

# Traits in the light of ecology and conservation of ground beetles

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"Look deep into nature, and then you will understand everything better."

- *Albert Einstein*

Nature awakens a great fascination in all of us and gives us a feeling of balance and peace of mind. Wherever you look, there is always something to discover. The plethora of habitats, species and various adaptation strategies is the true secret of nature's success. But nature's life insurance is in danger!

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## SUMMARY

We are in a phase of an alarming biodiversity loss, by scientist already referred to as Earth's sixth mass extinction. According to estimations, the current extinction rates are 100 to 1000 times higher than those predicted from fossil records. To counteract species loss and preserve the remaining biodiversity, with its important ecosystem functioning and services essential to human well-being, there is an urgent need to develop promising and long-term conservation strategies. In order to achieve these goals, extensive research to gain a better understanding of the general mechanisms underlying community diversity is of greatest importance. Especially, the identification of intrinsic ecological and distributional species traits is receiving increased attention in ecology and conservation biology research. Depending on the expression of their traits, species perform particular ecosystem functions and respond in a specific manner to environmental conditions. The identification of the effect of certain traits on community compositions can therefore significantly improve our understanding of species extinction processes and help to develop valuable and appropriate recommendations for conservation management. As trait-based analyses are applicable to different geographical, temporal and taxonomical scales, they may even allow for a broader generalization if similar results are found on different scales, i.e. for local species pools, the complete species pools of different habitat types or the entire species pool across several habitat types including different climatic regions.

Although insects make up the largest part of animal diversity and provide essential ecosystem services in form of e.g. pollination, pest control, and decomposition, the majority of studies on extinctions have mainly focused on vertebrates. Among invertebrates either charismatic taxa or those targeted by conservation laws have been investigated until now (e.g. butterflies or saproxylic beetles). Being highly species-rich and trait-diverse, ground beetles (Coleoptera: Carabidae) should be even more suitable for conducting trait-based analyses. Thus, using ground beetles as a model taxon, four case studies focusing on the analyses of traits form the basis of this doctoral thesis. The work of this thesis was conducted with the aim of gaining general insights on the influence of species traits on ground beetle community compositions, such as habitat occupancy and species vulnerability to extinction, for instance.

An important aspect when investigating species traits is the consideration of confounding factors which could influence the results, such as dependent relations between the different traits. Compiling a large dataset of 566 Central European species, I identified that dependent relations between the six tested traits of ground beetles (distribution range size, habitat specialization, body size, hind-wing morphology, breeding season and trophic level) are highly common. Across all identified dependent trait relations, the relation between body size and hind wing morphology or range size and hind wing morphology showed the strongest significant dependencies. Since the consideration of trait relations is necessary to provide reliable interpretations, all analyses of this thesis tested several traits simultaneously and considered possible trait interactions.

Studies on local communities found specific traits characterizing the local species pools of certain habitat types. Here, the species pools of seven different habitat types (coastal, forest, mountain, open, riparian, wetland and special habitat) were used to determine habitat-specific trait filters. The identified traits, characteristic for certain habitat types, were in most cases in accordance with the previous findings on local communities. Across Germany, the species of frequently disturbed habitat types, namely coastal, riparian and wetland habitats were characterized by small body size, high amount of

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macroptery, intermediate to high habitat specialization, spring breeding, and predatory feeding behavior. The species of stable habitat types (forest, mountain, and open habitats), however, were found to be generally larger in body size and more frequently breeding in autumn, further displaying greater variations in the other traits. The gained knowledge on the habitat-specific filtering of traits improve our understanding of the organization and assembly of communities, and can thereby help to detect alterations in the habitat-specific species pool due to natural or human-induced environmental changes.

Furthermore, traits can provide evidence on species occurrences and vulnerability to extinction. Three case studies of this thesis aimed to gain new insights on this topic, through the investigations on the following research questions; I. Which traits drive species extinction risks of Central European ground beetle species, II. How traits influence the species occurrences of 28 forest species within a large area in Central Europe, and III. Whether certain traits are related to long-term population trends of the species pool from an ancient forest in northern Germany. The results indicated, that depending on the habitat type and tested species pool, different traits prove to be good predictors for the vulnerability of species. Nevertheless, across different geographical and taxonomical scales, especially species with small range sizes and high habitat specialization faced a greater risk of extinction. Therefore, the two traits distributional range size and habitat specialization emerge as reliable predictors of ground beetles vulnerability to extinction. Interestingly, body size did not display a consistent response; while increasing body size led to higher extinction risk in riparian, wetland and open habitats and large macropterous species showed higher extinction risks across the entire species pool, smaller species showed long-term population declines in an ancient forest.

To summarize, this thesis presents a comprehensive picture of ground beetle species traits, providing valuable insights and a better understanding of the mechanisms driving changes in ground beetle diversity. On the basis of the results presented in this work, the efficiency of biodiversity protection can be increased by developing appropriate management and recovery plans, especially targeting species of threatened habitat types or 'functional groups' of species, exhibiting trait values strongly associated with a greater vulnerability to extinction.

## ZUSAMMENFASSUNG

Die Erde befindet sich in einer Phase mit alarmierendem Biodiversitätsverlust. Schätzungen zufolge sind aktuelle Aussterberaten um das 100 bis 1000 fache höher als von Wissenschaftlern aufgrund fossiler Daten vorhergesagt. Der enorme Verlust an biologischer Vielfalt wird daher in der Wissenschaft bereits als das „sechste Massensterben der Erdgeschichte“ bezeichnet. Um den Verlust der verbleibenden Biodiversität zu reduzieren und die Bereitstellung wesentlicher Ökosystemdienstleistungen als essentielle Grundlage für den Menschen zu sichern, ist es von zentraler Bedeutung erfolgversprechende und langfristige Schutzstrategien zum Erhalt der Biodiversität zu entwickeln. Um dies zu ermöglichen, ist es notwendig die allgemeinen Mechanismen, die der Diversität der Lebensgemeinschaften zugrunde liegen, umfassend zu untersuchen. Insbesondere die Erforschung von intrinsischen Artengemeinschaften (Traits) gewinnt dabei zunehmend an Bedeutung in den Forschungsfeldern der Ökologie und Naturschutzbiologie. Abhängig von der Ausprägung ihrer Traits erbringen Arten bestimmte Ökosystemfunktionen und reagieren spezifisch auf Umweltbedingungen. Aus diesem Grund kann der Einfluss bestimmter Traits auf die Zusammensetzung von Lebensgemeinschaften unser Verständnis von Aussterbeprozessen erheblich verbessern und dazu beitragen wertvolle und zielgerichtete Empfehlungen für das Naturschutzmanagement zu entwickeln. Dadurch, dass Trait-basierte Analysen auf verschiedenen geographischen, taxonomischen und zeitlichen Skalen anwendbar sind, können diese sogar eine breitere Verallgemeinerung ermöglichen. Dies gilt im Besonderen, wenn ähnliche Ergebnisse auf verschiedenen Skalen gefunden werden, d.h. für lokale Artenpools, Artenpools verschiedener Habitattypen oder den gesamten Artenpool über mehrere Lebensraumtypen einschließlich verschiedener Klimaregionen.

Obwohl Insekten den größten Teil der faunistischen Vielfalt ausmachen und essentielle Ökosystemleistungen in Form von beispielsweise Bestäubung, Schädlingsbekämpfung und Zersetzung erbringen, haben sich Studien bis dato vorwiegend auf Aussterbeprozesse von Vertebraten konzentriert. Bei den Invertebraten wurden bisher vor allem charismatische oder unter Naturschutz stehende Taxa untersucht (z.B. Schmetterlinge oder xylobionte Käfer). Da Laufkäfer (Coleoptera: Carabidae) jedoch sowohl artenreich als auch divers an Traits sind, sollten sie besonders gut für die Durchführung von Trait-basierten Analysen geeignet sein. Aufgrund dessen bilden vier Fallstudien, die sich auf die Analyse von Traits konzentrieren, die Grundlage für diese Doktorarbeit. Das Ziel dieser Arbeit war es, allgemeine Erkenntnisse über den Einfluss von Traits auf die Zusammensetzung von Lebensgemeinschaften zu gewinnen, wie z.B. dem Artvorkommen in Habitaten und der Aussterbewahrscheinlichkeit von Arten.

Ein wichtiger Aspekt bei der Untersuchung von Traits ist die Berücksichtigung von Störfaktoren, welche die Ergebnisse beeinflussen könnten, wie zum Beispiel mögliche Abhängigkeiten zwischen verschiedenen Traits. Anhand eines umfangreichen Datensatzes von 555 mitteleuropäischen Arten konnte festgestellt werden, dass abhängige Beziehungen zwischen den sechs getesteten Laufkäfer-spezifischen Traits (Größe des Verbreitungsgebietes, Habitatspezialisierung, Körpergröße, Hinterflügelausbildung, Reproduktionszeit und trophische Ebene) sehr häufig sind. Von den nachgewiesenen Trait-Beziehungen zeigten die Beziehungen zwischen Körpergröße und Hinterflügelausbildung als auch zwischen Größe des Verbreitungsgebietes und Hinterflügelausbildung die stärksten signifikanten Abhängigkeiten. Da die Berücksichtigung von Trait-Beziehungen somit notwendig ist, um zuverlässige Interpretationen zu liefern, wurde in allen Analysen dieser Arbeit mehrere Traits gleichzeitig getestet und mög-

liche Interaktionen zwischen diesen berücksichtigt.

In der Literatur wurden für lokale Laufkäfergemeinschaften bereits spezifische Traits nachgewiesen, die die Artenpools bestimmter Lebensraumtypen zu charakterisieren scheinen. In dieser Arbeit wurden die gesamten Artenpools von sieben verschiedenen Habitattypen (Küsten-, Wald-, Berg-, Offenland-, Ufer-, Feuchtgebiets- und Sonderhabitat) zur Bestimmung von habitatspezifischen Trait-Filtern genutzt. Die nachgewiesenen Traits, die für bestimmte Habitattypen charakteristisch waren, entsprachen in den meisten Fällen den bisherigen Ergebnissen über lokale Lebensgemeinschaften. In instabilen Habitattypen (Küsten-, Ufer- und Feuchtgebietshabitat) waren die Arten durch geringe Körpergröße, hohe Anzahl an flugfähigen Arten, mittlere bis hohe Habitatspezialisierung, Frühlingsreproduktion und Prädation gekennzeichnet. Arten stabiler Lebensraumtypen (Wald-, Berg- und Offenlandhabitat) waren generell größer, reproduzierten häufiger im Herbst und zeigten überdies größere Unterschiede in der Ausprägung der weiteren Traits. Die gewonnenen Erkenntnisse über die habitatspezifischen Trait-Filter verbessern unser Verständnis von der Organisation und Zusammensetzung von Lebensgemeinschaften. Zudem ermöglichen sie Veränderungen in den habitatspezifischen Artenpools zu erkennen. Diese können durch natürliche oder vom Menschen verursachte Umweltveränderungen hervorgerufen werden.

Traits können auch Hinweise auf das Vorkommen von Arten in Habitaten und deren Aussterbewahrscheinlichkeit liefern. Drei Fallstudien dieser Arbeit befassten sich daher damit neue Erkenntnisse in folgenden Forschungsfragen zu liefern: I. Welche Traits erhöhen das Aussterberisiko von 464 mitteleuropäischen Laufkäferarten; II. Wie beeinflussen Traits das Vorkommen von 28 Waldarten in mitteleuropäischen Wäldern, und III. Sind bestimmte Traits mit den langfristigen Populationstrends von Arten eines historisch-alten Waldes in Norddeutschland verbunden. Die Ergebnisse zeigten, dass sich je nach Habitattyp und untersuchtem Artenpool unterschiedliche Traits als gute Prädiktoren für die Verwundbarkeit von Arten erwiesen. Dennoch waren, über verschiedene geographische und taxonomische Skalen hinweg, vor allem Arten mit kleinen Verbreitungsgebieten und hoher Habitatspezialisierung am häufigsten einem größeren Aussterberisiko ausgesetzt. Diese beiden Traits erwiesen sich daher auch für Laufkäfer als zuverlässige Prädiktoren für die Aussterbewahrscheinlichkeit von Arten. Interessanterweise zeigten sich keine konsistenten Ergebnisse für die Körpergröße der Laufkäfer; Während sich das Aussterberisiko von Arten in Ufer-, Feuchtgebiets- und Offenlandhabitaten mit einer zunehmenden Körpergröße erhöhte und besonders große flugfähige Arten ein hohes Aussterberisiko über den gesamten Artenpool der Laufkäfer zeigten, waren in einem historisch-alten Wald vor allem kleinere Arten einem langfristigen Populationsrückgang ausgesetzt.

Insgesamt liefert meine Doktorarbeit ein umfassendes Bild über die Einflüsse von Traits und verbessert somit unser Verständnis über die Mechanismen, die Veränderungen in der Diversität von Laufkäfern verursachen. Aufbauend auf den Ergebnissen dieser Arbeit kann der Schutz der biologischen Diversität, sowie insbesondere von Arten bedrohter Habitattypen oder „funktioneller Artengruppen“ die höheren Aussterberisiken ausgesetzt sind, durch die Entwicklung geeigneterer Bewirtschaftungs- und Wiederherstellungspläne effizienter gestaltet werden.

# 1. GENERAL INTRODUCTION

## 1.1. Background: Biodiversity

Biological diversity (biodiversity) is essential for every ecosystem on Earth. It has profound effects on the health, resilience and functioning of ecosystems, which provide mankind with essential ecosystem services, such as biomass and food production, nutrient cycle or recreational experiences (Barton and Pretty, 2010; Hautier *et al.*, 2015; Hooper *et al.*, 2005; Loreau *et al.*, 2001). However, these services are threatened today, as we face an alarming loss of biodiversity (Ceballos *et al.*, 2015, 2017; Dirzo *et al.*, 2014). Ecological research assumes recent species extinction rates to be 100-1000 times higher than expected from fossil records and suggests future extinction rates to be even 10 times higher than this (Barnosky *et al.*, 2011; Pimm *et al.*, 1995). Therefore, scientists have addressed this global environmental phenomenon as the Earth's sixth mass extinction (Barnosky *et al.*, 2011; Ceballos *et al.*, 2015). Biodiversity is defined as the variability among all living organisms and their ecological complexes, including genetic, species and ecosystem diversity (Convention on Biological Diversity 1992). Several studies demonstrated that the loss of biodiversity is, alongside global environmental change, particularly triggered by human activities (Araújo and Rahbek, 2006; Barnosky *et al.*, 2011). Extrinsic human-induced processes, such as land use change, disturbance, habitat loss and fragmentation present the greatest immediate threats to biodiversity (Jantz *et al.*, 2015). For this reason, biodiversity loss is intensively discussed within the public and has become one of the most important research area in ecology and conservation biology (Hallmann *et al.*, 2017; Leather, 2018).

Although science constantly gains new insights on the mechanisms underlying species decline and extinction, our knowledge of the processes inducing biodiversity loss is still largely limited (Dirzo *et al.*, 2014). Today, many species have already gone extinct and it is expected that we will continue losing thousands of species annually (Mora *et al.*, 2013), if we do not take any actions. Therefore, it is a major concern in nature conservation management, to diminish the process of biodiversity loss and conserve ecosystem functionality. To achieve these goals and develop more effective conservation strategies, it is crucial to understand why certain species go extinct very rapidly even in protected areas, while other species increase in numbers and seem to adapt well to changing environmental conditions (Purvis *et al.*, 2000a). Thus, three important tasks need to be addressed in biodiversity research:

- I) Identification of taxa or species at high risk of extinction,
- II) Identification of extrinsic and intrinsic factors that drive extinction risks, and
- III) Development and implementation of convenient nature conservation management.

Among vertebrates, numerous studies have been carried out to identify threatened species and the factors driving their decline. As these studies provide a good knowledge base and emphasize the need to protect species, conservation measures for vertebrates are already carried out worldwide. However, for invertebrate species, which make up the majority of higher eukaryotic biodiversity (Ponder and Lumney, 1999; Scheffers *et al.*, 2012), research on the ongoing extinction events and their drivers is still limited (Chichorro *et al.*, 2018; Dirzo *et al.*, 2014). For example, for 67 % of vertebrate species, but only for less than 1 % of all described invertebrate species the conservation status is known (IUCN, 2018), of which about 40 % are already considered threatened (Collen *et al.*, 2012). This indicates, that the loss of biodiversity might be highly underestimated, as we might have already missed the majority of invertebrate extinctions (Dunn, 2005).

## 1.2. Species traits promote extinction risks

Some studies stated that extinction events are non-random across species (McKinney, 1997; Purvis *et al.*, 2000b). Besides extrinsic factors, intrinsic factors of species are discussed to influence species community compositions and extinction processes. Species traits are intrinsic ecological and distributional characteristics of species, which influence the performance and fitness of an organism by their effects on e.g. survival, growth and reproduction (McKinney, 1997; Violle *et al.*, 2007). Over the last two decades, studies on species traits have gained importance in biodiversity-related research (Chichorro *et al.*, 2018; Dirzo *et al.*, 2014; Schneider *et al.*, 2018; Violle *et al.*, 2007). It is suggested that particular traits of species make them more vulnerable to changing environmental factors and thus cause a higher risk of extinction (Henle *et al.*, 2004; McKinney, 1997; Purvis *et al.*, 2000a). Furthermore, ecosystem functions depend on the intrinsic traits of species occurring in an ecosystem (Díaz *et al.*, 2013).

Trait-based analyses can be conducted both, on individual species levels as well as on global biodiversity patterns (Díaz *et al.*, 2016), allowing wider applicability and generality in drawing conclusions across ecosystems (Kunstler *et al.*, 2016). Furthermore, shared similar responses to environmental changes of species with similar traits, enable the creation of 'functional groups' independently of species phylogenetic relatedness (Ribera *et al.*, 2001). This approach is particularly useful in predicting extinction risks (Fountain-Jones *et al.*, 2015; Kotiaho *et al.*, 2005) thereby enhancing the predictability of ecosystem functions, in general (see Moretti *et al.* 2017). Trait-based approaches can therefore significantly increase our understanding of the underlying mechanisms of community compositions (Van der Plas *et al.*, 2012), biodiversity loss and ecosystem functioning (de Bello *et al.*, 2010; Dirzo *et al.*, 2014), which will help to improve species protection and make conservation management more effective (Chichorro *et al.*, 2018).

In recent years the compilation of species trait data has shown to be somewhat problematic and time-consuming. Data on species traits had to be compiled from several literature sources, which partly used differing nomenclature and available trait information (Schneider *et al.*, 2018). The increasing availability of comprehensive trait-databases, dealing with different taxa, stimulated the use of trait-based approaches. Analyses on vertebrate traits, especially those of mammals and birds, have been conducted for quite some time (see McKinney 1997 for a historical comparative study) and have received most attention until now (Chichorro *et al.*, 2018). The traits most commonly identified to increase vertebrate extinction risks are large body size, distributional range size, rarity, high specialization and high trophic level (e.g. Cardillo 2003; Cardillo *et al.* 2005; Dirzo *et al.* 2014; Fisher and Owens 2004; Henle *et al.* 2004; Verde Arregoitia 2016). However, for some species traits, e.g. body size, studies reported varying results, indicating positive, negative or no relationships between the traits to species extinction risk. Blackburn and Gaston (1994) implied that this was due to the fact that the analyses were performed on different taxa from different habitat types and on different geographical or temporal scales.

In comparison with vertebrates, fewer trait-based studies have been conducted on invertebrates (e.g. Chichorro *et al.* 2018). However, since intrinsic factors for invertebrate extinction risks might strongly differ from those of vertebrates (Dunn, 2005), a direct transfer of driving traits from vertebrates to invertebrates is often difficult and might even be misleading. Moreover, the protective measures for vertebrates might not be effective for invertebrates. To ensure that conservation strategies on invertebrates are no longer neglected (Donaldson *et al.*, 2016; Schuldt and Assmann, 2010; Troudet *et al.*, 2017), it is important to increase our knowledge on invertebrate extinction risks with the help of trait-based studies (Whittaker *et al.*, 2005).

### 1.3. Ground beetles as model taxon

In recent years, comprehensive trait databases for different insect groups in Europe have been established (e.g. Gossner *et al.* 2015). Until now most studies linking species traits to insect species extinction risks deal with either charismatic taxa or those targeted by conservation laws, such as butterflies or saproxylic beetles (Essens *et al.*, 2017; Jeppsson and Forslund, 2014; Kotiaho *et al.*, 2005; Seibold *et al.*, 2015). These studies identified traits such as body size, range size or the degree of habitat specialization (niche breadth) to be important drivers of insect vulnerability. It is important to mention that due to their wide variety of traits, ground beetles should be even more suitable to analyze relationships between traits and species habitat occupancy or extinction risk, than less trait-diverse insect taxa, such as butterflies. The insect taxa of ground and tiger beetles (Coleoptera: Carabidae and Cicindelidae = ground beetles in the following) comprises a large number of well-documented and trait-diverse species (Kotze *et al.*, 2011; Lorenz, 2005). So far, about 39.000 extant ground beetle species are described worldwide (Lorenz, 2018). In the Western Palearctic region, more than 10.000 species are known (Löbl and Löbl, 2017), with as many as 566 species occurring in Germany (Schmidt *et al.*, 2016). Ground beetles are found in a wide variety of terrestrial and semi-aquatic ecosystems worldwide (Lövei and Sunderland, 1996) and their biology and ecology is well studied, especially in Europe (Lindroth, 1945; Lövei and Sunderland, 1996; Rainio and Niemelä, 2003; Thiele, 1977). They play a crucial role in the ecosystem food chain, with the majority of the species being predacious, while the rest being herbivorous or omnivorous (Kulkarni *et al.*, 2015; Lövei and Sunderland, 1996; Thiele, 1977). Additionally, the focal taxon contains not only eurytopic, but also stenotopic species, the latter being highly adapted to their ecological niche in a specific habitat type.

The loss of ground beetle species (Brooks *et al.*, 2012; Kotze and O'Hara, 2003) might have dramatic consequences on the delivery of ecosystem functions and services, such as natural pest and weed seed control (Balvanera *et al.*, 2006; Ceballos *et al.*, 2015).

Since 2014, a comprehensive trait database on ground beetles of the Palearctic region is available online ([www.carabids.org](http://www.carabids.org); Homburg *et al.* 2014b). This enables to analyze patterns of ground beetle species traits across habitat types as well as their relationship to species extinction risks, on a local as well as on a larger geographical scale. So far, most relationships of traits to ground beetle population decline, extinction risk or vulnerability to fragmentation, disturbance or habitat loss, were conducted on local community scales (see Table 1.1). However, to gain a better understanding of general mechanisms driving community compositions of ground beetles, it is necessary to analyze several species traits simultaneously, at different spatiotemporal and taxonomical scales.

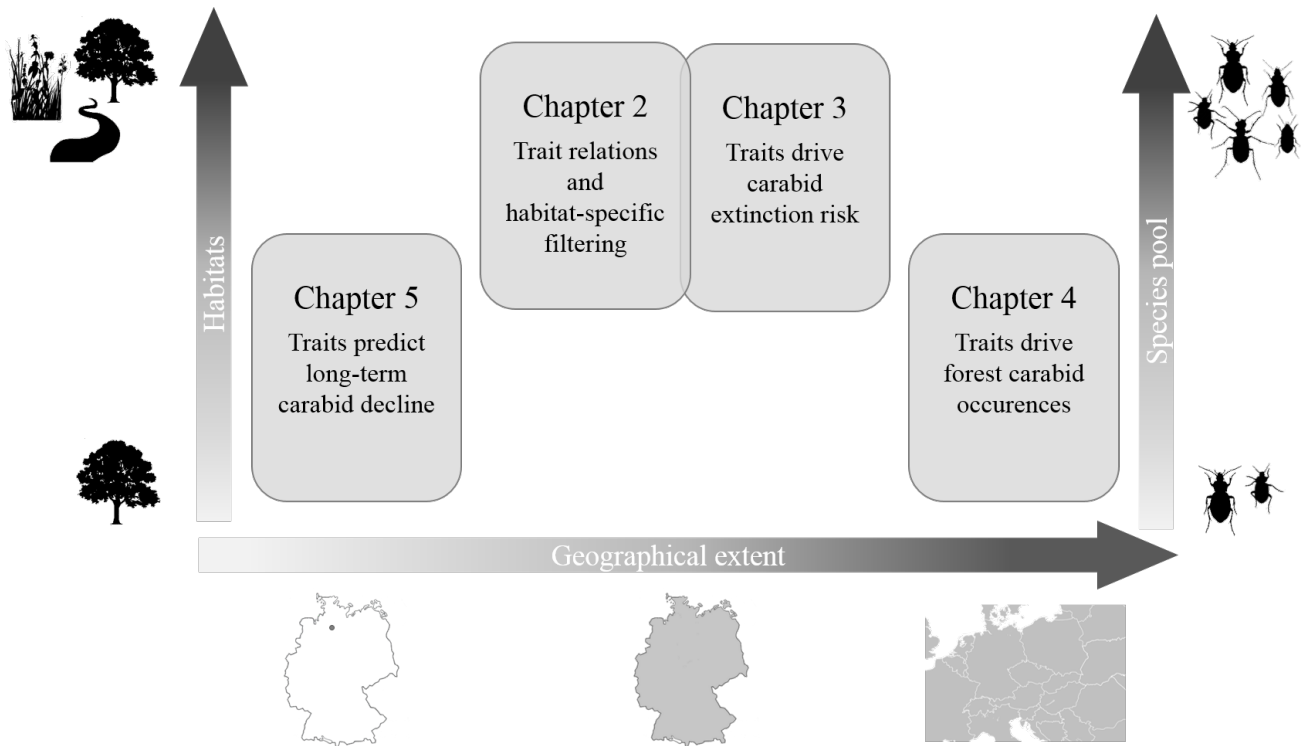
In summary, identifying general mechanisms driving community compositions of the trait-diverse ground beetle taxon, by conducting trait-based analyses, will help us to develop valuable and appropriate recommendations for conservation management. Furthermore, results from this taxon might be useful to shed light on processes driving diversity loss in less well-studied terrestrial arthropod taxa. This thesis aims to identify the importance of species traits for habitat occupancy, long-term population trends and species extinction risks of ground beetles. The four case studies of my cumulative dissertation vary in their geographical and taxonomical scales, ranging from local to transnational level, and from small to large species pools (see Fig. 1.1 for an overview).

**Table 1.1.** Species traits of carabid beetles and their assumed effect on species population decline and extinction risk or vulnerability to fragmentation, disturbance or habitat loss (+ = positive effect; - = negative effect, e.g. decreasing population decline, extinction risk or vulnerability with increasing distribution range size).

Trait	Trait explanation and values	Assumed trait effect / Source	
Taxonomy	Phylogenetic relatedness	None	Davies <i>et al.</i> (2000); Kotze and O'Hara (2003)
Distribution range size	Area in which the given species is recorded	-	Gaston and Fuller (2009)
Habitat specialization*	Degree of habitat /niche specialization, ranging from generalistic to highly stenotopic	+	Gaublomme <i>et al.</i> (2008); Jelaska and Durbesic (2009); Kotze and O'Hara (2003)
Habitat preference	Preferred habitat type	Mixed	Kotze and O'Hara (2003)
Body size	Average size of a species	+	Brooks <i>et al.</i> (2012); Davies <i>et al.</i> (2000); Halme and Niemelä (1993); Jelaska and Durbesic (2009); Kotze and O'Hara (2003)
Hind wing morphology	Brachypterous (= short-winged, flightless)	+	Driscoll and Weir (2005); Halme and Niemelä (1993); Jelaska and Durbesic (2009); Kotze and O'Hara (2003); de Vries <i>et al.</i> (1996); Wamser <i>et al.</i> (2012)
	Dimorphic (species with long and short-winged specimens)	-	
	Macropterous (= fully winged, predominantly flight-active)	-	
Trophic level	Predator	+	Davies <i>et al.</i> (2000); Liao <i>et al.</i> (2017); Schweiger <i>et al.</i> (2006)
	Omnivorous	-	
	Herbivorous	+	
Breeding season	Autumn breeder	Mixed,	den Boer (1968); den Boer and den Boer-Daanje (1990); Ribera <i>et al.</i> (2001)
	Spring breeder	depending	
	Variable breeding period (both spring and autumn breeder)	on habitat	
	Winter breeder		
Hibernation stage	Larvae	Mixed,	Ribera <i>et al.</i> (2001)
	Imago	depending	
	Larva and Imago (both)	on habitat	
Daily activity*	Diurnal	None	Ribera <i>et al.</i> (2001)
	Nocturnal		

\* Traits not yet listed in the dynamic database [www.carabids.org](http://www.carabids.org).





**Figure 1.1.:** Overview of the geographical and taxonomical scales addressed in the case studies of this thesis.

## 1.4. Aims, research questions and methods

This thesis deals with topics of great relevance for basic ecology as well as conservation biology and aims to:

- I) the identification of dependent relations between traits,
- II) the identification of variable trait filters across different habitat types,
- III) the detection of potential traits driving species occurrence and extinction risk.

Ecological analyses on species traits are discussed to be biased by phylogenetic effects (Grafen, 1989; Purvis, 2008), as closely related species are expected to share more similar species traits (Harvey and Pagel, 1991; Webb *et al.*, 2002). To evaluate a potential statistical bias arising from phylogenetic non-independent species, I accounted for a phylogenetic effect by using a species-by-species taxonomic distance matrix in all case studies. The use of a phylogenetic tree was not applicable, since a complete molecular phylogeny for all carabid beetle species considered in this study (i.e. a comprehensive phylogenetic tree) was unavailable. Nevertheless, the taxonomic hierarchies seem to be highly supported by molecular phylogenetic trees when available (e.g. Deuve *et al.* 2012; Ober and Maddison 2008).

### 1.4.1. Patterns and effects of ground beetle species traits across a large Central European species pool

The first two case studies of this thesis (Chapter 2 and 3) focused on a large Central European species pool of ground beetle species. To achieve the study objectives, I compiled ground beetle phylogenetic relatedness (calculated from taxonomic levels in Löbl and Smetana 2003, determined a main habitat

preference and degree of habitat specialization for each species (Bräunicke and Trautner, 2009). Additionally, I updated the ecological and distributional traits information, available on the trait-database [www.carabids.org](http://www.carabids.org) (Homburg *et al.*, 2014b), by performing detailed literature review and expert interviews. Through this, I was able to increase the database's trait information content on six species traits (distribution range size, mean body size, hindwing morphology, trophic level, reproduction period and hibernation stage) of 566 ground beetle species, from 79 % to 98 % of known trait information. Especially, information on trophic level, hibernation stage and reproduction period were still missing for many species. For instance, information on reproduction period was available for 42 % of the species before this work was started and increased to 95 % afterwards. The ascertained trait information will soon be incorporated and therefore be freely available in the dynamic database on [www.carabids.org](http://www.carabids.org). The updated trait information can be used in further analyses on species communities and functional diversity studies.

In **Chapter 2**, I present a study dealing with the questions of which species traits of ground beetles show dependent relations to each other and how habitat-specific filtering of traits varies between different habitat types. Dependent relations between traits were already found for many taxa, including ground beetles, e.g. body size x hind wing morphology (Davies *et al.*, 2000; Homburg *et al.*, 2013; Laube *et al.*, 2013). Still, traits are often tested separately and trait relations are ignored in ecological analyses (Davies *et al.*, 2004; Henle *et al.*, 2004; Laube *et al.*, 2013). However, since related traits are not independently of each other, not accounting for trait relations may lead to false interpretations. By testing for the correlation of six traits to each other, using a large species pool of 555 ground beetle species, I aimed to give general information about ground beetle trait relations, which should be considered in trait analyses (Laube *et al.*, 2013). Furthermore, studies on species pools of separate habitat types showed that species traits can largely vary between different habitat types. To our knowledge, most studies on ground beetle traits were examined on the local community level (Birkhofer *et al.*, 2017; Bonn, 2000; Jelaska and Durbesic, 2009). However, barely any study compared habitat-specific filters of traits between large numbers of habitat types or verified that the results identified on local communities can also be applied to the entire habitat species pool on a larger geographical extent. Here, I tested for trait variations between different habitat types by applying one-way analysis of variance. The aim was to identify habitat-specific filters with respect to ecological and distributional species traits, as it may offer a new analytic tool for both ecology and conservation biology.

In **Chapter 3**, I aimed to identify the relative importance of traits on ground beetle extinction risks, to expand our understanding of general patterns and mechanisms behind ground beetle vulnerability to extinction. Recent studies already identified population declines for ground beetles with large body size in the Great Britain (Brooks *et al.*, 2012) or with large body size, high habitat specialization, and low dispersal ability across Belgium, Denmark and the Netherlands (Kotze and O'Hara, 2003). I used 464 ground beetles species to identify which traits drive the extinction risks of Central European ground beetles. Applying an ordinal linear regression, the relationships of species extinction risks to seven ecological and distributional traits (distribution range size, habitat specialization, habitat preference, body size, hindwing morphology, trophic level and reproduction period) were analyzed. As a proxy for current species extinction risks, I used the recently updated Red List of carabid beetles in Germany (Schmidt *et al.*, 2016). To account for varying trait responses in different habitat types, I ran separate

models for the species pools of the habitat types forest, open, riparian and wetland. The results of this case study can help to formulate useful recommendations for the conservation management of different target habitat types, due to the general predictions across the entire species pool as well as habitat-specific perceptions made here.

#### 1.4.2. Effects of ground beetle species traits on the species persistence of smaller species pools of forests

While the first two case studies aimed to identify general patterns of ground beetle traits and their importance for extinction risks, in the second part of this thesis, I examined whether the broad findings of the previous chapters can be applied on local communities.

In **Chapter 4**, I analyzed whether a nestedness pattern could be found in forest ground beetle communities and which affect species traits show on species occurrences. A nested community composition has been shown to arise from diverse abiotic and biotic processes, including non-random colonization and extinction events (Atmar and Patterson, 1993; Wright *et al.*, 1998). Here, a small pool of 28 forest-dwelling ground beetle species was used, focusing not only on a local geographical scale (e.g. Weller and Ganzhorn 2004; Zalewski and Ulrich 2006), but also on a large dataset of ground beetle communities in 296 forest plots located in the three countries (Belgium, the Netherlands and Germany). As species were sorted according to their occurrences among plots, a nestedness analyses of communities can prove to be a valuable tool for identifying species that are more sensitive to habitat change and hence more prone to extinction (Bolger *et al.*, 1991; Martinez-Morales, 2005). These species can act as indicators for ecological conditions or species richness of an ecosystem. By using the nestedness by overlap and decreasing fill (NODF) approach, it was tested if species community compositions were ranked in a nested order. Furthermore, individual species occurrence ranks were calculated and used to determine whether species traits drive occurrence ranks, thereby, influencing species' vulnerability to extinction (Patterson and Atmar, 2000). Based on the results, specific implications for the habitat management of Central European forests were provided.

**Chapter 5** considers the long-term trend of a local ground beetle populations in an ancient forest and highlights traits that were significantly correlated with population declines. While several long-term monitoring programs exist for vertebrates, such as birds or mammals (cf. Battersby and Greenwood 2004; Schmeller *et al.* 2012), quantitative data from long-term surveys on insects are still limited. Nevertheless, some studies demonstrated long-term trends for a decline in insect species richness and biomass (Brooks *et al.*, 2012; Hallmann *et al.*, 2018; Kotze and O'Hara, 2003). To identify whether long-term population declines can also be found in the oldest and largest nature reserve of Germany, data of a continuous long-term survey over 24 years in an ancient forest of the nature reserve Lüneburger Heide was analyzed. This case study aimed to present the temporal dynamics of the species community, as well as to identify which species traits are characteristic for species with increasing or decreasing occurrences within the habitat. To shed light on these aspects, I used generalized linear models to test for temporal trends in species richness, functional diversity, phylogenetic diversity and biomass. Generalized linear mixed effects models was used to identify trait effects on species occurrences. Results of long-term surveys are very rare and therefore surely provide revealing insight for the development of local and global conservation measures for insect populations and communities.



## 2. ECOLOGICAL AND DISTRIBUTIONAL TRAITS VARY BETWEEN GROUND BEETLES OF DIFFERENT HABITAT TYPES IN CENTRAL EUROPE

Manuskript

D. Nolte, E. Boutaud, C. Drees, D.J. Kotze, A. Schuldt and T. Assmann

### **Abstract**

Species traits can vary considerably between species pools of different habitat types. For ground beetles, habitat filtering effects on traits have mostly been tested on local communities, with little known at larger geographical scales. When investigating trait-based approaches it is important to consider factors influencing trait interactions, for instance the relations between species traits, or phylogenetic relatedness of species. Here, we show that significant relations between traits of 555 Central European ground beetle species are common, e.g. body size x hind wing morphology or range size x hind wing morphology. Therefore, many traits cannot be considered independently of each other. Only a very small phylogenetic signal in the distribution of species across different habitat types was found, suggesting, that species traits differ irrespective of phylogenetic relatedness in different habitats. Our findings further highlight that traits already identified to characterize local species pools of particular habitat types can often also be confirmed at larger geographical scales. While species of frequently disturbed habitats (coastal, riparian and wetland habitats) are characterized by small body size, high frequency of macroptery, intermediate to high habitat specialization, spring breeding and mainly predatory feeding behaviour, species of more stable habitats (forest, mountainous and open habitats) display greater trait variations, but are generally of larger body size and more frequently breed in autumn, than species of frequently disturbed habitats. We argue that identifying relations between traits and determining habitat-specific filtering effects on traits at a broader geographic scale will provide new information, important for the analyses of ground beetles in ecology and conservation biology. A better understanding of the above-mentioned aspects can be used to detect natural or human-altered abiotic and biotic environmental conditions to provide more reliable recommendations for conservation management.

## 2.1. Introduction

Ground beetles are species-rich (Lorenz, 2005) and one of the taxonomically and ecologically best-known insect taxa. Especially in Europe, entomologists have studied ground beetles intensively for decades (e.g. Kotze *et al.* 2011; Lindroth 1945, 1949; Thiele 1977). In almost every terrestrial ecosystem, ground beetles occur in reasonable numbers and fulfil important functional roles as predators or herbivores (Kulkarni *et al.*, 2015; Lövei and Sunderland, 1996). Ground beetles show a wide range of habitat preferences, from eurytopic species, occupying all kinds of habitat types, to stenotopic species, being specialized to certain habitat types. It is hypothesized that species exhibit ecophysiological traits allowing them to adapt to specific resource availabilities, environmental conditions and disturbances of their preferred habitat type(s) (Thiele, 1977).

In the study of ground beetles, ecological traits have a long-lasting history, dating back to Larsson (1939) and Lindroth (1945). During recent years, the number of studies on species traits has increased considerably. For instance, since a comprehensive trait database for western Palaearctic ground beetles is available (Homburg *et al.*, 2014b), analysis of species traits in this group has become increasingly common (e.g. Boetzl *et al.* 2018; Gallé *et al.* 2018; Nolte *et al.* 2017; Schirmel *et al.* 2016; Spake *et al.* 2016). Many studies have analysed species traits, such as dispersal power, body size, specialization or breeding season, which seem to have a crucial effect on the adaptation of species to their environment (Brooks *et al.*, 2012; Dieckmann *et al.*, 1999; Kotze and O'Hara, 2003; Nolte *et al.*, 2017). With a few exceptions (e.g. Homburg *et al.* 2013) most studies on ground beetle traits refer to local communities (Birkhofer *et al.*, 2017; Bonn, 2000; Jelaska and Durbesic, 2009; Ribera *et al.*, 2001).

At the community level, specific ecological traits have been found to characterize different habitat types (see Table 2.1); for example, riparian communities which are composed of species which are generally smaller in size and have strong power of dispersal (Eyre *et al.*, 2001), while forest communities usually show the opposite (Blake *et al.*, 1994; Jelaska and Durbesic, 2009). However, it is not clear whether the habitat-specific filters on traits found locally also apply to the entire species pool of a habitat type at larger geographical scales. In addition to ecological traits, distributional traits are also increasingly being analysed. These can also explain a considerable part of differences between species, communities or trophic interactions (e.g. Purvis *et al.* 2000a; Schuldt *et al.* 2012). The size of a species' distributional range is used for the IUCN Red-List classification of species (e.g. IUCN 2017), as it is related to the probability of extinction of the species concerned (Lomolino *et al.*, 2006; Thomas *et al.*, 2004). Range size is therefore of direct importance from a conservational point of view (e.g. Nolte *et al.* 2017) and has to be taken into consideration when analysing communities in different habitats. Knowledge on habitat-specific filtering, due to species traits and the resulting detectability of possible changes in the filtering effect should improve our understanding of the organization and assembly of communities (cf. Wellborn *et al.* 1996) and may help in detecting changes in natural or human-altered abiotic and biotic environmental conditions (Koivula, 2011; Mouillot *et al.*, 2013).

However, when investigating species traits, the effects of phylogenetic relatedness and relations between traits should be considered (Laube *et al.*, 2013; Purvis *et al.*, 2000a). Analyses may be biased, because closely related species tend to inhabit more similar habitat types and show more similar species traits (Díaz *et al.*, 2013; Freckleton *et al.*, 2002). Relations between traits, for example body size x range size, are found for many taxa (Laube *et al.*, 2013; Lester *et al.*, 2007), and can therefore be expected in ground beetles. For instance, a generally known trait relation exists between adult body size and development

time. Such a relation between traits can arise when two traits are related to the same environmental variable, such as temperature in this case (e.g. Kingsolver and Huey 2008). Related traits, therefore, are not independently from each other and should not be analysed separately. However, at least to our knowledge, ground beetle trait relations have not yet been investigated in detail.

A better understanding of trait variation can only be gained from research at a broader geographic scale and by including a larger species pool. Based on a large dataset of Central European ground beetles, our aim is to analyse (a) relations between species traits, (b) phylogenetic effect on species distribution across habitat types and (c) the habitat-specific filter of ecological and distributional traits. Given the number of traits and habitat types, we did not present specific hypothesis, but expect certain traits to occur more often in the species pools of certain habitat types (see Table 2.1).

**Table 2.1.:** Carabid beetle traits used in the analyses (adopted from Homburg *et al.* 2014b) and hypothesized trends in the different habitat types.

Trait	Trait type	Trait explanations / value	Expected differences between habitat-specific species pools
Body size	continuous	Mean body size of adult beetles (mm)	Forest species have larger body size than those from other habitats (Blake <i>et al.</i> , 1994; Magura <i>et al.</i> , 2002), whereas species of riparian habitats are mostly small (Gerisch, 2011).
Distribution range size	continuous	Area of Palaearctic countries in which the given species is recorded (km <sup>2</sup> )	A high amount of endemic species occurs in mountainous habitats, which will therefore show low distribution range sizes (Habel and Assmann, 2010).
Habitat specialization	continuous	Number of habitat types not occupied in Germany (ranging from highly specialized (8) to broad generalist (1))	Species occurring in extreme habitats (e.g. those with low temperatures or high salinity) are more specialized than all others (Devictor <i>et al.</i> , 2010).
Hind wing morphology	ordinal	Brachypterous (= short winged, flightless) Dimorphic (species with long and short winged specimens) Macropterous (= long winged, predominantly flight-active)	The highest amount of brachypterous species can be found in stabile habitats, which persists for long time (e.g. forest habitats, Jelaska <i>et al.</i> 2011), while in less stable habitats (e.g. riparian, wetland habitats) species are mostly macropterous or sometimes dimorphic (Bonn <i>et al.</i> , 2002) which makes (re-) colonization easier and enables them to escape floodings.
Breeding season	nominal	Autumn breeder Spring breeder Variable breeding season (both spring and autumn breeder) Winter breeder	Increase of spring breeders in habitats with inundation probability (e.g. riparian habitats). Imagines survive floods with higher probability than larval instars (Cárdenas and Hidalgo, 2004). Increase of autumn breeders in habitats less disturbed during winter time (e.g. forest habitats, Halme and Niemelä 1993).
Trophic level	nominal	Herbivorous Omnivorous Predatory	Open habitats (e.g. pastures or meadows) have higher diversity and abundance of plants producing small seeds, which should increase the number of herbivorous species (Vanbergen <i>et al.</i> , 2010).

## 2.2. Material and Methods

### 2.2.1. Ground beetles and species traits

We compiled a dataset comprising all 566 ground beetle species occurring in Germany (Schmidt *et al.*, 2016). A catalogue published by the Society for Applied Carabidology (GAC) (Bräunicke and Trautner, 2009) provides numerous details about the habitat preferences of (Central European) ground beetle species. We used this information to classify the species into eight categories of main habitat preferences: coastal, forest, mountain, open, riparian, special, wetland habitats, and eurytopic species (coastal habitats comprise inland salt marshes, wetlands include all non-riparian sites influenced by the ground water table, and special habitats include caves, cellars and waste disposal sites). The habitat type that was indicated most frequently across all listed regions for a given species was chosen as the main habitat preference of the species. Species for which no main habitat preference was available (11 species) were excluded from the analysis, resulting in 555 ground beetle species used in the analysis. Eurytopic species were indicated to occur in at least in seven different main habitat types.

We further compiled a set of six species traits (Table 2.1), reflecting basic aspects of ground beetle ecophysiology and habitat selection (e.g. Thiele 1977). The majority of trait information was extracted from the [www.carabids.org](http://www.carabids.org) database (Homburg *et al.*, 2014b), such as body size, hind wing morphology, trophic level, breeding season or distribution range size. Missing trait information was complemented from the literature and, if necessary, expert knowledge. Range size was calculated as the sum of the countries' areas in which the species has been recorded according to the Catalogue of Palaearctic Coleoptera (Löbl and Smetana, 2003). Habitat specialization is represented by the number of habitats a species does not occur in, following the GAC catalogue (Bräunicke and Trautner, 2009). Thus, a higher value indicates a higher degree of habitat specialization.

### 2.2.2. Statistical analysis

All statistical analyses were performed in R, version 3.5.0 (R Core Team, 2018), using packages 'vegan' (Oksanen *et al.*, 2016), 'multcomp' (Hothorn *et al.*, 2008), 'rcompanion' (Mangiafico, 2018), 'ade4' (Jombart *et al.*, 2010), and 'nnet' (Venables and Ripley, 2002).

#### ***Analysis of phylogenetic relatedness***

To test for a phylogenetic signal in the ground beetle species pool across habitat types, we calculated Morans'*I* based on Abouheif (1999). This analysis considers relatedness by evaluation at a species' taxonomic distance matrix (based on taxonomical hierarchies) instead of using molecular phylogeny. We compiled the taxonomic distance matrix according to the Catalogue of Palaearctic Coleoptera (Löbl and Smetana, 2003; Nolte *et al.*, 2017). Molecular phylogeny by phylogenetic trees was not possible, since for several species no DNA sequences are available. However, where available, taxonomic hierarchies of carabid beetles are highly supported by current molecular phylogenetic trees (e.g. Deuve *et al.* 2012; Ober and Maddison 2008).



### ***Relations between traits***

We used all combinations of species traits to test whether a given trait depends on another trait. Tests between continuous traits (set of two numeric variables) were carried out using Spearman rank correlation, relations between continuous and categorical traits (combination of numeric and nominal variable) were analysed using one-way ANOVA and relations between categorical traits (sets of two nominal variables) were tested by Pearson's  $\chi^2$ -Contingency-Tests.

### ***Traits in different habitat types***

To compare the assemblages of ground beetles and their traits between different habitat types, we used principal coordinates analysis (PCoA). PCoA was based on Gower's dissimilarity coefficient, which is a commonly used measure of proximity for mixed data types (e.g. nominal, ordinal). Each species was only used for the analyses of its main habitat preference. Differences in continuous traits between species pools of different habitat types were tested using one-way ANOVA, using the traits body size, distribution range size and habitat specialization as response variables. Tukey post-hoc tests determined significant differences among means of the different habitat types. To test for differences in the categorical traits hind wing morphology, breeding season and trophic level between the species pools of different habitat types, we used Pearson's  $\chi^2$ -tests and performed multinomial logistic regression (MLR) for significant differences in trait characteristics between habitat types. MLR is an extension of binary logistic regression, allowing for the prediction of the probability of category membership for more than two categories of dependent or response variable, by using maximum likelihood estimation.

## **2.3. Results**

We classified one main habitat preference for each species of a set of 555 ground beetle species, all occurring in Germany; 33 % of the species are associated with open habitats (186 species), species of wetlands or riparian habitats both represented ca. 19 % each (both 103 species each), 14 % of the ground beetles preferred forest habitats (76 species) and few species were associated with mountainous (27 species), coastal (27 species) or special habitats (15 species). Eighteen species were classified as eurytopic, as they occur in almost all habitat types and do not indicate habitat preference at all.

### **2.3.1. Analysis of phylogenetic relatedness**

Our results showed a very weak, but significantly positive phylogenetic signal for the habitat preference of ground beetle species (Moran's  $I = 0.017$ , Standard observation = 10.411,  $P < 0.001$ ). The low value indicates that closely-related ground beetles show barely higher similarity in their habitat preference than expected by chance. Moran's  $I$  varies from 0, implying no explanatory power of species phylogeny, to 1, when the phylogeny fits completely with habitat preference.

### 2.3.2. Relations between traits

Spearman rank correlation revealed a significant relation only between the continuous traits range size and habitat specialization (Table 2.2). For most combinations of continuous to categorical traits, ANOVA analysis showed significant relations (Table 2.2, Fig. A.1a-g in Supplement). Only range size and habitat specialization were not significantly related to breeding season. All combinations of the categorical traits, hind wing morphology, breeding season and trophic level showed significant results (Table 2.2, Fig. A.1h-j in Supplement). The significant relations found between many species traits indicate that ground beetle traits are often dependent to each other within habitats.

**Table 2.2.:** Summary of analyses testing for relations between ground beetle species traits, using Spearman correlation ( $\rho$ -values), ANOVA (F-values) and Pearson's  $\chi^2$ -tests ( $\chi^2$ -values). Significant correlations are indicated in bold, Df = degrees of freedom.

	Body size	Distribution range size	Habitat specialization	Hind wing morphology	Breeding season
Distribution range size	$\rho = -0.04$ Df = 553				
Habitat specialization	$\rho = -0.02$ Df = 553	<b><math>\rho = -0.4</math> ***</b> <b>Df = 553</b>			
Hind wing morphology	<b>F = 77.69 ***</b> <b>Df = 2</b>	<b>F = 51.06 ***</b> <b>Df = 2</b>	<b>F = 20.94 ***</b> <b>Df = 2</b>		
Breeding season	<b>F = 16.23 ***</b> <b>Df = 3</b>	F = 2.22 Df = 3	F = 1.15 Df = 3	$\chi^2 = 29.60$ *** <b>Df = 6</b>	
Trophic level	<b>F = 4.48 *</b> <b>Df = 2</b>	<b>F = 15.55 ***</b> <b>Df = 2</b>	<b>F = 5.22 **</b> <b>Df = 2</b>	$\chi^2 = 44.50$ *** <b>Df = 6</b>	$\chi^2 = 66.40$ *** <b>Df = 9</b>

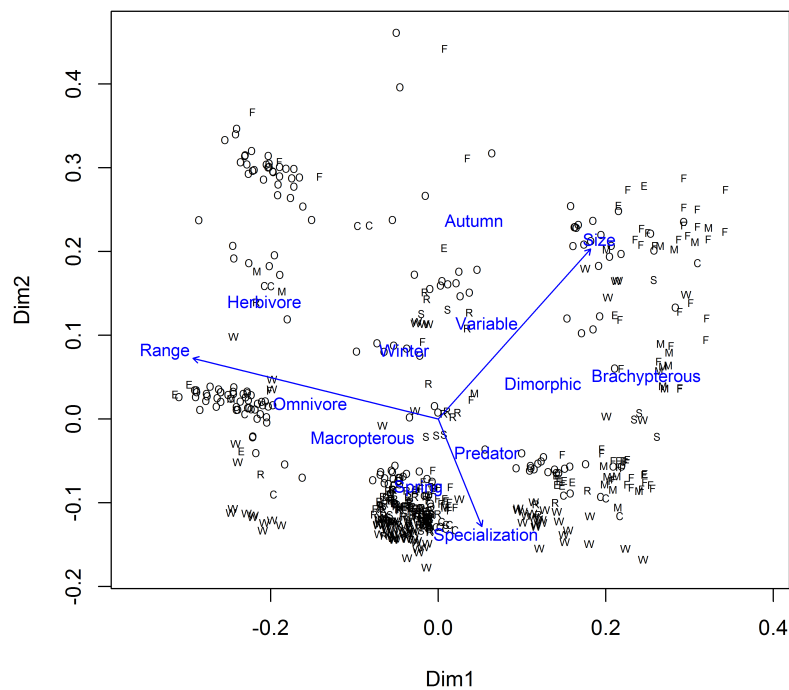
Significance levels: .P < 0.1; \*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001

### 2.3.3. Traits in different habitat types

Differences in ground beetle assemblages between habitat types, according to their species traits, were revealed by PCoA ordination analysis, which explained 67.7 % of the variance (Fig. 2.1). The first axis explained 27 %, while the second axis 22 % of variance.

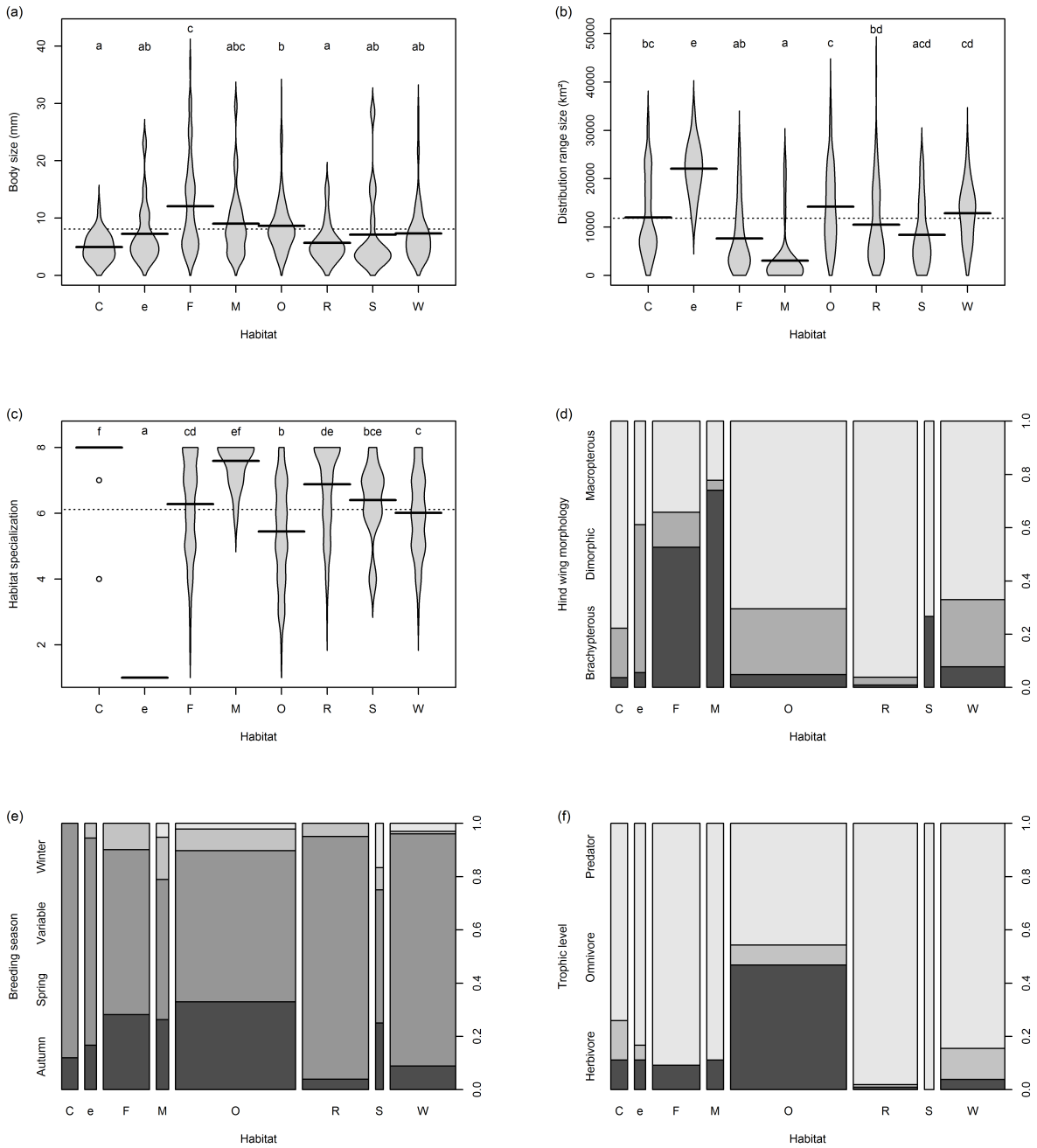
Body size was significantly different between species pools of different habitat types ( $F_{7, 547} = 11.53$ ,  $P < 0.001$ ). Forest species were larger on average, while ground beetles of coastal and riparian habitats were smallest (Figs 2.1, 2.2a). Similarly, distributional range size varied significantly between species of different habitat types ( $F_{7, 547} = 17.86$ ,  $P < 0.001$ ) with eurytopic species showing significantly larger ranges than species of all other habitat types. Species of open and wetland habitats have large range sizes, while species from mountainous habitats and, to a lesser extent, forest species have smaller ranges (Figs 2.1, 2.2b). We also showed significant differences in habitat specialization levels ( $F_{7, 547} = 57.07$ ,  $P < 0.001$ ); coastal and mountainous species, and to a lesser extent riparian species, showed the highest degree of habitat specialization, while species of open habitats were less specialized to their habitat (Figs 2.1, 2.2c).

Habitat types showed significant differences in hind wing morphology ( $\chi^2 = 241.94$ ,  $df = 14$ ,  $P < 0.001$ ), Table 2.3, Figs 2.1, 2.2d); forest and mountainous habitats had significantly more brachypterous species than open habitats, while all other habitat types are characterized by few brachypterous species. The highest proportion of dimorphic species was found for eurytopic species, while (almost) no dimor-



**Figure 2.1.:** Principal coordinates analysis (PCoA) summarizing the relationship of 555 ground beetle species with respect to their main habitat preferences and different species traits (Size = Body size; Range = Distribution range size; Specialization = Habitat specialization; Hind wing morphology: Brachypterous, Dimorphic and Macropterous; Breeding season: Autumn, Spring, Variable and Winter; Trophic level: Herbivore, Omnivore and Predator; Habitat types: C = coast, e = eurytopic, F = forest, M = mountain, O = open, R = riparian, S = special habitats and W = wetland).

phic species occurred in riparian, mountainous and special habitats. Species of riparian habitats were almost exclusively macropterous and, together with coastal, special, wetland and open habitats, had the highest proportions of macropterous species. The proportions of species with different breeding seasons varied among habitat types ( $\chi^2 = 90.56$ ,  $df = 21$ ,  $P < 0.001$ , Table 2.3, Fig. 2.2e); open habitat species had the highest proportion of autumn breeders, while it was significantly more probable to have spring breeders in riparian, wetland and coastal habitats. Most winter-reproducing species were found in special habitats. Trophic level proportions also differed significantly between habitat types ( $\chi^2 = 169.30$ ,  $df = 14$ ,  $P < 0.001$ , Table 2.3, Fig. 2.2f); species of open habitats showed the highest proportion of herbivore species with slightly more species being herbivores than predators. In all other habitats, significantly more predator species were found, with riparian and special habitats having almost only predator species. Omnivorous species occurred mostly in coastal, wetland and open habitats.



**Figure 2.2.:** Species trait variations of the different habitat types (C = coast, e = eurytopic, F = forest, M = mountain, O = open, R = riparian, S = special habitats and W = wetland). (a-c): Bean plots illustrate variation in (a) body size, (b) distributional range size and (c) habitat specialization (ranging from 1: not specialized to 8: highly specialized) of species with different habitat preferences. Black lines indicate means of the single habitat types and dashed line indicate the overall mean, letters above the 'beans' refer to significant differences after Tukey tests. (d-f): Proportions of the species trait characteristic (shown in different shades of grey) of (d) hind wing morphology, (e) breeding season, and (f) trophic level between species with different habitat preferences. The width of the bars correspond to species number within the habitat type.

**Table 2.3:** Multinomial logistic regression results testing the effect of species habitat preference on the categorical species traits hind wing morphology, breeding season and trophic level. Model estimates (SE).

Traits	Intercept (Open)	Coast	Eury- topic	Forest	Moun- tain	Riparian	Special habitats	Wetland
Hind wing morphology (brachypterous)								
Dimorphic	1.631*** (-0.36)	-0.021 (1.15)	0.671 (1.11)	-3.018*** (0.50)	-4.627*** (1.08)	-0.531 (1.21)	-14.777 (357.75)	-0.453 (0.54)
Macropterous	2.678*** (0.34)	0.367 (1.08)	-0.732 (1.12)	-3.035*** (0.42)	-3.882*** (0.57)	1.919 (1.06)	-1.666* (0.67)	-0.523 (0.50)
Breeding season (autumn)								
Spring	0.543*** (0.16)	1.449* (0.63)	0.997 (0.65)	0.245 (0.31)	0.15 (0.57)	2.603*** (0.53)	0.15 (0.72)	1.737*** (0.38)
Variable	-1.403*** (0.28)		0.304 (1.19)	0.604 (0.49)	0.892 (0.78)	1.626* (0.73)	0.304 (1.19)	-0.795 (1.09)
Winter	-2.725*** (0.51)				1.115 (1.21)		2.319* (1.04)	1.626 (0.84)
Trophic level (herbivore)								
Omnivore	-1.827*** (0.28)	2.114** (0.81)	1.134 (1.25)			1.826 (1.44)		2.925*** (0.64)
Predator	-0.023 (0.15)	1.92** (0.63)	2.038** (0.76)	2.311*** (0.42)	2.103*** (0.63)	4.638*** (1.01)		3.103*** (0.53)

Significance levels: .P < 0.1; \*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001

## 2.4. Discussion

Our analysis of 555 Central European ground beetle species illustrates that many species traits show clear relations to one other, e.g. large body size to brachypterous hind wing morphology, large distributional range size to macropterous hind wing morphology or breeding season to trophic level. Consequently, these traits cannot be considered independently. However, we did not find a clear phylogenetic signal on assemblages of different habitat types, leading to the conclusion that traits differ irrespective of phylogenetic relatedness. Furthermore, species with different traits are filtered depending on the habitat types.

### 2.4.1. Relations between species traits

Although it is likely to expect, that also ground beetles traits are interdependent, very few studies have examined this particular aspect (Gutierrez and Menéndez, 1997; Ribera *et al.*, 2001). We showed that many species traits are related to each other, with body size and hind wing morphology, as proxy for dispersal power, being particularly strong related. For the western Palaearctic, Homburg *et al.* (2013) confirmed on a large geographical scale, that flightless ground beetle species tended to be larger than winged species. Larger species, in particular, have to invest relatively more energy into active flight than smaller species, which may also drift passively by wind (Chapman *et al.*, 2005). In general, flight can lead to higher colonization efficiency and therefore be a specie's benefit. For large species, a trade-off can lead to a lower flight activity which increases survival rate. This relation is repeatedly postulated (e.g. Matalin 1997), however, we do not know of any empirical evidence for ground beetles. Moreover, Gillespie *et al.* (2017) showed that the flight activity period of smaller forest beetle species tends to be

longer than that of larger ones. Larger species may need higher temperatures for flight activity. This limited range of suitable weather conditions for large species could make them 'temporal specialists' (Ribeiro and Freitas, 2011).

The above-mentioned relation between body size and dispersal power leads to difficulties in the mechanistic interpretations of habitat or environmental filtering. For example, a comparison of the ground beetles of river banks with those of forests reveals striking and highly significant differences between these two traits. However, it is not clear whether it is one trait, only hind wing morphology or only body size that is adaptive here or whether both traits are affected. Dispersal power could be important for the colonization of river banks after flooding events. Since smaller species have greater power of dispersal (in terms of flight) than larger species, it is not clear whether riparian habitats also filter body size independently of dispersal power.

The second strongest relation was found between trophic level and breeding season. Open habitats generally have a high proportion of herbivorous ground beetles (Vanbergen *et al.*, 2010), due to a high availability of plant resources, especially seeds. We found the highest proportion of autumn breeders in the open habitat type where also half of the species are herbivorous. Although Ribera *et al.* (2001) suggested that more autumn breeders should be found in less disturbed sites, we assume that herbivory may be the predominant filter. Since the majority of plant resources, seeds in particular, are available during summer and autumn, a phenological coincidence with the food resource is possible (Talarico *et al.*, 2016). Hence, we cannot be certain whether breeding season is filtered independently of trophic level or whether herbivorous species, such as species of the genera *Ophonus*, *Harpalus* or *Amara* may be obliged to breed in the autumn (Talarico *et al.*, 2016).

The above-mentioned trait pairs, as well as the other significant relations between traits, enforces the notion why it is important to investigate trait relations, also for ground beetles. The interpretation of habitat-specific filtering effects and recommendations for conservation biology based on traits, will be most reliable when these trait relations are considered.

#### 2.4.2. Habitat-specific filtering of species traits

The proportion of species traits varied strongly between habitat types. Our results indicate that species of stable habitat types (forest, mountain, open and special habitats) are characterized by different traits than species of more unstable (coastal, riparian and wetland) habitats, which is in accordance with existing studies (e.g. Desender *et al.* 2005; Dhuyvetter *et al.* 2007).

Ripicolous species (of coastal, riparian and wetland habitats) were mainly characterized by small body size, high dispersal power (macroptery), high to medium habitat specialization (stenotopy), spring breeding and predatory feeding behaviour, in accordance with findings from local communities of ripicolous ground beetles (e.g. Bonn *et al.* 2002; Gerisch *et al.* 2012). Many traits are interpreted in the light of adaptation. In highly disturbed habitats, species are more at risk of local extinction, which should benefit species with higher dispersal ability (Southwood, 1977). High dispersal power enables ripicolous species to react quickly to frequent habitat disturbances, such as floods, and to cover larger distances by flight as well as quickly recolonize free habitat patches (Bonn, 2000; Gerisch, 2011; Ribera *et al.*, 2001). Furthermore, we observed breeding season to be associated with species habitat preference (Talarico *et al.*, 2016). In habitats disturbed by winter floods, the mortality rate is lower for spring breeders,

as they are in their sensitive larval stage, which is intolerant to hydraulic stress during summer time (Thiele, 1977). Autumn breeders, which larvae are exposed to a high flood probability during winter, or brachypterous species, which cannot react well to fast rising water levels, are therefore negatively affected by the habitat filtering, what may lead to a higher risk of extinction (Nolte et al. submitted).

Although a high habitat-specific filtering on traits can be expected for species of unstable habitat types, it is surprising that the traits characterising the habitat type's coast, riparian and wetland habitat, are so similar. We assume that the species of these habitat types have to respond to the same environmental factors, what thus benefit a group of species with specific traits (Gerisch *et al.*, 2012). Trait divergence due to competition seems not to be common locally and at the Central European species pool, and is not expected to be an important habitat filtering mechanism.

Expectably, eurytopic species displayed traits that optimized these species for survival in numerous habitat types. They possessed quite similar traits to those of ripicolous species, such as small body size and high proportion of macropterous species, which enable them to react quickly to habitat disturbances. They also showed low levels of habitat specialization, allowing them to colonize a high number of suitable habitat types, and a higher proportion of dimorphic species. Dimorphic species are known to benefit from their variable ecological strategy, the so called oogenesis-flight syndrome (Desender, 2000). During migration time dimorphic species profit from long winged individuals which have high colonization and reproduction rates, whereas under stable conditions the number of short winged individuals increases, which possess high establishment abilities (Aukema, 1991; Langellotto *et al.*, 2000).

In contrast, carabid beetles of more stable and less disturbed habitat types, such as forest, mountain, open and special habitat types generally displayed more differentiated traits. Stable habitat types were especially characterized by larger body size and higher percentages of autumn breeders, which seemed to be negative attributes in unstable habitat types. Natural selection reduces flight ability with increasing habitat stability (den Boer *et al.*, 1980), which explains why forest and mountainous species were largest and more often brachypterous in comparison to the species of most other habitat types (Brandmayr *et al.*, 2003; Magura *et al.*, 2002). In more stable habitats also the survival rate of winter larvae of autumn breeders increase, because of lower disturbance rates during winter time (Halme and Niemelä, 1993). The high variety of traits displayed in stable habitat types, may not only be caused by adaptations to different environmental condition in the habitat type (Talarico *et al.*, 2016) but also because of a low filtering effect due to a high stability of the habitat type. Besides all given explanations, certain traits can appear within a certain habitat types, not because the trait itself is filtered but because the trait is strongly related to another trait, which underlies the habitat filtering process.

## 2.5. Conclusion

We showed that Central European ground beetles are not structured by phylogenetic relatedness within habitat types. Consequently the habitat-specific filtering arise from different factors influencing species traits, such as trait relations or adaptation to environmental conditions in the habitat types, or both. Especially for communities of unstable habitat types, trait-based habitat filtering seems to play an important role. Nevertheless, further research is needed identifying which trait relations show synergetic effects on trait-based analyses. Besides this, also neglected traits of ground beetles, such as diurnal activity or preference for a certain substrate type should be considered in the future.

Here, we identified typical species traits characterizing habitat types on a larger geographical scale,

which will enable us to directly detect changes in the habitat filtering, when species numbers with untypical traits increase in the habitat. Therefore the knowledge of the habitat-specific filtering can be taken as early warning for anthropogenic landscape and habitat change.

## **Acknowledgements**

We thank Ingmar Harry, Pietro Brandmayr and Katharina Homburg for helping to complete the species trait dataset.



## A. Supplementary material

**Table A.1.:** Tukey test results displaying the effect of habitat preference on body size. Values presented are model estimates and significance levels (SE).

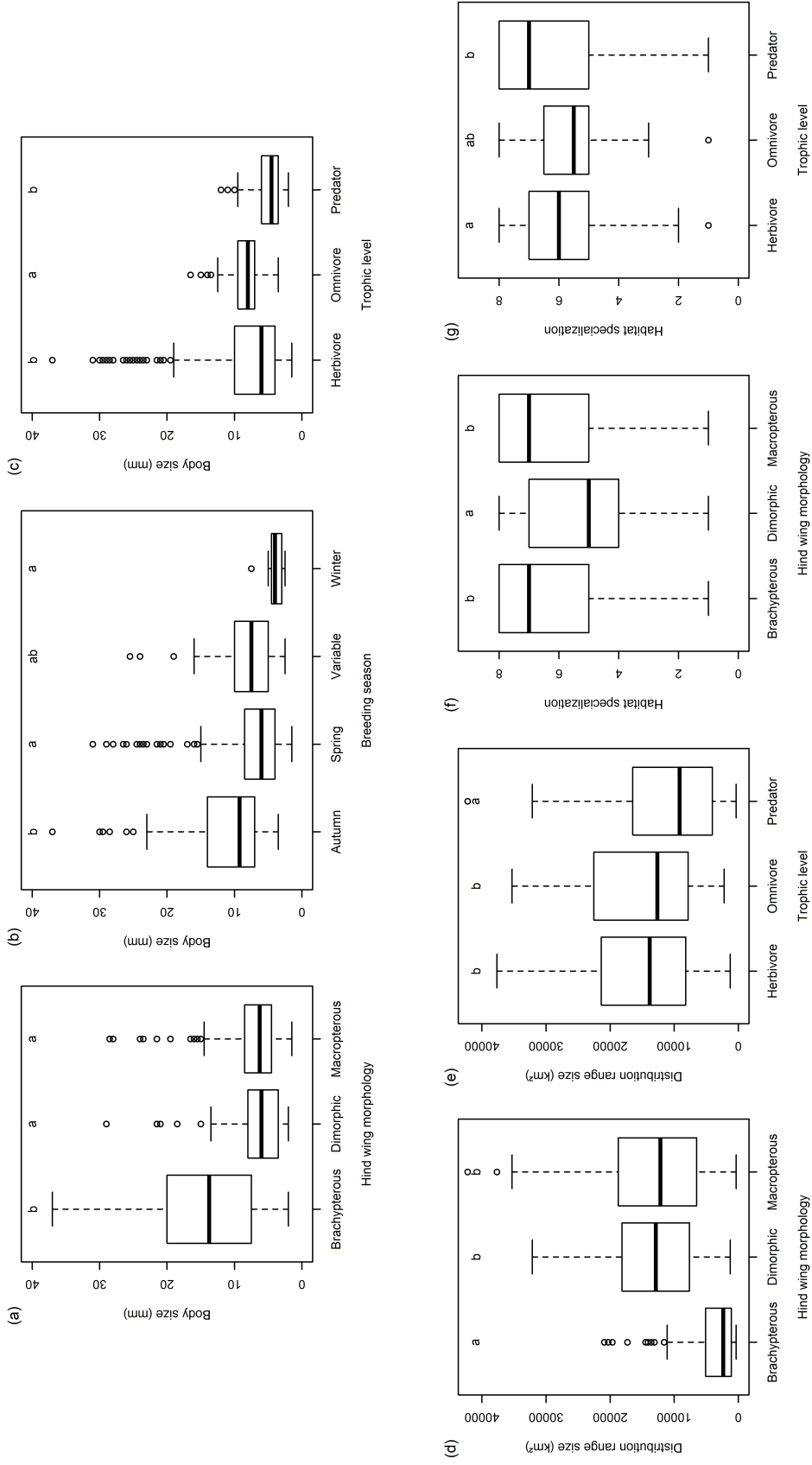
	Coast	Eurytopic	Forest	Mountain	Open	Riparian	Special habitat
Eurytopic	2.287 (1.58)						
Forest	<b>6.991***</b> <b>(1.16)</b>	<b>4.704*</b> <b>(1.36)</b>					
Mountain	4.056 (1.41)	1.769 (1.58)	-2.935 (1.16)				
Open	<b>3.685*</b> <b>(1.07)</b>	1.398 (1.28)	<b>-3.306***</b> <b>(0.70)</b>	-0.371 (1.07)			
Riparian	0.712 (1.12)	-1.575 (1.33)	<b>-6.279***</b> <b>(0.78)</b>	-3.344 (1.12)	<b>-2.973***</b> <b>(0.64)</b>		
Special habitat	2.170 (1.67)	-0.117 (1.82)	<b>-4.821*</b> <b>(1.47)</b>	-1.885 (1.67)	-1.515 (1.40)	1.459 (1.44)	
Wetland	2.377 (1.12)	0.090 (1.33)	<b>-4.614***</b> <b>(0.78)</b>	-1.679 (1.12)	-1.308 (0.64)	1.665 (0.72)	0.206 (1.44)

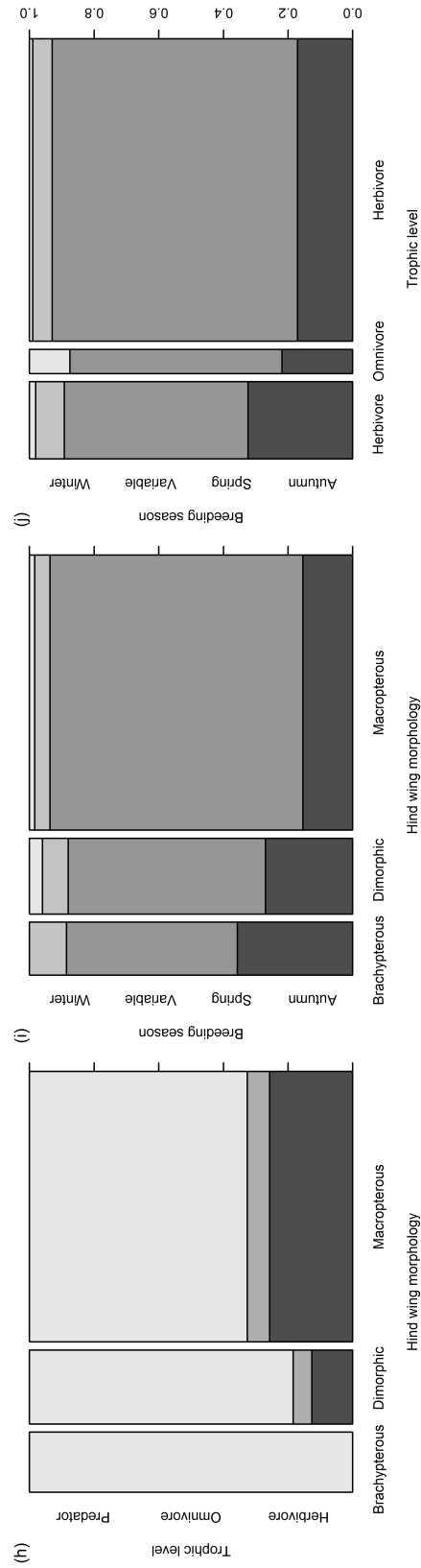
Significance levels: .P < 0.1; \*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001

**Table A.2.:** Tukey test results displaying the effect of species habitat preference on distributional range size. Values presented are model estimates and significance levels (SE).

	Coast	Eurytopic	Forest	Mountain	Open	Riparian	Special habitat
Eurytopic		<b>10062.1***</b> <b>(2242.6)</b>					
Forest	-4242.0 (1645.6)	<b>-14304.1***</b> <b>(1927.2)</b>					
Mountain	<b>-8957.6***</b> <b>(2005.8)</b>	<b>-19019.6***</b> <b>(2242.6)</b>	-4715.6 (1645.6)				
Open	2212.1 (1517.8)	<b>-7849.9***</b> <b>(1819.2)</b>	<b>6454.2***</b> <b>(994.2)</b>	<b>11169.7***</b> <b>(1517.8)</b>			
Riparian	-1504.2 (1593.4)	<b>-11566.2***</b> <b>(1882.8)</b>	2737.9 (1106.2)	<b>7453.4***</b> <b>(1593.4)</b>	<b>-3716.3**</b> <b>(905.2)</b>		
Special habitat	-3604.2 (2373.3)	<b>-13666.3***</b> <b>(2576.6)</b>	637.8 (2077.8)	5353.4 (2373.3)	-5816.4 (1978.2)	-2100.1 (2036.8)	
Wetland	860.1 (1593.4)	<b>-9202.0***</b> <b>(1882.8)</b>	<b>5102.1***</b> <b>(1106.2)</b>	<b>9817.7***</b> <b>(1593.4)</b>	-1352.0 (905.2)	2364.3 (1027.0)	4464.3 (2036.8)

Significance levels: .P < 0.1; \*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001





**Figure A.1.:** Significant relations between ground beetle species traits: (a-g): boxplots illustrate relations between (a) body size and hind wing morphology, (b) body size and breeding season, (c) body size and trophic level, (d) range size and hind wing morphology, (e) range size and trophic level, (f) habitat specialization and hind wing morphology and (g) habitat specialization and trophic level. Letters refer to significant differences after Tukey tests. (h-j): Relations between proportions of trait characteristics (shown in different shades of grey) of (h) trophic level and hind wing morphology, (i) breeding season and hind wing morphology, (j) breeding season and trophic level (for more information on statistics see Table 2.2).

**Table A.3.** Tukey test results displaying the effect of habitat preference on habitat specialization. Values presented are model estimates and significance levels (SE).

	Coast	Eurytopic	Forest	Mountain	Open	Riparian	Special habitat
Eurytopic	<b>-6.815***</b> (0.41)						
Forest	<b>-1.494***</b> (0.30)	<b>5.321***</b> (0.35)					
Mountain	-0.222 (0.37)	<b>6.593***</b> (0.41)	<b>1.272***</b> (0.30)				
Open	<b>-2.369***</b> (0.28)	<b>4.446***</b> (0.33)	<b>-0.874***</b> (0.18)	<b>-2.146***</b> (0.28)			
Riparian	<b>-0.931*</b> (0.29)	<b>5.884***</b> (0.35)	0.563 (0.20)	-0.709 (0.29)	<b>1.437***</b> (0.16)		
Special habitat	<b>-1.415*</b> (0.44)	<b>5.400***</b> (0.48)	0.079 (0.38)	-1.193 (0.44)	0.954 (0.36)	<b>-0.484***</b> (0.38)	
Wetland	<b>-1.805***</b> (0.29)	<b>5.010***</b> (0.35)	-0.311 (0.20)	<b>-1.583***</b> (0.29)	<b>0.563*</b> (0.16)	-0.874 (0.19)	-0.390 (0.38)

Significance levels: .P < 0.1; \*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001

### 3. HABITAT SPECIALIZATION, DISTRIBUTION RANGE SIZE AND BODY SIZE DRIVE EXTINCTION RISK IN CARABID BEETLES

Submitted article<sup>1</sup>

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#### **Abstract**

The worldwide biodiversity crisis is ongoing. To slow down, or even halt future species loss it is important to identify potential drivers of extinction risk. Species traits can help to understand the underlying process of extinction risk. In a comprehensive study on 464 carabid beetle species, we used ordinal logistic regression to analyze the relationship of species traits to extinction risk in Central Europe, taking phylogenetic relatedness into account. To consider varying trait responses in different habitat types, we also tested models for species groups associated with different habitat types (forest, open, riparian and wetland). Our results identified three traits of particular importance, with habitat specialization as most important predictor. Additionally, small distribution range (which is not considered in the categorization of this Red List) and large body size emerged as important predictors in the majority of models. Furthermore, large macropterous species showed high extinction risk. Overall, species associated with mountainous, coastal and open habitats generally revealed a high risk of extinction while most forest species showed a low extinction risk. However, forest species with predatory feeding behavior were threatened, as were wetland species that reproduce in autumn. Phylogenetic relatedness had no influence on how species traits predict carabid beetle extinction risk. In the light of these results, management and recovery plans for species which exhibit characteristic traits strongly associated with extinction risks, as well as the conservation and restoration of mountain, coastal and open habitats, have to be prioritized.

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### 3.1. Introduction

Biological annihilation (Ceballos *et al.*, 2015, 2017) is a contemporary possibility, threatening ecosystems and humans alike. Defaunation is experienced both locally (Hallmann *et al.*, 2017), and globally (Dirzo *et al.*, 2014), yet the loss of insect species may be highly underestimated (Dunn, 2005; Purvis *et al.*, 2000a). The decline in insect diversity as well as local population losses might have dramatic consequences for the provision of ecosystem services and functions (Balvanera *et al.*, 2006; Ceballos *et al.*, 2015). However, to understand the mechanisms behind biodiversity loss and to improve conservation strategies, general knowledge of the drivers of species extinction processes has to improve. Species are affected by many extrinsic factors, such as habitat loss, fragmentation, habitat quality or climate change (Fahrig, 2003; Purvis *et al.*, 2000b; Sala *et al.*, 2000), but their response to these extrinsic factors are to a large extent dependent on their intrinsic characteristics. Species of similar trait characteristics may show similar sensitivity to environmental change and have similar extinction risks, allowing for improved predictability of the effects of habitat alteration on species in general (see Moretti *et al.* 2017). Nevertheless, in comparison to a few charismatic groups, such as butterflies, dragonflies, damselflies or saproxylic beetles (Clausnitzer *et al.*, 2009; Essens *et al.*, 2017; Seibold *et al.*, 2015), less is known about the drivers of species extinction probabilities in other species-rich insect groups.

Here, we focus on the extinction risk of a species-rich and functionally important group of insects, carabid beetles. Carabid beetles (Carabidae) are taxonomically and ecologically well-known (Homburg *et al.*, 2014b) and a widely distributed taxon, occurring in decent numbers in almost every terrestrial ecosystem (Kotze *et al.*, 2011; Lövei and Sunderland, 1996), yet have also experienced a decrease in number (Brooks *et al.*, 2012; Schmidt *et al.*, 2016). These beetles perform important functional roles as predators of pest species and other invertebrates, or as granivores regulating weed seeds (Bohan *et al.*, 2011; Lövei and Sunderland, 1996), and provide an important opportunity to evaluate the effects of extirpation and extinction on ecosystems. Previous studies have discussed habitat specialization, body size and dispersal ability (hind wing morphology of carabid beetles) as potential predictors for species extinction risks in carabid beetles (Kotze and O'Hara, 2003; Nolte *et al.*, 2017). Additional drivers that may play a role in species vulnerability include distribution range size, diet, and reproduction as well as trait combinations. Furthermore, since most carabid species exhibit preference for a specific habitat type, and given that different habitat types often experience differences in anthropogenic development, habitat preference per se can influence extinction probability.

Our study aimed to identify the relative importance of carabid beetle traits linked to extinction risk, to prove, better define and substantiate established ideas about species extinction processes. For our analysis, we used the recently updated Red List status of carabid beetles in Germany as a proxy of the current species extinction risk. We selected a set of carabid beetle traits informed by earlier studies on the relationship of species traits and extinction risks (Henle *et al.*, 2004; Kotze and O'Hara, 2003; Terzopoulou *et al.*, 2015) and made predictions on whether these traits would be positively or negatively associated with extinction risk (Table 3.1). Analyzing species traits on a broader scale will enable us to predict species groups that are more prone to extinction. Based on these findings, we can provide useful recommendations for conservation management for the main target habitats and species (Barbaro and van Halder, 2009). These recommendations may also be applied to other countries and regions with a similar species pool, to counteract further insect loss which is currently under intensive public and scientific debate (Hallmann *et al.*, 2017; Leather, 2018).

**Table 3.1.:** Carabid beetle traits used in the analyses (adopted from Bräunicke and Trautner 2009; Homburg *et al.* 2014b) and their assumed effects in terms of extinction risk (a positive effect means an increase in extinction risks).

Trait	Trait type	Trait value	Assumed trait effect	Literature
Distribution range size	continuous	Area of Palearctic countries in which the given species recorded (km <sup>2</sup> )	Negative. Increasing distribution range size leads to lower extinction risk.	Gaston and Fuller (2009); Nolte <i>et al.</i> (2017)
Habitat specialization	continuous	Number of habitat types not occupied in Germany (ranging from highly specialized (8) to extreme generalist (1))	Positive. Extinction risk increases with habitat specialization (fewer suitable habitats).	Kotze and O'Hara (2003)
Habitat preference	nominal	Coastal (C) Eurytopic (E) Forest (F) Mountain (M) Open (O) Riparian (R) Special habitats (S, such as skeletal soils or caves) Wetland (W, does not include riparian habitats)	Mixed. Species related to a habitat type that has recently increased in Germany or Central Europe have lower extinction risks than species of habitat types that have decreased.	
Body size	continuous	Mean body size (cm)	Positive. Larger body size leads to a higher extinction risk.	Brooks <i>et al.</i> (2012); Dirzo <i>et al.</i> (2014); Kotze and O'Hara (2003)
Hind wing morphology	ordinal	Brachypterous (= short winged, flightless) Dimorphic (species with long and short winged specimens) Macropterous (= fully winged, predominantly flight-active)	Mixed. Dimorphic species show the lowest extinction risk due to their variable ecological strategy, with high dispersal power and establishment ability. Macropterous species benefit from higher dispersal powers than brachypterous species.	Kotze and O'Hara (2003); Nolte <i>et al.</i> (2017)
Trophic level	nominal	Herbivorous Omnivorous Predator	Negative. A higher trophic level leads to a higher extinction risk.	Davies <i>et al.</i> (2000)
Breeding season	nominal	Autumn breeder Spring breeder Variable breeding period (both spring and autumn breeder) Winter breeder	Mixed. Species with a variable breeding season have a lower extinction risk, while spring, autumn and winter breeder show higher extinction risks.	den Boer (1968); Nolte <i>et al.</i> (2017)

## 3.2. Methods

### 3.2.1. Carabid beetles and extinction risk

The classification of extinction risk in the German Red Lists of carabid beetles (Schmidt *et al.*, 2016) follows the approach of Ludwig *et al.* (2006), which is based on guidelines of the International Union for Conservation of Nature (IUCN); except in Germany, the size of the entire distribution range is not used in this classification. This approach is applied for all national Red Lists of Germany. After merging subspecies for which the highest stated Red List classification was used, 566 carabid beetle species remained in the dataset. Of these species, 36 % (201 species) are threatened and listed in categories between 'vulnerable' to 'regionally extinct'. The categories 'indeterminate' and 'rare' list 63 species (11 %), the category 'near threatened' 53 species (10 %) and 'least concern' 245 species (43 %), and data are deficient for 4 species (< 1 %) (cf. Schmidt *et al.* 2016). For this study, we re-coded the Red List classification to an ordinal variable between zero for 'least concern', and five for 'regionally extinct' (see Table B.1 in Supplement).

### 3.2.2. Species traits

For the majority of German carabid beetle species we were able to compile a set of seven species traits (Table 3.1), reflecting basic aspects of ecophysiology and habitat selection (e.g. Thiele 1977). Information about body size and hind wing morphology (which are dispersal ability parameters), trophic level and breeding season were extracted from the carabids.org database (Homburg *et al.*, 2014b) and complemented by a literature search and, if necessary, expert knowledge. Since the entire size of the distribution range of a species is not used in the determination of the Red List categories in Germany (Ludwig *et al.*, 2006), we used it here. As a proxy for the size of the entire distribution range we calculated the sum of the Palearctic countries' areas in which the given species has been recorded according to the Catalogue of Palearctic Coleoptera (Löbl and Smetana, 2003). Habitat specialization is represented by the sum of habitats a species does not occur in, following the catalogue published by the Society for Applied Carabidology (GAC) (Bräunicke and Trautner, 2009). Thus, an increasing value indicates an increasing degree of habitat specialization. We classified habitat preference into eight categories by using the habitat type that was most frequently indicated for a given species in the GAC catalogue (Bräunicke and Trautner 2009; Table 3.1).

### 3.2.3. Statistical analysis

Species with missing trait information or with a Red List classification of 'indeterminate', 'rare' or 'data deficient' were excluded from the analysis. We also excluded species classified as eurytopic since they were all classified as 'not threatened', which makes the applicability of the algorithms difficult; we performed a model including eurytopic species, but large standard errors were produced for the habitat preference of eurytopic species. The exclusion of eurytopic species did not influence our final results, as the calculated trait relationships were similar to the results we are presenting here. This resulted in the analysis of 464 carabid beetle species.

We fitted a proportional odds logistic regression model to evaluate the effect of species traits on extinction risk. All analyses were performed in R 3.4.1 (R Core Team, 2017) using the package 'ordinal' (Christensen, 2015). According to Grafen (1989), phylogenetic relationships between species can



lead to non-independency between species in statistical tests. A molecular phylogeny, as described by phylogenetic trees, was not applicable, because for most species no DNA sequences are available. However, taxonomic hierarchies of carabid beetles are highly supported by current molecular phylogenetic trees (e.g. Ober and Maddison 2008). Therefore, to account for a phylogenetic relationship we used the function 'phylo\_clmm' provided by Seibold *et al.* (2015). This function uses species-specific intercepts to avoid inflation of the degrees of freedom caused by species relationships. Species-specific intercepts were defined by a species-by-species taxonomic distance matrix based on taxonomical hierarchies according to the Catalogue of Palearctic Coleoptera (Löbl and Smetana, 2003; Nolte *et al.*, 2017). We performed five separate models. The general model included species of all habitat types ( $n = 464$  species). Additionally, we conducted four separate models for species preferring the habitat types forest (59 species), open (172 species), riparian (97 species) and wetland (95 species) (see Table 3.2). For species preferring coastal, mountainous and special habitats, models were not applicable due to low species numbers. In all models, the ordered Red List classification was used as an ordinal response variable and species traits as predictor variables. The models contained all seven variables and the interaction between body size and hind wing morphology. None of the explanatory variables were highly correlated (Spearman's rank correlation,  $\rho < 0.70$ ). To identify the best models we used backward selection based on Akaike's Information Criterion (AIC) until the AIC value stopped decreasing. Non-significant traits were left in the final models if they were involved in a significant interaction. To test for the effect of phylogeny on species extinction risk, we included phylogenetic taxonomy in all models, and compared these to models without phylogenetic taxonomy, using the conventional 'clm' function.

### 3.3. Results

The general model showed that extinction risk increased with increasing habitat specialization (Table 3.2, Fig. 3.1). Furthermore, small distribution range sizes, predatory feeding behavior and the interaction of increasing body size and macroptery also significantly promoted species extinction probability. The analysis of habitat preference showed that species of forests and special habitats (e.g., caves, cellars, waste disposal sites) had a significantly lower risk of extinction than species of open habitats (Fig. 3.2). Species of mountainous and coastal habitats showed the highest extinction risk. As main effects, body size and hind wing morphology solely did not contribute significantly to extinction risk. Results of the model without phylogenetic information remained identical (data not shown).

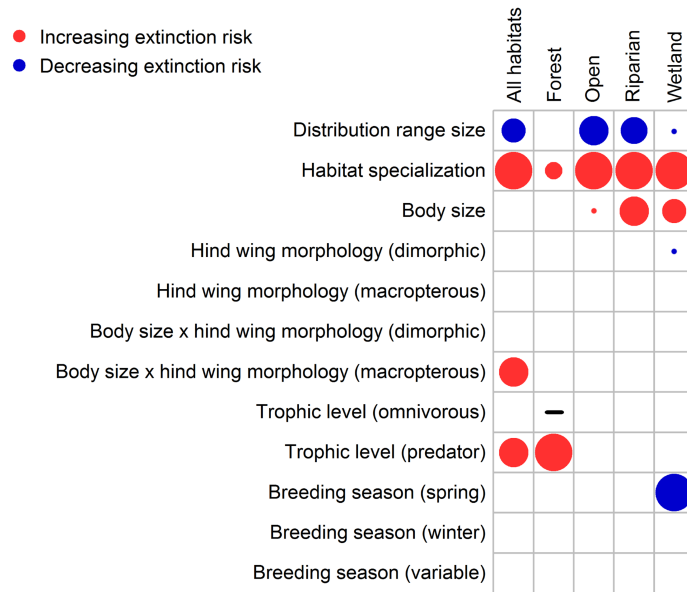
Analyses of species associated with specific habitat types (forest, open, riparian, wetland) showed both congruencies and differences to the general model (Table 3.2, Fig. 3.1). All four models showed an increase in extinction risk with increasing habitat specialization. In most final models, small distribution range size and large body size were associated (significantly or with a trend) with high extinction probability. Neither of these traits were, however, included in the final model for forest species. Here the risk of extinction was most strongly affected by trophic level: predatory forest species showed a significantly higher risk of extinction than herbivorous forest species. Hind wing morphology and breeding season were only included in the final model of wetland carabid species. In wetland species, autumn breeders showed a significantly higher extinction risk than spring breeders and a non-significantly higher risk than winter breeders or species with a variable reproduction period. Brachypterous wetland species were also at higher risk of extinction than dimorphic species. Similar to the general model, phylogenetic information did not affect the results of these habitat specific models.

**Table 3.2.:** Results of the proportional odds linear mixed-effects models with species-specific random intercepts on the basis of taxonomic hierarchy, to estimate the effects of carabid beetle species traits on extinction risk in all habitat types across Germany and for species of different habitat types.

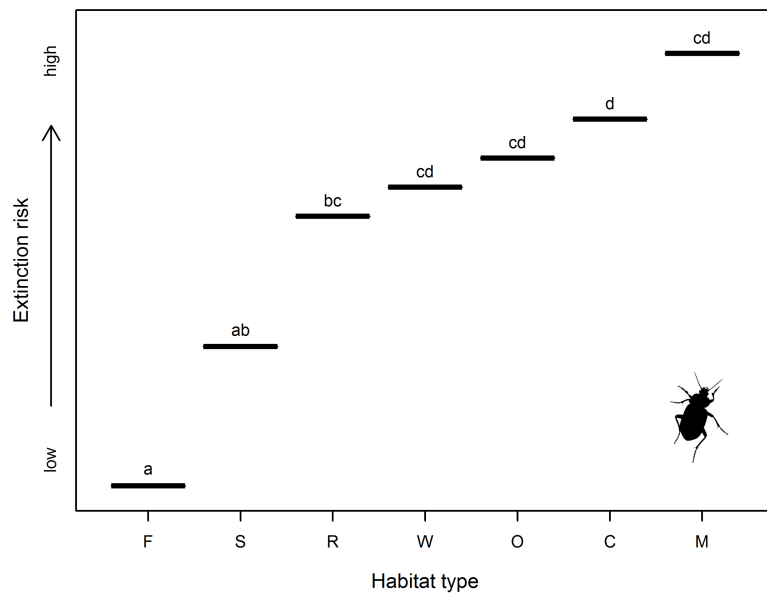
Variable	All habitats (n = 464)			Forest (n = 59)			Open (n = 172)			Riparian (n = 97)			Wetland (n = 95)		
	Estimate <sup>b</sup>	SE	z	Estimate <sup>b</sup>	SE	z	Estimate <sup>b</sup>	SE	z	Estimate <sup>b</sup>	SE	z	Estimate <sup>b</sup>	SE	z
Distribution range size	-0.47 ***	0.11	-4.18												
Habitat specialization	1.39 ***	0.14	9.81	1.26 *	0.54	-2.33	1.39 ***	0.21	-6.65	0.85 ***	0.23	3.75	2.11 ***	0.37	-5.76
Body size	0.14	0.23	0.60				0.28.	0.15	1.89	0.54 **	0.20	2.71	0.90 **	0.28	3.23
Hind wing morphology (brachypterous) <sup>a</sup>															
Dimorphic	-0.68	0.57	-1.19												
Macropterous	-0.17	0.53	-0.32												
Body size x hind wing morphology (body size x brachypterous) <sup>a</sup>															
Body size x dimorphic	0.35	0.34	1.03												
Body size x macropterous	0.63 *	0.27	2.31												
Trophic Level (herbivorous) <sup>a</sup>															
Omnivorous	0.43	0.47	0.90	trait character not present											
Predator	0.66 *	0.31	2.11	14.76 ***	0.73	20.14									
Breeding season (autumn) <sup>a</sup>															
Spring															
Winter															
Variable															
Habitat preference (open) <sup>a</sup>															
Forest	-3.04 ***	0.47	-6.49												
Wetland	-0.27	0.29	-0.91												
Riparian	-0.54	0.34	-1.59												
Coast	0.36	0.47	0.77												
Mountain	0.97	0.88	1.10												
Special habitat	-1.75 **	0.66	-2.67												

<sup>a</sup>Factor levels to which the categorical variables are compared are given in brackets.

<sup>b</sup>Significance levels: .p < 0.1, \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001



**Figure 3.1.:** Summary table of the results of the proportional odds linear mixed-effects models with species-specific random intercepts on the basis of taxonomic hierarchy to estimate the effects of species traits on the extinction risk of carabid beetle species in all habitat types across Germany, and for species of different habitat types. For categorical variables, factor levels are compared to carabid beetle species that are brachypterous, herbivorous and autumn breeders. Significant effects are shown with large circles ( $< 0.05$ , circle diameter represents value of the standard estimate, -: trait character not present, \*: trend effect  $p < 0.1$ )



**Figure 3.2.:** Relative extinction risk of species of different habitat types. Estimates of the variable habitat preference of the general model are used to compare species extinction risks. Letters above bars indicate significant differences between habitat groups (significant differences based on calculating the general model with varying intercepts). F = forest, S = special habitats, R = riparian, W = wetland, O = open, C =coastal, M = mountain

### 3.4. Discussion

Our general model including all species and the models including species of various habitat preference showed similar general results: increasing habitat specialization, decreasing distribution range size and larger beetle body size coincided with a higher extinction risk of carabid beetle. The general model further showed that larger species that are macropterous had high extinction risks, and that species preferring mountainous, coastal and open habitat types were more at risk of extinction than forest species. However, forest species with a predatory feeding behavior, and wetland species that breed in the autumn, showed high extinction risks. Phylogenetic relatedness had no influence on how species traits predict carabid beetle extinction risk.

#### 3.4.1. Species traits as drivers of extinction risk

Carabid beetle habitat specialization was the most important driver of extinction risk in all final models, except the forest habitat model where trophic level was more important (see Table 3.2). Indeed, Dunn (2005) has shown that narrow-habitat requirements are a more common driver of extinction in insects than in other animal taxa. Specialist species are particularly prone to extinction (Kotze and O'Hara, 2003; Terzopoulou *et al.*, 2015), due to their narrow niche and limited number of suitable habitats. During the last few decades, habitats of specialized species have decreased in size or have experienced severe disturbance, e.g., the fragmentation and disturbance due to land-use change, especially agricultural intensification and urban development, or wetland drainage and rectification measures on rivers (Hendrickx *et al.*, 2007; Maltby *et al.*, 2009). In addition, carabid beetle specialists show reluctance to move through unfavorable habitat, while generalists move more easily through the landscape as they can use various habitat types (Koivula *et al.*, 2002; Vermeulen, 1994). Functionally, a replacement of specialist species by broadly adapted generalists leads to the biotic and functional homogenization of biodiversity (McKinney and Lockwood, 1999), with subsequent implications for ecosystem functioning (Clavel *et al.*, 2011). Also (locally) rare species, which are those predominantly listed in red lists (cf. Ludwig *et al.* 2006), decrease with increasing land-use intensity and ecosystem functioning is negatively affected by the decrease of those species (Soliveres *et al.*, 2016).

Small distribution range size, large body size and high trophic level were further predictors of extinction risk in our study. The characteristics of these traits, as well as habitat specialists, are generally associated with low population densities (Blackburn *et al.* 2009; Gaston 2003; see also Pearson *et al.* 2014). Small populations are more prone to become regionally extinct since they often lack adaptability to climate or landscape changes (Gaston and Fuller, 2009), and are more vulnerable to stochastic events (Lande, 1993; Robles and Ciudad, 2012). Species with large distribution ranges can also exhibit low population densities due to habitat fragmentation, but generally have higher population densities (Brown, 1984; Gaston and Fuller, 2009; Kotze and O'Hara, 2003), and subsequently a lower risk of extinction since these populations are less likely to undergo simultaneous local extinction events. Importantly, the entire distribution range of a given species is often not a criterion used to assess the national threat status of species (Desender *et al.*, 2008b; Duelli, 1994; Ludwig *et al.*, 2006), but taking this trait into account might improve the Red List classification, at least for ground beetles.

Body size is considered a reliable predictor of extinction risk. For vertebrates, it is generally accepted that large bodied species are more prone to extinction than smaller species (Cardillo *et al.*, 2005; Dirzo

*et al.*, 2014), a pattern also found in invertebrates (Brooks *et al.*, 2012; Kotze and O'Hara, 2003). Large species tend to have smaller population sizes but also lower reproduction rates and require large, unfragmented and stable habitats, more so than small species (Matern *et al.*, 2008; Simberloff, 1994). In congruence to Nolte *et al.* (2017), we did not find an effect of body size on the extinction risk of forest species. Compared to other habitats, forests show more stable environmental conditions and are expanding in area in across Central Europe (e.g. Assmann 1999; FAO 2015), and forest species show less fluctuation in population densities (Günther and Assmann, 2004). Instead, trophic level was the most important predictor of forest species extinction risks. Higher extinction risks of species at higher trophic level (predators) is in agreement with the higher trophic-rank hypothesis (Davies *et al.*, 2000) but in contrast to the results of Nolte *et al.* (2017), who showed that herbivorous species are at lower occurrence ranks when studying community structure.

We expected hind wing morphology to be an important predictor of carabid beetle extinction risk, since it is closely related to a species' dispersal abilities (den Boer, 1977). However, species with individuals capable of flight (macropterous and dimorphic species) showed a lower extinction risk than brachypterous species only in the general model and for wetland species. Dimorphic species in particular have been identified to be least threatened by fragmentation and species decline (Barbaro and van Halder, 2009; Kotze and O'Hara, 2003; Nolte *et al.*, 2017). These species seem to benefit from a variable ecological strategy: during migration the number of individuals able to fly increases, which have a higher probability to successfully disperse and establish new populations, while under stable environmental conditions the number of flightless individuals increases, displaying higher fecundity and thus higher establishment abilities (den Boer *et al.*, 1980; Langellotto *et al.*, 2000; Zalewski *et al.*, 2012); also known as the oogenesis-flight syndrome (see Desender 2000). Macropterous species generally have a higher dispersal power and consequently better colonization and recolonization possibilities than brachypterous species (den Boer, 1990a). However, this general assumption does not hold with an increase in body size. Our results show that macropterous species show significantly higher extinction risks with increasing body size than brachypterous species (Table 3.2). This may be a consequence of large natural-like habitats that became more fragmented in cultural landscapes (Finck *et al.*, 2017). As macropterous species show stronger population fluctuations they need higher (re-) colonization to stabilize their occurrence. If the distance between suitable habitat patches is increasing, the dispersal power of even macropterous species may not be sufficient for colonization.

The breeding season of a species may influence survival rates, since the larval stage is the most sensitive in the life cycle of carabid beetles (Lövei and Sunderland, 1996). We found a significant influence of the trait breeding season only for species of wetland habitats. Anthropogenic changes in water regimes, changes of flood seasonality and magnitude as well as an increased frequency of winter floods (Petrov and Merz, 2009) may increase the mortality rate of wetland species during winter and early spring. During this period, individuals of autumn breeders are in their sensitive larval stage, which is more negatively affected by long lasting inundations than the imagines of spring breeders (Lövei and Sunderland, 1996).

### 3.4.2. Habitat preference as a drivers of extinction risk

Both habitat quality and quantity are crucial for the survival of a species. Over the last decades, land-use and habitat quantity have changed drastically (Fuchs *et al.*, 2015), and the proportion of long-term

endangered habitat types increased in Germany (Finck *et al.*, 2017). Habitats are more intensively used or converted into agricultural and urban land, resulting in habitat loss and fragmentation, which are considered major threats to endangered species (e.g. Fahrig 2003; Groom *et al.* 2006; Rands *et al.* 2010). Therefore, a strong and constant negative trend in habitat area is taken into account for species Red List classifications in Germany. Our results clearly show that species showing a strong preference for coastal, mountainous or open habitats face the highest risks of extinction and are in urgent need of protection, while most forest species are less threatened by extinction (see also Brooks *et al.* 2012). This result coincides with the respective decrease or increase in area covered by the given habitat types and the changes in habitat management in the anthropogenic landscape in Central Europe during the last decades. Especially coastal or open habitats, e.g. extensively grazed pastures or calcareous grasslands, face a dramatic decline in area (Wallis de Vries *et al.*, 2002), caused by intensification of land-use, especially pesticide and fertilizer use. Furthermore, mountainous habitats are subject to a drastic change in land-use; while accessibility dependent habitat abandonment and overgrazing, of the given habitats are frequent, cold and moist habitats are decreasing due to their sensitivity to global warming (Brooks *et al.*, 2012; Dieker *et al.*, 2011). However, not all habitats are decreasing in cover; forests have increased in area across Europe in the last two centuries (Assmann, 1999; FAO, 2012, 2015) and showed the lowest proportion of threatened species. The man-made habitat increase might be the reason why studies show that species associated with forests are often increasing in recent decades (Brooks *et al.*, 2012). But here especially the forest generalists might strongly benefit, while the forest specialists, on the other hand, depend more on habitat quality than on quantity. At least some of these habitat specialists are threatened (Nolte *et al.*, 2017).

### 3.4.3. Implication for nature conservation

This study covers most of the carabid beetle species found in Central Europe, so the results are also of interest to other Central European countries or regions. We show that extinction risk can be identified from certain carabid beetle traits; in particular habitat specialization, distribution range size and body size. Species that exhibit specific characteristics of these three traits in combination should be particularly the object of species' action plans and other activities that support these species. Even though only two carabid species occurring in Germany are listed in the annexes of the Natura 2000 Directive of the European Union (Council Directive - 92/43/EEC, Annex II), both hold the trait characteristics we identified leading to higher species extinction risks: (a) *Carabus variolosus*, a species with a long-term documentation of population decline (Breuning, 1926) with a very narrow specialization to habitats of headwater brooks with slowly flowing streams (Matern *et al.*, 2007). Moreover, this species has very small population sizes (Matern *et al.*, 2008) and a small distribution range, as it is restricted to Central Europe and the Carpathian Basin (Turin *et al.*, 2003). (b) *Carabus menetriesi*, a highly stenotopic species restricted to intact and constantly groundwater-influenced mesotrophic fens. The coincidence of small population sizes (Matern *et al.*, 2008) and a small distribution range is obvious (Müller-Motzfeld, 2005). Both species belong to the largest ground beetles in Germany and they show a small distribution range, with the more significant proportion located in Central Europe (Turin *et al.*, 2003). Therefore, this region has an important responsibility for the worldwide preservation of both species.

These examples show that the sometimes criticized choice of invertebrate species (Cardoso, 2012) listed by the Natura 2000 Directive of the European Union (Council Directive - 92/43/EEC) covers cara-

bid species that can be identified by other approaches as species of conservation concerns. Moreover, these species can act as umbrella species, as they are associated with other stenotopic carabid species that also show strong declines in Germany and in their entire distribution range (e.g. *Chlaenius sulci-collis*, Trautner and Rietze 2000). The preservation and regeneration of their habitats are a priority.

Second, we need to focus more on the conservation and restoration of habitat types that are decreasing in extent. Results of this study underline the importance of maintaining and restoring shrinking habitat types, especially mountainous, coastal and open habitats as well as wetlands. Without conservation efforts to protect these decreasing habitat types, we will continue to face massive insect species losses. The key to protect species of these habitat types is to reduce habitat artificialisation, increase habitat patch size (without decreasing other important habitat types), and to increase or restore habitat connectivity. If connectivity is not possible (e.g. for mountainous species), assisted migration may be an alternative under current changing environmental conditions, especially in the age of climate change (Homburg *et al.*, 2014a; Seddon *et al.*, 2014).

### **Acknowledgements:**

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## B. Supplementary material

**Table B.1.:** Categorization and nomenclature of extinction risks used by the IUCN and by Schmidt *et al.* (2016), including the ordinal code used in this paper.

Ordinal Red List code	IUCN categories	Categories in German	
5	RE: Regionally extinct	0: Ausgestorben oder verschollen	
4	CR: Critically endangered	1: Vom Aussterben bedroht	
3	EN: Endangered	2: Stark gefährdet	
2	VU: Vulnerable	3: Gefährdet	
1	NT: Near threatened	V: Vorwarnliste	
0	LC: Least concern	*: Ungefährdet	
	I: Indeterminate	G: Gefährdung anzunehmen	Not used in analyses
	R: Rare	R: Extrem selten	Not used in analyses
	DD: Data deficient	D: Daten ungenügend	Not used in analyses



## 4. FUNCTIONAL TRAITS DRIVE GROUND BEETLE COMMUNITY STRUCTURES IN CENTRAL EUROPEAN FORESTS: IMPLICATIONS FOR CONSERVATION

Published article

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### Abstract

Community metrics describing the structuring of ecological communities, such as nestedness and the potential linkages between functional traits and the occurrence of species, might hold important information for biodiversity conservation. The order in which species are ranked in nested communities, as well as species traits determining community composition, can help pinpoint species vulnerable to extinction. However, these patterns remain understudied for many taxa of conservation concern and across larger spatial scales. We used a large dataset of ground beetle communities in Central European forests to test for nestedness, variation in species composition, and whether species traits can explain species composition patterns. We found only weak evidence of nestedness of ground beetle communities. However, community compositions across regions were remarkably similar. Species traits explained over half the variance in the overall occurrence ranks of ground beetle species. Wing dimorphism, breeding in both spring and autumn, and hibernation as both larval instars and as imago coincided with increasing occurrence probability, probably due to the greater flexibility of such species to adapt to fluctuating environmental conditions. In contrast, predominantly granivorous species or those with smaller geographical ranges had small occurrence ranks. These results emphasise the importance of investigating the relationships between species traits and occurrence ranks to better understand the mechanisms which shape community composition, and these relationships should be taken into consideration in conservation contexts. Our results provide a basis for the development of more effective conservation strategies in Central European forests to protect threatened ground beetle species.

## 4.1. Introduction

Forests provide numerous ecosystem services, including the preservation of biodiversity. In Central Europe, especially in Germany, legal regulations have led to an ongoing, overall increase in forest coverage during the last two centuries (FAO, 2012; Fuchs *et al.*, 2013). Nevertheless, many forest species in Central Europe are threatened and red-listed (Binot-Hafke *et al.*, 2011; Desender *et al.*, 2008a), and forest management should therefore be influenced by conservation concerns. These conservation concerns need to be accounted on the regional level as usually, only a few species are ubiquitous, while the majority of species inhabit only few sites (e.g. Gaston 2003). The majority of threatened species belong to the latter category, and are more vulnerable to extinction. To preserve species diversity across forest ecosystems, it is crucial to understand the underlying mechanisms shaping community composition. Identified drivers can then be used to determine the extinction vulnerability of species, and to develop conservation measures aimed at the rarest and most threatened species (Wang *et al.*, 2015). This is especially important as rare species can have large effects on ecosystem functioning and on ecosystem services (Mouillot *et al.*, 2013; Soliveres *et al.*, 2016).

Nestedness analysis of communities is a valuable tool for identifying species which are sensitive to habitat changes and are hence more prone to extinction (Bolger *et al.*, 1991; Martinez-Morales, 2005). A nested community structure implies that species-poor sites are true subsets of species-rich sites (Patterson and Atmar, 1986). Although a perfectly nested pattern is rarely found in real-world ecosystems (Fischer and Lindenmayer, 2005), significant nested patterns have been shown for various habitat types and taxa (Schouten *et al.*, 2007; Wang *et al.*, 2013; Wright *et al.*, 1998). Although invertebrates make up the bulk of higher eukaryotic biodiversity, their community patterns and possible nestedness are not well understood. In Central Europe, ground beetles have been frequently studied in the context of conservation science (Pearce and Venier, 2006; Rainio and Niemelä, 2003) as they can serve as a model taxon for understanding biodiversity patterns. Nested communities have previously been reported for the genus *Carabus* on a European scale (Calatayud *et al.*, 2016) and for ground beetles on smaller geographic scales (within a region such as a city or a big lake and its surroundings) (Weller and Ganzhorn, 2004; Zalewski and Ulrich, 2006). However, to test for generality of nestedness in ground beetle communities and the applicability to forests and forest management, studies on a larger geographic scale (across regions) are necessary but to the best of our knowledge still missing. If nestedness occurs, conservation management can focus on preserving species-rich sites, as these are expected to contain most or all of the rare species (Fleishman *et al.*, 2002).

Among a plethora of factors (Ulrich *et al.*, 2009), extinction and (re-)colonization dynamics within the island biogeography framework are known to explain many nested community patterns (Cutler, 1991; Lomolino, 1996; Patterson and Atmar, 1986). Hence nestedness and other species occurrence patterns can be driven by environmental factors, such as habitat patch size, disturbance, and isolation (Wang *et al.*, 2013), as well as by species traits, such as trophic level and dispersal ability (Soga and Koike, 2012; Zalewski and Ulrich, 2006). Feeley *et al.* (2007) used the nestedness rank of a species, which is equivalent to the number of species incidences, as an indicator of extinction vulnerability in order to demonstrate the existence of a relationship between extinction vulnerability and species traits.

For European carabid beetle species, a large amount of information about the species traits is available in the literature, much of which has recently been assembled in an online database (Homburg *et al.*, 2014b). Species traits, such as flight capability, body size, and habitat specialization, are increasingly dis-

cussed as potential drivers of beetle community structure (Driscoll and Weir, 2005; Gerisch, 2011; Ribera *et al.*, 2001). Thus, species traits can be used to identify the mechanisms underlying community compositions of forest ground beetles. Additionally species traits are of great relevance for conservation management, as they offer an understanding of why some species are rare and face higher extinction vulnerability than others (Henle *et al.*, 2004; Soga and Koike, 2012). For example, species with low dispersal power or species with high habitat specialization are expected to be more prone to extinction (e.g. Kotze and O'Hara 2003). This knowledge can inform the development of more effective management strategies for preserving species diversity.

To identify the mechanisms underlying community compositions, we analysed a large dataset on the regional abundance of forest ground beetles, based on 296 forest plots in Germany, Belgium, and the Netherlands. In order to provide recommendations for nature conservation management, we address the following three questions:

- I) To which degree are the communities in the given landscapes nested?
- II) Is it possible to identify species vulnerable to regional extinction?
- III) Are species communities shaped by species traits?

## 4.2. Material and methods

### 4.2.1. Data compilation

We compiled seven regional datasets from several studies on epigeic active ground beetles in forests of Belgium, the Netherlands, and Germany (Table 4.1). All studies were carried out using pitfall traps at some points between 1981 and 2008, and covered at least the main activity period of the studied forest species. The seven datasets were each collected using slightly different methods, for example, different preservation fluids, which has been shown in laboratory experiments to not have a strong influence on catching rates (Gerlach *et al.*, 2009). Within the given datasets, the pitfall trapping method tends to be consistent (Table 4.1). Each dataset comprises catches from a continuous area with comparable climatic and edaphic parameters, such as Atlantic climate and sandy soils in the lowlands of Lower Saxony, as these parameters are known to have a strong influence on species composition (e.g. Assmann 1999; Desender 2005). We refer to the datasets as 'regions'. The number of forest plots per region ranged from 13 to 66, with a total of 296 forest plots. The forest plots differed slightly from each other, e.g. regarding the dominant tree species, forest size or habitat isolation (Assmann, 1999; Desender, 2005; Fischer *et al.*, 2010). While most of the plots represent isolated forests, plots in the Hainich-Dün and in the Schorfheide-Chorin (Table 4.1) are mostly located within large, continuous forests (Fischer *et al.*, 2010).

We only considered typical forest species, defined as those which reproduce exclusively in forests (Lindroth, 1985, 1986; Turin, 2000). We excluded species which can reproduce in forests as well as in other habitats as they are widely distributed and therefore not relevant to develop conservation strategies for specialized or rare forest species. Moreover, vagrant species were excluded from analyses as they exhibit probably different species traits, and thereby can interfere with the accuracy of the analyses. Nomenclature follows Schmidt *et al.* (2016).

**Table 4.1.:** Compiled datasets (regions), with numbers of forest plots used to test for nested patterns and species traits. Code refers to the abbreviation given to each region. The original data can be obtained in the cited source literature.

Region	Code	Number of plots	Source
Belgium: Flanders	BE	66	Desender <i>et al.</i> (2002); Gaublomme <i>et al.</i> (2008)
The Netherlands	NL	13	Heijerman and Turin (1989)
Germany: Eastern lowlands of Lower Saxony	LS	32	Assmann (unpublished); Gürlich (unpublished); Dülge (1988); Günther and Assmann (2004); Lohse (1981)
Germany: Schleswig-Holstein / Mecklenburg-Western Pomerania	SM	36	Buse (unpublished); Gürlich (unpublished); Meitzner <i>et al.</i> (2006)
Biodiversity-Exploratories			
Germany: Schorfheide-Chorin	SEW	50	Lange <i>et al.</i> (2014)
Germany: Hainich-Dün	HEW	49	Lange <i>et al.</i> (2014)
Germany: Schwäbische Alb	AEW	50	Lange <i>et al.</i> (2014)

#### 4.2.2. Species traits

A set of seven species traits reflecting basic aspects of ecophysiology and habitat selection (e.g. Thiele 1977), was selected for each species (Table 4.2). Information about body size and hind wing morphology, which are linked to dispersal ability, trophic level, breeding season, and hibernation stage were extracted from the carabids.org database Homburg *et al.* (2014b). We used the sum of the area of the countries in which the species has been recorded as a surrogate for geographic range size (Löbl and Smetana, 2003). The number of habitat types occupied by a given species was calculated from the catalogue published by the Society for Applied Carabidology (GAC, 2009). This catalogue defines species habitat preferences of ground beetles using 40 habitat types. A large degree of habitat specialization represents a wide niche, while lower numbers imply a narrow niche.

**Table 4.2.:** Species traits used in the trait-analysis. Source: Carabids.org database (Homburg *et al.*, 2014b)

Trait	Trait type	Trait value
Geographic range size	continuous	Extent of occurrence in the Palearctic realm (km <sup>2</sup> )
Degree of habitat specialization	continuous	Number of occupied habitat types in Central Europe
Body size	continuous	Mean body size (cm)
Hind wing morphology	ordinal	Brachypterous (flightless) Dimorphic (species with long and short winged specimens) Macropterous (predominantly flight-active)
Breeding season	nominal	Spring breeder Autumn breeder Both spring and autumn breeder
Trophic level	nominal	Granivore Predator
Hibernation stage	nominal	Imago Larval instars Both imago and larval instars

### 4.2.3. Data analysis

#### *Determination of nestedness*

For each region we constructed species  $\times$  plot presence – absence matrices with species occurrences as entries. We assessed the degree of nestedness in species composition among regions using Nestedness by Overlap and Decreasing Fill (NODF) (Almeida-Neto *et al.*, 2008) scaled between 0 and 1. NODF increases with increasing degree of nestedness. A convenient measure of how much a species or plot contributes to the total degree of nestedness is the nestedness contribution (NC) (Ulrich, 2010) of each species or each region ( $NC = NODF(i) - NODF$ , with  $NODF(i)$ , being the degree of nestedness excluding the focal species or plot  $i$ ). Species having  $NC < 0$  increase the overall degree of nestedness in the matrix.

To maximize the number of presences along the matrix diagonal, seriation was used to sort rows and columns of a matrix of species occurrences (rows) among plots (columns) (Leibold and Mikkelsen, 2002). Ulrich and Gotelli (2013) have shown that the rank correlation of row and column positions of all non-empty cells in the seriated matrix is a measure of directional species turnover ( $\beta$ -diversity) with good statistical properties. We used the respective coefficients of determination ( $R^2$ ) as the test statistic for species turnover across our sample plots.

Because raw scores of  $R^2$  and NODF depend on matrix fill and species richness, we used a null model approach (Gotelli and Ulrich, 2012) and compared observed scores with those obtained from 1000 matrices in which species occurrences within the species  $\times$  plot matrix were reshuffled according to two contrasting null assumptions, an equiprobable model (Wright *et al.*, 1998) and a proportional resampling model (Ulrich and Gotelli, 2010). In the first model, each cell has an equal probability of occurrences, while in the second model, occurrence probabilities are proportional to observed species abundances, though total row and column abundances remain fixed (the abundance-based IT null model of Ulrich and Gotelli 2010). Both models benchmark the end points of a continuum from maximally equitable to maximally constrained patterns of species spatial distribution, and allow for an assessment of the relative degree of species co-occurrences along this continuum (Ulrich and Gotelli, 2013). Nestedness and species turnover analyses were carried out using the software application *NODF* and *Turnover* (freely available on the homepage of W. Ulrich, [www.keib.umk.pl](http://www.keib.umk.pl)).

All other statistical analyses were computed in R 3.2.2 (R Core Team, 2014). We compiled species occurrence ranks for each region based on the order of the species in the respective seriated regional matrix. These species occurrence ranks were then used as a proxy for the frequency of species occurrences in the given region, assigning the highest rank to the most abundant species and absences a value of zero. The use of ranks instead of relative abundances reduces the bias due to non-linearity in species relative abundances inherent in such comparisons. We assessed the spatial distance decay in community composition using a Mantel test, with Euclidean distances for plots and Bray-Curtis distances for species occurrence ranks. To assess whether the species found in each region tend to have similar occurrence ranks across regions, we used Spearman's rank correlation on regional species occurrence ranks.

#### *Occurrence ranks and species traits*

Average occurrence ranks were calculated using the mean of the occurrence ranks of a given species in the individual regions. We used a linear model to assess the relationship between species traits and the

average species occurrence ranks. The average occurrence ranks were used as the dependent variable and species traits being the explanatory variables. Explanatory variables were tested for multicollinearity using Spearman's rank correlation (all  $\rho < 0.70$ , see Supplement, Table C.1). The average occurrence ranks as well as the geographic range size were square-root transformed. Furthermore, geographic range size, degree of habitat specialization and body size were z-score scaled (mean = 0, standard deviation = 1). To identify the main drivers of carabid beetle occurrence ranks, we used multi-model inference (Burnham and Anderson, 2002) based on Akaike's Information Criterion values corrected for small sample size (AICc). The models were automatically simplified and selected using the 'dredge' function (R package MuMIn, Barton 2016). We then generated average parameter estimates of the top-ranked models within  $\Delta\text{AICc} < 2$ , using the 'model.avg' function, and additionally calculated an average adjusted  $R^2$ .

To investigate a possible phylogenetic effect on the model results, taxonomic distances were compiled from the hierarchies of taxonomy as found in the Catalogue of Palaearctic Coleoptera (Löbl and Smetana 2003, see Supplement C.1, Table C.2 and C.3), which are highly supported by molecular phylogenetic trees (e.g. Ober and Maddison 2008). A classical phylogeny, as described by phylogenetic trees, was not applicable because from many species no DNA sequences are available. We ran a Mantel test between the distance matrix of the full model residuals and the taxonomic distances to test if the residual error of the models was affected by the taxonomic relationships among the beetle species.

## 4.3. Results

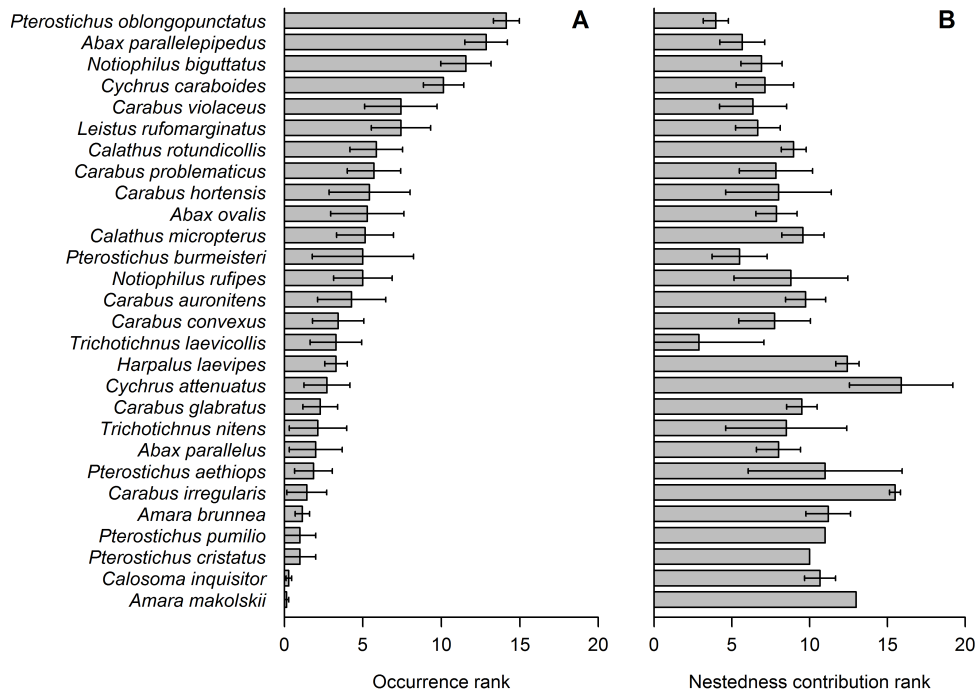
### 4.3.1. Patterns of richness and abundance

We analysed a dataset consisting of 142,109 individuals from 28 forest ground beetles species occurring in 296 forest plots. The number of species varied from 11 to 18 species per region, and from three to 15 species per forest plot. *Pterostichus oblongopunctatus*, *Abax parallelepipedus* and *Notiophilus biguttatus* were the most common species across all seven regions (Fig. 4.1A). Species with the lowest occurrence ranks were rare in all regions in which they occurred. We found significant correlations between the pair-wise Spearman's rank order in the occurrence ranks between the regions located in Belgium, the Netherlands and North Germany (BE, NL, LS, SM and SEW, all  $\rho > 0.53$ ,  $P < 0.01$ ). There was also a significant correlation between the occurrence rank orders in the low mountain regions of Germany (HEW and AEW;  $\rho = 0.63$ ,  $P < 0.01$ ). We did not find a significant correlation between the occurrence ranks of the northern and southern groups of sites.

### 4.3.2. Species co-occurrences

We found a significant nestedness pattern of species occurrences in all regions when compared to an equiprobable distribution, but only for two regions when compared to a proportional distribution (NODEF  $> 0.64$ , Table 4.3). Species turnover was always less than expected from the equiprobable null model, but higher than expected from the proportional null model (Table 4.3). Furthermore, we found a consistent lessening in similarity with increasing spatial distance between plots, although this was only statistically significant ( $P < 0.01$ ) in the regions LS, SM and HEW (Table 4.3).

Species nestedness contribution, a measure of how often a species occurs according to the overall degree of species loss among plots, decreased with increasing species occurrence ranks (Fig. 4.1B,



**Figure 4.1.:** Average rank of species occurrences (A) and nestedness contribution (B) ( $\pm$  one standard error) across the seven regions. Species with high average occurrence ranks were most frequent. Species with low nestedness contribution ranks contribute the most to the overall degree of nestedness in the community. Both rank orders were negatively correlated ( $\rho = -0.74$ ,  $P < 0.001$ , Spearman's rank correlation).

**Table 4.3.:** Species richness, number of plots, spatial autocorrelation of community structure (Mantel correlation), NODF, and  $R^2$ , and the respective effect sizes (observed score - expected scores) obtained from the equiprobable (EE) and proportional (IT) null models. Significant effect sizes ( $P < 0.01$ ) are bold-typed.

Region	Species	Plots	Spatial correlation	Score		EE null model		IT null model	
				NODF	$R^2$	NODF	$R^2$	NODF	$R^2$
BE	16	66	0.03	0.64	0.07	<b>0.24</b>	<b>-0.11</b>	<b>-0.15</b>	<b>0.06</b>
NL	11	13	0.16	0.78	0.01	<b>0.15</b>	<b>-0.11</b>	<b>0.15</b>	<b>0.01</b>
LS	17	32	<b>0.47</b>	0.66	0.07	<b>0.14</b>	<b>-0.06</b>	<b>-0.07</b>	<b>0.07</b>
SM	15	36	<b>0.30</b>	0.74	0.06	<b>0.20</b>	<b>-0.06</b>	<b>0.15</b>	<b>0.06</b>
SEW	15	50	0.13	0.71	0.01	<b>0.14</b>	<b>-0.08</b>	0.05	0.01
HEW	18	49	<b>0.22</b>	0.72	0.08	<b>0.21</b>	<b>-0.04</b>	<b>-0.07</b>	<b>0.07</b>
AEW	17	50	0.03	0.74	0.00	<b>0.11</b>	<b>-0.06</b>	<b>-0.03</b>	0.00

$\rho = -0.74$ ,  $P < 0.001$ , Spearman's rank correlation). The three most frequent species were also of major importance for the overall degree of nestedness, as the nestedness contribution ranks decreased with increasing species occurrence ranks (Fig. 4.1B).

### 4.3.3. Occurrence ranks and species traits

Multi-model inference revealed six models with  $\Delta\text{AICc} < 2$  (Table 4.4). Geographic range size and hind wing morphology were indicated as the most important variables explaining average occurrence ranks, as they were included in all top-ranked models (Table 4.4 and 4.5, Importance value = 1). Trophic level, breeding season and hibernation stage were not included in all top-ranked models, showing lower importance values of 0.34 - 0.63 (Table 4.4 and 4.5). Body size and habitat specialization did not appear in any of the top-ranked models. While the full model explained 67 % of the overall variance, the  $R^2$  averaged over the six top-ranked models was still 53 %. Model-averaging results showed a highly significant, positive effect of dimorphic hind wing morphology on average occurrence ranks. In addition, geographic range size and the potential to hibernate both as imago and as larval instars were positively and breeding in only one season negatively related with average occurrence ranks. Predatory feeding behaviour was positively related to average occurrence ranks in a single model only and showed a marginally significant effect in the model-averaging results. We additionally conducted a second approach with a 95 % confidence set of models, summing up Akaike weights from largest to smallest until the sum of their Akaike weights exceeds 0.95 (Burnham and Anderson, 2002). This approach showed similar results, as the added models comprise low explanatory power (see Supplement Table C.4 and C.5).

**Table 4.4.:** Most parsimonious mixed models between average occurrence ranks and species traits. Only the top-ranked models with  $\Delta\text{AICc} < 2$  are shown, ranked by AICc weight (grs: geographic range size, hwm: hind wing morphology, trl: trophic level, brd: breeding season, hb: hibernation stage).

Model	Explanatory variables included in model	df	$\Delta\text{AICc}$	AICc weight	Adjusted $R^2$
1	grs + hwm + trl + hb	8	0	0.13	0.57
2	grs + hwm + brd	7	0.5	0.10	0.52
3	grs + hwm	5	0.56	0.10	0.44
4	grs + hwm + trl	6	0.77	0.09	0.47
5	grs + hwm + trl + brd	8	1.48	0.06	0.55
6	grs + hwm + trl + brd + hb	10	1.77	0.05	0.64
Full	all selected traits	15	28.12	0	0.69

In our analysis between model residuals and taxonomic distances, we found no evidence of an effect of taxonomic relatedness of the beetle species on the model results (see Supplement, Table C.6), which is further supported by the wide spread of average occurrence rank values for species belonging to the same genus (e.g. *Carabus*, *Abax*, *Pterostichus*; Fig. 4.1).



**Table 4.5.:** Average parameter estimates and importance value of the six top-ranked models ( $\Delta AICc < 2$ , average  $R^2_{Adj.} = 0.53$ ). Significant results are bold-typed. Intercept: granivorous, macropterous, ground beetles breeding in spring and autumn, and hibernate as imago.

Explanatory variable	Estimate	Standard error	Adjusted SE	z-value	P-value	Importance value
Intercept	0.858	0.648	0.663	1.294	0.196	
Geographic range size	0.419	0.157	0.165	2.545	<b>0.011</b>	1.00
Hind wing morphology, dimorph	1.776	0.440	0.463	3.838	<b>&lt; 0.001</b>	1.00
Hind wing morphology, brachypterous	1.042	0.519	0.539	1.932	0.053	1.00
Trophic level, predator	0.727	0.393	0.415	1.752	0.080	0.63
Breeding season, autumn	-0.893	0.408	0.433	2.064	<b>0.039</b>	0.41
Breeding season, spring	-0.867	0.409	0.431	2.010	<b>0.044</b>	0.41
Hibernation stage, both imago and larval instars	0.887	0.358	0.379	2.340	<b>0.019</b>	0.34
Hibernation stage, larval instars	0.112	0.384	0.402	0.280	0.780	0.34

## 4.4. Discussion

Contrary to the results of previous studies on nestedness of ground beetle communities, we found only a weak or no nested pattern of carabid communities across seven regions in Central Europe. Nevertheless, we found consistent species occurrence ranks across regions. A suite of species traits were positively correlated with the average occurrence ranks. Large geographic range size together with the ability to hibernate both as larval instars and as imago and to breed in two seasons, predatory feeding behaviour and dimorphic hind wing morphology was positively correlated with higher species occurrences.

### 4.4.1. Nestedness of communities

We only found significant nested community patterns when comparing to a null model with equiprobable distribution of species, and only rarely when we used proportional occurrence probabilities as a null model. Our results are typical for communities which are either not nested or only slightly nested due to colonization dynamics (Ulrich *et al.*, 2009). Overall, the studied carabid communities do not follow a strong nested order. For this reason, preserving exclusively the most species-rich communities will not preserve the rare ones (Fischer and Lindenmayer, 2005). The weak evidence for nestedness which we found in the carabid communities of all seven regions cannot be a result of too small sample size, as our dataset is clearly one of the largest datasets published for insects in this context (cf. Soga and Koike 2012; Wright *et al.* 1998). We therefore conclude, like Ulrich and Gotelli (2007), that overall nested community patterns are less common than previously thought, including in ground beetles (e.g. Weller and Ganzhorn 2004; Zalewski and Ulrich 2006). Previous studies may be partly biased due to weaknesses in sampling or in statistical methodology, such as artefacts of passive sampling while using the Nestedness Temperature Calculator Program (NTC) (Fischer and Lindenmayer, 2002).

### 4.4.2. Species occurrence ranks

As far as we know, we are the first to demonstrate similar species occurrence ranks within forest carabid communities in different regions across Central Europe. As the study regions vary widely in terms of

fragmentation, edaphic parameters, and numerous other parameters, such a similarity in occurrence ranks is surprising. Recorded species with high occurrence ranks were usually highly abundant in all analysed regions, and therefore community compositions seem to be relatively stable across the studied regions. This result is consistent with previous studies which have demonstrated generally high abundances of these species (cf. Luka *et al.* 2009; Trautner *et al.* 2014). Species with low occurrence ranks did not occur in all of the regions, but always occurred in low abundances within the regions in which they occurred.

#### 4.4.3. Species traits shape community composition

We found that species average occurrence ranks can be explained by trait-driven mechanisms (Table 4.5). Palearctic geographical range size was positively correlated with average occurrence ranks. This concurs with the generally assumed positive association between the range size of a species and its local population sizes (cf. Gaston 2003), which is expected to influence the occurrence probability within sites. Consequently, larger geographic range sizes lead to an overall larger population size (Blackburn *et al.*, 2009), which in turn leads to a higher number of individuals which can exploit more potential habitats. These factors may mitigate the effects of fragmentation and habitat loss. Other studies have shown that a small geographic range size can serve as a strong predictor of extinction risk for various taxa (e.g. Gaston and Fuller 2009).

Three species trait characteristics which increase the flexibility of the given species to adapt to different environmental conditions coincide with high occurrence ranks. These trait characters were dimorphic hind wing morphology, breeding both in spring and in autumn and the ability to hibernate as larval instars and as imago. Hind wing morphology was the most important driver of carabid occurrence ranks. Differences in hind wing morphology have long been suggested as an important driver of carabid community composition as these differences can lead to differing dispersal abilities and consequently to different colonization and recolonization probabilities (den Boer, 1977). It is generally held that macropterous species have a higher dispersal power and a higher population turnover rate than brachypterous ones (den Boer, 1990a). However, species colonization probability is influenced by establishment ability as well (Gaston, 1994), which is expected to be higher in brachypterous carabid species (Aukema, 1991). We found that the probability of a high occurrence rank increases with hind wing dimorphism. Dimorphic species are assumed to have greater colonization rates, due to their variable ecological strategy (Kotze and O'Hara, 2003). These species may profit from higher colonization and reproduction rates if they are winged during the migration period. Whereas the number of flightless individuals, with higher establishment abilities, increases under stable habitat conditions (Aukema, 1991; Zalewski *et al.*, 2012). This micro-evolutionary process may explain why dimorphic species are less threatened by fragmentation and species decline (Barbaro and van Halder, 2009; Kotze *et al.*, 2003; Kotze and O'Hara, 2003).

Species with the ability to hibernate both as larvae and as imago as well as to breed in spring and in autumn coincide with high occurrence ranks. However, these two species traits were less important drivers of species occurrence ranks than hind wing morphology or geographic range size. Spake *et al.* (2016) found that species which overwinter as imago are associated with higher canopy cover, as it is shadier in the summer which reduces mortality due to larval desiccation. Species which are able to hibernate in both stages are less vulnerable to environmental conditions during hibernation, as they may

be able to adapt to environmental changes by shifting their reproductive period, a process which has been shown in *Abax parallelepipedus* (Lauterbach, 1964). Moreover, species hibernating in both stages as well as species using two breeding seasons may have a lower risk of extinction as they consist of different age classes, allowing them to better tolerate fluctuating abiotic and biotic conditions (Baumgartner *et al.*, 1997). Spreading the risk across time, here expressed by the different abilities of developmental stages to survive different environmental conditions, may lead to higher survival rates and consequently to more stable population sizes (den Boer, 1968).

While general theory tells us that species at higher trophic levels are more prone to extinction risk (Davies *et al.*, 2000), we found lower occurrence ranks for granivorous species than for predators. This can be due to the conservation programs of Central Europe, especially of Germany, which concentrate on encouraging natural-like dynamics in ecosystems (Brang *et al.*, 2014). In forests used for timber production, the removal of individual trees is currently the predominant forestry method in use (e.g. Loewe 1991), while clear-cutting or intensive thinning have decreased during the last decades. As a result, many forests are developing closed canopies, resulting in fewer herbs, grasses and fewer early successional tree species, reducing the food supply for granivorous carabids as they preferably feed on the seeds of grasses and herbaceous plants (e.g. Talarico *et al.* 2016). In our study the species with the lowest occurrence rank, *Amara makolskii* (syn. *Amara pseudocommunis*), forages on birch seeds (Burakowski, 1967), a pioneer tree species typical for early successional forests (Ellenberg and Leuschner, 2010).

Although recent studies have shown that larger species and species with higher habitat specialization show a strong population decline and are more prone to extinction (Brooks *et al.*, 2012; Kotze and O'Hara, 2003), we did not find evidence that body size or habitat specialization drives ground beetle occurrence ranks in Central European forests. In comparison with recent studies which included species from a large range of habitats, we studied only species specialized in forest habitats. The higher extinction vulnerability shown for larger ground beetles (Kotze and O'Hara, 2003) is explained by their generally low population densities. Especially the natural fluctuations of population densities trigger the extinction vulnerability. However, forest ground beetles show only low fluctuation in abundances (Günther and Assmann, 2004).

#### 4.4.4. Implications for habitat management of Central European forests

Our results suggest that occurrence ranks can be a useful tool to identify rare species. For example, *Abax parallelepipedus* showed one of the highest occurrence ranks and is known to have stable population dynamics (Chaabane *et al.*, 1996; Günther and Assmann, 2004) and consequently little genetic differentiation (Marcus *et al.*, 2015). In contrast, *Carabus irregularis*, a species which has high levels of genetic differentiation as a result of small population sizes or low gene flow (Homburg *et al.*, 2014a) and is listed as an endangered species in Germany (Schmidt *et al.*, 2016), had low occurrence ranks in our study. Thus, species of conservation concern can be identified by analysing occurrence ranks and species traits. Moreover, ecological properties derived from species traits of rare species lead to the following recommendations for habitat management.

It is likely that ground beetle species with low occurrence ranks across regions are especially sensitive to local extinction processes. Hence, macropterous forest-inhabiting carabid species, especially when they are granivorous and rely on seeds of early successional tree species, are in particular at risk

of extinction. Our results also show that brachypterous, forest-inhabiting carabid species are more susceptible to extinction than dimorphic species, and therefore conservation measures should account for these species. An example of such a conservation measure is assisted migration (Homburg *et al.*, 2014a), which has been shown to be effective in maintaining community composition, especially of ground beetles with low occurrence ranks and limited power of dispersal (Malausa and Drescher, 1991; Vigna Taglianti *et al.*, 2000). Ground beetles are a suitable taxon with which to test and develop protocols for the assisted migration of large, flightless insects, as they can be studied in enclosures over several generations. Such studies investigating the establishment of carabid populations have been conducted in the past (e.g. Schwöppe *et al.* 1998; de Vries 1996). Moreover, enclosures allow for the complete removal of introduced species to avoid potential introductions of species which may become invasive.

In conclusion, we suggest conservation efforts which encourage diverse forest management practices in order to support a wider range of species with low occurrence ranks, as brachypterous specialists of ancient woodland sites, such as *Carabus glabratus* have different habitat requirements than granivorous species, such as *Amara makolaskii*. It is important to create early successional stages of forests, such as silviculture with large gap creation or proper coppice systems, in addition to the maintenance of stable old-growth stands with high coverage (Isaia *et al.*, 2015; Negro *et al.*, 2009; Spake *et al.*, 2016). The current, predominant management strategies which encourage the transformation of forests to mature stands without early successional stages (Loewe, 1991), do not account for diverse species traits and the habitat requirements of some species.

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## C. Supplementary material

**Table C.1.:** Spearman's rank correlation coefficients ( $\rho$  values) for species traits.

	Geographic range size	Habitat specialization	Body size	Hind wing morphology	Breeding season	Trophic level
Habitat specialization	0.242					
Body size	-0.048	0.029				
Hind wing morphology	0.385	0.021	-0.593			
Breeding season	0.245	0.235	0.076	0.000		
Trophic level	-0.075	0.165	0.433	-0.615	0.000	
Hibernation stage	-0.037	0.127	0.194	-0.141	0.009	-0.026

### C.1. Generating a taxonomic distance matrix of the studies ground beetles species

For our analysis we compiled a taxonomic distance matrix, using six hierarchical levels, ranging from subgenus to family (Table C.2). For example, the two species *Carabus auronitens* and *Carabus violaceus* belong to the same genus *Carabus*, but to different subgenera. This results in a taxonomic distance of two. *Carabus violaceus* and *Abax ovalis* belong to different subfamilies which results in a taxonomic distance of six (Table C.3).

**Table C.2.:** Systematics of higher taxa and their hierarchy in the studied ground beetles. All species belong to the family of Carabidae.

Subfamily	Tribe	Subtribe	Genus	Subgenus	Species
Carabinae	Carabini	Carabina	<i>Calosoma</i>	<i>Calosoma</i>	<i>Calosoma inquisitor</i>
Carabinae	Carabini	Carabina	<i>Carabus</i>	<i>Chrysocarabus</i>	<i>Carabus auronitens</i>
Carabinae	Carabini	Carabina	<i>Carabus</i>	<i>Megodontus</i>	<i>Carabus violaceus</i>
Carabinae	Carabini	Carabina	<i>Carabus</i>	<i>Mesocarabus</i>	<i>Carabus problematicus</i>
Carabinae	Carabini	Carabina	<i>Carabus</i>	<i>Oreocarabus</i>	<i>Carabus glabratus</i>
Carabinae	Carabini	Carabina	<i>Carabus</i>	<i>Oreocarabus</i>	<i>Carabus hortensis</i>
Carabinae	Carabini	Carabina	<i>Carabus</i>	<i>Platycarabus</i>	<i>Carabus irregularis</i>
Carabinae	Carabini	Carabina	<i>Carabus</i>	<i>Tomocarabus</i>	<i>Carabus convexus</i>
Carabinae	Cychrini	Chychrina	<i>Cychrus</i>	<i>Cychrus</i>	<i>Cychrus attenuatus</i>
Carabinae	Cychrini	Chychrina	<i>Cychrus</i>	<i>Cychrus</i>	<i>Cychrus caraboides</i>
Harpalinae	Harpalini	Harpalina	<i>Trichotichnus</i>	<i>Trichotichnus</i>	<i>Trichotichnus laeicollis</i>
Harpalinae	Harpalini	Harpalina	<i>Trichotichnus</i>	<i>Trichotichnus</i>	<i>Trichotichnus nitens</i>
Harpalinae	Harpalini	Harpalina	<i>Harpalus</i>	<i>Harpalus</i>	<i>Harpalus laevipes</i>
Harpalinae	Pterostichini	Pterostichina	<i>Abax</i>	<i>Abax</i>	<i>Abax ovalis</i>
Harpalinae	Pterostichini	Pterostichina	<i>Abax</i>	<i>Abax</i>	<i>Abax parallelepipedus</i>
Harpalinae	Pterostichini	Pterostichina	<i>Abax</i>	<i>Abax</i>	<i>Abax parallelus</i>
Harpalinae	Pterostichini	Pterostichina	<i>Pterostichus</i>	<i>Bothriopterus</i>	<i>Pterostichus oblongopunctatus</i>
Harpalinae	Pterostichini	Pterostichina	<i>Pterostichus</i>	<i>Cheporus</i>	<i>Pterostichus burmeisteri</i>
Harpalinae	Pterostichini	Pterostichina	<i>Pterostichus</i>	<i>Cryobius</i>	<i>Pterostichus pumilio</i>
Harpalinae	Pterostichini	Pterostichina	<i>Pterostichus</i>	<i>Eosteropus</i>	<i>Pterostichus aethiops</i>
Harpalinae	Pterostichini	Pterostichina	<i>Pterostichus</i>	<i>Pterostichus</i>	<i>Pterostichus cristatus</i>
Harpalinae	Sphodrini	Calathina	<i>Calathus</i>	<i>Amphiginus</i>	<i>Calathus rotundicollis</i>
Harpalinae	Sphodrini	Calathina	<i>Calathus</i>	<i>Neocalathus</i>	<i>Calathus micropterus</i>
Harpalinae	Zabrini	Amarina	<i>Amara</i>	<i>Amara</i>	<i>Amara makolskii</i>
Harpalinae	Zabrini	Amarina	<i>Amara</i>	<i>Celia</i>	<i>Amara brunnea</i>
Nebriinae	Nebriini	Nebriina	<i>Leistus</i>	<i>Pogonophorus</i>	<i>Leistus rufomarginatus</i>
Nebriinae	Notiophilini	Notiophilina	<i>Notiophilus</i>	<i>Notiophilus</i>	<i>Notiophilus biguttatus</i>
Nebriinae	Notiophilini	Notiophilina	<i>Notiophilus</i>	<i>Notiophilus</i>	<i>Notiophilus rufipes</i>

**Table C.3.:** Systematics of higher taxa and their hierarchy in the studied ground beetles. All species belong to the family of Carabidae.

	Abax oval	Abax pallp	Abax para	Amar brun	Amar mako	Cala micr	Cala rotu	Calo inqu	Cara auro	Cara conv	Cara glab	Cara hort	Cara irre	Cara prob	Cara viol	Cych atte	Cych cara	Harp laev	Leis rufo	Noti bigu	Noti rufi	Pter aeth	Pter burm	Pter cris	Pter oblo	Pter pumi	Tric laev	
Abax	1																											
pallp																												
Abax para	1	1																										
Amar brun	5	5	5																									
Amar mako	5	5	5	2																								
Cala micr	5	5	5	5	5																							
Cala rotu	5	5	5	5	5	2																						
Calo inqu	6	6	6	6	6	6	6																					
Cara auro	6	6	6	6	6	6	6	3																				
Cara conv	6	6	6	6	6	6	6	3	2																			
Cara glab	6	6	6	6	6	6	6	3	2	2																		
Cara hort	6	6	6	6	6	6	6	3	2	2	2																	
Cara irre	6	6	6	6	6	6	6	3	2	2	2	2																
Cara prob	6	6	6	6	6	6	6	3	2	2	2	2	2															
Cara viol	6	6	6	6	6	6	6	3	2	2	2	2	2	2														
Cych atte	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5													
Cych cara	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	1												
Harp laev	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	6	6											
Leis rufo	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6										
Noti bigu	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5									
Noti rufi	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5	1								
Pter aeth	3	3	3	5	5	5	5	6	6	6	6	6	6	6	6	6	6	6	5	6	6	6						
Pter burm	3	3	3	5	5	5	5	6	6	6	6	6	6	6	6	6	6	6	5	6	6	6	2					
Pter cris	3	3	3	5	5	5	5	6	6	6	6	6	6	6	6	6	6	6	5	6	6	6	2	2				
Pter oblo	3	3	3	5	5	5	5	6	6	6	6	6	6	6	6	6	6	6	5	6	6	6	2	2	2			
Pter pumi	3	3	3	5	5	5	5	6	6	6	6	6	6	6	6	6	6	6	5	6	6	6	2	2	2	2		
Tric laev	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	6	6	6	3	6	6	6	5	5	5	5	5	
Tric nite	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	6	6	6	3	6	6	6	5	5	5	5	5	1

Abbreviations: Abax oval: *Abax ovalis*, Abax pallp: *Abax parallelepipedus*, Abax para: *Abax parallelus*, Amar brun: *Amara brunnea*, Amar mako: *Amara makolskii*, Cala micr: *Calathus micropterus*, Cala rotu: *Calathus rotundicollis*, Calo inqu: *Calosoma inquisitor*, Cara auro: *Carabus auronitens*, Cara conv: *Carabus convexus*, Cara glab: *Carabus glabratus*, Cara hort: *Carabus hortensis*, Cara irre: *Carabus irregularis*, Cara prob: *Carabus problematicus*, Cara viol: *Carabus violaceus*, Cych atte: *Cychrus attenuatus*, Cych cara: *Cychrus caraboides*, Harp laev: *Harpalus laevipes*, Leis rufo: *Leistus rufomarginatus*, Noti bigu: *Notiophilus biguttatus*, Noti rufi: *Notiophilus rufipes*, Pter aeth: *Pterostichus aethiops*, Pter burm: *Pterostichus burmeisteri*, Pter cris: *Pterostichus cristatus*, Pter oblo: *Pterostichus oblongopunctatus*, Pter pumi: *Pterostichus pumilio*, Tric laev: *Trichotichnus laevicollis*, Tric nite: *Trichotichnus nitens*.

**Table C.4.** 95% confidence set of models between average occurrence ranks and species traits. Set of models is constructed by summing up Akaike weights from largest to smallest until the sum of their Akaike weights exceeds 0.95 (grs: geographic range size, hwm: hind wing morphology, trL: trophic level, brd: breeding season, hb: hibernation stage, dhs: degree of habitat specialization, bs: body size).

Model	Explanatory variables included in model	df	$\Delta$ AICc	AICc weight
1	grs + hwm + trL + hb	8	0	0.133
2	grs + hwm + brd	7	0.5	0.103
3	grs + hwm	5	0.56	0.1
4	grs + hwm + trL	6	0.77	0.09
5	grs + hwm + trL + brd	8	1.48	0.063
6	grs + hwm + trL + brd + hb	10	1.77	0.055
7	grs + hwm + brd + hb	9	2.17	0.045
8	grs + hwm + hb	7	2.3	0.042
9	grs + hwm + dhs	6	2.57	0.037
10	grs + hwm + trL + dhs	7	2.72	0.034
11	hwm + trL + hb	7	2.88	0.031
12	grs + hwm + bs	6	3.83	0.02
13	hwm + trL + brd + hb	9	3.84	0.019
14	grs + hwm + trL + hb + dhs	9	3.86	0.019
15	grs + hwm + trL + hb + bs	9	3.97	0.018
16	grs + hwm + trL + bs	7	4.3	0.015
17	grs + hwm + brd + bs	8	4.43	0.014
18	grs + hwm + brd + dhs	8	4.47	0.014
19	hwm + trL + hb + dhs	8	5.42	0.009
20	grs + hwm + trL + brd + bs	9	5.67	0.008
21	hwm + brd + hb	8	5.83	0.007
22	grs + hwm + hb + dhs	8	5.84	0.007
23	grs + hwm + trL + brd + dhs	9	5.88	0.007
24	grs + hwm + dhs + bs	7	6.16	0.006
25	grs + hwm + hb + bs	8	6.21	0.006
26	grs + hwm + trL + brd + hb + bs	11	6.48	0.005
27	grs + hwm + brd + hb + dhs	10	6.48	0.005
28	grs + hwm + trL + dhs + bs	8	6.62	0.005
29	hwm + trL + hb + bs	8	6.71	0.005
30	grs + hwm + brd + hb + bs	10	6.81	0.004
31	grs + hwm + trL + brd + hb + dhs	11	6.93	0.004
32	trL + dhs	4	6.96	0.004
33	hwm + hb	6	7.06	0.004
34	grs + trL + dhs	5	7.25	0.004
35	hwm + trL + brd	7	7.58	0.003
36	hwm + trL	5	7.67	0.003
37	hwm + trL + dhs	6	7.82	0.003



**Table C.5.:** Average parameter estimates and importance value of the 95 % confidence set of models (Akaïke weights > 0.95, including 37 models). Significant results are bold-typed. Intercept: granivorous, macropterous, ground beetles breeding in spring and autumn, and hibernate as imago.

	Estimate	Standard error	Adjusted SE	z-value	P-value	Importance value
Intercept	0.877	0.633	0.649	1.352	0.177	
Geographical range size	0.416	0.157	0.165	2.519	<b>0.012</b>	0.91
Hind wing morphology, dimorph	1.727	0.477	0.499	3.458	<b>&lt;0.001</b>	0.99
Hind wing morphology, brachypterous	0.996	0.565	0.584	1.705	0.088	0.99
Trophic level, predator	0.764	0.407	0.429	1.780	0.075	0.56
Breeding season, autumn	-0.960	0.445	0.470	2.041	<b>0.041</b>	0.38
Breeding season, spring	-0.833	0.419	0.442	1.883	0.060	0.38
Hibernation stage, both imago and larval instar	0.925	0.400	0.421	2.196	<b>0.028</b>	0.44
Hibernation stage, larval instar	0.191	0.430	0.448	0.427	0.669	0.44
Habitat specialisation	0.114	0.166	0.173	0.661	0.509	0.17
Body size	-0.043	0.157	0.166	0.261	0.794	0.11

**Table C.6.:** Mantel r statistic and corresponding P-value (9999 permutations) evaluating the relationship between species taxonomic distances and distances of the model residuals. (Full model includes all species traits, most parsimonious model, showing the lowest AICc, includes the species traits geographic range size, hind wing morphology, trophic level and hibernation stage.)

	r-value	P-value
full model residual distances	-0.075	0.895
most parsimonious model residual distances	-0.050	0.816



## 5. WHERE HAVE ALL THE BEETLES GONE? LONG-TERM STUDY REVEALS CARABID SPECIES DECLINE IN A NATURE RESERVE IN NORTHERN GERMANY

Submitted article<sup>2</sup>

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### Abstract

1. The drastic insect decline has received increasing attention in scientific as well as in public media. Long-term studies of insect diversity trends are still rare, even though such studies are highly important to assess extent, drivers and potential consequences of insect loss in ecosystems.
2. To gain insights into carabid diversity trends of ancient and sustainably managed woodlands, we analysed data of carabid beetles from a trapping study that has been run for 24 years in an old nature reserve of Northern Germany, the Lüneburg Heath. We examined temporal changes in several diversity measures (e.g. biomass, species richness, functional diversity and phylogenetic diversity) and tested diverse species traits as predictor variables for species occurrence.
3. In contrast to recently published long-term studies of insect diversity, we did not observe a decline in biomass, but in species richness and phylogenetic diversity in carabids at our study site. Additionally, hibernation stage predicted the occurrence probability of carabids: Species hibernating as imagines or both imagines and larvae and breeding in spring showed strongest declines.
4. We assume the detected trends to be the result of external effects such as climate change and the application of pesticides in the surrounding. Our results suggest that the drivers for the insect decline and the responses are multifaceted. This highlights the importance of long-term studies with identification of the catches to, at best, species level to support the understanding of mechanisms driving changes in insect diversity and abundance.

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## 5.1. Introduction

In recent years, a drastic decline of insects has been detected in diverse habitats and ecosystems (Dirzo *et al.*, 2014; Hallmann *et al.*, 2017). Since then the insect decline has received a lot of attention, both in ecological and conservation research and in public media as the phenomenon might occur globally at a high pace, with yet unknown ecological consequences (Leather, 2018). However, to entomologists this decline was not surprising news since early compilations (Didham *et al.*, 1996), older studies (e.g. Driscoll and Weir 2005; Haskell 2000) or analyses of red lists and large-scaled inventories (e.g. Desender *et al.* 2010; Schmidt *et al.* 2016) have already shown an increasing number of threatened and vulnerable insect species.

One meaningful approach to deliver a better evidence base to understand extent, significance and potential drivers of the fate of insect populations and species is to carry out long-term studies on specific sites. Only in such studies changes in assemblages or population sizes across time can be related to possible explanatory factors such as land use or climatic changes (e.g. Dieker *et al.* 2011). Such studies can surely help to collect valuable information needed to develop effective conservation measures for insect populations, species, and communities. Currently, long-term data on species' occurrences revealing insights into insect diversity and abundance trends are rare (see for exception: Brooks *et al.* 2012; Hallmann *et al.* 2018). This is in contrast to several well-organised monitoring programs on birds and mammals (cf. Battersby and Greenwood 2004; Schmeller *et al.* 2012) that have already generated solid data over large temporal and spatial scales.

Insects are the most diverse taxon on Earth in terms of species numbers, with beetles representing the largest proportion of this group of organisms. Insects are of considerable importance for ecosystem functioning (Samways, 2005). Especially carabids can be used as indicators for habitat quality, environmental changes as well as ecosystem resilience (Koivula, 2011), and are of high importance for the assessment of environmental impacts as well as for the evaluation of conservation measures (e.g. Kotze *et al.* 2011; Thom *et al.* 2017). Thus, the implementation of suitable conservation strategies for such a functionally important taxon requires specifically designed long-term studies to enhance our understanding of potential drivers of diversity loss.

The few long-term trapping studies of carabids have focused mostly on heathland- and grassland species (e.g. Hallmann *et al.* 2018; van Noordwijk *et al.* 2017). On local and country level, long-term studies on carabids demonstrate in general a declining trend of species numbers and biomass (Hallmann *et al.*, 2018; Kotze *et al.*, 2011). Brooks *et al.* (2012) revealed a similar trend for open habitat types in Great Britain and presume land-use intensification in agricultural landscapes to be the main driver of species and biomass decline in carabids. In less intensively used forests and hedgerows, however, carabid abundance increased significantly (Brooks *et al.*, 2012). Since forest management in some regions (e.g. Central Europe) has developed to be less intensive and more sustainable than in previous centuries (Brang *et al.*, 2014; Niedersächsisches Ministerium für Ernährung Landwirtschaft und Forsten, 1997), carabid diversity and abundance may have increased also in Central European woodlands. In contrast, other arthropod taxa indicate a poor conservation status of Central European forests (Seibold *et al.*, 2015).

Traits suggest a mechanistic explanation for many ecological processes which cause extinction processes of species or the decrease of population densities as a consequence of land-use changes, especially of insect species (Birkhofer *et al.*, 2017; Davies *et al.*, 2000; Nolte *et al.*, 2017). Identifying the characteris-

tics which are common in those species which decline may enhance our understanding of the drivers of species loss.

Here, we analysed a long-term dataset on ground beetles from 24 years of continuous pitfall trapping. Our study site 'Hofgehölz Möhr' is located in an ancient woodland within the oldest nature reserve and largest inland conservation area of northern Germany, the Lüneburg Heath. Since the 1990s, the studied forest site is extensively used. Pitfall traps to inventory carabids were installed in 1994 and have been monitored continuously since then (cf. Günther and Assmann 2004). Thus, the site is well-suited to record long-term population trends and to study if the findings from British woodlands also apply to this specific area in mainland Europe, especially in long-term stable and sustainably managed woodlands. We specifically address the following research questions: (1) Have diversity, abundance and biomass of forest carabids changed over the last 24 years? (2) If there are changes, which traits are characteristic for the increasing or decreasing species? From the results of our long-term survey we will derive conservation strategies for woodland ground beetles.

## 5.2. Material and Methods

### 5.2.1. Study site

The study was initiated in 1994 at the 'Hofgehölz Möhr', an ancient woodland in Northern Germany near the town of Schneverdingen (cf. Günther and Assmann 2004). The site was already labelled as 'woodland' on historical maps dating back to the 18th century ('Kurhannoversche Landesaufnahme' 1774-1786), as well as on following ones and as such is assumed to have been continuously wooded since the last ice age. 'Hofgehölz Möhr', is located in the Lüneburg Heath Nature Reserve which was first designated in 1921 (219 km<sup>2</sup>) and expanded to its current size of 231.5 km<sup>2</sup> in 1993. Until the 1960s, the surrounding heathland, bog and fen areas were used for extensive agriculture, especially peat cutting and grazing. Since then, the utilization has been further reduced and some restoration measures (e.g. blocking of drainage ditches near the study area) occurred in 2003 and 2004. Nevertheless, the study site is not directly influenced by ground water table changes as the sites are located about one meter higher than the forest-adjacent open sites. The ancient woodland 'Hofgehölz Möhr' is about 4 ha in size but is today included in a forest of approximately 70 ha. The canopy layer of the studied Periclymeno-Fagetum forest is dominated by beech (*Fagus sylvatica*) and Common Oak (*Quercus robur*), the litter layer and humus have a relative low pH value (cf. von Oheimb *et al.* 2008). The forest site was completely left to natural development, with the exception of the removal of some Norway spruce (*Picea abies*) tree individuals in 2007 (pers. comm. D. Mertens, Verein Naturschutzpark e.V.).

### 5.2.2. Trapping

Since 1994, continuous trapping of ground beetles has been carried out with eight pitfall traps being open throughout each year. The traps (plastic cups, 10 cm diameter, 10.3 cm depth and 500 ml volume) were placed in a transect from North to South with 10-12 m distance between traps. The traps contained a mixture of ethanol (40%), water (30%), glycerol (20%) and acetic acid (10%) (cf. Renner 1980). Between March and October the traps were emptied fortnightly, between November and February monthly. Carabids from each trap were identified to species level and the number of individuals

per species per trapping period counted. Our analysis is based on data gathered from June 1994 until December 2017.

### 5.2.3. Data analysis

All statistical analyses were run in R (version 3.3.2, R Core Team 2016). Graphs were drawn using the 'ggplot2' package (version 2.2.1, Wickham and Chang 2016) in R. The number of species in a sample (or, in this case: year) is highly dependent on the number of individuals in this sample. Therefore, we calculated the species richness using a rarefaction approach based on the minimum number of individuals trapped in a year (425 in the year 2004). Species richness was calculated using the package 'vegan' (version 2.4-5, Oksanen *et al.* 2017).

For calculating functional diversity we compiled traits typically used for ground beetles (Birkhofer *et al.* 2017; Homburg *et al.* 2014b; Nolte *et al.* 2017; Table 5.1). Traits were compiled from [www.carabids.org](http://www.carabids.org) (Homburg *et al.*, 2014b), amended by information from Turin (2000) and Nolte *et al.* (2017) and from Bräunicke and Trautner (2009) for the habitat preferences. Functional diversity was calculated after Petchey and Gaston (2002, 2006) using the 'Gower' distance metric for building the cluster dendrogram (UPGMA method, package 'cluster', (version 2.0.5, Maechler *et al.* 2017, in R) based on a set of variables in which the levels of each trait variable were coded using two variables (Table 5.1). From the resulting cluster dendrogram the sum of the vertical cluster branch lengths for all occurring species (weighed by their abundance) represents the functional diversity of a specific community (here: the species set of a certain year).

We calculated the phylogenetic diversity for each year by calculation Rao's quadratic entropy (Rao's Q; Rao 1982) from a species-by-species taxonomic distance matrix (Euclidean distances) and a species-abundance matrix. Rao's Q is calculated as the variance in pairwise species dissimilarities (e.g. phylogenetic or functional) among the relative species abundances of all individuals in a community (de Bello *et al.*, 2010; Schuldt *et al.*, 2014). The taxonomic distances were calculated using taxonomical hierarchies according to the Catalogue of Palearctic Coleoptera (Löbl and Smetana, 2003; Nolte *et al.*, 2017). Since for many species no DNA sequences are available yet, a molecular phylogeny, as described in phylogenetic trees, was not applicable. Nevertheless in carabids, taxonomic hierarchies are highly supported by molecular phylogenies (cf. Ober and Maddison 2008).

Species biomass was calculated from mean body length after Booij *et al.* (1994) and multiplied by the number of individuals per year. The total biomass per year over all species was then calculated.

The calculated measures of diversity may not be independent from, but correlated to, each other. To assess relationships between them, Spearman Rank correlations were conducted. Resulting correlation probabilities were corrected for repeated testing using the False Discovery Rate (Benjamini *et al.*, 2001). Likewise, trait variables can be related to each other, i.e. the occurring sets of trait variable levels may not always be independent of each other. We thus checked for possible associations between the analysed trait variables by a set of  $\chi^2$ -Contingency-Tests (for sets of two nominal variables) or ANOVA with subsequent Tukey post-hoc tests (combination of numeric and nominal variables). The post-hoc-tests were run in the R package 'multcomp' (version 1.4.8, Hothorn *et al.* 2017). Repeated testing was accounted for by using the False Discovery Rate.

We tested for possible temporal linear changes in species numbers, species richness, phylogenetic and functional diversity as well as numbers of individuals and biomass using a General Linear Model

**Table 5.1.:** Trait variables and their levels for the 55 recorded ground beetle species. For different analyses, the trait variables were coded in different ways, as can be seen from the third and fourth column.

Trait variable	Explanation	Variable type and level(s) for calculation of functional diversity	Variable type and level(s) for analyses of relationships between trait variables	No. species in a trait level group
Body size, mean	Mean body length from tip of mandible to tip of elytra, in mm	-	Continuous	55
Body size, minimum	Minimal body length, measured as above, in mm	Continuous	-	55
Body size, maximum	Maximal body length, measures as above, in mm	Continuous	-	55
Wing development	Development of the alae, i.e. the second pair of wings	2 variables, nominal: 1 – 0: brachypterous 1 – 1: dimorphic 0 – 1: macropterous	Nominal, 3 levels: • brachypterous • dimorphic • macropterous	11 18 26
Habitat preference	Preferred habitat after Bräunicke and Trautner (2009)	2 variables, nominal: 1 – 0: forest species 1 – 1: eurytopic 0 – 1: other habitats	Nominal, 3 levels: • forest species • eurytopic • specialists for other habitats	15 18 22
Food preference	Preferred type of food	2 variables, nominal: 1 – 0: predator 1 – 1: omnivorous 0 – 1: herbivorous	Nominal, 3 levels: • predator • omnivorous • herbivorous	38 9 8
Hibernation type	Developmental stage in which species hibernates	2 variables, nominal: 1 – 0: imago 1 – 1: both stages 0 – 1: larva	Nominal, 3 levels: • imago • both stages • larva	34 9 12
Reproduction time	Season in which species reproduces	2 variables, nominal: 1 – 0: spring 1 – 1: indifferent 0 – 1: autumn 0 – 0: other	Nominal, 4 levels: • spring • both seasons • autumn • other	33 4 16 2

with 'Year' as the only explanatory variable. Model assumptions were checked graphically using diagnosis plots.

To test whether trait variables explained changes over time in the species occurrence (presence/absence) a Generalized Linear Mixed Effects Model (GLMM) with binomial errors and 'Species' as random term was used. Analysing the interaction between 'Year' and each of the following trait variables 'Body size', 'Food preference' and 'Hibernation type' allowed us to assess a possible change across time in the relative occurrence of species with a respective trait level. All other traits were significantly associated with the three chosen trait variables (Table 5.2), and, thus, not incorporated into the model. Models were run using the 'lme4' package (version 1.1.15, Bates *et al.* 2015). Models were simplified step-wise using likelihood ratio tests, starting with the two-way interactions, until only significant terms (or those included in significant interactions) remained (Crawley, 2007).

### 5.3. Results

Between June 1994 and December 2017 a total of 29,829 ground beetle individuals from 55 species were caught. 15 species were recorded with only one individual each (Table D.1, Supplemental Information). 15 species were forest specialists, 18 species eurytopic and 22 were specialists for other, adjacent habitat types. The number of species trapped in a year ranged from 11 (2016) to 31 (1998), with a median of 17.5 (interquartile range: 16-21) species per year.

#### 5.3.1. Measures of diversity

Both the number of species and the species richness declined significantly across years and there was a trend for a reduction in functional diversity (Table 5.2, Fig. 5.1a). In addition, the phylogenetic diversity decreased significantly over time (Table 5.2). While the number of species, species richness and functional diversity were significantly positively correlated to each other, the phylogenetic diversity was not correlated to either the species richness or the functional diversity (Table 5.3).

In contrast, there was no significant change in the total number of individuals (across all species) caught over the years (Table 5.2), which ranged from 425 (2004) to 2244 (1998). Likewise, the total biomass did not vary systematically over time (Table 5.2, Fig. 5.1c). The yearly total biomass varied between 140 g (2004) and 963 g (2008). Both measures (number of individuals and total biomass) were highly positively correlated (Table 5.3).

**Table 5.2.:** Results from GLMs testing for changes in community characteristics across 24 years for the complete species pool (55 species) and for woodland species (15 species) only. Intercepts represent averages for the year 1994. Significant effects are marked in bold.

Response		Coefficient	F <sub>1,22</sub>	P	R <sup>2</sup>
<b>All species: 55 species, 29,829 individuals</b>					
No. species	Intercept	22.53			
	<b>Year</b>	<b>-0.31</b>	<b>5.38</b>	<b>0.030</b>	<b>0.197</b>
Species richness (rarefied to 425 individuals)	Intercept	16.62			
	<b>Year</b>	<b>-0.19</b>	<b>8.84</b>	<b>0.007</b>	<b>0.289</b>
Functional diversity	Intercept	4.81			
	Year	-0.04	3.69	0.068	0.144
Phylogenetic diversity	Intercept	3.09			
	<b>Year</b>	<b>-0.03</b>	<b>8.99</b>	<b>0.007</b>	<b>0.290</b>
No. individuals	Intercept	1204.8			
	Year	3.19	0.04	0.846	0.002
Total biomass (kg)	Intercept	0.44			
	Year	0.009	1.63	0.215	0.069

#### 5.3.2. Trait relationships and affected traits

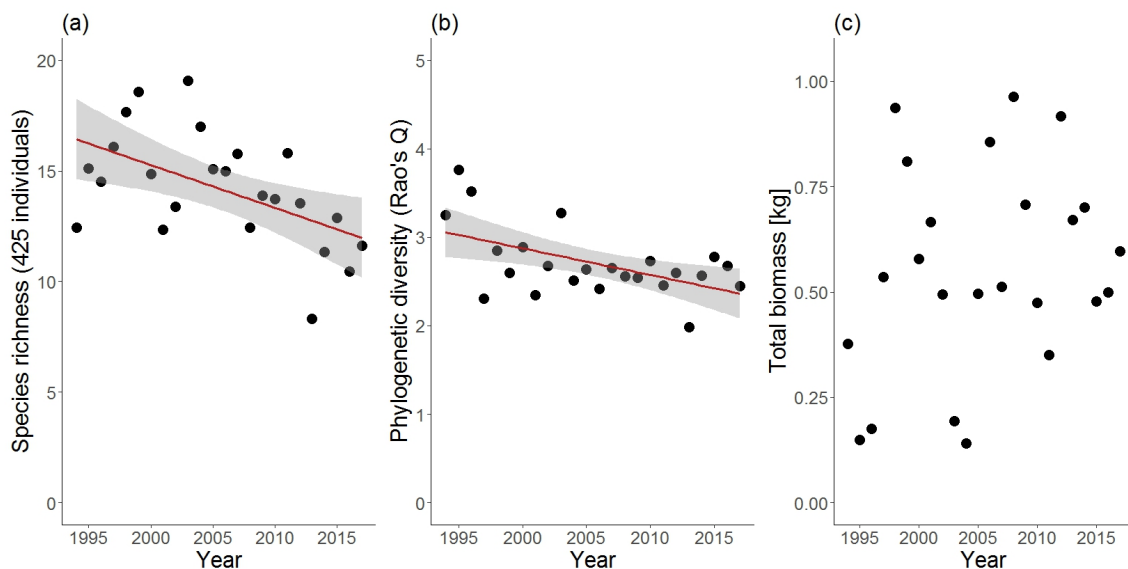
The recorded beetle species differ in their life-history-traits. However, not all of the traits varied independently from each other but were related in a certain way (Table 5.4). For instance, average body size of a species was significantly related to its wing-development (larger beetle species are less likely to fly, Fig. D.1a in Supplement) and to its habitat preference (forest species were significantly larger, Fig. D.1b in Supplement). The spring breeders were significantly smaller than the autumn breeders, while the



**Table 5.3:** Spearman rank correlations between different biodiversity measures. Significant correlations (after correction for multiple testing, cf. Benjamini *et al.* 2001) are indicated in bold; p-values are given in brackets.

	Species richness	Functional diversity	Phylogenetic diversity	No. individuals	Total biomass
No. species	<b>0.785 (&lt;0.001)</b>	<b>0.944 (&lt;0.001)</b>	-0.099 (0.644)	0.397 (0.055)	0.338 (0.106)
Species richness		<b>0.723 (&lt;0.001)</b>	0.203 (0.341)	-0.110 (0.609)	-0.213 (0.316)
Functional diversity			-0.101 (0.618)	0.417 (0.044)	0.328 0.118
Phylogenetic diversity				<b>-0.493 (0.015)</b>	-0.446 (0.030)
No. individuals					<b>0.877 (&lt;0.001)</b>

other species showed intermediate body sizes (Fig. D.1c in Supplement). Likewise, the reproduction time was significantly related to the hibernation type (most of the spring breeding species hibernated as adult beetles, Fig. D.1d in Supplement). The food preference was not significantly related to any of the other studied traits.

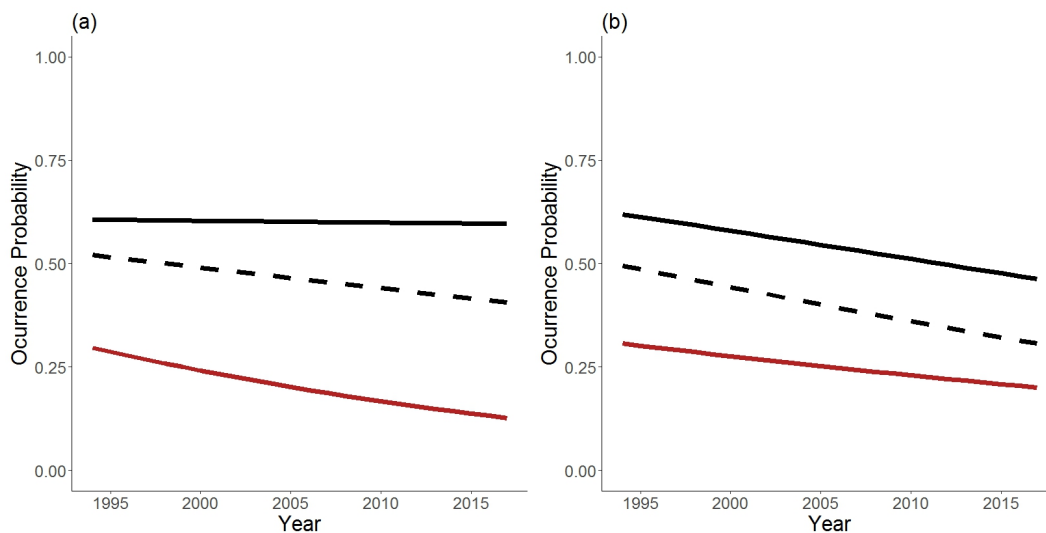


**Figure 5.1:** Rarefied species richness (a), phylogenetic diversity (b) and total biomass (c) across 24 years of study. The lines and the shaded areas indicate significant declines over time (GLM, 95 % confidence interval). For further details see Table 5.2.

The likelihood of a species being present declined differently depending on its body size (GLMM, 'Body size : Year',  $\chi^2 = 10.26$ ,  $df = 1$ ,  $P = 0.001$ ; Fig. 5.2a): the smaller the species the more pronounced was its decline (Fig. 5.2a). In addition, the decline in the likelihood of species' occurrence over time was explained by the developmental stage at hibernation (GLMM, 'Hibernation type : Year',  $\chi^2 = 7.42$ ,  $df = 2$ ,  $P = 0.024$ ; Fig. 5.2b): those species that hibernated as larva, were less likely to disappear over time than those hibernating as imago or as both stages ( $\chi^2 = 7.03$ ,  $df = 1$ ,  $P = 0.008$ ); the latter did not differ over time in their occurrence probability ( $\chi^2 = 1.41$ ,  $df = 2$ ,  $P = 0.493$ ; Fig. 5.2b). The food preference of a species did not predict the likelihood of its occurrence across time (GLMM, 'Food preference: Year',  $\chi^2 = 2.88$ ,  $df = 2$ ,  $P = 0.236$ ) or its presence independently of time (GLMM, 'Food preference',  $\chi^2 = 3.60$ ,  $df = 2$ ,  $P = 0.166$ ). A model, in which the variable 'Wing development' was additionally included, resulted in the same outcome (not shown).

**Table 5.4.:** Relationships between traits of the captured 55 species were assessed using contingency tables (exception: for relationships with the continuous variable body size ANOVAs were used). Indicated in bold are those test-statistics that remain significant after correction for multiple testing (False discovery rate after Benjamini *et al.* 2001). Underlined trait variables were used for further analysis.

	Wing development	Habitat preference	Food preference	<u>Hibernation type</u>	Reproduction time
<u>Body size</u>	<b><math>F_{2,52} = 49.78</math>, <math>p &lt; 0.001</math></b>	<b><math>F_{2,52} = 9.58</math>, <math>p &lt; 0.001</math></b>	$F_{2,52} = 1.03$ , $p = 0.365$	$F_{2,52} = 6.80$ , $p = 0.002$	<b><math>F_{3,51} = 3.74</math>, <math>p = 0.017</math></b>
Wing development		$\chi^2 = 24.95$ , <b><math>df = 4</math></b> <b><math>p &lt; 0.001</math></b>	$\chi^2 = 10.63$ , $df = 4$ $p = 0.031$	$\chi^2 = 8.84$ , $df = 4$ $p = 0.065$	$\chi^2 = 9.55$ , $df = 6$ $p = 0.145$
Habitat preference			$\chi^2 = 3.11$ , $df = 4$ $p = 0.539$	$\chi^2 = 7.87$ , $df = 4$ $p = 0.094$	$\chi^2 = 8.85$ , $df = 6$ $p = 0.182$
<u>Food preference</u>				$\chi^2 = 3.68$ , $df = 4$ $p = 0.452$	$\chi^2 = 6.43$ , $df = 6$ $p = 0.377$
<u>Hibernation type</u>					$\chi^2 = 64.52$ , <b><math>df = 6</math></b> <b><math>p &lt; 0.001</math></b>



**Figure 5.2.:** Changes in species occurrence probabilities depending on their body size (a) and hibernation type (b). For simplification of the presentation, two separate GLMMs with only the interaction between 'Body size : Year' and 'Hibernation : Year', respectively, and the main effects included in the interaction were run to create prediction lines for (a) and (b). Also, a three-level variable 'Body size class' was built from the continuous variable 'Body size' (statistics reported in the main text were based on the continuous variable; a). (a) Small species [ $< 10$  mm]: red line; medium sized species [ $10 - < 20$  mm]: dashed line; large species [ $\geq 20$  mm]: black line. (b) Species with hibernation as imago: black line; as larvae: red line; or at either stages: dashed line.

## 5.4. Discussion

In contrast to recently published long-term studies of flying insect diversity in Germany and the Netherlands (e.g. Hallmann *et al.* 2017, 2018), we did not observe a decline in biomass, but in species richness and phylogenetic diversity, and a declining trend in functional diversity in carabids at our study site. Our results of decreasing diversity measures are in accordance with surveys on many other studied insect taxa, such as butterflies, moths, and solitary bees (Fox *et al.*, 2014; Habel *et al.*, 2016; Potts *et al.*, 2010). In summary, the assumption that insect diversity is undoubtedly threatened is supported by this data.

However, it is difficult to infer that long-term insect decline appears as a uniform global trend over all regions, habitats and taxa, as the referred British study on carabid species concluded a positive population trend of carabids in woodland and hedges (Brooks *et al.*, 2012). The development of populations and community composition tends to be driven by more complex processes which are biased by local, regional and global factors such as land-use (change) and disturbance regimes (e.g. agricultural and forestry activities, including the usage of pesticides: Geiger *et al.* 2010; Nilsson *et al.* 2008; Woodcock *et al.* 2016), climate conditions and changes (Brandmayr and Pizzolotto, 2016; Habel *et al.*, 2016; Thom *et al.*, 2017), species traits (this study; Brooks *et al.* 2012; Nolte *et al.* 2017) and the interactions between these factors. Since it is difficult to disentangle the different mechanisms, we focus on the following main aspects.

### 5.4.1. Habitat

In their study of carabid species, Brooks *et al.* (2012) found carabids occurring in woodland and hedgerow habitats to be the only group with increasing abundance and richness trends. The authors assume habitat stability in woodland habitats to be a buffer against perturbations. As changes in forest management practices in Central Europe have put a better focus on preserving the ecological functions over the last decades (Brang *et al.*, 2014), we expected similar results for our study area, which is located in an ancient woodland and protected as nature reserve for almost a century. However, the extent of external effects are unknown, as the following example illustrates: East of the Lüneburg Heath Nature Reserve, insecticides against caterpillars feeding on oaks (e.g. the oak processionary (*Thaumetopoea processionea*), winter moth (*Operophtera brumata*) and green oak moth (*Tortrix viridana*)) have been applied between 2012 ('Landeszeitung', April 25, 2012) and 2018. The agent used, Diflubenzoron, is known to have negative effects also on non-target species, especially on other herbivorous species and their predators (Hassan *et al.*, 1994). Klenner (1994) found for Diflubenzoron-treated woodlands a reduced number of carabid individuals, especially of spring breeders. These carabids reproduce and have early larval instars during the application time of Diflubenzoron. The synchrony of the agent application and the occurrence of early larval instars imply causal negative effects of the insecticide on these non-target species. For agro-ecosystems, Geiger *et al.* (2010) already showed that pesticides, such as insecticides used for crop protection, do not only harm the target organisms. These products even have an immense negative effect on other insects (including those providing biological control, e.g. carabids) and thus are one driver of biodiversity loss (Purtauf *et al.*, 2005; Scherney, 1959; Thiele, 1977). The exact influence of pesticide applications in surrounding areas can only be assumed, since we are lacking data on precise insecticide usage near the nature reserve and measures of chemical influences on the study

plot. Specific research designs would be required to identify e.g. the drifting effects and their impacts on species and ecosystems.

#### 5.4.2. Species traits

As our results show species loss in an ancient habitat type, habitat stability may not be the most important factor shaping long-term trends of species abundances and occurrences. Trait-based studies are increasingly used to test hypotheses on species occurrence and extinction probabilities (e.g. Nolte *et al.* 2017). In times of dramatic insect decline, traits may be used to improve the understanding of extinction processes. However, the study of species traits cannot be made simply by consolidation or differentiating species by each trait independently. Species characteristics can be strongly correlated but not in a linear relationship over all species (cf. Davies *et al.* 2004; Laube *et al.* 2013). Our results show high correlation values between reproduction and hind wing development, the latter being the more obvious trait in carabid species but apparently not the one having the stronger effect in occurrence probability. Nolte *et al.* (2017) showed for a large-scale data set that dispersal ability is a suitable predictor for the extinction risk of woodland species, with dimorphic carabids being less vulnerable to extinction. In our study on the local level, however, species' dispersal ability represented by hind wing development appears to be the weaker predictor in contrast to reproduction period. In addition, we found other species characteristics such as body size or hibernation type to be good predictors for occurrence probability of species. In our study diversity loss is represented by a decreasing number of small species, whereas other studies found large carabids to be more prone to species decline (Brooks *et al.*, 2012; Kotze and O'Hara, 2003).

But as spring breeders may also be affected by insecticide applications in woodlands or arable fields in the surrounding, our recent results cannot disentangle which factor – global climate change or local pesticide application or both factors – are responsible for the observed species diversity trends.

#### 5.4.3. Climate change

In addition, we detected hibernation stage as a significant predictor of occurrence probability of carabids. Nevertheless, the traits hibernation stage and reproduction time of the species were closely associated. Species hibernating as imagines or both imagines and larval instars tend to face a stronger decline than species hibernating as larval instars only (this study; Lindroth 1949). Since species of these two hibernation types are more likely to be spring breeders, this trend is also true for this group of species. The larvae of spring breeders are active in summer and have to face higher temperatures and mostly lower humidity than species reproducing in autumn and hibernating as larvae. For instance, in habitats with a Mediterranean climate (low precipitation, but high temperatures during summer and mild, but rainy winters), spring breeders seem to be completely absent in woodlands (Brandmayr *et al.*, 1983; Timm, 2010). This is probably a consequence of the drought stress of larvae during summer, as larval instars are the most sensitive part of the life cycle in ground beetles (Lövei and Sunderland, 1996).

As a consequence of climate warming, some spring breeders tend to follow suitable climate conditions and show an uphill shift of their occurrences (Brandmayr and Pizzolotto, 2016). During the last seven decades, mean annual temperature increased by 1.9 °C and summer precipitation decreased by 5 to 10 percent in Lower Saxony. Moreover heat waves and drought periods during summer increased

significantly (Umweltbundesamt, 2018). Consequently, the strong declining trend of spring breeders can be the result of ongoing climate change. Further investigations linking species abundance and occurrence data to local climate conditions are required and planned for this sample in order to improve the knowledge on above-mentioned interrelations.

## 5.5. Conclusions

Our long-term study shows a decline of species numbers, and phylogenetic diversity of carabids in the oldest nature reserve of northern Germany. The study highlights the importance of long-term studies in which the individuals are identified to a low taxonomic (ideally down to species) level. Only this allows a deeper insight and, thus, the understanding of mechanisms driving local and global patterns of insect diversity and abundance.

In order to understand these patterns and the underlying mechanisms we need to design and, more importantly, carry out standardized and comparable long-term studies in different habitats (not only in protected areas but also intensively used agricultural and forestry landscapes): a large-scale and long-time insect monitoring would be necessary. This is of crucial importance when it comes to further enhancing the knowledge whether or not a global trend of an insect decline applies to all species and habitats. To support (or falsify) such a hypothesis, data availability, especially long-term approaches with standardized and comparable research designs and analytical approaches, must be improved or developed. From a conservation perspective, we also require better evidence on population trends of specific species groups in nature reserves in order to distinguish between local and global drivers for e.g. insect decline and to evaluate the success of conservation measures and interventions.

Using trait-based approaches to predict species occurrence probabilities appears very promising. Nevertheless, statistical analyses always have to account for trait correlations and ecological background knowledge has to validate model results.

## Acknowledgements

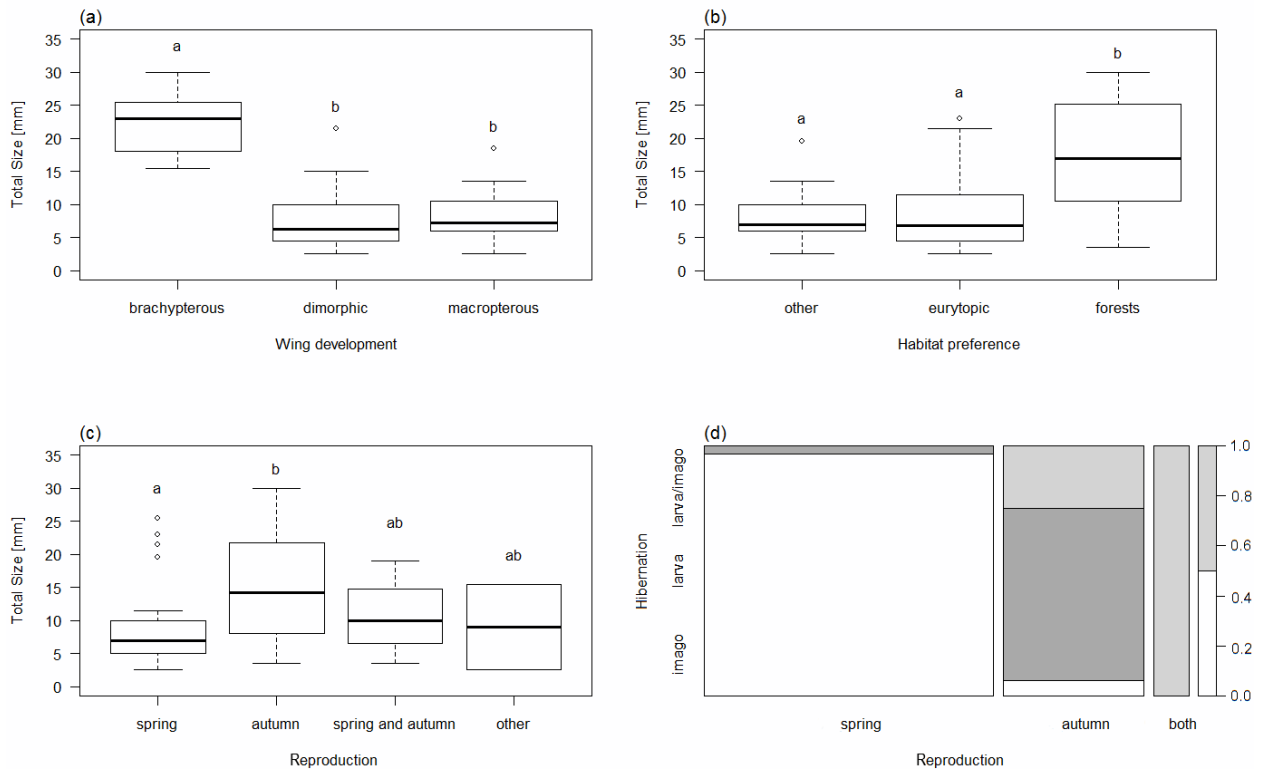
We thank Johannes Prüter, Johann Schreiner, Manfred Lütkepohl and Dirk Mertens for supporting this long-term survey. We are also grateful to Doris Blume-Winkler, Tobias Keienburg, Michael Kempken and many volunteers of the 'ecological year' (FÖJ) for emptying and reinstalling the traps, and Marianne Peters and some students for sorting and identifying a large part of the catches.

## D. Supplementary material

**Table D.1.:** Species caught in the study area with their habitat preference, traits and average total body size (min and max) and weight (calculated after Booij *et al.* 1994). The minimal and the maximal number of catches per year and the total number of catches over the whole study period (1994 – 2017) is also given (e: eurytopic, F: forest, O: open, W: wetlands; her: herbivorous, omn: omnivorous, pre: predatory; ma: macropterous, mi: micropterous, di: wing-dimorphic; im: imago, la: larva, la/im: larva/imago; au: autumn, sp: spring, sp/au: spring/autumn).

Species	Habitat pref.	Wing dev.	Food	Hibernation	Reproduction	Body size (mm)			Weight (mg)	No. of catches		
						Min	Max	Mean		Min	Max	Totals
<i>Abax parallelepidus</i>	F	mi	pre	la/im	sp/au	16	22	19	288	18	322	3302
<i>Abax parallelus</i>	F	mi	pre	im	other	13	18	15.5	158	0	1	2
<i>Agonum fuliginosum</i>	W	ma	pre	im	sp	5	7	6	10	0	2	5
<i>Agonum micans</i>	W	ma	pre	im	sp	5	7	6	10	0	2	3
<i>Agonum sexpunctatum</i>	O	ma	pre	im	au	6	9	7.5	18	0	1	1
<i>Amara consularis</i>	O	ma	her	la	au	7	9	8	22	0	1	1
<i>Amara familiaris</i>	e	ma	her	im	sp	5	9	7	15	0	1	1
<i>Amara municipalis</i>	O	ma	her	la	au	5	7	6	10	0	1	1
<i>Amara plebeja</i>	O	ma	her	im	sp	6	8	7	15	0	2	4
<i>Amara similata</i>	O	ma	omn	im	sp	7	10	8.5	27	0	1	2
<i>Amara tibialis</i>	O	ma	her	im	sp	4	5	4.5	4	0	1	1
<i>Anisodactylus binotatus</i>	e	ma	her	im	sp	8	12	10	43	0	2	7
<i>Asaphidion curtum</i>	F	ma	pre	im	sp	3	4	3.5	2	0	16	34
<i>Asaphidion flavipes</i>	O	ma	pre	im	sp	3	4	3.5	2	1	3	9
<i>Badister lacertosus</i>	W	ma	pre	im	sp	6	7	6.5	12	0	1	1
<i>Bembidion lampros</i>	e	di	pre	im	sp	2	4	3	1	0	58	158
<i>Bembidion properans</i>	e	di	pre	im	sp	3	4	3	2	0	1	1
<i>Bembidion quadrimaculatum</i>	e	ma	pre	im	sp	2	3	2.5	1	0	1	1
<i>Bembidion tetracolum</i>	e	di	pre	im	sp	4	6	5	6	0	1	2
<i>Bradycellus ruficollis</i>	W	di	omn	la/im	other	2	3	2.5	1	0	1	1
<i>Calodromius spilotus</i>	F	ma	pre	im	sp	3	4	3.5	2	0	1	1
<i>Carabus arvensis</i>	W	mi	pre	im	sp	16	23	19.5	311	0	1	4
<i>Carabus auronitens</i>	F	mi	pre	im	sp	16	35	25.5	689	15	198	1373
<i>Carabus convexus</i>	F	mi	pre	la	au	14	20	17	207	0	3	14
<i>Carabus glabratus</i>	F	mi	pre	la	au	26	34	30	1114	0	2	3
<i>Carabus granulatus</i>	e	di	pre	im	sp	13	30	21.5	416	0	3	9
<i>Carabus hortensis</i>	F	mi	pre	la	au	21	30	25.5	689	0	1	1
<i>Carabus nemoralis</i>	e	mi	omn	im	sp	18	28	23	507	0	93	258
<i>Carabus problematicus</i>	F	mi	pre	la	au	20	30	25	649	0	148	1043
<i>Carabus violaceus</i>	F	mi	omn	la	au	22	38	30	1114	32	622	7355
<i>Cychrus caraboides</i>	F	mi	pre	la	au	14	20	17	207	0	10	87
<i>Epaphius secalis</i>	W	ma	pre	la/im	au	3	4	3.5	2	0	2	6
<i>Harpalus latus</i>	e	ma	her	la/im	sp/au	8	11	9.5	37	0	8	16
<i>Harpalus quadripunctatus</i>	F	ma	her	la/im	sp/au	9	12	10.5	50	0	10	21
<i>Leistus rufomarginatus</i>	F	di	pre	la	au	7	9	8	22	0	19	181
<i>Limodromus assimilis</i>	F	ma	pre	im	sp	10	13	11.5	65	0	9	14
<i>Loricera pilicornis</i>	e	ma	pre	im	sp	6	8	7	15	0	16	79
<i>Nebria brevicollis</i>	e	ma	pre	la	au	9	14	11.5	65	0	213	740
<i>Nebria salina</i>	O	ma	pre	la/im	au	9	13	11	57	0	7	15
<i>Notiophilus biguttatus</i>	e	di	pre	im	sp	3	6	4.5	4	0	93	521
<i>Notiophilus palustris</i>	e	di	pre	im	sp	4	6	5	6	0	1	2
<i>Oxytelus obscurus</i>	W	di	pre	im	sp	4	6	5	6	0	1	1
<i>Poecilus cupreus</i>	O	ma	omn	im	sp	9	13	11	57	0	1	4
<i>Poecilus versicolor</i>	O	ma	pre	im	sp	8	12	10	43	0	5	10

Species	Habitat pref.	Wing dev.	Food	Hibernation	Reproduction	Body size (mm)			Weight (mg)	No. of catches		
						Min	Max	Mean		Min	Max	Totals
<i>Pseudophonus rufipes</i>	O	ma	omn	la/im	au	11	16	13.5	105	0	34	50
<i>Pterostichus melanarius</i>	e	di	omn	la/im	au	12	18	15	143	0	6	37
<i>Pterostichus minor</i>	W	di	pre	im	sp	6	8	7	15	0	1	1
<i>Pterostichus niger</i>	e	ma	pre	la	au	15	22	18.5	266	61	768	7212
<i>Pterostichus nigrita</i>	W	di	pre	im	sp	8	12	10	43	0	1	2
<i>Pterostichus oblongopunctatus</i>	F	di	pre	im	sp	9	12	10.5	50	63	1057	7089
<i>Pterostichus rhaeticus</i>	W	di	pre	im	sp	9	12	10.5	50	0	4	19
<i>Pterostichus strenuus</i>	e	di	omn	im	sp	5	7	6	10	0	11	67
<i>Stomis pumicatus</i>	O	di	pre	im	sp	6	8	7	15	0	1	1
<i>Synuchus vivalis</i>	e	di	omn	la	sp	5	8	6.5	12	0	1	1
<i>Trechus obtusus</i>	e	di	pre	la/im	sp/au	3	4	3.5	2	0	14	55



**Figure D.1:** Relationships between significantly related trait variables: Body size and wing development (a), body size and habitat preference (b), body size and reproduction (c), and reproduction and hibernation (d). In the box-whisker-plots different letters indicate significant differences (Tukey post-hoc tests,  $p < 0.05$ )





## 6. MAIN FINDINGS AND FUTURE PROSPECTS

Community ecology is one of the oldest disciplines in ecology. Besides abiotic factors especially competition has been intensively discussed to be a crucial underlying mechanism of community compositions for ground beetles (e.g. den Boer 1989; Loreau 1989). Modern research approaches in community ecology increasingly focus on the influence of species traits on e.g. species occurrences or extinction risks. To gain a better understanding of the influence of traits on community composition, it is necessary to analyze these relationships at different spatio-temporal and taxonomical scales. Especially studies including a high number of species with various traits and covering several habitat types or even different climatic regions may allow for a generalization of their results. Due to the large number of well-known and well-documented traits, ground beetles are a suitable entomological model taxon for trait-based approaches. This thesis analyzed a large set of ecological and distributional traits of a local as well as of a large Central European community, identifying that:

- I) dependent relations were common between many traits of ground beetles,
- II) phylogenetic relatedness did not seem to influence ground beetle community composition,
- III) species of unstable habitat types were characterized by a similar set of species traits, while traits were more dissimilar in stable habitat types,
- IV) certain species traits were more frequently found to be main drivers of species occurrences or extinction risks.

### 6.1. Relations between ground beetle traits

Identifying the effects of certain traits on community compositions can improve our understanding of extinction processes (Chichorro *et al.*, 2018). However, when using trait-based approaches for the investigation of species occurrence probabilities and extinction risks, relations between species traits have to be considered as traits may be interdependent on each other. Dependent relations between traits have already been confirmed for several taxa (e.g. Harvey and Pagel 1991; birds: Gaston and Blackburn 2000; Laube *et al.* 2013; butterflies/moth: García-Barros 2008; Mattila *et al.* 2006, or longhorn beetles: Jeppsson and Forslund 2014). For ground beetles, however, mostly studies dealing with the relation of certain traits to dispersal power have been described in literature (Gutierrez and Menéndez, 1997; Stevens *et al.*, 2014).

This thesis identified significant dependent relations for most combinations of ground beetle traits (see Chapter 2). Especially, hind wing morphology – with its trait characteristics, brachyptery, macroptery and dimorphism – was strongly related to the other tested traits. In accordance with Homburg *et al.* (2013), who found a positive relation between hind wing development and body size for widespread species, the results of this thesis showed that brachypterous species were significantly larger than macropterous or dimorphic species. In accordance with other studies (Dennis *et al.*, 2000; Gutierrez and Menéndez, 1997; Malmqvist, 2000), macropterous and dimorphic ground beetles also showed larger distribution range sizes, as they tend to have higher colonization and reproduction rates (den Boer *et al.*, 1980). However, a positive relation between range size and flight capacity does not seem to be generally valid but scale dependent, as some studies reported brachypterous species to be more

widespread at a regional scale (Gutierrez and Menéndez, 1997; Zalewski and Ulrich, 2006). On regional scales, brachypterous species might benefit from their expected higher establishment abilities. Consequently, the assumed relationship, that regionally widespread species are also widespread on a larger geographical scale (Gaston, 1994), cannot generally be confirmed for ground beetles. Furthermore, brachypterous and macropterous species were highly specialized, while dimorphic species were less specialized. A significant negative relation was observed between habitat specialization and distribution range size, as a wider habitat niche enables a species to colonize a larger number of suitable sites (Brown, 1984; Laube *et al.*, 2013; Slatyer *et al.*, 2013). However, when analyzing the species pools of habitat types individually, the relation between high habitat specialization and small range size could not be confirmed for all habitat types. In fact, this relation seemed to be habitat specific. While the expected relation was observed for species of most habitat types, forest species showed mainly low distribution range sizes although they were rather generalistic.

Consequently, these results (see Chapter 2 for further identified relations) highlight the difficulties in the interpretation of trait-based analyses due to dependent relations between species traits (additionally depending on the taxonomical and geographical scale). It is often difficult to predict general trait correlations and to determine which trait is the real driver of the observed pattern (Chichorro *et al.*, 2018). In example, for longhorn beetles Jeppsson and Forslund (2014) identified an influence of trait relations on their model: While for species overwintering as larvae a negative effect of species generation time on the prediction of extinction risk was found, the opposite trend was found for species overwintering as imago. If the overwintering type would have been neglected, no effect of generation time on extinction risk would have been observed. This shows, that model results can change crucially dependent on the choice of traits as explanatory variables – especially when only few or even only one trait is tested. If traits are interdependent, it may not be clear whether the observed effect really results from the tested trait or from its relationship to another trait. Moreover, a key trait could also have an impact on two or numerous other traits simultaneously. Thus, since the results of trait-based approaches can be biased, predictions of e.g. species decline or extinction risks, based on single or only few analyzed species traits, should be interpreted with caution (Davies *et al.*, 2004). Therefore, further research is needed to clarify which species traits are the key drivers of trait relations, which relations exhibit additive or non-additive synergetic trait effects and how strong these effects are (Davies *et al.*, 2004). To provide reliable predictions of species extinction risks for conservation planning, predictions should be based on trait analyses which take several traits simultaneously and their possible interactions into account (Mattila *et al.*, 2006), as performed in all case studies of this thesis.

### **6.1.1. Impact of phylogenetic relatedness on ground beetle trait approaches**

It is expected that closely related species share more similar species traits (Harvey and Pagel, 1991; Webb *et al.*, 2002) and show similar reactions to environmental conditions as well as environmental changes (Díaz *et al.*, 2013). This results in the question, whether ecological analyses on species traits are trait based by phylogenetic effects (Grafen, 1989; Purvis, 2008). However, clustered traits may occur within communities because of two reasons: I. because of close phylogenetic relatedness between species, in case of conserved traits within related lineages or II. similar traits may have evolved regardless of taxonomic relatedness, if traits were converged across different lineages (Weiher *et al.*, 2011). In this thesis, a very small effect of species' phylogenetic relatedness was found for the preferred main habitat

types of ground beetles (Chapter 2). In the other three case studies of this thesis (Chapters 3,4 and 5) as well as in the literature, no phylogenetic effect on community composition was found (e.g. Davies *et al.* 2000; Kotze and O’Hara 2003). Although not directly tested, these results suggest that ground beetle traits differ irrespectively of phylogenetic relatedness within communities.

Nevertheless, it is worth mentioning, that all previous studies as well as the case studies of this thesis used taxonomic hierarchies of ground beetles to test phylogenetic relationships, since molecular phylogeny was not available for all ground beetles examined in the studies. Although taxonomic hierarchies have been highly supported by molecular phylogenetic trees when available (e.g. Deuve *et al.* 2012; Ober and Maddison 2008), a phylogenetic effect might have been masked, as taxonomic hierarchies do not include information about the exact phylogenetic distances (branch lengths) between hierarchical clusters. In order to improve tests on potential phylogenetic effects in the future, research should also focus on creating a comprehensive phylogenetic tree of ground beetle species, e.g. by systematic barcoding (cf. German barcoding of life project (GBOL) see Geiger *et al.* 2016; Raupach *et al.* 2016) or other markers.

### 6.1.2. Species traits in ground beetles and their influence on biodiversity

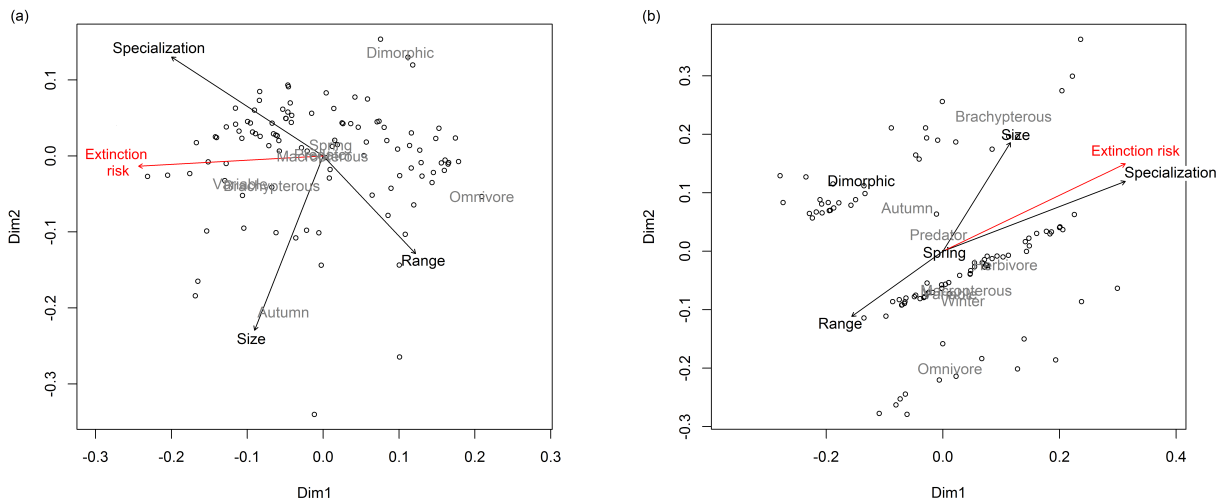
The interest in trait-based analyses has increased enormously during the last years. However, analyses are still focusing on vertebrates and leave insect taxa such as ground beetles mostly understudied (cf. Chichorro *et al.* 2018). This thesis, therefore, aims to cover research gaps in the general knowledge of habitat-specific trait filtering across the different habitat types occurring in Germany. Species pools of unstable habitat types (coastal, riparian and wetland habitats) were found to be characterized by highly similar trait values or trait characteristics, while they were less similar to species of stable habitat types (forest, mountainous and open habitats) (see Chapter 2). It was further demonstrated, that ground beetle extinction risks can be largely explained by species traits (see Chapter 3). Depending on the analyzed habitat type and the species pool, different traits were identified as drivers of ground beetle extinction risk. Distributional range size and habitat specialization, however, appeared to be more frequently identified as main drivers across the different habitat types than other traits. Species with small range sizes and high habitat specialization were in many cases at greater risk of extinction.

#### *Species traits of unstable habitats*

Species of unstable habitats were characterized by highly similar trait values or trait characteristics. They were mainly small bodied, macropterous, spring breeders and had predatory feeding behavior (Chapter 2). Our findings on a large species pool resembled findings of local species pools (e.g. Bonn *et al.* 2002; Gerisch *et al.* 2012), indicating high habitat-specific trait filtering in these habitat types. The concept of habitat filtering implies that ecologically similar species tend to co-occur more often in one habitat than expected by chance, because the species are filtered depending on their reaction to environmental conditions (Cornwell *et al.*, 2006; Weiher and Keddy, 2001). As already mentioned, similar reactions to environmental conditions may be caused by highly similar trait values or trait characteristics. This leads to the assumption, that trait characteristics which are only rarely found in these habitat types should increase species extinction risks significantly.

It is expected that in unstable habitat types disturbances (e.g. fluctuations of water level) will particularly affect the dispersal ability, i.e. species ability to fly and body size (e.g. Lamberts *et al.* 2009; Ribera





**Figure 6.1.:** Principal coordinate analysis (PCoA) summarizing the relationship between species traits and extinction risks of the species from (a) riparian and (b) wetland habitat. Traits revealed to significantly influence extinction risks (see Chapter 3) are indicated in black, not significant traits are indicated in grey and extinction risk is indicated in red, dots indicate individual species (Size = Body size; Range = Distribution range size; Specialization = Habitat specialization; Hind wing morphology: Brachypterous, Dimorphic and Macropterous; Breeding season: Autumn, Spring, Variable and Winter; Trophic level: Herbivore, Omnivore and Predator).

In unstable habitat types several species with low range sizes and high habitat specialization were found (Table 6.1, Fig. 6.1a, b), suggesting that no strong habitat-specific trait filter seemed to exist for these traits. Nevertheless, the results of this thesis identified increasing extinction risks for species with low range sizes (for riparian habitats) and high habitat specialization. Especially habitat specialists are often stated to be the ‘biggest losers’ of the current diversity crisis (e.g. Davies *et al.* 2004; Devictor *et al.* 2008b; Kotze and O’Hara 2003; McKinney and Lockwood 1999). Several studies identified specialization to strongly influence the underlying factors of community composition and confirmed specialization to be one of the key drivers for most taxa, including insects (cf. Chichorro *et al.* 2018; Dunn 2005; Fisher and Owens 2004; Powney *et al.* 2015). In accordance with these findings, specialization appeared to be a key driver for extinction risk of ground beetle species in unstable habitat types. Recent anthropogenic activities such as drainage or the lack of frequent inundations due to the reduction or absence of natural river dynamics (Bonn *et al.*, 2002; Hughes and Rood, 2003; Maltby *et al.*, 2009; Nienhuis and Leuven, 2001), transform especially the limited number of suitable microhabitats for habitat specialists (Bonn and Kleinwaechter, 1999; Boscaini *et al.*, 2000; Matern *et al.*, 2007).

In accordance with the habitat-specific trait filtering of unstable habitat types, extinction risk for spring breeding species was low (Table 6.1, Fig. 6.1a, b). For ground beetles, the breeding season of a species is strongly linked to the hibernation stage. Species predominantly breeding in spring hibernate as imago, while species breeding in autumn hibernate as larvae or both larvae and imago. In habitat types disturbed by flood events, species mostly reproduce in spring (Cárdenas and Hidalgo, 2004; Gerisch, 2011). The hibernating imagos of these species are less negatively affected and more likely to survive winter floods (Ribera *et al.*, 2001) while the sensitive larval instars develop in stable conditions during summer time and therefore avoid hydraulic stresses (cf. Cárdenas and Hidalgo 2007; Lövei and Sunderland 1996; Thiele 1977).

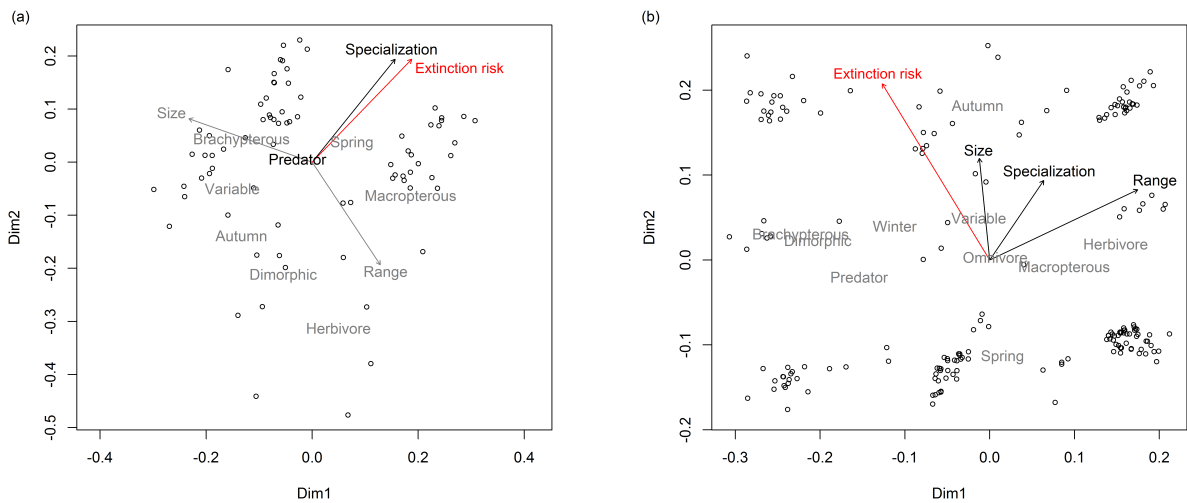
### ***Species traits of stable habitats***

Ground beetles of more stable habitat types were mostly characterized by larger body size, low habitat specialization, and a higher ratios of autumn breeders (Table 6.1, Fig. 6.2a, b).

Body size is the most studied species trait across taxa (Chichorro *et al.*, 2018). For different taxa an increasing body size was identified to lead to a higher species decline or extinction risk (vertebrates: e.g. Cardillo *et al.* 2005; Dirzo *et al.* 2014, invertebrates: Seibold *et al.* 2015; Terzopoulou *et al.* 2015), which was also shown for ground beetles (Brooks *et al.*, 2012; Kotze and O'Hara, 2003). Nevertheless, a comparative analysis across taxa (Chichorro *et al.*, 2018) did not find a distinct relationship between body size and extinction risk. The results of this thesis also revealed no clear tendency for the influence of body size on ground beetle extinction risk. Across all tested ground beetle species as well as for species of riparian and open habitat, species extinction risk increased with increasing body size (Table 6.1, Fig. 6.2b). However, for the entire forest species pool of Germany no significant effect of body size (or hind wing morphology) on species extinction risk was observed. Forest habitats often showed long-lasting habitat stability as well as an increase in area in some countries across Europe over the last years (e.g. Assmann 1999; FAO 2015). In long-term stable habitats dispersal of ground beetles is not mandatory. Hence, natural selection will reduce the ability to fly, as flightless species tend to have an advantage in reproduction (den Boer *et al.*, 1980; Desender and Turin, 1989), which therefore can lead to an increased body size (see Chapter 2). Merckx *et al.* (2018) also identified that the general trend towards smaller-sized species, as for example shown in Brooks *et al.* (2012), can be rescinded, when no positive relation between body size and dispersal power exists. This seems to be the case for forest ground beetles, where small species significantly declined over the last 24 years in an ancient woodland (Chapter 5). In accordance with these results, Kotze and O'Hara (2003) also found the effect of body size to be strongly dependent on the environmental conditions, as they found species larger than 11 mm to be more prone to decline when associated with e.g. open habitat type, but less prone to decline when associated with e.g. forest habitat type. Consequently, body size cannot be regarded as a convenient general predictor of extinction risk for ground beetles (cf. Chichorro *et al.* 2018).

Habitat specialization, however, was identified to be a suitable predictor of species extinction risk of unstable habitat types. Additionally was shown, that specialists of open and forest habitat types showed the highest extinction risks as well. This can also be seen in the habitat filtering of these habitat types (Table 6.1, Fig. 6.2a, b). Suitable sites for specialists have also decreased in open and forest habitat types during the last decades, due to e.g. habitat fragmentation or land-use change, triggered by agricultural intensification and urban development (e.g. Hendrickx *et al.* 2007). Especially in the highly fragmented Central European landscapes, specialists cannot move as easy as generalists through unfavorable habitats (Koivula *et al.*, 2002; Vermeulen, 1994) and can therefore get stuck in highly fragmented and declining habitat patches. Resulting in the general phenomenon that specialist get replaced by a few dominating generalists (Augenstein *et al.*, 2012; Habel *et al.*, 2016).

Apart from the fact that generally more ground beetles are spring breeders, a larger amount of autumn breeders was found in stable habitats types (see Chapter 2) in contrast to others. Low occurrence ranks (see Chapter 4) and decreasing long-term populations (see Chapter 5) were found for spring breeders testing local pools of forest species. Lower disturbance rates during winter time may increase the survival rates of autumn breeders in more stable habitat types (Halme and Niemelä, 1993). Additionally, a higher possibility of desiccation of the spring breeders' summer larvae was suggested by Spake



**Figure 6.2.:** Principal coordinate analysis (PCoA) summarizing the relationship between species traits and extinction risks of the species from (a) forest and (b) open habitat. Traits revealed to significantly drive extinction risks (see Chapter 3) are indicated in black, not significant traits are indicated in grey and extinction risk is indicated in red, dots indicate individual species. (Size = Body size; Range = Distribution range size; Specialization = Habitat specialization; Hind wing morphology: Brachypterous, Dimorphic and Macropterous; Breeding season: Autumn, Spring, Variable and Winter; Trophic level: Herbivore, Omnivore and Predator).

*et al.* (2016) to be an explanation why they found species that overwinter as adults to be linked to denser canopy cover. Nevertheless, on species extinction risks no significant effect of breeding season was observed for the entire open and forest species pool (see Chapter 3).

In the light of the ongoing anthropogenic landscape as well as climate change, the extinction risk of species might be further increased and the diversity of species reduced (Thom *et al.*, 2017). In habitat types characterized by highly similar trait values and trait characteristics of their species pool, certain management actions may lead to the loss of a large subset of habitat characteristic species (Díaz *et al.*, 2013), as species with similar traits are expected to show similar reactions to environmental changes. Especially species with small distributional range sizes and high habitat specialization are most prone to extinction. If the rare and specialized species are replaced by widespread generalists, the increase in homogenization of functional biodiversity (McKinney and Lockwood, 1999) might have dramatic negative effects on the ecosystem functioning of habitats (Clavel *et al.*, 2011). To halt biodiversity homogenization, disturbances have to be reduced (Devictor *et al.*, 2008a) and natural habitat dynamics or extensive managing practices with long traditions have to be reintroduced or continued, e.g. the rehabilitation of river floodplains and headwater areas (Matern *et al.*, 2007) or the traditional extensive grazing regimes on hill pastures and grasslands (Dieker *et al.*, 2011; Marini *et al.*, 2008).

Furthermore, rising global temperatures and changes in abiotic factors, e.g. soil moisture, will initiate altitudinal uphill shifts and latitudinal poleward shifts in climatic conditions, which all taxa, including ground beetle species, will have to follow (Drees *et al.*, 2011; Hickling *et al.*, 2006; Pizzolotto *et al.*, 2014; Thomas, 2010). In mountainous regions uphill shifts of ground beetle species have already been observed as consequence of climate warming and precipitation decrease (Brandmayr and Pizzolotto,

2016; Pizzolotto *et al.*, 2014). Spatial dispersal will be a major challenge for many species in the anthropogenically altered and highly fragmented Central European landscapes (Jaeger *et al.*, 2011). Völler *et al.* (2018) already noted that large and flightless species with low dispersal power, such as *Carabus hortensis*, might not be able to follow the spatial shifts in their climate niche and therefore may be caught in increasingly unsuitable habitat patches. For those species, assisted colonization/migration might be a necessary measure to maintain biodiversity on a global scale (e.g. Fuchs *et al.* 2010; Homburg *et al.* 2014a; IUCN/SSC 2013).

To conclude, this thesis provides a comprehensive picture of ground beetle species traits and helps to gain a better understanding of the mechanisms underlying species extinction risks, occurrences, and long-term decline, influencing community compositions and biodiversity loss. Based on this novel and informative knowledge, the efficiency of conservation planning for habitat protection and restoration can be increased. Conservation practices can be developed to protect entire 'functional groups' simultaneously, where species show high risks of extinction. However, our results might be taxon specific, as comparative studies concluded, that it is rather difficult to generalize the identified species traits as reliable predictors of extinction risk across all taxa (Cardillo and Meijaard, 2012; Chichorro *et al.*, 2018; Fisher and Owens, 2004). Therefore, conservation scientists should also tackle to investigate 'uncharismatic' or data-poor invertebrate taxa (Verde Arregoitia, 2016). Nevertheless, the new insights gained in this thesis can also help to develop more accuracy in trait-based models, as further studies should assess the robustness of the identified relationships between ground beetle traits and threats. Since a decline in microhabitat heterogeneity is assumed to be more harmful than large-scale landscapes changes (Hanski, 2005), research must also unravel how specific changes in microhabitat conditions or structures influence ground beetles with specific traits, in order to improve habitat management and permanently sustain global biodiversity.



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## APPENDIX

### Article overview and authors' contribution to articles

This is a cumulative dissertation including four articles that have either been published, submitted for publication or are close to submission for publication in international peer-reviewed journals. The articles are the result of the collaborative work of several authors. Table 6.2 gives an overview of my personal contributions to each article presented in this theses.

**Table 6.2.:** Overview of the articles in this thesis, my contribution, article publication status, the authors' contribution to the articles and my conference contributions. (WF = Weighting factor; IF = Impact factors of the international peer-reviewed journals, according to ISI Web of Knowledge)

Chapter	2	3	4	5
My contribution (WF)	predominant contribution (1.0)	predominant contribution (1.0)	predominant contribution (1.0)	important contribution (0.5)
Publication status, Journal (IF)	Manuscript prepared for submission	Submitted to Biodiversity and Conservation (2.828)	Published, Biological Conservation (4.660) DOI: 10.1016/j.biocon.2017.06.038	Submitted to Insect Conservation and Diversity (2.091)
<b>Specific contribution of all authors</b>				
Research question	DN, TA	DN, TA	DN, TA	TA, CD, KH
Study design	DN, TA	DN, TA	DN, TA	TA
Data collection	DN	DN	DN, MMG	PZ, EB, CD, KH
Statistical analysis	DN	DN, AS	DN, AS, WU	CD, KH, DN, WS
Manuscript preparation	DN, TA	DN, TA	DN, TA	KH, CD, EvR, TA, WS
Textualisation	DN, AS, CD, DJK, EB, TA	DN, AS, EB, JK, TA	DN, TA, AS, MMG, WU	KH, CD, EB, EvR, DN, TA, WS
Conference contributions	planned	planned	GAC 2018 ECM 2017 ISC 2016	

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### Versicherung

Ich versichere, dass alle in diesem Anhang gemachten Angaben jeweils einzeln und insgesamt vollständig der Wahrheit entsprechen.

Braunschweig, den 09. November 2018

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### Conferences

- GAC 2018 21. Meeting of the „Gesellschaft für angewandte Carabidologie“, February 16.-18., 2018, Freckenhorst. <http://www.angewandte-carabidologie.de/de/gac> | Talk
- ECM 2017 18. European Carabidologist Meeting, September 25.-29., 2017, Rennes (FRA). <https://colloque.inra.fr/18ecm> | Talk
- ISC 2016 4. International Symposium of Carabidology, September 20.-23., 2016, Athens (USA). | Poster

### Weighting factor

According to §12b and 14 of the Leuphana guideline for cumulative dissertations in Sustainability Science Dr.rer.nat [24th January 2012].

Author status	Weighting factor
Single author (Allein-Autorenschaft)	1.0
Co-author with predominant contribution (Überwiegender Anteil)	1.0
Co-author with equal contribution (Gleicher Anteil)	1.0
Co-author with important contribution (Wichtiger Anteil)	0.5
Co-author with small contribution (Geringer Anteil)	0

## List of Publications

### Peer-reviewed journals

- Homburg, K., Drees, C., Boutaud, E., **Nolte, D.**, Schuett, W., Zumstein, P., von Ruschkowski, E. and Assmann, T. (2019). Where have all the beetles gone? Long-term study reveals carabid species decline in a nature reserve in Northern Germany. *Insect Conservation and Diversity*, 12, 268-277. DOI: 10.1111/icad.12348<sup>3</sup>
- Nolte, D.**, Boutaud, E., Kotze, D. J., Schuldt, A., and Assmann, T. (2019). Habitat specialization, distribution range size and body size drive extinction risk in carabid beetles. *Biodiversity and Conservation*, 28, 1267-1283. DOI: 10.1007/S10531-019-01724-9<sup>3</sup>
- Assmann, T., Boutaud, E., Drees, C., Marcus, T., **Nolte, D.**, Starke, W., Terlutter, H., Völler, E. and Zumstein, P. (2017). Two new *Lebistina* Motschulsky, 1864 species from Kenya and Tanzania (Coleoptera, Carabidae, Lebiini). *African Invertebrates*, 58, 9. DOI: 10.3897/afrinvertebr.58.11456
- Nolte, D.**, Schuldt, A., Gossner, M.M., Ulrich, W. and Assmann, T. (2017). Functional traits drive ground beetle community structures in Central European forests: Implications for conservation. *Biological Conservation*, 213, 5–12. DOI: 10.1016/j.biocon.2017.06.038
- Birkhofer, K., Arvidsson, F., **Ehlers, D.**, Mader, V.L., Bengtsson, J. and Smith, H.G. (2015). Organic farming affects the biological control of hemipteran pests and yields in spring barley independent of landscape complexity. *Landscape Ecology*, 31, 567-579. DOI: 10.1007/s10980-015-0263-8

### Book publication

- Assmann, T., Boutaud, E., Finck, P., Härdtle, W., Matthiers, D., **Nolte, D.**, Von Oheimb, G., Riecken, U., Travers, E. und Ullrich, K. (2016). Halboffene Verbundkorridore: Ökologische Funktion, Leitbilder und Praxis-Leitfaden. *Naturschutz und Biologische Vielfalt*, 154. Bonn - Bad Godesberg. DOI: 10.19213/973154

### Conference contributions and talks

- Nolte, D.**, Schuldt, A., Gossner, M.M., Ulrich, W. und Assmann, T. (2018). Wie 'traits' uns helfen, die Zusammensetzung von Laufkäfergemeinschaften in Wäldern zu verstehen. 21. Jahrestagung der Gesellschaft für angewandte Carabidologie (GAC), Freckenhorst | Talk.
- Nolte, D.**, Schuldt, A., Gossner, M.M., Ulrich, W. and Assmann, T. (2017). Do species traits shape carabid communities in forests? 18th European Carabidologist Meeting (ECM), Rennes (FRA) | Talk.
- Ehlers, D.**, Boutaud, E. and Assmann, T. (2016). Evaluating the potential of semi-open corridors for epigeal arthropods. Oberseminar - Aktuelle Themen aus Tierökologie und Humanbiologie, Universität Potsdam, Potsdam | Talk.

<sup>3</sup>Updated information

- Ehlers, D.**, Boutaud, E. and Assmann, T. (2016). Are semi-open corridors a tool to overcome landscape fragmentation for both endangered open and woodland arthropods? 45th annual Meeting of the GfÖ (Gesellschaft für Ökologie), Marburg | Talk.
- Ehlers, D.**, Ulrich, W., Schuldt, A. and Assmann, T. (2016). Traits or competition – what drives community composition of woodland inhabiting carabids? 4th International Symposium of Carabidology, Athens (USA) | Poster.
- Ehlers, D.**, Boutaud, E. und Assmann, T. (2016). Lebensraumvernetzung durch halboffene Lebensräume und ihre Bedeutung für stenotope Arthropoden. Fachtagung zur ökologischen Funktion von halboffenen Verbundkorridoren, NNA Schneverdingen | Talk.
- Ehlers, D.**, Boutaud, E. und Assmann, T. (2015). Lebensraumvernetzung für Heiden – Die Bedeutung halboffener Lebensräume in Heiden und ihre Konsequenzen für stenotope Arthropoden. 13. Fachtagung Bundesfachausschusses (BFA) Entomologie im NABU, Berlin | Talk.
- Ehlers, D.**, Boutaud, E., Drees, C. and Assmann, T. (2014). Population density and spatial distribution of woodland inhabiting ground beetles (Coleoptera: Carabidae) – insights from a mark recapture study. 44th annual Meeting of the GfÖ (Gesellschaft für Ökologie), Hildesheim | Talk.

## Erklärungen

Hiermit erkläre ich, dass ich mich noch keiner Doktorprüfung unterzogen oder mich um Zulassung zu einer solchen beworben habe.

Ich versichere, dass die eingereichte Dissertation „*Traits in the light of ecology and conservation of ground beetles*“ noch keiner Fachvertreterin bzw. Fachvertreter vorgelegen hat, ich die Dissertation nur in diesem und keinem anderen Promotionsverfahren eingereicht habe und, dass diesem Promotionsverfahren keine endgültig gescheiterten Promotionsverfahren vorausgegangen sind.

Hiermit versichere ich weiter, dass ich die Abhandlung selbstständig und ohne unerlaubte Hilfsmittel verfasst habe. Anderer als der von mir angegebenen Hilfsmittel und Schriften habe ich mich nicht bedient. Alle wörtlich oder sinngemäß anderen Schriften entnommenen Stellen habe ich kenntlich gemacht.

Braunschweig, den 09. November 2018

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(Dorothea Nolte)