



Arthropod functional traits shaped by landscape-scale field size, local agri-environment schemes and edge effects

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Abstract

Agri-environment scheme (AES) approaches can be classified according to whether they prescribe management in non-productive areas, such as field boundaries and wildflower strips, or in productive areas, such as arable crops. Here we tested the ecological effectiveness of two popular AESs in Germany: wildflower strips next to winter wheat fields as off-field management and organic farming on winter wheat fields as on-field management. We selected ten landscapes along a field size gradient with three focal wheat fields, one conventional field with flower strip, one organic field and one conventional field without flower strip as a control. We sampled arthropods with pitfall traps at field edges and field interiors. We selected three ecological traits for spiders and carabids (body size, feeding trait, dispersal ability). We calculated community weighted mean values (CWM), and we used linear mixed effects models to test the effect of management type and transect position on CWM values. We found pronounced edge effects on most traits, and weaker effects of field size and AES in shaping functional traits. Smaller spiders, spiders with higher ballooning propensity and more web-builders were in the field interior than at the field edge, whereas carnivore carabids preferred field interiors. We also found a strong effect of landscape configuration, i.e. mean field size, as larger field size was positively related to more web-building spiders and more carnivore beetles. Flower strips enhanced populations of web-building spiders. Our results suggest that small-scale agriculture leading to high landscape-scale edge density has a major effect in shaping functional traits and potential ecosystems services in agricultural landscapes. Spider and carabid communities exhibit very different responses to edge vs. interior sites, and, based on the landscape-scale field size gradient emphasize the importance of landscape configuration in shaping the heterogeneity of the arthropods' traits and presumably ecosystem services in agricultural landscapes.

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Keywords: Organic farming; Flower strips; On-field vs off-field management; Body size; Feeding traits; Dispersal ability

Introduction

Land use change and the associated management intensification of agricultural areas have led to a dramatic decrease in farmland diversity worldwide, but especially in Europe (Batáry et al., 2020; Newbold et al., 2015). There is a

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widespread pattern of decline in insect diversity and abundance due to climate change, habitat loss and fragmentation, and deterioration of habitat quality (Didham et al., 2020; Hallmann et al., 2017). The decline of many insect populations urges an effective conservation strategy. Agri-environmental schemes (AESs) have been developed to mitigate the negative effects of agricultural intensification on biodiversity (The Council of the European Union, 2005). In intensively used croplands, AESs can be classified into two main categories: (1) schemes targeting productive areas such as organic farming, supporting low-intensity management systems through prohibiting pesticide and inorganic fertilizer inputs and (2) schemes applied to non-productive areas, e.g. field margins and hedgerows, focusing on areas taken out of production (Batáry, Dicks, Kleijn & Sutherland, 2015).

The effectiveness of AESs is influenced by landscape context and by the species pool of the landscape. Schemes applied to non-productive areas create semi-natural areas, thus they do not act only on the local scale, but they also have an effect on landscape scale through changing its heterogeneity. The beneficial effects of agri-environmental measures in conserving farmland biodiversity are predicted to be the strongest in structurally simple landscapes with 1–20% semi-natural habitats (Tscharntke, Klein, Kruess, Steffan-Dewenter & Thies, 2005). In addition, Batáry et al. (2015) showed in their meta-analysis that schemes focusing on non-production areas are more effective at conserving species richness than those aiming at productive areas.

Field edges are keystone features for biodiversity in agricultural landscapes, as semi-natural habitats are usually situated along them (Schirmel, Thiele, Entling & Buchholz, 2016). Arable fields are ephemeral habitats for arthropods because they are regularly disturbed by management such as ploughing. By contrast, semi-natural habitats such as field margin strips are temporally more stable areas in agricultural landscapes, offering suitable overwintering sites and resources for a wide range of arthropod species (Gallé et al., 2018; Geiger, Wäckers & Bianchi, 2009; Mestre et al., 2018). Field edges are often neighboured by semi-natural habitats such as grassy field margin strips or hedges and are permanent habitat strips that remain relatively undisturbed by agricultural management (Fischer et al., 2013). Thus, they host numerous arthropod species that are not able to persist in arable fields (Gallé et al., 2018).

The unstable nature of crop fields may lead to movement of arthropods from crop fields into adjacent non-crop habitats (Opatovsky & Lubin, 2012). This annual dispersal between crop fields and neighbouring semi-natural habitats was reported for predatory invertebrates (Madeira et al., 2016). Such spillover emphasizes the prominent role of landscape heterogeneity on biodiversity and ecosystem services. The two components of landscape heterogeneity are (1) composition, which can be measured as the diversity and abundance of different land use or land cover types and (2) configuration, referring to the size and spatial arrangement of land cover patches (Fahrig et al., 2011). The effects of

both components are relatively well documented for farmland arthropods, especially for spiders and carabids (e.g., Fahrig et al., 2015; Gallé, Happe, Baillod, Tscharntke & Batáry, 2019; Palmu, Ekroos, Hanson, Smith & Hedlund, 2014). Pest suppression shows complex responses to landscape composition (Karp et al., 2018), with landscape simplification negatively affecting biological control potential by reducing the richness of service-providing predators (Dainese et al., 2019). In summary, landscape composition, but also landscape configuration can determine natural enemy and pest populations according to a recent review (Haan, Zhang & Landis, 2020), and thus shape the efficiency of pest control (Tscharntke et al., 2016).

Several studies on biodiversity conservation efficiency of different AESs have focused on species richness and abundance of organisms. However, relatively little is known about AES effects on the functional diversity of arthropods (but see e.g. Gallé et al., 2019; Gayer, Lövei, Magura, Dietrich & Batáry, 2019). The trait-based functional diversity concept includes biologically important information directly into statistical models, thereby enhancing the generalisation of results (Gallé & Batáry, 2019). These results may also be used as a proxy for ecosystem functions and services, such as predation and natural control of pests. Biological control is an important regulating service that can increase crop production while contributing to the reduction of pesticide use (Naranjo, Ellsworth & Frisvold, 2015). Polyphagous invertebrate predators such as carabids and spiders effectively suppress pests, being important components of agricultural ecosystems (Losey & Denno, 1998). They are among the major contributors of biological pest-control, providing essential ecosystem services and promoting sustainable agriculture (Samu & Szinetár, 2002). Predator species differ in their potential to suppress pests (Birkhofer et al., 2016; Lang, Filser & Henschel, 1999). For example, web-building spiders are more effective in capturing mobile prey organisms, while active hunters feed more on sedentary or less mobile prey organisms (Michalko, Pekár & Entling, 2019). Therefore, it is important to account for species identity and species traits to draw general conclusions. Biological control efficiency of predatory arthropods depends on factors operating at different spatial scales from the local field to the landscape scale (Badenhausser et al., 2020; Rusch, Valantin-Morison, Sarthou & Roger-Estrade, 2010; Tscharntke et al., 2016).

We tested the ecological effectiveness of two popular AESs in Germany: wildflower strips next to winter wheat fields as off-field management and organic farming on winter wheat fields as on-field management. Furthermore, we tested the effect of local edge effects along a landscape-scale field size gradient on the functional traits of spiders and carabid beetles. We hypothesized that (1) management will affect trait composition, (2) landscape-scale field size will have an effect on functional trait state composition, (3) the contrast between field edges and interiors will affect trait composition.

Materials and methods

Study area and study design

We selected ten landscapes in Southern Lower Saxony (Germany) along a gradient of increasing landscape-scale field size during our two-year study (Appendix A). Economically the most important arable crop of the region is winter wheat (Batáry et al., 2017). In each landscape, we collected spiders and carabid beetles in three winter-wheat fields, with three different management regimes: conventional control, organic (on-field management), conventional with an adjoining 6–30 m wide flower strip (off-field management, CFS). The scheme for annual flower strips (“BS11 – einjährige Blühstreifen”) is the most popular in Lower Saxony (AES Lower Saxony, 2012). Seed mixtures contained at least five flowering plant species designed for providing flowers between June and October. Strips were planted until mid-April between the grassy margin and the field edge, and they were left untouched until February of the following year. In each landscape, the selected fields were situated within the area of one village close to each other with maximum distance of 3.7 km (1636 ± 176 , mean \pm SEM m in 2016 and 1666 ± 197 , mean \pm SEM m in 2017), in order to minimize edaphic and climatic differences among them. The selected fields belonged to 20 different farmers, as the conventional field and CFS fields within the same landscape belonged to the same farmer.

In each field we set up transects at two positions, (i) field edge between the first and second crop row, adjacent to a grassy margin, and (ii) the field interior, 10 m from field edge. Each transect was 20 m long and in parallel to the edge (Appendix B). Sampling was conducted over two consecutive years (2016 and 2017), thus we had 120 samples (10 landscapes \times 3 fields \times 2 transects \times 2 years). We changed fields in most cases due to crop rotation, and even farms in a few cases. The selected landscapes were digitalised based on the visual interpretation of the ArcGIS World Imagery, followed by ground truthing using ArcGIS software. To take into account potential landscape effects we measured mean arable field size within a 1000 m radius to characterize landscape configuration (3.41 ± 0.24 , mean \pm SEM ha; range 1.24 – 6.78 ha). All landscapes were dominated by agricultural land ($71.0 \pm 1.5\%$, mean \pm SEM, range 39.5 – 91.9).

Arthropod sampling and ecological traits

We collected spiders and carabids with two pitfall traps at each transect (120 traps per year). Traps were plastic cups inserted into the ground, flushed with the soil surface (diameter = 10 cm, depth = 25 cm). Traps were fitted with a metal grid to preclude vertebrate bycatches and white plastic to reduce dilution of the preservative (20×20 cm, 8–10 cm above ground) (Császár, Torma, Gallé-Szpisjak, Tölgyesi & Gallé, 2018). We used 50% ethylene-glycol and

water solution as preservative to reduce the surface tension. The traps were open for two one-week sampling periods in each year

We used three functional traits (body size, feeding trait, dispersal ability). Mean body size of each spider and carabid species was a continuous variable, based on literature data in mm following Nentwig, Blick, Gloor, Hänggi and Kropf (2019) for spiders and Homburg, Homburg, Schaefer, Schultdt and Assmann (2014) for carabids. We log transformed body size values, to downweight the high values attributed to length of large arthropods. To characterize feeding of species we used hunting strategy for spiders (two categories: active hunter code: 0, web builder code: 1) and feeding preference for carabids (three categories: herbivore code: 0, omnivore code: 0.5 and predator code: 1) according to Cardoso, Pekár, Jocqué and Coddington (2011) and Laroche (1990), respectively. Finally, we described dispersal ability with ballooning propensity for spiders (non-ballooning species code: 0, rarely ballooning code: 0.5 and frequently ballooning code: 1; Blandenier, 2009) and with wing system for carabids (reduced or no wings, code: 0, either with developed or with reduced wings, code: 0.5 and fully developed wings, code: 1; Hurka, 1996).

Data analysis

Prior the analyses, we pooled the data of the two pitfall traps and the sampling periods within year of the same transect for spiders and carabids separately. We calculated community weighted mean (CWM) values for all traits and each transect (Ricotta & Moretti, 2011) to characterize functional diversity using the R package ‘FD’ (Laliberte & Legendre, 2010).

We tested the effects of arable field size in the landscape, management and transect position on spider and carabid functional traits by general linear mixed-effects models (GLMM) using the function ‘lmer’ of the package ‘lme4’ (Bates, Maechler, Bolker & Walker, 2015). We employed the factors ‘transect position’ (edge vs. interior) and farm ‘management’ (organic, conventional and conventional with flower strip) as categorical predictor variables and landscape configuration (mean arable field size in 1000 m radius buffer) as continuous variable and their two-way interactions in the models. As we had two transects in the same field and several fields belonged to the same farmer, we included nested random effects, with ‘field’ nested in ‘farmer’, ‘farmer’ nested in ‘village’ and ‘village’ nested in ‘year’. Full model in R-syntax was “lmer(y ~ (mean field size+management+transect position)^2 + (1year/village/farmer/field)”. We calculated all potential models nested in the global model using the ‘dredge’ function of the package ‘MuMIn’ (Barton, 2016). We ranked all candidate models according to Akaike’s Information Criteria, corrected for small sample sizes (AICc). The models with $< 6 \Delta AICc$ of the best model (i.e. the model with the lowest AICc) were subjected to model averaging with function ‘model.avg’.

We linked spider and carabid traits to our predictor variables (i.e. mean field size, management and transect position) with the co-inertia analysis RLQ (Dolédec, Chessel, Ter Braak & Champely, 1996) using three data matrices: predictor variables \times sampling site (R), species \times sampling site (L) and arthropod traits \times species (Q), with the package ‘ade4’ (Dray & Dufour, 2007). This multivariate analysis provides an ordination plot to summarize the joint structure amongst the three tables (Dray et al., 2014). Furthermore, we performed permutation test (Monte Carlo randtest, $n = 10,000$) to test whether site and species scores can be explained significantly by trait-environment relationships (Dray et al., 2014).

Results

During the two-year study, we recorded a total of 6303 adult spiders belonging to 91 species (Appendix C). The

most abundant species were linyphiid spiders *Oedothorax apicatus* (33.7%), *Oedothorax retusus* (7.1%), *Erigone atra* (6.2%) and *Tenuiphantes tenuis* (6.2%), accounting for 42% of the samples. In total, we collected 12,196 carabid beetles of 80 species (listed in Appendix D). The four most abundant species, *Pterostichus melanarius* (36.7%), *Anchomenus dorsalis* (20.7%), *Metallina lampros* (7.3%) and *Poecilus cupreus* (6.4%), accounted for 71.3% of the samples.

Transect position strongly affected all trait indices, except for carabid flight ability. We found smaller spiders, spiders with higher ballooning propensity and more web-builders in the field interior than at the field edge (Fig. 1, Table 1). Increasing field size had an effect on hunting strategy of spiders, indicating a shift towards web-builders (Fig. 1, Appendix E). Spider hunting strategy was significantly related to management, as linear models and model averaging indicated a shift towards web builders in conventional fields with flower strip than conventional fields (Fig. 1, Appendix E). Furthermore, we found more carnivore carabids, as well

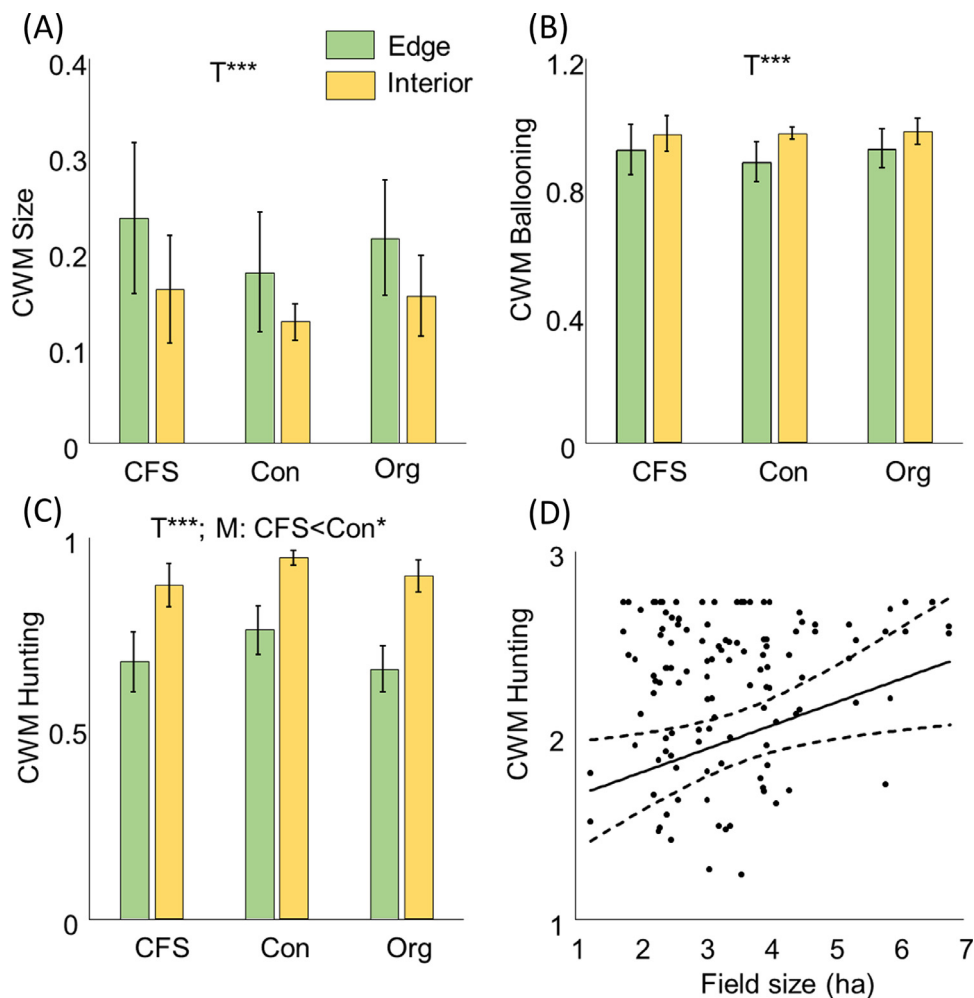


Fig. 1. Functional diversity indices of spider communities (A) Community weighted mean (CWM) of body size (continuous; in mm), ranging from 0 (smallest species) to 1 (largest species); (B) CWM ballooning (non-ballooning: 0, ballooning: 1); (C) CWM hunting strategy (active hunter: 0, web-builder: 1); (D) Effect of field size on CWM Hunting strategy. Error bars represent standard deviation. Transects (T), Management (M): conventional (Con); organic (Org); conventional with flower strip (CFS) and Field size (F). See Appendix F for model averaging results. Effect on each index including significance level are indicated above each plot, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 1. Summary table for GLMM results after multimodel averaging of best candidate models showing relative importance of each explanatory variable on spider functional diversity indices. The following traits were considered for spiders: body size (continuous variable in mm, log transformed values), feeding trait (web-builder, active hunter), dispersal ability (ballooning, non-ballooning species). CWM: Community weighted mean. For Carabids: body size (continuous variable in mm), feeding (herbivore, omnivore, predator), dispersal ability (marcopterous, dimorph wings, apterous/brachypterous).

Model ^a	Variable ^b	Relative importance ^c	Multimodel estimate ± 95% CI ^d		
Spiders					
CWM Size	Transect (E/I)	100%	−0.163 (−0.163)	±	0.040***
	Field size	18%	−0.033 (−0.006)	±	0.025**
	Manag.(Cfs/Con)	6%	−0.107 (−0.006)	±	0.070**
	Manag.(Cfs/Org)	6%	−0.025 (−0.001)	±	0.065
	Manag.(Org/Con)	6%	−0.082 (−0.004)	±	0.070**
CWM Hunting	Transect (E/I)	100%	0.440 (0.440)	±	0.091***
	Field size	17%	0.063 (0.010)	±	0.058*
	Manag.(Cfs/Con)	5%	0.170 (0.008)	±	0.157*
	Manag.(Cfs/Org)	5%	0.004 (0.001)	±	0.148
	Manag.(Con/Org)	5%	−0.069 (0.001)	±	0.126
CWM Ballooning	Transect (E/I)	100%	0.157 (0.157)	±	0.052***
Carabids					
CWM Size	Transect (E/I)	100%	0.073 (0.073)	±	0.049**
CWM Feeding	Transect (E/I)	100%	0.097 (0.097)	±	0.026***
	Field size	10%	0.028 (0.002)	±	0.023*
CWM Flight ability	—				

Management effect: Cfs (conventional with flower strip), Con (Conventional); Org (Organic).

^aModels were fitted with normal distribution.

^bTransect effect: E (edge) vs. I (interior) - positive value means higher number in interior.

^cEach variable's importance within the best candidate models ($\Delta AIC < 6$).

^dConditional and full model averages (in parenthesis) are given Significance levels: *: < 0.05 , **: < 0.01 , ***: < 0.001 .

as larger beetles, in field interiors than at field edges (Fig. 2, Table 1). Increasing field size had an effect on feeding of carabids, indicating a shift towards carnivore carabids (Fig. 2, Table 1). We did not find any significant interacting effects (Figs. 1 and 2). Further details of the models are given in Appendix E.

The RLQ analysis performed on spider data indicated a significant association between environmental attributes and species trait composition ($p < 0.001$, permutation test). The first RLQ axis separated the functional community composition based on management, while the second axis separated functional groups according to transect position and landscape. Web building spiders were associated with increasing field size, whereas larger spiders were associated with smaller field sizes and conventional fields with flower strip management. Ballooning spiders were associated with organic management and interior transect position (Fig. 3).

The carabid RLQ also showed a significant overall relationship between species trait composition and environmental attributes ($p < 0.01$, permutation test). First RLQ axis separated the functional composition based on management, second axis separated based on transect position and landscape. Carnivore beetles were associated with large fields. We found that larger carabids were associated with field interiors, whereas smaller beetles were associated with edges and conventional fields with flower strip management.

Carabids with good dispersal ability were associated with organic management.

Discussion

We found pronounced effects of the field edge compared to the field interior, as it affected all traits, with the exception of carabid flight ability. Smaller spiders, spiders with higher ballooning propensity and more web-builders were in the field interior than at the field edge, whereas carnivorous beetles were more abundant in the field interior. Management affected spider hunting strategy with more web-builders associated with conventional fields than conventional fields with flower strips (CFS). Furthermore, we found a strong effect of mean field size per landscape on the feeding traits of spiders and carabids, as increasing field size was associated with more web-building spiders and more carnivore beetles.

Landscape effect

Configurational landscape heterogeneity can be measured as density of field borders, which is negatively correlated with mean field size. Large fields correspond to low

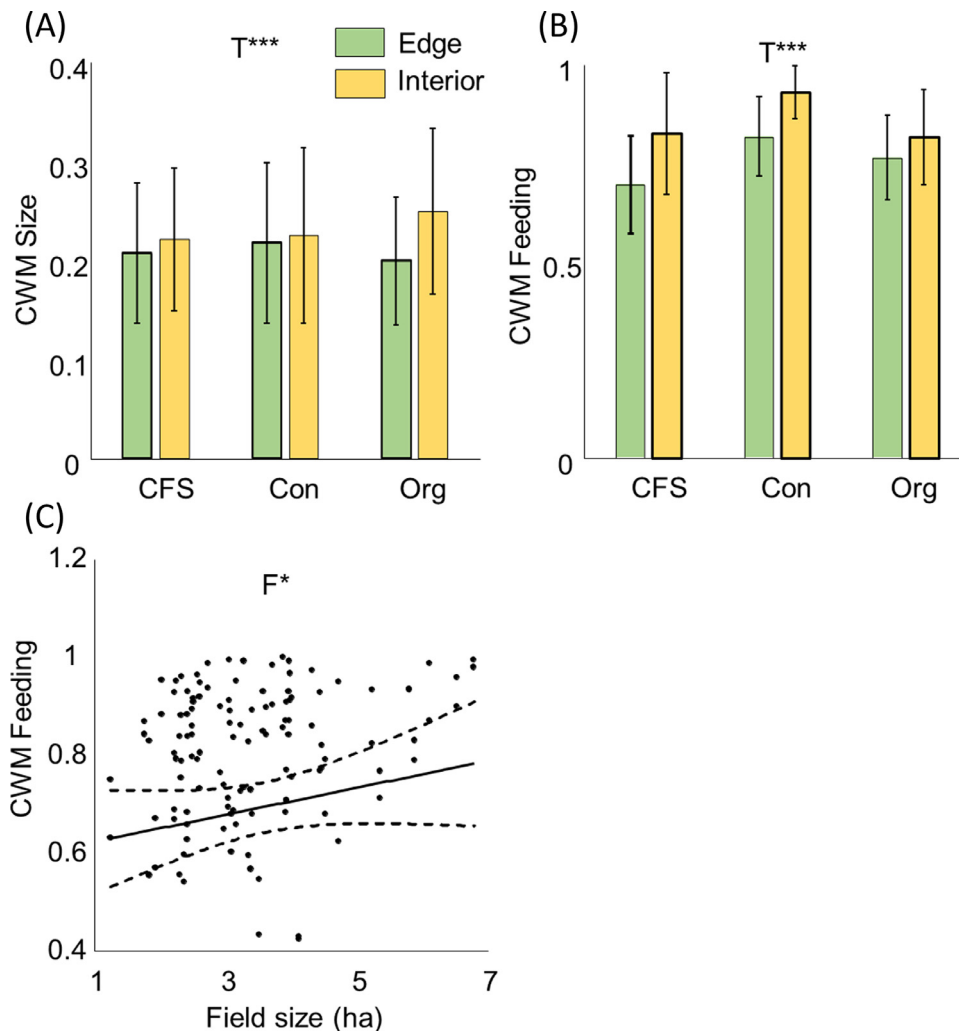


Fig. 2. Functional diversity indices of carabid communities. (A) CWM of body size (continuous; in mm), ranging from 0 (smallest species) to 1 (largest species); (B) Community weighted mean (CWM) Feeding (herbivore: 0, omnivore: 0.5 and carnivore: 1); (C) Effect of field size on CWM Feeding; (C), Error bars represent standard deviation. Transects (T), Management (M): conventional (Con); organic (Org); conventional with flower strip (CFS) and Field size (F). See Appendix F for model averaging results. Effect on each index including significance level are indicated above each plot, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

configurational heterogeneity at the landscape scale (Fahrig et al., 2011). Several studies demonstrated that landscape configuration does not have a strong effect on spider diversity in agricultural landscapes (e.g. Batáry et al., 2017; Gallé et al., 2018, 2019; Nardi, Lami, Pantini & Marini, 2019). However, we found that spider communities of larger fields were dominated by web-builders. Furthermore, large scale agriculture (i.e. low configurational heterogeneity) was also associated with small body size of spiders according to the RLQ ordination plot. The majority of agrobiont ground-dwelling spiders are lycosids (Samu & Szinetár 2002), which rarely balloon. The ground dispersal of lycosids is presumably slower than the aerial dispersal of the dominant web builder spider family, Linyphiidae. Therefore, during field colonization, lycosids may contribute less to early season pest control on large than on small fields. Predator body size is an efficient predictor of per capita prey consumption

and the reduction of prey biomass (Emmerson & Raffaelli, 2004). The low proportion of large spiders in landscapes with low configurational heterogeneity could result in lower mass of consumed prey items, and a lower biocontrol potential. In their synthesis, Martin et al. (2019) and Sirami et al. (2019) also suggested that high configurational heterogeneity can promote functional biodiversity and biological control in agroecosystems.

Local characteristics may affect carabid trait distribution more strongly than landscape structure (Gayer et al., 2019; Mader et al., 2017). However, several studies reported landscape filtering on flight ability (Hendrickx et al., 2009; Wamser, Diekotter, Boldt, Wolters & Dauber, 2012) and body size (Duflot, Georges, Ernoult, Aviron & Burel, 2014; Gallé et al., 2019). We found that carnivore carabid species were clearly associated with landscapes of larger fields, whereas small-scale landscapes were dominated by

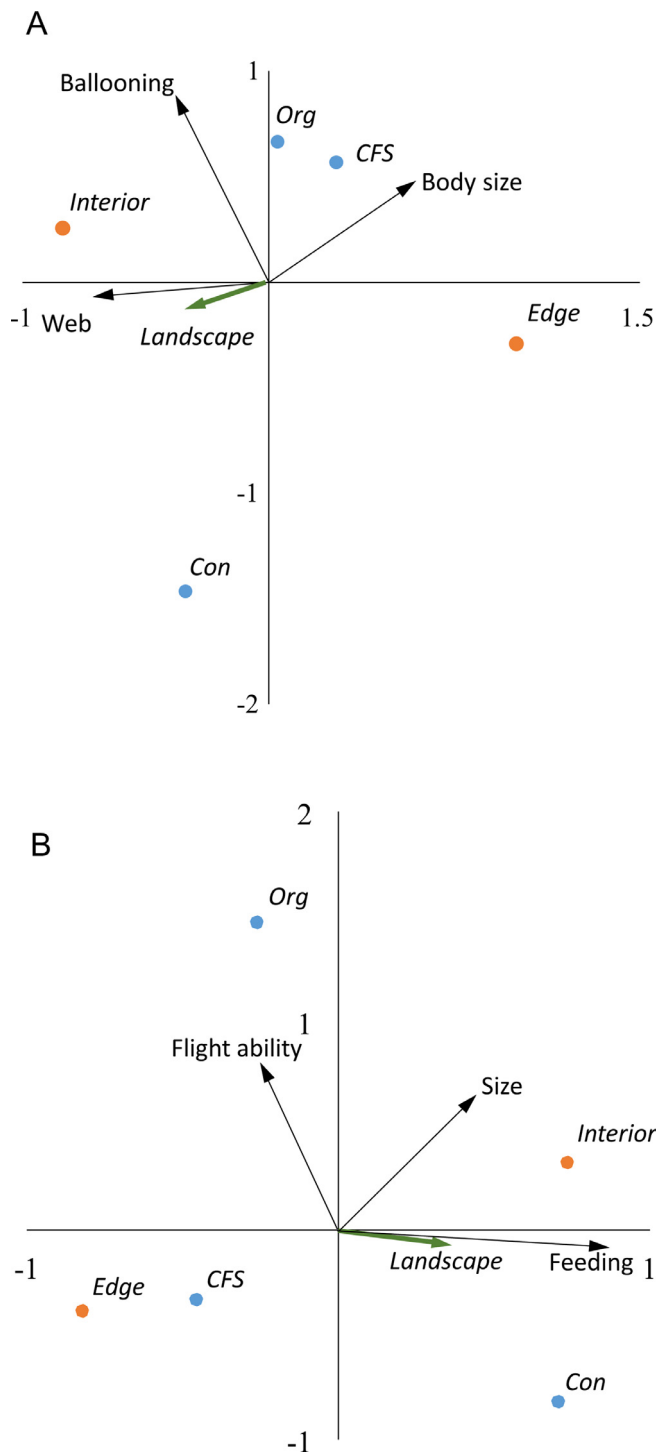


Fig. 3. Ordination plot of the RLQ analyses for spiders (A) and carabids (B). Management and transect descriptors (dots), landscape (green arrow), and species trait categories (black arrows) along the two first axes are indicated. Management: conventional (Con); organic (Org); conventional with flower strip (CFS).

herbivores. This is in line with the results of Labruyere, Bohan, Biju-Duval, Ricci and Petit (2016), who showed landscape scale effect on common herbivore carabids. Carabids in agricultural landscapes are considered to

be food-limited, they presumably depend on temporally stable food resources (Bommarco, 1998). In small-scale agricultural landscapes, the higher density of field margins may serve as important alternative trophic resources for herbivore beetles, as such configurational heterogeneity increases arable plant diversity (Alignier et al., 2020).

Off-field vs. on-field agri-environmental schemes

Conventional fields with flower strip management were situated near to organic fields on the spider RLQ ordination plot, indicating a similar trait composition of the two management types. Larger spiders with higher ballooning propensity characterize fields under CFS and organic management AES. Furthermore, we found more web builders in CFS fields than in conventional fields. The mean body size of predatory arthropods decreases with increasing management intensity (Blake, Foster, Eyre & Luff, 1994), and smaller predator size may result in lower biocontrol potential of spiders. Thus pest predation is probably higher in organic than in conventional fields (Birkhofer et al., 2016). As a consequence of increased propensity for aerial dispersal in fields under organic and CFS AES management, spiders presumably colonise field interiors of organic and CFS fields earlier than conventional fields and may impede pest outbreaks efficiently, also emphasizing the beneficial effect of both organic and CFS management on spider biocontrol potential. Web-building species rely more on structural properties of plants and therefore benefit from more complex vegetation in arable fields than ground-dwelling spiders (Diehl, Mader, Wolters & Birkhofer, 2013). Organic management leads to increased weed diversity (Henckel, Börger, Meiss, Gaba & Bretagnolle, 2015) and creates structurally more diverse habitats, also offering more potential web-attaching points for web builder spiders. Local web-building spider diversity at sites under low management intensity can contribute to aphid suppression even at the landscape scale, although, their per capita efficiency for aphid predation may decrease with increasing vegetation complexity (Diehl et al., 2013).

Well-dispersing carabids were associated with fields under organic management AES. Furthermore, we found smaller beetles in CFS fields. Organic farming does not always enhance carabid species richness compared to conventional fields, but may differ in species identity and trait composition (Purtauf et al., 2005). Carabids capable of flying may colonise organic fields rapidly, and may exert a controlling effect on weed and insect pest species. Although dispersal is enhanced by flight ability, carabid beetles can also disperse effectively on the ground. The distance that a carabid species can travel by walking is highly correlated with its size (Bertrand, Burel & Baudry, 2016), indicating that the community of CFS fields comprised relatively poor disperser species. CFS management may establish relatively stable complementary habitats,

flower strips may offer an opportunity for poor dispersers to colonise. We did not find a pronounced management effect on carabids. However, sown wildflowers have been shown to be beneficial for carabid abundance and species richness (Aviron et al., 2007). Perennial wildflower strips may offer overwintering sites and supplementary resources for carabids such as additional prey items for carnivores (Frank & Reichhart, 2004).

Edge effect

We found that transect position had a strong effect on almost all spider and carabid traits. Spiders were smaller in the field interior than in the field edge, whereas we found larger carabids in the field interior than in the field edge. The size of predator species plays an important role in prey-predator relationships, in terms of consumed species and predation rate, thereby influencing biological control potential (Rusch, Birkhofer, Bommarco, Smith & Ekblom, 2015). Field edges were beneficial for herbivorous beetles, presumably because they benefit from the richer flora they may feed on (Pecheur, Piqueray, Monty, Dufrière & Mahy, 2020). However, field interiors were dominated by carnivore carabids, as pest species may serve as an important food resource for them (Rusch et al., 2015). Arable fields are regularly disturbed by management, such as ploughing. The adjoining semi-natural habitats offer overwintering sites and supplementary resources for arthropods (Gallé et al., 2018) and harbour source populations for spillover towards arable fields. Field edges are situated close to these source habitats, benefiting species with low dispersal ability. In fact, species richness is typically higher at field edges than in the interiors of fields (Schmidt-Entling & Döbeli 2009). We found spiders with higher ballooning propensity in the field interior than in the field edges. Different dispersal strategies of arthropods appeared to result in specific distribution patterns of species traits in field edge and interior habitats (Gayer et al., 2019).

In conclusion, we found field interiors and edges had different trait state composition for carabids and spiders, emphasizing that small-scale agriculture with high landscape-scale edge density may enhance within-field functional diversity and presumably ecosystem services. This effect was stronger than the effect of off-field and on-field AESs, highlighting indirectly the importance of landscape configuration in shaping functional traits and presumably ecosystem services in agricultural landscapes.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2020.09.006.

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