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# Effects of experimentally planting non-crop flowers into cabbage fields on the abundance and diversity of predators

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Abstract Flowery field margins and intersowing of crops with flowers are used as management practices to promote arthropod biodiversity as well as biocontrol agents. Positive effects of enhancement (in abundance and species richness) of hymenopteran parasitoids on control of Lepidoptera pests have previously been demonstrated. However, effects on predatory arthropods, which may also serve as pest control agents, remain unclear. In an experimental study in cabbage fields we tested how sown flower strips on field margins and intersowing with cornflower affected the species richness, abundance and community composition of ground beetles and spiders. Furthermore, we investigated whether effects of flower margins are dependent on the distance from the field margins. We found that field margins generally harboured higher species richness, whereas effects on abundance were weaker. Intersown cornflower had positive effects on spider and ground beetle abundance, but affected species richness only weakly. Our results do not provide evidence for effects of distance from the flowery field margins on predator richness or

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abundance. Species composition was strongly affected by the habitat management actions. We conclude that habitat management practices like flower strips on field margins and intersowing with flowers, which are primarily added to attract and enhance parasitoids for pest control, also benefit biodiversity conservation in spiders and ground beetles. They also positively affect the abundance of these primarily predatory taxa, which adds to the biocontrol potential of non-crop flowering plants.

**Keywords** Araneae · Carabidae · Companion plants · Flower strips · Habitat management · Organic farming · Pest control

## Introduction

Habitat loss and the intensification of agriculture have led to a dramatic decline of biodiversity in Europe since the early twentieth century (Weibull et al. 2000; Stoate et al. 2001; Robinson and Sutherland 2002; Holland and Reynolds 2003; Haaland et al. 2011). This has been shown particularly clearly for ground beetles (Marggi 1992; Duelli 1994; Holland 2002; Huber and Marggi 2005; Kotze and O'Hara 2003; Luka et al. 2009). Biodiversity loss may impede ecosystem services (such as providing food, water, genetic resources, erosion control, pest regulation, soil formation, efficient nutrient cycling, pollination) and diminish the cultural value of a landscape (e.g. for recreation, aesthetics and spirituality; Gurr et al. 2003; MEA 2005; Tscharntke et al. 2005). However, biodiversity in agro-ecosystems can be managed, i.e. enhanced, by appropriate measures (Kromp and Steinberger 1992; Altieri 1999). Complex habitats benefit both biological control agents and biodiversity in general (Altieri and Letourneau 1982; Bianchi et al. 2006; Pisani Gareau and Shennan 2010). Therefore, subsidies for ecological compensation areas have been introduced across Europe to counter biodiversity loss (for Switzerland: Jordi 2010). Non-production areas set aside for compensation provide shelter, alternative food sources, undisturbed overwintering sites or larval development sites to a wide range of species and lead to a diversification of microclimate and vegetation structure (Dennis and Fry 1992; Landis et al. 2000; Pfiffner and Luka 2000; Geiger et al. 2009). Such measures have been demonstrated to increase pollinator species richness in adjacent fields (Franzen and Nilsson 2008), and they greatly increase the numbers of overwintering arthropod species with beneficial effects on agriculture (Pfiffner and Luka 2000; Hatteland et al. 2011). Compensation areas are often designed as strips in or along fields, consisting of a variety of semi-managed plant communities, among them flower mixtures (e.g., Pfiffner et al. 2009). Strips are often established along fields of cereals and root crops to increase populations of biological control agents (e.g. predatory insects, parasitoids), but little is known about the effects of compensation measures in vegetable crops. To enhance beneficial insects in cabbage cultures, intercropping with clover (e.g., Armstrong and McKinlay 1997; Finch and Kienegger 1997; Schellhorn and Sork 1997) or grass strips has been applied (e.g., Ryan et al. 1980). Weedy cabbage fields were shown to contain less insect pests than weedfree cultures (Schellhorn and Sork 1997).

The aim of this study was to investigate options for biodiversity management of grounddwelling, predatory arthropods (i.e., spiders and ground beetles) by experimental introduction of non-crop flowering plants in two spatial schemes. This involved establishing flower strips along field margins. However, because potential effects of flower strips could be restricted to the direct vicinity of the strips (Luka et al. 2001; Tylianakis et al. 2004; Lavandero et al. 2005), we also investigated effects of companion plants inside the field. We expected that these would attract target insects from the strips into the field and thus spread the effects of the strips.

Specifically we asked: (1) Do flower strips affect community properties of ground beetles and spiders? (2) Is the distance from flower strips on field margins related to community properties of ground beetles and spiders in fields? (3) Do the companion plants inside the fields affect community properties of ground beetles and spiders in fields?

Abundance of predators (i.e., individual numbers, regardless of species identity) is evidently related to biocontrol, whereas species richness is a variable relevant to both general conservation efforts (i.e., increasing alpha-diversity in the landscape) as well as biological pest control. Different predator species may differ in feeding niches, so they (potentially) prey on different pest organisms. We investigated experimental effects on both response variables. Ground beetles and spiders are well suited to address these questions because (1) they are species-rich and they occur in large numbers in agricultural as well as natural habitats (Hänggi 1989; Luka 1996; Blick et al. 2004). In Switzerland alone, 523 Carabidae (Luka et al. 2009) and 970 Araneae species (Blick et al. 2004; Hänggi and Stäubli 2012) are known. (2) Most ground beetles are polyphagous and all spiders are zoophagous, hence they act as natural control agents (Dempster 1967; Luff 1987; Luka 1996; Suenaga and Hamamura 1998; Gurr 2000; Holland 2002). Furthermore (3) the taxonomy of the European species is well studied (Müller-Motzfeld 2006; Luka et al. 2009) and their habitat requirements are well known and (4) they react sensitively and fast to environmental changes and are easily surveyed with reproducible methods (Nagel 1999; Rainio and Niemela 2003; Luka 2004). As a consequence, they are often utilized as bioindicators in conservation studies (but see Beck et al. 2013).

#### Materials and methods

#### Location and experimental design

We collected arthropods in seven organic white cabbage (*Brassica oleracea*) fields (mean area 8,800 m<sup>2</sup>) in the northern Swiss lowlands (see Table 1 for site details). A 3 m-wide flower strip (FS) was planted along one long margin of each field. Within each field we installed an area with companion plants (CP+) ( $12 \times 26$  m; cornflower (*Centaurea cyanus*) planted between cabbage at a density of 1 m<sup>-2</sup>). At 40 m distance an equally large area without companion plants (CP–) served as control. Cabbage fields had sizes of at least 50 × 100 m, hence edge effects on survey areas should be negligible. CP+ and CP– each contained a survey area "close" (5 m) and "far" (20 m) from the flower strip. The flower strip contained two survey areas adjacent to CP+ and CP–. Per survey area one pair of funnel traps, five meters apart, was set up (Fig. 1) from June 29th to September 9th.

The flower strips were sown in April 2010 with a seed mixture composed of 15 g Vicia sativa, 9 g Fagopyrum esculentum, 4 g Ammi majus and 2 g Centaurea cyanus and 70 g vermiculite (to facilitate sowing) per 100 g of mixture (provided by Fenaco Genossens-chaft, Sämereizentrum Niderfeld, Winterthur, Switzerland). This forb mixture ensured high ground coverage and inhibited the establishment of weeds. The cabbage plants were planted between May 19th and June 29th, 2010; companion plants were planted shortly thereafter (Table 1).

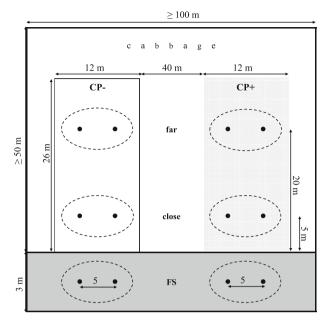
Table 1	Table 1 Location and characterization of study sites	laracterizatio	on of study sites							
Field	Municipality	Region	Coordinates <sup>a</sup>		Elevation (m) Area <sup>b</sup> (m <sup>2</sup> )	Area <sup>b</sup> (m <sup>2</sup> )	Strip length (m)	Flower strip sowing <sup>c</sup>	Cabbage planting <sup>c</sup>	CP planting <sup>c</sup>
A	Raperswilen	1	N 47° 37.676' E 09° 01.767'	N 47° 37.686' E 09° 01.874'	553	10,000	135	Apr. 7th	June 28/29th	June 29th
в	Engwilen	1	N 47° 37.310' E 09° 06.212'	N 47° 37.216' E 09° 06.228'	546	5,000	185	Apr. 7th	June 6th	June 9th
C	Lippoldswilen	1	N 47° 36.620' E 09° 06.980'	N 47° 36.600' E 09° 07.307'	501	26,000	415	Apr. 7th	June 5/11th	June 9th
D	Tägerwilen	1	N 47° 39.148' E 09° 06.610'	N 47° 39.123' E 09° 06.704'	520	3,200	128	Apr. 7th	June 5th	June 9th
Щ	Madiswil	7	N 47° 09.993' E 07° 47.443'	N 47° 10.004' E 07° 47.209'	530	6,000	93	Apr. 6th	June 1st	June 10th
ц	Madiswil	7	N 47° 09.686' E 07° 47.209'	N 47° 09.754' E 07° 47.228'	530	6,200	125	Apr. 6th	May 19th	June 9th
IJ	Wynau	2	N 47° 15.583' E 07° 49.709'	N 47° 15.626' E 07° 49.720'	470	5,000	136	Apr. 8th	May 25th	June 9th
CP con	CP companion plant									

<sup>a</sup> Coordinates (WGS84) of the flower strip extremities

<sup>b</sup> Total contiguous area planted with *Brassica* sp. <sup>c</sup> All dates in 2010

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Fig. 1 Experimental design: Cabbage field (*white area*) bordered by a flower strip (FS) (grey shaded area). Cabbage fields contained an area with comflowers (*Centaurea cyanus*) as companion plants (CP+, dotted) and a control area without companion plants (CP-, *white*). Six survey areas (dashed ellipses) containing two funnel traps each (filled circles) were set up. Seven fields in two regions were sampled (Table 1)



#### Measurements

Epigean arthropods were caught in funnel traps between June 29th and September 7th, 2010 (a period of 85 days). Traps were emptied fortnightly. Funnel traps consisted of a pipe of 10 cm diameter buried level to the soil surface, in which a funnel of 10 cm diameter was placed that ended in a 300 ml container filled to one-third with ethylene glycol (100 %) and a drop of soap (Gall-Seife flüssig, Permatin AG, Stein am Rhein, Switzerland) to reduce surface tension. To avoid flooding by rain water, traps were covered with a transparent plastic roof 5 cm above the ground.

All Carabidae and Araneae were identified to species level. The nomenclature of ground beetles followed Luka et al. (2009) corresponding to Löbl and Smetana (2003), that of spiders followed Platnick (2012). We measured activity density (i.e., number of individuals in traps) as a proxy of abundance, and species richness as a measure of diversity. Species richness may be affected by incomplete local sampling, but evaluation of species accumulation curves indicated that we assessed the local fauna at the sampling period quite completely (not shown).

In each sampling area a botanic inventory (ground coverage per plant species) was carried out according to Braun-Blanquet (1964) between July 29th and August 6th, 2010 to record both planted and spontaneous vegetation (i.e., weeds). Within the cabbage fields we surveyed an area of  $4 \times 12$  m, whereas survey areas within the flower strip were  $3 \times 12$  m in size.

# Analysis

All temporal replicates per trap were pooled per trap (see Fig. 1). Furthermore, for the analysis of habitat treatments (FS, CP+, CP-), the four traps within the same treatment

per field were pooled (Fig. 1). For comparisons of effects of companion plants and distance from flower strips, the two traps of each survey area (Fig. 1) were pooled.

We tested for effects of experimental habitat treatments (FS, CP+, CP–) with linear mixed effects models in R (R Development Core Team 2009; function *lme* of package *nlme*), using site as random factor. Species richness values and activity densities of spiders were normally distributed and data are reported as arithmetic mean plus or minus the standard error ( $\bar{x} \pm$  se). Activity densities of ground beetles were log-transformed to follow assumptions of parametric models. Therefore, means are reported as geometric mean times or divided by the multiplicative standard deviation ( $\bar{x}^**/s^*$ ; Limpert et al. 2001).

In a second step, we tested for effects of companion plant presence, distance from the flower strip, and their interaction, using only data from within the fields (i.e., not from flower strips) (CP+<sub>close</sub>, CP+<sub>far</sub>, CP-<sub>close</sub>, CP+<sub>far</sub>) with linear mixed effects models, using site as random factor. Activity densities and species richness were normally distributed and reported as arithmetic mean plus or minus the standard error ( $\bar{x} \pm$  se). Additionally, we applied a nested linear mixed effects model to investigate the effect of companion plant presence at the two distances from the flower strip, using only data from within the fields.

The influence of environmental and management variables on the faunal composition of ground beetles and spiders was studied using canonical correspondence analysis (CCA; software CANOCO for Windows 4.5, ter Braak and Smilauer 1998). Region, plant cover, plant species diversity and experimental habitat treatment were used as environmental predictors. We applied forward selection-CCA. The significance of effects were assessed by 499 Monte Carlo permutations, testing the eigenvalue of the axis associated with this variable (ter Braak 1996).

Carabidae species were classified as rare according to the Swiss Red List (Duelli 1994), whereas for rare Araneae we followed the most recent German Red List (Blick et al. 2013) as no Red List is available for Switzerland yet. Species were qualified as frequent if they occurred with at least nine individuals. We defined species to preferentially occur in one region or habitat type if at least 2/3 of individuals were found in that region or habitat type.

#### Results

#### Abundance and species richness

A total of 27,682 ground beetles belonging to 70 species and 9,942 spiders belonging to 65 species were caught. The most frequent ground beetles were *Harpalus rufipes* (28 % of carabid individuals), *Bembidion quadrimaculatum* (16 %) and *Poecilus cupreus* (13 %). The most frequent spiders were *Oedothorax apicatus* (62 % of spider individuals), *Erigone dentipalpis* (8.6 %) and *Pardosa agrestis* (6.6 %; Electronic Supplement). Per site medians were 3,538 specimens and 40 species of ground beetles, and 1,301 specimens and 29 species of spiders (Table 2).

Experimental habitat treatment (FS, CP+, CP–) generated significant differences in species richness of both taxa (Table 3). Flower strips sheltered 20 ground beetle species more (approx. 30 %) than the two habitat types within fields. Spider species richness was highest in flower strips and lowest in the treatment without companion plants. Ground beetle abundance was not significantly influenced by treatment type, and the effect was marginal for spiders. The significant effects were caused mainly by differences between flower strips and fields. Only spider species richness showed significantly higher values in the treatment without companion plants.

	FS	CP+ <sub>close</sub>	CP+ <sub>far</sub>	CP- <sub>close</sub>	CP- <sub>far</sub>
S (carab)	66	38	38	36	36
AD (carab)	13,961	3,500	3,895	3,365	2,961
S (spid)	54	32	31	28	25
AD (spid)	2,386	2,002	2,117	1,580	1,857

**Table 2** Total species richness (S) and activity density (AD) of treatments (FS, flower strip;  $CP\pm$ , with/ without companion plants, close and far from the flower strip)

Across seven fields (see Table 1) an average ( $\pm$ SE) of 3,954.6 ( $\pm$ 1258.9) ground beetle individuals of 39.4 ( $\pm$ 2.0) species and 1,335.2 ( $\pm$ 628.2) spider individuals of 28.3 ( $\pm$ 4.1) species were caught

**Table 3** Mean  $\pm$  SE of species richness (S) and activity density (AD) per taxon and habitat treatment (gmean\*/gse for carbid activity densities; see "Materials and methods") and test statistics of linear mixed effect models

	FS	CP+	CP-	$F_{df=12}$	р
S (carab)	$35.0^{a} \pm 1.3$	$22.9^{b} \pm 0.3$	$22.7^{\rm b} \pm 1.0$	84.0	< 0.001
AD (carab)	1,580.1 <sup>a</sup> */1.3	999.1 <sup>a</sup> */1.1	859.8 <sup>a</sup> */1.1	2.5	0.123
S (spid)	$23.0^{a} \pm 1.1$	$17.3^{b} \pm 1.1$	$14.3^{c} \pm 0.4$	23.9	< 0.001
AD (spid)	$340.9\pm47.0$	$588.4 \pm 116.6$	$491.0 \pm 100.4$	4.0	0.047

Different letters behind values indicate significant pairwise differences between treatments

Within the cabbage fields, companion plant presence positively affected spider species richness and abundance as well as ground beetle abundance (Table 4). However, there were no significant effects of distance from flower strips (Table 4). Companion plants did increase ground beetle activity densities far from the flower strip ( $F_{18} = 9.462$ , p = 0.006), but not close to the flower strip ( $F_{18} = 0.198$ , p = 0.662), whereas this effect was reversed for spider activity densities (near:  $F_{18} = 6.705$ , p = 0.018; far:  $F_{18} = 2.545$ , p = 0.128) and species richness (near:  $F_{18} = 6.927$ , p = 0.017; far:  $F_{18} = 4.051$ , p = 0.059).

using only	uuu nom om	in nords						
	CP+ <sub>close</sub>	$CP+_{far}$	CP- <sub>close</sub>	CP- <sub>far</sub>	Pres: F <sub>df=19</sub>	р	Dist: F <sub>df=19</sub>	р
S (carab)	18.9 ± 1.0	18.4 ± 1.3	18.6 ± 1.0	17.9 ± 1.1	0.231	0.636	0.410	0.530
AD (carab)	$500.0 \pm 54.6$	556.4 ± 83.3	$480.7 \pm 66.2$	$423.0\pm46.8$	5.486	0.003	0.000	0.984
S (spid)	$14.0 \pm 1.3$	$12.9\pm0.74$	$11.6\pm0.5$	$11.0\pm0.7$	11.265	0.003	1.802	0.195
AD (spid)	$286.0 \pm 63.0$	$302.4 \pm 58.0$	$225.7\pm49.7$	$265.3\pm52.3$	8.996	0.007	2.972	0.101

Table 4 Mean  $\pm$  SE of species richness (S) and activity density (AD) per taxon and habitat treatment, using only data from within fields

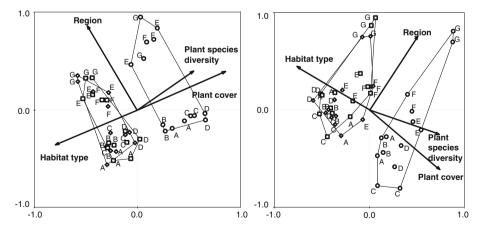
Test statistics from linear mixed effect models for effects of companion plant presence (*Pres*) and distance from flower strip (*Dist*) are given. Notably, effects of companion plants on the AD of Carabidae were stronger far from flower strips than near them, whereas the opposite was observed for effects on S and AD of spiders (details not shown)

## Effects on community composition

Region, plant ground cover and habitat treatment significantly affected species community composition (CCA: p < 0.008). Ground beetle and spider species community compositions differed, in particular, between flower strip and the two treatment types within fields. Plant ground cover explained most variability of species community composition, i.e. 18.3 and 16.4 % for ground beetles and spiders, respectively, followed by treatment type and region explaining ca. 15 % of compositional variance each, for both taxa. Plant species richness played a significant role only for ground beetles (explaining 13.6 % of variation). Additional analyses (not shown) could not establish significant effects of distance from field margins on community compositions.

The ordination of ground beetle data indicated that species communities of the two regions are distinct (Fig. 2). Communities of region 1 (fields A, B, C and D) are located on the bottom right of the ordination plot, whereas communities of region 2 (fields E, F and G) are on the top left. The same pattern, though less pronounced, is observed in the ordination of spider data (Fig. 2). Variation in ground beetle community composition between regions was related to known species-specific habitat preferences for xerophilous and pioneer flora habitats (region 1) as opposed to eurytopic species typical of arable land (region 2).

Eighteen of 70 recorded ground beetle species and 22 of 65 spider species occurred only in flower strips, nine species of each group with more than one individual. In contrast, only one ground beetle species (*Tachys bistriatus*) occurred exclusively within fields (60 individuals). Araneae species exclusive to cabbage fields were singletons (hence habitat preference is hard to judge), but seven frequent spiders species were more frequent in cabbage fields than in flower strips. Five rare, red-listed ground beetle species were found (49 specimens in total: *Amara kulti, A. littorea, Dolichus halensis, Porotachys bisulcatus, Trechoblemus micros*). Four of these occurred mainly in the flower strips. No spider species from the German Red List were found, but 3 recorded species (7 specimens in



**Fig. 2** Canonical correspondence analysis (CCA) plots of carabid (*left*) and spider (*right*) species community composition resemblance between habitat treatments (FS *circles*; CP+ *square*; CP- *diamonds*). *Letters* indicate fields (Table 1). *Arrow* orientation and length indicate direction and strength of correlations with the respective environmental predictors. Convex polygons enclose all sites of each habitat treatment. See Electronic Supplement for details on explained variance and significance of variables

total: *Drassyllus praeficus, Xerolycosa miniata, Robertus arundineti*) are red-listed for the southern German state of Baden-Württemberg (Nährig et al. 2003).

## Discussion

Potential of habitat management for conservation and pest control

Flower strips and companion plants are promoted for a double purpose in agriculture—on the one hand, they are expected to serve biodiversity conservation (Smith et al. 2008; Merckx et al. 2013), on the other hand they may promote the presence and abundance of biological pest control agents, such as predatory and parasitoid arthropods. Here we treated only ground-dwelling, predatory taxa, but similar studies on parasitoid Hymenoptera (e.g., Pfiffner et al. 2009; Géneau et al. 2012; Belz et al. 2013) showed evidence for the presence of both effects.

Our data clearly indicated that flower strips can enhance local species richness, hence contributing to the biodiversity of agricultural landscapes. Species richness of both ground beetles and spiders were higher in flower strips than in fields, they harboured a different species community than that found in fields (adding to the regional species richness), and they contained more species of national conservation relevance (i.e., red-listed taxa). This indicates the conservation potential of such management actions.

Data were more equivocal with regard to the effects of flowers on the pest control potential of these predatory taxa. Because ground beetles and spiders are less prey-specific than, e.g., parasitoids, we would expect pest-control benefits particularly from increased abundance, and less from increased species richness (despite potential effects of a larger prey spectrum, see "Introduction"). However, effects of flower strips on abundance (i.e., activity densities) were weak, whereas companion plants lead to significantly increased abundance when analysed separately from flower strip effects. This was particularly the case for ground beetles far from flower strips (despite the absence of other distance effects). Cultivating vegetable crops such as cabbage requires high intensity techniques (e.g., mechanical weed removal, fertilizer) compared to cereal crops, which may be related to the fact that stronger field margin effects onto ground beetles and spider communities had been found in earlier studies in cereal fields (Luka et al. 2001).

There is some support for companion plants increasing the density of predatory arthropods in fields far from pest control-managed field edges. This suggests that follow-up studies on the effects of these predators, i.e. on pest density and/or agricultural productivity, would be useful to allow an economic judgment on the use of companion plants for pest control (see above for established effects on parasitoids). Possibly effects of companion plants were weaker than those of flower strips simply because less species were used for the former than for the latter (i.e., one vs. four), which also affects structural complexity of the vegetation. However, economic constraints (i.e., the need to harvest cabbage) limit the choices for additional plants.

Ground beetles were found to be powerful biocontrol agents of cabbage pests in earlier studies (e.g., Schellhorn and Sork 1997; Shelton et al. 1983; Suenaga and Hamamura 1998, 2001). Dempster (1967), for example, estimated that over half of the mortality of the first two caterpillar instars of *Pieris rapae* (Lepidoptera) was due to predation by arthropods, especially the carabid *Harpalus rufipes*, and to lesser degrees *Abax parallelepipedus* and *Trechus quadristriatus*. On our study sites the pest species *P. rapae* occurred abundantly,

while predatory *H. rufipes* and *Bembidion quadrimaculatum* were the most frequently encountered ground beetles. *Harpalus rufipes* were most abundant in flower strips, whereas *B. quadrimaculatum* seemed to profit from companion plants.

Armstrong and McKinlay (1997) observed that cabbage cultures with natural weed cover had more ground beetles than dense cabbage cultures with dense white clover undergrowth. In contrast, Purvis and Curry (1984) observed no correlation between partial weed cover and trap contents. Schellhorn and Sork (1997) and Dempster (1969) demonstrated that crucifer cultures with weed cover contained fewer pests and higher predator abundance, particularly ground beetles. These studies and our results underline the potential of management measures on pest control by predators (e.g. Pfiffner et al. 2009; Géneau et al. 2012) as a surplus to documented effects by parasitoids.

Why do flowering plants affect predatory beetles and spiders?

Unlike parasitoid Hymenoptera, many of which are nectar-feeding as adults, only few ground beetles and none of the spiders utilize flowers as a food resource. This raises the question why the presence of flowers would affect their abundance and community structure. The habitat preferences of ground beetles are, at local scale, mainly linked to microclimate, i.e. moisture, temperature and light conditions (Thiele 1977). Furthermore, interspecific competition and vegetation density, which impair the mobility of some species, were identified as determinants of local species compositions (Dornieden 2005). Flower strips and companion plants most probably affect ground beetles and spiders by their impact on vegetation structure and consequent microclimatic changes. Furthermore, flower strips may promote the abundance and diversity of their (herbivorous) prey (Meek et al. 2002, Haaland et al. 2011; Bohan et al. 2011).

#### Conclusions

Apart from previously established benefits of flower strips and companion plants on parasitoids in vegetable fields, we found that such measures (particularly flower strips) clearly benefit conservation efforts in ground beetles and spiders (i.e., promoting species richness and the occurrence of rare species). Effects of habitat management measures on abundance of these predatory taxa were more equivocal, and follow-up studies will be required to evaluate how agronomically and economically relevant the pest control effects of these taxa are.

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