Patterns and drivers of biodiversity: insights from a hyperdiverse invertebrate taxon (Coleoptera: Carabidae)

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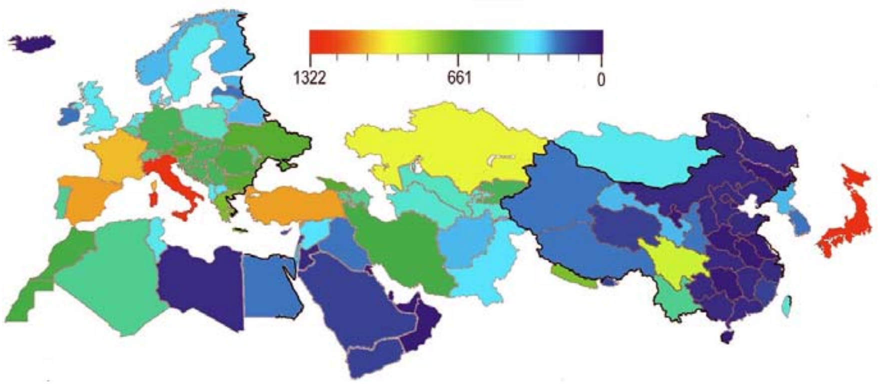

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Summary

Understanding the spatial distribution of biodiversity is central to ecological research and biodiversity conservation. Macroecology, which analyzes diversity patterns at broad scales, provides crucial information in this respect. However, despite their overwhelming diversity and their important roles in ecosystem functioning, invertebrates have largely been ignored in many aspects of macroecological research. In order to obtain a deeper understanding of general patterns in the distribution of biodiversity and to develop adequate strategies for its conservation, it is crucial to more strongly integrate invertebrate taxa into this research.

In this thesis, I analyze broad-scale distributions and potential drivers of species richness and endemism of carabid beetles (Coleoptera: Carabidae) as a highly diverse invertebrate model taxon, as well as the congruence between richness patterns of carabids and different invertebrate, vertebrate and plant taxa in the Palaearctic. Special attention is given to the western Palaearctic, for which carabid data is most comprehensive.

The results show that overall species richness distributions of carabid beetles are strongly determined by patterns of the widespread species, for which analysis of the comprehensive western Palaearctic data identified variables related to energy availability and water-energy balance to best explain broad-scale diversity distributions. Cold climates in northern latitudes and water limitation in some southern regions might explain the latitudinal gradient in carabid species richness across the Palaearctic, with highest richness in southern Europe, south-west China and Japan and decreasing richness towards the north and also towards the southernmost regions of the western and central Palaearctic. However, the dominant impact of widespread species masks effects of deviating determinants for large parts of carabid diversity, which are more restricted in their geographic distribution. While richness of these range-restricted, endemic species peaks at similar latitudes as total richness, it shows a much steeper latitudinal gradient. Low influence of current climate, absence from northern latitudes and a much stronger effect of topographic variability (as a proxy of history; promoting diversification processes and survival in changing climates along altitudinal gradients) on richness patterns of endemics as compared to widespread species point to a signal of history contained in the current spatial distribution of endemic carabids. A strong prevailing impact of history on these species might arise from limited dispersal abilities and inability to recolonize formerly glaciated areas. Separate analysis of highly range-restricted carabids adapted to belowground habitats supports these findings and suggests that historical processes and long-term stability of environmental conditions are probably major factors determining the distribution of highest richness of carabid beetles in the region studied.

These findings probably also apply to other organism groups and might account for the fact that broad-scale patterns of carabid diversity and the coarse-scale centers of highest total and endemic richness in many cases show fairly high congruence with those of other invertebrates, vertebrates and plants. However, taxon-specific characteristics and differences in the response to environmental factors influence the degree of congruence and show that future climate change might shift relationships between the diversity of different taxa. Yet, carabids are one of the taxa showing especially high covariation with patterns of many other organism groups and might thus help to better predict broad-scale patterns in the diversity also of taxa for which accurate data is missing so far. While the availability of reliable data limits comparison to other invertebrates to the western Palaearctic, general patterns can be extended to large parts of the whole Palaearctic in the cross-taxon analysis of carabids, vertebrates and plants. Regarding broad-scale biodiversity conservation strategies, the results indicate that biodiversity hotspots derived from data on vascular plants and vertebrates might indeed also capture a high diversity of invertebrates. Especially China qualifies as an outstanding multi-taxon hotspot of biodiversity in the Palaearctic, requiring intense biodiversity research and conservation effort. But even for the relatively well-documented western Palaearctic diversity, conservation legislation for invertebrates in many of the most biodiverse countries is insufficient. This thesis highlights the importance of single countries for invertebrate biodiversity and their special responsibility for specific taxa, urging for adequate consideration in the implementation of national and international conservation actions.

Altogether, this thesis provides information essential for a more general understanding of the broad-scale distribution of biodiversity. It raises attention to the potential but often ignored impact of history and shows that consideration of range size-related characteristics is central to elucidating driving factors and the mechanisms underlying broad-scale diversity distributions, especially as large parts of the global biodiversity are represented by invertebrates with low dispersal power. The results of this thesis further show that general characteristics in the broad-scale distribution of species richness apply to a broad range of different and phylogenetically unrelated taxa, including so far only insufficiently studied invertebrates. This knowledge can contribute to a better integration of the megadiverse invertebrates into broad-scale conservation strategies. In conclusion, this thesis analytically confirms patterns often hypothesized, but scarcely studied in detail so far and points out the high value of carabid beetles as a model taxon for macroecological analyses of highly diverse invertebrates.

Zusammenfassung

Ein zentrales Anliegen ökologischer und naturschutzfachlicher Forschung ist das Verständnis der räumlichen Verteilung von Biodiversität. Makroökologische Untersuchungen, welche Biodiversitätsmuster und deren zugrunde liegenden Mechanismen auf großskaligen Ebenen untersuchen, liefern in dieser Hinsicht entscheidende Einblicke. Trotz ihrer enormen Artenvielfalt und ihrer bedeutenden ökosystemaren Funktionen sind allerdings Invertebraten bisher in vielen Aspekten makroökologischer Forschung kaum berücksichtigt worden. Für ein tieferes Verständnis allgemeiner Muster und die Entwicklung adäquater Strategien für den Schutz von Biodiversität ist ein deutlich stärkerer Einbezug wirbelloser Taxa jedoch unerlässlich.

In dieser Arbeit analysiere ich die großräumige Verteilung des Gesamtartenreichtums sowie der Diversität endemischer Arten von Laufkäfern (Coleoptera: Carabidae) als hochdiverses wirbelloses Modelltaxon, deren potentielle Einflussfaktoren, sowie die Übereinstimmung zwischen Mustern der Diversitätsverteilung von Laufkäfern, anderen Invertebratengruppen, Wirbeltieren und Gefäßpflanzen in der Paläarktis. Der besondere Fokus liegt dabei auf der westlichen Paläarktis, für welche die umfassendsten Laufkäferdaten vorliegen.

Die Ergebnisse verdeutlichen, dass die großräumige Verteilung des Gesamtartenreichtums von Laufkäfern stark durch Verteilungsmuster weitverbreiteter Arten bestimmt wird. Die Analyse der umfassenden westpaläarktischen Daten weist Parameter, welche regionale Energie- und Wasserverfügbarkeit sowie das Verhältnis beider zueinander widerspiegeln, als Variablen mit hohem Erklärungswert für diese Muster aus. Kalte Klimate in nördlichen Breiten und begrenzte Wasserverfügbarkeit in einigen südlichen Regionen sind möglicherweise mit verantwortlich für die breitengradabhängige Verteilung des Laufkäfer-Artenreichtums. Letzterer erreicht höchste Werte in Südeuropa, Südwest-China und Japan und nimmt allgemein in Richtung Norden sowie im westlichen und mittleren Teil der Paläarktis auch zu den südlichsten Regionen hin ab. Allerdings überdeckt der starke Einfluss der weitverbreiteten Arten Effekte anderer Einflussgrößen, welche für einen großen Teil der Laufkäferdiversität, nämlich für die Vielzahl der Arten, welche geographisch stärker begrenzte Verbreitungsareale aufweisen, eine wichtige Rolle spielen. Während auch der Artenreichtum dieser in ihren Verbreitungsarealen stark eingeschränkten, endemischen Taxa höchste Werte in ähnlichen Breiten wie der Gesamtartenreichtum der Laufkäfer erreicht, zeigt er einen wesentlich steileren breitengradabhängigen Verteilungsgradienten. Ein geringer Einfluss gegenwärtiger Klimaverhältnisse, das Fehlen dieser Arten in nördlichen Breiten und ein deutlich stärkerer Effekt von topographischer Variabilität (die hier als Maß für historische Einflüsse gesehen werden kann, indem sie Artenbildungsprozesse und Überleben entlang von

Höhengradienten bei sich über längere Zeiträume wandelndem Klima fördert) auf Diversitätsmuster endemischer im Vergleich zu weitverbreiteten Arten deuten auf einen über historische Zeiträume wirkenden Einfluss hin, welcher sich in der gegenwärtigen Verbreitung endemischer Laufkäfer widerspiegelt. Ein solcher, immer noch andauernder Einfluss auf die endemischen Arten kann durch begrenztes Ausbreitungspotential und das Unvermögen zurückzuführen sein, ehemals durch eiszeitliche Gletscher bedeckte Gebiete wiederzubesiedeln. Die separate Analyse der besonders stark in ihrem Verbreitungsareal begrenzten Laufkäferarten subterraner Lebensräume bekräftigen diese Schlussfolgerungen und machen darüber hinaus deutlich, dass historische Prozesse und eine langzeitige Stabilität von Umweltbedingungen wahrscheinlich wesentliche Faktoren sind, welche die geographische Verteilung höchster Artendiversität der Laufkäfer bestimmen.

Diese Ergebnisse gelten mit großer Wahrscheinlichkeit auch für andere Organismengruppen und können als Erklärungsansatz dafür dienen, dass die großskaligen Muster der Laufkäferdiversität und die Zentren höchsten Arten- und Endemitenreichtums in vielen Fällen relativ hohe Übereinstimmung mit denen anderer Invertebraten und auch mit Mustern und Zentren von Wirbeltieren und Gefäßpflanzen aufweisen. Taxon-spezifische Eigenschaften und unterschiedlich starke Reaktionen auf verschiedene Umweltfaktoren beeinflussen dabei jedoch den Grad der Übereinstimmung zwischen einzelnen Taxa und zeigen, dass künftiger Klimawandel die Diversitätsbeziehungen zwischen verschiedenen Taxa verändern kann. Laufkäfer zählen allerdings zu den Artengruppen, welche sich durch besonders hohe Kovariation mit Mustern vieler anderer Organismengruppen auszeichnen und so helfen können, großflächige Verbreitungsmuster auch von Taxa abzuschätzen, für welche bisher keine ausreichende Datenbasis besteht. Während die Verfügbarkeit verlässlicher Daten den Vergleich mit anderen Invertebraten auf die westliche Paläarktis beschränkt, können durch die vergleichende Analyse von Laufkäfern, Wirbeltieren und Gefäßpflanzen allgemeine Muster der Diversitätsverteilung auf weite Teile der ganzen Paläarktis ausgeweitet werden. Im Bezug auf großflächige Strategien für den Schutz von Biodiversität deuten die Ergebnisse darauf hin, dass ‚Hotspots' der Biodiversität, welche auf der Basis von Pflanzen- und Wirbeltierdaten ausgewiesen wurden, auch einen hohen Artenreichtum wirbelloser Taxa erfassen können. Besonders China sticht dabei als bedeutendes Diversitätszentrum in der Paläarktis für eine Vielzahl von Organsimengruppen hervor, welches intensiven Schutz und weitere Erforschung der Biodiversität benötigt. Doch selbst für den relativ gut dokumentierten Artenreichtum von Invertebraten in der westlichen Paläarktis existiert in vielen der artenreichsten Länder nur eine unzureichende naturschutzfachliche Gesetzgebung. Die vorliegende Arbeit hebt die Bedeutung einzelner Länder und deren Verantwortung für die Biodiversität wirbelloser Tiere im Allgemeinen und für spezifische Taxa im Besonderen hervor und fordert eine angemessene Berücksichtigung dieser Taxa bei der Umsetzung von nationalen und internationalen Schutzbemühungen.

Insgesamt liefern die Ergebnisse der vorliegenden Arbeit wichtige Einsichten zu einem besseren und allgemeinen Verständnis der großräumigen Verteilung von Biodiversität. Sie machen auf den möglichen aber oft unbeachteten Einfluss historischer Prozesse aufmerksam und zeigen, dass Aspekte der Größe von Verbreitungsarealen der Arten unbedingt berücksichtigt werden müssen, um die Einflussfaktoren und Mechanismen aufzudecken, welche die großräumige Verteilung der Biodiversität bedingen. Dies ist besonders im Hinblick darauf von Bedeutung, dass ein Großteil dieser Diversität von Invertebraten mit geringem Ausbreitungsvermögen gestellt wird. Die Ergebnisse verdeutlichen darüber hinaus, dass generelle Muster in der großräumigen Verteilung des Artenreichtums für eine Vielzahl verschiedener und phylogenetisch nur entfernt verwandter Taxa zutreffen, auch für in dieser Beziehung bisher wenig untersuchte Invertebraten. Dieses Wissen kann zu einem besseren Einbezug der hochdiversen Invertebraten in großräumige Naturschutzstrategien beitragen. Die Arbeit bestätigt damit durch ihre Analysen Muster, welche oft vermutet, aber bisher kaum im Detail überprüft wurden und stellt dabei den hohen Wert von Laufkäfern als Modellgruppe für makroökologische Untersuchungen hochdiverser Invertebraten heraus.

Authors' contributions to manuscripts with multiple authors

The Chapters 2 to 5 and 7 are a series of manuscripts published in or submitted to international peer-reviewed journals.

Andreas Schuldt[1] is the overall author of all manuscripts presented in this thesis. He has personally developed the main ideas presented in the manuscripts, personally written all manuscripts, collected and analyzed the data for all manuscripts and created tables, figures, and appendices. He is also responsible for correspondence with editors and reviewers.

Thorsten Assmann[1] was the main supervisor for the analyses presented in the manuscripts. He gave input at various stages of the preparation of the manuscripts, from discussing the development of the main ideas to commenting on earlier drafts of the manuscripts.

Zhiheng Wang[2] and **Hongzhang Zhou**[3] helped in providing suitable data on plant species richness of Chinese provinces and commented on earlier versions of the manuscript presented in Chapter 4. Hongzhang Zhou also commented on earlier versions of the manuscript presented in Chapter 7.

Martin Baruffol[4], **Martin Böhnke**[5] **and Anne C. Lang**[1] provided data on woody plant species richness and basal diameter measurements of trees and shrubs of the forest stands studied within the context of the BEF China project (Chapter 7). **Karin Nadrowski**[6] gave input concerning statistical analyses of the data presented in Chapter 7 and commented on earlier versions of the manuscript. **Helge Bruelheide**[5] is the coordinator of the BEF China project and he as well as **Werner Härdtle**[1], **Goddert von Oheimb**[1] and **Winfried Voigt**[7] contributed to the preparation of the study and commented on earlier versions of the manuscript presented in Chapter 7.

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1 GENERAL INTRODUCTION

1.1 Background

Biodiversity, i.e. the variety of life in its genetic, taxonomic and ecological form, has become a central focus in ecology and a major concern in conservation biology over the last decades (Myers *et al.* 2000; Ricklefs 2004; Hillebrand and Matthiessen 2009). On the one hand, ecological research has made significant progress in documenting the profound effects species richness and functional diversity can have on ecosystem functioning, including important ecosystem 'services' such as biomass production, nutrient cycling and many other ecosystem properties essential to mankind (Andrews and O'Brien 2000; Hooper *et al.* 2005; Hector *et al.* 2007). On the other hand, however, we are becoming increasingly concerned with the rapid and to a large part human-induced decline in global biodiversity, with all its negative effects also on our own well-being (Root *et al.* 2003; Parmesan 2006; Kaiser-Bunbury *et al.* 2010). Land use and climate change pose severe threats to life on earth, with many species already having gone and many more expected to go extinct in near future (Samways 2007; Lee and Jetz 2008; Stork 2010). Recognition of these facts has triggered extensive research and international conservation efforts, which try to reduce this biodiversity loss (Myers *et al.* 2000; Whittaker *et al.* 2005; Brooks *et al.* 2006).

However, we are only beginning to understand the complex relationships and interactions between different components of overall diversity (e.g., between the diversity of different trophic levels or functional groups) and the consequences of losing diversity within one component for the diversity and functional integrity of other components (Duffy *et al.* 2007; Schmitz 2007; Tylianakis *et al.* 2008; Hillebrand and Matthiessen 2009). This is aggravated by the fact that scientific species names and documentation of species distributions so far only exist for a fraction of the global diversity of species (Samways 2007; Stork 2010). In order to truly understand ecological systems and to develop adequate measures for their conservation, better knowledge of biodiversity, of general patterns in the spatial distribution across different taxa and of the drivers of diversity is an essential prerequisite (Whittaker *et al.* 2005; Wolters *et al.* 2006; Field *et al.* 2009).

An approach which has gained increasing importance in biodiversity-related research over the last years is the adoption of a broader, macroecological perspective (Willig *et al.* 2003; Kerr *et al.* 2007). Patterns of diversity within and between taxa can be studied at different scales, with a local, regional or global extent. Classic ecological research has focused primarily on smaller scales and simplified systems or has studied subsystems to reduce the degree of complexity (Blackburn and Gaston 2004; Srivastava and Vellend 2005; Kerr *et al.* 2007). In contrast, the macroecological approach tries "*to take such a broad view of ecological systems that fine-scaled 'noise' is factored out and only the signal of broad general patterns remains*"

(Blackburn and Gaston 2004). As local assemblage structures are influenced by regional species diversity (Gaston and Blackburn 2000; He *et al.* 2005; Harrison and Cornell 2008), inclusion of such a broader perspective is indispensable for a general understanding of biodiversity (Ricklefs 2004).

Much progress has been made regarding our basic knowledge concerning central macroecological issues of patterns and drivers of diversity (Wolters *et al.* 2006; Gaston *et al.* 2008; Field *et al.* 2009). However, most of this knowledge is based on studies of only a very small proportion of the overall global biodiversity, with a strong bias towards few vertebrate and plant taxa (Hawkins *et al.* 2003; Qian and Ricklefs 2008). Invertebrate biodiversity, with its multitude of herbivores, detritivores, predators or parasitoids, by far exceeds the diversity of plants or vertebrates (Stork 2007), but has largely been ignored in many aspects of macroecological research (Whittaker *et al.* 2005; Baselga 2008). For a more general understanding of patterns and drivers of biodiversity than we have to date, it is thus of crucial importance to more strongly integrate these taxa into macroecological research (Whittaker *et al.* 2005; Ulrich and Fiera 2009). With invertebrates being heavily affected by species extinctions (Fonseca 2009; Stork 2010), this also applies to the development of effective conservation strategies facing the worldwide loss of biodiversity. Prominent strategies, such as the identification of biodiversity hotspots, presently lack adequate consideration of the megadiverse invertebrates (Myers *et al.* 2000; Brooks *et al.* 2006).

1.2 Carabid beetles as a model taxon for invertebrate macroecology

Insufficient documentation of the distribution of many taxa is one of the reasons for the paucity of studies incorporating invertebrates into research focusing on patterns of diversity over geographically extensive areas (Lovell *et al.* 2007; Hortal 2008). However, especially studies covering wider geographic ranges are of particular interest in understanding general patterns of overall biodiversity (Lamoreux *et al.*, 2006; Wolters *et al.*, 2006). With the distribution of species relatively well-documented across large parts of the Palaearctic, carabid beetles (Coleoptera: Carabidae) are one of the few and most diverse invertebrate taxa for which diversity patterns over such larger extents can be reliably analyzed. Of the worldwide 40 000 species, about 11 000 are known from the Palaearctic (Löbl and Smetana 2003; Lorenz 2005). A stable taxonomy exists for these species (Löbl and Smetana 2003) and avoids problems associated with taxonomic uncertainties, which may well arise in the analysis of other invertebrates (Isaac *et al.* 2004). Carabid beetles also offer the advantage over the few previously studied insect taxa of not only being remarkably species-rich in general, but also of featuring high richness of range-restricted and low mobile species.

Macroecological patterns of widespread and range-restricted species can differ substantially (Jetz and Rahbek 2002; Orme *et al.* 2005; Rahbek *et al.* 2007) and understanding these differences is of fundamental importance for biodiversity-related research (Szabo *et al.* 2009). As many invertebrates are characterized by low power of dispersal and restricted range sizes, results for carabids might also help to shed light on the distribution and determinants of the diversity of many less well-known invertebrate taxa, especially as carabids are not only taxonomically, but also ecologically highly diverse and represent a broad range of life-form types (Thiele 1977). Finally, with most carabids being predators, relationships between plant and invertebrate diversity can be assessed in a more general way than for instance possible with well-studied but phytophagous butterflies. Altogether, carabid beetles thus emerge as an exceptional and promising taxon to gain insight into macroecological patterns of highly diverse invertebrates.

Taking advantage of an extensive data basis for carabid beetles (Löbl and Smetana 2003), the analyses in the following chapters tackle issues concerning the spatial distribution of invertebrate diversity across the western (Europe and North Africa) and in part also across the eastern Palaearctic (central and east Asia). The Palaearctic comprises a broad range of boreal, temperate and subtropical regions and exhibits high spatial variation in biodiversity and environmental characteristics, making it an ideal subject for macroecological research.

1.3 Aims and hypotheses of this thesis

Among the topics which have dominated macroecological research since its emergence, two aspects have received special attention and are of great importance for both basic ecological and applied conservation biological research (Gaston 2000; Hawkins *et al.* 2003; Wolters *et al.* 2006; Field *et al.* 2009): The identification of general patterns in the distribution of species richness across different groups of organisms and the analysis of potential determinants of these patterns.

Using the highly diverse carabid beetles as a model taxon, this thesis aims to significantly increase our knowledge of the above aspects for the so far only insufficiently studied diversity of invertebrates and to contribute to a general understanding of macroecological patterns across different and phylogenetically unrelated organism groups. Throughout this thesis I will focus on species richness and endemism as two of the most commonly used measures of biodiversity (Hawkins *et al.* 2003; Brooks *et al.* 2006; Wolters *et al.* 2006), which allows for a good incorporation of the findings into the general framework derived from previous studies.

1.3.1 Patterns and drivers of invertebrate species richness and endemism

The first part of this thesis (Chapters 2 and 3) focuses on broad-scale patterns of carabid beetle diversity and its potential determinants across the western Palaearctic. Understanding the spatial distribution of species richness and endemism is not only key to determining the current status of biodiversity and to evaluate modern theories in ecology and biogeography, but also essential for predicting responses of biodiversity and adapting conservation strategies to global change (Ricklefs 2004; Kerr *et al.* 2007; Field *et al.* 2009).

In **Chapter 2**, I analyze species richness and endemism patterns of carabids across the well-sampled western Palaearctic, differentiating between patterns and potential environmental determinants of total species richness, the richness of widespread and the richness of range-restricted (endemic) species. For many previously studied taxa a strong impact of contemporary climate conditions on current diversity distributions is being assumed (e.g., Hawkins *et al.* 2003; Field *et al.* 2009). However, historical and evolutionary processes influencing diversification, extinction or dispersal are often alternatively or additionally considered (Wiens and Donoghue 2004; Mittelbach *et al.* 2007; Araújo *et al.* 2008). A combined effect of these aspects is probably relevant for current species richness distributions, but controversy exists over the relative roles of evolutionary or historical and contemporary impacts on these patterns (Hawkins and Porter 2003b; Montoya *et al.* 2007; Svenning and Skov 2007a; Araújo *et al.* 2008). The strength of current climate versus historical effects might depend on dispersal abilities of the species and especially for many range-restricted taxa, historical processes might still play an important role (Jetz *et al.* 2004; Svenning and Skov 2007a; Araújo *et al.* 2008). The analysis of carabid beetles offers an excellent opportunity to gain insight into these issues from an invertebrate perspective and to assess the relative importance of environmental and historical effects for a highly diverse insect taxon characterized by a large proportion of low mobile and range-restricted species.

With **Chapter 3**, this study is complemented by an analysis restricted to species richness distributions of carabid beetles which are adapted to belowground habitats and show reduced dispersal abilities due to their strong habitat specialization. Patterns in the diversity of belowground species are only poorly studied (Culver *et al.* 2006). Comparison of these patterns to those of total, widespread and endemic diversity in general can help to enhance our understanding of species richness distributions and of possible impacts of dispersal ability on current diversity patterns.

The **main hypotheses** guiding the analyses of **Chapters 2 and 3** are:

i) Species richness of carabid beetles in general probably follows a latitudinal cline, with high richness in southern and low richness in northern regions, as suggested from previous studies on less diverse taxa.

ii) I expect to find range-size related differences in the correlates of species richness: Widespread species probably have better been able to track climate changes and thus show stronger relation to current climate. In contrast, endemic species might have been less able to do so. Their restricted ranges could point to limited dispersal abilities.

iii) Weak links probably exist between belowground beetle diversity and current climatic conditions. Instead, a strong historical signal might be hypothesized to be found, reflecting the reduced dispersal abilities of the morphologically strongly adapted and low mobile subterranean carabid fauna.

1.3.2 General patterns in the distribution of diversity among invertebrates, vertebrates and plants

Based on the findings of the previous chapters, in the second part of the thesis (Chapters 4 and 5) I examine how the patterns observed for carabid beetles relate to those of other (invertebrate as well as vertebrate and plant) taxa and to what extent these patterns might be generalized over different and phylogenetically unrelated taxa. This issue is of special importance in ecological research as relationships between the diversity of different taxa can strongly influence species assemblages, the functioning of ecosystems and dynamics at regional scales (Hillebrand *et al.* 2008; Kissling *et al.* 2008). Moreover, regarding the global biodiversity decline, many conservation strategies rely on data of well-sampled vertebrates and plants (Brooks *et al.* 2006). For instance, identifying “hotspots” of highest diversity based on these taxa has become one of the successful strategies to allocate funding to regions of high conservation priority at continental and global scales (Myers and Mittermeier 2003). However, with little information on the degree to which diversity patterns of vertebrates and plants reflect those of the megadiverse invertebrates, the adequacy of these strategies for the conservation of global biodiversity is far from clear (Whittaker *et al.* 2005; Samways 2007).

Our understanding of general patterns in the distribution of diversity necessarily has to remain fragmentary as long as we only have insufficient knowledge concerning distribution patterns of large parts of the world’s biodiversity (Wolters *et al.* 2006; Samways 2007).

In **Chapter 4**, the analysis of the distribution of carabid beetle diversity is extended to the whole Palaearctic and patterns of species richness and endemism are compared to those of vertebrates and vascular plants. Assessing the extent of similarity and the differences between broad-scale distributions of the diversity of phylogenetically unrelated taxa allows for testing whether our present understanding of these distribution patterns, which is largely based on few well-studied taxa, is robust to the inclusion of species-rich invertebrates (Lamoreux *et al.* 2006). This comparison also helps to evaluate to what degree centers of high diversity of these taxa are congruent and thus to what extent well-established conservation strategies, such as the biodiversity hotspots approach, can account for invertebrate diversity. The few studies which have tried to incorporate invertebrates into analyses of cross-taxon congruence of diversity over larger geographic areas so far yielded varying results and were restricted to relatively species-poor taxa (e.g., Gaston and David 1994; Balmford and Long 1995; Pearson and Carroll 1998). High species richness and, in contrast to data on many other taxa, a dataset allowing for the analysis of both overall and endemic species richness promise important new results in this respect from the study of carabid beetles.

In **Chapter 5**, I further broaden the taxonomic scope to examine how species richness patterns of carabid beetles relate to those of other invertebrate taxa. Are the patterns observed for carabids representative of those of other invertebrates? For Europe, data on broad-scale distribution patterns of several invertebrate taxa has recently become available (e.g., Baselga 2008; Finch *et al.* 2008; Pautasso and Fontaneto 2008; Ulrich and Fiera 2009). I use this presently rare opportunity to analyze relationships between and congruence among spatial richness distributions of twelve invertebrate taxa. Here as well, data on vascular plants and vertebrates is incorporated to assess the extent to which generalizations can be made over the different organism groups. With reliable data on many other organism groups still missing, it is of special interest to identify taxa which well reflect diversity distributions of other and maybe less well-known taxa (Moritz *et al.* 2001; Wolters *et al.* 2006; Lovell *et al.* 2007). Carabid beetles might well qualify as one of these taxa representative of the diversity of many other organism groups. Inclusion of the many different invertebrate taxa also contributes to developing a more general perspective on centers of biodiversity and other conservation-based issues (Brooks *et al.* 2006). Considering that national conservation legislation for invertebrates in many biodiverse countries is insufficient, the analyses can also help to set priorities for invertebrate conservation at broader scales and to highlight the responsibility of individual countries for their highly diverse invertebrate fauna.

The **main hypotheses** guiding the analyses of **Chapters 4 and 5** are:

i) Congruence between unrelated invertebrate, vertebrate and plant taxa could be lower than for closely related taxa often considered so far (Grenyer *et al.* 2006). However, I hypothesize that carabid beetles show fairly high congruence with richness patterns of vascular plants and vertebrates, especially because of expected similarities in the influence of climate and other environmental factors on species richness patterns at broad scales.

ii) For the same reason, good congruence between carabid beetles and many other invertebrate taxa might be expected. Additionally, high species richness, the large number of range-restricted taxa and low mobility of many species might be characteristics which make carabids good predictors of the diversity of other invertebrates with likewise low mobility or small range sizes.

iii) In contrast, covariation between richness distributions of single invertebrate taxa and their relationship with the species richness of vertebrates or plants might be less strong. Deviations from the general latitudinal cline in species richness are known for some taxa and taxon-specific characteristics in the geographic distribution of diversity might have larger effects in species-poor than in species-rich taxa.

iv) While probably not comprising highest species numbers of all taxa, “hotspots” as centers of a generally high collective species richness of invertebrates, vertebrates and vascular plants might be identified, reflecting general latitudinal dependencies in the distribution of species richness at the broad scale of the analyses.

1.3.3 Additional material

In **Chapter 7**, I present as a supplement to the above broad-scale studies results from research on diversity relationships at local scales, conducted during the works for this thesis. They illustrate effects of biotic interactions, which are considered to influence patterns of diversity especially at local scales, on the relationship between plant species richness and insects, using the example of plant-herbivore interactions in a highly diverse subtropical forest ecosystem.

The **References** to Chapters 1-7 are listed in **Chapter 8**.

2 ENVIRONMENTAL AND HISTORICAL EFFECTS ON RICHNESS AND ENDEMISM PATTERNS OF CARABID BEETLES IN THE WESTERN PALAEARCTIC

Published article

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2.1 Abstract

Identifying determinants of spatial diversity gradients is in the focus of biodiversity-related research and has gained considerable importance regarding global change and conservation strategies. Despite their overwhelming diversity and the crucial role of invertebrates in ecosystem functioning, our understanding of factors driving broad-scale invertebrate diversity is limited. Tackling this issue, our study analyzes macroecological patterns of a highly diverse insect taxon across large parts of the Western Palaearctic. We used regression modelling to assess the influence of environmental factors on overall, widespread and restricted-range (endemic) carabid beetle diversity. Single-term regressions and variation partitioning among climatic, topographic and spatial variables showed that total carabid diversity as well as richness patterns of widespread species were most strongly correlated with spatially structured variables related to current climate (measures of ambient energy and, to a lesser degree, precipitation and AET). In contrast, restricted-range (endemic) species were most notably related to range in elevation. We discuss the possible role of this factor as a surrogate measure of historical processes and the impact of history on contemporary diversity distributions. Our results indicate that while overall diversity patterns of carabids strongly reflect current climate conditions, this primarily reflects the more widespread species, whereas the spatial distribution of restricted-range species is still significantly affected by historical processes. Thus, for a general understanding of determinants and mechanisms of broad-scale diversity, taking into account dispersal abilities and range sizes of species is essential, especially as large parts of global biodiversity are represented by invertebrates with low dispersal powers.

2.2 Introduction

The spatial heterogeneity and patterning of biodiversity, such as the often documented latitudinal richness gradient, have stimulated an enormous amount of scientific research (Willig *et al.* 2003). Identifying determinants of these spatial patterns and understanding the underlying mechanisms has become a central topic in ecology, biogeography and conservation biology (Ricklefs 2004; Gaston *et al.* 2008). As diversity patterns are often related to current climatic conditions, this topic is also highly relevant to predicting the effects of climate change on biodiversity, including future biodiversity shifts and losses based on global change scenarios (Kerr *et al.* 2007).

Large-scale geographic diversity patterns must ultimately be driven by the evolutionary/historical processes of speciation, extinction and dispersal (Jetz *et al.* 2004). Over time, environmental conditions have interacted with these processes, e.g., influencing dispersal (and thus isolation and speciation) of species via effects on their ecological and physiological requirements (Wiens and Donoghue 2004). Many studies have tested the ability of contemporary environmental characteristics to explain current diversity patterns and often reported strong covariation between diversity and modern day climate (Hawkins *et al.* 2003; Rodriguez *et al.* 2005; Qian *et al.* 2007; Whittaker *et al.* 2007; Baselga 2008; Hortal *et al.* 2008). However, it has proven difficult to derive robust mechanistic frameworks based entirely on these relationships (Currie *et al.* 2004). A growing number of studies try to combine ecological and evolutionary/historical aspects (e.g., Hawkins *et al.* 2007; Svenning and Skov 2007a; Araújo *et al.* 2008; Hortal *et al.* 2008; Qian 2008; Svenning *et al.* 2008), based on unifying theoretical frameworks (Ricklefs 2004; Wiens and Donoghue 2004; Rangel *et al.* 2007). Still, while some studies especially emphasize prevailing effects of history on current diversity distributions (e.g., Rahbek *et al.* 2007; Araújo *et al.* 2008), others underline the prominent role of contemporary environmental conditions in explaining large-scale diversity patterns (e.g., Kerr and Currie 1999; Hawkins and Porter 2003b). Interestingly, recent studies have shown that overall richness patterns are strongly influenced by the distribution patterns of the widespread, common species, which often covary more strongly with current climate than the restricted-range species. In contrast, the ranges of the latter might be much more dominated by persisting impacts of historical processes (Jetz and Rahbek 2002; Jansson 2003; Rahbek *et al.* 2007; Svenning and Skov 2007a).

Despite the enormous attention of biogeographers and ecologists to patterns of biodiversity and its possible determinants, studies analyzing spatial diversity patterns suffer from a bias towards specific organism groups, especially endothermic mammals and birds (Hawkins *et al.* 2003; Jetz *et al.* 2004). In order to assess the generality of the results found so far, there is a need for further studies on invertebrate taxa (Hawkins *et al.* 2003; Baselga 2008), which represent the bulk of faunal diversity. As ectothermic animals with an often low vagility, species-rich invertebrates especially qualify to test whether the often observed strong relationships with current climate are a general feature for the majority of animals and to what extent historical processes still dominate the distributional patterns of the many taxa with low dispersal abilities.

In our study, we analyze putative (i.e., correlation-based) determinants of total as well as widespread (non-endemic) and restricted-range (endemic) diversity patterns of carabid beetles (Coleoptera: Carabidae) across large parts of the Western Palaearctic. For species-rich predatory invertebrates, such as carabids, geographically extensive studies on driving factors of large-scale diversity distributions are scarce (cf. Hawkins *et al.* 2003). Relatively few studies have addressed diversity patterns of invertebrates and their determinants at broad scales and large spatial extents (e.g., Kerr and Currie 1999; Hawkins and Porter 2003b; Hawkins and Porter 2003a; Konvicka *et al.* 2006; Baselga 2008; Finch *et al.* 2008). In these studies, variables related to current climate have been reported to best explain the geographic variability in species richness of the respective taxa.

Carabid beetles differ distinctly from the invertebrate taxa previously studied in this context. They are remarkably species-rich (about 3,200 species known from our Western Palaearctic study region; Löbl and Smetana, 2003), are characterized by a large proportion of species with restricted ranges, are predominantly predators, and many species have low power of dispersal (Kotze and O'Hara 2003). The combination of these characteristics, in particular the large number of restricted-range species and low vagility of many species, might yield results deviating from those of previously studied taxa. For instance, retreat and recolonization processes due to glaciations might have caused Western Palaearctic diversity patterns of these low-mobility taxa to be poorly related to contemporary climate (Kotze and O'Hara 2003; Svenning and Skov 2007a; Araújo *et al.* 2008), as has been documented for distributions of restricted-range species of vertebrates and trees (Jansson 2003; Jetz *et al.* 2004; Svenning and Skov 2007a) and already much earlier for cave-dwelling beetles (Holdhaus 1954).

Thus, in our study we specifically aimed to assess the degree of covariation between measures of contemporary climate conditions (especially those related to energy and water-energy dynamics, as they are considered most influential, cf. Hawkins *et al.* 2003) and the distribution patterns of carabid beetle diversity. Differentiating between the richness of all species, just the widespread species, and just the restricted-range (hereafter, endemic) species, we analyzed climatic, topographic (which might contain a historical signal, see Discussion) and spatial models and partitioned the explained variance between these models to assess their relative effects on carabid beetle diversity. We specifically focused on the following questions: (1) Does total carabid diversity respond in a similar way as other taxa to environmental factors often suggested to determine spatial diversity patterns? (2) To what extent do the diversity patterns of widespread and endemic carabids correspond to these environmental factors? (3) How does the high proportion of endemic species influence the impact of current versus historical processes on total carabid diversity?

2.3 Methods

2.3.1 Species and environmental data

A database was compiled for carabid diversity (total, widespread, and endemic species richness; extracted from Löbl and Smetana 2003) and for potential predictor variables on a country level for all countries in the Western Palaearctic. Following the definitions in

Lumaret and Lobo (1996), species with range sizes <$6x10^5$ km² were classified as endemics, as opposed to widespread species with larger distribution ranges. Range sizes were estimated by summarizing the area of countries in which the species occurred and by taking into account known distribution patterns of species (e.g., species endemic to the Alps).

For invertebrates, country-level data is most comprehensive and accurate, as detailed surveys allowing for analyses across wider geographic ranges at finer scales are mostly missing (Lovell *et al.* 2007; Hortal 2008). Similar approaches have been used in biogeographical studies on other invertebrate and also on vertebrate taxa (e.g. Konvicka *et al.* 2006; Baselga 2008; Qian and Ricklefs 2008). To assess the degree of completeness of the data, we analyzed species accumulation curves (based on species discovery data) of carabid beetles for each country.

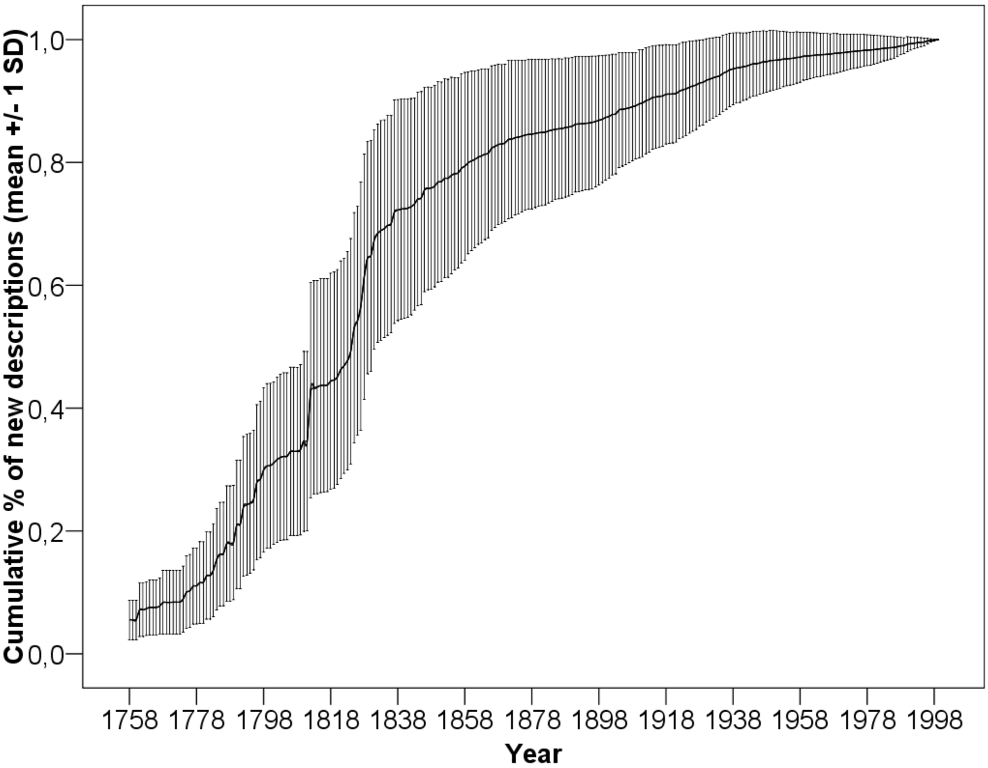

Figure 2.1. Species accumulation curve of the mean (+/- 1 SD) annual percentage of newly recorded carabid beetles per country in the Western Palaearctic study region.

Species richness in most European and North African countries reached a clear asymptote during the 20th century, often even earlier (Fig. 2.1). Only the most species-rich countries (Italy, Spain and Greece) still showed some increase in species numbers due to recent discoveries of mostly endogeic and cave-dwelling beetles (cf. Jiménez-Valverde and Ortuno 2007), which, however, does not affect the overall spatial richness pattern for this region. Discovery curves of global bird diversity and the British flora show similar shapes. Even for these taxa, which are considered to be well known, species numbers are still slightly but continuously increasing even at the end of the 20th century (Bebber *et al.* 2007). We excluded Turkey, European Russia and the Middle East from our dataset, as countries in these regions are in part less well sampled. We thus retained 39 countries (Europe and North Africa, excluding Iceland due to its strong insularity, and Andorra, Liechtenstein and Luxembourg because of their very small country sizes, Fig. 2.2) with well documented carabid beetle diversity (see also Assmann *et al.* 2008).

We selected eleven environmental variables as potential determinants of large-scale diversity gradients (Table 2.1, Supplementary Material: Table S2.1). These represent the main explanatory factors of recently intensively discussed hypotheses on the influence of contemporary processes as driving factors of diversity (based on ambient energy input, water-energy balance, productivity, climate and habitat heterogeneity; Willig *et al.* 2003, Currie *et al.* 2004). Climate data (temperature and precipitation variables, frost frequency) was obtained from Mitchell *et al.* (2002), who calculated country-level averages from the high-resolution data of New *et al.* (1999). Mean annual actual and potential evapotranspiration (AET and PET) were calculated using Thornthwaite's method (Thornthwaite and Mather 1963; Thornthwaite and Mather 1964; Black 2007). Elevation range (reflecting habitat heterogeneity as well as long-term possibilities for survival and speciation, i.e., a historical signal; see Discussion) was compiled from CIA (2008) along with midpoint latitude and longitude (quantifying the extent of spatial gradients in the diversity patterns).

2.3.2 Statistical analyses

We conducted separate analyses for overall species richness and richness of widespread and endemic species. First, we analyzed the relationships between single environmental variables and carabid diversity by single-term regressions. We checked for significant non-linear relationships in regressions, adding second- or third-order polynomial terms to predictor variables where appropriate (Quinn and Keough 2002). Variables were centered before computing polynomials to reduce collinearity between monomials (Legendre and Legendre 1998). Richness measures and area were $\log_{10}$-transformed to normalize their distributions.

We computed stepwise regression models for three sets of predictor variables (spatial, topographic and climatic) to test the ability of each model to explain total, widespread and endemic carabid diversity patterns. The spatial set consisted of the linear, quadratic and cubic terms of latitude and longitude. As multicollinearity of environmental variables can bias regression estimates, we excluded variables causing low tolerance values (<0.1) due to high covariation ($r > 0.9$) with other model variables of the same set (Quinn and Keough 2002). Partial regression analysis (variation partitioning) was used to assess the independent and shared statistical effects of the three predictor sets on carabid richness patterns (Legendre and Legendre 1998; Lobo *et al.* 2002; Hortal *et al.* 2008), i.e., the pure effects of climate, topography (in part reflecting a historical signal) and spatial variables (which might represent spatially structured variables not included in our analyses and broad-scale spatial patterns driven e.g. by postglacial recolonization, cf. Svenning and Skov 2005) and the overlap between them (e.g., the degree to which environmental factors are spatially structured, or the non-independent covariation between environmental variables).

Area was included as a covariable in the statistical analyses to account for the variation in country sizes. To further get an impression of possible scale-dependent effects on the results, we repeated the above analyses using a subset (about half) of our sampling units comprising only the larger countries ($>10^5$ km²). Smaller countries spanned a much smaller range of latitudes than the complete dataset including large countries (24 latitudinal degrees for small as compared to 39 degrees for large countries), hindering a direct comparison with results from the latter (as the warmest and coldest regions were excluded), so we did not analyze the smaller countries separately.

As spatial autocorrelation is often inherent in macroecological data and can inflate statistical errors of significance tests (Diniz-Filho *et al.* 2003), we recalculated significance of regressions using spatially corrected degrees of freedom. These were obtained by correlating observed and predicted values of regressions (Qian *et al.* 2007) according to the modified t-test by Dutilleul *et al.* (1993). Additionally, we generated spatial correlograms using Moran's I-coefficients of residuals from the non-spatial models (topography and climate) for carabids. Correlograms show the adequacy of a regression model to explain the spatial structure in the response variable, as represented by the reduction of spatial autocorrelation (Diniz-Filho *et al.* 2003).

We used SPSS 15.0 for Windows (SPSS Inc., Chicago) and SAM 2.0 (Rangel *et al.* 2006) for all statistical analyses.

2.4 Results

2.4.1 Total carabid diversity

Total carabid diversity showed a hump-shaped relationship with latitude, increasing from northern towards southern Europe and then decreasing again towards North Africa (Fig. 2.2a). There was no significant longitudinal gradient of species richness (Table 2.1). Several environmental variables significantly covaried with this pattern. Measures of ambient energy input (temperature, PET), mean annual precipitation and seasonal variability in precipitation showed quadratic relationships with carabid diversity, the latter peaking at intermediate values of these climatic factors. Range in elevation, March-November precipitation (a measure excluding the winter precipitation) and AET showed positive linear relationships with carabid species richness (Table 2.1). Area was not significantly related to total carabid diversity.

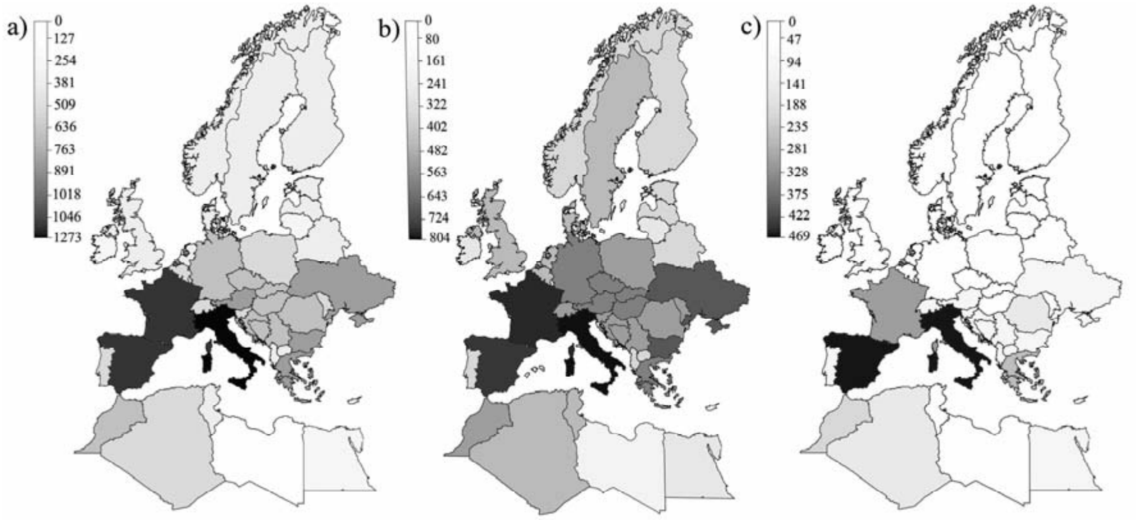

Figure 2.2. Total species richness (a) and richness of widespread (b) and endemic (c) species in the countries of the Western Palaearctic study region.

A quadratic function of PET as well as range in elevation were the strongest predictors when variables were analyzed separately (R^2 0.33 and 0.30, respectively). They were also the only factors entering the stepwise topographic and climatic models, respectively (Table 2.2). A combined environmental model with these factors accounted for 59% of the variability in the carabid data and removed all significant spatial autocorrelation (Supplementary Material: Fig. S2.1), indicating that the modelling results are unbiased by autocorrelation (Diniz-Filho *et al.* 2003). A purely spatial model with a cubic function of latitude ($lat\text{-}lat^2+lat^3$) accounted for 42% of the data variability. Together, the spatial, topographic and climatic models explained 65% of the variability in the pattern of total carabid diversity (Table 2.2). While range in elevation had the strongest *independent* effect on carabid richness (19.9% of explained variance), the spatially patterned climatic component (*shared* variation between climate and spatial variables) accounted for the largest part of the whole variation explained by all three models (27.1%; Fig. 2.3a). In contrast, the independent effect of climate was rather low (1.8%).

Table 2.1. Coefficients of determination for linear regressions of total, widespread and endemic carabid diversity against single environmental variables. Function: polynomial terms were fitted for curvilinear relationships (e.g., 'factor-factor^2' or 'factor+factor^2'), (+) indicates positive linear relationships.

	Total		*Widespread*		*Endemic*	
Variable	**function**	**R^2_{adj}**	**function**	**R^2_{adj}**	**function**	**R^2_{adj}**
Latitude (decimal degrees)	*lat-lat*^{2}*+lat*^{3}	0.42*	*lat-lat*^{2}	0.42*	*lat-lat*^{2}*+lat*^{3}	0.73**
Longitude (decimal degrees)	n.s.		n.s.		n.s.	
Area (km^2) ($\log_{10}$)	n.s.		n.s.		n.s.	
Elevation range (m)	*elev (+)*	0.30**	*elev (+)*	0.15*	*elev (+)*	0.68***
Mean annual temperature (°C)	*temp-temp*^{2}	0.27*	*temp-temp*^{2}	0.33*	*temp-temp*^{2}	0.42**
Mean temperature coldest month (°C)	n.s.		*cold-cold*^{2}	0.33*	*cold-cold*^{2}	0.32*
Mean temperature warmest month (°C)	n.s.		*warm-warm*^{2}	0.23*	*warm-warm*^{2}	0.37*
Temperature seasonality (°C)	n.s.		n.s.		*seast-seast*^{2}	0.20*
Mean annual precipitation (mm)	*prec-prec*^{2}	0.15*	*prec-prec*^{2}	0.24**	n.s.	
Mean precipitation March-November (mm)	*prec_mn (+)*	0.22*	*prec_mn (+)*	0.32*	n.s.	
Seasonality precipitation (mm)	*seasp-seasp*^{2}	0.11*	*seasp-seasp*^{2}	0.21**	n.s.	
Potential evapotranspiration (mm/yr)	*PET-PET*^{2}	0.33*	*PET-PET*^{2}	0.37**	*PET-PET*^{2}	0.52**
Actual evapotranspiration (mm/yr)	*AET (+)*	0.19*	*AET (+)*	0.27*	n.s.	
Frost frequency (days)	n.s.		n.s.		*frost (+)*	0.32*

p-values corrected for spatial autocorrelation: *** $p<0.001$; ** $p<0.01$; *$p<0.08$; n.s. not significant.

2.4.2 Diversity of widespread carabid beetles

Richness of widespread species was highly correlated with total carabid diversity (Pearson $r=0.97$; $p<0.001$). Widespread species represented 39% of all species analyzed, but accounted for 61-100% (mean 89%) of all species in the individual countries. As with total richness, diversity of widespread species was highest in southern Europe and decreased towards the north and further south (Fig. 2.2b). Similarly, there was no significant relationship with either longitude or country size (Table 2.1). Relationships with environmental variables were also very similar to those of total diversity, being hump-shaped for energy variables and overall precipitation and positively linear for range in elevation, March-November precipitation and AET (Table 2.1). However, range in elevation accounted for much less of the variation in single regressions than the climate variables. Again, *PET-PET*^{2} was selected as the only factor in the climatic multiple regression model (Table 2.2). Topography and climate together explained 53% of the carabid data variability (removing all significant spatial autocorrelation; Fig. S2.1), a spatial model alone 42% (Table 2.2). The partial regression analysis with all three models yielded results similar to those for total diversity (Fig. 2.3b). Again, range in elevation accounted for the largest *independent* fraction of explained variance (18.4%), whereas the independent contribution of climate was low (1.3%). However, the spatially structured climate component again had the highest overall value of explained variance (37.1%), which was even higher for widespread species than for total richness.

Table 2.2. Results (Coefficients of determination, F-values, degrees of freedom and probabilities) of regression modelling for total, widespread and endemic species diversity in the Western Palaearctic study region. Variable abbreviations see Table 2.1.

Modeltype	Model (function)	R^2_{adj}	F	df	p
Total					
Spatial (S)	$lat-lat^2+lat^3$	0.42	9.07	3, 35	< 0.001
Topographic (T)	*elev*	0.30	15.68	1, 37	< 0.001
Climatic (C)	$PET+PET^2$	0.33	8.81	2, 36	< 0.001
Combined (T+C)	$elev; PET+PET^2$	0.59	16.49	3, 35	< 0.001
Total (S+T+C)	$lat-lat^2+lat^3; elev; PET+PET^2$	0.65	9.88	6, 32	< 0.001
Widespread					
Spatial (S)	$lat-lat^2$	0.42	13.19	2, 36	< 0.001
Topographic (T)	*elev*	0.15	6.80	1, 37	0.013
Climatic (C)	$PET+PET^2$	0.37	10.55	2, 36	< 0.001
Combined (T+C)	$elev; PET+PET^2$	0.54	13.61	3, 35	< 0.001
Total (S+T+C)	$lat-lat^2; elev; PET+PET^2$	0.62	10.44	5, 33	< 0.001
Endemic					
Spatial (S)	$lat-lat^2+lat^3$	0.73	31.99	3, 35	< 0.001
Topographic (T)	*elev*	0.68	78.14	1, 37	< 0.001
Climatic (C)	$PET+PET^2$	0.52	19.62	2, 36	< 0.001
Combined (T+C)	$elev; PET+PET^2$	0.88	88.80	3, 35	< 0.001
Total (S+T+C)	$lat-lat^2+lat^3; elev; PET+PET^2$	0.92	60.27	6, 32	< 0.001

2.4.3 Diversity of endemic carabid beetles

While endemic carabids made up 61% of all carabid beetle species of our study area, they on average only represented 11% (ranging from 0-39%) of the number of species per country. Species numbers of endemics were more strongly correlated with total diversity (r=0.64; p=0.005) than with numbers of widespread species (Pearson r=0.47; p=0.048). The hump-shaped latitudinal gradient was stronger than for total or widespread species richness, with endemics completely missing in northern countries and most endemic species in southern Europe (Fig. 2.2c, Table 2.1). There was no significant longitudinal pattern of endemic richness across the study region and area also showed no significant effect (Table 2.1).

Environmental relationships differed from results for total or widespread species richness. While measures of ambient energy also were best fitted by polynomial terms, water and water-energy variables were not significantly related to endemic richness of carabids. Instead, there was a significant linear relationship with the annual number of frost days (Table 2.1). Range in elevation, which covaried positively with endemic richness across the whole study region, had the highest explanatory value of all variables when analyzed separately (68%). Polynomial terms of energy variables accounted for up to 52% in the data variability.

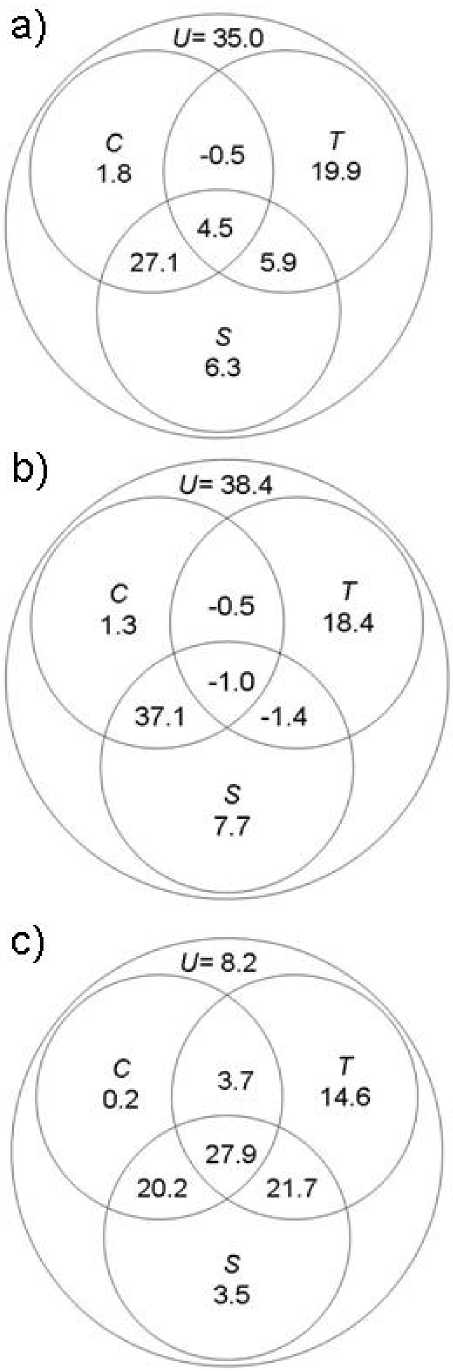

Figure 2.3. Variation partitioning for a) total diversity, b) richness of widespread species and c) endemic richness between independent and shared effects of spatial (S), topographic (T) and climate (C) models. U is the unexplained variation. All numbers indicate % of total variation.

PET-PET² was again selected as the only predictor in the climatic multiple regression model (Table 2.2). Topography and climate explained 88% of the variability in the endemic carabid pattern. Fitting these models removed almost all significant autocorrelation from the endemic species data, except for one medium distance class (Fig. S2.1), which indicates that these factors do not entirely account for the whole spatial structure in the diversity pattern of endemics. Variation partitioning between space, topography and climate again showed a strong independent effect of range in elevation and a weak independent effect of climate (Fig. 2.3c). However, shared components between space and climate and space and topography were equally high (20-22%), strengthening the overall impact of topography on endemic diversity. Another substantial part of the variation was shared by all three models together (27.9%), showing that large parts of the variation in the data of endemic species are explained by spatially structured components of the environmental factors (Fig. 2.3c).

Analysis of large countries

To assess the degree of spatial dependence of our results, we separately analyzed the large countries as a subset from our dataset with less variation in country size. Relationships between total, widespread and endemic species richness and single environmental variables were similar to results for the whole dataset, even though R^2 values slightly increased as the latitudinal gradients were more pronounced (Supplementary Material Table S2.2). Regression modelling yielded almost completely the same explanatory factors for the country-subset as for the whole dataset (Supplementary Material Table S2.3). Variation partitioning again showed a distinct independent variance fraction of topography and rather low independent values for climate (Supplementary Material Fig. S2.2). However, proportions of shared effects between spatially structured climate and spatially structured topography were especially higher in the endemic species dataset, which also had effects on total richness. In comparison to the whole dataset, it thus becomes more difficult to separate spatially structured effects of climate and topography.

2.5 Discussion

Invertebrates represent more than 95% of the global faunal diversity (Myers *et al.* 2000). However, disproportionately low consideration of most invertebrate taxa in large-scale studies on diversity patterns and its determinants across geographically extensive areas strongly biases our knowledge on these patterns towards relatively few well-studied taxa, predominantly vertebrates and plants (Hawkins *et al.* 2003). Our study on hyperdiverse carabid beetles originates from the necessity of a stronger focus on species-rich invertebrates to attain a comprehensive and general understanding of the spatial distribution of the world's biodiversity (Lovell *et al.* 2007).

While it is evident that the global patterning in biodiversity must ultimately be linked to evolutionary/historical processes (dispersal, isolation and diversification, extinction), it has subsequently evolved under the influence of environmental factors and their interactions with the former (Wiens and Donoghue 2004). There are differing views on the relative impact of modern day environmental conditions in this respect, even in the context of theories such as niche conservatism (Wiens and Donoghue 2004; Hawkins *et al.* 2007), which help linking evolutionary and ecological aspects related to the formation of diversity patterns. High covariation between large-scale species richness patterns of various organism groups and contemporary climate is often ascribed to a dominant impact of the latter on the spatial structure of diversity (Hawkins *et al.* 2003). However, recent studies showed that such relationships might be much more pronounced for widespread species than for species with restricted ranges (Jetz and Rahbek 2002; Jansson 2003; Svenning and Skov 2007a).

Carabid beetles are characterized by a high proportion of species with restricted ranges (endemics). This questions whether present-day environmental factors can explain diversity patterns of this hyperdiverse invertebrate taxon in a similar way as stated for previously studied taxa with deviating characteristics, especially in a region which has been severely affected by past glaciation events such as the Western Palaearctic.

In the present study total diversity of carabid beetles was significantly associated with single variables related to both available energy as well as water and water-energy balance, indicating similar possible constraints of climate on overall richness patterns of this highly diverse invertebrate taxon as often suggested for less species-rich invertebrate or vertebrate taxa as well as plants (Hawkins *et al.* 2003 and references therein; Konvicka *et al.* 2006; Whittaker *et al.* 2007; Baselga 2008; Finch *et al.* 2008). Unimodal relationships especially with measures of available energy (with decreasing diversity at high energy values) and a positive covariation with the amount of water availability during the vegetation period (*prec-mn*) in single-term regressions further indicate a pattern often reported from large-scale studies on various animal and plant taxa: Once a certain energy level has been reached, the relative importance of available energy often decreases, while other factors, such as the availability of water, become more important (Hawkins *et al.* 2003; Whittaker *et al.* 2007). This could also explain the lower diversity of carabid beetles in North Africa as compared to southern Europe. Energy values might be sufficiently high in both regions to not limit carabid diversity. However, there is a relative shortage of water (measured by various precipitation variables) in the North African region, which might depress diversity despite high energy values.

The richness pattern for widespread species showed relationships very similar to total richness, as might have been expected from the high correlation between total and widespread diversity and the fact that widespread species on average make up 89% of total richness in the single countries we analyzed. Results for total carabid diversity thus to a large part reflect patterns of widespread species. In contrast, large proportions of endemic carabids are strongly restricted to southern European countries, with northern Europe being more or less devoid of any endemics. This resulted in a stronger latitudinal gradient of endemic richness and pronounced relationships with spatially structured environmental variables. Unimodal relationships with temperature measures and a linearly decreasing relationship with frost frequency suggest an influence of these energy-related factors (while there was no significant relationship with precipitation measures) also on endemic, restricted-range species, as was also found by Baselga (2008) for cerambycid beetles and Svenning and Skov (2007a) for tree species in Europe. However, range in elevation was the single most important factor (explaining 68% of the variance in the data) predicting richness patterns of endemic carabids. In the analyses of total richness and especially of richness of widespread species, this factor was relatively less important in comparison to climatic factors.

These differences between widespread and endemic species, which affect the results for total richness, are also quite distinct when looking at the multiple regression models with the explained variance partitioned between climate, topography and spatial variables. These overall models accounted for large parts of the variation in the total, widespread and endemic species data (between 62 and 92%). Spatial variables independently accounted for only minor parts of the variation, indicating that climate and topography adequately capture most of the spatial patterning of diversity. In the total and especially in the widespread species data, most of the variation was explained by the spatially structured climate component. Comparatively lower proportions were accounted for by topography (i.e., range in elevation), again especially in the data of widespread species. In contrast, most of the variation in the data of endemic species is explained by the combination of the independent and spatially structured topography measure. The corresponding parts of climate account for a smaller fraction of the explained variance. Compared to widespread and total diversity, a large part of explained variation in endemics is being shared with both spatially structured climate and spatially structured topography. This might be due to the fact that a historical signal contained in elevation range, which we will show below might be relevant for the endemic richness pattern, could be more strongly spatially structured (due to a latitudinally structured impact of glaciation processes) than pure aspects of habitat heterogeneity reflected by this variable. Part of the explained variation in the data of endemic carabids may thus be attributed to shared effects of a historical signal of elevation range and spatial climate aspects.

Variation in elevation range is often suggested to reflect habitat heterogeneity (Kerr *et al.* 2001). Elevational zones differ in their small-scale environmental (especially climatic) characteristics and thus an increase in elevational zones is expected to increase habitat diversity. While habitat heterogeneity as a factor of the contemporary environment surely affects species diversity to a certain degree, elevational habitat diversity is also of importance regarding evolutionary processes. Small-scale habitat shifts along with elevational gradients in climatic features promote the spatial segregation and isolation of species and thus strongly affect diversification processes (Jetz *et al.* 2004; Rahbek *et al.* 2007). Often, regions with large elevational gradients are considered centers of speciation (Jansson 2003; Jetz *et al.* 2004). The impact of the major mountain ranges in Central and southern Europe on diversity patterns via effects of speciation and extinction are likely to have been amplified by the extensive glaciation events. Regions with high altitudinal ranges allowed species in these regions to respond to and to survive past climate changes (including glaciations) by climbing or descending to elevations offering suitable conditions (Hewitt 1999). In contrast, topographically less diverse regions did not allow for such short-distance migrations, increasing extinction probabilities in a changing climate. Thus, there is strong evidence that the effect of range in elevation on species richness patterns can contain an important historical signal. This interpretation is supported by our findings that topographic variability was a much stronger predictor for patterns of endemic carabid beetle diversity than for widespread species. Centers of endemism in our study region are located in mountainous countries considered the southern refugia of many species during the last ice age (e.g. Italy, Spain, the Balkans; Hewitt 1999; Drees *et al.* 2010). This is concordant with results found for vertebrates and plants with restricted ranges, which are clearly concentrated in regions with high topographic variability or climatically stable areas enabling species to effectively compensate climatic shifts and offering high potential for diversification (Jansson 2003; Jetz *et al.* 2004; Rahbek *et al.* 2007; Svenning and Skov 2007b). A signal of history contained in the endemic carabid pattern can also be derived from correlations of carabid diversity with plant species richness. As we do not assume a direct causal impact of plants on predominantly predatory carabids (even a causal link to herbivorous taxa is often supposed to be of minor importance at broad scales; Hawkins and Porter 2003a), we did not include plant diversity into regression analyses. Endemic carabids were much more strongly correlated with plants (Pearson r=0.88; p<0.001, corrected for spatial autocorrelation) than widespread carabids (r=0.62; p=0.014) and also overall carabid diversity (r=0.73; p=0.003). Many restricted, but also widespread plant species in Europe are thought to show strong dispersal limitation following Quaternary glaciations (Svenning and Skov 2007a; Svenning *et al.* 2008). Thus, especially high correlations between endemic carabids and plants might in part reflect a similarly strong and persisting impact of historical processes on both groups. These patterns also well correspond to the so called ‘Massifs de Refuge’, areas with high numbers of endemics of insects and plants assumed to represent common glacial refugia of the Western Palaearctic biota (Holdhaus 1954; Drees *et al.* 2010).

If topographic variability would primarily reflect contemporary habitat diversity, we would have expected a much stronger impact of elevation range also on widespread species (see also Kerr *et al.* 2001). However, this impact was only marginal in single-term regressions and also accounted for a much smaller amount of explained variation in the partitioning analysis for widespread species than climate variables. The variation in the data of widespread species actually explained by elevation range might in this case also be attributable to a larger part to the contemporary effect of available habitat diversity. There is a striking difference between the proportions of variance explained by independent and spatially structured components of elevation range in widespread and endemic richness patterns. The spatial component is much more important for endemics and might be additional evidence of the historical signal contained in this variable, which can be supposed to show a stronger spatial structure (due to the latitudinal dependencies of historical processes such as glaciations) than pure habitat diversity.

Altogether, our results suggest that a strong historical signal is still present in the richness pattern of endemic carabids, whereas widespread species and thus also total richness patterns appear to be less affected by such a signal. Similar results were reported in several studies on vertebrate and plant taxa (Jetz and Rahbek 2002; Rahbek *et al.* 2007; Svenning and Skov 2007a). For the latter two carabid groups, climate factors seem to be better predictors of richness distributions, as was also found for large-scale patterns of cerambycid beetles and widespread trees in Europe (Svenning and Skov 2007a; Baselga 2008) and also at smaller scales, e.g. for French dung beetles (Lobo *et al.* 2002). Widespread species might have better been able to track climate changes after the last major glaciations over larger geographic ranges due to a higher power of dispersal (Gutiérrez and Menéndez 1997; Araújo *et al.* 2008) or broad ecological niches (Hawkins *et al.* 2007; Lester *et al.* 2007), explaining their presence in northern regions. Yet, there is also a possibility of a more historical imprint, as current and past climate can be correlated (Araújo *et al.* 2008). In this case, climate stability over longer time periods might also be relevant to a certain degree for widespread species (Hawkins *et al.* 2007; Araújo *et al.* 2008). Of course, correlative analyses do not prove any causality of the relationships between diversity gradients and their putative determinants. Manipulative experiments would be needed to test for this, but are hardly feasible at macroecological scales (Lobo *et al.* 2002; Kerr *et al.* 2007). This is an issue common to all macroecological analyses and our study can only reveal from the set of variables we considered factors with the greatest probable influence on carabid diversity.

Relationships between climate factors and patterns of endemic carabids might well be attributable to current climate partially limiting the distribution of these species (Jiménez-Valverde *et al.* 2007). However, the strong indications of historical processes still affecting endemics also implies limited dispersal ability of many species restricted to their glacial refugia as an important mechanism determining present diversity patterns of endemic carabids. The majority of endemic carabids in our study are brachypterous (i.e., flightless due to reduced hindwings), which might strongly affect their dispersal abilities (Gutiérrez and Menéndez 1997; Kotze and O'Hara 2003). Dispersal limitation is also assumed to strongly influence distributions of European trees (Svenning and Skov 2007a) and amphibians and reptiles (Araújo *et al.* 2008). Both restrictive climate conditions and dispersal limitations might also conjointly influence these patterns in carabid beetles, as was suggested for flightless Iberian dung beetles (Lobo *et al.* 2006) and forest plants in nemoral Europe (Svenning *et al.* 2008). Yet, our results especially indicate an important role of dispersal limitation in restricting distributions of endemic carabids.

2.5.1 Analysis of large countries

Analyzing only large countries of our study region yielded results of single and multiple regressions similar to the analysis of the whole dataset, with the relative importance of the environmental variables being rather constant despite a reduction of the dataset. However, scale dependence is a common feature of diversity-environment-relationships (Rahbek and Graves 2001; Rahbek *et al.* 2007; Hortal *et al.* 2008), often resulting in larger influence of climate at larger scales (Hawkins *et al.* 2003; Hawkins *et al.* 2007; Hortal *et al.* 2008), and was also indicated in our study. Due to a more pronounced spatial gradient in carabid diversity, there was a stronger spatial structuring of variables in the variation partitioning of the large-country analyses, resulting in a less distinct separation between spatial effects of climate and topography. However, while somewhat blurring part of the explanatory power of variables in the partitioning analyses, these findings do not change the inferences drawn for carabid beetle diversity from analyses of the total dataset. Likewise, Baselga (2008) found no confounding effects of analyzing differently sized countries in his study on patterns of cerambycid beetles across European countries.

2.5.2 Conclusions

The results of our study provide information essential to a more general understanding of broad-scale diversity patterns, especially as insufficient data in many other species-rich, low mobile invertebrate taxa hinders extensive analyses of invertebrate distribution patterns. Our study shows that diversity patterns of highly diverse invertebrates can be shaped by both historical and contemporary processes. However, the degree to which these processes emerge as possible determinants of present richness patterns depends on range-size related characteristics of the species, such as dispersal abilities or niche breadth. Historical imprints in the diversity patterns are stronger in species with restricted ranges, whereas richness distributions of widespread species show high congruence with current climate conditions. We might test these relationships in a more direct way with reliable and accurate data quantifying these historical aspects, which at the moment is hardly available, and taking into account results from phylogenetic studies. However, our findings are supported by several studies reporting similar differences in the explanatory power of current and historical processes for restricted versus widespread species or total diversity within taxa. Even though widespread carabids comprise less than 40% of all carabid species known from our Western Palaearctic study region, they on average account for 89% of the total number of species within the single countries analyzed. This dominating impact of widespread species strongly masks the effects of deviating determinants of large parts of carabid diversity (i.e., the endemic species) when total diversity is analyzed. Thus, analyses of total diversity patterns that do not account for range-size related differences might miss essential information on driving factors and mechanisms underlying these patterns (Jetz and Rahbek 2002; Rahbek *et al.* 2007; Svenning and Skov 2007a; Araújo *et al.* 2008), as many organism groups feature high proportions of species with restricted ranges. We conclude that differentiating between widespread and more narrowly distributed species is needed for a more comprehensive understanding of the determinants of geographic patterns of biodiversity. Furthermore, this is also highly relevant to applied biodiversity research, where small-range species are often a special concern.

Acknowledgements

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2.6 Supplementary Material

Table S2.1. Summary statistics (mean, minimum and maximum values, standard deviation) of richness and environmental variables used in regression analyses.

Variable	Code	Mean	Min	Max	SD
Carabid species richness - total	-	469.9	87.0	1273.0	245.5
Carabid species richness - widespread species	-	402.1	81.0	804.0	159.0
Carabid species richness - endemics	-	67.8	0.0	469.0	109.0
Latitude (decimal degrees)	*lat*	46.5	25.0	64.0	9.5
Longitude (decimal degrees)	*long*	15.0	-8.0	33.0	11.3
Area (10^3 km²)	*area*	290.6	9.2	2381.7	473.3
Elevation range (m)	*elev*	2170.8	180.0	4809.0	1307.6
Mean annual temperature (°C)	*temp*	10.3	1.5	22.5	5.3
Mean temperature coldest month (°C)	*cold*	0.6	-11.3	12.9	6.4
Mean temperature warmest month (°C)	*warm*	19.6	11.7	32.4	4.8
Temperature seasonality (°C)	*seast*	19.0	9.8	26.6	3.8
Mean annual precipitation (mm)	*prec*	712.0	51.0	1537.0	313.7
Mean precipitation March-November (mm)	*prec_mn*	514.7	30.2	713.9	182.3
Seasonality precipitation (mm)	*seasp*	51.0	6.4	106.6	23.5
Potential evapotranspiration (mm/yr)	*PET*	709.1	461.6	1192.5	187.5
Actual evapotranspiration (mm/yr)	*AET*	504.3	56.4	683.7	151.6
Frost frequency (days)	*frost*	98.0	14.1	203.5	54.1

Table S2.2. Coefficients of determination for linear regressions of total, widespread and endemic carabid diversity against single environmental variables **for large countries** (>10^6 km²) of the study region. Function: polynomial terms were fitted for curvilinear relationships (e.g., 'factor-factor^2' or 'factor+factor^2'), (+) indicates positive linear relationships.

	Total		*Widespread*		*Endemic*	
Variable	**function**	R^2_{adj}	**function**	R^2_{adj}	**function**	R^2_{adj}
Latitude (decimal degrees)	$lat-lat^2+lat^3$	0.75*	$lat-lat^2+lat^3$	0.79*	$lat-lat^2+lat^3$	0.83**
Longitude (decimal degrees)	n.s.		n.s.		n.s.	
Area (km²) ($\log_{10}$)	n.s.		n.s.		n.s.	
Elevation range (m)	*elev (+)*	0.40**	*elev (+)*	0.25*	*elev (+)*	0.59**
Mean annual temperature (°C)	$temp-temp^2$	0.52*	$temp-temp^2$	0.58*	$temp-temp^2$	0.71**
Mean temperature coldest month (°C)	n.s.		$cold-cold^2$	0.54*	$cold-cold^2$	0.62*
Mean temperature warmest month (°C)	n.s.		n.s.		$warm-warm^2$	0.60*
Temperature seasonality (°C)	n.s.		n.s.		n.s.	
Mean annual precipitation (mm)	$prec-prec^2$	0.41*	$prec-prec^2$	0.55**	n.s.	
Mean precipitation March-November (mm)	*prec_mn (+)*	0.35*	*prec_mn (+)*	0.50*	n.s.	
Seasonality precipitation (mm)	n.s.		n.s.		n.s.	
Potential evapotranspiration (mm/yr)	$PET-PET^2$	0.57*	$PET-PET^2$	0.61*	$PET-PET^2$	0.75**
Actual evapotranspiration (mm/yr)	*AET (+)*	0.39*	*AET (+)*	0.54*	n.s.	
Frost frequency (days)	n.s.		n.s.		*frost (+)*	0.52*

p-values corrected for spatial autocorrelation: *** $p<0.001$; ** $p<0.01$; *$p<0.08$; n.s. not significant.

Table S2.3. Results (Coefficients of determination, F-values, degrees of freedom and probabilities) of regression modelling for total, widespread and endemic species diversity **for large countries** ($>10^6$ km^2) in the Western Palaearctic study region. Variable abbreviations see Table S2.1.

Modeltype	Model (function)	R^2_{adj}	F	df	p
Total					
Spatial (S)	$lat-lat^2+lat^3$	0.75	16.82	3, 16	< 0.001
Topographic (T)	*elev*	0.40	11.99	1, 18	0.003
Climatic (C)	$PET+PET^2$	0.57	11.36	2, 17	< 0.001
Combined (T+C)	$elev; PET+PET^2$	0.72	15.50	3, 16	< 0.001
Total (S+T+C)	$lat-lat^2+lat^3; elev; PET+PET^2$	0.93	28.88	6, 13	< 0.001
Widespread					
Spatial (S)	$lat-lat^2+lat^3$	0.79	21.05	3, 16	< 0.001
Topographic (T)	*elev*	0.25	5.99	1, 18	0.025
Climatic (C)	$cold-cold^2; prec-prec^2$	0.68	9.25	4, 15	< 0.001
Combined (T+C)	$elev; cold-cold^2; prec-prec^2$	0.84	17.58	5, 14	< 0.001
Total (S+T+C)	$lat-lat^2+lat^3; elev; cold-cold^2; prec-prec^2$	0.95	23.88	8, 11	< 0.001
Endemic					
Spatial (S)	$lat-lat^2+lat^3$	0.83	27.30	3, 16	< 0.001
Topographic (T)	*elev*	0.59	25.65	1, 18	< 0.001
Climatic (C)	$PET+PET^2$	0.75	25.27	2, 17	< 0.001
Combined (T+C)	$elev; PET+PET^2$	0.89	43.51	3, 16	< 0.001
Total (S+T+C)	$lat-lat^2+lat^3; elev; PET+PET^2$	0.96	48.91	6, 13	< 0.001

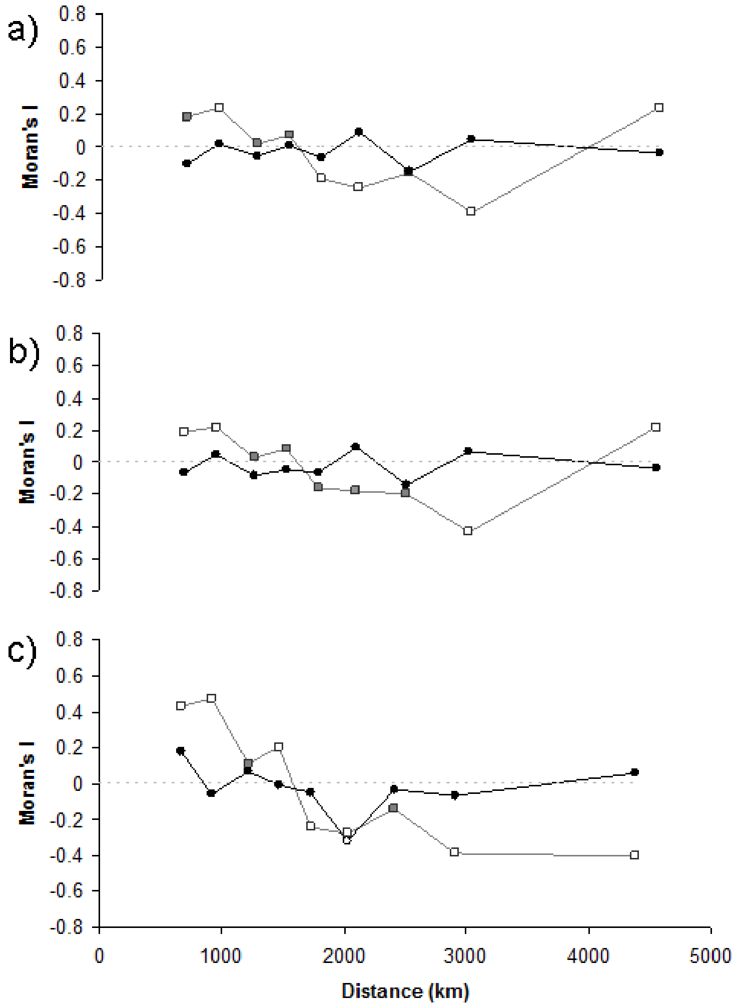

Figure S2.1. Spatial correlograms for carabid diversity before (grey line) and after (black line) fitting the environmental models: a) total diversity; b) widespread species diversity; c) endemic diversity. Open symbols: significant autocorrelation, filled symbols: no significant autocorrelation in the data.

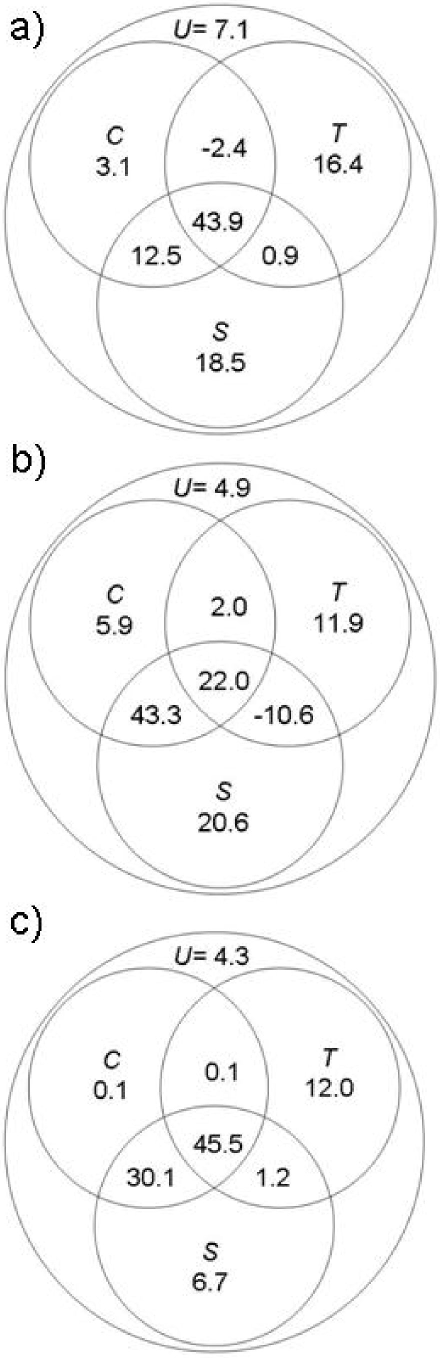

Figure S2.2. Variation partitioning for a) total diversity, b) richness of widespread species and c) endemic richness **of large countries** (>10^6 km²) between independent and shared effects of spatial (S), topographic (T) and climate (C) models. U is the unexplained variation. All numbers indicate % of total variation.

3 BELOWGROUND CARABID BEETLE DIVERSITY IN THE WESTERN PALAEARCTIC – EFFECTS OF HISTORY AND CLIMATE ON RANGE-RESTRICTED TAXA (COLEOPTERA: CARABIDAE)

Article in press, ZooKeys

A. Schuldt and T. Assmann

3.1 Abstract

Broad-scale patterns of subterranean diversity are a fascinating but neglected part of biodiversity research. Carabid beetles adapted to belowground habitats form a particularly species-rich part of the subterranean fauna. We studied large-scale diversity patterns of these belowground carabids across the western Palaearctic and evaluated potential impacts of historical and contemporary environmental conditions on the distribution of these taxa, using available species richness and environmental data on a country level. Regression modelling and variation partitioning showed a strong relationship between species richness and range in elevation. Potential effects of climatic variables, mainly those related to ambient energy input, were much weaker. We discuss the implications of this combination of effects, which suggests, concordant with the absence of subterranean carabids in northern and highest richness in southern Europe, a strong prevailing influence of historical processes on current richness distributions of these taxa. Previous studies did not provide clear indications for such an influence. In contrast to more mobile and widespread carabid beetles, dispersal limitation due to high adaptation of belowground carabids to subterranean habitats has probably hindered their recolonization of former permafrost and glaciated regions. Hotspots of highest belowground diversity are located in regions with an assumed long-term stability of environmental conditions, correlating with patterns of other dispersal-limited taxa such as many endemic plants. Our study provides important new information in the discussion of potential determinants of the distinct geographic patterns of belowground diversity. Moreover, it contributes to a better understanding of range size related differences previously found in the distribution of diversity and environmental dependencies of widespread and range-restricted species within the highly diverse carabid beetles.

Keywords: Cave fauna, endogeic, glaciations, geographic range, insects, latitudinal gradient, macroecology, permafrost, subterranean

3.2 Introduction

Studies on the spatial patterning of biodiversity and its potential determinants have gained much attention over the last decades, especially in light of global change and its assumed effects on the distribution and survival of many species (Kerr *et al.* 2007). In this regard, the diversity of belowground habitats has been studied only poorly, even though it comprises many rarely recorded and highly adapted species (Culver *et al.* 2006). These habitats are characterized by much lower temporal variability of the physical environment than the aboveground habitats (Wilkens *et al.* 2000; Assmann *et al.* 2010). Still, dependencies on environmental factors that have been identified as potential drivers of the distribution of diversity of many aboveground organism groups are being assumed also for subterranean diversity (Culver *et al.* 2006; Zagmajster *et al.* 2008). Especially productivity of the aboveground habitats, which again is determined by an interplay of energy input and water availability (Hawkins *et al.* 2003), has repeatedly been suggested as a possible factor influencing diversity in these subterranean habitats, which are often considered (and this particularly applies to caves) to be to a large part dependent on allochtonous input of resources (Gers 1998; Culver *et al.* 2006). Such a dependency on environmental factors could have far-reaching consequences for the strongly dispersal-limited belowground taxa regarding future shifts in environmental conditions due to climate change (Sharratt *et al.* 2000).

However, reduced dispersal abilities due to their strong habitat specialization also suggest that especially processes and environmental conditions over historical times have played important roles in the survival and present distribution of these species. Regions with high numbers of subterranean species have probably been subject to lower variability in environmental conditions over long time periods and a higher persistence of ecosystems than other western Palaearctic regions (Casazza *et al.* 2008; Assmann *et al.* 2010).

About 50% of the terrestrial fauna in subterranean habitats are beetles (Zagmajster *et al.* 2008). With more than 1,000 troglobiont and endogeic species described so far, carabid beetles make up a large part of this subterranean fauna in the western Palaearctic, which harbors one of the hotspots of highest diversity of terrestrial troglobites in the northern hemisphere (Casale *et al.* 1998; Culver and Sket 2000; Culver *et al.* 2006; Assmann *et al.* 2010). Carabids are thus also well suited to provide important insights into aspects of faunal diversity of subterranean habitats. Moreover, results from the study of the highly diverse subterranean carabid fauna also have implications for the understanding of general patterns in the distribution of biodiversity over large geographic extents. Schuldt and Assmann (2009) found differences in the potential impact of current climate and historical processes on overall diversity and that of widespread and endemic species of carabid beetles in the western Palaearctic, probably due to differences in the dispersal abilities of these taxa. Comparison of these patterns to those of the strongly range-restricted carabids living in belowground habitats can help to extend our understanding of the distribution of diversity and the possible mechanisms behind such range-size dependent diversity patterns.

The aim of our study was to analyze spatial patterns in the species richness of belowground carabids and their potential environmental determinants on a large scale across Europe and North Africa. Distinguishing between the carabid fauna of deeper soil horizons, beetles of the so-called superficial underground compartment (“milieu souterrain superficiel”, MSS; Juberthie 1979) as a macroporal system in rocky material, and obligate cave-dwellers is not possible for all regions of the western Palaearctic, as species known as specialized cave dwellers have also been recorded in the MSS (e.g., *Aphaenopidius kamnikensis* DROVENIK 1987, a carabid until recently known to occur only in caves; Drovenik *et al.* 2007). Thus, in our analysis we combine all species from these systems with an obligate subterranean way of living and use the term “belowground fauna” for these taxa from hereon. Species with the ability to fly and also occurring in aboveground habitats (e.g., species of *Limnastis*) were not treated as part of the belowground fauna.

Analyzing country-level species and environmental data, we hypothesize weak links between belowground diversity and current climatic conditions and a strong signal of history contained in broad-scale distribution patterns of belowground carabids. This would support and help to explain the previous findings concerning range size dependent differences between total, widespread and endemic richness of carabids in the response to large-scale environmental conditions (Schuldt and Assmann 2009).

3.3 Methods

3.3.1 Species and environmental data

Species numbers of carabid beetles were extracted from Löbl and Smetana (2003) for 39 countries of the western Palaearctic. The distribution of diversity for most invertebrates are not well documented at smaller scales over such large geographic extents, which hinders analysis on a more detailed scale or assigning reliable data to equal-area grids (Baselga 2008; Hortal 2008). In contrast, country-level data for carabid beetles in the western Palaearctic is quite comprehensive and allows accurate analysis of macroecological patterns for such a highly diverse insect taxon (Schuldt and Assmann 2009; Schuldt *et al.* 2009). In our analyses, we excluded Iceland due to its strong insularity as well as Andorra, Liechtenstein and Luxembourg because of their small country size. All species with a strict subterranean or cave-dwelling lifecycle, as documented in the literature and indicated by reduced and missing eyes, were classified as belowground species (see Table S3.1 in Supplementary Material for a list of the genera included). While total species richness is well documented for most western Palaearctic countries (Schuldt and Assmann 2009), new species are still being recorded from subterranean habitats in the most species-rich southern European countries. However, this does not affect the overall spatial pattern of species richness, neither for total nor for belowground carabid richness. We used patterns of total species richness of all carabids and the richness of widespread and endemic carabids (all extracted from Löbl and Smetana 2003) for comparison with distribution patterns of belowground beetles. Widespread (range sizes >6 x 10^5 km²) and endemic carabids (range sizes <6 x 10^5 km²) were classified following the definition of Lumaret and Lobo (1996). As we were also interested in the relationship with species richness of vascular plants, we compiled data for this taxon from Walter and Gillett (1998), Groombridge and Jenkins (2002) and CBD National Reports (www.cbd.in/countries).

For our analyses we used a set of environmental variables related to recently intensively discussed hypotheses (Willig *et al.* 2003) on the influence of climatic and topographic factors on the spatial distribution of species richness (see Table 3.1 for a complete list of variables used). Climate data was obtained as country-level averages of high-resolution data from Mitchell (2002) and comprised mean annual temperature, mean temperature of the coldest and the warmest month, temperature seasonality (difference between warmest and coldest month), mean annual precipitation, mean precipitation from March to November, seasonality in precipitation (difference between wettest and driest month) and the number of days with frost. Additionally, mean annual potential and actual evapotranspiration (PET and AET) were calculated using Thornthwaite's method (Thornthwaite and Mather 1963; Thornthwaite and Mather 1964; Black 2007). AET is often considered a surrogate measure for productivity (Hawkins *et al.* 2003). Finally, range in elevation (i.e. the difference between the highest and lowest elevation within each sampling unit) was compiled from CIA (2008) as a measure of both habitat heterogeneity as well as prevailing signals of evolutionary and historical processes (Schuldt and Assmann 2009). From the same source, we extracted midpoint latitude and longitude of the countries to quantify the spatial dimension of richness distributions.

3.3.2 Statistical analyses

Environmental correlates of species richness of belowground carabids were first analyzed in regressions with single environmental variables. Second- or third-order polynomials were added to the centred predictor variables in case of significant non-linear relationships. Species richness and country area were $\log_{10}$-transformed to normalize distributions.

We then used regression modelling to assess the separate and combined impact of three different sets of predictor variables (spatial, topographic and climatic) on the richness pattern of belowground carabids. Spatial, topographic and climatic factors might explain similar proportions of the variability in the observed richness patterns. Our approach allows us to handle the non-independence of predictor variables, which might show the same autocorrelated pattern but relate to different conceptual frameworks in the explanation of diversity patterns, and thus to identify the isolated influence of different sets of explanatory variables (Baselga 2008; Hortal *et al.* 2008). For each set, we computed stepwise regression models with backward elimination, excluding variables that caused low tolerance (<0.1) due to high multicollinearity (r >0.9) with other variables in the predictor sets (Quinn and Keough

2002). Variation partitioning was used to assess the independent (i.e., purely spatial, topographic and climatic) and shared (spatially structured and covarying) effects of the three predictor sets on belowground carabid richness in a combined model (Legendre and Legendre 1998; Hortal *et al.* 2008). We included area as a co-variable into the analyses to account for differences in country size.

Spatial autocorrelation can inflate statistical errors in analyses of geographic diversity patterns (Diniz-Filho *et al.* 2003). To account for this, we recalculated significance of regressions using spatially corrected degrees of freedom by correlating observed and predicted values of regressions (Qian *et al.* 2007) according to the modified t-test by Dutilleul (1993). Additionally, we checked the adequacy of our non-spatial regression on climate and topography to explain the spatial structure in the belowground carabid data by generating a correlogram with Moran's I coefficients, which show the reduction in spatial autocorrelation after fitting the regression model (Diniz-Filho *et al.* 2003). Moran's I values of zero indicate absence of spatial autocorrelation, whereas larger or smaller coefficients (usually ranging between +1 and -1) show the degree of positive or negative autocorrelation between neighboring sampling units. Non-significant values of Moran's I coefficients after fitting the explanatory variables indicate that the variables selected well account for the spatial pattern in the richness data (Diniz-Filho *et al.* 2003).

All statistical analyses were performed with SPSS 15.0 for Windows (SPSS, Chicago) and SAM 2.0 (Rangel *et al.* 2006).

3.4 Results

The distribution of species richness of carabids adapted to belowground habitats showed a clear and significant latitudinal gradient across the western Palaearctic (Table 3.1). Richness was highest in southern European regions (Fig. 3.1). This especially applies to Italy, which featured highest species numbers. Larger countries such as France and Spain had lower numbers and even for the Balkan Peninsula, species numbers were lower even when an area of comparable size and latitudinal extent was considered (i.e., Albania, Bosnia-Herzegovina, Greece, Macedonia and Serbia-Montenegro, which as a whole is slightly larger than Italy but harbors only 146 species as compared to 195 species for Italy). Even with Romania, Bulgaria and Croatia added to this latter region, which increases the area to more than twice the size of Italy, this region harbors only 36 more species than Italy.

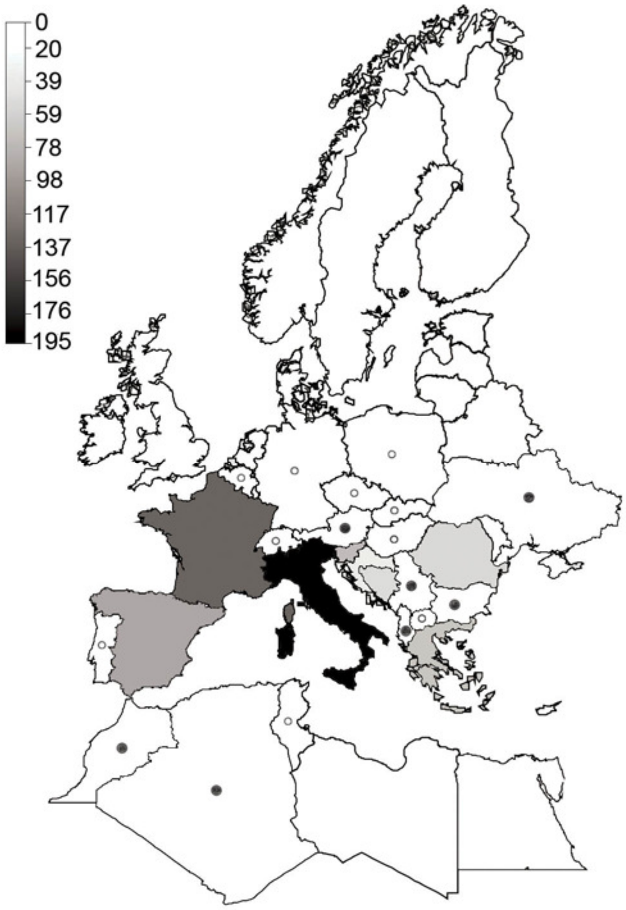

Figure 3.1. Distribution of species richness of belowground carabid beetles across the western Palaearctic, based on Löbl and Smetana (2003). Shadings and symbols indicate the number of species recorded for each country. Countries with 11-20 subterranean species are marked by a filled circle, countries with 1-10 species by an open circle. Countries for which no subterranean species have been recorded are white and without a symbol.

Species numbers decreased towards northern Europe and North Africa (Fig. 3.2a) and most countries completely lacked belowground carabids, especially in the northern part of Europe (Fig. 3.1). In contrast to latitude, subterranean carabids did not show a significant relationship with longitude. Species numbers were also not significantly related to the size of the countries analyzed (Table 3.1a). Several environmental variables were correlated with species richness of belowground carabids. Richness showed a linear increase with and was most strongly ($R^2=0.52$; $p<0.001$) related to range in elevation (Table 3.1a, Fig. 3.2b). Variables related to ambient energy input (PET, mean annual and mean temperature of the warmest month) showed a hump-shaped relationship with species richness (R^2 between 0.24 and 0.38; $p \leq 0.052$), which increased up to a certain level with increasing available energy and decreased again at highest levels of energy input (Table 3.1, Fig. 3.2c). Frost frequency was negatively related to species richness, whereas precipitation measures and AET were not significantly related to belowground carabid diversity (Table 3.1).

Regression modelling identified a polynomial term of latitude, the linear measure of elevation range and a quadratic term of PET as the best predictors of spatial, topographic and climatic models for species richness of belowground carabids (Table 3.1b). A combined model of elevation range and PET explained 69% of the variability in the carabid data. It removed all significant spatial autocorrelation from the carabid data. Moran's I coefficients in a spatial correlogram over ten distance classes were all close to zero and non-significant after fitting the model (see Supplementary Material Fig. S3.1: Spatial correlogram). This shows that these variables quite well account for the spatial structure in the distribution of subterranean carabid diversity and that modelling results are not affected by spatial autocorrelation (Diniz-Filho *et al.* 2003). The total model, adding a spatial component to these variables, did not increase the goodness of fit and explained 68% of the data variability (Table 3.1b). Variation partitioning showed that range in elevation had by far the strongest independent effect on species richness of belowground carabids, accounting for 19% of the explained variance. Together with the spatially structured effect of elevation range, this factor explained 30.1% of the carabid data variability (Fig. 3.3). In comparison, independent spatial and climatic as well as spatially structured climatic effects were weak. The shared variation for all three components together, i.e. spatially structured climatic and topographic effects, was 23.4% (Fig. 3.3).

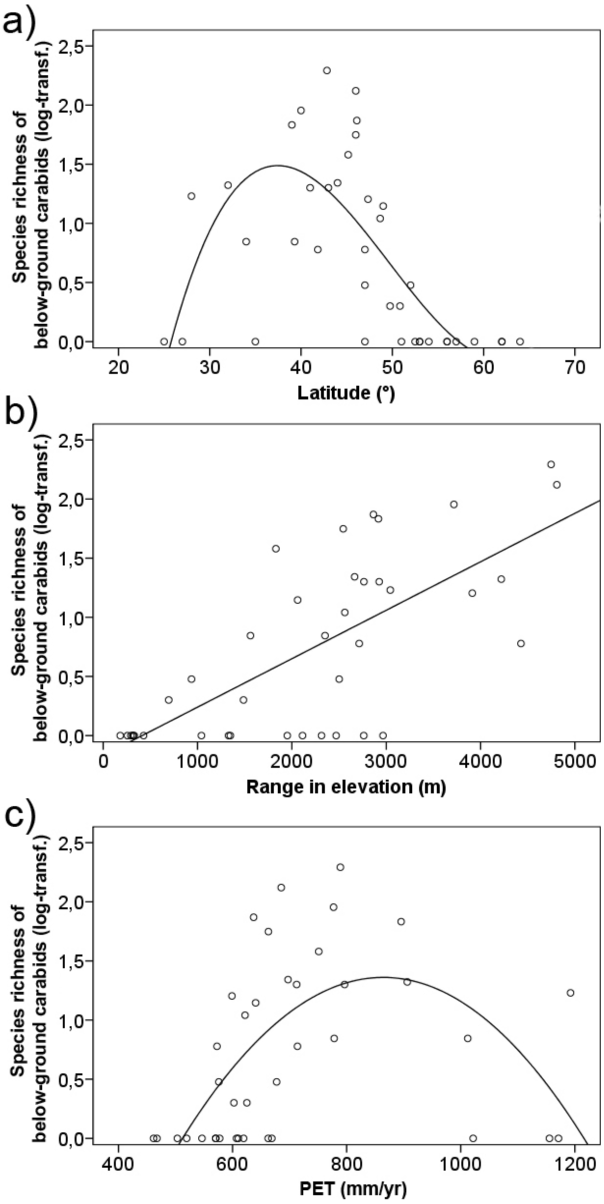

Figure 3.2. Relationship between species richness of belowground carabid beetles ($\log_{10}$-transformed) and (a) latitude ($R^2_{adj.}$=0.51; p=0.012), (b) range in elevation (i.e., topograohic variability; $R^2_{adj.}$=0.52; p<0.001) and (c) annual potential evapotranspiration ($R^2_{adj.}$=0.38; p=0.020) in the western Palaearctic.

Richness of belowground carabids was strongly correlated with total species richness of carabid beetles (Pearson' r=0.76; p<0.001, corrected for spatial autocorrelation), less strong with richness of widespread species (r=0.63; p=0.001) and most strongly with richness of endemic carabids (r=0.87; p<0.001). It was also highly correlated with species richness of vascular plants (r=0.86; p<0.001) across the western Palaearctic.

Table 3.1. Results (coefficients of determination, F-values, degrees of freedom and spatially corrected probabilities) of (a) regressions of belowground carabid species richness against single environmental variables and (b) regression modelling of species richness of belowground carabid beetles in the western Palaearctic.

Modeltype	Model (function)	R^2_{adj}	F	df	p
a) single regressions					
Latitude (decimal degrees)	$lat\text{-}lat^2+lat^3$	0.51	12.6	3, 35	0.012
Longitude (decimal degrees)	*n.s.*				
Area (km^2) (log_{10})	*n.s.*				
Elevation range (m)	*elev (+)*	0.52	38.7	1, 37	<0.001
Mean annual temperature (°C)	$mean\_temp\text{-}mean\_temp^2$	0.26	6.4	2, 36	0.042
Mean temperature coldest month (°C)	*n.s.*				
Mean temperature warmest month (°C)	$mean\_warm\text{-}mean\_warm^2$	0.24	5.8	2, 36	0.052
Temperature seasonality (°C)	*n.s.*				
Mean annual precipitation (mm)	*n.s.*				
Mean precipitation March-November (mm)	*n.s.*				
Seasonality precipitation (mm)	*n.s.*				
Potential evapotranspiration (mm/yr)	$PET\text{-}PET^2$	0.38	11.1	2, 36	0.020
Actual evapotranspiration (mm/yr)	*n.s.*				
Frost frequency (days)	*frost (-)*	0.14	5.0	1, 37	0.048
b) regression modelling					
Spatial (S)	$lat\text{-}lat^2+lat^3$	0.51	12.6	3, 35	0.012
Topographic (T)	*elev*	0.52	38.7	1, 37	<0.001
Climatic (C)	$PET\text{-}PET^2$	0.38	11.1	2, 36	0.020
Combined (T+C)	$elev;\ PET\text{-}PET^2$	0.69	26.5	3, 35	<0.001
Total (S+T+C)	$lat\text{-}lat^2+lat^3;\ elev;\ PET\text{-}PET^2$	0.68	13.5	6, 32	<0.001

3.5 Discussion

The spatial analysis of belowground carabids clearly identifies southern Europe, and especially Italy, as the region with highest species richness in the western Palaearctic. Generally, this region has been classified as one of the hotspots of overall terrestrial troglobiont diversity based on the comparison of local species numbers from single caves (Vigna Taglianti 1982; Culver and Sket 2000) and from the small-scale study of selected regions across Europe (Culver *et al.* 2006). Our study extends this knowledge to the regional scale for one of the most species-rich terrestrial belowground taxa using a spatially and temporally comprehensive dataset. So far, the diversity of separate subterranean groups has scarcely been studied in detail (Zagmajster *et al.* 2008). Moreover, in contrast to most previous studies focusing on obligate cave-dwellers, our study comprises a broader range of subterranean species, including those living in the superficial underground compartment (MSS; Juberthie 1979), and thus provides a more general picture of belowground diversity patterns.

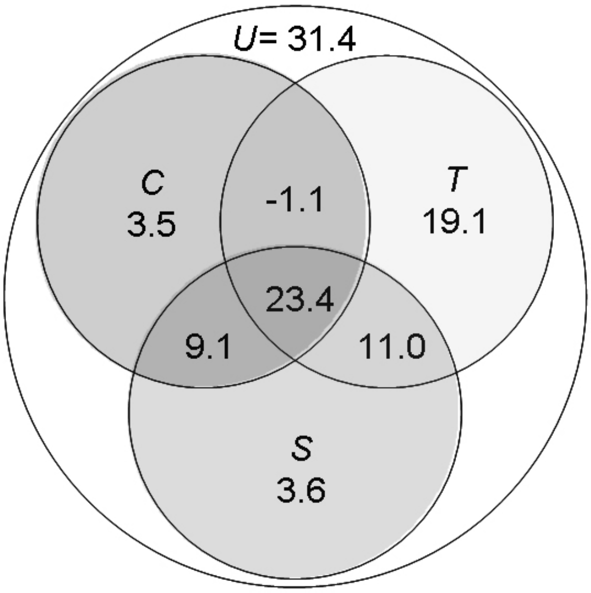

Figure 3.3. Partitioning of variation from regression modelling for species richness of belowground carabids. Values give the % of the total variation independent and shared effects of spatial (S), topographic (T) and climate (C) models account for in the explanation of richness patterns. U is the unexplained variation.

Species richness of carabid beetles adapted to belowground habitats significantly and most strongly covaried with range in elevation. To a certain extent, this might reflect effects of habitat heterogeneity and availability (Kerr and Packer 1997; Rahbek and Graves 2001), as mountainous regions are likely to feature extensive cave and karst systems. However, large karst areas also occur in regions which harbor only few or no belowground carabids at all (e.g., Belgium, England, Switzerland; see also Culver *et al.* 2006). Rather, our findings indicate a strong effect of historical processes on the present distribution patterns of belowground beetles. Regions with high altitudinal ranges can promote diversification processes through isolation and segregation along altitudinal gradients in environmental conditions (Jetz *et al.* 2004; Rahbek *et al.* 2007; see also Casale 2009). Moreover, topographically highly variable regions allow species to effectively compensate climatic shifts (Hewitt 1999) and not surprisingly, the highest belowground diversity of carabids was found in mountainous regions where probably the southern refugia of many taxa during the last ice age were located (Hewitt 1999; Casazza *et al.* 2008; Drees *et al.* 2010). The latitudinal pattern with a steep decrease in richness towards northern Europe, combined with relatively low effects of climate variables, yields further information regarding historical impacts. Due to their very specific habitat requirements and morphological adaptations, carabid beetles of belowground environments are strongly limited in their dispersal (Lamoreux 2004; Assmann *et al.* 2010). The lack of belowground species in central and northern Europe, despite suitable habitats, might be attributed to extinctions during Pleistocene glaciations and the inability of the range-restricted taxa to recolonize these regions (see also Schuldt and Assmann 2009). For many range-restricted and even for widespread vascular plants, effects of dispersal limitation on the current distribution across Europe have been suggested (Svenning and Skov 2007a; Svenning *et al.* 2008). Strong correlation between richness patterns of belowground carabids and vascular plants might indicate a similar historical signal prevailing in the distribution patterns of both taxa (cf. Hewitt 1999).

Concerning the distribution of hotspots of overall troglobiont diversity in Europe, Culver *et al.* (2006) found weak support for an influence of Pleistocene glaciations. Similarly, belowground carabids are also missing south of the former boundary of the Pleistocene ice sheet. However, the coarse-scale distribution of belowground carabid beetle diversity seems to largely conform to patterns postulated by Holdhaus (1954), who hypothesized that the occurrence of terrestrial cave fauna in Europe has been influenced by the spatial extent of permafrost soil, stretching much farther south than the ice sheet. According to his studies, the northern limit of these taxa runs along a line (the "Holdhaus-line") from the southern part of the Alps eastwards to the Carpathians (Holdhaus 1954; Drees *et al.* 2010). Concordance between the distribution of several groups of blind carabids and the theory of Holdhaus has also been found by Drees *et al.* (2010). Further re-examination on a more detailed scale will be needed to accurately evaluate these findings in light of the numerous new records of subterranean taxa from the last decades. While some species are considered to have survived in isolated refuges north of the Holdhaus-line (Holdhaus 1954), further deviations from the general pattern might be explained by postglacial range expansions (Drees *et al.* 2010). In contrast, an *Anillus* species recorded in park locations of Belgium (Desender 1986) and Germany (Malzacher 2000) was probably introduced with soil from the root system of trees imported from southern Europe. The survival of this species shows that suitable habitats also exist now in northern regions of Europe and can be seen as further evidence for strong effects of dispersal limitation on recolonization processes in the western Palaearctic (Drees *et al.* 2010).

As mentioned above, the influence of dispersal limitation might also become evident from the fact that current climate accounted for much smaller amounts of explained variation than elevation range in both single regressions as well as in regression modelling. Species with well-developed dispersal abilities are assumed to have tracked post-Pleistocene climate changes to a certain degree, and high covariation between species richness of many taxa and climatic variables support this view (reviewed by Hawkins *et al.* 2003). Within the highly diverse carabid beetles, the same is true for the richness of more mobile, widespread species, which is strongly related to climatic variables and much less to elevation range (Schuldt and Assmann 2009). In contrast, more range-restricted endemic species show the opposite pattern, with a strong impact of topographic variability and low influence of current climate pointing to prevailing effects of historical processes on distribution patterns (Schuldt and Assmann 2009). Our results for belowground beetles as part of the range-restricted carabids strongly support these findings and thus provide further insight into potential mechanisms underlying spatial distributions of diversity. They show that the significance of historical processes in explaining contemporary richness distributions might increase as dispersal abilities of the species decrease. In this respect, belowground carabids have a strong impact on overall patterns of the range-restricted (endemic) species. A larger influence of climate on these overall patterns of endemics (Schuldt and Assmann 2009) compared to belowground diversity, even though still secondary to effects of elevation range, indicates that postglacial range expansions are easier in above- than in the often spatially isolated belowground habitats (Porter 2007).

At least on the coarse scale of our analysis, we did not find evidence for the assumptions of Culver *et al.* (2006) that centres of highest belowground diversity might be located in regions of long-term high aboveground productivity. Current and past climate are correlated (Araújo *et al.* 2008) and AET as a measure of productivity (Hawkins *et al.* 2003) was not related to richness patterns of belowground carabids in our study. Rather, an influence of variables representing ambient energy input (temperature, PET) and the potential effects related to topographical variability suggest that in the western Palaearctic highest richness of these taxa is determined by historical/evolutionary processes a general long-term stability of environmental conditions (temperature) which supported survival and, especially regarding the strong signal of history, promoted diversification processes in belowground habitats (e.g., through isolation from other similar habitat patches or other phenomena relevant for evolutionary processes; Casale and Vigna Taglianti 2005).

3.6 Supplementary Material

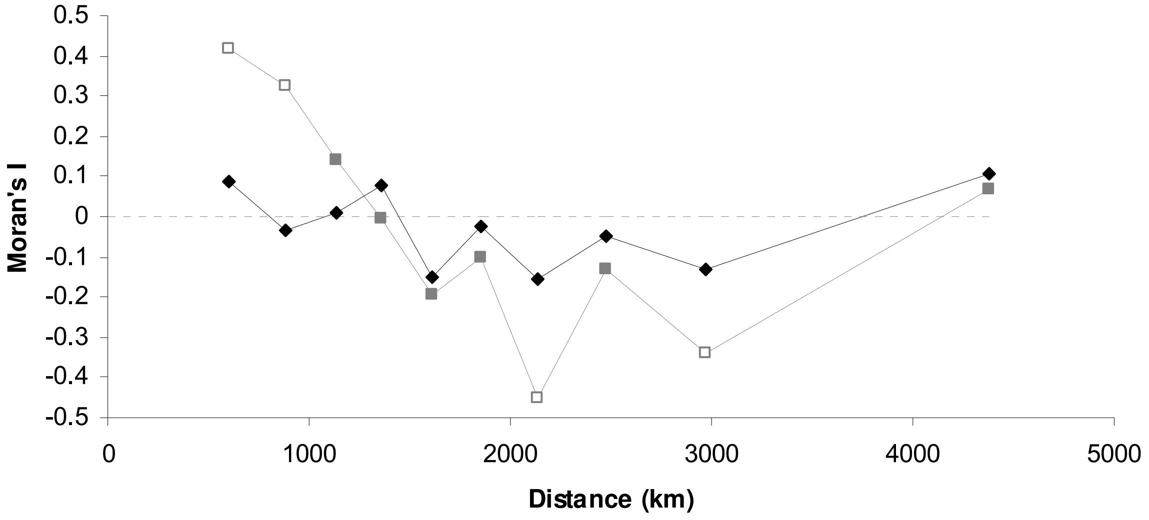

Figure S3.1. Spatial correlogram for below-ground carabid diversity before (grey line) and after (black line) fitting the environmental model. Open symbols: significant autocorrelation, filled symbols: no significant autocorrelation in the data.

Table S3.1. List of genera (in alphabetical order) of the belowground species analyzed. Data based on Löbl and Smetana (2003).

Arctaphaenops Meixner, 1925
Adriaphaenops Noesske, 1928
Agostinia Jeannel, 1928
Albanotrechus Casale & V.B. Guéorguiev, 1994
Allegrettia Jeannel, 1928
Allotrechiama Uéno, 1970
Alpiodytes Jeannel, 1957
Anillidius Jeannel, 1928
Anillopsidius Coiffait, 1969
Anillus Jacquelin du Val, 1851
Anophthalmus Sturm, 1844
Laemostenus Bonelli, 1810: only subgenus *Antisphodrus* Schaufuss, 1865
Aphaenopidius J. Müller, 1913
Aphaenopsis J. Müller, 1913
Aphaenotyphlus Españiol & Comas, 1985
Aphoenops Bonvouloir, 1862
Apocimmerites Belousov, 1998
Apoduvalius Jeannel, 1953
Arctaphaenops Meixner, 1925
Awatrechus Uéno, 1955
Binaghites Jeannel, 1937
Boldoriella Jeannel, 1928
Caecoparvus Jeannel, 1937
Chaetoduvalius Jeannel, 1928
Cimmerites Jeannel, 1928
Corcyranillus Jeannel, 1937
Coreoblemus Uéno, 1969
Croatotrechus Casale & Jalzic, 1999
Daiconotrechus Uéno, 1971
Dalmataphaenops Monguzzi, 1993
Dicropterus Ehlers, 1883
Doderotrechus Vigna Taglianti, 1968
Duvaliopsis Jeannel, 1928
Duvalius Delarouzée, 1859
Galiciotyphlotes Assmann, 1999
Geocharis Ehlers, 1883
Geotrechus Jeannel, 1919
Gotoblemus Uéno, 1970
Hydraphaenops Jeannel, 1926
Hydrotrechus Carabajal, Garcia & Rodriguez, 1999
Hypotyphlus Jeannel, 1937
Iberodytes Jeannel, 1949
Ildobates, Españiol 1966
Italaphaenops Ghidini, 1964
Kosswigia Jeannel, 1947
Lessinodytes Vigna Taglianti, 1982
Lovricia Pretner, 1979
Luraphaenops Giordan, 1984
Microtyphlus Linder, 1863
Nannotrechus Winkler, 1926
Neotrechus J. Müller, 1913
Orotrechus J. Müller, 1913
Paraphaenops Jeannel, 1916

Table S3.1. continued

Parazuphium: only *Parazuphium feloi* Machado, 1998
Parvocaecus Coiffait, 1956
Pheggomisetes Knirsch, 1923
Prioniomus Jeannel, 1937
Pseudanillus Bedel, 1896
Pseudaphaenops Winkler, 1912
Reicheadella Reitter, 1913
Reicheia Saulcy, 1862
Reicheidius Jeannel, 1957
Rhegmatobius Jeannel, 1937
Scotodipnus Schaum, 1860
Spelaeodytes L. Miller, 1863
Speleotyphlus Jeanne, 1973
Speluncarius Reitter, 1886
Speotrechus Jeannel, 1922
Stygiotrechus Uéno, 1958
Subilsia Españiol, 1967
Taurocimmerites Belousov, 1998
Trichaphaenops Jeannel, 1916
Troglocimmerites Ljovuschkin, 1970
Turkanillus Coiffait, 1956
Typhlocharis Dieck, 1869
Typhloreicheia Holdhaus, 1924
Typhlotrechus J. Müller, 1913
Winklerites Jeannel, 1937

4 INTEGRATING HIGHLY DIVERSE INVERTEBRATES INTO BROAD-SCALE ANALYSES OF CROSS-TAXON CONGRUENCE ACROSS THE PALAEARCTIC

Published article

A. Schuldt, Z. Wang, H. Zhou, and T. Assmann, Ecography 32 (2009): 1019-1030

4.1 Abstract

Our knowledge on broad-scale patterns of biodiversity, as a basis for biogeographical models and conservation planning, largely rests upon studies on the spatial distribution of vertebrates and plants, neglecting large parts of the world's biodiversity. To reassess the generality of these patterns and better understand spatial diversity distributions of invertebrates, we analyzed patterns of species richness and endemism of a hyperdiverse insect taxon, carabid beetles (about 11,000 Palaearctic species known), and its cross-taxon congruence with well-studied vertebrates (amphibians, reptiles) and plants across 107 units of the Palaearctic. Based on species accumulation curves, we accounted for completeness of the carabid data by separately examining the western (well-sampled) and eastern (partly less well-sampled) Palaearctic and China (deficient data). For the western Palaearctic, we highlight overall centers of invertebrate, vertebrate and plant diversity. Species richness and endemism of carabids were highly correlated with patterns of especially plant and amphibian diversity across large parts of the Palaearctic. For the well-sampled western Palaearctic, hotspots of diversity integrating invertebrates were located in Italy, Spain and Greece. Only analysis of Chinese provinces yielded low congruence between carabids and plants/vertebrates. However, Chinese carabid diversity is only insufficiently known and China features the highest numbers of annual new descriptions of carabids in the Palaearctic. Even based on the incomplete data, China harbors at least 25% of all Palaearctic carabid species. Our study shows that richness and endemism patterns of highly diverse insects can exhibit high congruence with general large-scale patterns of diversity inferred from plants/vertebrates and that hotspots derived from the latter can also include a high diversity of invertebrates. In this regard, China qualifies as an outstanding multi-taxon hotspot of diversity, requiring intense biodiversity research and conservation effort. Our findings extend the limited knowledge on broad-scale invertebrate distributions and allow for a better understanding of diversity patterns across a larger range of the world's biodiversity than usually considered.

4.2 Introduction

While biodiversity is decreasing globally at a fast rate, our knowledge on even basic patterns of diversity for large parts of the Earth's biota is still fragmentary (Wolters *et al.* 2006; Lovell *et al.* 2007). Identifying general patterns in the spatial distribution of biodiversity has become a central topic in geographical ecology and conservation biology. Relationships between species richness distributions of different taxa at various spatial scales have been used for hypothesis testing in biogeography (Hawkins *et al.* 2003; Gaston *et al.* 2008) and priority setting in conservation planning (Myers *et al.* 2000; Orme *et al.* 2005). At broad geographic scales, cross-taxon comparisons often show high concordance of diversity patterns between different organism groups (Grenyer *et al.* 2006; Wolters *et al.* 2006), based in part on similar latitudinal gradients in species richness (Hillebrand 2004). Which factors and mechanisms ultimately govern these patterns is subject to ongoing debate, even though an interplay between evolutionary and ecological processes is commonly assumed (Ricklefs 2004; Wiens and Donoghue 2004; Hawkins *et al.* 2007).

However, large-scale analyses of diversity patterns, especially of cross-taxon congruence, and the generalizations made from these are biased towards specific organism groups. While invertebrates make up about 95% of the global faunal diversity (Myers *et al.* 2000), strongly influencing processes and functioning of ecosystems (Partsch *et al.* 2006), studies on cross-taxon patterns and hotspots of diversity mainly cover plants and vertebrates (e.g., Myers *et al.* 2000; Qian and Ricklefs 2008). Invertebrates are largely omitted from these analyses and invertebrate species distributions are poorly understood (Moritz *et al.* 2001; Lovell *et al.* 2007). This is in part due to a lack of extensive distributional information for many invertebrate taxa in large parts of the world. Most studies actually incorporating invertebrates are strongly restricted in their geographic extent and usually remain at more local scales (e.g., Prendergast *et al.* 1993; Lund and Rahbek 2002; Gutiérrez and Menéndez 2007). Only few and rather species-poor insect taxa have previously been analyzed at larger (e.g., continental) levels, with varying results (Balmford and Long 1995; Pearson and Carroll 1998; Pearson and Carroll 1999). However, especially extensive studies covering wider geographic ranges are needed for invertebrates, as these are of particular interest in understanding general patterns of overall biodiversity (Lamoreux *et al.* 2006; Wolters *et al.* 2006).

Here, we analyze Palaearctic patterns of species richness and endemism (as two of the most commonly and broadly used measures of diversity) of carabid beetles and compare them to well-known patterns of vertebrates (amphibians, reptiles) and vascular plants. Many species of these taxa are characterized by a rather low mobility, which assures a consistent scale of analysis due to similarities in range sizes (as opposed to well-known but highly mobile birds or mammals; Hawkins and Pausas 2004) Unlike many other insect taxa, carabids offer an excellent opportunity to analyze macroecological patterns of invertebrates for several reasons: (1) Distributions are well-documented across a very large area (see Methods); (2) A comprehensive catalogue for the whole Palaearctic (Löbl and Smetana 2003) accounts for problems concerning taxonomic inflation (cf. Isaac *et al.* 2004); (3) In contrast to previously studied invertebrates, carabids are highly diverse (about 11,000 species described from the Palaearctic), feature a high proportion of endemics and a considerable variety of life-form types (including endogeic, tree-living or ectoparasitic species); (4) Being predominantly predatory, carabids allow for unbiased analyses of plant-invertebrate relationships. Our study comprises 107 geographic units across the Palaearctic, subdivided into three regions to account for the completeness of the carabid data.

We aimed to assess the extent to which results from comparisons of phylogenetically and functionally unrelated taxa can be generalized, irrespective of the underlying mechanisms. Are broad-scale diversity patterns of a highly diverse insect taxon concordant with those of so far predominantly studied vertebrates and plants? Congruence between these very distantly related groups could be lower than for closely related taxa often considered so far (Grenyer *et al.* 2006). However, carabid diversity in the western Palaearctic strongly covaries with environmental factors assumed to influence large-scale diversity distributions of vertebrates and plants (Schuldt and Assmann 2009). Based on these findings, we expect reasonable congruence in spatial patterns of species richness, endemism and also in coarse-scale centers of diversity between this speciose insect taxon and amphibians, reptiles and plants. Incorporating large-scale data from taxonomically and ecologically highly diverse invertebrates, our study helps to extend the limited knowledge on general diversity patterns to a larger range of the world's biodiversity.

4.3 Methods

4.3.1 Species richness data and scale of analysis

Defining an appropriate scale of analysis suitable to the accuracy of available data is a general problem in macroecological studies, even with well-known vertebrate data (Hurlbert and Jetz 2007; Hortal *et al.* 2008; Jetz *et al.* 2008). Due to the structure of the carabid beetle dataset, we used country-level diversity in our analyses. For species-rich invertebrates this scale is most comprehensive and accurate, as extensive surveys of large geographic regions on a more detailed scale are scarcely available from most regions of the world (Lovell *et al.* 2007; Hortal 2008). Trying to assign species data to finer levels (ecoregions or equal-area grids) would thus have inevitably decreased the precision of our study (see also Hortal *et al.* 2008). Although this limits our analyses to a rather coarse geographic scale, many studies using this approach have demonstrated its utility in analyzing large-scale patterns of diversity (e.g., Kerr and Burkey 2002; Pandit and Laband 2007; Keil *et al.* 2008a; Qian and Ricklefs 2008).

We created a country-level database compiling species richness data of carabid beetles (Coleoptera: Carabidae), amphibians, reptiles and vascular plants from 75 countries of the Palaearctic (geographic boundaries outlined in Löbl and Smetana 2003). China was divided into 33 provinces/autonomous regions to be in scale with the remaining dataset. For the same reason, we excluded Russia from statistical analyses, as we were not able to assign reliable species numbers of all taxa analyzed to subunits of this country. However, Russia only harbors a comparatively small number of endemic carabid beetles, so that only a very small proportion of Palaearctic carabids was excluded from our analysis. Our study is thus based on 107 units with an average size of 328,822 (± 510,242) km². To assess the robustness of our results we split the dataset and separately analyzed two subsets with reduced variation in country sizes, i.e., large countries (>10^5 km²) and small countries (<10^5 km²). Average unit sizes of these subsets were 523,351 (± 584,586) km² and 39,288 (± 31,103) km², respectively.

Species numbers (total and endemic) for plants and vertebrates were extracted from datasets representing comprehensive diversity assessments which are commonly used in biogeographical analyses (e.g., Brooks *et al.* 2002; Hobohm 2003; Grenyer *et al.* 2006). Amphibian data was obtained from IUCN (2007), reptile data from the former EMBL reptile database (Uetz and Hallermann 2007). Amphibian and reptile data for Chinese provinces was extracted from the CSIS database (http://www.chinabiodiversity.com; Xie and Sung 2007). Sources for vascular plant diversity were Walter and Gillett (1998), Groombridge and Jenkins (2002) and Hobohm (2008), supplemented by data from UNEP (http://earthtrends.wri.org), and CBD National Reports (http://www.cbd.int/countries). Chinese plant data (total numbers per province) was extracted from the College of Urban and Environmental Sciences (Peking University) database. Species numbers of carabids were obtained from the extensive compilation of Löbl and Smetana (2003). We used national endemics in our study as this data allowed robust comparison of endemism of the different taxa.

4.3.2 Completeness of the carabid dataset

Whereas species numbers of vertebrates and vascular plants are rather well known for large parts of the world (e.g., Lamoreux *et al.* 2006; Qian and Ricklefs 2008), assessments of invertebrate diversity, especially those of very species-rich taxa, are often incomplete (Gotelli and Colwell 2001). To account for this and to use reliable data comparable to well-studied vertebrates and plants, we analyzed species accumulation curves (using species discovery data; cf. Medellin and Soberon 1999; Cabrero-Sanudo and Lobo 2003) for carabid beetles in each of the countries of our study region. Analyses for the western Palaearctic region were also carried out by Schuldt and Assmann (2009), showing an adequate data basis of carabid beetle diversity in these countries. While it cannot be assumed for all of the countries of the western Palaearctic that the inventories are complete (as is difficult for any taxon, even for very well-known birds or plants; Bebber *et al.* 2007), accumulation curves for most countries become asymptotic during the 19th or 20th century (Fig. S4.1 in Supplementary Material). This is also indicated by closer analysis of faunistic data from European countries, where the increase in carabid species numbers within the last decades is very low for most of the countries (Table S4.1 in Supplementary Material), which underscores the results from our analysis using species discovery data. The solid carabid species inventories in most western Palaearctic countries assure powerful analysis of cross-taxon relationships. Countries east of this region are in part less well-sampled and accumulation curves do not reach a clear asymptote (Fig. S4.1). This is especially true for China, which shows strongly increasing species numbers. On average, 32% of the carabid species presently known from the Chinese provinces have been newly recorded over the last 50 years. In the same time span, for eastern Palaearctic countries this percentage was on average 22% and for western Palaearctic countries even only 4%. But especially within the last years, carabid species numbers in China have risen drastically (Fig. S4.1).

These findings necessitate cautious and critical interpretation of possible results. For this reason, we subdivided the dataset for analyses, based on the completeness of carabid data, into a western Palaearctic region (Europe and North Africa: well-known), the eastern parts of the Palaearctic (partly less well-known) and China (subdivided into provinces; deficient data) (Fig. S4.2). This subdivision also allows to evaluate observed patterns in the context of regional (historical) processes, as the three regions also represent geographical subdivisions of the Palaearctic.

4.3.3 Statistical analyses

We analyzed diversity patterns separately for the three subdivisions (see above) of our study region, using results from the well-sampled western Palaearctic region to help interpret eastern Palaearctic patterns.

For the analysis of diversity congruence, we calculated Pearson correlations between the total and endemic species richness of carabids, reptiles, amphibians and vascular plants. We used first-order partial correlation analysis (Legendre and Legendre 1998; Freckleton 2002), including country area as a covariable, to control for potentially confounding effects of the variance in country size. Both richness measures and area were $\log_{10}$-transformed to normalize and linearize the data.

Geographic richness data is often spatially autocorrelated, which can bias significance estimations of statistical tests by inflating Type I errors (Diniz-Filho *et al.* 2003). To account for this, we recalculated the statistical significance of the area-corrected cross-taxon correlations using spatially corrected degrees of freedom according to the method of Dutilleul (1993), which effectively corrects for spatial autocorrelation in the data (Legendre *et al.* 2002).

We additionally assessed the robustness of our results by dividing the dataset into large

($>10^5$ km²) and small ($<10^5$ km²) countries and separately reanalyzed cross-taxon relationships using these two sets of countries with areas within the same order of magnitude. Results similar to those for the total dataset would indicate that the latter are not significantly affected by the variation in country area and the grain size of our analysis (cf. Hortal *et al.* 2008).

Finally, for the western Palaearctic region we explored multivariate relationships between richness patterns of the four taxonomic groups by partial (controlling for area by including it as a covariable; Leps and Smilauer 2003) principal components analysis (PCA), depicting spatial richness distributions and indicating the overlap between taxon-specific centers of diversity (i.e., countries with highest total and endemic species richness, respectively, per unit area; Reid 1998). We also analyzed latitudinal gradients of diversity by regressing richness and endemism of each taxon on latitude (midpoint latitude for each country from CIA 2008). Area was again included as a covariable and second- or third-order polynomial terms of latitude were added to the model in case of significant non-linear relationships (Quinn and Keough 2002). Latitude was centered before computing polynomials to reduce collinearity between monomials. Partial regression analysis (Legendre and Legendre 1998; Hortal *et al.* 2008) was used to assess the independent effect of latitude (controlling for area) on species numbers. The variation in parameter estimates of the latitudinal gradients was tested with analysis of covariance, with taxon included as a categorical variable.

We used SPSS 15 (SPSS Inc., Chicago, USA) for correlation analyses, SAM 2.0 (Rangel *et al.* 2006) for spatial corrections and Canoco 4.5 (Ter Braak and Smilauer 2002) for multivariate analyses.

4.4 Results

In the western Palaearctic region, with very reliable carabid data, high (following Lamoreux *et al.* 2006) and significant correlations (coefficients of partial correlation analyses, including country area as a covariable, between 0.91 and 0.83) exist between total richness of carabid beetles, amphibians and vascular plants (Table 4.1). Reptile richness was also positively and significantly related to richness of the other taxa, but showed notably lower partial correlation coefficients (between 0.74 and 0.52). Endemic richness of the four taxa was significantly correlated in this region as well, with coefficients ranging from 0.88 to 0.49 (Table 4.1). Relationships between amphibians and carabids/plants and between reptiles and plants were slightly less strong for endemic richness compared to total richness patterns, whereas relationships between carabids and plants or reptiles and between reptiles and amphibians were slightly stronger for endemic richness patterns.

Table 4.1. Partial correlations (area included as covariable) of a) total and b) endemic species richness[a] between carabids, reptiles, amphibians and vascular plants across western (Europe/North Africa) and eastern (without China) Palaearctic countries and Chinese provinces.

	Carabid beetles			Reptiles			Amphibians		
	West P.	*East P.*	*China*	*West P.*	*East P.*	*China*	*West P.*	*East P*	*China*
a) total species richness									
Vascular plants	0.83***	0.90***	0.38*	0.74***	0.35	0.85**	0.84***	0.71*	0.84**
Amphibians	0.91***	0.68*	0.25	0.52***	0.33	0.85**			
Reptiles	0.53***	0.31	0.40						
b) endemic species richness									
Vascular plants	0.88***	0.79**	-[b]	0.59**	0.27	-[b]	0.49**	0.41	-[b]
Amphibians	0.62***	0.63**	0.50*	0.67***	0.73***	0.77***			
Reptiles	0.57**	0.27	0.66***						

[a] p-values corrected for spatial autocorrelation: ***p<0.001; **p<0.01; *p<0.05

[b] endemic plants not included in correlations across China, due to missing data

Within taxa, positive relationships between total and endemic richness were significant (coefficients between 0.63 and 0.50) for carabids, reptiles and plants, but not for amphibians (Table 4.2).

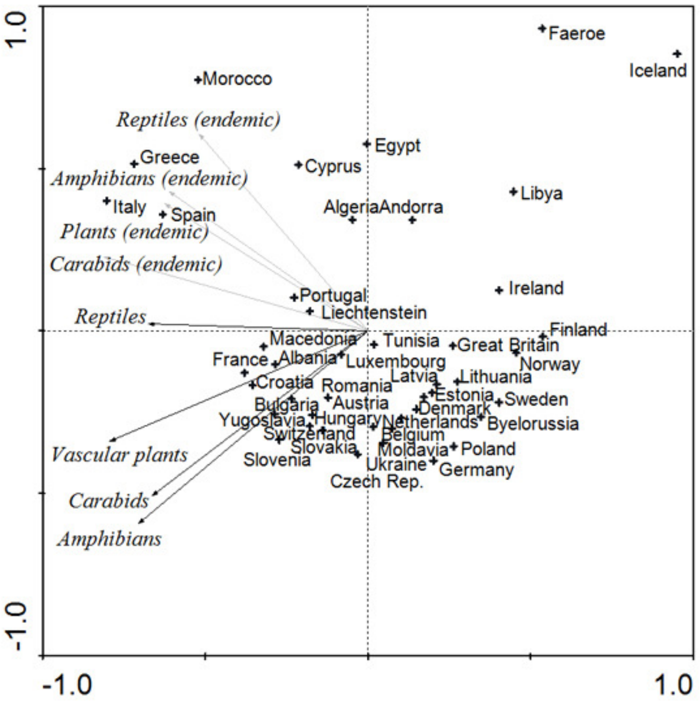

Figure 4.1. Ordination-plot of partial PCA (area included as covariable) showing western Palaearctic patterns of total (black species arrows) and endemic (grey species arrows) species richness of carabids, reptiles, amphibians and vascular plants. Standardized (Ter Braak and Smilauer 2002) eigenvalues for first (horizontal) and second (vertical) axis are 0.463 and 0.186, respectively. Cumulative percentage variance of species data is 79.8%.

The above relationships can also be easily retraced in the partial PCA ordination plot (Fig. 4.1), showing close relationships between total diversity of carabids, amphibians and vascular plants compared to total reptile richness, as well as congruence between endemism distributions of the four taxa (see also Fig. 4.3 and 4.4). It also indicates similarities between geographic patterns of total and endemic richness gradients across Europe and North Africa. Fig. 4.2

highlights this gradient, which is hump-shaped (significant polynomial terms of latitude-latitude^2 for richness and latitude-latitude^2+latitude^3 for endemism) for all four taxa. While model parameters significantly differed between taxa (taxon:latitude interactions in Ancova $F_{31,\ 144}=29.97$; $p<0.001$ for richness and $F_{55,\ 111}=24.73$; $p<0.001$ for endemism), carabids, plants and amphibians similarly show highest total richness at medium latitudes (the southern part of Europe), decreasing towards North Africa and northern Europe. A related pattern is apparent for endemic richness of especially carabids and plants, however, with the peak of highest endemism extending less into central Europe than that of total richness. Reptiles exhibit a somewhat deviating pattern, as total richness and endemism are highest in North Africa (Fig. 4.2). Yet, especially Italy, Spain and Greece combine high total as well as endemic richness of all four taxa, including reptiles, thus qualifying as important overall hotspots of diversity in the western Palaearctic region (Fig. 4.1). Serbia, Slovenia, Croatia and France also feature high total species richness of all four taxa, but have less significance concerning endemism.

Table 4.2. Within-taxon correlations (partial correlations with area as covariable) between total and endemic species richness[a] of carabids, reptiles, amphibians and vascular plants across western and eastern (without China) Palaearctic countries and Chinese provinces.

	West P.	*East P.*	*China*
Carabid beetles	0.50*	0.87**	0.90***
Reptiles	0.51*	0.57**	0.63**
Amphibians	0.28	0.72***	0.75**
Vascular plants	0.63*	0.91***	-[b]

[a] p-values corrected for spatial autocorrelation: ***p<0.001; **p<0.01; *p<0.05

[b] endemic plants not included in correlations across China, due to missing data

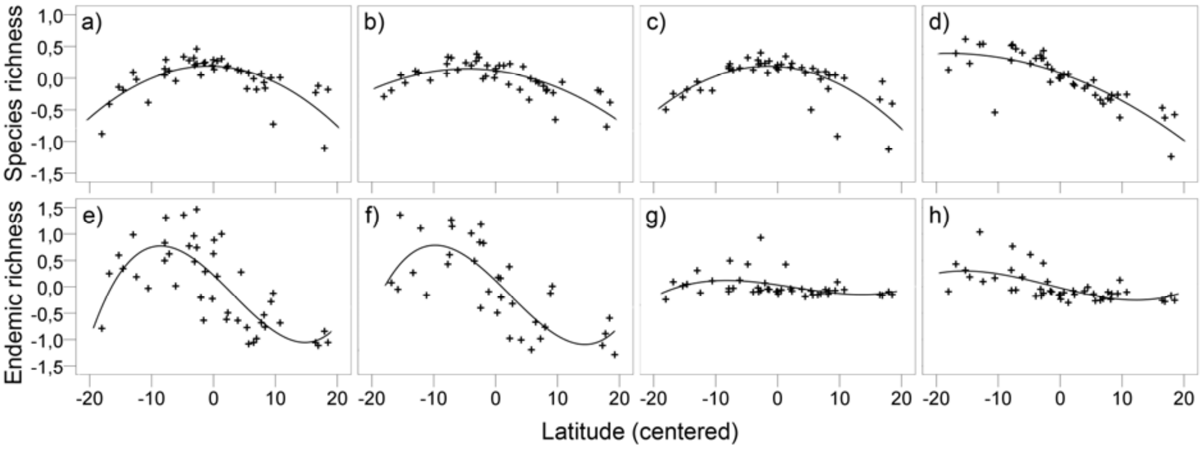

Figure 4.2. Latitudinal gradients of total/endemic species richness (log-transformed) of a/e) carabids, b/f) vascular plants, c/g) amphibians, and d/h) reptiles in the western Palaearctic. Partial regression plots (independent effects of area as a covariable factored out). Independent effects (R^2) of latitude on total (models for all taxa including latitude-latitude^2)/endemic richness (models: latitude-latitude^2+latitude^3): carabids 0.56/0.57; plants 0.61/0.55; amphibians 0.64/0.13; reptiles 0.50/0.36. Except for endemic amphibians (p=0.005) all p-values <0.001.

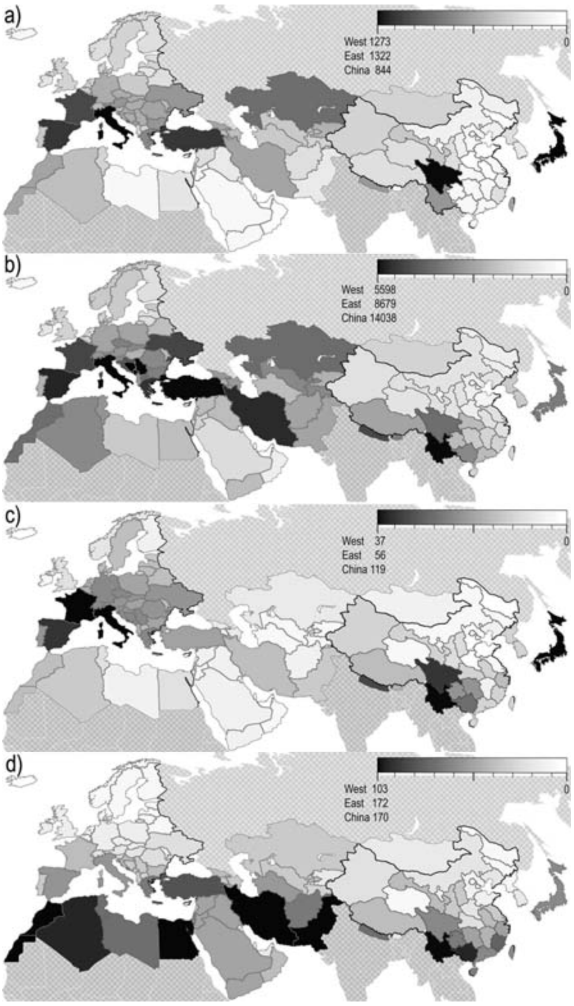

Figure 4.3. Patterns of total species richness of a) carabid beetles, b) vascular plants, c) amphibians, and d) reptiles across the Palaearctic (excluding Russia). Patterns were analyzed and are plotted separately for the western and eastern Palaearctic and China (bold lines show region borders) due to differences in the completeness of carabid species inventories (see Fig. S4.3 for comparison across the whole Palaearctic without considering the subdivision into regions). Checkered countries were not included in the analyses.

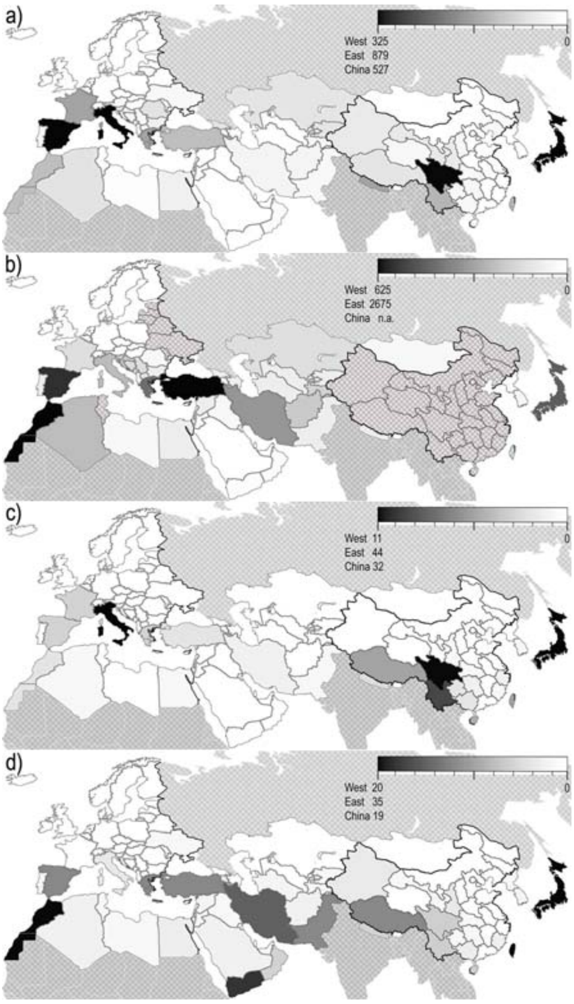

Figure 4.4. Patterns of endemic species richness of a) carabid beetles, b) vascular plants, c) amphibians, and d) reptiles across the Palaearctic (excluding Russia). Patterns were analyzed and are plotted separately for the western and eastern Palaearctic and China (bold lines show region borders) due to differences in the completeness of carabid species inventories (see Fig. S4.4 for comparison across the whole Palaearctic without considering the subdivision into regions). Checkered countries were not included in the analyses (missing data for endemic plants in China/eastern Europe).

Deviating patterns of reptile species richness become clearer when looking at cross-taxon congruence in the eastern Palaearctic region, where correlations between reptiles and amphibians or plants were rather weak (Table 4.1). Endemism patterns also deviated for the relationship between reptiles and plants, but not between reptiles and amphibians. In contrast, correlations between plant and amphibian richness and endemism are comparable to results from western Palaearctic countries, indicating that amphibian and plant diversity similarly covary across the whole Palaearctic. All three, amphibians, plants as well as reptiles, showed again high congruence of diversity across Chinese provinces (Table 4.1).

Integrating carabid beetles into eastern Palaearctic and Chinese diversity patterns requires cautious interpretation, due to less reliable carabid data from these regions. Like amphibians and plants, carabids exhibited weak relationships with reptile diversity (total as well as endemic) in the eastern Palaearctic, whereas correlations with the former two taxa were largely comparable to those using western Palaearctic data (Table 4.1; see also Fig. 4.3 and 4).

In contrast, for Chinese provinces, where carabid diversity is only insufficiently known, results for total diversity (but not for endemics) strongly deviated from patterns found for western Palaearctic and other Asian countries. Within taxa, concordance between total and endemic richness was rather high and significant for all four groups, also carabids, in both eastern regions (Table 4.2).

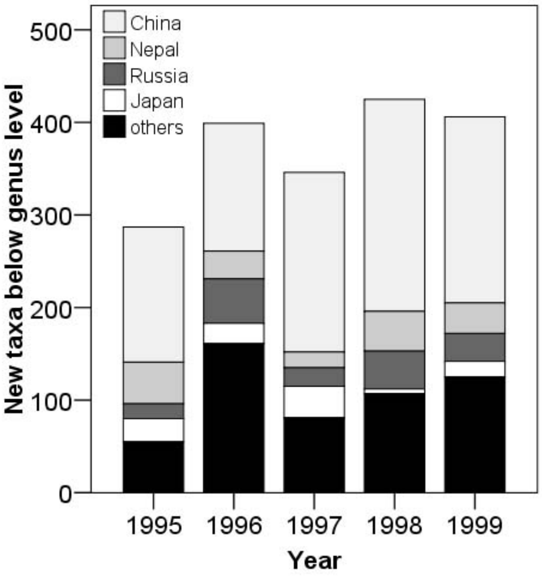

Figure 4.5. Numbers of carabid species and subspecies newly described for countries with highest increase in taxa (China, Nepal, Russia, Japan) and all other (mainly eastern) Palaearctic countries within the last five years contained in Löbl and Smetana (2003).

Vast undersampling of carabid beetles in China, in a dimension unparalleled by any other country in the Palaearctic, is implied by a closer analysis of description data for the last five years contained in Löbl and Smetana (2003): On average, about 50% of all new Palaearctic species and subspecies were described from China, whereas Nepal, featuring the second highest rate of new descriptions, only accounted for 9% (Fig. 4.5). The number (908) of species and subspecies newly described from China in these five years amounts to 28% of the total number of carabid (sub)species listed for China in Löbl and Smetana (2003). Provided that high correlations between carabids and plants/amphibians are characteristic for the whole Palaearctic, as might be inferred from our analyses, presently known numbers of carabids are much lower in most Chinese provinces than might be expected (Fig. 4.6).

Reanalyzing subsets of our data altogether yielded results similar to the analyses using all countries (Tables S4.2-S4.4 in Supplementary Material). Correlation coefficients and probability values of cross-taxon relationships in most cases showed low variability between

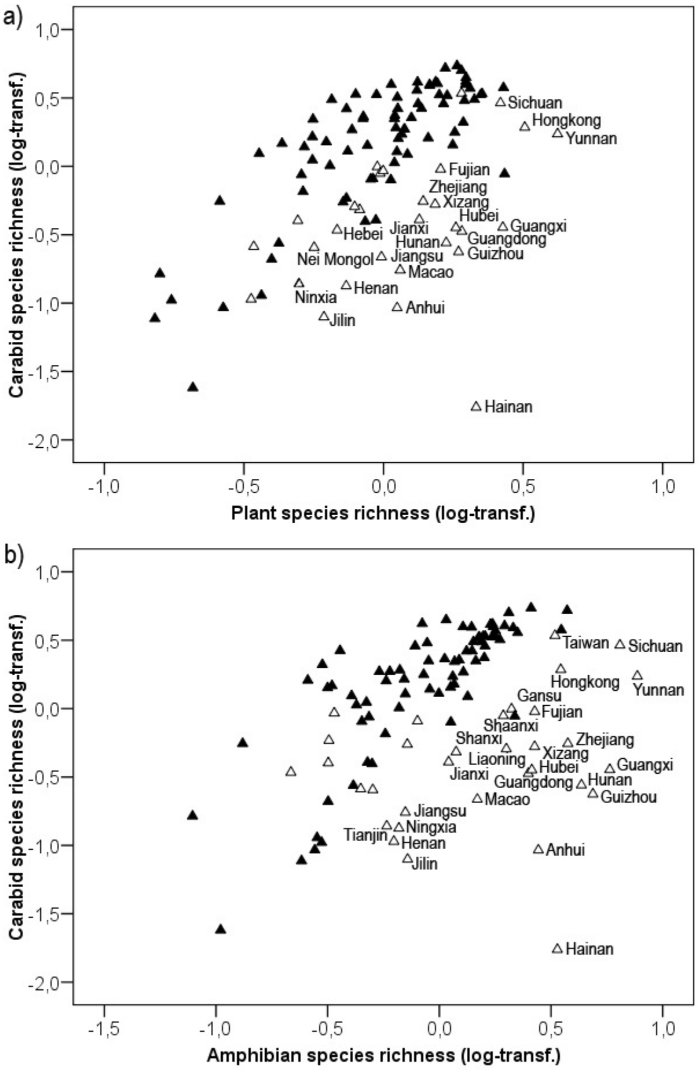

Figure 4.6. Relationships between species richness of carabid beetles and a) vascular plants, b) amphibians across the Palaearctic, with China represented by its provinces/autonomous regions (open triangles: Chinese provinces; filled triangles: all other countries). Partial regression plots (independent effects of area as a covariable factored out).

the total and small- and between the total and large-country datasets, supporting the robustness of the patterns found in the analyses using all countries. Values from large-country analyses in part tended to be slightly higher than those from the total or small-country analyses, however, without affecting the general results from the total and small-country analyses concerning significance and relative strength of the correlations. The same is true for larger differences between correlations of total richness of amphibians and plants/carabids in the eastern Palaearctic, where coefficients were higher for the small- than the large-country dataset. Yet, both analyses reflected the same general pattern as indicated by the results from the total dataset.

Notable differences only occurred in the analysis of endemism relationships. Here, correlations in the small-country dataset between reptiles and carabids/plants in the western Palaearctic as well as between amphibians and carabids in the eastern Palaearctic were weaker than in the large-country and total dataset and not significant. Likewise, the eastern Palaearctic correlation between endemic amphibians and plants was only significant for the large-country dataset. However, at least for the western Palaearctic these differences are most probably not due to scale-dependent effects but to the spatial clustering of the small countries in this region (see Discussion). Not surprisingly, correlation results were also rather low for the incompletely sampled carabid diversity in the small Chinese provinces. All other results using the small-country dataset showed similar congruence patterns as those of the whole dataset.

4.5 Discussion

Our study integrates data of hyperdiverse invertebrates into cross-taxon analyses to test for general patterns of broad-scale diversity across a wider range of organism groups than usually studied. However, this demands accurate consideration of the invertebrate data quality (Gotelli and Colwell 2001). The subdivision of our study region based on the completeness of the carabid data enables us to reliably analyze diversity patterns of carabid beetles for the well-sampled western Palaearctic (Europe and North Africa) and to cautiously interpret patterns of less completely sampled eastern Palaearctic regions. Of course, our species discovery curves can only give an estimate of the completeness of the species inventories for the countries of each region. However, considering the small changes in species numbers for many European countries over the last decades and the fact that increases in species numbers are detectable mainly in the already most species-rich countries, we are convinced that our analysis adequately reflects western Palaearctic richness patterns of carabids.

In our study, we use species richness and endemism as two of the most commonly and broadly applied diversity metrics in biogeographical analyses and conservation decisions (Lamoreux *et al.* 2006). To further explore congruence and complementarity in the patterns of diversity between taxa, the analysis of beta diversity patterns will be an important additional issue. Our dataset currently does not allow detailed analysis of the latter and future work should address these issues to compare different aspects of diversity. In our study, the analysis of endemism patterns in part approaches these questions of similarities between composition patterns, as it focuses on the singularity of faunal elements between countries.

At the large scale we considered, diversity distributions of amphibians, reptiles and vascular plants are sufficiently known across the whole Palaearctic (Brooks *et al.* 2002; Stuart *et al.* 2004; Grenyer *et al.* 2006; Qian and Ricklefs 2008). Our study yielded highly concordant diversity patterns of amphibians and vascular plants across the western and eastern Palaearctic regions and China. Except for China, where total reptile richness was highly correlated with richness of amphibians and plants (see also Qian 2007), reptile diversity distributions differed to some extent from those of the latter taxa. These differences were moderate in the western Palaearctic region, but very distinct across the eastern Palaearctic. For vertebrate and plant taxa, broad-scale studies generally found high cross-taxon congruence of species richness (Grenyer *et al.* 2006; Lamoreux *et al.* 2006; Wolters *et al.* 2006; Qian and Ricklefs 2008). Only reptile diversity patterns regionally deviated to some extent. This is explained by the physiological requirements of this taxon, which leads to reptiles being especially species-rich in warm, arid regions that are unfavourable to other taxa (Hawkins *et al.* 2003; Rodriguez *et al.* 2005; Whittaker *et al.* 2007). In our study, these regions are located mainly in the Middle

East and Asia (e.g., Pakistan, Israel), and thus deviating reptile patterns are most pronounced in our eastern Palaearctic study region.

The above findings from previous studies are concordant with our results and confirm that our country-approach accurately captures general large-scale patterns previously derived from comparisons using ecoregions or equal-area grids as sampling units. Here, we show that these patterns can be extended to species-rich invertebrates.

4.5.1 Cross-taxon relationships of carabids in the western Palaearctic

Total species richness

Total richness of carabid beetles was highly correlated with plant and amphibian richness across the western Palaearctic region. Similar to the latter two taxa, congruence with reptile patterns was slightly lower, but significant. Comparable studies are scarce and limited in their taxonomic or geographic extent. Pearson and Carroll (1998; 1999) analyzed continental distributions of tiger beetles (Cicindelidae), diurnal butterflies and birds in North America, Australia and India. Results varied with region, diversity of butterflies and birds showing highest correlations. However, testing only relationships between invertebrates and birds impedes applicability to a larger context. Range sizes differ considerably between insects and highly mobile birds, which shifts the scale of analysis between these groups and might blur correlations (Hawkins and Pausas 2004; Grenyer *et al.* 2006). Additionally, tiger beetles and diurnal butterflies are relatively species-poor taxa, representing but a very small fraction of invertebrate diversity and life-form types. In our study, we adopted a wider perspective by comparing species-rich beetles to plants and vertebrates with a likewise low mobility, which yielded more consistent results.

At an already smaller scale, Hawkins and Porter (2003a) state positive covariation between butterflies and plants across California. Many more studies integrated invertebrates in local-scale than in spatially extensive large-scale comparisons, usually finding weak cross-taxon relationships (e.g., Prendergast *et al.* 1993; Howard *et al.* 1998; Ricketts *et al.* 2002; Wolters *et al.* 2006; Lovell *et al.* 2007). Generally, correlations between taxa, including invertebrates, are suggested to be higher at larger scales and to decrease towards local scales (Wolters *et al.* 2006). Low congruence between taxa in small-scale studies is supposed to be caused by differences in habitat specificity and a strong influence of biotic interactions differentially determining diversity patterns at fine scales (Whittaker *et al.* 2001; Ricklefs 2004; Lovell *et al.* 2007). In contrast, large-scale patterns of diversity are probably strongly influenced by diversification processes and past and present environmental conditions, which are suggested to affect many taxa in a similar way (even though the relative impact of these factors is still being debated; Hawkins *et al.* 2003; Wiens and Donoghue 2004; Hortal *et al.*

2008). Latitudinal richness gradients were similarly hump-shaped for carabids, plants and amphibians, pointing to similar latitudinal dependencies. In fact, broad-scale patterns of carabid diversity closely covary with similar environmental factors as patterns of vertebrates and plants (Schuldt and Assmann 2009). Water-energy dynamics have repeatedly been found to be one of the main factors explaining richness distributions of these taxa (Hawkins *et al.* 2003; Whittaker *et al.* 2007; Schuldt and Assmann 2009). As mentioned above, physiological requirements of reptiles with a strong dependency on energy input rather than water-energy dynamics explain the deviating patterns with high richness in North Africa for this taxon. For a range of invertebrate taxa (Hawkins *et al.* 2003; Baselga 2008; Finch *et al.* 2008), similar patterns as those for carabids have been demonstrated, which indicates that the analysis of large-scale patterns of carabid diversity might help to better understand patterns of a wider spectrum of invertebrates, at least in Palaearctic regions.

Endemism and centers of diversity

In our study, we also found high congruence between endemism distributions of carabids, amphibians, reptiles and plants. Latitudinal gradients of endemism were very similar between carabids and plants. Amphibians (and also reptiles, with the exception of high endemism in North Africa) showed comparable patterns, though much less distinct as even the endemism hotspots harbor only few endemic amphibian (and reptile) species. Altogether, these similarities can probably be attributed to a larger part to the influence of historical processes. Endemics are characterized by small range sizes. Diversification processes in regions promoting isolation and offering small-scale environmental gradients (as the mountainous areas of southern Europe) as well as retreat or extinction of species in northern Europe during glaciation events and low recolonization rates of these low mobile taxa (with slight differences due to different dispersal abilities; see below) can have fostered these similar patterns (Araújo and Pearson 2005; Svenning and Skov 2007a).

Congruence of endemism patterns is well known for global vertebrate distributions at coarse scales (Lamoreux *et al.* 2006), as is also shown by our study across the whole Palaearctic. For invertebrates, there is only scant evidence in this regard. Balmford and Long (1995) studied performance of restricted-range birds as biodiversity indicators in 137 tropical countries, using tiger beetles and papilionid butterflies. Numbers of endemic beetles and butterflies were highly correlated with richness of restricted range birds. Lumaret and Lobo (1996) state similar rates of endemic species for geotrupid beetles, plants and amphibians in the Mediterranean Basin. Also at smaller scales, congruence between endemic invertebrates and vertebrates or plants can be high (Moritz *et al.* 2001).

Endemism of plants and vertebrates is often used to devise diversity hotspots ((Myers *et al.* 2000). The above results and reasonable overlap of endemism-centers in PCA-ordination suggest that such hotspots can also capture high proportions of endemic insects. Optimum hotspots would be those combining centers of both endemism and species richness, but little overlap has been found between patterns of these two within taxa, even at coarse scales (Orme *et al.* 2005; Ceballos and Ehrlich 2006; Lamoreux *et al.* 2006). In contrast, within-taxon correlations between total and endemic richness in our study were fairly high in most cases. Whereas the former studies compared global distributions, we focused on three Palaearctic regions. For the latter, diversity relationships can be stronger within taxa (Casazza *et al.* 2008), as these regions are characterized by distinct historical processes (e.g., glaciations) affecting diversity distributions. Different historical processes might lead to deviating patterns in other regions, thus affecting the outcome of global analyses. An indication of region-specific patterns can also be inferred from our analyses of within-taxon correlations, supporting the approach to analyze subdivisions of the Palaearctic. Correlations between species richness and endemism within taxa were higher for the eastern Palaearctic region and China than for the western Palaearctic. While this might to some part be an effect of less complete species inventories in the former regions (especially for China, where part of the species might only be known from their type localities so far and are thus classified as endemics), this probably primarily reflects a different impact of historical processes on these regions. The western Palaearctic was much more strongly affected by past glaciations. As a consequence, endemics are missing or are very rare in many European countries, while more widespread species were able to more easily recolonize these areas (Svenning and Skov 2007a; Schuldt and Assmann 2009). This leads to a stronger discrepancy between total and endemic species numbers in these countries and thus to lower within-taxon correlations.

For the western Palaearctic region, we might identify coarse centers of both total and endemic species richness for all taxa combined, based on reliable description data and the fairly high correlations between richness and endemism. While they do not necessarily contain the absolutely highest numbers for all taxa (as there is no complete overlap between richness and endemism hotspots and because of slightly deviating reptile diversity patterns), they nevertheless feature the highest possible collective diversity of invertebrates, vertebrates and plants (see also Gaston and David 1994; Dobson *et al.* 1997). With Italy, Spain and Greece as centers of highest diversity, our results incorporating species-rich carabid beetles very well correspond to the global hotspots network of Myers *et al.* (2000) considering primarily vascular plants. Supporting evidence that such hotspots might generally represent high numbers of invertebrates also comes from Meier and Dikow (2004), studying distribution patterns of predatory flies, and from our analyses of Chinese provinces (see below).

From the assumption that, among other factors, diversification processes play an important role in the patterning of diversity, one might expect correlations to be particularly high between endemic species. In most cases, coefficients were similar to those for total species richness. However, most notable for amphibians, especially in the western Palaearctic, congruence of endemism patterns with carabids and plants was lower than congruence of total species richness distributions. These findings might question the strength of the assumed impact of diversification processes on shaping distribution patterns. However, centers of endemism in the western Palaearctic are highly congruent between the four taxa, with Italy, Greece and Spain belonging to the top five countries with highest numbers of endemics in all taxa. Lower correlation coefficients for endemic compared to total richness are due to the fact that endemic amphibians (and also reptiles) are missing in most of central and Northern Europe, whereas endemic carabids and plants are also present (even though with few species) in these regions. Thus, while endemism centers strongly overlap, differences in the amplitude of latitudinal gradients (cf. Fig. 4.2) make correlations for endemic amphibians in part less strong than for total species richness, where latitudinal gradients are more similar to those of carabids and plants. For both carabids and plants, glacial refugia of some species farther north (i.e., in central Europe) than assumed for most species are known (Svenning and Skov 2007a; Drees *et al.* 2010). Araújo and Pearson (2005) point to a stronger dispersal limitation of amphibians (and reptiles) as compared to many plant species. Probably, these aspects of dispersal are reflected in the above patterns and especially influence the stronger range-restricted endemic species. Considering that endemism also reflects a part of beta diversity, showing the turnover of species with restricted ranges, these results undermine the importance of future studies analyzing beta diversity patterns in detail to relate these patterns to those of richness and endemism.

4.5.2 Eastern Palaearctic and Chinese patterns of carabid diversity

Results for carabids in the eastern Palaearctic region (without China) were similar to those from the western Palaearctic. Carabids showed high correlations with both total and endemic richness of amphibians and plants. Concordant with the latter two groups, relationships with reptiles were much weaker. While incomplete sampling in parts of this region cautions to careful interpretation of observed patterns, the high congruence with western Palaearctic patterns and consistent relationships between plants, amphibians, reptiles and carabids are striking and suggest relative robustness of the results. The most species-rich countries such as Japan and Nepal, which are also species-rich in vertebrates and plants, show the strongest annual increase in carabid numbers from new descriptions (Fig. 4.5). With complete data, we thus might actually expect correlations to be even higher for the eastern Palaearctic.

Altogether, even though we cannot exclude some degree of uncertainty due to the quality of the carabid data, the results imply that for the western as well as the eastern Palaearctic region (excluding China), patterns in the diversity distributions and cross-taxon relationships of carabid beetles can be adequately identified.

Interpretation of the cross-taxon relationships of carabid beetles in Chinese provinces is more complicated, as carabids are strongly undersampled and the influence of historical processes might differ from other parts of the Palaearctic (Qian *et al.* 2007). However, the strong undersampling of carabids in Chinese provinces suggests that the results showing only moderate to low congruence of carabid richness patterns with amphibian and plant diversity have only limited significance. Relationships between plant and amphibian richness across China were as strong as across the rest of the Palaearctic. Similarly, we observed high correlations between carabids and these taxa in the western and eastern Palaearctic, spanning the same latitudes as Chinese provinces. Based on these findings, we might also hypothesize relationships between carabids and plants or amphibians to grow stronger as completeness of carabid data in China increases.

Even with the so far available scant data on carabid beetles, Chinese provinces not only provide major centers of worldwide plant and vertebrate diversity (Myers *et al.* 2000). China probably qualifies as the most important center of overall diversity, including invertebrates, in the Palaearctic (see also Fig. S4.3 and S4.4 in Supplementary Material). With about 2,600 carabid species described so far (Löbl and Smetana 2003), it harbors about 25% of the approx. 11,000 species listed for the whole Palaearctic. The huge number of carabids newly described each year from China and the apparent undersampling in most provinces indicate that these figures are actually considerably higher than known to date. And even though we did not study complementarity of species between countries, high numbers of endemic carabids, vertebrates and plants highlight the uniqueness of the Chinese fauna and flora. Even at this coarse scale, these results have implications for conservation planning, giving weight to recommendations of strongly expanding conservation effort in southeast Asia and especially in China (Qian 2007; Soutullo *et al.* 2008).

4.5.3 Robustness of the results

Reanalyzing the data separately for large and small countries largely supports the robustness of our general findings. Correlation results were very similar between the total and large- and the total and small-country datasets in most cases. In part slightly higher correlation coefficients in the large-country analyses might indicate an influence of spatial scale. However, these results do not significantly affect the general findings of our analyses, as the total and the small-country datasets also yielded high and significant correlations in most of these cases, pointing to the same congruence patterns as the large-country dataset. Notable differences occurred in the small-country data of endemic amphibians (western and eastern Palaearctic) and reptiles (western Palaearctic) as well as in the small-province data of carabids in China. The latter is definitely due to the low quality of the Chinese carabid data and supports our view that the observed relationships for carabid beetles based on the current data available from China are not reliable. Low correlation results for endemic amphibians and reptiles in the western Palaearctic region do not really indicate a scale-dependence of our results. Rather, the spatial clustering of small countries in this region (they are concentrated at Central European latitudes; Schuldt and Assmann 2009) leads to small countries being completely (amphibians) or almost completely (reptiles) devoid of endemics. Thus, the results for small countries are geographically biased and not representative of patterns at the scale of this size category across the whole western Palaearctic (as is, in contrast, the data for large countries). Scale dependence thus only remains as an influential factor for the correlations of (endemic) amphibians with carabids and plants in the eastern Palaearctic. Large differences in scale are well known to affect cross-taxon correlations, with relationships generally reported to be stronger at larger scales (Grenyer *et al.* 2006; Wolters *et al.* 2006). However, even the small countries (mean size about 40,000 km^2) in our study reflect a rather large scale, which probably reduces effects of size differences between sampling units much stronger than in studies at finer resolutions and mostly (with some exceptions for eastern Palaearctic amphibians) yields robust results even with variable unit sizes.

4.5.4 Conclusions

Inevitably, studies comparing diversity patterns of different taxa will always suffer limitations from the resolution of available data and confounding factors which are difficult to control for (Whittaker *et al.* 2001; Hortal 2008). The coarse scale of our study limits its use in practical conservation issues requiring data from finer scales (Prendergast *et al.* 1993; Lovell *et al.* 2007). However, it is highly valuable in understanding general large-scale patterns of biodiversity, especially as geographically extensive analyses for hyperdiverse invertebrates will hardly be feasible at finer resolutions.

Data on invertebrates in the context of these biodiversity patterns is scarce. Our study shows that for a highly diverse insect taxon, large-scale patterns of species richness and endemism can exhibit a high degree of congruence with those known from plants or vertebrate taxa.

We showed that general latitudinal dependencies of distribution patterns of carabids, vertebrates and plants resulted in high cross-taxon correlations of diversity. Similar dependencies have been demonstrated for a variety of invertebrate taxa (but not for a comparable species-rich taxon as carabids), suggesting that our results might be relevant for many other invertebrates. Our analysis can only in part (looking at endemism distributions) touch on species composition patterns of the four taxa. One next step, which we are not yet able to analyze in detail, should be the comparison of beta diversity patterns to obtain a comprehensive picture of different components of diversity, as these components might differ regarding complementarity between taxa.

Confounding influences of different historical and evolutionary processes across the Palaearctic are rather low compared to global analyses (e.g., Qian and Ricklefs 2008) and are additionally accounted for by subdividing our study region into three parts. For the Palaearctic, our study indicates that hotspots of total and/or endemic richness previously derived from plant or vertebrate data can also include a large proportion of the diversity of invertebrate taxa. Although badly sampled for carabids, China emerges as a prominent Palaearctic hotspot not only for vertebrates and plants, but for invertebrate diversity as well. Focusing attention of future research and conservation effort on this region is thus highly recommended also from an invertebrate point of view.

Our study can only provide geographically limited information for one, though very species-rich, insect taxon. At the moment, the deficient data on invertebrate distributions in many parts of the world and also at finer grains in well-sampled regions makes analysis of further aspects of diversity patterns rather difficult. Yet, further studies are required to verify the observed patterns for other speciose invertebrates and for global analyses, as our focus on the Palaearctic excludes tropical regions. When adequate data is available, it will also be necessary to explore these relationships at smaller scales to obtain a comprehensive picture of the observed relationships (Whittaker *et al.* 2001). Still, by explicitly testing both species and endemic richness of a highly diverse insect taxon, our study extends the so far very limited knowledge on broad-scale invertebrate distributions and their relationships to better studied parts of the world’s biodiversity, analytically confirming hypothesized patterns that have scarcely been tested directly.

Acknowledgements

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4.6 Supplementary Material

Table S4.1. Increase in species numbers of carabid beetles in European countries/regions over the last decades. Compiled from checklists and monographs for countries with available data (for other countries, e.g. France, no updated checklists available or data difficult to compare between years due to differences in regions included in lists, e.g. Germany and neighboring countries differently defined and combined as "Central Europe"). Many newly recorded species in northern European countries are invasive species which have strongly extended their ranges over the last decades. Especially the most species-rich countries (e.g., Italy, Spain) still show some increase in species numbers, which, however, does not affect the overall spatial richness pattern for this region.

Country/Region	Old record	New record	References
Fennoscandia (incl. Sweden, Norway, Finland, Russian part of Kola Peninsula)	1948: 362	1985/86: 400[1]	Lindroth 1949: 423; Lindroth 1985; Lindroth 1986
Denmark	1841: 298	1983:314[1]	Bangsholt 1983
Britain and Ireland	1977: 342	2007: 355[1]	Luff 2007
Belgium	1950: 399	2008: 404[1]	Desender et al. 2008
Switzerland	1992: 505	2001: 509	Marggi 1992; Marggi and Luka 2001
Bulgaria	1988: 739	1995: 754[1]	Guérguiev and Guérguiev 1995
Italy	1993: 1290	2005: 1313	Brandmayr et al. 2005
Iberian Peninsula (Spain, Portugal)	1986: 972	2003: 1158	Jeanne and Zaballos 1986; Serrano 2003

[1] including several invasive species

[2] References:

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Table S4.2. Partial correlations (area included as covariable) of a) total and b) endemic species richness[a] between carabids, reptiles, amphibians and vascular plants across western (Europe/North Africa) and eastern (without China) Palaearctic countries and Chinese provinces **for large countries (>10^5 km²)**.

	Carabid beetles			Reptiles			Amphibians		
	West P.	*East P.*	*China*	*West P.*	*East P.*	*China*	*West P.*	*East P*	*China*
a) total species richness									
Vascular plants	0.89***	0.86***	0.48*	0.81**	0.37	0.87**	0.92***	0.56**	0.87***
Amphibians	0.95***	0.56*	0.47*	0.59*	0.4	0.84**			
Reptiles	0.60*	0.08	0.48*						
b) endemic species richness									
Vascular plants	0.91***	0.76***	-[b]	0.72*	0.24	-[b]	0.67*	0.64**	-[b]
Amphibians	0.74**	0.75**	0.61**	0.67**	0.74***	0.74***			
Reptiles	0.67*	0.22	0.72***						

[a] p-values corrected for spatial autocorrelation: ***p<0.001; **p<0.01; *p<0.07

[b] endemic plants not included in correlations across China, due to missing data

Table S4.3. Partial correlations (area included as covariable) of a) total and b) endemic species richness[a] between carabids, reptiles, amphibians and vascular plants across western (Europe/North Africa) and eastern (without China) Palaearctic countries and Chinese provinces **for small countries (<10^5 km²)**.

	Carabid beetles			Reptiles			Amphibians		
	West P.	*East P.*	*China*	*West P.*	*East P.*	*China*	*West P.*	*East P*	*China*
a) total species richness									
Vascular plants	0.80***	0.90*	0.28	0.72**	0.44	0.88*	0.76**	0.88*	0.80*
Amphibians	0.88***	0.82*	0.04	0.44*	0.28	0.90*			
Reptiles	0.57*	0.62	0.12						
b) endemic species richness									
Vascular plants	0.90**	0.86*	-[b]	0.45	0.40	-[b]	-[c]	0.30	-[b]
Amphibians	-[c]	0.36	0.35	-[c]	0.71*	0.92*			
Reptiles	0.31	0.36	0.55						

[a] p-values corrected for spatial autocorrelation: ***p<0.001; **p<0.01; *p<0.07

[b] endemic plants not included in correlations across China, due to missing data

[c] no endemic amphibians occurred in the small countries of the western Palaearctic region

Table S4.4. Within-taxon correlations (partial correlations with area as covariable) between total and endemic species richness[a] of carabids, reptiles, amphibians and vascular plants across western and eastern (without China) Palaearctic countries and Chinese provinces for a) large countries ($>10^5$ km^2) and b) small countries ($<10^5$ km^2).

	a) large countries			**b) small countries**		
Taxon	*West P.*	*East P.*	*China*	*West P.*	*East P.*	*China*
Carabid beetles	0.64*	0.92***	0.89***	0.37	0.88*	0.95***
Reptiles	0.63*	0.72**	0.72***	0.34	0.17	0.91*
Amphibians	0.49	0.86***	0.77***	-[c]	0.53*	0.93*
Vascular plants	0.73*	0.80***	-[b]	0.61*	0.94*	-[b]

[a] p-values corrected for spatial autocorrelation: ***$p<0.001$; **$p<0.01$; *$p<0.07$

[b] endemic plants not included in correlations across China, due to missing data

[c] no endemic amphibians occurred in the small countries of the western Palaearctic region

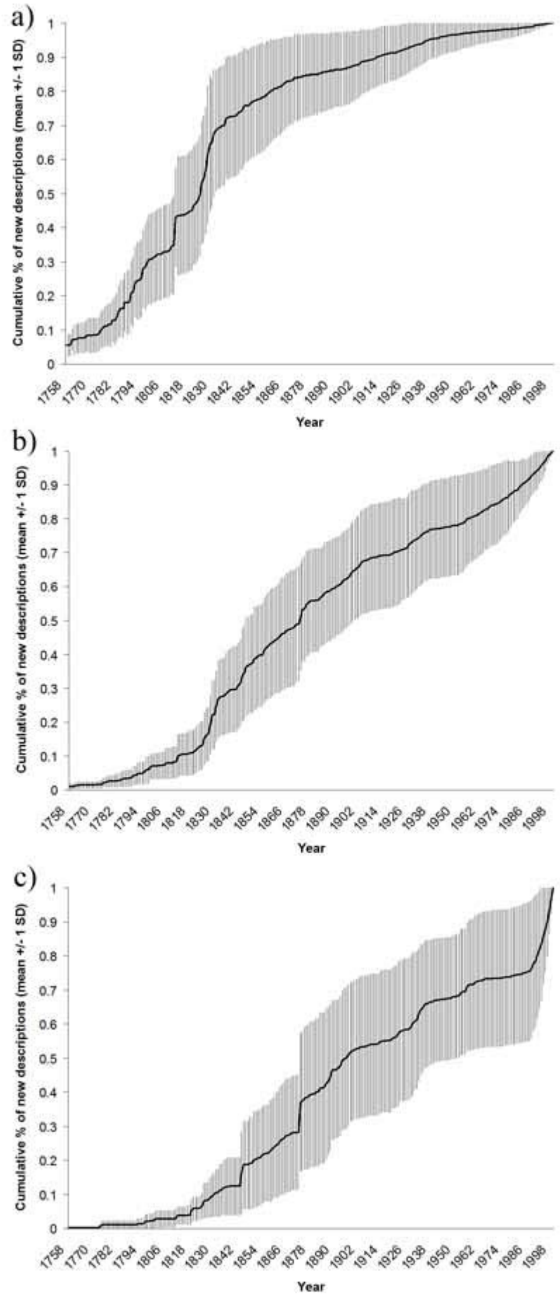

Figure S4.1. Species accumulation curves of the mean (+/- 1 SD) annual percentage of newly recorded carabid beetles per country in a) the western b) the eastern Palaearctic and c) Chinese provinces.

Figure S4.2. Subdivision of the Palaearctic (excluding Russia) into three subregions based on the completeness of carabid species inventories.

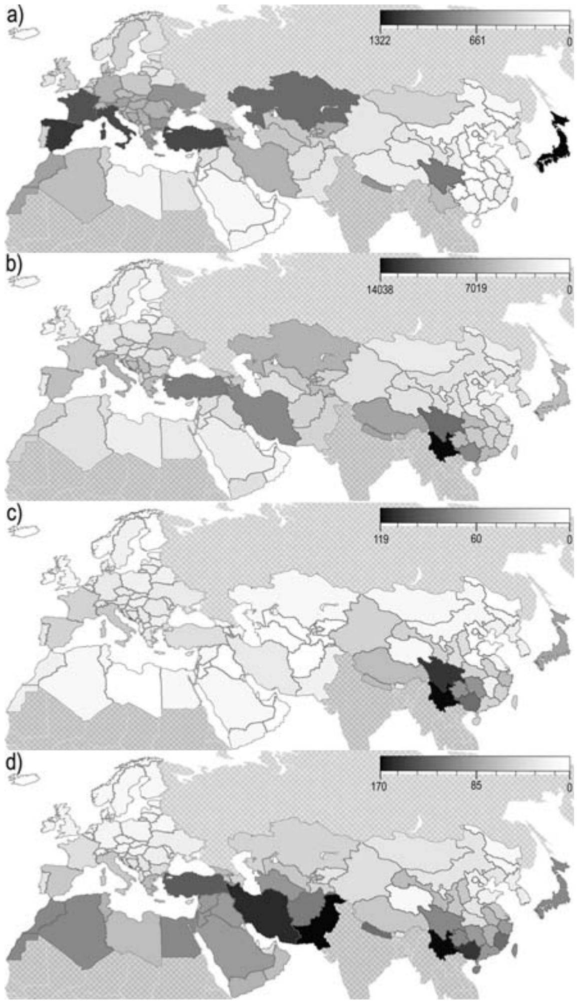

Figure S4.3. Patterns of total species richness of a) carabid beetles, b) vascular plants, c) amphibians, and d) reptiles for the whole Palaearctic, not divided by subregions (excluding Russia; checkered countries not included in the analysis).

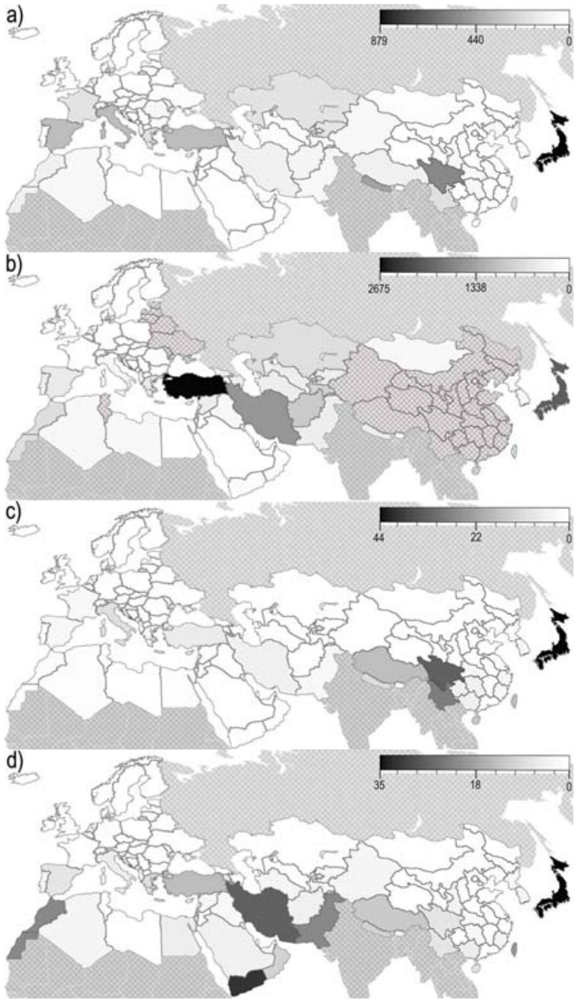

Figure S4.4. Patterns of endemic species richness of a) carabid beetles, b) vascular plants, c) amphibians, and d) reptiles for the whole Palaearctic, not divided by subregions (excluding Russia; checkered countries not included in the analysis: e.g., missing data for endemic plants in China/eastern Europe).

5 INVERTEBRATE DIVERSITY AND NATIONAL RESPONSIBILITY FOR SPECIES CONSERVATION ACROSS EUROPE – A MULTI TAXON APPROACH

Submitted manuscript

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5.1 Abstract

Invertebrates are important in ecosystem functioning, but with worldwide declining biodiversity, a lack of knowledge concerning their diversity distributions and adequate integration into conservation strategies has become evident. We analyzed congruence between species richness patterns of twelve invertebrate taxa across Europe and compared these patterns to those of so far predominantly studied vertebrates and plants. Species richness of most taxa peaked in southern Europe, making it possible to identify coarse centers of high collective diversity. However, the strength of covariation between diversity patterns strongly depended on the respective taxa, with ground beetles emerging as one of the invertebrate taxa well reflecting diversity distributions of many invertebrates, vertebrates and plants. Ants and plants showed similarly strong cross-taxon correlations. In contrast, correlations of vertebrates with invertebrates were in part less strong, questioning whether conservation strategies based on the former adequately account for diversity of invertebrates as a whole. Environmental variables were strongly related to species richness distributions and significantly influenced the strength of cross-taxon correlations. However, differences between taxa in the potential impact of current climate on diversity distributions indicate that future climate change might affect relationships between richness patterns of different taxa. Our findings raise attention to the necessity and also the use of incorporating invertebrates, for instance represented by the highly diverse ground beetles, into conservation decisions and biogeographical research. It also highlights the importance of single countries for European biodiversity and their responsibility for specific invertebrate taxa, urging for adequate consideration in the implementation of national and international conservation actions.

Keywords: Biodiversity conservation, climate change, cross-taxon correlation, hotspot, history, insect

5.2 Introduction

Invertebrates make up a large part of the world’s biodiversity (Stork 2007). They are essential in controlling and maintaining processes which are crucial for the functioning of ecosystems and the basis for economically important ecosystem services (Weisser and Siemann 2004). However, we are just beginning to fully understand the actual extent of their direct and indirect effects and lack adequate knowledge of the role of their diversity in this respect (Weisser and Siemann 2004). This is highly problematic, as the accelerating and to a large part human-induced global loss of biodiversity also heavily affects invertebrates (Samways *et* *al.* 2010). Integrating invertebrates into conservation strategies is thus imperative to effectively protect biodiversity and its influence on ecosystem functioning and services (Cassola and Pearson 2000; Lovell *et al.* 2007; Buse *et al.* 2008). So far, however, invertebrates are often ignored in conservation planning especially at larger scales, where decisions, such as the allocation of funds to regions of highest conservation priority, are largely based on the study of few taxa, mostly vascular plants or charismatic vertebrates (Myers *et al.* 2000; Lamoreux *et al.* 2006; Samways 2007). To what degree broad-scale diversity patterns of these taxa reflect diversity distributions of invertebrates has been studied only insufficiently (Pearson and Carroll 1998; Moritz *et al.* 2001; Whittaker *et al.* 2005). Moreover, there is also little information on how well spatial diversity patterns of the few invertebrates studied so far reflect broad-scale distribution patterns of the many other, unstudied invertebrate taxa (Samways 2007). This is to a large part due to insufficient documentation of distribution patterns of many invertebrates, which makes it hard to incorporate data of these taxa into analyses over large geographic extents (Hurlbert and Jetz 2007; Hortal 2008). Comprehensive data to identify continental or global networks and hotspots of diversity including invertebrates is hardly available at the small scales needed for reserve selection. Presently, diversity patterns of most invertebrate taxa can be analyzed most reliably only at coarser scales (Gaston and David 1994; Baselga 2008; Hortal 2008). However, this coarse-scale data can be used to map spatial patterns in the general distribution of diversity, to highlight regions of highest biodiversity for geographically extensive areas and to assess potential shifts in the distribution of diversity due to climate change (Myers *et al.* 2000; Ceballos and Ehrlich 2006; Kerr *et al.* 2007). In fact, many regional and global conservation strategies make use of such coarse-scale data even for plants and vertebrates (e.g., Olson and Dinerstein 1998; Myers *et al.* 2000; Lamoreux *et al.* 2006). Including invertebrate data and considering as many different organism groups as possible is necessary to design consistent conservation actions.

In contrast to many other regions of the world, for the western Palaearctic and especially for Europe a range of large-scale datasets for various invertebrate taxa have recently become available through taxon-specific research and projects such as the Fauna Europaea database (e.g., Van Swaay and Warren 1999; Baselga 2008; Finch *et al.* 2008; Pautasso and Fontaneto 2008; Ulrich and Fiera 2009). In our study, we use this excellent opportunity to analyze the degree of congruence between large-scale species richness distributions of twelve different invertebrate taxa as well as vascular plants and vertebrates across Europe. We aimed to determine to what extent spatial patterns in species richness of different unwinged or winged insect and other invertebrate taxa can be generalized and how far plants and vertebrates, as the focal taxa in most biodiversity studies, reflect those patterns. Generally, diversity patterns are assumed to covary fairly well between different taxa at large scales, whereas this covariation gets weaker at smaller scales (Wolters *et al.* 2006). Discrepancies between taxa at large scales might thus indicate general differences in the spatial diversity distribution of different taxa and a need for adequate conservation strategies (Leroux and Schmiegelow 2007). Our study highlights countries with a special responsibility for the conservation of invertebrate diversity in Europe. It can further identify taxa representative of other invertebrates, helping to put results of biodiversity research on single invertebrate taxa in a wider taxonomic context (McGeoch 1998; Moritz *et al.* 2001). In this regard, we are especially interested in the performance of ground beetles, as high species richness of this insect taxon has been shown to coincide with centers of plant and vertebrate diversity across the whole Palaearctic (Schuldt *et al.* 2009) and as it is often used as a biodiversity indicator also at smaller scales (McGeoch 1998; Gutiérrez *et al.* 2004). Climate change might play an important role in future diversity distributions and relationships between taxa (Kerr *et al.* 2007; Samways 2007). For this reason, we also check for cross-taxon correlations after accounting for environmental effects, such as current climate, on species richness patterns to assess to what extent correlations are influenced by current environmental conditions.

With the multitude of taxa analyzed, our study helps to better understand relationships between broad-scale invertebrate, vertebrate and plant diversity and provides important information for urgently needed conservation strategies with an extensive taxonomic scope.

5.3 Methods

5.3.1 Species richness and environmental data

We compiled species richness data of twelve invertebrate taxa (Table 5.1) as well as of reptiles, amphibians, mammals and vascular plants for 33 European countries. The data was obtained from the following, recently published macroecological studies on these taxa: spiders (Araneae: Finch *et al.* 2008), springtails (Collembola: Ulrich and Fiera 2009), mayflies, stoneflies and caddisflies (Ephemeroptera, Plecoptera, Trichoptera: Pautasso and Fontaneto 2008), dragonflies (Odonata: extracted from the Fauna Europaea database at www.faunaeur.org), aphids (Aphididae: Pautasso and Powell 2009), ants (Formicidae: Schlick-Steiner *et al.* 2008), butterflies (Lepidoptera-Rhopalocera: Van Swaay and Warren 1999), mosquitoes (Culicidae: Foley *et al.* 2007) and longhorn beetles (Cerambycidae: Baselga 2008). Schuldt *et al.* (2009) compiled richness data for ground beetles (Carabidae) from Löbl and Smetana (2003) and the well-documented data on reptiles (Uetz and Hallermann 2007), amphibians (IUCN 2006) and vascular plants (Walter and Gillett 1998;

Groombridge and Jenkins 2002) from reliable diversity assessments commonly used in biogeographical studies (Brooks *et al.* 2002; Grenyer *et al.* 2006). Mammal data was obtained from the World Resources Institute database (<earthtrends.wri.org>; cf. Qian and Ricklefs 2008).

Even though the documentation of large-scale invertebrate distributions has much advanced in recent years, detailed information allowing reliable analyses of spatial patterns on predefined scales and with the use of equal-area grids is not yet available for many invertebrate taxa (Hurlbert and Jetz 2007; Hortal 2008). So far, country-level data is most comprehensive and precise for most of these taxa and many studies have demonstrated its utility in the analysis of broad-scale macroecological patterns (e.g., Keil *et al.* 2008a; Qian and Ricklefs 2008; Schuldt *et al.* 2009). Countries also have the political responsibility of implementing conservation decisions, which further legitimates this scale of analysis from a biodiversity conservation point of view (New 2009). We accounted for differences in country size in our statistical analyses (see below) and excluded Andorra, Liechtenstein and Luxembourg due to their very small country size as well as Iceland due to its strong insularity. Previous studies have shown that this dataset yields robust results not affected by matters of scale (Schuldt *et al.* 2009).

Environmental variables hypothesized to influence large-scale species richness distributions, representing measures of ambient energy input, water-energy balance, productivity as well as climatic and habitat heterogeneity (Hawkins *et al.* 2003; Willig *et al.* 2003) were compiled from several sources. Climate data (mean annual temperature/precipitation, mean temperature of the warmest/coldest month, temperature seasonality [difference between warmest and coldest month], mean precipitation March-November, seasonality in precipitation [difference between driest and wettest month], frost frequency) was extracted from Mitchell *et al.* (2002) as country-averages from the high-resolution data of New *et al.* (1999). Mean annual potential and actual evapotranspiration (PET and AET) were calculated using Thornthwaite's method (Thornthwaite and Mather 1964; Black 2007). Range in elevation, reflecting both habitat heterogeneity as well as a historical signal related to survival and speciation (Jetz *et al.* 2004), and geographic midpoint coordinates were obtained from CIA (2008).

5.3.2 Statistical analyses

We used partial principal components analysis (PCA), including country-area as a covariable (Leps and Smilauer 2003), to highlight multivariate patterns in the geographic richness distribution of the 16 taxa in a multivariate analysis. Prior to the analyses, richness data and country area were $\log_{10}$-transformed to normalize their distributions.

In a more detailed analysis, we then used first-order partial correlations (Pearson's r) with area as a covariable (Legendre and Legendre 1998) to determine to which degree the single taxa studied each covary with the diversity of other invertebrates and, in a second analysis, with the diversity of only vertebrates and plants. For these analyses we used a set of 28 countries for which we had richness data for most taxa (excluding Albania, Croatia, Macedonia, Moldova and Serbia). Correlations with springtails were calculated for 21 countries, as data for several countries was missing or not reliable (Ulrich and Fiera 2009). Species richness patterns can covary to a large part due to a similar influence of environmental factors on diversity distributions. We used ordinary least squares regression in a backward elimination procedure to factor out the influence of significant environmental variables on spatial diversity patterns. As multicollinearity of predictor variables can bias regression outcomes, we excluded predictors that caused low tolerance values (<0.1) in the regressions due to high correlation with other variables (Quinn and Keough 2002). Polynomial terms of predictor variables were added in case of significant non-linear relationships with species richness data (Legendre and Legendre 1998). With the environmentally independent richness data obtained from the regressions we recalculated correlations to see to what extent relationships between taxa were retained after factoring out large-scale environmental effects.

We accounted for spatial autocorrelation in our data, which can bias the outcome of statistical tests (Diniz-Filho *et al.* 2003), by recalculating probabilities of our correlations using spatially corrected degrees of freedom according to Dutilleul *et al.* (1993). In the same way, we corrected the statistical significance of the regression analyses, correlating observed and predicted values of the regressions and using spatial corrections (Qian *et al.* 2007).

We used Canoco 4.5 (Ter Braak and Smilauer 2002) for PCA, SPSS 15 (SPSS, Chicago, USA) for partial correlations and regressions and SAM 3.0 (Rangel *et al.* 2006) for spatial corrections.

5.4 Results

Species richness of most invertebrate taxa analyzed generally showed an increase from northern Europe towards southern and south-eastern European regions (Figs 1 and 2). Deviations from these patterns could be observed especially in aphids, with high richness in Central Europe. The large-scale distribution of diversity of vascular plants, amphibians and mammals was comparable to that of most invertebrates, whereas reptiles showed a stronger increase in species numbers towards south-western Europe (Figs 1 and 2). The mean values of partial correlations between the single taxa and the studied invertebrate taxa, which were

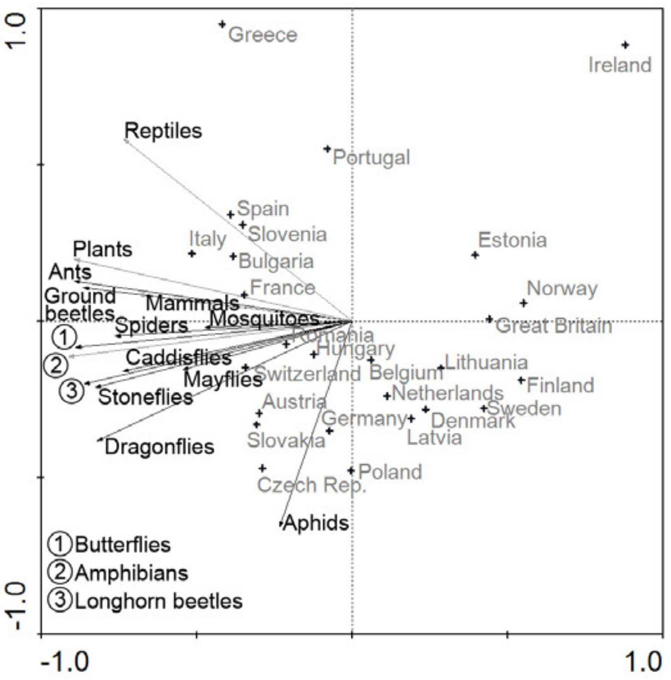

Figure 5.1. Ordination plot from partial PCA (area as covariable) showing the distribution of species richness of invertebrates (black arrows; springtails and Byelorussia, Croatia, Macedonia, Moldova, Serbia and Ukraine not included due to missing data for some taxa), vertebrates and vascular plants (grey arrows) across Europe. Standardized eigenvalues for first (horizontal)/second (vertical) axis are 0.58/0.08. Cumulative percentage variance of species data explained by both axes is 79.2%.

fairly high in most cases, support these findings of a general concordance in large-scale richness patterns of many taxa across Europe (Fig. 5.3a). However, a closer look at these direct comparisons at the same time reveals large variation in the taxon-specific strength of correlation with the richness patterns of the single invertebrate taxa analyzed. For instance, correlation coefficients between butterfly richness and the richness of other invertebrates varied between 0.19 and 0.85, coefficients involving longhorn beetle diversity ranged from 0.25 to 0.95 (Fig. 5.3a; Table S5.1 in Supplementary Material). In contrast, springtails (for which data on seven European countries was missing, though), stoneflies or mosquitoes showed lower variation. On average, coefficients for correlations with other invertebrates varied by an r of 0.56 within the single taxa, and even with the strong effect of deviating aphid patterns removed, the mean variation of Pearson's r was 0.39 (Fig. 5.3a; Table S5.1). Invertebrates which generally showed high concordance with richness patterns of many other invertebrate taxa were especially ants, spiders, stoneflies, caddisflies and ground beetles. Concordance with diversity distributions of other invertebrates was low for aphids, mayflies and mosquitoes. In general, correlations between amphibians or vascular plants and invertebrates were also fairly high, but showed strong variation depending on the invertebrate taxon considered (Fig. 5.3a). Reptile richness, and in several cases also mammal richness, was less strongly correlated with invertebrate diversity. In contrast, diversity of all vertebrate taxa was highly correlated with plant diversity and especially ants and ground beetles showed strong correlations with both vertebrate and plant diversity (Fig. 5.3c). Aphid diversity was only weakly related to the species richness of vertebrates or plants, whereas most other invertebrates had coefficients between 0.37 and 0.91 in correlations with amphibians, reptiles, mammals and plants (Table S5.1).

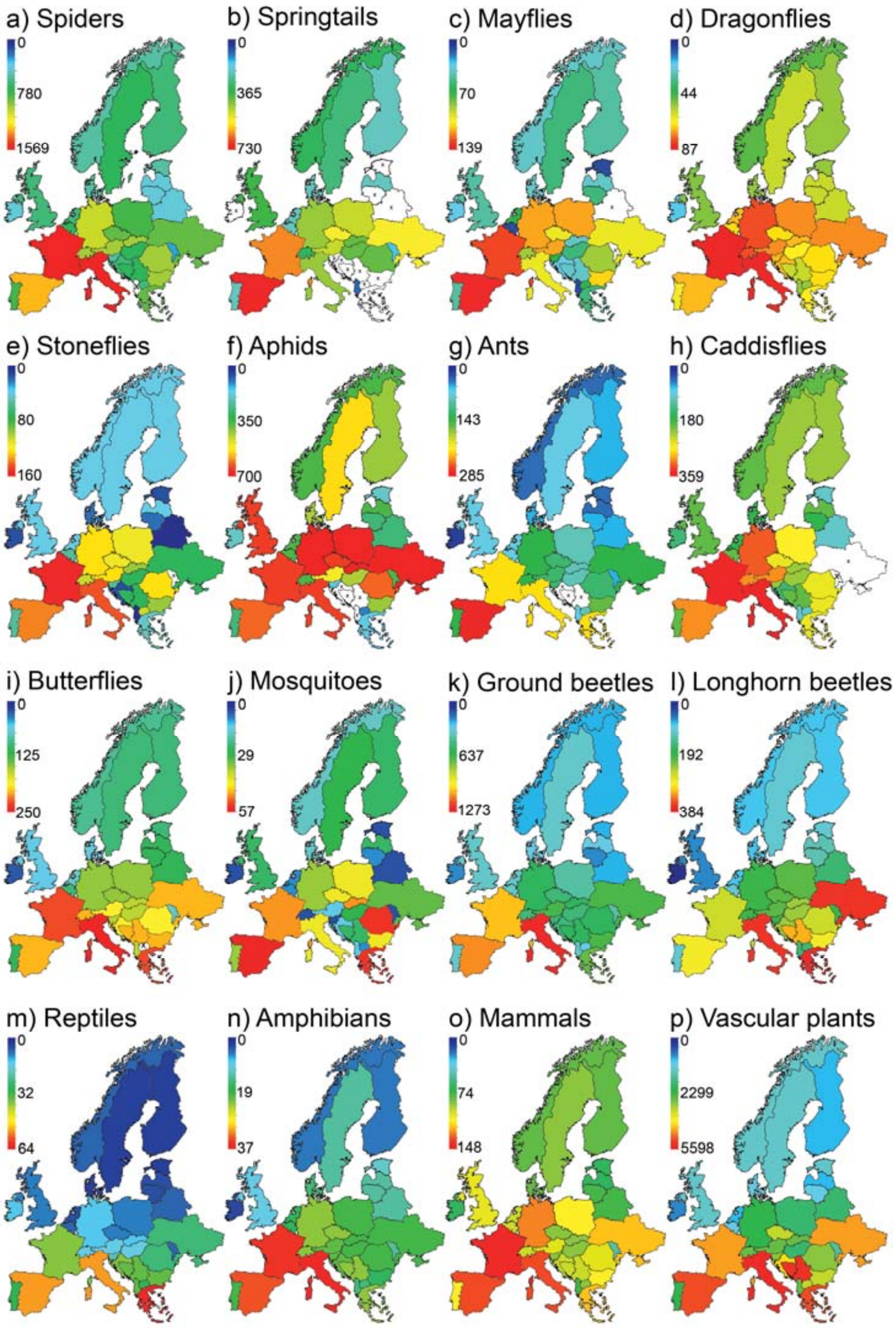

Figure 5.2. Patterns of species richness of the sixteen studied taxa across Europe. Countries with missing data are left white and are marked by "x".

To see to what degree similarities between diversity patterns of the different taxa are retained after accounting for the influence of environmental factors affecting species richness, we factored out significant environmental variables by multiple regression. Species richness of most taxa covaried with similar variables, most notably range in elevation and variables related to energy input (temperature) or water-energy balance (AET, temperature, precipitation) (Table 5.1). These variables accounted for 32-83% of the variability in the richness data of the different taxa. Correlations between invertebrate taxa were much lower with these variables factored out and in many cases non-significant after correcting for spatial autocorrelation (Table S5.1, Fig. 5.3b). Coefficients ranged from around zero to 0.90, with an average of 0.41. Especially spiders and ground beetles as well as ants, butterflies and dragonflies still showed relatively high and significant correlations with the environmentally corrected richness of many, but not all, other invertebrate taxa (Fig. 5.3b). Plants, amphibians and mammals were also most strongly related to the former taxa, whereas reptiles showed no or even negative relationships with invertebrates after factoring out environmental influences (Fig. 5.3b). These results are also reflected in the generally low but highly variable correlation coefficients between environmentally independent richness patterns of most invertebrates and vertebrates or plants (Fig. 5.3d).

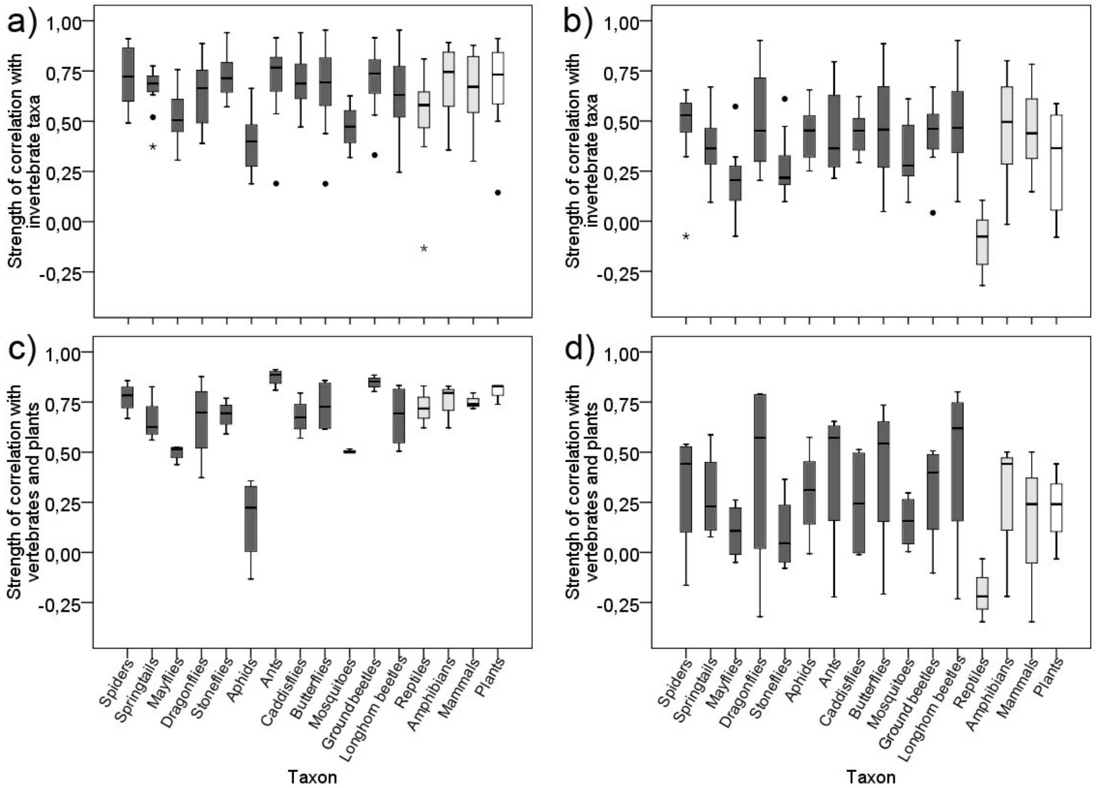

Figure 5.3. Variability in the correlation coefficients for the relationships between species richness of the single study taxa (invertebrates: dark grey, vertebrates: light grey and plants: white boxplots) and richness of a-b) (other) invertebrate taxa and c-d) vertebrate taxa and vascular plants; a) and c) show cross-taxon correlations with area as a covariable, b) and d) show cross-taxon correlations with the impact of environmental variables factored out.

Table 5.1. Minimal linear models (with coefficients of determination, F-values, degrees of freedom and spatially corrected probabilities) for the relationship between species richness of the studied taxa and environmental variables* across Europe. Variables ordered by decreasing t-statistics.

Taxon	Model	R^2_{adj}	F	df	p_{corr}
Spiders	elev+prec_mar_nov+log_area-mean_prec	0.77	26.5	4, 27	<0.001
Springtails	AET-AET^2+log_area+elev	0.69	17.4	3, 19	<0.001
Mayflies	elev+log_area	0.41	11.4	2, 28	<0.001
Dragonflies	elev+mean_warm-PET+prec_mar_nov	0.35	5.29	4, 28	0.002
Stoneflies	elev+AET+AET^2-seas_prec	0.66	22.5	3, 28	<0.001
Aphids	log_area	0.32	14.8	1, 28	0.001
Ants	elev+mean_warm-seas_prec	0.77	37.7	3, 27	<0.001
Caddisflies	elev+log_area	0.48	14.7	2, 28	<0.001
Butterflies	elev+seas_temp+mean_warm+AET	0.83	37.9	4, 27	<0.001
Mosquitoes	log_area+PET	0.50	17.3	2, 30	<0.001
Ground beetles	elev+mean_temp-seas_prec+seas_temp	0.73	22.3	4, 28	<0.001
Longhorn beetles	seas_temp+elev+mean_temp	0.69	24.3	3, 29	<0.001
Reptiles	PET+log_area	0.80	62.9	2, 30	<0.001
Amphibians	mean_temp+elev+seas_temp	0.51	12.2	3, 29	0.002
Mammals	elev+log_area+mean_temp-seas_prec	0.73	22.5	4, 28	<0.001
Plants	elev+mean_temp+seas_temp	0.81	46.4	3, 29	<0.001

*log_area: $\log_{10}$-transformed country area; elev: range in elevation; mean_temp: mean annual temperature; mean_warm/cold: mean temperature of warmest/coldest month; seas_temp: temperature seasonality; mean_prec: mean annual precipitation; prec_mar_nov: mean precipitation March-November; seas_prec: precipitation seasonality; AET: annual actual evapotranspiration; PET: annual potential evapotranspiration.

5.5 Discussion

5.5.1 Hotspot regions in Europe

We found high correlations between species richness patterns of many invertebrate taxa, and in many cases also high congruence with patterns of vertebrates and plants across Europe. On the coarse scale we considered, centers of high collective diversity can thus be identified, comprising high species richness of plants, vertebrates as well as of most of the invertebrates studied. These hotspots of biodiversity are located in regions of southern Europe (e.g., Italy) which are considered to form one of the world's 'hottest' hotspots of plant and also vertebrate diversity (Myers *et al.* 2000). Our study shows that such broad-scale centers of plant and vertebrate diversity can also integrate high diversity of invertebrates, a pattern often hypothesized but scarcely studied in detail so far (Samways 2007). Diversity distributions in Europe have been severely affected by Pleistocene glaciations and the hotspot regions we identified are known as glacial refugia of many animal and plant species (Hewitt 1999; Taberlet and Cheddadi 2002). Long-term climatic stability and the resulting potential for diversification and survival have probably made these regions persisting centers of high diversity of many organism groups in Europe (Jetz *et al.* 2004; Araújo *et al.* 2008). At least for our study region, the influence of history might in part be reflected by the strong covariation of diversity patterns of many taxa with range in elevation. While often used as a proxy of habitat heterogeneity, topographic variability can promote isolation and diversification and enable survival of species during past climate changes by offering suitable climate conditions along elevational gradients (Hewitt 1999; Jetz *et al.* 2004). Of course, the patterns we found could be strongly influenced by region-specific historical processes, as Europe features a particular geography and has a strong history of glaciations (Hewitt 1999). Yet, results for the highly diverse ground beetles from eastern parts of the Palaearctic indicate that these patterns might also hold for other regions less affected by glaciation events (Schuldt *et al.* 2009).

5.5.2 Diversity congruence between invertebrates, vertebrates and plants

However, even though almost all taxa (except aphids, for which species radiations in temperate regions might explain deviating patterns; Ortiz-Rivas *et al.* 2004) showed highest richness in southern Europe and a decrease towards northern latitudes, the strength of this gradient and congruence across different countries varied to some degree between taxa. Thus, while centers of diversity identified in our study capture high species richness of most taxa, they do not necessarily comprise highest richness of all organism groups (see also Prendergast *et al.* 1993; Gaston and David 1994). Besides range in elevation, variables related to energy availability and water-energy balance seem to have a strong influence on richness distributions of plants, vertebrates as well as invertebrates at large spatial scales (cf. Hawkins *et al.* 2003). However, the strength of the relationship with these variables and thus the impact of topography, energy and water balance differ between taxa, leading to differences in the spatial distribution and cross-taxon congruence of species richness. One reason for these deviations might be differences in dispersal abilities. For amphibians, plants and ground beetles, current distributions of many species in the western Palaearctic have been suggested to be limited by their dispersal power, with these species often being hindered to recolonize the more northern and formerly glaciated regions (Svenning and Skov 2007a; Araújo *et al.* 2008; Schuldt and Assmann 2009). In contrast, other taxa with a higher proportion of more mobile species (e.g., mammals and insect groups where most species are able to fly) have been able to expand their distribution ranges with changing climate and can thus show less steep latitudinal richness gradients (Hillebrand 2004). However, for most invertebrate taxa more detailed studies are needed to permit full evaluation of this potential mechanism. Further aspects, such as lifecycle (e.g., aquatic versus terrestrial), physiological requirements (e.g., dependence of reptiles on energy input) and evolutionary aspects (e.g., aphids with temperate species radiation), certainly also significantly influence congruence in richness patterns between taxa.

Factoring out environment strongly reduced the covariation between species richness of the different taxa, clearly showing the impact of environmental factors on the degree of diversity concordance. However, environment-corrected richness patterns of most invertebrates, vertebrates and plants were still moderately (even though non-significantly in many cases) correlated (see also Qian and Ricklefs 2008), indicating the influence of general evolutionary processes of diversification on current species richness patterns (Wiens and Donoghue 2004). Yet, climate and regional processes (e.g., glaciations) have significantly altered these patterns and their congruence between taxa (Qian and Ricklefs 2008). The varying effects of energy input and water availability on species richness patterns of different taxa indicate that future climate change could differently affect taxon-specific diversity distributions and thus shift congruence patterns between organism groups.

5.5.3 Evaluation of diversity patterns based on single taxa

Taxa which best represented current diversity distributions of both invertebrate and vertebrate/plant species richness on this coarse scale were especially ants, ground beetles and vascular plants, followed by e.g. spiders. In contrast, taxa such as mayflies, aphids, mosquitoes and others much less reflected diversity patterns of other invertebrates. In part, these patterns were retained also after factoring out environmental influences. Ground beetles have been shown to covary fairly well with both species richness and endemism patterns of plants and vertebrates across large parts of the whole Palaearctic (Schuldt *et al.* 2009). With accurate data on many other invertebrates missing for eastern Palaearctic regions, they might thus help to model broad-scale diversity patterns and hotspots of many other taxa.

While invertebrates like ground beetles or ants also well represented vertebrate diversity across Europe, vertebrates showed much higher variability in correlations and lower congruence with invertebrates (especially reptiles and in part mammals). Moritz *et al.* (2001) reported similar patterns on a smaller scale, with invertebrates better representing vertebrate diversity than vice versa. These findings might have implications for the evaluation of biogeographical patterns and conservation strategies based solely on data of specific vertebrate taxa (Grenyer *et al.* 2006; Lamoreux *et al.* 2006). Vertebrate data might in part be less reliable to estimate overall invertebrate diversity, even though they capture patterns of certain invertebrates quite well. However, these patterns are probably strongly scale-dependent. Small-scale studies in single countries or local reserves generally indicate that covariation between diversity patterns of different invertebrate taxa or congruence with vertebrate or plant diversity are often weak (Prendergast *et al.* 1993; Wolters *et al.* 2006;

Lovell *et al.* 2007), but the opposite has also been documented (e.g., Moritz *et al.* 2001; Schouten *et al.* 2009). Further studies are needed to clarify to what degree the patterns observed in our study also apply to diversity distributions across Europe at finer resolutions and to what extent regional conservation strategies can profit from biodiversity congruence between vertebrates, plants and different invertebrate taxa. At present, however, insufficient data for many invertebrates at small scales across geographically extensive areas, even across Europe, can introduce a high degree of uncertainty to such analyses (Hurlbert and Jetz 2007). In contrast, our country-level analysis is based on relatively robust data and provides information important for the evaluation and improvement of conservation efforts on a national and thus politically very relevant level.

5.5.4 Implications for conservation

Socio-economic and political factors influencing conservation decisions have strong effects on the national level. Moreover, it is the responsibility of national governments to implement national and international programs and treaties concerned with biodiversity conservation. With the multitude of organism groups analyzed and with an extensive incorporation of highly diverse invertebrates, our study allows us to point out countries with an especially high responsibility for the conservation of European biodiversity, without being restricted to the diversity of only vertebrates and plants as most previous studies. Highest species richness of the sixteen taxa is represented by only five countries (Table 5.2) and even after accounting for country area, especially Italy, but also France, Spain and Greece belong to the top five countries with highest species richness for most taxa (Table 5.2). Our findings highlight not only the general importance of these countries for overall biodiversity in Europe, but also their specific responsibility for those (invertebrate) taxa which reach their highest diversity in these countries. These taxa require far more consideration in national conservation legislation and in national strategies for European and international directives such as the EU Habitats Directive or the Convention on Biological Diversity. ‘Red listing’ species on the basis of their distribution and the threats they face is one strong means to implement national conservation needs (New 2009), but with the exception of butterflies (cf. Van Swaay and Warren 1999), such legislation is largely missing for invertebrates in many of the highly biodiverse southern European countries. Invertebrates are also strongly underrepresented in the above international conservation programs, often because of insufficient knowledge on their distributions (Samways 2007). Our study can help to formulate national priorities, which might be set for those invertebrate taxa, such as ground beetles for Italy, ants for Spain or longhorn beetles for Greece (Table 5.2), featuring an especially high diversity in the respective countries. With more fine-scaled data becoming available and for the analysis of single countries, future studies will go into more detail. With our analysis, we provide a basis for discussion and future research on the much neglected integration of invertebrates into biodiversity and conservation issues. Our study focuses on species richness, which is one of the most commonly used measures of diversity, but of course other aspects such as endemism and species turnover need to be addressed in the future, as far as the invertebrate data quality permits reliable analyses. However, the above countries have been shown to harbor high numbers of endemic animals and plants, so that these countries also play very important roles regarding aspects of endemism and beta-diversity (Myers *et al.* 2000; Baselga 2008; Schuldt *et al.* 2009).

Table 5.2. Countries with high responsibility for biodiversity conservation in Europe, based on the ranking of all European countries in species richness of the sixteen studied taxa.

Country	*Italy*	*France*	*Spain*	*Greece*	*Ukraine*	*others*[a]
Total number of species[b]	11 248	10 177	10 413	8 203	8 419	Austria and Czech Republic: high biodiversity of six taxa when accounting for country area; Bulgaria and Slovenia: high biodiversity of four taxa when accounting for country area
Country area (10³ km²)	294	546	500	131	604	
Highest (bold) or top five ranking in species richness of	**Caddisflies**[c] **Butterflies**[c] **Ground beetles**[c] **Amphibians**[c] **Vascular plants**[c] Spiders[c] Dragonflies[c] Stoneflies Aphids Ants[c] Mosquitoes Longhorn beetles[c] Reptiles[c] Mammals[c]	**Spiders**[c] **Dragonflies**[c] **Stoneflies** **Mammals**[c] Springtails Mayflies Aphids Ants[c] Caddisflies Butterflies Mosquitoes Ground beetles[c] Reptiles Amphibians[c] Vascular plants	**Springtails**[c] **Mayflies** **Ants**[c] **Mosquitoes** Spiders Stoneflies Butterflies Ground beetles[c] Reptiles Amphibians[c] Mammals Vascular plants	**Longhorn beetles**[c] **Reptiles**[c] Butterflies[c] Mosquitoes[c] Ants[c] Ground beetles[c] Amphibians Vascular plants[c]	**Aphids** Springtails Butterflies Ground beetles Longhorn beetles[c] Mammals Vascular plants	

[a] countries with lower total but relatively high species richness when accounting for country area
[b] sum over all sixteen studied taxa
[c] top five ranking also after accounting for country area (regression of log-transformed species richness on log-transformed country area)

5.5.5 Conclusions

Broad-scale patterns can be relevant for various aspects of biogeography and biodiversity conservation (Lamoreux *et al.* 2006; Kerr *et al.* 2007) and with the absence of more fine-scaled data these patterns are highly informative for many regions of the world. Our study shows that at coarse scales certain invertebrate taxa represent diversity of other invertebrates quite well and that they can also show high congruence with diversity patterns of so far predominantly studied plants or vertebrates. Even though limited to a rather coarse scale, our study raises attention to the necessity and the use of incorporating invertebrates into conservation decisions. It further highlights the responsibility of individual European countries, such as Italy, France and Spain, for their highly diverse invertebrate fauna, which needs much stronger consideration in the implementation of national legislation and international conservation actions. One of the taxa which show high diversity congruence with invertebrates as well as with vertebrates and plants, and which might thus be used to assess general patterns in invertebrate diversity distributions, are ground beetles. Probably, they capture patterns in the variation of species richness of different taxa quite well because their extraordinary species richness and high proportion of endemic species results in fine-scaled diversity distributions with high information content for other taxa (cf. Moritz *et al.* 2001). Of course, our study is restricted to the European subcontinent, but high correlations between ground beetles and vertebrates or vascular plants over large parts of the Palaearctic indicate that the results found might also be relevant for other regions (Schuldt *et al.* 2009). With a better availability of invertebrate data in the future, the patterns we found need to be reassessed at finer resolutions and should consider further diversity aspects, such as endemism and beta-diversity, to obtain a comprehensive picture of invertebrate diversity distributions and hotspots.

Acknowledgements

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5.6 Supplementary Material

Table S5.1. Correlation matrix for the relationships between species richness of the sixteen study taxa. Upper values from partial correlation with area as covariable, lower values (italicized) for correlations with environmental variables factored out.

	Spiders	Springtails	Mayflies	Dragonflies	Stoneflies	Aphids	Ants	Caddisflies	Butterflies	Mosquitoes	Ground beetles	Longhorn beetles	Reptiles	Amphibians	Mammals	Plants
Spiders	-	0.67*	0.51	0.72**	0.89***	0.49	0.86**	0.87**	0.72*	0.57*	0.91***	0.63*	0.67*	0.79**	0.85**	0.78**
Springtails	_0.46_	-	0.63*	0.52	0.77*	0.66	0.71*	0.69*	0.69	0.37	0.74*	0.75*	0.62	0.63*	0.56	0.83*
Mayflies	_-0.07_	_0.25_	-	0.47	0.71*	0.31	0.59*	0.76*	0.48	0.32	0.53	0.43	0.44	0.52*	0.53	0.51
Dragonflies	_0.50**_	_0.28_	_0.26_		0.67*	0.43	0.79***	0.66*	0.84***	0.39	0.71**	0.89***	0.37	0.88***	0.73**	0.67*
Stoneflies	_0.32_	_0.19_	_0.16_	_0.17_	-	0.57*	0.76**	0.94***	0.70*	0.63**	0.81**	0.59*	0.59	0.70**	0.77*	0.69*
Aphids	_0.66***_	_0.49_	_0.32_	_0.45*_	_0.30_	-	0.19	0.47	0.19	0.40	0.33	0.25	-0.13	0.36	0.30	0.14
Ants	_0.53*_	_0.36_	_0.30_	_0.66***_	_0.21_	_0.25_	-	0.77*	0.85**	0.54*	0.92***	0.79**	0.81**	0.89***	0.88**	0.91***
Caddisflies	_0.50*_	_0.33_	_0.57*_	_0.53_	_0.47*_	_0.62*_	_0.29_	-	0.68*	0.51*	0.80*	0.57	0.57	0.68*	0.80*	0.66*
Butterflies	_0.61***_	_0.46*_	_0.05_	_0.72***_	_0.17_	_0.32_	_0.73***_	_0.39_	-	0.44	0.79**	0.95***	0.62	0.83***	0.62	0.86**
Mosquitoes	_0.43*_	_0.10_	_0.22_	_0.20_	_0.61***_	_0.56**_	_0.23_	_0.52*_	_0.22_	-	0.57*	0.47*	0.50*	0.50*	0.52*	0.50*
Ground beetles	_0.56**_	_0.67***_	_0.04_	_0.36*_	_0.33_	_0.45**_	_0.51*_	_0.32_	_0.46*_	_0.39_	-	0.72*	0.80**	0.85***	0.85**	0.88***
Longhorn beetles	_0.56**_	_0.47_	_0.17_	_0.82***_	_0.10_	_0.46*_	_0.73***_	_0.43_	_0.89***_	_0.26_	_0.55**_	-	0.51	0.83***	0.59	0.80**
Reptiles	_-0.16_	_0.08_	_-0.05_	_-0.14_	_0.10_	_-0.01_	_-0.22_	_0.01_	_-0.21_	_0.00_	_-0.10_	_-0.23_	-	0.62*	0.72*	0.84**
Amphibians	_0.51**_	_0.31_	_0.26_	_0.81***_	_-0.02_	_0.57*_	_0.61***_	_0.48_	_0.73***_	_0.23_	_0.47*_	_0.80***_	_-0.22_	-	0.80**	0.83**
Mammals	_0.54**_	_0.15_	_0.18_	_0.73***_	_0.37_	_0.33_	_0.65**_	_0.51*_	_0.57**_	_0.30_	_0.33_	_0.69***_	_-0.35_	_0.50*_	-	0.74*
Plants	_0.37_	_0.59_	_0.03_	_0.25_	_-0.08_	_0.29_	_0.54*_	_-0.01_	_0.52**_	_0.08_	_0.51*_	_0.55**_	_-0.03_	_0.44*_	_0.241_	-

p-values corrected for spatial autocorrelation: ***p<0.001; **p<0.01; *p≤0.05.

6 GENERAL DISCUSSION AND CONCLUSIONS

This thesis is the first to bring together critical aspects of broad-scale distribution patterns and of the potential determinants of species richness and endemism for a highly diverse – both in terms of species richness and ecological variability – insect taxon over such a large geographic area. The main findings are in accordance with the hypotheses formulated in the introduction. They can be combined to a more comprehensive picture regarding broad-scale diversity distributions of this invertebrate taxon and contribute to a better understanding of general macroecological patterns across a broader spectrum of the global biodiversity than usually considered.

6.1 Macroecological insights from a highly diverse insect taxon

Broad-scale species richness and endemism distributions of carabid beetles can be modelled fairly well for large parts of the Palaearctic and show distinct spatial patterns. Both measures of diversity peak in southern regions of Europe and Asia and decline towards northern regions both in the western as well as in the eastern (including China) Palaearctic. In the western and central parts, species numbers also decrease towards the southernmost regions (North Africa, Saudi Arabia). These patterns appear to be strongly influenced by current climatic as well as historical processes, with their relative effects varying between widespread and restricted-range species. High covariation between current climate and the richness of widespread species and a strong signal of history emerging in the patterns of species with restricted distribution ranges might be attributable to differences in niche breadth and dispersal abilities of these species. The more mobile and widespread species (which might also have broader ecological niches) have probably been able to track climate changes relatively well, whereas dispersal limitation in many range-restricted species might be a key factor for the restricted distribution patterns of these taxa. Extinctions during past glaciations and subsequent disability to recolonize formerly glaciated areas have probably had a strong impact on the current distributions of these species (cf. Hewitt 1999). Closer analysis of the highly range-restricted carabid beetles adapted to belowground habitats reinforces these findings, which are also strongly supported by recent studies on vascular plants, amphibians and reptiles in this region (Svenning and Skov 2007b; Araújo *et al.* 2008). The present study is the first to address these important findings for a highly diverse invertebrate taxon.

Overall patterns of carabid beetles primarily reflect patterns of the widespread species, as these make up on average about 90% of the species present in the single countries sampled. Considering the strong covariation of species richness of widespread carabids with both measures of energy and water availability, it is not surprising that total richness decreases towards dry regions such as North Africa or Saudi Arabia and towards cold northern regions.

Present diversity patterns are often ascribed to a dominant impact of current climate on the spatial structure of diversity (Hawkins *et al.* 2003; Field *et al.* 2009), but studies need to go into more detail. Altogether, range-restricted species make up more than 60% of the total number of carabid beetle species in the western Palaearctic. In the analysis of total species richness, effects of history on a large part of total carabid beetle diversity are thus masked by the strong impact of widespread species on overall patterns (see also Rahbek *et al.* 2007). Ignoring these effects might miss essential information on driving factors and mechanisms underlying these patterns. Dispersal abilities and range sizes of species need to be taken into account in order to obtain a general understanding of the broad-scale distribution of biodiversity and the mechanism underlying these patterns (Rahbek *et al.* 2007; Szabo *et al.* 2009), especially as large parts of the global biodiversity are characterized low mobile and range-restricted species (Gaston 1996). This is also relevant to biodiversity conservation, as many species of conservation concern have small range sizes (Myers *et al.* 2000; Bonn *et al.* 2002; Lee and Jetz 2008). For the prediction of the future performance and shifts in current distribution patterns not only of these taxa, but of biodiversity in general, knowing the relative role of specific effects is essential (Araújo *et al.* 2008). This is of particular importance in light of global environmental change, and macroecological studies have much to offer in this respect (Kerr *et al.* 2007; Algar *et al.* 2009). With the study of potential determinants of the diversity of an extraordinarily species-rich insect taxon, this thesis provides a basis for further and more detailed analyses tackling these issues from an invertebrate perspective.

Carabid beetles are just one, even though extraordinarily species-rich, invertebrate taxon and comparison to other taxa is needed to put results into a wider taxonomic context. The analyses of Chapters 4 and 5 show that broad-scale species richness and endemism distributions of carabid beetles covary fairly well with patterns of many other invertebrate as well as with vertebrate and plant taxa. This congruence of richness distributions is probably due to a similar influence of environmental factors and historical processes on species richness patterns of many taxa at this broad scale (Hawkins *et al.* 2003; Hillebrand 2004). The results of this thesis show that general characteristics in the broad-scale distribution of species richness apply to a broad range of taxa, including so far only insufficiently studied but highly diverse invertebrates.

High congruence with other invertebrates indicates that distribution patterns of carabid species richness can be representative of broad-scale patterns of many other invertebrate taxa. Carabid beetles might thus help to better predict patterns in the diversity also of taxa for which accurate data is missing so far. Probably, carabids capture patterns in the variation of species richness of different taxa quite well because their extraordinary species richness and high proportion of endemic species results in fine-scaled diversity distributions with high information content for other taxa (cf. Moritz *et al.* 2001). Many other invertebrate taxa are less well-suited to reflect general patterns in diversity distributions, for instance because they show distributions deviating from more general patterns or because their low species richness does not adequately capture distribution patterns of more species-rich taxa (Moritz *et al.* 2001; Hillebrand 2004).

Still, general patterns in the broad-scale distribution of species richness can be identified for most of the taxa analyzed, including collective centers of diversity which comprise high species richness of plants, vertebrates as well as of many invertebrates. Devising such hotspots of high diversity has become a successful strategy which allows priority setting for biodiversity conservation at continental or global scales (Myers and Mittermeier 2003; Brooks *et al.* 2006). However, such prominent conservation strategies are largely based on a very limited proportion of global biodiversity and focus primarily on vascular plants and vertebrates (Whittaker *et al.* 2005; Brooks *et al.* 2006). This thesis provides insights which can contribute to a better integration of species-rich invertebrates into these strategies. While the availability of reliable data for most invertebrate taxa restricts the analysis to the comparison of species richness patterns across a subsection of the western Palaearctic, general trends can be extended to large parts of the whole Palaearctic and to patterns of both total end endemic species richness with the analysis of carabid beetles. The results from Chapters 4 and 5 indicate that in the Palaearctic hotspots of total and endemic richness previously derived from plant or vertebrate data (i.e., southern Europe and south-west China; Myers *et al.* 2000) can indeed also include a large proportion of the diversity of invertebrate taxa (see also Meier and Dikow 2004; Tixier and Kreiter 2009). While this pattern has often been hypothesized, it has scarcely been studied in detail so far (Samways 2007). The analyses in this thesis further show that these centers of high overall and endemic species richness are located in regions with an assumed long-term stability of environmental conditions which supported survival and, especially considering the effects of historical processes such as glaciations also in the surroundings of these regions, a high potential for diversification (cf. Jetz *et al.* 2004).

Especially China emerges as a prominent Palaearctic hotspot not only for vertebrates and plants (Myers *et al.* 2000; Tang *et al.* 2006), but also for invertebrate diversity. At the same time, the analyses show the necessity of more detailed biodiversity assessments for invertebrates such as carabid beetles and a stronger focus of conservation efforts in this region (see also Soutullo *et al.* 2008). Even many of the western Palaearctic countries harboring a high diversity of invertebrates miss adequate legislation for the conservation of invertebrates and need to more rigorously implement national (such as Red Lists; New 2009) and international (e.g., the EU Habitats Directive) conservation actions for these taxa. In this case, results from this thesis can help to formulate national priorities, which might be set for those invertebrate taxa with an especially high diversity in the respective countries.

Altogether, the results of this thesis provide information essential to a more general understanding of the distribution of biodiversity at broad scales. Of course, macroecological analyses are necessarily limited to correlative approaches and the causality of observed relationships is difficult to prove, as experimental manipulation is hardly feasible at the scales and geographic extents considered (Lobo *et al.* 2002). However, with thorough statistical analysis and careful evaluation of the results, macroecological studies have proven effective in advancing the fields of both basic and applied ecology in many aspects (Myers *et al.* 2000; Kerr *et al.* 2007; Field *et al.* 2009). This thesis extends the limited knowledge on patterns and drivers of invertebrate diversity and its relationship with so far predominantly studied parts of the global diversity. It can help to better integrate invertebrates into conservation planning at broader scales and identifies carabid beetles as an invertebrate taxon of high value for such broad-scale studies in ecology and conservation biology.

6.2 Future research needs

Despite a recent increase in attention to macroecological patterns of invertebrate diversity (e.g., Konvicka *et al.* 2006; Baselga 2008; Keil *et al.* 2008b; Ulrich and Fiera 2009), there is still much to learn. With more detailed data becoming available in the future, further aspects of invertebrate diversity distributions need to be addressed. Future studies should take into account additional characteristics of diversity, such as the spatial turnover in species (beta diversity). The analysis of endemism patterns in this thesis can only in part touch on this issue by showing the singularity of faunal elements across countries. Striving for a more global perspective and including matters of scale will also be necessary. Due to the available data, results of this thesis are restricted to the Palaearctic, which largely excludes tropical regions. Highest biodiversity of many taxa can be found in the tropics, but comprehensive data from these regions is scarce (Balmford and Long 1995; Stork 2007). Global datasets are available for species-poor tiger beetles or mosquitoes (Cassola and Pearson 2000; Foley *et al.* 2007), but even these still show strongly increasing species numbers in regions such as the Neotropics or southeast Asia (Cassola and Pearson 2000). With an improvement of the data quality also for the Palaearctic, the scale-dependence of the observed patterns for carabids can be assessed. Mechanisms determining diversity patterns at more local scales can differ from those at larger scales and cross-taxon correlations of diversity have often been found to be weaker at such local scales (Whittaker *et al.* 2001; Wolters *et al.* 2006), but the opposite has also been documented (e.g., Moritz *et al.* 2001; Schouten *et al.* 2009). At present, however, insufficient data for many invertebrates at small scales across geographically extensive areas, even across Europe, can introduce a high degree of uncertainty to such analyses (Hurlbert and Jetz 2007). Reliable data for invertebrates is currently still restricted in many cases to relatively coarse scales.

7 ADDITIONAL STUDY: DIVERSITY RELATIONSHIPS AT LOCAL SCALES

As mentioned in the introductory part to this thesis, different scales of perception can be examined and need to be combined in the study of biodiversity and its relationships and effects among different taxa (Rahbek 2005; Hortal *et al.* 2010). The diversity of invertebrates and its association with and effects on other parts of the faunal and floral biodiversity need more thorough investigation also at smaller scales (Samways 2007; Stork 2007). How broad-scale patterns of diversity scale down to more local levels is subject to intense and much debated research (Hillebrand and Blenckner 2002; He *et al.* 2005; Harrison and Cornell 2008). At local scales, biotic interactions are hypothesized to strongly affect diversity patterns (He *et al.* 2005; but see Kissling *et al.* 2008 for broad-scale effects). At the scale of ecosystems and local assemblages, the study of relationships between biodiversity and ecosystem functioning is one of the major topics which currently dominate ecological research (Hillebrand and Matthiessen 2009; Caliman *et al.* 2010).

Besides the study of macroecological patterns, an additional focus of my research is thus the analysis of invertebrate diversity also at these local scales. Studies on the relationship between the diversity of invertebrates and other taxa and its effects on processes within ecosystems are limited in many cases to relatively species-poor systems (e.g., Vehviläinen *et al.* 2007; Schuldt *et al.* 2008; Sobek *et al.* 2009). Actual effects of diversity are often difficult to separate from effects of species composition in these studies (Hooper *et al.* 2005). A stronger focus on species-rich ecosystems might help to overcome certain limitations of such studies (Unsicker *et al.* 2006). From a region identified also in the macroecological studies of this thesis to harbor an extraordinary species richness of invertebrates, vertebrates and plants and requiring much more attention in biodiversity research, this chapter provides first results of my studies on invertebrate diversity in a species-rich ecosystem. They were conducted in a highly diverse subtropical forest system of southeast China within the framework of the BEF (Biodiversity and Ecosystem Functioning) China project and are included here as additional material compiled during my thesis. They serve to illustrate the effects of biotic interactions on the relationship between the diversity of different taxa, using plant-insect interactions as a potentially important driver of these relationships with strong implications for research on biodiversity and ecosystem functioning (Baraza *et al.* 2007; Schmitz 2008).

TREE DIVERSITY PROMOTES INSECT HERBIVORY IN SUBTROPICAL FORESTS OF SOUTHEAST CHINA

Article in press

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7.1 Summary

1. Insect herbivory can strongly affect ecosystem processes, and its relationship with plant diversity is a central topic in biodiversity–functioning research. However, very little is known about this relationship from complex ecosystems dominated by long-lived individuals, such as forests, especially over gradients of high plant diversity.
2. We analyzed insect herbivory on saplings of ten tree and shrub species across 27 forest stands differing in age and tree species richness in an extraordinarily diverse subtropical forest ecosystem in China. We tested whether plant species richness significantly influences folivory in these highly diverse forests or whether other factors play a more important role at such high levels of phytodiversity.
3. Leaf damage was assessed on 58 297 leaves of 1284 saplings at the end of the rainy season in 2008, together with structural and abiotic stand characteristics.
4. Species-specific mean damage of leaf area ranged from 3 to 16%. Herbivory increased with plant species richness even after accounting for potentially confounding effects of stand characteristics, of which stand age-related aspects most clearly covaried with herbivory. Intraspecific density dependence or other abiotic factors did not significantly influence overall herbivory across forest stands.
5. *Synthesis*. The positive herbivory–plant diversity relationship indicates that effects related to hypotheses of resource concentration, according to which a reduction in damage by specialized herbivores might be expected as host plant concentration decreases with increasing plant diversity, do not seem to be major determinants for overall herbivory levels in our phytodiverse subtropical forest ecosystem. We discuss the potential role of host specificity of dominant herbivores, which are often expected to show a high degree of specialisation in many (sub)tropical forests. In the forest system we studied, a much higher impact of polyphagous species than traditionally assumed might explain the observed patterns, as these species can profit from a broad dietary mix provided by high plant diversity. Further testing is needed to experimentally verify this assumption.

Key-words: BEF China, biodiversity, ecosystem functioning, Gutianshan, resource concentration, succession, trophic interactions, Zhejiang

7.2 Introduction

Increasing awareness that the human-induced loss of biodiversity may affect important ecosystem services has triggered extensive research on the relationship between biodiversity and ecosystem functioning. Focusing primarily on the producer level, much progress has been made in understanding the effects of plant diversity on productivity and nutrient cycling (Hooper *et al.* 2005; Hector *et al.* 2007). However, ecosystem processes such as plant production or nutrient cycling are strongly influenced by complex interactions between trophic levels, which need to be considered adequately to fully understand diversity–functioning relationships (Thebault and Loreau 2006; Duffy *et al.* 2007). Invertebrates, representing the bulk of faunal diversity, play a major role in this respect (Weisser and Siemann 2004). An interaction of considerable importance is herbivory by phytophagous insects. This can have a profound impact on ecosystem processes, especially as herbivores may directly influence growth and species composition at the producer level (Coley and Barone 1996; Mulder *et al.* 1999; Hartley and Jones 2004; Frost and Hunter 2008).

Relationships between plant diversity and herbivores have been studied predominantly in agricultural and grassland systems (Andow 1991; Tonhasca and Byrne 1994; Scherber *et al.* 2006b; Unsicker *et al.* 2006). Many of these studies found a decrease in herbivores and herbivory with increasing plant species richness (e.g., Andow 1991; Hambäck *et al.* 2000; Unsicker *et al.* 2006) and often related this to resource-concentration effects as suggested by Root's (1973) hypothesis for specialized herbivores. With increasing plant diversity this hypothesis predicts a decrease in specialist herbivore loads (which can result in reduced herbivory), as host finding can be hindered by the increasing number of non-host plants (Root 1973). In contrast, other studies (often those incorporating much more diverse plots than usual intercropping experiments) report the opposite effect of increasing herbivore loads or damage with increasing plant diversity (e.g., Mulder *et al.* 1999; Otway *et al.* 2005; Scherber *et al.* 2006b). Colonization and population dynamics might explain such patterns in specialist herbivores (Otway *et al.* 2005), whereas generalist herbivores can directly profit from dietary mixing and increase their consumption in more diverse plots (Unsicker *et al.* 2008) or spill over from more-preferred to less-preferred plant species (White and Whitham 2000).

Recently, forests have come into the focus of the diversity–functioning debate as more complex systems dominated by long-lived individuals and providing crucial ecosystem services (Scherer-Lorenzen *et al.* 2005). Varying effects of plant diversity on herbivore loads or damage have also been reported for these systems (Jactel and Brockerhoff 2007; Vehviläinen *et al.* 2007; Sobek *et al.* 2009). However, analyses of forest diversity have so far mostly considered only low levels of plant diversity, often restricted to comparisons between monocultures and two- or three-species mixtures (reviewed by Jactel *et al.* 2005). In contrast to grassland systems, there is a lack of studies on plant–insect interactions over gradients of high tree diversity. Yet, this issue is of high concern for the extraordinarily species-rich subtropical and tropical forests, where herbivory is one of the dominant interactions (Coley and Barone 1996; Eichhorn *et al.* 2006). A wealth of studies in these species-rich forests have analyzed effects of distance and density dependence on the growth and survival of young trees neighboring conspecific adults (cf. Hyatt *et al.* 2003). However, differences in stand diversity have not been considered in these studies. While not generally confirmed as a community-wide effect (Hyatt *et al.* 2003), several studies found higher herbivory and mortality of saplings closer to adult trees of the same species (e.g., Blundell and Peart 2004; Norghauer *et al.* 2006), concordant with the hypothesis of Janzen (1970) and Connell (1971) predicting herbivore spillover from conspecific trees to neighboring saplings. This is also concordant with resource-concentration theory, as specialized herbivores are often considered to dominate herbivore communities in these forests (Barone 1998; Barone 2000; Dyer *et al.* 2007). These studies imply that there might also be an effect of tree diversity on herbivory at medium to high species richness of trees, as the abundance of single tree species is likely to decrease in forest stands with increasing tree diversity. Interestingly, to our knowledge, this issue has not been addressed directly for highly diverse subtropical forests.

Here, we analyze herbivory on saplings of ten tree and shrub species in three successional stages of semi-natural forest in subtropical China along a tree richness gradient from medium to high diversity (25-68 woody species per 900 m^2). We chose saplings because of their importance in maintaining high stand diversity and because they represent an especially vulnerable stage within the tree life cycle. We tested whether potential effects of tree species richness on insect herbivory are detectable even in such extraordinarily species-rich subtropical forests or whether only structural (e.g. stand density) and abiotic factors play an important role for herbivory at such high levels of phytodiversity. Strong effects of plant diversity on herbivory have especially been reported from studies incorporating monocultures or low-diversity treatments. However, whether these effects persist or level out in highly diverse plant communities (cf. Hooper *et al.* 2005) has not been studied sufficiently (Unsicker *et al.* 2006). Our study across a gradient of medium to high tree diversity provides insight into the herbivory–plant diversity relationship beyond the level approached in most previous studies, but which is very relevant for the phytodiverse (sub)tropical forests. In addition to richness effects, intraspecific density-dependent effects of the proportion of the target species in the tree and shrub layer on herbivore damage of saplings might emerge. We assessed the relative statistical support for the hypotheses that (i) both plot conditions and species richness or target species density, or (ii) plot conditions alone, or (iii) only richness and/or target species density alone are important predictors of the observed pattern in herbivory across the study plots. Considering the reported high specialization of many insect herbivores in similarly species-rich forests, we might expect a decrease in overall herbivore damage on saplings with increasing plant species richness across our diversity gradient. To our knowledge, our study is the first to explicitly test the effects of tree diversity on this important plant–insect interaction for a very species-rich subtropical forest ecosystem.

7.3 Materials and methods

7.3.1 Study site and plot selection

Our study was conducted in the Gutianshan National Nature Reserve (29°14’N, 118°07’E), Zhejiang Province, in southeast China. The reserve, established in 1975 as a National Forest Reserve, comprises about 8000 ha of semi-evergreen broad-leaved forest at an elevation of 300-1260 m a.s.l. It is characterized by subtropical monsoon climate, with a mean annual temperature of 15.3 °C and mean annual precipitation of about 2000 mm. The parent rock of the mountain range is granite, with soil pH ranging from 5.5 to 6.5 (Hu and Yu 2008).

In the context of the project “BEF (Biodiversity and Ecosystem Functioning) China”, 27 study plots of 30 × 30 m were established in the nature reserve (H. Bruelheide *et al.*, unpublished data) Plot locations were randomly chosen within strata of different plot age from suitable forest stands distributed across the whole nature reserve, limited by inaccessibility and steep topography (areas with an inclination >55° were excluded) of parts of the reserve. In total there were nine replicates of each young (about 10 to 20 years old), middle-aged (about 40 to 50 years old) and old (>70 years old) forest stands, differing in species richness of trees and shrubs. Within each of the three successional stages, species richness of woody plants similarly varied between plots from a minimum of 25-30 to a maximum of 55-68 species. The scale of foraging of insect herbivores might vary between species and thus also the scale of perception of plant diversity. To account for this, we checked diversity patterns and their relationship with herbivory levels also for smaller subsamples of trees within the study plots. Due to their status as a national nature reserve, the forest stands have not been managed over the last decades and thus have been subject to low anthropogenic influence.

7.3.2 Study species and herbivory assessment

Ten evergreen tree and shrub species were selected to study folivory on saplings in relation to tree species diversity and stand characteristics: *Ardisia crenata* Sims, *Camellia fraterna* Hance, *Castanopsis eyrei* (Champ. ex Benth.) Tutch., *Cyclobalanopsis glauca* (Thunb.) Oerst., *Eurya muricata* Dunn, *Lithocarpus glaber* (Thunb.) Nakai, *Loropetalum chinense* (R. Br.) Oliv., *Machilus thunbergii* Sieb. et Zucc., *Neolitsea aurata* (Hayata) Koidz. and *Schima superba* Gardn. et Champ. These ten species on average accounted for 40% of all individuals and 45% of the total biomass (as approximated by their local relative basal area) in the tree and shrub layer of the study plots. In each plot, a maximum of ten saplings of each species (with a height between 20 and 100 cm, which was recorded for each sapling as a covariate for the statistical analysis) were randomly sampled by crossing the whole plot along parallel transects. All species were present and sampled in most of the plots and missing values for single species in single plots were accounted for in the statistical analysis. The degree of foliar damage by insects, defined as the combined removal of photosynthetic tissue by leaf-chewing, mining and galling (and, if visible, sucking) insects, was assessed for all leaves of the saplings to estimate overall damage levels for each individual. Most folivory damage could clearly be attributed to feeding patterns caused by mainly herbivorous lepidopterans and several beetle families observed during the assessment. Only senescent leaves or leaves heavily damaged by fungi were excluded from the assessment.

Sampling was conducted once on each plot at the end of the rainy season in June-July 2008, recording standing levels of insect herbivory (Blundell and Peart 1998). While these are not necessarily representative of total annual herbivory, sampling at the end of the rainy season represents the degree of damage during one of the most important parts of the growing season, when water availability is best for plant growth, and when herbivory might thus have the greatest impact (Coley and Barone 1996; Hawkes and Sullivan 2001). Insect herbivore damage was estimated using percentage classes of herbivore damage (White and Whitham 2000; Scherber *et al.* 2006b; Vehviläinen *et al.* 2007; Sobek *et al.* 2009). Each leaf was assigned to one of six percentage classes of tissue removal (0%; <1%; 1-5%; >5-15%; >15-35%; >35%). The six classes were defined beforehand and appropriateness of the estimates was checked by analyzing samples of randomly collected leaves. The latter were digitally scanned and the degree of herbivory was determined using Adobe Photoshop CS3 to calculate pixel ratios of removed to estimated total tissue of each leaf (cf. Unsicker *et al.* 2006). Herbivore damage was assessed by one person only (A.S.) to prevent variability in estimation accuracy. In the statistical analyses, we used mean percentage of herbivory from the sampled and scanned leaves for each percentage class (0%; 0.5%; 3%; 9%; 23%; 55%).

7.3.4 Predictors of herbivore damage

To test whether tree species diversity or other environmental parameters are able to explain differences in herbivory between the 27 forest stands, we used variables representing important plot characteristics, recorded during the 2008 growing season. Species richness of woody plants was based on the complete inventory of all tree and shrub individuals >1 m height in the plots. Diameter at breast height (d.b.h.) was recorded for all trees >10 cm d.b.h. in the whole plot and for all individuals >3 cm d.b.h. in a central plot of 10 × 10 m. From this we calculated sums of species-specific basal area as well as the total basal area of all trees and shrubs per plot as approximations of plant biomass. To test whether the biomass of the respective species (i.e. the concentration of this specific food resource) affects overall herbivory, we used the local relative basal area of conspecifics in the tree and shrub layer of each plot (which was strongly correlated with the absolute basal area of the target species in the study plots: $r=0.94$, $p<0.001$), henceforth referred to for simplicity as 'dominance'. Variables representing structural and abiotic plot conditions were altitude, aspect (divided into linear north-south and east-west gradients), canopy and herb cover, stand age, tree density and total basal area per plot (Table 7.1).

7.3.5 Statistical analysis

Analyses were performed using R 2.7.1 (R Development Core Team 2008). Percentage data of insect herbivore damage were arcsine-square-root-transformed and dominance of target species was $\log_{10}$-transformed to account for non-normal or heteroscedastic error terms in the analyses. For our analyses, we used mean herbivore damage per individual nested within species to account for non-independent measurements (see below). We checked for significant non-linear relationships between herbivory and the predictors by analyzing second-order polynomials of the predictors.

Prior to the analysis of herbivory patterns, we conducted a dimension reduction in the set of explanatory variables related to stand structural and abiotic conditions (including stand age) by principal components analysis (PCA), as we were primarily interested in the main effects of a combined set of abiotic variables. Variable reduction by PCA allows extraction of a set of uncorrelated principal components (PC) which represent a large fraction of the variability of the original variables in reduced dimensionality (Legendre and Legendre 1998; Quinn and Keough 2002). The analyses were conducted on the standardized values of the variables using a correlation matrix. All PCs with eigenvalues higher than the mean were selected for further analyses. Structural and abiotic variables were reduced to a condensed set of three PCs. PC1 primarily represented stand age as well as age-dependent aspects of stand structure and biomass, together with age-related effects of other abiotic conditions (Table 7.1). PC2 and PC3 summed up further effects of abiotic characteristics (altitude, herb cover and aspect) related to growing conditions (such as temperature and light availability) independent of stand age. The three PCs together explained 73% of the variation in the structural and abiotic variables. Results from the analyses using the reduced set of PCs were compared to results using all eight PCs in a backward elimination procedure and to results of partial least-squares regression to verify that all relevant information for the relationships between the stand structural and abiotic parameters and herbivore damage was included in the reduced set of PCs (see Appendix S1 in Supporting Information for details on these additional methods and results). None of the omitted PCs significantly contributed to the herbivory pattern, and comparing our results to the alternative analysis using partial least-squares regression for dimension reduction did not yield deviating results (Appendix S1).

Table 7.1. Component loadings and eigenvalues of principal components (PC) selected from PCA reduction analysis on environmental variables (most influential variables in bold).

Variable	*PC 1*	*PC 2*	*PC 3*
Stand age	**0.88**	-0.24	-0.11
Total basal area	**0.82**	-0.15	-0.07
Tree density	**-0.72**	**0.56**	-0.14
Canopy cover	**-0.65**	0.23	0.24
Herb cover	-0.47	**-0.70**	-0.27
Altitude	0.45	**0.57**	**-0.51**
Aspect (East-West)	0.47	**0.50**	-0.06
Aspect (North-South)	0.41	0.14	**0.81**
Cumulative proportion explained (%)	*40.1*	*59.1*	*72.7*
Eigenvalue	*3.21*	*1.52*	*1.10*

Different insect herbivores might have different scales of perception of plant diversity. To assess whether diversity patterns and the species richness–herbivory relationship are consistent across different spatial scales at a subplot level, we analyzed correlations between species richness of woody plants at the plot level and rarefied richness (for random draws of 20, 50, 100 and 150 plant individuals, respectively), as well as correlations between herbivory levels and the different richness measures. Rarefied values were calculated with the vegan package in R (Oksanen *et al.* 2008).

Herbivory patterns were analyzed using linear mixed-effects models (Pinheiro and Bates 2000) in an information theoretic approach (Burnham and Anderson 2004) with the package lme4 in R (Bates and Meaechler 2009). A maximal model, with all variables and interactions of interest, was fitted including stand age and structure (PC1 from the above

PCA), abiotic plot conditions (PCs 2 and 3), species richness of trees and shrubs, and dominance as fixed effects. We also included sapling height and the total number of leaves of each sapling to take into account sapling apparency or dilution effects on herbivory levels owing to differences in size or leaf number. As we were interested in the potential influence of stand age on richness or dominance effects, we also included the interactions between stand age and richness/dominance. Species identity, with individuals nested within species, and plot were considered as crossed random effects, taking into account the hierarchical structure of the data (Pinheiro and Bates 2000). We also tested for interactions between species identity and species richness of woody plants, comparing model fit with this interaction included to model fit without this interaction in the random effects structure with a likelihood ratio test (Pinheiro and Bates 2000). The following three hypotheses were considered to explain differences in herbivore damage across plots: (a) both plot characteristics and richness/dominance, (b) plot characteristics only or (c) richness and/or dominance alone are important predictors of herbivory. As the number of predictors was small and any combination of the fixed variables might influence the degree of insect herbivory, we used an ‘all-subsets’ approach with information-theoretic selection criteria (Quinn and Keough 2002; Burnham and Anderson 2004), including the age:richness/dominance interactions for those cases where both stand age and richness/dominance were present. Model fit was assessed and models were ranked based on Akaike’s Information Criterion (AICc for small sample sizes; Burnham and Anderson 2004). For each of the three hypotheses above, we selected the three best-fit models, i.e. those with lowest AICc values, and compared their performance calculating ΔAICc as the difference in AICc between the candidate and the best-fit model. Models with $\Delta AICc \leq 2$ are considered to be equally likely, while larger values indicate a lack of fit and lower explanatory power relative to the best model (Burnham and Anderson 2004). In case of differences ≤ 2, the model with the smaller number of predictors was preferred. The package languageR with the function pvals.fnc for mixed models was used to assess the significance of the model parameters (Baayen 2009), with p-values based on Markov chain Monte Carlo sampling (Baayen *et al.* 2008). Model residuals were checked for modelling assumptions of normality and homogeneity of variances. While mixed models are a powerful tool to deal with missing values (Pinheiro and Bates 2000) and species-specific effects can be tested with interaction terms, we additionally checked for a potential bias introduced by differential abundance of sapling species in the samples along the diversity gradient. The data were reanalyzed after excluding *C. glauca*, the only species showing higher relative abundance in species-rich compared with species-poor plots.

7.4 Results

In total, 58 297 leaves from 1284 saplings of the 10 study species were sampled. Mean herbivory of saplings differed between species, with highest damage levels (13-17%) in *C glauca* and *L. glaber* and lowest levels (3-4%) in *A. crenata* and *C. fraterna* (Fig. 7.1a). Mean overall percentage of herbivory for the ten species was 8%. Herbivory generally increased from the young to the older plots (Fig 1b). Total species richness of the plots was strongly correlated with rarefied richness at all levels (Pearson correlations: r=0.72/0.80/0.86/0.88 for correlations with mean richness of 20/50/100/150 plant individuals; p<0.01 in all cases). Similarly, mean herbivory levels were strongly related to species richness of woody plants at all levels (r=0.52/0.56/0.59/0.60; p<0.01 for mean richness of 20/50/100/150 plant individuals and r=0.48; p<0.05 for species richness at the plot level), indicating that diversity and herbivory relationships at smaller scales are well represented by our analysis at the plot level.

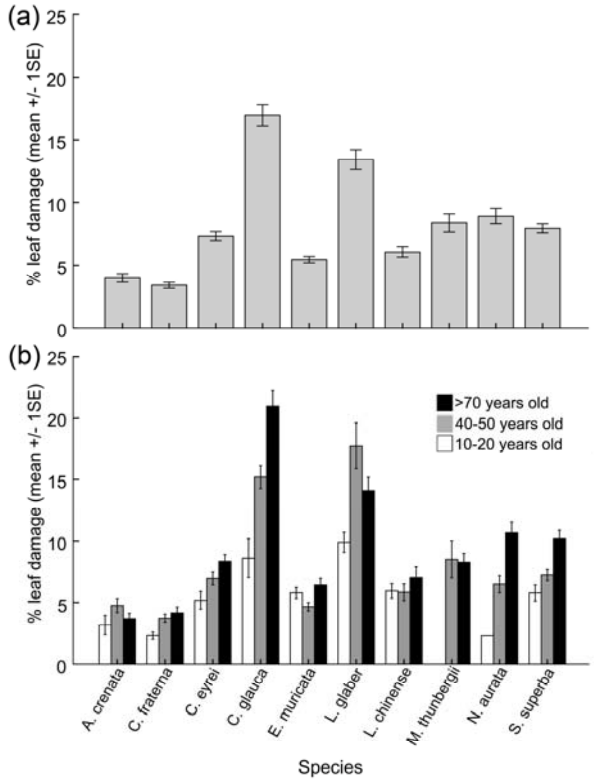

Figure 7.1. Mean percentage (+/- 1 SE) of leaf consumption for saplings of the ten study species (*Ardisia crenata, Camellia fraterna, Castanopsis eyrei, Cyclobalanopsis glauca, Eurya muricata, Lithocarpus glaber, Loropetalum chinense, Machilus thunbergii, Neolitsea aurata* and *Schima superba*): (a) mean values per plot, (b) mean values per age class.

Mixed-effects modelling showed a substantially better fit of models including both plot characteristics and species richness rather than only one of these (Table 7.2). The best-fit models contained both stand age and structure (PC 1, which primarily reflects stand age-related differences in biotic and abiotic conditions) and species richness as predictors, and the model with only these two variables had the lowest AICc. Models with a ΔAICc ≤ 2 additionally included one more predictor, either dominance or the PC1–richness interaction. However, the estimated effects of these variables were not significantly different from zero (Table 7.2). The same was true for effects of abiotic plot conditions other than stand age-related effects and of dominance or sapling height in the models considering only plot characteristics or only richness and dominance. Stand age and structure (PC1) and species richness were the most important parameters in these models as well. There was no effect of potential interactions between species identity and species richness. Including this interaction in the random effects structure did not significantly improve model fit (Likelihood ratio test with χ^2=4.7; d.f.=2; p=0.1).

Table 7.2. Results from linear mixed-effects modelling. For each predictor set (a-c), the three best-fit models (lowest AICc) are shown, with regression estimates (± SE) for the predictors included*. ΔAICc is the difference in AICc values between the candidate and the overall best-fit (in bold) model. Estimated effects of predictors in italics are not significantly different from zero (based on Markov chain Monte Carlo sampling).

Model	AICc	ΔAICc
a) Plot characteristics and species richness		
0.0116 (±0.0031) PC1+0.0012 (±0.0005) richness	**-2555.8**	**0**
-0.0028 (±0.0144) PC1+0.0011 (±0.0006) richness+0.0004 (±0.0004) PC1:richness	-2555.0	0.8
0.0115 (±0.0030) PC1+0.0012 (±0.0005) richness*-0.0030 (±0.0036) dominance*	-2554.3	1.5
b) Only plot characteristics		
0.0126 (±0.0032) PC1	-2552.6	3.2
0.0126 (±0.0032) PC1*-0.0022 (±0.0054) PC3*	-2550.7	5.1
0.0126 (±0.0032) PC1*-0.0043 (±0.0119) sapling height*	-2550.6	5.2
c) Only species richness and dominance		
0.0015 (±0.0006) richness	-2545.8	10.0
0.0015 (±0.0006) richness*-0.0037 (±0.0036) dominance*	-2544.8	11.0
0.0015 (±0.0006) richness*-0.0041 (±0.0119) sapling height*	-2544.2	11.6

*PC1: Principal component 1 from PCA dimension reduction (Table 7.1), primarily reflecting stand age-related differences in biotic and abiotic conditions; PC3: Principal component 3 (see Table 7.1); richness: species richness of trees and shrubs; PC1:richness: interaction between stand age/structure and species richness

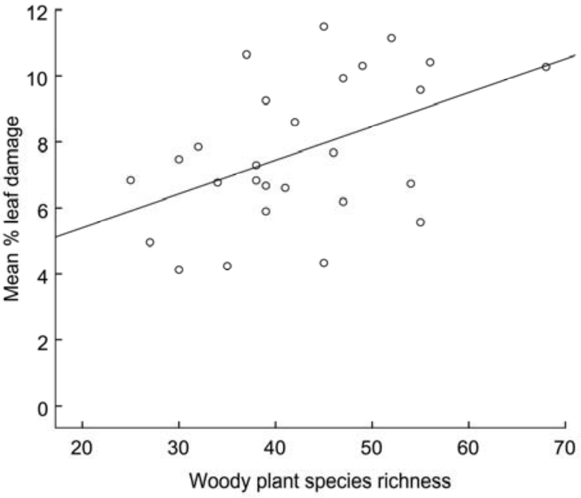

Figure 7.2. Mean percentage of leaf damage per plot due to insect herbivory in relation to species richness of trees and shrubs across a diversity gradient of 27 study plots in subtropical China (β=0.001; p=0.025).

Relative abundance of most sapling species was constant over the samples of the 27 plots. Only the proportion of *C. glauca* saplings significantly increased with increasing species richness of the plots ($F_{1,25}$=12.1; p=0.001), whereas the proportion of *L. chinense* decreased ($F_{1,25}$=5.2; p=0.031). As *C. glauca* featured highest damage levels of all species studied (whereas *L. chinense* showed medium herbivore damage; Fig. 7.1a), the data were reanalyzed after excluding *C. glauca* saplings. However, mixed-model results did not differ from those of the overall analysis (see Appendix S2). There was also no significant effect of sapling proportions on herbivory levels for any of the species (not shown).

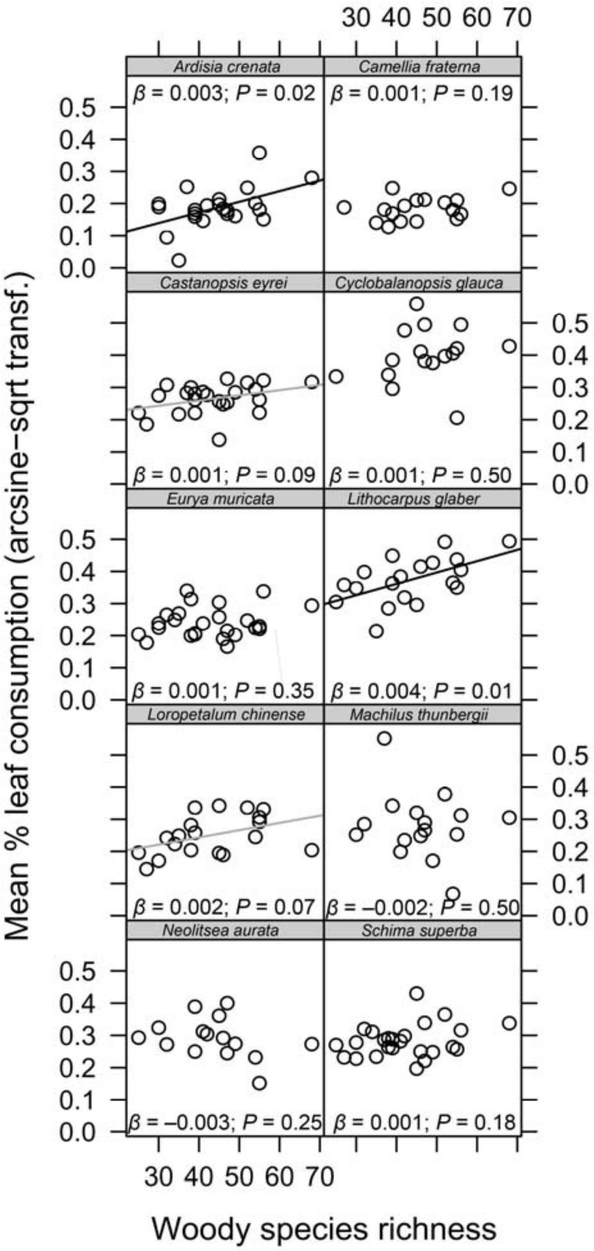

Figure 7.3. Relationship between herbivore damage of the single study species (arcsine-square-root-transformed) and species richness of woody plants across the diversity gradient of 27 study plots in subtropical China. Regression slopes (β; with their probabilities p) from single regressions show sign and magnitude of the relationships, regression lines indicate significant (black) and close to significant (grey) relationships.

The best mixed model in our analysis, with species richness and stand age and structure (PC1) as fixed effects, accounted for 41% of the variation in the herbivory data. Species identity accounted for most of the variation in the random-effects structure (38.7% as compared to the plot effect of 3.8%). This strong intercept effect underlines the large differences in species-specific susceptibility to insect herbivory (cf. Fig. 7.1a). The degree of herbivory over all species was positively related to both stand age and structure and woody plant species richness. As can be inferred from this model, however, stand age and structure had a stronger impact on herbivore damage than species richness. This is also shown by the substantially smaller AICc value for the model including only stand age and structure compared to the model including only richness (Table 7.2). With respect to plant species richness, our model predicts an increase in herbivory of about 1% with an increase in richness by 10 tree and shrub species (Table 7.2, Fig. 7.2). Across the richness gradient of the 27 study plots, this amounts to an overall increase in mean herbivore damage of about 5% from the least to the most species-rich plots, which is a doubling of mean herbivory over all species from about 5% to 10% (Fig. 7.2). While mixed-model results indicate a general and significant overall increase in herbivore damage, single regressions for the study species show that this pattern was most pronounced for *L. glaber* and *A. crenata* and also for *C. eyrei* and *L. chinense* (Fig. 7.3). Even though not significant in the single species analyses, most other species also showed a tendency towards increasing damage with higher stand diversity, with regression estimates of β=0.001 close to the overall mixed-model estimate. Only patterns in *M. thunbergii* and *N. aurata* slightly deviated (Fig. 7.3). However, this did not have an effect on the overall pattern, as is also shown by the better fit of the mixed model excluding separate parameters for each species through a species-richness interaction. Significance levels in the single regressions must be interpreted with care, since they are subject to multiple testing. However, while with α=0.05 we would expect one species out of 20 to show a significant effect by chance, our analysis finds two significant relationships in 10 species, which additionally have the same direction. The mixed-model results further confirm the general positive relationship between plant diversity and herbivory.

Measures of rarity could not explain the species-specific susceptibility to herbivory: the mean rate of herbivore damage of the ten species analyzed was not related to their general dominance in the studied forest ecosystem (i.e. the basal area each species accounted for across all 27 study plots) (Pearson correlation r=-0.03; p=0.93).

7.5 Discussion

While observational studies have to take a range of potentially confounding factors into account, they have the advantage of providing near-natural conditions and fully established communities of animals and plants with a multitude of interactions that might not have developed in the same way in artificial experiments (Scherber *et al.* 2006b; Unsicker *et al.* 2006; Leuschner *et al.* 2009). This is especially important for the study of ecosystems dominated by long-lived individuals, such as forests, where successional processes can strongly influence the outcome of analyses (Leuschner *et al.* 2009). With a paucity of long-term experimental setups studying the relationship between biodiversity and ecosystem functions in forests, observational studies provide essential insights into the role of biodiversity in influencing processes and interactions in these ecosystems (Scherer-Lorenzen *et al.* 2005; Leuschner *et al.* 2009).

7.5.1 Effects of plant species richness on herbivory

Our study of foliar damage on saplings in subtropical forests shows that tree species diversity can be important in influencing insect herbivory even in an extremely species-rich forest ecosystem. Interestingly, our results indicate an altogether positive relationship between plant diversity and herbivory in these forest stands. This is in contrast to many studies reporting a decrease in herbivory with increasing plant diversity both in forests and in other systems (Andow 1991; Hambäck *et al.* 2000; Massey *et al.* 2006; Unsicker *et al.* 2006; Jactel and Brockerhoff 2007; Sobek *et al.* 2009). However, these studies usually considered gradients of species richness in plant communities much less diverse than those of our study, the latter of which feature a relatively high species richness already in the least diverse plots. Hypotheses to explain the pattern reported in the above studies comprise those on resource-concentration and on predator effects formulated by Root (1973). In many of the studied systems, specialized herbivores are considered to cause the largest amount of damage to plants. The resource-concentration hypothesis, originating from agroecosystem studies, but often also considered relevant for other systems, predicts lower specialist herbivore loads (and, as generally assumed, lower resulting plant damage) in more diverse plant communities. Specialists might have difficulties locating their hosts in more diverse stands due to reduced host plant abundance and distracting effects (e.g. optical, olfactory) of non-host plants. Herbivore communities of the highly phytodiverse forests occurring in the tropics and subtropics are also typically considered to be dominated by specialized, oligophagous species with a much stronger impact on damage levels than polyphagous species (Erwin 1982; Barone 1998; Barone 2000; Dyer *et al.* 2007). Considering the above theory, we might thus have expected lower herbivore damage in the more diverse stands of our study.

However, the fact that we found the opposite pattern is consistent with a range of recent studies (Mulder *et al.* 1999; Prieur-Richard *et al.* 2002; Scherber *et al.* 2006b; Vehviläinen *et al.* 2007). In these studies (mainly of grassland systems), this positive effect was also repeatedly found over higher gradients of plant diversity than usually considered (where diversity effects often depend on the identity of the plants added to a system; cf. Unsicker *et al.* 2006). One reason for this pattern could be a higher impact of generalist, polyphagous insects and a comparatively lower influence of specialist herbivores in these systems (Basset 1999; White and Whitham 2000; Jactel and Brockerhoff 2007). Polyphagous herbivores can profit from and are able to cause greater damage in more diverse stands, which provide a greater variety of resources for these taxa (Pfisterer *et al.* 2003; Joshi *et al.* 2004; Jactel and Brockerhoff 2007; Unsicker *et al.* 2008). White and Whitham (2000) suggested the use of the term ‘associational susceptibility’ for those cases where plant species experience an increase in herbivore damage from a spill-over (which might occur for several reasons such as resource depletion or preference shifts) of generalist herbivores feeding on neighboring plant species. Associational susceptibility depends on the host preferences of the generalist herbivore and the palatability of the respective plant species (White and Whitham 2000). Higher plant diversity increases the probability of suitable plant species associations for generalist herbivores and thus the probability of higher damage in systems dominated by generalist herbivores. A possible explanation for our findings could thus be a much stronger impact of generalist herbivores on overall herbivore damage in our subtropical forest than often hypothesized for such highly diverse systems. Such strong effects of generalists on herbivory or a less narrow specialization of the herbivore community than traditionally assumed has also been found to occur in similarly species-rich tropical forests (Basset 1999; Novotny *et al.* 2002; Novotny and Basset 2005). Even though we lack systematic data on feeding preferences of herbivorous insects for our study region, observations during our census show that single species which feed on a broad range of tree species can cause substantial leaf damage. For instance, adults of the curculionid *Heterapoderus sulcicollis* (Jekel 1860) were observed feeding on at least eight tree species of different genera and families. In comparison, related weevils from temperate regions are more restricted to single or few tree species (cf. Kippenberg 1981). As we recorded total leaf damage, we cannot directly differentiate between effects of different functional herbivore groups. However, the largest part of the damage was caused by leaf-chewing lepidopterous larvae and beetles (see Materials and methods), taxa which are often considered to comprise many generalist feeders also in tropical forests (Novotny and Basset 2005). Future work in the forest stands and on the newly established tree plantations of the BEF China project will further clarify dietary preferences of dominant insect herbivores and specific effects of different functional groups.

Supporting evidence for our findings also comes from our consideration of potential effects of target species dominance. The Janzen–Connell hypothesis (Janzen 1970; Connell 1971) predicts less strong effects of specialist herbivores on growth and mortality of saplings when young trees grow at a greater distance from adult trees of the same species or at lower densities of neighboring conspecifics. A recent meta-analysis by Hyatt *et al.* (2003) found no general support for intraspecific distance dependence of herbivory on saplings, which was present in only some of the species studied so far. Distance and density effects probably depend on the herbivore community (i.e. the dominance of specialists or generalists) associated with each species (Barone 2000). The lack of a positive effect of the dominance of the target species in the tree and shrub layer in our study thus also suggests that polyphagous insect herbivores indeed play an important role in determining herbivory levels in highly diverse subtropical forests. At least in the sum of herbivory effects, which as a whole influence fitness and survival of the saplings, resource-concentration effects related to the hypotheses of Root or Janzen and Connell do not seem to have a strong impact on the overall damage levels of the ten species studied in our subtropical forest system. Likewise, effects predicted from the natural enemies hypothesis do not appear to significantly influence overall herbivory levels observed in our study system. This hypothesis suggests that greater diversity and abundance of predators with increasing plant diversity causes a reduction of herbivore loads and damage in more diverse plant communities, because of a broader spectrum and a temporally more stable availability of prey as well as a greater variety of niches (Root 1973). While support for this hypothesis has been reported from several studies of less diverse systems (e.g., Sobek *et al.* 2009), the effect of predators might depend on the system studied (Vehviläinen *et al.* 2007). We presently lack information on predator diversity in our plots and further research is needed to evaluate predator–herbivore relationships in our study system.

7.5.2 Effects on single species

The strength of positive relationships between plant diversity and herbivore damage varied to some extent between species. This might be due to differences in the palatability of the species and the feeding preferences of dominant generalist herbivores, such that the study species show different degrees of associational susceptibility (White and Whitham 2000). Our study treated sapling species as random effects, so that the general positive trend of herbivore damage with tree species richness would be expected for a randomly drawn species of the dominant tree species pool (cf. Pinheiro and Bates 2000). The mixed model shows that differences between species in their response to plant diversity are consistent with the assumption of an increase of herbivore damage with diversity, independent of species identity. As proportions of the heavily damaged *C. glauca* increased in the samples of the more diverse stands, this species might have potentially affected the overall results. However, the mixed-model analysis takes into account potential species-specific effects, and results from the additional reanalysis of the data after excluding *C. glauca* did not differ from the overall analysis, showing that the patterns found were not affected by distribution characteristics of, e.g. particularly herbivore-prone species.

As specified in Materials and methods, these ten species belong to the most common plant species in our subtropical forest ecosystem. Theories on the origin of the extraordinary species richness of subtropical and tropical forests suggest that herbivorous insects might contribute to high plant diversity by differentially affecting common and rare plant species (Janzen 1970; Connell 1971; Givnish 1999). The newly established tree plantations of the BEF China project might help to further investigate this issue, as we are unable to fully test these assumptions with our current data (rare species are difficult to sample in statistically sufficient numbers in our forest stands). For our ten study species, we did not find indications of decreasing susceptibility to herbivory with decreasing commonness of the species.

Whether the species richness effect suggested by our results can significantly affect, either by itself or in an interaction with other factors, the fitness or survival of the saplings analyzed depends on the capacities of the single species to compensate leaf damage and requires further testing. Species already experiencing high levels of herbivory (e.g. *L. glaber*) might be more affected by an increase in herbivory across the diversity gradient than species with generally low damage levels (e.g. *C. fraterna*). However, effects on plant fitness have already been found at even lower damage levels than those reported in our study (Scherber *et al.* 2006a). Altogether, as our study species accounted on average for 40% of all plant individuals in the tree and shrub layer, the overall positive effect of plant species richness on herbivory applies to a substantial part of the plant communities of the studied subtropical forest system.

7.5.3 Effects of stand age and abiotic conditions

Models considering both species richness and plot conditions were the best-fit in our statistical analysis, and stand age and structure played an important role in these models. Herbivore damage increased with stand age, which was the main factor with the highest loading on the first principal component in the dimension reduction of structural/abiotic variables. At the same time, tree density and canopy cover were negatively and total basal area of trees and shrubs positively related to stand age. Also, several other abiotic variables covaried with stand age. It is well known that abiotic conditions as well as the composition of and interactions within the biotic community, and thus their potential impact on herbivory, change with the successional development of an ecosystem (Poorter *et al.* 2004; Vilà *et al.* 2005; Vehviläinen *et al.* 2007; Leuschner *et al.* 2009). However, even after accounting for these strong effects, we did find significant effects of plant diversity on herbivory. Beyond age-related differences, variables related to important abiotic conditions which might, directly or indirectly, influence herbivory (e.g. light and temperature conditions; Coley and Barone 1996; Howlett and Davidson 2001) did not have additional explanatory power. This suggests that the gradient in abiotic conditions across the 27 study plots may be too small to have a severe impact on either leaf quality or herbivore communities of our study species beyond stand age-related effects (see also Howlett and Davidson 2001; Eichhorn *et al.* 2006). It further indicates that, despite the observational character of our study, the positive effects of stand diversity on herbivory are unlikely to be artificially caused by underlying and covarying abiotic conditions of the plots.

7.5.4 Conclusions

Our study documents a positive relationship between the degree of insect herbivory and plant diversity in a highly diverse subtropical forest system for a substantial part of the whole plant community, even after accounting for stand age and environmental variability. Our findings of increasing herbivory with an increase in plant species richness suggest that effects expected from classical hypotheses on plant diversity–herbivory relationships do not seem to play a major role in overall herbivory patterns of the species analyzed in our study system. One possible mechanism explaining the contrasting results of other herbivory studies could be differences in the degree of host specificity of dominant species in the herbivore community, indicating a higher impact of generalist herbivores in our study than usually assumed for such phytodiverse forests. Additionally, our study comprises levels of plant diversity beyond the scope of most forest plantation experiments or previous observational studies. Of course our results are limited to above-ground herbivory of young understorey trees, but as the performance of saplings determines diversity of the forest stands in the long run, they are essential for a general understanding of plant–herbivore interactions in forests. Large-scale experimental studies focusing on similar systems, such as the newly established tree plantations of the BEF China project (H. Bruelheide *et al.*, unpublished data), will help to establish the causative mechanisms underlying these patterns.

Acknowledgements

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7.6 Supplementary Material

Appendix 7.1 Details on methods and results of PCA validation

The parameters most strongly correlated with herbivory were stand age, total basal area, tree density and canopy cover (Table S7.1), all of which loaded most strongly on PC1, the only PC retained in the all-subsets analysis. Herbivory increased with stand age and total basal area, while it decreased with tree density and canopy cover.

Table S7.1. Component loadings and eigenvalues of all principal components (PC) from PCA reduction analysis on environmental variables as well as Pearson correlations of the single parameters and of each PC with mean herbivory per plot.

Variable	*Correlation with leaf damage*	*PC 1*	*PC 2*	*PC 3*	*PC 4*	*PC 5*	*PC 6*	*PC 7*	*PC 8*
Stand age	r=0.66; p<0.001	0.88	-0.24	-0.11	0.26	-0.09	-0.10	0.12	0.24
Total basal area	r=0.55; p=0.003	0.82	-0.15	-0.07	0.21	0.42	0.08	0.21	-0.16
Tree density	r=-0.55; p=0.003	-0.72	0.56	-0.14	0.07	-0.17	0.00	0.36	0.01
Canopy cover	r=-0.54; p=0.003	-0.65	0.23	0.24	0.38	0.53	0.11	-0.08	0.12
Herb cover	r=-0.13; p=0.504	-0.47	-0.70	-0.27	-0.20	0.03	0.41	0.08	0.06
Altitude	r=0.03; p=0.866	0.45	0.57	-0.51	0.26	-0.18	0.31	-0.15	-0.01
Aspect (East-West)	r=0.22; p=0.254	0.47	0.50	-0.06	-0.65	0.32	0.05	0.02	0.09
Aspect (North-South)	r=0.25; p=0.206	0.41	0.14	0.81	0.00	-0.24	0.30	0.05	0.00
Cumulative proportion explained (%)		*40.1*	*59.1*	*72.7*	*82.5*	*91.2*	*96.0*	*98.8*	*100*
Eigenvalue		*3.21*	*1.52*	*1.09*	*0.78*	*0.69*	*0.38*	*0.22*	*0.11*
Corrleation with leaf damage (Pearson's r)		0.64	-0.27	0.04	-0.10	-0.03	-0.11	0.20	0.09
Probability		<0.001	0.165	0.841	0.629	0.871	0.580	0.315	0.645

Retaining Principal Components (PCs) from PCA dimension reduction with eigenvalues higher than the mean is a standard approach to select those PCs with highest information content for further analysis (Quinn and Keough 2002). However, additional PCs might theoretically be relevant in a regression on a response variable, as PCs are primarily optimised to account for the variation in the predictor and not directly in the response variable. We thus tested the robustness of our method and the results using two different approaches.

First of all, we tested whether inclusion of any of the PCs with eigenvalues <1 and not chosen in our all-subsets analysis significantly contributed to explaining the variance in the herbivory data. Starting with the maximal model of our all-subsets approach, as defined in the Materials and Methods section, but including all PCs instead of only the first three, we conducted a mixed model analysis with backward elimination. Unlike with the original variables, including all eight PCs is possible as the components are orthogonal and thus there is no collinearity and instability in the estimates of the regression coefficients (Quinn and Keough 2002). Using backward elimination was preferred over an all-subsets approach as the number of predictors was much higher than in the all-subsets analysis using only three PCs.

Insignificant variables were removed from the maximal model one by one, with each step checked by a likelihood-ratio test, until a minimal adequate model was obtained where further deletion of parameters would have lead to significant changes in deviance (Scherber *et al.* 2006b; Crawley 2007). The minimal model obtained was identical to the best-fit model in the all-subsets analysis using only the PCs with eigenvalues higher than the mean (cf. Table 7.2), with only PC1 and species richness retained (Table S7.2). All other PCs did not significantly increase model fit and were successively removed, showing that our analysis using only the first three PCs includes all relevant information on stand structural and abiotic aspects for the analysis of herbivory patterns.

Table S7.2. Results for the minimal adequate model of mixed effects modelling with backward elimination*.

Fixed effects	*Estimate*	*Std. Error*	*t value*	p_{MCMC}
Intercept	0.2108	0.0329	6.40	0.001
Woody plant species richness	0.0012	0.0005	2.35	0.0198
PC1	0.0116	0.0031	3.79	0.008

*starting with a maximal model including as fixed effects: PCs1-8 (cf. Table S7.1), species richness, dominance, sapling height and number of leaves, interactions of richness and dominance with PC1.

Additionally, we compared our results to a mixed model approach using components for stand structural and abiotic aspects derived from partial least squares (pls) regression. Pls regression yields components based on the direct relationship between the predictors and the response variable (Mevik and Wehrens 2007). However, it is not possible to take into account the hierarchical structure in our dataset (species and individuals nested in plots) with the pls regression procedure and it is not able to handle missing values intrinsically (Mevik and Wehrens 2007). In our case, pls regression is only possible on mean values of herbivory (averaged over all species) per plot and component loadings do not directly reflect effects on species-specific levels of herbivory (and might thus introduce a bias into the estimation of regression slopes). We thus performed a pls regression of stand structural and abiotic parameters (cf. Table 7.1) on mean herbivory values per plot, using the package pls for R (Wehrens and Mevik 2007). Components relevant for the explanation of the variation in herbivory were selected on the basis of the root mean squared error of prediction (RMSEP) (Mevik and Wehrens 2007). The pls separated our first PC axis into three orthogonal components, with total basal area loading strongest on PLS1, tree density loading strongest on PLS2, and stand age loading strongest on PLS3 (Table S7.3). Given that PLS1 explains most variance in herbivory, followed by PLS3, one would come to the conclusion, that the effect of total basal area can be separated from stand age. However, since the pls was performed on mean values within plots, these results may also reflect a simple bias in species incidence within plots. The interpretation is further complicated by the contrasting results when including the PLS components into the mixed model together with species richness.

Table S7.3. Loadings of the main variables on the components (PLS1-3) selected from partial least squares (pls) regression.

Variable	*PLS1*	*PLS2*	*PLS3*
Stand age			0.80
Total basal area	1.00		
Tree density		-0.95	0.16
Canopy cover			-0.53
Herb cover			-0.29
Altitude		-0.33	
Aspect (East-West)			
Aspect (North-South)			
Sum of squares loadings	1.00	1.01	1.02
Cumulative Variance Explained in the response variable	30.24	37.04	53.54

We used the three components in an all-subsets mixed model approach, with the same model structure as in the all-subsets analysis using PCs (see Materials and Methods), but substituting the three pls components for the PCs. The best-fit model contained species richness and pls components PLS3 and PLS1 (Table S7.4). Component PLS3, with high loadings of primarily stand age and to a lesser degree canopy cover, had a much higher effect on herbivory than component PLS1, which reflected total basal area of the plots. Thus, the importance of PLS3 and PLS1 flipped when accounting for the nested structure of the data as well as for diversity. The interpretation of the two PLS axes is difficult, since they may include a bias of species incidence within plot (see above). Results are still very similar to the all-subsets approach using PCs (Table 7.2), with both approaches identifying species richness and the components related most strongly to stand age and total basal area as the most important variables.

Table S7.4. Results from linear mixed-effects modelling using data from partial least squares (pls) regression. For each predictor set (a-c), the three best-fit models (lowest AICc) are shown, with regression estimates (± standard error) for the predictors included*. ∆AICc is the difference in AICc-values between the candidate and the overall best-fit (in bold) model. Estimated effects of predictors in italics are not significantly different from zero (based on Markov chain Monte Carlo sampling).

Model	AICc	∆AICc
a) Plot characteristics and species richness		
0.0007 (±0.0004) PLS3+0.0011 (±0.0006) richness+0.000002 (±0.0000006) PLS1	**-2554.8**	**0**
0.0007 (±0.0004) PLS3+0.0011 (±0.0007) richness+0.000002 (±0.0000006) PLS1*-0.0029 (±0.0036) dominance*	-2553.4	1.4
0.0007 (±0.0003) PLS3+0.0011 (±0.0005) richness+0.000002 (±0.0000005) PLS1*-0.0053 (±0.0122) sapling height*	-2553.0	1.8
b) Only plot characteristics		
0.0009 (±0.0003) PLS3+0.000002 (±0.0000005) PLS1	-2552.7	2.1
0.0009 (±0.0003) PLS3+0.000002 (±0.0000006) PLS1*-0.0042 (±0.0121) sapling height*	-2550.8	4.0
0.0009 (±0.0003) PLS3+0.000002 (±0.0000006) PLS1*-0.0000005 (±0.00002) PLS2*	-2550.7	4.1
c) Only species richness and dominance		
0.0015 (±0.0006) richness	-2545.8	9.0
0.0015 (±0.0007) richness*-0.0037 (±0.0036) dominance*	-2544.8	10.0
0.0015 (±0.0006) richness*-0.0041 (±0.0119) sapling height*	-2544.2	10.6

*PLS1, PLS2, PLS3: Components 1, 2 and 3 from pls regression (Table S7.3); richness: species richness of trees and shrubs; PLS3:richness: interaction between stand age/structure and species richness.

Appendix 7.2 Mixed model results excluding *C. glauca*

Table S7.5. Results from linear mixed-effects modelling excluding data from *Cyclobalanopsis glauca* (Thunb.). For each predictor set (a-c), the three best-fit models (lowest AICc) are shown, with regression estimates (± standard error) for the predictors included*. ∆AICc is the difference in AICc-values between the candidate and the overall best-fit (in bold) model. Estimated effects of predictors in italics are not significantly different from zero (based on Markov chain Monte Carlo sampling).

Model	AICc	∆AICc
a) Plot characteristics and species richness		
0.0110 (±0.0030) PC1+0.0012 (±0.0005) richness	**-2423.7**	**0**
-0.0031 (±0.0129) PC1+0.0010 (±0.0005) richness+0.0003 (±0.0003) PC1:richness	-2422.8	0.9
0.0110 (±0.0030) PC1+0.0012 (±0.0005) richness*-0.0117 (±0.0123) sapling height*	-2422.5	1.2
b) Only plot characteristics		
0.0118 (±0.0033) PC1	-2421.0	2.7
0.0118 (±0.0033) PC1*-0.0110 (±0.0123) sapling height*	-2419.6	4.1
0.0118 (±0.0033) PC1*-0.0038 (±0.0075) number of leaves*	-2419.1	4.6
c) Only species richness and dominance		
0.0015 (±0.0006) richness	-2415.6	8.1
0.0015 (±0.0006) richness*-0.0105 (±0.0123) sapling height*	-2414.1	9.6
0.0015 (±0.0006) richness*-0.0025 (±0.0038) dominance*	-2413.8	9.9

*PC1: Principal component 1 from PCA dimension reduction (Table 7.1), primarily reflecting stand age-related differences in biotic and abiotic conditions; PC3: Principal component 3 (see Table 7.1); richness: species richness of trees and shrubs; PC1:richness: interaction between stand age/structure and species richness

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List of Publications

Peer reviewed journal and book publications

Schuldt A, Assmann T (submitted) Invertebrate diversity and national responsibility for species conservation across Europe – a multi-taxon approach.

Schuldt A, Assmann T (submitted) Patterns and hotspots of carabid beetle diversity in the Palaearctic – insights from a hyperdiverse invertebrate taxon.

Bruelheide H, Böhnke M, Both S, Fang T, Assmann T, Baruffol M, Bauhus J, Buscot F, Chen XY, Ding BY, Durka W, Erfmeier A, Fischer M, Geißler C, Guo D, Guo LD, Härdtle W, He JS, Hector A, Kröber W, Kühn P, Lang AC, Nadrowski K, Pei K, Scherer-Lorenzen M, Shi X, Scholten T, Schuldt A, Trogisch S, von Oheimb G, Welk E, Wirth C, Wu YT, Yang X, Yu M, Zeng X, Zhang S, Zhou H, Ma K, Schmid B (submitted) Community assembly during secondary forest succession in a Chinese subtropical forest.

Schuldt A, Assmann T (2010) Belowground carabid beetle diversity in the western Palaearctic – effects of history and climate on range-restricted taxa (Coleoptera: Carabidae). ZooKeys (in press)

Schuldt A, Baruffol M, Böhnke M, Bruelheide H, Härdtle W, Lang AC, Nadrowski K, von Oheimb G, Voigt W, Zhou, H, Assmann T (2010) Tree diversity promotes insect herbivory in subtropical forests of southeast China. Journal of Ecology, doi: 10.1111/j.1365-2745.2010.01659.x

Drees C, Brandmayr P, Buse J, Dieker P, Gürlich S, Habel J, Harry I, Härdtle W, Matern A, Meyer H, Pizzolotto R, Quante M, Schäfer K, Schuldt A, Taboada A, Assmann T (2010) Poleward range expansion without a southern contraction in *Agonum viridicupreum* (Coleoptera: Carabidae). ZooKeys (in press)

Assmann T, Drees C, Matern A, Schuldt A (2010) *Eucamaragnathus desenderi*, a new ground beetle species from Africa (Coleoptera, Carabidae). ZooKeys (in press)

Assmann T, Casale A, Drees C, Habel JC, Matern A, Schuldt A (2010) The dark side of relict species biology. Cave animals as ancient lineages. In: Habel JC, Assmann T (eds) Relict species – Phylogeography and conservation biology. Springer, Heidelberg

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Schuldt A, Fahrenholz N, Brauns M, Migge-Kleian S, Platner C, Schaefer M (2008) Communities of ground-living spiders in deciduous forests: Does tree species diversity matter? Biodiversity and Conservation 17: 1267-1284

Further Publications

Dörrie H, Grüneberg C, Paul S, Schuldt A *et al.* (2006) Brutvögel im Göttinger Kerngebiet 1948-1965-2005/2006. Naturkundliche Berichte zur Fauna und Flora in Süd-Niedersachsen 11: 68-80

Schuldt A, Cling S, Waltert M (2005) Zur Entwicklung der Heuschreckenfauna des Kerstlingeröder Feldes, Göttingen, in den Jahren 1993 und 2001 bis 2004. *Articulata* 20: 125-138

Talks and Poster presentations

Schuldt A, Assmann T (2009) Macroecology of carabid beetles - species richness endemism and cross-taxon congruence across the Palaearctic. Talk at the 14th European Carabidologist Meeting. Westerbork, Netherlands, 17.09.2009

Schuldt A, Assmann T (2009) Hotspots of diversity and cross-taxon congruence of a hyperdiverse insect taxon, vertebrates and plants across the Palaearctic. Poster presentation at the Symposium "Biodiversity Hotspots - Evolution and Conservation". Luxembourg, 26.-28.03.2009

Schuldt A, Assmann T (2009) Insect herbivory on tree and shrub saplings in subtropical forests. Talk at the Conference on the experimental design of the Biodiversity Ecosystem Functioning Experiment (BEF-China) in Xingangshan (Jiangxi Province). Gutianshan, China, 16.03.2009

Curriculum Vitae

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EDUCATION

Oct 2007 – May 2010	Leuphana University Lüneburg, Germany PhD (Dr. rer. nat.) studies Thesis: "Patterns and drivers of biodiversity: insights from a hyperdiverse invertebrate taxon (Coleoptera: Carabidae)"
Feb 2007	University of Göttingen, Germany Diploma in Biology Diploma thesis: "Spider communities (Arachnida: Araneae) of deciduous forests – Studies on the effects of tree diversity"
Oct 2001 – Feb 2007	University of Göttingen, Germany Studies of Biology
2000	Städtisches Gymnasium Schleiden (High School), Germany Abitur

PROFESSIONAL EXPERIENCE

Apr 2007 – Sep 2007	University of Oldenburg, Germany Research assistant
Aug 2000 – Apr 2001	Biological Station Rieselfelder Münster, Germany „Freiwilliges Ökologisches Jahr" (voluntary gap year of environmental service)

SCHOLARSHIPS

Oct 2007 – May 2010	PhD scholarship, Leuphana University Lüneburg

Lüneburg, 29.03.2010

Erklärung

Ich versichere, dass ich die eingereichte Dissertation “Patterns and drivers of biodiversity: insights from a hyperdiverse invertebrate taxon (Coleoptera: Carabidae)” selbstständig und ohne unerlaubte Hilfsmittel verfasst habe. Anderer als der von mir angegebenen Hilfsmittel und Schriften habe ich mich nicht bedient. Alle wörtlich und sinngemäß den Schriften anderer Autorinnen und Autoren entnommenen Stellen habe ich kenntlich gemacht.

Hiermit erkläre ich, dass die Abhandlung in der gegenwärtigen oder einer anderen Fassung noch keinem anderen Fachbereich vorgelegen hat. Den Inhalt der Dissertation habe ich noch nicht im Rahmen einer Diplom- oder anderen Prüfungsarbeit verwendet.

Lüneburg im März 2010