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COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Management intensity at field and landscape levels affects the structure of generalist predator communities

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Abstract Agricultural intensification is recognised as a major driver of biodiversity loss in human-modified landscapes. Several agro-environmental measures at different spatial scales have been suggested to mitigate the negative impact of intensification on biodiversity and ecosystem services. The effect of these measures on the functional structure of service-providing communities remains, however, largely unexplored. Using two distinct landscape designs, we examined how the management options of organic farming at the field scale and crop diversification at the landscape level affect the taxonomic and functional structure of generalist predator communities and how these effects vary along a landscape complexity gradient. Organic farming as well as landscapes with longer and more diversified crop rotations enhanced the activity-density of spiders and rove beetles, but not the species richness or evenness. Our results indicate that the two management options affected the functional composition of communities, as they primarily enhanced the activity-density of functionally similar species. The two management options increased the functional similarity between spider species in regards to hunting mode and habitat preference. Organic farming enhanced the functional similarity of rove beetles. Management options at field and landscape levels were generally more important predictors of community structure when compared to landscape complexity. Our study highlights the importance of considering the functional composition of generalist predators in order to understand how agro-environmental measures at various scales shape community assemblages and ecosystem functioning in agricultural landscapes.

Keywords Agri-environmental measures · Biological pest control · Community composition · Crop rotation · Functional diversity · Natural enemies · Organic farming · Traits

Introduction

The application of agrochemicals at the local scale and a strong reduction in habitat diversity at the landscape scale are the main drivers of the ongoing biodiversity loss under agricultural intensification (Kleijn et al. 2009, 2011; Stoate et al. 2001). Biodiversity, commonly measured as the number of species, is often related positively to the delivery of ecosystem services (Cardinale et al. 2012). The species composition of communities is an important additional component of biodiversity, but the identity and functional traits of species are often ignored in studies examining the

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effects of agricultural intensification (Moonen and Bàrberi 2008). Understanding the impact of agricultural intensification on species composition and trait diversity may lead to a better understanding of how to conserve biodiversity and how to improve predictions about the delivery of ecosystem services under future environmental change (Bommarco et al. 2013).

Naturally occurring generalist predators, such as spiders or ground-living beetles, contribute to the important ecosystem service of biological control of insect crop pests (Thies et al. 2011). Several recent studies provide strong evidence that landscape composition is an important factor affecting natural enemy communities in agroecosystems. Species richness and density of generalist predators are often found to be higher in complex landscapes, but the majority of these studies focussed on species richness or density measures (Chaplin-Kramer et al. 2011). These metrics provide useful baseline information, but analysing the effects of agricultural intensification on species and functional composition may provide more direct links to ecosystem functioning (Martin et al. 2013). Environmental factors act as filters that determine the species composition of communities and their life history traits. Thus, analysing impacts of agricultural intensification and land use change on both the taxonomic and functional composition of natural enemies might improve predictions about how communities will react to future environmental changes. Moreover, a large majority of studies focussing on natural enemies and biological pest control only considered a limited number of taxa (Gagic et al. 2012; Lohaus et al. 2013). There is a need for more multi-taxa approaches that link landscape structure to the functional composition of assemblages, because such studies will provide a holistic view of processes that shape communities of service-providing organisms in agricultural landscapes.

Several agro-environmental measures such as conversion to organic farming, grassland extensification, and preservation of specific biotopes to mitigate the negative effects of agricultural intensification are implemented throughout Europe (Kleijn et al. 2006). Their value for biodiversity conservation has been challenged and has been suggested to depend on landscape complexity. Local management options are suggested to be more effective in structurally simple landscapes rather than in extremely simplified or in complex landscapes ("intermediate landscape-complexity hypothesis"; Kleijn et al. 2011; Tscharntke et al. 2005, 2012). According to this hypothesis, biodiversity and associated ecosystem services are maximised in structurally very complex landscapes resulting in no noticeable benefits of additional management options at the field scale. Extremely simplified landscapes (e.g. dominated by arable land), in contrast, host a rather poor species pool that would not allow for positive effects of management options on biodiversity and the delivery of ecosystem services. However, there are few rigorous tests of such interactions between landscape context and management options at different scales on the functional diversity of service-providing communities (Tscharntke et al. 2012). Studies examining effects of management options on biodiversity and ecosystem services often consider implementation at the field scale, and almost nothing is known about outcomes at larger spatial scales (but see Rundlöf et al. 2008; Rusch et al. 2013).

Among on- and off-field management options, conversion to organic farming and diversified crop rotations have been suggested recently as promising tools to enhance provisioning of ecosystem services (Bennett et al. 2011; Bommarco et al. 2013). Organic farming combines a set of practices and is known to primarily enhance the abundance of natural enemies at the field scale (Bengtsson et al. 2005), with less predictable effects on species richness of ground beetles or spiders (Birkhofer et al. 2012). Almost nothing is known about the impact of organic farming on the functional structure of natural enemy communities. Diversification of cultivated plants in space and time has been suggested as a potential management option to improve the provision of ecosystem services (Bennett et al. 2011). For instance, diversified crop rotations are known to improve soil structure, reduce disease and weed pressure, or increase pollination services (Bommarco et al. 2013). Thus, including leys into crop rotations may result in an enhanced provision of intermediate ecosystem services such as nutrient retention, pollination or biological control. However, effects of a diversification of agricultural landscapes on the structure of service-providing communities remain unknown. It has been suggested that positive effects of organic farming on natural enemies may stem primarily from longer and more diversified crop rotations and particularly the inclusion of ley into the rotation (Bengtsson et al. 2005; Fuller et al. 2005). Rigorous tests of the independent effect of crop rotation on biodiversity and ecosystem services regardless of other correlated variables, such as the use/non-use of chemical fertilizers, are still lacking.

In this study, we analysed how organic farming at the field scale and crop diversification at the landscape scale affect the taxonomic and functional composition of generalist predator communities and how these effects vary along a landscape complexity gradient. We specifically studied how activity-density, taxonomic diversity, species composition, functional diversity, and functional redundancy of generalist predator communities are influenced by these management options. We hypothesize that (1) activity-density, species richness and evenness of generalist predator communities will be highest under organic farming and in landscapes with more diversified crop rotations; (2) functional diversity of predator communities should decrease with land-use intensification, indicated by a higher functional diversity in fields under organic farming or embedded in landscapes with more diversified rotations; and (3) the positive effect of these two management options will be most pronounced at an intermediate level of landscape complexity.

Methods

Study designs

Two study designs were established in the province of Skåne in southern Sweden. The ley design consisted of 24 conventionally managed spring barley fields selected along two orthogonal gradients: a gradient of the average proportion of ley in the landscape and a gradient of landscape complexity. The organic design consisted of 18 spring barley fields (9 organic and 9 conventional) selected along a similar landscape complexity gradient. These study designs allowed us to respectively test for the effects of crop rotation length at the landscape scale and farming system on predator communities along a gradient of landscape complexity. Spearman's correlations between major landscape variables are shown in Table S1.

The average amount of ley in the landscape between 2009 and 2011 was used as a proxy for crop rotation length and diversity at the landscape scale. Ley is temporary grassland composed of perennial crops intended for seed production, forage silage and hay that forms part of crop rotations on arable land. It is often kept for 2–3 years in the crop rotation, but sometimes longer, and is managed less intensively than annual crops (Jordbruksverket 2006). The proportion of ley included in short-term rotation is approximately constant when the total amount of ley varies (Jordbruksverket 2006), making the proportion of ley in the landscape a suitable proxy for its use in crop rotations. In southern Sweden, typical crop sequences that include 2 years of ley are 6-years long, and they are thus longer, less disturbed, and more diverse than intensive 3-year crop sequences that consist exclusively of annual crops such as spring barley, winter oilseed rape and winter wheat. Landscapes with high average proportions of ley can therefore be considered more diverse and less disturbed compared to landscapes with low average proportions of ley.

For both designs, landscape complexity was defined as the combination between the amount of semi-natural pastures and the length of field borders (Persson et al. 2010). These two variables were combined by principal component analysis(PCA). The first axis of the PCA was used as a measure of landscape complexity for field selection and data analyses. Larger values on the first PCA axis represent more complex landscapes, with higher amounts of pastures and with more field borders, whereas lower values represent more simple landscapes with lower amounts of pasture and fewer field borders. Additional details can be found in Rusch et al. (2013).

Fields were selected using the information on land-use available from the Integrated Administration and Control System (IACS), a database maintained by the Swedish Board of Agriculture. We first selected landscapes with similar levels of complexity (i.e. similar values on the first PCA axis) in a 1-km radius with low, medium and high average proportions of ley in the landscape (for details see Rusch et al. 2013). We used the same procedure to select farms in the organic design. We selected nine farms that had been under organic management for at least 10 years spanning from −1.66 to 2.35 along the first axis of the PCA and nine conventional farms spanning a comparable gradient (−1.32 to 1.91).

Sampling

In each field, ground-dwelling predators were monitored in a 20 × 100 m area that was not treated with insecticides and located at the field edge. Three pitfall traps (diameter 12 cm; depth 12 cm) were placed along a transect located in the middle of the experimental area, 10 m apart from the edge and each other. Pitfall traps were kept open for two periods of 7 days each during the aphid colonisation and aphid population growth phase (first period: from 30 May to 10 June 2011; second period: from 20 June to 1 July). Collected samples were stored in 70 % ethanol and ground beetles, spiders, and rove beetles were identified to species. Samples from the 2 week-long periods were pooled prior to analysis.

Measures of functional diversity

For each taxonomic group we collected information on functional traits from the literature. For ground beetles we used body size, wing morphology, breeding season, and diet preferences (Table S2). Spiders were characterized by body size, hunting mode, habitat preference, and preference for different strata (Table S2). Rove beetles were classified according to diet of adults and body size (Table S2). These traits were selected because they indicate differences in ecological strategies and are relevant to how species respond to environmental variation (see references in Table S2).

We used trait information to calculate four indices of functional diversity: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis) (Laliberté and Legendre, 2010). Functional richness is calculated as the volume of trait space occupied by a community and corresponds to a multidimensional range. Functional evenness combines the evenness of species spacing in trait space with the evenness of abundance distribution, and gives information about the regularity of the abundance distribution in trait space. Functional divergence represents how the abundance distribution diverges from the centre of the functional space (see Villéger et al. 2008). Functional dispersion, which is the mean distance in trait space of individual species to the centroid of all species, is independent of species richness and takes into account the relative abundance of species (Laliberté and Legendre 2010). The FD package, which implements a distance-based approach using a Gower dissimilarity matrix, was used to compute multidimensional functional diversity indices (Laliberté and Shipley 2011). Using Gower's distance makes it possible to take into account continuous, ordinal, nominal, multi-choice nominal, and binary variables. We did not compute functional diversity indices for rove beetles due to the limited number of traits available for this group.

In addition, we analysed how the activity-density of predator species with particular traits varies along farming systems and landscape gradients. These analyses of individual traits provide information about shifts in trait values within communities. For nominal traits, activity densities of predators were calculated separately for each group (spiders, ground beetles and rove beetles) in each design and for each trait modality. For continuous traits, we calculated the mean trait value of all species in the community weighted by their relative abundances for each group.

Measures of functional redundancy

To examine how functional redundancy within communities is affected by landscape and management options, we first classified species into functional groups using Ward's clustering method on a Gower dissimilarity species × traits matrix for each taxonomic group. The number of functional groups was determined by visual inspection of the resulting dendrogram. Following Laliberté et al. (2010), we calculated the functional redundancy of each functional group (i.e. number of species per group), and ranked values within each functional group to control for inter-group differences. For each taxonomic group in each design we calculated $n \times Fg$ functional redundancy values, where n is the number of sites and Fg is the number of functional groups resulting from the cluster analysis.

Data analysis

For each generalist predator group the response variables were: activity-density, species richness, community evenness (Pielou index), functional diversity indices (FRic, FEve, FDiv, FDis) and predator activity-density in each trait modality. We analysed raw species richness for each group as our sampling effort was standardised across sites.

We first used general linear models to test for the effect of different predictors on each response variable separately for each design. In the organic design, we examined the influence of farming systems and landscape complexity, including the interaction. In the ley design, we tested for the effect of landscape complexity and the average proportion of ley in the landscape, including the interaction. For each model, a validation procedure was then applied to check that underlying statistical assumptions were not violated. If residuals were not distributed normally or if heteroscedasticity was detected, we transformed the response variables (log, square root, or arcsine square root transformation) to meet the assumptions of the model. Model simplification was done using a stepwise selection procedure based on the Akaike information criterion adjusted for small sample sizes (AICc). If data transformations did not improve homogeneity of variances (i.e. if there was evidence for unequal variance in the residuals), we applied a generalised least square (GLS) modeling approach. The GLS approach makes it possible to model the heterogeneity of the variance as it allows the introduction of a range of variance-covariate structures (Zuur et al. 2009). The optimal error structure was determined by starting with a model without any variance-covariate terms and comparing this model with GLS models that contained specific variance structures. GLS models with different error structures were compared using the AICc, likelihood ratio-tests and graphical validation (Zuur et al. 2009). Once the optimal error structure was defined, the optimal fixed structure was identified with a manual backward selection procedure using likelihood ratio tests (fitted by maximum likelihood). Numerical output of the optimal model was obtained by refitting the model with REML following Zuur et al. (2009).

Distance-based permutational statistics were used for the analyses of community composition. This is an appropriate method to account for a large number of species (dependent variables) and activity density tables that are dominated by zeros (e.g. McCune and Grace 2002). Community composition based on activity density data for all spider, ground and rove beetle species was compared between sites by calculating the Bray-Curtis distances from untransformed data at each site. We did not transform activity density data prior to distance calculations, so that species contributions to differences between sites are weighed according to their activity densities. The resulting resemblance matrices for spider, ground and rove beetle communities were analysed for differences between organically and conventionally managed fields by permutational analysis of covariance with the average PC1 in a 1,000 m radius as a covariate and farming system as a fixed factor (including the interaction).

Non-metric multidimensional scaling was used to illustrate significant results with discriminating species between organically and conventionally managed fields being identified by similarity percentage analysis (SIMPER). Vectors for these species are shown in nonmetric multidimensional scaling (NMDS) plots based on multiple correlation coefficients ($R > 0.4$). The vector for PC1 was added as an additional vector to all NMDS plots. The resulting tri-plots show the similarity between organically and conventionally managed sites in terms of community composition (symbols and their distance), the preferences of discriminating species for a particular subset of sites (arrows) and the PC1 gradient (line). In the ley design we analyzed the relationship between the two continuous predictor variables PC1 and average area of ley in a 1,000 m radius and community composition using distance-based linear models (Legendre and Anderson 1999). To select predictor variables for the most parsimonious model we used forward selection based on the AICc for small sample sizes. Species with strong relationships (Pearson $R > 0.4$) to the selected predictors are shown as vectors in the NMDS plots, with values of the selected predictors superimposed as circles.

For each design, the effects of predictors on overall functional redundancy in communities were examined using generalized linear mixed models using site as a random effect to take into account the fact that there were several functional redundancy values per site (i.e. one value per functional group for each site). We used Gaussian or Poisson distribution as appropriate. In case of overdispersion, the standard errors were corrected using a quasi-GLM. The models were simplified by sequentially removing all non-significant terms, while respecting marginality.

Results

In total, 4,377 spiders of 72 species, 2,911 ground beetles of 65 species and 1,243 rove beetles of 53 species were trapped in the ley design. In the organic design, we trapped 2,535 spiders of 59 species, 2,655 ground beetles of 53 species, and 1,282 rove beetles of 53 species.

Ley design

Activity-density, species richness and community evenness

In the ley design, the activity-density of spiders increased with the proportion of ley in the landscape (Table 1 and S3; Fig. 1). Species richness of spiders was not affected by landscape complexity or the proportion of ley (Table 1 and S3). The evenness of spider communities was negatively related to the proportion of ley in the landscape and positively related to landscape complexity (Fig. 1). For ground beetles and rove beetles no effects were found for landscape complexity or the proportion of ley in the landscape on the activity-density, species richness, and evenness (Table 1).

Community composition

The species composition of spider communities tended to be related to the proportion of ley in the landscape ($R^2 = 0.09$; $P = 0.06$), with *Pardosa palustris* and *P. pratívaga* being more common at sites with more ley (Fig. 2a). Spider community composition was not related to landscape complexity ($R^2 = 0.02$; $P = 0.87$). In contrast, the community composition of ground beetles was related to landscape complexity ($R^2 = 0.13$; $P = 0.004$), with activity densities of *Bembidion lampros* and *Pterostichus melanarius* being negatively related to landscape complexity (PC1) (Fig. 2b). The composition of ground beetle communities was not related to the proportion of ley ($R^2 = 0.06$; $P = 0.24$). The community composition of rove beetles was related to the proportion of ley in a 1 km radius ($R^2 = 0.07$; $P = 0.049$), with *Aleochara bipustulata* and *Philonthus cognatus* being more common at sites with more ley and *Aloconota gregaria and Anotylus insecatus* preferring sites with a lower proportion of ley in the landscape (Fig. 2c). Rove beetle community composition was not related to landscape complexity (PC1) values ($R^2 = 0.05$; $P = 0.29$).

Functional diversity

Functional richness, evenness and divergence of spiders were affected neither by landscape complexity nor by the proportion of ley. However, functional dispersion of spiders was negatively related to the proportion of ley in the landscape (Table 1 and S4). This indicates that, as the proportion of ley in the landscape increased, functionally more similar spider species tended to be favoured. Functional diversity indices for ground beetle communities were not related to the proportion of ley or landscape complexity. Analyses were not performed on rove beetles due to limited trait information that was available.

The activity-density of ground running spiders and of spiders with preferences for meadows increased with the proportion of ley in the landscape (Table 1 and S5). Similarly, spiders with a preference for soil surface and herb layer increased with the proportion of ley in the landscape (Table 1 and S5). The mean body size of spiders was not related to landscape complexity or the proportion of ley in the landscape (Table 1).

Individual trait analyses for ground beetles indicated that the activity-density of autumn breeders decreased with the proportion of ley in the landscape (Table 1 and S5). No effect of landscape complexity or the proportion of ley in the landscape was found on mean body size of ground

Table 1 Summary of effects of the two management options (organic farming at the field scale and the proportion of ley in the landscape) along landscape complexity gradients on the taxonomic and functional structure of predator communities in cereal fields

	Ley design			Organic design		
	% of ley	PC1	Interaction	Organic	PC1	Interaction
Spiders						
Activity-density	+			(+)		
Species richness			(+)			
Evenness	–	+				
FRic						
FEve				–		
FDiv						
FDis	–		(+)			
FRedundancy						
Hunting mode						
Folliage runners				+		
Ground runners	+			+		
Wand sheet						
Ambushers						
Space Web						
Orb weaver						
Preferred habitat						
Forest						
Moor						
Meadow	+			+		
Arable				+		
Ruderal						
Shrub						
Preferred strata						
Under stone						
Soil surface	+					
Herb layer	+					
Shrub layer					+	
Tree trunk					+	
Tree canopy						
Body size						
Ground beetles						
Activity-density						
Species richness						
Evenness						
FRic						
FEve						
FDiv						
FDis					(−)	
FRedundancy						
Diet						
Carnivorous						
Phytophagous						
Omnivorous						
Breeding season						
Autumn breeder	–					
Spring breeder						

Table 1 continued

	Ley design			Organic design		
	% of ley	PC1	Interaction	Organic	PC1	Interaction
Wing morphology						
Macropterous						
Dimorphic						
Brachypterous						
Body size						
Rove beetles						
Activity-density				+		
Species richness						
Evenness				–		
FRedundancy				+		
Diet						
Carnivorous				+		
Omnivorous						
Mycetophagous						
Body size	+					

Only significant and marginally significant (in parenthesis) results are presented in the table. See Supplementary materials for further statistical details. Multiple traits analysis was not performed for rove beetles due to limited trait information that was available

beetles as well as on activity-density of ground beetles for each modality of diet or wing morphology (Table 1).

The mean body size of rove beetles increased with the proportion of ley in the landscape (Table 1 and S5; Figure S1). Individual trait analyses for rove beetle diet revealed no effect of landscape complexity or the proportion of ley in the landscape.

Functional redundancy

In the ley design, three, five, and two functional groups were respectively identified for spiders, ground beetles, and rove beetles by cluster analyses. Similar levels of functional redundancy were found for spiders, ground beetles, and rove beetles along the proportion of ley and the landscape complexity gradient (Table 1; Figure S2).

Organic design

Activity-density, species richness and community evenness

Activity-density of spiders tended to be affected by the farming systems with more individuals in the organic (182.7 ± 40.3) than in the conventional fields (101.6 ± 17) (Table 1 and S6; Fig. 3). No differences in activity-density of ground beetles were found between farming systems. More rove beetles were trapped in the organic (mean ± SE; 106.8 ± 28.9) compared to the conventional (36.5 ± 8.15) farming system (Table 1 and S6; Fig. 3). The activity-densities of spiders, ground beetles and rove beetles were not related to landscape complexity (Table S6). Species richness of spiders, ground beetles and rove beetles were not affected by farming system or landscape complexity (Table S6). The evenness of rove beetle communities was lower in the organic (0.71 ± 0.04) compared to the conventional fields (0.85 ± 0.02) (Table S6). Evenness of ground beetles and spiders did not differ between farming systems or along the landscape complexity gradient.

Community composition

The community composition of spider species differed between farming systems (Table S7a), with *P. palustris* (63 vs 18 individuals field^{-1}) and *P. agrestis* (42 vs 1 individual field^{-1}) being more common in organically managed fields (Fig. 4a). *Pardosa prativaga* (17 vs 30 individuals field^{-1}) exhibited the opposite preference with higher activity density in conventionally managed fields. Spider community composition was not related to landscape complexity (Table S7). Ground beetle community composition was not affected by farming system and not related to landscape complexity (Table S7b). The community composition of rove beetles was affected by farming system (Table S7c), with three species from the genus *Aleochara* (*A. bilineata*, 10 vs 3 individuals field^{-1}; *A. bipustulata*, 46 vs 3 individuals field^{-1} and *A. curtula*, 7 vs 2 individuals field^{-1}) showing higher activity densities in organically managed fields (Fig. 4b). Two species (*Aleochara brevipennis* and *P. cognatus*) were more common in fields embedded in more complex landscapes, whereas *Aloconota gregaria* occurred more often in fields embedded in more simple landscapes.

Functional diversity

The functional evenness of spiders was negatively affected by organic farming (Table 1 and S8). The functional

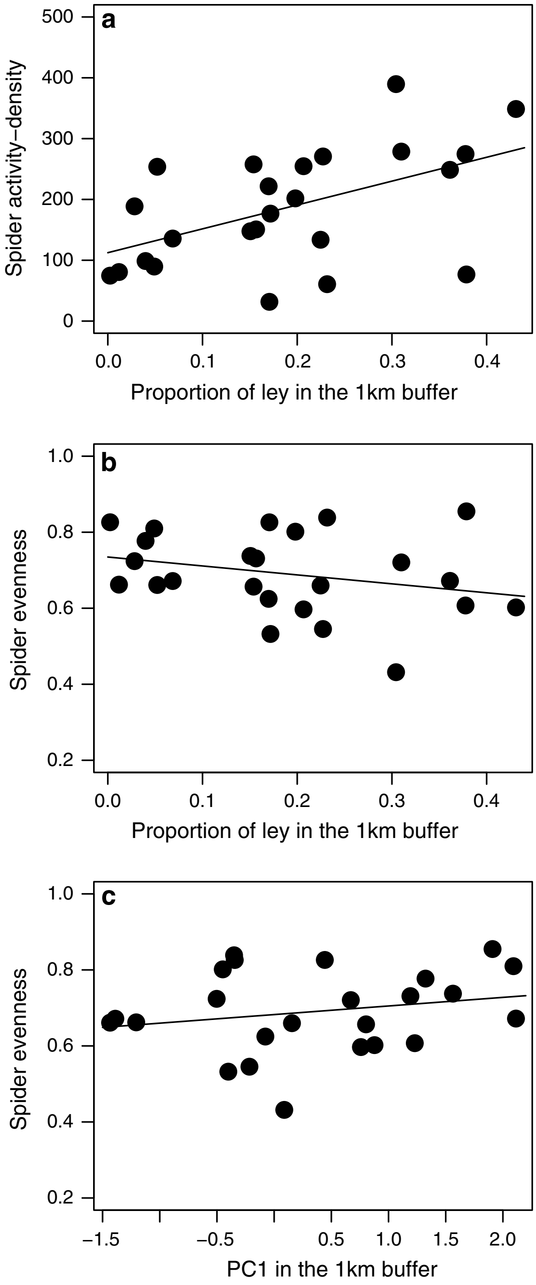

Fig. 1 Relationships between the average proportion of ley in a 1 km radius and spider **a** activity-density, **b** evenness, and **c** relationships between landscape complexity (PC1) and spider evenness. Results were obtained after stepwise multiple regression analyses. See Table S3 for statistics

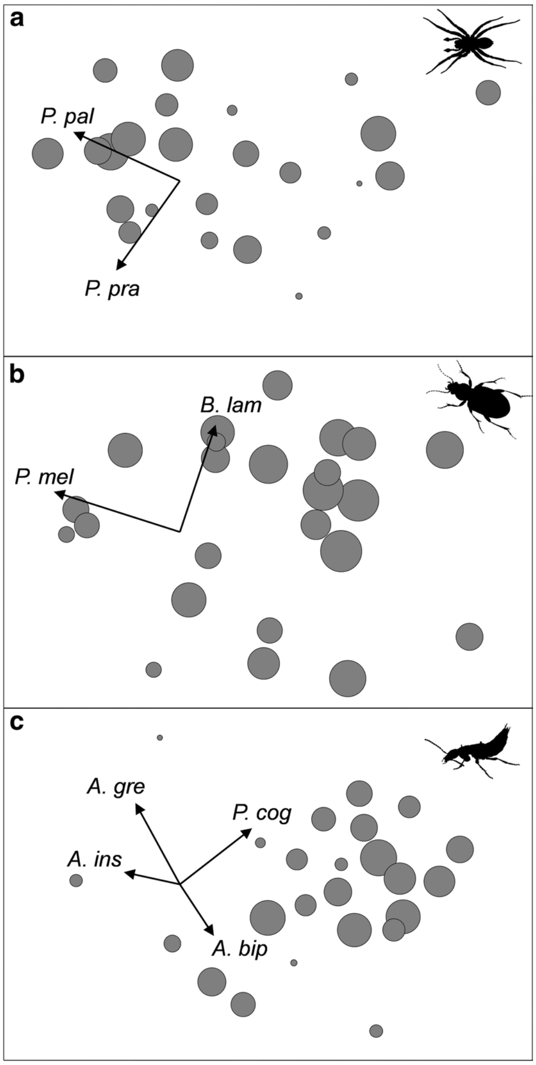

Fig. 2 Nonmetric multidimensional scaling (NMDS) ordination based on the community composition of **a** spiders (2-d stress 0.11), **b** ground beetles (2-d stress 0.17) and **c** rove beetles (2-d stress 0.19) with symbols scaled according to the area of ley around each site for **a** and **c** and according to the landscape complexity (PC1) value of each site for **b**. Vectors are superimposed for species that had a multiple correlation coefficient >0.4. For species abbreviation see "Results" section

dispersion of ground beetles tended to decrease with landscape complexity (Table 1 and S8). No other functional diversity metrics were significantly related to farming system or landscape complexity in the analysed taxa.

The individual trait analyses for spiders revealed that the activity-density of foliage running and ground running spiders, as well as the activity-density of spiders with preferences for meadow and arable land, tended to be higher in organic farming systems (Table 1 and S9). Spiders with preferences for shrub layer and tree trunk habitats tended to have higher activity-densities in more complex landscapes (Table 1 and S9). Farming system and landscape complexity did not significantly affect mean body size of spiders.

Farming system or landscape complexity did not significantly affect individual trait values of ground beetles for body size, diet, breeding season and wing morphology (Table 1 and S9).

More carnivorous rove beetles were found in organic fields compared to conventional fields (Table 1 and S9). Farming systems and landscape complexity did not affect mean body size of rove beetles significantly.

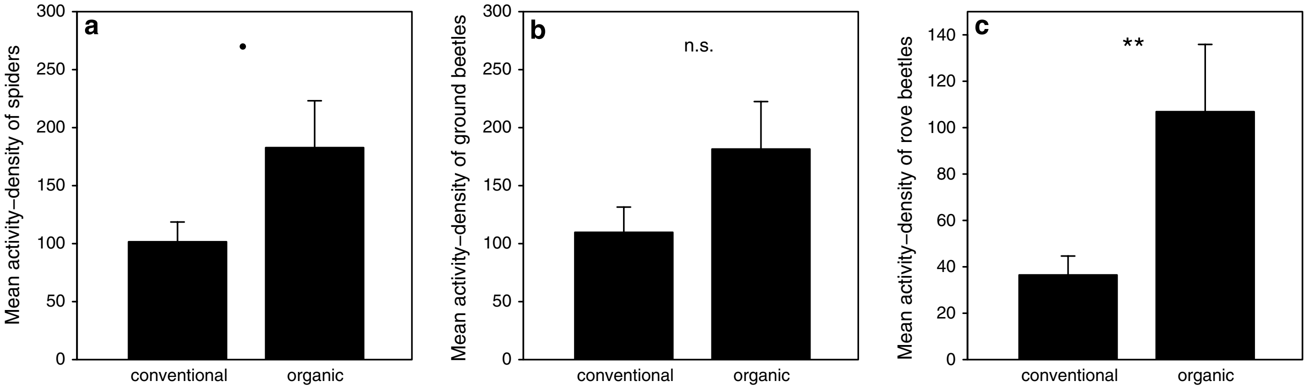

Fig. 3 Activity density of **a** spiders, **b** ground beetles, and **c** rove beetles in organic and conventional barley fields. •$P < 0.01$, **$P < 0.001$, *ns* not significant

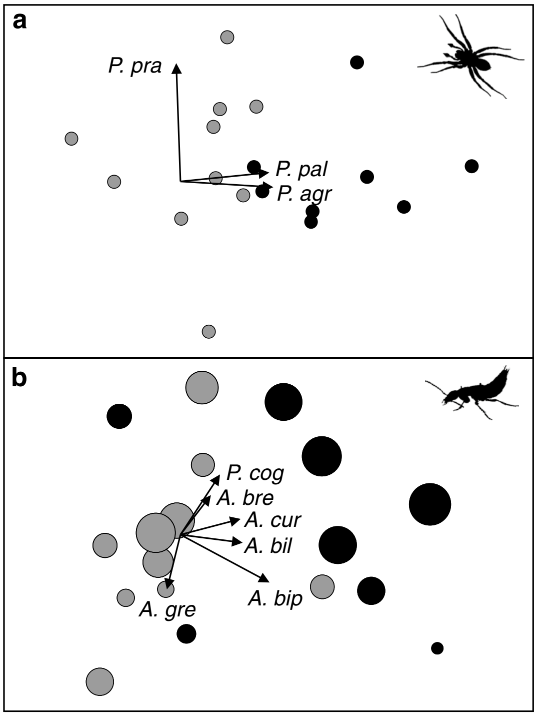

Fig. 4 NMDS ordination based on the community composition of **a** spiders (2-d stress 0.12) in conventionally (*filled circles*) and organically (*filled circles*) managed barley fields, and **b** rove beetles (2-d stress 0.15) in conventionally (*filled circles*) and organically (*filled circles*) managed barely fields with symbols scaled according to the PC1 value of each site (range −17 to 24). Vectors are superimposed for species that had a multiple correlation coefficient >0.4. For species abbreviation see "Results" section

Functional redundancy

Four, six, and two functional groups were identified for spiders, ground beetles and rove beetles respectively, by cluster analyses. The functional redundancy of spider and ground beetle communities was not related to any predictor, but functional redundancy of rove beetles was significantly higher in organic compared to conventional fields (Table 1 and S10; Fig. S3).

Discussion

In this study, we analyzed how crop diversification in the landscape and organic farming at the field scale affected the community structure of generalist predators in cereal fields along a landscape complexity gradient. Our analyses revealed that management options, either at the local or the landscape scale, were more important in explaining the taxonomic and functional structure of generalist predators than landscape complexity. Our approach further highlights how analysis of complementary aspects of community structure provides valuable insights about how intensification shapes natural enemy communities in agricultural landscapes.

Activity-density, species richness and evenness

We first hypothesized that the two management options would increase activity-density, species richness and evenness of generalist predator communities. This hypothesis was partly confirmed for the activity-density of predators as we found that more diverse crop rotation at the landscape scale as well as organic farming at the field scale tended to increase the activity-density of all natural enemies pooled together. In the ley design, the higher activity-density of predators was due mainly to the increase in activity-density of spiders whereas in the organic design it was due mainly to higher activity-density of rove beetles and spiders. Perennial habitats, such as ley, are known to be a major source of immigration of spiders in spring as they are used as overwintering sites (Lemke and Poehling 2002; Öberg and Ekbom 2006). This explains the higher activity-density in fields embedded in landscapes with higher proportions of ley. Moreover, our results are in line with well-known effects of organic farming on abundance of predatory insects (Bengtsson et al. 2005; Tuck et al. 2014) and with results of specific studies on spiders (Schmidt et al. 2005) and rove beetles (Andersen and Eltun 2000). The positive effect of organic farming suggests more favourable habitat conditions that could result from the absence of synthetic pesticides, higher prey availability and lower intraguild predation due to higher structural within-field complexity, the use of organic fertilizers and the higher amounts of organic material in the soil (Langellotto and Denno 2004; Birkhofer et al. 2008; Rusch et al. 2010).

Contrary to our expectations, the results of our study indicated that extended and more diverse crop rotations as well as organic farming did not enhance species richness and evenness of generalist predators. In fact, we found that both management options tended to decrease evenness of predators, particularly of spiders in the ley design and rove beetles in the organic design. These results differ from recent results by Crowder and Snyder (2010) showing greater evenness of natural enemies in organic compared to conventionally managed fields. This difference can be explained by the fact that these two management options only increased the activity-density of a few predator species with similar functional traits (see below). In addition, Crowder and Snyder (2010) reported some cases where evenness of natural enemies was lower in organic fields.

The result that farming system did not affect the activity-density, species richness and evenness of ground beetles is supported by results from other studies (Winqvist et al. 2011 and references therein). It has been demonstrated that ground beetles are affected by specific farming practices such as crop type, soil tillage or pesticide applications (Holland and Luff 2000), but the overall effect of farming systems remains unclear (Winqvist et al. 2011; Birkhofer et al. 2012). This may be explained by the high variability of practices potentially used under organic farming, antagonistic effects of crop management on ground beetle communities, or high tolerance to disturbance.

Contrary to recent findings from Chaplin-Kramer et al. (2011), we did not detect any effect of landscape complexity on species richness of generalist predators. However, we found a positive effect of landscape complexity on evenness of spider species in the ley design, indicating that complex landscapes may provide resources for a higher number of species compared to rather homogeneous landscapes which favour only a few species that are well adapted to arable fields (agrobiont species).

Functional diversity and life-history traits

We initially hypothesized that functional diversity of predator communities would be higher in landscapes with high proportions of ley and in organic fields. Our results showed that the two management options did not affect predator functional diversity per se but that they shaped functional community composition as they differentially affected species depending on their life-history traits.

We found that more diversified rotations in the landscape as well as organic farming increased the functional similarity of spider communities. Indeed, our results showed that both functional dispersion and functional evenness in spider communities were significantly lower in landscapes with high proportions of ley and in organic fields. Furthermore, our analyses revealed that spider communities were functionally more similar with respect to hunting mode and habitat preference in organic fields and with increasing proportions of ley in the landscape. In particular, ground running spiders (*P. agrestis* and *P. prativaga*), as well as spiders with preferences for meadows, benefited from both management options. Higher activity-densities of three rove beetle species that functionally resemble each other (i.e. *A. bilineata*, *A. bipustulata* and *A. curtula*) were recorded in organic fields. This suggests that environmental filtering, mediated by habitat requirements and life-history traits of predators and associated to spillover processes, is responsible for such changes in predator communities. Spider species that hunt on the ground and with a preference for meadows may prefer leys and organic farming over cereal fields as they may be able to hunt and reproduce better in those systems (Bell et al. 2001). Moreover, cursorial spiders, such as *Pardosa* spp., often occur at low densities in the field centre and are more affected by a reduced availability of overwintering sites at the landscape level as they have lower dispersal abilities compared to ballooning spiders (Schmidt and Tscharntke 2005). Our results suggest that both organic farming and longer crop rotations increase the success of crop colonisation for cursorial species.

The observed higher functional redundancy of rove beetles in organic fields is in accordance with recent studies showing that land-use intensification reduces functional redundancy in communities of taxa such as plants, birds and mammals (Flynn et al. 2009; Laliberté et al. 2010). In organic fields, communities of rove beetles and the pest control service they provide might be more stable over time and less vulnerable to future disturbance (Hooper et al. 2005).

The positive relationship between the proportion of ley in the landscape and mean body size of rove beetles supports the hypothesis that species with larger body sizes are more vulnerable to disturbance (Blake et al. 1994; Ewers and Didham 2006). Landscapes with shorter and less diversified crop rotations are characterized by higher levels of disturbance than landscapes with a high proportion of ley. Global size-density relationships predict that small species generally occur at higher densities compared to larger species (White et al. 2007), suggesting that small-sized invertebrate predators should have a lower probability of local extinction and therefore be less affected by disturbance (Magura et al. 2006). Moreover, larger organisms usually have lower reproductive rates than smaller species and are therefore more sensitive to temporal variability in resource availability and local extinctions (Ribera et al. 2001). Surprisingly, no effects of the two management options or of landscape complexity were found on the mean body-size of spiders and ground beetles in the present study. This may indicate that other processes are more important in shaping body-size distribution in these communities, or that other correlated traits are masking the relationship between body size and landscape complexity (Ewers and Didham 2006; Henle et al. 2004).

Interactions between management options and landscape complexity

Finally, we hypothesized that the effect of the two management options on activity-density, taxonomic or functional diversity of predators would be modulated by the surrounding landscape. Following the intermediate disturbance hypothesis, we initially predicted that taxonomic and functional diversity would be maximized at an intermediate level of landscape complexity (Connell 1978). However, our results did not support this intermediate landscape-complexity hypothesis (Tscharntke et al. 2012). In fact, landscape complexity did not seem to influence the effects of different management options on activity-density and species richness of generalist predators. This might be due to different landscape composition or lower range of variation in landscape complexity in our studied area compared to other regions where this hypothesis has been validated (Batáry et al. 2011). This result indicates that, at least in the region where the study was performed, management options, such as organic farming or diversifying crop rotations, are promising options to enhance activity-density of predators irrespective of the proportion of semi-natural habitats in the landscape.

Conclusions

The results of our study demonstrate that management options aiming at decreasing agricultural intensification, such as organic farming or crop rotation diversification, affect predator community composition through effects on species that share similar traits. Environmental changes did not alter composite indices of functional diversity (e.g. functional richness, functional evenness).Single trait values, however, were affected and this suggests that analysis of individual traits facilitates understanding of predator community responses to farming practices. These results are consistent with a recent study comparing the performance of individual and composite indices in linking environmental variables and functional composition to ecosystem functions (Butterfield and Suding 2013). Composite indices might be more relevant when describing general changes in functional diversity based on large trait databases or when investigating multiple ecosystem processes (Mouillot et al. 2011).

Our results show that management options were more important than landscape complexity in explaining structural aspects of generalist predator communities in cereal. Specifically, the activity-density of functionally similar species was enhanced by the proportion of ley in the landscape or by organic farming regardless of landscape complexity. This increase in activity-density of generalist predators does not necessarily imply an increase in the delivery of natural pest control services as different types of interactions (i.e. positive, negative or neutral) can occur between predator species. Future studies should link changes in community structure to the delivery of ecosystem services to assess the effectiveness of management options on the flow of ecosystem services in agroecosystems.

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