

Pest control potential of adjacent agri-environment schemes varies with crop type and is shaped by landscape context and within-field position

Fabian A. Boetzl  | Maren Schuele | Jochen Krauss  | Ingolf Steffan-Dewenter 

Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Würzburg, Germany

Correspondence

Fabian A. Boetzl
Email: fabian.boetzl@uni-wuerzburg.de

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Abstract

1. Increasing natural pest control in agricultural fields is an important aim of ecological intensification. Combined effects of landscape context and local placement of agri-environmental schemes (AES) on natural pest control and within-field distance functions of natural pest control agents have rarely been addressed but might affect the distribution of biocontrol providers. Importantly, it is currently unknown whether ecosystem services provided by adjacent AES are consistent for different crop types during crop rotation.
2. In this study, we assessed whether crop rotation from oilseed rape to cereals altered within-field distance functions of ground-dwelling predators from adjacent agri-environmental fields along a gradient in landscape context. Additionally, we recorded crop pests, predation rates, parasitoids as well as crop yields on a total of 30 study sites.
3. Distance functions varied between trophic levels: Carabid richness decreased while densities of carabid beetles, staphylinid beetles as well as crop yields increased towards the field centres. Distance functions of parasitoids and pests were modulated by the amount of semi-natural habitat in the surrounding landscape, while the effects of adjacent AES were limited.
4. Distance decay functions found for ground-dwelling predators in oilseed rape in the previous year were not always present in cereals. Increasing distance to the field edge also increased effects of crop rotation on carabid beetle assemblages, indicating a source habitat function of field edges.
5. *Synthesis and applications.* Distance functions of natural pest control are not universal and the effects of agri-environmental schemes (AES) in different adjacent crops during crop rotation vary and depend on ecological contrasts. A network of semi-natural habitats and spatially optimized AES habitats can benefit pest control in agricultural landscapes, but constraints as a result of crop type need to be addressed by annually targeted, spatially shifting agri-environment schemes for different crops.

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KEY WORDS

cereals, distance gradient, ecological intensification, ecosystem services, ground-dwelling predators, parasitoids, pest control, semi-natural habitats

1 | INTRODUCTION

Increasing natural pest control in agricultural fields is one of the main goals of ecological intensification. As many different biotic factors influence crop yields, ecological intensification aims at understanding and fostering these biotic relations and at replacing external fertilizer and pesticide input by biodiversity-mediated functions to make modern agriculture more sustainable (Bommarco, Kleijn, & Potts, 2013; Garibaldi et al., 2019).

A widely implemented approach to increase ecosystem services in agricultural landscapes is the creation of agri-environmental scheme (AES) habitats as safe-havens for biodiversity and ecosystem service providers (Ekroos, Olsson, Rundlof, Watzold, & Smith, 2014; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). The benefits of AES in increasing species richness and abundance of plants and animals in croplands have been shown (Batáry, Báldi, Kleijn, & Tscharntke, 2011). However, effectiveness varies between the types of AES implemented (Batáry, Dicks, Kleijn, & Sutherland, 2015) and it is largely unknown whether and how effectively AES support ecosystem services in adjacent crops (but see Dainese, Montecchiari, Sitzia, Sigura, & Marini, 2017). In Central Europe, many habitats currently created under AES (e.g. temporary flower strips or fields) are tailored to support pollinators and potential off target effects on other ecosystem services like pest control are poorly understood and rarely investigated (but see Tschumi et al., 2016).

Recent comprehensive synthesis studies unveiled landscape level drivers of natural pest control in agricultural landscapes. Both landscape composition and configuration were shown to be important drivers with landscape simplification decreasing natural enemy richness and thereby weakening natural pest control (Dainese et al., 2019; Haan, Zhang, & Landis, 2019; Karp et al., 2018). Edge density as a measure of landscape complexity, proportion of semi-natural habitat (SNH) as a measure of landscape composition as well as crop diversity in agricultural landscapes benefit natural enemies, pest control and ultimately increase yields (Martin et al., 2019; Redlich, Martin, & Steffan-Dewenter, 2018). However, translating these findings into practical management for ecological intensification is complex as most landscape characteristics cannot easily be restructured. While AES habitats are an accessible means by which policy makers can enhance diversity in agricultural landscapes, the landscape types with the greatest benefits remain unclear (as suggested by Tscharntke, Batáry, and Dormann (2011)).

Apart from landscape level drivers, the distribution of pest control agents could also be modulated by local crop rotation and within-field distance decay functions (Boetzl, Krimmer, Krauss, & Steffan-Dewenter, 2019; Fusser et al., 2018). Crop rotation is a

widely used method to counter weeds, diseases and pests by disrupting continuous host availability to maintain soil fertility. Previous studies on natural pest control and crop rotations focused on the landscape level aspect of crop rotations and not on changes within the same fields or interactions with adjacent habitats (e.g. Rusch, Birkhofer, Bommarco, Smith, & Ekbom, 2014; Rusch, Bommarco, Jonsson, Smith, & Ekbom, 2013). Apart from crop type, crop rotation, however, changes specific management regimes (soil management, fertilization and agrochemical input) potentially affecting spillover and within-field distribution of natural enemies and ecosystem services provided by adjacent AES habitats. The direct effects of crop rotation on local ecosystem service providers are, however, rarely assessed.

Field edges differ from field centres as they undergo less intensive management and are more affected by spillover from adjacent habitats (Boetzl, Krimmer, et al., 2019; Tscharntke, Rand, & Bianchi, 2005). Yet, the extent of these effects on pest control and yields as well as the role of adjacent habitats remains unclear. To address this question, distance gradients have received more attention in recent years, but few studies have actually addressed more than two within-field distances (e.g. Birkhofer, Wolters, & Diekötter, 2014; Van Vooren et al., 2018; Woodcock et al., 2016) which limit the value of datasets as no predictions of distance functions are possible. Moreover, most existing datasets only contain single trophic levels and represent snapshots as they do not cover longer time periods. In a large field study conducted in winter oilseed rape with adjacent AES habitats tailored to support pollinators, distance decay functions of ground-dwelling predators (Boetzl, Krimmer, et al., 2019) and pollinators (Krimmer, Martin, Krauss, Holzschuh, & Steffan-Dewenter, 2019) were reported. Distance decay functions of pollinators were buffered by increasing amount of SNHs in the surrounding landscape (Krimmer et al., 2019). In total, however, data on distance functions, especially across different trophic levels, is still very limited and if distance functions are affected by different adjacent habitats, landscape context or crop type remains poorly understood. Furthermore, no studies have so far addressed how crop rotation and the consequent replacement of crop types adjacent to AES habitats affects their provision of pest control services.

In this study, we investigated whether different trophic levels (agricultural pests, ground-dwelling predators and flying parasitoids), predation rates and crop yields depend on distance from the field edge, SNH in the surrounding landscape and/or adjacent AES habitat presence and type within one large-scale field study throughout the growing period. We assessed (a) how different pest control agents, pests and crop yields are affected by distance, landscape context (proportion of SNH) and adjacent AES habitats, (b) whether distance

decay functions persist during crop rotation in a different crop (from oilseed rape to cereals) as well as (c) if crop rotation shifted carabid beetle assemblages in the same sites between years and how this depended on distance, proportion of SNH and adjacent AES habitat type.

2 | MATERIALS AND METHODS

2.1 | Study design

The study design comprised 30 study sites with five different treatments consisting of four different adjacent AES habitats (new flowering fields, refreshed flowering fields, continuous flowering fields (CAP greenings) established on regular agricultural fields and permanent semi-natural calcareous grasslands) and controls with an adjacent arable field. In each field, all measurements were taken along a continuous distance gradient with three distances per field from the field edge (at the side of the adjacent AES habitat) into the field centres (1–65 m). Distances varied with field size (Supporting Information 1; Table S1).

For this study, we used the same study design and study sites as in Boetzel, Krimmer, et al. (2019) and Krimmer et al. (2019). Following the typical crop rotation, winter cereals followed the previous field culture (oilseed rape; Table S1). All studied winter cereal fields were managed conventionally, have undergone very similar management regimes in the study region and were therefore considered comparable.

To assess landscape level effects, non-overlapping landscapes with a radius of 1 km around all study sites formed a gradient of SNH within each treatment ranging in total from 3.6% to 31.6%. SNH included only permanent habitats (forest edges, field margins, bank borders, roadside vegetation, small wood groves, hedgerows, orchard meadows and extensive pastures as well as semi-natural calcareous grasslands and grassland taken out of agricultural production; see Krimmer et al., 2019 for more information).

2.2 | Data collection

Along the distance transects, different variables were recorded over the vegetation period from early April until crop harvest in early July 2017 (Figure 1): (a) pest densities using sweep netting; (b) parasitoid densities using crossed window traps; (c) ground-dwelling predators (carabid beetles, staphylinid beetles and spiders) using pitfall traps; (d) predation rates on the ground using aphid sentinel prey cards (Boetzel, Konle, & Krauss, 2019) and (e) crop yields. The factors (a), (b) and (d) were recorded during the sensitive period of milk ripening where cereals are both very attractive to pests and very sensitive to pest pressure. Detailed descriptions of all methods and sampling schemes are provided in Supporting Information 1.

2.3 | Statistical analyses

All statistical analyses were performed in R 3.6.1 for Windows (R Development Core Team, 2019), using the packages `LME4` (Bates, Machler, Bolker, & Walker, 2015), `LME4TEST` (Kuznetsova, Brockhoff, & Christensen, 2017), `MULTCOMP` (Hothorn, Bretz, & Westfall, 2008), `VEGAN` (Oksanen et al., 2019) and `GGEFFECTS` (Lüdecke, 2018).

For all responses obtained from passive traps (pitfall & window traps), we calculated per day activity densities throughout the sampling period (to account for occasional trap losses, 1.6% for both trap types combined). Species richness was the accumulated number of species at the end of the sampling period. For pest densities and predation rates, measured values were first averaged between replicates per plot (sampling distance per site) and then summed over the sampling period to obtain an accumulated pest pressure and predation value.

As calcareous grasslands are naturally located within landscapes that have a high proportion of SNH, they had significantly higher SNH percentages than all other AES types (linear model: $F_{4,25} = 4.96$, $p = 0.004$). We therefore excluded the fields bordering calcareous

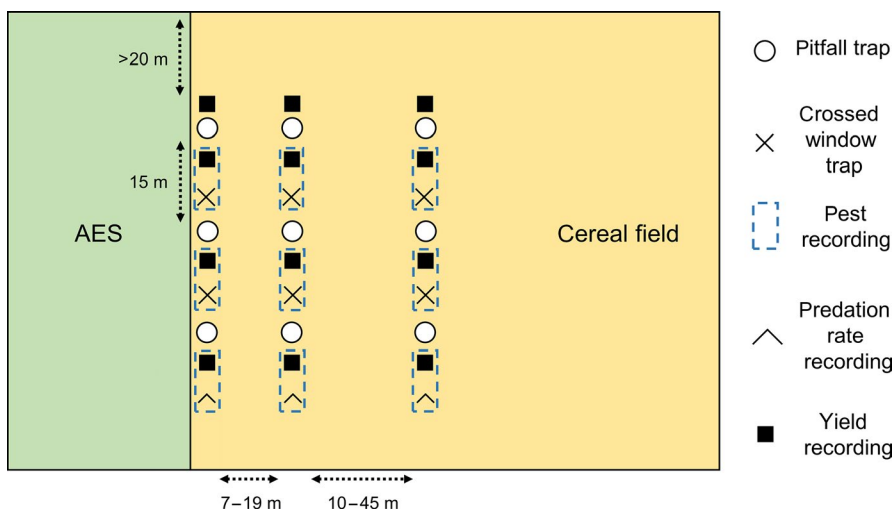


FIGURE 1 Schematic representation of the study design with symbols representing methods used and distances between within-field positions and between pitfall trap transects (circle: pitfall trap for ground-dwelling predator recording; cross: crossed window trap for parasitoid recording; dashed square: sweep netting for pest density assessment; angle: predation rate recording using aphid sentinel prey cards; square: yield harvest)

grasslands in all models investigating distance functions and SNH (models including these sites are shown in Table S3).

For all responses, we tested models including the fixed effects 'distance', 'SNH' and 'AES habitat type' as well as the interactions 'AES habitat type: distance' and 'SNH: distance' while 'study site ID' was used as random intercept. To select the best model for different hypothetical distance functions, distance was included in different ways: (a) linear, (b) quadratic (for hump-shaped patterns) or logarithmic (for asymptotic patterns). For these comparisons, 'distance' and 'SNH' were rescaled in order to allow comparability among models. We compared the resulting models using the likelihood ratio approach and if models were significantly different, the best model was selected based on AIC (otherwise, the simple linear distance model was kept). Activity densities of carabid beetles, spiders and densities of cereal leaf beetle (CLB) larvae were square root transformed to improve normality. If significant differences between adjacent AES habitats types were detected, we performed Tukey-HSD post hoc tests (function 'glht').

Changes between carabid beetle assemblages over crop-rotation were investigated based on Bray-Curtis similarities between the assemblages in the same distance and site in both years. Moreover, we assessed if crop rotation did change species assemblages using a PERMANOVA ('adonis', Bray-Curtis dissimilarities, 999 permutations) on a species-abundance table containing the pooled data of all within-field distances per site (species proportions). Additionally, we calculated Bray-Curtis similarities between carabid assemblages caught in both years in the same within-field distances. Similarities were compared in a linear mixed effects model using 'study site ID' as random intercept (following the same procedures described above).

For the figures, we predicted the best model with 95% confidence intervals over the gradients of distance or SNH we investigated. If significant distance: SNH interactions were present, we predicted distance functions for the SNH levels 5%, 10%, 15% and 20%.

3 | RESULTS

Throughout the vegetation period, we caught 128,826 carabid beetles (~2.5 times the amount of the previous year in oilseed rape) from 119 species (one species less than in the previous year; Table S2), 84,979 staphylinid beetles (~1.9 times the amount of the previous year), 86,682 spiders (~3.1 times the amount of the previous year) and 5,056 parasitoid wasps in the studied fields. For the analyses, we only used non-granivorous carabid beetles to predict pest control potential which were 117,391 individuals (~3.2 times the amount of the previous year) from 79 species (one species less than in the previous year; Table S2). In pest recordings, we observed a total of 1,815 CLB larvae (*Oulema* sp.) on all transects. We used a total of 2,160 aphids of which 1,255 (58.1%) were consumed during predation rate assessments. Ultimately, we harvested a total of 45,282

ears containing 1,274,688 grains with a total weight of approximately 45.3 kg.

3.1 | Effects of within-field distance and SNH

Carabid species richness was driven by a distance decay from the field edges towards the field centres declining by 10% within 65 m (Table 1; Figure 2a). Carabid activity density, however, was increasing towards the field centres by 17% (Table 1; Figure 2b). The densities of CLBs and parasitoids were moderated by both SNH proportion and distance to the field edge; they increase towards the field centres in landscapes with low SNH (at 5% SNH: 30% in CLBs and 24% in parasitoids) and decrease in landscapes with comparably high SNH (at 20% SNH: 29% in CLBs and 30% in parasitoids; Table 1; Figure 2e,f). The same trend was found for carabid beetle activity densities, however, not significant (Table 1; Figure S1). The activity density of staphylinid beetles followed a hump-shaped pattern increasing by 22% from the edge to the peak at 45 m near the field centres (Table 1; Figure 2c). There was no significant distance function found for spider activity density or predation rates (Table 1; Figure 2d,g). Crop yields increased by 31% from the field edges towards the centres, reaching 95% of the maximum yield after 27 m and peaking at 49 m (Table 1; Figure 2h).

Carabid beetle activity densities tended to decrease by 81% with increasing SNH while spider activity densities were decreasing by 40% from landscapes with low SNH to landscapes with high SNH (Table 1; Figure 3a,b). On the contrary, predation rates tended to increase by 75% from landscapes with low SNH towards landscapes with high SNH (Table 1; Figure 3b).

3.2 | Effects of adjacent AES

We did not find effects of adjacent AES habitat type or controls without adjacent AES habitat on densities of ground-dwelling predators, parasitoids, CLBs or yields (Table 1). However, predation rates were highest in fields adjacent to refreshed flowering fields and did not differ significantly in fields bordering the other AES habitat types (Table 1; Figure S2).

3.3 | Similarity between carabid assemblages in both years

Carabid beetle assemblages within the crop fields changed with crop rotation between the years (PERMANOVA crop field centres, $F_{1,59} = 5.02$, $p = 0.001$) while carabid assemblages in adjacent AES habitats did not change significantly (PERMANOVA, $F_{1,52} = 0.89$, $p = 0.669$; Figure S3). We therefore expect that the observed changes were driven by the change in crop type and not by annual variation. Although total species richness decreased by one species from 120 to 119 species (0.9%), 12 species were

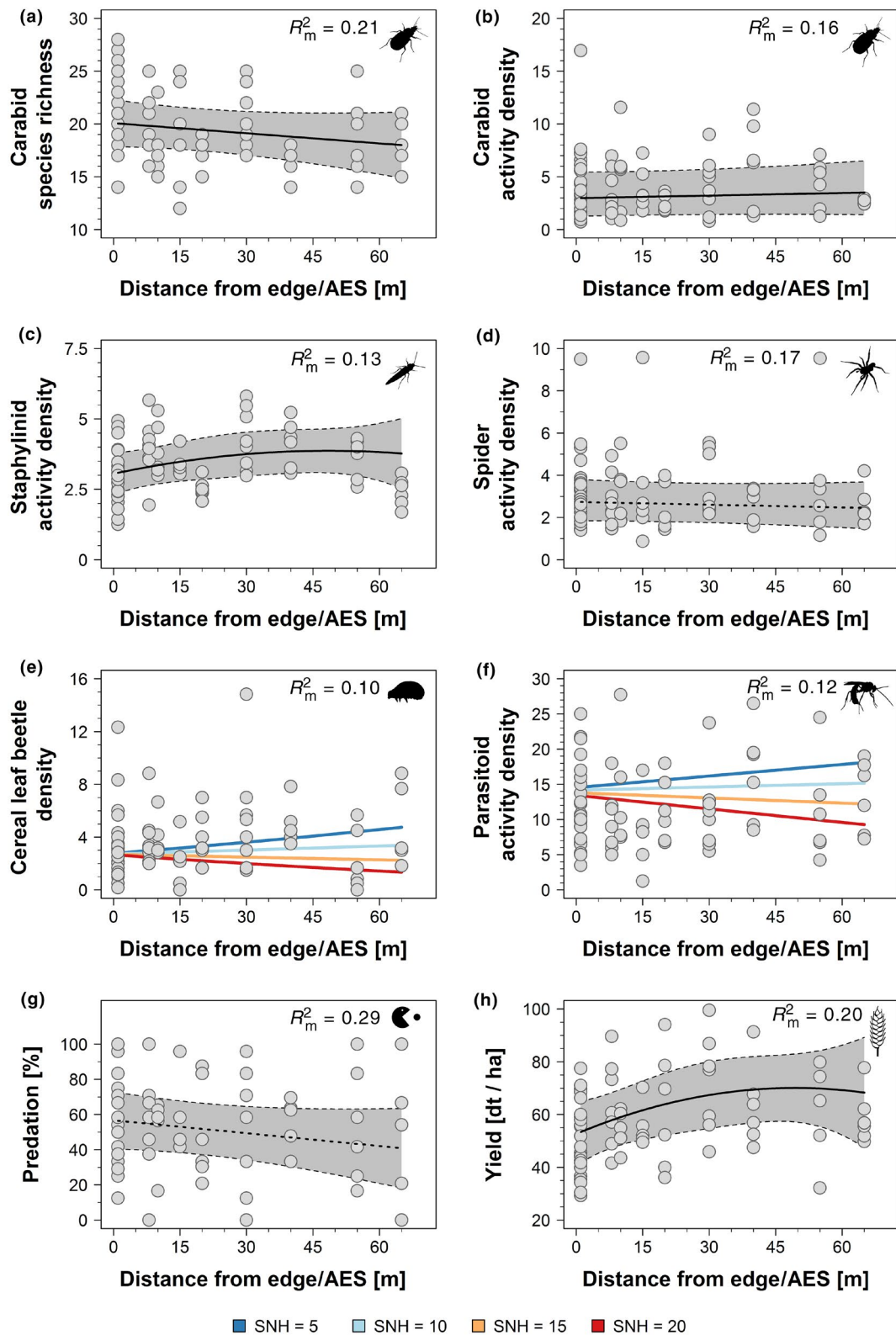


FIGURE 2 Distance functions of the different responses investigated: (a) carabid beetle species richness (excluding exclusively granivorous species), (b) carabid beetle activity density (excluding exclusively granivorous species), (c) staphylinid beetle activity density and (d) spider activity density, (e) cereal leaf beetle and (f) parasitoid activity density, (g) predation rates and (h) crop yields. Model predictions (obtained from the full model), partly with 95% confidence intervals (a, b, c, d, g and h). Colours represent predictions for five different semi-natural habitats (SNH) levels (5%, 10%, 15% and 20%) wherever the interaction between distance and SNH was significant. Solid lines indicate significant distance functions, dotted lines non-significant distance functions, R_m^2 is the marginal R^2 value of the model (Statistics see text and Table 1)

TABLE 1 Results obtained from linear mixed effects models (lmer) including a random intercept for 'study site ID' on different responses. *df*=degrees of freedom (numerator, denominator); *F*- and *p*-values obtained by type II sums of squares ANOVA with Kenward–Roger approximation; bold printing indicates significant $p < 0.5$; Significance levels: (*) $p < 0.1$, * $p < 0.5$, ** $p < 0.1$; R_m^2 =marginal R^2 ; R_c^2 =conditional R^2 . Distance: ¹linear component, ²quadratic component.

Response/factors	Distance as	<i>df</i>	<i>F</i>	<i>p</i>	R_m^2	R_c^2
Carabid species richness						
AES habitat type	Linear	3, 22	1.71	0.195	0.21	0.60
Distance ¹		1, 49	9.02	0.004**		
SNH		1, 24	0.88	0.358		
Distance ¹ : AES habitat type		3, 49	0.60	0.616		
Distance ¹ : SNH		1, 49	0.69	0.410		
Carabid activity density						
AES habitat type	Linear	3, 21	0.38	0.771	0.16	0.88
Distance ¹		1, 47	4.24	0.045*		
SNH		1, 22	3.89	0.061(*)		
Distance ¹ : AES habitat type		3, 47	0.48	0.695		
Distance ¹ : SNH		1, 48	3.28	0.077(*)		
Staphylinid activity density						
AES habitat type	Quadratic	3, 22	0.14	0.932	0.13	0.61
Distance ¹		1, 45	0.52	0.473		
Distance ²		1, 44	11.60	0.001**		
SNH		1, 25	0.33	0.573		
Distance ¹ : AES habitat type		3, 45	0.48	0.700		
Distance ² : AES habitat type		3, 44	0.97	0.414		
Distance ¹ : SNH		1, 47	0.57	0.456		
Distance ² : SNH		1, 45	0.02	0.897		
Spider activity density						
AES habitat type	Linear	3, 21	0.51	0.679	0.17	0.81
Distance ¹		1, 48	0.59	0.448		
SNH		1, 22	5.53	0.028*		
Distance ¹ : AES habitat type		3, 48	0.26	0.855		
Distance ¹ : SNH		1, 48	0.36	0.551		
Parasitoid activity density						
AES habitat type	Linear	3, 21	0.82	0.495	0.10	0.83
Distance ¹		1, 48	1.13	0.294		
SNH		1, 22	1.85	0.188		
Distance ¹ : AES habitat type		3, 48	0.45	0.718		
Distance ¹ : SNH		1, 48	5.86	0.019*		
Cereal leaf beetle density						
AES habitat type	Linear	3, 22	0.62	0.609	0.12	0.74
Distance ¹		1, 48	4.74	0.034*		
SNH		1, 23	1.46	0.239		
Distance ¹ : AES habitat type		3, 48	0.31	0.820		
Distance ¹ : SNH		1, 48	4.34	0.043*		
Predation rates						
AES habitat type	Linear	3, 22	3.40	0.036*	0.29	0.65
Distance ¹		1, 49	2.52	0.119		
SNH		1, 24	3.85	0.061(*)		
Distance ¹ : AES habitat type		4, 49	1.59	0.203		
Distance ¹ : SNH		1, 49	0.55	0.461		

(Continues)

TABLE 1 (Continued)

Response/factors	Distance as	df	F	p	R _m ²	R _c ²
Yield [dt/ha]						
AES habitat type	Quadratic	3, 21	0.53	0.668	0.20	0.59
Distance ¹		1, 41	4.61	0.038*		
Distance ²		1, 40	8.23	0.007**		
SNH		1, 25	0.81	0.376		
Distance ¹ : AES habitat type		3, 42	0.16	0.925		
Distance ² : AES habitat type		3, 41	0.57	0.641		
Distance ¹ : SNH		1, 43	0.09	0.760		
Distance ² : SNH		1, 42	0.41	0.527		
Similarity of carabid assemblages between years						
Distance ¹	Linear	1, 50	7.45	0.009**	0.09	0.77

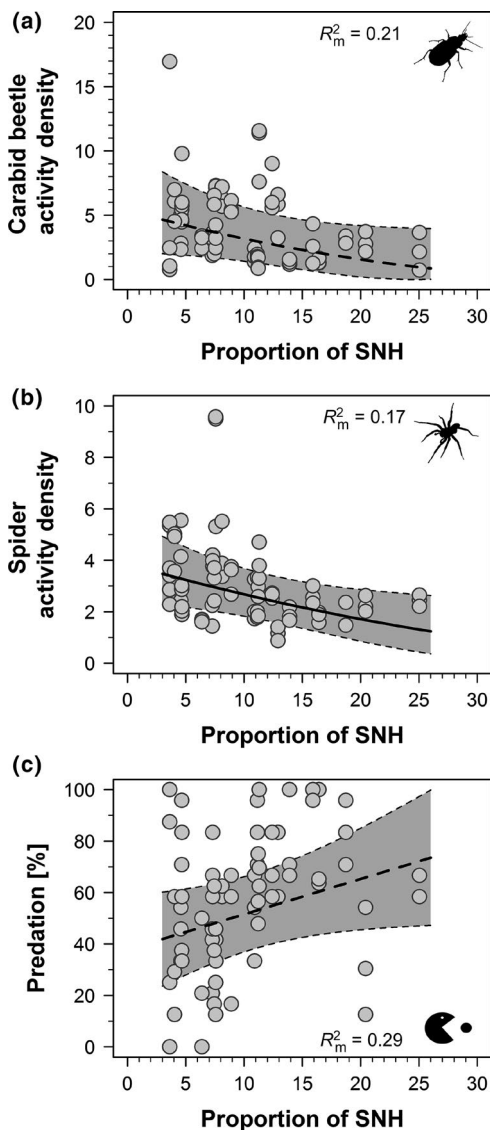


FIGURE 3 Carabid beetle activity density (a), spider activity density (b) and predation rates (c) in relation to landscape level semi-natural habitats (SNH). Model predictions with 95% confidence intervals. Dotted lines indicate non-significant relations, R_m² is the marginal R² value of the model (statistics see text and Table 1)

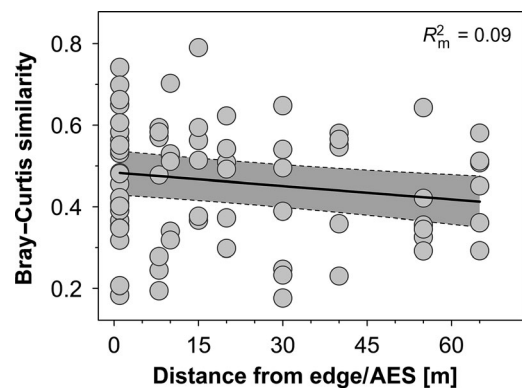


FIGURE 4 Bray-Curtis similarity of carabid beetle assemblages in the same within-field distances at the same sites between oilseed rape (2016) and winter cereals (2017). Model prediction with 95% confidence interval, R_m² is the marginal R² value of the model (statistics see text and Table 1)

exclusively found in 2016 and 11 species were exclusively found in 2017 bringing the total species number over both years to 130. Assemblages recorded in 2017 (winter cereals) were most similar to the ones recorded in 2016 (winter oilseed rape) near the field edges and similarity decreased towards the field centres by 15% (Table 1; Figure 4).

4 | DISCUSSION

Our results have broad implications for the spatiotemporal management of AES habitats at local and landscape scales as we found strong differences in their effectiveness among different crop types and depending on landscape context. Apart from a clear distance decay of carabid species richness, distance functions of the densities of natural pest control agents and pests were not as clear as expected. Carabid beetle densities increased towards the field centres while staphylinid beetle densities and crop yields showed a hump-shaped distance function peaking near the field centres. Increasing SNH in the surrounding landscapes decreased

densities of spiders irrespective of within-field distance. Moreover, SNH modulated distance functions of pest and parasitoid densities. However, adjacent AES did not have clear effects on pest control agents, pests or crop yields in the responses investigated. The distance functions found for ground-dwelling predators partly contradict the universal distance decay functions found in the previous year which indicates that distance functions changed with crop rotation.

4.1 | Distance functions of natural pest control and yields

Carabid beetle species richness was driven by a clear distance decay which seems to be a general pattern as it was previously found for oilseed rape (Boetzel, Krimmer, et al., 2019), pumpkin (Fusser et al., 2018) and winter cereals (Anjum-Zubair, Schmidt-Entling, Querner, & Frank, 2010; Clough et al., 2007). Species preferring adjacent habitats regularly disperse into the edges of arable fields and add to the species pool already present in the fields, a process called spillover (Tschantke, Rand, et al., 2005). This effect is typically decreasing with increasing distance to the field edge as these species are filtered out by changes in conditions within the field or limited mobility.

Contrary to the distance decay found for activity densities of ground-dwelling predators in winter oilseed rape, we did not detect such uniform functions in winter cereals. While both carabid and staphylinid beetle densities increased towards the field centres, there was no clear distance function for spider densities. Distance effects on ground-dwelling predators in winter cereals were contradicting in previous studies. Several studies found increased activity densities of carabid beetles in field centres compared to field edges and concluded that this pattern might arise from productivity-driven pest accumulations in the field centres (Anjum-Zubair et al., 2010; Birkhofer et al., 2014). However, other studies have found either no relationship between within-field position and carabid densities (Batáry, Holzschuh, Orci, Samu, & Tschantke, 2012) or a decrease from the field edges towards field centres (Pollier, Tricault, Plantegenest, & Bischoff, 2019). Carabid densities and carabid species richness followed reverse trends within fields, indicating that fewer species coping well with agricultural management reached high densities in field centres.

Crop yields per unit area are expected to decrease towards field edges as management intensity and inputs are lower near the edge due to mechanical limitations and legal regulations. In contrast to Raatz et al. (2019), edge effects on yields reached 10 m farther into the field and crop yields reached 95% of the maximum only after 27 m. This suggests that distance functions of crop yields are not necessarily consistent across studies. We expect that crop yields are affected by habitat context management but also by the magnitude of local ecosystem services or pest spillover, a factor not assessed by Raatz et al. (2019). Our results indicate that especially in small fields, edge effects reduce yields significantly.

4.2 | SNH effects on pest control and distance functions

Decreased pest densities in the field centres together with predation rates marginally increasing with increasing landscape SNH proportion indicate that complex landscapes favour natural pest control which is in line with previous studies (Karp et al., 2016; Martin et al., 2019; Rusch et al., 2016). SNH also modulated densities of the natural enemies carabid beetles (marginally), parasitoid wasps (which are attracted to their hosts) and spiders likely driven by prey availability. As natural enemies were most abundant in landscapes with low SNH and high densities of pests, predators potentially disperse if local pest densities are too low. However, predation rates tended to increase with increasing SNH. An explanation for this contradiction could be the independent measuring of predation rates and natural enemy densities in our design. We used aphid cards to record predation rates during the essential period of milk ripening while predators were accumulated over the whole growing period. Both measures, therefore, cover different timeframes and relations might be disguised. With this method, it is also impossible to control which predators are responsible for prey removal although we recorded the most important ground-dwelling predators. A positive relation between natural pest control and the proportion of SNHs in a landscape has previously been reported (Karp et al., 2016; Rega et al., 2018; Sutter, Albrecht, Jeanneret, & Diekötter, 2018). Whether this relation is visible, however, depends on the type of sentinel prey used which might explain why it was only marginally significant in our study (McHugh, Moreby, Lof, van der Werf, & Holland, 2020).

The densities of CLBs and parasitoids were modulated by landscape SNH, decreasing towards the field centres in landscapes with high SNH and increasing in landscapes with low SNH. We assume lower parasitoid densities arose from reduced host densities in complex landscapes. Landscape-mediated effects on pests and parasitoids were most pronounced in the field centres and decreased towards the field edges. Field edges underlie a magnitude of different stressors influencing insect populations (e.g. gradients of management intensity, spillover and colonization effects) whereas conditions in field centres are much more controlled and stable. While our results for field centres are in line with the findings of Grab, Danforth, Poveda, and Loeb (2018), the distance patterns found for CLBs and parasitoids differ from previously reported patterns (Pollier et al., 2019). Previous studies generally neglected possible interactions of distance and landscape complexity, often only assessing densities in field centres (e.g. Grab et al., 2018). Our study design allowed us to investigate effects of distance and SNH on predator densities independently. We assume that different patterns for distance functions previously reported in the literature could have arisen from modulation by landscape level SNH.

Our results suggest that distance functions, apart from depending on crop type, often interact with landscape characteristics such as SNH. In studies not addressing or standardizing landscape parameters, distance functions might be biased. However, little is

known which landscape level parameters influence distance functions across different trophic levels. Different taxa are affected by different aspects of landscapes they utilize (e.g. parasitoids need floral nectar sources in contrast to ground-dwelling predators; Tschardtke, Rand, et al., 2005) and the definitions of SNH in the literature vary with geographic location and individual preferences of authors. Therefore, more research is needed to clarify how distance functions respond to the surrounding landscape and how they can be managed to better exploit ecosystem service potentials.

4.3 | Effects of adjacent AES habitats

Agri-environmental schemes are widely implemented to benefit biodiversity-mediated ecosystem services in agricultural landscapes. In particular, the AES habitats investigated in this study are established to foster and ensure pollinator populations. AES habitats, however, have occasionally been shown to benefit pest control (Fusser et al., 2018; Mestre et al., 2018; Pollier et al., 2019). Beneficial effects of adjacent AES habitats varied between years. In oilseed rape, AES habitats benefitted ground-dwelling predator assemblages at the trait level (body size and diet; Boetzl, Krimmer, et al. (2019)). Effects of AES habitats on adjacent crops, however, are potentially disguised or buffered by ecological contrast between AES habitats and the adjacent crops (Marja et al., 2019). In our study, this contrast is larger in oilseed rape than in cereal cultures. One important factor that might have influenced the activity patterns of ground-dwelling predators is microclimate and shading. While oilseed rape has a closed canopy already early in the season retaining a dark, cool and moist microclimate at the ground, cereals remain largely open resulting in light and dry conditions. In contrast to Marja et al. (2019), we assume that a small contrast between AES habitat and crop is beneficial for ground-dwelling predators as species supported by the AES habitats cannot persist in adjacent crop habitats if the contrast is too large. We assume the relatively low contrast between AES habitats and cereal fields facilitated ground-dwelling predator spillover into the fields while the high contrast between AES habitats and oilseed rape fields filtered out ground-dwelling predators resulting in distance decay functions.

Predation rates were higher in fields adjacent to refreshed flowering fields than in all other fields, although predator communities or densities did not differ. Predation rates, however, cannot simply be linked to predator densities recorded in our study due to the method of recording used (see above). Ultimately, elevated predation rates could also be driven by other co-factors such as density-dependent aggregation of pests and predators.

Contrary to our results, Tschumi et al. (2016) observed clear negative effects of adjacent AES habitats (flower strips) on densities of CLB larvae and consequently positive effects on crop yields in winter wheat. CLB larvae densities measured in Tschumi et al. (2016) were up to five times higher than densities measured in this study which potentially disguises effects. Our data show that relations might not be general and that effects of AES habitats are

potentially blurred by other factors. However, we studied the effects of AES habitats during the growing season. We assume AES habitats benefit pest control essentially by providing undisturbed habitats for overwintering and by providing pest control agents for recolonization of the fields after disturbances (i.e. soil management or harvest; see Schneider, Krauss, Boetzl, Fritze, & Steffan-Dewenter, 2016).

4.4 | Crop rotation affects pest control services and species assemblages

Edges are important predictors for many ecosystem service agents on the landscape level as high edge density increases landscape complexity and thereby the diversity of micro-habitats that allow species to persist, procreate and flourish also after crop harvest (Martin et al., 2019; Tschardtke, Klein, et al., 2005). Distance decay functions of ecosystem service agents originating from edges would be expected. However, in winter cereals, distance functions were not uniform and partly depended on landscape context (while they had been independent from landscape level SNH in oilseed rape in the previous year). Apparently, distance decay functions are not universal and potentially affected by a multitude of different factors. As many of these are still unknown, predicting distance functions for pest control potentials remains difficult. More research is needed to identify effects of different crop rotations and how these depend on management and ecological contrast between crops.

Carabid species assemblages differed clearly between the study years as the field crop and the associated management changed. This difference was most pronounced in the field centres and decreased towards the field edges. This illustrates the importance of field edges to stabilize and secure predator assemblages as they buffer crop- and management-driven assemblage shifts and allow different species to persist in a landscape over crop rotation. Together with increased species richness of carabid beetles towards field edges, this indicates that carabid assemblages in field centres are a subset of the local species pool of arable lands filtered by crop type and associated management. Simplifying landscapes by increasing field sizes for higher efficiency in modern agriculture might therefore be harmful in the long term as species affected by crop rotation-driven assemblage shifts cannot find refuge in adjacent permanent habitats or field margins. Sirami et al. (2019) showed that decreasing field sizes (and therefore increasing landscape complexity as well as margin to field ratio) benefits biodiversity across multiple levels. Increasing field sizes might eventually eliminate dispersal limited, perennial species from the local species pools by reducing the amount and availability of suitable source and refuge habitats. As natural pest control is closely linked to predator diversity (Dainese et al., 2019), simple landscapes with large field sizes and low complexity might ultimately erode natural pest control potentials.

5 | CONCLUSIONS

Under the current regime of conventional high input agriculture, farmers regulate pests by agrochemicals and cereal crop yields by fertilizer input. At the same time, natural pest regulation is not fully exploited or even hampered by pesticide applications (Krauss, Gallenberger, & Steffan-Dewenter, 2011). As this system is both cost-intensive and potentially harmful to biodiversity-mediated ecosystem functioning, replacements for inputs will be needed in the future. Understanding the distance functions underlying the distribution of beneficial ecosystem service providers as well as their interactions with landscape composition will be essential for the planning of agricultural landscapes under ecological intensification policies. Distance functions, however, are not universal—depending on the measured variable, distance functions are affected by crop type, landscape context or habitat configurations. This explains contradicting results obtained from previous studies and emphasizes the need for a deeper, holistic understanding of these functions and their drivers. Our results show that natural pest control is working in small as well as large fields. Field edges or margin habitats, however, are important to secure predator diversity in agricultural landscapes throughout management changes. We therefore recommend a network of margin structures (such as AES habitats) in agricultural landscapes to foster natural pest control as suggested by Martin et al. (2019). Also, SNHs in agricultural landscapes are beneficial and need to be conserved. Policymakers are advised to stop and preferably reverse simplification of agricultural landscapes. Effects of AES habitats on natural pest control in adjacent fields are not universal and affected by ecological contrast between the habitats and the adjacent crops as found by Marja et al. (2019) for pollinators. This relationship between AES habitats and adjacent crop fields could be exploited in the future to maximize benefits. AES habitats could be improved to provide refuges and resources to a variety of ecosystem service providers at the same time (e.g. open soil patches for ground-nesting bees and wasps, flower resources for pollinators and parasitoids) to achieve both supporting pollination services as well as enhancing natural pest control. To better target ecosystem services, AES habitats need to be tailored more specifically towards a function they should fulfil in interaction with the adjacent crop (e.g. AES habitats could be used to pull pests from the crop or to provide reservoirs of predators that can persist in the adjacent crop). Only if the effects of adjacent habitats, edge proximity and the distribution of ecosystem service agents within a field and across agricultural landscapes are understood, pest control potentials can be predicted precisely and utilized to the potential maximum. Within the framework of ecological intensification, these functions will be needed to reach an optimum between field size and ecosystem service potential to maximize yields in a sustainable way.

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AUTHORS' CONTRIBUTIONS

F.A.B., J.K. and I.S.-D. designed the study; F.A.B. and M.S. conducted fieldwork; F.A.B. analysed data and wrote the first draft of the manuscript. All authors interpreted the results, revised the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.mcvdncjxn> (Boetzel, Schuele, Krauss, & Steffan-Dewenter, 2020).

ORCID

Fabian A. Boetzel  <https://orcid.org/0000-0001-5121-3370>

Jochen Krauss  <https://orcid.org/0000-0003-2304-9117>

Ingolff Steffan-Dewenter  <https://orcid.org/0000-0003-1359-3944>

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