



RESEARCH ARTICLE

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

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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, & Tschardtke, 2011; Sutcliffe et al., 2015; Tschardtke, 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; Tschardtke 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 (Laliberte & 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

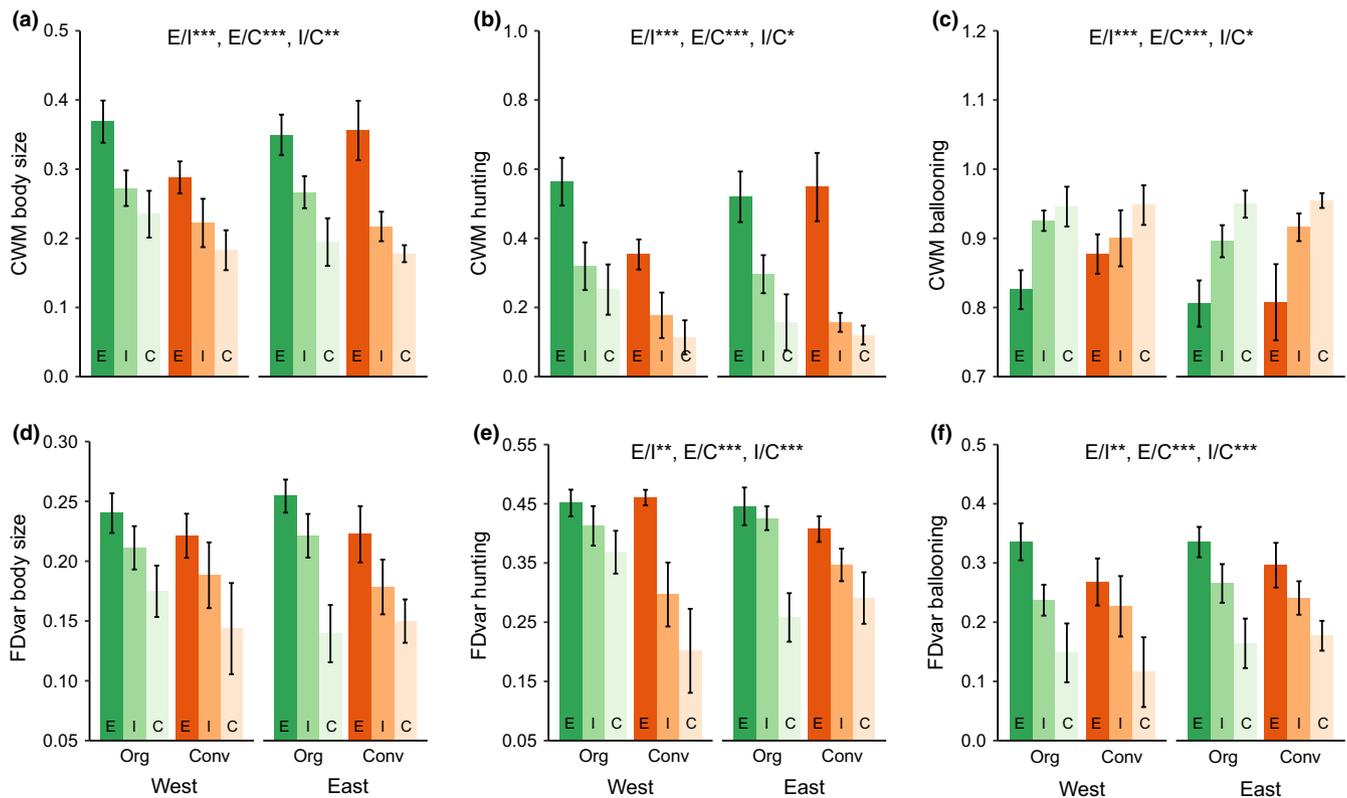


FIGURE 1 Functional diversity indices of spider communities in organic (Org) and conventional (Conv) fields in small-scale (West) and large-scale (East) agricultural landscapes. (a) Community weighted mean (CWM) of body size (continuous in mm and ranged between 0 and 1); (b) CWM hunting strategy (active 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.	<i>p</i> -value	Corr. coeff.	<i>p</i> -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

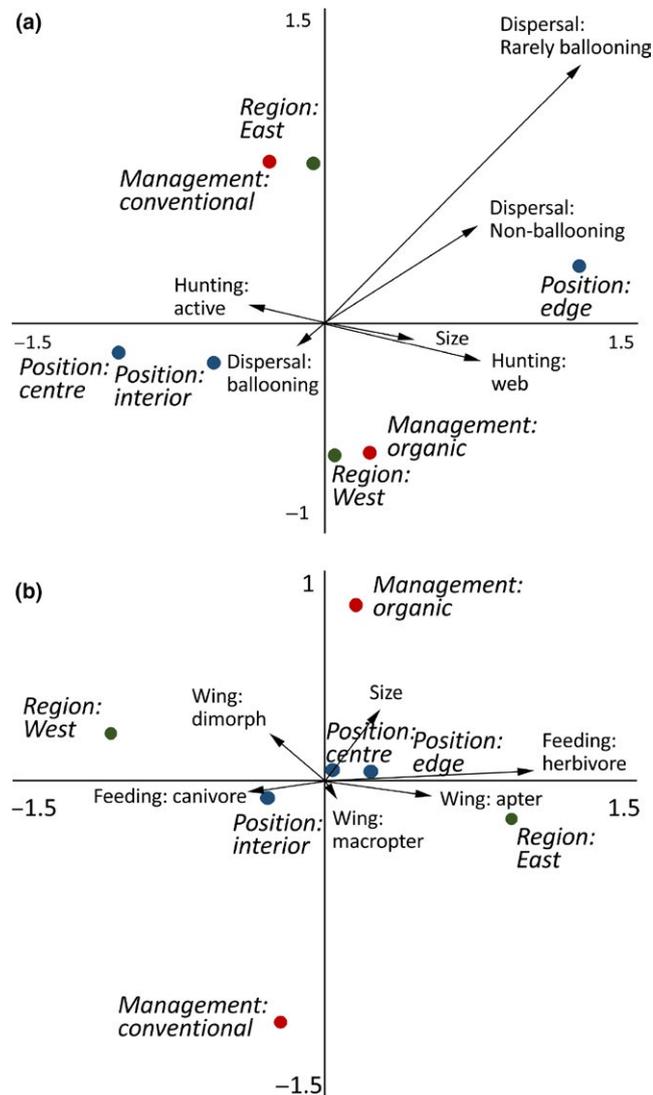


FIGURE 2 Ordination plots of landscape, management and transect descriptors (dots), and species trait categories (arrows) along the two-first axes of the RLQ analysis, for (a) spiders and (b) carabid beetles

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 (Tschardt 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, & Tschardt, 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 (Tschardt 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

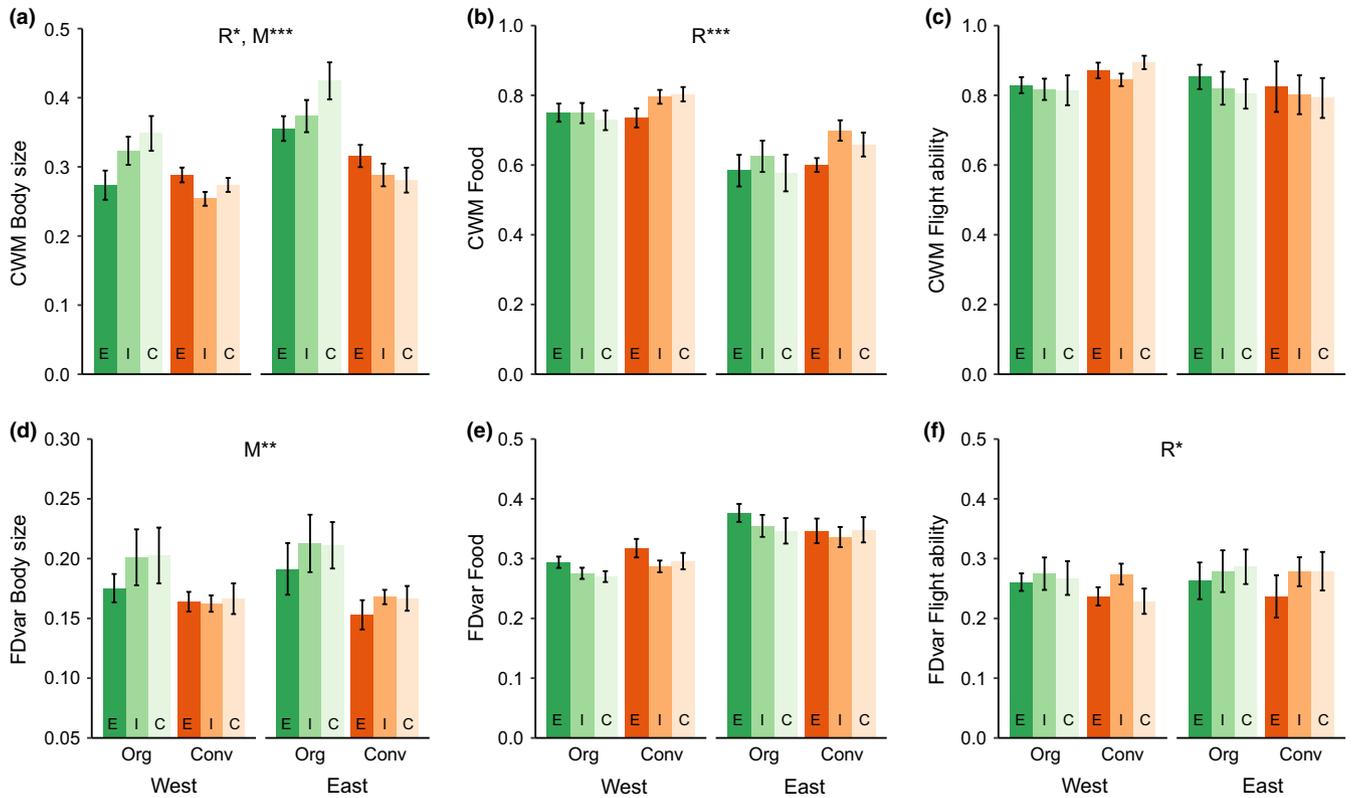


FIGURE 3 Functional diversity indices of carabid communities. (a) Community weighted mean (CWM) Body size (continuous in mm); (b) CWM Food (herbivore: 0, omnivore: 0.5 and carnivore: 1); (c) CWM Flight ability (apterous/brachypterous: 0, macropterous:1); (d) Functional divergence (FDvar) Body size; (e) 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, Dossall, & 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, & Tschantke, 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 (Thorbek & 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).

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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, Tschardtke, & Batáry, 2018).

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SUPPORTING INFORMATION

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