+Birch	0.985	0.001
Lomaspilis marginata	Pine+Birch	0.791	0.033
Scopula sp.	Pine+Mixed	0.894	0.007
Iotaphora admirabilis	Pine+Oak	0.886	0.006
Larentiinae sp.10	Larch+Pine+Oak	0.816	0.045
Epholca auratilis	Larch+Mixed+Oak+Birch	0.967	0.036
Phanerothyris sinearia	Larch+Pine+Mixed+Oak	0.995	0.005

6.3.3. Insect species turnover rates

The NMDS ordination plots based on the CNESS dissimilarity matrices showed that, for dominant ground beetle species (minimum shared sample size, m=1), pine and oak forest harboured distinct communities from other forest types, whereas other sites formed one cluster, with two outliers representing mixed forest habitats. This pattern was slightly different for rare species, where pine and oak forests still reflected distinct species compositions, but the other forest types were also more notably differentiated by their species composition. Overall, oak, pine and mixed forests showed a greater β-diversity in both dominant and rare species of carabids than birch and larch forest (see Figure 32). The picture was pronouncedly different for geometrid moths, where birch forests showed the greatest dissimilarity in species composition, with the other forest types forming a relatively close cluster. Plots showed a similar pattern for both common and rare species, with overall differentiation according to forest types being much weaker than in ground beetles (Figure 32 c, d).

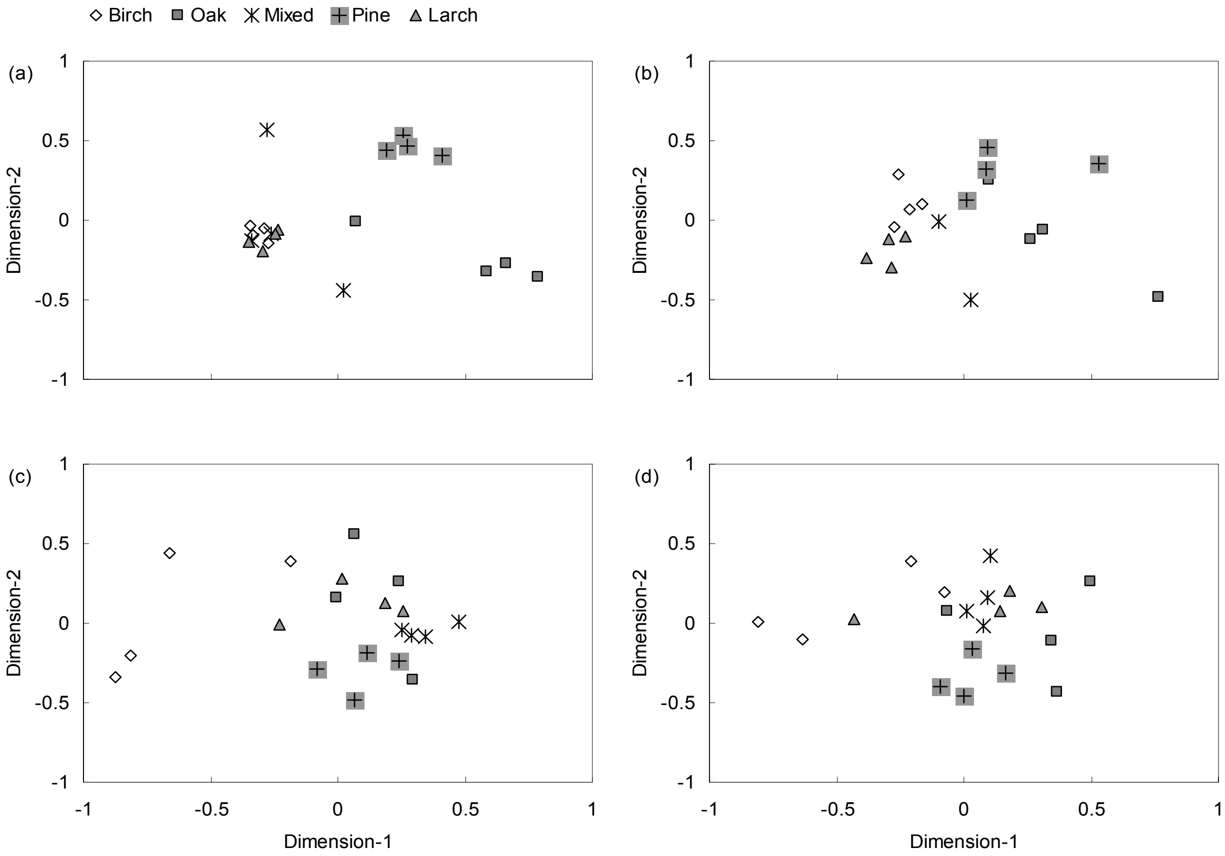

Figure 32 NMDS ordination plots based on the CNESS dissimilarity matrix between all sampling plots of carabids for sample size *m*=1 (a, stress=0.1) m=23 (b, stress=0.14), and of geometrids for sample size *m*=1 (c, stress=0.13) and *m*=29 (d, stress=0.18)

6.3.4. Species composition of plants

Two dimensional scaling based on the "Jaccard" similarity for incidence data of the understory plant layer composition showed that there was no distinctive cluster for any of the five habitats. Oak forests harboured the most distinct assemblages, but also contained one outlier (Figure 33). Mantel tests showed that the CNESS matrix of carabids emphasizing the most common species (*m*=1) was significantly correlated with the matrix of understory plants (r=0.32, P=0.003). No correlation was observed between species composition of common geometrid species and the undergrowth vegetation layer. When focusing on rare species (*m*=23 for carabids and *m*=29 for geometrids), neither carabids nor geometrids was correlated with undergrowth vegetation layer.

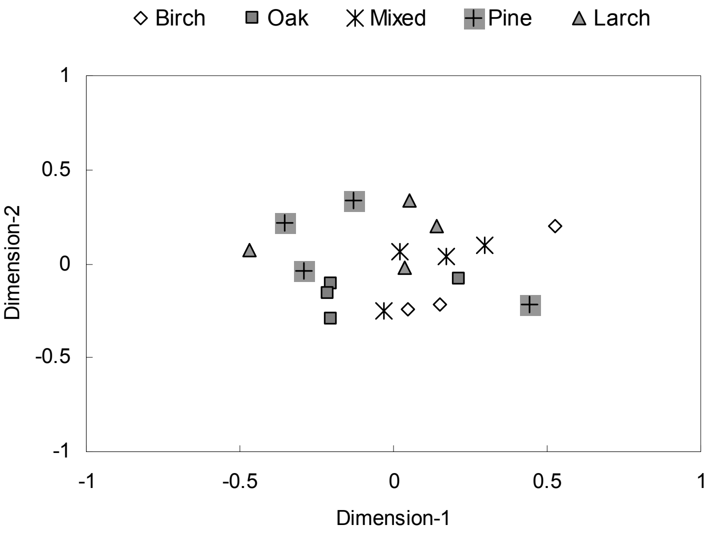

Figure 33 NMDS ordination plots based on 'Jaccard' index for understory layer (stress=0.11).

6.4. <u>Discussion</u>

6.4.1. Overall number of species on Donling Mountain

Based on previous studies, a total of 23 carabid species caught in the study area is a high number recorded. In a previous study, Yu et al. (2010) discovered 19 species of carabids in their study area near BFERS in DLM; another study by the same group later reported 17 carabid species (Yu et al., 2014) from that area. Additionally, Yu et al. (2002) also sampled 10 species in the genus *Carabus* in DLM between 1000m and 2300m.. In comparison, I only recorded 7 *Carabus* species, with 6 of these being the same species already found by Yu et al. (2002). One of the missing species in my sample, *Carabus brandti* Faldermann, was actually found in the sample sites outside my main study area. *Carabus granulatus* Linne and one unidentified morpho-species were rare in Yu et al. (2002)'s sample and therefore will most likely have been missed in my sampling. Similarly, species only represented by very few individuals in my sample, such as *Carabus kruberi* Fischer, could easily have been missed by Yu et al. (2002)'s sampling. The only common species missing from my samples is *Carabus sculptipennis* Chaudoir, of which Yu et al. (2002) reported 84 individuals in sampling sites near BFERS. As species sorting and identification for both of our studies were carried out by the IZ-CAS, the lack of this species in my samples is unlikely due to misidentification. A possible reason is due to the seasonal variation, as Yu et al. (2002)'s sampling was carried out from April to October, while mine was restricted to the period from June to September. Unfortunately, very little information is available for the ecological status of *Carabus sculptipennis*. Another possible cause for this species to lack from my samples is that I used saturated salt-water as killing agent, while Yu et al. (2002) used a mixture of vinegar, sugar, alcohol and water as trapping fluid (see Yu et al., 2006b), and *Carabus sculptipennis* might be specifically attracted to this latter mixture. The above two reasons can also potentially explain the lack of other missing species in comparison to Yu et al.'s studies (e.g. Yu et al., 2002, 2010, 2014) in this area. Finally, as Yu et al. (2002)'s sampling was conducted in 1998-2000, differences could also be related to environmental change or other factors leading to an overall change in the local species pool over the last 12 years.

To the best of my knowledge, my study represents the first occasion that an extensive study of geometrid moths is conducted in DLM. The recorded 165 species is a substantial number, which is even higher than my records from Changbai Mountain of

155 species despite the substantially smaller study area and lack of strong altitudinal variations between plots at DLM (see Chapter 3). This number of geometrid moths is also relatively high when compared with other studies of plantation and secondary forests in northern China. A total of 75 species from 1000 specimens were recorded in secondary forests in the Ziwu mountains, Gansu province (Jiang & Zhang, 2001), and 110 species based on 14,692 individuals were collected in plantation forests and agricultural fields on the Bashang Plateau of Heibei Province (Axmacher et al., 2011, see discussion in Chapter 3). Additionally, results also indicated that manual collection will add a number of species that are otherwise missed by automatic light trapping, rendering manual sampling a very good complementary approach to automatic light traps (see also Axmacher & Fiedler, 2004; Brehm & Axmacher, 2006).

6.4.2. α-diversity and species composition for different forests

The general α-diversity levels of both carabids and geometrids were similar for native oak forest and pine plantation forest. It contrasts Yu et al. (2010)'s suggestion that plantation forests of native pine support fewer ground-dwelling beetle species than secondary oak forest. This outcome also contrasts studies from other temperate regions such as North America and Europe, where a higher α-diversity of carabids has been recorded in native forest types in comparison to conifer plantations (Elek et al., 2001; Fahy & Gormally, 1998; Finch, 2005; Magura et al., 2003). The slightly lower diversity of carabids in larch than pine plantation may partly be attributable to a higher density of ground cover in this latter forest (Warren-Thomas, 2011), as higher density of ground cover can potentially reduces the activity of forest specialist carabid species (Niemelä et al., 1996; Niemelä et al., 1992). Nevertheless, rarefaction of the samples showed a similar number of geometrids species occurring in these two plantation forests when standardized for sample size.

The observed significant differences in carabid assemblage composition between plantation and secondary forests are consistent with the study by Maeto and Sato (2004) in the temperate region of Japan. These authors reported that the species composition of ants allowed a clear differentiation between plantation and secondary forests. This also resonates with previous studies (Magura et al., 2003; Magura et al., 2000; Ohsawa, 2004; Yu et al., 2006a, 2010) reporting that conifer plantations support an altered species composition and distribution of beetles compared to native broad-leaved forests. In contrast to carabids, differences in species composition of geometrid moths for both rare and dominant species between mainly secondary (oak and mixed) forests and plantation (larch and pine) forests were very limited. This possibly relates to the fact of geometrid moths have a higher mobility than carabids, resulting in geometrids moving more commonly across the finely grained mosaic of different forest types and hence showing a lower dissimilarity in the species composition. This pattern can also partly explain the significant correlation between β-diversity of carabids and vegetation, but not for geometrid moths. The difference in species composition pattern between the two investigated insect groups also highlights their varying associations with vegetation and environmental conditions (Axmacher et al., 2011).

Although the study area comprises a distinctive forest mosaic (Ma et al., 1995), species compositions in the understory layer were not very heterogeneous. The differences in carabid assemblages between different forest types within the forest mosaic indicates that carabid species composition can indicate habitat fragmentation, whereas single carabid species may perform poorly in doing so. In contrast, geometrid species appear to contain good indicator species for different habitat type(s) within a relatively small geographical area, while overall species composition performs poorly in differentiating between different habitats. The difference between carabid and geometrid assemblages in their responses to habitat mosaics may result from the difference of their feeding guilds. Although the food sources of many geometrid species are not yet clearly established, selected indicator geometrids are likely depending on specific host plant species or small host plant groups, while predatory carabids are more likely to be more indirectly affected via the different micro-climatic conditions at different forest habitats (Rykken et al., 1997). My results suggest that different arthropod taxa have a distinctly varying suitability to be used as bioindicator in forest management practices (Maleque et al., 2009).

6.4.3. Synthesis

Overall, all sampling plots were contained in a relatively small area in this study. The high α-diversity of carabids and geometrids in this study suggest that DLM harbours a high insect biodiversity that needs to be more widely recognized. My results also indicate that in DLM, old age conifer plantation forests can harbour insect diversity levels similar to secondary oak forests of similar age. These plantation forests therefore have a high biodiversity conservation importance. Nonetheless, the low distinctiveness in the species composition of geometrid moths between different forest habitats indicates that some species might acutally have migrated in from neighbouring forest types. For a comprehensive comparison of the diversity between secondary and plantation forests, studies in a wider geographical area are required.

Chapter 7. Comparison of insect diversity patterns in mature, secondary and plantation forests in temperate North China

Summary

Results from Chapter 6 showed that plantation forests harboured similar levels of α-diversity to secondary forests in Dongling Mountain. The vicinity of different forest mosaics in DLM may however have affected the results due to edge effects. This chapter investigated three wider geographical areas in the temperate region of northern China: Changbaishan Natural Reserve (CNR), Dongling Mountain (DLM) and Bashang Plateau (BSP), where sampling plots representing primary forest, secondary forest and plantation forest habitats were selected, respectively. The chapter focused on a comparison of α- and β-diversity of the three core study taxa; understory plants, ground beetles and geometrid moths. Results showed that the α-diversity of understory plants and carabid beetles was highest at BSP and lowest at DLM; while α-diversity for geometrids peaked at DLM and was lowest at BSP. For β-diversity, CNR showed the lowest dissimilarity values in species composition for all three taxa. Results therefore suggested that in temperate areas in northern China, the wide range of protected larch plantation forests potentially play a considerable role in biodiversity conservation in relation to understory plants and ground-dwelling arthropods. Nonetheless, specific attention still needs to be paid to the last remaining primary forests like the ones encountered at CNR.

7.1. Introduction

In Chapter 6, I have established that plantation forests in Dongling Mountain (DLM) harboured similar levels of α-diversity to secondary forest. One potential problem of this comparison is nonetheless the relative vicinity of the different forest types (Carnus et al., 2006; Chazdon et al., 2009), as transient species particularly in mobile geometrid moths may be infrequently recorded amongst each forest types (Barlow et al., 2007b). It is often difficult to avoid the impact of edge effects in diversity studies based in finely grained forest mosaics (Lopez-Barrera et al., 2005; Pardini et al., 2009) such as DLM. To enhance the general understanding of the role plantation and secondary forests play in biodiversity conservation, an additional comparison between mature, plantation and secondary forest sites from a wider geographical area will have great significance.

Chapter 3 already provided baseline information on the diversity of carabids and geometrids in a primary forest in northeast China—Changbaishan Natural Reserve (CNR), while Chapter 6 provided a basic overview of the diversity status of these two taxa in a major secondary forest region with some plantation elements in forests near Beijing (DLM). Large scale pure plantation forests have been planted in large areas of neighbouring Hebei province including the mountains between Beijing and the Inner Mongolian Plateau, where both carabids and geometrids have been studied by staff from UCL and the China Agricultural University on the Bashang Plateau (BSP) Mountains (see Chapter 2). A comparison of these three study regions which chiefly represent pristine, secondary and plantation forests can therefore allow valuable new insights into the larger-scale importance of these forests to biodiversity conservation.

Apart from geometrids and carabids, plant diversity was also recorded in all three areas. Given that tree species have been planted in BSP and partly also DLM, they are not very suitable indicators of phyto-diversity. Understory plants were therefore selected as key representatives of the forest plant diversity status. The understory layer plays a dominant role in forest ecosystem functioning because of its high functional and compositional diversity, its numerous interactions across tropic levels and its key role in forest succession (Dyer et al., 2010; Hosseini et al., 2010; Nilsson & Wardle, 2005; Pringle & Fox‐Dobbs, 2008). Understory plants have been used successfully in diversity studies investigating different land use types and forest succession stages (Aubin et al., 2008; Brunet et al., 2011; Hosseini et al., 2010;

Ramadhanil et al., 2008; Xiong et al., 2008).

The overall objectives of this chapter are to compare the α-diversity of understory plants, carabids and geometrids in the three areas dominated by primary, secondary and plantation forests, respectively, and to analysis the similarity in species composition of the three taxa in these areas. The main hypotheses are that the primary forest (CNR) harbours the highest diversity for all three taxa, following by the secondary forest (DLM), with the plantation forest (BSP) harbouring the lowest diversity levels. It is furthermore hypothesised that the generally patterns in the species composition are distinctly different between the study areas, while there is also a notable overlap in species between the different areas, with both primary forest and forest plantation sharing more species with the secondary forest habitats than with each other.

7.2. Sampling sites selection and data analysis

As indicated in Chapter 2, the plantation forest area investigated at BSP contained 8 plantation forest plots (details of sampling methods can also be found in: Axmacher et al., 2011; Wang, 2010). In DLM, samples of all 12 secondary forest plots located in oak, mixed and birch forest near BFERS were used for comparison. In CNR, all 11 sites in mixed coniferous and broad-leaved (MCBF) forests below 1000m were selected. The MCBF sites were selected to account for the latitude differences between the study areas and as this is the forest zone in CNR with the most similar annual temperature and precipitation regimes to both DLM and BSP. In the following sections of this chapter, CNR, DLM and BSP will specifically refer to data coming restrictedly from the 31 above-mentioned sampling plots.

To minimize between-sample variations in the same area, data were pooled for α-diversity analysis. Individual-based rarefaction methods (see Appendix 1, equation 1) were use to compare the α-diversity of geometrids and carabids. Sample-based rarefactions for incidence data were used for understory plants (Appendix 1, equation

2), as plant species abundance was not recoded in DLM and BSP. In addition, species rank-abundance plots were used to compare species dominance patterns between the study areas.

Compositions of geometrid subfamilies and carabid feeding guilds were also calculated. Carabid feeding categories were classified according to Harvey et al. (2008), Yu et al. (2010), Oelbermann and Scheu (2010), ElSayed and Nakamura (2010), Zhu et al. (1999), Hering and Plachter (1997) and based on personal communications with experts from the IZ-CAS. Species were classified as either carnivores, omnivores or phytophagous. Species from the same genus were considered as belonging to the same feeding guilds when detailed information was missing. To analyse the β-diversity, dissimilarity matrices were calculated for each taxa. The matrices for understory plants were calculated based on the 'Jaccard' index (Appendix 1, equation 8) according to incidence (presence-absence) data, while dissimilarity matrices for carabids and geometrids were calculated based on chord-normalized expected species shared (CNESS) with emphasis on dominant species (m=1, Appendix 1, equation 9) based on abundance data. Non-metric multidimensional scaling (NMDS) ordinations were used to visualize similarity patterns in the three taxonomic groups.

CNESS results were calculated by the software COMPAH (Gallagher, 1998). The remaining calculations and statistics were carried out in R (R Development Core Team, 2011), using the package 'vegan' (Oksanen et al., 2012) to calculate the 'Jaccard' index and to carry out the NMDS.

7.3. **Results**

7.3.1. α-diversity

In total, the three study sites contained 295 understory plant species. Of these, 69 species were recorded in CNR and 61 were observed in DLM, whereas 190 species were recorded in BSP. Incidence based sample-size rarefaction showed a similar pattern to the observed specie richness, with BSP being substantially more diverse in the number of understory plant species. Rarefaction curves showed a slightly higher number of understory plant species at CNR than DLM (Figure 34).

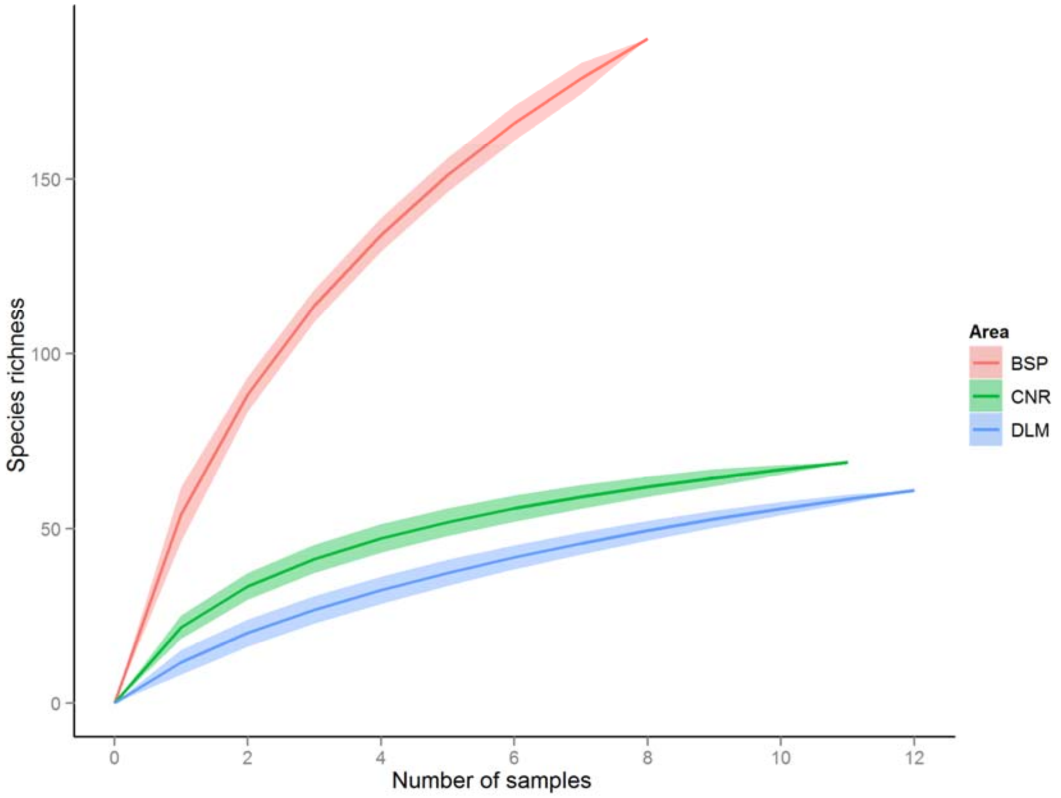

Figure 34 Rarefaction curves of understory plant species richness in the different study areas (shaded areas represent 95% confidence intervals)

A total of 2571 carabids representing 74 species were collected in the plots representing the three study areas. Of these, 1178 individuals representing 30 species were recorded at CNR; 714 individuals representing 21 species at DLM and 679 individuals representing 33 species at BSP. Rarefaction curves again showed a similar trend to the observed species richness, with BSP having the highest rarefied species richness and DLM reaching the lowest estimated value (Figure 35). In comparison between the three areas, the dominant ground beetle species take up similar proportions in the assemblages (Figure 36). In CNR, carabid assemblages were dominated by *Pterostichus vladivostokensis* Lafer, *Pt. orientalis* Motschulsky and *Pt.*

interruptus Dejean, accounting for 62.5% of all individuals. The assemblages in DLM were dominated by *Pt. acutidens* Fairmaire, *Carabus crassesculptus* Kraatz and *Carabus manifestus* Kraatz, which accounted for 65.8% of all individuals. At BSP, the three dominant species *Pt. fortipes* Chaudoir, *Pseudotaphoxenus mongolicus* Jedlicka and *Pt. gebleri* Dejean accounted for 60.1% of the sampled individuals. The pattern of rare species (accounting for less than 1% of the specimens in the samples, and with a log value lower than -2) was different between the three areas: BSP had 21 species and CNR had a very similar number of 20 species, while samples at DLM only contained 12 rare species (Figure 36).

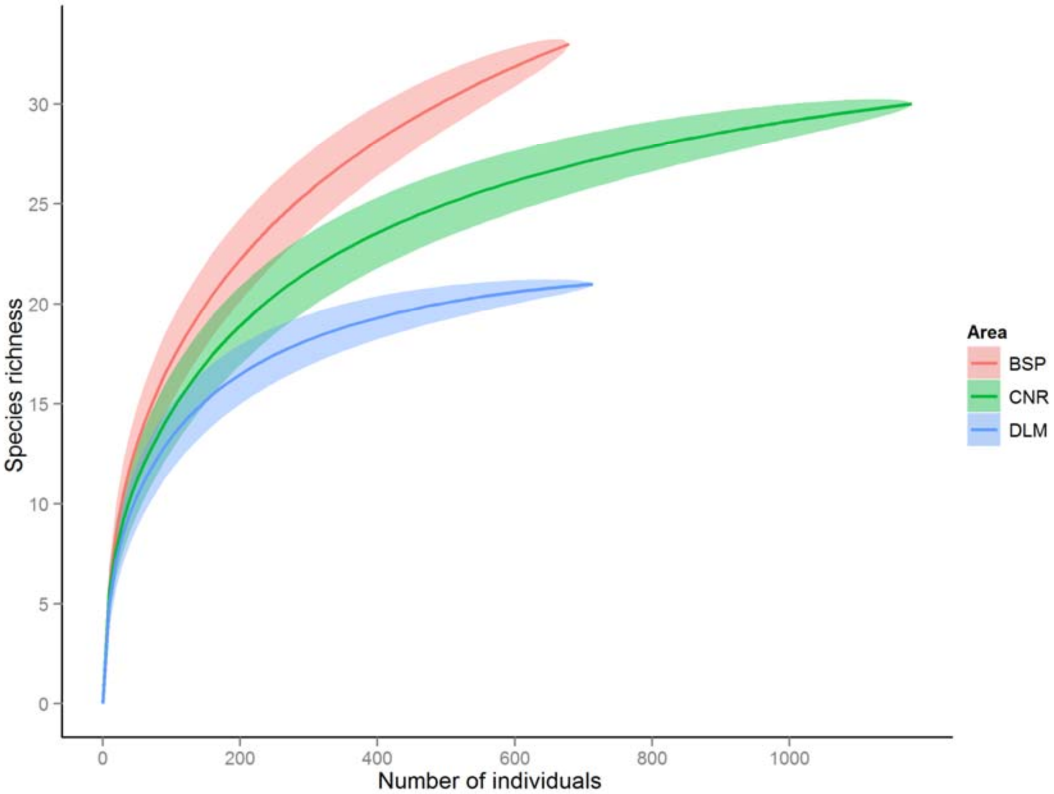

Figure 35 Rarefaction curves of carabids in different areas (shaded areas represent 95% confidence intervals)

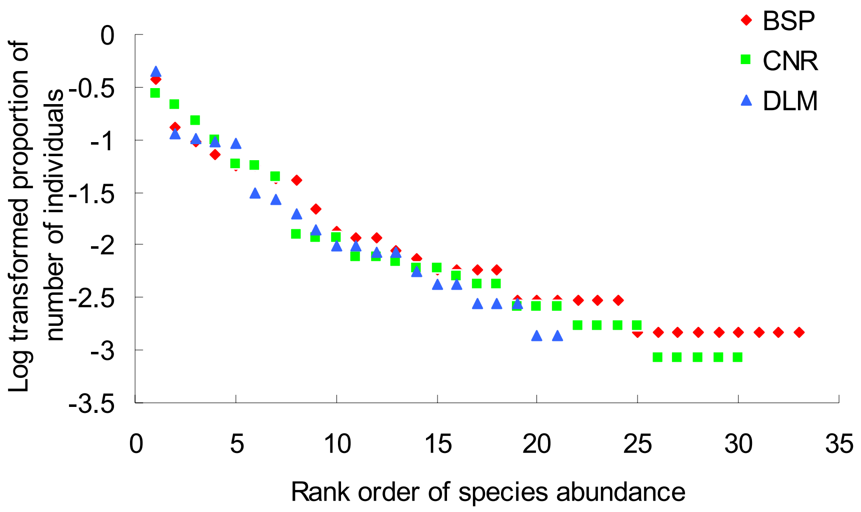

Figure 36 Rank–abundance distribution of carabid species in CNR, DLM and BSP.

A total of 6980 geometrid moths representing 286 species were observed in the three study areas. At the study sites in the CNR where 2589 individuals were collected, these represented 111 species. At DLM, 1017 individuals were sampled which were separated into 128 species. At BSP, the 3374 geometrid moths sampled represented 76 species. Rarefaction showed that DLM had a notably higher species richness of geometrids than the other sites. CNR occupied an intermediate position in relation to species richness, while BSP contained the lowest species richness (Figure 37). The high α-diversity in DLM was partly related to the low level of dominance and high proportion of rare species (Figure 38). In DLM, the three most specimen-rich species *Phanerothyris sinearia* Guenée, *Hypomecis punctinalis* Scopoli and *Alcis picata* Butler accounted for only 22.8% of the overall individuals. In CNR, the most dominant species *Abraxas suspecta* Warren, *Endropiodes abjecta* Butler and *Hypomecis* sp. represented 41.4% of sampled specimens, while in BSP, the three most abundant species *Alcis repandata* Linnaeus, *Epirrhoe hastulata* Hübner and *Alcis castigataria* Bremer accounted for a total of 39.8%. For rare species, DLM had 100 species accounting for less than 1% towards the total number of individuals, which is higher than CNR (93 species) and BSP (57 species).

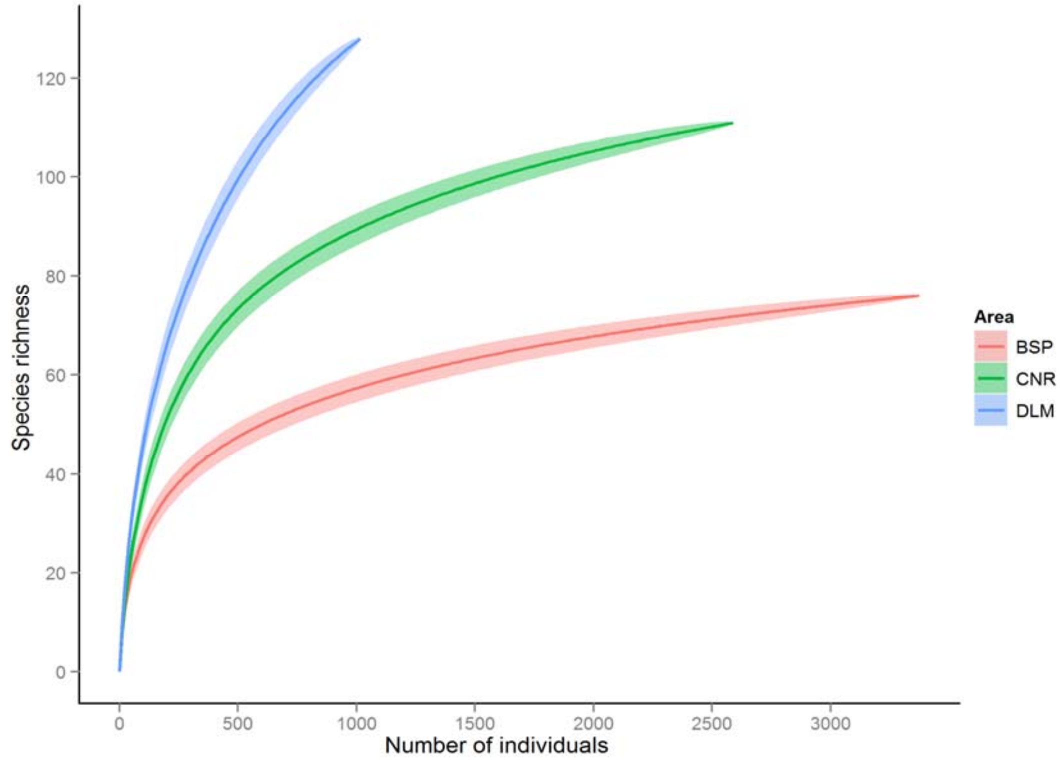

Figure 37 Rarefaction curves of geometrids for the different study areas (shaded areas represent 95% confidence intervals)

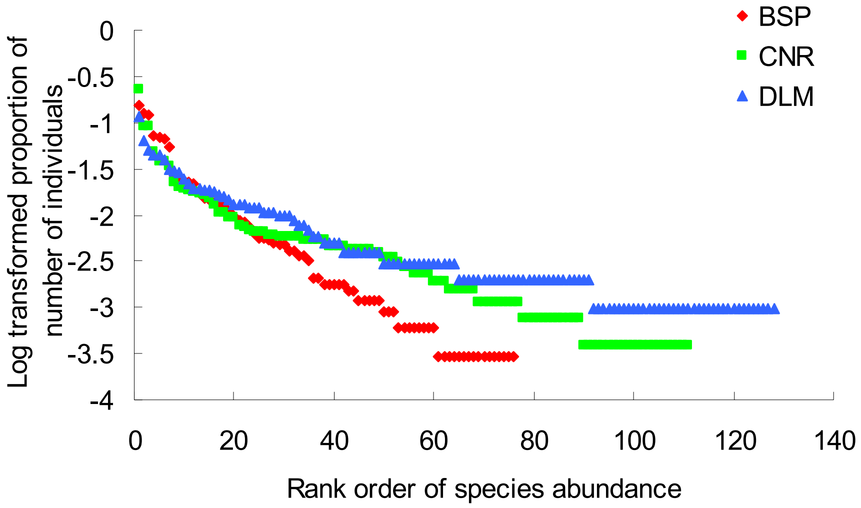

Figure 38 Rank–abundance distribution of geometrid species in CNR, DLM and BSP.

7.3.2. *Species composition, turnover and similarities*

In relation to species composition, CNR shared more understory plant species with DLM than with BSP (Figure 39). In BSP, 175 out of the 190 understory plant species were unique (92%), while the proportion of unique species for understory plants in CNR was also high (84%), but much lower in DLM (64%).

For carabids, CNR again shared more species with DLM than with BSP. Both CNR and BSP had as high number of unique species of carabids (26 species), but the structure of the assemblages was quite different. In total, unique species accounted for 70.6% of the sampled individuals in CNR, while this number decreased to 62.3% and 36.8% in DLM and BSP, respectively. The 5 species BSP shared with DLM already accounted for 62% of all specimens caught at BSP.

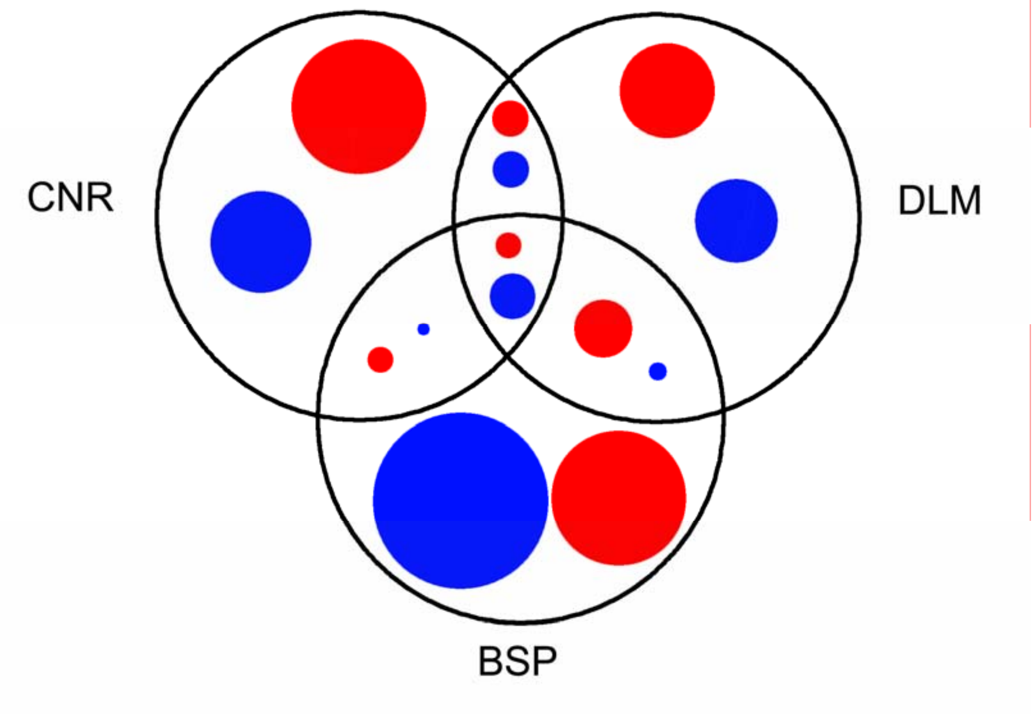

Figure 39 Proportion of shared and unique species between the three study areas (blue dots represent understory plants and red dots represent carabid species, with dot size representing the proportion of the number of species).

Omnivores were the most abundant carabid feeding guild at all three study areas, with 13 species representing 77.3% of all sampled individuals at CNR, 8 species (60.9%) at DLM and 13 species (49.3%) at BSP (Figure 40). Nontheless, at both DLM (11 species) and BSP (14), carnivores were the most species-rich group (Figure 40). For phytophagous, CNR and DLM harboured only 2 species, each, accounting for 0.2% and 6.7% of the total number of individuals, respectively, while this number was much higher at BSP. Here, 13 phytophagous species accounted for 16.9% of all individuals.

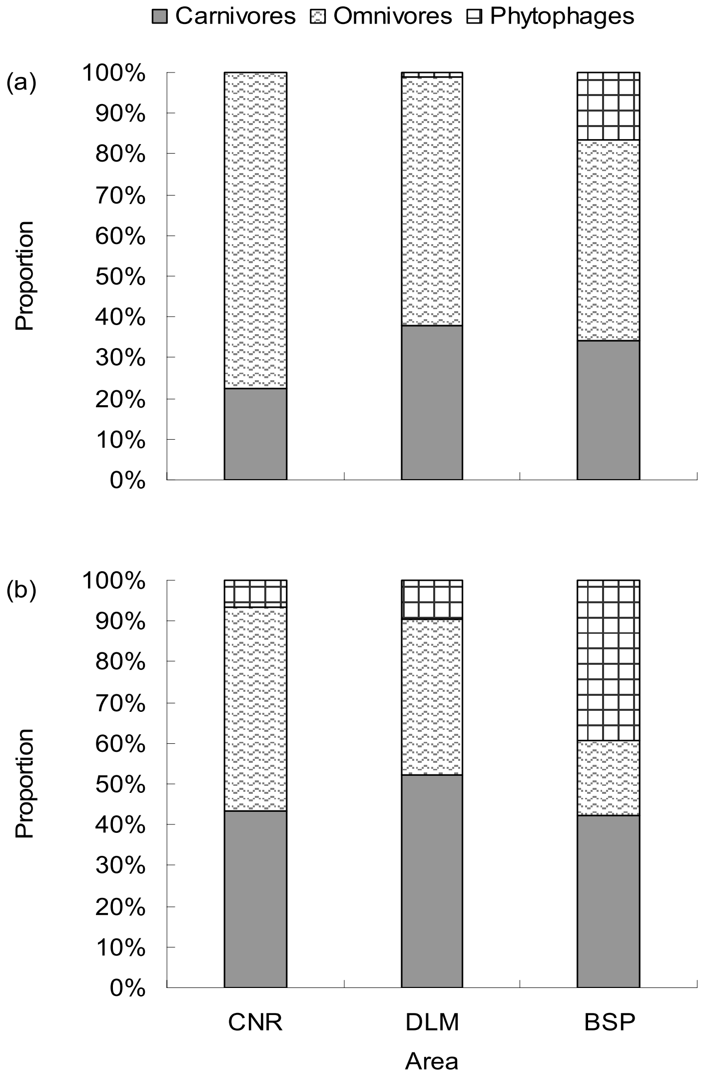

Figure 40 Carabid feeding guild composition in relation to (a) abundance and (b) species richness at CNR, DLM and BSP

As specimens of geometrids were sorted and identified together for CNR and DLM and some of these species were only sorted to morphospecies level pending DNA analysis, while most species from BSP were identified to species level using DNA barcoding, BSP was not included in the analysis of shared common species of geometrid moths. When comparing geometrid species between CNR and DLM, 25 species occurred at both areas, with the remaining 86 species (representing 65.9% of specimens) and 103 species (representing 76.1% of the sampled specimens) were unique at CNR and DLM, respectively. Among the 25 shared species, 17 accounted for less than 1% of abundance at CNR and 16 at DLM.

For the composition of individual subfamilies of geometridae moths, the subfamily Ennominae was the most abundant subfamily in all three areas, but their proportion decreased from 84.5% in CNR to 74.1% in DLM and 44.0% in BSP (Figure 41a). The proportional abundance of Larentiinae, on the contrary, increased from 11.3% to 13.1% and 36.3% when comparing CNR with DLM and BSP, respectively. In addition, very few members of the subfamily Sterrhinae were observed in CNR which only accounted for 0.6% of the overall abundance, while this group was much more strongly represented in samples from DLM (7.5%) and BSP (15.4%) (Figure 41a). However, differences of proportional species richness were not as pronounced between the three areas (Figure 41b), with the proportion of species belonging to Ennominae being slightly higher in CNR (56.8%) than DLM and BSP, where they accounted for similar values of 43% and 44.7%, respectively.

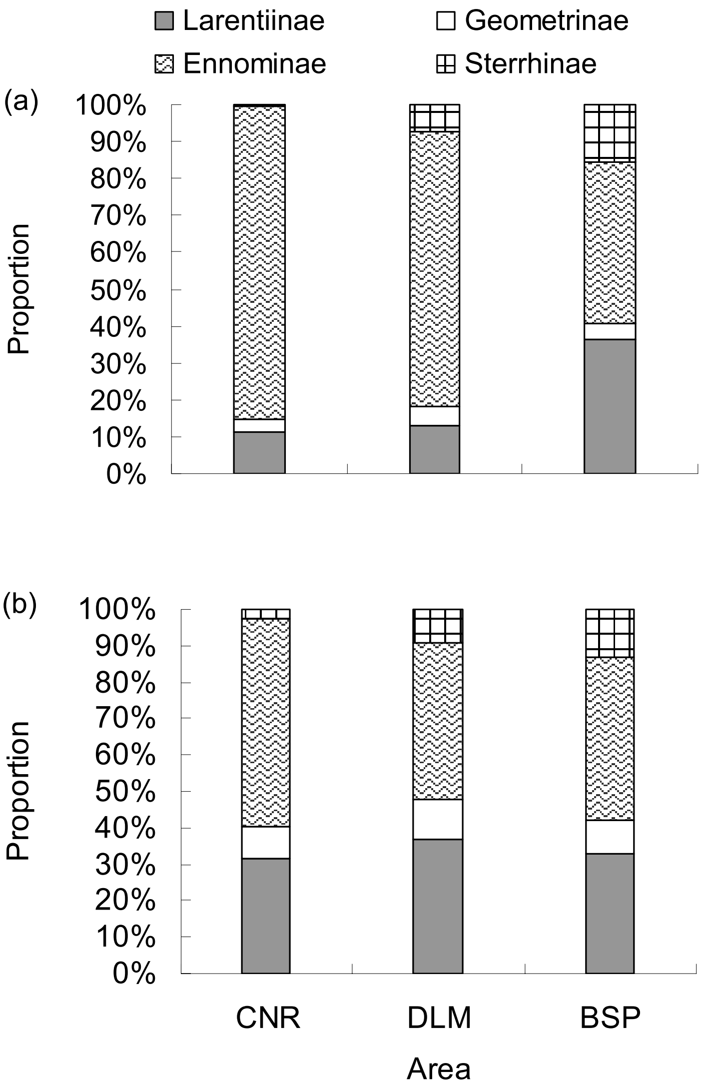

Figure 41 Geometrid subfamily composition in relation to (a) abundance and (b) species richness at CNR, DLM and BSP

When comparing the β-diversity between the three areas, plant species composition of the understory layer showed three very distinctive clusters, each representing one of the study areas. Sampling sites at CNR and BSP formed two particularly tight clusters, while sites in DLM were more spread-out, indicating a higher β-diversity in DLM than at the other two sites (see Figure 42a). The species composition pattern for carabids again was clearly differentiated again into the three study areas in the ordination diagram. In this diagram, CNR assemblages were still grouped into a denser cluster than BSP and DLM (Figure 42b). Species composition for geometrids was again only compared between CNR and DLM because morphospecies are not comparable with species from BSP. Results also showed two distinct clusters for these two areas, and DLM again had a higher β-diversity than CNR.

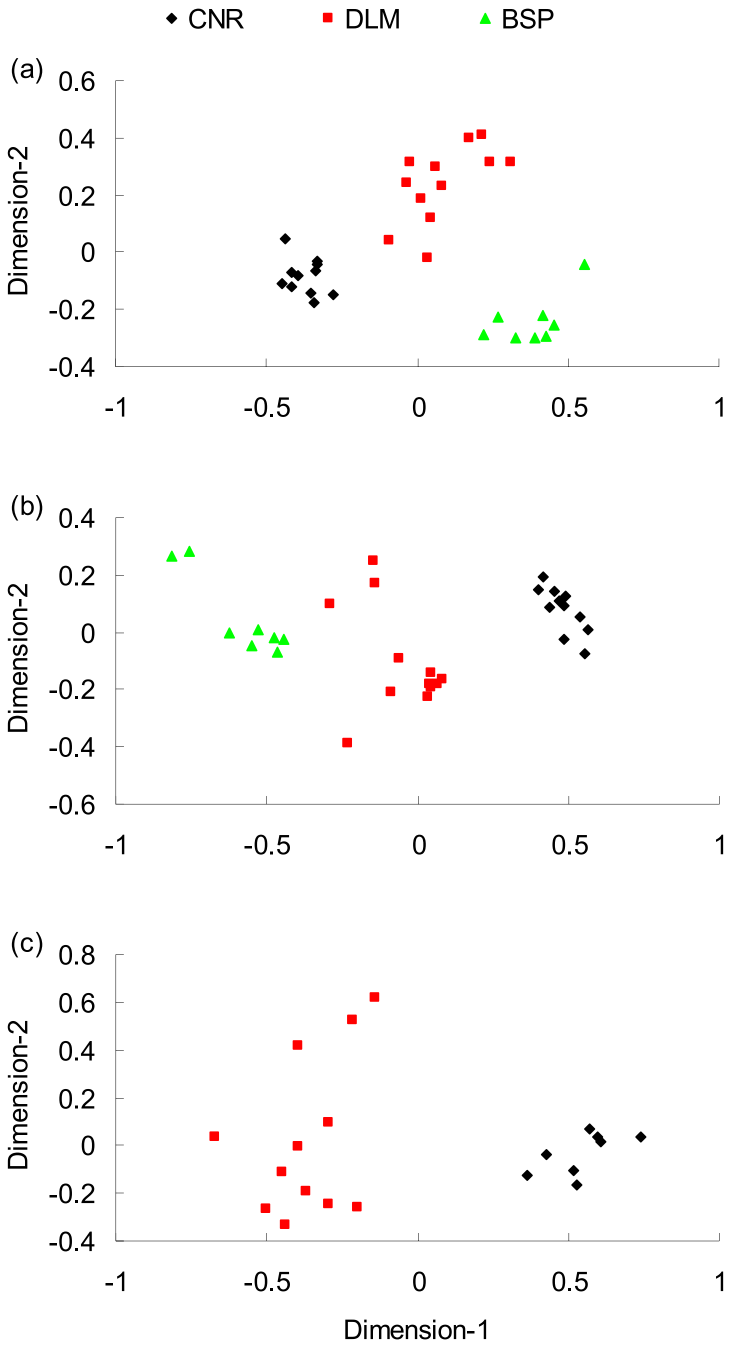

Figure 42 NMDS ordination plots for (a) understory plants based on 'Jaccard' (incident data) dissimilarity matrices, and based on CNESS dissimilarity matrices for sample sizes m=1 for (b) carabids and (c) geometrids .

7.4. Discussion

7.4.1. Plants and carabids

Probably the most striking finding presented in this chapter is the extremely high diversity in undergrowth plants in the plantation forests of BSP. BSP also harboured unique species other than other two areas. In BSP, the earliest larch plantations were planted in the late 1980s with the aim of forest habitat restoration, and since then, these forest plantations have been well protected. A few previous studies have shown that native timber plantations can increase biodiversity though the provision of opportunities for understory plant regeneration (Ashton et al., 2001; Carnevale & Montagnini, 2002). This relates for example to increasing topsoil nutrient contents, facilitating the influx of site-sensitive tree, shrub and herb species (Grubb, 1995). Another possible reason is that trees in plantation forests at BSP are less densely planted than trees in naturally generated secondary forest (DLM) and mature forest (CNR) ecosystems. This would result in less canopy closure in the BSP forests and hence a higher species richness and density in understory plants (Lemenih et al., 2004). The factor can also partly explain the high species richness for carabids at BSP, as many carabid species prefer areas with open canopies (Butterfield et al., 1995; Humphrey et al., 1999). Unfortunately, tree density or canopy closure were not recorded here. Unfortunately, tree density or canopy closure were not recorded here. The high diversity of understory plants in the BSP could also be interpreted as fitting the intermediate disturbance hypothesis (IDH) (Grime, 1973; Connell, 1978). The IDH not only refers to direct human disturbance in forest management, but also seems fitting in forest succession (Bongers et al., 2009; Chazdon, 2003; Kessler, 1999; Molino & Sabatier, 2001). With more than 30 years of restoration history, vegetation succession is arguably at an intermediate stage, resulting in a high diversity of understory vegetation assemblages.

In addition, the high diversity of understory plants also relates to the fact that forest plantations in BSP were established on former grassland habitats. These habitats were relatively weakly disturbed before the plantations were established but harboured typical, highly diverse steppe grassland assemblages, resulting in the plantation area harbouring a mixture of grassland and forest species of an overall high diversity. This is also reflected in the great similarity in carabid species composition between forests and grasslands in this area (Liu et al., 2012). The observed, high diversity of carabids could also partly be contributed to the high diversity of understory plants in BSP, which is likely to result in a wide range of microclimatic conditions and humus layer depths, hence providing suitable habitats for a wide range of ground-dwelling invertebrates (Carnus et al., 2006) such as carabids.

Due to the high diversity of understory plants at BSP, it is not surprising that carabid phytophages account for a higher proportion at BSP than at the other two areas. Previous studies have reported positive relationships between the abundance of carabid phytophages and plant species richness (Harvey et al., 2008), as high plant diversity will potentially provide more food resources for those herbivore species (Haddad et al., 2001). It nonetheless needs to be pointed out that 10 of the 13 phytophagous species at BSP were *Harpalus spp*. This genus was classified as phytophagous according to Harvey et al. (2008)'s sorting, while some other studies classified members of this group as omnivores (ElSayed & Nakamura, 2010).

7.4.2. Geometrid moths

As limited geometrid species appear in grassland, it is therefore also resonablethat BSP did not harbour a high diversity of geometrid moths. Amongst the three study areas, the highest diversity of geometrids occurs in DLM, which can be related to two reasons. The first possible reason relates to the slight difference in sampling methods. Automatic light trapping was used in BSP and CNR, while manual catching was additionally used as complementary approach to the automatic light trapping in DLM (see Chapter 2), and manual collection techniques generated additional species that were not collected at the light traps (see Chapter 6).

Another possible explanation for such a high diversity in DLM relates to the environmental heterogeneity of this area, which relates to the strong heterogeneity in the tree species composition. In this area, deforestation started more than 200 years ago, resulting in the natural forest being almost completely depleted. As already introduced in the previous chapter, forest reforestation and afforestation conducted in this area result in a fine forest mosaic. The high vegetation heterogeneity in DLM can also be expected to relate to the high β-diversity observed here. In contrast to carabids, geometrids have generally a higher mobility, so that catches of geometrids in secondary forest plots might also contain some species originating from other forest types such as the pine and larch plantations (see discussion in Chapter 6).

7.4.3. Species composition overlap

In spite of the large geographical distance between the three forest areas, there is still substantial overlap in understory plant and insect species. Interestingly, most species of geometrids shared between CNR and DLM are not dominant species, with the same trend observed for carabids in these two areas, too. This is in contrast to the BSP, where the most dominant carabid species was also recorded in DLM, while the unique species were mainly rare. Endangered carabid species have been reported from plantation forests also in other countries, such as the species *Holcaspis brevicula* Butcher in New Zealand pine plantation forests (Brockerhoff et al., 2005), and three nationally spare species in the genera *Trechus* and *Pterostichus* in pine and spruce plantation forests in Britain (Jukes et al., 2001). It can therefore be speculated that plantation forests in BSP can also potentially sustain suitable habitats for rare species of carabids, although the knowledge base for ground beetles in China is insufficient for a detailed evaluation of the occurrence patterns of nationally or regionally rare and threatened species.

7.4.4. Synthesis

The comparison of the primary forests in CNR with secondary forest sites at DLM and plantation forests at BSP, α-diversity showed different patterns for understory plants, carabid beetles and geometrid moths. It therefore again indicates that diversity correlations across trophic levels may be weak under natural conditions and results of between-area comparisons depend on target taxa, so that results from a simple taxon are insufficient in providing clear guidance for the development of overarching biodiversity conservation strategies. All three areas harboured relatively high levels of α-diversity for the three taxa investigated, suggesting a high conservation value of the forests in the wider region. It should also be noticed in this regard that criticism raised about China's plantations causing an overall decrease of species diversity primarily in the vegetation (e.g. Cao, 2008; Cao et al., 2010a) were mainly focused on fast-growing, water-inefficiency *Populus* spp. plantations. Different choices of tree species used in plantations however commonly result in very different ecological outcomes for forest ecosystem communities (see reviews by e.g. Aubin et al., 2008; Brockerhoff et al., 2008; Carnus et al., 2006). My results indicate that the wide range of protected larch plantation forests in northern China might potentially be of considerable conservation value, not only for vegetation restoration and in preventing soil erosion and land degradations, but also in sustaining high biodiversity levels for ground-dwelling arthropods such as carabids. Furthermore, the remaining primary forests in northern China such as that encountered at the CNR harbour a distinct composition of insect and plant species and require particular conservation attention.

Chapter 8. Discussion and conclusion

8.1. General diversity of ground beetles and geometrid moths in study areas

Insects are extremely important ecosystem components, while their diversity patterns are widely ignored in current approaches to biodiversity conservation and widely unknown, which is also true for the temperate forest ecosystems of Northern China. The main focus of this research was to investigate insect diversity patterns in mountain forests of northern China, and to establish the relationship between different insect assemblages, the vegetation and core environmental condition. In addition, the research also aimed to provide insights into the insect diversity status in large-scale secondary and plantation forests in northern China.

This study focuses on two distinct insect taxa: ground beetles (Coleoptera: Carabidae) as a family mainly representing predatory insects, and geometrid moths (Lepidoptera: Geometridae), a group of chiefly herbivorous insects. The main study area was located on Changbai Mountain in Jilin Province, which is covered by one of the last pristine forests in Northern China. To the best of my knowledge, the total catches (4844 individuals of carabids and 9285 individuals of geometrids, representing 47 and 155 species, respectively) is the highest number of species recorded from the study area to date (Chen et al., 2007; Liu et al., 2007a), and the number is also comparable with catches from other temperate regions in China (Axmacher et al., 2011; Jiang, 2006; Yu et al., 2006b) and Europe (Avgın, 2006; Skalski et al., 2011). The comparatively high diversity of Changbai Mountain's insect fauna supports the general assumption that this area generally harbours high levels of biodiversity. It also reflects the importance of the establishment of the National Natural Reserve in the 1960s at the Changbai Mountain region, which contributes significantly towards the protection of its biodiversity from human disturbances.

The second study area, Dongling Mountain which is located on the western boundary of Beijing, contributes a substantial proportion towards the overall forest cover of

Beijing. A total of 23 species of ground beetles recorded from this area is a high number in comparison with previous studies (Yu et al., 2002, 2006, 2010, 2014). I also present the first comprehensive sample of geometrid moths for a forested area in Beijing. A total of 165 moth species is a substantial number when compared to other studies in temperate forests in China (Axmacher et al., 2011; Jiang & Zhang, 2001). The vast majority of my samples are kept at the Institute of Zoology, Chinese Academy of Sciences, where it can provide a valuable reference for further studies of geometrids in Beijing and the Hebei Province.

8.2. Main findings and lessons for biodiversity conservation

When modelling the relationship between plant diversity, principal components representing the main gradients in plant species composition and elevation with the diversity of carabids and geometrids, the changing elevation was the most important predictor of changes in both the α-diversity of carabid and geometrid moths. This trend suggests that phytodiversity poorly represents the diversity patterns of the species-rich arthropod assemblages in the invesigated temperate forest ecosystems. My work highlights that previous plant-focused conservation strategies might be risky to ensure the conservation of mega-diverse arthropods, and that it is important to establish a baseline knowledge of the biodiversity status for different taxa, so that biodiversity conservation strategies can adequately consider the diversity status of arthropods representing the bulk of species in most terrestrial habitats. Additionally, neither recorded patterns in predatory arthropod abundance and diversity support traditional top-down control theories, nor does the herbivorous arthropod diversity support traditional bottom-up control theories. These traditional hypotheses that are suitable for less complex ecosystems of low diversity appear to play a much less pronounced role in highly complex forest ecosystems.

The impact of climate change on the biodiversity status of invertebrates in particular is another important topic that requires substantial attention. My work unfortunately can only provide a basic and indirect insight into changes of insect diversity with changes in the environmental conditions. Results nonetheless showed that a variety of plant families have positive links to the diversity of carabids and geometrids, and many of these families declined in species richness over the past half-century. Due to the pressure of raising temperature, both plants and insects are also assumed to move toward higher altitudes, a trend which was clearly demonstrated for parts of the vegetation which indicates the high risk of extinction for species living in the uppermost forest ecosystems.

This work also highlights the importance of plantation and secondary forests in biodiversity conservation. Over the past 50 years, large-scale, well-protected plantation and secondary forests have been established throughout China, but the conservation value of these forests has been widely unclear. The establishment of these forests has been criticized for lacking proven biodiversity conservation value. Some have even argued that they may result in substantial ecosystem and biodiversity degradation (Cao et al., 2010b; Sayer et al., 2004; Xu, 2011). My results however suggest that the wide range of protected larch plantation forests in northern China might potentially be of considerable biodiversity conservation value, providing suitable habitats for ground-dwelling arthropods such as carabids. Nonetheless, the distinct species composition of insects and plants in the primary forest clearly reflect that the remaining pristine forest remnants require particular attention in relation to biodiversity conservation.

8.3. Further work

Further work is still required for a better understanding of arthropod diversity patterns in temperate forests in China and how these patterns respond to global change. First, more diverse arthropod groups should be included in further studies. The selection of these taxa could include a wider range of predatory arthropod taxa such as spiders and ants, and herbivores such as butterflies and bark beetles, with additional detailed surveying techniques employed such as caterpillar collection and detailed leaf damage assessments. This could decrease the taxon-specific bias in the information of arthropod diversity patterns.

Additionally, long-term monitoring of insect diversity patterns is suggested in order to get better insights how arthropod diversity changes with the changing environment. This research has provided basic information of how plant species composition changed in the last five decades. The relationships between insects and plants are however indirect; hence plant information can only give a first indication of how insect diversity might change over time. Insect diversity trends based on temperature-focussed models (Chapter 5) are also very limited and basic, while information from long-term monitoring is probably the only way to get a direct indication of the real developments.

Furthermore, climate data from more than one meteorological station are required to realistically create a spatial model and subsequently map the insect distribution in the entire CNR area and also to better understand the potential interactions between insect diversity and climatic variables,. According to my knowledge, there are at least three meteorological stations located at CNR at different elevational levels. Apart from the Songjiang station from which my climatic data was obtained, a station is located at about 1300m asl and another is located at the top of Changbai Mountain (about 2600m), but their data are chiefly inaccessible. Apart from meteorological stations, there are also many small data loggers set by different research groups in a variety of the forests on Changbaishan. Unfortunately, there is no proper information-sharing system, and this wealth of climatic data was not available for my research. Further works based on this study should hence include the obtaining of detailed climatic records from different locations across the mountain.

Finally, studies from other temperate forests in North China can provide complementary information to substantiate results from this study. Ideal study areas for mature forests in northeast China include Liangshui and Fenglin Natural Reserves in Heilongjiang Province that belong to the Xiaoxinganling Mountain range, and Hanma Natural Reserves in the Daxinganling Mountain range located at the boundary between Heilongjiang Province and Inner Mongolia. Both Xiaoxinganling and Daxinganling Mountain ranges also include large-scale plantation forests. Additionally, Saihanba plantation forest located between Hebei Province and Inner Mongolia is also an ideal place to study the biodiversity status of forest plantations. Detailed large scale studies can give a much better overall view of insect diversity patterns in China’s temperate forests, while to establish such a broad study area and monitoring networks requires huge financial inputs.

8.4. Conclusion

The primary focus of this thesis was to investigate the biodiversity status of two species-rich insect taxa, ground beetles and geometrid moths, in the forested mountain habitats of Northern China. This thesis demonstrated that α-diversity of the two insect taxa decreases significantly with increasing elevation. In the complex forest ecosystems in northern China, the relationship between plant diversity and the diversity of insects are only weakly established, with observed positive links believed to be chiefly driven by changes in the same underlying environmental factors. Traditional ecological theories such as top-down control that work well in grassland and agricultural ecosystems may therefore not be applicable in the complex temperate forest ecosystems. In practice, my work highlights some areas that require specific attention for insect biodiversity conservation in the Changbai Mountain region. These areas include more attention given to Korean Pine forests, a forest habitat that has a unique species composition of plants and insects, but was ignored in previous conservation strategies, as well as the diverse impacts of climate change on the different forest habitats. When designing future conservation strategies, the traditional plant-focus approaches may not be sufficient for the conservation of mega-diverse insect taxa, and more biodiversity knowledge for these individual taxa needs to be considered. Finally, my work also suggests that in my study region in Northern China, secondary and plantation forests not only harbour high level of insect diversity, but they also harbour unique species, which underlines the potential value of China’s large-scale afforestation and reforestation projects for biodiversity conservation.

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Appendix 1. Expression of used biodiversity measurements

Equation No.	Equation Name	Equation Expression	Explanation
1	Hurlbert-Rarefaction	$E(S_n) = \sum_{i=1}^{S}\left[1-\frac{\binom{N-N_\mathrm{i}}{n}}{\binom{N}{n}}\right]$	‘$E(S_n)$’ is the expected number of species for samples containing ‘n’ individuals collected randomly without replacement; ‘n’ is the rarefied number of individuals; ‘N’ is the total number of individuals and ‘N_i’ is the observed number of individuals of the ‘i^{th}’ species
2	Shinozaki-Rarefaction	$E(S_\mathrm{q}) = \sum_{i=1}^{S}\left[1-\frac{\binom{Q-F_\mathrm{i}}{\mathrm{q}}}{\binom{Q}{\mathrm{q}}}\right]$	Assumes that the study area is divided into ‘Q’ quadrats of which ‘q’ quadrats are sampled, while ‘F_i’ individuals are observed for the ‘i^{th}’ species
3	Simpson’s diversity static	$\gamma = \sum_{i=1}^{S}\mathrm{p}_i = \sum_{i=1}^{S}\left[\frac{\mathrm{N}_i(\mathrm{N}_i-1)}{N(N-1)}\right]$	‘γ’ refers to the Simpson’s proportion-based static; ‘S’ refers to the number of observed species; ‘p_i’ refers to the individuals’ proportion for the ‘i^{th}’ species; ‘N_i’ is the observed number of individuals of the ‘i^{th}’ species and ‘N’ is the total number of individuals

4	Shannon (-Wiener/Weaver/Wienert) diversity	$\mathrm{H} = -\sum_{i=1}^{S} p_i \log p_i$, where $p_i = \frac{N_i}{N_t}$	'H' represents the Shannon-Wiener diversity or entropy; 'S' is the number of species observed; 'pi' refers to the individuals' proportion for the 'ith' species; 'Ni' refers to number of individuals in the 'ith' species and 'Nt' is total number of individuals in the sample
5	Fisher's α	$S = \alpha \ln(1 + \frac{N}{\alpha})$	'α' is the value of Fisher's α index; 'S' is the number of species, and 'N' is total number of individuals. The 'N' is very large in most cases, resulting in '$1 + \frac{N}{\alpha}$' approximately equalling to '$\frac{N}{\alpha}$', so that the equation can simply be expressed as '$S = \alpha \ln(\frac{N}{\alpha})$'.
6	Chao 1	$S_{est} = S_{obs} + \frac{F_1^2}{2F_2}$	'S_{est}' is the estimated number of species and 'S_{obs}' is the observed number of species; 'F_1' is the number of singletons (species represented by only one individual) and 'F_2' is the number of doubletons (species represented by only two individuals in the sample)

7	Abundance-based Coverage Estimator (ACE)	$S_{\mathrm{ACE}}=\mathrm{S}_{\mathrm{abund}}+\frac{\mathrm{S}_{\mathrm{rare}}}{C_{ACE}}+\frac{\mathrm{F}_1}{C_{ACE}}\max\left\{\frac{S_{rare}\sum_{\mathrm{i=1}}^{10}i(i-1)F_i}{\mathrm{C}_{\mathrm{ACE}}(N_{rare})(N_{rare}-1)}-1,0\right\}$	‘S_{abund}’ is the number of abundant species with more than 10 individuals; ‘S_{rare}’ is the number of rare species with no more than 10 individuals; ‘F_1’ is the number of species with one individual, ‘F_i’ is the number of species with i individuals; ‘N_{rare}’ is the overall number of individuals for rare species; and ‘C_{ACE}’ refers to the sample coverage estimate for the sub-sample, which is equal to ‘$1-\frac{\mathrm{F}_1}{N_{rare}}$’
8	Jaccard index	$\beta_J=\frac{a}{a_1+a_2-a}$	‘a’ is the number of species in common for both samples, ‘a_1’ is the number of species in sample 1 and ‘a_2’ is the number of species in sample 2
9	Chord-normalized expected species shared (CNESS)	$CNESS_{ij\|m}=\sum_{k=1}^{S}\left[1-\frac{\binom{N_i-N_{ik}}{m}}{\binom{N_i}{m}}\right]\times\left[1-\frac{\binom{N_j-N_{jk}}{m}}{\binom{N_j}{m}}\right]$	‘S’ is the total number of species; ‘i’ and ‘j’ are the ‘i^{th}’ and ‘j^{th}’ sample, ‘N_{ik}’ is the abundance of the ‘k^{th}’ species in the ‘i^{th}’ sample; ‘N_i’ is the number of individuals in the ‘i^{th}’ sample, ‘m’ is the sample size.

Appendix 2. Number of carabid individuals for each species sampled in different forests in Changbai Mountain (MCBF: mixed coniferous and broad-leaved forest; KPF: Korean Pine Forest; MCF: mixed coniferous forest; SMCF: sub-alpine mixed coniferous forest; BF: birch forest).

Species	**Forest Type**					**Total**
	MCBF	**KPF**	**MCF**	**SMCF**	**BF**	
Agonum sp.1	9	0	0	1	1	11
Amara tumida Morawitz	0	0	0	0	5	5
Asaphidion sp.1	1	0	0	0	0	1
Carabus aurocinctus Motschulsky	0	0	116	645	138	899
Carabus billbergi Mannerheim	14	15	0	1	0	30
Carabus canaliculatus Adams	52	0	31	0	7	90
Carabus constricticollis Kraatz	0	0	1	0	0	1
Carabus fraterculus Reitter	3	0	0	1	0	4
Carabus granulatus Linne	8	0	0	0	0	8
Carabus seishinensis Lapouge	70	7	12	0	0	89
Carabus venustus Morawitz	0	11	144	117	52	324
Carabus vietinghoffi Adams	15	0	23	0	0	38
Cychrus morawitzi Gehin	14	0	12	3	0	29
Harpalus laevipes Zetterstedt	0	1	0	1	0	2
Harpalus ussuricus Mlynar	1	0	0	0	1	2
Harpalus xanthopus Gemminger & Harold	1	0	0	0	0	1
Leistus niger Gebler	67	11	24	12	12	126
Leistus sp.1	0	0	0	7	8	15
Loricera pilicornis Fabricius	0	0	0	2	16	18
Morphodactyla coreica Solsky	0	0	8	157	70	235
Nebria pektusanica Horvatovich	0	0	0	1	0	1
Notiophilus reitteri Spaeth	0	0	1	1	0	2
Pristosia sp.1	5	0	9	2	0	16
Pristosia sp.2	5	4	0	0	0	9
Pristosia sp.3	0	0	2	6	0	8
Pterostichus adstrictus Eschscholtz	117	82	32	33	1	265
Pterostichus comorus Jedlicka	2	3	129	415	354	903
Pterostichus gibbicollis Motschulsky	3	0	0	0	0	3
Pterostichus horvatovichi Kirschenhofer	6	0	0	1	0	7

Pterostichus interruptus Dejean	176	3	83	26	5	293
Pterostichus jankowskyi Tschitscherine	7	0	0	0	0	7
Pterostichus mandzhuricus Lustshnik	2	0	0	0	0	2
Pterostichus microcephalus Motschulsky	1	0	0	0	0	1
Pterostichus nigrita Paykull	2	0	0	0	0	2
Pterostichus orientalis Motschulsky	256	54	79	79	16	484
Pterostichus sp.1	0	0	0	106	160	266
Pterostichus sp.2	3	0	13	59	11	86
Pterostichus sp.3	0	0	0	0	1	1
Pterostichus sp.4	0	0	0	0	2	2
Pterostichus subovatus Motschulsky	0	0	0	0	2	2
Pterostichus tuberculiger Tschitscherine	0	0	3	0	0	3
Pterostichus vladivostokensis Lafer	319	34	40	38	63	494
Synuchus agonus Tschitscherine	7	10	9	4	3	33
Synuchus sp.1	9	0	0	1	0	10
Synuchus sp.2	1	0	0	0	0	1
Trechus sp.1	0	0	0	2	0	2
Trichotichnus coruscus Tschitscherine	2	1	0	0	0	3
Total observed number of individuals	**1178**	**236**	**771**	**1721**	**928**	**4834**
Total observed number of species	**30**	**13**	**20**	**26**	**21**	**47**
Estimated number of species	**33**	**14**	**21**	**37**	**24**	**54**
Sampling completeness	**91%**	**93%**	**95%**	**70%**	**88%**	**87%**

Appendix 3. Number of geometrid moth individuals for each species sampled in different forests in Changbai Mountain (MCBF: mixed coniferous and broad-leaved forest; KPF: Korean Pine Forest; MCF: mixed coniferous forest; SMCF: sub-alpine mixed coniferous forest; BF: birch forest)

Species	Forest Type					Total
	MCBF	KPF	MCF	SMCF	BF	
Abraxas grossudariata Linneaus	8	3	2	0	0	13
Abraxas suspecta Warren	595	21	28	14	5	663
Agathia carissima Butler	4	0	0	0	0	4
Alcis sp.1	0	30	191	119	10	350
Alcis sp.2	12	14	5	28	17	76
Amraica superans Butler	2	0	0	0	0	2
Angerona prunaria Linneaus	40	7	29	0	0	76
Anticypella diffusaria Leech	15	0	0	0	0	15
Aracima muscosa Butler	1	0	0	0	0	1
Arichanna melanaria Butler	0	11	69	23	108	211
Asthena sp.1	2	0	3	0	0	5
Baptria sp.1	0	0	0	1	0	1
Biston betularia Linnaeus	1	8	3	0	4	16
Brabira artemidora Oberthur	0	2	0	0	1	3
Bupalus vestalis Staudinger	0	0	7	2	0	9
Cabera griseolimbata apotaeniata Wehrli	49	3	8	0	0	60
Carige cruciplaga Walker	9	0	0	0	0	9
Cepphis advenaria Hubner	3	0	1	0	0	4
Chiasmia sp.1	1	0	147	61	7	216
Cleora insolita Butler	9	0	2	2	1	14
Comibaena tancrei Graeser	0	2	0	0	0	2
Comostola sp.1	3	1	0	0	0	4
Crocallis elinguaria Linnaeus	0	0	1	0	0	1
Culpinia diffusa Walker	1	0	1	0	0	2
Cusiala sp.1	10	0	0	0	0	10
Cusiala stipitaria Oberthur	1	0	0	0	0	1
Deileptenia mandshuriaria Bremer	17	0	0	0	0	17
Deileptenia sp.1	0	5	4	39	0	48
Dysstroma cinereata Moore	2	2	0	0	11	15
Dysstroma citrate Linnaeus	0	0	4	0	17	21
Dysstroma latefasciata Staudinger	1	0	0	12	63	76

Dysstroma sp.1	0	0	0	1	0	1
Dysstroma truncate Hufnagel	2	0	1	12	14	29
Ecliptopera silaceata Denis et Schiffermüller	42	25	3	13	2	85
Ectropis sp.1	6	0	0	0	1	7
Eilicrinia wehrlii Djakonov	2	0	0	0	1	3
Endropiodes abjecta Butler	241	0	12	33	3	289
Ennominae sp.1	6	0	0	0	0	6
Ennominae sp.2	0	0	3	0	0	3
Ennominae sp.3	0	0	3	0	0	3
Ennominae sp.4	0	0	0	0	4	4
Ennominae sp.5	1	0	0	0	0	1
Ennominae sp.6	10	0	2	2	0	14
Ennominae sp.7	0	1	0	0	0	1
Ennominae sp.8	0	0	0	1	0	1
Ennominae sp.9	0	3	0	0	0	3
Ennominae sp.10	2	0	0	0	0	2
Ennominae sp.11	0	0	0	0	7	7
Ennominae sp.12	0	0	12	0	0	12
Ennominae sp.13	1	0	0	0	0	1
Ennominae sp.14	2	0	0	0	0	2
Ennominae sp.15	0	7	1	0	0	8
Ennominae sp.16	12	0	0	0	0	12
Ennominae sp.17	1	0	0	0	0	1
Ennominae sp.18	1	1	2	1	0	5
Ennominae sp.19	0	0	14	0	0	14
Ennominae sp.20	1	0	0	0	0	1
Ennominae sp.21	2	0	0	0	0	2
Epholca arenosa Butler	24	0	4	0	0	28
Epirrhoe supergressa Prout	14	0	0	2	0	16
Euchristophia cumulate Christoph	6	4	230	13	0	253
Euliptopera umbrosaria Motschulsky	3	2	5	4	3	17
Eulithis convergenata Bremer	4	1	0	0	0	5
Eulithis ledereri Bremer	2	0	0	0	0	2
Eulithis prunata Linnaeus	15	0	4	5	2	26
Eulithis pyropata Bubner	11	0	0	0	0	11
Euphyia cineraria Butler	9	1	1	5	3	19
Eupithecia gigantean Staudinger	3	0	1	0	0	4
Eupithecia sp.1	2	0	0	0	3	5
Eupithecia sp.2	1	0	21	0	0	22
Eustroma aerosa Butler	33	13	4	14	8	72

Eustroma reticulate obsdeta Djakonov	4	3	5	3	0	15
Eustroma sp.1	0	5	0	1	0	6
Exangerona prattiaria Leech	44	0	0	0	0	44
Gandaritis fixseni Bremer	14	13	0	0	0	27
Garaeus mirandus Butler	2	0	5	12	3	22
Geometra glaucaria Menetries	58	2	0	0	0	60
Geometra rana Oberthur	17	14	18	5	3	57
Geometrinae sp.1	0	4	17	0	0	21
Geometrinae sp.2	3	0	0	0	0	3
Geometrinae sp.3	1	0	0	0	0	1
Geometrinae sp.4	4	0	0	0	0	4
Glaucorhoe undaliferaria Motschulsky	17	1	0	0	0	18
Heterarmia sp.1	18	5	13	0	0	36
Heterolocha laminaria Herrich-Schhäffer	24	0	6	0	0	30
Heterothera serraria Lienig	0	0	13	132	1	146
Hydrelia flammeolaria Hufnagel	7	3	5	1	1	17
Hydriomena impluviata Denis & Schiffermüller	0	0	3	368	449	820
Hydriomena sp.1	0	0	0	0	1	1
Hypomecis roboraria Denis & Schiffermüller	126	47	1	1	2	177
Hypomecis sp.1	235	6	16	9	2	268
Hypomecis sp.2	12	0	1	0	0	13
Hypomecis sp.3	88	0	61	6	9	164
Hypomecis sp.4	1	0	0	0	0	1
Hypomecis sp.5	15	0	33	0	0	48
Hypomecis sp.6	0	0	63	35	0	98
Hysterura sp.1	11	3	0	10	1	25
Iotaphora admirabilis Oberthur	2	0	0	0	0	2
Jankowskia fuscaria Leech	28	0	4	0	0	32
Larentiinae sp.1	12	1	0	1	1	15
Larentiinae sp.2	1	0	0	0	0	1
Larentiinae sp.3	0	0	0	0	1	1
Larentiinae sp.4	0	0	0	0	1	1
Larentiinae sp.5	1	0	0	0	0	1
Larentiinae sp.6	16	22	21	16	1	76
Larentiinae sp.7	1	0	0	0	0	1
Larentiinae sp.8	0	0	0	1	6	7
Larentiinae sp.9	5	0	0	0	0	5
Larentiinae sp.10	3	0	0	0	0	3

Larentiinae sp.11	0	0	1	2	0	3
Larentiinae sp.12	0	0	2	1	0	3
Larentiinae sp.13	1	0	0	0	0	1
Lomaspilis marginata Linnaeus	3	0	0	0	0	3
Lomographa bimaculata Fabricius	99	0	0	0	0	99
Lomographa sp.1	16	0	4	2	6	28
Lomographa sp.2	7	0	3	0	0	10
Lomographa sp.3	27	0	18	0	0	45
Lomographa sp.4	1	0	3	0	0	4
Lomographa sp.5	14	1	0	0	0	15
Lomographa sp.6	11	0	8	2	2	23
Menophra senilis Butler	4	0	2	3	0	9
Mesastrape fulguraria Walker	19	1	1	2	1	24
Mesoleuca albicillata Linnaeus	0	0	1	7	2	10
Mesoleuca mandshuricata Bremer	0	0	5	1	4	10
Naxa psilonaxa seriaria Motschulsky	11	0	0	0	0	11
Odontopera bidentata harutai Inoue	15	0	13	137	83	248
Ophthalmitis albosignaria Bremer & Grey	11	0	0	1	0	12
Ophthalmitis irrorataria Bremer & Grey	3	0	3	0	0	6
Ourapteryx similaria Leech	0	4	0	0	0	4
Parectropis extersaria Hubner	97	0	3	3	1	104
Pareulype consanguinea Butler	0	0	4	0	0	4
Pareulype sp.1	6	0	0	2	2	10
Philereme transversata Hufnagel	0	0	0	0	1	1
Photoscotosia atrostrigata Bremer	0	0	0	1	1	2
Phthonosema tendinosaria Bremer	1	0	0	0	0	1
Plagodis pulveraria Linnaeus	46	0	7	75	81	209
Plagodis reticulata Warren	14	0	3	4	0	21
Plemyria rubiginata Denis et Schiffermüller	5	0	0	0	0	5
Psyra boarmiata Graese	53	3	1	15	0	72
Rheumaptera latifasciaria Leech	0	0	0	1	0	1
Selenia sp.1	0	2	0	7	29	38
Selenia sp.2	48	2	2	2	1	55

Selenia tetralunaria Hufnagel	0	0	0	1	2	3
Semiothisa sp.1	0	0	0	0	4	4
Spilopera debilis Butler	15	3	29	96	9	152
Tanaoctenia dehaliaria Wehrli	0	1	0	0	0	1
Thera variata Denis et Schiffermüller	0	0	0	1	0	1
Timandra apicirosea Prout	4	1	0	0	0	5
Triphosa dubitata Linnaeus	5	7	25	13	165	215
Venusia cambrica Curtis	3	2	34	328	553	920
Viidaleppia quadrifulta Prout	0	0	0	1	0	1
Xanthorhoe biriviata Borhauson	20	0	4	124	28	176
Xanthorhoe fluctuate malleda Inoue	0	1	0	3	1	5
Xanthorhoe sp.1	14	2	39	123	251	429
Xenortholitha exacra Wehrli	1	0	0	0	0	1
Total observed number of individuals	**2589**	**326**	**1328**	**1966**	**2004**	**8213**
Total observed number of species	**111**	**50**	**76**	**66**	**59**	**156**
Estimated number of species	**130**	**57**	**84**	**82**	**77**	**185**
Sampling completeness	**85%**	**88%**	**90%**	**80%**	**77%**	**84%**

Appendix 4. Number of carabid individuals for each species sampled in different forests in Dongling Mountain

Species	Forest Type					Total
	Pine	Oak	Mixed	Larch	Birch	
Amara sp.	2	0	0	1	0	3
Asaphidion semilucidum Motschulsky	0	1	1	0	0	2
Carabus canaliculatus Adams	0	0	2	11	8	21
Carabus crassesculptus Kraatz	61	15	27	54	38	195
Carabus kruberi Fischer	2	0	1	0	0	3
Carabus manifestus Kraatz	23	6	1	6	67	103
Carabus smaragdinus Duftschmid	1	0	0	0	0	1
Carabus sui Imura & Zhou	3	2	0	0	0	5
Carabus vladimirskyi Dejean	7	63	3	1	0	74
Harpalus bungii Chaudoir	1	0	0	0	0	1
Harpalus coreanus Tschitscherine	2	0	3	2	0	7
Harpalus laevipes Zetterstedt	0	0	1	14	5	20
Notiophilus impressifrons Morawitz	5	3	0	1	0	9
Panagaeus davidi Fairmaire	0	0	1	0	0	1
Pristosia sp	2	5	1	3	0	11
Pseudotaphoxenus mongolicus	14	7	3	1	12	37
*Pterostichus acutidens*Fairmaire	6	22	86	208	208	530
Pterostichus adstrictus Eschscholtz	9	1	8	5	60	83
Pterostichus fortipes Chaudoir	0	14	0	0	2	16
Pterostichus interruptus Dejean	0	0	2	0	5	7
Pterostichus subovats Motschulsky	3	2	4	0	1	10
Synuchus sp.	9	8	6	20	5	48
Trichotichnus sp.	0	1	1	0	2	4
Total number of individuals	**150**	**150**	**151**	**327**	**413**	**1191**
Total number of species	**16**	**14**	**17**	**13**	**12**	**23**

Appendix 5. Number of geometrid individuals for each species sampled in different forests in Dongling Mountain

Species	Forest Type					
	Pine	**Oak**	**Mixed**	**Larch**	**Birch**	**Total**
Abraxas grossudariata Linneaus	1	0	0	0	29	30
Abraxas sp.1	1	0	0	0	12	13
Agathia carissima Butler	2	1	0	0	0	3
Alcis picata Butler	7	2	2	2	15	28
Alcis sp.1	0	0	0	1	0	1
Alcis sp.2	0	0	0	0	1	1
Angerana prunaria Linneaus	7	2	8	2	7	26
Anticypella diffusaria Leech	2	1	0	0	1	4
Arichanna melanaria Butler	19	1	0	1	45	66
Auaxa cesadaria Walker	0	0	0	1	0	1
Bizia aexaria Walker	2	0	0	0	0	2
Bupalus vestalis Staudinger	2	0	0	0	0	2
Cabera exanthemata insulate Inoue	2	0	2	1	1	6
Cabera griseolimbata apotaeniata Wehrli	20	8	2	9	5	44
Cabera sp.1	3	0	2	3	2	10
Cabera sp.2	1	7	3	1	2	14
Cabera sp.3	4	5	11	10	6	36
Chartographa ludovicaria praemutans Prout	4	2	1	1	0	8
Chartographa tabiolaria Oberthür	2	2	0	0	0	4
Chlorissa gelida Butler	1	0	0	0	1	2
Cleora insolita Butler	0	0	0	0	13	13
Comibaena cassidara Guenee	2	0	1	1	0	4
Comibaena nigromacularia Leech	0	0	5	0	0	5
Conchia mundataria Cramer	0	1	0	0	0	1
Ctenognophos sp.1	11	22	10	29	32	104
Ctenognophos sp.2	1	1	1	0	0	3
Ctenognophos tetarte Wehrli	1	0	0	0	0	1
Ctenognophos ventraia kansubia Wehrli	0	0	1	0	0	1
Deileptenia sp.1	1	4	8	14	4	31
Deileptenia sp.2	0	3	0	0	0	3

Diaprepesilla flavomarginaria Bremer	4	1	0	0	0	5
Ecliptopera umbrosaria Motschulsky	0	1	0	0	0	1
Ectropidia expramata Walker	2	2	3	3	6	16
Endropiodes abjecta Butler	13	2	12	5	11	43
Ennominae sp.1	0	0	0	0	1	1
Ennominae sp.2	2	2	9	2	0	15
Ennominae sp.3	1	0	0	0	0	1
Ennominae sp.4	0	0	0	0	2	2
Ennominae sp.5	6	1	0	0	0	7
Ennominae sp.6	2	0	2	1	0	5
Ennominae sp.7	0	0	0	0	2	2
Ennominae sp.8	1	0	0	0	0	1
Ennominae sp.9	0	0	0	0	1	1
Ennominae sp.10	0	0	0	1	0	1
Ennominae sp.11	0	1	0	0	0	1
Epholca auratilis Prout	5	12	17	26	17	77
Epipristis transiens Sterneck	1	0	0	0	0	1
Epirrhoe supergressa albigressa Prout	18	4	4	3	3	32
Eucosmabraxas placida propinqua Butler	0	2	1	3	0	6
Eulithis convergenata Bremer	2	1	1	2	2	8
Eulithis ledereri Bremer	0	0	0	1	1	2
Eustroma aerosa Butler	0	2	1	1	0	4
Euthecia sp.1	0	0	0	2	0	2
Euthecia sp.2	1	1	0	0	0	2
Euthecia sp.3	0	0	0	1	0	1
Euthecia sp.4	4	1	2	5	0	12
Exangerona prattiaria Leech	3	3	32	15	6	59
Gandaritis flavomacularia Leech	0	0	1	1	0	2
Geometra glaucaria Menetries	1	2	13	0	4	20
Geometra valida Felder et Rogenhofer	6	5	2	2	0	15
Geometrinae sp.1	2	0	0	0	0	2
Geometrinae sp.2	0	0	0	0	1	1
Geometrinae sp.3	1	0	1	0	0	2
Geometrinae sp.4	0	1	0	0	0	1
Gnophos serratilinea Sterneck	4	4	5	12	4	29
Gnophos sp.1	1	0	0	1	0	2
Hemistola parallelaria Leech	1	0	1	1	1	4
Hemithea aestivaria Hübner	0	1	1	0	0	2
Heterarmia conjunctaria Leech	23	6	19	15	27	90

Heterolocha laminaria Herrich-Schäffer	1	0	1	2	0	4
Heterophleps sp.1	2	0	0	2	0	4
Hirasa sp.1	1	0	1	6	2	10
Hirasa sp.2	1	1	1	0	0	3
Horisme brevifasciaria Leech	8	4	5	5	1	23
Horisme radicaria Harpe	2	1	0	1	0	4
Horisme sp.1	0	1	1	6	1	9
Horisme tersata Denis et Schiffermüller	9	0	1	8	1	19
Hydrelia flammeolaria Hufnagel	0	0	0	4	2	6
Hydrelia sp.1	3	2	1	7	3	16
Hypomecis punctinalis Scopoli	0	0	0	0	1	1
Hypomecis roboraria Denis & Schiffermüller	2	0	0	1	0	3
Hypomecis sp.2	1	0	0	0	0	1
Idaea sp.1	6	4	1	4	0	15
Iotaphora admirabilis Oberthür	4	7	2	0	1	14
Laciniodes denigrate abiens Prout	0	0	0	0	1	1
Larentiinae sp.1	8	0	1	2	0	11
Larentiinae sp.2	15	3	1	1	0	20
Larentiinae sp.3	4	3	1	7	0	15
Larentiinae sp.4	0	1	0	8	2	11
Larentiinae sp.5	3	1	2	0	0	6
Larentiinae sp.6	0	0	0	4	0	4
Larentiinae sp.7	5	2	1	1	5	14
Larentiinae sp.8	2	2	0	0	0	4
Larentiinae sp.9	1	1	1	1	0	4
Larentiinae sp.10	4	2	0	5	0	11
Larentiinae sp.11	3	2	0	0	0	5
Larentiinae sp.12	2	2	2	0	0	6
Larentiinae sp.13	0	2	0	1	0	3
Larentiinae sp.14	0	3	0	0	0	3
Larentiinae sp.15	0	0	1	0	4	5
Larentiinae sp.16	0	2	0	0	0	2
Larentiinae sp.17	0	1	1	0	0	2
Larentiinae sp.18	0	1	0	0	0	1
Larentiinae sp.19	0	0	0	1	0	1
Larentiinae sp.20	0	1	0	0	0	1
Larentiinae sp.21	1	0	0	0	0	1
Larentiinae sp.22	1	0	0	0	0	1
Larentiinae sp.23	0	0	0	0	1	1
Larentiinae sp.24	1	0	0	0	0	1
Larentiinae sp.25	0	0	1	0	0	1

Larentiinae sp.26	1	0	0	0	0	1
Larentiinae sp.27	0	0	0	0	1	1
Larentiinae sp.28	0	0	0	0	1	1
Larentiinae sp.29	1	0	0	0	0	1
Larentiinae sp.30	1	0	0	0	0	1
Larentiinae sp.31	0	0	1	0	0	1
Larentiinae sp.32	0	0	0	1	0	1
Lobophora halterata Hufnagel	0	1	0	0	2	3
Lomaspilis marginata Linnaeus	5	0	0	0	2	7
Lomographa simplicior Butler	1	1	1	0	0	3
Maxates sinuolata Inoue	0	1	0	1	0	2
Maxates sp.1	2	0	0	0	0	2
Medasina sp.	1	3	3	0	6	13
Melanthia procellata inexpectata Warnecke	0	1	1	1	0	3
Menophra harutai Inoue	4	3	9	11	18	45
Microcalicha melanosticta Hampson	2	0	0	0	0	2
Micronidia sp1	1	4	10	9	6	30
Naxa seriaria Motschulsky	26	0	0	0	0	26
Odontopera bidentata harutai Inoue	1	0	1	0	0	2
Odontopera bilinearia Wehrli	1	0	0	0	0	1
Ophthalmitis albosignaria albosignaria Bremer & Grey	4	0	1	5	0	10
Ophthalmitis cordularia Swinhoe	3	0	1	1	2	7
Ophthalmitis irrorataria Bremer & Grey	3	0	0	1	0	4
Ourapteryx similaria Leech	14	4	4	3	10	35
Paradaria sp.1	0	0	1	0	0	1
Parectropis sp.1	2	0	0	0	0	2
Phanerothyris sinearia Guenée	64	18	96	35	2	215
Phthonosema tendinosaria Bremer	0	0	0	1	0	1
Plagodis pulveraria Linnaeus	11	2	3	1	0	17
Plagodis reticulata Warren	3	13	1	5	18	40
Pomecis sp.1	0	0	0	4	0	4
Pseudostegania defectata Christoph	3	0	0	0	0	3
Psyra sp.1	3	0	0	2	2	7
Scopula sp.	45	5	8	0	0	58
Selenia sordidaria Leech	0	0	4	0	2	6
Semiothisa sp.1	0	0	0	0	3	3
Stegania cararia Hübner	0	0	1	0	0	1

Sterrhinae sp.1	3	5	6	5	9	28
Sterrhinae sp.2	0	1	2	5	7	15
Sterrhinae sp.3	4	0	1	0	0	5
Sterrhinae sp.4	18	2	4	3	2	29
Sterrhinae sp.5	0	0	0	0	2	2
Sterrhinae sp.6	0	1	0	0	1	2
Sterrhinae sp.7	0	0	1	0	1	2
Sterrhinae sp.8	1	0	2	2	7	12
Sterrhinae sp.9	0	0	0	1	0	1
Sterrhinae sp.10	0	1	0	0	0	1
Sterrhinae sp.11	0	2	1	0	0	3
Thera Britannica Truner	0	0	3	3	1	7
Thetidia albocostaria Bremer	3	0	0	0	0	3
Thetidia chlorophyllaria Hedemann	3	1	1	0	0	5
Venusia sp.1	4	1	1	3	2	11
Venusia sp.2	1	0	0	1	0	2
Xanthorhoe quadrifasciata Clerck	1	0	0	2	4	7
Xenortholitha propinguata Kollar	31	0	2	2	0	35
Total number of individuals	**561**	**236**	**380**	**364**	**401**	**1942**
Total number of species	**104**	**79**	**80**	**81**	**69**	**165**