

Aus dem Institut für Natur- und Ressourcenschutz
der Christian-Albrechts-Universität zu Kiel

**Diversity effects of wildflower strips in relation to
their spatial arrangement and landscape
complexity on the non-target group of prey-
hunting wasps**

Dissertation

zur Erlangung des Doktorgrades
der Agrar- und Ernährungswissenschaftlichen Fakultät
der Christian-Albrechts-Universität zu Kiel

vorgelegt von
Uta Sophie Hoffmann, M.Sc.
aus Freudenberg, Siegen-Wittgenstein

Kiel, 2020

Dekan: Prof. Dr. Dr. Christian Henning
Erstgutachter: Prof. Dr. Tim Diekötter
Zweitgutachter: Prof. Dr. Volkmar Wolters

Tag der mündlichen Prüfung: 17.06.2020

Gedruckt mit Genehmigung
der Agrar- und Ernährungswissenschaftlichen Fakultät
der Christian-Albrechts-Universität zu Kiel

Table of Contents

Summary.....	1
Zusammenfassung.....	3
General Introduction	7
Chapter 1: Spatially concerted installation may boost biodiversity effects of aculeate wasps on sown wildflower strips promoted by landscape context and connectivity	14
Chapter 2: Prey-dependent benefits of sown wildflower strips on solitary wasps in agroecosystems.....	27
Chapter 3: The suitability of sown wildflower strips as hunting grounds for spider-hunting wasps of the genus Trypoxylon depends on landscape context.....	40
General Discussion	52
References	55
Appendix	66
Acknowledgements/ Danksagung	73
Curriculum Vitae.....	75

Summary

Wildflower strips, as an agri-environmental scheme, aim at counteracting the dramatic decline in insect diversity in agricultural landscapes. By providing flower resources this measure is thought to promote especially pollinators such as wild bees. Previous studies suggest that the effectiveness of wildflower strips is highest in landscapes with a simple structure, where wildflower strips create a high ecological contrast to the surrounding landscape. So far it has not been investigated, however, whether their effectiveness may be strengthened if several, rather than single, wildflower strips are created in close proximity to each other, particularly in cleared landscapes. In addition, there is hardly any knowledge on whether non-target organisms, such as herbivores or their natural enemies, benefit from wildflower strips. Here, I studied the benefits of a concerted installation of wildflower strips to the non-target group of prey-hunting wasps.

Using a common design, I followed three hypotheses-based approaches to quantify the species richness and abundances of predatory wasps (Aculeata) on wildflower strips and their development over the three years of study (CHAPTER 1), to examine prey quantity and quality in one caterpillar- and one spider-hunting wasp (CHAPTER 2) and to study spider-prey composition (CHAPTER 3) in relation to the landscape context and connectivity of wildflower strips. The study utilized 11 wildflower strips (isolated) that in a radius of 500 m had no other wildflower strip (isolated) and 11 wildflower strips (connected) with at least one wildflower strip in their surrounding of which the closest one (satellite) was also sampled for spider-hunting wasps using yellow pan traps. Applying GIS-based landscape analyses, isolated and connected wildflower strips were selected with independently varying proportions of grassland and semi-natural habitats in their surroundings as a measure of landscape complexity. Trap nests installed in increasing distances to isolated and connected wildflower strips were used to examine their utilization as hunting grounds by wasps.

Species richness of prey hunting wasps on isolated wildflower strips increased with landscape complexity. The richness of wasps on connected sites did not vary with

landscape complexity and was as low as on isolated sites at the low end of the complexity gradient. When taken together, however, wasp richness on connected sites and their satellites was still independent of landscape complexity but as high as isolated sites at the high end of the landscape complexity gradient. Over the three years of the study, the abundance of wasps grew most strongly in simple landscapes with several wildflower strips installed (CHAPTER 1). I could show that the caterpillar-hunting wasp *Ancistrocerus nigricornis* built more cells in proximity to wildflower strips and with increasing amount of surrounding grassland. The weight of collected caterpillars increased with amount of grassland on connected wildflower strips, whereas on isolated sites the effect was reversed. Number of caterpillar individuals per brood cell were negatively correlated with their weight and with amount of semi-natural habitats (CHAPTER 2). In contrast, the spider-hunting wasp *Trypoxylon figulus* built more cells with increasing distance of nests to wildflower strips. If there were few strips, *T. figulus* built more cells in grassland-rich landscapes, whereas low shares of grassland were compensated when several wildflower strips were present (CHAPTER 2). The similarity between spider communities in nests and in flowering strips decreased with the distance to the next wildflower strips, but the percentage of surrounding grasslands modulated this relationship. This concurred with an observed positive effect of grassland on spider species richness in trap nests, especially if wildflower strips were distant from the nests (CHAPTER 3).

The results highlight that wildflower strips not only benefit the prominently targeted group of pollinators but also the non-target group of prey-hunting wasps. For the first time it was shown that these diversity benefits of wildflower strips may be boosted by a concerted installation of several wildflower strips, particularly in simple landscapes. It seems that this effect is driven by an increased connectivity of habitat elements in these landscapes that allows more species to utilize and benefit from the forage resources created by wildflowers strips. This thesis substantiates the importance of wildflower strips for species richness and trophic interactions in agroecosystems and may help to develop further this agri-environmental scheme and increase its effectiveness in the future.

Zusammenfassung

Die Anlage von Blühflächen wird als Maßnahme im Rahmen von Agrarumweltprogrammen eingesetzt, um dem dramatischen Rückgang der Insektendiversität in der Agrarlandschaft entgegenzuwirken. Von den vielfältigen Blütenressourcen sollen besonders Bestäuber wie Wildbienen profitieren. Vorherige Studien zeigen, dass die Effektivität der Blühflächen aufgrund ihres hohen ökologischen Kontrastes zur umgebenden Landschaft in einfach strukturierten Landschaften am höchsten ist. Bisher ungewiss ist, ob ihre Effektivität gesteigert werden kann, wenn nicht nur einzelne, sondern mehrere Blühflächen in räumlicher Nähe zueinander angelegt werden. Diese Konnektivität der Blühflächen könnte besonders in strukturarmen Landschaften deren Effektivität steigern. Darüber hinaus ist wenig bekannt, inwieweit auch andere Taxa neben den Zielarten von den Blühflächen profitieren, wie Herbivore und ihre natürlichen Feinde. In dieser Arbeit untersuche ich die Wirkung der räumlichen Anordnung von Blühflächen auf die wenig beachtete Gruppe der prädatorischen Wespen (Aculeata).

In drei hypothesenbasierten Ansätzen habe ich die Diversität prädatorischer Wespen sowie deren Beutenutzung über drei Studienjahre im Kontext der Landschaftskomplexität und der Konnektivität der Blühflächen untersucht. Die Untersuchungsflächen für den Fang der Wespen mit Gelbschalen (KAPITEL 1) waren 11 Blühflächen (isoliert), ohne weitere Blühfläche in einem Radius von 500 m, sowie 11 Blühflächen (vernetzt), mit wenigstens einer weiteren Blühfläche in der Umgebung, von der jeweils die nächstgelegene Blühfläche (Satellit) ebenfalls beprobt wurde. Durch eine GIS-gestützte Landschaftsanalyse wurden die isolierten und vernetzten Blühflächen so ausgewählt, dass sie entlang eines unabhängigen Gradienten des Anteils Grünland und naturnaher Habitate in ihrer Umgebung als Maß der Landschaftskomplexität lagen. Ob die Blühflächen auch zur Beutejagd der Wespen genutzt werden, wurde in Nistfallen, die in steigender Distanz zu den in Kapitel 1 untersuchten Blühflächen aufgestellt wurden, beobachtet (KAPITEL 2 + 3). Dabei habe ich die Quantität und Qualität der in die Nester eingetragenen

Beutetiere einer raupen- und einer spinnenjagenden Wespenart (KAPITEL 2), sowie die Artenzusammensetzung der erbeuteten Spinnen (KAPITEL 3) untersucht.

Die Anzahl der Wespenarten auf isolierten Blühflächen stieg mit der Landschaftskomplexität an. In Landschaften mit vernetzten Blühflächen hingegen ist die Anzahl der Arten unabhängig von der Landschaftskomplexität; hier kommen gleich viele Arten wie auf isolierten Blühflächen nur in komplexen Landschaften vor. Über die drei Untersuchungsjahre stieg die Abundanz der Wespen am stärksten in einfachen Landschaften mit vernetzten Blühflächen an (KAPITEL 1). Des Weiteren zeige ich, dass von der raupenjagenden Wespe *Ancistrocerus nigricornis* sowohl in geringerer Entfernung zur Blühfläche als auch bei steigendem Anteil Grünland mehr Brutzellen angelegt wurden. Das Gewicht der ins Nest eingetragenen Raupen stieg bei vernetzten Blühflächen mit dem Anteil an Grünland an. Die Anzahl der Raupen pro Brutzelle war dabei negativ mit deren Gewicht und dem Anteil an naturnahen Habitaten korreliert (KAPITEL 2). Die Anzahl an Brutzellen der spinnenjagenden Grabwespe *Trypoxylon figulus* stieg mit steigender Distanz der Nistfallen zu den Blühflächen an. Dabei wurden bei isolierten Blühflächen mehr Brutzellen gebaut, allerdings nur in Landschaften mit hohem Grünlandanteil, wohingegen der Effekt in strukturarmen Landschaften durch die Anlage mehrerer Blühflächen ausgeglichen wurde (KAPITEL 2). Mit steigender Distanz zur Blühfläche wich die Artenzusammensetzung der eingetragenen Spinnen zunehmend von jener der Blühflächen ab. Dieser Effekt war jedoch beschränkt auf komplexe Landschaften, was mit dem beobachteten positiven Effekt des Grünlandanteils auf die Anzahl der Spinnenarten in den Nistfallen übereinstimmte, besonders bei höherer Distanz zu den Blühflächen (KAPITEL 3).

Mit dieser Arbeit zeige ich, dass Blühflächen nicht nur Bestäuber als eigentliche Zielgruppe fördern, sondern auch die weniger beachteten prädatorischen Wespen. Erstmals wird gezeigt, dass deren positive Wirkung auf die Artenvielfalt durch die Anlage mehrerer vernetzter Blühflächen gesteigert werden kann, besonders in einfach strukturierten Landschaften. Dieser positive Effekt der Blühflächen kann auf die gesteigerte Konnektivität der einzelnen Habitatslemente zurückgeführt werden. Die höhere Vernetzung der Landschaft erlaubt es mehr Arten, die Blühfläche mit ihren bereitgestellten Nahrungsressourcen zu nutzen. Diese Arbeit stützt die

Bedeutung von Blühflächen für die Vielfalt der Arten und trophischen Interaktionen in Agrarökosystemen und kann dazu beitragen, die Effektivität zukünftiger Agrarumweltprogramme zu steigern.



General Introduction

Worldwide biodiversity decline is one of the biggest challenges we face to date and in the coming decades (Steffen *et al.*, 2015; Cardoso *et al.*, 2020). It is driven by the loss of natural habitats especially in agricultural regions (Benton *et al.*, 2003; Foley *et al.*, 2005; Seibold *et al.*, 2019) and accelerated by climate change (de Chazal & Rounsevell, 2009; Lister & Garcia, 2018). Therefore, to counteract the decline of farmland biodiversity, wildflower strips are put into place (Kleijn & Sutherland, 2003; Whittingham, 2006). While these flower-rich elements have originally been targeted at promoting flower-visiting insects such as bees or butterflies (Ouvrard *et al.*, 2018), also non-target insect groups may benefit from their implementation due to also providing ample resources other than pollen or nectar (Grass *et al.*, 2016; Baulechner *et al.*, 2019). In addition to poor knowledge on the effects of wildflower strips on the diversity of non-target organisms, little is known on how the spatial arrangement of wildflower strips may affect their efficiency that to date has solely been attributed to landscape structural complexity and the created contrast (Tschardt *et al.*, 2005; Scheper *et al.*, 2013). Therefore, I studied if wildflower strips benefit the non-target group of prey-hunting wasps and whether the creation of multiple versus single wildflower strips can increase the biodiversity benefits of this measure.

Agricultural landscapes have been shaped by human activities over centuries, forming ecosystems of high spatial and temporal heterogeneity (Benton *et al.*, 2003; Hendrickx *et al.*, 2007). As such, for a long time, agricultural landscapes have provided habitats to a diverse set of species. This has started to change in the middle of the 20th century since when an increased mechanization and specialization has led to drastic changes in the cultivated area as well as to a loss and fragmentation of (semi-)natural habitats (Foley *et al.*, 2005; Emmerson *et al.*, 2016). Robinson & Sutherland (2002) quantified a loss of 50% of all hedgerows in Great Britain, and also other linear landscape elements that were once corridors for dispersing species vanished from agricultural landscapes (Krewenka *et al.*, 2011). Overall, the once heterogeneous agricultural mosaic transformed into a homogenous landscape of ever-growing arable fields.

From a biodiversity perspective, crop and, as a side effect, also remaining non-crop habitats became degraded due to the increasing use of synthetic fertilizers and pesticides since the 1950's (Geiger *et al.*, 2010). Increasing yields with high nitrogen inputs decreased plant species richness across Europe (Baessler & Klotz, 2006), amplified by the application of herbicides. Since plants represent the basic food resource for heterotrophs (Hass *et al.*, 2019), the loss of plant species distorts plant-insect interactions (Rossetti *et al.*, 2017) and is recognized as one of the main drivers for the decline of higher trophic levels such as herbivores, wild bees, predators or parasitoids (Scheper *et al.*, 2014; Balzan *et al.*, 2016). Thus, the loss of plant resources may decrease the overall abundance and diversity of consumers (Tilman *et al.*, 2001). Plant diversity and the quality of the agricultural matrix also determine its permeability, an essential aspect in increasingly fragmented agricultural landscapes.

Habitat fragmentation in modern agricultural landscapes results in a loss and isolation of (semi-)natural habitats. With fragmentation distances grow between remaining natural or semi-natural habitat patches that are surrounded by an increasingly hostile agricultural matrix (Fahrig, 2001; Öckinger *et al.*, 2012). As the quality of the surrounding landscape matrix together with the species' dispersal abilities determine landscape connectivity (Tischendorf & Fahrig, 2000; Ricketts, 2001), a decreasing number of species can meet their demands in these simplified landscapes (Tilman *et al.*, 2001). Particularly affected by habitat fragmentation are small and less mobile species (Jauker *et al.*, 2013) and multi-habitat users that are spatially constricted to their respective foraging and nesting sites and therefore dependent on good matrix quality to enable movement between these habitat elements (Jauker *et al.*, 2009). The isolation and loss of foraging resources resulted in the decline of the abundance and species richness of, for example, wild bees (Holzschuh *et al.*, 2008; Bommarco *et al.*, 2012a), hoverflies (Meyer *et al.*, 2009; Beduschi *et al.*, 2018), and butterflies (van Swaay *et al.*, 2006).

Not only are abundance and species richness of different taxa affected by these changes in agricultural landscape but also associated ecosystem services might be at risk (Mckenzie *et al.*, 2013). One much-noticed ecosystem service is the pollination by flower-visiting insects. Up to 75% of all food crops have been shown to be dependent on insect pollination (Power, 2010; Ollerton *et al.*, 2011). Besides honey

bees, wild bees provide important pollination services to many crops (Kremen *et al.*, 2002; Klein *et al.*, 2007) and increase their yields (Bommarco *et al.*, 2012b). Another important ecosystem service that is negatively affected by observed decline in biodiversity is biological control (Dirzo *et al.*, 2014). This service is provided by parasitoid and predatory insects that are highly affected by habitat fragmentation (Kruess & Tscharntke, 1994; Rusch *et al.*, 2010) which may also be an effect of their higher trophic level (Tscharntke *et al.*, 2002).

Prey-hunting wasps are multi-habitat users that depend on a high landscape heterogeneity and connectivity of their foraging and nesting sites (Holzschuh *et al.*, 2009). Beside floral resources for adult nutrition, they depend on the availability of prey arthropods for the provisioning of their brood cells (Armstrong & Stamp, 2003). It was shown that small distances between suitable foraging habitats and nesting sites increases wasps' fitness by reducing foraging time (Stamp, 2001; Klein *et al.*, 2004). The connectivity of suitable habitats may also be enhanced by linear grassy elements in the landscape (Öckinger & Smith, 2007; Holzschuh *et al.*, 2009). Wildflower strips may act in a similar way and besides increasing the connectivity may also provide floral resources for adults (Scheper *et al.*, 2015) and arthropod prey for larvae (Blaauw & Isaacs, 2014)

Since the 1980's, agri-environmental schemes (AES) were implemented as part of the Common Agricultural Policy (CAP) of the EU in order to integrate nature conservation goals into agricultural practice (Ovenden *et al.*, 2008). A common measure within these schemes is the sowing of wildflower strips on former arable fields. Wildflower strips are targeting mainly at flower-visiting insects like bees, bumblebees or butterflies that benefit from the high availability of flower resources (Winfree, 2010). However, it has been discussed that wildflower strips do not always meet their aim at promoting farmland biodiversity (Kleijn & Sutherland, 2003). This failure was attributed to a lack of source populations in intensively used landscapes (Duelli & Obrist, 2003). It was also argued that wildflower strips may benefit mainly common generalist species (Kleijn *et al.*, 2006; Haaland *et al.*, 2011; Wood *et al.*, 2017). In contrast, a positive correlation of plant species richness on flower-visiting insects (Tscharntke & Steffan-Dewenter, 2001) reveals their high potential to promote flower visitors.

High flower densities over a long seasonal period, especially in late summer when there is often a lack of foraging resources, attract a diverse community of flower visitors as well as herbivores (Grass *et al.*, 2016). High abundances of herbivores, in turn, attract predatory insects that feed on them (Rusch *et al.*, 2010). Therefore, wildflower fields may promote also non-target species (Ovenden *et al.*, 2008; Grass *et al.*, 2016; Baulechner *et al.*, 2019). These organisms may spill over into the adjacent land uses and contribute to ecosystem services at a local and landscape scale. It was shown, for instance, that high abundances of natural enemies and flower visitors on wildflower strips increased ecosystem service, like biological control (Blaauw & Isaacs, 2015; Tschumi *et al.*, 2016) and pollination (Albrecht *et al.*, 2007; Krimmer *et al.*, 2019) on adjacent crops. Therefore, wildflower strips contribute to more than species richness and abundances but also to ecosystem stability by diverse species interactions.

The positive effect of wildflower strips on biodiversity, however, is strongly determined by the landscape context (Batary *et al.*, 2011; Scheper *et al.*, 2013). It was shown that wildflower strips are most effective when the created ecological contrast is high. This is especially true when wildflower strips are established in simple compared to cleared and complex landscapes (Tschardtke *et al.*, 2005; Scheper *et al.*, 2013). While in complex landscapes, the installation of wildflower strips may create only a weak ecological contrast (Scheper *et al.*, 2013) and species are diluted across a heterogeneous set of abundant resources, in cleared landscapes, distances between habitat elements and new wildflower strips may be large and the intervening matrix act as a strong dispersal filter for small individuals (Gámez-Virúés *et al.*, 2015) and less mobile species (Dufлот *et al.*, 2014), resulting in small source populations.

If the installation of multiple compared to single wildflower strips may influence this landscape effect is unexplored so far. Studies indicate that wildflower strips can increase connectivity of suitable habitats for insects (Haaland *et al.*, 2011). The installation of multiple wildflower strips on landscape scale could bridge the unsuitable agricultural landscape matrix by increasing dispersal abilities of species. Several wildflower strips therefore may have the same attributes as stepping-stones between source habitats (Baum *et al.*, 2004) and could increase the effectiveness of wildflower strips in cleared landscapes (Tschardtke *et al.*, 2005; Beduschi *et al.*

al., 2018). However, there might be a high importance of a planning of wildflower strips as AES on landscape scale by considering already existing sites before installing additional wildflower strips.

Hence, in this thesis I examine the effects of single versus multiple wildflower strips in different landscape complexities on the diversity of the non-target group of predatory wasps. For doing so, 33 wildflower strips were selected along a landscape complexity gradient in an agricultural region in central Germany. Of these wildflower strips, 11 were isolated in that they had no other wildflower strips in a surrounding of 500m (“isolated”), whereas 11 others had one or more satellite wildflower strips in their surrounding (“connected”) of which we investigated the nearest (“satellite”). Landscape complexity was measured as the amount of grassland and semi-natural habitats in the radius of 500 m around the central wildflower strip. Different approaches were used to study the effects of wildflowers strips, their landscape context and spatial arrangement on (i) predatory wasp diversity in general (CHAPTER 1) and on (ii) predator-prey interactions of selected species (CHAPTERS 2 & 3).

CHAPTER 1: SPATIALLY CONCERTED INSTALLATION MAY BOOST BIODIVERSITY EFFECTS OF SOWN WILDFLOWER STRIPS

In this study, I explore whether the installation of multiple wildflower strips in concert increases their effectivity in promoting local wasp diversity. Several wildflower strips may improve patch connectivity within the agricultural matrix and therefore promote suitability of wildflower strips for prey-hunting wasps. Therefore, I survey species richness and abundances of wasps on wildflower strips using yellow pan traps over three years. Central study sites are either connected to additional wildflower strips within a landscape sector of 500 m radius or the only wildflower strips in the landscape sector. For exploring interacting effects of landscape complexity and the factor of wildflower strip connectivity, study sites are selected along a gradient of the amount of grasslands and semi-natural habitats in the surrounding landscape matrix. I examine species richness and abundance of prey-hunting wasps over three study years and hypothesize that species richness and abundance of wasps benefit from landscape complexity (amount of grassland and semi-natural habitats), and that multiple wildflower strips can compensate for

low landscape complexity by increasing habitat connectivity. Thus, the effectiveness might be highest if several wildflower strips are installed in landscapes of low complexity.

CHAPTER 2: PREY-DEPENDENT BENEFITS OF SOWN WILDFLOWER STRIPS ON SOLITARY WASPS IN AGROECOSYSTEMS

The species richness of wasps on wildflower strips may be a consequence of habitat quality regarding nectar resources for adult wasps. Yet, the utilization of wildflower strips by wasps may also be attributed to the availability of prey for nutrition of wasps' larvae. In the second study, I aim to specify the effects on total wasp community (CHAPTER 1) by assessing whether wildflower strips are used for hunting prey by the caterpillar-hunting mason wasp *Ancistrocerus nigricornis* CURTIS (Hymenoptera: Vespidae) and the spider-hunting digger wasp *Trypoxylon figulus* LINNAEUS (Hymenoptera: Crabronidae). I examine the nest building of these species using trap nests that are placed in increasing distances to the wildflower strips. The benefits for solitary wasps may not only be driven by high quantity of prey on wildflower strips in the proximity of their nests but also by higher prey quality. Therefore, I record the number of built brood cells, as well as number of collected prey items, caterpillar weight and spider species richness per brood cell of the respective wasp species. I test whether the distance between nests and the closest isolated or connected wildflower strip, landscape complexity and their interaction affect the number of brood cells and prey attributes. I hypothesize that both wasp species benefit from high quality and quantity of prey but that the distance to wildflower strips and the landscape complexity is crucial for their use of wildflower strips.

CHAPTER 3: THE SUITABILITY OF SOWN WILDFLOWER STRIPS AS HUNTING GROUNDS FOR SPIDER-HUNTING WASPS OF THE GENUS TRYPOXYLON DEPENDS ON LANDSCAPE CONTEXT

In order to examine the use of wildflower strips as hunting grounds for wasps, I examine the similarity of spider species richness occurring on wildflower strips and in nests of wasps of the genus *Trypoxylon* in trap nests along a distance gradient between nests and wildflower strips. After studying the benefits of wildflower

strips on total wasp diversity in general (CHAPTER 1) and the reproduction and prey quantity and quality of two trap-nesting species (CHAPTER 2), I here focus on available and utilized prey composition of spider-hunting wasps. I hypothesize, that collected spiders become more dissimilar to spider species on wildflower strips with increasing distance between the two locations and with increasing landscape complexity. I assume that wildflower strips are attractive foraging habitats to wasps, if they are located in low distance to the nesting sites. If wildflower strips are too far away, however, wasps may search for spider prey in other habitats where different spider species are abundant.

1. Spatially concerted installation may boost biodiversity effects of aculeate wasps on sown wildflower strips promoted by landscape context and connectivity

Uta S. Hoffmann | Frank Jauker | Daniela Warzecha |
Volkmar Wolters | Tim Diekötter

Manuscript in preparation

1.1 Abstract

Biodiversity effects of sown wildflower strips are driven by the ecological contrast with the surrounding matrix and thus moderated by landscape context. Maximal effectiveness of this agri-environment scheme (AES) has been shown in simple as compared to cleared or complex landscapes. Yet, so far it has not been investigated whether benefits of wildflower strips may be boosted if they were not individually installed but in concert. To answer this question, we studied aculeate wasp diversity in 33 wildflower strips in an agricultural landscape in central Germany. Of these wildflower strips, 11 had no other wildflower strip in a surrounding of 500m (“isolated”), whereas 11 others (“connected”) had at least one satellite wildflower strip in their surrounding of which we investigated the nearest (“satellite”). We found that species richness of wasps in isolated wildflower strips increased with increasing shares of grassland in their surroundings. In contrast, wasp species richness in connected wildflower strips started similarly low as for isolated ones at the low end of the grassland gradient but showed no increase along the gradient. Yet, pooling species richness of connected wildflower strips and their satellite sites resulted in an equally high value throughout the grassland gradient as for isolated wildflower strips at the high end of the gradient. The ratio of wasp abundance of the years 2013 and 2011, i.e. the relative gain in abundances across the study period, declined on connected wildflower strips along the gradient of semi-natural habitats, whereas on isolated wildflower strips there was no decline in the ratio. Higher abundance ratios in landscapes with lower amounts of semi-natural habitats concur with previous findings that wildflower strips are more effective in promoting biodiversity in more simple than complex landscapes. For the first time, our results show, that the biodiversity effects of sown wildflower strips in simple landscapes can be boosted by installing wildflower strips not singly but in concert. Together with a more precise identification of tipping points along the landscape complexity gradient, these new findings may help to increase the efficiency of AES in modern agroecosystem in the future.

1.2 Introduction

Agricultural intensification has increased the fragmentation of semi-natural habitats like field margins, hedgerows, fallows or pastures in modern agro-ecosystems (Foley *et al.*, 2011). This loss and isolation of resources for foraging, nesting or overwintering resulted in a dramatic loss of biodiversity (Benton *et al.*, 2002; Foley *et al.*, 2005). Wildflower strips have been implemented in many European countries as a prominent agri-environmental scheme (AES) to counteract this loss (Haaland *et al.*, 2011; Whittingham, 2011). The benefits of wildflower strips have been argued to be maximal in simple as compared to cleared or complex landscapes (Tscharntke *et al.*, 2005; Scheper *et al.*, 2013). It is unclear, however, whether installing multiple wildflower strips in concert overcomes this functional deficit and changes their context-dependent efficiency. Thus, we studied the effect of single *versus* multiple wildflower strips on species richness and abundance of prey-hunting wasps along a gradient of agricultural landscape complexity.

Flower-visiting insects are an obvious target group of wildflowers strips. Wildflower strips have thus frequently been shown to benefit the diversity of solitary wild bees (Feltham *et al.*, 2015), bumblebees (Carvell *et al.*, 2007) or butterflies (Haaland & Bersier, 2011). Accordingly, plant species composition in seed mixtures has become a focus of interest, and how flower composition interacts with pollinator traits such as rarity, to improve conservation efforts (Kleijn *et al.*, 2006; Ouvrard *et al.*, 2018; Warzecha *et al.*, 2018). Often overlooked are herbivorous insects such as true bugs or butterflies in their larval stages (Huusela-Veistola *et al.*, 2016), that may benefit from the diverse plant biomass provided by wildflower strips, and higher trophic levels that in turn may increase due to bottom-up effects (Scherber *et al.*, 2010; Ramsden *et al.*, 2014). Along this line, wildflower strips have been shown to also positively affect non-target groups such as spiders (Campbell *et al.*, 2019) or predatory wasps (Hoffmann *et al.*, 2018, 2020).

Generally, species responses to landscape structure are trait dependent (Duflot *et al.*, 2014) and the various taxa supported by wildflower strips likely differ in their response to the implementation of wildflower strips in relation to the landscape context (e.g. Heard *et al.* 2007; Tscharntke *et al.* 2012) the landscape dependency

in the effectiveness of wildflower strips is understudied for most taxa, in the general context of AES implemented measures were more effective at enhancing diversity in structurally simple than in cleared or complex landscapes (Tschardt *et al.*, 2012; Scheper *et al.*, 2013). This is because in cleared landscapes, wildflower strips represent attractive habitat islands but often with a strong dispersal filter for a reduced regional species pool (Duflot *et al.*, 2014; Gámez-Virúés *et al.*, 2015), while in complex landscapes, the connectivity is high but the created contrast is weak due to many resource-rich habitats in close proximity. In the context of wildflower strips, a matrix dependency was evident for prey-hunting wasps where wildflower strips improved nesting activity, yet only if strips were close to nesting habitats and well connected by high shares of grassland (Hoffmann *et al.*, 2018). As connectivity between landscape elements seems to be crucial for flower-visiting multi-habitat users (Jauker *et al.*, 2009), installing multiple wildflower strips in concert rather than individually may boost their benefits to biodiversity and potentially change their context-dependency.

Aculeate wasps (Hymenoptera: Aculeata) are multi-habitat users. Like bees, adult wasps depend on nectar as energy source, while their larvae, in contrast to bees, are dependent on arthropod prey such as caterpillars, spiders, flies or hemipterans (Witt, 1998). While nectar as well as their arthropod prey may well be found in wildflower strips or grasslands (Hoffmann *et al.*, 2018, 2020), nesting sites are often found in nearby woody habitats (Holzschuh *et al.*, 2009; Coudrain *et al.*, 2013). Besides providing foraging resources, grass-strip corridors (Holzschuh *et al.*, 2009) or the amount of grassland (Hoffmann *et al.*, 2018, 2020) may also facilitate wasp movement between different landscape elements in agricultural landscapes. With their necessity to commute repeatedly between different habitat elements, wasps make a prime taxonomic group for studying the effects of interspersing multiple wildflower strips into the landscape matrix in which they forage.

Here, we aimed at revealing the effect of installing single *versus* multiple wildflower strips in concert on the abundance and species richness of the functionally important guild of wasps. For doing so, we collected the abundance and species richness of wasps with yellow pan traps over three years in 33 wildflower strips

that were situated in differently structured landscapes and either installed as single wildflower strips or in concert. We specifically hypothesized that (i) wasp communities in single wildflower strips are primarily restricted by a dispersal filter (i.e. species richness and abundance increase with amount of semi-natural elements or grassland in the surrounding increasing landscape permeability), (ii) multiple wildflower strips overcome this landscape filter by increasing connectivity at the landscape scale (i.e. species richness and abundance become independent from landscape complexity) and (iii) benefits of wildflower strips to wasp communities over time are thus greatest with a concerted installation of multiple wildflower strips in simple landscapes.

1.3 Material and Methods

1.3.1 Study area

The three-year study took place in the district of Marburg-Biedenkopf (Hesse, Germany), a region which is dominated by agricultural area (44 %) and forest (41%). In 2011 as part of an AES (HIAP - Hessisches Integriertes Agrarumweltprogramm) more than 200 wildflower strips were sown on former arable fields with a seed mixture containing wild herbs and cultural plants which are considered to be attractive for flower visitors. As part of the subsidy scheme, farmers were contracted to refrain from any management for five years. The 33 similarly sized (0.3 ± 0.04 ha) wildflower strips covered a broad geographic range (distance between sites 911–9,856 m; $2,520 \pm 1,919$ m standard deviation STD). Of these study sites, 22 sites were divided in the isolation classes: “isolated” (only the focal wildflower strip was present in a 500 m radius) and “connected” (at least one additional wildflower strip present in a 500 m radius). Additional 11 sites were selected as “satellite” sites, representing the closest neighbouring wildflower strip to each “connected” site. All together the study sites covered independent gradients in the amount of permanent grassland (pastures and grasslands; 5.5 – 34.3 %; 21.0 ± 8.2 % STD), semi-natural habitats (hedges, gardens, fallows, alluvial meadows, clear cuttings, tree rows, quarries, orchards, and the respective wildflower strips; 5.0 – 14.4 %; mean 10.4 ± 2.2 % STD) and area of arable land (16.8 – 81.6

%; 45.8 ± 21.1 % STD) at the landscape scale (radius 500 m around the focal study site). Landscape analyses were carried out using ArcGIS 10.4 (ESRI, Ca., USA).

1.3.2 Wasp collection

For surveying wasp diversity, we placed two yellow pan traps in the center of each focal wildflower strip with an inter-trap distance of 10 m. In “connected” study sites we additionally placed traps in the “satellite” wildflower strip located closest to the focal site. Traps were installed in the field from beginning of June to the end of July in the years 2011 to 2013, insect samples were collected weekly. We selected all individuals of the aculeate wasp families Pompilidae, Sapygidae, Tiphiidae, Vespidae and Crabronidae (Hymenoptera: Apocrita, Aculeata). All individuals were determined to species level. Sampled wild bees were used for associated studies (e.g. Warzecha et al., 2016).

1.3.3 Statistical analyses

Analyses were performed with R 3.5.1 (R Development Core Team, 2018). We calculated species richness and abundance of wasps per study site pooled for both traps and all three study years. To quantify changes of abundances over time, we calculated for each study site an abundance ratio (LN transformed, with 1 added to account for zeros in the dataset; Scheper *et al.*, 2015) by dividing wasp abundances in 2013, representing the established wildflower strip, by abundances in 2011, representing the status quo when wildflower strips were newly sown on former arable fields without a flowering aspect yet. Social species of the family Vespidae were excluded from abundance-based models, because unrecorded proximity to nests may bias analyses (967 individuals in 2011, compared to 20 individuals in 2012 and 88 in 2013), but remained in models on species richness. Explanatory variables were amount of grassland and semi-natural habitats in the surrounding landscape (radius 500 m around the focal study site), considered to represent landscape complexity.

We first plotted total abundance and total species richness for each isolation class (focal study sites “connected” and “isolated”, satellite site “satellite” and accumulated values of “connected + satellite”). Because abundance or species richness of

“connected+satellite” sites are accumulated values of connected and satellite sites and thus not independent from their underlying sites, we refrained from a global test of isolation class on abundance or species richness. Instead, we tested for the pairwise differences between “connected” and “isolated”, “satellite” and “isolated”, as well as “connected+satellite” and “isolated” sites using t-tests. For testing the interacting effects of isolation and landscape complexity (measured as the percentage area of semi-natural habitats or grassland) on total abundance and species richness of wasps and the abundance ratio we used an ANCOVA analysis based on linear models. In these models, we used “connected” and “isolated” sites only. For model selection, a manual forward selection procedure was used. In this procedure the isolation class entered the model first and remained in the model, the two variables of landscape complexity and their interactions with the isolation class were added successively (first percentage area of semi-natural habitats, second percentage area of grassland) and removed when a set P -level of 0.05 was not achieved. Model residuals were checked for normal distribution and homoscedasticity.

1.4 Results

Overall, we collected 2548 aculeate wasp individuals out of 111 species over the three years. The social wasp species *Vespula germanica* FABRICIUS, *V. vulgaris* LINNAEUS and *Dolichovespula sylvestris* SCOPOLI (Hymenoptera: Vespidae) were the most abundant species with 1426 (56%) of all individuals. The most abundant solitary wasp species was *Tiphia minuta* FABRICIUS (Hymenoptera: Tiphiidae) with 162 individuals, followed by *T. femorata* VAN DER LINDEN and *Pemphredon lethifer* SHUCKARD (Hymenoptera: Crabronidae) with 117 and 103 individuals, respectively. The most diverse wasp families were Crabronidae with 66 species and Pompilidae with 17 species.

With on average $26.64 (\pm 14.37 \text{ STD})$ individuals on connected and $21.18 (\pm 13.39)$ individuals on satellite sites, the total abundance of wasps over the period of three years was on average 1.64 ($p = 0.082$), respectively 2.06 ($p = 0.016$) times lower than on isolated sites with $43.73 (\pm 24.36)$ individuals (Fig. 1a). Together, connected and their satellite sites showed a similar average total wasp abundance over the period of three years (47.82 ± 22.8) than isolated sites ($p = 0.689$). With 16.27

(± 4.1) species on connected and 16.45 (± 5.35) on satellite sites, the total wasp species richness over the period of three years was on average 1.24 ($p = 0.073$), respectively 1.26 ($p = 0.1$) times lower than on isolated sites with 20.73 (± 6.54) (Fig. 1b). With an average of 25.91 (± 5.82), the total species richness of wasps over the period of three years on connected and satellite sites together was 1.25 times higher than on isolated sites ($p = 0.073$).

The total abundance of wasps over the period of three years was neither affected by landscape complexity, isolation class nor their interaction. In contrast, the total species richness per site was driven by an interacting effect of landscape complexity, here measured as the amount of grassland in the surrounding landscape, and the isolation class of wildflower strips ($F_{3,18} = 3.92$; $p = 0.026$; $R^2_{\text{adj}} = 0.29$; Table 1). For isolated wildflower strips, the total species richness of wasps increased with amount of strips species permanent grassland, while for connected wildflower strips the species richness did not vary with the amount of permanent grassland and, with a mean of 16.3 (± 4.1), the species richness remained nearly as low as for the isolated sites at the low end of the grassland gradient. If connected sites and their satellite were pooled, however, and plotted in the same graph (this data was not part of the regression model), species richness on average remained constant

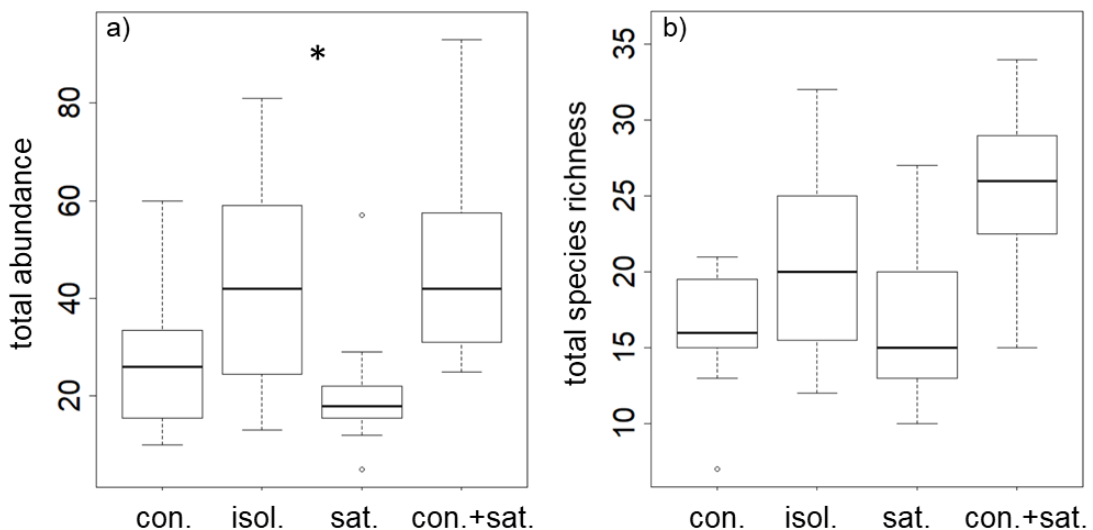


Fig. 1: Total abundance (a) and species richness (b) of aculeate wasps on wildflower strips distributed along the isolation classes: isolated (“iso”) and connected wildflower strips (focal strip “con.”, satellite strip “sat.”, and the accumulated species richness of the focal and its satellite strip “con.+sat.”).

along the grassland gradient but this time with a mean of $25.9 (\pm 5.8)$ being similarly high as the species richness of isolated sites at the high end of the grassland gradient (Fig. 2).

The abundance ratio was interactively affected by landscape complexity, measured as the amount of semi-natural habitats, and the isolation of wildflower strips ($F_{3,18} = 3.74$; $p = 0.030$; $R^2_{\text{adj}} = 0.28$; Table 1). With a mean of around $0.39 (\pm 0.99)$, the abundance ratio on isolated wildflower strips did not change along the gradient of semi-natural habitats. For connected wildflower strips, however, the abundance ratio was high at the low end of the semi-natural habitat gradient, but steeply declined with an increasing amount of semi-natural habitats to even negative values at the high end of the gradient (Fig. 3).

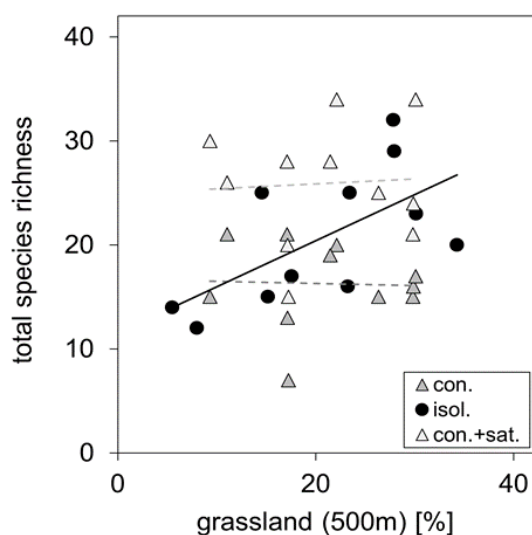


Fig. 2: Species richness of aculeate wasps as an interaction between the amount of grassland [%] in a 500 m radius and isolation class of wildflower strips (isolated strips, black circles; connected, dark grey triangles). As a visual reference accumulated species richness of connected focal and their satellite strips are plotted (light triangles).

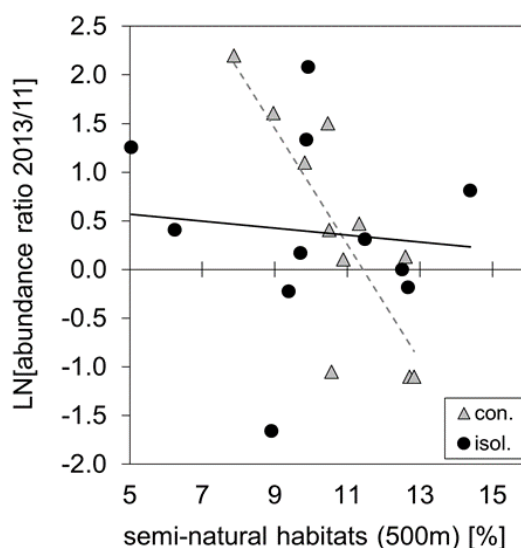


Fig. 3: The relative change in aculeate wasp abundance between 2011 and 2013 [LN] as an interaction between amount of semi-natural habitats [%] in a 500 m radius around the focal wildflower strip and the isolation class of wildflower strips (connected strips, grey triangles; isolated strips, black circles).

Table 1: Results for all ANCOVA models.

dependent	explanatory variable	d.f.	Estimate	t	p	model p, R²
abundance					<i>n.s.</i>	
species richness	isolated	1,22	20.80	14.17	>0.001	0.026, 0.29
	grassland	1,22	-0.02	-0.10	0.920	
	grassland:isolated	1,22	0.44	2.68	0.016	
LN [abundance ratio13/11 +1]	connected	1,22	0.62	2.23	0.039	0.030, 0.28
	semi-natural	1,22	0.08	-0.35	0.731	
	semi-natural :connected	1,22	-1.32	-3.33	0.004	

1.5 Discussion

The effectiveness of wildflower strips in promoting farmland diversity is generally considered to be highest in simple landscapes (Tschardt *et al.*, 2005). While previous studies focused on single wildflower strips, here, we show for the first time that the concerted installation of multiple wildflower strips modulates this landscape dependency and boosts the effectiveness of this AES when landscape complexity is low. Our study thus highlights the potential of coordinating the installation of wildflower strips at the landscape scale. Revealing general diversity benefits of wildflower strips to the non-target group of predatory wasps, our study emphasizes the importance of this AES for species richness and multifunctionality in agroecosystems.

Wildflower strips are implemented mainly to meet the foraging demands of flower visitors, such as butterflies and wild bees (Carvell *et al.*, 2007; Ouvrard *et al.*, 2018). Lately, it was shown for two caterpillar- respectively spider-hunting wasp species that also these taxa benefit from wildflower strips (Hoffmann *et al.*, 2018, 2020). Here, these benefits were shown for aculeate wasps in general, yet that the utilization of wildflower strips is landscape dependent as it was shown in the two species-specific studies (Hoffmann *et al.*, 2018, 2020). This landscape dependency, however, was modulated by the availability of single *versus* multiple wildflower

strips. When there was only one single wildflower strip at the landscape scale, the species richness of wasps increased with the amount of grassland in the surrounding landscape. A high amount of grassland elements within the agricultural matrix was previously shown to benefit wild bee dispersal since it provides valuable resources for adult and larval nutrition (Jauker *et al.*, 2009) and may also increase the connectivity between nesting and foraging sites of multi-habitat users (Holzschuh *et al.*, 2009; Krewenka *et al.*, 2011; Hoffmann *et al.*, 2018). Aculeate wasps have low foraging distances similar to wild bees and therefore depend on landscape composition in the proximity of their focal nesting site (Steffan-Dewenter, 2003); in landscapes with low matrix quality distances between suitable habitat patches become insurmountable for these species (Diekötter *et al.*, 2008; Jauker *et al.*, 2009; Zurbuchen *et al.*, 2010). Thus, in landscapes with low matrix quality, wildflower strips may pose important habitat island for wasps. Yet, depending on how poor the agricultural matrix is, the installation of one single wildflower strip might not be enough to promote the diversity of wasps or other insects.

In the present study, the species richness of wasps in connected wildflower strips was relatively low over all landscape complexities when only the focal strip was considered. When considering the focal wildflower strip and its associated satellite site as a unit, however, species richness increased to highest values independent of the surrounding landscape matrix (Fig. 2). On the one hand, this indicates that wildflower strips installed in proximity may act in concert on agro-biodiversity. On the other hand, it suggests that the landscape dependency of wildflower strips in their biodiversity effects may be modulated by the spatial arrangement of their installation.

It was argued that the ecological contrast created by wildflower strips is one of the main drivers of their effectiveness and that this contrast is greatest in simple landscapes (Scheper *et al.*, 2013). Furthermore, cleared landscapes often exhibit a reduced regional species pool (Tschardt *et al.*, 2012; Rösch, 2015) and exert a strong dispersal filter on species (Dufnot *et al.*, 2014; Cadotte & Tucker, 2017). In cleared landscapes, the concerted installation of multiple wildflower strips may rise the ecological contrast by increasing floral diversity at the landscape scale as well as by providing undisturbed elements for nesting (Cope *et al.*, 2019) or over-

wintering (Hoffmann *et al.* under review). At the same time the availability of several wildflower strips at the landscape scale may increase the connectivity of landscape elements for multi-habitat users like prey-hunting wasps. Accordingly, the abundance of two selected wasp species, measured as the number of brood cells in one year, related positively to connected wildflower strips and good matrix quality (Hoffmann *et al.*, 2018). Ideally, such fitness effects of wildflower strips accumulate over the years and result in higher total abundances of the respective species towards the end of the agri-environmental scheme.

An increase in the abundance of wasps on wildflower strips over the three years of this experiment was apparent in landscapes at the lower end of the amount of semi-natural habitats and particularly so when wildflower strips were installed in concert rather than isolated in these landscapes. While these results generally accord to those of the intermediate-landscape complexity hypothesis (Tscharntke *et al.*, 2012; Scheper *et al.*, 2013), they are new in that it has been shown for the first time that this landscape dependency may be modulated by a concerted installation of wildflower strips also for longer-lasting abundance effects. Most likely, several wildflower strips in concert raise resource levels and the ecological contrast to levels sufficiently high to induce community or population growth over time (Kleijn *et al.*, 2018). Additionally, a concerted installation of wildflower strips may contribute to the connection of the necessary resources at the landscape scale, as indicated by highest effects towards the low end of the complexity gradient in the category of simple landscapes.

Besides fostering dispersal in agricultural landscapes, a positive effect of connected wildflower strips on abundance and species richness may be attributed to a sole area effect following the established theory of island biogeography (MacArthur & Wilson, 2001) and the species-area relationship (Holt *et al.*, 1999). In our design, we cannot correct for such an area effect. It has previously been shown, however, that a collection of small fragments of resource-rich calcareous grasslands contributed disproportionately to the overall species richness across a wide range of taxonomic groups (plants, leafhoppers, true bugs, snails) even though their joint area was about three times smaller than that of the two largest fragments to which they were compared to (Rösch *et al.*, 2015). It was argued that this effect could be due

to the greater geographic extent covered by many small than few large fragments. Because the spatial scale of the landscape sectors with either single or multiple wildflower strips in our study was comparatively small (radius 500 m around the focal study site), we suggest resource heterogeneity among wildflower strips as one of the factors that may lead to stronger biodiversity effects of spatially concerted as compared to single wildflower strips. Such a resource heterogeneity may result from different seed mixtures used or differences in the establishment of the same seed mixture among different wildflower strips (Warzecha *et al.*, 2018). Another factor contributing to the higher diversity effect of spatially concerted than single wildflower strips may be a clearer resource partitioning among species (Fründ *et al.*, 2013; Polidori *et al.*, 2013).

This study contributes to enhancing the effectiveness of AES. We show that especially in landscapes where wildflower strips were so far considered as insufficient, the concerted installation of several wildflower strips, potentially of similar total area, can boost their individual effectivity in promoting farmland biodiversity. There is a need of identifying the tipping points along the gradient of landscape complexity, at which level the installation of several wildflower strips become redundant. Hence, future AES should consider landscape context at the planning of new locations of wildflower strips to increase their efficiency for farmland biodiversity.

1.6 Acknowledgements

Special thanks to Karina Weiß and Michael Zerbe of Amt für Ländliche Räume Marburg Biedenkopf for their cooperation and the farmers who supported our study. Thanks to Stefan Tischendorf for determination of wasp individuals of families Crabronidae and Tiphiidae. To associated students Aziza Boufarra, Moritz Gorski, Lisa Keller, Anton Müller, Patricia Schmidt for their contribution in data collection and field work. To Mario Hasler for statistical advice.

2. Prey-dependent benefits of sown wildflower strips on solitary wasps in agroecosystems

Uta S. Hoffmann | Frank Jauker | Jonathan Lanzen | Daniela Warzecha |
Volkmar Wolters | Tim Diekötter

Similar version of this chapter published as:

Hoffmann US, Jauker F, Lanzen J, Warzecha D, Wolters V & Diekötter T (2018): Prey-dependent benefits of sown wildflower strips on solitary wasps in agroecosystems. *Insect Conservation and Diversity*, 11: 42–49.

<https://doi.org/10.1111/icad.12270>

2.1 Abstract

Sown wildflower strips can support insects that collect pollen for their larvae. How these strips affect flower visitors with carnivorous larvae, however, is almost unknown. We studied the impact of wildflower strips and their surroundings on two common solitary wasps: the caterpillar-hunting *Ancistrocerus nigricornis* CURTIS and the spider-hunting *Trypoxylon figulus* LINNAEUS. Trap-nest locations at 22 semi-natural habitats in central Germany formed independent gradients in landscape complexity and distance to either one or several wildflower strips in their surroundings. For each brood cell, we recorded the number of prey items, total caterpillar weight and spider species richness. *Ancistrocerus nigricornis* built more cells in proximity to wildflower strips and with increasing amount of surrounding grassland. Fewer prey items provided in landscapes with large shares of semi-natural habitats suggest that in these landscapes high-quality prey is available. In contrast, *T. figulus* built more cells with increasing distance of nests to wildflower strips. If there were few strips, *T. figulus* built more cells in grassland-rich landscapes, whereas low shares of grassland were compensated when several wildflower strips were present. Benefits of flowering strips for *T. figulus* seem related to flower resources for adults, rather than through prey provisioning. In conclusion, wildflower strips promote prey-hunting wasps through species-specific effects on adult and larval food provisioning. Considering the differential effects of wasps on crop pests (caterpillars) and natural enemies (spiders), the functional role of wildflower strips in agroecosystems may be much greater than assumed when solely focusing on pollination.

2.2 Introduction

Flower-rich agri-environmental schemes (AES) (e.g. sown wildflower strips) aim to promote farmland biodiversity by creating resource-rich habitats to counteract increasing fragmentation of semi-natural habitats, a main driver of species loss in agro-ecosystems over the past decades (Fahrig, 2003; Foley *et al.*, 2005; Rossetti *et al.*, 2017). Associated with this species loss, key ecosystem services such as pollination (Kremen *et al.*, 2002; Vanbergen & Initiative, 2013) or biological pest control

(Winqvist *et al.*, 2011; Rusch *et al.*, 2013) may be at risk in agro-ecosystems. So far, the efficiency of sown wildflower strips in promoting biodiversity has mainly been discussed for wild bee pollinators (Carvell *et al.*, 2007; Scheper *et al.*, 2015). In contrast, we know considerably less about their effects on flower-visiting wasps, some of which are important biological control agents in agricultural systems (Harris, 1994). Here, we were interested in potential benefits for flower-visiting wasps whose larvae depend on arthropod prey.

In the past, field margins, hedges, streams and pastures were abundant in agricultural landscapes (Batáry *et al.*, 2015). Today, however, these semi-natural landscape elements are rare and often fragmented (Foley *et al.*, 2011). If present, they have been shown to positively affect the abundance and species richness of trap-nesting bees and wasps in agricultural landscapes (Steffan-Dewenter, 2002; Diekötter & Crist, 2013). In addition, small distances between resources utilized for nesting and foraging can reduce foraging duration of solitary bees (Zurbuchen *et al.*, 2010), resulting in less time needed for finishing one breeding cell and therefore increasing reproduction rates. The connectivity of different habitat elements for e.g. foraging or nesting, however, may not only be determined by inter-patch distance but also by the quality of the interjacent landscape matrix (Jauker *et al.*, 2009; Holzschuh *et al.*, 2010).

Solitary wasps, like wild bees, depend on a diverse set of landscape elements which provide adult and larval food as well as suitable nesting and overwintering sites to successfully complete their life cycle (Tschardt *et al.*, 1998; Potts *et al.*, 2005). However, in contrast to wild bees that feed exclusively on plant resources as larvae and adults, wasps utilize nectar and pollen as adults and require arthropod prey such as caterpillars or spiders for offspring nutrition.

In addition to pollen and nectar, sown wildflower strips are likely to provide arthropod prey. The occurrence and abundance of caterpillars is mainly determined by the availability of host plants (Alanen *et al.*, 2011; Blake *et al.*, 2011; Woodcock *et al.*, 2012); however, species richness and abundance of butterflies also benefit from the diversity in plant resources provided by wildflower strips at the local and landscape scale (Feber *et al.*, 1996; Aviron *et al.*, 2011). In addition, the presence of wildflower strips may not only positively affect prey quantity, but also quality of

prey. Caterpillars often show higher body weights and relative growth rates when feeding on high quality plant species or plant parts (Burghardt & Fiedler, 1996; Liu *et al.*, 2010). Like butterflies, spiders benefit in species richness and abundance from wildflower strips at a local scale due to a highly structured vegetation cover and the absence of disturbances (e.g. mowing) (Bell *et al.*, 2001; Blake *et al.*, 2013). At a landscape scale, wildflower strips increased the density of various spider families and, subsequently, biological control in adjacent wheat (Schmidt-Entling & Döbeli, 2009) or blueberry (Blaauw & Isaacs, 2015) fields. Thus, since prey arthropods benefit from sown wildflower strips, solitary wasps hunting for caterpillar or spider prey may also positively respond to the according AES.

Here, we studied whether the caterpillar-hunting wasp species *Ancistrocerus nigricornis* CURTIS (Hymenoptera: Eumenidae) and spider-hunting wasp *Trypoxylon figulus* LINNAEUS (Hymenoptera: Crabronidae) benefit from sown wildflower strips. The two species were selected because they are generally abundant and because they may show contrasting effects on ecosystem functioning due to their different prey spectrum. In particular, we hypothesized that (i) independent of the kind of their larval prey, *A. nigricornis* and *T. figulus* benefit in their abundance from sown wildflower strips, and that (ii) these benefits result from either higher quality (*A. nigricornis*) or quantity of prey (*T. figulus*) provided by wildflower strips. In addition, we tested (iii) whether these effects were dependent on the landscape composition surrounding nest locations, i.e. the availability of alternative foraging habitats.

2.3 Material and Methods

2.3.1 Study area

The study was conducted in the district of Marburg-Biedenkopf (Hesse, Germany), a region covering approximately 1,260 km² of which 44 % is under agricultural use and 41 % is forest. As part of an AES (HIAP - Hessisches Integriertes Agrarumweltprogramm) in 2011 more than 200 wildflower strips were sown on former arable fields with one of four perennial seed mixtures. As part of the subsidy scheme, farmers had to agree to refrain from any management for five years. For our study,

we selected 22 hedgerows or forest edges as study sites. These hedgerows were selected so that half of them contained only one sown wildflower strip (isolated) and the other half several (connected) wildflower strips in a radius of 500 m around them. Furthermore, study sites were selected in such a way that both groups (isolated vs. connected) spanned a distance gradient (0 - 381 m, isolated: mean 214 ± 106 m standard deviation, connected: 178 ± 130 m, t-test = 0.19) to similar sized sown wildflower strips (0.3 ± 0.04 ha). Additionally, they covered independent gradients in the amount of permanent grassland (pastures and grasslands) and semi-natural habitats (hedges, gardens, fallows, alluvial meadows, clear cuttings, tree rows, quarries, orchards, and the respective wildflower strip). Other explanatory variables were the percentage area of arable land and forest edge in the sectors around selected sites. The area of forest edges was calculated by multiplying the length of forest boundaries in each sector by 10 m (Jauker *et al.*, 2012). Landscape analyses were carried out using ArcGIS 10 (ESRI, Ca., USA).

2.3.2 Solitary trap-nesting wasps and their prey

In April 2012, two trap nests were placed in each of the 22 selected study sites. The trap nests were established at a distance of 10 m to each other and left in the field until August. Each trap nest was made of two plastic tubes with a length of 27 cm and a diameter of 10 cm and fixed with iron belts to a wooden post 140 cm above the ground aligned in north-south direction. Each of the plastic tubes was filled with approximately 130 internodes of common reed (*Phragmites australis* Cav.) with diameters between 4 mm and 12 mm (Gathmann *et al.*, 1994). The traps were checked once a week for newly built nests to collect data on the prey of the trap-nesting wasps. We carefully removed every sealed reed internode, indicating completed wasp's nest, from the plastic tube and replaced it by an empty internode of similar size (Coudrain *et al.*, 2013). If wasps had not yet developed into larvae and thus prey was untouched, prey was taken from half of the brood cells per nest; otherwise fewer cells were used for prey analysis. We counted caterpillar or spider prey items for each emptied brood cell and determined spiders to species level. For caterpillars, we measured the dry weight per brood cell after drying the caterpillar samples in a compartment dryer under 45°C for 2 days. After taking prey from the cells, the nests were closed with tape and residual cells incubated first at room

temperature to allow spring species to hatch in the same year. From September 2012, remaining cells were stored within a climate chamber (4 °C) to simulate winter until hatching in the following spring. Upon hatching in 2013, two individuals per nest were determined to species level; all other individuals were released back to nature. Analyses focused on the caterpillar-hunting *A. nigricornis* and spider-hunting *T. figulus*, two species that together constituted 81 % of all nests recorded in this study.

2.3.3 Statistical analyses

For statistical analyses, data of both trap nests per site were pooled. Dependent variables included number of nests and number cells. In the main analyses, only the number of cells was used as a measure of wasp abundance because both variables were strongly correlated. The number of prey items, prey species richness and prey dry weight were only analyzed for those sites in which the wasp species occurred. To achieve a normal distribution, the number of cells for both species were $\log(x+1)$ -transformed. Prior to model building, the four land-use variables were tested for inter-correlation. Generalized linear models (GLM) were used to test for effects of the following independent variables: area percentage of grassland, area percentage of arable land, area percentage of semi-natural habitats and the area percentage of forest edges, as well as the distance to the next wildflower strip and flower strip connectivity (factor with two levels: isolated or connected). Furthermore, we tested for interacting effects of connectivity and the four land-use variables on the dependent variables.

For model selection, a manual forward selection procedure was used. In this procedure distance to the next wildflower strip and connectivity were entered first and remained in the model until the four land-use variables and their interactions with connectivity successively entered or left the model based on a set p-level of 0.05 in predefined order: grassland, arable land, forest edge, semi-natural habitat. Only then were distance to the next wildflower strip and connectivity, representing the main gradients in this study, removed from the model in case they did not show a significant relationship with the tested dependent variable. Additionally, we used an exponential linear mixed-effects model (R Package “lme4”) to test for correlation between weight of collected caterpillar individuals and overall number of collected

prey items per cell in *A. nigricornis*, using study site as random factor. Spatial autocorrelation was disproved using Moran's I for dependent variables number of cells by *A. nigricornis* ($p = 0.16$), number of collected prey items per cell ($p = 0.23$), mean prey weight per cell ($p = 0.79$) and number of cells by *T. figulus* ($p = 0.88$). Statistical analyses were carried out in R 3.2.2 (R Development Core Team 2014).

2.4 Results

Within the 44 trap-nests the caterpillar-hunting wasp *A. nigricornis* built 199 nests with 1227 brood cells; spider-hunting wasp species *T. figulus* built 193 nests with 935 brood cells. A total of 4037 caterpillars, 7.5 ± 4.0 per brood cell, were collected from 541 of the 1227 brood cells of *A. nigricornis*. A total of 1227 spider individuals, 3.2 ± 1.5 per brood cell, were collected from 382 of the 935 brood cells of *T. figulus*. The most abundant spider species, *Phylloneta impressa*, composed 83.1% of all prey individuals.

For *A. nigricornis*, the number of brood cells per study site was negatively affected by the distance of trap nests to the nearest wildflower strip (Fig. 1a) and positively by the amount of grassland (Fig. 1b) in the surrounding landscape. This final model explained 57% (R^2_{adj}) of the variation ($F_{2,19} = 14.76$, $p < 0.001$; Table 1). The number of collected prey items per brood cell was negatively affected by the amount of semi-

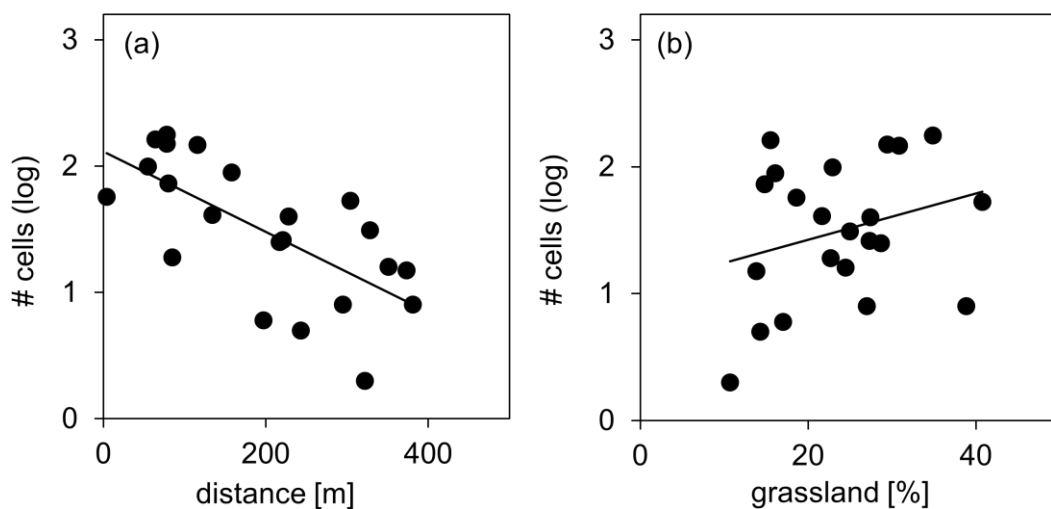


Fig. 1: Number of brood cells built by the caterpillar-hunting wasp *Ancistrocerus nigricornis* as a function of (a) distance to next sown wildflower strip and (b) amount of grassland within a radius of 500 m around the study sites.

natural habitats in the surrounding landscape ($F_{1,19} = 10.69$, $R^2_{\text{adj}} = 0.33$, $p = 0.004$; Fig. 2, Table 1). Furthermore, weight of caterpillar individuals correlated negatively with the overall number of collected prey items per cell ($R^2_{\text{adj}} = 0.34$, $p < 0.001$, Fig. 3). The total average weight of collected caterpillars per brood cell, however, interactively depended on the percentage of grasslands and the connectivity of wildflower strips at landscape scale ($F_{3,17} = 4.36$, $R^2_{\text{adj}} = 0.34$, $p = 0.019$; Table 1). When nesting sites were poorly connected to foraging habitats (i.e. landscapes with isolated wildflower strip), the amount of grassland in the surrounding

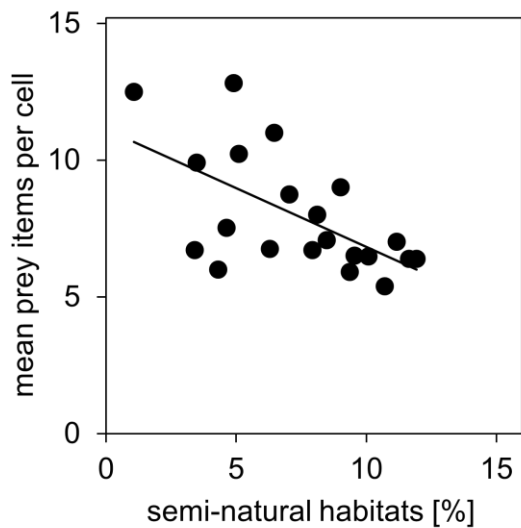


Fig. 2: Mean prey items per cell collected by the caterpillar-hunting *Ancistrocerus nigricornis* correlated with the amount of semi-natural habitats within a radius of 500 m around the study sites.

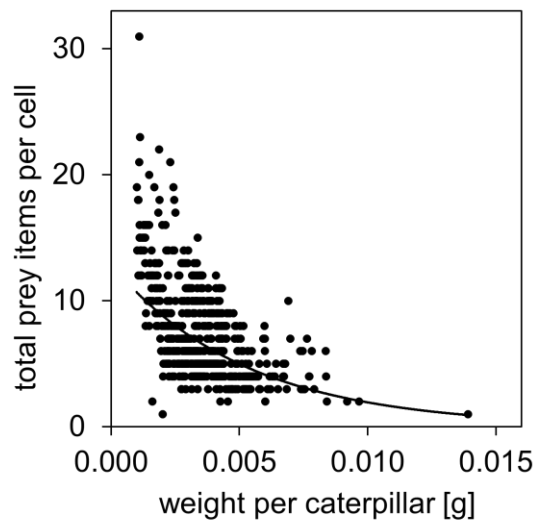


Fig. 3: Number of prey items per cell collected by the caterpillar-hunting *Ancistrocerus nigricornis* correlated with the weight per caterpillar per cell.

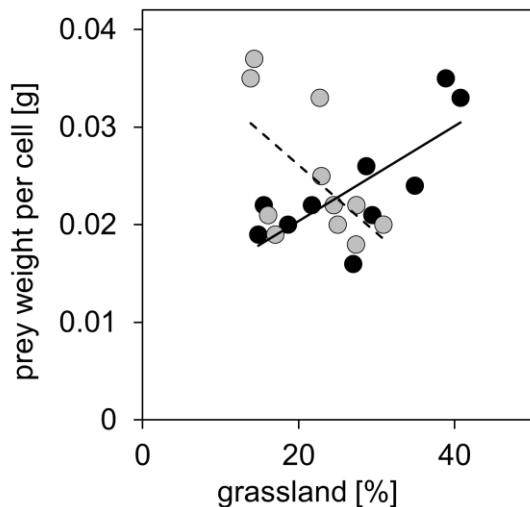


Fig. 4: Average weight of prey per brood cell collected by the caterpillar-hunting wasp *Ancistrocerus nigricornis* as a function of percentage area of grassland within a radius of 500 m around the study site in landscapes with an isolated wildflower strip (grey circles ●) and connected wildflower strips (black circles ●).

landscape had a negative effect on the weight of collected caterpillars (Fig. 4). In contrast, when nesting sites were well connected to foraging habitats (i.e. landscapes with several wildflower strips), the weight of caterpillars increased with the amount of grassland (Fig. 4).

For *T. figulus*, the number of brood cells per study site increased with the distance of trap nests to the next wildflower strip (Fig. 5a). In addition, the number of cells was positively correlated with the amount of grassland if wildflower strips were isolated (Fig. 5b) but was unaffected when wildflower strips were connected (Fig. 5b). The final model explained 71% of the variation ($F_{4,17} = 14.05$, $p < 0.001$; Table 1). Neither the number of prey items per cell ($F_{1,11} = 2.85$, $R^2_{\text{adj}} = 0.13$, $p = 0.120$) nor the species richness of spider prey ($F_{1,11} = 1.28$, $R^2_{\text{adj}} = 0.02$, $p = 0.282$) was affected by any landscape variable.

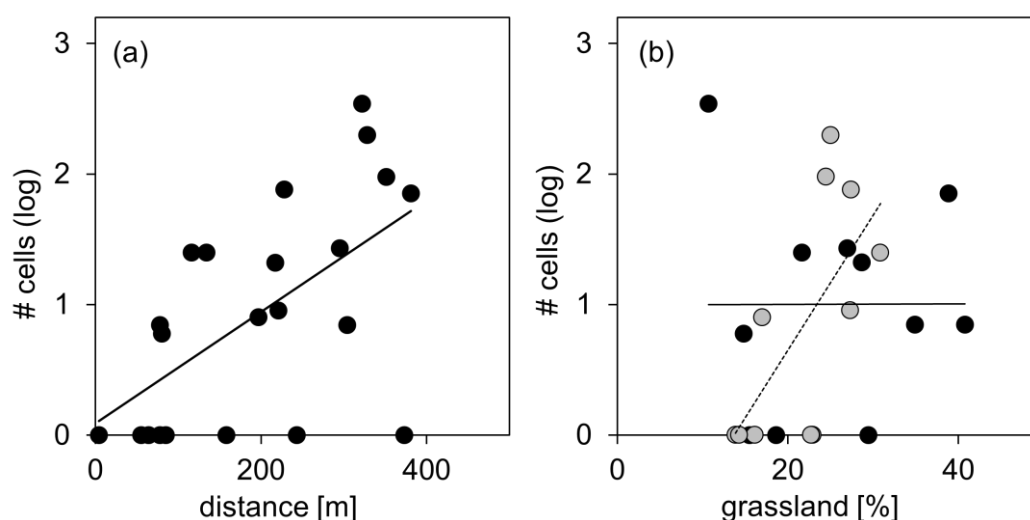


Fig. 5: Number of built brood cells by the spider-hunting wasp *Trypoxylon figulus* as a function of (a) distance to next sown wildflower strip and (b) the amount of grassland within a radius of 500 m around the study sites in landscapes with an isolated wildflower strip field (grey circles ●) and connected wildflower strips (black circles ●).

Table 1: Model results for all dependent variables. Explanatory variables and the adjusted R² are given for the most parsimonious model. Models were reduced using a stepwise forward selection.

Species	Dependent	Explanatory	Direction	d.f.	t-value	P	(whole model) Adjusted R ² , P
<i>A. nigricornis</i>	Number of cells	Distance	–	1,19	–5.50	<0.001	0.57; <0.001
		Grassland	+	1,19	2.33	0.016	
	Prey items	Semi-natural habitats	–	1,19	–3.27	0.004	0.33; 0.004
		Weight of prey	–	1,5288	–16.31	<0.001	
	Weight of prey	Connectivity	+	1,17	3.54	0.003	0.34; <0.001
		Grassland	+	1,17	2.61	0.018	
Connectivity: grassland		–	1,17	–3.50	0.003		
<i>T. figulus</i>	Number of cells	Distance	+	1,17	6.17	<0.001	0.71; <0.001
		Connectivity	–	1,17	–5.33	<0.001	
		Grassland	–	1,17	–1.83	0.084	
		Connectivity:grassland	+	1,17	5.2	<0.001	
	Prey items					<i>n.s.</i>	
	Weight of prey					<i>n.s.</i>	

2.5 Discussion

We found that sown wildflower strips, in addition to previously demonstrated benefits for wild bees, can also promote prey-hunting wasps in agricultural landscapes. Yet, benefits for solitary prey-hunting wasps were prey-dependent. While the caterpillar-hunting wasp *A. nigricornis* clearly benefitted from a proximity to sown wildflower strips, the spider-hunting wasp *T. figulus* did not appear to do so. In fact, *T. figulus* showed reduced nest-building activity close to wildflower strips. This negative effect on *T. figulus* was less pronounced than the positive on *A. nigricornis*. Thus, our findings contribute to the accumulating body of evidence on the beneficial effects of sown wildflower strips for species diversity and ecosystem service provisioning in agroecosystems.

Ancistrocerus nigricornis and *T. figulus* were the dominant species of solitary trap-nesting wasps in our study area. Thus, like Kleijn et al. (2015) showed for wild bee pollinators, the responses of these wasps to wildflower strips and landscape composition will largely determine the provisioning of ecosystem services and disservices associated with this guild. For *A. nigricornis*, the number of brood cells decreased with the distance of trap nests from sown wildflower strips. This indicates that sown wildflower strips provide ample resources for this wasp species allowing for efficient nest building in the proximity of these AES elements. Due to their plant species richness and abundance, sown wildflower strips will not only boost caterpillar-hunting wasps via energetically rich nectar (Fabian *et al.*, 2014), but

also via abundant prey. Even though caterpillar prey in nests of *A. nigricornis* consisted exclusively of microlepidoptera, it seems likely that, similar to macrolepidoptera (Aviron *et al.*, 2011; Haaland & Bersier, 2011; van Halder *et al.*, 2017), this group of small butterflies benefits from the diversity and quantity of plants in the wildflower strips. Thus, wildflower strips, with much smaller areas, seem to facilitate ecological functioning similarly to grasslands that were also shown to affect wasp fitness positively. The benefits of large shares of grassland, constituting a considerably larger but less structural heterogeneous area than wildflower strips may be attributed to either a better connectivity of nesting sites with foraging resources (Ricketts, 2001; Holzschuh *et al.*, 2009) or to a better resource provisioning by the grassland itself (Jauker *et al.*, 2009).

Field (1992) showed for the sphecid wasp *Ammophila sabulosa* LINNAEUS, that nest building may be facilitated by utilizing small prey caterpillars that were captured and transported to the nest faster than large ones. The utilization of heavier prey, in contrast, may allow for fewer prey items to be provisioned in each cell, if the total weight of larval food determines brood cell completion (Polidori *et al.*, 2005). Indeed, the number of collected caterpillars per brood cell decreased with the individual weight of caterpillars in our study. Thus, the negative relationship between the number of prey items per cell and the amount of resource-rich semi-natural habitats (including wildflower strips) in our results suggests that in resource-rich landscapes heavier prey is available. Accordingly, prey weight per cell increases with amount of grassland and wildflower strips in the landscape matrix, suggesting that landscape connectivity benefits wasp fitness as available prey can be found more effectively and be transported faster to the nests. Given the common variation in ecological patterns, the interactive effect of the amount of grassland and the connectivity of wildflower strips on the total prey weight per cell suggests benefits of diverse landscapes and AES to nest provisioning in solitary wasps by providing both high quality and quantity in caterpillar prey. Although the high total prey weight in landscapes with a small amount of grassland and isolated wildflower strips indicates that high ecological contrast may increase the effectiveness of wildflower strips (cf. Scheper *et al.*, 2013). The effectiveness of AES especially within highly diverse landscapes on the promotion of various components of biodiversity needs to be studied in further detail.

In contrast to *A. nigricornis*, in the spider-hunting wasp *T. figulus* the number of brood cells per study site increased with increasing distance to wildflower strips. *Trypoxylon figulus* is considered as a generalist predator (Witt, 1998). Here and in a previous study (Coudrain *et al.*, 2013), brood cells were predominantly provisioned with the web-building spider species *Phylloneta impressa* KOCH (Araneae: Theridiidae). Because complementary work in our study area revealed similar abundances of *P. impressa* in arable land and wildflower strips (Mader *et al.*, 2016), the negative effect of proximity to flowering strips may indicate a conflict in landscape suitability regarding foraging for adult flower and larval prey resources. It seems that *T. figulus* is attracted to wildflower strips for adult feeding requirements (Fabian *et al.*, 2014), but that larval spider prey, although present, is less effectively caught in structurally diverse wildflower strips than simple arable fields (cf. Rypstra *et al.* 2007). Accordingly, the presence of multiple wildflower strips compensates negative effects of a landscape matrix with low shares of high quality grassland on the fitness of adult wasps, for example by connecting agricultural and late successional habitat elements (Rösch *et al.*, 2015). Single flowering strips could not deliver such fitness benefits for wasps in this landscape context, substantiating the importance of managed habitat connectivity for the reproduction of *T. figulus* in degraded landscapes. In an agricultural landscape matrix with high shares of good quality grassland, in contrast, wasp reproduction was also high even when only single flowering strips were present.

In conclusion, our study adds to the importance of sown wildflower strips for species richness and multifunctionality in agroecosystems. Our data suggests that *A. nigricornis* and *T. figulus*, the two most abundant solitary wasp species in our study, can be supported by the installment of wildflower strips through the provisioning of high quantity and quality of larval and adult food. Sown wildflower strips seemed to have biggest effects when their installment created ecological contrasts or improved habitat connectivity. Yet, in order to be able to assess the overall effect of wildflower strips on ecosystem functioning in agricultural landscapes, the relative effects of wasps on herbivores (e.g. caterpillars) and antagonists (spiders) as well as spillover of organisms from and to wildflower strips need to be quantified in future studies.

2.6 Acknowledgements

We thank Mr. Zerbe and Mrs. Weiss of Amt für Ländliche Räume Marburg Biedenkopf for their cooperation and the farmers who supported our study. Thanks to Elvira Sereda and Sergej Sereda for determination of spiders, John Herrmann for statistical advice and proofreading and two anonymous reviewers for their helpful comments that improved the manuscript.

This is the pre-print of the article published in *Insect Conservation and Diversity*. The final authenticated version is available online at:

<https://doi.org/10.1111/icad.12270>

3. The suitability of sown wildflower strips as hunting grounds for spider-hunting wasps of the genus *Trypoxylon* depends on landscape context

Uta S. Hoffmann | Frank Jauker | Eva Diehl | Viktoria L. Mader | Daniela Fiedler |
Volkmar Wolters | Tim Diekötter

Similar version of this chapter published as:

Hoffmann US, Jauker F, Diehl E, Mader VL, Fiedler D, Wolters V, Diekötter T (2020): The suitability of sown wildflower strips as hunting grounds for spider-hunting wasps of the genus *Trypoxylon* depends on landscape context. *Journal of Insect Conservation* 24: 125-131.

<https://doi.org/10.1007/s10841-019-00190-6>

3.1 Abstract

Subsidized wildflower strips aim at counteracting insect species loss in agricultural landscapes. Little is known yet about their effects on insects that not only feed on pollen and nectar but also hunt for arthropod prey for larval nutrition. Here, we provide new evidence that wildflower strips may benefit the provisioning of larval prey for spider-hunting wasps. Woody semi-natural habitats in central Germany were selected as trap-nest locations along independent gradients in distance to wildflower strips and percentage of grassland in the surrounding landscape. From these nests, spider individuals hunted by wasps of the genus *Trypoxylon* (Crabronidae) were collected. In addition, spiders were collected in the associated wildflower strips and the similarity between spider communities in nests and in flowering strips was calculated. The similarity of spider communities decreased with the distance to the next wildflower strips, but the percentage of surrounding grasslands modulated this relationship. This concurred with an observed positive effect of grassland on spider species richness in trap nests, especially if wildflower strips were distant from the nests. In contrast, landscape context did not affect spider species richness in wildflower strips. In conclusion, our results suggest that wildflower strips are used by *Trypoxylon* wasps for hunting spiders as prey for larvae, yet only if strips are close to nesting habitats and well connected by high shares of grassland. Our results substantiate the importance of wildflower strips for species richness and trophic interactions in agroecosystems.

3.2 Introduction

Current studies report a dramatic decline of insect diversity during the last decades (Dirzo *et al.*, 2014; Fox *et al.*, 2014; Woodcock *et al.*, 2016). Agricultural intensification is considered to be a main driver of this loss (Foley *et al.*, 2005; Rossetti *et al.*, 2017). The establishment of wildflower strips within agri-environmental schemes (AES) aims at counteracting this loss (Haaland *et al.*, 2011; Whittingham, 2011). While benefits of wildflower strips to nectar- and pollen collecting insects such as wild bees or butterflies have frequently been shown (Scheper *et al.*, 2015; Grass *et al.*, 2016; Ouvrard *et al.*, 2018), their effects on other arthropods have only

recently received attention in agro-ecological research (e.g. Tschumi et al. 2015; Baulechner et al. 2019). For solitary wasps, benefits of wildflower strips likely depend on the collected prey (Hoffmann *et al.*, 2018). Here, we focused on spider-hunting wasps and how wildflower strips affect their prey availability in a landscape context.

Similarly to wild bees, adult wasps depend on flowering plants as a nectar source. For larval nutrition, though, female mud-dauber wasps of the genus *Trypoxylon* LATREILLE (Hymenoptera: Crabronidae) collect spiders, of which several individuals are provisioned in one brood cell (Witt, 1998). Related to these food requirements and their abundance in agricultural landscapes (Schüepp *et al.*, 2011; Ebeling *et al.*, 2012), *Trypoxylon* spp. wasps may be important for the provisioning of ecosystem services such as pollination and of disservices like regulation of biological control by spiders in agroecosystems (c.f. Kleijn et al. 2015).

Based on the reported positive effect of plant diversity on richness and abundance of spider-hunting wasps (Fabian *et al.*, 2014), flower-rich habitats, such as wildflower strips, might represent attractive foraging sites not only in terms of adult nutrition on nectar, but also nest provisioning in the form of spider prey. Spider species richness and abundance were shown to increase with plant diversity and vegetation coverage, both on the local (Diehl *et al.*, 2013) and landscape scale (Schmidt-Entling & Döbeli, 2009). Structurally diverse non-crop habitats promote web-building farmland spiders (Bell *et al.*, 2001) and attract especially large spider species (Mader *et al.*, 2017). Moreover, Pekár (2000) frequently found webs of *Phylloneta impressa* KOCH (Araneae: Theridiidae) on blue tansy *Phacelia tanacetifolia* BENTHAM (Boraginaceae), a plant species with high coverages in sown wildflower strips.

As cavity-nesting species, however, *Trypoxylon* spp. additionally depend on nearby woody habitats for nesting. Moreover, the quality of the intervening matrix is often crucial for such multi-habitat users, modulating the movement of individuals between landscape elements (Jauker *et al.*, 2009). Accordingly, *Trypoxylon* wasps are most common in open landscapes (Coudrain *et al.*, 2013) with a large amount of grassland (Hoffmann *et al.*, 2018). Under these conditions, wildflower strips may compensate for poor matrix quality, but only when they are well connected at the

landscape level (Hoffmann *et al.*, 2018). Whether benefits of wildflower strips are attributed to flower availability for adults or prey availability for provisioning larvae, however, remains unresolved so far.

Here, we studied whether wildflower strips are suited for promoting *Trypoxylon* wasps by providing high spider prey availability. We compared spiders collected into trap nests by *Trypoxylon* spp. individuals and spider communities in associated wildflower strips along a gradient of landscape complexity. We hypothesized that (i) the number of brood cells of *Trypoxylon* spp. is higher in complex landscapes, (ii) the spider species richness in *Trypoxylon* spp. nests increases in more complex compared to simple landscapes, and (iii) the similarity of spider species between *Trypoxylon* spp. nests and associated wildflower strips decreases with increasing distance between these two habitats and decreases with landscape complexity.

3.3 Material and Methods

3.3.1 Study area

The study was conducted in the district of Marburg-Biedenkopf (Hesse, Germany), a region with 44% of the area under agricultural management. In this area, wildflower strips were sown as part of an AES in 2011 (Hessian Integrated Agri-environmental Program HIAP). According to the scheme, no tillage and no application of fertilizers or pesticides was allowed for five years. For our study, we selected the hedgerows nearest to 11 wildflower strips as trap-nest locations, covering a gradient in distance between hedgerows and wildflower strips of 53 - 386 m (mean 235 ± 131 m standard deviation). Wildflower strips were similar in size (0.3 ± 0.04 ha). Additionally, selected sites represented an independent gradient in area percentage of surrounding grassland (pastures and permanent grasslands; 15 - 29%) and semi-natural habitats (hedges, gardens, fallows, alluvial meadows, clear cuttings, tree rows, quarries, orchards, and the respective wildflower strip; 4 - 17%) in a sector of 500 m radius. This radius was chosen based on the maximal foraging range of similar sized solitary hymenoptera (Gathmann & Tschardt, 2002; Coudrain *et al.*, 2013). Percentage area of arable land (23 - 65%) and forest edges (0 - 4%) in the sectors around selected sites were quantified. Forest edges are

considered potential nesting habitats (cf. Coudrain et al. 2013), as opposed to the forest interior, and their area was calculated by multiplying the length of forest boundaries in each sector by 10 m (Jauker *et al.*, 2012). Landscape analyses were carried out using ArcGIS 10 (ESRI, Ca., USA).

3.3.2 Sampling of solitary wasps and their prey

In May 2013, two trap nests were installed in each of the 11 selected study sites with an inter-trap distance of 10 m. Trap nests consisted of a plastic tube of 27 cm length and 10 cm diameter, filled with approximately 130 internodes of common reed (*Phragmites australis* CAV.) with randomized diameters between 4 mm and 12 mm (Gathmann *et al.*, 1994). Internodes sealed with clay, indicating a completed wasp nest, were carefully removed from the trap nest and replaced by empty ones of similar diameters once a week until the first week in August. Nests of other wasp genera and wild bees were quantified in the same way and used for a different survey.

Removed nests were cautiously cut open and the number of brood cells built by wasps were counted. From approximately half of the brood cells with collected prey, spiders were removed, counted and classified to species level. Then nest internodes were closed again with adhesive tape. From September 2013 on, remaining cells were stored in a climate chamber (4°C) to simulate winter until hatching in following spring. After hatching, two individuals per nest were collected, pinned and classified to species level. All other hatching individuals were released back into nature on the grounds of the university. Analyses were confined to the wasp genus *Trypoxylon*, which accounted for 91% of all spider-hunting individuals in our sample. Within this genus, 88% of the individuals belonged to the species *T. figulus* LINNAEUS, among less abundant species were *T. attenuatum* SMITH and *T. clavicerum* LEPELETIER & SERVILLE.

3.3.3 Spider collection on wildflower strips

Previous studies on prey choice of spider-hunting wasps revealed a preference for web-building over ground-dwelling spider species (Polidori *et al.*, 2005; Polidori & Andrietti, 2007). Therefore, we randomly hand-sampled approximately 30 web-

building spider individuals in each of the 11 wildflower strips under dry weather conditions in late June / early July 2013 (Mader *et al.*, 2016), a method which has been approved in previous studies (Magurran & McGill, 2011; Diehl *et al.*, 2013). Collected spiders were frozen for storage and successively classified to species level.

3.3.4 Statistical analyses

Data of the two traps per site were pooled by summarizing the number of brood cells for both traps. Since number of brood cells of *Trypoxylon* spp. showed a Poisson error distribution we performed a Generalized Linear Model (GLM) with corresponding error family settings. Linear models (lm) were used to analyze normal-distributed number of prey items per brood cell, species richness of spiders per *Trypoxylon* spp. brood cell and species richness of hand-collected spiders on wildflower strips. Independent variables were area percentage of grassland, semi-natural habitats, arable land and forest edges, as well as distance to next wildflower strip. A manual forward selection procedure was used to select final models. In this procedure, distance to next wildflower strip entered the model first and remained in the model until the four land-use variables and their interaction with distance successively entered the model in a predefined order: semi-natural habitats, arable land, grassland and forest edge. Based on a p-level of 0.05, non-significant landscape variables were not retained in the model. Only if land-use variables did not show a significant relationship, distance to wildflower strip, as the main factor in this study, was removed from the model and the landscape variables were tested consecutively. For visual presentation of interacting effects between the continuous explanatory variables in the figures, we split percentage of grassland into two categories, 'high' and 'low', separated by the median.

Spider community composition of trap nests and wildflower strips were compared using the Jaccard index (J):

$$J = 2 BCI / (1 + BCI)$$

The underlying Bray-Curtis dissimilarity index was calculated using R function *vegdist* in package *vegan* (Oksanen *et al.*, 2018):

$$BCI_{ij} = \frac{\sum_{k=1}^n |x_{ik} - x_{jk}|}{\sum_{k=1}^n (x_{ik} + x_{jk})}$$

where BCI is the dissimilarity between spider species (x) captured by *Trypoxylon* spp. in trap-nests (i) and available on wildflower strips (j) for each study site (k). The values range from zero to one, whereby one indicates most dissimilar and zero identical communities. Since *Trypoxylon* spp. were absent from two study sites, those were excluded from statistical analysis on community similarity.

All statistical analyses were carried out in R 3.2.2 (R Development Core Team 2014).

3.4 Results

In total, 1129 brood cells in 258 nests along our study sites were built by cavity nesting bee and wasp species. Individuals of the genus *Trypoxylon* spp. were the most abundant spider-hunting wasps, with 374 brood cells built in 93 nests in nine of the eleven study sites. The number of brood cells of *Trypoxylon* spp. was driven by an interacting effect of the amount of grassland in the surrounding area and the distance between nesting site and the next wildflower strip ($R^2_{\text{adj}} = 0.96$, $p < 0.001$; Table 1). In landscapes with high shares of grassland, the number of brood cells increased with increasing distance of trap nests from wildflower strips; in landscapes with low shares of grassland the number of brood cells was low and did not change with the distance of nests to the wildflower strip (Fig. 1). Other landscape variables had no effect on the number of brood cells.

A total of 630 spider individuals belonging to ten species were extracted from 198 brood cells. On average, *Trypoxylon* spp. collected 5.3 ± 2.0 spider individuals per cell independent of any landscape variable in our study. The mean species number per cell was 2.8 ± 1.1 . *Phylloneta impressa* was the most abundant spider species (82% of all individuals found in trap nests). A significant interaction suggests that the number of spider species caught by *Trypoxylon* spp. per site was jointly affected by the distance of nests to the next wildflower strip and the area percentage of

grassland in the surrounding landscape ($F_{3,5} = 9.29$, $R^2_{\text{adj}} = 0.76$, $p = 0.017$; Table 1). In landscapes with high shares of grassland the number of spider species in brood cells increased with distance between nests and wildflower strips, while in landscapes with low shares of grassland it rather decreased with distance (Fig. 2). Other landscape variables had no effect on the number of spider species in brood cells.

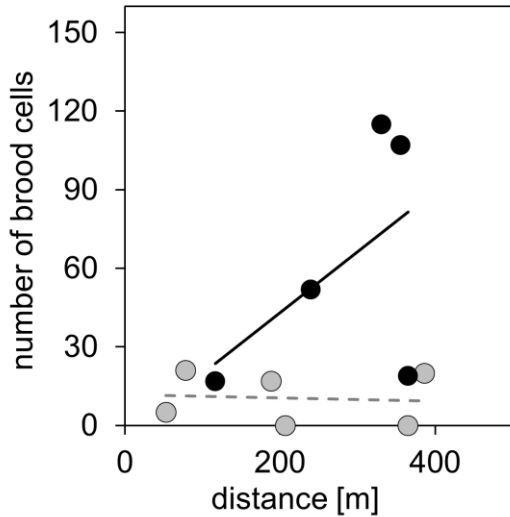


Fig. 1: Number of brood cells of *Trypoxylon* as a function of distance to next wildflower strip, interacting with the area percentage of grassland in the surrounding landscape. Amount of grassland was divided at the median (21%) into the categories low grassland percentage (grey circles ●) and high grassland percentage (black circles ●).

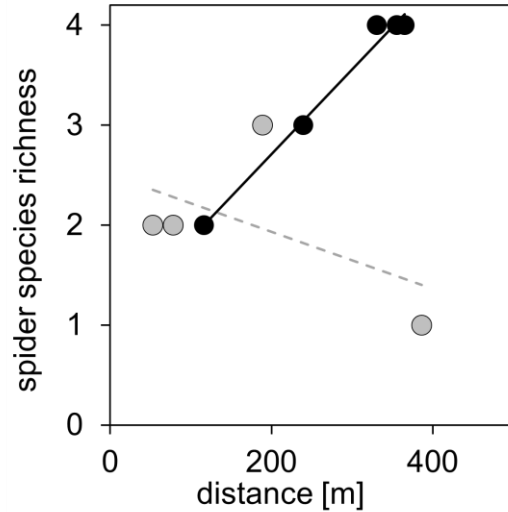


Fig. 2: Spider species richness of prey individuals in nests of the solitary wasp *Trypoxylon* as a function of distance to next wildflower strip, interacting with the area percentage of grassland in the surrounding landscape. Amount of grassland was divided at the median (21%) into the categories low grassland percentage (grey circles ●) and high grassland percentage (black circles ●).

A total of 15 spider species were recorded in wildflower strips. The mean richness per site was 3.9 ± 1.5 species and did not correlate with any landscape variable. The most abundant spider was *P. impressa*. It accounted for 73% of all hand-collected spider individuals, without this share being modulated by any explanatory variable. A significant interaction indicates that the community dissimilarity (J) of spiders found in trap-nests of *Trypoxylon* spp. and spiders hand-collected on wildflower strips was mutually affected by the trap nest distance to the wildflower strips and the area percentage of grassland in the surrounding landscape

($F_{3,5} = 7.08$, $R^2_{adj} = 0.70$, $p = 0.030$; Table 1). In landscapes with high shares of grassland, communities of spiders became more dissimilar with increasing distance between traps and wildflower strips while in landscapes with low shares of grassland the dissimilarity did not change along the distance gradient and was equally high as for the most distant traps in landscapes with a lot of grassland (Fig. 3). The community dissimilarity was unaffected by other landscape variables.

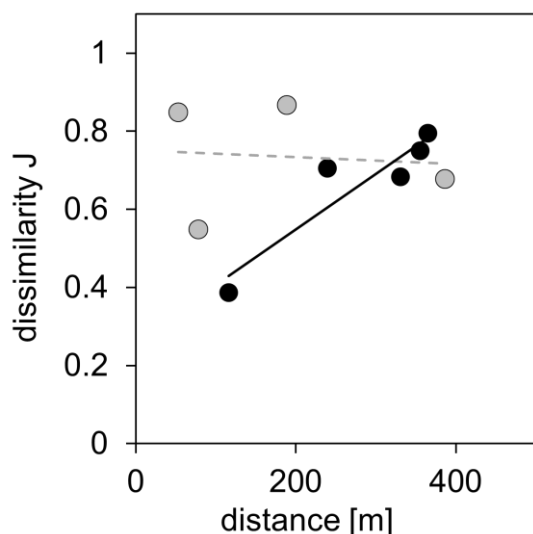


Fig. 3: Jaccard dissimilarity index (J) of spider communities as prey within trap nests compared to available spiders on wildflower strips. Plotted as a function of distance to next wildflower strip, interacting with the area percentage of grassland in the surrounding landscape. Amount of grassland was divided at the median (21%) into the categories low grassland percentage (grey circles ●) and high grassland percentage (black circles ●).

Table 1: Model results for all dependent variables. Explanatory variables and the adjusted R^2 are given for the most parsimonious model. Final models were selected using a stepwise forward selection method.

Dependent	Explanatory	Direction	d.f.	t-value	P	(whole model) Adjusted R ² ; P
number of brood cells of <i>Trypoxylon</i> spp.	distance		1,11	-2.315	0.021	
	grassland		1,11	-0.156	0.876	0.96; <0.001
	distance:grassland		1,11	4.335	<0.001	
spider species in trap nests	distance	-	1,9	-3.424	0.019	
	grassland	-	1,9	-2.470	0.057	0.76; 0.017
	distance:grassland	+	1,9	4.002	0.010	
Jaccard dissimilarity	distance	-	1,9	-3.127	0.026	
	grassland	-	1,9	-4.291	0.008	0.70; 0.030
	distance:grassland	+	1,9	3.483	0.018	
spider species on wildflower strips						n.s.
number of prey items per brood cell						n.s.

3.5 Discussion

While numerous studies have focused on the effects of wildflower strips on nectar- and pollen-feeding insects, few have considered how these strips affect resource availability for prey-hunting wasps in agricultural landscapes. Our results suggest that also spider-hunting wasps of the genus *Trypoxylon* utilize wildflower strips to collect spider prey for feeding their larvae, yet only when wildflower strips are close to nests and well connected by high shares of grassland. Thus, our results contribute to the evidence that wildflower strips offer resources not only to flower-visiting but also prey-hunting hymenoptera.

In landscapes with high shares of grassland, the number of brood cells of *Trypoxylon* spp. increased with increasing distance of nests from wildflower strips whereas in landscapes with low shares of grassland the number of brood cells was low and did not change with the distance of nests to the wildflower strip (Fig. 1). Grassland can provide flowering plants as a nectar source for adult nutrition and spiders as larval food. Concerning solitary wasps, it additionally increases the connectivity between nesting and other foraging sites (Holzschuh *et al.*, 2009; Krewenka *et al.*, 2011). This may enable solitary wasps to provide more brood cells with spiders per unit time if grasslands are abundant. Yet, when shares of grasslands are high and sown wildflower strips close, *Trypoxylon* spp. may choose to search for its presumed preferred prey species in wildflower strips. As the vertical structure is usually more complex in wildflower strips than in grasslands, though, fewer spiders might be caught per unit time in wildflower strips than in grassland, leading to fewer cells built.

Spider-hunting digger wasps have been shown to prefer web-building over ground-dwelling spiders as their prey (Polidori *et al.*, 2005; Polidori & Andrietti, 2007). This is consistent with our finding that the prey of *Trypoxylon* spp. was dominated by the most abundant web-building spider species, *P. impressa* (cf. Coudrain *et al.* 2013; Hoffmann *et al.* 2018). *Phylloneta impressa* builds three dimensional tangle webs within the vegetation (Pekár, 2000; Jurczyk *et al.*, 2012) and dominates the spider communities of both flowering fields and cereal fields in our study region (Mader *et al.*, 2016). Based on the consistent interaction of the distance between

nests and sown flowering strips and the landscape share of grassland and the absence of any effect of the amount of arable land, we suppose flowering strips to be preferred over arable fields in foraging for *P. impressa*.

The richness of spider species hunted by Trypoxylon spp. increased with the distance of nests to the next wildflower strip, but only in grassland dominated landscapes. Considering the known dominance of *P. impressa* in nests of Trypoxylon (cf. Coudrain et al. 2013; Hoffmann et al. 2018) and the fact that *P. impressa* was equally dominant across wildflower strips (Mader *et al.*, 2016), the observed pattern suggests a shift towards less preferred prey with increasing distances of nests from foraging habitats providing this preferred prey when alternative hunting grounds are more readily available or flowering strips are less well connected. With prey-predator-size relations being higher in spider-hunting than in other groups of predatory wasps (De Beaumont, 1964; Fabian *et al.*, 2014), a trade-off between prey quality and carrying distance may explain this shift. Whether fitness costs are related to such a prey shift remains unclear to date. Previous studies on the genus *Polistes* show that predatory wasps are able to distinguish between prey of different quality (Stamp, 2001; Armstrong & Stamp, 2003). A diet of unpalatable prey resulted in smaller nests or colonies built and in smaller wasps and reduced the proportion of males produced (Stamp, 2001). So far it remains unknown, however, how prey choice affects the reproduction of Trypoxylon spp. and whether lower numbers of brood cells will be compensated by higher emergence ratios or better body condition of individuals from cells provisioned with *P. impressa*.

Spiders predominantly capture insects, including both pest (e.g. herbivores) and beneficial species (e.g. pollinators) (Birkhofer & Wolters, 2012; Birkhofer *et al.*, 2013). As spider-hunters, Trypoxylon spp. thus significantly increase the diversity of trophic interactions and likely contribute to ecosystem stability (cf. Sanders et al. 2018). Our results suggest that wildflower strips are suitable foraging habitats for spider-hunting wasps. This highlights the potential of sown wildflower strips to increase biodiversity beyond classical pollinators (Baulechner *et al.*, 2019). For this to become fully effective, however, considerable attention has to be paid to the landscape context, in particular the connectedness between these new foraging habitats and existing nesting sites.

3.6 Acknowledgements

Establishment and maintenance of the study sites was funded by the federal state of Hesse (Germany) as part of the regional Hessian Integrated Agri-environmental Program (HIAP). Thanks to Michael Zerbe and Karina Weiß of Amt für Ländlichen Raum Marburg-Biedenkopf for their cooperation and the farmers who supported our study. We are grateful to Daniela Warzecha for selecting the study sites, funded by the German Federal Environmental Foundation (DBU). Thanks to Daniela Warzecha and Anna Hörner for spider collection and to Elvira Sereda and Sergei Sereda for determination of spider species. Thanks to two anonymous reviewers for helpful comments that improved the manuscript.

This is a pre-print of the article published in *Journal of Insect Conservation*. The final authenticated version is available online at:

<https://doi.org/10.1007/s10841-019-00190-6>.

General Discussion

Wildflower strips aim at mitigating biodiversity loss in agricultural landscapes. Their effectivity in promoting farmland biodiversity, however, has been shown to strongly correlate with their landscape context. In landscapes in which wildflower strips create a high ecological contrast, their effectivity seems highest. Here, I showed that the installation of multiple wildflower strips can increase their effectivity where single wildflower strips would be insufficient. Wildflower strips can increase habitat connectivity and resource availability especially for multi-habitat users. I showed for the first time, in addition to previously demonstrated benefits for wild bees, that prey-hunting wasps use wildflower strips as hunting grounds to collect prey items for their nests, but that connectivity and landscape context crucially determine wildflower functionality. My work contributes to new approaches in the design and implementation of agri-environmental schemes for multifunctional agricultural landscapes of the future.

Most wildflower strips target wild bees by increasing flower diversity and therefore providing a diverse set of foraging resources. Besides wild bees, however, wildflower strips might attract also herbivorous insects (Pfiffner & Wyss, 2003; Nicholls & Altieri, 2013) and their natural enemies (Walton & Isaacs, 2011; Tschumi *et al.*, 2016). Here I showed that also the non-target group of prey-hunting wasps was promoted by wildflower strips, but that these benefits to wasps – similar to wild bees (Holzschuh *et al.*, 2007; Batary *et al.*, 2011) – depended on landscape context. Over time, the abundance of wasps increased in landscapes with only small amounts of semi-natural habitats especially on connected wildflower strips (CHAPTER 1). The amount of grassland increased species richness on isolated wildflower strips, whereas in landscapes with multiple wildflower strips the species richness was independent from landscape context and similar high as on isolated wildflower strips in complex landscapes (CHAPTER 1). Thus, high landscape complexity contributes to either a better connectivity of landscape elements by linking foraging and nesting sites (Ricketts, 2001; Holzschuh *et al.*, 2009) or by providing foraging resources itself (Jauker *et al.*, 2009). Low complexities in contrast may act as a dispersal filter for small and less mobile species. However, the

effect of landscape complexity seems to be modulated by the spatial arrangement of wildflower strips.

So far, research did not consider whether the installation of multiple wildflower strips in concert may promote their benefits by increasing habitat connectivity. Here, I show for the first time that multiple wildflower strips compensate low landscape complexities by increasing connectivity of other semi-natural habitats for prey-hunting wasps (CHAPTER 1). Single wildflower strips in agricultural dominated landscapes might be too isolated to be used by wasps with small foraging ranges. However, multiple wildflower strips installed on a landscape scale may mutually increase their effectivity by reducing foraging distances for multi-habitat users like prey-hunting wasps by either increasing the wasps' fitness (CHAPTER 2) or by providing foraging resources (CHAPTER 2+3).

Prey-hunting wasps are promoted by wildflower strips not only via energetically rich nectar for adult wasps' nutrition (Fabian *et al.*, 2014), but also via abundant prey (Walton & Isaacs, 2011; Grass *et al.*, 2016). This latter benefit to prey-hunting wasps may not only be attributed to high prey quantity on wildflower strips, but also to higher prey quality. Here, weight of collected prey items was increased by landscape complexity and the connectivity of wildflower strips. Since wasps collected less but heavier prey items to provision their brood cells with ample larval food resources (CHAPTER 2), this may cause reproduction benefits, what is shown in turn by the increased number of brood cells in complex landscapes (CHAPTER 2). Nevertheless, there may be a trade-off between high prey quality and carrying distance to nesting sites, as prey species in wasps' nests became more dissimilar to available prey species on wildflower strips with increasing distance between them (CHAPTER 3). Since foraging distances are limited by the weight of prey (Fabian *et al.*, 2014), this pattern implies a shift towards less preferred prey if distances between foraging habitats and nesting sites become too high. This distance effect indicates that the impact radius of wildflower strips is limited by the dispersal abilities of organisms, that on average may be similar for prey-hunting wasps as it was shown for bees (Gathmann & Tschardt, 2002; Steffan-Dewenter *et al.*, 2002; Jauker *et al.*, 2013). Therefore, a concerted installation of multiple wildflower

strips increases the movement of individuals between nesting and foraging habitats and promote wasp populations especially in more homogenous landscapes.

Wildflower strips are a suitable measure for promoting not only flower visitors but also taxa on higher trophic levels, like I show for prey-hunting wasps. Landscape effects on wasps on wildflower strips are similar to those shown for wild bees. Thus, optimizing wildflower strips as commonly used AES for flower visitors may conserve not only pollinators but also non-target species like wasps. For examined prey-hunting wasps the distance to next wildflower strip was crucial for their utilization, thereby the connectivity of wildflower strips by installing them in concert improved their reachability. In landscapes with low matrix quality single wildflower strips were not able to facilitate fitness benefits for prey-hunting wasps but the installment of multiple wildflower strips increases their effectivity. This shows that wildflower strips as a commonly used AES are even functional in landscapes that were hitherto attributed with low effectivity. New approaches are needed for future AES; however, results show that planning of wildflower strip locations at a landscape scale must become practice (cf. McKenzie et al. 2013). With this approach the effectiveness of agri-environmental schemes can be maximized by increasing landscape heterogeneity on a large scale, not only for promotion of farmland biodiversity but also ecosystem stability by increasing predator-prey interactions and ecosystem services.

References

- Alanen, E.-L., Hyvönen, T., Lindgren, S., Härmä, O. & Kuussaari, M. (2011) Differential responses of bumblebees and diurnal Lepidoptera to vegetation succession in long-term set-aside. *Journal of Applied Ecology*, **48**, 1251–1259.
- Albrecht, M., Duelli, P., Müller, C., Kleijn, D. & Schmid, B. (2007) The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland. *Journal of Applied Ecology*, **44**, 813–822.
- Armstrong, T.R. & Stamp, N.E. (2003) Effects of prey quantity on predatory wasps (*Polistes dominulus*) when patch quality differs. *Behavioral Ecology and Sociobiology*, **54**, 310–319.
- Aviron, S., Herzog, F., Klaus, I., Schüpbach, B. & Jeanneret, P. (2011) Effects of wildflower strip quality, quantity, and connectivity on butterfly diversity in a Swiss arable landscape. *Restoration Ecology*, **19**, 500–508.
- Baessler, C. & Klotz, S. (2006) Effects of changes in agricultural land-use on landscape structure and arable weed vegetation over the last 50 years. *Agriculture, Ecosystems and Environment*, **115**, 43–50.
- Balzan, M. V., Bocci, G. & Moonen, A.C. (2016) Utilisation of plant functional diversity in wildflower strips for the delivery of multiple agroecosystem services. *Entomologia Experimentalis et Applicata*, **158**, 304–319.
- Batary, P., Baldi, A., Kleijn, D. & Tscharrntke, T. (2011) Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 1894–1902.
- Batáry, P., Dicks, L. V., Kleijn, D. & Sutherland, W.J. (2015) The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, **29**, 1006–1016.
- Baulechner, D., Diekötter, T., Wolters, V. & Jauker, F. (2019) Converting arable land into flowering fields changes functional and phylogenetic community structure in ground beetles. *Biological Conservation*, **231**, 51–58.
- Baum, K.A., Haynes, K.J., Dilleuth, F.P. & Cronin, J.T. (2004) The Matrix enhances the effectiveness of Corridores and Stepping Stones. *Ecology*, **85**, 2671–2676.
- Beaumont, J. De. (1964) *Hymenoptera: Sphecidae. Insecta Helvetica, Fauna 3*. Société Entomologique Suisse, Lausanne, Schweiz.
- Beduschi, T., Kormann, U.G., Tscharrntke, T. & Scherber, C. (2018) Spatial community turnover of pollinators is relaxed by semi-natural habitats, but not by mass-flowering crops in agricultural landscapes. *Biological Conservation*, **221**, 59–66.
- Bell, J.R., Wheeler, C.P. & Cullen, W.R. (2001) The implications of grassland and heathland management for the conservation of spider communities: a

- review. *Journal of Zoology*, **255**, S0952836901001479.
- Benton, T.G., Bryant, D.M., Cole, L. & Crick, H.Q.P. (2002) Linking agricultural practice to insect and bird populations: A historical study over three decades. *Journal of Applied Ecology*, **39**, 673–687.
- Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, **18**, 182–188.
- Birkhofer, K., Entling, M.H. & Lubin, Y. (2013) Agroecology. Trait composition, spatial relationships, trophic interactions. In *Spider Research in the 21st century. Trends & Perspective* (ed. by Penney, D.). Siri Scientific Press, Manchester, UK, pp. 200–229.
- Birkhofer, K. & Wolters, V. (2012) The global relationship between climate, net primary production and the diet of spiders. *Global Ecology and Biogeography*, **21**, 100–108.
- Blaauw, B.R. & Isaacs, R. (2014) Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *Journal of Applied Ecology*, **51**, 890–898.
- Blaauw, B.R. & Isaacs, R. (2015) Wildflower plantings enhance the abundance of natural enemies and their services in adjacent blueberry fields. *Biological Control*, **91**, 94–103.
- Blake, R.J., Woodcock, B.A., Westbury, D.B., Sutton, P. & Potts, S.G. (2011) New tools to boost butterfly habitat quality in existing grass buffer strips. *Journal of Insect Conservation*, **15**, 221–232.
- Blake, R.J., Woodcock, B.A., Westbury, D.B., Sutton, P. & Potts, S.G. (2013) Novel management to enhance spider biodiversity in existing grass buffer strips. *Agricultural and Forest Entomology*, **15**, 77–85.
- Bommarco, R., Lundin, O., Smith, H.G. & Rundlof, M. (2012a) Drastic historic shifts in humble-bee community composition in Sweden. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 309–315.
- Bommarco, R., Marini, L. & Vaissière, B.E. (2012b) Insect pollination enhances seed yield, quality, and market value in oilseed rape. *Oecologia*, **169**, 1025–1032.
- Burghardt, F. & Fiedler, K. (1996) The influence of diet on growth and secretion behaviour of myrmecophilous *Polyommatus icarus* caterpillars (Lepidoptera: Lycaenidae). *Ecological Entomology*, **21**, 1–8.
- Cadotte, M.W. & Tucker, C.M. (2017) Should Environmental Filtering be Abandoned? *Trends in Ecology and Evolution*, **32**, 429–437.
- Campbell, J.W., Milne, M., Dinh, B.T., Daniels, J.C. & Ellis, J.D. (2019) Spider (Araneae) abundance and species richness comparison between native wildflower plantings and fallow controls in intensively managed agricultural areas. *Arthropod-Plant Interactions*.
- Cardoso, P., Barton, P.S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., *et al.* (2020) Scientists' warning to humanity on insect extinctions.

- Biological Conservation*, **242**, 108426.
- Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D. & Nowakowski, M. (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology*, **44**, 29–40.
- Chazal, J. de & Rounsevell, M.D.A. (2009) Land-use and climate change within assessments of biodiversity change: A review. *Global Environmental Change*, **19**, 306–315.
- Cope, G.C., Campbell, J.W., Grodsky, S.M. & Ellis, J.D. (2019) Evaluation of nest-site selection of ground-nesting bees and wasps (Hymenoptera) using emergence traps. *Canadian Entomologist*, **151**, 260–271.
- Coudrain, V., Herzog, F. & Entling, M.H. (2013) Effects of Habitat Fragmentation on Abundance, Larval Food and Parasitism of a Spider-Hunting Wasp. *PLoS ONE*, **8**, 1–7.
- Diehl, E., Mader, V.L., Wolters, V. & Birkhofer, K. (2013) Management intensity and vegetation complexity affect web-building spiders and their prey. *Oecologia*, **173**, 579–589.
- Diekötter, T., Billeter, R. & Crist, T.O. (2008) Effects of landscape connectivity on the spatial distribution of insect diversity in agricultural mosaic landscapes. *Basic and Applied Ecology*, **9**, 298–307.
- Diekötter, T. & Crist, T.O. (2013) Quantifying habitat-specific contributions to insect diversity in agricultural mosaic landscapes. *Insect Conservation and Diversity*, **6**, 607–618.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014) Defaunation in the Anthropocene. *Science*, **345**, 401–406.
- Duelli, P. & Obrist, M.K. (2003) Regional biodiversity in an agricultural landscape: The contribution of seminatural habitat islands. *Basic and Applied Ecology*, **4**, 129–138.
- Duflot, R., Georges, R., Ernoult, A., Aviron, S. & Burel, F. (2014) Landscape heterogeneity as an ecological filter of species traits. *Acta Oecologica*, **56**, 19–26.
- Ebeling, A., Klein, A.M., Weisser, W.W. & Tscharrntke, T. (2012) Multitrophic effects of experimental changes in plant diversity on cavity-nesting bees, wasps, and their parasitoids. *Oecologia*, **169**, 453–465.
- Emmerson, M., Morales, M.B., Oñate, J.J., Batáry, P., Berendse, F., Liira, J., *et al.* (2016) How Agricultural Intensification Affects Biodiversity and Ecosystem Services. In *Advances in Ecological Research* (ed. by Dumbrell, A.J., Kordas, R.L. & Woodward, G.). Academic Press, Oxford, pp. 43–97.
- Fabian, Y., Sandau, N., Bruggisser, O.T., Aebi, A., Kehrli, P., Rohr, R.P., *et al.* (2014) Plant diversity in a nutshell: Testing for small-scale effects on trap nesting wild bees and wasps. *Ecosphere*, **5**, 1–18.
- Fahrig, L. (2001) How much habitat is enough? *Biological Conservation*, **100**,

65–74.

- Fahrig, L. (2003) Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487–515.
- Feber, R.E., Smith, H. & MacDonald, D.W. (1996) The Effects on Butterfly Abundance of the Management of Uncropped Edges of Arable Fields. *Journal of Applied Ecology*, **33**, 1191–1205.
- Feltham, H., Park, K., Minderman, J. & Goulson, D. (2015) Experimental evidence that wildflower strips increase pollinator visits to crops. *Ecology and Evolution*, **5**, 3523–3530.
- Field, J. (1992) Patterns of nest provisioning and parental investment in the solitary digger wasp *Ammophila sabulosa*. *Ecological Entomology*, **17**, 43–51.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., *et al.* (2005) Global consequences of land use. *Science*, **309**, 570–574.
- Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., *et al.* (2011) Solutions for a cultivated planet. *Nature*, **478**, 337–342.
- Fox, R., Oliver, T.H., Harrower, C., Parsons, M.S., Thomas, C.D. & Roy, D.B. (2014) Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *Journal of Applied Ecology*, **51**, 949–957.
- Fründ, J., Dormann, C.F., Holzschuh, A. & Tschardtke, T. (2013) Bee diversity effects on pollination depend on functional complementarity and niche shifts. *Ecology*, **94**, 2042–2054.
- Gámez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., Jong, H. de, *et al.* (2015) Landscape simplification filters species traits and drives biotic homogenization. *Nature Communications*, **6**, 8568.
- Gathmann, A., Greiler, H.-J. & Tschardtke, T. (1994) Trap-nesting bees and wasps colonizing set-aside fields: succession and body size, management by cutting and sowing. *Oecologia*, **98**, 8–14.
- Gathmann, A. & Tschardtke, T. (2002) Foraging ranges of solitary bees. *Journal of Animal Ecology*, **71**, 757–764.
- Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., *et al.* (2010) Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology*, **11**, 97–105.
- Grass, I., Albrecht, J., Jauker, F., Diekötter, T., Warzecha, D., Wolters, V., *et al.* (2016) Much more than bees—Wildflower plantings support highly diverse flower-visitor communities from complex to structurally simple agricultural landscapes. *Agriculture, Ecosystems & Environment*, **225**, 45–53.
- Haaland, C. & Bersier, L.-F. (2011) What can sown wildflower strips contribute to butterfly conservation?: an example from a Swiss lowland agricultural landscape. *Journal of Insect Conservation*, **15**, 301–309.

- Haaland, C., Naisbit, R.E. & Bersier, L.-F. (2011) Sown wildflower strips for insect conservation: a review. *Insect Conservation and Diversity*, **4**, 60–80.
- Halder, I. van, Thierry, M., Villemey, A., Ouin, A., Archaux, F., Barbaro, L., *et al.* (2017) Trait-driven responses of grassland butterflies to habitat quality and matrix composition in mosaic agricultural landscapes. *Insect Conservation and Diversity*, **10**, 64–77.
- Harris, A.C. (1994) *Ancistrocerus gazella* (Hymenoptera: Vespoidea: Eumenidae): A potentially useful biological control agent for leafrollers *planotortrix octo*, *p. excessana*, *ctenopseustis obliquana*, *c. herana*, and *epiphyas postvittana* (Lepidoptera: Tortricidae) in New Zealand. *New Zealand Journal of Crop and Horticultural Science*, **22**, 235–238.
- Hass, A.L., Brachmann, L., Batáry, P., Clough, Y., Behling, H. & Tschardtke, T. (2019) Maize-dominated landscapes reduce bumblebee colony growth through pollen diversity loss. *Journal of Applied Ecology*, **56**, 294–304.
- Heard, M.S., Carvell, C., Carreck, N.L., Rothery, P., Osborne, J.L. & Bourke, A.F.G. (2007) Landscape context not patch size determines bumble-bee density on flower mixtures sown for agri-environment schemes. *Biology Letters*, **3**, 638–641.
- Hendrickx, F., Maelfait, J.P., Wingerden, W. Van, Schweiger, O., Speelmans, M., Aviron, S., *et al.* (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *Journal of Applied Ecology*, **44**, 340–351.
- Hoffmann, H., Peter, F., Herrmann, J.D., Donath, T. & Diekötter, T. (under review) Benefits of wildflower fields as overwintering habitats for ground-dwelling arthropods depend on landscape structural complexity. *under review*.
- Hoffmann, U.S., Jauker, F., Diehl, E., Mader, V., Fiedler, D., Wolters, V., *et al.* (2020) The suitability of sown wildflower strips as hunting grounds for spider-hunting wasps of the genus *Trypoxylon* depends on landscape context. *Journal of Insect Conservation*, **24**, 125–131.
- Hoffmann, U.S., Jauker, F., Lanzen, J., Warzecha, D., Wolters, V. & Diekötter, T. (2018) Prey-dependent benefits of sown wildflower strips on solitary wasps in agroecosystems. *Insect Conservation and Diversity*, **11**, 42–49.
- Holt, R.D., Lawton, J.H., Polis, G.A. & Martinez, N.D. (1999) Trophic Rank and the Species-Area Relationship. *Ecology*, **80**, 1495–1504.
- Holzschuh, A., Steffan-Dewenter, I., Kleijn, D. & Tschardtke, T. (2007) Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. *Journal of Applied Ecology*, **44**, 41–49.
- Holzschuh, A., Steffan-dewenter, I. & Tschardtke, T. (2009) Grass Strip Corridors in Agricultural Landscapes Enhance Nest-Site Colonization by Solitary Wasps. *Ecological Applications*, **19**, 123–132.
- Holzschuh, A., Steffan-Dewenter, I. & Tschardtke, T. (2008) Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos*, **117**,

354–361.

- Huusela-Veistola, E., Hyvönen, T., Norrdahl, K., Rinne, V., Saarijärvi, I. & Söderman, G. (2016) Different response of two Hemiptera species groups to sown wildflower strips: True bugs and leafhoppers. *Agriculture, Ecosystems and Environment*, **222**, 93–102.
- Jauker, B., Krauss, J., Jauker, F. & Steffan-Dewenter, I. (2013) Linking life history traits to pollinator loss in fragmented calcareous grasslands. *Landscape Ecology*, **28**, 107–120.
- Jauker, F., Diekötter, T., Schwarzbach, F. & Wolters, V. (2009) Pollinator dispersal in an agricultural matrix: Opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecology*, **24**, 547–555.
- Jauker, F., Peter, F., Wolters, V. & Diekötter, T. (2012) Early reproductive benefits of mass-flowering crops to the solitary bee *Osmia rufa* outbalance post-flowering disadvantages. *Basic and Applied Ecology*, **13**, 268–276.
- Jurczyk, M., Wolters, V. & Birkhofer, K. (2012) Utilization of prey-rich patches leads to reproductive advantages for clustered individuals of a web-building spider. *Écoscience*, **19**, 170–176.
- Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., Esteban, J. De, Fernández, F., *et al.* (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, **9**, 243–254.
- Kleijn, D., Linders, T.E.W., Stip, A., Biesmeijer, J.C., Wäckers, F.L. & Bukovinszky, T. (2018) Scaling up effects of measures mitigating pollinator loss from local- to landscape-level population responses. *Methods in Ecology and Evolution*, **9**, 1727–1738.
- Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, **40**, 947–969.
- Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., *et al.* (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications*, **6**, 7414.
- Klein, A.-M., Steffan-Dewenter, I. & Tscharntke, T. (2004) Foraging trip duration and density of megachilid bees, eumenid wasps and pompilid wasps in tropical agroforestry systems. *Journal of Animal Ecology*, **73**, 517–525.
- Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., *et al.* (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 303–313.
- Kremen, C., Williams, N.M. & Thorp, R.W. (2002) Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences*, **99**, 16812–16816.
- Krewenka, K.M., Holzschuh, A., Tscharntke, T. & Dormann, C.F. (2011)

- Landscape elements as potential barriers and corridors for bees, wasps and parasitoids. *Biological Conservation*, **144**, 1816–1825.
- Krimmer, E., Martin, E.A., Krauss, J., Holzschuh, A. & Steffan-Dewenter, I. (2019) Size, age and surrounding semi-natural habitats modulate the effectiveness of flower-rich agri-environment schemes to promote pollinator visitation in crop fields. *Agriculture, Ecosystems & Environment*, **284**, 106590.
- Kruess, A. & Tscharntke, T. (1994) Habitat Fragmentation, Species Loss, and Biological Control. *Science*, **264**, 1581–1584.
- Lister, B.C. & Garcia, A. (2018) Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proceedings of the National Academy of Sciences*, **115**, E10397–E10406.
- Liu, Z., Scheirs, J. & Heckel, D.G. (2010) Host Plant Flowering Increases Both Adult Oviposition Preference and Larval Performance of a Generalist Herbivore. *Environmental Entomology*, **39**, 552–560.
- MacArthur, R.H. & Wilson, E.O. (2001) *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- Mader, V., Birkhofer, K., Fiedler, D., Thorn, S., Wolters, V. & Diehl, E. (2016) Land use at different spatial scales alters the functional role of web-building spiders in arthropod food webs. *Agriculture, Ecosystems and Environment*, **219**, 152–162.
- Mader, V., Diehl, E., Fiedler, D., Thorn, S., Wolters, V. & Birkhofer, K. (2017) Trade-offs in arthropod conservation between productive and non-productive agri-environmental schemes along a landscape complexity gradient. *Insect Conservation and Diversity*, **10**, 236–247.
- Magurran, A.E. & McGill, B. (2011) *Biological Diversity - frontiers in measurement and assessment*. Oxford University Press, New York.
- Mckenzie, A.J., Emery, S.B., Franks, J.R. & Whittingham, M.J. (2013) Landscape-scale conservation: Collaborative agri-environment schemes could benefit both biodiversity and ecosystem services, but will farmers be willing to participate? *Journal of Applied Ecology*, **50**, 1274–1280.
- Meyer, B., Jauker, F. & Steffan-Dewenter, I. (2009) Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic and Applied Ecology*, **10**, 178–186.
- Nicholls, C.I. & Altieri, M.A. (2013) Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. *Agronomy for Sustainable Development*, **33**, 257–274.
- Öckinger, E., Bergman, K.-O., Franzén, M., Kadlec, T., Krauss, J., Kuussaari, M., *et al.* (2012) The landscape matrix modifies the effect of habitat fragmentation in grassland butterflies. *Landscape Ecology*, **27**, 121–131.
- Öckinger, E. & Smith, H.G. (2007) Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, **44**, 50–59.

- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., *et al.* (2018) Package “vegan”: Community Ecology Package. *Green Food: An A-to-Z Guide*.
- Ollerton, J., Winfree, R. & Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos*, **120**, 321–326.
- Ouvrard, P., Transon, J. & Jacquemart, A.-L. (2018) Flower-strip agri-environment schemes provide diverse and valuable summer flower resources for pollinating insects. *Biodiversity and Conservation*, **27**, 2193–2216.
- Ovenden, G.N., Swash, A.R.H. & Smallshire, D. (2008) Agri-environment schemes and their contribution to the conservation of biodiversity in England. *Journal of Applied Ecology*, **35**, 955–960.
- Pekár, S. (2000) Webs, diet, and fecundity of *Theridion impressum* (Araneae: Theridiidae). *European Journal of Entomology*, **97**, 47–50.
- Pfiffner, L. & Wyss, E. (2003) Use of sown wildflower strips to enhance natural enemies of agricultural pests. In *Ecological Engineering for Pest Management: Advances in Habitat Manipulation for Arthropods* (ed. by Gurr, G.M., Wratten, S.D. & Altieri, M.A.). CSIRO Publishing, Melbourne, Australia, pp. 165–186.
- Polidori, C. & Andrietti, F. (2007) Factors affecting spider prey selection by *Sceliphron mud-dauber* wasps (Hymenoptera: Sphecidae) in northern Italy. *Animal biology*, **57**, 11–28.
- Polidori, C., Boesi, R., Isola, F. & Andrietti, F. (2005) Provisioning patterns and choice of prey in the digger wasp *Cerceris arenaria* (Hymenoptera: Crabronidae): the role of prey size. *European Journal of Entomology*, **102**, 801–804.
- Polidori, C., Santoro, D. & Blüthgen, N. (2013) Does prey mobility affect niche width and individual specialization in hunting wasps? A network-based analysis. *Oikos*, **122**, 385–394.
- Potts, S.G., Vulliamy, B., Roberts, S., O’Toole, C., Dafni, A., Ne’eman, G., *et al.* (2005) Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology*, **30**, 78–85.
- Power, A.G. (2010) Ecosystem services and agriculture: tradeoffs and synergies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2959–2971.
- Ramsden, M.W., Menéndez, R., Leather, S.R. & Wäckers, F. (2014) Optimizing field margins for biocontrol services: The relative role of aphid abundance, annual floral resources, and overwinter habitat in enhancing aphid natural enemies. *Agriculture, Ecosystems and Environment*, **199**, 94–104.
- Ricketts, T.H. (2001) The Matrix Matters: Effective Isolation in Fragmented Landscapes. *The American Naturalist*, **158**, 87–99.
- Robinson, R.A. & Sutherland, W.J. (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, **39**, 157–176.

- Rösch, V. (2015) *Landscape context of habitat fragmentation and the diversity of plants, arthropods and snails on calcareous grasslands*.
- Rösch, V., Tschardtke, T., Scherber, C. & Batáry, P. (2015) Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments. *Oecologia*, **179**, 209–222.
- Rossetti, M.R., Tschardtke, T., Aguilar, R. & Batáry, P. (2017) Responses of insect herbivores and herbivory to habitat fragmentation: a hierarchical meta-analysis. *Ecology Letters*, **20**, 264–272.
- Rusch, A., Bommarco, R., Jonsson, M., Smith, H.G. & Ekbom, B. (2013) Flow and stability of natural pest control services depend on complexity and crop rotation at the landscape scale. *Journal of Applied Ecology*, **50**, 345–354.
- Rusch, A., Valantin-Morison, M., Sarthou, J.-P. & Roger-Estrade, J. (2010) *Biological Control of Insect Pests in Agroecosystems. Advances in Agronomy*. Elsevier Ltd.
- Rypstra, A.L., Schmidt, J.M., Reif, B.D., DeVito, J. & Persons, M.H. (2007) Tradeoffs involved in site selection and foraging in a wolf spider: effects of substrate structure and predation risk. *Oikos*, **116**, 853–863.
- Sanders, D., Thébault, E., Kehoe, R. & Frank van Veen, F.J. (2018) Trophic redundancy reduces vulnerability to extinction cascades. *Proceedings of the National Academy of Sciences*, **115**, 2419–2424.
- Scheper, J., Bommarco, R., Holzschuh, A., Potts, S.G., Riedinger, V., Roberts, S.P.M., *et al.* (2015) Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. *Journal of Applied Ecology*, **52**, 1165–1175.
- Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G., *et al.* (2013) Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss - a meta-analysis. *Ecology Letters*, **16**, 912–920.
- Scheper, J., Reemer, M., Kats, R. van, Ozinga, W.A., Linden, G.T.J. van der, Schaminée, J.H.J., *et al.* (2014) Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. *Proceedings of the National Academy of Sciences*, **111**, 17552–17557.
- Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., *et al.* (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, **468**, 553–556.
- Schmidt-Entling, M.H. & Döbeli, J. (2009) Sown wildflower areas to enhance spiders in arable fields. *Agriculture, Ecosystems and Environment*, **133**, 19–22.
- Schüepf, C., Herrmann, J.D., Herzog, F. & Schmidt-Entling, M.H. (2011) Differential effects of habitat isolation and landscape composition on wasps, bees, and their enemies. *Oecologia*, **165**, 713–721.
- Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D.,

- et al.* (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, **574**, 671–674.
- Stamp, N.E. (2001) Effects of prey quantity and quality on predatory wasps. *Ecological Entomology*, **26**, 292–301.
- Steffan-Dewenter, I. (2002) Landscape context affects trap-nesting bees, wasps, and their natural enemies. *Ecological Entomology*, **27**, 631–637.
- Steffan-Dewenter, I. (2003) Importance of Habitat Area and Landscape Context for Species Richness of Bees and Wasps in Fragmented Orchard Meadows. *Conservation Biology*, **17**, 1036–1044.
- Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C. & Tscharncke, T. (2002) Scale-Dependent Effects of Landscape Context on Three Pollinator Guilds. *Ecology*, **83**, 1421.
- Steffen, W., Richardson, K., Rockstrom, J., Cornell, S.E., Fetzer, I., Bennett, E.M., *et al.* (2015) Planetary boundaries: Guiding human development on a changing planet. *Science*, **347**, 1259855–1259855.
- Swaay, C. van, Warren, M. & Loïs, G. (2006) Biotope Use and Trends of European Butterflies. *Journal of Insect Conservation*, **10**, 189–209.
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., *et al.* (2001) Forecasting agriculturally driven global environmental change. *Science*, **292**, 281–284.
- Tischendorf, L. & Fahrig, L. (2000) How should we measure landscape connectivity? *Landscape Ecology*, **15**, 633–641.
- Tscharncke, T., Gathmann, A. & Steffan-Dewenter, I. (1998) Bioindication using trap-nesting bees and wasps and their natural enemies: Community structure and interactions. *Journal of Applied Ecology*, **35**, 708–719.
- Tscharncke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters*, **8**, 857–874.
- Tscharncke, T. & Steffan-Dewenter, I. (2001) Succession of bee communities on fallows. *Ecography*, **24**, 83–93.
- Tscharncke, T., Steffan-Dewenter, I., Kruess, A. & Thies, C. (2002) Contribution of Small Habitat Fragments to Conservation of Insect Communities of Grassland-Cropland Landscapes. *Ecological Applications*, **12**, 354.
- Tscharncke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., *et al.* (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, **87**, 661–685.
- Tschumi, M., Albrecht, M., Collatz, J., Dubsy, V., Entling, M.H., Najar-Rodriguez, A.J., *et al.* (2016) Tailored flower strips promote natural enemy biodiversity and pest control in potato crops. *Journal of Applied Ecology*, **53**, 1169–1176.
- Tschumi, M., Albrecht, M., Entling, M.H. & Jacot, K. (2015) High effectiveness

- of tailored flower strips in reducing pests and crop plant damage. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20151369.
- Vanbergen, A.J. & Initiative, T.I.P. (2013) Threats to an ecosystem service: pressures on pollinators. *Frontiers in Ecology and the Environment*, **11**, 251–259.
- Walton, N.J. & Isaacs, R. (2011) Influence of Native Flowering Plant Strips on Natural Enemies and Herbivores in Adjacent Blueberry Fields. *Environmental Entomology*, **40**, 697–705.
- Warzecha, D., Diekötter, T., Wolters, V. & Jauker, F. (2016) Intraspecific body size increases with habitat fragmentation in wild bee pollinators. *Landscape Ecology*, **31**, 1449–1455.
- Warzecha, D., Diekötter, T., Wolters, V. & Jauker, F. (2018) Attractiveness of wildflower mixtures for wild bees and hoverflies depends on some key plant species. *Insect Conservation and Diversity*, **11**, 32–41.
- Whittingham, M.J. (2006) Will agri-environment schemes deliver substantial biodiversity gain, and if not why not? *Journal of Applied Ecology*, **44**, 1–5.
- Whittingham, M.J. (2011) The future of agri-environment schemes: biodiversity gains and ecosystem service delivery? *Journal of Applied Ecology*, **48**, 509–513.
- Winfree, R. (2010) The conservation and restoration of wild bees. *Annals of the New York Academy of Sciences*, **1195**, 169–197.
- Winqvist, C., Bengtsson, J., Aavik, T., Berendse, F., Clement, L.W., Eggers, S., *et al.* (2011) Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. *Journal of Applied Ecology*, **48**, 570–579.
- Witt, R. (1998) *Wespen beobachten, bestimmen*. Naturbuch Verlag, Augsburg.
- Wood, T.J., Holland, J.M. & Goulson, D. (2017) Providing foraging resources for solitary bees on farmland: current schemes for pollinators benefit a limited suite of species. *Journal of Applied Ecology*, **54**, 323–333.
- Woodcock, B.A., Bullock, J.M., Mortimer, S.R., Brereton, T., Redhead, J.W., Thomas, J.A., *et al.* (2012) Identifying time lags in the restoration of grassland butterfly communities: A multi-site assessment. *Biological Conservation*, **155**, 50–58.
- Woodcock, B.A., Isaac, N.J.B., Bullock, J.M., Roy, D.B., Garthwaite, D.G., Crowe, A., *et al.* (2016) Impacts of neonicotinoid use on long-term population changes in wild bees in England. *Nature Communications*, **7**, 12459.
- Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S. & Dorn, S. (2010) Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation*, **143**, 669–676.

Appendix

Tab. 1: Abundance (individuals per year) and occurrence (study sites per year) of wasp species collected with yellow pan traps on the 33 wildflower strips (Chapter 1) over three years of study.

(sub)family	species	abundance			occurrence		
		2011	2012	2013	2011	2012	2013
Eumeninae	<i>Allodyneres delphinalis</i>	0	1	2	0	1	1
	<i>Ancistrocerus claripennis</i>	3	1	3	3	1	3
	<i>Ancistrocerus gazella</i>	1	2	3	1	2	3
	<i>Ancistrocerus nigricornis</i>	0	1	3	0	1	3
	<i>Ancistrocerus oviventris</i>	0	0	1	0	0	1
	<i>Ancistrocerus trifasciatus</i>	1	5	2	1	3	2
	<i>Gymnomerus laevipes</i>	0	0	3	0	0	3
	<i>Odynerus spinipes</i>	0	1	1	0	1	1
	<i>Symmorphus bifasciatus</i>	0	0	1	0	0	1
	<i>Symmorphus crassicornis</i>	0	1	0	0	1	0
	<i>Symmorphus murarius</i>	0	2	0	0	1	0
Pompilidae	<i>Agenioideus cinctellus</i>	0	2	0	0	2	0
	<i>Anoplius nigerrimus</i>	0	6	18	0	6	8
	<i>Arachnospila anceps</i>	0	4	3	0	3	3
	<i>Arachnospila abnormis</i>	0	1	0	0	1	0
	<i>Arachnospila anceps</i>	2	0	0	2	0	0
	<i>Arachnospila minutula</i>	1	1	6	1	1	3
	<i>Arachnospila spissa</i>	1	4	5	1	1	3
	<i>Auplopus carbonarius</i>	0	2	2	0	2	2
	<i>Calicurgus hyalinatus</i>	0	0	3	0	0	2
	<i>Dipogon nitidum</i>	0	0	1	0	0	1
	<i>Priocnemis agilis</i>	0	0	1	0	0	1
	<i>Priocnemis fennica</i>	0	0	1	0	0	1
	<i>Priocnemis hyalinata</i>	0	0	4	0	0	2
	<i>Priocnemis obstrusiventris</i>	0	1	0	0	1	0
	<i>Priocnemis pertubator</i>	0	5	11	0	3	9
	<i>Priocnemis susterei</i>	0	0	1	0	0	1
	<i>Priocnemis vulgaris</i>	0	0	3	0	0	3
Sapygidae	<i>Sapygina decemguttata</i>	0	2	0	0	2	0
Crabronidae	<i>Astata boops</i>	2	1	0	2	1	0
	<i>Astata minor</i>	0	1	0	0	1	0
	<i>Cerceris rybyensis</i>	0	2	0	0	2	0
	<i>Crabro cribrarius</i>	1	7	1	1	5	1

APPENDIX

<i>Crabro peltarius</i>	1	0	0	1	0	0
<i>Crossocerus assimilis</i>	0	1	0	0	1	0
<i>Crossocerus cetratus</i>	0	3	2	0	3	1
<i>Crossocerus congener</i>	0	1	0	0	1	0
<i>Crossocerus distinguendus</i>	0	0	1	0	0	1
<i>Crossocerus megacephalus</i>	8	2	4	7	2	3
<i>Crossocerus nigrinus</i>	6	3	3	5	3	3
<i>Crossocerus palmipes</i>	0	2	0	0	2	0
<i>Crossocerus podagricus</i>	2	2	0	2	2	0
<i>Crossocerus vagabundus</i>	3	1	1	3	1	1
<i>Crossocerus varus</i>	1	3	0	1	3	0
<i>Didineis lunicornis</i>	0	1	0	0	1	0
<i>Diodontus luperus</i>	1	1	0	1	1	0
<i>Diodontus tristis</i>	0	1	0	0	1	0
<i>Ectemnius borealis</i>	5	4	9	3	4	7
<i>Ectemnius cavifrons</i>	1	11	0	1	3	0
<i>Ectemnius continuus</i>	3	36	23	3	12	11
<i>Ectemnius dives</i>	0	2	1	0	2	1
<i>Ectemnius guttatus</i>	0	0	1	0	0	1
<i>Ectemnius lapidarius</i>	2	25	16	1	11	8
<i>Ectemnius lituratus</i>	0	12	0	0	2	0
<i>Ectemnius rubicola</i>	3	5	4	3	5	2
<i>Ectemnius ruficornis</i>	0	19	0	0	4	0
<i>Ectemnius sexinctus</i>	0	3	0	0	2	0
<i>Entomognathus brevis</i>	2	0	0	1	0	0
<i>Gorytes fallax</i>	0	1	0	0	1	0
<i>Gorytes laticinctus</i>	3	1	0	3	1	0
<i>Gorytes planifrons</i>	0	1	0	0	1	0
<i>Lestiphorus bicinctus</i>	0	1	3	0	1	1
<i>Lindenius albilabris</i>	1	2	1	1	2	1
<i>Lindenius panzeri</i>	1	0	0	1	0	0
<i>Mellinus arvensis</i>	1	0	0	1	0	0
<i>Mimesa bicolor</i>	0	1	0	0	1	0
<i>Mimumesa dahlbomi</i>	0	0	2	0	0	1
<i>Nitela spinolae</i>	0	1	0	0	1	0
<i>Nysson spinosus</i>	0	12	2	0	7	2
<i>Nysson trimaculatus</i>	0	0	1	0	0	1
<i>Oxybelus bipunctatus</i>	1	0	0	1	0	0
<i>Passaloecus borealis</i>	0	5	1	0	4	1
<i>Passaloecus brevilabris</i>	2	4	1	2	3	1
<i>Passaloecus corniger</i>	1	9	3	1	6	3
<i>Passaloecus insignis</i>	1	5	4	1	3	3
<i>Passaloecus singularis</i>	0	6	3	0	5	3
<i>Passaloecus turionum</i>	0	4	6	0	4	6

REFERENCES

	<i>Pemphredon clypealis</i>	1	0	0	1	0	0
	<i>Pemphredon enslini</i>	6	6	0	5	5	0
	<i>Pemphredon inornata</i>	7	5	9	7	5	9
	<i>Pemphredon lethifer</i>	22	51	30	12	20	16
	<i>Pemphredon lugubris</i>	0	2	2	0	2	1
	<i>Pemphredon morio</i>	6	2	0	4	1	0
	<i>Pemphredon mortifer</i>	0	1	0	0	1	0
	<i>Pemphredon rufiger</i>	1	3	2	1	3	1
	<i>Pemphredon rugifer</i>	0	1	0	0	1	0
	<i>Pemphredon wesmaeli</i>	0	0	1	0	0	1
	<i>Psenus brevitarsis</i>	0	9	0	0	5	0
	<i>Psenus fulvicornis</i>	0	1	0	0	1	0
	<i>Psenus laevigatus</i>	0	1	0	0	1	0
	<i>Trypoxylon attentuatum</i>	0	1	6	0	1	6
	<i>Trypoxylon clavicerum</i>	1	2	2	1	2	2
	<i>Trypoxylon figulus</i>	17	26	16	3	9	8
	<i>Trypoxylon medium</i>	0	1	1	0	1	1
	<i>Trypoxylon minus</i>	1	4	1	1	3	1
Vespinae	<i>Dolichovespula adulterina</i>	1	0	1	1	0	1
	<i>Dolichovespula media</i>	10	0	1	9	0	1
	<i>Dolichovespula norwegica</i>	8	0	0	5	0	0
	<i>Dolichovespula omissa</i>	1	0	0	1	0	0
	<i>Dolichovespula saxonica</i>	10	0	6	6	0	3
	<i>Dolichovespula sylvestris</i>	318	1	64	28	1	17
	<i>Polistes dominula</i>	28	18	9	15	8	5
	<i>Polistes nimpha</i>	1	5	2	1	4	2
	<i>Polistes vulgaris</i>	2	0	0	1	0	0
	<i>Vespa crabro</i>	10	0	1	6	0	1
	<i>Vespula germanica</i>	210	0	4	26	0	4
	<i>Vespula rufa</i>	1	0	0	1	0	0
	<i>Vespula vulgaris</i>	791	0	38	31	0	17
Tiphiidae	<i>Methocha articulata</i>	0	3	1	0	3	1
	<i>Tiphia femorata</i>	44	55	18	13	13	7
	<i>Tiphia minuta</i>	14	127	21	3	24	12

APPENDIX

Tab. 2: Overall plant species of the four seed mixtures (*Lebensraum 1*, *Veitshöchheimer Bienenweide*, *ODIN-Blühfläche 2 Kranichsteiner Mischung*, *ODIN-Blühfläche*) used for wildflower strips in the agri-environmental scheme “HIAP” (2011-2015).

family	species	family	species
Apiaceae	<i>Daucus carota</i>	Hypericaceae	<i>Hypericum perforatum</i>
Apiaceae	<i>Carum carvi</i>	Lamiaceae	<i>Salvia pratensis</i>
Apiaceae	<i>Heracleum sphondylium</i>	Lamiaceae	<i>Origanum vulgare</i>
Apiaceae	<i>Pastinaca sativa</i>	Lamiaceae	<i>Clinopodium vulgare</i>
Apiaceae	<i>Foeniculum vulgare</i>	Lamiaceae	<i>Prunella vulgaris</i>
Apiaceae	<i>Coriandrum sativum</i>	Lamiaceae	<i>Leonurus cardiaca</i>
Apiaceae	<i>Anthriscus sylvestris</i>	Lamiaceae	<i>Thymus pulegioides</i>
Apiaceae	<i>Petroselinum sativum</i>	Linaceae	<i>Linum usitatissimum</i>
Apiaceae	<i>Anethum graveolens</i>	Linaceae	<i>Linum austriacum</i>
Asteraceae	<i>Helianthus annuus</i>	Malvaceae	<i>Malva sylvestris</i>
Asteraceae	<i>Achillea millefolium</i>	Malvaceae	<i>Malva moschata</i>
Asteraceae	<i>Anthemis tinctoria</i>	Malvaceae	<i>Malva sylvestris</i>
Asteraceae	<i>Cichorium intybus</i>	Malvaceae	<i>Malva mauritanica</i>
Asteraceae	<i>Centaurea scabiosa</i>	Malvaceae	<i>Malva verticillata</i>
Asteraceae	<i>Artemisia campestris</i>	Malvaceae	<i>Malva alcea</i>
Asteraceae	<i>Silybum marianum</i>	Onagraceae	<i>Oenothera biennis</i>
Asteraceae	<i>Calendula officinalis</i>	Papaveraceae	<i>Papaver rhoeas</i>
Asteraceae	<i>Centaurea cyanus</i>	Plantaginaceae	<i>Plantago lanceolata</i>
Asteraceae	<i>Centaurea jacea</i>	Poaceae	<i>Setaria italica</i>
Asteraceae	<i>Leucanthemum irtutianum</i>	Poaceae	<i>Anthoxanthum odoratum</i>
Asteraceae	<i>Artemisia vulgaris</i>	Poaceae	<i>Cynosurus cristatus</i>
Asteraceae	<i>Crepis biennis</i>	Poaceae	<i>Phleum pratense</i>
Asteraceae	<i>Tanacetum vulgare</i>	Poaceae	<i>Poa pratensis</i>
Asteraceae	<i>Leucanthemum vulgare</i>	Poaceae	<i>Secale multicaule</i>
Asteraceae	<i>Carduus nutans</i>	Polygonaceae	<i>Fagopyrum esculentum</i>
Asteraceae	<i>Inula helenium</i>	Ranunculaceae	<i>Nigella sativa</i>
Asteraceae	<i>Solidago virgaurea</i>	Resedaceae	<i>Reseda luteola</i>
Asteraceae	<i>Tanacetum corymbosum</i>	Resedaceae	<i>Reseda lutea</i>
Fabaceae	<i>Medicago sativa</i>	Rosaceae	<i>Sanguisorba minor</i>
Fabaceae	<i>Onobrychis viciifolia</i>	Rosaceae	<i>Agrimonia eupatoria</i>
Fabaceae	<i>Trifolium pratense</i>	Rubiaceae	<i>Galium verum</i>
Fabaceae	<i>Lotus corniculatus</i>	Rubiaceae	<i>Galium album</i>
Fabaceae	<i>Medicago lupulina</i>	Rubiaceae	<i>Galium mollugo</i>
Fabaceae	<i>Trifolium incarnatum</i>	Scrophulariaceae	<i>Verbascum nigrum</i>
Fabaceae	<i>Vicia sepium</i>	Scrophulariaceae	<i>Verbascum lychnitis</i>
Fabaceae	<i>Trifolium hybridum</i>	Scrophulariaceae	<i>Verbascum thapsus</i>
Fabaceae	<i>Vicia pannonica</i>	Scrophulariaceae	<i>Verbascum phoeniceum</i>
Fabaceae	<i>Vicia sativa</i>	Scrophulariaceae	<i>Verbascum densiflorum</i>
Fabaceae	<i>Ornithopus sativus</i>	Caryophyllaceae	<i>Silene vulgaris</i>

REFERENCES

Fabaceae	<i>Trifolium resupinatum</i>	Caryophyllaceae	<i>Cerastium holosteoides</i>
Fabaceae	<i>Trigonella caerulea</i>	Caryophyllaceae	<i>Silene alba</i>
Fabaceae	<i>Lathyrus pratensis</i>	Caryophyllaceae	<i>Silene dioica</i>
Fabaceae	<i>Melilotus officinalis</i>	Caryophyllaceae	<i>Silene flos-cuculi</i>
Fabaceae	<i>Anthyllis vulneraria</i>	Boraginaceae	<i>Borago officinalis</i>
Fabaceae	<i>Onobrychis arenaria</i>	Boraginaceae	<i>Echium vulgare</i>
Fabaceae	<i>Trifolium montanum</i>	Boraginaceae	<i>Phacelia tanacetifolia</i>
Fabaceae	<i>Trifolium repens</i>	Boraginaceae	<i>Myosotis arvensis</i>
Fabaceae	<i>Trifolium rubens</i>	Brassicaceae	<i>Barbarea vulgaris</i>
Fabaceae	<i>Trigonella foenum gr.</i>	Brassicaceae	<i>Sinapis alba</i>
		Caprifoliaceae	<i>Dipsacus fullonum</i>



Acknowledgements/ Danksagung

The whole work of this thesis could not have been possible without help and support of many gorgeous people. To them, I am very grateful:

First, I want to say thank you to my supervisor Tim Diekötter for giving me the opportunity to write this dissertation and for supporting me during all these years. You and Frank Jauker always gave good advice and drove success not only during my PhD work, but also during my master programm, bringing the best out of me. Without both of you I would never have come so far.

Thanks to Volkmar Wolters for molding my passion for agroecology and integrating me in the working group in Giessen University after my studies. I enjoyed my time in Giessen in the Department for Animal Ecology with my very nice colleagues Birgit Jauker, Daniela Warzecha, Viktoria Mader, Eva Diehl, Katharina John, Ralf Sauerbrei, Keiko Sasaki, Christian Krippes, Andrea Früh-Müller, Dennis Baulechner, Nora Rütz, Klemens Ekschmitt, Elisabeth Pohlen, Elvira Sereda and Birgit Aue.

During field work around Giessen and Marburg I had a lot of help by many student helpers and collogues. Therefore, I want to thank especially Daniela Warzecha, Patricia Schmidt, Anton Müller, Aziza Bouffara, Stefanie Ettlting and Anna Hörner; it was always a pleasure to have your companionship during field work and in our little insect lab. Also, thanks to all the farmers in Hesse and the *Amt für Ländlichen Raum* who supported this research project.

After finishing the field work for my PhD thesis, I moved to Kiel to work in a research project in the Department of Landscape Ecology at Kiel University while finishing this PhD thesis. Thanks to the whole working group for the warmly welcome and the nice work climate in OS75. Big thanks to Tobias Donath, Heinrich Reck, Heiko Schmäuser, Charlotte Hegge, Kerrin Müller, Henrike Möhler, Katrin Schwarz, Franziska Peter, Maren Jähne, Julia Roos, Marie Perennes, Henriette Beye, Christian Hertz-Kleptow, Henning Nissen, Ulrich Holst, Andreas Tränkner, Ulrich Fehlberg, Eugen Görzen, Hannes Hoffmann, Jonas Paul and John Hermann. Every day I enjoyed working in the institute, also our social activities

besides work where always great. My student helper made the work in my research project much easier. Thank you: Karina Borisova, Jessica Vollrath, Anna-Lena Kolze, Camilla Gillis-Adelman (a DAAD research intern from Canada), Katharina Wieggers, Lisa Bern-Seifert and Lukas Loose. The Sunday excursions with the “JuZos” (young zoologists) were always educational and enjoyable, thanks to all who were involved.

Special thanks to Michael Kuhlmann for enabling access to the collection of bees and wasps in the Zoological Museum of Kiel, also for good advices and for giving me the opportunity to work as a lecturer in the Institute for Zoology at Kiel University after finishing my research project. Also, thanks for good teamwork in the Aculeate Working Group of Schleswig-Holstein (AG Stechimme).

Thanks to my friends, roommates and fellow students who accompanied this part of my way and enriched my life in all those years, even if we see each other rather rarely: Christina, Lena, Tabea, David, Patricia, Miriam, Lisa, Maren, my Giessen-people: Miriam, Lisa, Wiebke, Sarah, Mario, Patricia S., Daniela, Melanie, Deborah, and my last roommates in Kiel Christoph and Arne, we had a lot of fun in the past years.

Lennart, meeting you was the best happening to me. Thank you for all your love and encouragement. I´m looking forward to all next years coming in our beautiful home and paradise garden.

Finally, I thank my family in Büschergrund who supported me during my studies. My parents Christiane and Theo, and Anne, Philipp, Heiner, Lara, Lina, Elise, Emil, Bosse, Ludo and Mathilde - you backed me up all the time. Without all of you I wouldn´t have come so far. There is no place like home...

Curriculum Vitae

Personal Data

Name	Uta Sophie Hoffmann
Place of birth	Freudenberg, Germany
Nationality	German

Education

2015 – 2020	PhD thesis Institute for Natural Resource Conservation, Land- scape Ecology, Kiel University, Germany
2011 – 2013	Master of Science Biology Justus-Liebig-University, Giessen, Germany
2008 – 2011	Bachelor of Science Biology Justus-Liebig-University, Giessen, Germany
1999 – 2008	High school Fürst-Johann-Moritz Gymnasium, Siegen, Germany

Career

since 2019	Zoologist Department of Species Conservation and Environ- mental Planning, Administration of District Schleswig-Flensburg, Germany
since 2017	Lecturer Institute for Zoology, Kiel University, Germany
2015 – 2019	Scientific employee Institute for Natural Resource Conservation Kiel University, Germany
2013 – 2015	Scientific Assistant Institute for Animal Ecology and Institute for Plant Ecology Giessen University, Germany
2013	Internship Department for Environment and Rural Affairs, Lower nature conservation authority, Giessen, Germany

Publications and Contributions to Conferences

Hoffmann US, Jauker F, Wolters V, Diekötter T (**in preparation**) Spatially concerted installation may boost biodiversity effects of sown wildflower strips.

Hoffmann US, Donath TW, Diekötter T, Peter F (**submitted**) Considering sown wildflower fields as an efficient measure to reduce visitation rates of honeybees and other pollinating insects on *Jacobaea vulgaris*.

Hoffmann US, Jauker F, Mader VL, Diehl E, Fiedler D, Wolters V, Diekötter T (**2020**) The suitability of sown wildflower strips as hunting grounds for spider-hunting wasps of the genus *Trypoxylon* depends on landscape context. *Journal of Insect Conservation* 24: 125-131.

Hoffmann US, Jauker F, Wolters V, Diekötter T (**2018**) Semi-natural habitats stabilize wasp communities on wildflower strips. *The 48th annual conference of the Ecological Society of Germany, Austria and Switzerland*. Talk

Hoffmann US, Jauker F, Lanzen J, Warzecha D, Wolters V, Diekötter T (**2018**) Prey-dependent benefits of sown wildflower strips on solitary wasps in agroecosystems. *Insect Conservation and Diversity* 11: 42-49

Hoffmann US, Mader VL, Diehl E, Wolters V, Diekötter T, Jauker F (**2016**) Utilization of subsidized flowering fields by spider-hunting wasps. *The 46th annual conference of the Ecological Society of Germany, Austria and Switzerland*. Poster

Hoffmann US, Jauker F, Lanzen J, Wolters V, Diekötter T (**2015**) Subsidized flowering fields promote prey-hunting wasps through increased habitat connectivity. *The 45th annual conference of the Ecological Society of Germany, Austria and Switzerland*. Talk