



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

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## 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.

**Keywords** Agri-environmental schemes · Biological control · Landscape complexity · Prey-hunting wasps · Trophic interaction

## 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; Hallmann et al. 2017). 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,

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of which several individuals are provisioned in one brood cell (Witt 1998). Related to these food requirements and their abundance in agricultural landscapes (Schüpp 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 and 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.

## Materials and methods

### 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 5 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  $235 \pm 131$  m standard deviation). Wildflower strips were similar in size ( $0.3 \pm 0.04$  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 and Tschamtk 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).

### 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.

### 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 and 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 and McGill 2011; Diehl et al. 2013). Collected spiders were frozen for storage and successively classified to species level.

### 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 ( $J$ ):

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

The underlying Bray–Curtis dissimilarity index was calculated using R function *vegdist* in package *vegan* (Oksanen et al. 2012):

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

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 Core Team 2014).

## Results

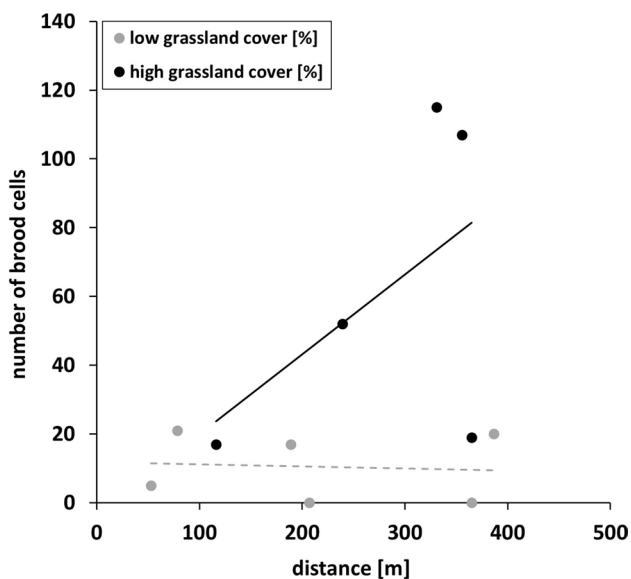
In total, 1129 brood cells in 258 nests along our study sites where built by cavity nesting bee and wasp species. Individuals of the genus *Trypoxylon* spp. were the most abundant spider-hunting wasps, with 374 brood cells built in 93 nests in nine of the eleven study sites. The number of brood cells 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 ( $R^2_{adj} = 0.96$ ,  $p < 0.001$ ; 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  $5.3 \pm 2.0$  spider individuals per cell independent of any landscape variable in our study. The mean species number per cell was  $2.8 \pm 1.1$ . *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

**Table 1** Model results for all dependent variables

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

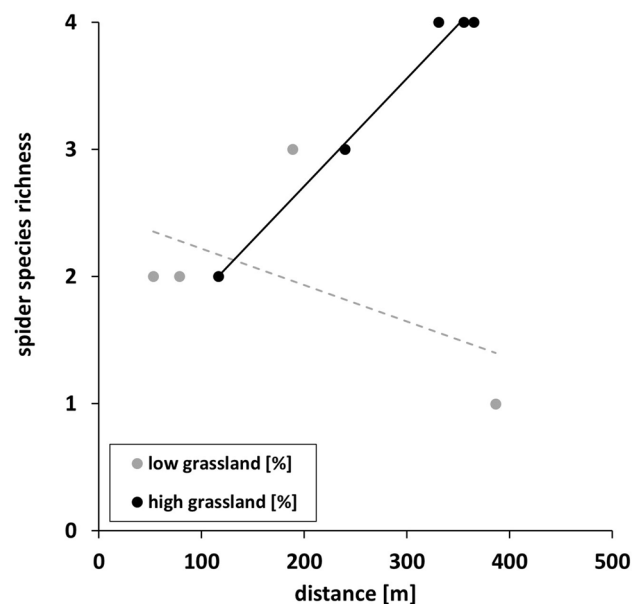
Explanatory variables and the adjusted  $R^2$  are given for the most parsimonious model. Final models were selected using a stepwise forward selection method



**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)

surrounding landscape ( $F_{3,5} = 9.29$ ,  $R^2_{adj} = 0.76$ ,  $p = 0.017$ ; 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.

A total of 15 spider species were recorded in wildflower strips. The mean richness per site was  $3.9 \pm 1.5$  species and



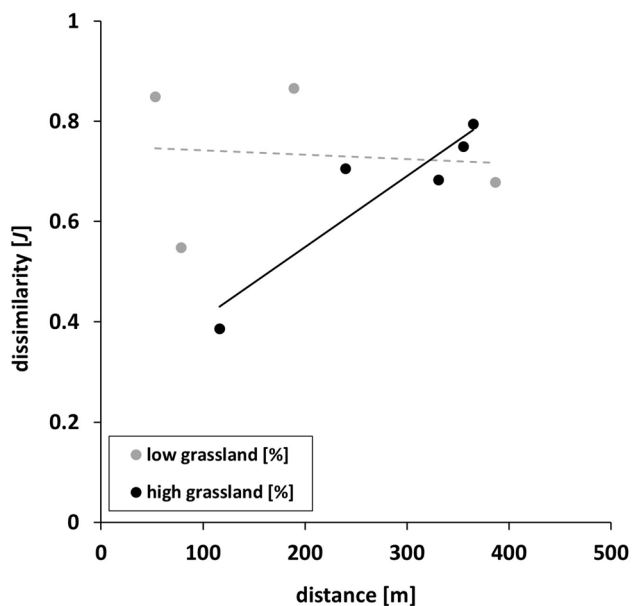
**Fig. 2** Spider species richness of prey individuals in nests of the solitary wasp *Trypoxylon* as a function of distance to next wildflower strip, interacting with the area percentage of grassland in the surrounding landscape. Amount of grassland was divided at the median (21%) into the categories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

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 ( $F_{3,5} = 7.08$ ,  $R^2_{\text{adj}} = 0.70$ ,  $p = 0.030$ ; 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.

## 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.



**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)

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 and 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 and 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 and 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 (c.f. 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 (c.f. 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.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** The authors also complied with journal's ethical standards regarding the integrity of the research and its presentation. The presented research involved the collection of cavity-nesting wasps and their spider prey. The work conforms to the legal requirements of Germany including those relating to conservation, and to the journal's policy on these matters. Every effort was made to reduce the impact of our research on local populations. This included the release of all but one reference individual per nest back to nature.

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