

## RESEARCH ARTICLE

# Landscape-level crop diversity benefits biological pest control

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**Abstract**

1. Landscape-level crop diversification is a promising tool for ecological intensification, whereby biodiversity and ecosystem services are enhanced, and pesticide applications reduced. Yet evidence for the effects of crop diversity at multiple scales and in different landscape contexts is lacking. Here, we investigate the potential benefits and context dependencies of multiscale crop diversity on natural enemies and overall biological control in winter wheat. Simultaneously, we examine the mediating effects of bird predation on aphid regulation in this system.
2. Eighteen conventional winter wheat fields were selected along two independent gradients of crop diversity and semi-natural habitat cover (SNH). We assessed biological control using a natural enemy exclusion experiment ("Open Treatment," "Bird Enclosure," "Full Enclosure"). Biological control, predator and parasitoid densities within cages were analysed as functions of landscape (crop diversity  $\times$  SNH), bird predation (yes/no) and temporal change (three surveys) on six spatial scales (100–3,000 m).
3. Crop diversity rather than SNH enhanced aphid regulation in our study system. Biological control in fields with high landscape-level crop diversity was 8%–33% higher than in low-diversity landscapes, with main effects observed on scales <500 m.
4. Predator and parasitoid densities increased with crop diversity on small (100–250 m) and large (2,000–3,000 m) spatial scales respectively. Nevertheless, our findings suggest that natural enemies other than birds, parasitoids and aerial arthropods facilitated biological control.
5. *Synthesis and applications.* Our study shows that landscape-level crop diversification can improve biological control in agroecosystems. Therefore, increased crop diversity could lower dependence on insecticides while enhancing yield stability through ecological intensification of farming. We also highlight the need to assess biological control rather than natural enemy abundances to avoid bias due to sampling artefacts or species interactions. Finally, simple measures of crop diversity (e.g. "effective number of crop types") help in science communication and the development of farm management guidelines.

**KEYWORDS**

aphids, crop diversity, ecological intensification, farmland biodiversity, parasitoids, pest control, predators, spatial scales

## 1 | INTRODUCTION

Worldwide, natural enemy communities and biological pest control suffer from increased homogenization of food production and the removal of natural habitats (Altieri, 1999; Rusch et al., 2016). In addition, replacement of biological control agents with chemical insecticides results in long-term risks (biodiversity loss, pesticide resistance, groundwater contamination) that largely outweigh the perceived short-term yield and cost benefits (Wilson & Tisdell, 2001). However, ecological intensification practices such as field-scale diversification via flower plantings (Gurr et al., 2016; Letourneau et al., 2011) and extensification of agricultural processes (pesticide reductions; Jonsson et al., 2012) can enhance natural enemies and biological control (Bommarco, Kleijn, & Potts, 2013). Scaling up, landscape complexity (e.g. the quantity of semi-natural habitat; Chaplin-Kramer & Kremen, 2012; Gardiner et al., 2009; Schmidt et al., 2003) and interannual changes in host plant cover (Bosem Baillod, Tscharnkte, Clough, & Batáry, 2017; Schneider, Krauss, Riedinger, Holzschuh, & Steffan-Dewenter, 2015) also contribute to biological control. It is yet unclear whether increasing the number of crop types cultivated within a landscape has similar benefits.

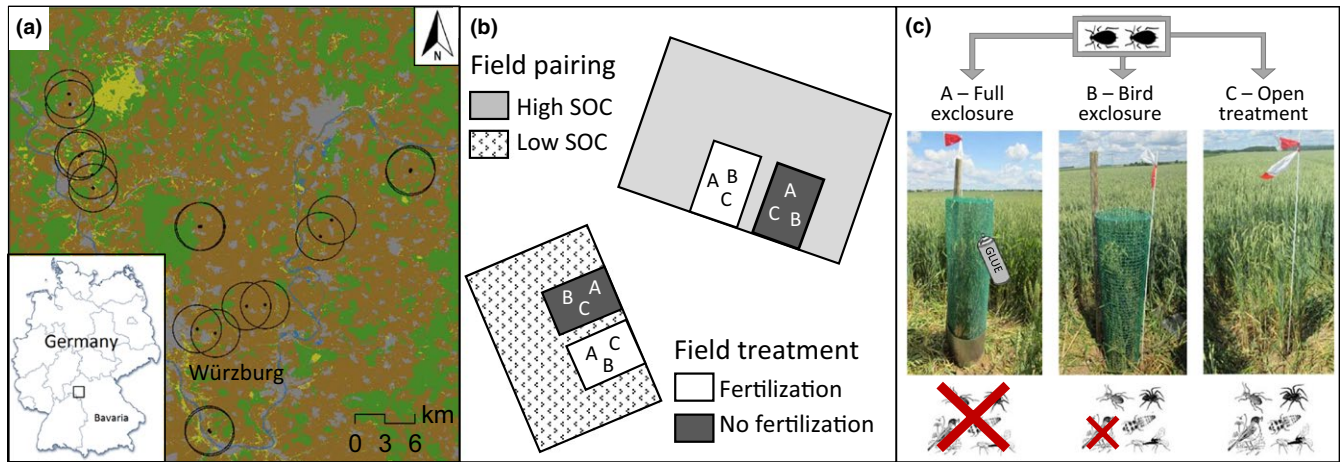
In theory, landscape-level crop diversification (hereafter “crop diversity”) should enhance natural enemies by providing diverse plant-derived resources such as pollen, nectar and shelter throughout the year (Fahrig et al., 2011; Schellhorn, Gagic, & Bommarco, 2015). Biological control can thereby be sustained in landscapes where non-crop resources are scarce (Martin, Seo, Park, Reineking, & Steffan-Dewenter, 2016; Tscharnkte et al., 2016). Furthermore, crop diversity precludes yield losses due to cropland conversion or plant competition common to small-scale diversification practices (Lin, 2011), while enhancing global food security and resilience against climate change via functional redundancy of beneficial organisms (Aguilar et al., 2015; Bommarco et al., 2013; Lin, 2011; Schellhorn et al., 2015). Nevertheless, few studies explore the link between crop diversity and natural enemy density or richness (e.g. Fahrig et al., 2015; Palmu, Ekroos, Hanson, Smith, & Hedlund, 2014). Even fewer do so for the biological control service these organisms provide (Bosem Baillod et al., 2017; Chaplin-Kramer & Kremen, 2012; Holland et al., 2012), although the mostly positive relationship between enemy diversity and biological control (Altieri, 1999; Harrison et al., 2014) can be disrupted by antagonistic species interactions (Letourneau, Jedlicka, Bothwell, & Moreno, 2009; Straub, Finke, & Snyder, 2008).

Whether and at which spatial scale biological control responds to crop diversity depends on the specialization, life history and movement capability of different natural enemy guilds and their relative importance to pest suppression (Chaplin-Kramer, O'Rourke, Blitzer, & Kremen, 2011; Henri et al., 2015; Martin et al., 2016; Rusch, Bommarco, Jonsson, Smith, & Ekbom, 2013; Shackelford et al., 2013). For example, specialist natural enemies (e.g. parasitoids) often respond to smaller spatial scales than large-bodied generalists (Chaplin-Kramer et al., 2011). In systems with parasitoid-mediated biological control, landscape

complexity at small-spatial scales can therefore enhance pest suppression (Schmidt et al., 2003). Yet the relative importance of specialist parasitoids, epigeal or aerial arthropod predators and insectivorous birds is highly disputed and varies among systems (Caballero-López et al., 2012; Dainese, Schneider, Krauss, & Steffan-Dewenter, 2017; Holland et al., 2012; Martin, Reineking, Seo, & Steffan-Dewenter, 2013; Rusch et al., 2013; Schmidt et al., 2003; Tamburini, De Simone, Sigura, Boscutti, & Marini, 2015). At the same time, crop diversity benefits might only emerge in resource-depleted, simplified landscapes with low semi-natural habitat cover. Here, crop diversification adds essential resources otherwise lacking in the non-crop matrix (Josefsson, Berg, Hiron, Pärt, & Eggers, 2017; Tscharnkte, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). However, correlations between crop diversity and semi-natural habitat often impede our ability to infer causal relationships (Fahrig et al., 2011, 2015). Disentangling the independent and interacting effects of both variables across multiple spatial scales is of prime importance—both for separate natural enemy guilds and overall biological control.

Owing to differences in the mobility and specialization of natural enemies, cereal-aphid-antagonist food webs in temperate agroecosystems are well suited for multiscale landscape studies on biological control. Aphids (Hemiptera: Sternorrhyncha), most notably the species *Sitobion avenae* (Fabricius), are major pests in these systems (Dedryver, Le Ralec, & Fabre, 2010). The suite of associated natural enemies ranges from specialized biological control agents such as parasitoids (Hymenoptera, Parasitica) and ladybird larvae (Coleoptera: Coccinellidae) to generalist predators such as ground beetles (Coleoptera: Carabidae) and spiders (Araneae, various families). Additionally, insectivorous birds can suppress pests but might also constrain insect-mediated biological control via intraguild predation on intermediate predators (Martin et al., 2013; Mooney et al., 2010). In cereal systems, this so-called omnivorous intraguild predation is potentially more disruptive than coincidental intraguild predation (intermediate predators consuming parasitoid larvae with their aphid host) due to large differences in body size (Straub et al., 2008).

In this study, we aimed to gain a comprehensive understanding of the potential benefits and context dependencies of multiscale crop diversity in conventional winter wheat systems. We used repeated pest and natural enemy surveys within a natural enemy exclusion experiment to evaluate the link between crop diversity and biological pest control, while testing for interacting effects with semi-natural habitat cover across six spatial scales (100 to 3,000 m radii around fields). Additionally, the complex natural enemy community in this system allowed us to evaluate the individual contribution of different natural enemy guilds to biological control and their response to crop diversity. We hypothesized that crop diversity increases overall biological control (i) and the density of arthropod natural enemies (ii), yet these benefits depend on spatial scale and natural enemy guild (parasitoids vs. predators). We further assumed that crop diversity effects are most pronounced in landscapes with low semi-natural habitat cover (low-landscape complexity) (iii). Finally, we



**FIGURE 1** Experimental set-up of the natural enemy exclusion experiment in winter wheat using sentinel aphid populations of *Sitobion avenae*. (a) Nine field pairs were selected along independent gradients of crop diversity and semi-natural habitat cover in central Germany. Shown are 3 km radii around fields. (b) Each pair comprised two fields of contrasting soil organic matter content (high/low). Fertilizer treatments (no/yes) were applied on the subplot scale. (c) Each subplot received three exclusion treatments: “Full Exclusion” (all natural enemies excluded), “Open Treatment” (all natural enemies present) and “Bird Exclusion” [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

assessed whether natural enemy guilds differ in their contribution to overall biological control (iv) and whether insectivorous birds constrain biological control by affecting arthropod enemies and their ability to suppress aphids (v).

## 2 | MATERIALS AND METHODS

### 2.1 | Study area and experimental design

The study took place in an intensively cultivated region of c. 40 × 40 km in Lower Franconia/Germany (49°47'N, 9°57'E), an area dominated by high-input crops such as cereal, sugar beet and maize. Here, we selected 18 conventional winter wheat fields along independent gradients of crop diversity and semi-natural habitat at six spatial scales. The research was conducted within the project LIBERATION (“Linking farmland Biodiversity to Ecosystem seRvices for effective ecological intensificATIOn”), which explored the interactive effects of landscape simplification and local management on pests and antagonists. Following the joint design (Figure 1, Appendix S1 in Supporting Information), fields were grouped in nine pairs of contrasting soil organic carbon content (=SOC, high/low). A fertilizer treatment (yes/no) was applied in two experimental subplots at the field edge. Both SOC and fertilization might influence pests and natural enemies, yet these relationships and effects on yields are investigated elsewhere (Gagic et al., 2017). We nevertheless accounted for both factors in the statistical analyses. However, pest densities (preliminary analyses), natural enemies and biological control were unaffected by SOC and fertilization in our exclusion experiment (Table 1, Figure S1, Appendix S1). This corroborates previous studies related to the grain aphid *Sitobion avenae* (Garratt, Wright, & Leather, 2010) and biological control (van Gils, van der Putten, & Kleijn, 2016). Hence, local management factors are not discussed further.

### 2.2 | Landscape variables

Crop diversity (CropDiv, overall range 0–1.48) was calculated on six spatial scales (100, 250, 500, 1,000, 2,000, 3,000 m radii around fields) as Shannon Wiener Index in the “vegan” package in R (Oksanen et al., 2015). The index used 12 arable crop categories provided by the Bavarian State Ministry of Nutrition, Agriculture and Forestry: cereals, 1–2-year fallows, cultivated flowers, temporary grassland, legumes, maize, oilseed rape, root crops, sunflower, vegetables and other industrial crops (Table S1). To ease interpretation of CropDiv, we also calculated the “effective number of crops” using  $\exp(\text{CropDiv})$  (=ENCS, Table S1; Jost, 2006). ENCS estimates the number of equally abundant crop types required to achieve a specific amount of CropDiv and associated levels of biological control. We use ENCS to illustrate diversification effects in a way that improves communication of research results to farmers and policy makers and helps in the development of farm management guidelines.

Semi-natural habitat cover (=SNH, overall range 1.2%–76.9%) included perennial grassland, orchard meadows, hedgerows, forest edges and grass margins along rivers and roads. SNH was calculated in ArcMap v. 10 (ESRI) using official digital topological maps ATKIS DTK 25 (Bayerische Vermessungsverwaltung, 2010, Table S1). Correlations of CropDiv with SNH and other influential landscape factors not included in analyses (crop cover (Caballero-López et al., 2012), field size (Fahrig et al., 2015) and habitat diversity (Gardiner et al., 2009; Martin et al., 2016) were low at all spatial scales (Pearson’s  $|r| \leq .51$ , Table S2).

### 2.3 | Biological control

Overall levels of biological control and the influence of bird predation on aphid suppression were assessed with a natural enemy exclusion experiment (Figure 1b,c; Appendix S1). Three standardized

**TABLE 1** Sum of model weights ( $\sum w_i$ ) of predictor variables included in scale-specific models for biological control (BCI), predator (PR) and parasitoid (PA) density. Predictor variables were crop diversity (CropDiv), semi-natural habitat cover (SNH), survey interval (S), bird exclusion (B) and interactions of CropDiv with survey and SNH. Covariates included aphid densities (A), fertilization treatment (F) and field soil organic matter content (SOC). Bold numbering signifies  $\sum w_i$  where 95% confidence intervals of estimates excluded zero. Parenthesis highlights the presence of interactions. Hyphens indicate predictor variables not included in the full model

Scale																		
100 m			250 m			500 m			1,000 m			2,000 m			3,000 m			
Response			Response			Response			Response			Response			Response			
BCI	PR	PA	BCI	PR	PA	BCI	PR	PA	BCI	PR	PA	BCI	PR	PA	BCI	PR	PA	
Predictor variables																		
CropDiv	(1)	0.99	0.29	(1)	0.86	0.26	(1)	0.55	(0.69)	0.31	0.32	(0.79)	0.33	0.92	(0.98)	0.3	0.55	
SNH	0.29	0.61	0.24	0.31	0.53	0.26	0.42	0.4	(0.73)	0.57	0.29	0.62	0.33	0.34	0.59	0.37	0.26	
S <sup>a</sup>	(1)	1	—	(1)	1	—	(1)	1	—	(1)	1	(1)	1	—	(1)	1	—	
B	0.47	0.32	0.22	0.44	0.25	0.32	0.48	0.31	0.3	0.46	0.31	0.32	0.31	0.29	0.44	0.31	0.22	
Interactions																		
CropDiv:	0.09	0.15	b			0.07	0.11	0.04	0.22	0.07	0.6	0.13	0.05	0.04	0.13	0.06	0.14	
SNH															0.28	0.04	0.04	
CropDiv: S <sup>a</sup>	0.99	0.64	—	1	0.19	—	1	0.07	—	0.91	0.04	—	0.65	0.03	—	0.97	0.03	—
Covariates																		
A	—	1	1	—	1	1	—	1	1	—	1	1	—	1	—	1	1	
F	0.3	0.26	0.25	0.26	0.3	0.32	0.28	0.27	0.34	0.28	0.27	0.35	0.29	0.27	0.31	0.27	0.25	
SOC	0.3	0.36	0.36	0.25	0.37	0.35	0.25	0.36	0.34	0.3	0.31	0.39	0.28	0.31	0.27	0.31	0.35	

<sup>a</sup>Temporal effects of survey interval not tested for parasitoid density (data restricted to day 15).

<sup>b</sup>Interaction not selected in models with  $\Delta AIC_c \leq 7$ .

populations of *Sitobion avenae* were established in each fertilization subplot (initial aphid density ~100). We then exposed populations to one of three exclusion treatments: "Open Treatment" (aerial and epigeal invertebrate predators, parasitoids and birds), "Bird Exclusion" (birds excluded) and "Full Exclusion" (all natural enemies excluded). Aphid densities in each exclusion treatment (total  $n = 108$ , 6 cages per field) were recorded non-destructively on 10 randomly selected tillers in 5-day intervals (days 0, 5, 10, 15). We estimated the overall level of biological control attributable to natural enemies by comparing 5-day aphid growth rates in treatments allowing access to some or all natural enemies ("Open Treatment," "Bird Exclusion") with growth rates in the baseline treatment ("Full Exclusion") of the same subplot. This biological control index (=BCI; Gardiner et al., 2009; Appendix S1) ranges from zero (no pest suppression) to one (high pest suppression). Negative values were set to zero (Gardiner et al., 2009). The index was calculated separately for "Open Treatments" and "Bird Exclusions," thereby yielding 216 BCI estimates (two treatments  $\times$  two subplots  $\times$  18 fields  $\times$  three 5-day survey intervals). The difference in BCI between the two open treatments was used to investigate the effect of birds on biological control.

## 2.4 | Sampling of arthropod enemies

Biological control relates to a variety of biodiversity components (Harrison et al., 2014). One such component, natural enemy richness, can negatively affect pest suppression via antagonistic species interactions (Letourneau et al., 2009; Straub et al., 2008). While we specifically tested for bird intraguild predation by manipulating taxonomic richness of predator groups, we otherwise aimed to avoid this potential bias by using the abundance of arthropod enemies instead. Furthermore, enemy abundance drives the magnitude of biological control, whereas species richness is mostly thought to increase the stability of this ecosystem service (Harrison et al., 2014; Shackelford et al., 2013). We recorded the density of leaf-dwelling natural enemies on 10 randomly selected tillers during the last three aphid surveys. Due to the low occurrence of individual subgroups, all arthropod predators were pooled across families ("predator density" for days 5, 10, 15). To avoid double counting, we used the number of parasitized aphids on day 15 as estimate of parasitoid density (Shackelford et al., 2013). This allowed us to compare the effect of CropDiv on large arthropod predators and small specialist parasitoids, assess their contribution to overall biological control and potential mediating effects of bird predation via intraguild predation.

## 2.5 | Statistical analysis

We assessed the scale-dependent and landscape-specific effect of CropDiv on overall BCI (hypotheses i + iii) by building separate linear mixed effect models with Gaussian error distribution for each spatial scale (Table S3). We concurrently tested for the contribution of bird predation to BCI (hypothesis v) and temporal delays in CropDiv effects. Therefore, explanatory variables for each scale-specific landscape model were CropDiv, SNH, bird exclusion (yes/no), CropDiv  $\times$  SNH

and CropDiv  $\times$  survey. We controlled for fertilization (yes/no) and SOC (low/high) by adding both factors as covariates. All models used a nested random structure (pair/field/subplot/cage).

Effects of CropDiv, SNH and bird predation on predator and parasitoid densities (hypotheses ii, iii + v) were analysed with a similar model structure by fitting generalized linear mixed effects models with Poisson error distribution (Table S3). These landscape models also accounted for aphid density (fixed term). No temporal effects were investigated for parasitoid densities (data restricted to day 15). Using parasitism rate as response yielded similar results (aphids<sub>parasitized</sub>/aphids<sub>total</sub>, binomial error distribution); therefore, only the effects on parasitoid densities are shown to improve comparability with arthropod predators.

Two additional linear mixed effect models (Gaussian distribution) investigated the influence of predator and parasitoid densities on BCI (hypothesis iv, Table S4). Potential modulating effects of bird predation (hypothesis v) and changes over time (predator model only) were assessed by including interactions with bird exclusion and survey date.

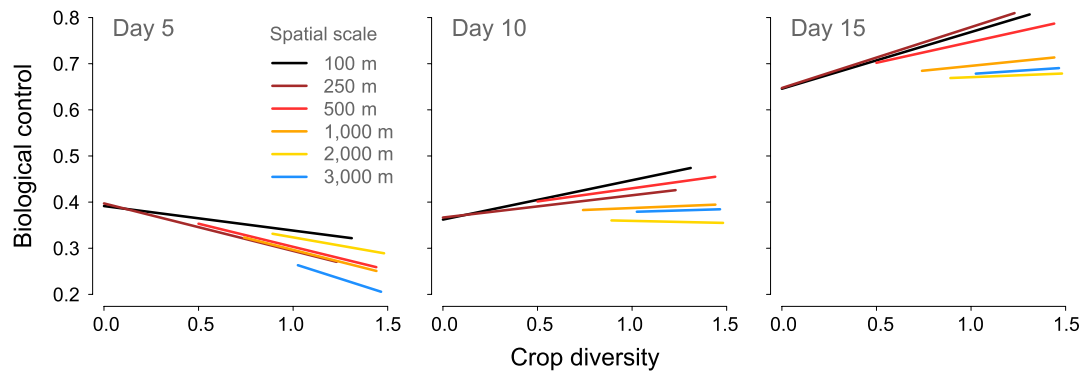
All continuous explanatory variables were z-standardized. Normality and homoscedasticity of model residuals were validated graphically. We found no significant overdispersion in Poisson models ( $p > .12$ ) or multicollinearity of independent variables (variance inflation factors  $< 3$ ; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Residual spatial dependence was rejected for all models ( $p > .19$ , Moran's  $I$  test). We calculated marginal (fixed effects) and conditional (random and fixed effects) coefficients of determination ( $R^2$ ) to assess overall model fit (Tables S3–S5; function "r.squaredGLMM"; Nakagawa & Schielzeth, 2013). Full landscape models with the highest  $R^2$  indicate the spatial scale with the greatest predictive value. Marginal model fit (average across all scales  $\pm SE$ ) was reasonably high for all landscape models (BCI:  $0.21 \pm 0.01$ , predator density:  $0.23 \pm 0.01$ , parasitoid density:  $0.3 \pm 0.03$ ) and for models relating predator and parasitoid densities to BCI ( $R^2 = .2$  and  $R^2 = .13$  respectively).

We employed an information-theoretic approach (Burnham & Anderson, 2002) to quantify the strength of alternative competing models with  $\Delta AIC_c < 7$  (Burnham, Anderson, & Huyvaert, 2011). Model averaging across the model sets yielded estimates with associated confidence intervals (95% CIs), and the sum of Akaike weights ( $\sum w_i$ ) for each predictor variable (Tables S5 and S6).  $\sum w_i$  (range 0–1) can act as indicator of relative variable importance; yet, due to some controversy relating to its use, we focus on effects where 95% CIs of estimates exclude zero (Galipaud, Gillingham, David, & Dechaume-Moncharmont, 2014). All analyses were performed using the packages "nlme" (Pinheiro, Bates, DebRoy, Deepayan, & R Development Team, 2016), "lme4" (Bates, Maechler, Bolker, & Walker, 2015), "MuMIn" (Barton, 2013), "ape" (Paradis, Claude, & Strimmer, 2004) and "base" implemented in R v.3.2.2 (R Development Team, 2016).

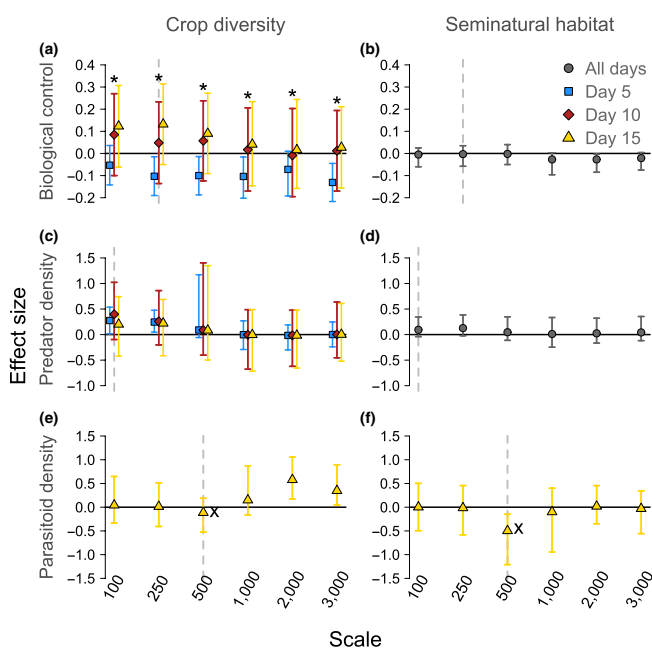
## 3 | RESULTS

Over the 15-day survey period, we counted 65 601 aphids across all exclusion treatments. Of the 576 natural enemies recorded, the majority





**FIGURE 2** Multiscale effects of crop diversity on biological control estimated for day 5, 10 and 15 of the natural enemy exclusion experiment. Regression lines show predicted results based on model-averaged estimates (including models with  $\Delta AIC_c \leq 7$ ) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 3** Effect of crop diversity (CropDiv) and semi-natural habitat (SNH) on biological control (a, b), predator (c, d) and parasitoid density (e, f) at six spatial scales. Values are model-averaged estimates  $\pm 95\%$  confidence intervals ( $\Delta AIC_c \leq 7$ ). CIs excluding zero indicate effect sizes with strong support. In biological control and predator models, estimates were calculated for separate survey intervals for CropDiv or across survey intervals for SNH. Estimates for parasitoid density were calculated for day 15 only. Effect sizes  $> 0$  indicate a positive regression slope between standardized landscape predictors and response variables (positive effect). Estimates of CropDiv  $\times$  survey and CropDiv  $\times$  SNH interactions with CIs excluding zero are marked with asterisks and "x", respectively, yet only estimates of main landscape effects are shown here. The most predictive scales (highest  $R^2$  values of the full models) are indicated by dashed vertical lines [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

were aerial or vegetation-dwelling predators such as Coccinellidae (adults 28.5%, larvae 13.9%), Araneae (26.7%, mostly Linyphiidae) and Syrphidae (larvae 12.7%). On day 15, the number of parasitized aphids observed in cages ranged from 0 to 10 (mean  $\pm$  SE "Bird Enclosure"

$1.17 \pm 0.43$ , "Open Treatment"  $1.47 \pm 0.03$ ). Mean aphid densities in cages without natural enemies ("Full Enclosures"  $250.67 \pm 17.49$ ) were 3.13 times higher than in "Bird Enclosures" ( $80.03 \pm 8.92$ ) and 2.29 times higher than in "Open Treatments" ( $109.42 \pm 12.01$ ). This difference, and consequently estimates of BCI, increased over time (Figures 2 and S2).

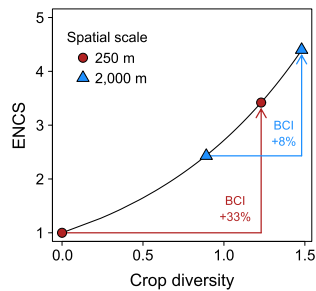
### 3.1 | Scale-dependent crop diversity effects

The benefits of CropDiv to BCI varied with time and scale considered (Figures 2 and 3, Table 1). Across all landscapes, BCI correlated negatively with CropDiv in the first survey period (day 0–5, Figures 2a and 3a). However, in subsequent surveys, this relationship reversed (CropDiv  $\times$  survey interaction). CropDiv on small-spatial scales (100, 250 and 500 m) had the strongest positive effect on BCI, which weakened with increasing spatial scale (Figures 2b,c and 3a). Translated to ENCS, an increase from one to three dominating crop types at the most predictive 250 m scale (highest  $R^2$ ) equated to an average 33% rise in biological control (Figure 4). In contrast, a similar increase in CropDiv at 2,000 m scale (second highest  $R^2$ ) only improved BCI by around 8%. Due to the contrasting relationships over time, high diversity landscapes (CropDiv  $> 1.38$ , ENCS  $> 4$ ) showed the strongest temporal increase in BCI, which more than tripled over the 15-day survey period (BCI means  $\pm$  SE across all spatial scales: day 5 =  $0.18 \pm 0.04$ , day 10 =  $0.32 \pm 0.04$ , day 15 =  $0.76 \pm 0.03$ , Figure 2).

The density of arthropod predators increased over time and with CropDiv at small-spatial scales (100 m and 250 m, Figure 3c, Table 1). Large-scale CropDiv also positively affected parasitoids (2,000 and 3,000 m, Figure 3e, Table 1). In addition, both natural enemy groups showed strong density dependence with aphids (Table 1, Figure S1b,c).

### 3.2 | Landscape-dependence of crop diversity effects

The effect of CropDiv on BCI and predator densities was not influenced by SNH (no CropDiv  $\times$  SNH interaction, Table 1, Figure 3b,d). The only observed interaction relates to parasitoid densities at



**FIGURE 4** Conversion of crop diversity (CropDiv) to “effective number of crops” (ENCS, Jost, 2006). CropDiv was calculated as Shannon Wiener index based on 12 arable crop types (Table S1). Therefore, ENCS ( $\exp[\text{CropDiv}]$ ) indicates the number of equally abundant crop types required to achieve a specific CropDiv. In this graphic, crop diversification increases from the bottom left (low diversification) to the top right (high diversification). Benefits of crop diversification to BCI are shown for two spatial scales: on small scales (250 m, circles), BCI increased by 33%, on larger scales (2,000 m, triangles) by 8%. Illustrated using minimum and maximum CropDiv/ENCS values (Table S1) and model-averaged estimates of BCI for the two most predictive scales (highest  $R^2$  values of full models) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

the most predictive 500 m scale (Table 1). Here, the response to CropDiv changed from positive to negative with increasing landscape complexity.

### 3.3 | Natural enemies and biological control

We found no relationship between BCI and the density of arthropod predators ( $\sum w_i = 0.55$ , estimate [95% CIs] =  $-0.007$  [ $-0.1, 0.08$ ]) or parasitoids ( $\sum w_i = 0.88$ , estimate =  $-0.02$  [ $-0.07, 0.02$ ]). Furthermore, the presence of birds did not affect overall biological control (Figure S1, Tables 1 and S6) or aphid suppression by predators and parasitoids (bird exclusion  $\times$  predator:  $\sum w_i = 0.18$ , estimate [95% CIs] =  $-0.006$  [ $-0.116, 0.05$ ]; bird exclusion  $\times$  parasitoid:  $\sum w_i = 0.47$ , estimate =  $-0.003$  [ $-0.139, 0.003$ ]).

## 4 | DISCUSSION

Our study explored the scale- and landscape-specific influence of crop diversification on biological control of aphids in winter wheat. By disentangling the effects of landscape-level crop diversity and semi-natural habitat cover (SNH) on six spatial scales, we demonstrate that crop diversity augments natural enemies and biological control (BCI). On small scales below 500 m, an increase from one to three dominating crop types enhanced BCI by up to 33%. This contradicts previous studies linking biological control primarily to non-crop landscape composition and configuration rather than crop diversity (Holland et al., 2012; Rusch et al., 2013). Instead, our findings corroborate recent evidence for benefits of crop diversification on aphid suppression (Bosem Baillod et al., 2017). Opposed to our predictions, arthropod predators and parasitoids did not differ greatly in

the strength of their response to crop diversity and SNH. However, our findings suggest that natural enemies other than birds or the recorded arthropod predators and parasitoids were responsible for pest suppression in our system. This highlights the need to study the ecosystem service itself rather than individual natural enemy guilds.

### 4.1 | Time and scale effects

We found delayed biological control most likely linked to the deferred arrival of predators and higher attractiveness of treatment patches with increasing aphid densities (Chaplin-Kramer, de Valpine, Mills, & Kremen, 2013; Martin et al., 2016). Furthermore, the response of BCI to crop diversity switched from negative to positive during the course of the exclusion experiment. This suggests that initial dilution-concentration effects (Bosem Baillod et al., 2017; Schneider et al., 2015) were replaced by diversity- and abundance-mediated processes. Importantly, we show that the benefits of crop diversity would have gone unnoticed in experiments lasting less than 10 days or restricted to a single-spatial scale (e.g. 1,000 m, commonly used in ecological studies). Crop diversity was most influential on small (<500 m, biological control, predator densities) and large (>2,000 m, parasitoid densities) spatial scales, whereas SNH had no or weak effects across all scales.

To our knowledge, scale effects on overall biological control using comparable crop diversity indices and exclusion experiments have not previously been investigated. However, two recent studies report reduced aphid densities (1,000 m scale; Bosem Baillod et al., 2017) and increased levels of predation by epigeal predators (750 m scale; Holland et al., 2012) with crop diversification in similar cereal systems in Germany and the UK respectively. These effects occurred on slightly larger scales than in our system. Yet, scale-specific differences in the response to landscape variables are common and depend on study region and system. For example, non-crop landscape complexity may influence overall or taxon-specific pest suppression and predator densities either at small (<500 m; Holland et al., 2012; Tamburini et al., 2015), intermediate (>500 m–2,000 m; Bosem Baillod et al., 2017; Chaplin-Kramer et al., 2013; Gardiner et al., 2009; Rusch et al., 2013) or large-spatial scales (>2,000 m; Chaplin-Kramer et al., 2013; Gardiner et al., 2009; Woltz, Isaacs, & Landis, 2012). Due to their specialist diet and greater dispersal limitation, specialist parasitoids may be less responsive to resource diversification than generalist predators and influenced more locally (Chaplin-Kramer et al., 2011). Nevertheless, strong responses to large-scale landscape complexity were reported elsewhere and compare well with our findings (1,500–2,000 m; e.g. Thies, Steffan-Dewenter, & Tschardtke, 2003).

### 4.2 | Semi-natural habitat and landscape interactions

Perennial non-crop structures are important sources of natural enemies in agroecosystems (Bosem Baillod et al., 2017; Tschardtke et al., 2005), and therefore have the potential to enhance pest regulation (Rusch et al., 2016). Yet a growing evidence base suggests that

natural habitat is not a panacea to improve biological control (Martin et al., 2016; Tschardt et al., 2016). Some predators, especially those primarily relying on crop resources, benefit from non-crop removal, so that SNH enhancement might weaken overall biological control (Caballero-López et al., 2012; Shackelford et al., 2013). Alternatively, local habitat disturbance and pesticide intensity can override resource-related landscape complexity effects (Jonsson et al., 2012). Natural habitat cover may also act as barrier to dispersal for natural enemies, lead to host/prey dilution or provide more favourable resources, thereby drawing natural enemies away from the crops (Holland et al., 2012; Ratnadass, Fernandes, Avelino, & Habib, 2012). This could explain the negative effect of SNH on parasitoid densities at the 500 m scale, especially in landscapes with a diversity of additional crop resources. In contrast, higher crop diversity in simple landscapes might sustain parasitoids by providing alternative hosts across the season, as seen here (Schellhorn et al., 2015). Apart from this interaction between crop diversity and landscape complexity, we found no evidence for landscape-dependent effects of crop diversification (Rusch et al., 2013; Woltz et al., 2012).

#### 4.3 | Natural enemies and biological control

We expected natural enemy guilds to differ in their contribution to biological control, but this hypothesis was not confirmed. Surprisingly, we observed no correlations of biological control with the density of specialist parasitoids and (aerial) arthropod predators, although both groups were enhanced by crop diversification at different scales. These findings suggest that taxa not captured well with our sampling method, particularly epigeal Carabidae and Staphylinidae, or cryptic leaf-dwelling Chrysopidae, were primary drivers of pest suppression in our system. Epigeal predators can be important biocontrol agents (Martin et al., 2013; Tamburini et al., 2015) and contribute to increased predation in oilseed rape fields (Dainese et al., 2017) and crop-diversified landscapes (Holland et al., 2012). However, they are generally less mobile and more likely to depend on crop rather than non-crop resources (Shackelford et al., 2013). Our results support this idea owing to strong small-scale effects of crop diversity on BCI, yet a lack of correlation with SNH at the same scales.

Our findings and previous research therefore highlight the importance of assessing overall biological control rather than the density of natural enemy guilds alone. Sampling deficits related to distinct guilds could mask influential correlations (Henri et al., 2015). Moreover, species-specific predation and overall parasitism rates may not translate to high-biological control owing to species interactions at the community level (Letourneau et al., 2009; Shackelford et al., 2013; Tamburini et al., 2015; Woltz et al., 2012). For example, insectivorous birds interfere with pest suppression by feeding on intermediate predators (Martin et al., 2013; Mooney et al., 2010). In our study, we did not observe reductions in overall biological control in the presence of birds (Tamburini et al., 2015). However, the strength of intraguild predation by birds is known to vary strongly, depending on the system (temperate vs. tropical) or pest organism studied (e.g. chewing vs. sap-sucking insects; Straub et al., 2008).

#### 4.4 | Synthesis and management implications

Agricultural landscapes are primarily crafted by market forces dictating farmers choices of what, where and how to produce (Bowman & Zilberman, 2013). Hence, the scope for implementing beneficial diversification practices is often limited. Societal, economic and bureaucratic obstacles deter conventional farmers from joining agri-environment schemes (state-subsidized wildlife conservation programs such as off-field flower plantings) or creating natural habitat in an attempt to extensify farming (e.g. by reducing insecticide applications, Lin, 2011; Wilson & Tisdell, 2001). Policy-based tools such as the inclusion of "crop diversification" in the European Common Agricultural Policy ("Greening", EU Regulation No. 1307/2013) can favour positive changes. Nevertheless, potential "Greening" benefits are probably lower than expected, as the minimum number of crops that needs to be grown is low (c. 3 crop species, Josefsson et al., 2017; Pe'er et al., 2014). Furthermore, the lacking requirement to cultivate functionally different crops could result in resource bottlenecks for natural enemies (Schellhorn et al., 2015). Our study indicates that at least three functional crop groups (not crop species *per se*) ought to be cultivated to increase biological control. Hence, the conversion of crop diversity to "effective number of crop types" (ENCS) can aid in the development of appropriate farm management guidelines that facilitate ecosystem services, and in the communication of research results to farmers and policy makers.

Although hypothesized links between crop diversity and yield, agrochemical usage, ecosystem resilience and farm economic stability need yet to be confirmed (Aguilar et al., 2015; Lin, 2011), our study is one of the first to highlight the importance of crop diversity for biological control. From a farmer's perspective, landscape-level crop diversification for the sake of biological control is a promising alternative to on-field or non-crop diversification measures. Increasing the number of crop types on small landscape scales allows for a certain flexibility of implementation using extended crop rotation schemes and co-operation with neighbouring farms. Considering the adverse effects of agricultural intensification and climate change, this finding opens new potential pathways for the future of sustainable farming.

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#### AUTHORS' CONTRIBUTIONS

E.M., S.R. and I.S.D. conceived the idea and designed methodology; S.R. collected and analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.



## DATA ACCESSIBILITY

Data available in the Dryad Digital Repository <https://doi.org/10.5061/dryad.g10f7> (Redlich, Martin, & Steffan-Dewenter, 2018).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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