


RESEARCH ARTICLE

Landscape configuration, organic management, and within-field position drive functional diversity of spiders and carabids

Róbert Gallé^{1,2}  | Anne-Kathrin Happe^{2,3} | Aliette Bosem Baillod^{2,4} |
Teja Tscharnatke² | Péter Batáry^{2,5} 

¹Department of Ecology, University of Szeged, Szeged, Hungary

²Agroecology, University of Goettingen, Göttingen, Germany

³Ecological Networks, Technische Universität Darmstadt, Darmstadt, Germany

⁴Agricultural Landscapes and Biodiversity Group, Research Station Agroscope Reckenholz-Taenikon ART, Zürich, Switzerland

⁵GINOP Sustainable Ecosystems Group, MTA Centre for Ecological Research, Tihany, Hungary

Correspondence

Róbert Gallé

Email: galle.robert@gmail.com

Funding information

Deutsche Forschungsgemeinschaft, Grant/Award Number: BA 4438/1-1

Handling Editor: J. Scott MacIvor

Abstract

1. Agricultural management intensity and landscape heterogeneity act as the main drivers of biodiversity loss in agricultural landscapes while also determining ecosystem services. The trait-based functional diversity approach offers a way to assess changes in community functionality across agroecosystems. We focused on carabids and spiders, because they are an important component of crop field biodiversity and have significant biological control potential.
2. We assessed the effect of small- vs. large-scale agricultural landscapes, organic farming, and within-field position on functional diversity of spiders and carabids. We sampled pairs of organic and conventional winter wheat fields in small-scale agricultural landscapes (former West Germany) and in neighbouring large-scale agricultural landscapes (former East Germany). We sampled arthropods with funnel traps in transects at field edges, field interiors (15 m from edge), and field centres.
3. The gradient from field edges towards the centres played an important role: spider body size decreased; ballooning ability increased, and hunting strategy switched from active hunters to more web-builders—presumably, due to higher microhabitat stability in the field centre. Higher trait diversity of spiders in field edges suggested higher biocontrol potential in small-scale agriculture. In contrast, carabid feeding switched from herbivores to carnivores, presumably due to higher pest densities inside crop fields. Furthermore, small-scale agricultural landscapes and organic management supported larger, i.e., less dispersive carabids.
4. *Synthesis and applications.* In our research, spiders were more sensitive to edge effects and less sensitive to management and landscape composition than carabids. Smaller fields and longer edges, as well as organic management increase carabid functional diversity, which may increase resilience to environmental change. Since many spider species are confined to field edges, the effect of within-field position on functional diversity is more important in small-scale agricultural landscapes with more edge habitat than in large-scale agricultural landscapes. Our findings suggest that European Union policy should acknowledge the high benefits of small-scale agriculture for the functional role of major predators such as spiders and carabid beetles, as the benefits are equal to those from a conversion to organic agriculture.

KEYWORDS

agricultural management, arthropods, edge effect, functional diversity, functional trait, landscape heterogeneity, organic farming, pest control

1 | INTRODUCTION

Biodiversity loss in agricultural landscapes has been driven by the spread of intensive agricultural management, which has led to a decline in ecosystem services such as biological pest control (Batáry, Báldi, Kleijn, & Tscharntke, 2011; Sutcliffe et al., 2015; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). The intensification of local agricultural practices, such as fertilizer and pesticide use, together with landscape simplification, such as enlarged farmland size, decreases the number of crop types and the amount of seminatural landscape elements. These processes are all potential contributors for the loss of biodiversity (Bertrand, Burel, & Baudry, 2016; Ekroos, Olsson, Rundlöf, Wätzold, & Smith, 2014).

Organic agricultural methods are reported to increase biodiversity in the agricultural landscape (Tuck et al., 2014); however, the effect of organic farming is highly heterogeneous, the results are taxon-specific (Bengtsson, Ahnström, & Weibull, 2005), and the effectiveness may depend on the landscape context (Batáry et al., 2011; Tscharntke et al., 2012). Low-intensity agricultural land use is enhanced by different incentives in many countries. In the European Union, agrienvironment schemes are a major source of nature conservation funding and exist in all member states (Batáry, Dicks, Kleijn, & Sutherland, 2015). The main aim of the programs focusing on organic farming is to reduce management intensity through abolishment of pesticide and inorganic fertilizer inputs (Tuck et al., 2014).

In agricultural landscapes, spatial heterogeneity, which is a combination of compositional and configurational heterogeneity (Dufлот, Georges, Ernoult, Aviron, & Burel, 2014; Fahrig et al., 2011), is regarded as an important driver of biodiversity. Landscape composition can be measured as the variety and abundance of different cover types, whereas configuration refers to the complex spatial arrangement, size, and position of landscape elements or the cumulative length of edges (Concepción, Díaz, & Baquero, 2008; Fahrig et al., 2011). Landscape structure is particularly important for arthropod assemblages, as several studies found an increase in spider and carabid diversity with spatial heterogeneity (e.g., Fahrig et al., 2015; Palmu, Ekroos, Hanson, Smith, & Hedlund, 2014). However, studies addressing configurational heterogeneity controlling for compositional heterogeneity are scarce (Pasher et al., 2013; Perović et al., 2015). Recent research has shown that several species of the same taxonomic group may respond differently to landscape configurational heterogeneity gradients (Dufлот et al., 2014; Neumann, Griffiths, Hoodless, & Holloway, 2016). Here, we addressed the effect of high landscape configurational heterogeneity, which can be obtained by reducing field sizes (Fahrig et al., 2011).

The historical division of Germany after the World War II resulted in different landscape structures of the former East and West Germany. After the collectivization in the 1950s, agricultural management in East Germany switched to large-scale homogeneous agriculture. The differences in landscape structure are still visible (Batáry et al., 2017). The average farm size is six times bigger in the Eastern part of Germany (Batáry et al., 2017), offering the opportunity to study the effect of configurational landscape heterogeneity under similar agricultural management and climatic conditions.

Trait-based functional diversity can be defined as the relative abundance, range, and dispersion of functionally meaningful life-history trait values of organisms. It relates the functional trait characteristics of species to ecosystem properties and functioning (Díaz et al., 2007; Petchey & Gaston, 2006). For example, the higher functional diversity of predatory arthropods of agroecosystems implies not only different hunting strategies and prey items, but also a higher potential for biological pest control (Letourneau & Bothwell, 2008). Thus, the functional diversity approach offers a useful tool to assess ecosystem functions and services (Díaz & Cabido, 2001). Recent research shows increasing interest in the link between functional diversity and land use change (Sams et al., 2017), with some studies focusing on the effect of configurational heterogeneity on invertebrate functional diversity (Neumann et al., 2016; Perović et al., 2017). However, there is a need to address the effects of land use change on functional diversity along a landscape heterogeneity gradient (De Lima, Dallimer, Atkinson, & Barlow, 2013). Furthermore, relatively little is known about the effect of edges on the functional diversity of arthropods (but see e.g., Gallé, Szabó, Császár, & Torma, 2018; Krauss, Gallenberger, & Steffan-Dewenter, 2011).

Many carabid beetles and all spiders are polyphagous predators commonly found in winter wheat (*Triticum aestivum*). They are among the most important biological control agents of winter wheat pests (Diekötter, Wamser, Wolters, & Birkhofer, 2010). The aim of our study was to compare the effectiveness of organic farming for conservation of spider and carabid functional diversity in small- vs. large-scale agriculture, and thereby to assess the effect of configurational heterogeneity on within-field patterns of functional diversity. We selected pairs of organic and conventional fields in small-scale agricultural landscapes in the former West (lower Saxony) and in large-scale agricultural landscape in the former East (Thuringia) Germany. We hypothesized that (a) smaller fields have higher functional diversity than large fields, (b) organic farming supports more functional diversity than conventional farming, and (c) contrast between field edges and centres is lower in small fields than in large fields. The overall goal of our study was to provide evidence how landscape structure, organic farming, and within-field position shape spider and carabid functional diversity.

2 | MATERIALS AND METHODS

2.1 | Study sites

We selected nine pairs of organic and conventional winter wheat fields in Thuringia, in the Eastern part of Germany and another nine pairs in the Western part of Germany in Lower Saxony ($N = 36$). We selected winter wheat as it is the economically most important arable crop of the region (Batáry et al., 2017). The average size of organic fields was 21.7 ± 5.5 ha (East, mean \pm SEM) and 3.7 ± 0.7 ha (West) and the average size of conventional fields was 18.3 ± 2.1 ha (East) and 3.3 ± 0.3 ha (West) (for further details and map see Batáry et al., 2017). The major difference in the landscape structure between East and West was due to landscape configuration. Configurational heterogeneity was higher in the West with 70% more field edges (11.0 ± 0.8 km East organic (mean \pm SEM); 10.8 ± 0.6 km East conventional; 18.3 ± 1.3 km West organic, and 19.5 ± 1.2 km West conventional).

We selected fields belonging to one pair within the area of one village close to each other (2598 ± 583 m East [mean \pm SEM]; 1101 ± 216 m West). We selected three villages with one pair of organic and conventional fields (in both East and West) and we had three villages with two organic and conventional field pairs resulting in a cross-nested sampling design (Batáry et al., 2017). We explored the functional diversity pattern within fields with transects at three positions, (a) field edge, (b) field interior, 15 m from field edge, and (c) field centre, 120 and 75 m from field edge in large and small fields, respectively (Figure S1).

2.2 | Arthropod sampling and ecological traits

We collected arthropods using a pair of funnel traps at each transect inserted into the ground, flushed with the soil surface (diameter = 10 cm, depth = 25 cm). We used 50% ethylene-glycol and water solution as preservative and a few drops of odourless detergent (Drogerie Markt, Denkmittel Spülmittel Ultra Sensitive) to reduce the surface tension. The traps were applied with a funnel to reduce vertebrate by-catches and a plastic roof (25×25 cm, 8–10 cm aboveground level) to prevent the dilution of preservative (Lange, Gossner, & Weisser, 2011). In each transect, we placed traps at least 10 m from each other. There were two 1-week long sampling periods with 5 weeks break between them. We chose sampling dates in mid-May and late June (2013) before the full ripening of wheat. The funnel trap contents were preserved in 70% alcohol for further identification. Adult spiders and carabids were identified to species using standard keys (Hurka, 1996; Nentwig, Blick, Gloor, Hänggi, & Kropf, 2017). Voucher specimens are stored in the collection of Agroecology, University of Göttingen (carabids) and in the collection Department of Ecology, University of Szeged (spiders).

We selected three ecological traits for spiders and carabids (body size, feeding trait, dispersal ability). Average body size of each species was given as continuous variable using literature data in mm following Nentwig et al. (2017) for spiders and Homburg, Homburg,

Schaefer, Schuldt, and Assmann (2014) for carabids. We ranged body size values between 0 and 1 to down weight the high values attributed to length of large arthropods. We used spider hunting strategy (web-builder, active hunter; coded as 0 and 1, respectively) and carabid feeding preference (herbivore, omnivore and carnivore; coded as 0, 0.5 and 1, respectively) as feeding trait (Cardoso, Pekár, Jocqué, & Coddington, 2011; Larochelle, 1990). Finally, we classified spider species as either frequently ballooning (code: 1), rarely ballooning (code 0.5) or nonballooning species (code: 0; Blandenier, 2009) and carabid species wing system as macropterous (fully developed wings, code: 1), dimorph (either with developed or with reduced wings, code: 0.5), or apterous/brachypterous (reduced or no wings, code: 0; Hurka, 1996; Hendrickx et al., 2009), which corresponds to the dispersal ability of species.

2.3 | Data analysis

We analysed transects ($N = 108$), thus we pooled data from the two funnel traps and two collection periods (Madeira et al., 2016), for spiders and carabids separately. We calculated community weighted mean values (CWM), i.e., the average of trait values weighted by the relative abundances of each species for each trait at each transect position (Lavorel et al., 2008; Ricotta & Moretti, 2011). We also calculated functional divergence (FDvar), which shows higher values when the abundance is increasing towards either one or both margins of the trait distribution, and which is lower when abundance is concentrated towards the average value of the trait (Pla, Casanoves, & Di-Rienzo, 2012). We calculated FDvar indices according to Lepš, de Bello, Lavorel, and Berman (2006), and we used the R package (FD) to calculate CWM indices (Laliberté & Legendre, 2010).

To test whether landscape configuration, management type, transect position, and their second-order interactions had a significant effect on the trait composition and functional diversity of spiders and carabids, we used linear mixed effects models and model averaging. We used lmer (lme4, Bates, Maechler, Bolker, & Walker, 2014) models with random effect terms that included "field pair" embedded in "village" and "farmer". The suite of all possible linear combination of predictor variables of the above models was used to generate parameter estimates for landscape configuration, field management, and within-field position. Akaike's Information Criteria corrected for small sample sizes (AIC_c) was calculated to rank candidate models. The models with $<6 \Delta AIC_c$ of the best model (i.e., the model with the lowest AIC_c) were used for model averaging (Bolker et al., 2009; Richards, 2008) with the R package MuMIn (Barton, 2009).

We used a three-table ordination method, the RLQ analysis to test the direct link between environmental conditions and spider or carabid species trait attributes. This analysis uses three data matrices (Matrix R: landscape and management attributes by sites, Matrix L: species by sites, Matrix Q: species by traits). The RLQ analysis is an extension of coinertia analysis, which simultaneously takes into account the information contained in the tables R, L, and Q. It graphically summarizes and represents the main costructure in the

three matrices (Dray, Chessel, & Thioulouse, 2003). The overall significance of the relationships between variables of the R-tables and species traits of the Q-tables was assessed by a Monte-Carlo test with 5000 permutations on total inertia of the RLQ analyses. Finally, we tested the link between site scores and environmental variables using Kendall tau rank correlation coefficients. We tested the link between species scores and trait values using Kendall tau for categorical variables and Spearman correlations for body size, the only continuous variable (Carrié et al., 2017). Analyses were conducted in R using the ade4 package (Dray & Dufour, 2007).

3 | RESULTS

3.1 | Spiders

From the 36 winter wheat fields, we recorded 4769 adult spiders belonging to 71 species (Appendix S1). The most abundant species were aerial dispersers such as linyphiid spiders, *Oedothorax apicatus* (Blackwall, 1850) and *Erigone dentipalpis* (Wider, 1834), representing 45.5% of all spider individuals caught. We captured 56 species and 2124 individuals in conventional fields; 53 species and 2645 individuals in organic fields; 57 species and 2159 individuals in East Germany; 48 species and 2600 individuals in West Germany.

Transect position strongly affected all trait indices (CWM, FDvar) of functional diversity, except FDvar body size. We found a significantly higher proportion of web-builders, and larger bodied spiders at the edge than in the field centre. Whereas more active hunters and ballooning spiders occurred in the centre than in the edge. FDvar for hunting strategy and ballooning was significantly related to within-field position, as linear models and model averaging indicated higher values in the field edges than in the centre; however, landscape configuration and organic management had no significant effect (Figure 1, Appendix S2). We did not find any significant effect of interactions.

The spider RLQ analysis indicated a significant relationship between environmental attributes and species trait composition ($p < 0.001$, permutation test). The first two RLQ axes explained 90.5% of the total inertia (64.6% and 25.6%, respectively). The RLQ plot revealed that web-building, nonballooning, and large spiders were associated with edge habitats. Ballooning spiders were associated with interior and centre transect position (Table 1, Figure 2a).

3.2 | Carabids

From the two sampling periods, we collected 14986 carabid beetles belonging to 89 species. The most abundant species were

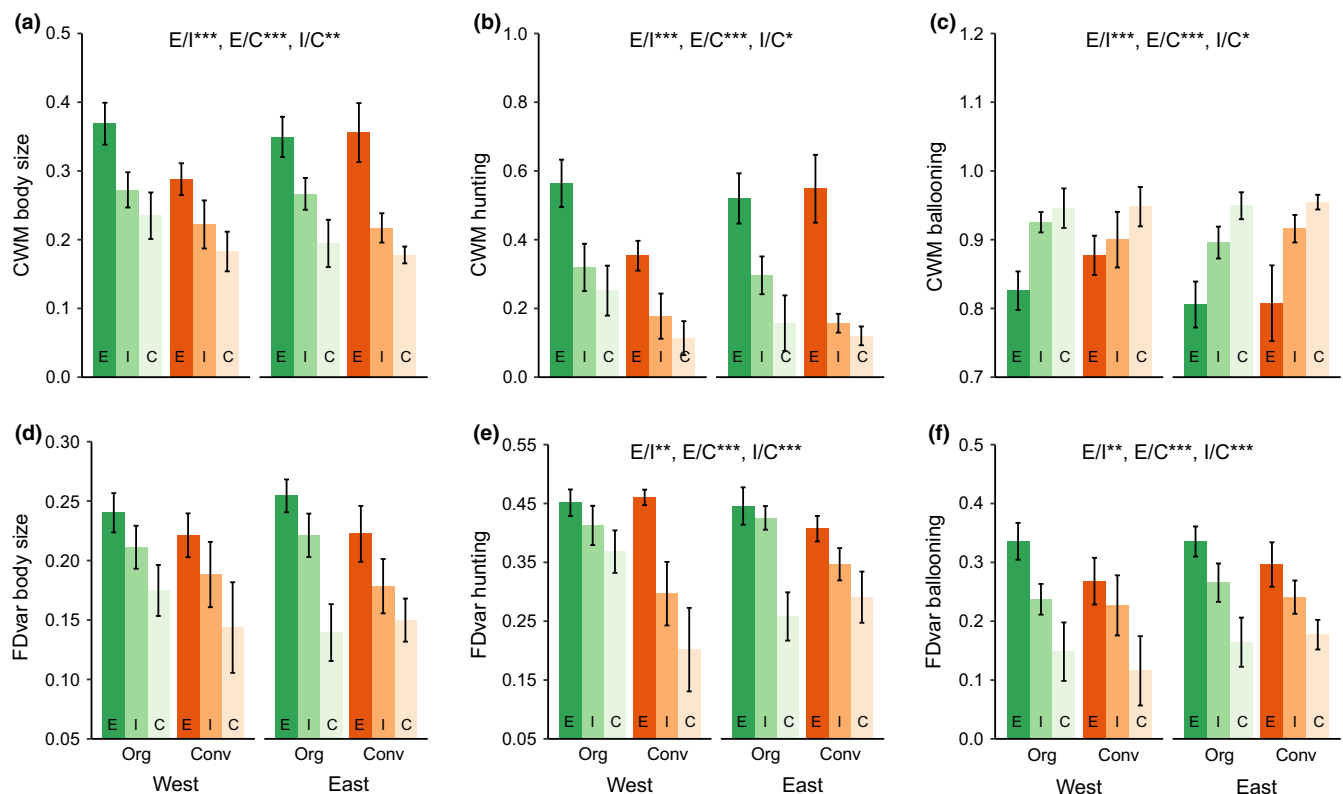


FIGURE 1 Functional diversity indices of spider communities in organic (Org) and conventional (Conv) fields in small-scale (West) and large-scale (East) agricultural landscapes. (a) Community weighted mean (CWM) of body size (continuous in mm and ranged between 0 and 1); (b) CWM hunting strategy (active hunter: 0, web-builder: 1); (c) CWM ballooning (nonballooning: 0, ballooning: 1); (d) Functional divergence (FDvar) size; (e) FDvar hunting strategy; (f) FDvar ballooning; Transects: E: field edge; I: interior; C: centre (see Table S2 for model averaging results) * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

TABLE 1 Correlations between the first two RLQ axes with both environmental descriptors and species traits. Correlation coefficient (corr. coeff.) for factorial variables is Kendall's tau, for the only continuous variable (body size) it is Spearman's rho

	First RLQ axis		Second RLQ axis	
	Corr. coeff.	p-value	Corr. coeff.	p-value
Spiders, environmental variables				
Region (E/W)	0.164	0.045	0.615	<0.001
Management (C/O)	0.369	<0.001	0.492	<0.001
Transect position (Centre)	0.565	<0.001	0.001	0.999
Transect position (Interior)	0.130	0.112	-0.261	0.002
Transect position (Edge)	-0.696	<0.001	0.261	0.002
Spiders, traits				
Body size	-0.544	<0.001	0.091	0.448
Dispersal: ballooning	-0.475	<0.001	-0.206	0.035
Dispersal: probable ballooning	0.225	0.021	0.257	0.008
Dispersal: nonballooning	0.352	<0.001	-0.001	0.998
Hunting: web/active	-0.563	<0.001	0.493	<0.001
Carabids, environmental variables				
Region (E/W)	0.738	<0.001	0.369	<0.001
Management (C/O)	0.287	<0.001	0.738	<0.001
Transect position (Centre)	0.001	0.999	0.001	0.999
Transect position (Interior)	-0.261	0.001	-0.174	0.034
Transect position (Edge)	0.261	0.001	0.174	0.034
Carabids, traits				
Body size	0.186	0.080	0.366	<0.001
Feeding: carnivore	-0.486	<0.001	0.026	0.763
Feeding: omnivore	0.257	0.003	-0.008	0.921
Feeding: herbivore	0.399	<0.001	-0.029	0.733
Flight ability: macropterous	0.059	0.496	-0.069	0.424
Flight ability: dimorph	-0.060	0.489	0.110	0.207
Flight ability: apterous	-0.001	0.901	-0.031	0.718

Anchomenus dorsalis (Pontoppidan, 1763) and *Poecilus cupreus* (Linne, 1758), representing 37.3% of the total carabid abundance (Appendix S3). We identified 72 species and 6240 individuals from conventional fields; 71 species and 8622 individuals from organic fields; 78 species and 8045 carabids from East Germany, 67 species and 6851 carabids from West Germany. Region had a significant effect on carabids, as we found larger species (CWM of size) and more carnivorous carabids (CWM food) with higher variance in feeding preference (FDvar food) in large- than in small-scale agricultural landscapes. Organic management had a significant negative effect on the variance in flight ability (FDvar flight ability) and we found larger carabids and larger variance of carabid body size in organic than conventional fields (CWM size and FDvar size). We did not find any significant effect of interactions (Figure 3, Appendix S4).

The RLQ analysis performed on carabid data also showed a significant overall association between species trait composition and environmental attributes ($p < 0.01$, permutation test). First and second RLQ axes explained 84.12% of the total inertia (59.6% and 24.5%, respectively). Herbivore and apterous carabids were associated with edge position and large-scale agriculture, whereas carnivore carabids with interior position (Table 1, Figure 2b).

4 | DISCUSSION

In accordance with our hypotheses (1) and (2), we found positive effects of increasing landscape configurational heterogeneity (i.e., smaller field size in West Germany) and organic management on carabid functional diversity. Concerning hypothesis (3), transect

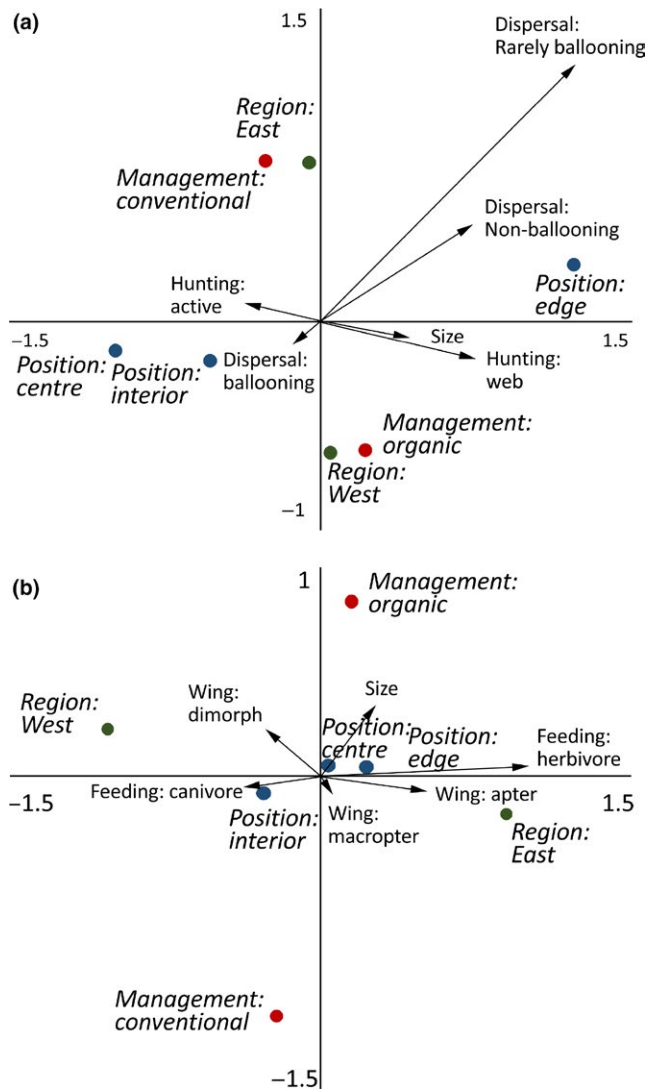


FIGURE 2 Ordination plots of landscape, management and transect descriptors (dots), and species trait categories (arrows) along the two-first axes of the RLQ analysis, for (a) spiders and (b) carabid beetles

position affected spider but not carabid communities, irrespective of landscape configuration and management type, with higher functional diversity towards the field edges.

4.1 | Landscape effects

Smaller field sizes at a landscape scale indicate a higher density and, thereby, presumably connectivity, through seminatural linear habitats (e.g., field margins, road verges), and thus, higher landscape configurational heterogeneity. We found that variation in carabid dispersal ability decreased with lower landscape configurational heterogeneity while higher configurational heterogeneity (small fields in our study) was associated with lower dispersal ability and smaller carabids. Body size of carabids is known to relate to their epigeic dispersal ability, with larger species moving longer distances than smaller carabids (Homburg, Schuldt, Drees, & Assmann, 2013).

Landscape simplification, including reduced habitat quantity and lower matrix quality, may have a negative effect on species with high dispersal probabilities through increased dispersal mortality (Tscharrntke et al., 2012). The decrease in carabid abundance, may result in lower biocontrol potential.

Landscape configuration had no effect on spider functional diversity according to the regression models. In line with these results, Martin, Seo, Park, Reineking, and Steffan-Dewenter (2016) did not find significant effects of landscape configuration on spiders. However, landscape configurational heterogeneity increases with the density of seminatural habitat-arable field interfaces that may facilitate the spillover of predator arthropods from edges into neighbouring fields (Martin, Reineking, Seo, & Steffan-Dewenter, 2013). It may also increase the pool of species related to natural and seminatural habitats due to small-scale habitat diversity (Purtauf et al., 2005). Thus, complex landscapes are generally associated with increased diversity of generalist arthropods (Chaplin-Kramer, O'Rourke, Blitzer, & Kremen, 2011), irrespective of management type (Schmidt, Roschewitz, Thies, & Tscharrntke, 2005). Higher species diversity does not necessarily mean a stronger functional differentiation (Bello, Lepš, Lavorel, & Moretti, 2007), but may increase resilience to environmental change and thereby, sustain ecosystem functioning (Tscharrntke et al., 2012). However, the effect of configurational heterogeneity may not be uniform along a landscape composition gradient, changing with the amount of suitable habitat (Villard & Metzger, 2014).

4.2 | Management effect

Organic farming increases biodiversity according to a recent meta-analysis (Tuck et al., 2014). In our study, we confirmed the positive effect of organic farming on carabid functional diversity. Several earlier studies suggested that organic management may not enhance carabid species richness; however, organic and conventional fields may differ in species composition (Purtauf et al., 2005) and abundance (Birkhofer, Bezemer, Hedlund, & Setälä, 2012; Diekötter, Wamser, Dörner, Wolters, & Birkhofer, 2016; but see Diekötter et al., 2010; Jonason, Smith, Bengtsson, & Birkhofer, 2013). Organic fields may be more suitable habitats for arthropods than conventional fields. The lower management intensity and omission of pesticides reduce arthropod mortality (Schmidt et al., 2005), and increase structural complexity of the habitat through higher weed density (Weiner, Griepentrog, & Kristensen, 2001). The heterogeneous habitat structure provides a broad spectrum of food resources, high prey abundance, and more potential sites for web-building spiders (Diekötter & Crist, 2013).

Our results showed a positive effect of organic farming on CWM of carabid body size. The mean body size of the individuals may decrease with increasing management intensity (Blake, Foster, Eyre, & Luff, 1994). Larger carnivorous and herbivorous carabid species require more and larger food items, which determines their functional role in biological pest control and weed-seed predation (Honek, Martinkova, Saska, & Pekar, 2007; Wheeler, 1988). Rusch, Binet, Delbac, and Thiéry (2016) provided evidence that mean predator body size is among the best

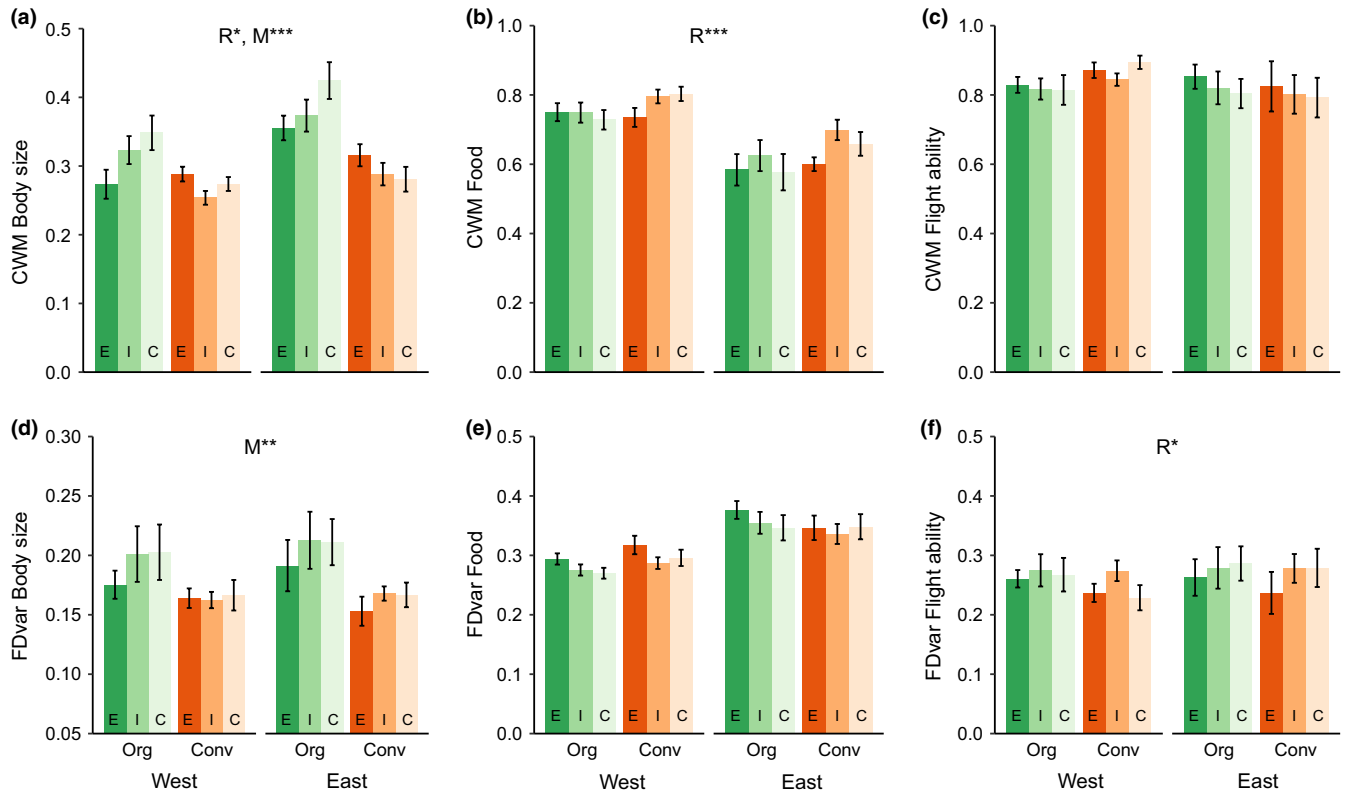


FIGURE 3 Functional diversity indices of carabid communities. (a) Community weighted mean (CWM) Body size (continuous in mm); (b) CWM Food (herbivore: 0, omnivore: 0.5 and carnivore: 1); (c) CWM Flight ability (apterous/brachypterous: 0, macropterous: 1); (d) Functional divergence (FDvar) Body size; (e) FDvar Food; (f) FDvar Flight ability; Transect: E: field edge; I: interior, C: centre. Effects of region (R), management (M) and transect on each index including significance level are indicated above each plot (see Table S4 for model averaging results) * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

predictors of predation rates. An increased predator size leads to higher per capita predation rates and more efficient reduction of prey density and biomass (Emmerson & Raffaelli, 2004). However, predator body size may also relate to prey size preferences (Brose, 2010). Here, we showed that organic management was related to higher FDvar values, a higher variation in carabid size. This variation indicates a wider food preference of the carabid fauna in organic fields compared to conventional fields and thus a strong contribution of carabids to both insect pest and weed control in organic farming. Weed species diversity and cover is higher in organic than in conventional fields (Batáry et al., 2017). The weed control potential of carabids in arable fields is well known (Bohan, Boursault, Brooks, & Petit, 2011), since carabids can significantly reduce the weed-seed stock (Diekötter et al., 2016; Kulkarni, Dosdall, & Willenborg, 2015). Trichard, Alignier, Biju-Duval, and Petit (2013) detected local management and landscape effects on carabid diversity and weed seed predation; however, seed predation is temporally highly variable during the crop cycle (Westerman, Wes, Kropff, & Van der Werf, 2003).

4.3 | Edge effect

In agricultural landscapes, the majority of seminatural habitats are situated along the field edges (Schirmel, Thiele, Entling, & Buchholz, 2016). Species diversity and arthropod abundance are enhanced by the seminatural habitats (Dainese, Luna, Sitzia, & Marini, 2015). Field

edges are less disturbed habitats than crop interiors due to less effective weed and pest management, spillover from neighbouring habitats (Marshall & Moonen, 2002), favourable spatial habitat structure, microclimate, and alternative food sources (Bianchi, Booij, & Tscharntke, 2006). Such habitat parameters may play a prominent role in shaping the trait composition of spiders and carabids in herbaceous field margins (Schirmel et al., 2016). Crop management reduces the abundance of ground-dwelling arthropods, e.g., ploughing causes direct mortality and emigration due to disturbance and altered habitat structure. Thus, many species overwinter in field margins and colonize the arable fields from these seminatural habitats (Thorbeck & Bilde, 2004). The ground-dwelling movement of spiders is an effective short-distance dispersal mode, and dispersal by ballooning allows spiders to rapidly colonize remote habitats (Schmidt et al., 2005). We found smaller spiders with higher ballooning propensity in field interiors and centres than in edges suggesting the prominent role of ballooning dispersal in agricultural landscapes. The different dispersal strategy of spiders could result in a different distribution pattern of spiders.

5 | CONCLUSIONS

Our results highlight that reduced management intensity of local farming practices, i.e., organic agriculture, and higher landscape

heterogeneity, i.e., small-scale agriculture, promote the functional diversity of carabids. The small-scale agriculture in the West was characterized by more predatory carabids with smaller body size, which has been shown to increase predation rates in cereal fields (Rusch, Birkhofer, Bommarco, Smith, & Ekbohm, 2015). Organic management appeared to favour larger carabids, but also a higher variation in body size of beetles suggesting a higher response diversity to environmental change. Larger body size and higher overall trait diversity of ground-dwelling spiders in field edges were related to an enhanced spider biocontrol in small-scale agricultural landscapes, due to their high edge density. Maintenance or restoration of seminatural edge habitats and small-scale agriculture is needed to maintain heterogeneity in agricultural landscapes sustaining functionally diverse arthropod communities and potential biocontrol. Functional trait composition and diversity indices are more sensitive to habitat quality and landscape scale changes than alpha diversity indices, such as species richness (Gallé, Gallé-Szpisjak, & Torma, 2017; Rusch et al., 2015; Schirmel et al., 2016), and provide an insight into community–environment interactions and their effect on ecosystem functioning (e.g., Laliberté et al., 2010; Rusch et al., 2016).

ACKNOWLEDGEMENTS

This paper is the product of the project, “Biodiversity and associated ecosystem services in small- vs. large-scale agriculture” (DFG BA 4438/1-1). We are grateful to P. Császár for the identification of carabid beetles, and to D. Molnár for assisting in field work. P.B. was supported by the Economic Development and Innovation Operational Programme of Hungary (GINOP-2.3.2-15-2016-00019).

AUTHORS' CONTRIBUTIONS

P.B., and T.T. conceived the study; P.B., R.G., A.-K.H., and T.T. developed the study; R.G., A.-K. H., and P.B. collected data; R.G. identified spiders; R.G. analysed data with substantial input from A.B.B. and P.B.; R.G. wrote the paper with substantial input from all authors.

DATA ACCESSIBILITY

Data available via the Zenodo digital repository <https://doi.org/10.5281/zenodo.1285239> (Gallé, Happe, Baillod, Tscharnkte, & Batáry, 2018).

ORCID

Róbert Gallé  <http://orcid.org/0000-0002-5516-8623>

Péter Batáry  <http://orcid.org/0000-0002-1017-6996>

REFERENCES

Barton, K. (2009). MuMIn: R functions for model selection and model averaging. R package version 0.12.0. Retrieved from <http://r-forge.r-project.org/projects/mumin>

- Batáry, P., Báldi, A., Kleijn, D., & Tscharnkte, T. (2011). Landscape-moderated biodiversity effects of agri-environmental management – A meta-analysis. *Proceedings of the Royal Society B-Biological Sciences*, 278, 1894–1902. <https://doi.org/10.1098/rspb.2010.1923>
- Batáry, P., Dicks, L. V., Kleijn, D., & Sutherland, W. J. (2015). The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, 29, 1006–1016. <https://doi.org/10.1111/cobi.12536>
- Batáry, P., Gallé, R., Riesch, F., Fischer, C., Dormann, C. F., Mußhoff, O., ... Tscharnkte, T. (2017). The former iron curtain still drives biodiversity-profit trade-offs in German agriculture. *Nature Ecology & Evolution*, 1, 1279–1284. <https://doi.org/10.1038/s41559-017-0272-x>
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version, 1(7).
- Bello, F., Lepš, J., Lavorel, S., & Moretti, M. (2007). Importance of species abundance for assessment of trait composition: An example based on pollinator communities. *Community Ecology*, 8, 163–170. <https://doi.org/10.1556/ComEc.8.2007.2.3>
- Bengtsson, J., Ahnström, J., & Weibull, A. C. (2005). The effects of organic agriculture on biodiversity and abundance: A meta-analysis. *Journal of Applied Ecology*, 42, 261–269. <https://doi.org/10.1111/j.1365-2664.2005.01005.x>
- Bertrand, C., Burel, F., & Baudry, J. (2016). Spatial and temporal heterogeneity of the crop mosaic influences carabid beetles in agricultural landscapes. *Landscape Ecology*, 31, 451–466. <https://doi.org/10.1007/s10980-015-0259-4>
- Bianchi, F. J. J. A., Booij, C. J. H., & Tscharnkte, T. (2006). Sustainable pest regulation in agricultural landscapes: A review on landscape composition: Biodiversity and natural pest control. *Proceedings of the Royal Society B-Biological Sciences*, 273, 1715–1727. <https://doi.org/10.1098/rspb.2006.3530>
- Birkhofer, K., Bezemer, T. M., Hedlund, K., & Setälä, H. (2012). Community composition of soil organisms under different wheat farming systems. In T. Cheeke, D. C. Coleman, & D. H. Wall (Eds.), *Microbial ecology in sustainable agroecosystems* (pp. 89–111). Boca Raton, FL: CRC Press. <https://doi.org/10.1201/CRCADVAGROECO>
- Blake, S., Foster, G. N., Eyre, M. D., & Luff, M. L. (1994). Effects of habitat type and grassland management-practices on the body-size distribution of carabid beetles. *Pedobiologia*, 38, 502–512.
- Blandenier, G. (2009). Ballooning of spiders (Araneae) in Switzerland: General results from an eleven-year survey. *Arachnology*, 14, 308–316. <https://doi.org/10.13156/arac.2009.14.7.308>
- Bohan, D. A., Boursault, A., Brooks, D. R., & Petit, S. (2011). National-scale regulation of the weed seedbank by carabid predators. *Journal of Applied Ecology*, 48, 888–898. <https://doi.org/10.1111/j.1365-2664.2011.02008.x>
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., ... White, J. S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24, 127–135. <https://doi.org/10.1016/j.tree.2008.10.008>
- Brose, U. (2010). Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Functional Ecology*, 24, 28–34. <https://doi.org/10.1111/j.1365-2435.2009.01618.x>
- Cardoso, P., Pekár, S., Jocqué, R., & Coddington, J. A. (2011). Global patterns of guild composition and functional diversity of spiders. *PLoS ONE*, 6, e21710. <https://doi.org/10.1371/journal.pone.0021710>
- Carrié, R., Andrieu, E., Cunningham, S. A., Lentini, P. E., Loreau, M., & Ouin, A. (2017). Relationships among ecological traits of wild bee communities along gradients of habitat amount and fragmentation. *Ecography*, 40, 85–97. <https://doi.org/10.1111/ecog.02632>
- Chaplin-Kramer, R., O'Rourke, M. E., Blitzer, E. J., & Kremen, C. (2011). A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters*, 14, 922–932. <https://doi.org/10.1111/j.1461-0248.2011.01642.x>

- Concepción, E. D., Díaz, M., & Baquero, R. A. (2008). Effects of landscape complexity on the ecological effectiveness of agri-environment schemes. *Landscape Ecology*, 23, 135–148. <https://doi.org/10.1007/s10980-007-9150-2>
- Dainese, M., Luna, D. I., Sitzia, T., & Marini, L. (2015). Testing scale-dependent effects of seminatural habitats on farmland biodiversity. *Ecological Applications*, 25, 1681–1690. <https://doi.org/10.1890/14-1321.1>
- De Lima, R. F., Dallimer, M., Atkinson, P. W., & Barlow, J. (2013). Biodiversity and land-use change: Understanding the complex responses of an endemic-rich bird assemblage. *Diversity and Distributions*, 19, 411–422. <https://doi.org/10.1111/ddi.12015>
- Díaz, S., & Cabido, M. (2001). Vive la difference: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, 16, 646–655. [https://doi.org/10.1016/S0169-5347\(01\)02283-2](https://doi.org/10.1016/S0169-5347(01)02283-2)
- Díaz, S., Lavorel, S., de Bello, F., Quetier, F., Grigulis, K., & Robson, M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 20684–20689. <https://doi.org/10.1073/pnas.0704716104>
- Diekötter, T., & Crist, T. O. (2013). Quantifying habitat-specific contributions to insect diversity in agricultural mosaic landscapes. *Insect Conservation and Diversity*, 6, 607–618. <https://doi.org/10.1111/icad.12015>
- Diekötter, T., Wamser, S., Dörner, T., Wolters, V., & Birkhofer, K. (2016). Organic farming affects the potential of a granivorous carabid beetle to control arable weeds at local and landscape scales. *Agricultural and Forest Entomology*, 18, 167–173. <https://doi.org/10.1111/afe.12150>
- Diekötter, T., Wamser, S., Wolters, V., & Birkhofer, K. (2010). Landscape and management effects on structure and function of soil arthropod communities in winter wheat. *Agriculture, Ecosystems & Environment*, 137, 108–112. <https://doi.org/10.1016/j.agee.2010.01.008>
- Dray, S., Chessel, D., & Thioulouse, J. (2003). Co-inertia analysis and the linking of ecological data tables. *Ecology*, 84, 3078–3089. <https://doi.org/10.1890/03-0178>
- Dray, S., & Dufour, A. B. (2007). The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, 22, 1–20.
- Duflot, R., Georges, R., Ernout, 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., Olsson, O., Rundlöf, M., Wätzold, F., & Smith, H. G. (2014). Optimizing agri-environment schemes for biodiversity, ecosystem services or both? *Biological Conservation*, 172, 65–71. <https://doi.org/10.1016/j.biocon.2014.02.013>
- Emmerson, M. C., & Raffaelli, D. (2004). Predator–prey body size, interaction strength and the stability of a real food web. *Journal of Animal Ecology*, 73, 399–409. <https://doi.org/10.1111/j.0021-8790.2004.00818.x>
- Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., ... Martin, J. L. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, 14, 101–112. <https://doi.org/10.1111/j.1461-0248.2010.01559.x>
- Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., & Tischendorf, L. (2015). Farmlands with smaller crop fields have higher within-field biodiversity. *Agriculture, Ecosystems and Environment*, 200, 219–234. <https://doi.org/10.1016/j.agee.2014.11.018>
- Gallé, R., Gallé-Szpisjak, N., & Torma, A. (2017). Habitat structure influences the spider fauna of short-rotation poplar plantations more than forest age. *European Journal of Forest Research*, 136, 51–58. <https://doi.org/10.1007/s10342-016-1008-1>
- Gallé, R., Happe, A. K., Baillod, A. B., Tscharrntke, T., & Batáry, P. (2018). Data from: Landscape configuration, organic management and within-field position drive functional diversity of spiders and carabids. *Zenodo*, <https://doi.org/10.5281/zenodo.1285239>
- Gallé, R., Szabó, Á., Császár, P., & Torma, A. (2018). Spider assemblage structure and functional diversity patterns of natural forest steppes and exotic forest plantations. *Forest Ecology and Management*, 411, 234–239. <https://doi.org/10.1016/j.foreco.2018.01.040>
- Hendrickx, F., Maelfait, J. P., Desender, K., Aviron, S., Bailey, D., Diekötter, T., ... Bugter, R. (2009). Pervasive effects of dispersal limitation on within-and among-community species richness in agricultural landscapes. *Global Ecology and Biogeography*, 18, 607–616. <https://doi.org/10.1111/j.1466-8238.2009.00473.x>
- Homburg, K., Homburg, N., Schaefer, F., Schuldt, A., & Assmann, T. (2014). carabids.org – A dynamic online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conservation and Diversity*, 7, 195–205. <https://doi.org/10.1111/icad.12045>
- 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>
- Honek, A., Martinkova, Z., Saska, P., & Pekar, S. (2007). Size and taxonomic constraints determine the seed preferences of Carabidae (Coleoptera). *Basic and Applied Ecology*, 8, 343–353. <https://doi.org/10.1016/j.baae.2006.07.002>
- Hurka, K. (1996). *Carabidae of the Czech and Slovak republics*. Zlín, Czech Republic: Ing. Vit Kabourek.
- Jonason, D., Smith, H. G., Bengtsson, J., & Birkhofer, K. (2013). Landscape simplification promotes weed seed predation by carabid beetles (Coleoptera: Carabidae). *Landscape Ecology*, 28, 487–494. <https://doi.org/10.1007/s10980-013-9848-2>
- Krauss, J., Gallenberger, I., & Steffan-Dewenter, I. (2011). Decreased functional diversity and biological pest control in conventional compared to organic crop fields. *PLoS ONE*, 6, e19502. <https://doi.org/10.1371/journal.pone.0019502>
- Kulkarni, S. S., Dosdall, L. M., & Willenborg, C. J. (2015). The role of ground beetles (Coleoptera: Carabidae) in weed seed consumption: A review. *Weed Science*, 63, 355–376. <https://doi.org/10.1614/WS-D-14-00067.1>
- Laliberte, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299–305. <https://doi.org/10.1890/08-2244.1>
- Laliberte, E., Wells, J. A., DeClerck, F., Metcalfe, D. J., Catterall, C. P., Queiroz, C., ... Mayfield, M. M. (2010). Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters*, 13, 76–86. <https://doi.org/10.1111/j.1461-0248.2009.01403.x>
- Lange, M., Gossner, M. M., & Weisser, W. W. (2011). Effect of pitfall trap type and diameter on vertebrate by-catches and ground beetle (Coleoptera: Carabidae) and spider (Araneae) sampling. *Methods in Ecology and Evolution*, 2, 185–190. <https://doi.org/10.1111/j.2041-210X.2010.00062.x>
- Larochelle, A. (1990). *The food of carabid beetles (Coleoptera: Carabidae, incl. Cicindelinae)*. Fabreries, QC: Association des Entomologistes Amateurs du Québec.
- Lavorel, S., Grigulis, K., McIntyre, S., Williams, N. S. G., Garden, D., Dorrough, J., ... Bonis, A. (2008). Assessing functional diversity in the field – Methodology matters!. *Functional Ecology*, 22, 134–147.
- Lepš, J., de Bello, F., Lavorel, S., & Berman, S. (2006). Quantifying and interpreting functional diversity of natural communities: Practical considerations matter. *Preslia*, 78, 481–501.
- Letourneau, D. K., & Bothwell, S. G. (2008). Comparison of organic and conventional farms: Challenging ecologists to make biodiversity functional. *Frontiers in Ecology and the Environment*, 6, 430–438. <https://doi.org/10.1890/070081>
- Madeira, F., Tscharrntke, T., Elek, Z., Kormann, U. G., Pons, X., Rösch, V., ... Batáry, P. (2016). Spillover of arthropods from cropland to protected calcareous grassland – The neighbouring habitat matters. *Agriculture, Ecosystems and Environment*, 235, 127–133. <https://doi.org/10.1016/j.agee.2016.10.012>
- Marshall, E. J. P., & Moonen, A. C. (2002). Field margins in northern Europe: Their functions and interactions with agriculture. *Agriculture*,

- Ecosystems and Environment*, 89, 5–21. [https://doi.org/10.1016/S0167-8809\(01\)00315-2](https://doi.org/10.1016/S0167-8809(01)00315-2)
- Martin, E. A., Reineking, B., Seo, B., & Steffan-Dewenter, I. (2013). Natural enemy interactions constrain pest control in complex agricultural landscapes. *Proceedings of the National Academy of Sciences of the USA*, 110, 5534–5539. <https://doi.org/10.1073/pnas.1215725110>
- Martin, E. A., Seo, B., Park, C. R., Reineking, B., & Steffan-Dewenter, I. (2016). Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. *Ecological Applications*, 26, 448–462. <https://doi.org/10.1890/15-0856>
- Nentwig, W., Blick, T., Gloor, D., Hänggi, A., & Kropf, C. (2017). Spiders of Europe. Retrieved from www.araneae.unibe.ch
- Neumann, J. L., Griffiths, G. H., Hoodless, A., & Holloway, G. J. (2016). The compositional and configurational heterogeneity of matrix habitats shape woodland carabid communities in wooded-agricultural landscapes. *Landscape Ecology*, 31, 301–315. <https://doi.org/10.1007/s10980-015-0244-y>
- Palmu, E., Ekroos, J., Hanson, H. I., Smith, H. G., & Hedlund, K. (2014). Landscape-scale crop diversity interacts with local management to determine ground beetle diversity. *Basic and Applied Ecology*, 15, 241–249. <https://doi.org/10.1016/j.baae.2014.03.001>
- Pasher, J., Mitchell, S. W., King, D. J., Fahrig, L., Smith, A. C., & Lindsay, K. E. (2013). Optimizing landscape selection for estimating relative effects of landscape variables on ecological responses. *Landscape Ecology*, 28, 371–383. <https://doi.org/10.1007/s10980-013-9852-6>
- Perović, D., Gámez-Virués, S., Börschig, C., Klein, A. M., Krauss, J., Steckel, J., ... Westphal, C. (2015). Configurational landscape heterogeneity shapes functional community composition of grassland butterflies. *Journal of Applied Ecology*, 52, 505–513. <https://doi.org/10.1111/1365-2664.12394>
- Perović, D. J., Gámez-Virués, S., Landis, D. A., Wäckers, F., Gurr, G. M., Wratten, S. D., ... Desneux, N. (2017). Managing biological control services through multi-trophic trait interactions: Review and guidelines for implementation at local and landscape scales. *Biological Reviews*, 93, 306–321.
- Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: Back to basics and looking forward. *Ecology Letters*, 9, 741–758. <https://doi.org/10.1111/j.1461-0248.2006.00924.x>
- Pla, L., Casanoves, F., & Di-Rienzo, J. (2012). *Quantifying Functional Biodiversity*. Series: Springer Briefs in Environmental Science. Berlin: Springer Editorial. ISBN 978-94-007-2647-5. <https://doi.org/10.1007/978-94-007-2648-2>
- Purtauf, T., Roschewitz, I., Dauber, J., Thies, C., Tscharnkte, T., & Wolters, V. (2005). Landscape context of organic and conventional farms: Influences on carabid beetle diversity. *Agriculture, Ecosystems & Environment*, 108, 165–174. <https://doi.org/10.1016/j.agee.2005.01.005>
- Richards, S. A. (2008). Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology*, 45, 218–227.
- Ricotta, C., & Moretti, M. (2011). CWM and Rao's quadratic diversity: A unified framework for functional ecology. *Oecologia*, 167, 181–188. <https://doi.org/10.1007/s00442-011-1965-5>
- Rusch, A., Binet, D., Delbac, L., & Thiéry, D. (2016). Local and landscape effects of agricultural intensification on carabid community structure and weed seed predation in a perennial cropping system. *Landscape Ecology*, 31, 2163–2174. <https://doi.org/10.1007/s10980-016-0390-x>
- 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 and Applied Ecology*, 16, 250–259. <https://doi.org/10.1016/j.baae.2015.02.003>
- Sams, M. A., Lai, H. R., Bonser, S. P., Veski, P. A., Kooyman, R. M., Metcalfe, D. J., ... Mayfield, M. M. (2017). Landscape context explains changes in the functional diversity of regenerating forests better than climate or species richness. *Global Ecology and Biogeography*, 26, 1165–1176. <https://doi.org/10.1111/geb.12627>
- Schirmel, J., Thiele, J., Entling, M. H., & Buchholz, S. (2016). Trait composition and functional diversity of spiders and carabids in linear landscape elements. *Agriculture, Ecosystems & Environment*, 235, 318–328. <https://doi.org/10.1016/j.agee.2016.10.028>
- Schmidt, M. H., Roschewitz, I., Thies, C., & Tscharnkte, T. (2005). Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. *Journal of Applied Ecology*, 42, 281–287. <https://doi.org/10.1111/j.1365-2664.2005.01014.x>
- Sutcliffe, L., Batáry, P., Báldi, A., Dicks, L., Herzon, I., Kleijn, D., ... Tscharnkte, T. (2015). Harnessing the biodiversity value of Central and Eastern European farmland. *Diversity and Distributions*, 21, 722–730.
- Thorbek, P., & Bilde, T. (2004). Reduced numbers of generalist arthropod predators after crop management. *Journal of Applied Ecology*, 41, 526–528. <https://doi.org/10.1111/j.0021-8901.2004.00913.x>
- Trichard, A., Alignier, A., Biju-Duval, L., & Petit, S. (2013). The relative effects of local management and landscape context on weed seed predation and carabid functional groups. *Basic and Applied Ecology*, 14, 235–245. <https://doi.org/10.1016/j.baae.2013.02.002>
- Tscharnkte, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – Ecosystem service management. *Ecology Letters*, 8, 857–874. <https://doi.org/10.1111/j.1461-0248.2005.00782.x>
- Tscharnkte, T., Tylianaskis, J., Rand, T., Didham, R., Fahrig, L., Batáry, P., ... Kleijn, D. (2012). Landscape moderation of biodiversity patterns and processes – Eight hypotheses. *Biological Reviews*, 87, 661–685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>
- Tuck, S. L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L. A., & Bengtsson, J. (2014). Land-use intensity and the effects of organic farming on biodiversity: A hierarchical meta-analysis. *Journal of Applied Ecology*, 51, 746–755. <https://doi.org/10.1111/1365-2664.12219>
- Villard, M. A., & Metzger, J. P. (2014). Beyond the fragmentation debate: A conceptual model to predict when habitat configuration really matters. *Journal of Applied Ecology*, 51, 309–318. <https://doi.org/10.1111/1365-2664.12190>
- Weiner, J., Griepentrog, H. W., & Kristensen, L. (2001). Suppression of weeds by spring wheat *Triticum aestivum* increases with crop density and spatial uniformity. *Journal of Applied Ecology*, 38, 784–790. <https://doi.org/10.1046/j.1365-2664.2001.00634.x>
- Westerman, P. R., Wes, J. S., Kropff, M. J., & Van der Werf, W. (2003). Annual losses of weed seeds due to predation in organic cereal fields. *Journal of Applied Ecology*, 40, 824–836. <https://doi.org/10.1046/j.1365-2664.2003.00850.x>
- Wheeler, C. P. (1988). Predator-prey size relationships in some Pterostichini (Coleoptera: Carabidae). *Coleopterists Bulletin*, 42, 237–240.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Gallé R, Happe A-K, Baillod AB, Tscharnkte T, Batáry P. Landscape configuration, organic management, and within-field position drive functional diversity of spiders and carabids. *J Appl Ecol*. 2019;56:63–72. <https://doi.org/10.1111/1365-2664.13257>

Appendix S1. Trait values and abundances (N) of collected spider species. hunting: web-builder (0), active hunter (1); ballooning: ballooning (1), non-ballooning (0), body size values (in mm) were ranged between 0 and 1.

	Hunting	Ballooning	Body size	N
Dysderidae				
<i>Dysdera erythrina</i> (Walckenaer, 1802)	1	0	1.000	1
<i>Harpactea lepida</i> (C. L. Koch, 1838)	1	0	0.458	1
Theridiidae				
<i>Enoplognatha ovata</i> (Clerck, 1757)	0	1	0.369	1
<i>Enoplognatha thoracica</i> (Hahn, 1833)	0	1	0.216	2
<i>Phylloneta impressa</i> (L. Koch, 1881)	1	1	0.261	1
<i>Robertus arundineti</i> (O. P.-Cambridge, 1871)	0	1	0.088	11
<i>Robertus neglectus</i> (O. P.-Cambridge, 1871)	0	1	0.064	4
Linyphiidae				
<i>Agyneta rurestris</i> (C. L. Koch, 1836)	0	1	0.093	31
<i>Araeoncus humilis</i> (Blackwall, 1841)	0	1	0.034	4
<i>Bathypantes gracilis</i> (Blackwall, 1841)	0	1	0.064	68
<i>Centromerus sellarius</i> (Simon, 1884)	0	0.5	0.123	2
<i>Ceratinella brevis</i> (Wider, 1834)	0	0.5	0.044	2
<i>Collinsia inerrans</i> (O. P.-Cambridge, 1885)	0	1	0.088	22
<i>Dicymbium nigrum</i> (Blackwall, 1834)	0	1	0.078	6
<i>Diplocephalus picinus</i> (Blackwall, 1841)	0	0.5	0.054	1
<i>Diplostyla concolor</i> (Wider, 1834)	1	1	0.137	27
<i>Dismodicus bifrons</i> (Blackwall, 1841)	0	1	0.081	1
<i>Erigone dentipalpis</i> (Wider, 1834)	0	1	0.093	930
<i>Leptorhoptrum robustum</i> (Westring, 1851)	0	1	0.251	4
<i>Micrargus herbigradus</i> (Blackwall, 1854)	0	1	0.078	55
<i>Microneta viaria</i> (Blackwall, 1841)	0	1	0.088	1
<i>Oedothorax apicatus</i> (Blackwall, 1850)	0	1	0.137	1243
<i>Oedothorax retusus</i> (Westring, 1851)	0	1	0.123	29
<i>Panamomops sulcifrons</i> (Wider, 1834)	0	1	0.000	2
<i>Pelecopsis parallela</i> (Wider, 1834)	1	1	0.004	5
<i>Sintula corniger</i> (Blackwall, 1856)	0	1	0.064	1
<i>Porrhomma microphthalmum</i> (O. P.-Cambridge, 1871)	0	1	0.049	66
<i>Tapinocyba insecta</i> (L. Koch, 1869)	0	0.5	0.044	2
<i>Tenuiphantes flavipes</i> (Blackwall, 1854)	0	1	0.078	75
<i>Tiso vagans</i> (Blackwall, 1834)	0	1	0.073	1
<i>Troxochrus scabriculus</i> (Westring, 1851)	0	1	0.049	2
<i>Walckenaeria acuminata</i> Blackwall, 1833	0	1	0.177	1
<i>Walckenaeria atrotibialis</i> (O. P.-Cambridge, 1878)	0	1	0.113	6
<i>Walckenaeria capito</i> (Westring, 1861)	0	0.5	0.162	1
<i>Walckenaeria unicornis</i> O. P.-Cambridge, 1861	0	0.5	0.064	1
<i>Walckenaeria dysderoides</i> (Wider, 1834)	0	0.5	0.177	2
<i>Walckenaeria nudipalpis</i> (Westring, 1851)	0	1	0.073	3
<i>Walckenaeria vigilax</i> (Blackwall, 1853)	0	1	0.098	3
Tetragnathidae				
<i>Pachygnatha degeeri</i> Sundevall, 1830	0	1	0.221	609

	Hunting	Ballooning	Body size	N
<i>Pachygnatha listeri</i> Sundevall, 1830	0	1	0.261	30
Lycosidae				
<i>Alopecosa farinosa</i> (Herman, 1879)	1	0.5	0.704	1
<i>Alopecosa cuneata</i> (Clerck, 1757)	1	0.5	0.605	50
<i>Alopecosa pulverulenta</i> (Clerck, 1757)	1	0.5	0.753	146
<i>Aulonia albimana</i> (Walckenaer, 1805)	1	1	0.270	2
<i>Pardosa agrestis</i> (Westring, 1861)	1	1	0.334	53
<i>Pardosa amentata</i> (Clerck, 1757)	1	1	0.507	442
<i>Pardosa palustris</i> (Linnaeus, 1758)	1	1	0.458	243
<i>Pardosa prativaga</i> (L. Koch, 1870)	1	1	0.492	27
<i>Pardosa pullata</i> (Clerck, 1757)	1	1	0.359	156
<i>Piratula uliginosa</i> (Thorell, 1856)	1	0.5	0.310	3
<i>Piratula latitans</i> (Blackwall, 1841)	1	0.5	0.226	2
<i>Trachyzelotes pedestris</i> (C. L. Koch, 1837)	1	0	0.551	3
<i>Trochosa ruricola</i> (De Geer, 1778)	1	0	0.901	90
<i>Trochosa terricola</i> Thorell, 1856	1	0	0.901	156
<i>Xerolycosa miniata</i> (C. L. Koch, 1834)	1	0	0.472	1
Agelenidae				
<i>Inermocoelotes inermis</i> (L. Koch, 1855)	0	0	0.901	2
Hahnidae				
<i>Hahnia pusilla</i> C. L. Koch, 1841	0	0	0.004	5
Miturgidae				
<i>Zora spinimana</i> (Sundevall, 1833)	1	1	0.467	2
Phrurolithidae				
<i>Phrurolithus festivus</i> (C. L. Koch, 1835)	1	0	0.133	15
<i>Phrurolithus minimus</i> C. L. Koch, 1839	1	0	0.133	1
Gnaphosidae				
<i>Drassyllus praeficus</i> (L. Koch, 1866)	1	0	0.512	3
<i>Drassyllus pusillus</i> (C. L. Koch, 1833)	1	0	0.310	60
<i>Haplodrassus minor</i> (O. P.-Cambridge, 1879)	1	0	0.236	4
<i>Haplodrassus signifer</i> (C. L. Koch, 1839)	1	0	0.679	6
<i>Micaria pulicaria</i> (Sundevall, 1831)	1	0	0.236	6
Thomisidae				
<i>Ozyptila praticola</i> (C. L. Koch, 1837)	1	0.5	0.251	2
<i>Ozyptila simplex</i> (O. P.-Cambridge, 1862)	1	1	0.216	2
<i>Xysticus cristatus</i> (Clerck, 1757)	1	1	0.433	3
<i>Xysticus kochi</i> Thorell, 1872	1	1	0.596	21
<i>Xysticus ulmi</i> (Hahn, 1831)	1	1	0.423	4
Salticidae				
<i>Talavera petrensis</i> (C. L. Koch, 1837)	1	0.5	0.174	1

Appendix S2. 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: body size (continuous variable in mm), feeding trait (web-builder, active hunter), dispersal ability (ballooning, non-ballooning species). CWM: Community weighted mean; FDvar: Functional divergence.

Model ^a	Variable ^b	Relative importance (%) ^c	Multimodel estimate \pm 95 % CI ^d	
CWM Size (0.32/0.69;2)	Management (O/C)	6	0.040	\pm 0.054
	Transect (E/I)	100	-0.090	\pm 0.029***
	Transect (E/C)	100	-0.143	\pm 0.029***
	Transect (I/C)	100	-0.047	\pm 0.029**
CWM Hunting (0.37/72;3)	Region (W/E)	4	0.015	\pm 0.138
	Management (O/C)	15	0.107	\pm 0.130
	Transect (E/I)	100	-0.258	\pm 0.064***
	Transect (E/C)	100	-0.335	\pm 0.064***
	Transect (I/C)	100	-0.076	\pm 0.064*
CWM Ballooning (0.15/0.47;1)	Transect (E/I)	100	0.095	\pm 0.033***
	Transect (E/C)	100	0.120	\pm 0.033***
	Transect (I/C)	100	0.040	\pm 0.033*
FDvar Size (0.21/0.50;1)	Transect (E/I)	100	-0.034	\pm 0.025
	Transect (E/C)	100	-0.082	\pm 0.025
	Transect (I/C)	100	0.047	\pm 0.025
FDvar Hunting (0.25/0.46;2)	Management (O/C)	11	0.055	\pm 0.072
	Transect (E/I)	100	-0.070	\pm 0.039**
	Transect (E/C)	100	-0.161	\pm 0.039***
	Transect (I/C)	100	-0.090	\pm 0.039***
FDvar Ballooning (0.19/0.54;1)	Transect (E/I)	100	-0.066	\pm 0.039**
	Transect (E/C)	100	-0.157	\pm 0.039***
	Transect (I/C)	100	0.091	\pm 0.039***

^aModels were fitted with normal distribution (marginal/conditional R^2 of full model; number of candidate models, $\Delta AIC < 6$).

^bRegion effect: W (West) vs. E (East) - positive value means higher number in West vs. East; Management effect: O (Organic), C (Conventional); Edge effects: C (Centre), E (Edge), I (Interior).

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

^dSignificance levels: *: < 0.05 , **: < 0.01 , ***: < 0.001 .

Appendix S3. Trait values and abundances (N) of collected carabid species. Food: herbivore (0), omnivore (0.5) and carnivore (1); flight ability: marcopterous (1), dimorph (0.5) and apterous/brachypterous (0); body size values (in mm) were ranged between 0 and 1.

	Food	Flight ability	Body size	N
<i>Abax ovalis</i> (Duftschmid, 1812)	1	0	0.468	3
<i>Abax parallelus</i> Duftschmid, 1812	1	0	0.574	12
<i>Acupalpus meridianus</i> (Linnaeus, 1761)	1	1	0.063	37
<i>Agonum muelleri</i> (Herbst, 1784)	1	1	0.234	98
<i>Agonum sexpunctatum</i> (Linnaeus, 1758)	1	1	0.234	8
<i>Amara aenea</i> DeGeer, 1774	0.5	1	0.212	87
<i>Amara apricaria</i> (Paykull, 1790)	0.5	1	0.234	4
<i>Amara aulica</i> Panzer, 1796	0.5	1	0.446	2
<i>Amara bifrons</i> Gyllenhal, 1810	0.5	1	0.170	4
<i>Amara communis</i> Panzer, 1797	0.5	1	0.170	3
<i>Amara consularis</i> Duftschmid, 1812	0.5	1	0.255	1
<i>Amara convexior</i> Stephens, 1828	0.5	1	0.255	3
<i>Amara familiaris</i> Duftschmid, 1812	0.5	1	0.212	127
<i>Amara lunicollis</i> Schiodte, 1837	0.5	1	0.234	3
<i>Amara montivaga</i> Sturm, 1825	0.5	1	0.255	9
<i>Amara ovata</i> Fabricius, 1792	0.5	1	0.276	121
<i>Amara plebeja</i> Gyllenhal, 1810	0.5	1	0.212	97
<i>Amara similata</i> Gyllenhal, 1810	0.5	1	0.276	89
<i>Anchomenus dorsalis</i> (Pontoppidan, 1763)	1	1	0.191	3554
<i>Anisodactylus binotatus</i> (Fabricius, 1787)	0.5	1	0.361	3
<i>Anisodactylus poeciloides</i> (Stephens, 1828)	0.5	1	0.404	1
<i>Asaphidion flavipes</i> (Linnaeus, 1761)	1	1	0.063	50
<i>Badister bullatus</i> Schrank, 1798	1	1	0.127	26
<i>Badister lacertosus</i> Sturm, 1815	1	1	0.191	1
<i>Badister sodalis</i> Duftschmid, 1812	1	1	0.063	13
<i>Bembidion guttula</i> Fabricius, 1792	0	1	0.021	22
<i>Bembidion lampros</i> (Herbst, 1784)	1	0.5	0.042	1040
<i>Bembidion lunulatum</i> Geoffroy, 1785	1	1	0.063	10
<i>Bembidion obtusum</i> Audinet-Serville, 1821	0.5	0	0.021	223
<i>Bembidion quadrimaculatum</i> (Linnaeus, 1761)	1	1	0.021	26
<i>Bembidion tetracolum</i> Say, 1823	1	0.5	0.127	16
<i>Brachinus crepitans</i> Linnaeus, 1758	0.5	1	0.255	495
<i>Brachinus explodens</i> Duftschmid, 1812	1	1	0.148	71
<i>Carabus fuscipes</i> Goeze, 1777	1	0.5	0.425	22
<i>Calathus melanocephalus</i> (Linnaeus, 1758)	0.5	0.5	0.234	1
<i>Carabus auratus</i> Linnaeus, 1761	1	0	0.914	415
<i>Carabus auronitens</i> Fabricius, 1792	1	0	1.000	1
<i>Carabus convexus</i> Fabricius, 1775	1	0	0.638	12
<i>Carabus granulatus</i> Linnaeus, 1758	1	1	0.829	347
<i>Carabus nemoralis</i> O.F. Müller, 1764	1	0	0.893	15
<i>Cicindela campestris</i> Linnaeus, 1758	1	1	0.425	1
<i>Clivina fossor</i> (Linnaeus, 1758)	0.5	0.5	0.170	56

	Food	Flight ability	Body size	N
<i>Dyschirius globulosus</i> (Say, 1823)	1	1	0.127	21
<i>Trechus secalis</i> (Paykull, 1790)	1	1	0.617	21
<i>Harpalus affinis</i> (Schränk, 1781)	1	0.5	0.021	42
<i>Harpalus distinguendus</i> (Duftschmid, 1812)	1	0	0.063	107
<i>Harpalus latus</i> (Linnaeus, 1758)	0.5	1	0.340	782
<i>Harpalus luteicornis</i> Duftschmid, 1812	0.5	1	0.297	111
<i>Harpalus rubripes</i> (Duftschmid, 1812)	0	1	0.319	36
<i>Harpalus signaticornis</i> (Duftschmid, 1812)	0.5	1	0.191	3
<i>Harpalus tardus</i> Panzer, 1796	0.5	1	0.340	21
<i>Leistus ferrugineus</i> (Linnaeus, 1758)	0	1	0.191	6
<i>Leistus rufomarginatus</i> (Duftschmid, 1812)	0	1	0.297	8
<i>Loricera pilicornis</i> (Fabricius, 1775)	1	0	0.191	2
<i>Microlestes maurus</i> Sturm, 1827	1	0	0.255	2
<i>Molops elatus</i> Fabricius, 1801	1	1	0.212	478
<i>Molops piceus</i> Panzer, 1793	1	0.5	0.000	18
<i>Nebria brevicollis</i> Fabricius, 1792	0.5	0	0.553	31
<i>Nebria salina</i> Fairmaire & Laboulbène, 1854	1	0	0.404	3
<i>Notiophilus aestuans</i> Dejean, 1826	1	1	0.404	5
<i>Notiophilus biguttatus</i> Fabricius, 1779	1	1	0.382	6
<i>Notiophilus palustris</i> (Duftschmid, 1812)	1	1	0.106	65
<i>Ophonus azureus</i> (Fabricius, 1775)	1	0.5	0.106	42
<i>Ophonus laticollis</i> Mannerheim, 1825	1	0.5	0.127	18
<i>Ophonus puncticollis</i> (Paykull, 1798)	0	0.5	0.234	2
<i>Panagaeus bipustulatus</i> Fabricius, 1775	0	0.5	0.319	49
<i>Patrobus atrorufus</i> (Stroem, 1768)	0	1	0.319	1
<i>Philorhizus notatus</i> Stephens, 1827	1	1	0.255	2
<i>Platynus assimilis</i> Paykull, 1790	1	0.5	0.212	26
<i>Poecilus cupreus</i> Linnaeus, 1758	1	0.5	0.276	1
<i>Poecilus versicolor</i> (Sturm, 1824)	1	1	0.021	32
<i>Harpalus rufipes</i> (De Geer, 1774)	0.5	1	0.404	2047
<i>Pterostichus burmeisteri</i> Heer, 1838	1	1	0.382	218
<i>Pterostichus macer</i> (Marsham, 1802)	0	1	0.340	1540
<i>Pterostichus madidus</i> (Fabricius, 1775)	1	0	0.489	9
<i>Pterostichus melanarius</i> (Illiger, 1798)	1	1	0.468	42
<i>Pterostichus niger</i> (Schaller, 1783)	1	0.5	0.617	1
<i>Pterostichus oblongopunctatus</i> (Fabricius, 1787)	0.5	0.5	0.553	1648
<i>Pterostichus ovoideus</i> (Sturm, 1824)	1	1	0.702	29
<i>Pterostichus strenuus</i> (Panzer, 1796)	1	1	0.361	1
<i>Pterostichus vernalis</i> Panzer, 1796	1	0.5	0.212	1
<i>Stomis pumicatus</i> (Panzer, 1796)	0.5	0.5	0.170	37
<i>Syntomus truncatellus</i> (Linnaeus, 1761)	1	1	0.191	64
<i>Synuchus vivalis</i> Illiger, 1798	1	0	0.212	18
<i>Trechoblemus micros</i> (Herbst, 1784)	1	0.5	0.021	1
<i>Trechus quadristriatus</i> (Schränk, 1781)	1	0.5	0.212	23
<i>Zabrus tenebrioides</i> Goeze, 1777	1	1	0.106	2
<i>Dyschirius globulosus</i> (Say, 1823)	1	1	0.063	3
<i>Trechus secalis</i> (Paykull, 1790)	0	1	0.553	232

Appendix S4. Summary table for GLMM results after multimodel averaging of best candidate models showing relative importance of each explanatory variable on carabid functional diversity indices. The following traits were considered: body size (continuous variable in mm), feeding trait (herbivore, omnivore, carnivore), dispersal ability (macropterous, dimorph, apterous/brachypterous). CWM: Community weighted mean; FDvar: Functional divergence.

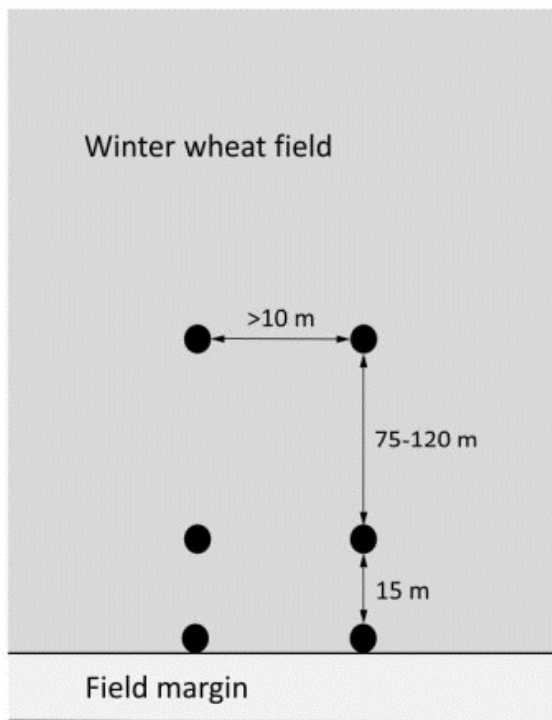
Model ^a	Variable ^b	relative importance (%) ^c	Multimodel estimate \pm 95 % CI ^d
CWM Size (0.42/0.66;3)	Region (W/E)	9	0.046 \pm 0.035*
	Management (O/C)	5	0.071 \pm 0.037***
CWM Food (0.35/0.75;4)	Region (W/E)	8	0.129 \pm 0.076***
	Management (O/C)		0.038 \pm 0.050
CWM Flight ability (0.67/0.75;2)	Management (O/C)		0.042 \pm 0.073
FDvar Size (0.18/0.74;2)	Management (O/C)	3	0.042 \pm 0.028**
FDvar Food (0.33/0.69;2)	Region (W/E)	5	-0.060 \pm 0.073
FDvar Flight ability (0.17/0.73;2)	Region (W/E)	7	-0.041 \pm 0.028*

^aModels were fitted with normal distribution (marginal/conditional R^2 of full model; number of candidate models, $\Delta AIC < 6$)

^bRegion effect: W (West) vs. E (East) - positive value means higher number in West vs. East; Management effect: O (Organic), C (Conventional); Edge effects: C (Centre), E (Edge), I (Interior).

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

^dSignificance levels: *: < 0.05 , **: < 0.01 , ***: < 0.001 .



Appendix Fig S1. Within-field sampling design. Position of pitfall traps (dots) in winter wheat field (grey square).