

Effects of environmental heterogeneity
on diversity, spatial distribution and trophic
interactions of terrestrial arthropod predators

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Fotos: Sergej Sereda

For my daughters Lea and Nana



“If we knew what it was we were doing, it would not be called research, would it?”

- Albert Einstein

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Summary

The on-going decline of biodiversity is likely to alter important ecosystem functions and services, such as biological control of pests, due to a loss of predator species from ecosystems. Predictions about changes in predator diversity require reliable estimates of the composition of arthropod communities in local habitats. This composition at least partly results from effects of environmental heterogeneity on the spatial distribution and trophic interactions of arthropod predator species.

“Assessment”, “Distribution”, “Function” and “Service” are four major topics of biodiversity research. These aspects are addressed in the four core chapters of this cumulative dissertation and focus on how decisions about the sampling design affect the quality of biodiversity inventories in environmentally heterogeneous habitats and how environmental heterogeneity affects the spatial distribution and the functional role of terrestrial arthropod predators. To understand the effect of environmental heterogeneity on arthropod predator diversity and distribution the aspects “Assessment” and “Distribution” were studied in unmanaged forest ecosystems (Chapters 1 & 2). The aspect “Function” focusing on effects of heterogeneity in structure and resource availability on the litter-decomposer-predator food chain and the aspect “Service” focusing on the contribution of natural enemies to aphid suppression were studied in managed agricultural ecosystems (Chapters 3 & 4). This switch from forest systems (Chapters 1 & 2) to primarily agricultural systems (Chapters 3 & 4) was motivated by a stronger focus on applied aspects (ecosystem services such as decomposition and biological control) in agricultural systems. The aspects “Assessment”, “Distribution” and “Function” focused on generalist predators (spiders and ground beetles) and their potential prey (Collembola), while the aspect “Service” focused on aphid control by natural enemies (generalist and specialist predators).

The first study (Chapter 1, “Assessment”) addresses the question how the design of sampling schemes in biodiversity inventories affects the precision of diversity assessment by comparing systematic and stratified sampling designs. The results suggest that stratified sampling based on expert knowledge about habitat heterogeneity is more effective than systematic sampling. Arrangement of pitfall traps in a stratified design covers a more diverse range of microhabitats and therefore provides a more complete picture of the existing community in a given sample area. Thus, the quality of future inventories will be considerably improved by incorporating information on habitat heterogeneity.

The second study (Chapter 2, “Distribution”) is closely related to the former study and focuses on the effect of environmental heterogeneity on the spatial distribution of abundant spider species and Collembola groups in the same forest floor habitat. It complements study 1 by adding information on habitat needs of selected taxa in heterogeneous habitats. The distribution of three spider species was

affected by habitat heterogeneity such as moss or litter coverage estimated from forest inventory data. In addition, the distribution of one spider species was negatively related to the local availability of prey. The distribution of Collembola, in contrast, was only related to environmental heterogeneity. Considering biotic and abiotic factors is crucial when studying the distribution of individuals in heterogeneous habitats. Chapter 1 and 2 highlight the need for doing so in both biodiversity inventories and long-term monitoring studies with a conservation background.

Investigations on the aspects “Function” and “Service” in managed systems covered studies on the functional role of arthropod predators in food webs and on the provision of pest control services. To understand how environmental heterogeneity not only affects diversity (chapter 1 & 2), but also modulates the contribution of arthropod predators to ecosystem processes, I also quantified the effect of the addition of wheat and maize litter on the litter-decomposer-predator food chain in both conventionally and organically managed wheat fields (Chapter 3, “Function”). The activity density of generalist predators was significantly higher in experimental plots with maize compared to wheat litter plots and under organic farming. Collembola did not numerically respond to litter addition, though they incorporated a high share of maize-born carbon (as estimated by carbon stable isotope ratios). Two spider species were more closely linked to the decomposer prey that consumed maize in organically managed fields and one carabid species showed this pattern in conventionally managed fields. Litter mass loss was highest in plots that received wheat litter under organic management and was negatively related to predator activity density. Addition of crop residues from a growing crop under organic management may be a promising strategy to synergistically promote decomposition processes and activity density of natural enemies in agricultural fields.

Concerning the aspect “Service”, the meta-analysis demonstrated that aphid control by natural enemies is mediated by top-down (degree of prey specialization in predators) and bottom-up (host plant group) drivers and climatic conditions. Generalist predators significantly reduced aphid numbers, but not to the same extent as specialist predators or assemblages of specialists and generalists. Moreover, natural enemies were more effective on aphid populations colonizing grass or herb crops, but did only marginally affect those inhabiting nitrogen-rich legume plants. These findings show that environmental heterogeneity affects arthropod predators at spatio-temporal levels beyond the scales addressed in the previous case studies (Chapters 1-3). This suggests that agricultural fields differing in the availability of plant functional groups in the surrounding area may provide different levels of pest control services. In addition, the meta-analysis revealed that climatic conditions affect predator-prey interactions at the global scale. More specifically, biological control of pests by natural enemies was stronger in regions with more

severe climatic events. This finding has important implications for future alterations of pest control levels in the face of climate change.

In conclusion, this dissertation highlights the importance of accounting for environmental heterogeneity when assessing the diversity and distribution of arthropod predator communities. The results are not only relevant for progress in basic research, but also have strong implications for applied sciences and practical approaches in the face of future changes in land use and climate. Functions and services may directly be affected by alterations of environmental heterogeneity at both small and higher spatial scales. A better understanding of the relationships among predators or between predators and their prey in habitats with different levels of environmental heterogeneity will considerably improve our predictive capacity concerning the function of terrestrial arthropod predators under conditions of environmental change.

Zusammenfassung

Der andauernde Rückgang der Biodiversität beeinflusst wichtige Ökosystemfunktionen und -dienstleistungen. Vor diesem Hintergrund kann der Verlust räuberischer Arthropodenarten die biologische Schädlingskontrolle – als Dienstleistung in terrestrischen Ökosystemen bereitgestellt von natürlichen Feinden – beeinträchtigen. Eine Prognose der Veränderungen der Arthropodendiversität erfordert verlässliche Daten über die Zusammensetzung von Gemeinschaften in unterschiedlichen Lebensräumen. Die Gemeinschaftszusammensetzung wird durch die Heterogenität der Umwelt, die damit verbundenen Unterschiede in der räumlichen Verteilung von Arten und schließlich auch durch die trophischen Interaktionen zwischen Prädatoren und ihrer Beute beeinflusst.

Die vier Hauptaspekte der Biodiversitätsforschung – “Erfassung”, “Verteilung”, “Funktion” und “Service” – bilden daher die Grundthemen der vier Kapitel dieser vorliegenden kumulativen Dissertation. Deren Schwerpunkte sind der Einfluss des Probenahmeverfahrens auf Biodiversitätserfassungen in heterogenen Habitaten sowie der Einfluss der Umweltheterogenität auf die räumliche Verteilung und die funktionelle Rolle von terrestrischen Arthropoden. Um den Effekt der Umweltheterogenität auf Arthropodengemeinschaften zu analysieren, wurden die Aspekte “Erfassung” und “Verteilung” in unbewirtschafteten Waldökosystemen untersucht (Kapitel 1 und 2). Die Auswirkungen erhöhter struktureller Komplexität und Ressourcenqualität eines Lebensraums auf die Streu-Zersetzer-Räuber-Nahrungskette wurden unter dem Aspekt “Funktion” experimentell untersucht (Kapitel 3). Abschließend wurde unter dem Aspekt “Service” eine Meta-Analyse über den Beitrag der natürlichen Feinde zur Kontrolle von Blattlauspopulationen in bewirtschafteten Agrarökosystemen durchgeführt (Kapitel 4). Mit dem Wechsel von unbewirtschafteten Waldökosystemen in Kapitel 1 & 2 zu bewirtschafteten Agrarökosystemen in den beiden folgenden Kapiteln verschiebt sich der Schwerpunkt dieser Dissertation von der Grundlagenforschung zu stärker angewandten Fragestellungen innerhalb der Biodiversitätsforschung. Spinnen und Laufkäfer als generalistische Prädatoren und Collembolen als ihre potentielle Beute waren die Zielgruppen der Kapitel “Erfassung”, “Verteilung” und “Funktion”. Da in Agrarökosystemen Getreideschädlinge erhebliche Ernteverluste verursachen können, stand unter dem Aspekt “Service” die Blattlauskontrolle durch natürliche Feinde im Fokus, wobei sowohl generalistische als auch spezialisierte Prädatoren Berücksichtigung fanden.

Die erste Studie (Kapitel 1, “Erfassung”) konzentriert sich auf die Qualität der Biodiversitätserfassung mithilfe von zwei unterschiedlichen Probenahmeverfahren. Das stratifizierte Probenahmeverfahren, welches auf einer von Experten festgelegten Auswahl der Fallenstandorte basierte, erwies sich als effektivere Methode im Vergleich zur traditionell bei Waldinventuren durchgeführten systematischen

Beprobung. Durch die stratifizierte Anordnung der Fallen wurden verschiedene Mikrohabitate besser abgedeckt, was eine vollständigere Erfassung der Gemeinschaftszusammensetzung ermöglichte. Für zukünftige Studien, die eine vollständige Erfassung der Diversität als Ziel verfolgen, könnte eine stratifizierte, auf Expertenwissen basierende Beprobung eine höhere Qualität der Inventur versprechen.

Die zweite Studie (Kapitel 2, "Verteilung") über die Wirkung von Umweltheterogenität auf die räumliche Verteilung von Spinnen und Collembolen fügte ergänzt die unter "Erfassung" behandelte methodische Fragestellung um Erkenntnisse über die realisierte ökologische Nische ausgewählter Taxa im Lebensraum Wald. Die Verteilungsmuster von drei Spinnenarten waren durch eine enge Beziehung zur Heterogenität in Bezug auf die Verteilung von Moos- und Streudeckung charakterisiert. Die lokale Beuteverfügbarkeit beeinflusste die räumliche Verteilung einer weiteren Spinnenart. Demgegenüber wurde die räumliche Verteilung der Collembolen ausschließlich durch die Umweltheterogenität bestimmt. Aus diesen Ergebnissen leitet sich die Notwendigkeit ab, bei Untersuchungen der räumlichen Verteilung von Arthropoden in heterogenen Habitaten sowohl biotische als auch abiotische Faktoren einzubeziehen. Beide Studien unterstreichen die Wichtigkeit der Berücksichtigung von Umweltheterogenität bei Biodiversitätserfassungen und langfristigen Monitoring-Studien.

Der angewandte Aspekt der Biodiversitätsforschung wurde in Kapitel 3 und 4 durch Studien über die funktionelle Rolle der Arthropoden in Nahrungsnetzen und die Bereitstellung der ökosystemaren Dienstleistung "biologische Schädlingskontrolle" in bewirtschafteten Systemen repräsentiert. Als Erstes zeigt sich das eine experimentelle Veränderung der Umweltheterogenität mittels Einbringen von Ernteabfällen (Weizen- bzw. Maisstreu) auf konventionell und ökologisch bewirtschafteten Weizenfeldern die Streu-Zersetzer-Räuber-Nahrungskette beeinflusst (Kapitel 3, "Funktion"). Die Aktivitätsdichte generalistischer Prädatoren war signifikant höher auf den experimentellen Flächen, die mit Maisstreu manipuliert wurden, im Vergleich zu Flächen, auf denen Weizenstreu ausgebracht wurde. Demgegenüber zeigten die Collembola zwar keine numerische Reaktion auf erhöhte Streumengen, der prozentuale Anteil des aus Maisstreu aufgenommenen Kohlenstoffs war aber erhöht. Zwei von drei untersuchten Spinnenarten waren auf ökologisch bewirtschafteten Agrarflächen Teil der Maiskohlenstoff-Nahrungskette und eine von zwei untersuchten Laufkäferarten zeigte dieses Muster auf konventionell bewirtschafteten Feldern. Hoher Streuzersetzung konnte nur auf ökologisch bewirtschafteten Feldern beobachtet werden und nur auf Teilflächen, auf denen Weizenstreu ausgebracht wurde. Das Ausbringen von Ernteabfällen der angebauten Feldfrucht auf ökologisch bewirtschafteten Getreideflächen könnte daher sowohl die Zersetzerleistung als auch die Dichte wichtiger Raubarthropoden fördern.

Die unter dem Aspekt "Service" durchgeführte Meta-Analyse verdeutlichte, dass die Kontrolle von Blattlauspopulationen durch natürliche Feinde sowohl "top-down" (Spezialisierung der Prädatoren auf

bestimmte Beutegruppen) als auch "bottom-up" (Gruppe der Wirtspflanze) reguliert wurde. Generalistische Prädatoren reduzierten zwar signifikant die Größe von Blattlauspopulationen, waren dabei aber weniger effektiv als Spezialisten oder gemischte Räbergemeinschaften, die sich beiden funktionellen Gruppen zusammensetzten. Natürliche Feinde waren dann effektiver, wenn sich Blattlauspopulationen auf Gräsern oder Kräutern etablierten, nicht aber auf stickstoffreichen Leguminosen. Diese Ergebnisse zeigen, dass die Auswirkung der Umweltheterogenität auf die Funktion von räuberischen Arthropoden auch auf größeren räumlichen Skalen wirksam war, als solche, die in Kapitel 1 bis 3 untersucht wurden. So können z. B. in der Landschaft verteilte Flächen mit diversen, funktionellen Pflanzengemeinschaften verschiedene Intensitäten der Schädlingskontrolle bereitstellen. Darüber hinaus wirkten sich klimatische Faktoren, d. h. hohe Variationen von Niederschlag und Temperatur, positiv auf die Blattlauskontrolle durch natürliche Feinde aus. Angesichts des globalen Klimawandels wäre es vorteilhaft, diese Erkenntnisse zukünftig bei agrarwirtschaftlichen Bewirtschaftungsplänen zu berücksichtigen, welche auch die biologische Schädlingskontrolle miteinbeziehen.

Zusammenfassend lässt sich festhalten, dass die vorliegende Dissertation die Bedeutung der Umweltheterogenität für die Biodiversitätserfassung von Prädatoren besonders hervorhebt. Grundlagenforschung im Hinblick auf die Erfassung der biologischen Vielfalt erlangt dann eine praktische Relevanz, wenn die gewonnenen, empirischen Erkenntnisse in eine angewandte Perspektive überführt werden, die sowohl den globalen Landnutzungs- als auch den Klimawandel integriert. Wichtige ökologische Funktionen und ökosystemare Dienstleistungen werden durch die Heterogenität der Umwelt auf kleinen und großen räumlichen Skalen beeinflusst. Ein besseres Verständnis der Beziehungen zwischen Räubern untereinander oder zwischen Räubern und ihrer Beute in unterschiedlich heterogenen Lebensräumen kann die Prognose über die Auswirkungen der zukünftigen Landnutzungsänderungen auf Arthropodengemeinschaften in terrestrischen Ökosystemen verbessern.

Introduction

Biodiversity is declining worldwide and is therefore a focus of current ecological research (Wolters & Hotes 2010). Anthropogenic management is a major threat to biodiversity and has led to a homogenization of ecosystem functions and services in managed systems (e.g. arable land) compared to unmanaged systems (e.g. protected areas; MacDougall et al. 2013). In terrestrial ecosystems arthropod predators are abundant and are involved in ecosystem functioning (e.g. food webs) and provide important services (e.g. biological pest control; Symondson et al. 2002). To conserve diversity and promote associated services, knowledge on the current state of biodiversity based on appropriate assessments is indispensable (Collen et al. 2013). In local habitats, the diversity and composition of arthropod communities at least partly results from the effects of environmental heterogeneity, e.g. climatic conditions or the availability of resources, on the spatial distribution and trophic interactions of arthropod predator species.

According to Baur's book on the basic principles of biodiversity (2010), the four main aspects of biodiversity research are "Assessment", "Distribution", "Function" and "Service" (Fig. 1). In the present dissertation the effect of habitat heterogeneity on these aspects is covered in four chapters. In detail, the chapters address the questions how decisions about sampling designs affect the quality of biodiversity inventories in environmentally heterogeneous habitats ("Assessment"; chapter 1), how environmental heterogeneity affects the spatial distribution ("Distribution"; chapter 2), the functional role of terrestrial arthropod predators in the litter-decomposer-predator food chain ("Function"; chapter 3) and the associated service of biological pest control ("Service"; chapter 4).

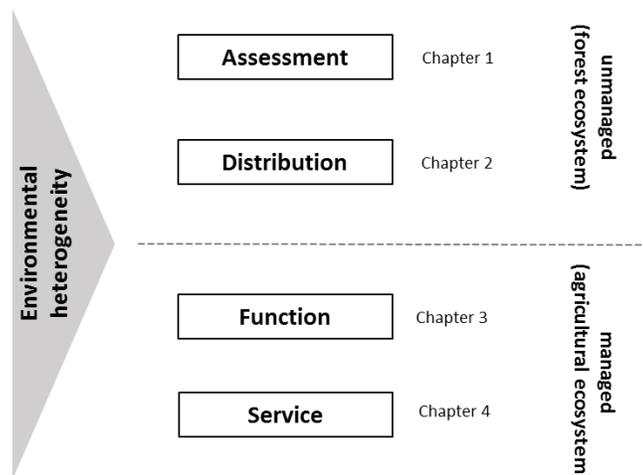


Figure 1 Outline of this cumulative dissertation. The effects of environmental heterogeneity on the main aspects of biodiversity research "Assessment", "Distribution", "Function" and "Service" (adapted from Baur 2010) studied in unmanaged (Chapters 1 & 2) and managed ecosystems (Chapters 3 & 4).

The aspects “Assessment” and “Distribution” were studied in unmanaged forest ecosystems (Chapters 1 & 2), while the aspects “Function” and “Service” were studied in agricultural systems (Chapter 3 & 4). The switch from forests to primarily agricultural systems to address the last aspects “Function” and “Service” is due to the importance of such applied research questions in developing sustainable farming systems compared to more basic research questions which require a high level of environmental heterogeneity in the first two aspects “Assessment” and “Distribution”.

Forests cover over 31 % of world’s surface (FAO 2010) providing a range of habitats for different plants, animals and microorganisms and unmanaged forest systems often are hotspots of biodiversity (Myers et al. 2000). To promote biodiversity conservation, strict forest reserves (German: “Naturwaldreservate”) were established in different regions of Germany (Bunker et al. 2005, Dorow et al. 2007). These unmanaged forest areas provide a baseline for undisturbed ecosystems in terms of diversity and relationships between species and their environment. Such semi-primary forests are less affected by local anthropogenic disturbances compared to more intensively managed ecosystems (Dupouey et al. 2002). Hence, these unmanaged systems are ideal areas to study the effects of environmental heterogeneity on established dynamics of temporal or spatial patterns in arthropod predator diversity and distribution without human impact when focusing on the two aspects of biodiversity “Assessment” and “Distribution”.

A precise assessment of biodiversity is the first step in biodiversity research and only a detailed understanding of communities allows a reliable prediction of changes in community structure and facilitates the development of conservation strategies. Biodiversity assessment includes knowledge about the life- and evolutionary history of organisms, species richness, rarity, endemism and distribution of species (Steele & Pires 2011). Sampling efficiency is an important prerequisite in the design of biodiversity inventories (Oliver et al. 1999), but can be challenging in environmentally complex habitats. Comprehensive inventories in habitats with high level of environmental heterogeneity therefore often require long-term effort and can be expensive, but the precision of diversity estimates and the success of biodiversity inventories may depend on such actions (Colwell & Coddington 1994).

The causes for a non-random distribution of organisms in space and interactions that determine the spatial distribution of individuals are among the fundamental questions in ecology (Townsend et. al 2002). Biodiversity is not distributed evenly in space, as some species are extremely abundant in some habitat areas but may be absent in others (Habel et al. 2013). These spatial distribution patterns play a profound role in shaping ecological processes such as competition, predation and mating systems (Borregaard et al. 2008), but may also affect the outcome of biodiversity assessments based on decisions made by the researchers. For a reliable inventory of biodiversity, a-priori knowledge about the spatial distribution of species inhabiting environmentally heterogeneous habitats is crucial (Keitt et al. 2002). This knowledge

facilitates the choice of sampling strategies and helps avoiding oversampling (Holland et al. 1999). Considerations of spatial aspects further have implications for the design of field studies, as results and interpretation depend on the distribution of the target taxa (Hayek & Buzas 1997). The spatial distribution can be influenced by environmental heterogeneity, as species at the local scale in forests for example form aggregations that mirror the distribution of suitable microhabitats, e.g. soil covered with litter, moss or deadwood (Niemelä et al. 1992, Ettema & Wardle 2002). This environmental heterogeneity is one of the most important factors regulating spatial and temporal patterns of organisms in terrestrial ecosystems (Bardgett et al. 2005). Hence, determining the factors that explain spatial patterns in arthropod communities is a prerequisite to predict the effect of habitat change on biodiversity (Illan et al. 2010).

Agricultural ecosystems are temporally less stable systems compared to forests (Connor et al. 2011). Continuous input of organic matter, agrochemicals and management practices such as harvest, soil management or irrigation are important anthropogenic disturbances in agricultural systems. The land used for agriculture compiles 50% of the world's terrestrial surface and has been used by humans for millennia in order to produce food, fibers, energy and other products (Tilman et al. 2002). However, anthropogenic activities led to unavoidable modifications of environmental heterogeneity, possibly followed by changes in biodiversity and trophic interactions. Thus, studies performed in such managed habitats provide insights in effects of anthropogenic alterations in habitat heterogeneity on arthropod communities and associated ecosystem functions and services when dealing with the aspects of biodiversity "Function" and "Service".

Many ecosystem functions¹ are sensitive to biodiversity decline (Naeem et al. 1999) and habitat alterations as a consequence of anthropogenic disturbances may negatively affect ecosystem functions (Hooper et al. 2005). For example, predators in terrestrial food webs can structure invertebrate communities through top-down effects (Preisser et al. 2005) and anthropogenic management practices may alter the availability of resources required by arthropod predators for optimal performance. Such alterations can lead to modifications of the structure of food webs in agricultural fields through bottom-up processes (Landis et al. 2000). Generalist arthropod predators (e.g. spiders, carabid beetles) in agricultural systems, for example, feed on herbivorous prey (e.g. aphids) or on decomposer prey (e.g. Collembola) and such mixed diets contribute significantly to a higher fitness of arthropod predators (Toft & Wise 1999). Anthropogenic alterations of the availability of basal resources (e.g. plant residue management) in agroecosystems may indirectly affect the function of arthropod predators via a trophic cascade that includes decomposer prey (Duyck et al. 2011).

¹ Function refers to the role of organisms within an ecological system, to the overall processes that maintain a system and to the services a system provides for humans or other organisms (Jax 2005).

An ecosystem service is a function of ecosystems that helps to sustain human welfare (Daily et al 1997, de Groot et al. 2002). In agricultural systems one specific ecosystem service, namely conservation biological control of pests provided by natural enemies (Barbosa 1998), has become an important component of more sustainable agricultural systems. Until recently the research on biological control of pests has primarily focused on highly specialized predators and strategies to maximize the efficiency of pest reduction by such species (Symondson et al. 2002). However the focus on specialist predators that only feed on one or a few pest species is moving towards predators with a broader prey spectrum (Welch et al. 2012). Generalist predator populations are present in arable fields early in the growing season before pest species colonize fields due to their ability to survive on decomposer prey and a higher resistance to disturbances (Wissinger 1997). Environmental heterogeneity may affect arthropod predators and their contribution to pest control. Sensitivity of pests and arthropod predators to climatic conditions may, for example, determine the damage by pests to host plants and the success of arthropod predators in pest control (Abbott et al. 2014). Understanding these climate-mediated effects is of particular importance, as it has implications for management strategies that try to mitigate the effect of future climate change on the ecosystem service of pest control.

The present dissertation focuses on two major groups of arthropod generalist predators, spiders (Araneae) and ground beetles (Carabidae), and their two most important prey groups from the belowground decomposer (springtails, Collembola) and aboveground herbivore (aphids, Aphidina) subsystem and the following section provides some background about these taxa. Spiders and carabid beetles are dominant predators present in all terrestrial ecosystems and are two diverse groups with more than 44.500 spider (Platnick 2014) and 40.000 carabid beetle (Lövei & Sunderland 1996) species described. As generalist predators most of these species consume insects on the ground surface or vegetation in forests (Perry 1994) and arable systems (Lövei & Sunderland 1996) and can therefore affect decomposer and herbivore prey populations and associated ecosystem services such as decomposition (Wise 2004) and biological control (Birkhofer et al. 2008). Generalist predators do not only act as biocontrol agents that regulate pest populations and prevent outbreaks in agricultural systems (Nyffeler & Benz 1987, Holland 2002, Rusch et al. 2013), but probably have an equally important role in forests (Mason et al. 1997). Spiders and carabid beetles are sensitive to environmental change or changes in a habitat structure (Bell et al. 2001, Uetz 1991, Horne 2007) and hence these groups may be used as indicators for management effects (Prieto-Benitez & Mendez 2011). Collembola are an abundant prey group comprising a considerable proportion of the diet of generalist predators in agricultural (Sunderland 1975, Agustí et al. 2003) and forest habitats (Chen & Wise 1997). In comparison to other prey groups (e.g. aphids, Diptera), the high quality of collembolan prey has been suggested to play a major role for the establishment of predator

populations early in the growing season and thus potentially affects pest suppression later in the season (Bilde et al. 2000). Aphids are common herbivore prey in agricultural systems infesting a wide range of arable and horticultural crops (Powell & Pickett 2003). Different aphid species damage plants directly by phloem sucking or indirectly by the transmission of plant viruses (Alford 2011) thus causing considerable economic losses in agriculture (e.g. Östman et al. 2003).

Research questions and hypothesis

Four studies were used to identify how the four aspects of biodiversity research (“Assessment”, “Distribution”, “Function” and “Service”) are affected by environmental heterogeneity (environmental conditions and availability of resources). Using different approaches, ranging from descriptive inventories over manipulative field experiments to meta-analyses of the existing literature, these studies focus on the importance of decisions about designs for biodiversity assessment of arthropods on the forest floor habitat (methodological approach, Chapter 1), factors responsible for the spatial distribution of arthropods in heterogeneous forest habitats (modeling approach, Chapter 2), effect of crop residue addition on detritus-based food chain and decomposition processes in agricultural system (experimental approach, Chapter 3) and effects of predator specialization, host plant and climatic conditions on the ecosystem service of aphid biological control (meta-analytical approach, Chapter 4).

Specific research questions were formulated and the following hypotheses were tested and are discussed in the four chapters:

- 1) “Assessment”: Which sampling design is most suitable to assess arthropod diversity during biodiversity inventories in forests?

The main hypothesis in the first study was that a stratified design based on expert knowledge provides a more complete estimate of spider diversity than a systematic design based on a regular grid of sample locations.

- 2) “Distribution”: What are the main factors responsible for the formation of spatial distribution patterns in spider species and collembolan prey in an environmentally heterogeneous forest floor habitat?

The hypotheses tested were that (a) environmental heterogeneity causes aggregated distributions of spiders, with different environmental conditions differentially affecting distantly related spider species and (b) activity density of spiders is higher in the patches with high collembolan activity density.

- 3) “Function”: What litter type (maize vs. wheat) strengthens the predator-decomposer-detritus food chain in organically and conventionally managed wheat fields?

The main hypotheses tested were that: (a) the addition of litter compared to litter-free control plots increases the activity-density of Collembola and thereby generalist predators. The most pronounced effects are expected in conventionally managed fields that provide limited alternative microhabitat structure in addition to wheat tillers (microhabitat structure-mediated effect), (b) the addition of wheat litter increases the activity-density of Collembola and generalist predators more than the addition of maize litter with lower resource quality (resource-mediated effect), (c) maize litter is primarily incorporated into the litter-decomposer-predator food chain in resource-poor conventionally managed fields and that (d) positive effects of litter addition on Collembola activity density lead to higher litter mass loss from litter bags.

- 4) "Service": How is the ecosystem service of aphid control affected by predator specialization, host plant and climatic conditions?

The hypotheses tested were that the effect of predators on aphid population size is (a) strongest in the presence of both generalist and specialist predators (additive effect), (b) weakest for aphid populations on plant groups that are rich in nitrogen and (c) strongest in areas with high climate seasonality.

Chapter outline

Chapter 1: Assessing spider diversity on the forest floor: expert knowledge beats systematic design

Elvira Sereda, Theo Blick, Wolfgang H.O. Dorow, Volkmar Wolters & Klaus Birkhofer – published in Journal of Arachnology (2014) 42:44–51

This chapter aims at comparing the assessment of spider diversity on the forest floor either by (i) a regular grid of pitfall traps (systematic design) or (ii) an expert-based distribution of traps (stratified design). The study was conducted in the strict forest reserve Locheiche situated in the National Park Kellerwald-Edersee (Hesse, Germany). Estimates of species richness, rarefied species richness and activity density calculated per trap were significantly higher in the stratified compared to the systematic design as hypothesized (1). The community composition based on the presence or absence of sampled species or on log-transformed activity densities differed significantly between the sampling designs. Three species contributed most to the significant dissimilarity between designs. *Pardosa saltans* Töpfer-Hofmann (Lycosidae) was more common in traps of the stratified design and *Tenuiphantes zimmermanni* (Bertkau) and *Walckenaeria cuspidata* Blackwall (both Linyphiidae) were more common in traps of the systematic design. In general, community composition in the systematic design varied less between trap locations compared to the stratified design. The results of this study show that a stratified design based on expert knowledge is better suited for complete biodiversity inventories of spider communities on the forest floor as it provides more comprehensive estimates of diversity and community composition. Stratified sampling designs are thus proposed for strict inventories in European forests and the use of systematic designs should be reserved for surveys in more homogeneous habitats or spatial analyses.

Chapter 2: Spatial distribution of spiders and epedaphic Collembola in an environmentally heterogeneous forest floor habitat

Elvira Sereda, Theo Blick, Wolfgang H.O. Dorow, Volkmar Wolters & Klaus Birkhofer- published in Pedobiologia (2012) 55: 241– 245

Describing distribution patterns of species and disentangling the factors responsible for the formation of spatial patterns in animal communities are crucial for understanding food web interactions. In the second chapter the data on the four most abundant spider species sampled in the systematic design (see chapter 1) was used to describe their spatial distribution in a beech dominated forest floor habitat. Additionally, the spatial distribution of three surface active Collembola groups was analyzed. The observed patterns were related to measures of environmental heterogeneity, overall predator activity (all ground beetles and spiders) and prey availability (all Collembola). Environmental heterogeneity was assessed based on moss cover or litter cover and the number of deadwood items on the forest floor. The distribution of spider species (particularly distantly related spider species) was affected by different abiotic properties as hypothesized in 2a. The distribution of *Coelotes terrestris* was positively related to the cover of moss, but negatively related to litter cover. The distribution of *Tenuiphantes zimmermanni* was negatively related to moss cover. The distribution of *Tapinocyba insecta* was negatively related to moss cover and the local availability of prey that contrasts hypothesis 2b. The distribution of Collembola was negatively related to local litter cover (*Lepidocyrtus* spp.) and positively related to the amount of medium-sized deadwood items (all other Entomobryidae). This chapter emphasizes the importance of taking environmental heterogeneity into account when performing ecological studies, as different habitat properties differentially affected the local activity density of spider species and Collembola and thus considerably contributed to the understanding of distribution patterns.

Chapter 3: The addition of crop residues affects a detritus-based food chain depending on litter type and farming system

Elvira Sereda, Volkmar Wolters & Klaus Birkhofer- submitted in Journal of Applied Ecology

The addition of litter resources derived from the crop plant itself or from other plants may not only increase food availability for decomposers (resource-mediated effects), but may also directly alter the habitat structure for decomposers and generalist predators (structure-mediated effects). Chapter 3 focuses on the effect of wheat (*Triticum aestivum* L.) and maize (*Zea mays* L.) litter resources on Collembola, generalist predator communities (spiders and ground beetles) and decomposition rates in organically and conventionally managed wheat fields. Further, differences between carbon incorporation from the maize or wheat plant biomass energy channel into the tissues of abundant predator species and Collembola taxonomic groups were analysed by means of stable isotope analysis. The experiment was conducted in three conventionally and three organically managed wheat fields around Giessen (Hesse, Germany). The activity density of predators was significantly higher in plots with maize litter compared to plots with wheat litter and under organic farming not confirming hypotheses 3a & b. In contrast, the activity density of Collembola was not significantly affected by litter type or farming system. Litter mass loss was highest in plots that received wheat litter under organic management and was negatively related to predator activity density. A high percentage of maize-borne carbon was observed in *Lepidocyrtus* spp. (57% and 39% in organically and conventionally managed fields respectively) compared to predator species (only 0-6% for spiders and 0-16% for carabids). Two spider species were more closely linked to the decomposer prey that consumed maize in organically managed fields and one carabid species showed this pattern in conventionally managed fields that contrasts hypothesis 3c. High litter decomposition levels, decomposer and generalist predator numbers were only observed in organically managed fields in wheat litter plots. The addition of crop residues from the growing crop under organic management may therefore be a promising farming practice to synergistically promote decomposition services and activity density of natural enemies.

Chapter 4: Effects of predator specialization, host plant and climate on biological control of aphids by natural enemies: a meta-analysis

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In temperate zones aphids are severe pests of crops causing significant economic damage. The biological control of aphids by natural enemies is an essential ecosystem service and of particular importance in pesticide-free farming systems. In the fourth chapter, knowledge about the effectiveness of different predator groups (specialists, generalists and assemblages of both specialists and generalists) for aphid control and the role of host plants and climatic conditions in aphid-predator interactions was summarized using a meta-analytical approach. The data used in this meta-analysis was extracted from the scientific literature that compared the size of aphid population in presence of different groups of natural enemies to the size of aphid population in absence of natural enemies. Specialist predators were the most effective biocontrol agents, as aphid reduction was higher in treatments where specialist predators were present, either alone or together with generalist predators not confirming hypothesis 4a about additive effects. Generalist predators also reduced aphid numbers effectively, though not to the same extent as specialist predators. The success of biological control of aphids by natural enemies in temperate regions is also modulated by bottom-up effects as aphids feeding on grasses and herbs were reduced more effectively compared to aphids feeding on legumes in line with hypothesis 4b. The meta-analysis further indicated that climatic conditions such as higher seasonality in precipitation and temperature facilitate aphid predation by natural enemies supporting hypothesis 4c. Facing climate change, the conditions under which natural enemies contribute successfully to the control of aphid pests should be considered in the development of future pest management strategies.

Results and Conclusions

The four main aspects of biodiversity research - “Assessment”, “Distribution”, “Function” and “Service”- address how environmental heterogeneity affect the diversity, spatial distribution and functional role of terrestrial arthropod predators in managed and unmanaged systems. Arthropod predators were selected as model group to address these issues, because they are numerically abundant, diverse and involved in important ecosystem functions and services. In the unmanaged forest system the aspects “Assessment” and “Distribution” focused on the effect of environmental heterogeneity on arthropod predator diversity and distribution (Chapter 1 & 2). In the managed system the aspects “Function” and “Service” added to the better understanding of the distribution of generalist predators by focusing on the effects of environmental heterogeneity on trophic interactions of terrestrial arthropod predators (Chapter 3 & 4).

The studies presented in this dissertation illustrate that the all the four main aspects of biodiversity research listed above are fundamentally affected by environmental heterogeneity of both environmental conditions (Chapter 1, 2 & 4) and resource availability and quality (Chapter 2, 3 & 4). The results show that environmental conditions had a positive effect on the aspects “Assessment” and “Service” and mixed effects on the aspect “Distribution”, while resource availability affected positively or negatively the aspects “Function” and “Distribution” respectively and had a mixed effect on the aspect “Service” (Fig. 2). These results fill important knowledge gaps regarding biodiversity assessments and factors responsible for the formation of spatial patterns, food web interactions between arthropod predators and their prey and associated ecosystem services.

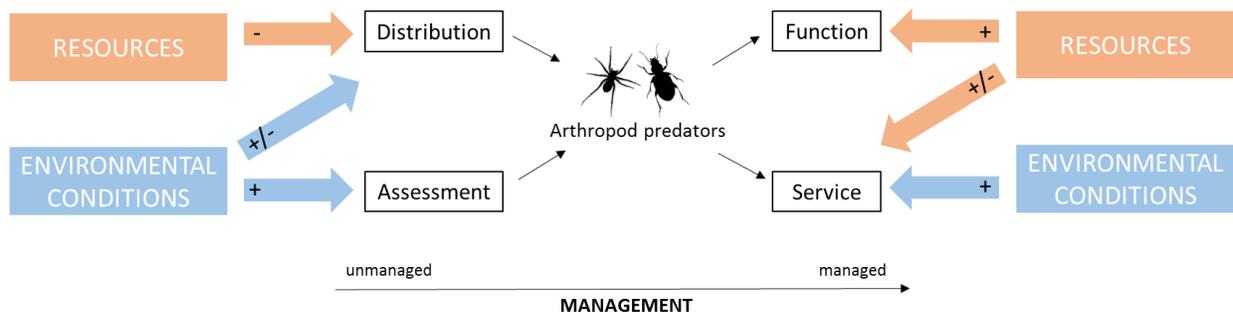


Figure 2 Summary of the identified effects of environmental heterogeneity (environmental conditions and resources) on the four main aspects of biodiversity research (“Assessment”, “Distribution”, “Function” and “Service”) in communities of arthropod predators in unmanaged and managed systems. Symbols in arrows stand for the effects of environmental heterogeneity that had a positive (+), negative (-) and mixed effects (+/-) on the aspects of biodiversity in the present dissertation.

Environmental conditions are important drivers of arthropod diversity (“Assessment”), spatial distribution (“Distribution”) and service provision (“Service”) (Chapter 1, 2 & 4). The quality of inventories and the understanding of distribution patterns in arthropod predators were generally improved by incorporating information about environmental heterogeneity. Spider diversity was higher when sampled with a stratified compared to a systematic design (Chapter 1) and activity densities of different spider species were related to a range of environmental variables (e.g. moss, litter cover, deadwood density, Chapter 2). The more comprehensive inventory by the stratified design is best explained by the arrangement of traps that cover a diverse range of microhabitats based on expert knowledge (Chapter 1). These results highlight the importance of considering environmental heterogeneity when assessing arthropod communities in heterogeneous habitats. Chapter 2 highlights the effect of specific environmental conditions on the distribution of arthropod predator species and potential prey which already became evident in chapter 1 documenting how important it is to account for environmental differences in biodiversity inventories. On a global scale, climatic conditions affect predator-prey interactions as biological control of pests by natural enemies was stronger in regions with more severe climate events (Chapter 4). This finding is particularly important to develop future management strategies that focus on conservation biological control under climate change.

Arthropod communities are also affected by the distribution and quality of resources as shown in this dissertation by approaching the aspects “Distribution”, “Function” and “Service” (Chapter 2, 3 & 4). In terms of resource distribution, only the activity density of one spider species (*Tapinocyba insecta*) was negatively related to the local availability of potential prey (Chapter 2). However, resource quality may also affect entire food web compartments (predator-decomposer-detritus food chain, Chapter 3) and the performance of arthropod predators in pest suppression (Chapter 4). Addition of maize litter promoted the activity density of generalist predators under organic farming, whereas the activity density of Collembola was not significantly affected by litter type or farming system. However, the analysis of naturally occurring C and N stable isotopes suggested that Collembola incorporated higher percentage of maize-borne carbon than predators. Two spider species (*Oedothorax apicatus* and *Walckenaeria vigilax*) were more closely linked to the decomposer prey that consumed maize in organically managed fields and one carabid species (*Bembidion lampros*) showed this pattern in conventionally managed fields (Chapter 3). In terms of arthropod predator performance, aphid suppression by predators was bottom up modulated, as predators were more effective in aphid suppression on grasses or herbs compared to legume crops (Chapter 4). These results of this meta-study show that environmental heterogeneity affects arthropod predators at scales beyond the previous case studies (Chapters 1-3), as fields with different

plant functional groups in the landscape may be expected to provide different levels of pest control services.

To conclude, this dissertation highlights the importance of accounting for environmental heterogeneity when assessing the diversity and composition of arthropod predator communities. This result of more basic research is shown to be relevant from an applied perspective in the face of global land use and climate change, as functions and services may directly be affected by environmental heterogeneity at small and large spatial scales. In terms of conservation effort, the choice of a stratified sampling design allows reliably assessments of the diversity of arthropod predators and should therefore be selected for strict inventory surveys. An a-priori understanding on the most influential environmental drivers of the spatial distribution of species is crucial to successfully establish such designs. In terms of applied aspects, the functional role of predators in predator-aphid prey interactions deserves particular attention in legume crops. The addition of crop residues may be a promising technique to naturally enhance abundances of natural enemies and to contribute significantly to pest control, independent of the farming system context. The results presented in this dissertation are further important in the face of global change, as a better understanding of the spatial relationships and trophic interactions of arthropod predators allow predictions about the consequences of future land-use and climate changes for the function of arthropod predators in terrestrial ecosystems.

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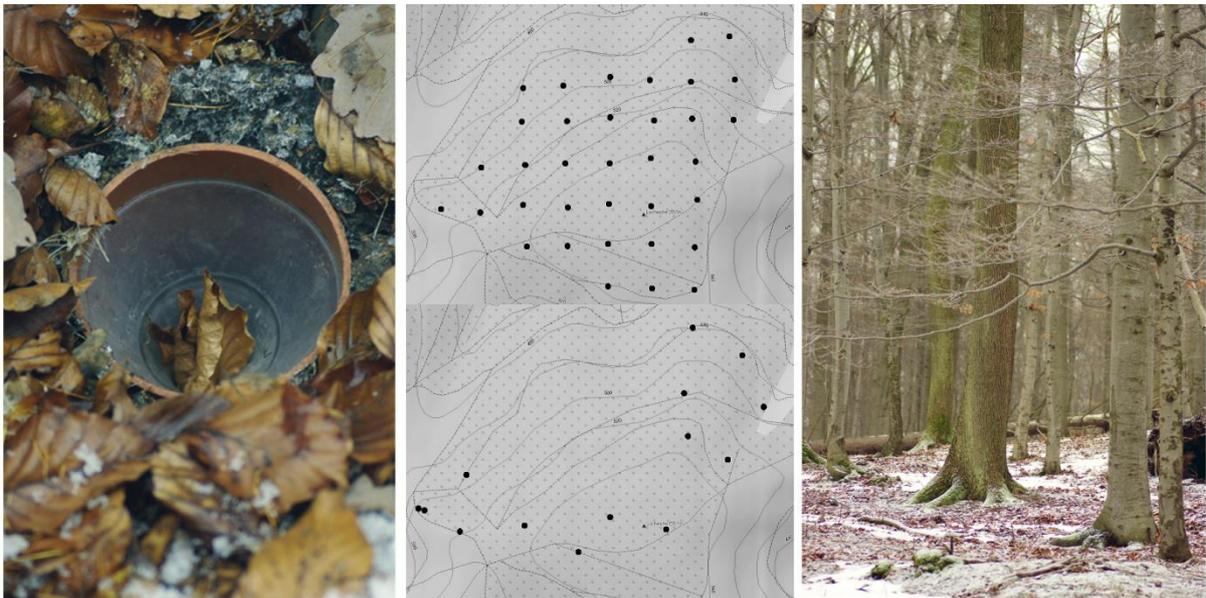
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CHAPTERS

Chapter 1: Assessing spider diversity on the forest floor: expert knowledge beats systematic design

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Assessing spider diversity on the forest floor: expert knowledge beats systematic design

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Abstract. The design of sampling schemes affects the results of biodiversity inventories. As an approach for quantifying the implications of such effects, we compared data on spider communities sampled in a beech-dominated forest floor habitat by 1) a regular grid of pitfall traps (systematic design) and 2) an expert-based distribution of traps (stratified design). We tested whether the two designs would lead to similar conclusions about the diversity and composition of ground-dwelling spider communities. Estimates of species richness, rarefied species richness and activity density calculated per trap were significantly higher in the stratified than in the systematic design. The community composition based on the presence or absence of sampled species or based on log-transformed activity densities differed significantly. Most of the dissimilarity between the community estimates of the two designs was attributable to three species, with *Pardosa saltans* Töpfer-Hofmann 2000 being more common in traps of the stratified design and *Tenuiphantes zimmermanni* (Bertkau 1890) and *Walckenaeria cuspidata* Blackwall 1833 being more frequently observed in traps of the systematic design. Our study suggests that a stratified sampling design is better suited for inventory surveys of spider communities of forest-floor habitats, as trap locations of this design reflect specific habitat needs. It is important to note that inventories are a major field for the application of such designs and that greater care is needed for the application of inferential statistics. For example, the non-randomness that is caused by expert selection of sampling sites may violate fundamental assumptions of simple linear models.

Keywords: Araneae, biodiversity, inventory, expert-based sampling, regular sampling, sampling design

Biodiversity research provides crucial information for the development of conservation strategies (Brooks et al. 2004). Strict inventories that generate comprehensive taxonomic lists for a discrete spatiotemporal unit are thus prerequisites for protecting species richness (Longino & Colwell 1997). Moreover, reliable estimates of species composition are needed to enable researchers to monitor biodiversity changes successfully (Dorow et al. 1992; Colwell & Coddington 1994; Buckley & Roughgarden 2004). As a contribution to this issue, we compared estimates of diversity and species composition of ground-dwelling spiders in a forest-floor habitat of a beech forest with two different sampling designs (systematic vs. stratified; e.g., Southwood & Henderson 2000).

Systematic designs that are based on a regular distribution of sampling locations in a study area (Woodcock 2005) are a common approach in diversity surveys (e.g., sampling transects for flower-visiting insects: Rundlöf et al. 2008). However, such a design depends on a priori decisions on the distance between sampling points in relation to the scale of environmental heterogeneity and the mobility of the focal taxa. A regular placement of sampling locations further assumes that environmental gradients which affect the analysed taxa are constant over the study area and do not vary over different spatial scales (Quinn & Keough 2002). Systematic designs may therefore be most appropriate for homogeneous habitats with weak or very simple environmental gradients. Dorow et al. (2007) suggested that stratified sampling of pre-defined subpopulations provides an appropriate alternative for biodiversity inventories, since it may improve precision by taking account of specific habitat types (see also Hayek & Buzas 1997). In stratified designs, specific microhabitats can be selected based on expert knowledge, and this approach may thus provide a more precise

estimate of diversity in heterogeneous study regions than random sampling (Southwood & Henderson 2000). In general, subjective selection of sampling locations biases analyses of ecological data by preconceptions of the investigator (Hirzel & Guisan 2002). However, subjectivity may be necessary and valid for certain research questions (McCune & Grace 2002). A strict inventory of species richness in heterogeneous habitats, for example, may only be reliable if the sampling design is biased by expert knowledge toward locations that support rare species and habitat specialists. An important assumption for using data from stratified designs is that information about the stratum is included as a predictor in statistical models (Quinn and Keough 2002). Comparative studies on the trade-offs between systematic and stratified designs are generally rare (Hirzel & Guisan 2002) and not available for invertebrate communities in temperate forests.

Our study focused on spiders, because this taxon forms a diverse group in temperate forests, and species are sensitive to environmental heterogeneity (Wunderlich & Blick 2006; Ziesche & Roth 2008; Birkhofer et al. 2010). Data were collected with pitfall traps in a 34.8 ha area for 16 months. The spatial arrangement of traps either followed a systematic design (regular grid) or a stratified design (expert-based selection of 14 pre-defined habitat structures). We hypothesize that the design based on expert knowledge would provide a more complete estimate of spider diversity than the systematic design based on a regular grid.

METHODS

Study site and sampling.—The study was conducted in the strict forest reserve “Locheiche” located in the National Park Kellerwald-Edersee in the northern part of Hesse, Germany

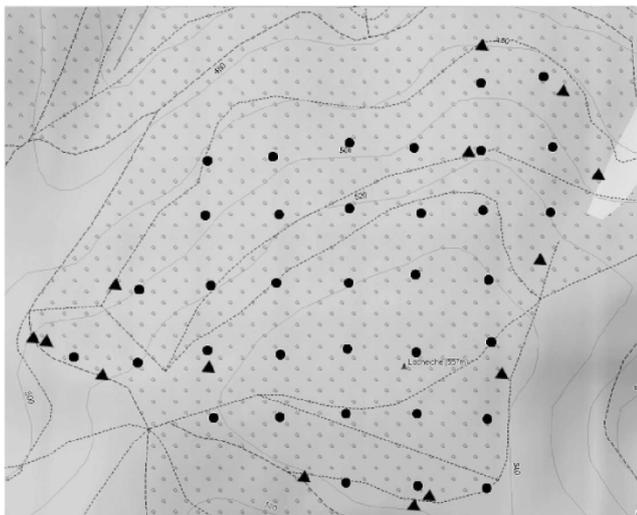


Figure 1.—Trap locations (points) in the 34.8 ha study area in the Kellerwald strict forest reserve “Locheiche” with the systematic (circles, one trap per point) and the stratified design (triangles, three traps per point).

(480–555 m a.s.l.; 51°08'30.45"N, 08°59'21.82"E) as a part of the long term studies in the forest reserves of Hesse (Dorow et al. 2010). The forest has not been managed since 1988, and beech trees (*Fagus sylvatica* L.) of an age of 81–120 years grow on the north and west exposed slopes of the study area. Additional tree species are *Quercus petraea* (Mattuschka) Liebl., *Larix decidua* Mill., *Acer pseudoplatanus* L. and *Picea abies* (L.) H. Karst. The annual mean temperature is 7.6°C, and the average annual precipitation is 765 mm (www.naturwaelder.de). The soil type is a cambisol with a pH of 5.1 in the uppermost horizon (Harmonized World Soil Database 2009).

In total, 77 funnel pitfall traps (diameter 10 cm, filled with approximately 200 ml of 70% ethanol and 99.5% glycerin at a

ratio of 2:1) were placed on the forest floor (for details see Dorow et al. 1992). Thirty-five traps were arranged in a regular grid with an inter-trap distance of 100 m (systematic design, referred to as SYS below: Fig. 1), and 14 triplets of traps (42 traps in total) were placed at pre-defined locations with a distance of 5 m between traps in a triplet (stratified design, referred to as STR below: Fig. 1, Table 1). We account for these differences in inter-trap distances within and between designs in our analyses (see statistical analysis). Forest inventory points at 100×100 m grid intersections were established on the forest floor, and pitfall traps of the systematic design were placed next to these standardized locations. Locations of the traps in the stratified design were defined based on an inspection of the study area and structures outlined in Table 1. Traps were open for 16 months (29 October 2008 to 23 March 2010) and were emptied every 4 weeks. In winter, traps were not emptied before spring due to snow cover from 11 December 2008 to 25 March 2009 and from 25 November 2009 to 23 March 2010. Spiders were determined using standard keys (Roberts 1987, 1995; Nentwig et al. 2013), and the nomenclature followed Platnick (2013). Juveniles were only identified to the family level and were not included in the analysis.

Statistical analysis.—Before analyses commenced diversity metrics were corrected for differences in sampling effort between designs (systematic: 35 traps vs. stratified: 42 traps) by using the following approach. Traditional diversity metrics, such as species richness (including species richness that was rarefied to a minimum of 24 individuals observed in one trap), activity density or the inverse Simpson index were calculated as means per trap over the 16 month study period and are presented as average values per trap. As the capture probability of pitfall traps varies with both activity and density of the species, the term activity density should be used (Heydemann 1957). To make the results more intuitive we used the inverse of the Simpson index instead of its original formulation, as an increase in the inverse index reflects an increase in diversity (Magurran 1988).

Table 1.—Description of trap locations in the stratified (1–14) and systematic design (201–235). Note that each location of the stratified design was sampled with three pitfall traps.

Trap ID	Description
1	Beech-spruce-larch forest with needle and leaf litter
2	Border of forest-driveway with <i>Avenella flexuosa</i>
3	Border of forest-driveway with grasses and <i>Urtica dioica</i>
4	Woodrush beech forest, underlayer without herb layer
5	Woodrush beech forest, stony hilltop
6	Dense beech young stands with maple
7	Charcoal pile with <i>Cardamine bulbifera</i>
8	Edge of the forest with several shrub species
9	Charcoal pile with grass and young beech stands
10	Glade with grass and young beech stands
11	Young spruce plantation
12	Mixed beech-oak-larch forest
13	Border of forest-driveway, stony, poor herb layer
14	Border of forest-driveway, with young stands of beech and larch
201–206, 208–224, 226, 227, 230–232, 235	Forest floor covered with beech litter, without herb layer
225, 228, 229, 233, 234	Forest floor covered with beech and needle litter, without herb layer
207	Forest floor with grass and young stands of beech

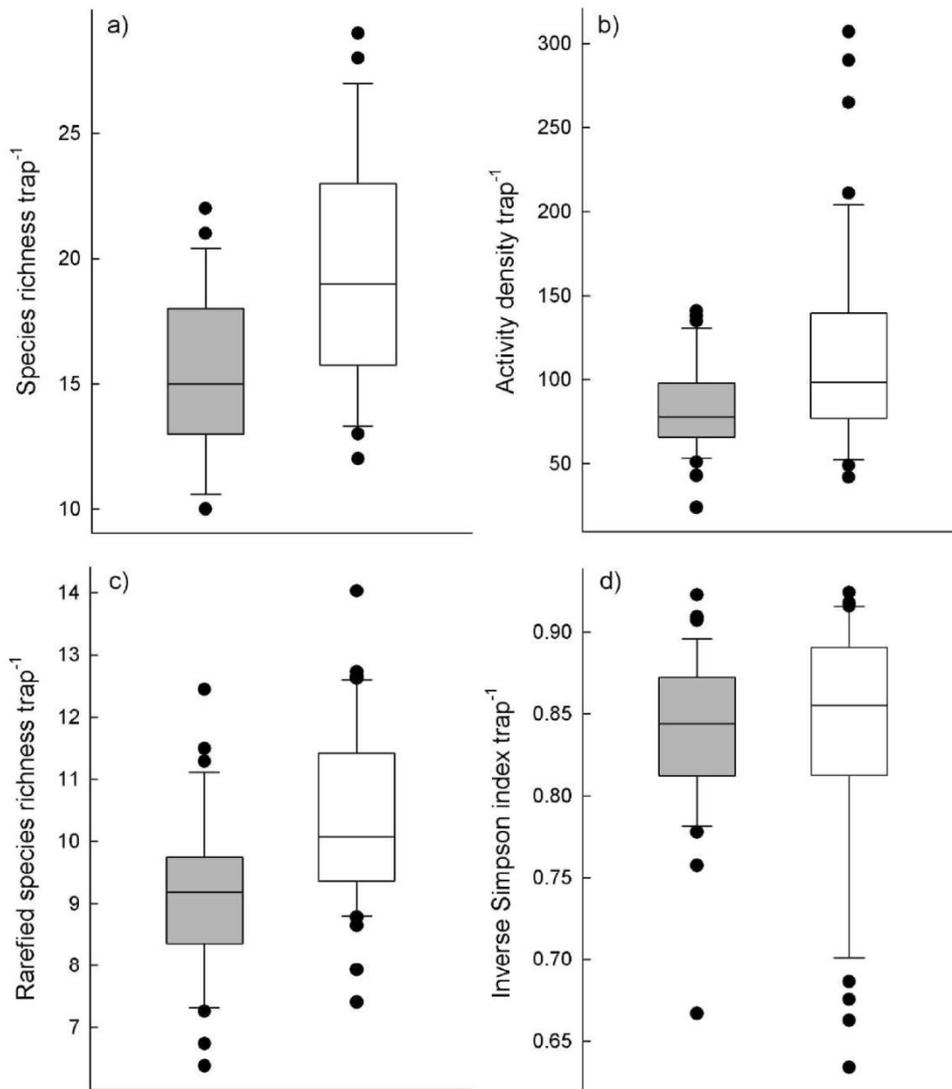


Figure 2.—Median, 75 and 95% quartiles and outliers for a) species richness, b) activity density, c) rarefied species richness ($n = 24$) and d) inverse Simpson index per pitfall trap for spider assemblages sampled in a systematic (SYS, gray) or stratified (STR, white) design.

Diversity and abundance metrics were compared between designs by one-way permutational analysis of variance with permutation of residuals under a reduced model and design (systematic vs. stratified) as fixed factor (PERMANOVA: Anderson 2001). We included X and Y coordinates of all trap locations as co-variables in our models to account for the fact that some traps within, but also between, designs were located more closely to each other. All univariate tests were based on Euclidean distances and 10,000 permutations. The univariate PERMANOVA based on Euclidean distances is analogous to a traditional one-way ANOVA, but P-values are obtained from permutations (Anderson and Millar 2004). We thus avoid the assumption of normality in our statistical models (e.g., Anderson et al. 2008) and show all results using box and whisker plots as recommended by Dytham (2003) for such data.

To assess the differences in community composition between sampling designs, we calculated resemblance matrices based on

Sørensen (presence or absence of species) or Bray-Curtis ($\log x+1$ -transformed activity densities) distances between traps in both designs. We log-transformed activity density data to weigh down the contribution of abundant species to differences between the two designs and to emphasize the importance of rare species (Clarke et al. 2006). We used principal coordinate analysis (PCO) based on Bray-Curtis distances to visualize the dissimilarity of communities between traps from both designs (Clarke & Warwick 2001). To explore the individual contribution of species to dissimilarities between the two designs, we used similarity percentage analysis (SIMPER; Clarke & Warwick 2001). We further tested for homogeneity of multivariate dispersion by comparing the distances of communities per traps to group centroids between both designs (PERMDISP routine). All analyses were performed using PRIMER version 6.1.13 with the PERMANOVA + add-on version 1.0.3 (PRIMER-E, Plymouth, UK: Anderson et al. 2008).

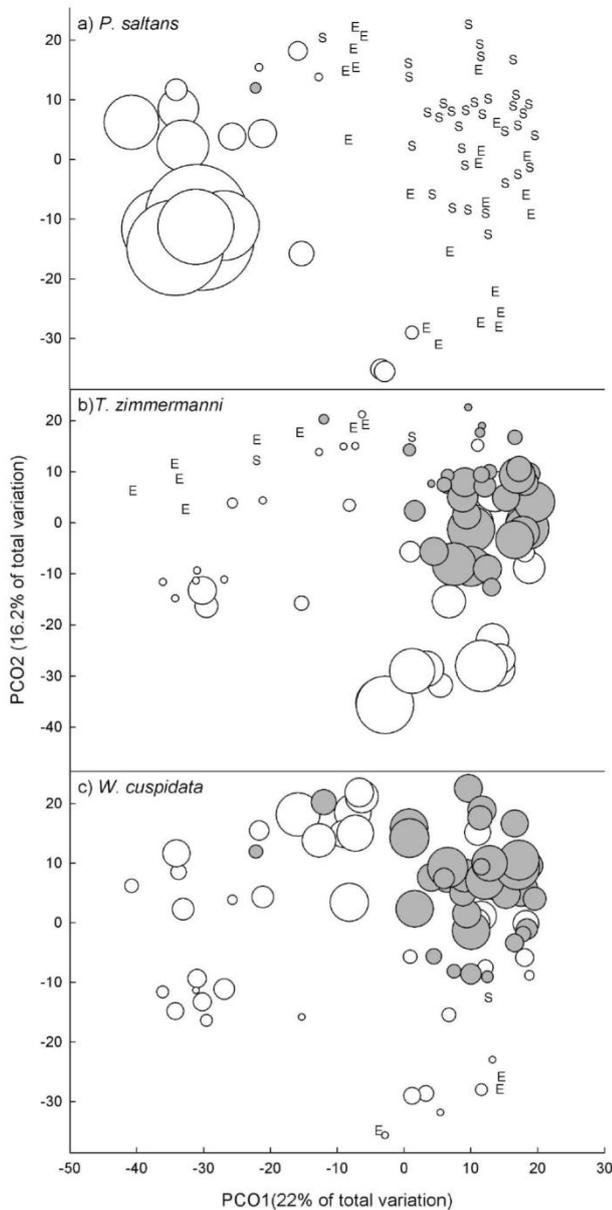


Figure 3.—Principal coordinates analysis based on Bray-Curtis similarities of log-transformed activity density data from all traps. The size of the bubbles corresponds to the number of individuals sampled in each pitfall trap in the systematic (SYS, gray) or stratified (STR, white) design for a) *Pardosa saltans* (bubble size range: 1–173 individuals), b) *Tenuiphantes zimmermanni* (1–62 individuals) and c) *Walckenaeria cuspidata* (1–39 individuals). Letters stand for traps that did not contain any individuals from the species in the stratified (expert-based, E) or systematic (S) sampling. Note that bubbles may overlap.

RESULTS

In total, 8012 adult spiders were sampled from 96 species in 14 families (see Appendix 1). Traps in the STR design contained 90 species, of which 42 were exclusively found in the STR design. Traps of the SYS design contained 54 species, of which 6 were exclusively found in the SYS design. Species

richness (pseudo- $F_{1,74} = 31.59$, $P < 0.001$) and activity density (pseudo- $F_{1,74} = 13.99$, $P < 0.001$) per trap were significantly lower in the SYS than in the STR design (Figs. 2a,b). Rarefied species richness was also significantly lower in the SYS design (Fig. 2c; pseudo- $F_{1,74} = 17.18$, $P < 0.001$). The inverse Simpson index did not differ significantly between designs (Fig. 2d; pseudo- $F_{1,74} = 1.10$, $P = 0.301$).

Community composition based on the presence or absence of species in traps (Sørensen similarity, pseudo- $F_{1,74} = 7.04$, $P < 0.001$) or based on log-transformed activity densities (Fig. 3, Bray-Curtis similarity, pseudo- $F_{1,75} = 8.02$, $P < 0.001$) differed significantly between the two designs. Although both designs shared 47 out of 96 species, similarity percentage analyses indicated that three common species contributed most to the significant dissimilarity between communities (Fig. 3). *Pardosa saltans* Töpfer-Hofmann 2000 was more common in traps of the STR design (mean abundance of 51 individuals across all traps) and almost absent from the SYS design (only two individuals were collected in one trap of the systematic design). In contrast, *Tenuiphantes zimmermanni* (Bertkau 1890) and *Walckenaeria cuspidata* Blackwall 1833 were more frequently observed in traps of the SYS design. In general, the multivariate dispersion of community composition was significantly smaller in the SYS design, indicating that community composition varied less between traps than in the STR design (PERMDISP; $F_{1,75} = 49.18$, $P < 0.001$).

DISCUSSION

Our study suggests that the stratified design provides a more representative estimate of diversity and a more comprehensive summary of community composition in the study area than a systematic design. Species richness was higher in the stratified design, and the number of exclusive species only sampled with this design was almost an order of magnitude higher than for the systematic design. However, expert knowledge is needed to select sample locations in stratified designs in order to sample all relevant microhabitats. In contrast, systematic designs do not require such knowledge, but decisions about the extent of the sampling area, the number of sample points and the inter-point distances also require a priori assumptions.

It has been previously suggested that systematic designs may not adequately represent the composition of communities, since environmental gradients that acted on the mammal species studied were not covered (Read et al. 1988; Pearson & Ruggiero 2003). The effectiveness of stratified methods to sample rare species in heterogeneous habitats was also highlighted for plant communities in coastal wetlands (Croft & Chow-Fraser 2009). In our study, the number of unique spider species was seven times higher in the stratified design, even though the same sampling technique was used and the survey lasted over the same period (16 months). Differences between designs were attributed to some common spider species; for example, *P. saltans* was predominantly collected by traps in the stratified design. This pattern highlights preferences of *P. saltans* for particular forest habitats (e.g., Hendrickx et al. 2001) that were only sampled in the stratified design. This observation also demonstrates the danger of missing specific habitat types if trap locations are arranged in a regular grid that is related to the number, size and distribution of habitats in the study area.

Tenuiphantes zimmermanni and *W. cuspidata* were more frequently observed in traps of the systematic design, but both species were also present at particular locations of the stratified design. This pattern reflects the rather broad habitat preferences of these two sheet-web weavers.

Community composition of spiders in individual traps was significantly more homogeneous in the systematic design than in the stratified design, reflecting a more diverse range of microhabitats sampled in the stratified design. The vast majority of Central European beech forests consist of a relatively uniform stand of dense beech trees without a shrub and herb layer (Standovár & Kenderes 2003; Gálhidy et al. 2006). These areas are interspersed by small patches of different structure (e.g., wayside herbs, seepage springs, glades, rocks). To cover such elements in a systematic design requires an enormous effort and resources that may not be available for biodiversity inventories. Although the study presented here clearly illustrates that a stratified sampling design is more efficient than a systematic design, we acknowledge that the observed differences may be limited to the study location. Thus additional studies are needed to confirm our results for other habitats in general.

To conclude, our results suggest that forest surveys aiming at strict inventories of ground-active arthropods should not be based on systematic designs even in moderately heterogeneous study areas. That approach is more expensive and provides a less precise estimate of diversity and community composition. We propose, instead, that stratified designs should be used for strict inventories in European forests if expert knowledge is available and that the use of systematic designs should be reserved for spatial analyses (e.g., Birkhofer et al. 2011; Sereda et al. 2012) or surveys in more homogeneous habitats (e.g., Diekötter et al. 2010). It is important to note that inventories are a major field for the application of such designs and that greater care is needed for the application of inferential statistics. For example, the non-randomness that is caused by expert selection of sampling sites may violate fundamental assumptions of simple linear models.

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Appendix 1.—Species and number of individuals (juveniles excluded) sampled by the systematic (SYS) and the stratified (STR) approach.

Family/Species	SYS	STR
Agelenidae		
<i>Coelotes terrestris</i> (Wider 1834)	507	479
<i>Histopona torpida</i> (C. L. Koch 1837)	115	87
<i>Inermocoelotes inermis</i> (L. Koch 1855)	129	213
<i>Malthonica silvestris</i> (L. Koch 1872)	21	18
Amaurobiidae		
<i>Amaurobius fenestralis</i> (Ström 1768)	26	29
Clubionidae		
<i>Clubiona compta</i> C. L. Koch 1839	0	1
<i>C. reclusa</i> O. P.-Cambridge 1863	0	1
<i>C. terrestris</i> Westring 1851	1	6
Dictynidae		
<i>Cicurina cicur</i> (Fabricius 1793)	128	211
Dysderidae		
<i>Dysdera erythrina</i> (Walckenaer 1802)	0	1
<i>Harpactea hombergi</i> (Scopoli 1763)	0	8
Gnaphosidae		
<i>Drassodex lesserti</i> (Schenkel 1936)	0	2
<i>Haplodrassus signifer</i> (C. L. Koch 1839)	0	1
<i>H. silvestris</i> (Blackwall 1833)	1	16
<i>H. umbratilis</i> (L. Koch 1866)	0	1
<i>Micaria pulicaria</i> (Sundevall 1831)	0	2
<i>Zelotes clivicola</i> (L. Koch 1870)	0	17
<i>Z. erebeus</i> (Thorell 1871)	0	3
<i>Z. subterraneus</i> (C. L. Koch 1833)	0	128
Hahniidae		
<i>Hahnia helveola</i> Simon 1875	3	7
<i>H. pusilla</i> C. L. Koch 1841	0	17
Linyphiidae		
<i>Agyneta conigera</i> (O. P.-Cambridge 1863)	0	1
<i>Asthenargus paganus</i> (Simon 1884)	0	2
<i>Bathyphantes gracilis</i> (Blackwall 1841)	0	1
<i>B. nigrinus</i> (Westring 1851)	0	1
<i>Bolyphantes alticeps</i> (Sundevall 1833)	0	5
<i>Centromerus brevivulvatus</i> Dahl 1912	1	0
<i>C. cavernarum</i> (L. Koch 1872)	2	66
<i>C. dilutus</i> (O. P.-Cambridge 1875)	54	167
<i>C. pabulator</i> (O. P.-Cambridge 1875)	1	48
<i>C. sylvaticus</i> (Blackwall 1841)	21	134

Appendix 1.—Continued.

Family/Species	SYS	STR
<i>Ceratinella brevis</i> (Wider 1834)	1	35
Linyphiidae		
<i>Dicymbium tibiale</i> (Blackwall 1836)	28	35
<i>Diplocephalus cristatus</i> (Blackwall 1833)	0	1
<i>D. latifrons</i> (O. P.-Cambridge 1863)	1	13
<i>D. picinus</i> (Blackwall 1841)	51	122
<i>Diplostyla concolor</i> (Wider 1834)	1	65
<i>Drapetisca socialis</i> (Sundevall 1833)	3	0
<i>Entelecara erythropus</i> (Westring 1851)	0	1
<i>Erigone atra</i> Blackwall 1833	0	1
<i>Formiphantes lephthyphantiformis</i> (Strand 1907)	0	1
<i>Gonatium rubellum</i> (Blackwall 1841)	26	40
<i>Helophora insignis</i> (Blackwall 1841)	0	42
<i>Jacksonella falconeri</i> (Jackson 1908)	8	0
<i>Lepthyphantes minutus</i> (Blackwall 1833)	0	1
<i>L. nodifer</i> Simon 1884	0	1
<i>Linyphia hortensis</i> Sundevall 1830	0	3
<i>Macrargus rufus</i> (Wider 1834)	36	34
<i>Maso sundevalli</i> (Westring 1851)	0	2
<i>Micrargus herbigradus</i> (Blackwall 1854)	26	130
<i>Microneta viaria</i> (Blackwall 1841)	36	26
<i>Monocephalus fuscipes</i> (Blackwall 1836)	0	1
<i>Nerienne clathrata</i> (Sundevall 1830)	1	1
<i>N. emphana</i> (Walckenaer 1841)	1	0
<i>Nusoncus nasutus</i> (Schenkel 1925)	1	1
<i>Obscuriphantes obscurus</i> (Blackwall 1841)	0	1
<i>Palliduphantes pallidus</i> (O. P.-Cambridge 1871)	1	3
<i>Pocadicnemis pumila</i> (Blackwall 1841)	0	1
<i>Porrhomma campbelli</i> F. O. P.-Cambridge 1894	4	1
<i>P. pallidum</i> Jackson 1913	7	13
<i>Pseudocarorita thaleri</i> (Saaristo 1971)	4	3
<i>Saloca diceros</i> (O. P.-Cambridge 1871)	26	64
<i>Tapinocyba insecta</i> (L. Koch 1869)	327	256
<i>T. pallens</i> (O. P.-Cambridge 1872)	64	161
<i>T. praecox</i> (O. P.-Cambridge 1873)	0	1
<i>Tenuiphantes alacris</i> (Blackwall 1853)	4	2
<i>T. cristatus</i> (Menge 1866)	1	15
<i>T. flavipes</i> (Blackwall 1854)	10	73
<i>T. mendei</i> (Kulczyński 1887)	4	12
<i>T. tenebricola</i> (Wider 1834)	1	34
<i>T. tenuis</i> (Blackwall 1852)	0	7
<i>T. zimmermanni</i> (Bertkau 1890)	443	487
<i>Thyreosthenius parasiticus</i> (Westring 1851)	1	0
<i>Walckenaeria acuminata</i> Blackwall 1833	0	11
<i>W. corniculans</i> (O. P.-Cambridge 1875)	24	45
Linyphiidae		
<i>W. cucullata</i> (C. L. Koch 1836)	47	111
<i>W. cuspidata</i> Blackwall 1833	566	407
<i>W. dysderoides</i> (Wider 1834)	8	7
<i>W. mitrata</i> (Menge 1868)	0	1
<i>W. obtusa</i> Blackwall 1836	4	14
Liocranidae		
<i>Agroeca brunnea</i> (Blackwall 1833)	0	4
<i>Apostenus fuscus</i> Westring 1851	0	2
Lycosidae		
<i>Alopecosa pulverulenta</i> (Clerck 1757)	0	12
<i>Pardosa amentata</i> (Clerck 1757)	0	1
<i>P. pullata</i> (Clerck 1757)	0	1
<i>P. lugubris</i> (Walckenaer 1802)	0	45
<i>P. saltans</i> Töpfer-Hofmann 2000	2	1018

Appendix 1.—Continued.

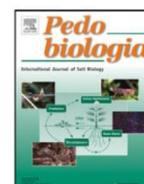
Family/Species	SYS	STR
<i>Trochosa terricola</i> Thorell 1856	2	75
<i>Xerolycosa nemoralis</i> (Westring 1861)	0	1
Salticidae		
<i>Euophrys frontalis</i> (Walckenaer 1802)	0	3
<i>Neon reticulatus</i> (Blackwall 1853)	9	9
Segestriidae		
<i>Segestria senoculata</i> (Linnaeus 1758)	0	3
Tetragnathidae		
<i>Metellina segmentata</i> (Clerck 1757)	1	0
<i>Pachygnatha degeeri</i> Sundevall 1830	3	1
Theridiidae		
<i>Robertus lividus</i> (Blackwall 1836)	33	41
<i>R. scoticus</i> Jackson 1914	7	4
Total:	2833	5179

Chapter 2: Spatial distribution of spiders and epedaphic Collembola in an environmentally heterogeneous forest floor habitat

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Spatial distribution of spiders and epedaphic Collembola in an environmentally heterogeneous forest floor habitat

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ABSTRACT

Describing the biotic and abiotic processes that are responsible for the formation of spatial patterns in predators and their prey is crucial for improving our understanding of food–web interactions. We studied the spatial distribution of four abundant spider species and three common groups of epedaphic Collembola prey in a beech-dominated (*Fagus sylvatica*) forest floor habitat and related the observed patterns to environmental heterogeneity, overall predator activity (all ground beetles and spiders) and prey availability (all Collembola) at the local scale. Spiders and epedaphic Collembola were sampled over 392 days in a spatially explicit design based on a regular grid of 25 pitfall traps (inter-trap distance 100 m). Environmental heterogeneity was characterized by cover of moss and litter as well as the amount of dead wood at each trap location. We first used the index of dispersion to characterize the spatial distribution of spider species and Collembola and then related the observed patterns to environmental heterogeneity, predator and prey availability while testing for spatial autocorrelation within the same models. All taxa were significantly more aggregated than expected from the assumption of random distribution. The distribution of spider species was positively (*Coelotes terrestris*) or negatively (*Tenuiphantes zimmermanni* and *Tapinocyba insecta*) related to the cover of moss and negatively related to litter cover (*C. terrestris*) or the local availability of prey (*T. insecta*). The distribution of Collembola was negatively related to local litter cover (*Lepidocyrtus* spp.) and positively related to the amount of medium deadwood pieces (all other Entomobryidae). Our study suggests that none of the spider species preferred areas of low overall predator activity density. Moreover, it does not indicate association of spider species to prey-rich areas at the analyzed scale of 100 m. It further highlights the importance of environmental heterogeneity, as different habitat properties differentially affected the local activity density of spiders and Collembola and thus considerably contributed to the understanding of distribution patterns.

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Introduction

Explaining the distribution of species in space remains one of the major challenges in ecology (e.g. Cornulier and Bretagnolle 2006). A particular difficulty concerning most invertebrates is that the processes creating spatial patterns often remain hidden in small and cryptic species (Ettema and Wardle 2002). This is a major shortcoming, since these species significantly contribute to both richness and functioning of terrestrial communities (Van der Putten et al. 2004). A better understanding of how the spatial distribution of small and cryptic species is differentially affected by abiotic and biotic processes will therefore be crucial for identifying drivers of community composition and for assessing patterns of biodiversity (Margules and Pressey 2000; Keitt et al. 2002). In the study reported

here, we approached this issue by investigating the distribution of four abundant spider species and three groups of their potential collembolan prey in relation to the spatial pattern of biotic and abiotic habitat properties on the floor of a beech (*Fagus sylvatica* L.) forest in Germany.

Two closely linked processes contribute to the formation of spatial patterns of individual species: biotic interactions and response to environmental heterogeneity. Concerning biotic interactions, many ground-dwelling spider species have been shown to intensively compete for resources (Marshall and Rypstra 1999). Moreover, ground-active spiders are frequently involved in intraguild predation (Birkhofer and Wolters 2012) and are often cannibalistic (Wise 1993). As a consequence, predator–predator interactions may affect habitat choice (Eichenberger et al. 2009) and the overall spatial distribution of spiders (e.g. Birkhofer et al. 2006). Predator–prey interactions provide another class of biotic factors affecting the distribution of spiders (e.g. Sih 2005). Collembola, for example, are important prey of forest-living spiders (Kajak

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1995; Rusek 1998; Lawrence and Wise 2000) and may even occupy microhabitats with less suitable environmental conditions to avoid areas with high spider activity density (Birkhofer et al. 2010).

The effect of environmental heterogeneity on the formation of spatial patterns relates to factors such as microclimatic conditions or specific structural features of the habitat (Morris 2000). On the forest floor, dead wood, moss cover and litter have been shown to be particularly important structures creating complex environmental conditions that affect habitat choice of ground-dwelling arthropods (e.g. Grear and Schmitz 2005; Ziesche and Roth 2008). Neglecting these structural features when analyzing spatial patterns may thus lead to oversimplified descriptions of spatial relationships (Birkhofer et al. 2010). Considering the importance of both Collembola in decomposition processes (Lawrence and Wise 2000) and spiders as predators in arthropod food-webs (Wise 2004), a better understanding of the spatial relationships of these two groups is essential for disentangling the factors driving biodiversity on the floor of forest ecosystems.

Using the index of dispersion (Upton and Fingleton 1985) and distance based linear models (Legendre and Anderson 1999) we describe the spatial distribution of the taxa investigated and their relationship to biotic and abiotic habitat properties. The study was carried out in a pure beech (*F. sylvatica* L.) forest reserve in Germany. We hypothesized that (1) environmental heterogeneity causes aggregated distributions, with abiotic habitat properties differentially affecting different taxa (particularly distantly related spider species), (2) competitive interactions among predators may lead to aggregation of spider species in predator-poor areas and that (3) spiders are more active in patches with high collembolan activity density.

Materials and methods

Study site and sampling

The study was conducted in the strict forest reserve “Locheiche” located in the National Park “Kellerwald-Edersee” in the northern part of Hesse, Germany (480–555 m a.s.l.; center of sample grid: 51°8′30.45″N, 8°59′21.82″E). The forest has not been managed since 1988 and beech trees (*F. sylvatica* L.) between 81 and 120 years of age are growing on north and west exposed slopes in the study area. Additional tree species are *Quercus petraea* (Matuschka) Liebl., *Larix decidua* Mill., *Acer pseudoplatanus* L. and *Picea abies* (L.) H. Karst. The annual mean temperature is 7.6 °C and the average annual precipitation is 765 mm (www.naturwaelder.de). The soil type is a cambisol with a pH of 5.1 in the uppermost horizon (Harmonized World Soil Database 2009).

Twenty five pitfall traps (diameter 10 cm, filled with 200 ml of 70% ethanol and glycerin, for details see Dorow et al. 1992) were placed in a regular grid on the forest floor (5 × 5 traps, inter-trap distance = 100 m). Traps were open throughout 392 days (from October 29, 2008 to November 25, 2009) and were emptied every 4 weeks except in winter (December 11, 2008 to March 25, 2009). Environmental heterogeneity at the forest floor was defined based on moss and litter cover and the number of dead wood items around each trap location. Moss cover was recorded in quadrats of 5 m × 5 m centered at each pitfall trap, litter cover and the number of deadwood items were quantified in a radius of 2.5 m around each pitfall trap (McElhinny et al. 2005). This definition of forest floor heterogeneity was used because of the known preferences of epedaphic Collembola and spiders for moss, litter and deadwood-rich habitats (Uetz 1976; Bultman and Uetz 1982; Evans et al. 2003; Varady-Szabo and Buddle 2006; Salamon et al. 2008). The total number of Collembola as well as the total number of spiders and ground beetles were used as proxies for either prey or predator

activity density, respectively at each trap location. The probability of falling into a pitfall trap varies with both activity and density of the organisms caught. Hence the term activity density should be used (e.g. Heydemann 1957).

Statistical analysis

Four abundant spider species that were present in at least 24 pitfall trap sites, *Coelotes terrestris* (Wider) (Agelenidae), *Tenuiphantes zimmermanni* (Bertkau), *Tapinocyba insecta* (L. Koch) and *Walckenaeria cuspidata* Blackwall (all Linyphiidae), were selected for spatial analyses. The number of individuals of each spider species and of three groups of abundant epedaphic Collembola (*Lepidocyrtus* spp., other Entomobryidae and Tomoceridae, always present in traps) sampled over the study period was pooled for each trap location. These data were used to calculate the index of dispersion (ID) as an overall measure of the deviation from a random (Poisson) distribution. Index values below 1 suggest a more regular distribution, values above 1 indicate that individuals occur clustered compared to a random distribution. Results of a chi-square test are provided to indicate significance of this deviation. We used distance-based linear models (Legendre and Anderson 1999) to relate the activity density of each spider species and the three Collembola groups to environmental characteristics (moss cover, litter cover and amount of deadwood) and to predator or prey activity density, while also testing for spatial autocorrelation by including the trap coordinates as potential predictors. Activity densities of each spider species or Collembola group at each trap location were transformed into a resemblance matrix using Bray–Curtis distances. Distance-based linear models then used the following indicator groups of predictor variables to predict variation in activity density: (1) location (*x* and *y* coordinates of trap locations), (2) litter cover, (3) amount of deadwood (divided in size classes <2 cm, 2–<7 cm and 7–20 cm), (4) moss cover, (5) overall predator activity density (ground beetles and all spiders, excluding individuals of the modeled species) and (6) overall Collembola activity density. Selection of the most parsimonious model was based on a stepwise variable selection using the AICc selection criteria for small sample sizes. Statistical significance of the selected indicator groups of predictor variables was assessed at an alpha level of 0.05 and tested against 9999 permutations.

Results

In total 1319 adults of the four dominant spider species *C. terrestris* (346 males, 49 females), *T. zimmermanni* (59 males, 239 females), *T. insecta* (193 males, 58 females) and *W. cuspidata* (81 males, 294 females), 5089 ground beetles and 33,651 Collembola (21,007 *Lepidocyrtus* spp., 4344 other Entomobryidae and 8300 Tomoceridae) were sampled. *T. zimmermanni* and *W. cuspidata* showed two peaks in activity density in March and August, and in April and October respectively. *T. insecta* and *C. terrestris* only showed one peak from April to March, and from August to September respectively (Fig. 1a). Collembola were present throughout the sampling period, and different groups showed peaks in March and July to October (Fig. 1b).

Spiders

All spider species and Collembola groups showed a highly significant over-dispersion in the study area (Figs. 2–4). Locations of clusters differed between taxa and biotic or abiotic habitat properties explained significant portions of the variation in activity densities for all taxa (Araneae and Collembola) with the exception of *W. cuspidata* and Tomoceridae where no model solution was found. The activity density of *T. zimmermanni* ($R^2 = 0.33$; $P < 0.001$)

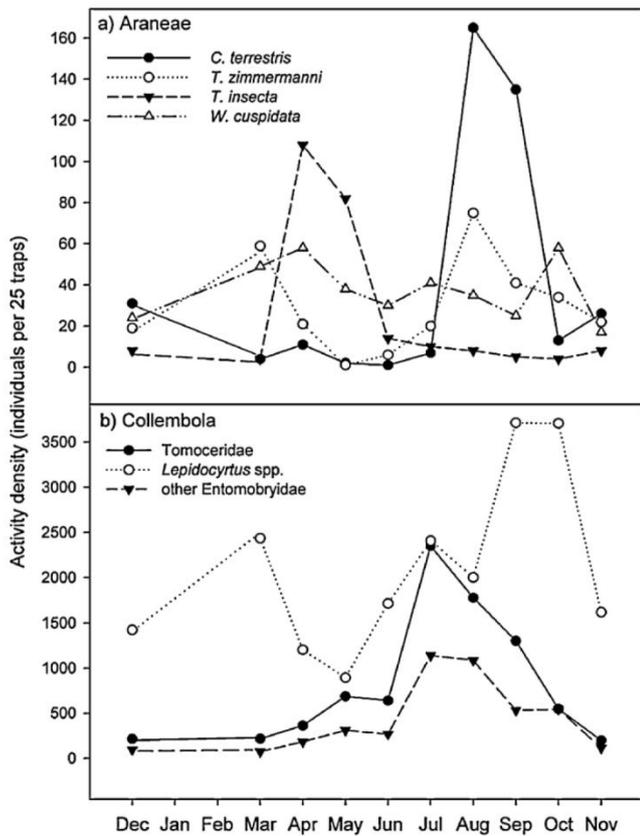


Fig. 1. Activity density of (a) spider species and (b) Collembola groups during the study period.

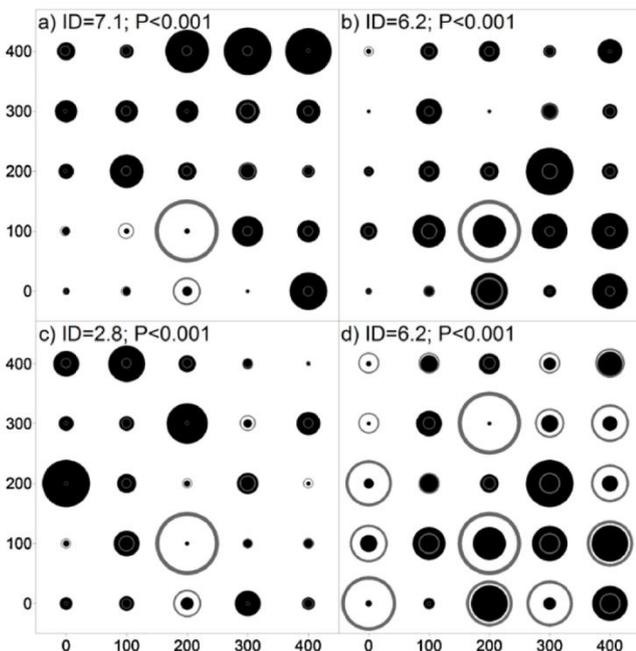


Fig. 2. Distribution of spider species (black bubbles) and (a–c) moss cover (grey circles, cover classes 0–5) or (d) litter cover (grey circles, cover classes 1.5–5) in the study area for (a) *T. zimmermanni* (0–31 ind.), (b) *C. terrestris* (2–38 ind.), (c) *T. insecta* (4–24 ind.) and (d) *C. terrestris* (2–38 ind.) including the index of dispersion (ID) and *P*-values for a deviation from a Poisson distribution.

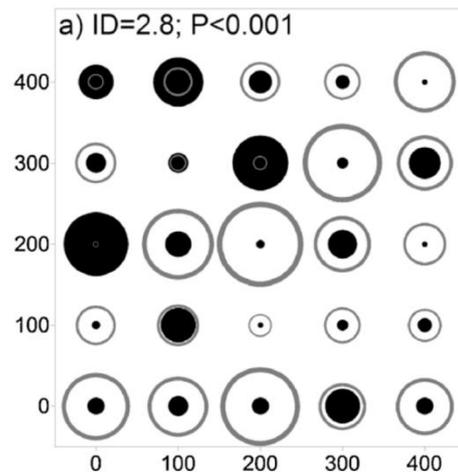


Fig. 3. Distribution of *T. insecta* (4–24 ind.) and overall Collembola prey activity density (grey circles, 936–2102 ind.) in the study area including the index of dispersion (ID) and *P*-values for a deviation from a Poisson distribution.

and *C. terrestris* ($R^2 = 0.23$; $P = 0.027$) was significantly related to trap location. After accounting for trap location, the most parsimonious model further indicated a statistical trend for a negative relationship between *T. zimmermanni* and moss cover ($R^2 = 0.09$; $P = 0.056$; Fig. 2a) and a positive trend between *C. terrestris* and moss cover ($R^2 = 0.10$; $P = 0.051$; Fig. 2b). The most parsimonious model for *C. terrestris* further showed a significant negative relationship to litter cover ($R^2 = 0.13$; $P = 0.014$; Fig. 2d). Together these predictors explained 42% (*T. zimmermanni*) and 46% (*C. terrestris*) of the variation in activity density in these species. The only spider species with a significant negative relationship to prey activity density was *T. insecta* ($R^2 = 0.15$; $P = 0.041$; Fig. 3). Additionally, moss cover was selected as second predictor with a statistical trend for a negative relationship ($R^2 = 0.11$; $P = 0.068$, Fig. 2c), together explaining 26% of the variation in *T. insecta* activity density.

Collembola

The activity density of the Collembola genus *Lepidocyrtus* was significantly related to the trap locations ($R^2 = 0.26$; $P = 0.031$) and after accounting for this indicator, it was negatively related to litter cover ($R^2 = 0.14$; $P = 0.034$; Fig. 4a), together explaining 40% of the variation. The activity of other genera from the family Entomobryidae was also explained by trap location ($R^2 = 0.31$; $P = 0.005$), but the amount of medium deadwood (diameter 2–<7 cm) elements ($R^2 = 0.16$; $P = 0.036$; Fig. 4b) and not litter cover was the second predictor together explaining 47% of the variation in activity density. The activity density of individuals from the family Tomoceridae was not explained by any predictors in our models (Fig. 4c).

Discussion

Our analysis of the spatial patterns of four dominant spider species and their potential epedaphic collembolan prey in a heterogeneous forest floor highlights the importance of considering biotic and abiotic processes when studying the distribution of individuals in heterogeneous habitats. While the distribution of spiders was generally affected by habitat heterogeneity, with positive and negative relationships to moss or litter cover in particular, activity densities in one species were also related to overall prey activity density. In contrast, Collembola activity density was not significantly related to predator activity density and only showed a

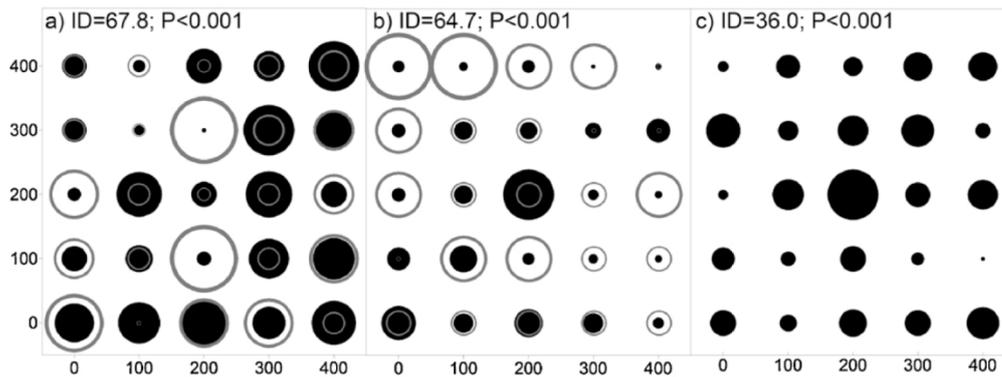


Fig. 4. Distribution of Collembola groups (black bubbles) and (a) litter cover (gray circles, cover classes 1.5–5) or (b) amount of deadwood (gray circles, diameter 2–7 cm, amount classes 0–3) in the study area for (a) *Lepidocyrtus* spp. (358–1147 individuals), (b) other Entomobryidae (41–522 ind.) and (c) Tomoceridae (111–631 ind.) including the index of dispersion (ID) and *P*-values for a deviation from a Poisson distribution.

significant relationship to environmental heterogeneity in terms of litter cover or the amount of medium deadwood elements.

Abiotic factors have frequently been demonstrated to affect the spatial distribution of spiders (Uetz et al. 1999; Ziesche and Roth 2008). Similarly, various authors have shown that biotic interactions may impact spider distribution, with factors such as limited dispersal of juveniles from the maternal burrow (Lubin et al. 1998), conspecific cuing (Hodge and Storfer-Isser 1997) or association to prey (Birkhofer et al. 2011) leading to aggregation. Competitive interactions, in contrast, lead to a more regular distribution (Birkhofer et al. 2007). Our analyses showed trends of specific patch preferences for the three spider species *T. insecta*, *T. zimmermanni* and *C. terrestris*, as the first two species were negatively related to moss cover, whereas the activity density of *C. terrestris* was positively related to moss cover, but negatively related to litter cover. Some linyphiids have been shown to prefer moss-rich habitats on the forest floor (Larrivée et al. 2005; Nentwig et al. 2011), but our study does not support this finding for the analyzed species. It rather suggests a negative relationship between the activity density of the analyzed forest-living linyphiids and moss cover. In contrast, the larger agelenid species *C. terrestris* preferred moss-rich, but litter-poor habitat patches. This species constructs a silk lined tube as retreat, which relies on mosses to attach the adjacent sheet-web (Tretzel 1961). These results only partly support our first hypothesis, as distantly related species (linyphiids vs. agelenids) showed inverse relationships to the same abiotic variable (moss cover).

Our analyses further suggest that none of the spider species investigated preferred areas of low overall predator activity density (Carabidae and Araneae). This not only contradicts our second hypothesis, but also the conclusions drawn from an investigation carried out by Birkhofer et al. (2007). Since the latter study focused on a much smaller scale of spatial resolution, however, the deviating results presented here may be explained by the fact that the distributional patterns of most animal species vary with spatial scale (Taylor et al. 1978). Moreover, considering that spider species have been demonstrated to show competitive interactions and intraguild predation in laboratory experiments (e.g. Harwood and Obrycki 2005), our results highlight the need for evaluating results gained in such artificial micro-environments in light of the factors governing interactions at appropriate ecological scales. In contrast to our second hypothesis, competition among ground-active predators did not play a major role for the spatial distribution of individuals at the scale at which our forest floor study was performed.

Our study was not primarily designed for analyzing collembolan distribution at a level of spatial resolution that is suited

for determining the factors causing aggregative responses of microarthropods (see also Ettema and Wardle 2002). Although activity densities of two groups were correlated to litter cover or the amount of deadwood, it is more likely that environmental heterogeneity (e.g. soil humidity) affects the distribution of Collembola at smaller scales (Grear and Schmitz 2005). However, changes in prey density associated with the aggregation of Collembola may nevertheless be very relevant for more mobile predators such as spiders (e.g. Birkhofer et al. 2011). *C. terrestris* is a specialized predator of beetles (Petto 1990), but linyphiids frequently feed on Collembola that can provide up to 36% of the prey items to linyphiid diets (Sunderland et al. 1986). In our study, only one out of four spider species showed a significant (but negative) relationship to local variations in collembolan prey availability. Collembolan prey was available throughout the year including the activity density peaks of all analyzed spider species. Together, these results do not support our hypothesis that forest-floor inhabiting spiders are generally more active in patches with high availability of potential Collembola prey.

Spatially explicit aspects of food web interactions have been largely ignored in empirical and theoretical studies of communities (Van de Koppel et al. 2005). This is a major shortcoming, since understanding ecological networks remains one of the greatest scientific challenges in the face of global ecosystem change (Bascompte 2009). Studying the processes that affect the spatial distribution of predators are particularly important in this context, as a better understanding of the relationships among predators as well as those between predators and their prey may allow predictions about the consequences of future changes in diversity for trophic interactions.

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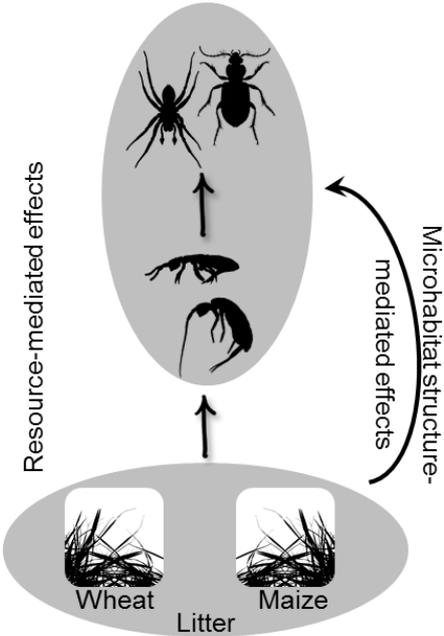
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Chapter 3: The addition of crop residues affects a detritus-based food chain depending on litter type and farming system

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Submitted in Basic and Applied Ecology



Abstract

The addition of crop residues is a common farming practice to increase the organic carbon content of agricultural soils with particular importance in organically managed crops. Residues can either be added from the crop plant itself or from other plants and the type of litter may differentially affect decomposer populations. Effects of litter addition may cascade up to affect generalist predator numbers via trophic cascades or modifications of structural microhabitat properties. Wheat and maize litter were added to organically and conventionally managed wheat fields and effects on generalist predator and Collembola numbers, litter decomposition and carbon utilization as estimated by stable isotope analyses were studied. The activity density of predators was significantly higher in plots with maize litter compared to plots with wheat litter and under organic farming. In contrast, the activity density of Collembola was not significantly affected by litter type or farming system. Litter mass loss was highest in plots that received wheat litter under organic management and was negatively related to predator activity density. Individuals of *Lepidocyrtus* spp. (Collembola) incorporated high percentages of maize-borne carbon compared to predator species. Two spider species were more closely linked to the decomposer prey that consumed maize in organically managed fields and one carabid species showed this pattern in conventionally managed fields. High litter decomposition levels, decomposer and generalist predator numbers were only observed in organically managed fields in wheat litter plots. The addition of crop residues from the growing crop under organic management may therefore be a promising farming practice to synergistically promote decomposition services and activity density of natural enemies.

Keywords: Araneae; Carabidae; Collembola; crop residues, litter quality; mulching; organic farming; predator-prey interactions; stable isotopes; trophic cascades

Introduction

The addition of crop residues increases soil organic carbon content (Kumar & Goh 1999) and enhances densities of natural enemies (Médiène et al. 2011) in agricultural fields. Residue management is therefore an important farming practice in organically fertilized systems (e.g. organic farming, Zehnder et al. 2007) which has been proposed to mitigate the loss of biodiversity due to agricultural intensification (Tuck et al. 2014) and may at the same time synergistically increase decomposition and pest control services. Abundances of generalist predators and Collembola are often higher under organic farming (Birkhofer et al. 2012), but few studies have focused on functional consequences of individual farming practices in organic and non-organic farming systems (Letourneau & Bothwell 2008) or on how resource addition may alter trophic interactions in agricultural fields (Duyck et al. 2011).

Trophic links between predators and prey from the belowground system may be directly affected by the addition of crop residues (Halaj & Wise 2002). Litter resources that are either added from a different crop or from the standing crop may indirectly enhance generalist predator numbers via trophic cascades that include decomposer prey (Scheu 2001). These cascading effects are explained by the energy-shunt hypothesis (Oksanen et al. 1997) under which decomposer taxa benefit from the addition of a litter resource and generalist predators then show a numerical response to the enhanced availability of decomposer prey (Fig. 1a, “resource-mediated effects” sensu Diehl, Wolters & Birkhofer 2012). Such trophic cascades have been documented in vegetable gardens (Halaj & Wise 2002), forests (Miyashita, Takada & Shimazaki 2003) and conventionally managed cereal fields (Birkhofer, Wise & Scheu 2008a). However, the addition of litter resources does not only increase food availability, but also alters the microhabitat structure (Fig. 1a, “microhabitat structure-mediated effects” sensu Diehl, Wolters & Birkhofer 2012). These alterations of habitat structure may lead to numerical responses by generalist predators independent of trophic cascades, which are often driven by a more favourable microclimate in areas with more complex microhabitat structure (e.g. Diehl, Wolters & Birkhofer 2012).

The addition of straw mulches is a common agricultural practice in vegetable crops (Snyder & Wise 1999) and cereals in tropical or arid regions (Buerkert, Bationo & Dossa 2000). The food chain that includes straw mulches, Collembola and generalist predators is an ideal study system to identify effects of the addition of different litter types on decomposition processes and resource utilization in agricultural systems (Halaj & Wise 2002).

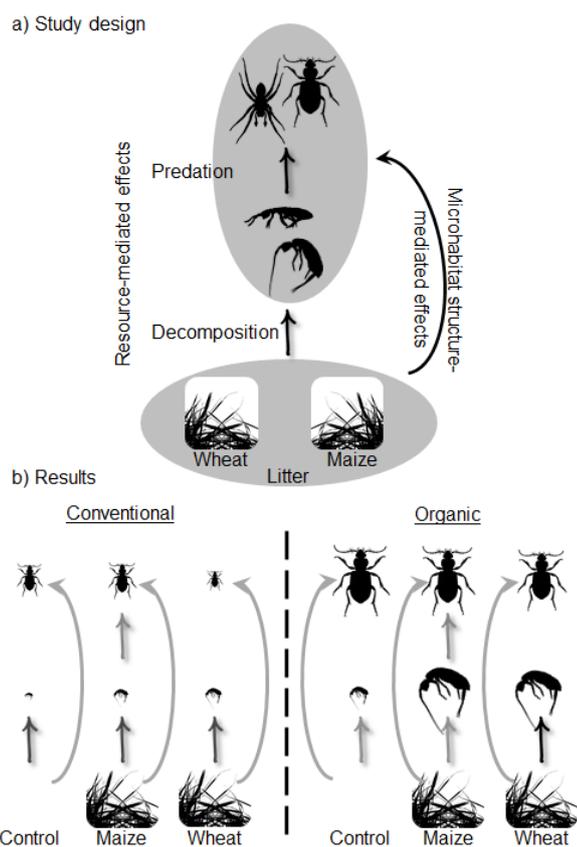


Figure 1 Overview of a) the general study design with litter treatments and potential resource- or microhabitat structure-mediated effects on organisms (Collembola and arthropod generalist predators) or processes (decomposition and predation) and b) summary of effects in conventionally and organically managed wheat fields. Symbols for organisms are scaled according to the mean activity density in the respective treatments, decomposition arrows reflect the results of litter mass loss (Fig. 3), predation arrows reflect the incorporation of maize-borne carbon by predators in maize litter plots (Fig. 5) and arrows for microhabitat structure-mediated effects are based on the contrast test of litter versus control effects (Tab. 1). Darker arrows suggest a stronger link than lighter arrows (black to dark grey to light grey).

Generalist predators consume significant numbers of Collembola in agricultural systems (Bilde, Axelsen & Toft 2000) and Collembola are generally abundant in agroecosystems of temperate regions. The consumption of Collembola prey contributes to a higher fitness of generalist predators (Toft & Wise 1999) and Collembola are important secondary decomposers of plant litter (Rusek 1998). However, the availability of basal resources in agroecosystems is often a limiting factor for decomposer populations (Oelbermann, Langel & Scheu 2008) and the addition of crop residues may therefore not only promote populations of natural enemies, but could potentially lead to higher decomposer activity at the same time.

Here we studied the “microhabitat structure-” and “resource-” mediated effects of experimentally added wheat and maize litter on a litter-decomposer-predator food chain in

organically and conventionally managed wheat fields. We aimed to understand what litter type would be superior to promote beneficial effects of crop residue addition on decomposition, natural enemy and decomposer numbers and if such effects depend on the farming system. Maize litter is of poor quality for decomposers compared to wheat litter (Albers, Schaefer & Scheu 2006), primarily due to its high fibre and lignin content (Scheunemann, Scheu & Butenschoen 2010). Using these two litter resources of contrasting quality and different carbon stable isotope signature further provides an opportunity to understand how different litter resources are incorporated in the body tissue of consumers by means of stable isotope analyses (Birkhofer et al. 2011, Traugott et al. 2013). We hypothesize that: (1) the addition of litter compared to litter-free control plots increases the activity-density of Collembola and thereby generalist predators. The most pronounced effects are expected in conventionally managed fields that provide limited alternative microhabitat structure in addition to wheat tillers (microhabitat structure-mediated effect), (2) the addition of wheat litter increases the activity-density of Collembola and generalist predators more than the addition of maize litter with lower resource quality (resource-mediated effect) and that (3) maize litter is primarily incorporated into the litter-decomposer-predator food chain in resource-poor conventionally managed fields. Finally, we hypothesize that (4) positive effects of litter addition on Collembola activity density lead to higher litter mass loss from litter bags.

Materials and Methods

Study site

The experiment was conducted in three conventionally and three organically managed wheat fields located in an area approximately 3 km west and 19 km north of Giessen (Hesse, Germany). The average annual temperature in the study area is 9.3°C and the annual precipitation is 693 mm (WorldClim database, Hijmans et al. 2005). All fields are located on podzolic brown earth soils. Conventional fields received a total of 130 kg organic and inorganic N per ha and herbicides or growth hormones were applied prior to the study. Organic fields received the equivalent of 160 kg N per ha by means of a legume rotation. Organically managed fields were under pesticide-free management for more than three years prior to this study.

Experimental design and sampling

Three 3x3 m plots were established in each wheat field in April 2011. One plot received maize (*Zea mays* L.) litter and a second plot received wheat (*Triticum aestivum* L.) litter at levels at which the ground was completely covered by litter. The amount of litter was therefore not standardized by mass, but by surface cover. Litter was dried at 60°C for 120 hours prior the experiment and distributed evenly to cover the entire 9 m² soil surface. The third plot served as control and did not

receive any litter. Wheat and maize litter (shoot and leaves) were shredded to fragments of approximately 3.5 x 1 cm prior to the establishment of treatments to avoid any impact of structural differences between litter fragments. However, wheat fragments were naturally thinner and minor differences in the shape and size of litter fragments developed over the period of the experiment, with wheat fragments being more clumped than maize litter fragments.

To estimate litter mass loss due to decomposition during the experiment one litter-bag (mesh size 4mm, 25 cm x 25 cm) filled with 20 g dried wheat litter (for litter preparation see previous section) was placed in each plot. Litterbags were weighed prior to and after the experiment and the mass loss of dried litter was then used to estimate decomposition (Kampichler & Bruckner 2009). Surface-active Collembola, spiders and carabid beetles were sampled from 1 July 2011 to 14 July 2011 immediately before the harvest with two pitfall traps established in the centre of each plot (10 cm diameter, depth 13 cm, 50 cm distance, filled with 70% ethylenglycol and an odour-free tenside). The use of pitfall traps to estimate the availability and activity of surface-active Collembola is justified as we studied the role as potential prey for surface-active predators and litter mass loss from litter bags on the soil surface. Both, the density and activity of a species affect the number of individuals caught by pitfall traps and the term activity density is therefore used instead of abundance (Thiele 1977). Spiders and carabid beetles were counted and determined to species level and Collembola were counted, with individuals from the genus *Lepidocyrtus* sorted for stable isotope analyses (see Supplementary material Appendix 1).

Stable isotope analysis

Stable isotope analyses were only performed in maize litter plots, as this was the only treatment with a high availability of two resources with markedly different carbon isotope signatures (a precondition for two-source mixing models). The two abundant resources (wheat plants and maize litter) from experimental plots were dried at 60°C for three days and were then pulverized in a ball mill. Animal tissue (≈ 0.25 mg) and plant material (≈ 2.5 mg) were transferred into tin capsules. For each replicate of large spider (*Pardosa sp.*) and carabid species (*Pterostichus melanarius* (Illiger, 1798)) a subsample of one individual that was homogenized with a ball mill was used per stable isotope sample. To reach an appropriate weight for smaller species 2-3 individuals of *Oedothorax apicatus* (Blackwall, 1850), *Walckenaeria vigilax* (Blackwall, 1853), *Bembidion lampros* (Herbst, 1784) and 20-25 individuals of *Lepidocyrtus* spp. were pooled per sample. We analysed three replicates for each taxon in each farming system. Stable isotope ratios were determined by a coupled system of an elemental analyzer (Thermo Scientific FLASH 2000, Italy) and a mass spectrometer (Thermo Scientific DELTA V Advantage Isotope Ratio MS (IRMS), Germany). Stable isotope ratios were calculated as δX (‰) = $[(R_{\text{sample}}/R_{\text{standard}})-1] \times 1000$, where R_{sample} is the $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$ ratio of the sample and R_{standard} the

respective ratio of the standard (Peterson & Fry 1987). Wheat flour (IA-R001, Iso-Analytical, UK: $\delta C = -26.43$, $\delta N = 2.55$), Glycine (Fluka AG, Switzerland: $\delta C = -30.95$, $\delta N = 2.06$) and Acetanilide (Indiana University, Department of Geological Sciences, Biogeochemical Laboratories, USA; $\delta C = 29.5$, $\delta N = 19.56$) served as standard and for internal calibration. Two-source mixing models based on $\delta^{13}C$ isotope ratios of resources (wheat plants and maize litter) and $\delta^{13}C$ isotope ratios of animal tissue were used to estimate the contribution of maize-borne carbon to the diet of predator species and Collembola (Phillips & Gregg 2001). Ethylenglycol like other preservatives (e.g. formalin or ethanol) may affect stable isotope values (Carabel, Verísimo & Freire 2009), but we used the same trapping fluid for only 14 days in all traps. We therefore expect effects of the trapping fluid on isotope values to be small and comparable across all samples.

Statistical analysis

Differences in activity density of predators and Collembola and litter mass loss were compared between treatments by permutational analysis of variance with permutation of residuals under a reduced model (Anderson 2001). Farming system and litter type were included as fixed factors and field was included as a random factor nested in farming system. In line with our hypotheses we added two contrasts to our models: i) no litter versus litter (maize and wheat) to test for microhabitat structure-mediated effects (hypothesis 1) and ii) wheat versus maize litter to test for resource-mediated effects (hypothesis 2). We are aware that replication for the factor farming system is low ($N=3$). Our results do not document patterns that would be expected over all organically and conventionally managed winter wheat fields across central Germany, but may still highlight the context dependency of litter addition effects on litter-decomposer-predator food chains. All permutational analyses of variance were based on Euclidean distances and P-values were estimated as a result of 9999 data permutations. The Pearson correlation coefficient was used to characterize relationships between litter mass loss and activity densities of generalist predators or Collembola. All statistical analyses were performed in the Primer-E software (Clarke & Gorley 2006) with the Permanova+ add-on (Anderson, Gorley & Clarke 2008). The Pearson correlation coefficient was calculated in Statistica 10.0 (StatSoft Inc, 2011).

Results

We sampled 1007 individuals from 53 predator species in conventionally and 1959 individuals from 63 predator species in organically managed cereals fields (Supplementary material Appendix 1). We sampled 6580 individuals of surface-active Collembola in conventionally and 20356 individuals in organically managed cereals fields.

The litter type affected predator numbers significantly (Tab. 1), with the activity density being 1.7 times higher in maize compared to wheat litter plots if accounting for field identity in our model (Tab. 1, Fig. 2a: note that it is only 1.3 times higher in this figure as it does not account for field identity). Litter addition did not affect the activity density of Collembola significantly (Tab. 1). The activity density of generalist predators was 2.2 times higher in plots under organic farming compared to plots under conventional management (Tab. 1, Fig. 2b). The activity density of Collembola did not differ significantly between farming systems.

Table 1 Results of permutational analyses of variance of mixed models with the two fixed factors “farming system” (organic versus conventional) and “litter treatment” (wheat, maize or litter-free control) and the random factor “field” nested in farming system. *A priori* contrasts are defined as litter (maize and wheat) versus control (C1) and high (wheat) versus low (maize) quality litter (C2). Significant effects of fixed factors are in bold.

Source	df	Activity density				Litter mass loss	
		Predators		Collembola		Pseudo-F	P
		Pseudo-F	P	Pseudo-F	P		
farming system	1	12.72	0.023	3.35	0.139	5.90	0.070
litter treatment	2	5.39	0.032	0.61	0.561	9.39	0.010
litter vs. no litter (C1)	1	1.75	0.211	1.5	0.247	3.18	0.103
high vs. low quality (C2)	1	10.9	0.049	1.03	0.765	8.40	0.047
Field (farming system)	4	9.64	0.005	0.79	0.574	1.12	0.422
farming system x litter treatment	2	0.53	0.606	0.25	0.787	6.63	0.022
farming system x C1	1	0.12	0.734	0.58	0.465	2.44	0.151
farming system x C2	1	0.84	0.413	0.02	0.705	5.54	0.080
Residuals	8						
Total	17						

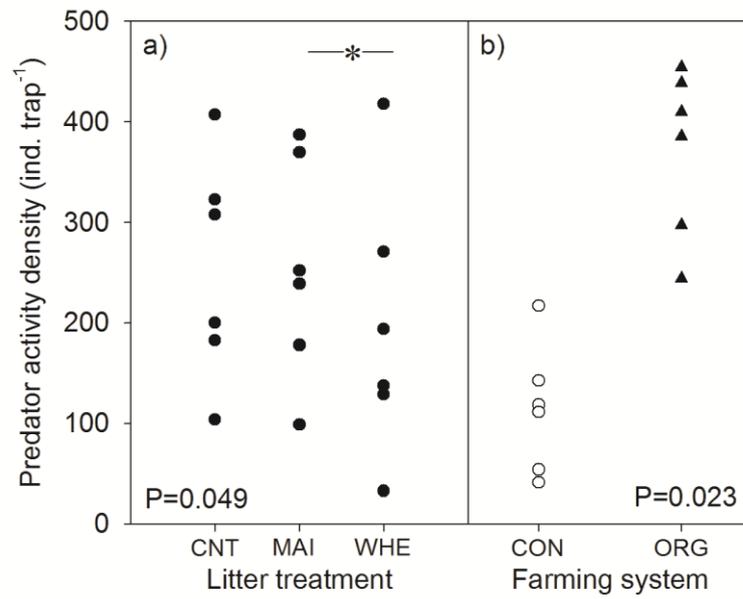


Figure 2 Strip plots for activity density of ground-running generalist predators in a) litter-free control plots (CNT), plots with maize (MAI) or wheat (WHE) litter and in b) conventionally (CON, o) and organically (ORG, ▲) managed cereal fields.

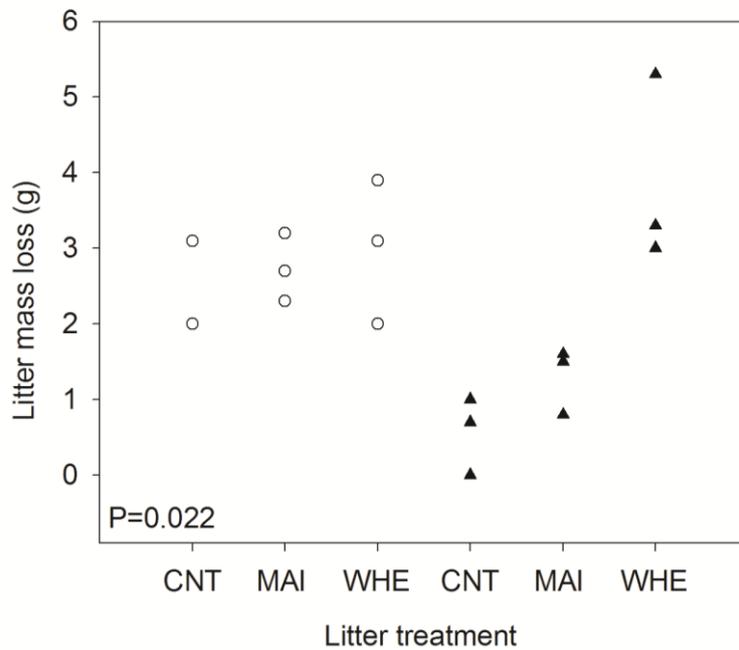


Figure 3 Strip plots for litter mass loss due to decomposition in conventionally (o) and organically (▲) managed cereal fields and in litter-free control plots (CNT), plots with maize (MAI) or wheat (WHE) litter.

Litter mass loss was significantly related to the activity density of predators independent of farming system (Fig. 4; $R=-0.55$, $P=0.018$), but with a more pronounced negative relationship in organically

managed ($R=-0.63$, $P=0.069$) compared to conventionally managed fields ($R=-0.24$, $P=0.533$; Fig. 4). The activity density of Collembola was not significantly related to litter mass loss ($R=-0.17$, $P=0.501$).

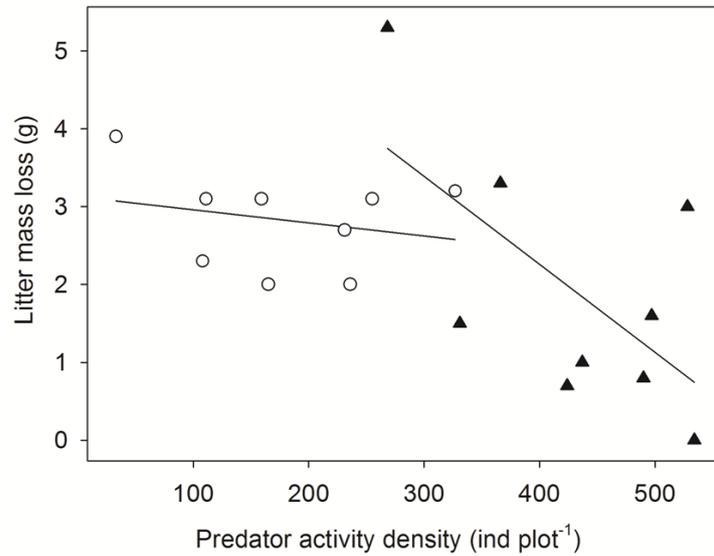


Figure 4 Relationship between predator activity density and litter mass loss in conventionally (○) and organically (▲) managed cereal fields.

The percentage of maize-borne carbon in the body tissue of individuals from the genus *Lepidocyrtus* deviated significantly from zero (Fig. 5).

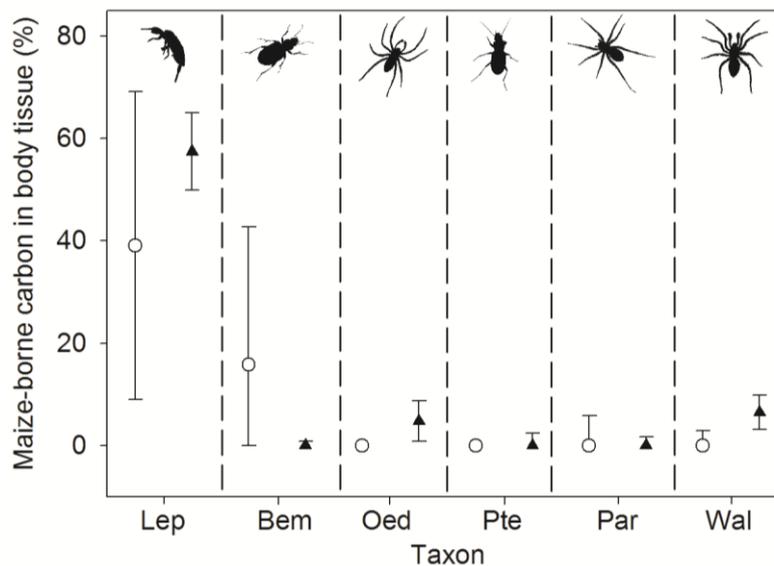


Figure 5 Mean percentage (\pm 95% confidence envelopes) of maize-borne carbon incorporated in the tissue of the most abundant Collembola taxon (*Lepidocyrtus* spp.) and ground-running generalist predator taxa: *Bembidion lampros*, *Oedothorax apicatus*, *Pterostichus melanarius*, *Pardosa* sp. and *Walckenaeria vigilax* in maize litter plots of conventionally (○) or organically (▲) managed winter wheat fields. Estimates are derived from two-source mixing models based on $\delta^{13}C$ isotope ratios of wheat and maize litter (sources) and animal tissue.

Lepidocyrtus spp. on average incorporated significantly more maize-borne carbon in maize litter plots in organically (57%) compared to conventionally (39%) managed fields ($P=0.007$). *Bembidion lampros* on average incorporated 16% of its carbon from the maize channel under conventional farming, whereas maize-borne carbon incorporation was not observed under organic farming (Fig. 5). Two spider species (*O. apicatus* and *W. vigilax*, Fig. 5) were linked to the maize energy channel, but incorporated relatively low percentages of maize-borne carbon in their diet (5-6%). This contribution differed significantly from zero under organic farming and no incorporation of maize-borne carbon was evident for these species under conventional farming (Fig. 5).

Discussion

The addition of crop residues primarily affected the litter-decomposer-predator food chain via resource-mediated effects, but depending on farming system and litter type (Fig. 1b). Litter decomposition was highest in wheat litter plots under organic management and was negatively related to predator activity density in organically managed fields. Two spider species were more closely linked to prey that consumed maize litter in organically managed fields, but one carabid species showed the opposite pattern.

Our first hypothesis assuming effects of litter addition on Collembola and predator communities independent of litter type was not supported (microhabitat structure-mediated effects). Positive effects of litter addition on predator populations were previously documented (Halaj & Wise 2002; Schmidt et al. 2004; Oelbermann, Langel & Scheu 2008) and microclimatic conditions are known to contribute to such effects (Holland & Luff 2000). The addition of maize litter in our study resulted in a 1.7 times higher activity density of predators in maize litter plots compared to wheat litter plots. Predator activity density between litter-free control plots and maize litter plots did not differ significantly. These results suggest that the addition of structure *per se* did not enhance predator activity density in our study. Activity density of Collembola was not significantly affected by litter addition, which stands in contrast to previous results from forest ecosystems (e.g. Chauvat, Zaitzev & Wolters 2003). Collembola may have experienced suitable habitat conditions throughout most areas in the agricultural fields during our study period and may have not been attracted by additional litter (but see Birkhofer et al. 2011).

A relatively high percentage of maize-born carbon could be observed in decomposers of the genus *Lepidocyrtus* indicating that they were linked to maize carbon pools especially under organic management and contradicting our third hypothesis. Collembola switch between different resources depending on availability and management practices (Mebes & Filser 1998; Ngosong et al. 2009), but it remains unclear why Collembola primarily utilized maize litter under organic management.

Bacteria and fungi are the most important primary decomposers in agricultural soils (Kennedy 1999) and the biomass of these organisms is often higher in organically managed wheat fields (Birkhofer et al. 2008b, Kong et al. 2011; Ullrich et al. 2011). Higher rates of primary decomposition of maize litter by bacteria and fungi under organic management may have promoted incorporation of maize-borne carbon into the studied decomposer food-chain.

Maize-borne carbon could not be detected in all analysed predator taxa indicating a limited utilization of maize-consuming decomposer prey by most predator species. However, some predator species were linked to maize carbon pools, but the low percentage of incorporated maize-borne carbon (only 0-6% for spiders and 0-16% for carabids) suggests a lag in time for carbon incorporation in higher trophic levels (see also Albers, Schaefer & Scheu 2006). The two spider species showed incorporation of maize-borne carbon in organically managed fields, where maize incorporation by Collembola was highest. Both spider species from the family Linyphiidae are known to feed on Collembola prey comprising more than 36% of their diet (Sunderland, Fraser & Dixon 1986). The limited incorporation of maize-borne carbon by predators may also be a result of preferences for prey that primarily fed other resources (e.g. herbivores, see Birkhofer et al. 2011).

Maize litter is known to be of poor quality for decomposers due to high fibre and lignin content (Scheunemann, Scheu & Butenschoen 2010), but it can provide about 1.7 times more carbon than wheat litter (Wilhelm et al. 2004). Hence, maize litter plots in contrast to our second hypothesis may act as “islands” of organic matter attracting decomposers more than wheat litter plots. We did not find a significant effect of different litter types on Collembola activity density. The 1.7 times higher activity density of predators in maize litter plots compared to wheat litter plots may have caused active avoidance of maize plots by Collembolans (e.g. Vucic-Pestic et al. 2010, Birkhofer, Scheu & Wiegand 2010) and higher predation risk could reduce the value of carbon “islands”. Litter mass loss was significantly affected by litter treatment depending on farming system, with highest losses in wheat plots of organically managed fields. This result supports our explanation of higher maize-borne carbon incorporation in decomposer tissue under organic management, as a higher biomass of primary decomposers may have promoted wheat litter mass loss in organically managed plots. However, the observed mass losses from litter bags were also generally high in conventionally managed fields which probably had fewer naturally occurring litter sources (e.g. arable weeds; Bengtsson, Ahnström & Weibull 2005). The overall negative relationship between litter mass loss and predator activity density as well as the lower predator activity density in wheat litter plots suggest that decomposer taxa (including other taxa than Collembola) were negatively affected or avoided predation through spiders and ground beetles. However, in contrast to our fourth hypothesis decomposition was not related to activity densities of Collembola.

Our study suggests that microhabitat structure-mediated effects on predators are weak and that resource-mediated effects of litter addition on predators depend on species. Resource-mediated effects on decomposers and decomposition depend on farming system and litter type. The demonstrated context dependency of an individual farming practice offers a chance to improve selected farming systems. The addition of wheat residues to wheat fields under organic management is a promising practice to synergistically promote decomposition process and natural enemy numbers. The ecological intensification of agricultural production (Bommarco, Kleijn & Potts 2013) can only be accomplished if such context-dependencies and synergies are better understood and if future studies aim to demonstrate risks and benefits of individual farming practices under different conditions.

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Supporting information

The addition of crop residues affects a detritus-based food chain depending on litter type and farming system

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Supplementary material

Appendix 1. Activity density of spiders, carabid beetles and Collembola in conventionally (CON) and organically (ORG) managed fields.

Family/Species	CON	ORG
Clubionidae		
<i>Clubiona reclusa</i>	0	1
Gnaphosidae		
<i>Micaria pulicaria</i>	2	6
<i>Zelotes latreillei</i>	1	0
<i>Zelotes lutetianus</i>	1	0
Linyphiidae		
<i>Araeoncus humilis</i>	5	5
<i>Bathyphantes gracilis</i>	6	67
<i>Bathyphantes nigrinus</i>	0	1
<i>Centromerus sylvaticus</i>	0	1
<i>Collinsia inerrans</i>	7	9
<i>Dicymbium nigrum</i>	1	2
<i>Diplostyla concolor</i>	33	13
<i>Erigone atra</i>	155	56
<i>Erigone dentipalpis</i>	68	11
<i>Erigonella hiemalis</i>	1	0
<i>Meioneta affinis</i>	3	2
<i>Meioneta rurestris</i>	49	11
<i>Mermessus trilobatus</i>	4	1
<i>Micrargus subaequalis</i>	9	1
<i>Oedothorax apicatus</i>	203	842
<i>Oedothrax fuscus</i>	13	0
<i>Oedothrax retusus</i>	40	30
<i>Pelecopsis paralella</i>	1	0
<i>Porrhomma errans</i>	0	1
<i>Porrhomma oblitum</i>	0	2
<i>Porrhomma microphthalmum</i>	2	0
<i>Tenuiphantes tenuis</i>	6	21
<i>Walckenaeria atrotibialis</i>	1	0
<i>Walckenaeria vigilax</i>	38	127
Lycosidae		
<i>Pardosa agrestis</i>	7	3
<i>Pardosa lugubris</i>	0	4
<i>Pardosa palustris</i>	35	7
<i>Pardosa prativaga</i>	1	0
<i>Pardosa pullata</i>	19	7
<i>Pardosa amentata</i>	15	20
<i>Trochosa ruricola</i>	9	15

<<Continued from Appendix 1

Family/Species	CON	ORG
Salticidae		
<i>Euophrys frontalis</i>	1	0
Tetragnathidae		
<i>Pachygnatha clercki</i>	24	49
<i>Pachygnatha degeeri</i>	74	11
Theridiidae		
<i>Enoplognatha thoracica</i>	1	0
<i>Robertus neglectus</i>	2	2
Thomisidae		
<i>Ozyptila simplex</i>	4	1
<i>Xysticus kochi</i>	2	0
<i>Xysticus ulmi</i>	0	1
Total:	843	1330
Carabidae		
<i>Abax parrallelepipedus</i>	0	2
<i>Agonum muelleri</i>	0	4
<i>Amara communis</i>	0	33
<i>Amara familiaris</i>	0	1
<i>Amara ovata</i>	0	1
<i>Amara similata</i>	0	1
<i>Anchomenus dorsalis</i>	3	28
<i>Asaphidion flavipes</i>	0	2
<i>Bembidion lampros</i>	26	237
<i>Bembidion properans</i>	2	6
<i>Bembidion quadrimaculatum</i>	0	1
<i>Brachinus explodens</i>	1	0
<i>Calathus fuscipes</i>	1	2
<i>Calathus melanocephalus</i>	0	3
<i>Carabus auratus</i>	0	1
<i>Carabus granulatus</i>	0	1
<i>Carabus violaceus</i>	0	18
<i>Clivina fossor</i>	0	1
<i>Harpalus affinis</i>	2	10
<i>Harpalus latus</i>	0	1
<i>Harpalus rufipes</i>	49	49
<i>Loricera pilicornis</i>	1	2
<i>Microlestes minutulus</i>	3	0
<i>Notiophilus palustris</i>	5	2
<i>Notiophilus substriatus</i>	1	0
<i>Ophonus rufibarbis</i>	1	0
<i>Poecilus cupreus</i>	8	96
<i>Poecilus versicolor</i>	0	4
<i>Pterostichus melanarius</i>	52	101
<i>Pterostichus strenuus</i>	0	2

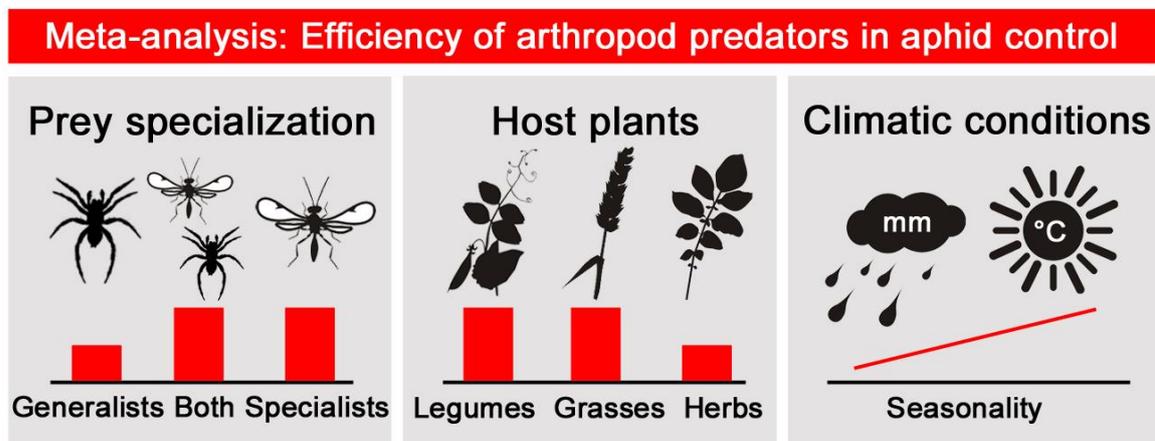
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Family/Species	CON	ORG
<i>Pterostichus vernalis</i>	2	8
<i>Stomis pumicatus</i>	1	0
<i>Synuchus vivalis</i>	0	1
<i>Trechus obtusus</i>	0	2
<i>Trechus quadristriatus</i>	6	8
<i>Zabrus tenebrioides</i>	0	1
Total:	164	629
Tomoceridae	3	11
Entomobryidae		
<i>Lepidocyrtus spp.</i>	2180	7367
other Entomobryidae	3949	148
Sminthuridae	89	206
Isotomidae	359	12624
Total:	6580	20356

Chapter 4: Effects of predator specialization, host plant and climate on biological control of aphids by natural enemies: a meta-analysis

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REVIEW

Effects of predator specialization, host plant and climate on biological control of aphids by natural enemies: a meta-analysis

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Summary

1. Aphids are among the most severe invertebrate pests of crops and cause high economic losses. The control of aphids by natural enemies is an essential ecosystem service with high relevance to management strategies applied in agricultural plant production and horticulture. However, the current knowledge on the effectiveness of specialist and generalist predators in aphid control with respect to host plants and climatic conditions has not yet been summarized in a meta-analytical approach.

2. We collected 60 studies providing 168 independent cases of predator exclusion experiments to analyse how predator and host plant group and climatic conditions affect aphid control by natural enemies.

3. Effects of natural enemies on aphid populations were strongest in assemblages that included specialist predators, either alone or with generalist predators. Generalists alone also reduced aphid numbers significantly, but not to the same extent as specialists.

4. Effects of natural enemies were weaker on aphid populations feeding on legumes compared with aphids on grasses or herbs. The percentage reduction of aphids feeding on grasses, herbs or legumes was higher in treatments with assemblages or specialists alone compared with generalists with the largest difference on grasses.

5. According to all field studies from the temperate zone, effects of natural enemies on aphid populations were strongest in areas with high precipitation seasonality. A relationship between predator effects and temperature seasonality was only found for the USA.

6. *Synthesis and applications.* Specialist predators alone or assemblages of specialists and generalists had the strongest effect on aphid populations, especially when either feeding on grasses and herbs or when exposed to extreme weather events. The control of aphids by natural enemies is most promising in grass and herb crops, whereas it is less suited for controlling aphids in legume crops. Facing climate change, the effect of extreme weather events on aphid control by natural enemies will have further implications for developing management strategies for aphid control in the future.

Key-words: aphididae, biocontrol, climate seasonality, effect size, generalist predator, meta-regression, pest suppression, pesticide-free management, predator–prey interaction, specialist predator

Introduction

Aphids are among the most severe invertebrate pests of crops (Dedryver, Le Ralec & Fabre 2010), with the annual economic loss through aphid infestation ranging from 10 to 250 million US\$ in North America (Brewer &

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Elliott 2004). Aphids primarily threaten crops in temperate regions (Holman 2009), where damage to plants is caused by sap-sucking, honeydew deposition and virus transmission (Alford 2011). Several management strategies have been developed over the last decades to reduce aphid populations using natural control mechanisms (e.g. Ferron & Deguine 2005). The demand for such strategies has been driven by socioeconomic changes such as increasing pesticide costs as well as economic and environmental benefits from the production of organically farmed crops (Menzler-Hokkanen 2006). The biological control of aphids by natural enemies has thus become an important component of pesticide-free management strategies (Zehnder *et al.* 2007) such as conservation biological control (Barbosa 1998). This approach may be an effective way of reducing crop plant damage (e.g. Östman, Ekblom & Bengtsson 2003), but it is also associated with considerable uncertainties, since the strength of predator effects on pest numbers depends on a range of external factors (Rusch *et al.* 2010). Unfortunately, the increasing number of studies addressing biological control of aphid populations so far has not been analysed using an integrative approach that would allow for a synoptic evaluation based on the current state of knowledge on this issue. The meta-analysis presented here aims to fill this gap of knowledge, with a particular focus on the modulating effect of the factors predator and plant group as well as climate seasonality.

Natural enemies of aphids include taxa that are specialized on single or few aphid species as prey (e.g. parasitic wasps, Desneux *et al.* 2009), predators that are primarily aphidophagous (e.g. coccinellids and lacewing larvae, Dixon 2000) and generalist predators that frequently feed on other prey in addition to aphids (e.g. spiders or ground beetles, Birkhofer & Wolters 2012). Specialization may increase the per capita efficiency of pest reduction (Schmidt *et al.* 2003). Specialized groups such as parasitoids and aphidophagous predators are hence commercially applied for biological control of aphids (Van Lenteren 2003). In contrast, generalist predators are primarily utilized by means of conservation biological control (Barbosa 1998), as they do not depend on the availability of aphid prey and are thus already present at early stages of aphid colonization to contribute to biological control (Oksanen *et al.* 1997). However, experiments have suggested that the simultaneous presence of these two predator groups may enhance aphid suppression compared to treatments with one functional group only (additive effects; Thies *et al.* 2011). Alternatively, the joint occurrence of specialists and generalists may reduce aphid suppression, for example, through intraguild predation (e.g. Snyder & Ives 2001) or behavioural changes in one predator group (nonadditive effects, League-Pike & Shulman 2009). Considering the ambiguous state of knowledge on this issue, one key question we wanted to address with the meta-analysis presented here is whether generalists, specialists or assemblages of the two func-

tional groups are more effective in controlling aphid populations.

Effects of natural enemies on aphids may be modulated by interactions between aphids and their host plant. The host physiological phenotype hypothesis predicts that host plants with short-lived and nutrient-rich tissue have a greater potential to support aphid populations (Cronin *et al.* 2010). As nitrogen availability is a limiting factor for most herbivores (Mattson 1980), population growth of aphids has been shown to be positively related to the nitrogen content of plants (Schütz, Bonkowski & Scheu 2008). Legumes (Fabaceae *s.l.*), therefore, may be particularly prone to fast population growth of aphids, as N-fixation by associated rhizobia leads to a generally higher nitrogen concentration in the tissues of this plant family compared with nonlegume plants (e.g. Scherer-Lorenzen 2004). To take account of potential plant effects on the effectiveness of biological control, we focus on whether the impact of natural enemies on aphids varies between groups of host plants that are known to differ in C : N ratios (e.g. Kahmen *et al.* 2006).

Global variation in weather and climate affects all trophic levels and potentially alters interactions in food webs (Stenseth *et al.* 2002; Van der Putten *et al.* 2004). Aphids are sensitive to climatic conditions, with extreme rainfall and drought events or low winter temperatures directly causing mortality or reducing population growth (Hulle *et al.* 2010). For instance, rain can increase predation risk by dislodging aphids from plants and forcing them to move between plants (e.g. Narayandas & Alyokhin 2006). As direct and indirect mortality in response to extreme climate events may facilitate pest control by predators, our meta-analysis also investigates whether climate seasonality changes the effect strength of natural enemies on aphid populations.

We used published data from predator exclusion experiments to analyse the overall effect of predator or host plant group and climate seasonality on biological control of aphid populations by natural enemies. The following hypotheses were tested: the effect of natural enemies on aphid population size is (i) strongest in treatments with both generalist and specialist predators (additive effect), but if tested in isolation, specialists are more successful in controlling aphids than generalists; (ii) weakest for aphid populations on plant groups that are rich in nitrogen; and (iii) strongest in areas with high climate seasonality.

Materials and methods

LITERATURE SURVEY

We conducted a systematic review of primary literature published in peer-reviewed journals between 1960 and 2010 including the search terms 'predat*' (e.g. predator and predation) and 'aphid*' (e.g. Aphididae or aphids) in the title, abstract or keywords section, using the ISI Web of Knowledge (www.isiknowledge.com). Literature published between 1960 and 2009 was searched

between April and June 2010, and the literature published in 2010 was searched in January 2011. We included manipulation experiments conducted in the laboratory, glasshouse or field that compared densities of aphid populations in treatments with arthropod predators ('predator-present' treatment) to aphid populations in treatments with predator exclusion ('predator-absent' treatment). For analysing the effect of climatic seasonality, only field studies were considered. Aphid densities were reported as number of aphids per experimental unit or plant, biomass of aphids or percentage of aphid survival. Predator exclusion treatments included studies that used microcosms, mesh plant sleeves or clip cages. Arthropod predator treatments included studies using single species or assemblages that were either introduced or native arthropod predators. If a study provided two predator-present treatments including (i) a cage control (i.e. treatments in which physical conditions generated by the cage were mimicked); and (ii) uncaged plots (nonmanipulated area of the same size), we used the cage control. The selection of studies included in our meta-analyses may be biased, as studies with significant results and large sample sizes are more likely to be published than nonsignificant results ('file-drawer problem'). We calculated the fail-safe N number to identify whether the 'file-drawer problem' biased our meta-analyses. The fail-safe N number is the number of additional nonsignificant cases that we would need to incorporate to change a significant into a nonsignificant result (Borenstein *et al.* 2009).

DATA TREATMENT

The statistical unit of our meta-analyses is defined as a data set that compares aphid density in a predator-present treatment to aphid density in a predator-absent treatment within one experiment (referred to as case). Mean aphid density, standard deviation and sample size for the two different treatments were collected from text sections and tables of studies or from published graphs using SIGMAPLOT 10.0 (Systat Software Inc, Richmond, CA, USA, 2006). If not provided, standard deviations were calculated from other variance measures such as standard errors or confidence intervals. When sample size was given as a range, we used the mean value of replicate numbers for analysis. Note that a single study may report multiple cases from independent experiments. Independent cases are separate experiments that were established at different study sites, in different years, with different predator or aphid species or densities, different plant individuals or plant species. The following designs were not considered as independent cases and were excluded from meta-analyses: (i) treatments with different predator species that were compared with the same predator-absent treatment. We only used one of the predator-present treatments for meta-analysis, selected using the following order of criteria: largest sample size, lowest variance and, for a few cases, generalists over specialists (to balance sample size between categories). If this order of criteria did not lead to a selection, cases were selected randomly; (ii) multiple aphid species counted within the same experimental unit. Here, we used the mean density of all aphid species; (iii) multiple sample dates during 1 year, but within the same experimental unit. If cases appeared with multiple sample dates during 1 year, we only included one sample date with the highest aphid density in the predator-absent treatment. We used this date as it corresponds to the most severe aphid infestation and as selecting this point in aphid dynamics was the only way to standardize data selection

between the different studies. An a-priori analysis of the relationship between the duration of studies until peak densities were reached and the reduction of aphid numbers comparing predator and control treatments did not suggest a strong effect of experimental duration on aphid reduction (Pearson $R = 0.16$). We collected metadata for each case, including the group of the host plant and predator species, the experimental set-up (e.g. glasshouse or field), geographic location, date and duration of the experiment (see Appendix S1 in Supporting Information). We did not collect measures of landscape complexity around field sites, as historic data on the landscape context was not available for the majority of regions (but see Chaplin-Kramer *et al.* 2011).

STATISTICAL ANALYSES

We performed three meta-analyses using (i) the whole data set ($N = 168$ cases); (ii) a data set categorized by predator functional group: generalist predators (GP; polyphagous; including Araneae, Carabidae, Staphylinidae, Heteroptera; $N = 26$), specialist predators (SP; mono- and oligophagous; including Coccinellidae, Chrysopidae, Hymenoptera; $N = 62$) or an assemblage of both functional groups (AS; $N = 80$) used in the predator-present treatment; and (iii) a data set categorized by plant group: legumes ($N = 40$ including 8 cases with generalist predators, 6 cases with specialist predators and 26 cases with an assemblage of both in the predator-present treatment), grasses ($N = 93$; GP = 6, SP = 50 and AS = 37) or herbs ($N = 31$; GP = 11, SP = 4 and AS = 16). Three cases used mixed assemblages of plants and were thus excluded from this analysis.

To measure effect strength of natural enemies on aphid populations, we calculated the effect size for each case. We used the bias-corrected Hedges' g , which is one of the most common effect size measures (Osenberg, Sarnelle & Goldberg 1999). It is calculated as the difference between the means of the predator-absent and predator-present treatment divided by the within-treatments standard deviation, pooled across treatments and multiplied by a factor that corrects for small samples sizes (Hedges 1981). Positive effect sizes indicate a lower aphid density in predator-present treatments compared with predator-absent treatments. Effect sizes from single cases were combined to the mean Hedges' g for all cases (first meta-analysis) or for individual categories (second and third meta-analyses) using a random-effects model. The contribution of each case was weighted by the inverse value of the case's variance. A random-effects model assumes that cases in our meta-analyses are a random sample of a distribution of effect sizes, that is, the true effect size may vary from case to case (e.g. when different predator species were used). The calculated summary effect is thus an estimate of the mean of all relevant true effects (Borenstein *et al.* 2009). Categories (predator or plant groups) differ significantly if their 95% confidence intervals do not overlap. To test for effects of predator and plant group on the magnitude of aphid reduction, we used percentage reduction between predator-present and predator-absent treatment values from each case and statistically compared these values by two-way ANOVA.

We further performed a meta-regression with a global data set that was limited to field studies ($N = 101$ cases, excluding glasshouse studies) to explore whether precipitation seasonality (variation in annual mean precipitation expressed as a coefficient of variation) or temperature seasonality (variation in annual mean temperature expressed as a standard deviation*100) at each study location affects the observed effect size. We further analysed two

separate data sets from regions with sufficient data (USA: $N = 76$; Europe: $N = 18$) and accounted for possible spatial autocorrelation between study locations using spatial correlations. In these analyses, we correlated effect size to seasonality of precipitation or temperature (Spearman's rank correlation), while using geographically effective degrees of freedom based on the coordinates of study sites to test for statistical significance (e.g. Legendre & Legendre 1998). Dutilleul's (1993) estimator for the effective number of degrees of freedom was used and the magnitude of spatial autocorrelation was estimated for distance between study locations up to 1100 km (USA) and 750 km (Europe). Spatially explicit climatic data (resolution of 1 km^2) was obtained from the WORLDCLIM data base (<http://worldclim.org/>; Hijmans *et al.* 2005) using ARCGIS (version 9.3, ESRI ArcMap[™], Redlands, CA, USA). Method of moments was used to explore the relationship between climatic data (precipitation seasonality, temperature seasonality) and Hedges' g for each case. A mixed-effect model was used to calculate the summary effect. The contribution of each case was weighted by the inverse of the case's variance. All meta-analyses and meta-regression approaches were conducted using Comprehensive Meta-Analysis (version 2, Biostat[®], Englewood, NJ, USA). Analyses of spatial autocorrelation were conducted using the software SAM (Rangel, Diniz & Bini 2010).

Results

Of the 2245 reviewed studies, 60 (2.7%) were included in our meta-analysis, yielding 168 independent cases. The fail-safe N number in our meta-analysis was 72052, that is, our data set with 168 cases would need to include 72052 additional nonsignificant cases to disregard our significant result. The first study that provided appropriate data for our meta-analyses was published in 1983. The years with the most studies were 2008 ($N = 7$), 2004 ($N = 6$) and 2007 ($N = 5$), and studies were predominantly conducted in temperate ecosystems (Fig. 1). The effect size for individual cases showed that 132 of 168 cases had significantly lower aphid densities in the predator-present treatment compared with the associated predator-absent treatment (Fig. 2). In one case (see Appendix S1, study number 47), aphid density was significantly higher in the predator present than in the associated predator-absent treatment. In 35 cases, the presence of arthropod predators had no significant effect on aphid densities. Summarized for all cases, aphid densities were significantly lower in the presence of predators ($g = 1.85$, 95% CI = 1.67–2.03, $P < 0.001$).

PREDATOR FUNCTIONAL GROUP

The meta-analyses of the categorized data revealed significantly lower aphid densities in the presence of generalist predators ($g = 1.12$, 95% CI = 0.69–1.55, $P < 0.001$), specialist predators ($g = 1.91$, 95% CI = 1.62–2.19, $P < 0.001$) and assemblages of both functional groups ($g = 2.08$, 95% CI = 1.81–2.35, $P < 0.001$) compared with the absence of predators (Fig. 3a). For specialists and assemblages of predators, mean Hedges' g was signifi-

cantly higher (1.7 and 1.9 times) compared with treatments with only generalist predators. The mean effect size of treatments with only specialist predators did not differ significantly from means of assemblage treatments. In line with the results for effect strength, the percentage of aphid reduction in all host plant groups was significantly higher in predator treatments with an assemblage or specialists compared with predator treatments with generalists (Fig. 4a–c; interaction predator \times plant group; $F_{2,153} = 10.85$; $P < 0.001$). However, the contribution of generalist predators to the percentage of aphid reduction was lowest in experiments with grasses (Fig. 4b; $F_{4,153} = 3.17$; $P = 0.016$).

HOST PLANT GROUP

Significantly lower aphid densities were observed in all plant groups for predator-present treatments compared with predator-absent treatments (legumes: $g = 1.34$, 95% CI = 1.01–1.65, $P < 0.001$; grasses: $g = 1.91$, 95% CI = 1.67–2.15, $P < 0.001$; herbs: $g = 2.12$, 95% CI = 1.70–2.53, $P < 0.001$; Fig. 3b). The mean effect size of predator-present treatments was significantly higher (1.8 times) for aphid densities on herbs compared with legumes. Mean effect sizes on grasses did not differ significantly from herbs and legumes.

CLIMATE SEASONALITY

Effect sizes of all field experiments ($N = 101$) were significantly related to precipitation seasonality (slope = 0.010, $P = 0.044$; Fig. 5), showing a positive relationship between aphid control by natural enemies and seasonality in precipitation. In contrast, temperature seasonality was not related significantly to effect size (slope < 0.001, $P = 0.065$). When accounting for potential spatial autocorrelation between sample locations in the USA (Fig. 6a), the effect size in this region was positively related to seasonality in temperature (Fig. 6c; $N_{\text{corrected}} = 74$, $R_S = 0.252$, $P_{\text{corrected}} = 0.002$), with no significant relationship to seasonality in precipitation (Fig. 6b; $N_{\text{corrected}} = 74$, $R_S = 0.139$, $P_{\text{corrected}} = 0.575$). In Europe (Fig. 7a), effect size was not significantly related to seasonality in temperature (Fig. 7c; $n_{\text{corrected}} = 16$, $R_S = -0.558$, $P_{\text{corrected}} = 0.078$) or seasonality in precipitation (Fig. 7b; $N_{\text{corrected}} = 16$, $R_S = -0.315$, $P_{\text{corrected}} = 0.097$). In general, cases in the USA were more variable in effect size and included a wider range of precipitation and temperature seasonality values compared with the cases in Europe (but note the smaller N for Europe).

Discussion

Our meta-analysis synthesizes results of a wide variety of independent studies that investigated the effect of predators on aphid populations, while accounting for the fact that designs (e.g. number of replicates) differed between

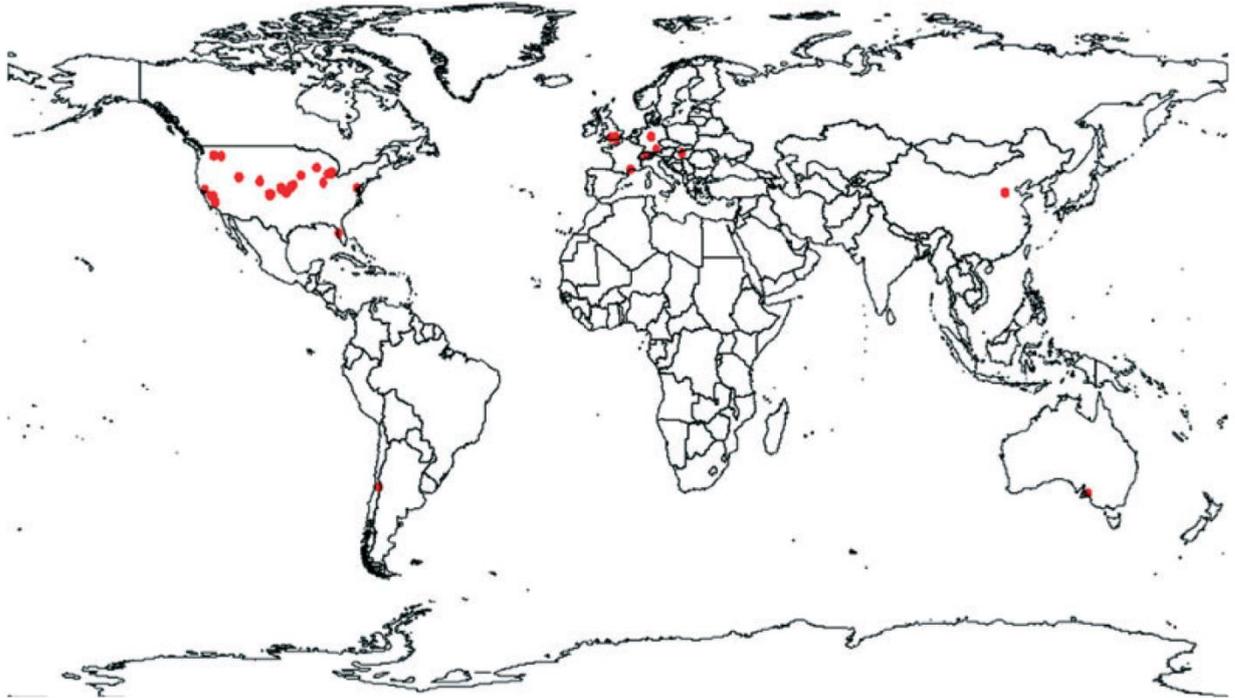


Fig. 1. Distribution of study locations in temperate regions providing data for our meta-analyses (N = 59; location of one laboratory study was not specified). Note that points may overlap.

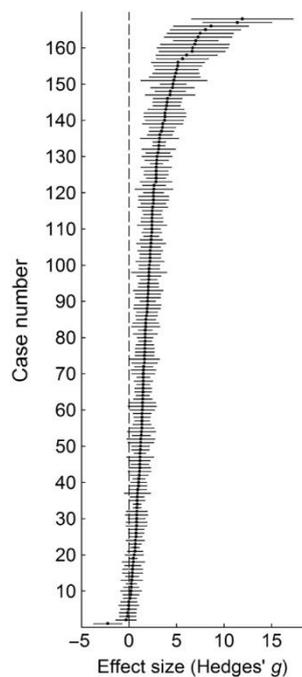


Fig. 2. Forest plot showing the effect size (Hedges' $g \pm 95\%$ CI) for each case in our meta-analyses (N = 168). Case numbers indicate references corresponding to IDs in Appendix S1. Predator effects are significant if 95% confidence intervals do not overlap with zero.

studies. We did find overwhelming evidence that predators significantly suppress aphids. Only 36 of 169 independent cases did not indicate a significant effect of predators on

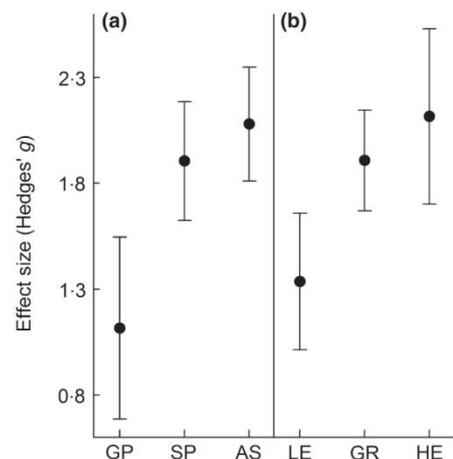


Fig. 3. Mean effects sizes (Hedges' $g \pm 95\%$ CI) for predator effects on aphid densities in (a) different categories of predator functional groups: generalist predators (GP, N = 26), specialist predators (SP, N = 62) or assemblages (AS, N = 80) and in (b) plant groups: legumes (LE, N = 40), grasses (GR, N = 93) and herbs (HE, N = 31).

aphid populations and only a single study suggests that aphid numbers were higher in the presence of predators. We are aware that meta-analytical approaches have been criticised because of methodological issues (Philibert, Loyce & Makowski 2012) or because empirical work is not adequately valued (Kueffer *et al.* 2011). While we cannot change the attitude of journals towards publishing significant effects (file-drawer problem), we minimized

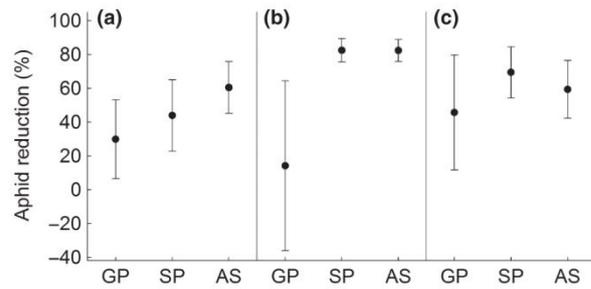


Fig. 4. Mean percentage of the reduction of aphid numbers in case studies with (a) legumes, (b) grasses or (c) herbs comparing effects of generalist (GP) and specialist (SP) predator or assemblage (AS) treatments (\pm 95% CI).

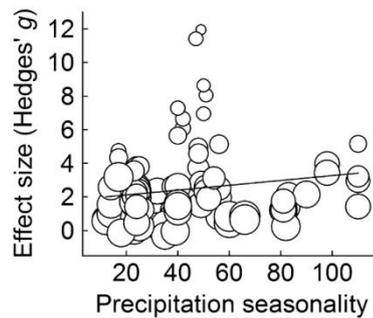


Fig. 5. Relationship between effect size (Hedges' g) and precipitation seasonality in field experiments ($N = 101$). Individual cases are indicated by circles, size of the circles is proportional to the case's weight estimated by meta-regression. Note that cases may overlap.

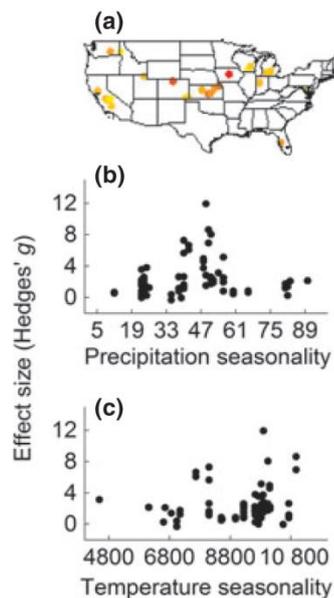


Fig. 6. Cases from field studies in the USA with (a) distribution of study locations and colours according to effect size (light yellow $g = -0.32$ to red $g = 11.93$; for overlapping cases, the case with largest Hedges' g is shown) and relationship between effect size and (b) seasonality in precipitation ($R_S = 0.139$, $P_{\text{corrected}} = 0.575$) and (c) seasonality in temperature ($R_S = 0.252$, $P_{\text{corrected}} = 0.002$). Note that best-fit lines are not shown as relationships are analysed with Spearman's rank correlations using geographically effective degrees of freedom.

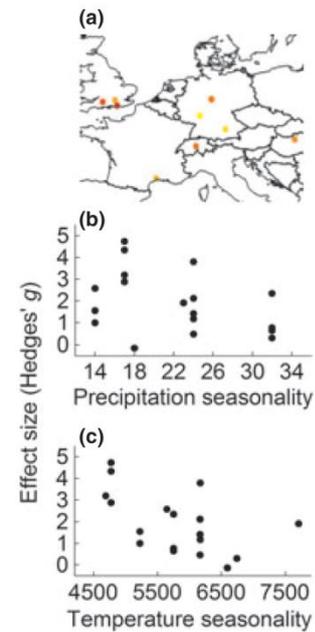


Fig. 7. Cases from field studies in Europe with (a) distribution of study locations and colours according to effect size (light yellow $g = -0.14$ to red $g = 4.73$; for overlapping cases, the case with largest Hedges' g is shown) and relationship between effect size and (b) seasonality in precipitation ($R_S = -0.558$, $P_{\text{corrected}} = 0.078$) and (c) seasonality in temperature ($R_S = -0.315$, $P_{\text{corrected}} = 0.097$). Note that best-fit lines are not shown, as relationships are analysed with Spearman's rank correlations using geographically effective degrees of freedom.

methodological issues by weighing for a study's precision, using an effect strength estimator with well-known properties and by analysing data with random-effect models. The biological control of herbivore populations by natural enemies is an indispensable ecosystem service, particularly in less intense farming systems (Tilman *et al.* 2002; Zehnder *et al.* 2007), and our results contribute to a better understanding of the underlying factors that alter this service.

PREDATOR FUNCTIONAL GROUP

We hypothesized that the effect of natural enemies on aphid population size is strongest in treatments with both generalist and specialist predators (additive effect), but that if tested in isolation, specialists are more successful in controlling aphids than generalists. The effect of arthropod predators on aphid populations was indeed strongest in treatments that included both generalist and specialist predators, but this effect, in contrast to the first half of our hypothesis, was not additive. However, specialists alone were more successful in controlling aphids than generalists, thus supporting the second half of our hypothesis. Nonadditive interactions among multiple predator species may either enhance predation risk of a shared prey by facilitation (synergism) or may reduce it due to interference or intraguild predation (Schmitz 2007;

Carey & Wahl 2010). Our analysis on the interactive effect of generalist and specialist predators tends to support the reduction hypothesis. One explanation might be that generalist predators reduce aphid control by specialists through intraguild predation (e.g. Snyder & Ives 2001). Specialized parasitoids, for example, are particularly vulnerable to intraguild predation, as their offspring develops within aphid hosts (i.e. the shared prey; Brodeur & Rosenheim 2000). Interference may have additionally reduced the effect of joint predation by causing behavioural changes among predators and prey (Bilu & Coll 2007). Overall, the results of our meta-analysis support classical biological control strategies that primarily rely on high per capita consumption rates of specialist predators (Schmidt *et al.* 2003) particularly if host plants are grasses. Nevertheless, the potential of generalist predators may be underestimated by our approach, as the data available did not allow us to account for temporal dynamics, for example, particularly strong effects of generalist predators early in the growing season (Scheu 2001; Birkhofer *et al.* 2008).

HOST PLANT GROUP

In line with our second hypothesis, the results of the meta-analysis suggest that the effect of arthropod predators on aphid populations was weakest on legumes that are rich in nitrogen compared with the other plant groups tested, particularly in treatments with only one predator group. Aphids reach maximum fecundity faster when reared on host plants with high nutrient availability (Stadler, Dixon & Kindlmann 2002). Thus, a more rapid growth of aphid populations on nitrogen rich legumes may not suffer as much from predation compared with slower growing aphid populations on herbs and particularly grasses. In addition, aphids that feed on host plants with a low C : N ratio have a high nutritional quality for predators (Couture, Servi & Lindroth 2010). As a consequence, specialist predators feeding on aphid prey inhabiting legumes may have to consume only a comparatively small number of prey organisms to fulfil their physiological demands. Thus, aphid reduction is lower on plants with high nutrient availability such as legumes compared with plants with poor nutritional quality such as grasses. This argument is consistent with the conclusion of Awmack & Leather (2002) that higher-trophic level interactions between herbivorous insects and their predators and parasitoids is modulated by the impact of the prey's diet on prey quality.

CLIMATE SEASONALITY

Our third hypothesis is supported, as the results of the meta-analysis indicate that the effect of natural enemies on the size of aphid populations increases with precipitation seasonality in temperate regions and with temperature seasonality in the USA. Drought and extreme

rainfall events, common in areas with high seasonality in precipitation and temperature, are known to cause mortality in aphid populations (McVean & Dixon 2001; Karley *et al.* 2004). Temperature seasonality may facilitate predator effects, as aphids are often more sensitive to extreme temperature fluctuations than their predators (Bale *et al.* 2002). Effects of temperature extremes are stronger on above-ground herbivores compared to soil-dwelling predators (e.g. carabids and spiders), as temperature directly affects development rate, population density and host plant exploitation by herbivorous insects. In contrast, populations of ground-active predators are less affected by climate extremes, as temperature fluctuations are buffered at the soil layer. High frequencies of extreme temperature events can further reduce aphid densities, without altering the foraging ability and offspring production of an aphid parasitoid (Bannerman, Gillespie & Roitberg 2011). The effect of temperature seasonality may be more pronounced in the USA because of the larger range of temperature seasonality in the USA as compared to Europe in our study. The biological control of aphids seems to be facilitated by higher precipitation or temperature seasonality in ecosystems.

CONCLUSIONS

Our meta-analysis shows that the success of biological control of aphids by natural enemies within the biomes covered by the available data set (i.e. predominantly temperate regions) is modulated by both bottom-up (group of host plants) and top-down (predator functional group) effects. Specialist predators and assemblages of specialists and generalists are particularly effective in reducing the numbers of aphid species that feed on grasses or herbs. The control of aphids by natural enemies is most promising in grass and herb crops, whereas it is less suited for controlling aphids in legume crops. The finding that climatic conditions such as higher seasonality in precipitation and temperature facilitate aphid predation may have significant implications for the effect of future climate change on the ecosystem service of pest control. To consolidate the trends revealed by our meta-analytical approach, future studies should cover a larger range of climatic conditions and should also include additional threats to biological control, such as elevated CO₂ levels or pest invasions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Studies providing cases for meta-analysis with experimental set-up, predator functional group and host plant group.

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List of publications

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Diehl E, **Sereda E**, Wolters V & Birkhofer K (2013) Effects of predator specialization, host plant and climate on biological control of aphids by natural enemies: a meta-analysis. *Journal of Applied Ecology* 50: 262-270

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