

Landscape elements as potential barriers and corridors for bees, wasps and parasitoids

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ABSTRACT

Habitat loss and fragmentation in agricultural landscapes lead to severe declines of abundance and richness of many insect species in the remaining isolated semi-natural habitats. We analysed possible barrier effects of large hedges and corridor effects of narrow grass strips that were hypothesized to affect foraging and dispersal of hymenopterans. We selected calcareous grasslands in the vicinity of Göttingen (Germany), which harbour high Hymenoptera diversity and are starting points for foraging and dispersal in the landscape. We installed pan traps to sample bees (i) on the grasslands; (ii) on grassland edges behind adjacent hedges (potential barriers) and without hedges; (iii) on grass strips in 100 m distance to the grassland, which were connected or unconnected to the grassland; and (iv) unconnected (isolated) grass strips in 300 m and 750 m distance to test for corridor and isolation effects on abundance and species richness of foraging wild bees. Additionally we provided trap nests for bees, wasps and their parasitoids on the grasslands and the strips. Species abundance and richness declined with increasing isolation from grasslands for foraging solitary bees, trap-nesting bees, wasps and parasitoids, but not for foraging bumblebees. Hedges did not confine movement of foraging bees. We found no mitigating effects of (100 m) corridor strips on any of the observed groups. We conclude that conservation of semi-natural habitats as sources of bee and wasp diversity is important and that grass strips act as sinks rather than corridors when high quality patches are nearby.

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1. Introduction

Fragmentation and loss of habitat caused by agricultural intensification has been identified as one of the biggest threats to biodiversity in agricultural landscapes, causing a reduction of abundance and diversity of insects in remaining, isolated habitat patches (Benton et al., 2003; Fahrig, 2003; Saunders et al., 1991; Tilman et al., 2001; Winfree et al., 2009). Corridors have often been proposed as a strategy to connect habitat fragments and mitigate negative effects of fragmentation (Haddad et al., 2003; Sutcliffe and Thomas, 1996). On the other hand, barrier effects of hedgerows are also known to restrict movement of some invertebrate species (Dover and Fry, 2001; Kuefler et al., 2010), although the knowledge of corridor and barrier effects on the movement and dispersal of bees and wasps and their parasitoids is limited (Holzschuh et al., 2009; Zurbuchen et al., 2010). Bees and wasps contribute widely to ecosystem services such as pollination of crops and wild plants (Cane, 1997; Winfree et al., 2007) and biological control (Klein et al., 2007; Tylianakis et al., 2005), but are increasingly threatened

by fragmentation (Larsen et al., 2005; Ricketts et al., 2008; Tschardt and Brandl, 2004).

The number of wild bees has decreased over the last centuries because of vanishing nesting and food resources in the intensively managed agricultural landscape (Biesmeijer et al., 2006; Kremen et al., 2002; Steffan-Dewenter et al., 2005). This problem is intensified by the ongoing loss of managed honeybees due to increasing pressure by pests and diseases and low economic return (De la Rua et al., 2009; Downey and Winston, 2001; Potts et al., 2010; Watanabe, 1994). Predatory wasps, nesting in tree trunks or branches in semi-natural habitats, are also challenged by the modification of the agricultural landscape (Tylianakis et al., 2006). Without suitable nesting habitats the predation of pest organisms by these predatory wasps is likely to decrease with increasing isolation (Holzschuh et al., 2009). Higher trophic levels are supposed to suffer even more from isolation of habitat patches (Albrecht et al., 2007; Holt et al., 1999).

Linear landscape elements, such as grass strips or hedgerows, are considered as conservation tools for enhancing biodiversity in the agricultural landscape through mitigating negative isolation effects (Beier and Noss, 1998; Rosenberg et al., 1997). Yet, the empirical evidence for corridor effects of such narrow habitat strips is

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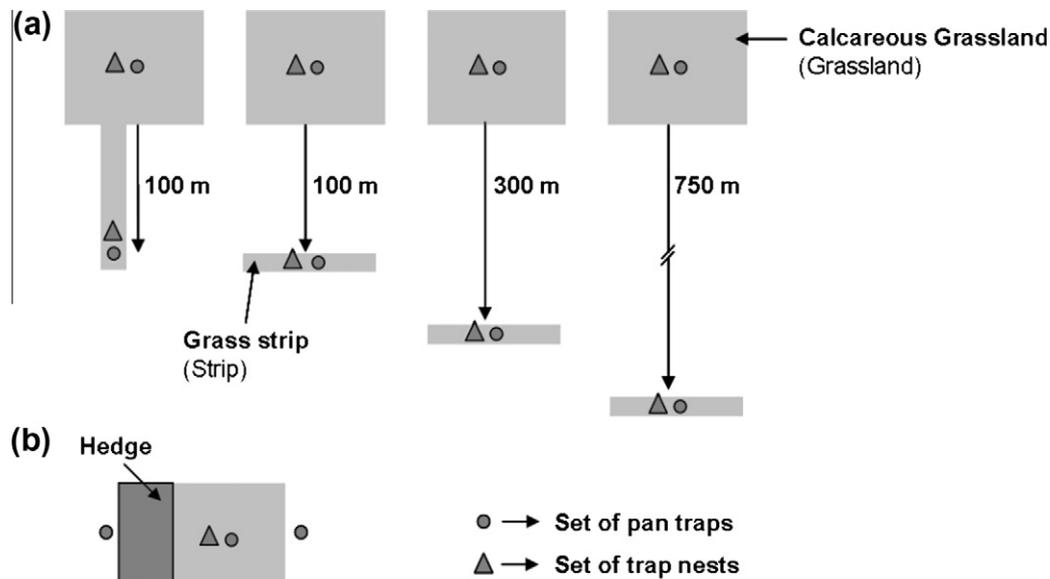


Fig. 1. Experimental design. All sites were embedded in the agricultural landscape matrix. Corridor experiment: (a) Trap nests and pan traps were installed in the middle of each calcaereous grassland and parallel to these in connected and unconnected grassy strips in the given distances (100 m, 300 m, 750 m). Barrier experiment: (b) On five calcaereous grasslands with hedges on one side, pan traps were exposed behind the hedge and on the edge without hedge to test for possible barrier effects.

limited and taxon-specific. Many studies investigating corridor effects on plants and animals have been conducted in a forest matrix with cleared grassland plots (Damschen et al., 2006; Haddad and Tewksbury, 2005; Tewksbury et al., 2002; Townsend and Levey, 2005), and these results cannot be readily transferred to the situation in intensively used agricultural landscapes. There are even studies indicating negative effects of corridors, such as grassy strips in open landscapes, proliferating pests or invasive species (Alofs and Fowler, 2010; Proches et al., 2005). Moreover, corridors in fragmented landscapes could enhance parasitoid species richness and abundance as well, affecting host populations in alternative habitats.

Hedges have been shown to be valuable landscape elements for conservation of bird, mammal and arthropod populations (Brambilla et al., 2007; Michel et al., 2007; Pollard and Holland, 2006; Varchola and Dunn, 2001), including cavity nesting bees and wasps, which construct their nests in the branches of hedges (Holzschuh et al., 2009). However, hedges can also function as obstacles for invertebrates, enhancing isolation effects as shown for lepidopteran species (Fry, 1995) and for carabid beetles (Mauremooto et al., 1995).

Our main objectives in this study were to assess whether hedges inhibit colonization of habitat patches and whether grass strips function as corridors for wild bees, predatory wasps and their parasitoids. The grass strips, situated along crop field margins and up to three metres wide, are common in agricultural landscapes in central Europe. We selected grass strips connected to species rich calcaereous grassland and unconnected grass strips varying in distance from the grassland. We expected connectivity to matter for foraging of wild bees and colonization success of trap-nesting bees and wasps. In addition we focused on hedgerows that separated the potential grass strip corridor from the grassland to test whether hedges can function as barriers inhibiting the movement of wild bees.

To our knowledge, our study is the first to use these typical grass strips of varying distances to semi-natural source habitats of wild bees to test for potential corridor and also potential barrier effects of hedgerows on bees and wasps and their parasitoids in the agricultural landscape. Specifically, our hypotheses were:

- (i) Abundance and species richness of wild bees and trap-nesting wasps and their parasitoids decline with increasing isolation from the source habitat.
- (ii) Abundance and species richness of wild bees and trap-nesting wasps are higher on grass strips that are connected to a semi-natural habitat than on unconnected grass strips.
- (iii) Hedges can function as an obstacle and restrict foraging movements of wild bees.
- (iv) Parasitism rates of hosts in the trap nests decline with increasing isolation and are higher in connected than unconnected strips.

2. Material and methods

2.1. Experimental sites

The study took place in summer 2007 in the vicinity of the city of Göttingen, located in the south of Lower Saxony, Germany. Göttingen is surrounded by shell limestone, featuring extensively managed calcaereous grasslands, which are protected conservation areas. These calcaereous grasslands are known to be valuable habitats for many flowering plant species and a huge variety of bee and wasp species (WallisDeVries et al., 2002). They are nutrient-poor locations and created by grazing by goats, sheep or small horses. The calcaereous grasslands host nesting resources for cavity nesting bee and wasp species, such as shrubs and hedges, which partly surround the grasslands (Steffan-Dewenter and Tschardtke, 1999). The dry, sandy soil with only bare vegetation is attractive for ground-nesting bees.

For our experiment we selected 17 calcaereous grasslands, which we considered to be source habitat for dispersal and daily foraging of bees and wasps. The mean area of the grasslands was 2.7 ± 0.8 ha (mean \pm SEM; min = 0.1 ha, max = 16.9 ha). Focusing on isolation and possible corridor effects, we observed hymenopteran movement on narrow, approximately 3 m broad grass strips connected and unconnected to the grassland.

Data were collected (i) directly at source grasslands ($n = 17$); (ii) at connected grass strips located 100 m from the grassland ($n = 13$); at unconnected grass strips located (iii) 100 m ($n = 8$);

(iv) 300 m ($n = 6$) and (v) 750 m ($n = 11$) from the grassland (Fig. 1). The calcareous grasslands are high-quality habitats and therefore not directly comparable to the low-quality grass strips; they were used as benchmark, since abundance and species richness are expected to be maximal on these grasslands. It was not possible to find calcareous grasslands with adjacent grass strips of all required isolation levels. Thus, the number of grass strip replicates differs among treatments. Flower density and the width of grass strips did not differ among treatments (strip width: lme, $F_{3,9} = 3.50$, $P = 0.063$; flower density: lme, $F_{3,9} = 0.33$, $P = 0.805$).

To test for possible barrier effects of hedges, we selected five calcareous grasslands with a dense hedge on one edge, which was larger than ten square metres and higher than two metres. Four of these grasslands were also used in the corridor and isolation experiments, therefore the set of pan traps in the centre of the grasslands could be used for both experimental set ups.

2.2. Survey of foraging bees and trap-nesting bees and wasps

We installed a total of 110 pan traps in the centre of the calcareous grasslands and on the grass strips in the mentioned distances from the traps on the grassland. To account for foraging movements of wild bees, we chose pan traps, which attract the bees by their colour (Westphal et al., 2008). One set of pan traps comprised two plastic soup bowls in yellow and blue, sprayed with UV-reflecting colour (Sparvar®) and filled with a mixture of ethylene glycol and water plus one drop of detergent. They were placed at one metre height on a wooden pole. Pan traps were exposed for 3 weeks (from 17th of July to 7th of August) and emptied at weekly intervals. On four locations the pan traps were destroyed, so we had to exclude them from analyses. Thus, the pan trap data set was reduced to (i) 16 source grasslands; 12 connected grass strips (ii) in 100 m, seven unconnected grass strips in (iii) 100 m and five grass strips in 300 m distance from the grassland. We installed additionally 11 sets of pan traps: one set in the centre of each grassland, one set directly behind the hedge facing the wheat field, and one set on the opposite side at the edge of the calcareous grassland next to a wheat field (Fig. 1b).

Trap nests are an established tool to assess the colonization activity of nesting specialists, such as cavity nesting bees and wasps, as well as the distribution and activity of their parasitoids (Tscharrntke et al., 1998). We placed in total 216 trap nests on the grasslands and grass strips, located 20 cm besides the pan traps at a height of 1.30 m. One set of trap nests consisted of a wooden pole with four plastic tubes with a diameter of 10.5 cm, each filled with approximately 200 reed internodes of diameters between 0.2 cm and 1.0 cm. The trap nests were put out from 15th of April to the 5th of October 2007. The occupied reed internodes were dissected and brood cells were counted. The numbers of parasitized brood cells, dead and undeveloped larvae were recorded. The occupied reed internodes were stored in glass vials at 4 °C for 6 weeks to simulate winter season and after that at room temperature to stimulate larval development. Emerging adults (hosts and parasitoids) were identified to species level. If no adult emerged, features of the nest and larval food were used to identify the genus or subfamily. Empty brood cells of eumenid wasps were assumed to belong to the bivoltine *Ancistrocerus nigricornis*, since offspring of the first generation emerged before trap collecting. We used no trap nests in the barrier experiment since hedges are nesting sites for most above-ground-nesting bee and wasp species and we hence expected no barrier effect of hedges for these groups.

All bees and wasps were identified to species level. *Bombus terrestris* and *Bombus lucorum* were pooled to *B. terrestris* agg. Bumblebees and solitary bees were analysed separately. The semi-social species of the genus *Lasioglossum* were included in the group of the solitary bees, while the domesticated honeybees

(*Apis mellifera*) were excluded from any analysis. We focused on the following species groups: foraging solitary bees, foraging bumblebees, trap-nesting bees and trap-nesting wasps, and the parasitoids of trap-nesting bees and wasps. Trap-nesting wasps were further divided into four functional groups with respect to the prey for their larvae. The first group consisted of wasps of the genus *Ancistrocerus* spp., which attack lepidopteran larvae (Schmid-Egger, 2004). The second group consisted of wasps of the genus *Symmorphus* spp., which are specialized on larvae of Chrysomelidae and Curculionidae (Budriené, 2003). Species richness of the genus *Symmorphus* was not analysed, because only two species occurred and one of these was present in two nests only. The third group consisted of the aphid-preying genera *Passaloecus*, *Pemphredon* and *Psenulus* (Sphecidae). Finally the fourth group consisted of the spider-preying genera *Trypoxylon* (Sphecidae), *Dipogon* and *Auplopus* (Pompilidae).

2.3. Vegetation survey

On the grass strips we recorded the species richness of flowering plants and the flower cover in the middle of July on a transect of 25 m in each direction of the traps. Flower cover was generally very low ($0.97\% \pm 0.06\%$, mean \pm SEM, min = 0.40%, max = 1.76%, $n = 38$ grass strips) with on average 7.4 ± 0.59 plant species per grass strip (mean \pm SEM, min = 4, max = 20). The average width of the grass corridors was $1.06 \text{ m} \pm 0.56 \text{ m}$ (mean \pm SEM, min = 0.37 m, max = 2.42 m, $n = 38$ grass strips).

2.4. Statistical analyses

Species richness is the total number of species per pan trap set or trap nests on each grassland and grass strip. Abundances in pan traps are the mean number of individuals caught over the two traps of a pan trap set and three rounds. Abundances in trap nests are the total numbers of brood cells per trap nest set. To assess the effect of grass strip isolation, we fitted linear mixed-effects models with isolation level as fixed factor and site as random factor. Response variables were the abundance and species richness of wild bees in the pan traps and the colonization, species richness and parasitism rates of trap-nesting bees and wasps and the functional groups of wasps. The random factor corrected for the fact that grass strips of different isolation level surrounding one grassland were not independent from each other. Abundances of *Symmorphus* spp. were too low to conduct a linear mixed-effects model analysis, so we used a Pearson's χ^2 -test with presence-absence matrix. Parasitism rates were calculated by dividing the parasitized brood cells by the number of all host brood cells. Parasitism rates were analyzed only for sites with a number of host brood cells >0 and not analysed for the functional wasp groups separately, since the number of parasitism events was too low. We also tested whether parasitoid species richness and parasitism rate depended on host species richness and included the isolation level as additional explanatory variable in the model. We analysed barrier effects of hedges, employing mixed-effect models with abundance and species richness of foraging bees as dependent variable, trap locations as fixed factor (centre of grassland vs. edge of the grassland with hedge vs. edge of the grassland without hedge) and site as random factor. Corridor effects on abundance and species richness were tested by strip type as fixed factor (connected grass strips in 100 m vs. unconnected grass strip in 100 m) and site as random factor. To fulfil the criteria of normality of errors the data for species richness, abundance and number of brood cells were $\log_{10}(x + 1)$ -transformed. The percentage values of parasitism rates were arcsine-square-root transformed (Crawley, 2007). The statistical analyses were conducted using R (version 2.10.0; R Development Core Team, 2009) and the package nlme (Pinheiro et al.,

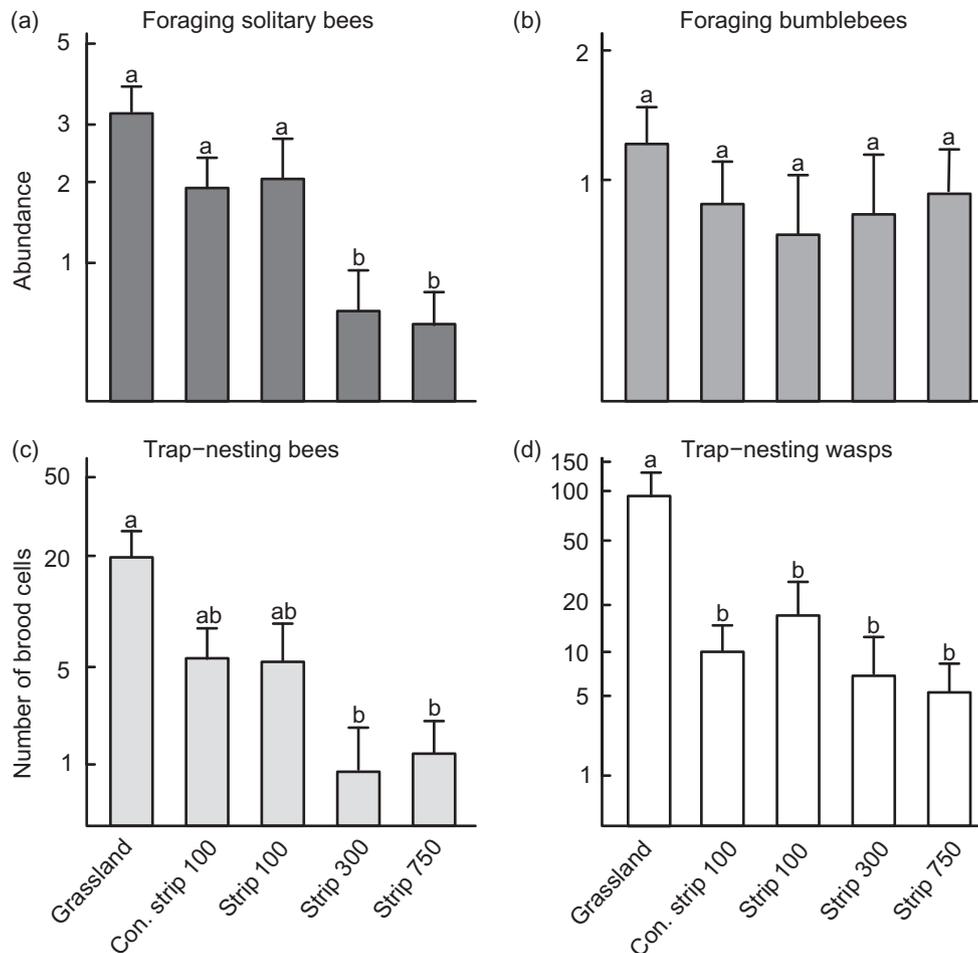


Fig. 2. Abundance of foraging bees. Abundance of (a) foraging solitary bees and of (b) foraging bumblebees in the pan traps and the number of brood cells of (c) trap-nesting bees and (d) trap-nesting wasps in the trap nests of the grassland, the connected strip in 100 m (con. strip 100) and the unconnected grass strips in 100 m, 300 m and 750 m. Figures are based on mean values + SEM, *P*-values are corrected after pairwise post hoc comparisons using the Holm method.

2009). If results showed significant *P*-values, they were tested with the post hoc general linear hypothesis test, using the packages *multcomp* and *multcompView* (Hothorn et al., 2008). *P*-values were corrected using the Holm method for multiple comparisons (Aickin and Gensler, 1996).

3. Results

In the intact 102 pan traps of the corridor experiment we caught in total 488 individuals. These were 203 bumblebees of 11 species (including *Psithyrus* spp.) and 285 solitary bee individuals of 36 species, mainly represented by the genus *Lasioglossum* (211 individuals). In the additional 24 pan traps of the barrier study 301 foraging bees were caught. The dominant genus was again *Lasioglossum* with 229 individuals (for details check Table A1 in the Appendix A).

In the trap nests, bees and wasps built 3675 brood cells. In total, we found 13 species of six bee genera. The most abundant genus of bees was *Hylaeus*, present in 436 brood cells, followed by *Chelostoma* with 196 and *Heriades* with 117 brood cells. Overall we identified 23 wasp species of 12 genera. The most abundant wasp genera were the spider predators of the genus *Trypoxylon*, which built 1100 brood cells, the predators of lepidopteran larvae, constructing 804 brood cells and the aphid predators *Passaloecus* spp. with 761 brood cells.

The parasitism rate in the trap nests was $19.2 \pm 2.6\%$ (mean \pm SEM, min = 0%, max = 58.3%, *N* = 3675). We found 13

species of (klepto-) parasitoids and one predator species (larvae of *Megatoma undata*), which we included in the analysis of parasitism. Seven parasitoid species attacked bees only, four species attacked wasps only and three parasitoid species were found in both bee and wasp nests (for details concerning trap-nesting bees, wasps, their prey and their parasitoids, check Table A2 in the Appendix A).

3.1. Isolation effects with increasing distance from the source habitat

We tested for isolation effects by comparing the abundance and species richness of foraging bees and trap-nesting bees and wasps on the grassland to the connected grass strip in 100 m distance and the isolated grass strips in 100 m, 300 m and 750 m distance.

The abundance of foraging solitary bees and trap-nesting bees was significantly reduced in the isolated grass strips at 300 m and 750 m distance (Fig. 2a and c). Species richness of foraging solitary bees was lower in the grass strip in 750 m, whereas the species richness of trap-nesting bees declined already from 300 m distance onwards (Tables 1 and 2).

Wasps were divided into four functional groups: predators of lepidopteran larvae, predators of chrysomelid larvae, predators of spiders and predators of aphids. Number of brood cells and species richness of all trap-nesting wasps, as well as the functional groups of trap-nesting wasps and their parasitoids, were significantly higher on the grassland than the grass strips (Table 2 and Figs. 2d, 3 and 4b). An exception were the predators of lepidopteran larvae that

Table 1
Results of the linear mixed-effect-models testing the effects of isolation on species richness and abundance of foraging bees, trap-nesting bees and wasps and three functional groups of trap-nesting wasps, comparing the grassland, Connected grass strip in 100 m distance (con. strip 100) and grass strips (strips) in mentioned distances. (Predators of chrysolimid larvae were excluded, since no linear mixed-effect model was conducted, due to low sample size). Values are for the full model and for pairwise post hoc comparisons after Holm correction.

	Foraging solitary bees		Foraging bumblebees		Trap-nesting bees		Trap-nesting wasps		Lepidopteran larvae predators		Aphid predators		Spider predators	
	$F_{4,21}$	P	$F_{4,21}$	P	$F_{4,25}$	P	$F_{4,25}$	P	$F_{4,25}$	P	$F_{4,25}$	P	$F_{4,25}$	P
<i>Species richness</i>														
Full model	5.4	0.004	0.3	0.904	8.3	<0.001	11.3	<0.001	3.4	0.024	11.3	<0.001	17.5	<0.001
Grassland – con. strip 100 m		1.000				0.085		<0.001		0.087		0.009		<0.001
Grassland – strip 100 m						0.238		0.216		0.145		0.334		<0.001
Grassland – strip 300 m		0.128				0.005		<0.001		0.119		0.002		<0.001
Grassland – strip 750 m		0.007				<0.001		<0.001		0.806		<0.001		<0.001
Con. strip 100 m – strip 100 m		1.000				1.000		0.340		1.000		0.450		1.000
Strip 100 m – strip 300 m		0.083				0.192		0.754		1.000		0.450		1.000
Con. strip 100 m – strip 750		0.001				0.056		0.360		1.000		0.030		0.642
Strip 100 m – strip 300 m		0.281				0.150		0.150		1.000		0.099		1.000
Strip 100 m – strip 750		0.023				0.046		0.016		1.000		0.002		1.000
Strip 300 m – strip 750		1.000				1.000		0.754		1.000		0.450		1.000
<i>Abundance</i>														
Full model	9.74	<0.001	0.7	0.624	7.5	<0.001	17.6	<0.001	1.7	0.181	38	<0.001	38.0	<0.001
Grassland – con. strip 100 m		0.118				0.143		<0.001				0.003		<0.001
Grassland – strip 100 m		0.396				0.167		0.042				0.354		<0.001
Grassland – strip 300 m		0.002				0.003		0.010				<0.001		<0.001
Grassland – strip 750 m		<0.001				0.001		<0.001				<0.001		<0.001
Con. strip 100 m – strip 100 m		1.000				1.000		1.000		1.000		0.354		1.000
Strip 100 m – strip 300 m		0.024				1.667		1.000				0.354		1.000
Con. strip 100 m – strip 750		0.006				1.667		1.000				0.017		1.000
Strip 100 m – strip 300 m		0.048				0.193		1.000				0.016		1.000
Strip 100 m – strip 750		0.012				0.193		0.696				<0.001		1.000
Strip 300 m – strip 750		1.000				1.000		1.000				0.416		1.000

Table 2
Grass strip type and distance at which species richness and abundance significantly decline compared with species richness and abundance on calcareous grasslands for connected strips in 100 m (con. strip 100) and grass strips (strip) in the mentioned distances.

	Significant decline of species richness	Significant decline of abundance
Foraging solitary bees	Strip 750	Strip 300
Foraging bumblebees	No decline up to strip 750	No decline up to strip 750
Trap-nesting bees	Strip 300	Strip 300
Trap-nesting wasps	Con. strip 100	Con. strip 100
Wasps: predators of lepidopteran larvae	No decline up to strip 750	No decline up to strip 750
Wasps: predators of chrysolimid larvae	NA	Con. strip 100
Wasps: predators of aphids	Con. strip 100	Con. strip 100
Wasps: predators of spiders	Con. strip 100	Con. strip 100
Parasitoids of trap-nesting bees	No decline up to strip 750	No decline up to strip 750
Parasitoids of trap-nesting wasps	Con. strip 100	Con. strip 100

showed no response to increasing isolation of the grass strips (lme: $F_{4,25} = 1.554$, $P = 0.217$) (Fig. 3a), but species richness was lower on the connected grass strip in 100 m distance compared to the isolated grass strips (Tables 1 and 2). We found no effect of isolation on the abundance and species richness of foraging bumblebees (Tables 1 and 2, Fig. 2b) and on the parasitoids of trap-nesting bees (Table 3).

Parasitism rates of trap-nesting wasps were highest on the grassland and were significantly lower on the grass strip in 750 m distance (Table 3, Fig. 4a). Species richness of trap-nesting bees and wasps was positively correlated with the number of brood cells (lme: bees, $F_{1,14} = 22.54$, $P < 0.001$; wasps, $F_{1,19} = 63.5$, $P < 0.001$) and species richness of parasitoids increased with the species richness of hosts (lme: bees, $F_{1,14} = 29.28$, $P < 0.001$; wasps, $F_{1,19} = 85.18$, $P < 0.001$).

3.2. Corridor effects

The models including the grassland and all grass strips showed no significant differences in abundance or species richness be-

tween the connected and Unconnected grass strips in 100 m distance (Table 1). When directly comparing the two 100 m grass strips in the model, we found no significant effect for any of the observed groups (abundance: solitary foraging bees, lme: $F_{1,3} = 6.90$, $P = 0.08$; bumblebees, lme: $F_{1,3} = 0.26$, $P = 0.643$; species richness: solitary foraging bees, lme: $F_{1,3} = 0.02$, $P = 0.66$; bumblebees, lme: $F_{1,3} = 0.24$, $P = 0.655$). Also abundance and species richness of trap-nesting bees and wasps did not differ between the two grass strip types (abundance: bees, lme: $F_{1,4} = 0.03$, $P = 0.879$; wasps, lme: $F_{1,4} = 0.01$, $P = 0.913$; species richness: bees, lme: $F_{1,4} = 0.013$, $P = 0.914$; wasps, lme: $F_{1,4} = 0.044$, $P = 0.844$, for results for the functional groups of wasps see Table A3 in the Appendix A).

3.3. Barrier effects of hedges

We compared the abundance and species richness of foraging bees in the pan traps on the grassland with the foraging bees caught on the edge of the grassland (i) behind a hedge and (ii) without a hedge. There was no detectable barrier effect on foraging solitary bees and foraging bumblebees (abundance: solitary

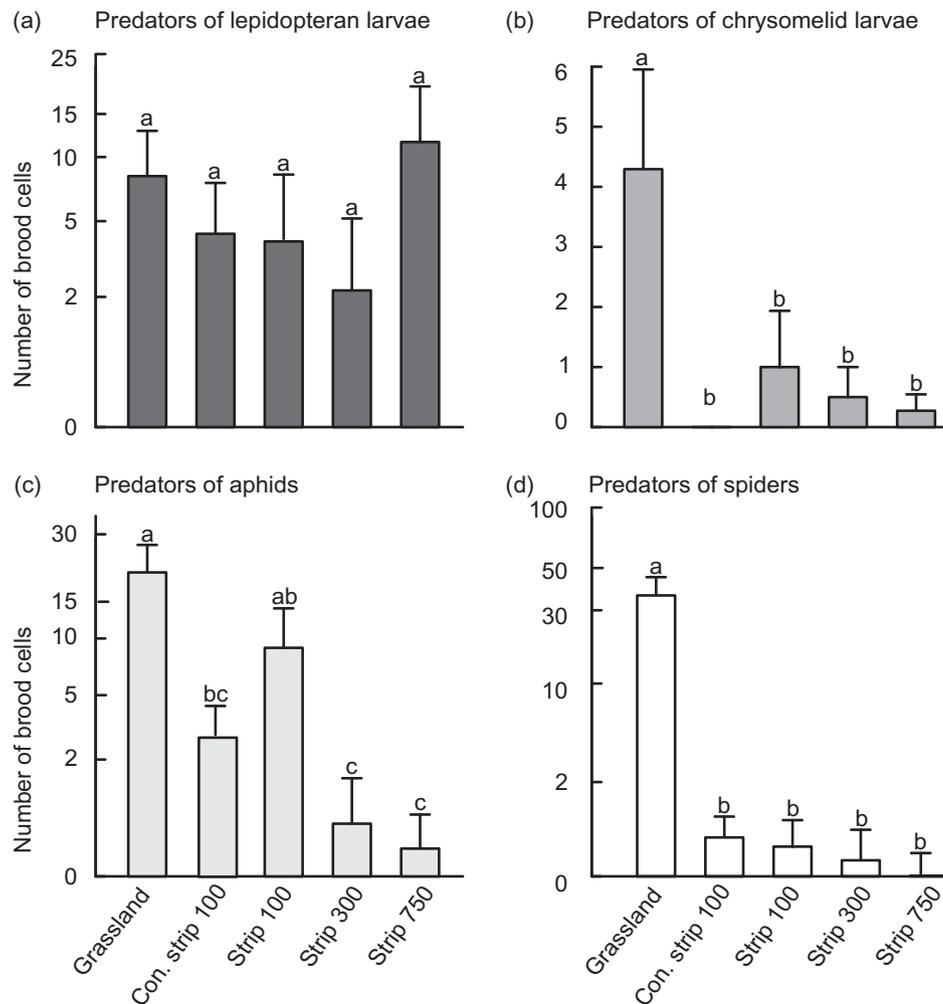


Fig. 3. Abundance of the four functional groups. Mean number + SEM of brood cells for the functional groups of wasps in the trap nests of the grassland, the connected strip in 100 m (con. strip 100) and the unconnected grass strips (Strip) in 100 m, 300 m and 750 m. (a) Predators of lepidopteran larvae (*Ancistrocerus* spp.), (b) predators of chrysomelid larvae (*Symmorphus* spp.), (c) aphid predators and (d) spider predators. *P*-values are for the full model and for pairwise post hoc treatment comparisons using the Holm method.

foraging bees, lme: $F_{2,8} = 0.88$, $P = 0.452$; bumblebees, lme: $F_{2,8} = 0.28$, $P = 0.762$; species richness: solitary foraging bees, lme: $F_{2,8} = 0.24$, $P = 0.788$; bumblebees, lme: $F_{2,8} = 0.24$, $P = 0.787$).

4. Discussion

The results of this study showed that isolation of narrow grass strips from large grassland negatively affected wild bees, predatory wasps and their parasitoids in the agricultural landscape, while neither hedges inhibited nor connecting grass strips facilitated dispersal. Habitat isolation affected nearly all observed guilds negatively. Abundance and species richness declined with increasing distance to the nearest grassland. Bees and wasps preferred the calcareous grassland as nesting habitat and starting point for daily forays. Exceptions from this pattern were the species richness and abundance of bumblebees, the abundance of predators of lepidopteran larvae and the abundance and species richness of parasitoids of bees. Abundance and species richness of foraging solitary bees declined with increasing distance from the source patch from a distance of 300 m onwards. Gathmann and Tschardtke (2002) linked the foraging distance of bees to their body length, with bigger bees flying considerably longer distances than small bee species (see also Greenleaf et al., 2007). In fact, most of the captured foraging solitary bees were

small with body sizes between five to nine millimetres, which suggests, according to Gathmann and Tschardtke (2002), a foraging distance of 200–250 m and thus explains the rapid decline from a distance of 300 m onwards. The ground-nesting bees sampled in the pan traps showed a similar pattern to that found for the abundance and species richness of the trap-nesting bees, which declined also with increasing distance and were significantly lower on the grass strip in 300 m distance. This is in line with studies dealing with the negative impact of increasing isolation from species rich grassland and habitat patches on the abundance of flower-visiting bees (Albrecht et al., 2007; Steffan-Dewenter and Tschardtke, 1999).

Abundance and species richness of trap-nesting wasps were significantly higher on the calcareous grasslands than on the grass strips. These findings suggest that wasps prefer high-quality habitats, but have the ability to colonize alternative habitats and to cover distances up to 750 m. When taking a closer look at the wasps by splitting the data set into functional groups regarding their prey, we found that spider predators and aphid predators were more abundant on the grassland. The predators of chrysomelid larvae were only found on the grasslands. According to Budriené (2003), these wasps prefer chrysomelid prey associated with trees and curculionid larvae on flowering herbs, which appeared to be the reason why they were restricted to

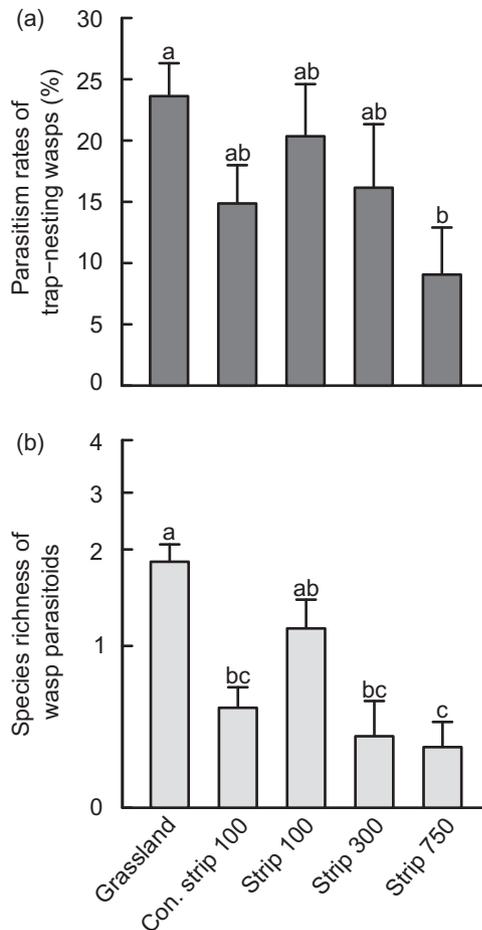


Fig. 4. Parasitism rates of wasps and species richness of wasp parasitoids. (a) Parasitism rates (%) of trap-nesting wasps and (b) species richness of wasp parasitoids on the grassland and the grass strips, based on mean values + SEM. *P*-values are for the full model and for pairwise post hoc treatment comparisons using the Holm method.

Table 3

Effects of the grassland and the different strips, (connected strip in 100 m = con. strip 100; grass strips = strip plus the distance of 100 m, 300 m and 750 m from the grassland), on the parasitism rate, species richness of parasitoids and the number of parasitized brood cells for trap-nesting bees and wasps. Values are for the full model and for pairwise post hoc treatment comparisons after Holm correction.

Trap-nesting wasps	Parasitism rate		Species richness of parasitoids		Parasitized brood cells	
	$F_{4,20}$	<i>P</i>	$F_{4,20}$	<i>P</i>	$F_{4,20}$	<i>P</i>
Full model	3.429	0.027	15.320	<0.001	15.7	<0.001
Grassland – con. strip 100 m		0.174		<0.001		<0.001
Grassland – strip 100 m		1.000		0.205		0.004
Grassland – strip 300 m		1.000		0.002		0.004
Grassland – strip 750 m		0.043		<0.001		<0.001
Con. strip 100 m – strip 100 m		1.000		0.072		1.000
Strip 100 m – strip 300 m		1.000		0.892		1.000
Con. strip 100 m – strip 750		1.000		0.588		1.000
Strip 100 m – strip 300 m		1.000		0.070		1.000
Strip 100 m – strip 750		0.230		0.006		1.000
Strip 300 m – strip 750		1.000		0.892		1.000
Trap-nesting bees	$F_{4,15}$		$F_{4,15}$		$F_{4,15}$	
Full model	0.265	1.454	1.950	0.155	1.458	0.264

the calcareous grasslands. We did not find connectivity effects on the distribution of predators of lepidopteran larvae, in contrast to

the study of Holzschuh et al. (2009), which focused on isolation from forest edges rather than grasslands. Forest edges are hosting more nesting sites than calcareous grasslands and are therefore more likely to function as source habitat for this species group.

The numbers of the aphid predators also declined with distance to the grassland yet were highest on the grass strips in 100 m distance. These aphid predators appeared to colonize even inferior nesting habitats when the prey availability in the surrounding wheat fields was high (Danks, 1970). In this case, grass strips function as alternative habitat with a possible impact on biological control of aphid populations in adjacent crops. The richness of the spider-hunting guild dropped off rapidly between the grassland and any grass strips. This suggests that these genera are less flexible in terms of colonizing new nesting habitats. The most abundant genus of this group, *Trypoxylon*, hunts sheet web building spiders (Bellmann, 2005), which are key spiders in grassland (Curry, 1994). *Trypoxylon* uses grasslands as starting points for dispersal in other habitats in the agricultural landscape (Schmidt and Tschamtkke, 2005; Thomas and Jepson, 1997).

Foraging bumblebees were distributed equally over the grassland and all grass strips, with no significant difference in species richness or abundance, even at 750 m distance. The very common generalist species *B. terrestris*, *B. lucorum* and *Bombus lapidarius* prefer field edges and banks as nesting sites (Kells and Goulson, 2003). These bumblebee species are not dependent on high quality habitat patches, as shown by Goulson et al. (2006). In contrast, Öckinger and Smith (2007) found more bumblebees on field margins at 100 m compared to 1000 m distance from the next seminatural grassland. This implies that there could be a distance effect for bumblebees on larger scales, which is consistent with the study by Westphal et al. (2006) showing landscape-wide bumblebee responses and the study by Knight et al. (2009), where the effective radius of available nesting and foraging sites for *Bombus pascuorum* was 1000 m.

No significant corridor effect was found for any of the observed species groups. This is in line with the study by Collinge (2000), who did not find differences in the abundance of hymenoptera between the sites with and without corridors in a grassland matrix. Our results suggest that native bees do not orientate themselves on structures like field margins but have their specific foraging radius that they scan for adequate food and nesting resources.

The lack of a corridor effect for trap-nesting species can potentially be explained by their occurrence being limited by suitable nesting sites. Abundance and species richness of trap-nesting bees and wasps is linked to the supply of suitable nesting sites in the focal habitat (Gathmann et al., 1994; Steffan-Dewenter, 2003; Tschamtkke et al., 1998). The connected and the isolated grass strip in 100 m distance provided equal amounts of nesting resources. With additional nesting sites in the surrounding, grass strips could function as alternative habitats enhancing dispersal of trap-nesting bees and wasps and their ecosystem services.

Larger individuals with high dispersal abilities such as many bumblebees may experience effects of connected vs. unconnected grass strips only on larger scales. Parasitism rates of wasps were significantly higher on the grassland than on the grass strip in 750 m distance, supporting results of Tschamtkke et al. (1998). Species richness of wasp and bee parasitoids was positively correlated (i) with species richness of hosts and (ii) the number of parasitized brood cells, supporting the findings of Holzschuh et al. (2009, 2010) and Tylianakis et al. (2006). We did not find isolation effects for parasitoids of bees, which may be due to the low numbers of trap-nesting bees and therefore low numbers of parasitism events.

Large hedgerows had no barrier effect on foraging pollinators. Since hedgerows are valuable nesting habitats for trap-nesting bees and wasps (Holzschuh et al., 2009), we focused on ground-nesting bees. Several studies found barrier effects of hedges, for example in carabid beetles (Mauremooto et al., 1995). Flying insects seem to be more flexible in terms of crossing barriers, but their movement may be negatively influenced by hedgerows, leading to changes of directions or return to source habitat patches (Dover and Fry, 2001). In contrast to this, foraging bees did not appear to be affected, possibly also because hedgerows function as foraging habitat for bees (Freemark et al., 2002; Hannon and Sisk, 2009).

5. Conclusions

Our findings showed that isolation distances of grass strips affected most Hymenoptera groups, while separating functional groups is crucial for understanding differences in sensitivity. Hedgerows are no barriers for wild bees including small ground-nesting bees and are not inhibiting dispersal of these bees into the adjacent agricultural landscape. We reject the hypothesis that grass strips, connecting habitats at a 100 m distance, function as corridors for wild bees, cavity-nesting wasps and their parasitoids. Common bumblebee species used grassland and grass strips similarly. Grass strips offer an additional foraging habitat when flower-

ing species are promoted and mowing frequency remains low. In addition, nesting sites such as hedgerows or tree trunks help cavity nesting bees and wasps maintaining their diversity (Holzschuh et al., 2009). Our results emphasize that large semi-natural habitats such as calcareous grasslands need to be protected as sources of bee and wasp diversity. Increasing the quality of grass strips may support bee and wasp diversity by serving as low-quality habitat (Brown and Paxton, 2009), in particular when embedded in a large scale habitat matrix, while small-scale habitat connectivity did not appear to be very important.

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Appendix A

See Tables A1 and A2.

Table A1
Survey of bee genera caught in the pan traps.

Genera	No. of individuals
Bombus	203
Andrena	27
Chelostoma	5
Halictus	10
Hylaeus	16
Lasioglossum	211
Megachile	5
Panurgus	1
Sphecodes	9
Stelis	1
Sum	488

Table A3

Results of the linear mixed-effect model with site as random factor, testing the connected and unconnected strip in 100 m distance in terms of abundance and species richness for the functional groups of wasps (Predators of lepidopteran larvae, predators of spiders and predators of aphids). Predators of chrysomelid larvae are excluded, because sample size on the grass strips was too low.

	Abundance		Species richness	
	$F_{1,4}$	P	$F_{1,4}$	P
Predators of lepidopteran larvae	0.55	0.500	0.230	0.660
Predators of spiders	0.086	0.784	0.134	0.733
Predators of aphids	0.228	0.660	0.500	0.520

Table A2

Survey of individuals occupying the trap nests. Prey of predatory wasps, parasitism rates, and parasitoids found in the nests of all genera are included.

	No. of brood cells	Parasitized brood cells	Parasitism rate %	Parasitoids	
<i>Trap-nesting bees</i>					
Chelostoma	196	34	17.35	<i>Stelis minuta</i> , <i>Trichrysis cyanea</i> , <i>Sapyga clavicornis</i> , <i>Melittobia acasta</i> , Ichneumonidae	
Heriades	117	12	10.26	<i>Sapyga decemguttata</i> , <i>Stelis</i> spp.	
Hylaeus	436	24	5.05	<i>Gasteruption assectator</i> , <i>Gasteruption jaculator</i> , <i>Melittobia acasta</i> , Ichneumonidae	
Megachile	90	18	20	<i>Coelioxys mandibularis</i> , <i>Coelioxys inermis</i> , <i>Melittobia acasta</i> , Ichneumonidae	
Osmia	25	3	12	<i>Melittobia acasta</i>	
Sum	872	93	10.67		
<i>Trap-nesting wasps</i>					
<i>Prey</i>					
Ancistrocerus	Lepidopteran larvae	219	12	5.48	<i>Chrysis ignita</i> , <i>Melittobia acasta</i>
Auplopus	Spiders	1	0	0	
Crossocerus	Diptera	51	7	13.73	<i>Melittobia acasta</i> , <i>Megatoma undata</i>
Dipogon	Spiders	31	2	6.45	<i>Chrysis</i> spp.
Discoelius	Lepidopteran larvae	4	0	0	
Eumenidae spec.	Lepidopteran larvae	494	139	28.14	<i>Chrysis ignita</i> , <i>Melittobia acasta</i> , Ichneumonidae,
Nitela	Diptera	8	1	12.5	<i>Melittobia acasta</i>
Passaloecus	Aphids	738	45	6.1	<i>Melittobia acasta</i> , <i>Trichrysis cyanea</i> , <i>Omalus aeneus</i>
Pemphredon	Aphids	2	0	0	
Psenulus	Aphids	25	0	0	
Spilomena	Thysanoptera	44	0	0	
Symmorphus	Chrysomelid larvae	86	6	6.98	<i>Chrysis ignita</i> , <i>Melittobia acasta</i>
Trypoxylon	Spiders	1100	379	34.45	<i>Melittobia acasta</i> , <i>Trichrysis cyanea</i> , Ichneumonidae
Sum		2803	591	21.09	

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