



**HAL**  
open science

## **In-field cover crop strips support carabid communities and shape the ecological trait repartition in maize fields**

Coralie Triquet, Anthony Roume, Alexander Wezel, Vincent Tolon, Aurélie Ferrer

### ► **To cite this version:**

Coralie Triquet, Anthony Roume, Alexander Wezel, Vincent Tolon, Aurélie Ferrer. In-field cover crop strips support carabid communities and shape the ecological trait repartition in maize fields. *Agricultural and Forest Entomology*, 2023, 25 (1), pp.152-163. 10.1111/afe.12540 . hal-03813213

**HAL Id: hal-03813213**

**<https://isara.hal.science/hal-03813213v1>**

Submitted on 22 Nov 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# In-field cover crop strips support carabid communities and shape the ecological trait repartition in maize fields

Coralie Triquet<sup>1</sup>, Anthony Roume<sup>1</sup>, Alexander Wezel<sup>1</sup>, Vincent Tolon<sup>1</sup>, Aurélie Ferrer<sup>1</sup>

<sup>1</sup>Agroecology and Environment Research Unit, Isara, 23 rue Jean Baldassini, 69364 Lyon, France

Corresponding author: Coralie Triquet, [triquet.coralie@gmail.com](mailto:triquet.coralie@gmail.com)

Original paper published in *Agricultural and Forest Entomology*, *afe.12540*, 1-12, September 2022. <https://doi.org/10.1111/afe.12540>

## Abstract

1. The enhancement of pest regulation service in crops depend for a large part on the capacity of agroecological practices to increase the presence of key species or functional traits in arthropod communities within fields.

2. We investigated the effects of undestroyed strips of winter cover crops in maize fields on carabid community composition, and on the distribution of three ecological traits: diet, wing status and body size.

3. We found that the community composition and the distribution of ecological traits in the in-field cover crop strips had commonalities with both adjacent cropped areas and field margins. Some species were recorded mostly or only in the strips, indicating that strips could support carabid species and help increase local diversity from the first year of establishment.

4. The activity-density of *Poecilus cupreus* and *Pterostichus melanarius* was higher in the cropped proximity of the strip, and the body size was influenced by the distance from the strip.

5. Our results suggest that carabid communities are shaped by the habitat type, but the influence of such agroecological infrastructures on communities of adjacent crops is minor beyond a distance of 10 meters. However, overall species abundance was increased and thus potentially provided enhanced pest regulation.

## Keywords

Carabidae, mid-field vegetation strip, winter cover crop, edge effect, ecological traits, pest regulation, conservation biological control

# 1. Introduction

Biodiversity loss has been recorded in the last years, with entomofauna being particularly endangered (Didham et al., 2020; Sánchez-Bayo and Wyckhuys, 2019; Wagner, 2020). Agricultural activities are identified as one of the main drivers of arthropod biodiversity loss (Seibold et al., 2019; Stoate et al., 2001) with the intensification of land use and landscape simplification in agricultural landscapes (Holland et al., 2016). However, the primary role of entomofauna and their associated ecosystem services provision (e.g. pollination, pest and weed regulation) for agricultural production has been widely demonstrated (Albrecht et al., 2020; Dainese et al., 2019).

Decreasing detrimental disturbances and increasing plant diversity and semi-natural habitats inside and outside the agricultural production area is an efficient approach to mitigate the loss of vulnerable arthropod species (Ekroos et al., 2016). In this respect, agri-environmental schemes have been developed in the EU policies and proposed to farmers, aiming to address this challenge and increase biodiversity and ecosystem services in agricultural landscapes (Dainese et al., 2019). Among them, different agroecological infrastructures (AEI) are targeted such as vegetation strips. Generally placed at the edge of cropped fields, they have a particular interest for multiple ecosystem services, e.g. water regulation and purification, and prevention of soil erosion. Many studies have shown the attractiveness of vegetation strips for a large range of beneficial arthropods (Campbell et al., 2019; Holland et al., 2016; Kujawa et al., 2020; Triquet et al., 2022), including pollinators when they contain flowers (Amy et al., 2018; Haaland et al., 2011). They can offer food resources, shelter (Griffiths et al., 2008; Landis et al., 2005) and overwintering habitat for ground-dwelling arthropods (Landis et al., 2000; Pywell et al., 2005), and thus are expected to deliver ecosystem services to adjacent cropping (Bianchi et al., 2013).

The effectiveness of ecosystems delivery by entomofauna from vegetation strips thus relies on the spillover of the beneficial arthropods into adjacent fields (Bianchi et al., 2006; Blitzer et al., 2012). Such spillover and the effect of AEI in general on the adjacent crops have been mainly investigated through the measurement of the abundance and richness of beneficial arthropods. Some studies showed such spillover effect (Gayer et al., 2019; Woodcock et al., 2016), but in others this could not be clearly observed (Kujawa et al., 2020; Triquet et al., 2022). Indeed, little is known about this process, and particularly about the impact of AEI on the composition and the ecological trait distribution of arthropod communities in adjacent

fields at different distances from the AEI (Boetzl et al., 2018; Gallé et al., 2020; Gayer et al., 2019; Pecheur et al., 2020). Yet, pointed out that taxonomic and functional diversity of natural enemies plays a crucial role to enhance and maintain natural pest control and weed regulation in crops (Crowder et al., 2010; Northfield et al., 2010; Rusch et al., 2015). Carabids have been particularly studied as they have a high contribution to pest and weed regulation in arable crops (Bohan et al., 2011; Kulkarni et al., 2015). This contribution is driven by their feeding characteristics and dispersal ability, of which ecological traits such as body size, diet and wing status give an indication (Bertrand et al., 2016; Emmerson and Raffaelli, 2004). For example, smaller species with a higher dispersal ability seem more capable to penetrate into cropped areas and consume pests in the centre of fields, while larger predatory carabids are able to consume a higher amount of pests and bigger prey, but may also feed on smaller predators resulting in intra-guild predation (Rusch et al., 2015; Williams et al., 2010). Thus, the effect of AEI on carabids community composition and more particular on their traits repartition will have an impact on the ecosystem services delivered in the adjacent crop, and with this on the functionality of the AEI.

Beyond the lack of knowledge about their functionality, vegetation strips and wildflower strips remain poorly adopted in France because of technical and economic constraints such as the additional working time and costs needed for implementation and maintenance (Uyttenbroeck et al., 2016). Agroecological practices such as integration of AEI, if they are based on common practices and easy to implement in existing cropping systems, can be easily adopted by farmers (Pearsons and Tooker, 2017; Pe'er et al., 2017). For example, maintaining a strip of a previous winter cover crop in the middle of a spring crop has been recently documented and showed potential for ground-dwelling arthropods support and the enhancement of predatory activities in maize fields (Triquet et al., 2022). However, the effects of such mid-field cover crop strips on the composition of carabid communities and the distribution of their ecological traits remain to be explored. In this study, we tested these effects for the first year of implementation of mid-field cover crop strips, and compared the results with the community composition and distribution of ecological traits in permanent grassy field margins. We hypothesized that the strip, by providing an uncropped habitat in the middle of the field, could support a carabid community and traits distribution patterns reflecting a mix between the species from the surrounding cropped area and the permanent field margin. We also hypothesized an edge effect around the strip within the cropped area due to spillover or attractiveness of some species. We therefore predicted that:

1. The carabid community in the preserved cover crop strip is composed of a mix of some species from the cropped area and the permanent field margin, with activity-densities in the same order of magnitude;
2. In the cover crop strip, the distribution of ecological traits of carabids reflects the combination of the ecological traits of the field margin and of the cropped area;
3. The distribution of ecological traits in the cover crop strip evolves during the season towards a margin-like ecological trait distribution (because the strip remains longer undisturbed and vegetation characteristics evolve more towards those of perennial herbaceous habitats);
4. In the cropped area, distance from the strip influences the carabid community composition and the spatial distribution of their ecological traits, in particular the trait distribution in the close proximity to the cover crop strip will have some common points with the cover crop strip, due to spillover or aggregation of some species.

## 2. Materials and methods

### 2.1. Experimental design

The field trials took place on 12 conventionally managed fields, on commercial farms located in the region Auvergne-Rhône-Alpes (France), in the Rhône, Ain, Isère and Drôme districts. The climate in the study area is temperate semi-continental with Mediterranean influence during summer. The fields were located in landscapes dominated by conventional specialized arable cropping systems and mixed crop livestock systems. Field experiments were conducted on twelve different maize fields, five in 2019 and seven in 2020, which size ranging from 1.1 to 5.7 ha. The mean distance between strips was 46 km (from 0.2 to 95 km). No insecticides were applied on the fields during the experiment.

In the middle of each field, a strip of 5 m width and 110 m length of the previous winter cover crop sown in autumn the year before was preserved, and remained uncultivated and not mowed during the whole maize cultivation cycle, from sowing in April-May to harvest in October. This strip was connected to a grassy field margin (Fig. 1). The vegetation of the strip was composed of a commercial cover crop mixture sown with 37.5 % ray grass (*Lolium multiflorum*, in 2019) and/or rye (*Secale cereal*, in 2020), 35 % Crimson clover (*Trifolium*

*incarnatum*, in 2019) or Alexandria clover (*Trifolium alexandrinum*, in 2020), 15 % Turnip Rape (*Brassica rapa* subsp. *Oleifera*), and 12.5 % Phacelia (*Phacelia tanacetifolia*). The changes in the Poaceae and clover species composition between 2019 and 2020 was necessary to adapt the practice to farmers' constraints and expectations.

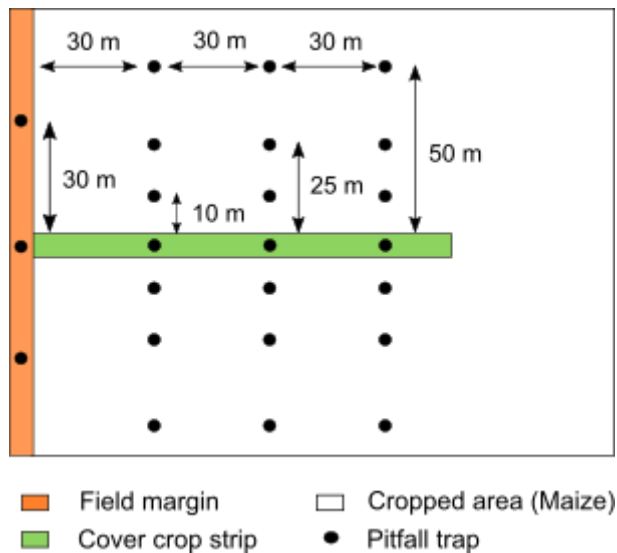


Figure 1. Sampling design of the field experiment. Each black dot represents a sampling point where a pitfall trap was installed.

## 2.2. Arthropod sampling and ecological traits

Carabids were monitored using pitfall traps (10 cm opening diameter, 15 cm depth, filled with of a 30% propylene glycol solution with a drop of detergent) protected from rain by a plastic roof (Woodcock, 2005). The pitfall traps were placed in the cover crop strip, in the connected grassy field margin and in the cultivated area at 10 m, 25 m and 50 m from the strip (defined as the five studied “zones” in the article). Traps were placed in and around the strip along three parallel transects as shown in Figure 1. There were in total five sampling periods: before winter cover crop ploughing (initial stage, IS), at the maize seeding (S), at the 4 leaves (4L) and 8 leaves (8L) stages of maize development, and after maize harvest (final stage before the cover crop strip destruction, FS). Pitfall traps were active during 48 hours for each sampling period.

Carabids were identified at the species level. We selected three ecological traits of carabids linked with their feeding and dispersal characteristics: diet (predatory, polyphagous, phytophagous), wing status (macropterous, dimorphic, wingless; giving indication of dispersal ability), body size (size classes: class A  $\leq 5$  mm, class B  $\leq 10$  mm, class C  $\leq 15$

mm, class D  $\leq$  25 mm and class E  $>$  25 mm). These ecological traits were determined according to the available literature (Jeannel, 1942, 1941; Lindroth, C.H., 1988; Ribera et al., 2001).

### ***2.3. Data analysis***

We first explored graphically the activity-density variations of each species through sampling periods (IS, S, 4L, 8L and FS) in order to identify major changes in community compositions in the five sampled zones (margin, strip, 10 m, 25 m, 50 m). We conducted compositional dissimilarity analyses based on Bray-Curtis distances to assess the impact of site, sampling period and zone on the differences in community compositions. For this, analysis of similarity (ANOSIM) and Permutational analysis of variance (PERMANOVA) were conducted with 9999 permutations, respectively using `anosim` and `adonis2` functions of the R `vegan` package (Faith et al., 1987; Warton et al., 2012). We selected the R value of ANOSIM analysis as an indicator of the dissimilarity between groups (from 0 to 1, 1 being the highest dissimilarity, R compares the mean of ranked dissimilarities between groups to the mean of ranked dissimilarities within groups). We used the  $R^2$  values from the PERMANOVA models as quantification of the magnitude of change in communities among groups (explained by site, sampling period or zone). In addition, a pairwise PERMANOVA (multilevel comparison) analysis was conducted for the variable “zone” (Martinez Arbizu, 2020).

To detect the potential species significantly associated to groups of sites or zones, we computed indicator species analyses by calculating the Point Biserial correlation coefficient (De Cáceres and Legendre, 2009) with 9999 permutations, with the function `multipatt` from the R package `indicspecies` (De Cáceres et al., 2010). Each analysis was carried out using data from Initial Stage (IS) to Final Stage (FS), and for comparison was repeated using only data from the three sampling periods during maize development (S, 4L, 8L) which are close in time (from April to beginning of July) and avoid the major changes occurring after IS and before FS: ploughing and maize harvest. We also used this method to check if the main species were not associated with only one site.

Analyses looking at ecological traits instead of species composition of community were then performed to explore a potential similar distribution and evolution in time of ecological traits in the different zones among sites. In order to assess the relations between environmental variables (sampling period and zone) and ecological traits of carabids, co-inertia RLQ

analysis (Dray et al., 2014) was conducted with the ade4 R package. A trajectory scatter plot was used for the visualization of the spatio-temporal evolution of traits distribution in carabid community. Data used for the RLQ analysis were pooled by zones, by sampling periods, and by sites. A Monte Carlo randtest (9999 permutations, function randtest of ade4 package) was computed to test the overall association between ecological traits and environmental variables. The fourth corner method was used to determine pairwise significant associations between ecological traits and environmental variables (Dray et al., 2014).

All statistical analyses were conducted using R, version 4.1.0 (R Development Core Team, 2021).

### 3. Results

A total of 4162 carabids were sampled in the 1352 pitfall traps taken into account all sampling periods. In total, 76 different carabid species were collected. The three most abundant species were *Anchomenus dorsalis*, *Poecilus cupreus*, and *Pterosticus melanarius* (see complete list of carabid species in Supporting Information A). From the delimitation of the strip (i.e. from the “S” sampling period), the strip harboured 35% *A. dorsalis* of total species abundance, 13% *P. cupreus*, and 5% *P. melanarius*, and in the cropped area there were 37% *P. melanarius*, 20% *P. cupreus* and 10% *A. dorsalis*. In the grassy margin, we counted 23% of *A. dorsalis*, 9% of *P. melanarius* and 2% of *P. cupreus*.

#### 3.1. Community species composition

The carabid community composition was significantly different between sites ( $p < 0.001$ ), and the effect of site was stronger than the effect of zone or sampling period ( $R = 0.269$  from IS to FS,  $R = 0.340$  from S to 8L, Table 1). PERMANOVA analysis showed that the effect of the interaction between site and zone and between site and sampling period were highly significant ( $p < 0.001$ , Table 1), indicating that the variation of community composition between zones and periods differed among sites, taking into account the full sampling period or only the main maize growing period. The  $R^2$  outcomes of the PERMANOVA indicated that the site explained approximately 21% of the community composition of carabids, and zone and sampling period together (with their interaction) explained only 6% of the variations in the community (Table 1).



Table 1. Outcomes of ANOSIM, PERMANOVA and pair-wise PERMANOVA analyses on carabids community composition, with all sampling periods (IS to FS) or grouped for maize growth period (S to 8L). R value of ANOSIM analysis compares the mean of ranked dissimilarities between groups to the mean of ranked dissimilarities within groups. A low R value indicates closer community composition between groups. Significant results are in bold ( $p$ -value $<0.05$ ).

	Full period (from IS to FS)			During maize growth (from S to 4L)				
ANOSIM								
Site	R: 0.269 p-value: <b>1e-04</b>			R: 0.340 p-value: <b>1e-04</b>				
Period	R: 0.098 p-value: <b>1e-04</b>			R: 0.041 p-value: <b>1e-04</b>				
Zone	R: 0.060 p-value: <b>1e-04</b>			R: 0.082 p-value: <b>1e-04</b>				
PERMANOVA								
	df	R <sup>2</sup>	Pr(>F)	df	R <sup>2</sup>	Pr(>F)		
Site	11	0.173	<b>1e-04</b>	11	0.214	<b>1e-04</b>		
Period	4	0.049	<b>1e-04</b>	2	0.025	<b>1e-04</b>		
Zone	4	0.032	<b>1e-04</b>	4	0.042	<b>1e-04</b>		
Site:Period	41	0.124	<b>1e-04</b>	22	0.087	<b>1e-04</b>		
Site:Zone	44	0.075	<b>1e-04</b>	44	0.096	<b>1e-04</b>		
Period:Zone	16	0.024	<b>1e-04</b>	8	0.013	<b>2e-04</b>		
<i>residual</i>	686	0.524		537	0.524			
<i>total</i>	806	1		628	1			
Pairwise PERMANOVA on Zone								
	R <sup>2</sup>		p-value		R <sup>2</sup>		p-value	
margin vs 0m	0.0103		<b>0.04</b>		0.021		<b>0.01</b>	
margin vs 10m	0.0401		<b>0.01</b>		0.044		<b>0.01</b>	
margin vs 25m	0.0406		<b>0.01</b>		0.050		<b>0.01</b>	
margin vs 50m	0.0279		<b>0.01</b>		0.028		<b>0.01</b>	
0m vs 10m	0.0359		<b>0.01</b>		0.053		<b>0.01</b>	
0m vs 25m	0.0378		<b>0.01</b>		0.060		<b>0.01</b>	
0m vs 50m	0.0295		<b>0.01</b>		0.045		<b>0.01</b>	
10m vs 25m	0.0014		1.00		0.001		1.00	
10m vs 50m	0.0047		0.37		0.006		0.38	
25m vs 50m	0.0039		0.81		0.007		0.16	

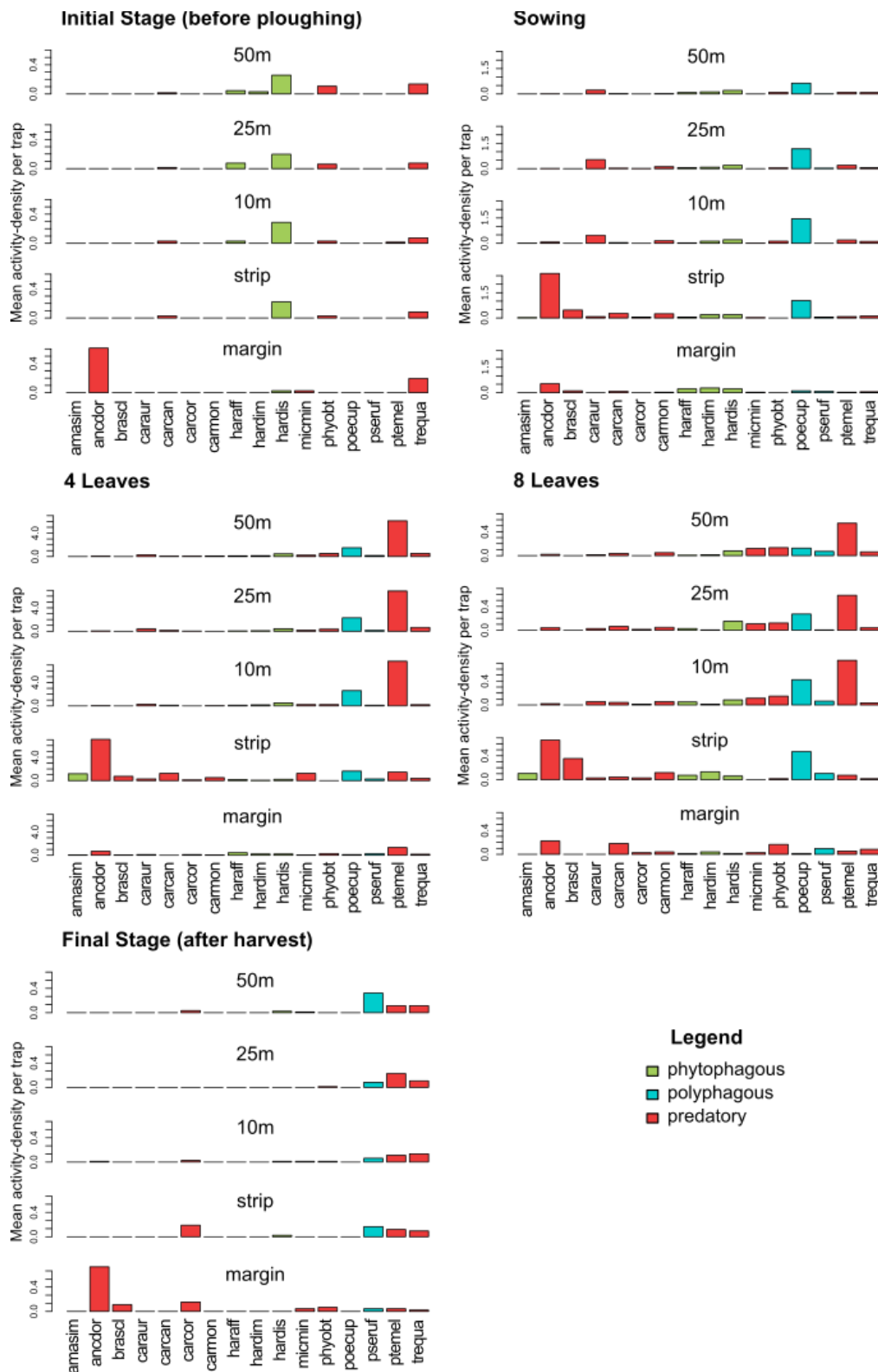


Figure 2. Mean activity-density per trap of the 15 main species (> 50 individuals) and *Amara similata* in the 5 zones, for each sampling period. Red bars represent predatory species, blue bars polyphagous species and green bars phytophagous species. Code names correspondence is available in Supporting Information A.

At the beginning of the experiment (IS), we could observe two distinct carabid communities: one in the margin and the other in the winter cover crop. Then, from the S sampling period, three different communities can be detected: in the margin, in the crop, and in the strip (the later with a mix of species present in the margin and in cropped area communities), which changed at 4L with the addition of carabid species (Fig. 2). The community composition was significantly different among zones ( $p < 0.001$ ) and among sampling periods ( $p < 0.001$ , Table 1). The PERMANOVA analysis validated these significant effects ( $p < 0.001$  for both zone and period) and indicated a significant interactive effect between zone and sampling period ( $p < 0.001$  from IS to FS,  $p < 0.001$  from S to 8L, Table 1), highlighting that the community composition among zones changed differently through time, even during the main maize growth period (see Supporting Information C showing beta diversity). The pairwise multilevel comparison showed that the community was not significantly different between the 3 sampling zones within the crop (10 m, 25 m, 50 m; Table 1).

Looking at indicator species analyses by groups of zones, *A. dorsalis* was significantly associated with the strip zone, ( $p < 0.001$ , Supporting Information B). It was indeed observed from IS sampling period in the margin, and then colonized during S also the strip where it became the most abundant until maize harvest (Fig. 2). *P. cupreus* was observed from S to 8L in the strip and in the cropped area, and was the most frequently found at 10 m from the strip. We further could observe a gradient of decreasing activity-density of *P. cupreus* from 10 m to 50 m from the strip in the cropped area (Fig. 2). This was validated by the indicator species analysis showing that *P. cupreus* was significantly associated with the “0 m + 10 m + 25 m” zone group (corresponding to strip and the closest part of the cropped area from the strip) ( $p < 0.001$ , Supporting Information B). *P. melanarius* was significantly associated with the “10 m + 25 m + 50 m” zone group (corresponding to the cropped area,  $p < 0.001$  from IS to FS and  $p < 0.001$  from S to 8L, Supporting Information B), and was observed from S to FS in the strip and the cropped area, with an important peak at 4L in the cropped area. As for *P. cupreus*, it was the most abundant at 10 m from the strip and with a gradient of decreasing activity-density from 10 m to 50 m from the strip (Fig. 2). Finally, the genera *Harpalus* was sampled in all three zones but some species were only found in the strip and in the margin. Species from the genera *Carabus* were observed from S in the margin, and later mostly found in the strip at 4L sampling period. Other species such as *Brachinus scolpeta* and *Amara similata* were recorded mainly in the strip (Fig. 2, see Supporting Information A for the

composition of the community), which were significantly associated only to the strip or the grassy margin (Supporting Information B).

### 3.2. Ecological traits composition

The carabid communities were dominated by strictly predatory species in every habitat (68% in the field margin, 72% in the strip, and 65% in the crop, see Figure 3). Cumulating the sampling periods from S to FS, the ecological trait distribution in the strip was more similar to the cropped area regarding the diet trait, but more similar to the margin regarding the morphological traits (wing status and body size, Fig. 3).

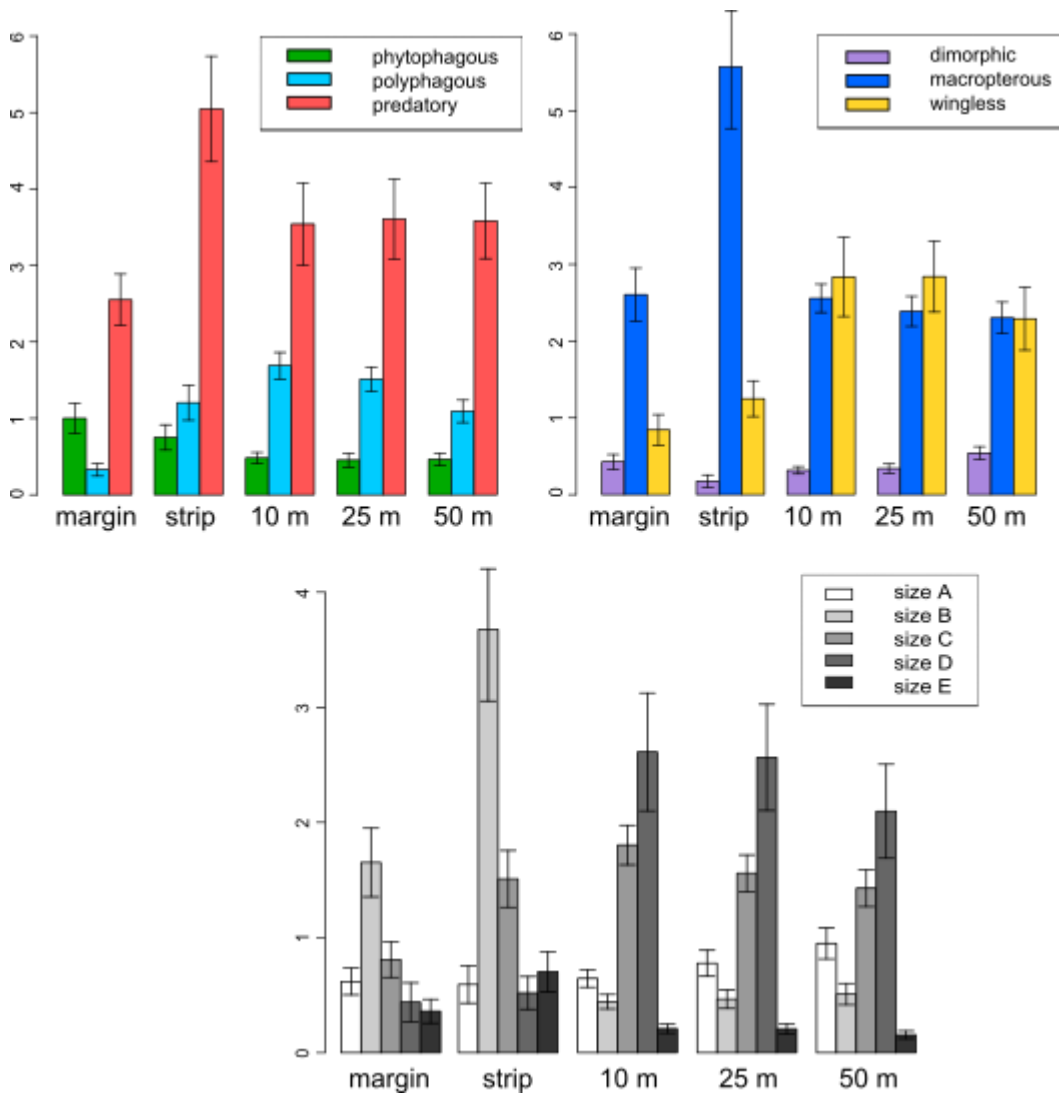


Figure 3. Mean activity-density by trap of carabids, grouped by ecological traits (diet, body size, wing status) in the five zones (strip, 10 m, 25 m, 50 m, margin). The activity-densities take into account all sampling periods with the preserved strip (from Sowing to Final Stage) and all experimental sites. Standard deviations are shown.

The RLQ analysis showed a significant overall association between ecological traits composition and environmental variables (Monte Carlo randtest,  $p < 0.05$ ). The two first RLQ axes explained 74% of the total inertia (47% and 27%, respectively).

At the initial stage (IS), the trait distribution was quite similar in every zone (top right part of scatter plot in Fig. 4a), with a specific presence of small dimorphic and phytophagous species (right part of scatter plot in Fig. 4b). This period was also characterised by a lower abundance of the medium sized (size C) and polyphagous species. At the beginning of maize growth (S and 4L), a shift appeared in the cropped area (10 m, 25 m and 50 m) that hosted more medium sized and polyphagous species (bottom left part of Fig. 4a, b). This pattern also affected to a lower extent the strip and the margin (bottom right part of Fig. 4a, b). From the 8L sampling period and until the harvest (FS), the 25 m and 50 m zones were clearly occupied by large (class D) and wingless species (top left part of Fig. 4a, b). The trait distribution at 10 m did not change at 8L but followed the same shift toward large and wingless species at FS. From 8L, the margin remained associated to small and dimorphic species until the end of the harvest (FS), while the strip included more medium sized and polyphagous species than before (bottom left part of Fig. 4a, b, trait distribution close to what was observed during maize growth in the cropped area).

Fourth corner analysis applied to the carabids data showed a significant negative association between the body size class B and the zones at 25 m and 50 m from the strip in the crop ( $p = 0.0385$ , Fig. 5). This outcome confirmed the rapid shift toward large species of the farthest cropped area from the strip observed in the Figure 4, but the relatively small data set and the correction applied on p-values due to numerous tests probably explained a lack of significant results.

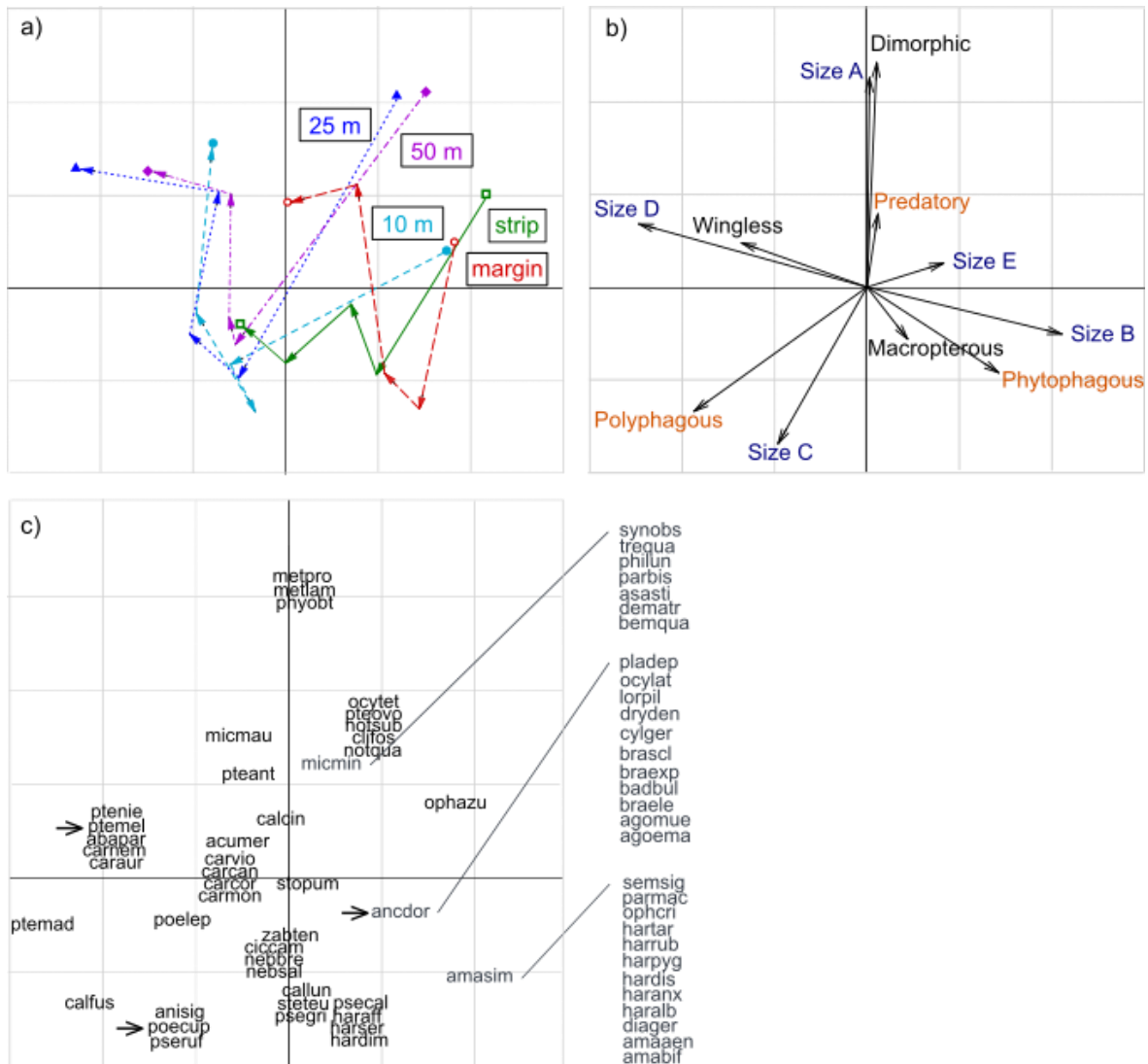


Figure 4. Ordination plot of the RLQ co-inertia analysis on carabids community, with a) trajectory scatter plot of each zone through time (IS, S, 4L, 8L and FS), b) ecological traits of carabids, and c) carabid species (code names correspondence see Supporting Information A). Note that by definition the RLQ analysis often highlights the traits that highly specific to a habitat or period (e.g. dimorphic, phytophagous or polyphagous), but the widespread traits appear to be non-discriminant (e.g. predatory, wingless or macropterous).

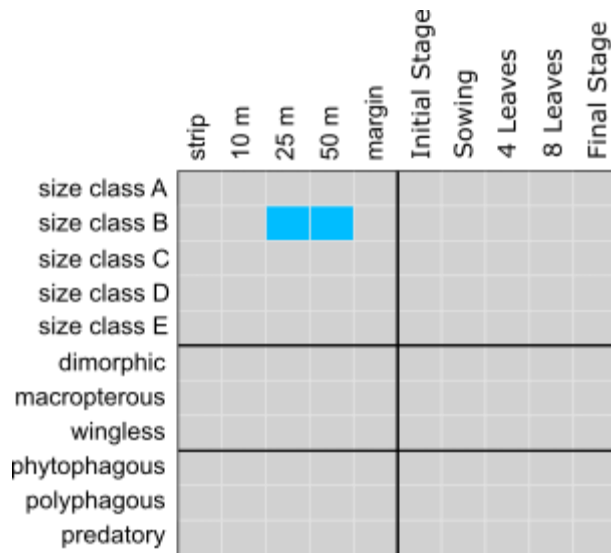


Figure 5. Results of fourth-corner statistics for the pairwise associations between environmental variables and carabids ecological traits. Coloured squares represent significant associations (red positive; blue negative) at the  $p < 0.05$  level.

## 4. Discussion

### 4.1. Differences in communities of the field margin, the strip and the cropped area

The field margin, the cover crop strip and the cropped area had a significantly different community composition. This is consistent with previous studies showing that community species composition is different between uncropped and cropped areas (Boetzl et al., 2018; Pecheur et al., 2020), and between perennial field margins and recently established vegetation strips (Maas et al., 2021).

The differences of community composition between zones were significantly impacted by the period effect, even during the maize growth, showing the rapid evolution of carabid communities in the agroecosystem along with seasons and human interventions. The initial carabid community of the winter cover crop has been disturbed by the ploughing and sowing in the cropped area, and consequently showing a different community than in the undestroyed cover crop strip. The strip community did not comprise only a mix of the species of the field margin and the cropped area, as we predicted, but some species were also found mostly (e.g. *Brachinus scolpeta*, *Amara similata*, *Carabus cancellatus*) or only (e.g. *Syntomus obscuroguttatus*) in the strip. This observation is coherent with some ecological traits of these species. Indeed, *Amara spp.* are known to be mostly found in non-cropped habitats where the soil is less compacted and easier to dig galleries in (Pywell et al., 2005;

Thomas et al., 2001). *B. sclopeta* is indicated to have an affinity with rapeseed (Marrec et al., 2015), and its presence in the strips could potentially be explained by the plant composition of the cover crop, which includes turnip rape being a plant closely related to rapeseed. These different outcomes show that implementing such vegetation strips can not only support carabid species within fields from the first year of establishment, but also, by hosting a community different from a crop area or a perennial field margin, can support local diversity or species richness. In the same way, the singular characteristics of the margins in term of carabid community confirm the absolute importance of protecting the perennial field margins to preserve species that are dependent on stable habitats and their associated ecosystem functions (Maas et al., 2021).

The effect of habitat type on carabid communities has also been observed on the distribution of ecological traits. First of all, we observed that the overall ecological trait distribution in the strip had similarities with both the margin and the cropped area, as we predicted. At the initial stage, the trait distribution was quite similar in the field margin and the cover crop field, with mainly very small species (less than 5 mm), and then this distribution started to have a different trajectory. During the maize growth (i.e. from S to 8L corresponding to the period from April to July), we recorded the highest activity-density of carabids, with polyphagous, wingless and large species (sized between 10 and 25 mm) more present in the cropped area. Likewise, previous studies have shown a higher proportion of polyphagous and more mobile species (i.e. larger and/or winged carabids, Homburg et al., 2013) in cropped fields than in uncropped habitats (Boetzel et al., 2018; Gayer et al., 2019), probably linked with their higher ability to live in more frequently disturbed habitats (Cardarelli and Bogliani, 2014) and with particular species known to breed in field centre areas such as *P. melanarius* (Holland et al., 2009; Jowett et al., 2019). During the same period, the cover crop strip and the field margin hosted more phytophagous and macropterous species. They hosted also more species of two distinct groups of size: small carabids (5 to 10 mm), and very large carabids (more than 25 mm) corresponding to species of the genera *Carabus*, mostly found in the cover crop strip. These results are partly consistent with previous studies that reported a higher proportion of phytophagous and smaller carabids in vegetation strips or field margins than in crops (Baulechner et al., 2019; Birkhofer et al., 2014; Gallé et al., 2020). The higher density and richness of plants in vegetation strips and grassy margins provide a more abundant and diverse food resource for phytophagous species and favour their presence (Kulkarni et al., 2015). The strip had a tall vegetation with large flowering plants (e.g.



phacelia, turnip rape), which was more heterogeneous but less dense than the vegetation of the field margin (mainly composed of grasses). Consequently, the strip probably provided a more suitable habitat for the largest carabids (*Carabus spp.*) which cannot easily disperse in a dense vegetation (Ng et al., 2018; Rouabah et al., 2015).

#### ***4.2. Effect of the distance from the strip into the adjacent crop***

The two dominant species in the field (*P. cupreus* and *P. melanarius*) were the most abundant in the cropped area at 10 m from the strip, but not in the strip, validating our fourth prediction concerning species composition. This affinity with the proximity of the strip could be interpreted both as a spillover effect from the strip (Holland et al., 2009; Schellhorn et al., 2014), or as a phenomenon of aggregation towards the strip (Bianchi et al., 2010). However, the latter explanation fits better with our results as the activity-density of *P. cupreus* and *P. melanarius* was not at a high level in the strip. Therefore, the strip cannot be considered as a preferred habitat acting as a source habitat generating a spillover effect into the adjacent crop for these two species (Bianchi et al., 2013; Blitzer et al., 2012; Jowett et al., 2019). The cover crop strip comprised several flowering plant species, which attracted many arthropods, including flying insects which can be prey for many ground-dwelling predatory arthropods (González-Chang et al., 2019; Holland et al., 2016). Consequently, a high amount of prey in the proximity of the strip could have attracted these entomophagous carabids (Anjum-Zubair et al., 2010), potentially leading, in turn, to an increased pest regulation in the zone (Triquet et al., 2022; Woodcock et al., 2016). However, unobserved but possible drawbacks of the attractiveness of the strip for many arthropods could be the increase of flying crop pests, and the concentration of local carabids in the strips, hence reducing their abundance in the cropped area and creating an ecological trap when the strip is destroyed after maize harvest (Ganser et al., 2019).

Regarding the distribution of ecological traits, the body size class was the most affected by the distance from the strip. During the maize growth, small carabids (between 5 mm and 10 mm) were less present in the farthest zones from the strip in the cropped area. Thus, in the vicinity of the strip, we recorded more small carabids such as these associated with the strip, indicating a possible spillover effect of some species from the strip (Schellhorn et al., 2014) in search for food resources (Tschardt et al., 2007). This effect of distance from the strip on carabids size validates our fourth prediction concerning ecological traits, and it is

consistent with previous studies showing that the size of carabids increased with the distance of the field margin or an AEI (Boetzel et al., 2018; Gallé et al., 2020; Pecheur et al., 2020).

#### ***4.3. Influence of the experimental site and possible links with landscape context***

The species composition of carabids community significantly differed among experimental sites, and the effect of the site was stronger than the effect of the zone or the sampling period. In this context, the analysis of the communities through ecological traits allowed us to detect other relevant trends in the evolution of carabid communities in different habitats, beyond species identity. We found a distinct overall distribution of ecological traits of carabids in the three habitats, reflecting the capacity of different habitat to provide different resources more fitting with the needs and abilities of different carabids species to use these habitats (e.g. more phytophagous species where more weed seeds are available, smaller species where the density of vegetation is high). However, we did not find significant pairwise associations between ecological traits and zone or sampling period (except for size class B and 25 m + 50 m zones). This outcome prompts to take precautions in generalizing our observations.

Indeed, the carabids communities are known to be strongly influenced by the local characteristics (e.g. in-field agricultural interventions) and the landscape compositional and configurational heterogeneity. At the field scale, the crop type (Aguilera et al., 2020; Labruyere et al., 2016; Rusch et al., 2014), the cropping management type (e.g. organic vs. conventional), cropping practices (Gallé et al., 2020, 2019; Gayer et al., 2019), and the local soil and climate conditions can modify local species pool and shape the traits distribution in carabids communities. In our case, cropping management and practices were generally similar, although farmers adapted the timing and intensity of interventions to their particular constraints.

At the landscape scale, the effect on arthropods regarding the proportion of semi-natural habitats (including field margins) and their spatial configuration has been widely studied (Gallé et al., 2020, 2019; Duflot et al., 2014). A more heterogeneous landscape, with more semi-natural habitats, smaller cultivated fields and a higher length of field margins is known to increase activity-density, species richness and functional diversity of carabids, (Badenhausser et al., 2020; Landis et al., 2005; Martin et al., 2019; Sirami et al., 2019).

## Conclusion

Our study provides new insights into the species and ecological trait distribution in carabid communities within three different habitat types in agroecosystems: preserved cover crop strips, grassy margins and cropped maize field. Our results indicate that preserved cover crop strips in maize fields can help enhance the carabid diversity at least at field level, from the first year of establishment, but probably also in the larger agricultural landscape. This highlights the good dispersal capacity and adaptability of carabid communities in agroecosystems. The cover crop strips had an influence on the community of the adjacent cropped area, with more *P. melanarius* and *P. cupreus*, and more small carabids, in the proximity to the strip. However, spillover effects in our study were limited, an increased number of cover crop strip implementation in space (farm or landscape scale) and time (over years) could lead to a higher occurrence of some carabids and greater resilience of the carabid community in cultivated landscapes. Moreover, we found major predatory species that were associated with margins, but they did not always occur densely within them, probably because of the limited size of the margins. This might have limited also the spillover effect into crop areas. In this respect, it needs to be taken into account that the effects of such strips on carabids community composition and structure in agroecosystems can vary among cultivated fields or territories (Concepción et al., 2012; Karp et al., 2018), and thus having varying spillover and potential resilience effects. Thus further research should investigate the influence of the interactions between local and landscape characteristics on the efficiency of agroecological practices regarding ecosystem functions and services. This could be of prime importance for the development of innovative agroecological practices, which are also realistic for implementation on farmers' fields, and understand the conditions of success for an increase of pest and weed seed control in the cropping systems.

### Authors' contributions

C.T, A.F., A.R., and A.W. designed the study; C.T and A.R. conducted data collection; A.R. identified carabids; C.T. analysed data with the support of V.T.; C.T. wrote the first draft of the manuscript. All authors revised the manuscript and gave final approval for publication.

## Acknowledgments

We thank Lucile Toniutti, Thomas Lhuillery and Manon Bouvier for their technical assistance, and Sandrine Leblond for her help and support in the design of the study. We would like to thank the farmers of the study site for allowing us to conduct our experiment on their fields. This work was funded by Isara and by BASF France division Agro.

## Declaration of Competing Interest

The authors declare that they have no conflict of interest.

## Supporting information

Additional supporting information may be found online in the Supporting Information section.

## Data Availability Statement

Data available via Zenodo at [DOI] (Triquet et al., 2022).

## References

- Aguilera, G., Roslin, T., Miller, K., Tamburini, G., Birkhofer, K., Caballero-Lopez, B., Lindström, S.A.-M., Öckinger, E., Rundlöf, M., Rusch, A., Smith, H.G., Bommarco, R., 2020. Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats. *J. Appl. Ecol.* 57, 2170–2179. <https://doi.org/10.1111/1365-2664.13712>
- Albrecht, M., Kleijn, D., Williams, N.M., Tschumi, M., Blaauw, B.R., Bommarco, R., Campbell, A.J., Dainese, M., Drummond, F.A., Entling, M.H., Ganser, D., Arjen de Groot, G., Goulson, D., Grab, H., Hamilton, H., Herzog, F., Isaacs, R., Jacot, K., Jeanneret, P., Jonsson, M., Knop, E., Kremen, C., Landis, D.A., Loeb, G.M., Marini, L., McKerchar, M., Morandin, L., Pfister, S.C., Potts, S.G., Rundlöf, M., Sardiñas, H., Sciligo, A., Thies, C., Tscharnke, T., Venturini, E., Veromann, E., Vollhardt, I.M.G., Wäckers, F., Ward, K., Wilby, A., Woltz, M., Wratten, S., Sutter, L., 2020. The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis. *Ecol. Lett.* 23, 1488–1498. <https://doi.org/10.1111/ele.13576>
- Amy, C., Noël, G., Hatt, S., Uyttenbroeck, R., Van de Meutter, F., Genoud, D., Francis, F., 2018. Flower Strips in Wheat Intercropping System: Effect on Pollinator Abundance and Diversity in Belgium. *Insects* 9, 114. <https://doi.org/10.3390/insects9030114>
- Anjum-Zubair, M., Schmidt-Entling, M.H., Querner, P., Frank, T., 2010. Influence of within-field position and adjoining habitat on carabid beetle assemblages in winter

- wheat. *Agric. For. Entomol.* no-no. <https://doi.org/10.1111/j.1461-9563.2010.00479.x>
- Badenhausser, I., Gross, N., Mornet, V., Roncoroni, M., Saintilan, A., Rusch, A., 2020. Increasing amount and quality of green infrastructures at different scales promotes biological control in agricultural landscapes. *Agric. Ecosyst. Environ.* 290, 106735. <https://doi.org/10.1016/j.agee.2019.106735>
- Baulechner, D., Diekötter, T., Wolters, V., Jauker, F., 2019. Converting arable land into flowering fields changes functional and phylogenetic community structure in ground beetles. *Biol. Conserv.* 231, 51–58. <https://doi.org/10.1016/j.biocon.2019.01.005>
- Bertrand, C., Burel, F., Baudry, J., 2016. Spatial and temporal heterogeneity of the crop mosaic influences carabid beetles in agricultural landscapes. *Landsc. Ecol.* 31, 451–466. <https://doi.org/10.1007/s10980-015-0259-4>
- Bianchi, F.J.J.A., Booij, C.J.H., Tschardtke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc. R. Soc. B Biol. Sci.* 273, 1715–1727. <https://doi.org/10.1098/rspb.2006.3530>
- Bianchi, F.J.J.A., Schellhorn, N.A., Buckley, Y.M., Possingham, H.P., 2010. Spatial variability in ecosystem services: simple rules for predator-mediated pest suppression. *Ecol. Appl.* 20, 2322–2333. <https://doi.org/10.1890/09-1278.1>
- Bianchi, F.J.J.A., Schellhorn, N.A., Cunningham, S.A., 2013. Habitat functionality for the ecosystem service of pest control: reproduction and feeding sites of pests and natural enemies. *Agric. For. Entomol.* 15, 12–23. <https://doi.org/10.1111/j.1461-9563.2012.00586.x>
- Birkhofer, K., Wolters, V., Diekötter, T., 2014. Grassy margins along organically managed cereal fields foster trait diversity and taxonomic distinctness of arthropod communities. *Insect Conserv. Divers.* 7, 274–287. <https://doi.org/10.1111/icad.12051>
- Blitzer, E.J., Dormann, C.F., Holzschuh, A., Klein, A.-M., Rand, T.A., Tschardtke, T., 2012. Spillover of functionally important organisms between managed and natural habitats. *Agric. Ecosyst. Environ.* 146, 34–43. <https://doi.org/10.1016/j.agee.2011.09.005>
- Boetzl, F.A., Krimmer, E., Krauss, J., Steffan-Dewenter, I., 2018. Agri-environmental schemes promote ground-dwelling predators in adjacent oilseed rape fields: Diversity, species traits and distance-decay functions. *J. Appl. Ecol.* 56, 10–20. <https://doi.org/10.1111/1365-2664.13162>
- Bohan, D.A., Boursault, A., Brooks, D.R., Petit, S., 2011. National-scale regulation of the weed seedbank by carabid predators: Carabid seed predation. *J. Appl. Ecol.* 48, 888–898. <https://doi.org/10.1111/j.1365-2664.2011.02008.x>
- Campbell, J.W., Kimmel, C.B., Grodsky, S.M., Smithers, C., Daniels, J.C., Ellis, J.D., 2019. Wildflower plantings harbor increased arthropod richness and abundance within agricultural areas in Florida ( USA ). *Ecosphere* 10. <https://doi.org/10.1002/ecs2.2890>

- Cardarelli, E., Bogliani, G., 2014. Effects of grass management intensity on ground beetle assemblages in rice field banks. *Agric. Ecosyst. Environ.* 195, 120–126. <https://doi.org/10.1016/j.agee.2014.05.004>
- Concepción, E.D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E.J.P., Tschardtke, T., Verhulst, J., 2012. Interactive effects of landscape context constrain the effectiveness of local agri-environmental management: Landscape constrains the effectiveness of local management. *J. Appl. Ecol.* no-no. <https://doi.org/10.1111/j.1365-2664.2012.02131.x>
- Crowder, D.W., Northfield, T.D., Strand, M.R., Snyder, W.E., 2010. Organic agriculture promotes evenness and natural pest control. *Nature* 466, 109–112. <https://doi.org/10.1038/nature09183>
- Dainese, M., Martin, E.A., Aizen, M.A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L.G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L.A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D.S., Kennedy, C.M., Kleijn, D., Kremen, C., Landis, D.A., Letourneau, D.K., Marini, L., Poveda, K., Rader, R., Smith, H.G., Tschardtke, T., Andersson, G.K.S., Badenhausser, I., Baensch, S., Bezerra, A.D.M., Caballero-Lopez, B., Cavigliasso, P., Classen, A., Cusser, S., Dudenhöffer, J.H., Ekroos, J., Fijen, T., Franck, P., Freitas, B.M., Garratt, M.P.D., Gratton, C., Hipólito, J., Holzschuh, A., Hunt, L., Iverson, A.L., Jha, S., Keasar, T., Kim, T.N., Kishinevsky, M., Klatt, B.K., Klein, A.-M., Krewenka, K.M., Krishnan, S., Larsen, A.E., Lavigne, C., Liere, H., Maas, B., Mallinger, R.E., Pachon, E.M., Martínez-Salinas, A., Meehan, T.D., Mitchell, M.G.E., Molina, G.A.R., Nesper, M., Nilsson, L., O'Rourke, M.E., Peters, M.K., Ple, M., Ramos, D. de L., Rosenheim, J.A., Rundlöf, M., Rusch, A., Sáez, A., Scheper, J., Schleuning, M., Schmack, J.M., Sciligo, A.R., Seymour, C., Stanley, D.A., Stewart, R., Stout, J.C., Sutter, L., Takada, M.B., Taki, H., Tamburini, G., Tschumi, M., Viana, B.F., Westphal, C., Willcox, B.K., Wratten, S.D., Yoshioka, A., Zaragoza-Trello, C., Zhang, W., Zou, Y., Steffan-Dewenter, I., 2019. A global synthesis reveals biodiversity-mediated benefits for crop production. *Sci. Adv.* 5, 14. <https://doi.org/10.1126/sciadv.aax0121>
- De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* 90, 3566–3574. <https://doi.org/10.1890/08-1823.1>
- De Cáceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. *Oikos* 119, 1674–1684. <https://doi.org/10.1111/j.1600-0706.2010.18334.x>
- Didham, R.K., Basset, Y., Collins, C.M., Leather, S.R., Littlewood, N.A., Menz, M.H.M., Müller, J., Packer, L., Saunders, M.E., Schönrogge, K., Stewart, A.J.A., Yanoviak, S.P., Hassall, C., 2020. Interpreting insect declines: seven challenges and a way forward. *Insect Conserv. Divers.* 13, 103–114. <https://doi.org/10.1111/icad.12408>
- Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S., ter Braak, C.J.F., 2014. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* 95, 14–21. <https://doi.org/10.1890/13-0196.1>

- Duflot, R., Georges, R., Ernoult, A., Aviron, S., Burel, F., 2014. Landscape heterogeneity as an ecological filter of species traits. *Acta Oecologica* 56, 19–26. <https://doi.org/10.1016/j.actao.2014.01.004>
- Ekroos, J., Ödman, A.M., Andersson, G.K.S., Birkhofer, K., Herbertsson, L., Klatt, B.K., Olsson, O., Olsson, P.A., Persson, A.S., Prentice, H.C., Rundlöf, M., Smith, H.G., 2016. Sparing Land for Biodiversity at Multiple Spatial Scales. *Front. Ecol. Evol.* 3. <https://doi.org/10.3389/fevo.2015.00145>
- Emmerson, M.C., Raffaelli, D., 2004. Predator–prey body size, interaction strength and the stability of a real food web. *J. Anim. Ecol.* 73, 399–409. <https://doi.org/10.1111/j.0021-8790.2004.00818.x>
- Faith, D.P., Minchin, P.R., Belbin, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69, 57–68. <https://doi.org/10.1007/BF00038687>
- Gallé, R., Geppert, C., Földesi, R., Tschardtke, T., Batáry, P., 2020. Arthropod functional traits shaped by landscape-scale field size, local agri-environment schemes and edge effects. *Basic Appl. Ecol.* 48, 102–111. <https://doi.org/10.1016/j.baae.2020.09.006>
- Gallé, R., Happe, A., Baillod, A.B., Tschardtke, T., Batáry, P., 2019. Landscape configuration, organic management, and within-field position drive functional diversity of spiders and carabids. *J. Appl. Ecol.* 56, 63–72. <https://doi.org/10.1111/1365-2664.13257>
- Ganser, D., Knop, E., Albrecht, M., 2019. Sown wildflower strips as overwintering habitat for arthropods: Effective measure or ecological trap?, *Agric. Ecosyst. Environ.* 275, 123–131. <https://doi.org/10.1016/j.agee.2019.02.010>.
- Gayer, C., Lövei, G.L., Magura, T., Dieterich, M., Batáry, P., 2019. Carabid functional diversity is enhanced by conventional flowering fields, organic winter cereals and edge habitats. *Agric. Ecosyst. Environ.* 284, 106579. <https://doi.org/10.1016/j.agee.2019.106579>
- González-Chang, M., Tiwari, S., Sharma, S., Wratten, S.D., 2019. Habitat Management for Pest Management: Limitations and Prospects. *Ann. Entomol. Soc. Am.* 112, 302–317. <https://doi.org/10.1093/aesa/saz020>
- Griffiths, G.J.K., Holland, J.M., Bailey, A., Thomas, M.B., 2008. Efficacy and economics of shelter habitats for conservation biological control. *Biol. Control* 45, 200–209. <https://doi.org/10.1016/j.biocontrol.2007.09.002>
- Haaland, C., Naisbit, R.E., Bersier, L.-F., 2011. Sown wildflower strips for insect conservation: a review: Wildflower strips for insect conservation. *Insect Conserv. Divers.* 4, 60–80. <https://doi.org/10.1111/j.1752-4598.2010.00098.x>
- Holland, J.M., Bianchi, F.J., Entling, M.H., Moonen, A.-C., Smith, B.M., Jeanneret, P., 2016. Structure, function and management of semi-natural habitats for conservation biological control: a review of European studies: Structure, function and management of semi-natural habitats for biological control. *Pest Manag. Sci.* 72, 1638–1651. <https://doi.org/10.1002/ps.4318>

- Holland, J.M., Birkett, T., Southway, S., 2009. Contrasting the farm-scale spatio-temporal dynamics of boundary and field overwintering predatory beetles in arable crops. *BioControl* 54, 19–33. <https://doi.org/10.1007/s10526-008-9152-2>
- Homburg, K., Schuldt, A., Drees, C., Assmann, T., 2013. Broad-scale geographic patterns in body size and hind wing development of western Palaearctic carabid beetles (Coleoptera: Carabidae). *Ecography* 36, 166–177. <https://doi.org/10.1111/j.1600-0587.2012.07488.x>
- Jeannel, R., 1942. Coléoptères Carabiques. Tome II. Faune Fr. 40.
- Jeannel, R., 1941. Coléoptères Carabiques. Tome I. Faune Fr.
- Jowett, K., Milne, A.E., Metcalfe, H., Hassall, K.L., Potts, S.G., Senapathi, D. and Storkey, J., 2019. Species matter when considering landscape effects on carabid distributions. *Agric. Ecosyst. Environ.* 285, 106631. <https://doi.org/10.1016/j.agee.2019.106631>.
- Karp, D.S., Chaplin-Kramer, R., Meehan, T.D., Martin, E.A., DeClerck, F., Grab, H., Gratton, C., Hunt, L., Larsen, A.E., Martínez-Salinas, A., O'Rourke, M.E., Rusch, A., Poveda, K., Jonsson, M., Rosenheim, J.A., Schellhorn, N.A., Tscharrntke, T., Wratten, S.D., Zhang, W., Iverson, A.L., Adler, L.S., Albrecht, M., Alignier, A., Angelella, G.M., Zubair Anjum, M., Avelino, J., Batáry, P., Baveco, J.M., Bianchi, F.J.J.A., Birkhofer, K., Bohnenblust, E.W., Bommarco, R., Brewer, M.J., Caballero-López, B., Carrière, Y., Carvalheiro, L.G., Cayuela, L., Centrella, M., Četković, A., Henri, D.C., Chabert, A., Costamagna, A.C., De la Mora, A., de Kraker, J., Desneux, N., Diehl, E., Diekötter, T., Dormann, C.F., Eckberg, J.O., Entling, M.H., Fiedler, D., Franck, P., Frank van Veen, F.J., Frank, T., Gagic, V., Garratt, M.P.D., Getachew, A., Gonthier, D.J., Goodell, P.B., Graziosi, I., Groves, R.L., Gurr, G.M., Hajian-Forooshani, Z., Heimpel, G.E., Herrmann, J.D., Huseeth, A.S., Inclán, D.J., Ingrao, A.J., Iv, P., Jacot, K., Johnson, G.A., Jones, L., Kaiser, M., Kaser, J.M., Keasar, T., Kim, T.N., Kishinevsky, M., Landis, D.A., Lavandero, B., Lavigne, C., Le Ralec, A., Lemessa, D., Letourneau, D.K., Liere, H., Lu, Y., Lubin, Y., Luttermoser, T., Maas, B., Mace, K., Madeira, F., Mader, V., Cortesero, A.M., Marini, L., Martinez, E., Martinson, H.M., Menozzi, P., Mitchell, M.G.E., Miyashita, T., Molina, G.A.R., Molina-Montenegro, M.A., O'Neal, M.E., Opatovsky, I., Ortiz-Martinez, S., Nash, M., Östman, Ö., Ouin, A., Pak, D., Paredes, D., Parsa, S., Parry, H., Perez-Alvarez, R., Perović, D.J., Peterson, J.A., Petit, S., Philpott, S.M., Plantegenest, M., Plečaš, M., Pluess, T., Pons, X., Potts, S.G., Pywell, R.F., Ragsdale, D.W., Rand, T.A., Raymond, L., Ricci, B., Sargent, C., Sarthou, J.-P., Saulais, J., Schäckermann, J., Schmidt, N.P., Schneider, G., Schüepp, C., Sivakoff, F.S., Smith, H.G., Stack Whitney, K., Stutz, S., Szendrei, Z., Takada, M.B., Taki, H., Tamburini, G., Thomson, L.J., Tricault, Y., Tsafack, N., Tschumi, M., Valantin-Morison, M., Van Trinh, M., van der Werf, W., Vierling, K.T., Werling, B.P., Wickens, J.B., Wickens, V.J., Woodcock, B.A., Wyckhuys, K., Xiao, H., Yasuda, M., Yoshioka, A., Zou, Y., 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proc. Natl. Acad. Sci.* 115, E7863–E7870. <https://doi.org/10.1073/pnas.1800042115>
- Kujawa, K., Bernacki, Z., Kowalska, J., Kujawa, A., Oleszczuk, M., Sienkiewicz, P., Sobczyk, D., 2020. Annual Wildflower Strips as a Tool for Enhancing Functional



- Biodiversity in Rye Fields in an Organic Cultivation System. *Agronomy* 10, 1696. <https://doi.org/10.3390/agronomy10111696>
- Kulkarni, S.S., Dossall, L.M., Willenborg, C.J., 2015. The Role of Ground Beetles (Coleoptera: Carabidae) in Weed Seed Consumption: A Review. *Weed Sci.* 63, 355–376. <https://doi.org/10.1614/WS-D-14-00067.1>
- Labruyere, S., Ricci, B., Lubac, A., Petit, S., 2016. Crop type, crop management and grass margins affect the abundance and the nutritional state of seed-eating carabid species in arable landscapes. *Agric. Ecosyst. Environ.* 231, 183–192. <https://doi.org/10.1016/j.agee.2016.06.037>
- Landis, D.A., Menalled, F.D., Costamagna, A.C., Wilkinson, T.K., 2005. Manipulating plant resources to enhance beneficial arthropods in agricultural landscapes. *Weed Sci.* 53, 902–908. <https://doi.org/10.1614/WS-04-050R1.1>
- Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat Management to Conserve Natural Enemies of Arthropod Pests in Agriculture. *Annu. Rev. Entomol.* 45, 175–201. <https://doi.org/10.1146/annurev.ento.45.1.175>
- Lindroth, C.H., 1988. The ground-beetles (carabidae) of fennoscandia. A zoogeographic study., Smithsonian Institution Libraries and National Science Foundation. ed.
- Maas, B., Brandl, M., Hussain, R.I., Frank, T., Zulka, K.P., Rabl, D., Walcher, R., Moser, D., 2021. Functional traits driving pollinator and predator responses to newly established grassland strips in agricultural landscapes. *J. Appl. Ecol.* 1365-2664.13892. <https://doi.org/10.1111/1365-2664.13892>
- Marrec, R., Badenhauer, I., Bretagnolle, V., Börger, L., Roncoroni, M., Guillon, N., Gauffre, B., 2015. Crop succession and habitat preferences drive the distribution and abundance of carabid beetles in an agricultural landscape. *Agric. Ecosyst. Environ.* 199, 282–289. <https://doi.org/10.1016/j.agee.2014.10.005>
- Martin, E.A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M.P.D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S.G., Smith, H.G., Al Hassan, D., Albrecht, M., Andersson, G.K.S., Asís, J.D., Aviron, S., Balzan, M.V., Baños-Picón, L., Bartomeus, I., Batáry, P., Burel, F., Caballero-López, B., Concepción, E.D., Coudrain, V., Dänhardt, J., Diaz, M., Diekötter, T., Dormann, C.F., Dufnot, R., Entling, M.H., Farwig, N., Fischer, C., Frank, T., Garibaldi, L.A., Hermann, J., Herzog, F., Inclán, D., Jacot, K., Jauker, F., Jeanneret, P., Kaiser, M., Krauss, J., Le Féon, V., Marshall, J., Moonen, A., Moreno, G., Riedinger, V., Rundlöf, M., Rusch, A., Scheper, J., Schneider, G., Schüepp, C., Stutz, S., Sutter, L., Tamburini, G., Thies, C., Tormos, J., Tschardt, T., Tschumi, M., Uzman, D., Wagner, C., Zubair-Anjum, M., Steffan-Dewenter, I., 2019. The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecol. Lett.* 22, 1083–1094. <https://doi.org/10.1111/ele.13265>
- Martinez Arbizu, P., 2020. pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.4.

- Ng, K., Barton, P.S., Blanchard, W., Evans, M.J., Lindenmayer, D.B., Macfadyen, S., McIntyre, S., Driscoll, D.A., 2018. Disentangling the effects of farmland use, habitat edges, and vegetation structure on ground beetle morphological traits. *Oecologia* 188, 645–657. <https://doi.org/10.1007/s00442-018-4180-9>
- Northfield, T.D., Snyder, G.B., Ives, A.R., Snyder, W.E., 2010. Niche saturation reveals resource partitioning among consumers. *Ecol. Lett.* 13, 338–348. <https://doi.org/10.1111/j.1461-0248.2009.01428.x>
- Pearsons, K., Tooker, J., 2017. In-Field Habitat Management to Optimize Pest Control of Novel Soil Communities in Agroecosystems. *Insects* 8, 82. <https://doi.org/10.3390/insects8030082>
- Pecheur, E., Piqueray, J., Monty, A., Dufrêne, M., Mahy, G., 2020. The influence of ecological infrastructures adjacent to crops on their carabid assemblages in intensive agroecosystems. *PeerJ* 8, e8094. <https://doi.org/10.7717/peerj.8094>
- Pe'er, G., Zinngrebe, Y., Hauck, J., Schindler, S., Dittrich, A., Zingg, S., Tschardt, T., Oppermann, R., Sutcliffe, L.M.E., Sirami, C., Schmidt, J., Hoyer, C., Schleyer, C., Lakner, S., 2017. Adding Some Green to the Greening: Improving the EU's Ecological Focus Areas for Biodiversity and Farmers. *Conserv. Lett.* 10, 517–530. <https://doi.org/10.1111/conl.12333>
- Pywell, R.F., James, K.L., Herbert, I., Meek, W.R., Carvell, C., Bell, D., Sparks, T.H., 2005. Determinants of overwintering habitat quality for beetles and spiders on arable farmland. *Biol. Conserv.* 123, 79–90. <https://doi.org/10.1016/j.biocon.2004.10.010>
- Ribera, I., Dolédec, S., Downie, I.S., Foster, G.N., 2001. Effect of Land Disturbance and Stress on Species Traits of Ground Beetle Assemblages. *Ecology* 82, 1112–1129. [https://doi.org/10.1890/0012-9658\(2001\)082\[1112:EOLDAS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1112:EOLDAS]2.0.CO;2)
- Rouabah, A., Villerd, J., Amiaud, B., Plantureux, S., Lasserre-Joulin, F., 2015. Response of carabid beetles diversity and size distribution to the vegetation structure within differently managed field margins. *Agric. Ecosyst. Environ.* 200, 21–32. <https://doi.org/10.1016/j.agee.2014.10.011>
- Rusch, A., Birkhofer, K., Bommarco, R., Smith, H.G., Ekbom, B., 2015. Predator body sizes and habitat preferences predict predation rates in an agroecosystem. *Basic Appl. Ecol.* 16, 250–259. <https://doi.org/10.1016/j.baae.2015.02.003>
- Rusch, A., Birkhofer, K., Bommarco, R., Smith, H.G., Ekbom, B., 2014. Management intensity at field and landscape levels affects the structure of generalist predator communities. *Oecologia* 175, 971–983. <https://doi.org/10.1007/s00442-014-2949-z>
- Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: A review of its drivers. *Biol. Conserv.* 232, 8–27. <https://doi.org/10.1016/j.biocon.2019.01.020>
- Schellhorn, N.A., Bianchi, F.J.J.A., Hsu, C.L., 2014. Movement of Entomophagous Arthropods in Agricultural Landscapes: Links to Pest Suppression. *Annu. Rev. Entomol.* 59, 559–581. <https://doi.org/10.1146/annurev-ento-011613-161952>

- Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., Weisser, W.W., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* 574, 671–674. <https://doi.org/10.1038/s41586-019-1684-3>
- Sirami, C., Gross, N., Baillod, A.B., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miguet, P., Vuillot, C., Alignier, A., Girard, J., Batáry, P., Clough, Y., Violle, C., Giralt, D., Bota, G., Badenhausser, I., Lefebvre, G., Gauffre, B., Vialatte, A., Calatayud, F., Gil-Tena, A., Tischendorf, L., Mitchell, S., Lindsay, K., Georges, R., Hilaire, S., Recasens, J., Solé-Senan, X.O., Robleño, I., Bosch, J., Barrientos, J.A., Ricarte, A., Marcos-Garcia, M.Á., Miñano, J., Mathevet, R., Gibon, A., Baudry, J., Balent, G., Poulin, B., Burel, F., Tscharncke, T., Bretagnolle, V., Siriwardena, G., Ouin, A., Brotons, L., Martin, J.-L., Fahrig, L., 2019. Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proc. Natl. Acad. Sci.* 116, 16442–16447. <https://doi.org/10.1073/pnas.1906419116>
- Stoate, C., Boatman, N.D., Borralho, R.J., Carvalho, C.R., Snoo, G.R. de, Eden, P., 2001. Ecological impacts of arable intensification in Europe. *J. Environ. Manage.* 63, 337–365. <https://doi.org/10.1006/jema.2001.0473>
- Thomas, C.F.G., Parkinson, L., Griffiths, G.J.K., Garcia, A.F., Marshall, E.J.P., 2001. Aggregation and temporal stability of carabid beetle distributions in field and hedgerow habitats: *Spatial distributions of carabid beetles*. *J. Appl. Ecol.* 38, 100–116. <https://doi.org/10.1046/j.1365-2664.2001.00574.x>
- Triquet, C., Roume, A., Tolon, V., Wezel, A., Ferrer, A., 2022. Undestroyed winter cover crop strip in maize fields supports ground-dwelling arthropods and predation. *Agric. Ecosyst. Environ.* 326, 107783. <https://doi.org/10.1016/j.agee.2021.107783>
- Tscharncke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.M., Nouhuys, S. van, Vidal, S., 2007. Conservation biological control and enemy diversity on a landscape scale. *Biol. Control* 43, 294–309. <https://doi.org/10.1016/j.biocontrol.2007.08.006>
- Uyttenbroeck, R., Hatt, S., Paul, A., Boeraeve, F., Piqueray, J., Francis, F., Danthine, S., Frederich, M., Dufrière, M., Bodson, B., Monty, A., 2016. Pros and cons of flowers strips for farmers. A review. *Biotechnol Agron Soc Env.* 12.
- Wagner, D.L., 2020. Insect Declines in the Anthropocene. *Annu. Rev. Entomol.* 65, 457–480. <https://doi.org/10.1146/annurev-ento-011019-025151>
- Warton, D.I., Wright, S.T., Wang, Y., 2012. Distance-based multivariate analyses confound location and dispersion effects. *Methods Ecol. Evol.* 3, 89–101. <https://doi.org/10.1111/j.2041-210X.2011.00127.x>
- Williams, I.H., Ferguson, A.W., Kruus, M., Veromann, E., Warner, D.J., 2010. Ground Beetles as Predators of Oilseed Rape Pests: Incidence, Spatio-Temporal Distributions and Feeding, in: Williams, I.H. (Ed.), *Biocontrol-Based Integrated Management of Oilseed Rape Pests*. Springer Netherlands, Dordrecht, pp. 115–149. [https://doi.org/10.1007/978-90-481-3983-5\\_4](https://doi.org/10.1007/978-90-481-3983-5_4)

Woodcock, B.A., 2005. Pitfall trapping in ecological studies, in: *Insect Sampling in Forest Ecosystems*. Wiley Online Library, pp. 37–57.

Woodcock, B.A., Bullock, J.M., McCracken, M., Chapman, R.E., Ball, S.L., Edwards, M.E., Nowakowski, M., Pywell, R.F., 2016. Spill-over of pest control and pollination services into arable crops. *Agric. Ecosyst. Environ.* 231, 15–23. <https://doi.org/10.1016/j.agee.2016.06.023>

## Supporting Information A: List of carabid species ranked by abundances in the three habitats (margin, strip and cropped area)

Code names correspondences:

abapar: <i>Abax parallelus</i> (Duftschmid, 1812)	lorpil: <i>Loricera pilicornis</i> (Fabricius, 1775)
acumer: <i>Acupalpus meridianus</i> (Linne, 1761)	metlam: <i>Metallina lampros</i> (Herbst, 1784)
agoema : <i>Agonum emarginatum</i> (Gyllenhal, 1827)	metpro: <i>Metallina properans</i> (Stephens, 1828)
agomue : <i>Agonum muelleri</i> (Herbst, 1784)	micmau: <i>Microlestes maurus</i> (Sturm, 1827)
amaaen: <i>Amara aenea</i> (De Geer, 1774)	micmin: <i>Microlestes minutulus</i> (Goeze, 1777)
amabif: <i>Amara bifrons</i> (Gyllenhal, 1810)	nebbre: <i>Nebria brevicollis</i> (Fabricius, 1792)
amasim: <i>Amara similata</i> (Gyllenhal, 1810)	nebsal: <i>Nebria salina</i> Fairmaire & Laboulbène, 1854
andcor: <i>Anchomenus dorsalis</i> (Pontoppidan, 1763)	notqua: <i>Notiophilus quadripunctatus</i> Dejean, 1826
anisig: <i>Anisodactylus signatus</i> (Panzer, 1796)	notsub: <i>Notiophilus substriatus</i> G.R. Waterhouse, 1833
asasti: <i>Asaphidion stierlini</i> (Heyden, 1880)	ocylat: <i>Ocydromus latinus</i> (Netolitzky, 1911)
badbul: <i>Badister bullatus</i> (Schränk, 1798)	ocytet: <i>Ocydromus tetracolos</i> (Say, 1823)
bemqua: <i>Bembidion quadrimaculatum</i> (Linne, 1761)	ophazu: <i>Ophonus azureus</i> (Fabricius, 1775)
braele: <i>Brachinus elegans</i> Chaudoir, 1842	ophcri: <i>Ophonus cribricollis</i> (Dejean, 1829)
braexp: <i>Brachinus expodens</i> Duftschmid, 1812	parbis: <i>Paratachys bistriatus</i> (Duftschmid, 1812)
brascl: <i>Brachinus sclopeta</i> (Fabricius, 1792)	parmac: <i>Parophonus maculicornis</i> (Duftschmid, 1812)
calcin: <i>Calathus cinctus</i> Motschulsky, 1850	philun: <i>Philochthus lunulatus</i> (Geoffroy in Fourcroy, 1785)
calfus: <i>Calathus fuscipes</i> (Goeze, 1777)	phyobt: <i>Phyla obtusa</i> (Audinet-Serville, 1821)
callun: <i>Callistus lunatus</i> (Fabricius, 1775)	pladep: <i>Platyderus depressus</i> (Audinet-Serville, 1821)
caraur: <i>Carabus auratus</i> Linne, 1761	poecup: <i>Poecilus cupreus</i> (Linne, 1758)
carcan: <i>Carabus cancellatus</i> Illiger, 1798	poelep: <i>Poecilus lepidus</i> (Leske, 1785)
carcor: <i>Carabus coriaceus</i> Linne, 1758	polcon: <i>Polistichus connexus</i> (Geoffroy in Fourcroy, 1785)
carmon: <i>Carabus monilis</i> Fabricius, 1792	psecal: <i>Pseudoophonus calceatus</i> (Duftschmid, 1812)
carnem: <i>Carabus nemoralis</i> Müller, 1764	psegri: <i>Pseudoophonus griseus</i> (Panzer, 1797)
carvio: <i>Carabus violaceus subsp. purpurascens</i> Fabricius, 1787	pseruf: <i>Pseudoophonus rufipes</i> (De Geer, 1774)
ciccam: <i>Cicindela campestris</i> Linne, 1758	pteant: <i>Pterostichus anthracinus</i> (Illiger, 1798)
clifos: <i>Clivina fossor</i> (Linne, 1758)	ptemad: <i>Pterostichus madidus</i> (Fabricius, 1775)
cylger: <i>Cylindera germanica</i> (Linne, 1758)	ptemel: <i>Pterostichus melanarius</i> (Illiger, 1798)
dematr: <i>Demetrias atricapillus</i> (Linne, 1758)	ptenie: <i>Pterostichus niger</i> (Schaller, 1783)
diager: <i>Diachromus germanus</i> (Linne, 1758)	pteovo: <i>Pterostichus ovoideus</i> (Sturm, 1824)
dryden: <i>Drypta dentata</i> (Rossi, 1790)	semsig: <i>Semiophonus signaticornis</i> (Duftschmid, 1812)
haraff: <i>Harpalus affinis</i> (Schränk, 1781)	steteu: <i>Stenolophus teutonius</i> (Schränk, 1781)
haralb: <i>Harpalus albanicus</i> Reitter, 1900	stopum: <i>Stomis pumicatus</i> (Panzer, 1796)
haranx: <i>Harpalus anxius</i> (Duftschmid, 1812)	synobs: <i>Syntomus obscuroguttatus</i> (Duftschmid, 1812)
hardim: <i>Harpalus dimidiatus</i> (Rossi, 1790)	tacpar: <i>Tachyura parvula</i> (Dejean, 1831)
hardis: <i>Harpalus distinguendus</i> (Duftschmid, 1812)	trequa: <i>Trechus quadristriatus</i> (Schränk, 1781)
harpyg: <i>Harpalus pygmaeus</i> Dejean, 1829	zabten: <i>Zabrus tenebrioides</i> (Goeze, 1777)
harrub: <i>Harpalus rubripes</i> (Duftschmid, 1812)	
harser: <i>Harpalus serripes</i> (Quensel in Schönherr, 1806)	
harsma: <i>Harpalus smaragdinus</i> (Duftschmid, 1812)	
hartar: <i>Harpalus tardus</i> (Panzer, 1797)	

For each species, rank, abundance (Ab.), and proportion in the habitat (%) are given. Bold species are the 3 main species; grey boxes highlight the species found exclusively in the strip (however in low abundances). These abundances take into account all sampling periods with an existing strip (from Sowing to Final Stage).

<u>Strip</u>	rank	Ab.	%	<u>Margin</u>	rank	Ab.	%	<u>Crop</u>	rank	Ab.	%
<b>andcor</b>	<b>1</b>	<b>267</b>	<b>35,3</b>	<b>andcor</b>	<b>1</b>	<b>80</b>	<b>23,2</b>	<b>ptemel</b>	<b>1</b>	<b>1078</b>	<b>37,3</b>
<b>poecup</b>	<b>2</b>	<b>98</b>	<b>13</b>	<b>ptemel</b>	<b>2</b>	<b>31</b>	<b>9</b>	<b>poecup</b>	<b>2</b>	<b>577</b>	<b>20</b>
brascl	3	54	7,1	phyobt	3	20	5,8	hardis	3	140	4,8
<b>ptemel</b>	<b>4</b>	<b>39</b>	<b>5,2</b>	haraff	4	17	4,9	caraur	4	135	4,7
carcan	5	35	4,6	hardim	5	17	4,9	trequa	5	117	4
amasim	6	29	3,8	pseruf	6	17	4,9	phyobt	6	116	4
carmon	7	26	3,4	carcan	7	16	4,6	pseruf	7	78	2,7
micmin	8	23	3	hardis	8	13	3,8	micmin	8	73	2,5
pseruf	9	21	2,8	trequa	9	12	3,5	carmon	9	48	1,7
hardim	10	17	2,2	carcor	10	11	3,2	ptemad	10	47	1,6
hardis	11	16	2,1	metlam	11	11	3,2	hardim	11	43	1,5
trequa	12	16	2,1	brascl	12	10	2,9	carcan	12	38	1,3
braele	13	14	1,9	haranx	13	10	2,9	asasti	13	36	1,2
carcor	14	14	1,9	harser	14	10	2,9	cylger	14	35	1,2
caraur	15	10	1,3	<b>poecup</b>	<b>15</b>	<b>7</b>	<b>2</b>	haraff	15	34	1,2
haraff	16	10	1,3	micmin	16	6	1,7	anisig	16	33	1,1
metlam	17	9	1,2	carmon	17	5	1,4	metlam	17	29	1
asasti	18	6	0,8	hartar	18	5	1,4	<b>andcor</b>	<b>18</b>	<b>26</b>	<b>0,9</b>
pteant	19	5	0,7	ophazu	19	5	1,4	metpro	19	23	0,8
nebsal	20	4	0,5	cylger	20	4	1,2	pteant	20	20	0,7
ptemad	21	4	0,5	micmau	21	4	1,2	nebbre	21	19	0,7
anisig	22	3	0,4	ptemad	22	4	1,2	ptenie	22	17	0,6
calfus	23	3	0,4	dryden	23	3	0,9	calfus	23	15	0,5
cylger	24	3	0,4	nebsal	24	3	0,9	bemqua	24	14	0,5
dematr	25	3	0,4	parmac	25	3	0,9	nebsal	25	14	0,5
ophazu	26	3	0,4	amaaen	26	2	0,6	carcor	26	13	0,4

<b>Strip</b>	rank	Ab.	%	<b>Margin</b>	rank	Ab.	%	<b>Crop</b>	rank	Ab.	%
synobs	27	3	0,4	caraur	27	2	0,6	notqua	27	10	0,3
agomue	28	2	0,3	haralb	28	2	0,6	ophazu	28	9	0,3
amaaen	29	2	0,3	harrub	29	2	0,6	ciccam	29	4	0,1
amabif	30	2	0,3	pladep	30	2	0,6	psecal	30	4	0,1
nebbre	31	2	0,3	amabif	31	1	0,3	amaaen	31	3	0,1
acumer	32	1	0,1	amasim	32	1	0,3	calcin	32	3	0,1
badbul	33	1	0,1	asasti	33	1	0,3	haranx	33	3	0,1
bemqua	34	1	0,1	braexp	34	1	0,3	harrub	34	3	0,1
braexp	35	1	0,1	diager	35	1	0,3	harser	35	3	0,1
carnem	36	1	0,1	harsma	36	1	0,3	micmau	36	3	0,1
carvio	37	1	0,1	metpro	37	1	0,3	stopum	37	3	0,1
dryden	38	1	0,1	nebbre	38	1	0,3	badbul	38	2	0,1
metpro	39	1	0,1	polcon	39	1	0,3	ocylat	39	2	0,1
phyobt	40	1	0,1	pteovo	40	1	0,3	ophcri	40	2	0,1
ptenie	41	1	0,1	steteu	41	1	0,3	parbis	41	2	0,1
semsig	42	1	0,1					tacpar	42	2	0,1
stopum	43	1	0,1					acumer	43	1	0
zabten	44	1	0,1					agoema	44	1	0
								amasim	45	1	0
								callun	46	1	0
								carvio	47	1	0
								dematr	48	1	0
								harpyg	49	1	0
								harsma	50	1	0
								lorpil	51	1	0
								ocytet	52	1	0
								philun	53	1	0
								poelep	54	1	0
								psegri	55	1	0
								steteu	56	1	0

## Supporting Information B: Indicator species analysis results by zone groups

Multilevel pattern analysis: 9999 permutations

Significance level (alpha): 0.05

Significance codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

### First analysis: full sampling period (from Initial stage to Final Stage)

Total number of species: 76

Selected number of species: 19

Number of species associated to 1 group: 14

Number of species associated to 2 groups: 2

Number of species associated to 3 groups: 2

Number of species associated to 4 groups: 1

List of species associated to each combination:

Group	species	stat	p.value
Group margin	haranx	0.207	0.0001 ***
	hartar	0.186	0.0001 ***
	harser	0.155	0.0003 ***
	micmau	0.137	0.0037 **
	pladep	0.124	0.0167 *
	parmac	0.117	0.0137 *
Group 0m	<b>andcor</b>	<b>0.334</b>	<b>0.0001 ***</b>
	brascl	0.231	0.0001 ***
	amasim	0.191	0.0001 ***
	braele	0.160	0.0001 ***
	carmon	0.129	0.0075 **
	dematr	0.108	0.0497 *
	carcan	0.102	0.0500 *
Group 50m	ptenie	0.124	0.01 **
Group margin+0m	carcor	0.167	4e-04 ***
Group 10m+25m	caraur	0.131	0.0059 **
Group 0m+10m+25m	<b>poecup</b>	<b>0.192</b>	<b>1e-04 ***</b>
Group 10m+25m+50m	<b>ptemel</b>	<b>0.165</b>	<b>2e-04 ***</b>
Group margin+10m+25m+50m	phyobt	0.136	0.0023 **



**Second analysis: during maize growth (from Sowing to 8 Leaves stage)**

Total number of species: 76

Selected number of species: 21

Number of species associated to 1 group: 17

Number of species associated to 2 groups: 1

Number of species associated to 3 groups: 2

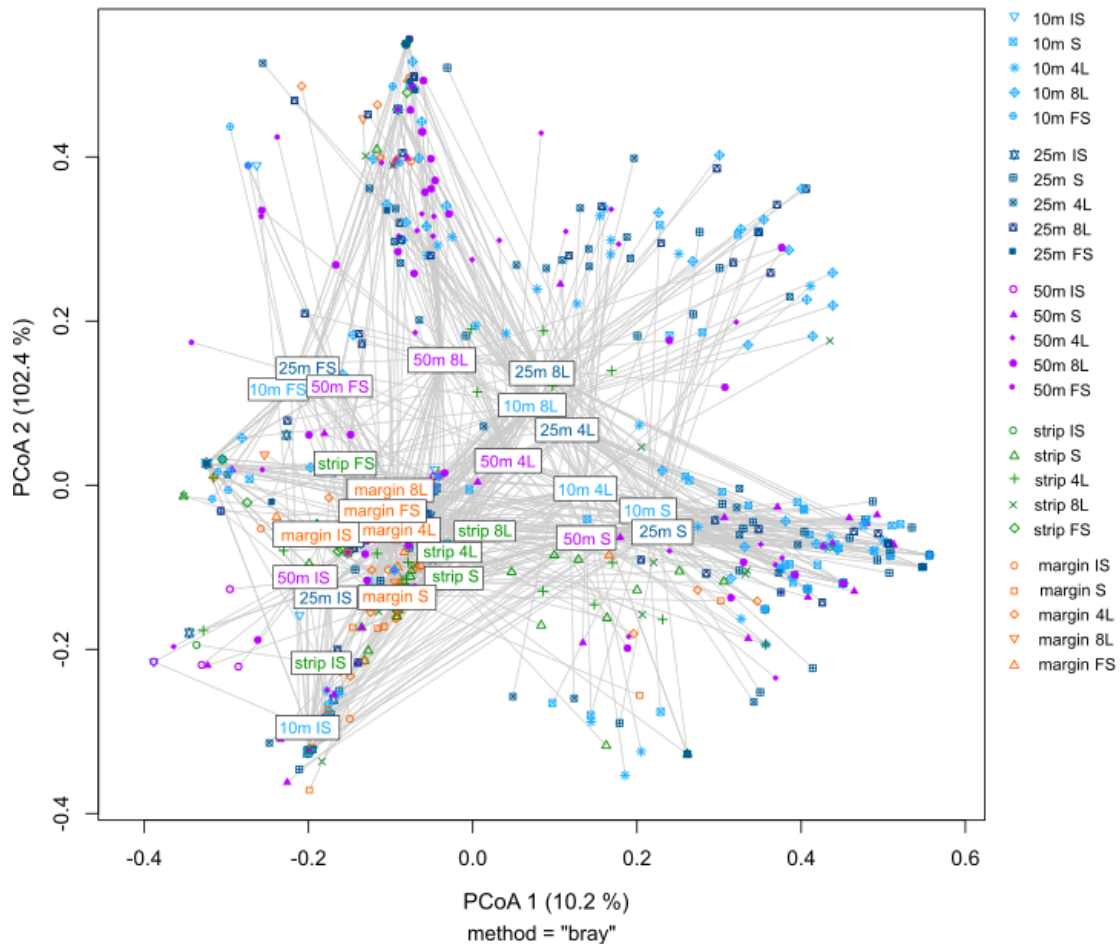
Number of species associated to 4 groups: 1

**List of species associated to each combination:**

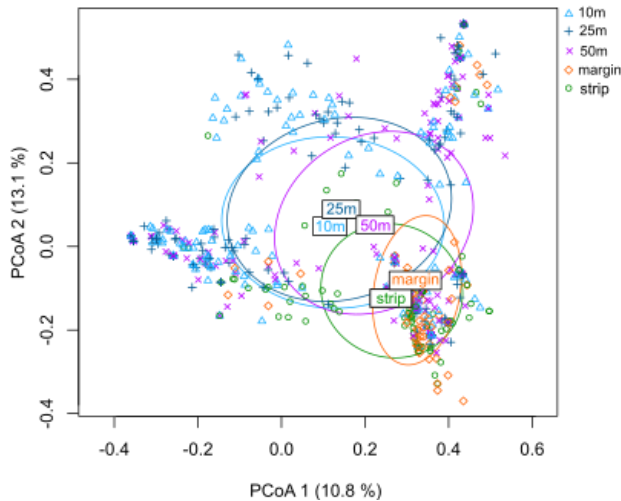
Group	species	stat	p.value
Group margin	haranx	0.246	0.0001 ***
	hartar	0.195	0.0006 ***
	harser	0.183	0.0004 ***
	haralb	0.145	0.0137 *
	pladep	0.145	0.0137 *
	parmac	0.138	0.0167 *
	micmau	0.136	0.0150 *
	haraff	0.133	0.0158 *
	dryden	0.119	0.0444 *
Group 0m	<b>andcor</b>	<b>0.448</b>	<b>0.0001 ***</b>
	brascl	0.277	0.0001 ***
	amasim	0.218	0.0001 ***
	braele	0.183	0.0001 ***
	carmon	0.150	0.0053 **
	dematr	0.141	0.0235 *
	agomue	0.133	0.0401 *
Group 50m	ptenie	0.147	0.0087 **
Group 10m+25m	caraur	0.146	0.0068 **
Group 0m+10m+25m	<b>poecup</b>	<b>0.219</b>	<b>1e-04 ***</b>
Group 10m+25m+50m	<b>ptemel</b>	<b>0.181</b>	<b>7e-04 ***</b>
Group margin+10m+25m+50m	phyobt	0.148	0.006 **

## Supporting Information C: Multivariate dispersion

Effect of zone and sampling period (IS, S, 4L, 8L, FS) on the multivariate dispersion of species composition. Taxonomic  $\beta$ -diversity is measured as the distance of factors to their group centroid using Bray-Curtis, represented on the first two axes of a PCoA. Additional PcoA showing only zones (without IS period) and sites are presented with the sd ellipses.



Species dispersion - zones without IS sampling period



Species dispersion - sites

