Convergent evolution of functional traits and implications for the structure and assembly of communities

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Content

Summary

In order to understand and counteract the causes and consequences of the current biodiversity crisis, it is necessary to understand the mechanisms and processes that influence how animal communities assemble. This understanding must go far beyond species numbers, there are other components of biodiversity such as phylogenetic and functional diversity, which give a more informative picture of ecological relationships. Nevertheless, for most animal groups, the relationship between phylogenetic diversity, functional traits and their responses to environmental changes is not clear. This is because for many traits the actual function and the evolutionary patterns and adaptations are often insufficiently understood. Therefore, in this thesis, I combine three approaches and examine the reaction of ground beetle communities to agri-environmental measures in a field investigation (study 1). In the two other studies, I trace the altered biodiversity pattern which I found in the carabid communities of the first study back to evolutionary mechanisms derived from a phylogenetic analysis (study 2) and a series of laboratory experiments (study 3).

With the first study, I demonstrate that agri-environmental measures increase the proportion of medium-sized herbivorous ground beetle species in the community and change the phylogenetic structure, but not the phylogenetic or species diversity. At the same time, however, the proportion of species with functionally unique trait combinations increases. In the second study this pattern could be attributed to the convergent evolution of food preferences, which are linked to morphological adaptations. This explains the consistently high phylogenetic diversity even in functionally more similar communities with altered phylogenetic structure. The specialized mandible shapes are of essential adaptive value, which *inter alia* could be demonstrated in laboratory experiments with species specialized on Collembola. In addition, generalist species not only showed lower capture efficiency, but also severe weight loss and increased mortality when fed only with Collembola. However, species with highly specialized morphological adaptations are still able to access alternative prey. My results indicate a strong selection pressure on these morphological adaptations regarding herbivory and Collembola as food. Since this finding establishes a strong ecological relationship between feeding groups and their preferred food, these species should therefore not be ecologically classified as omnivorous due to their ability to feed on other food resources as substitutes. It is concluded that phylogenetic diversity cannot predict functional diversity, at least not if it is based on convergent traits as feeding and body size. Even though flowering strips have a particularly positive effect on the number of herbivorous species, a high phylogenetic diversity is maintained due to the convergent evolution of this trait. High phylogenetic diversity can have a positive effect on the function, resistance and resilience of these communities. Phylogenetic and functional diversity are therefore crucial biodiversity components to maintain the function of communities and ecosystems and should be of central interest in conservation efforts.

Zusammenfassung

Um die Ursachen und Konsequenzen der aktuellen Biodiversitätskrise zu verstehen und entgegen wirken zu können, ist es nötig die Mechanismen und Prozesse zu verstehen, welche beeinflussen, wie sich Tiergemeinschaften zusammenstellen. Dieses Verständnis muss weit über Artenzahlen und Umweltfaktoren hinausgehen, andere Biodiversitätskomponenten wie die phylogenetische und funktionelle Diversität in Gemeinschaften geben ein informativeres Bild über ökologische Zusammenhänge. Dennoch ist bei den meisten Tiergruppen der Zusammenhang zwischen phylogenetischer Diversität, funktionellen Merkmalen und deren Reaktionen auf Umweltveränderungen nicht klar. Das ist unter anderem darin begründet, dass bei vielen Merkmalen die tatsächliche Funktion und auch die evolutiven Muster und Anpassungen oftmals unzureichend verstanden sind. Deshalb kombiniere ich in dieser Thesis drei Ansätze und untersuche in einer Feld-Untersuchung (Studie 1) die Reaktion von Laufkäfergemeinschaften auf Agrarumweltmaßnahmen. In zwei weiteren Studien führe ich die veränderten Biodiversitätsmuster die in den Gemeinschaften der ersten Studie nachgewiesen werden konnten in einer phylogenetischen Studie (Studie 2) und einer Reihe von Laborexperimenten (Studie 3) auf evolutionsbiologische Mechanismen zurück.

Mit der ersten Studie zeige ich das Agrarumweltmaßnahmen den Anteil mittelgroßer herbivorer Laufkäferarten in der Gemeinschaft erhöht und die phylogenetische Struktur verändert, aber nicht die phylogenetische oder Artendiversität an sich. Gleichweise erhöht sich aber der Anteil von Arten mit funktionell einzigartigen Merkmalskombinationen. Dieses Muster konnte ich in einer weiteren Studie darauf zurückführen, dass Nahrungspräferenzen mit morphologischen Anpassungen verbunden und mehrfach konvergent entstanden sind. Dies erklärt die gleichbleibende hohe phylogenetische Diversität auch bei funktionell ähnlicher werdenden Gemeinschaften und veränderter phylogenetische Struktur. Die spezialisierten Mandibelformen haben einen starken adaptiven Wert, was am Beispiel von Arten welche auf Collembola spezialisiert sind in Laborexperimenten nachgewiesen werden konnte. Zudem zeigten generalistische Arten nicht nur eine geringere Fangeffizienz, sondern auch eine starke Gewichtsabnahme und eine erhöhte Mortalität, wenn diese nur mit Collembola gefüttert wurden. Dennoch können Arten welche hochspezialisierte morphologischen Anpassungen aufweisen auf andere Beute ausweichen. Meine Ergebnisse weisen auf einen starken Selektionsdruck auf diese morphologischen Anpassungen bezüglich Herbivorie und Collembola als Nahrung hin. Da dies eine starke ökologische Beziehung zu der präferierten Nahrung begründet, sollten diese Arten daher nicht aufgrund ihrer Fähigkeit

ersatzweise andere Nahrung aufnehemn zu können, ökologisch als Omnivore klassifiziert werden. Daraus lässt sich schlussfolgern, dass phylogenetische Diversität keine Vorhersagen über funktionelle Diversität liefern kann, zumindest, wenn diese auf konvergenten Merkmalen wie Nahrungsweise und Körpergröße basiert. Auch wenn Blühstreifen vor allem positiv auf herbivore Arten wirken, kann aufgrund der konvergenten Evolution dieses Merkmals eine hohe phylogenetische Diversität erhalten bleiben. Eine hohe phylogenetische Diversität kann positiv auf die Funktion, Resistenz und Resilienz dieser Gemeinschaften wirken. Phylogenetische und funktionelle Diversität sind daher entscheidende Biodiversitäts-Komponenten und sollten von zentraler Bedeutung in Naturschutzmaßnahmen sein.

Introduction

The relationship between biodiversity and ecosystem functioning is still not fully understood (Balvanera et al., 2006; Bannar-Martin et al., 2017; Hagan, Vanschoenwinkel, & Gamfeldt, 2021). To counteract the current biodiversity crisis, it is crucial to identify biodiversity-components, which are suitable to detect community responses to environmental change and can be linked to ecosystem functioning.

I will focus on a major challenge in using phylogenetic information to assess Biodiversity at the community level: convergent evolution of traits. The coexistence of distantly related species with shared traits can result in complex relationships between different diversity components. This is known from studies addressing high taxonomic levels such as vertebrates (Huang, Stephens, & Gittleman, 2012). For example, pollination, which involves various coevolutionary adaptations, has evolved several times in birds, mammals, and reptiles (Olesen & Valido, 2003; Ratto et al., 2018). If a community consists of three pollinator species, the functional diversity is certainly higher if these are one hummingbird, one bat and one lizard compared to a community with three species of bees. In this example, phylogenetic distance increases the information on the diversity of the community while functional diversity, if based on a single trait, gives little new information. Arguably the first and still most frequently used approach to measure phylogenetic diversity is calculating the sum of all branch lengths (Faith 1992). Since its development in the early 1990s, the use of phylogenetic diversity (PD) in community ecology is controversially discussed (Faith, 1992; Kelly, Grenyer, & Scotland, 2014; Srivastava, Cadotte, MacDonald, Marushia, & Mirotchnick, 2012; Tucker, Davies, Cadotte, & Pearse, 2018; Venail et al., 2015; Winter, Devictor, & Schweiger, 2013). Indeed, Faith (1992) already cautioned that phylogenetic diversity is prone to convergent traits but advocate it as a measure of “feature diversity” and its value for conservation evaluation. The use of phylogenetic diversity as a proxy for functional traits or community assembly mechanisms cannot be generally substantiated (Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015). In this thesis, however, I demonstrate that phylogenetic measures can give a complementary view to functional trait diversity and contributes to community ecology by extending our understanding of biodiversity on different levels: ecological, functional and evolutionary. Although implications for ecosystem functioning on a broad scale are already discussed for plants, studies in animals just emerge recently and the phylogenetic diversity – functional diversity relationship for most taxa is not well understood (Tucker et al., 2018).

Biodiversity - a functional and phylogenetic perspective

Biodiversity can be defined as “the variability among living organisms [...] such as diversity within species, between species and of ecosystems” (Convention on Biological Diversity (CBD) 1992, p. 3). This definition includes the genetic diversity within species and between species, as well as species numbers but since its first definition it has been extendet to include abundances, ecological functions, and interactions in communities (Bermudez & Lindemann-Matthies, 2020; Hooper et al., 2005; Luna, Corro, Antoniazzi, & Dáttilo, 2020). Accordingly, there are many definitions and measures of biodiversity (Mace, Norris, & Fitter, 2012; Schwarz et al., 2017). Despite the conceptual variety of the term biodiversity, species richness is the most common used metric to describe the current biodiversity crisis which is considered to be the incipient sixth mass extinction events by some researchers (Barnosky et al., 2011). Species richness alone, however, is not reliable as a measurement of biodiversity to predict ecosystem functioning or services and the consequences of human induced environmental changes (Cadotte et al., 2011; Gagic et al., 2015; Mace et al., 2012). Functional diversity of communities, for example, is crucial to help maintain the functions and services of ecosystems (Bongers et al., 2021; Laureto, Cianciaruso, & Samia, 2015). Thus, the ecological functions of species in a community cover the concept of biodiversity outlined above more comprehensively, but the related functional traits of species are often unknown.

To circumvent this knowledge gap, phylogenetic diversity (Faith, 1992b) is often proposed as a proxy for functional diversity based on the assumption of trait similarity in related species (Boyle & Adamowicz, 2015; Webb et al., 2002). While this assumption may be accurate at broad taxonomic and spatial scales (e.g. Huang, Stephens, & Gittleman, 2012), the relation between phylogenetic diversity and functional diversity is not well understood in many taxonomic groups and has been shown unreliable in many cases (Mazel et al., 2018a). Consequently, phylogenetic patterns cannot generally be expected to predict community assembly processes (Box 1), but can give insights in how diversification patterns in lineages can control community structure (Gerhold et al., 2015; Losos, 2011). The journal “Ecology” dedicated an entire special issue on phylogenetic community ecology to emphasize that combined knowledge of phylogenetic structure, trait and community data is necessary to understand the evolution and assembly of communities (Webb et al., 2006). Since then many studies highlighted the complementarity of phylogenetic pattern to other biodiversity measures as species richness or functional diversity (e.g.: Gumbs et al., 2020; Li et al., 2020; Staab et al., 2021).

Instead of using phylogenetic patterns as proxies in community assembly, there are more promising venues to utilize evolutionary methods in community ecology. These methods help understanding how biodiversity components at the species, functional and evolutionary level are interrelated, and how present-day coexistence is explained by evolutionary patterns of lineages and trait diversification. I address the gap between ecology and evolutionary biology by examining the evolution of functional groups, including their adaptive morphology, and linking the phylogenetic diversity of these groups to human induced changes in community composition. This is crucial to address pressing questions on how future changes will affect ecosystem functioning, while building on the evolutionary history of a community as the fundamental component of biodiversity.

Trait based framework of community assembly and why phylogeny matters

The drivers of assembly processes need to be understood to estimate causes and consequences of environmental changes for different biodiversity components. Focusing on trait-environment relationships fosters a mechanistic understanding of the assembly and structuring of communities (McGill et al., 2006). Community assembly is often described as a series of filtering processes from a species pool which can be neutral (e.g. dispersal ability, Jetschke & Hubbell, 2002) or deterministic and niche based (Weiher et al., 2011). Niche-based processes are reactions of species functional traits to environmental factors or other species. An environmental filter will result in communities comprised of species with traits that enable the persistence under certain environmental conditions and can therefore increase trait similarity in communities (Webb, Ackerly, McPeek, & Donoghue, 2002). This would reduce functional richness by excluding species with different functional traits which are not suitable under these environmental conditions. Interaction filter, including competition or resource partitioning, can produce over dispersed trait distributions due to exclusion of similar species (McGill, Enquist, Weiher, & Westoby, 2006). Classical ecological theory predicts that competition is higher between similar species than species with ecological differences. However, communities are often comprised of highly similar species. Even at a global scale, the assumption of competitive exclusion is not well supported (Kunstler et al., 2016), because trait difference can stabilize species coexistence and competitive imbalances driving exclusion (Adler, Fajardo, Kleinhesselink, & Kraft, 2013; Levine, 2016).

I will focus on niche-based processes to determine how environmental factors, for example resource availability, will affect the functional and phylogenetic community structure. The

response of a community to the environment are not just reflected in compositional changes due to filtering processes (presence-absence), but changes of the abundance of species will also alter community structure and functioning (e.g. de la Riva et al., 2016). Relative species abundance modified by environmental filtering is known to change the competitive dominance pattern within communities (Perronne, Munoz, Borgy, Reboud, & Gaba, 2017). Moreover, species occurrence might be driven by traits other than species abundance (Cingolani, Cabido, Gurvich, Renison, & Díaz, 2007). Indeed, based on observational data, it is difficult to strictly distinguish environmental filtering processes, which act on survival, reproduction and thus persistence of species in a certain environment, from other processes (Cadotte & Tucker, 2017). However, to understand the mechanisms behind the effect of environmental change on communities and to link it to ecosystem functions, a profound knowledge of the trait-environment relationships is crucial. Therefore, in this dissertation, I compare presence absence and abundance-based
measures from observational data to environmental change and link traits to their adaptive function. Trait-based abundance-weighted approaches appear to be best suited to predicting ecosystem functioning and productivity (Gagic et al., 2015; Manning & Cutler, 2018).
A major challenge to foster a mechanistic understanding of community assembly, is to define functional groups and functional traits (chapter 2 & 3) and link these to environmental responses (chapter 1) or functions (Violle et al., 2007). Functional groups share ecological functions or “roles” in a community, contributing equally to ecosystem processes. Thus, functional traits can be any characteristics of an organism that affect performance or fitness including morphological, physiological, and behavioral or live history traits (Nock, Vogt, & Beisner, 2016).

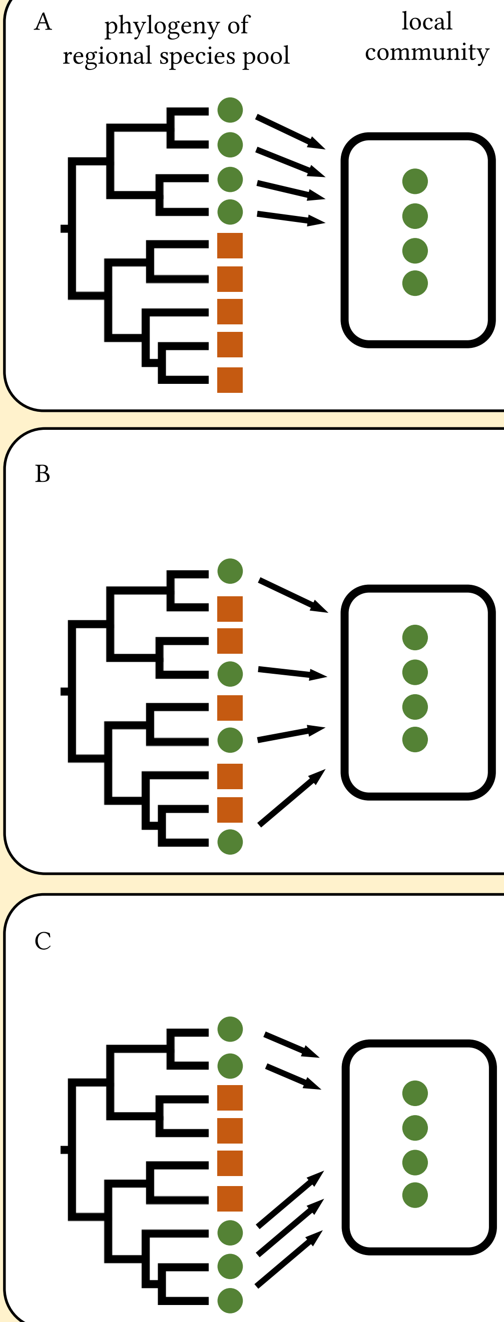
Despite some attempts in unifying definitions of functional traits (Schneider et al., 2019), there are still many obstacles ahead. Trait selection is a crucial and complicated task to conduct meaningful studies on functional trait – environment relationships. The functional role of the trait must be clearly established: is it either a response trait or an effect trait (Nock et al., 2016). Response traits are sensitive to environmaental change, food specialisation for example is a response trait to resource availability. Pollination is an effect trait (but can also be a response trait) that alter the function of pollination in an ecosystem. Finally, trait selection should consider species and scale dependent trait-environment relationship (Perronne et al., 2017).

Traits are often selected without considering these aspects, as the functional role is unclear in many cases. This is true for one of the most commonly used functional traits in animals:

the feeding type. For example, the classification as ‘omnivorous’ is based on a vague definition of resource use and will thus include species, which are functionally highly different. Some omnivorous species, however, may actually respond to similar limitations in resource availability. Some generalist species are omnivorous, but are morphologicallyspecialised (deVries, Stock, Christy, Goldsmith, & Dawson, 2016; Robinson & Wilson, 1998). Furthermore, focusing only on single traits will not reveal differential responses to resource availability. Small carnivores, for example, rely on different prey than large carnivores and consequently react to the availability of other resource. Accordingly, to understand trait-based community assembly, multivariate explanations are necessary.

The classical multivariate measure of functional diversity is functional richness (FR), which is proportional to the number of traits in a community. This metric is measured as the convex hull of all traits after a dimensional reduction (Schleuter, Daufresne, Massol, & Argillier, 2010). Functional richness is effective to reveal changes if the total amount of traits in a community is affected. Other measures which includ multiple traits and can be weighted by abundance and express the distribution of traits in a community. Functionally redundant species share functional roles in the community (Laureto et al., 2015), but their definition depends on the traits measured (Petchey & Gaston, 2006). Loosing functional redundant species in a community can be less relevant for ecosystem functions than loosing unique species. Redundant species, however, can increase the resilience of communities (Pillar et al., 2013). Consequently, in chapter 1, the application of functional originality, the inverse redundancy, measures how many unique trait combinations per species are present in a community. Compared to functional richness, this measure can be better linked to ecosystem functioning, resistance and resilience. These multivariate trait-based indices are more suitable to detect changes in functional community assembly. Single measures or even single traits might be insufficient to connect environmental changes to species and community responses. This issue is addressed in chapter 1 by comparing multiple measures of functional diversity.

Box 1: Environmental filtering of specific traits can result in different patterns of phylogenetic diversity in a community. Phylogenetic signal in traits is not suitable to evaluate if PD is a good proxy for FD (trait diversity), specifically if traits evolved convergently but are phylogenetically conserved in multiple clades (C). The schematic example shows three communities with four species each, were the same environmental filter selects for a specific character state (green circles) of one trait. Phylogenetic pattern of trait evolution determine the relation of FD and PD in the three communities.



Traits with phylogenetic signal

Environmental filter results in low trait diversity and low PD

Trait diversity (or FD) correlates with phylogenetic diversity

Additional traits (red squares) in the community would highly increase PD

Traits are overdispersed

PD and FD are not correlated which is implied by the lack of a phylogenetic signal in trait distribution

Environmental filter results in low trait diversity but high PD.

PD is strongly correlated with SR

Traits have a phylogenetic signal but evolved convergently in multiple clades

PD is not a good proxy for FD despite a phylogenetic signal. Community assembly processes cannot be inferred by PD

If species are removed from the community, PD will remain high. PD is weakly correlated with SR

If the environment filters for a trait, which evolved just in closely related species, and accordingly has a strong phylogenetic signal, a close relationship between phylogenetic and functional diversity are often assumed (Flynn, Mirotchnick, Jain, Palmer, & Naeem, 2011).

Complex pattern of repeated evolution and filtering of different traits can obscure this relationship (Box 1). However, niche differentiation can lead to divergence in additional traits to enable coexistence of different species. Consequently, the correlation between phylogetic diversity and functional diversity becomes stronger with increasing number of traits (Tucker et al., 2018). In fact, Faith acknowledged already in the early 1990s that phylogetic diversity captures overall "feature diversity" rather than individual trait differences (Faith, 1992). However, conservation measures still often focus on specific functions (e.g., pollination). By establishing conservation strategies aiming for specific groups, it can be valuable to avoid reduction in phylogetic diversity or even increase it to maintain diversity of unknown features that may increase resistance and resilience of communities. Equally to the functional measures mentioned above, by including abundance or more complex measures of phylogenetic community structure (for example MPD, as applied in chapter 1) otherwise overlooked changes in community structures can be detected (Tucker et al., 2017). Therefore, a profound understanding of the evolution of functional groups as well as the functional link between traits and the environment is crucial to understand assembly processes and their impact on biodiversity.

Carabids, traits and agri-environmental schemes

Carabid beetles (Coleoptera: Carabidae) are a well suited model for studying environment – species relationships, such as the consequence of environmental change. The taxon is extensively studied with more than 6700 publications regarding the key word "carabid*, and 1700 in the combination with the key word "environment*" (Web of science January 2022, but see also (Kotze et al., 2011a). Carabids are common in almost all terrestrial habitats worldwide, except the polar regions (Lövei & Sunderland, 1996). Life-history and ecological information is well documented for many species, which can make them useful indicator organisms (Koivula, 2011). Additionally, carabids are early responders to environmental change (Koivula, 2011, Kotze et. al., 2011) which gives the opportunity to link species traits to occurrence and changes in abundance based on environmental factors. It is no surprise that carabid communities are already used to monitor environmental change in forests and agricultural landscapes (Butterfield, Luff, Baines, & Eyre, 1995; Kromp, 1990; Pearce & Venier, 2006; Rainio & Niemela, 2003; Streiff, Veyrier, Audiot, Meusnier, & Brouat, 2005). Their reactions to environmental change are associated with functional traits (Cole et al., 2002; Jung, Lee, Lee, & Lee, 2018). The most important functional traits associated with these responses are linked to dispersal ability (e.g. body length and flight ability), trophic behaviour (Pakeman

& Stockan, 2014) and trophic groups (Purtauf, Dauber, & Wolters, 2005; Vanbergen et al., 2010). However, the classification of trophic groups for most species is based on broad categories and often founded on limited laboratory studies or gut content analyses. Isotope signatures from field studies show that trophic grouping is possible, but they also indicates a high flexibility of some carabids with respect to their major food source (Kamenova, Leroux, Polin, & Plantegenest, 2018; Zalewski et al., 2014).

The strongly developed ability to use alternative food sources is probably one explanation for the evolutionary and ecological success of carabids and allows them to persist also in rapidly changing environments. Even within species or individuals, composition of food sources can change dependent on local and landscape characteristics or time of the year (Araújo, Bolnick, & Layman, 2011; Fawki & Toft, 2005; Mader, Diehl, Wolters, & Birkhofer, 2018). However, consumption of alternative food sources that are likely to have less nutritional value than the primary food can even prevent the development of successive generations (Giglio, Brandmayr, Talarico, & Giulianini, 2012; Jorgensen & Toft, 1997). Therefore, one major focus of this thesis is to classify trophic groups of carabids based on the evolution of adaptive morphology in order to identify essential food resources. Specialised feeding behaviour requires the evolution of such adaptations.

The exploitation of new food resources is often followed by adaptive radiations which can result in highly diverse phylogenetic clades. For example, in beetles, herbivory has evolved several times, driving adaptive radiation and increasing diversification rates in almost all lineages (McKenna et al., 2019). This results in phylogenetic pattern with strong phylogenetic signals, but also converged lineages and will ultimately affect patterns of functional and phylogenetic diversity in beetle communities. Classical carabid taxonomy already indicates that herbivory evolved at least twice in Carabids, but this has never been tested in a phylogenetic framework. There are at least two distinct taxonomic groups which feed mainly on seeds: Harpalinii and Zabrinii. Observational descriptions of their mandibles support the assumption that both groups have evolved specific mandible morphologies (Acorn & Ball, 1991; Honek, Martinkova, & Jarosik, 2003) which are advantageous for seed consumption over mandibles of carnivores (Wallin, 1988). However, this thesis is the first study combining morphometric- and phylogenetic approaches to verify these observations and shed light on the evolution of herbivory in carabids.

Besides herbivory there are other feeding specialist in carabids. Of particular note are at least three carabid genera (*Leistus*, *Notiophilus, Loricera*) occurring in central Europe, which are specialised to feed on Collembola. Special adaptations are required to efficiently hunt Collembola, given their effective escape behaviour (Bauer, 1985; Hintzpeter & Bauer, 1986; Yin, Cai, Huang, & Li, 2017). These include setal traps in night active species (*Leistus* and *Loricera*) or enlarged eyes in day active species (*Notiophilus*; Erikstad, 1989; Ernsting & Isaaks, 1997; Ernsting & Jansen, 1978). Mandible morphology, however, has never been analysed regarding morphological adaptations. Therefore, I analyse responses of collembolan specialists to environmental change, classify their mandible morphology in a phylogenetic framework and evaluate the efficiency of these adaptations.

Based on this framework I link morphological adaptations of major carabid feeding groups to their evolutionary history to understand community based reactions in diversity pattern. Resource mediated responses of carabids are often associated with other traits. For example *Amara* spp. and *Harpalus* spp. prefer different seeds (Honek et al., 2003). Weed control by seed feeding carabids in agricultural landscape is mainly driven by large carabids (Fischer, Riesch, Tscharntke, & Batáry, 2021). Therefore, multivariate trait approaches, for example combining feeding preferences with body size, are necessary to assess functional responses of carabids to environmental factors. The combination of dispersal and resource related traits shows that species from the same trophic group might react differently to environmental factors at the local or landscape scale depending on their size and flight ability (Liu et al., 2015; Ignacio Ribera, Dolédec, Downie, Foster, & Apr, 2001). However, studies applying a multivariate approach to assess the effects on overall functional diversity in a community of carabids are scarce. Including multivariate diversity indices can increase our understanding of changes in carabid diversity as a response to environmental factors. For example, multivariate functional indices will show a different response to local or landscape factors than species richness alone (Schirmel, Thiele, Entling, & Buchholz, 2016). For example, along successional gradients functional dispersion, a measure of functional similarity, increases in carabids (Schirmel, Blindow, & Buchholz, 2012).

The additionall use of phylogenetic information to detect community level responses of carabids to environmental gradiants can give complementary results to traditional measures (Gayer, Lövei, Magura, Dieterich, & Batáry, 2019; Magura, 2017). Understanding trait-based community assembly of carabids in a phylogenetic context can help directing management strategies towards more target-oriented conservation aims. For example, rather than aiming for conserving a maximum number of feeding groups, conservation strategies should aim to increase diversity in these groups by also increasing phylogenetic diversity in a community. The functional redundancy of species from different lineages can increase ecosystem stability and resistance. Likewise, the conservation of herbivorous species from different lineages might contribute to their potential to increase ecosystem services as seed feeder by increasing the amount of specialists that evolved in different groups.

Chapter synthesis

This dissertation aims to integrate approaches from the disciplines evolutionary biology and ecology into the study of community assembly of carabids (Fig. 1). For that reason, I investigate the evolution of functional traits to explain pattern of community assembly. Chapter 1 addresses the influence of land use change on functional- and phylogenetic diversity. Chapter 2 focuses of on feeding groups as a functional group, which showed a strong response in chapter 1 and link morphological adaptations to their ecological function. For this purppose, I used the mandible shape as a functional adaptation to specific feeding modes (chapter 3). The main focus was on whether the patterns found in chapter one, particularly the convergence of functional groups, can be traced down to morphological adaptations and whether these show similar pattern. The finding that specialists are morphologically very similar suggests a strong selective pressure on morphological adaptation to specific feeding types. However, morphological specialisation does not always coincide with ecological specialisation. Consequently, the third study aimed to experimentally demonstrate the adaptive advantage of specialised mandibles. I thus conducted feeding experiments to verify the hunting efficiency of specialised species compared to generalists.

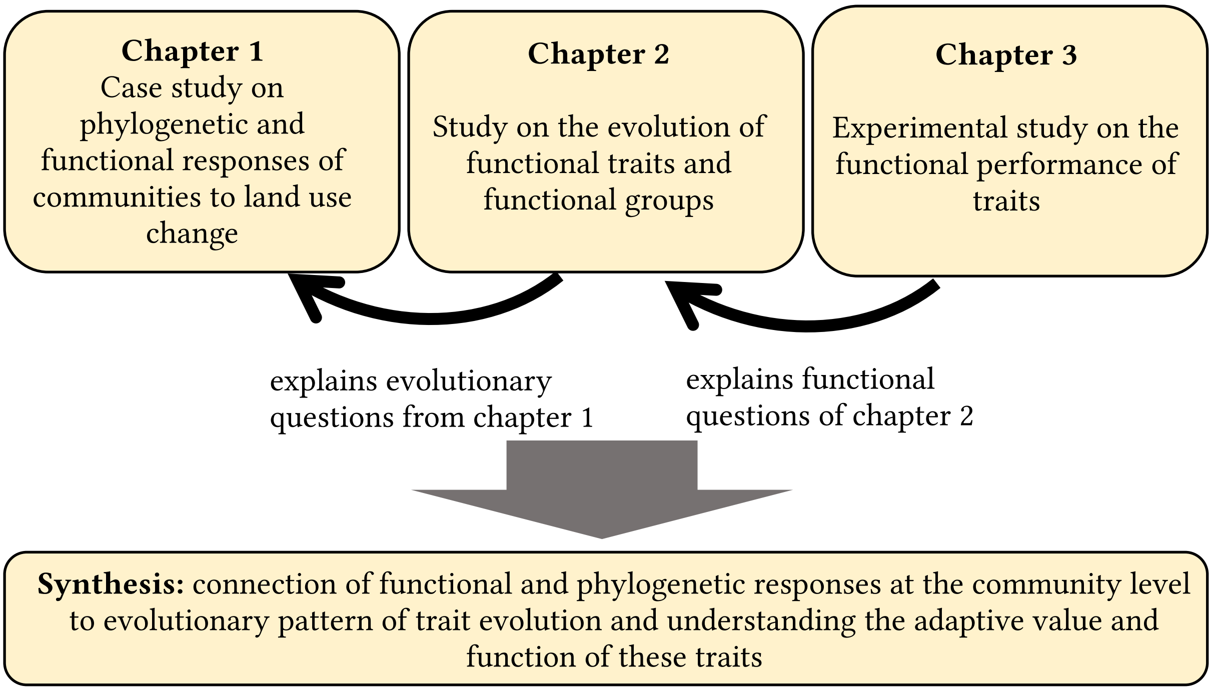


Fig.1: Synthesis of the three studies represented as chapters in this dissertation. Chapters two and three explain causal relationships from the preceeding studies.

To develop a more comprehensive understanding of the evolutionary ecology of functional groups in carabids and the present-day consequences of environmental change, this dissertation investigates the following general hypothesis:

1. The conversion of arable land to flowering fields changes the functional and phylogenetic composition of carabid communities (chapter 1).
2. Convergent evolution results in feeding groups which are phylogenetically highly diverse (chapter 1 & 2). Phylogenetic and functional diversity are not related in this case.
3. The repeated evolution of feeding groups is coupled with morphological adaptations in mandible shape (chapter 2). These adapations are the driving response traits to changes in resource availability as demonstrated in Chapter 1.
4. The adaptive value of a functional morphology towards a specific food can be confirmed by an enhanced hunting success (Chapter 3).

Conclusion and implications

In the following chapters, I demonstrate how evolutionary information can help to understand ecological processes such as community assemblies and how trait evolution characterise and shape biodiversity. I show that the effects of land-use change on communities can result in functional changes, which cannot be detected by species richness or similar traditional measures (chapter 1). Confirming my hypothesis 1 and 2, as a result of the convergent evolution of functional traits, phylogenetic diversity is not affected by changes of functional groups in these communities. This is substantiated by the fact that feeding types evolved several times, therefore decoupling the relationship between trait difference and phylogenetic distance (chapter 1 & chapter 2). The convergent evolution of feeding types is substantiated by shared specialised mandible morphology in each feeding group (hypothesis 3 and chapter 2). The efficiency of these specialized mandible shapes is established in chapter 3 to confirm their adaptive value and accordingly hypothesis 4. Consequently, this thesis successfully links the evolution of morphological adaptations to ecological functions and responses of different biodiversity components to land use change. This allows for a comprehensive understanding of the evolutionary ecology of carabid feeding groups. My studies thus contribute to a causal understanding of the relations between different biodiversity components.

As confirmed by many studies, single functional traits can be highly usefull to detect species responses to environmental change. The results summarized in this thesis show that including multiple traits and phylogenetic information can improve our understanding of functional community assembly. For example, within a trophic group, different phylogenetic lineages can evolve differences in body sizes. These separate lineages will react differently to resource availability due to differential resource use, obscuring community assembly pattern when only the trophic group is used as a response trait. Due to their evolutionary distance these different lineages probably evolved many different undetected traits (Faith´s "feature diversity", Faith 1992). Therefore, the inclusion of multiple response traits combined with phylogenetic information can be more informative to increase our understanding of the response of functional diversity to environmental factors compared to traditional single-trait measures. To evaluate the success of conservation efforts, research should not only focus on how to protect functional groups but also on a high phylogenetic diversity within these groups. Increasing the evolutionary distinctiveness in functional groups can positively affect resistance, resilience and ecosystem services, but these connections despite being discussed already in the early 90s are still understudied (Hipp et al., 2015). However, due to the fast technological progress over the last decades, the application of phylogenetic methods in conservation now becomes possible.

The value of flowering fields for insect diversity and especially for carabids has been confirmed in recent years. Indeed, carabids are one of the early responders to the establishment of this agri-environmental measure showing increased species richness in new flowering fields, while other taxa rely on temporal continuous flowering fields (Boetzl et al., 2021). This is supported by the results in chapter 1 which showed fast responses of carabid community structure right after the establishment of flowering fields which were decoupled from species richness. Chapter 1 shows that the establishment of flowering fields changes functional diversity and increases the amount of herbivorous species which is confirmed by a recent study (Gayer et al., 2019). Flowering fields not only increase the number or abundance of herbivore species. The positive effect on distinct evolutionary lineages of herbivores with differed traits, increased functional originality and ecosystem services as seed removal are likely to be more efficient. The distinct evolutionary lineages differ in body size, degree of specialisation and probably unknown traits regarding live history and physiological adaptation. In communities with a few species per trophic group the loss of some species might exclude a whole functional group without having any species as a functional buffer. The increase of biodiversity in flowering fields (Boetzl et al., 2021) is likely to enhance crop yields (Rischen, Frenzel, & Fischer, 2021). Flowering fields are, however still understudied in regard to non-pollinator diversity. This includes also the effect of flowering fields on soil-fauna, for example Collembola, which are an essential food resource for some specialised carabids as demonstrated in chapter 3. Because of the convergent evolution of Collembola specialists, there could be a strong effect on the phylogenetic structure in carabid communities. For example, if these genera are present, phylogenetic diversity will be maintained high and obscure effects on phylogenetic structure if other taxa are removed from the community. This indicates that the efficiency of flowering fields will depend on multiple trophic networks, from soil-fauna to plant seed-diversity. It should therefore be considered that indirect effects from soil type, previous treatments and crop rotation through multiple trophic networks will regulate the effect on different components of biodiversity. Even for specialist, changes in landscape composition will influence the importance of alternative prey to overcome food shortages (Carbonne et al., 2020). The continuing research on the application of agri-environmental schemes will show the long term and large-scale landscape effect on carabid biodiversity. Particularly important is to consider different special scales and landscape factors and how traits related to dispersal ability alter the response of trophic groups.

The results of the studies summarized in this dissertation demonstrate how different biodiversity components should be used complementary and not as proxies for each other in order to understand how communities are affected by land use and to evaluate counter measures. Instead of inferring assembly processes based on phylogenetic pattern my results highlight that phylogenies can be much more useful in community ecology. It is crucial to first understand the phylogenetic distributions of traits and the trait-environment relationships, as I demonstrated for carabid beetles, then it is possible to build new hypotheses predicting community responses to environmental changes (see also Davies, 2021).

Chapter overview

Chapter 1: Converting arable land into flowering fields changes functional and phylogenetic community structure in ground beetles

Published March 2019 in Biological Conservation

Short summary: The conversion of arable land to flowering fields increased herbivorous species richness but not total richness, species diversity or phylogenetic diversity. However, species were more closely related to each other compared to null models and functional originality increased.

Contribution: first Author, conceptualisation, analyses and lead in writing

Chapter 2: Convergent evolution of specialized generalists: Implications for phylogenetic and functional diversity of carabid feeding groups

Published October 2020 in Ecology and Evolution

Short summary: Carabid feeding groups evolved convergent mandible morphologies as an adaptation to specific food resources.

Contribution: first Author, conceptualisation, analyses and lead in writing

Chapter 3: Carabid adaptation to a collembolan diet: hunting efficiency and nutritional value

Published November 2021 in Ecological Entomology

Short summary: Collembolan specialists have a higher hunting efficiency due to their adaptive mandible morphology. Generalist carnivores which are known to feed occasionally on collembolans decreased dramatically in weight when fed only collembolans and had a high mortality rate. Specialisation of collembolan feeder however does not constrain these species to collembolans as the only food resource.

Contribution: first Author, conceptualisation, analyses and lead in writing

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CHAPTERS

Chapter 1

Converting arable land into flowering fields changes functional and phylogenetic community structure in ground beetles

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Abstract

Agri-environmental schemes aim to promote biodiversity in agricultural landscapes. However, knowledge about the impact of these measures on diversity components beyond species richness, especially for non-target species and their ecological functions, is still very poor. Here, we investigated the response of ground beetle communities to the conversion of arable land into flowering fields, focusing on the relationship between biodiversity components and the evolutionary relationship among functional groups.

Land-use conversion from arable land to flowering fields has changed the phylogenetic community composition of ground beetles towards a phylogenetically clustered community. This is due to an increase in closely related medium-sized herbivorous species and a decrease in evolutionarily distinct small carnivorous species. Phylogenetic clustering did not result in a reduction of functional richness, but it increased the number of unique trait combinations of species within the local communities. This suggests a low ecological redundancy among herbivorous species. Because species richness, functional richness and phylogenetic diversity were unaffected by conversion, phylogenetic community structuring was predominantly driven by species turnover rather than by numerical changes.

Flowering fields can act as refuges for herbivorous carabids that potentially affect the surrounding agricultural landscape by providing important ecosystem services such as weed control. To understand the impact of habitat transformation on carabid biodiversity, it was more informative to relate response traits to phylogenic and functional diversity than to use single diversity measures such as species richness. This conclusion might also apply to many other taxa.

Keywords: Agri-environmental scheme; biodiversity; phylogenetic diversity; functional diversity; trait evolution; carabid diversity

Highlights

- Carabid species richness was unaffected by habitat conversion
- Communities in flowering fields were phylogenetically clustered
- Phylogenetic clustering did not reduce phylogenetic diversity or functional diversity
- Arable land was dominated by carnivorous carabid species
- In flowering fields, closely related medium-sized herbivorous species increased

Introduction

Management intensification is a major driver of biodiversity loss in agricultural landscapes (Foley et al., 2005; Sala et al., 2000). To counteract this decline, great efforts have been made to reduce agricultural intensification by establishing agri-environmental schemes (Kleijn et al., 2006). The measures associated with these schemes often lead to habitat islands, which significantly differ in resource composition and availability from the surrounding agricultural landscape. These islands act as local environmental filters that will theoretically promote the establishment of target taxa with specific ecological or functional traits. Subsidized flowering fields, for example, are targeted at flower visitors to counteract pollinator loss in agricultural landscapes. The effectiveness of such measures is controversial, however, even for target species (Kleijn et al., 2006; Kleijn & Sutherland, 2003; Tscharntke et al., 2005). Non-target species, like carabid beetles in flowering fields, have been addressed by only a few studies so far. This constitutes a serious lack of knowledge, since one could hypothesize, for example, that the local reduction or offset of agricultural management adversely affects taxa that are well adapted to arable land (Birkhofer et al., 2015). On the other hand, there is evidence that flowering strips or fields can actually increase the richness of some of these taxa (Mader et al., 2017; Tschumi et al., 2015). Hence, the aim of this study was to fill this knowledge gap by investigating the response of a non-target group to the local conversion of arable land into flowering fields: carabid beetles.

Carabids are well adapted to arable landscapes (Andersen, 2000). However, different species or functional groups significantly differ in their response to land-use changes and management intensity (Diekötter et al., 2010; Fusser et al., 2017; Kotze & O'Hara, 2003; Purtauf et al., 2004, 2005). For example, large-scale land-use intensification puts large micropterous species with poor dispersal capability at a disadvantage, compared to small and macropterous species with high dispersal capabilities (Ribera et al., 2001; Wamser et al., 2012). Moreover, fragmentation of habitats in intensively managed regions may adversely affect species with life history cycles that include hibernation in undisturbed natural or semi-natural habitats (Frank & Reichhart, 2004; Wamser et al., 2011). Thus, certain agri-environmental measures may benefit carabid communities by increasing the permeability of agricultural landscapes and providing additional resources to species that are not restricted to arable land (Schirmel et al., 2016).

The establishment of flowering fields is intended to mitigate pollinator loss. However, these fields also provide ample resources for herbivorous carabids and additionally alter the prey spectrum for carnivorous species. They can therefore serve as important refuges for species that have become less abundant in impoverished agricultural landscapes. The associated changes in species composition and richness alter the communities' functional diversity, with considerable feedbacks to the functioning, robustness and resilience of the ecosystem (Cadotte et al., 2011; D'Andrea & Ostling, 2016; Hillebrand & Matthiessen, 2009; Loreau & Hector, 2001). Functional diversity, in turn, can be positively related to phylogenetic diversity, but this depends on the number of traits included in the functional diversity measure and the processes of trait evolution (Tucker et al. 2018). Assuming that differences in traits among species accumulate over time, phylogenetic distance should reflect differences in traits and niche space (Kraft et al., 2007). It is unclear, however, whether the use of phylogenetic diversity measures has any meaning in conservation strategies and whether phylogenetic richness or rather phylogenetic structure of communities is affected by traits responding to habitat change (Winter et al., 2013). To understand and forecast changes at the community level as a response to environmental change, responding traits must be correlated with the environment (Cadotte & Tucker, 2017; Cavender-Bares et al., 2009) and analyzed in a phylogenetic framework (Cadotte et al., 2009, 2011).

Therefore, the aim of this study was to identify traits that respond to habitat conversion of arable land to flowering fields and to analyze how these trait responses affect phylogenetic community structure and functional diversity. Against this background, we hypothesized that the number of herbivorous species will increase due to the increased resource availability. Similarly, carnivorous species might profit from the habitat conversion due to higher structural diversity and associated prey diversity. We expected a shift in average body size due to a disadvantage for small species in colonizing newly established habitats and a stronger response in carnivorous species due to a higher variability in body size. Because we expected a phylogenetic signal for feeding guilds and body size, a community shift towards the most benefitting guilds will alter the phylogenetic community structure and modify functional diversity of the communities.

Methods

Study area and sampling

The sampling sites were located in the district of Marburg-Biedenkopf in central Hesse, Germany. The study region covers an area of approximately 1260 km^2 and is covered by 44% agricultural use, 41% forest and 14% settlement and traffic. The region of temperate climate receives 600 (central region) to 1,000 (peripheral region) mm rainfall per year at 6 (peripheral) to 9 °C (central) mean annual temperature. The two sampling periods were similar in temperature (mean 2011: 9.5 °C; 2012: 10 °C) and precipitation (sum 2011: 559.0 l/m^2; 2012: 662,9 l/m^2). For a detailed climatic comparison of both sample years and periods, see Appendix Table A4-A6).

Inter-site distances ranged from 57.7 km maximum to 1.57 km minimum (see Appendix Table A3 for geographical coordinates). When flowering fields were established, farmers were required to apply distinct flower mixtures and abandon land management for five years in order to receive subsidies. All sites were used for conventional cereal grain or energy plant production in the previous year (for details see Appendices Table A3).

We collected carabid beetles at 22 study sites before the abandonment of land use in 2011 and after the establishment of flowering fields in 2012. Land management was abandoned in autumn 2010 and flower mixtures were applied in Mai 2011. Carabid beetles were collected with pitfall traps, which were active for 14 days at the beginning of June in 2011 and in 2012. Three pitfall traps were aligned in the center of 22 of these sites with inter-trap distances of 10 m. All specimens were identified to species level.

Species diversity and community composition

We first calculated local species richness at all sites for the two years to evaluate changes in the taxonomic community structure before and after habitat transformation. Species similarity for each site between years was calculated based on the Sörensen index (Dixon, 2003). The overarching trend of interannual changes was analyzed by correlating the matrices of Sörensen similarities of sites between years using a Mantel test with 999 permutations (Dixon, 2003). A significant correlation indicates that a similar response to habitat conversion among sites is based on similar species identities in the local communities. All statistical analyses were performed using R version 3.2.2 ((R Development Core Team, 2013).

Functional traits

Trait analysis was done using the information compiled on Carabids.org (Homburg et al., 2014). Data include categorical (feeding preferences, larval or adult hibernation, reproduction time, wing morphology and flight ability) and continuous traits (minimum and maximum body size, eye size in proportion to head size). To evaluate the role of functional traits in community responses to habitat transformation, we calculated Gower distance matrices of the trait distribution for each community by means of the function “daisy” of the R package cluster (Maechler et al., 2013). This approach corresponds to the concept underlying the measure 'functional diversity' (FD), which is defined as the total branch length of the trait distance matrix (Petchey & Gaston, 2002). We then calculated the mean pairwise trait distance (MPTD) for each community based on the Gower distance matrixes, using the R package picante (Kembel et al., 2010). MPTD indicates how similar (i.e. clustered) a community is to a specific trait or combination of traits. MPTD were tested against a simulation of null models (1,000 generations) with random shuffling of species over the distance matrix. Calculation of the standardized effect size (ses) of MPTD describes the difference between observed values and randomized null models:

$$sesMPTD = \frac{MPTD_{observed} - mean(MPTD_{null})}{sd(MPTD_{null})}$$

For better comparability with other studies, we used sesMPTD^{-1}, which equals the widely used nearest relative index NRI (Webb et al., 2002). Thus, positive values indicate clustering of species with similar traits, while negative values indicate an overdispersed distribution of traits (low similarity). MPTD was calculated for all possible trait combinations (n = 64). We then computed the total community functional richness (FR) and functional originality (D'Andrea and Ostling, 2016) based on the R scripts provided by (Mouillot et al., 2013). FR is a measure for the volume of the calculated multidimensional space occupied by all species of a community. FOri quantifies the isolation of species in the calculated functional trait space occupied by a given commmunity. High values of FOri characterise communities with species with unique trait combinations and thus with low functional redundancy. Both calculations are expressed as a percentage of the maximal richness or originality observed in the species pool. To analyse differences in MPTD, FR and FOri before and after the conversion we performed a two-sample Wilcoxon (Mann Whitney) test.

Phylogenetic reconstruction

Cytochrome oxidase I (COI) sequences were obtained from *GenBank®* for each species sampled (Appendix Table A2). Sequences were aligned using the muscle algorithm in MEGA version 6 (Tamura et al., 2013). We determined GTR+Γ+I as the best nucleotide substitution model using jModelTest 2.1.5. (Guindon & Gascuel, 2003; Posada, 2008). Ultrametric phylogenetic trees were reconstructed using the software BEAST v1.8 (Drummond et al., 2012) with 10 000 000 Marcov Chain Monte Carlo (MCMC) generations under a relaxed molecular clock model and based on a yule speciation process. Due to the problems of COI in resolving deeper phylogenetic relationships, especially in the tribe Sphodrini, we used the topology published by (Ruiz et al., 2009)) as a backbone to constrain relationships between genera in this tribe (for applied constraints and used outgroups see Appendix Table A2) with the program BEAUTY v2.2 (Drummond et al., 2012). Posterior probabilities below 50% were collapsed to polytomies before further analyses.

Phylogenetic structure

To evaluate changes in the phylogenetic community structure before and after habitat transformation, phylogenetic diversity measures for each site were calculated for the two years using the R package picante (Kembel et al., 2010; R Development Core Team, 2013). We used the indices phylogenetic diversity (PD) and mean pairwise distance (MPD). The choice of these indices is based on the analyses of (Tucker et al., 2017), who identified PD as an "anchor" index for richness and MPD for divergence out of 70 available mostly redundant phylogenetic indices. PD is a measure of phylogenetic distance of members in a community. It is calculated as the sum of the branch length of all members in a community. MPD is a measure of phylogenetic clustering or relatedness and is calculated as the mean pairwise distance between all members in a community (MPD). Since MPD is particularly sensitive to clustering at the deeper level of the phylogeny, we calculated the mean nearest taxon distance (MNTD), which rather responds to clustering at the species level. MNTD is calculated as the mean distance to the nearest neighbor in the phylogeny of each species in the community. MPD and MNTD were tested against a simulation of null models (1,000 generations), with random shuffling of species over the tips of the phylogeny. We calculated both measures based on both presence-absence and abundance data. The parameters sesMPD and sesMNTD quantify the difference between observed values and randomized null models:

$$sesMPD = \frac{MPD_{observed} - mean(MPD_{null})}{sd(MPD_{null})}$$

$$sesMNTD = \frac{MNTD_{observed} - mean(MNTD_{null})}{sd(MNTD_{null})}$$

As in the trait analyses, we used $sesMPD^{-1}$ and $sesMNTD^{-1}$ for a better comparability with other studies, since both measures are based on the calculation for the nearest taxon index (NRI) that equals $sesMPD^{-1}$. Hence, positive values indicate clustering of species and negative values a random distribution over the phylogeny. Differences in sesMPD and sesMNTD before and after habitat conversion we tested by performing two-samples Wilcoxon (Mann Whitney) tests.

In a final step, we analyzed whether (i) specific trait responses to habitat conversion drive phylogenetic clustering, and (ii) responding traits are indeed phylogenetically conserved. Therefore, we first correlated the sesMPTD with the sesMPD values for all communities in the two years. We then calculated the phylogenetic signal *K* for each trait with the R package picante running 1000 simulations (Blomberg et al., 2003; Kembel et al., 2010; R Development Core Team, 2013). This test compares the observed phylogenetic distribution of a trait to the distribution under a Brownian motion model of trait evolution (Blomberg et al., 2003).

Results

Species composition and functional diversity

A total of 6,814 carabids from 84 species was captured. Local species richness and phylogenetic diversity (PD) did not change after the conversion to flowering fields (Table 1). In contrast, species composition had changed considerably in terms of both density and occurrence frequency (Fig.1). The study sites only shared less than half of the species before and after habitat transformation (Sörensen Index; mean = 0.43, min = 0.14, max = 0.71) and similarity between sites was not correlated between years (Mantel test; p = 0.57). Abundant small carnivorous species (e.g. members of the genera *Bembidion*, *Acupalpus, Clivina*) disappeared from many sites in the second year (Fig.1). Large and medium-sized carnivorous species decreased considerably in abundance (e.g. *Pterostichus melanarius*) and occurrence frequency (*Agonum muelleri*). In general, medium-sized herbivorous species (members of the genera *Harpalus*, *Amara, Anisodactylus*) responded positively to the habitat conversion in terms of abundance and frequency of occurrence (Fig. 1, Fig 4). *Anisodactylus binotatus*, for example, which occurred at only two sites in the first year, was found at 20 flowering fields after conversion. Similarly, *Pterostychus vernalis* was found in an additional 10 sites in flowering fields compared to the first year. “Food preference” was the only trait which changed from random distribution in arable fields towards an equal distribution in flowering fields (sesMPD: 2011: -0.007, 2012: -0.911, Wilcoxon test: $p < 0.001$). Arable fields were dominated by carnivorous species, while the proportion of carnivorous and herbivorous species was identical in the flowering fields (Fig. 4a & b). While functional diversity (FD) did not change between arable and flowering fields, functional originality was significantly higher in the latter (Tab 1).

Comparing all possible combinations of trait-based sesMPD values, clustering only occurred in the second year and was confined to the continuous traits “body size” (sesMPD: 2011: -0.79;

2012: 1.91, Wilcoxon test: $p < 0.001$, Fig. 2) and “proportion of eye size to head size” (sesMPD: 2011:-0.74, 2012: 0.86, Wilcoxon test: $p < 0.001$). The term “Body size” refers only to minimum body size since this parameter had a slightly stronger effect then maximum body size, but the direction of the effect was identical for the two parameters. “Proportion of eye size to head size” was excluded from the phylogenetic community structure analysis, since only 10 out of 22 sites switched from random to clustered distribution (but see Fig. A2 in the Appendix). All other trait combinations of the second year only weakly clustered with “body size”. The clustering of sesMPD for “body size” is due to the dominance of medium-sized species in the flowering fields, to the detriment of small-sized species in the arable fields before the conversion (Fig. 3).

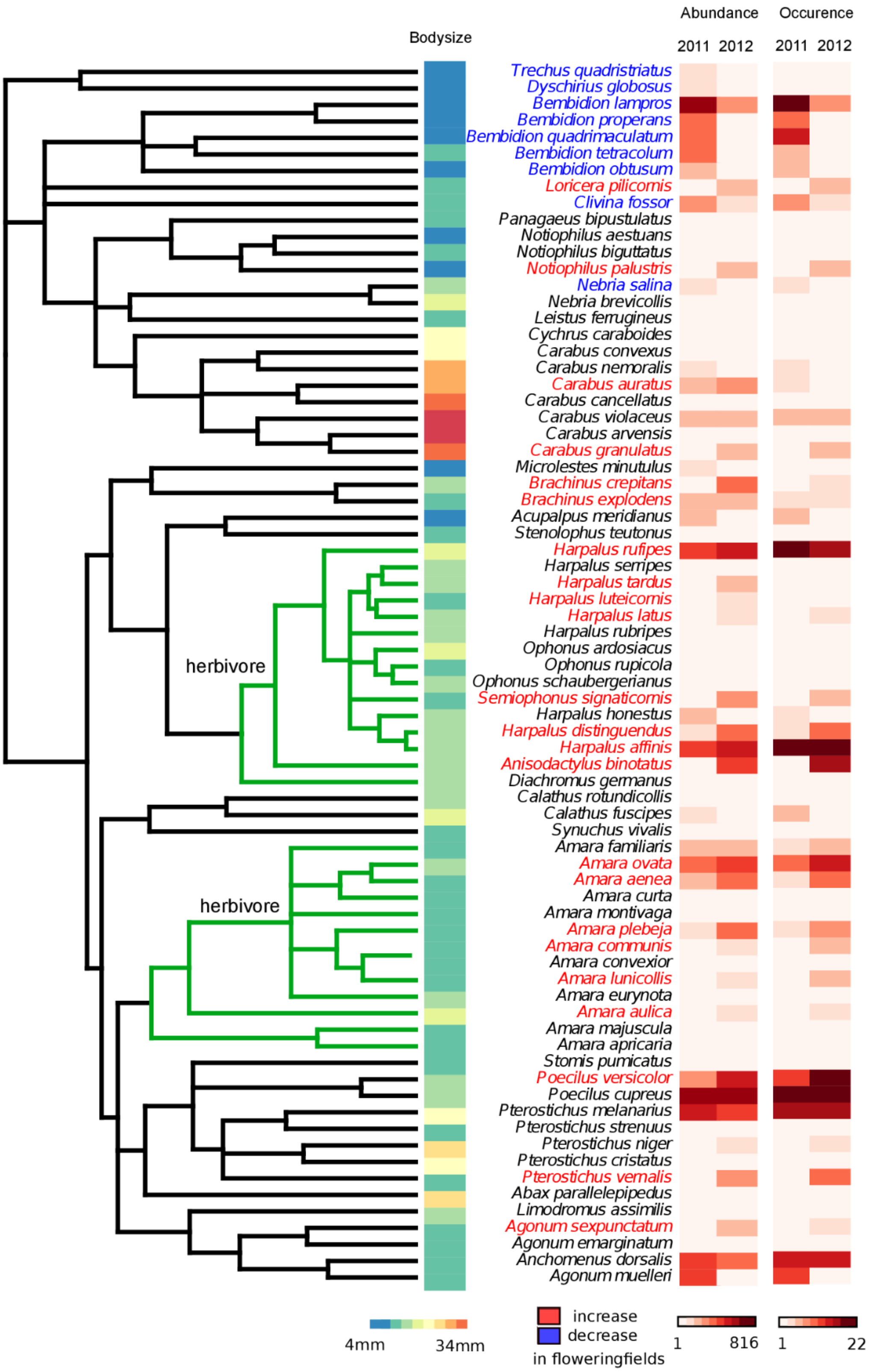

Fig. 1: Phylogenetic distribution of the two responding traits body size (minimum body size given here, but equally applicable to maximum body size) and feeding preference and species responses to the conversion to flowering fields. Groups with preferred herbivory lifestyle are marked in green in the phylogeny. The heat map next to the phylogeny shows the distribution of body sizes. Species that increased in abundance and/or occurrence frequency after the conversion to flowering fields are marked in red. Species that decreased are marked in blue. Overall abundance and occurrence frequency (the number of sample sites where a species is present) are shown in the four heat maps on the right. Posterior probabilities below 50% are collapsed into polytomies.

Table 1: Diversity indices measured between the years. The median, min and max values are for all 22 sites. P values for the U tests are given based on the differences between community values before and after conversion.

	Arable land before conversion			Flowering fields after conversion			Wilcoxon Test	
Index	min	median	max	min	median	max	W	p value
PD	1.23	2.062	3.4	1.05	1.97	2.71	210	0.220
SR	7	12	19	6	12	19	216	0.943
FOri	0.12	0.25	0.50	0.24	0.34	0.66	435	< **0.001**
FR	0.28	0.51	0.88	0.29	0.51	0.83	211	**0.140**
sesMPD (*-1)	-1.61	-0.46	1.80	-0.29	1.71	4.22	468	< **0.001**
sesMNTD (*-1)	-2.31	1.19	1.24	-1.84	1.89	1.31	329	**0.013**
sesMPDabundance	-1.65	-0.66	1.60	0.26	1.31	2.21	456	< **0.001**
sesMNTDabundance	-1.79	0.78	1.47	0.17	0.99	2.35	287	0.068

PD: phylogenetic diversity, SR: species richness; FOri: functional originality; FR: functional richness, ses: standardized effect size, MPD: mean pairwise distance, MNTD: Mean nearest taxon distance;

Phylogenetic structure

Carabid communities had a significantly higher sesMPD in flowering fields than in arable fields (p < 0.001, Table 1, Fig. 2 b & c), with 21 out of 22 sites being phylogenetically clustered in flowering fields (values >1; Fig. 2 b). Thus, communities were more closely related in the flowering fields and were more closely related than in randomly generated null communities. The response of sesMNTD to habitat conversion was weak. When weighted by species abundance, the effect of habitat conversion on sesMPD was also strong, but no effect on sesMNTD could be detected (Table 1). This indicates clustering at deeper phylogenetic levels rather than at the species level.

We found strong correlation between sesMPD and sesMPTD for the trait "body size" in the two years (Fig. 2 b, 2011: Spearman rank rho = 0.73, p < 0.001; 2012: Spearman rank rho = 0.90, p < 0.001). Body size and food preference in carabids was phylogenetically conserved and exhibited a phylogenetic signal (Blomberg´s $K > 1$), i.e. closely related species tend to have a more similar size and similar food preference than expected under Brownian motion (Blomberg et al., 2003). However, the food preference for herbivory evolved independently in two distinct taxa, Harpalini and Zabrini (Fig 1).

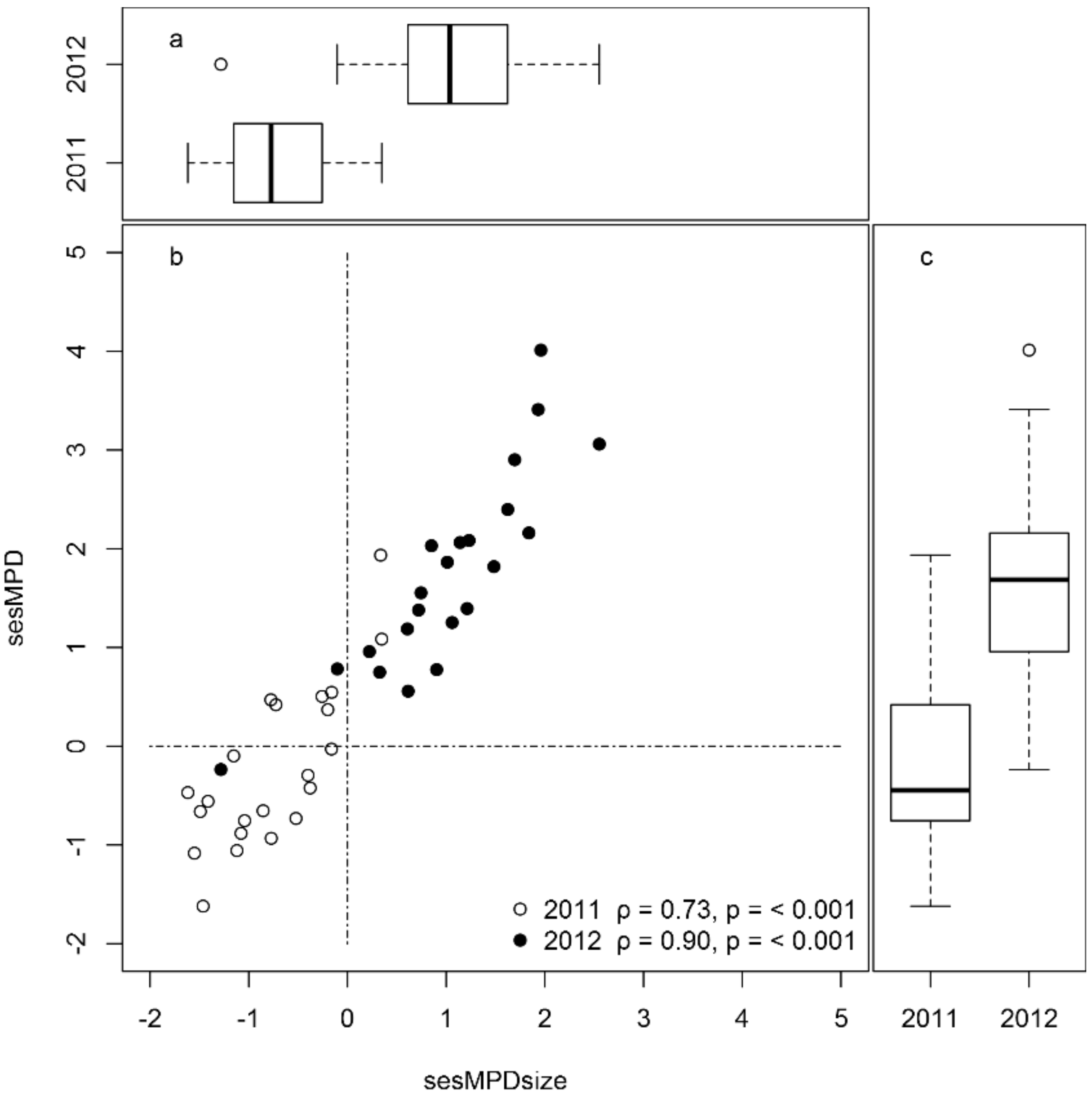

Fig 2: Relation between the similarity in body size (sesMPDsize) and phylogenic similarity (sesMPD) (a). Spearman rank rho and p values are given in the legend. Both body size similarity sesMPDsize (b) and phylogenetic similarity sesMPD (c) were clustered after conversion (positive values) compared to randomized null models.

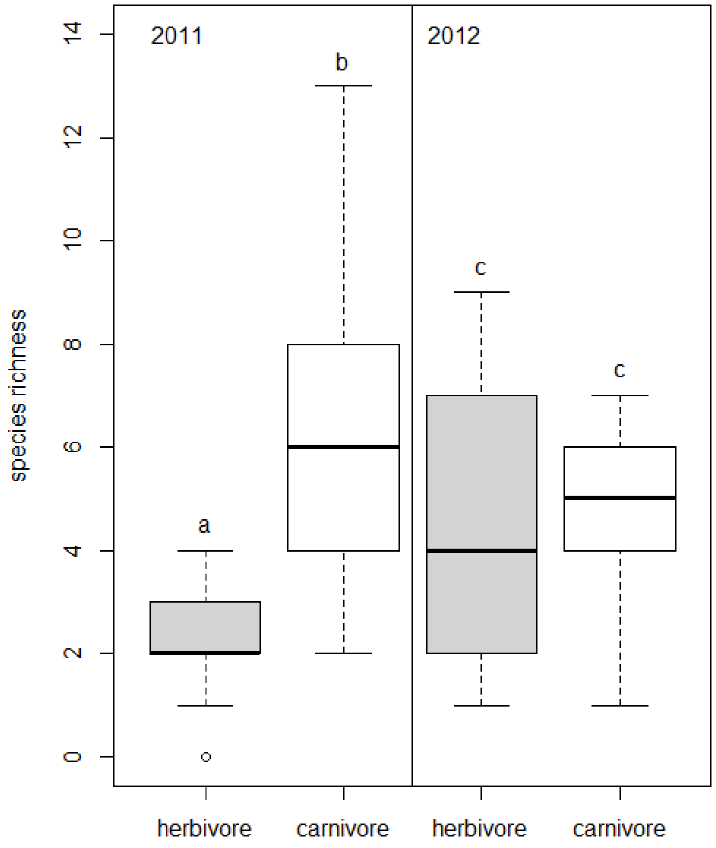

Fig 3: Herbivorous and carnivorous species richness in arable fields before conversion in 2011 and after conversion to flowering fields in 2012.

Discussion

The conversion of arable land to flowering fields aims to reduce pollinator loss in agricultural landscapes. To quantify the consequences for non-target groups, we investigated the effect of this measure on different diversity components of carabids. Our results show that the increase in the proportion of medium-sized herbivores and the decrease in the proportion of small carnivores after the conversion significantly changed the phylogenetic community structure and increased functional originality. In contrast, species richness, functional diversity (FD), and phylogenetic diversity (PD) remained unaffected. Considering, however, that the sites shared less than half of the species before and after habitat transformation, the establishment of flowering fields within a matrix of arable land definitely enriches carabid communities at the landscape scale. The stimulation of herbivorous species suggests that flowering fields, similar to grass banks (MacLeod et al., 2004), may contribute to the reduction of undesired weeds in intensive agricultural land by enhancing the populations of pest controlling carabid species (Diekötter et al., 2016; Honek et al., 2003a; Kulkarni, Dosdall, & Willenborg, 2015). *Harpalus rufipes*, which was abundant in flowering fields, can adversely affect crops such as strawberries (Briggs, 1965; French et al., 1968), but recent literature does not support the assumption that this and other herbivorous species found in our study sites play a significant role as crop pests.

Changes in vegetation structure not only affect herbivorous carabids, but likewise alter hunting efficiency, enemy pressure and microhabitat conditions for carnivorous species (Brose, 2003). Therefore, structural heterogeneity and stable temperature conditions, which are typical for flowering fields, usually promote the diversity of predatory arthropods (Diehl et al., 2012; MacLeod et al., 2004; Thomas et al., 1992). One might thus expect that flowering fields will also increase the species richness of carnivorous carabids (Tschumi et al., 2016). On the contrary, and in accordance with our hypothesis, we found that the positive effect of flowering fields was confined to medium-sized herbivorous species, while small carnivorous species even declined. This decline may be explained by the fact that the feeding strategies of small carnivorous species like Bembidion are best supported by simple structures and bare ground ((Batáry et al., 2012), which leads to a preference of these taxa for intensively managed landscapes and disturbed habitats (Blake et al., 1994; Pakeman and Stockan, 2014; Ribera et al., 1999). Small carnivorous species are known to prey on different small pest species (Burn, 1982; Grafius & Warner, 1989; Lemay et al., 2018) and their loss may thus limit their role as pest control agents.

Because the two traits “herbivory” and “body size” have a strong phylogenetic signal, the increase in medium-sized herbivore species and the parallel decline of small carnivores led to phylogenetically clustered carabid communities in flowering fields. This additionally explains the fact that the trait “body size” was also clustered. These effects of habitat conversion on phylogenic and functional community structure were equivalent for all communities. Moreover, the low share of identical species between sites indicates a general functional and not a species-specific response.

It has been suggested that the effect of environmental filtering on carabid assemblages is particularly important in less disturbed habitats with taller vegetation (Pakeman and Stockan, 2014). This is consistent with our finding of a phylogenetic community clustering in flowering fields, but not on arable land. Conventionally, this could be explained by environmental filtering (Webb et al., 2002). However, since phylogenetic clustering might also result from competitive exclusion, which can alternatively induce overdispersion, phylogenies are not well suited to infer assembly processes from phylogenetic patterns (Kraft et al., 2007; Mayfield and Levine, 2010)(Gerhold et al., 2015). This is supported by our result that the distinct response of carabid communities to habitat conversion altered phylogenetic structure without affecting phylogenetic (PD) or functional diversity (FD). The co-occurrence of many closely related and ecologically similar species nevertheless suggests that competition probably did not play a major role in the assembly of the carabid communities investigated in our study (Vamosi and Vamosi, 2007). However, the fact that functional originality increased in flowering fields, while functional richness did not change (i.e. the number of traits remained the same, but species with unique trait combinations increased), indicates avoidance of competition among herbivorous carabids via niche partitioning (Srivastava et al., 2012a). As becomes obvious through our phylogenetic tree and the analyses of trait distribution, convergent evolution of herbivory in the tribes Harpalini and Zabrini strongly contributed to the potential of unique trait combinations. These two taxa differ in breeding season, activity time and body size (Homburg et al., 2014) and therefore feed on seeds from a different set of plant species (Honek et al., 2007a).

Conclusion

The analysis of both functional traits and phylogenetic structure allowed us to focus on ecological complementarity rather than on species richness, which is often associated with ecological redundancy (Bommarco et al., 2013). Our results indicate that the establishment of flowering fields increases the amount of functional originality contained in the individual carabid communities. The protection of functional originality is essential for conserving the functional diversity of ecosystems (Mouillot et al., 2008). Flowering fields thus seem to be a promising measure for promoting the structural and functional richness not only of pollinators, but also of non-target taxa such as carabids in agricultural landscapes. By providing a refuge habitat for a broad spectrum of herbivorous carabid species, they might increase essential ecosystem services such as weed control. The decline in small carnivorous species, however, might reduce ecological pest control. Concerning our methodological approach, phylogenetic diversity has been proposed as a proxy for the otherwise often difficult to measure functional diversity (Cadotte et al., 2009; Webb et al., 2002). In contrast, our results support the emerging view that phylogenetic diversity alone is an insufficient measure for conservation strategies (Mazel et al., 2018b; Winter et al., 2013). In accordance with (Cadotte and Tucker, 2017), we therefore suggest relating response traits and their phylogenetic pattern to the environment to understand how communities are structured according to environmental conditions. As our work concentrated on the initial phase of flowering field establishment and a relatively short period within years, a temporal extension of this framework constitutes a promising revenue for future research.

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Supporting information: Chapter 1

Appendix

Table A1: Traits used for the functional trait analyses for all sampled species compiled from Carabids.org (Homburg et. al., 2014).

	Predator	Omnivore	Herbivore	Visual hunter	Snail hunter	Collembolan hunter	Imago hibernation	Larval hibernation	Reproduction in spring	Short winged	Winged	Dimorphic	Min size	Max size	Eye size % of head size
Abax parallelepipedus	1	0	0	0	0	0	0	0	0	1	0	0	16	22	50
Acupalpus meridianus	0	1	0	0	0	0	1	0	0	0	1	0	3	4	50
Agonum emarginatum	0	0	0	0	0	0	1	0	1	0	1	0	8	9	50
Agonum muelleri	1	0	0	0	0	0	1	0	0	0	1	0	6	9	50
Agonum sexpunctatum	1	0	0	1	0	1	1	0	0	0	1	0	6	9	50
Amara aenea	0	0	1	0	0	0	0	1	0	0	1	0	6	8	25
Amara apricaria	0	0	1	0	0	0	0	1	0	0	1	0	6	9	25
Amara aulica	0	0	1	0	0	0	1	0	0	0	1	0	10	15	25
Amara communis	0	0	1	0	0	0	1	0	0	0	1	0	5	7	25
Amara convexior	0	0	1	0	0	0	1	0	0	0	1	0	7	9	25
Amara curta	0	0	1	0	0	0	1	0	0	0	1	0	5	7	25
Amara eurynota	0	0	1	0	0	0	1	0	0	0	1	0	9	13	25
Amara familiaris	0	0	1	0	0	0	0	1	0	0	1	0	5	9	25
Amara fusca	0	0	1	0	0	0	1	0	0	0	1	0	7	9	25
Amara lunicollis	0	0	1	0	0	0	0	1	0	0	1	0	6	9	25
Amara majuscula	0	0	1	0	0	0	1	0	0	0	1	0	8	9	25
Amara montivaga	0	0	1	0	0	0	1	0	0	0	1	0	7	9	25
Amara ovata/similata	0	0	0	0	0	0	1	0	0	0	1	0	7	10	25
Amara plebeja	0	0	1	0	0	0	0	0	0	0	1	0	6	8	25
Amara proxima	0	0	1	0	0	0	1	0	0	0	1	0	7	8	25
Anchomenus dorsalis	1	0	0	0	0	0	1	0	0	0	1	0	5	8	50
Anisodactylus binotatus	0	0	1	0	0	0	1	0	1	0	0	1	9	12	25
Asaphidion flavipes	1	0	0	1	0	0	0	1	1	0	1	0	3	4	50
Bembidion lampros	1	0	0	1	0	0	1	0	1	0	0	1	2	4	50
Bembidion lunatum	1	0	0	1	0	0	1	0	1	0	0	1	5	6	50
Bembidion obtusum	1	0	0	1	0	0	1	0	1	0	1	0	2	3	50
Bembidion properans	1	0	0	1	0	0	1	0	1	0	0	1	3	4	50
Bembidion quadrimaculatum	1	0	0	1	0	0	0	0	0	0	1	0	2	3	50
Bembidion tetracolum	1	0	0	1	0	0	0	0	0	0	1	0	4	6	50
Brachinus crepitans	0	0	0	0	0	0	0	1	0	0	0	1	6	10	25
Brachinus explodens	0	0	0	0	0	0	0	1	0	0	0	1	4	7	25

Calathus fuscipes	1	0	0	0	0	0	0	1	0	0	0	1	10	14	25
Calathus melanocephalus	1	0	0	0	0	0	0	0	0	1	0	0	6	9	50
Calathus rotundicollis	1	0	0	0	0	0	0	0	0	1	0	0	8	11	25
Carabus arvensis	0	0	0	0	0	0	0	0	0	1	0	0	35	30	25
Carabus auratus	1	0	0	0	0	0	0	0	0	0	0	1	20	27	25
Carabus cancellatus	1	0	0	0	0	0	0	0	0	1	0	0	19	33	25
Carabus convexus	1	0	0	0	0	0	0	0	0	1	0	0	14	20	25
Carabus granulatus	1	0	0	0	0	0	0	0	0	0	1	0	13	30	25
Carabus nemoralis	1	0	0	0	0	0	0	0	0	0	0	1	18	28	25
Carabus violaceus	0	0	0	0	0	0	0	0	0	1	0	0	22	38	25
Clivina collaris	1	0	0	0	0	0	1	0	0	0	1	0	4	5	25
Clivina fossor	1	0	0	0	0	0	0	1	0	0	0	1	5	7	25
Cychrus caraboides	1	0	0	0	1	0	0	0	1	0	1	0	14	20	25
Diachromus germanus	0	0	1	0	0	0	1	0	1	0	1	0	7	10	25
Dyschirius globosus	1	0	0	1	0	0	0	0	0	0	0	1	2	3	50
Harpalus affinis	0	0	1	0	0	0	0	0	1	0	1	0	8	12	25
Harpalus distinguendus	0	0	1	0	0	0	1	0	1	0	1	0	7	11	25
Harpalus honestus	0	0	1	0	0	0	0	0	0	0	1	0	7	10	25
Harpalus latus	0	0	1	0	0	0	1	0	1	0	1	0	8	11	25
Harpalus luteicornis	0	0	1	0	0	0	0	1	0	0	1	0	6	7	25
Harpalus serripes	0	0	1	0	0	0	0	0	0	0	1	0	8	12	25
Harpalus rubripes	0	0	1	0	0	0	0	1	0	0	1	0	9	12	25
Harpalus tardus	0	0	1	0	0	0	1	0	0	0	1	0	6	7	25
Harpalus signaticornis	1	0	0	1	1	0	1	0	0	0	1	0	7	11	25
Leistus ferrugineus	1	0	0	1	0	1	0	0	0	0	1	0	5	8	50
Limodromus assimilis	0	0	0	0	0	0	0	0	0	0	1	0	10	12	25
Loricera pilicornis	1	0	0	1	0	1	1	0	0	0	0	1	6	8	50
Microlestes minutulus	1	0	0	0	0	1	1	0	0	0	0	1	2	3	50
Nebria brevicollis	1	0	0	1	0	0	1	0	0	0	1	0	9	14	50
Nebria salina	1	0	0	0	0	0	1	0	0	0	1	0	9	13	50
Notiophilus aestuans	1	0	0	1	0	1	1	0	0	0	1	0	4	5	50
Notiophilus biguttatus	1	0	0	1	0	1	1	0	0	0	1	0	3	6	50
Notophilus palustris	0	0	0	0	0	0	1	0	0	0	1	0	3	5	50
Ophonus ardosiacus	0	0	1	0	0	0	1	0	0	0	1	0	10	14	25
Ophonus puncticollis	0	0	1	0	0	0	1	0	1	0	1	0	6	10	25
Ophonus rupicola	0	0	1	0	0	0	1	0	1	0	1	0	7	9	25
Ophonus schaubergerianus	0	0	1	0	0	0	0	0	0	1	0	0	7	10	25
Ophonus subquadratus	0	0	1	0	0	0	0	0	0	0	0	1	6	8	25
Panagaeus bipustulatus	0	0	0	0	0	0	0	0	0	0	0	1	6	8	50
Poecilus cupreus	0	1	0	0	0	0	0	0	0	1	0	0	9	13	50
Poecilus versicolor	1	0	0	1	0	1	0	0	0	0	0	1	8	12	50
Pseudophonus rufipes	0	0	0	0	0	0	0	0	0	0	0	1	11	16	25
Pterostichus cristatus	1	0	0	0	0	0	1	0	0	0	1	0	12	18	25
Pterostichus melanarius	1	0	0	1	1	0	0	0	0	0	0	1	12	18	25
Pterostichus niger	1	0	0	0	0	0	0	0	0	0	0	1	15	22	25
Pterostichus pumilio	0	0	0	0	0	0	0	0	0	0	0	1	4	6	25
Pterostichus strenuus	1	0	0	1	0	1	0	0	0	0	0	1	5	7	25

Pterostichus vernalis	1	0	0	0	0	0	0	0	0	0	0	0	6	7	25
Stenolophus teutonus	0	1	0	0	0	0	0	0	0	0	0	0	5	7	50
Stomis pumicatus	1	0	0	0	0	0	0	0	0	0	0	0	6	8	50
Synuchus vivalis	0	0	0	0	0	0	0	0	0	0	0	0	5	9	25
Trechus obtusus	0	0	0	0	0	0	0	0	0	0	0	0	3	4	25
Trechus quadristriatus	0	0	0	0	0	0	0	0	0	0	0	0	3	4	25

Table A2: Genbank access numbers of COI sequences used in this study. The program Beauty was used to set constrains on the tree topology based on Ruiz et al. (2009) for the Tribe Sphodrini and the genera Amara and Pterostichus. As outgroups for phylogenetic analyses of the carabid dataset we used *Dysyticus harrisii* and *Geotrupes spiniger.*

Genbank Accession Number	Species	Constrain1	Constrain2
KM448743.1	*Abax parallelepipedus*	Sphodrini	
KJ966817.1	*Acupalpus meridianus*	Sphodrini	
KJ961760.1	*Agonum emarginatum*	Sphodrini	
KJ962454.1	*Agonum muelleri*	Sphodrini	
KJ961883.1	*Agonum sexpunctatum*	Sphodrini	
KJ961903.1	*Amara aenea*	Sphodrini	Amara
KJ966483.1	*Amara apricaria*	Sphodrini	Amara
KJ961751.1	*Amara aulica*	Sphodrini	Amara
KJ962110.1	*Amara communis*	Sphodrini	Amara
KM446682.1	*Amara convexior*	Sphodrini	Amara
KM446850.1	*Amara curta*	Sphodrini	Amara
KJ964361.1	*Amara eurynota*	Sphodrini	Amara
KJ963389.1	*Amara famelica*	Sphodrini	Amara
KJ962483.1	*Amara familiaris*	Sphodrini	Amara
KJ962433.1	*Amara lunicollis*	Sphodrini	Amara
KJ966578.1	*Amara majuscula*	Sphodrini	Amara
KM441035.1	*Amara montivaga*	Sphodrini	Amara
KJ962941.1	*Amara ovata*	Sphodrini	Amara
KJ961745.1	*Amara plebeja*	Sphodrini	Amara
KJ964098.1	*Anchomenus dorsalis*		
KJ961844.1	*Anisodactylus binotatus*	Sphodrini	
KJ962221.1	*Asaphidion pallipes*		
KJ963189.1	*Bembidion lampros*		
KJ963203.1	*Bembidion obtusum*		
KJ961866.1	*Bembidion properans*		
KJ962844.1	*Bembidion quadrimaculatum*		
KJ963727.1	*Bembidion tetracolum*		
KM441050.1	*Brachinus crepitans*		
KM446858.1	*Brachinus explodens*		
KJ965504.1	*Calathus ambiguus*		
KJ963720.1	*Calathus fuscipes*		
KJ962712.1	*Calathus melanocephalus*		
KM442710.1	*Calathus rotundicollis*		
KM441386.1	*Carabus arvensis*		
JQ646600.1	*Carabus auratus*		

HM909075.1	*Carabus cancellatus*		
JQ646582.1	*Carabus convexus*		
KJ962008.1	*Carabus granulatus*		
KJ962198.1	*Carabus nemoralis*		
KJ962034.1	*Carabus violaceus*		
HM909098.1	*Clivina fossor*		
KJ962991.1	*Cychrus caraboides*		
KM441477.1	*Diachromus germanus*		
KJ962700.1	*Dyschirius globosus*		
KJ962241.1	*Harpalus affinis*	Sphodrini	
KJ967303.1	*Harpalus distinguendus*	Sphodrini	
KM451044.1	*Harpalus honestus*	Sphodrini	
KJ962172.1	*Harpalus latus*	Sphodrini	
KJ964640.1	*Harpalus luteicornis*	Sphodrini	
KJ962558.1	*Harpalus rubripes*	Sphodrini	
KJ964139.1	*Harpalus rufipes*	Sphodrini	
KM448641.1	*Harpalus serripes*	Sphodrini	
KJ963464.1	*Harpalus tardus*	Sphodrini	
KJ962205.1	*Leistus ferrugineus*		
KM449803.1	*Limodromus assimilis*		
KJ962979.1	*Loricera pilicornis*		
KJ963951.1	*Microlestes minutulus*		
KJ962291.1	*Nebria brevicollis*		
KM444378.1	*Nebria salina*		
KJ966200.1	*Notiophilus aestuans*		
KJ967196.1	*Notiophilus biguttatus*		
KJ966848.1	*Notiophilus palustris*		
KM444919.1	*Ophonus ardosiacus*	Sphodrini	
KM448271.1	*Ophonus rupicola*	Sphodrini	
KM441497.1	*Ophonus schaubergerianus*	Sphodrini	
KM444298.1	*Panagaeus bipustulatus*		
KJ964542.1	*Poecilus cupreus*	Sphodrini	Pterostichus
KJ962185.1	*Poecilus versicolor*	Sphodrini	Pterostichus
KM448091.1	*Pterostichus cristatus*	Sphodrini	Pterostichus
KJ962344.1	*Pterostichus melanarius*	Sphodrini	Pterostichus
KJ961928.1	*Pterostichus niger*	Sphodrini	Pterostichus
KM443059.1	*Pterostichus pumilio*	Sphodrini	Pterostichus
KJ964557.1	*Pterostichus strenuus*	Sphodrini	Pterostichus
KJ962522.1	*Pterostichus vernalis*	Sphodrini	Pterostichus
KM452585.1	*Semiophonus signaticornis*	Sphodrini	
KM446423.1	*Stenolophus teutonus*		
KJ962339.1	*Stomis pumicatus*		
KJ963702.1	*Synuchus vivalis*	Sphodrini	
KJ963008.1	*Trechus quadristriatus*		
KU874915.1	*Dytiscus harrisii*	Outgroup	
KM446049.1	*Geotrupes spiniger*	Outgroup	

Table A3: Details about the location of all sampling sites are given by the community district and the X and Y coordinates. Land-use characterization is provided by the proportion of agriculturally used area in a 500m radius and by the crop type in 2010.

ID code	prop. agriculture	district	Point X	Point Y	previus crop 2010
c36	0.49	Halsdorf	3.497.918.649	5.642.703.718	*Hordeum vulgare*
c42	0.82	Halsdorf	3.495.520.679	5.641.069.827	*Triticum aestivum*
i45	0.68	Halsdorf	3.494.634.979	5.640.856.057	*Hordeum vulgare*
i76	0.85	Bracht	3.491.314.698	5.642.344.065	*Hordeum vulgare*
c81	0.72	Schwarzenborn	3.490.498.009	5.640.772.738	*Avena sativa*
i86	0.50	Schwarzenborn	3.489.723.239	5.640.242.336	*Brassica napus L. var. napus*
c90	0.65	Betziesdorf	3.490.652.838	5.636.219.559	*Hordeum vulgare*
i92	0.62	Schoenstadt	3.488.742.290	5.639.103.099	*Triticum aestivum*
c120	0.96	Niederasphe	3.477.326.151	5.645.694.829	*Not available*
c124	0.57	Niederasphe	3.476.103.352	5.646.289.624	*Brassica napus L. var. napus*
c125	0.77	Weihershausen	3.476.937.258	5.627.951.798	*Avena sativa*
i129	0.82	Dilschhausen	3.475.450.505	5.630.943.242	*Triticale*
i130	0.58	Friebertshausen	3.474.561.372	5.626.404.248	*Hordeum vulgare*
i137	0.94	Treisbach	3.475.231.434	5.643.181.167	*Hordeum vulgare*
i138	0.44	Frohnhausen	3.474.150.567	5.648.516.595	*Brassica napus L. var. napus*
i144	0.36	Runzhausen	3.467.990.799	5.629.102.476	*Avena sativa*
c174	0.38	Dernbach	3.464.704.759	5.627.561.811	*Triticum aestivum*
c192	0.39	Gladenbach	3.471.608.485	5.625.780.897	*Secale cereale*
c196	0.46	Gladenbach	3.471.647.472	5.627.020.364	*Hordeum vulgare*
c204	0.42	Schwabendorf	3.492.192.054	5.640.299.070	*Not available*
i212	0.77	Ernsthausen	3.497.780.834	5.639.357.985	*Avena sativa*
i226	0.41	Bellnhausen	3.480.804.192	5.618.776.957	*Triticum aestivum*

Table A4: Annual temperature maximum and minimum in °C for the year 2011 and 2012 as obtained by the weather station closest to the study sites (Cölbe) and compiled from the database on wetterkontor.de

	max	min	l/m²
2011	32.8	-11	559
2012	34.4	-18	662

Table A5: Mean temperature and precipitation for the different seasons in 2011 and 2012 as obtained by the weather station closest to the study sites (Cölbe) and compiled from the database on wetterkontor.de. Deviations of the mean for a 30 year period are given in the column "dev".

	temperatur		percipitation	
	mean	dev	mean	dev
summer 2011	17,3	-0,1	231,6	124%
spring 2011	10,7	+1,6	47,3	29%
winter 2010/2011	0,1	-1,2	161	88%
sommer 2012	17,3	-0,1	225	120%
spring 2012	10,3	+1,2	137,4	85%
winter 2011/2012	2	+0,7	221,8	122%

Table A6.: Minimum, maximum and mean temperature and precipitation for each day and the whole period when pitfall traps were active.

	min °C	max °C	mean °C	perc. l/m^2
05.06.2011	15	29	20.30	3.5
06.06.2011	16.3	27.5	19.40	0.8
07.06.2011	16.1	25.8	20.10	10
08.06.2011	8.2	18	15.20	0.5
09.06.2011	6.5	20	14.10	0
10.06.2011	11.2	20.4	15.40	1.2
11.06.2011	8.6	20.3	14.90	0.1
12.06.2011	6.4	21.5	14.80	0
13.06.2011	9.2	22	16.30	0
14.06.2011	12.9	27.2	19.20	0
15.06.2011	10.2	25.6	18.10	0.1
16.06.2011	12.5	25.2	17.60	3.8
17.06.2011	7.1	21.7	16.40	1.1
18.06.2011	11.8	19.6	16.10	0.1
19.06.2011	11.3	17.6	13.60	0.5
26.06.2012	8.3	21.4	14.9	0
27.06.2012	8.5	22.8	16.5	0.7
28.06.2012	14.3	27.6	21.2	2.4
29.06.2012	16.4	28	21.1	3.8
30.06.2012	14.6	27.1	20.9	0.3
01.07.2012	11.1	21.1	18	1
02.07.2012	10.1	18.2	14.9	1.2
03.07.2012	13.1	25.8	19.1	0
04.07.2012	11	28	20.3	0
05.07.2012	15.3	27.4	20.6	6.4
06.07.2012	14.1	24	18.8	0.8
07.07.2012	12.9	26	19.3	0.2
08.07.2012	12.2	22.3	17.1	8
09.07.2012	14.5	23.2	18	5.4
10.07.2012	12.8	23.4	17	7.7
period 2011	**6.40**	**29.00**	**16.77**	**1.45**
period 2012	**8.30**	**28.00**	**18.51**	**2.53**

Fig A1: Frequencies of body sizes before conversion in 2011 and after conversion to flowering fields in 2012 (skewness: 2011 = 0.84, 2012 = 1.21; kurtosis 2011 = 2.463 2012 = 3.103).

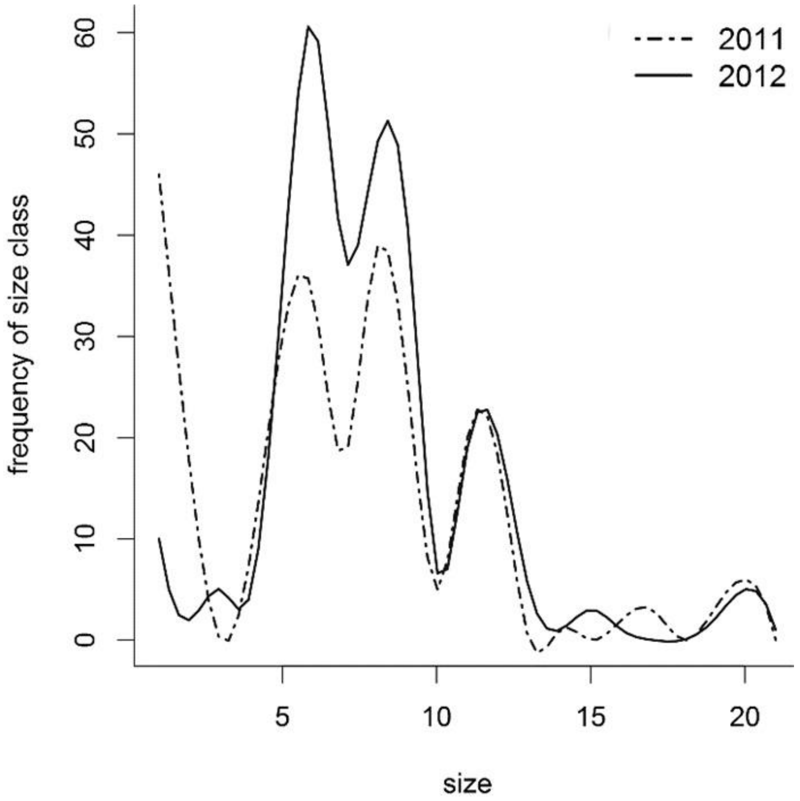
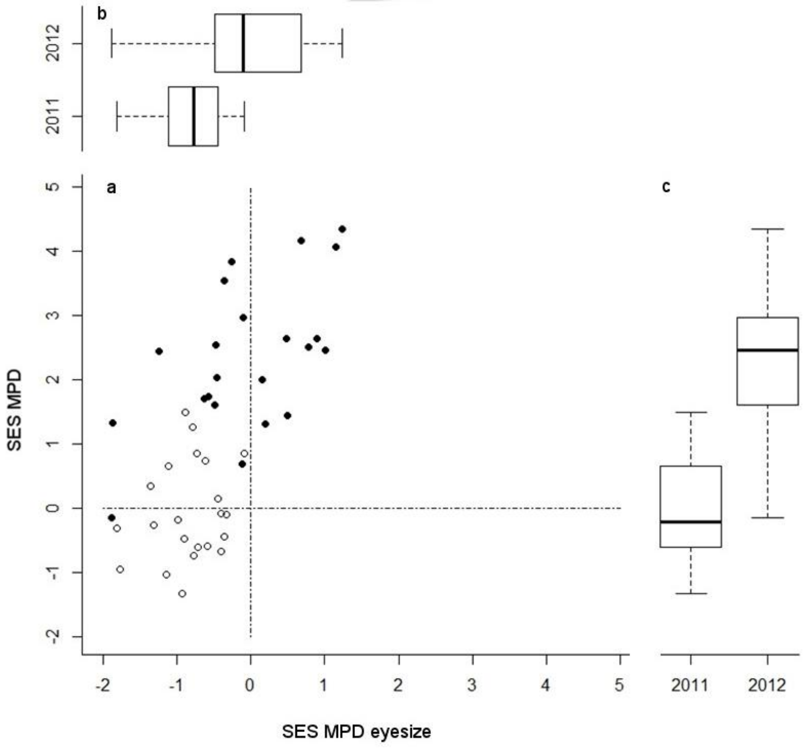


Fig A2: Relation between the similarity in eye size (SES MPD eyesize) and phylogenic similarity (sesMPD) (a). Both eye size similarity SES MPDsize (b) and phylogenetic similarity sesMPD (c) were clustered after conversion (positive values) compared to randomized null models.



Chapter 2

Convergent evolution of specialised generalists: implications for phylogenetic and functional diversity of carabid feeding groups

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Short title: Convergent evolution of specialised generalists

Abstract

1. Closely related species are often assumed to be functionally similar. Phylogenetic information is thus widely used to infer functional diversity and assembly of communities. In contrast, evolutionary processes generating functional similarity of phylogenetically distinct taxa are rarely addressed in this context.
2. To investigate the impact of convergent evolution on functional diversity (FD) and phylogenetic diversity (PD), we reconstructed the phylogenetic structure of carabid trophic groups. We then analysed the mandible shapes using geometric morphometrics to link specialisation in functional morphology with feeding specialisation among herbivores, generalist carnivores, and specialised consumers of Collembola.
3. Our results show that carabid feeding groups are paraphyletic. Herbivory evolved at least twice and specialisation to Collembola predation at least three times. Species within feeding groups share a remarkably similar mandible morphology, which evolved convergently. While specialised mandibles of herbivores and collembolan specialists represent an adaptation to their main food source, the particular mandible morphologies do not necessarily reflect the degree of food specialisation within feeding groups. Only a few species with a specialised herbivorous mandible may occasionally feed on animals, but the range of specific food resources in generalist carnivore species is large, despite an almost identical mandible shape.
4. Thus, convergent evolution in specialised feeding groups reverses the relationship between PD and functional similarity compared to generalist carnivores. We conclude that phylogenetic relationship is a poor proxy of FD in carabids. Moreover, the inconsistencies between relatedness, morphological adaptation and ecological function requires caution in the characterisation of functional groups. Rather than assuming general relationships between PD and FD, we suggest integrating the analysis of evolutionary processes into functional community analyses.

Keywords: functional groups, functional morphology, geometric morphometrics, ecological specialisation, evolutionary ecology, morphological adaptation.

Introduction

Convergent evolution is a key issue of evolutionary biology and has important implications for the development of ecological concepts (Harmon et al., 2005). It can shape communities (Losos, 1992; Melville et al., 2006; Webb et al., 2002), adaptive radiation (Muschick et al., 2012) and whole ecosystems (Losos et al., 1998; Mahler et al., 2013). Consequently, taking into account convergent evolution as a key mechanism that modulates biodiversity is vital for understanding ecological patterns and processes. For example, species with similar resource use (i.e. feeding groups or guilds) evolved multiple times in different communities, resulting in a remarkable resemblance of trophic patterns (Blondel, 2003). However, the implications of convergent evolution are barely addressed in community ecology. This is surprising, considering the increasing relevance of phylogenetic distance as a proxy for ecological differences in community analyses (Flynn et al., 2011; Kraft et al., 2015). Since it is often assumed that phylogenetic diversity (PD) correlates with functional diversity (FD), PD is often used for assessing community assembly processes and ecological functioning (Cadotte et al., 2009; Cavender-Bares et al., 2009; Srivastava et al., 2012a). However, the relationship between PD and FD remains controversial and strongly depends on trait selection and taxonomic scale (Cadotte et al., 2017; Mazel et al., 2018a; Tucker et al., 2018; Wilcox et al., 2018).

We focus on two topics that challenge the hypothesis of a general relationship between FD and PD. First, we examine the assumption that this relationship is offset by convergent evolution only in distantly related species (cf. (Cadotte et al., 2017). Second, we address the question whether the assignment to functional groups without considering adaptation, specialisation and phylogenetic relationships can bias the conclusions drawn about community structure and assembly. Members of functional groups that are predefined based on coarse taxonomic criteria can have a high overlap in resource use (e.g. guilds *in sensu stricto*, see Simberloff and Dayan 1991; Blondel 2003) or little to no overlap (e.g. generalist carnivores or predators). The degree of resource use overlap thus determines their ecological similarity (or ‘functionality’) and their reaction to environmental changes.

The use of specific resources requires a specific functional morphology, which should reflect the degree of specialization (Ricklefs 2012; Dehling et al. 2016). Consequently, convergence in feeding habits requires the independent evolution of morphological adaptations. Our study builds upon the necessity to understand evolutionary processes and morphological adaptations before making general assumptions on the relationship between FD and PD. Carabid beetles are well suited for this purpose, because they comprise several functional groups (here: feeding groups) with different implications for community assembly

(Cole et al., 2002b; Ribera et al., 1999; Schirmel et al., 2016). For example, herbivorous species can either be specialised on certain seeds or feed on a wide range of seeds (Honek et al., 2007b), but occasionally even consume insects (Talarico et al., 2016). Some of these preferences are restricted to specific taxa, e.g. certain *Harpalus* and *Amara* species are strongly specialised in seeds (Hengeveld, 1979; Honek et al., 2007b). Similarly, while several carnivorous carabids are specialised to prey on collembolans, annelids or molluscs (Kotze et al., 2011), many generalists occasionally also feed on these taxa (Roubinet et al., 2018). Carabid feeding groups thus cover a wide range of specialisation levels. In addition, herbivorous species contrast to carnivorous species in having a high overlap in resource use. They can therefore be considered as guilds (Blondel, 2003) exposed to strong interspecific competition, while competition among carnivorous carabids is likely to be low, due to low overlap in resource use.

The analysis of carabid communities is hampered by the fact that the assignment of many species to feeding groups is still based on potentially misleading laboratory observations or a very limited set of field data. This might lead to a serious misinterpretation of the processes driving carabid community assembly. A profound understanding of the relationship between mandible morphology and its adaptive value for exploiting certain food sources could thus be very helpful to overcome this gap in knowledge (Acorn & Ball, 1991; Evans & Forsythe, 1985, 2009; Forsythe, 1983). So far, however, neither the suitability of mandible morphology as a proxy for ‘feeding groups’ nor the associated phylogenetic restrictions have been sufficiently investigated. The same applies to the question of whether mandible morphology reflects the degree of trophic specialisation in carabids.

By combining morphological measurements with functional and phylogenetic parameters, we investigate the influence of convergent evolution on the relationship between PD and FD. Specifically, we hypothesise that (1) feeding groups of carabids originate from convergent evolutionary lines, resulting in a high phylogenetic diversity, and (2) mandible morphology evolved convergently as an adaptation to the main food source.

Methods

Selection of species and definition of feeding groups

We selected 32 species of carabids, which can be assigned by their main food resource to one of four feeding groups (Table 1): herbivores, generalist carnivores, collembolan specialists and one genus (*Carabus*) of large carnivores (Fawki et al., 2003; Freude et al., 2004; Hengeveld, 1980; Homburg et al., 2014; Honek et al., 2003b; Turin et al., 2003). To analyse the degree of convergent evolution within these groups, we include at least the two species with different degrees of specialisation to the same feeding group. We follow the nomenclature and taxonomy of (Freude et al., 2004).

Herbivorous species were selected from the four genera *Ophonus*, *Anisodactylus*, *Harpalus,* and *Amara* of the two tribes Harpalini and Zabrini, which are known to consist of seed-feeding carabids (Talarico et al., 2016). We took special care to include species with a different degree of specialisation, from granivorous specialists (*Ophonus* spp.) to generalist species (*Harpalus rufipes, Amara similata*), to investigate whether morphological adaptations are reflected in the degree of specialisation. We included species with different body sizes (e.g. *Amara aenea* with a max. size of 8.5 mm and *Amara aulica* with 15 mm), since this parameter can constrain the type of seeds that are accessible as a food resource.

Three genera of collembolan specialists (*Loricera*, *Leistus*, *Notiophilus*) are each represented by one species per genus. Members of all three genera are highly specialised and evolved various morphological adaptations to capture collembolans (Bauer, 1981, 1985; Freude et al., 2004; Yin et al., 2017).

Generalist carnivorous species were selected from several tribes (Pterostichini, Bembidini, and Nebrini). *Nebria brevicollis* (a generalist carnivore, Šerić Jeleska, Franjević, Jeleska, & Symondson, 2014) belongs to the same tribe as *Leistus* (Nebrini). *Poecilus cupreus* is often categorised as an omnivorous species that occasionally consumes seeds, whereas its sister species *P. versicolor* is described as a carnivorous generalist (Homburg et al., 2014). *Pterostichus melanarius* is a generalist predator (McKemey et al., 2003), also known as an effective snail predator occasionally consuming seeds (Kulkarni et al., 2015).

Carabus species feed on large prey with a preference for snails and earthworms but also insects and other arthropods (Turin et al., 2003). This genus was selected to allow comparison against medium and small generalist carnivores such as *Pterostichus melanarius*, which also feed on annelids and snails.

Phylogenetic reconstruction

Gene sequences for phylogenetic reconstruction were obtained from GenBank for 18s ribosomal RNA, 28s ribosomal RNA, cytochrome oxidase subunit 1 (COI) and elongation factor 1 alpha (EF1a). Sequence length varied across specimens between 647 bp and 4665 bp (Table 1). COI was available for all but two species. For most genera, at least one species was included with COI, 18s and 28s. EF1a was available for at least one species per tribe. The beetles *Trachypachus holmbergi* (Trachpachyidae) and *Noterus clavicornis* (Noteridae) served as outgroup. Phylogenetic analyses included two additional species of the genus *Leistus*, in order to increase the phylogenetic resolution in the tribe Nebrini, though specimens for morphological analyses were not available for these species. For *Notiophilus palustris* only COI sequences are available on GenBank. Therefore, we included *Notiophilus semiopacus* in the phylogenetic analyses and enforced monophyly for these genera. Each gene sequence was aligned using the muscle algorithm in MEGA version 6 (Tamura et al., 2013). Genes were assembled using the program SequenceMatrix 1.8 (Vaidya et al., 2011). We used jModeltest 2.1.5 (Guindon & Gascuel, 2003; Posada, 2008) to determine the best nucleotide substitution model for each gene. For all genes, the general time reversible model (GTR) or a close derivative was determined as the best-suited explanation for DNA evolution. Therefore, we chose the GTR+Γ+I model for further analyses. Based on this DNA model, we reconstructed ultrametric phylogenetic trees using the software BEAST v1.8 (Drummond et al., 2012) based on five independent runs of each 10,000,000 Markov Chain Monte Carlo (MCMC) generations under a strict molecular clock model and based on a Yule speciation process. The MCMC runs were examined using Tracer 1.7.1 (Rambaut et al., 2018) to ensure an adequate effective sample size (ESS, >150) and convergence of the MCMC.

Table 1. DNA sequences used for phylogenetic reconstruction in this study. Numbers in brackets indicate number of indels (in.).

Taxon	Total length	18s	28s	COI	EF1a
Abax parallelepipedus	3875 bp	2082 (176 in.)	1146 (128 in.)	647	
Agonum muelleri	4405 bp	2082 (186 in.)	971 (122 in.)	646 (17 'N')	706 (173 'N', 1 in.)
Amara aenea	3759 bp	2082 (202 in.)	971 (100 in.)		706 (1 in.)
Amara apricaria	3852 bp	2082 (196 in.)	1123 (136 in.)	647	
Amara aulica	1345 bp	476 (115 in.)	222 (20 in.)	647	
Amara ovata	647 bp			647	
Amara plebeja	647 bp			647	
Amara similata	1343 bp	474 (79 in.)	222 (22 in.)	647	
Anisodactylus binotatus	2951 bp	2082 (201 in.)	222 (23 in.)	647	
Bembidion tetracolum	3844 bp	2063 (131 in.)	1134 (175 in.)	647	
Calathus fuscipes	2082 bp	2082 (201 in.)			
Carabus cancellatus	3857 bp	2082 (184 in.)	1128 (188 in.)	647	
Carabus nemoralis	3906 bp	2082 (185 in.)	1177 (187 in.)	647	
Carabus violaceus	1774 bp		1127 (182 in.)	647	
Harpalus affinis	4380 bp	2082 (201 in.)	945 (136 in.)	647	706 (2 in.)
Harpalus latus	647 bp			647	
Harpalus luteicornis	647 bp			647	

Harpalus rubripes	1343 bp	474 (75 in.)	222 (23 in.)	647	
Harpalus rufipes	2798 bp	474 (75 in.)	971 (140 in.)	647	706 (1 in.)
Leistus ferrugineus	2728 bp	2081 (147 in.)		647	
Leistus rufomarginatus	647 bp			647	
Leistus spinibarbis	647 bp			647	
Loricera pilicornis	3606 bp	2041 (165 in.)	222 (34 in.)	637	706 (1 in.)
Nebria brevicollis	3817 bp	2041 (131 in.)	1129 (101 in.)	647	
Noterus clavicornis	3837 bp	2076 (1 'N', 160 in.)	1114 (213 in.)	647	
Notiophilus palustris	647 bp			647	
Notiophilus semiopacus	3216 bp	2082 (172 in.)	1134 (147 in.)		
Ophonus ardosiacus	647 bp			647 (1 'N')	
Ophonus azureus	647 bp			647	
Ophonus laticollis	2729 bp	2082 (201 in.)		647	
Poecilus cupreus	1879 bp	1010 (112 in.)	222 (24 in.)	647	
Poecilus versicolor	2803 bp	996 (111 in.)	1160 (114 in.)	647	
Pterostichus melanarius	4728 bp	2082 (187 in.)	1293 (128 in.)	647	706 (1 in.)
Synuchus vivalis	4406 bp	2082 (202 in.)	971 (136 in.)	647	706 (15 'N', 1 in.)
Trachypachus holmbergi	4612 bp	2082 (83 in.)	1177 (159 in.)	647	706 (1 in.)

bp = base pairs; COI = cytochrome oxidase subunit 1; EF1a = elongation factor 1 alpha

Morphological analyses

Morphological adaptations of the different feeding groups were assessed based on mandible morphology. Specimen for morphological analysis are part of the collection at the department of animal ecology at the JLU and were collected in Hesse in 2011-2012. All specimen, including the mandibles, remains in the collection after dissection. First, the mandibles of three individuals per species were photographed after removing them from the head capsule using a digital microscope (Keyence VHX-2000, KEYENCE Corp., Osaka, Japan). Then, nine landmarks (LM) were set on homologous structures occurring on the ventral site of the left mandible of all species by means of the program TPSDig 1.4 (Rohlf, 2004) (Fig. 1). Mandible outline and ridges/grooves were characterised as eight curves using 205 semilandmarks (SL). Each curve was placed between two LM. Nomenclature for the mandibular morphology follows (Acorn & Ball, 1991). LM 1 was set at the tip of the incisor and LM 2 at the tip of the terebral tooth. The mandible outline in between was connected with a curve of 30 SL. The ventral groove was delimited by LM 3 and LM 4 and connected by a curve of 10 SL. The inferior retinacular ridge was characterised by a curve of 30 SL between LM 1 and LM 9. LM 5 and LM 6 delimited the primary mandibular joint; its outline was characterised by a curve of 20 SL. LM 7 and LM 8 are connected by a curve of five SL. The lateral outline of the mandible was defined by a curve of 30 SL connecting LM 1 and LM 8. The posterior outline of the mandible was defined by a curve of 60 SL between LM 4 and LM 7.

The R package 'geomorph' 3.1.0 (Adams et al., 2016; Adams & Otárola-Castillo, 2013) was used to perform a Generalised Procrustes Analysis (F. James Rohlf, 1999). Based on the GPA coordinates, an ANOVA was performed to test for statistical differences between the four feeding groups. SL were superimposed based on the minimum bending energy criterion (Bookstein, 1997). Generalised Procrustes coordinates were visualised with a principal component analysis (PCA) including the reconstruction of the phylomorphospace. The mean shape of the three individuals per species was calculated and the phylogenetic tree was superimposed on the first and the second principal component of the morphospace to construct a phylomorphospace. Outgroups and species from the phylogenetic analyses not represented in the morphological dataset were excluded. To eliminate a potential bias caused by the highly derived mandible of the genus *Carabus*, we conducted a second analysis without this group.

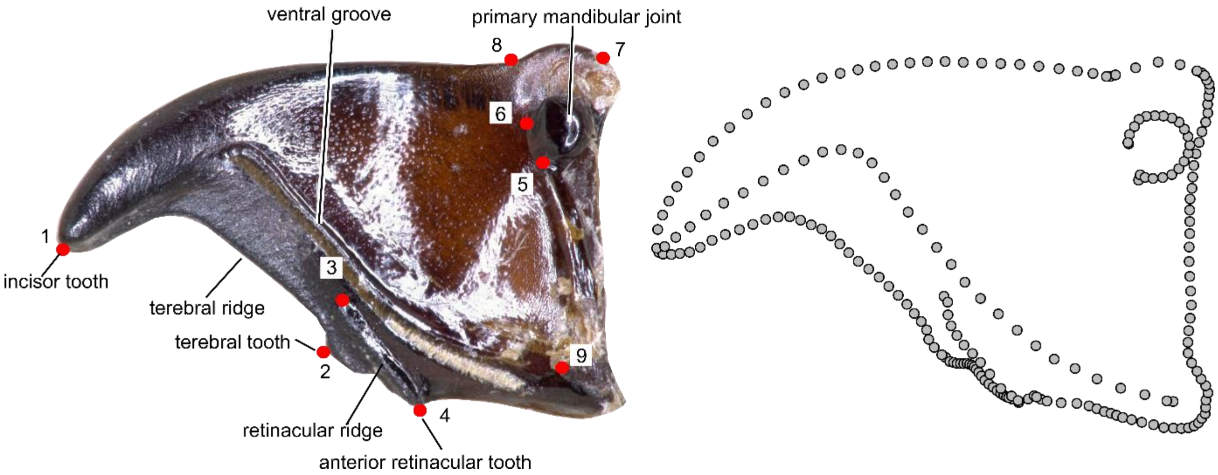

Fig. 1. Position of the nine landmarks and 205 semilandmarks along eight curves used to characterise the mandible shape. The example shows the ventral side of the left mandible of *Harpalus rufipes*. The right image displays the position of the SL after sliding.

Results

Phylogenetic relationship within feeding groups

We found strong phylogenetic structure within the feeding groups. According to the reconstructed phylogeny, herbivores, generalist carnivores and collembolan specialists are not monophyletic groups (Fig. 2). Herbivory evolved independently at least twice and specialisation to collembolan feeding three times. The two clades of herbivores as well as the three collembolan specialist clades each form monophyletic groups with generalist carnivores which supports our hypothesis. The herbivorous tribe Zabrini and the generalist carnivore tribe Pterostichini are monophyletic. The other herbivorous tribe Harpalini is a sister group to the monophyletic Zabrini-Pterostichini clade. Due to our limited data and sampling, uncertainties remain as to the phylogenetic position of some groups. However, our results are consistent with other studies (see below) and the phylogenetic tree is well supported. Only, our phylogenetic reconstruction placed the generalist carnivore *Abax parallelepipedus* as a sister taxon to all Harpalinae. This position is questionable since the genus is well known to be a member of the Pterostichini (Li et al., 2020) (cf. Li et. al. 2020) and might be a result of the very limited data, with only one sequence available for this species. Collembolan specialists belong to three tribes, each forming monophyletic groups with other feeding groups: Loricerini, Nebrini and Notiophilini. Nebrini. Carabini are opposed to all other taxa. Nebrini include *Leistus* and *Nebria* and are a sister tribe to Carabini and Notiophilini. The herbivorous species of the tribes Zabrini and Harpalini form clades with the generalist carnivorous tribes Pterostichini and Sphodrini, respectively. *Loricera* represents a clade closely related to the Harpalinae (López-López & Vogler, 2017). The monophyly of Pterostichini and Zabrini and its placement as a sister taxon to Harpalini is consistent with the finding of other studies and supports the convergence of the herbivorous tribes (Ruiz et al., 2009a). We can confirm the collembolan specialist genus *Leistus* as a member of the otherwise generalist carnivorous tribe Nebrini (Freude et al. 2004). The collembolan specialists *Loricera* spp. belong in a discrete tribe, which is probably closely related to Harpalinae (compare to López-López and Vogler 2017).

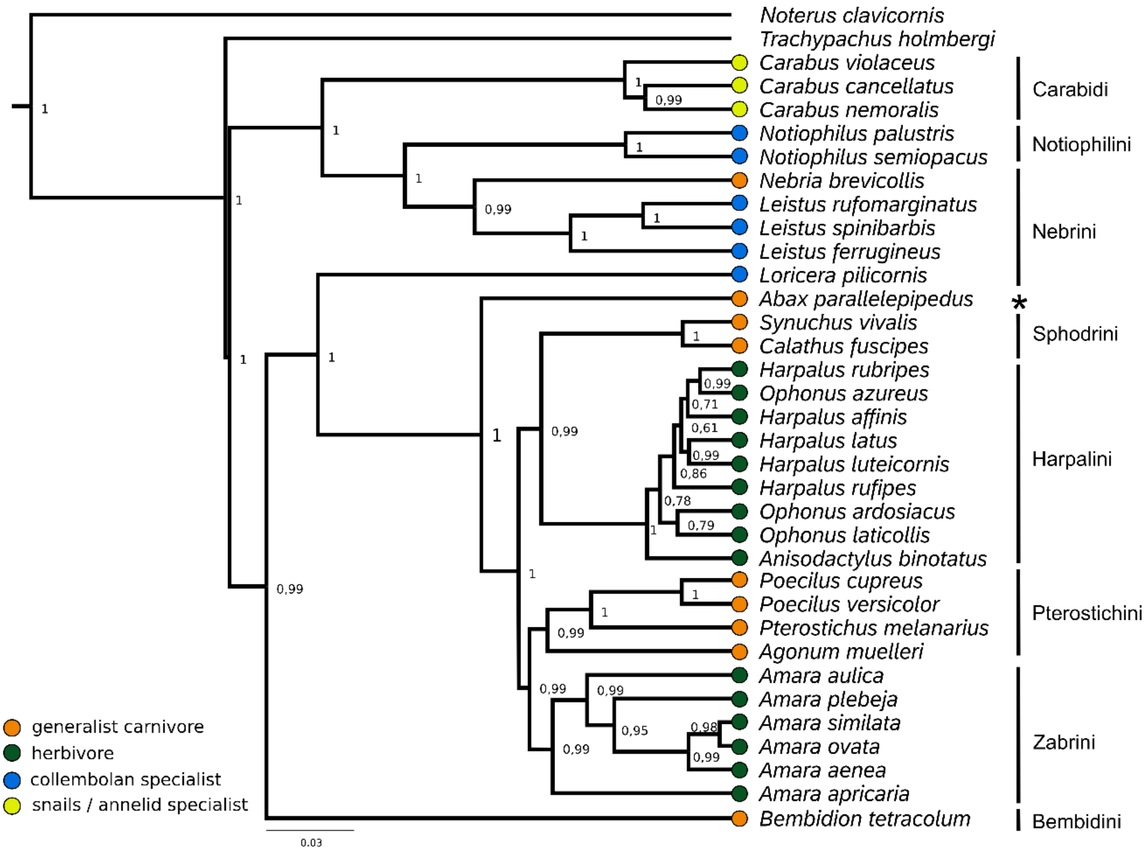

Fig. 2. Ultrametric phylogenetic tree based on 18s, 28s, COI, and ef1. Tribes are indicated on the right. Posterior probabilities are given at each node. The asterisks highlight that *Abax parallelepipedus* is generally considered to belong to the tribe Pterostichini

Convergent evolution in functional morphology

The four feeding groups (herbivores, generalist predators, collembolan specialists and species of the genus *Carabus*) can be identified and grouped according to their mandible morphology (ANOVA $p < 0.001$, Fig. 3). Mollusc-annelid specialists are separated from all other morphotypes (PCA, see Appendix 1). Since this strong effect masked obvious differences among other groups, further analyses were confined to the remaining feeding groups (Fig. 3). The first two PCs explain 57.4 % of the total variance (PC 1: 32.9%, PC 2: 24.5%; see Supplementary Material for detailed results). The phylomorphospace analysis based on the mean PC scores of the three individuals per species revealed no corresponding phylogenetic clustering, but indicate convergence of morphotypes (Fig. 4). PC 1 separates herbivorous species from all other feeding groups (Fig. 3, Fig. 4). Adaptation to herbivory obviously selects for very stout mandibles with a rectangular proximal base and much bigger primary mandibular joints (Fig. 4) compared to the other two groups, likely to enable the shredding of tough plant material and seeds. The terebral tooth, retinacular tooth, retinacular ridge and the ventral groove form wide ridges and broad structures probably as an adaptation towards seed consumption (Fig. 2, cf. Acorn & Ball, 1991). The phylomorphospace (Fig. 4) highlights the strong selection pressure favouring the convergent evolution of this specific mandible shape as an adaptation to herbivory. Herbivorous species show a greater within- than between-species variation, so their mandible morphology cannot be assigned to a specific species. Conversely, at the species or at least the genus level, the collembolan specialists and most generalist carnivores form discrete groups in the morphospace (Fig. 3). The tooth structure in the posterior area of the carnivore mandible is more delicate compared to the herbivore mandibles. Moreover, the incisor of carnivorous species is more strongly bent and has a more articulated cutting edge. PC 2 separates collembolan specialists from generalist carnivores (Fig. 3, Fig. 4). The most prominent feature separating collembolan specialists from the other groups is the position and much smaller size of the primary mandibular joint, which connects the mandible to the head capsule (Fig. 1, Fig. 3). Further, the cutting edge formed by the ventral groove of the pointy and delicate incisor of collembolan specialists is hardly visible. Herbivores and collembolan specialists each evolved morphologically highly specialised mandibles, clearly separating feeding groups. The stout mandibles of both tribes show many morphological adaptations towards seed predation (Acorn & Ball, 1991). Additionally to the findings of Acorn & Ball (1991), we point out the enlargement of the mandibular joint and the more ridge-like structure of the posterior teeth as an adaptation towards seed consumption. The latter probably serves a more grinding function than the more delicate structures with many single teeth in generalist carnivores.

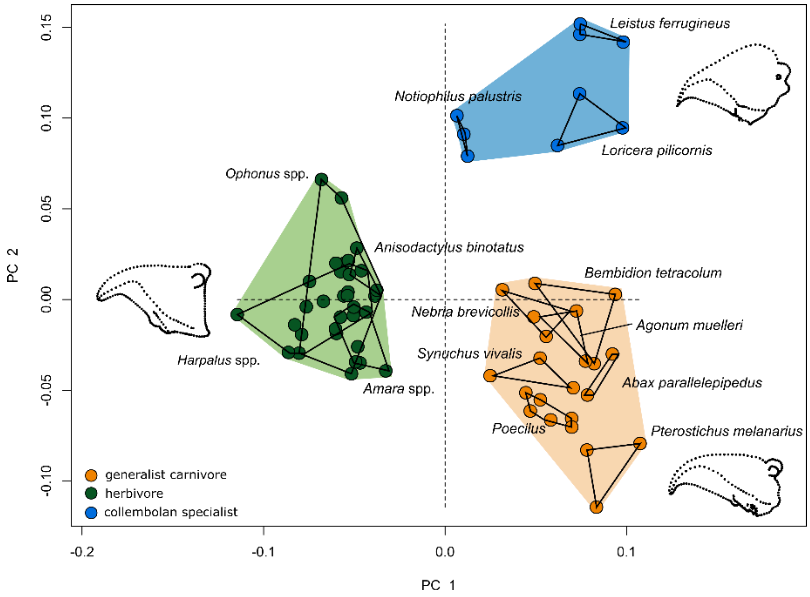

Fig. 3. Morphospace of herbivorous (green), generalist carnivorous (orange), and collembolan specialists (blue). PC1: 33%, PC: 25% of the total variance. Each species is represented by three individuals. The three groups differed significantly in mandible shape based on the GPA coordinates (ANOVA $p < .001$).

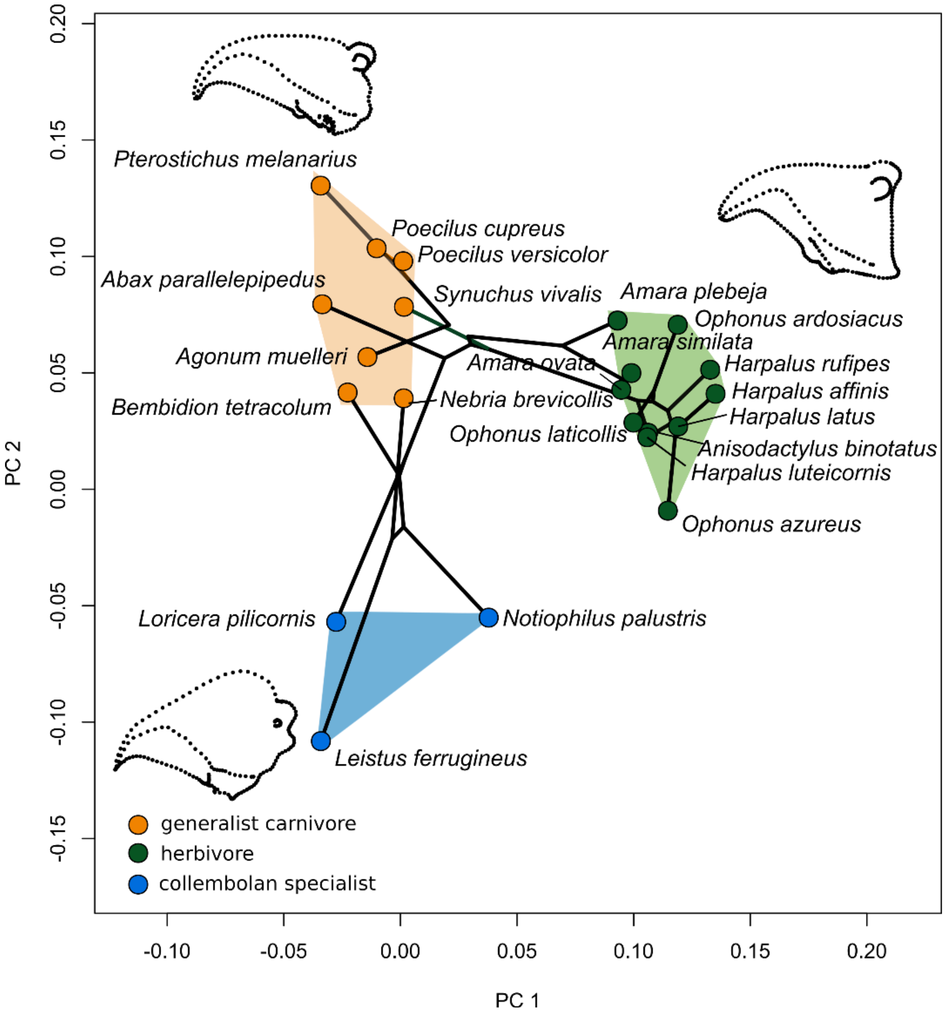

Fig. 4. Phylomorphospace of all species excluding the mollusc specialists (*Carabus*), showing the convergent pattern of phylogenetic relationships among feeding groups

Discussion

Convergent evolution of carabids resulted in phylogenetically diverse feeding groups with remarkably similar adaptations in mandible morphology. Our study demonstrates that mandible shape is a good predictor for the primary food source in specialised feeding groups such as herbivores and collembolan specialists. It also shows that there is no general relationship between functional similarity and phylogenetic diversity (PD). The relationship is even reversed between specialist feeding groups such as herbivores and collembolan specialists compared to generalist carnivores.

Convergent evolution resulted in high PD in the herbivorous and collembolan specialist feeding groups. Generalist carnivores are comprised of multiple unrelated groups and, accordingly, also phylogenetically highly diverse. Thus, PD per se is a poor predictor of functional diversity (FD) in carabid communities and might not be affected at all by community responses of feeding groups to environmental change (Baulechner et al., 2019).

We found evidence that convergence can cause a discrepancy between phylogenetic and functional divergence not just at broad taxonomic scales (Cadotte et al., 2017) but even within a family at the genus level. Therefore, in line with other recent studies (Mazel et al., 2018a), we find that PD does not reliably capture FD and should not be used alone to assess community assembly or functionality. In particular, assembly processes such as competition should not be derived from single measures such as PD.

Our results indicate strong selection pressures for the mandible shape to access specific food resources. However, mandible specialisation does not necessarily reflect the degree of specialisation and the overlap in resource use. There are many specialists that exclusively feed on seeds, such as the genus *Ophonus* or some *Amara* species, which are even specialised on the seeds of specific plant species (Honek et al., 2003b). Despite the overall similarity in specialised morphology, these groups contain many species with a generalist diet. *Harpalus rufipes,* for example, preys on a variety of seeds but also on slugs, spiders and insects. Moreover, prey spectrum and the degree of specialisation vary across seasons (El-Danasoury et al., 2017; Loughridge & Luff, 1983; Roubinet et al., 2018). *Amara similata* is known to feed on aphids, but granivory plays a vital role in its diet (Jorgensen & Toft, 1997). Yet mandible morphology does not reflect the differences in the degree of specialisation. A comparable inconsistency in phenotypic and ecological specialisation, which is termed Liem's paradox, has also been documented for other taxa such as cichlid fish (Binning et al., 2009; Liem, 1980). Morphological specialisation of generalist species might be a competitive advantage when other food sources are scarce (Robinson & Wilson, 1998). The morphological specialisations in herbivorous species can be sustained via natural selection as an adaptation as "specialised generalists" given that the access to this resource is ecologically and evolutionarily crucial. Accordingly, the herbivore mandible shape is a good indicator for seeds as a primary food source and supports the classification, despite the occasional carnivorous behaviour of some species.

On the other hand, many generalist carnivores occasionally feed on seeds or collembolans and are therefore often considered omnivorous in community analyses. For example, *Poecilus cupreus* is widely considered omnivorous and *P. versicolor* carnivorous ((Bargmann, Heegaard, Hatteland, Chipperfield, & Grytnes, 2016), (Homburg et al., 2014)), although *P. cupreus* may eat seeds under starvation in laboratory conditions (own unpubl. observation). A functional distinction between the two species, based solely on single observations (Homburg et al., 2014; Lindroth, 1986), may bias analytical results regarding community assembly. As we could not find any adaptation towards seed consumption in the mandible morphology of carnivorous generalists, and considering the strong adaptation to seed predation we found in herbivorous species, the ecological relevance of seed consumption in generalist carnivores is questionable. Since mandibles of generalist carnivores are not robust enough to handle seeds as a primary food source, they would get severely battered over time (Wallin, 1988). In addition, there are no studies providing evidence that generalist carnivores rely on seeds under natural conditions or have any influence on plant occurrence by seed predation. Jointly categorizing carnivores that occasionally ingest seeds and highly adapted herbivores that regularly consume large amounts of seeds as "omnivores" results in an inconsistent feeding group.

Thus, feeding groups of carabids are too inconsistent to be useful in the analysis of ecological communities. Overlap in resource use is high among herbivores but very low (or even non-existent) among generalist carnivores. Moreover, herbivores might also react differently to different ecological conditions depending on their degree of specialisation. Despite both being herbivorous, for example, Zabrini and Harpalini strongly differ in the types of seeds ingested, due to strong differences in body size (Honek et al., 2007b). We therefore suggest avoiding the term “guild” to classify feeding groups in carabids, a term that has often been used inconsistently in the past anyway (Simberloff & Dayan, 1991). This is supported by the poor evidence of competition for food sources (Kotze et al., 2011b) in carabids and the fact that a generalist carnivorous species might occupy different trophic niches (Zalewski et al., 2014). Only collembolan specialists and some herbivores might form guilds in the strict sense, because of the strong similarity in their food spectra. This is reflected in their highly specialised mandibles and the associated high degree of different morphological adaptations, such as setae traps to catch collembolans (Bauer, 1985; Yin et al., 2017).

The high diversity in resource use also becomes evident through the different number of species occurring in the individual feeding groups. In fact, the degree of specialisation and species richness are negatively related to each other. With more than 350 species, generalist carnivores constitute the most species-rich feeding group in central Europe. The herbivorous tribes encompass approximately 55 species and occur in almost every central European habitat. Conversely, the diversity of collembolan specialists is low (Barševskis, 2007; Freude et al., 2004).

Conclusion

The repeated convergent evolution of feeding groups obscures a clear relationship between relatedness and ecological functioning regarding the food resource. Equally, the range of specialist species to generalists cannot be explained by phylogenetic relation or morphological adaptation but through convergent evolution. Specialisation and generalism can be driven by competition and can have evolutionary (niche evolution) and ecological (e.g. competitive exclusion) consequences (Poisot et al., 2011). Therefore, community assembly processes such as competitive exclusion cannot be inferred by phylogenetic pattern alone. The same accounts for other assembly processes such as environmental filters, which might select closely related or convergently evolved distantly related species.

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Conflict of interest
The authors report no competing interest.

Data availability statement
Mandible landmarks and genebank accession numbers for phylogenetic reconstructions are provided in the supporting information.

Author contribution
D.B. conceived the ideas and designed the methodology, collected and analysed the data and took the lead in writing the manuscript. T.N. contributed critically to the analyses and the writing of the manuscript. V.W. and F.J. contributed critically to developing the idea and to the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting information: Chapter 2

The clear separation of Carabus species from all remaining groups masked obvious differences among other groups. Therefore, further analyses were confined to the remaining feeding groups.

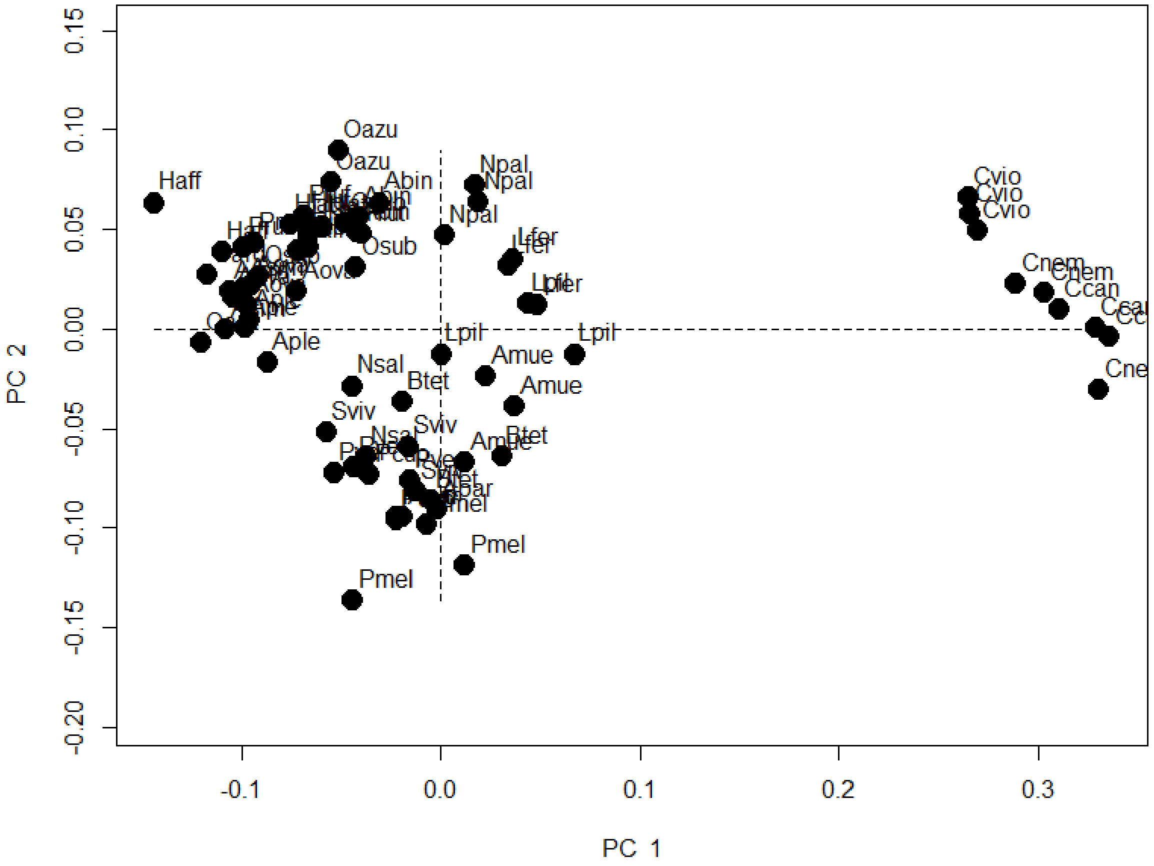

Fig. 1. Plot of the tangent space of the mandible of all investigated species. The genus *Carabus* is clearly separate from all other species on PC 1.

Chapter 3

Carabid adaptation to a collembolan diet: hunting efficiency and nutritional value

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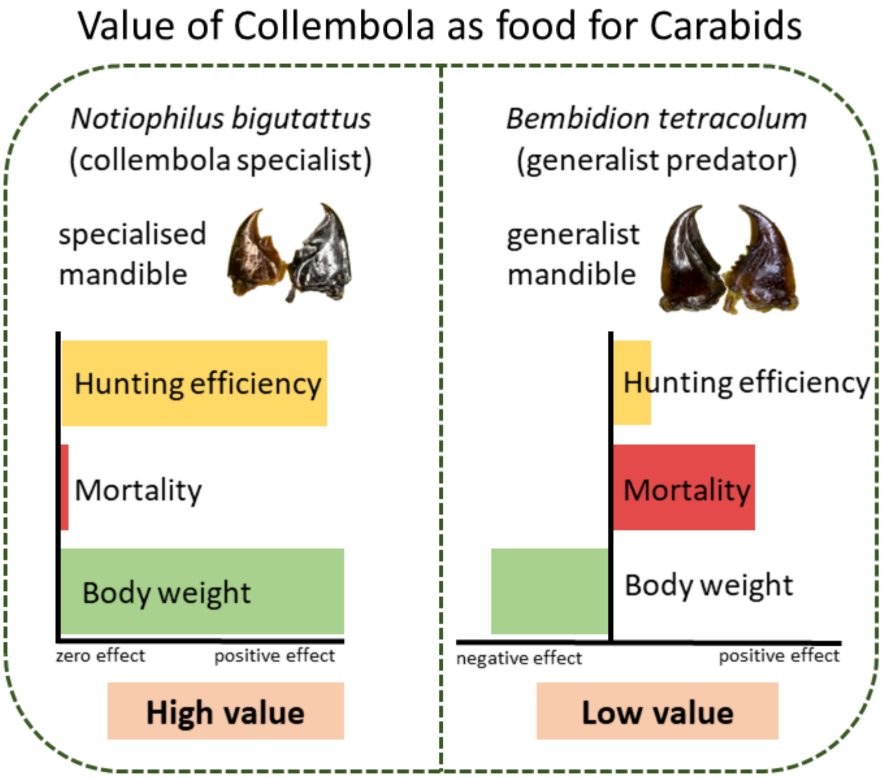
Short title: Hunting efficiency of specialized carabids

Graphical abstract



Highlights

- The enhanced hunting efficiency of *N. biguttatus* on Collembola compared to generalist species supports the hypothesis that the convergent evolution of mandibles in collembolan specialist carabids is highly adaptive.
- When subjected to a pure collembolan diet, the mortality of generalist species was higher than that of collembola specialists.
- When fed only with collembola, body weight of specialist species increased whereas that of generalist species decreased over time.

Abstract

1. Collembola are an important potential food source for carnivorous arthropods living on the soil surface. Nevertheless, due to their effective evasive maneuvers, Collembola are not an easy prey. Several carabid groups, however, have evolved morphological specializations to overcome this otherwise effective defense strategy. The adaptive value of this specialization is still unclear, since some generalist carabids also consume collembolans.
2. Feeding experiments with the collembolan specialist *Notiophilus bigutattus* and four generalist carnivorous carabids revealed that the specialized species is more efficient in hunting Collembola than the generalist species.
3. A comparison between specialized and generalist carabid species subjected to a pure collembolan diet further suggests that Collembola are only a dietary supplement for generalists: The generalist carnivore *Bembidion lampros* decreased in weight and had a higher mortality rate when fed exclusively with collembolans.
4. Analogously, a third experiment shows that edaphic mites or other non-collembolan soil arthropods are just a nutritional supplement for *N. biguttatus*, since mortality increased when they were fed exclusively with these groups. The adaptation toward Collembola as prey, in contrast, does not constrain *N. biguttatus,* since they even increased in weight when fed with drosophila.
5. The enhanced hunting efficiency of *N. biguttatus* on Collembola compared to generalist species supports the hypothesis that the convergent evolution of mandibles in all collembolan specialist carabids is highly adaptive. The advantage of specialization most probably is reinforced by the fact that generalist carabids are not real competitors for specialists, due to their poor efficiency in utilizing collembolans.

Keywords: Collembola specialists, feeding behavior, food specialization, *Notiophilus*, *Bembidion*, mandible morphology

Introduction

Collembolans are an important and abundant prey for various arthropod groups (Gomez-Polo, Alomar, Castañé, & Agustí, 2016). Due to the effective evasive maneuvers of epigeic and many hemiedaphic species that use tail-like appendages to fling themselves into the air, however, collembolans are no easy prey. Therefore, several morphological specializations for capturing collembolans have evolved in different arthropod groups (Yin et al., 2017). Ground beetles are among the most abundant carnivorous predatory arthropods and many species feed on collembolans (Homburg et al., 2014; Kotze et al., 2011; Ribera, McCracken, Foster, Downie, & Abernethy, 1999; Ignacio Ribera et al., 2001; Šerić Jeleska, Franjević, Jeleska, & Symondson, 2014). Most of them are generalist carnivores that only occasionally use this food source, such as members of the genera *Bembidion*, *Poecilus*, *Pterostichus* and *Asaphidion.* Only a few species are specialists with a well-documented high hunting efficiency on collembolans, such as members of the genera *Leistus*, *Loricera* and *Notiophilus* (Bauer, 1981, 1985; Ernsting & Jansen, 1978). Morphological adaptations seem crucial as a specialization toward a primary diet on collembolans. Other coleopteran taxa, such as species from the family Staphylinidae, evolved a protrusible labium to hunt Collembola (Bauer & Pfeiffer, 1991). In carabids, these adaptations include setal traps in the genera *Leistus* and *Loricera* (T Bauer, 1985; Hintzpeter & Bauer, 1986), which mostly hunt at night using olfactorial cues. Species of the genus *Notiophilus*, in contrast, do not possess comparable morphological adaptations, but hunt during the day aided by their highly enlarged eyes. However, common to all species of the genera *Loricera*, *Leistus* and *Notiophilus* is a convergently evolved specialized mandible shape as an adaptation to hunting collembolans (Baulechner et al., 2020). Compared to generalist carabids, Collembola specialists show a smaller primary mandibular joint, a more delicate and pointed incisor tooth and lack retinacular ridges (Baulechner et al., 2020). While these adaptations are most likely responsible for an increased hunting efficiency towards elusive and delicate prey, they hinder consumption of food items requiring high mandible pressure (such as ‘hard’ arthropods or seeds). Specialists like *Notiophilus* may nevertheless also feed on other small prey to some extent (Hengeveld, 1979, 1980).

Generalist carnivores, which occasionally feed on collembolans, lack these mandible adaptations and should therefore be less efficient predators. To our knowledge, however, this hypothesis has never been validated experimentally. Moreover, the nutritional value and thus the ecological relevance of collembolans in the diet of generalist carnivores has yet to be proven. Physiological factors may play a role in this context. For example, egg production and adult body weight of *Bembidion lampros* (Herbst, 1784) are adversely affected when larvae are fed with a single collembolan species only (Bilde, Axelsen, & Toft, 2000). It remains unclear, however, whether a mixed diet including collembolans as alternative prey is more suitable for generalists (Bilde et al., 2000). In this study, we compare the value of collembolans as a main food source between generalist and specialist species. We aim to test the hypotheses that morphological adaptations increase hunting efficiency in Collembola specialists compared to generalist carnivores (H1), and that a pure collembolan-based diet benefits Collembola specialists but not generalist carnivores (H2). Moreover, we hypothesize that the morphological specialization does not necessarily lead to the exclusion of other prey and does not result in a strict ecological specialization toward collembolans (H3). Since the value of alternative prey items such as mites and other soil organism is not well documented for Collembola specialists, this aspect is also evaluated.

Methods

Specimen and prey collection

Carabids of the species *Notiophilus bigutattus* (Fabricius, 1779), a collembolan specialist, and the generalist carnivores *Bembidion lampros* (Herbst, 1784), *Asaphidion flavipes* (Linnaeus, 1761), *Poecilus versicolor* (Sturm, 1824), and *Pterostichus melanarius* (Illiger, 1798) were captured with pitfall traps or by hand in central Hessen in close proximity to the city of Giessen. Prey items were hand collected or extracted from soil cores obtained from the same locality where the beetles were captured, using a modified Macfadyen extractor (Macfadyen, 1961). The collection tubes were equipped with wet tissue paper to provide enough humidity. The extraction was carried out at 40 °C for 4 days and animals were removed from the collection tubes every day. Soil and litter organisms were sorted into Collembola, mites, and 'others' (mainly insect larvae, dipterans, spiders and staphylinid beetles). As collembolan prey we include epigeic species of the families Isotomidae and Entomobryidae. Since living collembolans could not be determined to species level, they were instead classified as small (<2mm), medium (2mm-3.5mm), and large (4mm-6mm). Size class of collembolans initially entered analyses as a confounding factor but was ultimately dropped because it did not improve or affect any statistical result. Flightless *Drosophila melanogaster* (Meigen, 1830) were obtained from a pet shop.

Feeding experiment 1 - Hunting efficiency

The experiments were conducted in 2018 and 2019, between June and August. For each of the five species included (*N. bigutattus*, *B. lampros*, *A. flavipes*, *P. versicolor*, *P. melanarius*), 13 to 35 individuals per species were used in a total of 212 experimental trials (110 individuals in total). Accordingly, approx. half of the individuals entered one trial, the remaining individuals entered multiple trials which were conducted at least two days apart (see Table 1 for number of trials per species). Until the start of each trial each individual was kept in a separate plastic container with a diameter of 10 cm. The bottom was covered with cellulose filter paper and water was sprayed in the container each day to increase humidity. Folded tissue paper as refuges and a small cup with water were provided. Before each experimental trial, carabids were kept without food for two days. For each experimental trial, carabids were placed in a new container at room temperature (18°C), avoiding direct light and observer shadow and left for 5 minutes to resume normal behavior. The ground was covered with cellulose filter paper so that the beetles had sufficient grip but no refuges when hunting. One collembolan was placed in the middle of the container and the number of capture attempts were recorded until the prey was successfully captured. Experiments were aborted after 15 minutes if no attempt was successful. From this data, two parameters were calculated: i) overall hunting success per species (percentage of trials that resulted in captured prey, regardless of the number of attempts); ii) Average hunting success of a species (percentage of attempts that resulted in captured prey). If a specimen failed to capture the prey within 15 min, the average hunting success rate was set at 0%, irrespective of the number of attempts. We also provide the total amount of capture attempts and the mean number of attempts for successful and unsuccessful experiments.

Feeding experiment 2 - Effect of collembolans as prey on body weight and survival

Individuals of the collembolan specialist *Notiophilus bigutattus* (n = 23) and the generalist carnivore *Bembidion lampros* (n = 18) were kept separately for up to 19 days in 2018, with collembolan prey items in plastic containers (diameter 15cm). To provide sufficient moisture, the container floor was covered with plaster and watered daily. Additionally, a small plastic cup with water was provided. Food was provided *ad libitum*, ensuring that there were at least five Collembola per container each day. Dead collembolan prey was removed. Prior to these trials, carabids were starved for two days within the same containers. Carabids that died within two days were excluded from the experiment and are not included in the analyses. To rule out a higher mortality rate under laboratory conditions we kept 10 individuals of *B. lampros* in a 30 cm container with forest soil and litter from the same location where the beetles were collected. We added fresh forest soil and litter every few days to provide enough soil and litter fauna as food. We checked for survival every 2 to 3 days until the end of all experiments.

Feeding experiment 3 - Effect of alternative prey on body weight and survival

Similar to feeding experiment 2, feeding experiment 3 was set up for 15 days in the summer of 2019 to evaluate the performance of the collembolan specialist *N. biguattatus* on alternative prey taxa. A total of 29 individuals of *N. biguattatus* were kept separately in plastic containers and fed *ad libitum* with one of three prey item treatments: at least five mites (n = 9), at least five drosophila (n = 11), or a randomly distributed assortment of soil arthropods (n = 9). Feeding started two days after the carabids were placed into the containers. Dead and partly consumed prey was replaced daily. As a reference we used the same data of collembolans fed to *N. bigutattus* as described above.

Measurements and statistical analyses

For Experiment 1, descriptive statistics reporting the successful and unsuccessful hunting attempts were used to calculate the overall and mean and median hunting success rate. To account for multiple trials of individual carabids we compared the linear mixed effect model with beetle identity as a random factor against a simple model without random factors (lmne-function of the R package lmne version 3.1; Pinheiro et al., 2020). Both models showed comparable AIC and BIC (appendix Table 1) and we thus used the simpler gls model for subsequent analyses of hunting efficiency.

In feeding experiments 2 & 3, the body weight of each beetle was measured with a Sartorius 0.01mg half-microbalance every second or third day until the end of the experiment or until the beetle died. Weight gain or loss over the course of the experiment was calculated in percent of the first day of the experiment. We calculated the proportion of experiments in which individuals did not survive until the end of the experiment as the mortality rate. Further, we calculated the mean number of days a species survived in the experiment. We tested the correlation between body weight and time for the feeding experiments by fitting a linear mixed model with beetle ID as a random variable and tested for autocorrelation between day and ID using the lmne function of the R package lmne version 3.1 (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2020). These models reached a higher AIC and BIC value than models without temporal autocorrelation and without ID as random variables and were therefore used for subsequent analyses (appendix table 2-5). For feeding experiment 2 with collembolans fed to *N. bigutattus* and *B. lampros,* we used species as a factor and day (of experiment) as a continuous predictor variable as well as the interaction between these two parameters. For feeding experiment 3 with different prey items fed to *N. bigutattus*, we used prey item as a categorical and day (of experiment) as continuous independent predictor variables and as interaction terms. Models were fitted with a Restricted Maximum Likelihood Estimation (RMLE). Residuals were analyzed for normal distribution. To evaluate the effect of time, species and the interaction of the two, we used the Anova function from the R package car 3.0-8 (Fox & Weisberg, 2019) to calculate Wald-chi-square tests for fixed effects. We conducted a posthoc test for multiple comparisons with a tukey adjustment using the R Package multcomp 1.4-13 (Hothorn, Bretz, & Westfall, 2008) and lsmeans 2.30-0 (Lenth, 2016).

Results

Feeding experiment 1 - Hunting efficiency

N. bigutattus had the highest overall success rate (gls, $p = < 0.001$, appendix Table 2), effectively capturing collembolans in 77% of the trials. The generalist species had much lower success rates of 19% to 35% (Table 1). *N. bigutattus* also had the highest average hunting success (Fig 1) and thus needed the fewest number of attempts to capture a collembolan. On average, 50 % of the individuals were successful at the first attempt (median Fig 1). Generalist carnivores were considerably less efficient: The median hunting success rate was 0 and the mean hunting success rate was lower than 20% (5 attempts until success) for the generalist species *B. tetracolum*, *P. melanarius* and *P. versicolor*, while *A. flavipes* had a slightly higher mean and median hunting success rate than the other generalist species (Fig 1).

Tabel 1: Total number of trials and attempts to capture prey, overall hunting success rate and mean successful and unseccessful attempts per experiment. Trials are the number of repetitions performed for each species. Overall successrate is the percentage of trails resulting in successful capture of the prey.

		overall		**mean attempts per experiment**	
	trials	success rate	attempts	successful	unsuccessful
N. bigutattus	86	**77 %**	178	**2.3**	1.4 (1-8)
B. lampros	80	19 %	293	5.8	3.2 (1-17)
A. flavipes	34	35 %	105	4.8	2.2 (1-11)
P. versicolor	36	14 %	262	9.2	7.0 (1-35)
P. melanarius	16	31 %	52	2.6	3.5 (3-7)

In experiments not resulting in the capture of the prey item, *N. bigutattus* abandoned the hunt after fewer attempts than the generalist carnivores and required fewer attempts in successful experiments (Table 1). In successful trials, *P. melanarius* required a similar number of attempts to *N. bigutattus*, but was successful in just 31% of the experiments and conducted more attempts in unsuccessful experiments (Table 1). *P. versicolor* had the highest mean number of attempts in unsuccessful and in successful experiments (Table 1). On average, for all species, the number of attempts was lower in unsuccessful experiments than in successful experiments. However, specific individuals conducted a high number of attempts in unsuccessful experiments. For example, *B. tetracolum* attempted to capture the prey between 10 and 17 times in 7 trials and *P. versicolor* between 20 and 35 times in 50 % of the trials.

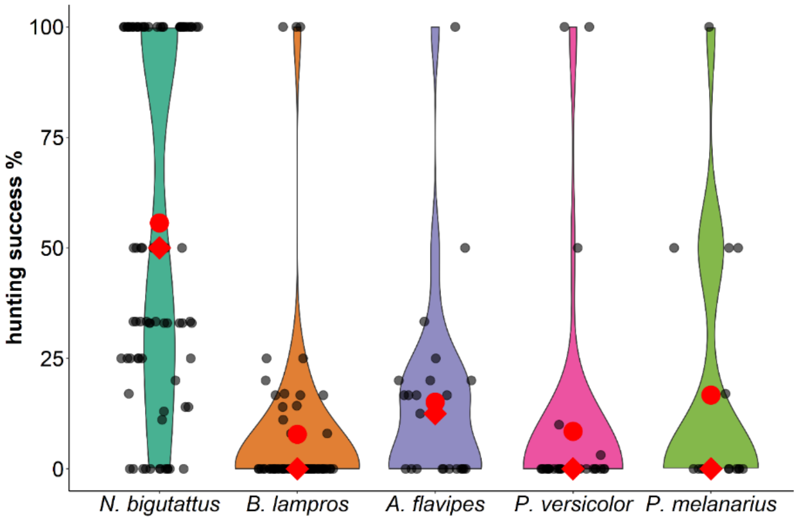


Fig 1. Hunting success of the specialist *N. bigutattus* in % compared to the four generalist species. Width of the violin-plot corresponds to the data distribution. Red circles indicate the mean and red diamonds the median. Hunting success indicates how many attempts it takes an individual to successfully capture a collembolan (100% = 1 attempt, 50% = 2 attempts, etc.)

Feeding experiment 2 - Effect of collembolans as prey on body weight and survival

The final linear mixed effect model that best explained the changes in body weight based on the AIC and BIC values included the variables species, day and the interaction between the two fixed effects (appendix Table 3). The interaction between species and day was highly significant ($Pr > \chi_2 = <0.001$, appendix Table 3). When fed only with collembolans, the weight of the collembolan specialist *N. biguttatus* increased (Fig 2). Only four *N. bigutattus* individuals did not survive until the end of the experiment, resulting in a mortality rate of 17.3%. In contrast, the weight of the generalist carnivore *B. tetracolum* decreased (Fig 2). *B. tetracolum* showed a high mortality rate of 83% during the experiment and survived on average 9.6 days. In the control group fed with diverse microarthropods, however, nine of ten *B. tetracolum* individuals survived for more than 19 days (5 individuals survived for 8 months), which rules out a higher mortality in captivity.

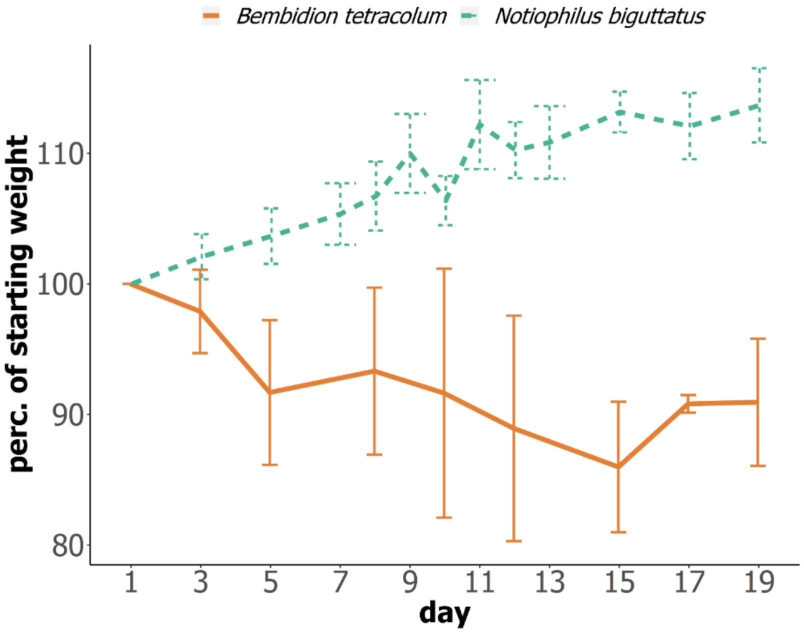


Fig 2. Percentage changes in the weight of the generalist *B. tetracolum* (solid line) and the specialist *N. biguttatus* (dotted line) when fed with pure collembolan diet. Mean values and standard error (vertical bars) are shown.

Feeding experiment 3 - Effect of alternative prey on body weight and survival

All prey groups had a statistically different effect on body weight of the collembolan specialist *N. biguttatus* (adjusted p values of the Tukey HSD posthoc test; appendix Table 5 & Table 6). Body weight increased when fed with Drosophila or Collembola, but it increased more when fed with Drosophila (Fig 3, appendix Table 5 & Table 6). Mortality rate was lowest when fed with Drosophila (0%), also compared to a collembolan diet (17.3%, see section above).When fed only with mites or other soil arthropods, body weight of *N. bigutattus* decreased in both cases (Fig 3, appendix Table 6 & Table 7). Mites and a mixed arthropod diet both resulted in a high mortality rate of 77% (mean survival of 8.3 days when fed with mites and 6.8 days when fed with other arthropods). None of the *N. bigutattus* individuals fed with mites or mixed arthropods survived more than 13 days.

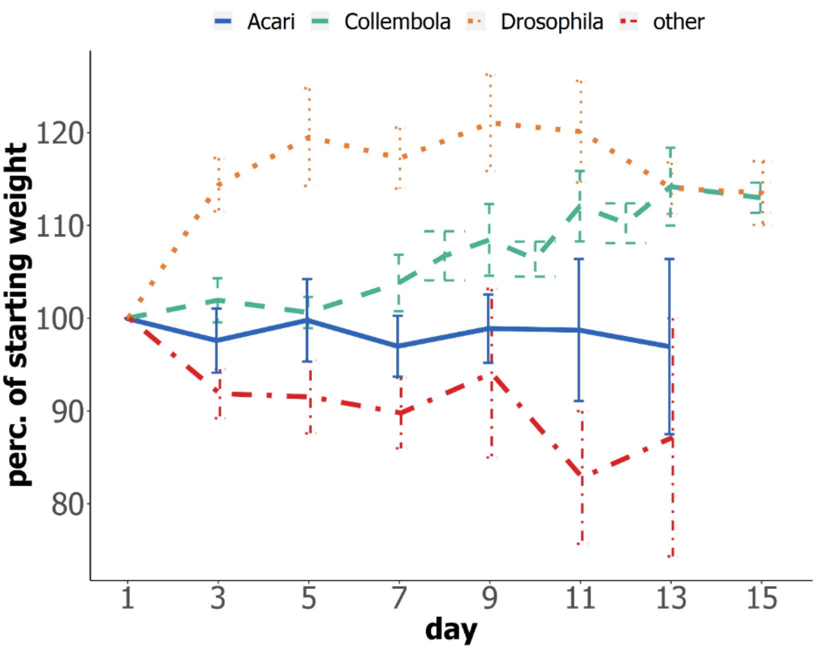


Fig 3. Percentage changes in body weight of *N. biguttatus* when fed with different prey. Mean values and standard error (vertical bars) are shown. The term "other" refers to a mixed diet of random soil arthropods.

Discussion

The role of Collembola as prey for many generalist carnivores has probably been overestimated. Our results suggest that highly evolved morphological specializations are necessary to efficiently feed on collembolans. The generalist species in this study are known to feed, at least occasionally, on collembolans. We show, however, that they are inefficient hunters compared to the collembolan specialist *N. bigutattus*. Moreover, the generalist carnivore *B. lampros* had a high mortality rate and a significant decrease in body weight when fed solely with Collembola. This is most likely caused by the low hunting success rate and suggests that collembolans are not an essential food item for generalist carnivore carabids.

Without any morphological specializations for collembolan prey, generalist carnivores seem less well equipped to efficiently use collembolans as a primary food source. Several different complex morphological specializations have evolved in various taxa to enable them to feed on collembolans, like saeta traps in *Leistus* and *Loricera*. *N. bigutattus* is lacking comparable morphological structures, but has evolved as a fast visual hunter with overlapping frontal vision (Ernsting & Jansen, 1978b; Bauer, 1981b; Ribera et al., 1999a). *N. bigutattus* even outperformed *Asaphidion*, which has a comparable visual overlap (Bauer, 1985b), in terms of hunting efficiency. Consequently, mandible morphology appears to be the prevailing common trait evolved in carabid collembolan specialists (Baulechner et al., 2020) and can be used to identify true feeding specializations in carabids. This is consistent with the observation of a strong link between morphology and dietary specialization in the animal kingdom (Aguirre, Herrel, van Damme, & Matthysen, 2002; Grant & Grant, 1996), although mismatches are also common (Bouton, Os, & Witte, 1998; Brandl, Robbins, & Bellwood, 2015; deVries et al., 2016; Ungar, Grine, & Teaford, 2008). Our study confirms that the morphological specialization to a certain food source does not necessarily imply the inability to use other prey items, since drosophila was a valuable alternative food resource for *Notiophilus* spp. and mites at least appeared not to be disadvantageous in terms of body weight change. Exploiting alternative resources is crucial for specialists when the preferred resource is scarce (Fontaine, Collin, & Dajoz, 2008; Robinson & Wilson, 1998; Ungar et al., 2008). During droughts in summer, for example, collembolan densities are exceptionally low (Pflug & Wolters, 2001), while mites are more drought tolerant (Perdue & Crossley, 1989; Santonja et al., 2017). When fed with mites only, however, mortality of *N. bigutattus* increased, probably due to a large share of oribatid mites, which were regularly approached and captured, but always released unharmed after a short handling between the mandibles. If at all, just non-oribatid mites should be considered as additional food for *N. bigutattus*, which to our knowledge has never been specified in the literature. Therefore, classification as a Collembola specialists should be based on the fact that collembolans make a substantial contribution to the diet of a species, with morphological or behavioural adaptations confirming predominant use of the target prey. Gut content analyses or anecdotal observations alone, in contrast, may overestimate the occasional consumption of collembolans by scavengers or other generalists in carabids. The term specialist is often used subjectively, so it should be specified which type of specialization is present (e.g., ecological vs. adaptive specialist) and in which way or if at all it is constrained to a narrow range of food (Ferry-Graham, Bolnick, & Wainwright, 2002). This is even more important in the classification of generalist carnivores, since Collembola are regularly found in their diet.

Collembolans are not a valuable primary food source for generalist carnivorous carabids. Our results show that *Pterostichus*, *Poecilus* and *Bembidion* have a very low and *Asaphidion* a low hunting success (Bauer, 1985a), which resulted in a high mortality rate. This finding is supported by the fact that generalist carnivores are able to consume dead rather than live Collembola (Mundy, Allen-Williams, Underwood, & Warrington, 2000), whereas *N. bigutattus* prefers live to dead collembolans (Mundy et al., 2000). Accordingly, density-dependent relationships with Collembola abundances in ecological studies should only be expected for true collembolan specialists, such as *Notiophilus* spp., *Leistus* spp. and *Loricera pilicornis*. For example, when collembolan abundance is enhanced, the abundance of the collembolan specialist *Loricera pilicornis* increases, but not the overall carabid abundance (Birkhofer, Wise, & Scheu, 2008). Similar reactions might be expected from *N. bigutattus* and other species of this genera, but evidence is lacking so far. Still, collembolans might serve as an additional food resource for generalist carnivorous carabid species when other prey is not available. In structurally complex organically managed wheat fields, collembolans might compensate for a temporal lack of aphid prey for *B. lampros* (Birkhofer, Wolters, & Diekötter, 2011). The decreased egg production and larval development resulting in lower weight of adult *B. lampros*, however, suggests short-term effects only (Bilde et al. 2000). Our results suggest that Collembola are only an additional food resource and are not valuable enough as an exclusive food.

Considering that Collembola were already widespread and abundant more than 200 million years before Coleoptera diversified (Leo, Carapelli, Cicconardi, Frati, & Nardi, 2019; Misof et al., 2014; Whalley & Jarzembowski, 1981; Yin et al., 2017), surface dwelling Collembola had most likely developed their escape mechanisms long before carabids appeared as potential predators. The response of generalists in our feeding experiments shows that the efficiency of these mechanisms holds for most carabids up to the present day. However, the findings for *N. bigutattus* suggest that the ability to overcome this barrier opened a nutritional niche for certain carabid species that allowed them to successfully reduce food competition with other species, while still being able to use alternative food sources. The fact that the ability to use Collembola as preferred prey evolved independently in different genera of carabids and other taxa indicates the ecological relevance of this process. However, there are still many open questions concerning the density dependency between Collembola specialists and their prey, as well as the influence of land use, prey availability, and competition on prey choice.

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Supporting information: Chapter 3

We tested the correlation between hunting success fitting a linear mixed model with beetle ID as a random variable and ID using the lme function of the R package lmne version 3.1 (Pinheiro et al., 2020). We compared AIC and BIC values for this model with a simpler model (gls, general least square) without beetle ID as a random factor. The model with the lowest AIC and BIC values were selected for further analyses.

Feeding experiment 1 - Feeding experiment 1 - Hunting efficiency

Formula and R code for Model$_{\text{lme1}}$ and Model$_{\text{gls1}}$ using the lme function of the R package lmne version 3.1 (Pinheiro et al., 2020):

Model$_{\text{lme1}}$ = lme (success ~ genus, random = ~1|ID, data = data, method = "REML", na.action = na.omit)

Model$_{\text{gls1}}$ = gls (success ~ genus, data = data, method = "REML", na.action = na.omit)

Table 1: Comparison of AIC and BIC values for Model$_{\text{lme0}}$ with ID as a random variable and the Model$_{\text{gls0}}$ (general least square) without random variable.

	Model	df	AIC	BIC	logLik	Test	L.Ratio	p-value
Model$_{\text{lme1}}$	1	7	2042.110	2065.439	-1014.055			
Model$_{\text{gls1}}$	2	6	2040.347	2060.343	-1014.173	1vs2	0.33566	0.626

Table 2: Model$_{\text{gls0}}$ posthoc test for pairwise comparisons with Tukey adjustment using the R Package multcomp 1.4-13 (Hothorn et al., 2008) and lsmeans 2.30-0 (Lenth, 2016).

contrast	estimate	SE	df	t.ratio	p.value
A.flavipes-B.lampros	0.074	0.079	103	0.936	0.882
A.flavipes-N.bigutattus	-0.409	0.077	103	-5.338	<0.001
A.flavipes-P.melanarius	-0.018	0.104	103	-0.173	1.000
A.flavipes-P.versicolor	0.069	0.088	103	0.784	0.935
B.lampros-N.bigutattus	-0.482	0.054	103	-8.9	<0.001
B.lampros-P.melanarius	-0.091	0.089	103	-1.033	0.840
B.lampros-P.versicolor	-0.004	0.070	103	-0.064	1.000
N.bigutattus-P.melanarius	0.391	0.087	103	4.505	0.001
N.bigutattus-P.versicolor	0.478	0.067	103	7.108	<0.001

We tested the correlation between body weight and time for the feeding experiments by fitting a linear mixed model with beetle ID as a random variable and tested for autocorrelation between day and ID using the lme function of the R package lmne version 3.1 (Pinheiro et al., 2020). We compared AIC and BIC values for this model with a simpler model (gls, general least square) without temporal autocorrelation and without beetle ID as a random factor. The model with the lowest AIC and BIC values were selected for further analyses.

Feeding experiment 2 - Effect of collembolans as prey on body weight and survival

Formula and R code for Model$_{lme1}$ and Model$_{gls1}$ using the lme function of the R package lmne version 3.1 (Pinheiro et al., 2020):

Model$_{lme2}$ = lme (percent ~ day * species, random = ~1|ID, correlation = corAR1 (form = ~ day | ID), data = data, method = "REML", na.action = na.omit)

Model$_{gls2}$ = gls (percent ~ day * species, data = data, method = "REML", na.action = na.omit)

Table 3: Comparison of AIC and BIC values for Model$_{lme2}$ with temporal autocorrelation and ID as a random variable and the Model$_{gls2}$ (general least square) without random variable or autocorrelations.

	Model	df	AIC	BIC	logLik	Test	L.Ratio	p-value
Model$_{lme2}$	1	7	2068.947	2094.084	-1027.473			
Model$_{gls2}$	2	6	2145.282	2166.828	-1066.641	1vs2	78.33566	<.0001

Table 3: Analysis of Deviance Table (Type II tests) for Model$_{lme1}$ using the Anova function from the R package car 3.0-8 (Fox & Weisberg, 2019)

	Chisq	Df	Pr(>Chisq)
day	35.35	1	<0.001
species	8.27	1	0.004
day:species	21.04	1	<0.001

Feeding experiment 3 - Effect of alternative prey on body weight and survival

Table 4: Comparison of AIC and BIC values for model3 with temporal autocorrelation and ID as a random variable and the model4 (general least square) without random variable or autocorrelations.

	Model	df	AIC	BIC	logLik	Test	L.Ratio	p-value
Model$_{lme3}$	1	11	2519.6	2561.8	-1248.8			
Model$_{gls3}$	2	9	2634.7	2669.2	-1308.3	1vs2	119.1	<.001

R code for model1 and Model$_{\text{gls2}}$ using the lme function of the R package lmne version 3.1 (Pinheiro et al., 2020).:

Model$_{\text{lme3}}$= lme(percent ~ day * prey, random = ~1|ID, correlation = corAR1 (form = ~ day | ID), data = data, method = "REML", na.action = na.omit)

Model$_{\text{gls3}}$ = gls(percent ~ day * prey, data = data, method ="REML", na.action=na.omit)

Table 5: Analysis of Deviance Table (Type II tests) for Model$_{\text{lme2}}$ using the Anova function from the R package car 3.0-8 (Fox & Weisberg, 2019)

	Chisq	Df	Pr(>Chisq)
day	74.38	1	<0.001
prey	26.74	3	<0.001
day:prey	18.64	3	0.001

Table 6: Posthoctest for Model$_{\text{lme3}}$ prey species in

Prey	day	lsmean	SE	df	lower.CL	upper.CL
Other	7.71	9.01E+01	2.28	341	84.4	95.8
Acari	7.71	9.83E+01	2.03	341	93.2	103.4
Collembola	7.71	105.8	0.79	341	103.9	107.8
Drosophila	7.71	114.8	1.12	341	112	117.6

Degrees-of-freedom method: df.error
Confidence level used: 0.95
Conf-level adjustment: sidak method for 4 estimates
P value adjustment: tukey method for comparing a family of 4 estimates
significance level used: alpha = 0.05

Table 7: Posthoc test with pairwise comparisons for Model$_{\text{lme3}}$ with Tukey adjustment using the R Package multcomp 1.4-13 (Hothorn et al., 2008) and lsmeans 2.30-0 (Lenth, 2016).

contrast	estimate	SE	df	t.ratio	p.value
Acari - other	8.21	3.06	341	2.684	0.038
Collembola - other	15.76	2.42	341	6.521	<.0001
Collembola - Acari	7.55	2.18	341	3.464	0.003
Drosophila - other	24.74	2.54	341	9.721	<.0001
Drosophila - Acari	16.53	2.32	341	7.122	<.0001
Drosophila - Collembola	8.98	1.37	341	6.553	<.0001

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Curriculum Vitae

Research Experience

Since 2018	**Research associate BeeContour:** Streifenanbausysteme zur Förderung von Bienen und weiteren Bestäuberinsekten in der Agrarlandschaft
Since 2018	**Research associate RESOILIENCE:** Resilience of invertebrate communities in grasslands (DFG Biodiversity exploratories).
Since 2017	**Doctoral student** at the Department of Animal Ecology and Systematics, JLU Giessen: Convergent evolution of functional traits and its implications for carabid community assembly.
Since 2011	**Freelance Biologist** (Environmental consultant, Biodiversity Assessment)
2013-2018	**Research associate** (part time) at the Department of Animal Ecology and Systematics, JLU Giessen
2013-2018	**Environmental consultant** “Planungsbüro Gall”; Specialist for Bats, Reptiles, Amphibians and Beetles
2013-2017	**Adjunct teacher** (“Lehrbeauftragter”, part time) at the Department of Animal Ecology and Systematics, JLU Giessen
2013	**Lecturer** (Lehrkraft für besondere Aufgaben, LFBA)
2011-2012	**Research associate, DFG Project** (German Research Association) Project (EN 987/1-1): Coevolution of spinturnicid mites and their bat hosts; Project coordination and preparation of proposal for DFG research grand (Prof. Encarnação, JLU Giessen)
2009-2011	**Master student** at the Justus Liebig University (JLU) of Giessen Major field of study: **Ecology & Conservation biology** Additional courses: Phylogenetics, Bioinformatics, Evolutionary Biology, Plant Ecology (global adaptation & stress ecology) **Master Thesis:** Coevolution of wing mites and their bat hosts - Codivergence or adaptive radiation (Prof. Dr. Encarnação, Department of animal Ecology and Systematics; Mammalian Ecology Group, JLU Giessen)
2006-2011	**Research assistant** (part time, Department of Animal Ecology and Systematics, JLU Giessen) • Determination of Carabids: o Biodiversity exploratories (SOILFOODWEB, 2007-2011) o BIOPLEX (2007-2011) o BIOLOG Europe (2007-2009) • Determination and capture of Apidae (Prof. Wolters, JLU Gießen, 2006)
2007	**Field assistant:** PhD. Thesis of Stesha Pasachnik, University of Tennessee (Genetic structure of the *Ctenosaura melanosterna* clade)

2006- 2008	**Student field work** (summer breaks) IRBS, Utila, Honduras: population ecology and genetics of *Norops utilensis* (Prof. Dr. Wolters, JLU Giessen)
2006-2009	**Study of Biology** at Justus Liebig University of Giessen Major field of study: **Ecology, Zoology & Biophilosophy** **Bachelor Thesis:** Primer establishment for AFLP population genetic analyses for two Anole lizards: *Norops utilensis* and *N. bicaorum* (Prof. Dr. Wolters, Department of Animal Ecology and Systematics, JLU Giessen)
2005	**Field assistant:** Diploma Thesis of Ullrich Schulte, Universität Bielefeld (Development of a monitoring concept for the Utila spiny-tailed iguana, C*tenosaura bakeri*)
2003-2004	**Apprenticeship:** "staatlich geprüfter Umweltschutztechnischer Assistent, UTA (free transl.: Environmental Conservation Technical Assistant)
2003	**Internship** (Mar-Sep): Iguana research and breeding station (IRBS), Utila, Honduras, guided tours breeding station, mangrove forest etc.; maintenance of the breeding program.
2001	**Volonteer** (Jun-Aug): Iguana research and breeding station (IRBS), Utila, Honduras

Teaching (Department of Animal Ecology and Systematics, JLU Giessen)

2021	Assistenz in organismischer Biologie, V-OB-ASO
2021	Evolution of Plants and Animals, V-OB-EPT
2013-2020	Micro- and macroevolution of animals (Mikro und Makroevolution der Tiere, V-ZO-MMT): three classes on: Nomenclature, Taxonomy, evolutionary ecology.
Since 2016	Nature conservation for undergraduates (Biologische Grundlagen des Naturschutzes, Naturschutzrechts und der Umweltbildung, V-NS-1)
Since 2015	Nature conservation for undergraduates (Fachexkursionen im Naturschutz, V-NS-2)
Since 2012	Animal ecology for undargraduates (A4-TÖE)
Since 2010	Biodiversity and Morphology (Beetles and Herpetofauna, V-TÖ-BDF)
Since 2010	Arthropod determination for biologists (K2-BEX)
2013, 2015	Introduction to Animal Biology for undergraduates (K1-ALB)
2011	Mammalian ecology for master students (Bioacustic analyses of bats)
	Mammalian ecology for master students (Scientific writing and citing)
2010	Mammalian ecology for undergraduates (Bioacustic analyses of bats)

Conference contributions

2021	Multidimensional trait response drives assembly processes of edaphic microarthropod communities in grasslands, Poster, 50th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland "Ecology - Science in Transition, Science for Transition
2021	RESOILIENCE: Resilienz der Invertebratengemeinschaften in Grünlandböden Biodiversitäts Exploratories annual assembly
2020	Biodiversitäts Exploratorien Jahrestagung: RESOILIENCE: Resilienz der Invertebratengemeinschaften in Grünlandböden
2019	Biodiversitäts Exploratorien Jahrestagung: RESOILIENCE: Resilienz der Invertebratengemeinschaften in Grünlandböden
2018	Convergent evolution of feeding characteristics in Carabids (Talk) 21. Annual meeting Gesellschaft für Angewandte Carabidologie
2017	Convergent Evolution of Herbivory and mandible morphology in carabids (poster) “Ecology Across Borders” Joint annual Meeting of the British ecological society and the Ecological Society of Germany, Austria and Switzerland)
2015	Phylogenetic and functional response of carabid community structure to conversion of arable land in flowering fields (talk) 45th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland “Ecology for a Sustainable Future”
2014	Mating at summer sites: Implications for conservation and population genetic structure in Daubenton’s bats (talk at the 88th Annual Meeting of the German Society for Mammalian Biology)
2011	Coevolution of spinturnicid mites and their bat hosts (talk) 104th annual conference of the German Zoological Association (DZG)
2011	Seasonal-, sex and age specific variations in ectoparasite load of European bats (talk) 104th *annual conference* of the *German Zoological* Association, (DZG)
2011	Flughautmilben an mitteleuropäischen Fledermäusen - was können uns Parasiten über ihren Wirt sagen? (poster) 10. Fachtagung der BAG Fledermausschutz im NABU in Benediktbeuern Fledermäuse zwischen Kultur und Natur
2011	Flughautmilben der Bechsteinfledermaus, Alte Merkmale in neuem Licht (poster) Fachtagung - Populationsökologie und Habitatansprüche der Bechsteinfledermaus *Myotis bechsteinii*
2008	Population ecology of *Norops utilensis* (talk); DGHT AG Iguana, annual meeting
2008	Conservation of *Ctenosaura bakeri*: Perspectives;(talk) DGHT AG Iguana, annual meeting
2007	Development and conservation on Utila; Population ecology of *Norops utilensis* (talk) IUCN SSC Iguana Specialist Group, annual meeting, Utila, Honduras

Publications

Baulechner D, Jauker F, Wolters V (2021) Carabid adaptation to a collembolan diet: hunting efficiency and nutritional value. *Ecological Entomology*, doi.org/10.1111/een.13106

Provost, G. Le, Thiele, J., Westphal, C., Penone, C., Allan, E., Neyret, M., […], **Baulechner, D.**, et al. (2021) Contrasting responses of above- and belowground diversity to multiple components of land-use intensity. *Nature Communications*, 12, 3918. doi.org/10.1038/s41467-021-23931-1

Baulechner, D., Jauker, F., Neubauer, T. A., & Wolters, V. (2020). Convergent evolution of specialized generalists: Implications for phylogenetic and functional diversity of carabid feeding groups. *Ecology and Evolution.* doi: 10.1002/ece3.6746

Baulechner, D., Diekötter, T., Wolters, V., & Jauker, F. (2019). Converting arable land into flowering fields changes functional and phylogenetic community structure in ground beetles. *Biological Conservation*, *231*, 51–58. doi: 10.1016/j.biocon.2019.01.005

Baulechner, D. Becker, N. I., & Encarnação, J. A. (2013). Host specificity in spinturnicid mites: Do parasites share a long evolutionary history with their host*? Journal of Zoological Systematics and Evolutionary Research.* doi: 10.1111/jzs.12021

Encarnação, J. A., **Baulechner, D.**, & Becker, N. I. (2012). Seasonal variations of wing mite infestations in male Daubenton's bats (Myotis daubentonii) in comparison to female and juvenile bats. *Acta Chiropterologica*, *14*(1). doi: 10.3161/150811012X654367

Book Chapter

Baulechner, D, Becker, N. I., & Encarnação, J. A. (2011). Wing mites in Bechsteins bats: new light shed on old traits. In: Population ecology and habitat requirements of Bechstein´s bat Myotis Bechsteinii, Editor Markus Dietz, 309-317. ISBN 978-3-00-043875-2

Declaration

I declare that I have completed this dissertation single-handedly without the unauthorized help of a second party and only with the assistance acknowledged therein. I have appropriately acknowledged and cited all text passages that are derived verbatim from or are based on the content of published work of others, and all information relating to verbal communications. I consent to the use of an anti-plagiarism software to check my thesis. I have abided by the principles of good scientific conduct laid down in the charter of the Justus Liebig University Giessen „Satzung der Justus-Liebig-Universität Gießen zur Sicherung guter wissenschaftlicher Praxis“in carrying out the investigations described in the dissertation.