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At Which Spatial Scale Does Crop Diversity Enhance Natural Enemy Populations and Pest Control? An Experiment in a Mosaic Cropping System

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Abstract: The importance of plant richness to enhance the presence, biodiversity and efficiency of natural enemies in agricultural systems has largely been studied and demonstrated these last decades. Planting and preserving non-crop plants or manipulating crop richness in fields are practices that have proven their efficiency. However, the impact of crop-richness continuity in space and time on pests and natural enemies at a landscape scale remains poorly studied. In a two-year study, we assessed the effect of crop richness (single crop vs. multiple crops) on pest and natural enemy abundance and spillover in a field experiment in north-east China. Overall, we found crop diversity had a limited impact on pest and natural enemy abundance at the spatial scale tested (0.025 vs. 0.2 ha). The total pest and natural enemy abundances were not different between single-crop and multi-crop plots in either year, and the community composition at the functional group level was mostly determined by the crop but not crop diversity. However, we found that crop diversity influenced the numeric response of ladybirds to aphids in wheat; their negative response (higher abundance where aphid abundance was lower, suggesting predation) was attenuated in multi-crop plots (no correlation of aphid and ladybird abundance, suggesting the use of alternative resources). This pattern was not found in maize. Finally, crop succession enhanced the spillover of ladybirds from wheat and maize to cotton plots but with limited benefits for aphid control. Because of these limited impacts, we hypothesized that crop diversity may benefit natural enemy populations and enhance pest control at larger spatial scales; while we found similar abundances of ladybirds between our small (0.025–0.2 ha) plots and in large (2 ha) close-by cotton fields, aphid abundances were more than ten times higher in large cotton fields. Our study highlights the need to accurately estimate the spatial scale at which crop biodiversity may benefit pest control, in relation to the ecology of the target pest and natural enemies.

Keywords: aphid; ladybirds; spillover; crop succession; arthropod movement; dispersal; landscape complexity

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1. Introduction

Increased agricultural productivity has been achieved via the intensive use of chemical fertilizers and pesticides and at the expense of biodiversity, which is now threatened [1–4]. Ecological intensification, a knowledge-intensive process requiring the optimal management of ecosystem functions and biodiversity to improve agricultural yields [5] has a huge potential to reduce the negative impacts of human activity while sustainably maintaining agricultural productivity [6–8]. Integrated Pest Management (IPM) is a systemic approach relying on the careful use of synthetic pesticides in combination with ecological management, to maintain sustainable crop production [9,10]. Enhancing ecological processes by which pest populations are controlled by their natural enemies is essential to reduce our dependency on chemical pesticides (e.g., [11]).

Conservation biological control aims to enhance and maintain alternative food resources and habitat quality for pests' natural enemies naturally present in agroecosystems, notably by increasing plant and habitat diversity within or around fields [12–14]. These food resources—including alternative arthropod prey/hosts and pollen and nectar floral resources [15–18] —associated with shelter/nesting sites are major drivers of natural enemy population dynamics in agricultural landscapes [12,19,20]. It is generally admitted that enhancing plant diversity at the field- or at the landscape-level boosts biological control services in agricultural landscapes by providing resources to natural enemies [21–23]. At the field scale—generally between 0.5 ha and 10 ha—increasing plant diversity enhances biological pest control and reduces pest abundance [22]. At the landscape scale—generally between 50 ha and 1000 ha—increasing the proportion of semi-natural habitats can promote biological control [12,24,25]. However, most studies looked at the impact of the relative proportion of natural areas—considered as resource-rich habitats for natural enemies—versus cropped areas (resource-poor habitats), thereby oversimplifying complex agro-ecosystems [26] (but see [27–29] for more complex examples). For instance, the effect of increased heterogeneity or spatio-temporal resource continuity at the landscape scale, driving arthropod movement [30] has been little studied. In particular, how the manipulation of cultivated crop diversity at different spatio-temporal scales affects the movement and population dynamics of pests and their natural enemies requires further research [31,32].

Arthropod movement is influenced by many factors. First, it can be driven by herbivore-induced plant volatiles (HIPVs) [33] at different spatial scales. This strong dependence on olfactory cues has led to the development of several agricultural practices to enhance pest management at field scales, including companion cropping, push–pull and attract-and-reward strategies [22,34,35]. Second, the movement and abundance of natural enemies can be driven by landscape-scale factors such as landscape composition and configuration [36,37]. Composition relates to the presence of different resource types (for example wild plant species or crops) available to arthropods in the landscape, while configuration relates to the spatial arrangement, shape and size of the different landscape elements (e.g., cultivated fields and semi-natural elements) [38–40]. Landscape composition and configuration are therefore inherently related to crop spatial organization and succession. Crop succession (the time of planting and harvest) can induce spillover, that is, the exportation of an arthropod community to surrounding areas following a massive increase in population densities in the origin area [2,41–43]. If spillover of natural enemies happens from semi-natural habitats to adjacent crop fields, this can result in increased pest control among crops [44]. Spillover is directly related to arthropod movement capacity, and is dependent on their size and dispersal capacity. For example, large predators like ladybirds, carabids and spiders can travel many kilometers [45,46], whereas parasitoids that are smaller hardly travel more than a few kilometers for foraging and mating [47]. Therefore, different functional groups of natural enemies respond to different spatial scales, relative to their movement capacity (landscape configuration) [48] and their specific ecology (diet needs, nesting sites, etc.; landscape composition) [24].

One way to enhance resources for natural enemies in agricultural landscapes is to increase the proportion of non-cropped areas. However, this may represent a non-acceptable cost for farmers due to reduced cropped areas and potentially reduced yields if non-cropped areas are taken from productive land [49,50]. Another possibility is to increase within-field crop diversity by using agricultural techniques like companion cropping, but this may require specific expertise and possibly new equipment [51]. In north-eastern China, the agricultural landscape is composed of a mosaic of small fields (usually from 0.2 to 0.5 ha) planted with a variety of crop plants [52]. In such landscape, the spatial arrangement and cultivated diversity of crop fields may strongly influence arthropod movements and biological control, yet this remains insufficiently understood.

In this study, we tested the effect of increasing crop diversity at a field scale on arthropod abundance and diversity, and pest biological control in a two-year field experiment in the Hebei province of China. In 2017, we planted all crops simultaneously, varying the number of crops planted in 0.3 ha plots. In 2018, we planted crops successively in plots of 0.2 ha following agricultural practices, to test the impact of temporal crop succession on arthropod spillover. We sought to answer the following questions: Q1. Does biocontrol efficacy increase with crop diversity? We hypothesized that (H1.1.) overall natural enemy abundance and diversity should increase with increased crop diversity in a given area through increased resource diversity and availability, and therefore pest abundance should decrease. However, this should be modulated by (H1.2.) pest and natural enemies' ecology (polyphagy and their ability to use alternative food resources, along with their dispersal capacity), and by (H1.3.) differences in their capacity to detect and respond to their target pest abundances. Q2. Does crop diversity in a sequential design increase natural enemy spillover? We expected that (H2.1.) natural enemies should appear earlier in areas of higher crop diversity through increased proximity of sequentially managed crops and hence the increased accessibility of complementing food sources. If so, (H2.2.) pest abundance should decrease earlier. Q3. Does the scale at which crop diversity is increased have an effect on the abundance of the arthropods? We expected that (H3.1.) functional groups characterized by a large movement capacity may be little affected, but that (H3.2.) resource concentration may increase the abundance of arthropods specialized on a restricted range of resources at larger scales.

2. Material and Methods

2.1. Experimental Designs

To assess the effect of crop diversity on arthropod abundance and diversity, two experiments were conducted at the Langfang Experimental Station (39.53° N, 116.70° E) in the Hebei Province of China. In 2017, we assessed the effect of crop diversity on the abundance and diversity of pests and associated natural enemies by simultaneously establishing between one and six crop plants in similar-sized plots. In 2018, we also assessed the effect of a spatial and temporal crop succession on the spillover of natural enemies between crops by establishing and harvesting the different crop plants at different times following agricultural practices. No chemical product was applied in the field, and weeds were regularly removed by hand.

The first experiment was established in a field of 1.2 ha (65 × 180 m). The field was divided into 21 plots of 15 × 20 m each (0.3 ha), themselves divided into 12 subplots of 5 × 5 m each (0.025 ha) and planted quasi-simultaneously with either one crop (single-crop), four or six different crops (multi-crop; Figures S1A, S2A and S3). The plots were separated by 5 m of bare ground. The crops were tomato, maize, or cabbage for the one-crop treatment; tomato, maize, cabbage, and cotton for the four-crop treatment; and tomato, maize, cabbage, cotton, wheat, and soybean for the six-crop treatment. Due to logistical limitations, we only collected data on three crops: tomato, maize, and cabbage in one subplot in each one-crop plots and in three subplots in each four-crop and six-crop plots (randomly chosen among all possible subplots of each plot). The other plots (dark grey on Figure S1A) were not sampled. This allowed a balanced design with three sampled subplots per crop and per treatment (N = 3).

The second experiment was established in a field of 0.98 ha (130 × 75 m). The field was divided into 25 plots of 10 × 20 m (0.2 ha), themselves divided into eight sub-plots of 5 × 5 m (0.025 ha) planted with either one or four crops (200 subplots in total; Figure S1B). Crops were planted successively following local agricultural practices (Figure S2B), allowing a spatio-temporal crop diversification and the observation of arthropod movement. The plots were separated by 5 m of bare ground. The crops planted were either wheat, maize, cotton, or cabbage in single-crop plots, and all four in multi-crop plots. Each plot was replicated five times (N = 5) in a semi-randomized pattern where the same plot type did not appear in two adjacent plots. In the multi-crop plots, each crop was planted in two non-adjacent subplots selected randomly.

2.2. Insect Sampling

Non-destructive samplings were conducted nine times each year, from 20 June to 21 August 2017 and from 30 April to 4 October 2018. We visually counted all arthropods present on five entire plants (1 plant = 3 tillers for wheat) equitably distributed in a subplot on each sampling day, carefully inspecting all plant parts. In addition, a pitfall trap was placed in the middle of each subplot and collected 48 h later to catch ground-dwelling predators (Carabidae and spiders). All arthropods observed were identified in situ to the family and to the species when possible, and classified in the following functional groups (Table S1): aphids, Lepidoptera, Aleyrodidae, hemipteran bugs (mostly Miridae and some rare Pentatomidae), Chrysomelidae and thrips for pests; and Coccinellidae, Chrysopidae, Syrphidae, aphid parasitoids (parasitized aphid mummies) and Anthocoridae for natural enemies. Identifications to the species in 2018 were performed by expert taxonomists, and only a few specimens could not be identified to the species. Note that hemipteran bugs are recognized to notably prey upon aphids and other species [53–55], but their impact as pests is quite high in the region and therefore they were only considered as pests here as a simplification. The number of arthropod individuals of each functional group counted on the five plants of a subplot was summed to obtain one value per functional group per subplot per sampling day. For the sake of simplicity, we thereafter use the term abundance to refer to this number per five plants.

To expand our analysis to larger spatial scales (Q3), ladybirds and aphids were also sampled both years every five days from mid-June to early September (16 sampling dates) in three 2 ha cotton fields 1 km distant from the experiment site. Insects were counted on the entire plant on 50 different cotton plants randomly chosen in the center of the field, and counts were compared to numbers per plant in our cotton subplots (at the subplot and plot scale) in 2017 and 2018. Agricultural practices were identical to those in the experiment, including the lack of use of pesticides.

2.3. Statistical Analyses

All statistical analyses were performed with R version 3.6.3 [56]. Spatial autocorrelation in arthropod numbers was tested a priori for each functional group, week, and year separately using Moran's autocorrelation test (R library 'ape', function 'Moran.I') [57]. We found that only one (2%) and two (5%) week-functional groups were autocorrelated in 2017 and 2018, respectively, but none were autocorrelated in either year after correcting tests' p-values for multiple testing [58](R function 'p.adjust' with correction method 'BH') [56]. Therefore, and for simplicity, spatial autocorrelation was thereafter accounted for via random effects. In all tests except otherwise stated, the crop was specified as a fixed effect to account for differences in numbers due to crop (plant size, shape, and density), and random effects were the subplot nested in the plot, accounting for repeated measures through time and space. The model distribution was chosen to account for data distribution skewness and overdispersion. The significance of fixed effects was estimated through a stepwise regressive type-II model comparison with an ANOVA based on χ^2 tests for Generalized Linear Mixed Models (GLMMs) and Linear Mixed Models (LMMs), and Fisher tests for multivariate analyses. The absence of residual heteroscedasticity and overdispersion was verified a posteriori in the best GLMM model (functions 'plot(simulateResiduals())' and 'testDispersion'; R library 'DHARMa') [59]. When fixed effects were found significant at $p < 0.05$, a post hoc comparison of means between effects groups was performed to assess which levels were significantly different (R functions 'emmeans' for combinations of factorial effects and 'emtrend' for combinations of factorial effects and covariables; R library 'emmeans') [60].

2.3.1. Effect of Crop Diversity on Natural Enemy and Pest Abundances and Diversity

To understand how biocontrol efficacy increases with crop diversity (Q1), we first assessed if higher crop diversity at plot level positively affected the abundance and diversity of natural enemies while negatively affecting that of pests (hypothesis H1.1.). To this aim, we used count data during the periods of high crop diversity each year, i.e., from 26 June to 21 August 2017 (all eight weeks with all crops), and from 17 May to 11 July 2018 (three weeks with at least three crops).

First, we analyzed the total pest and natural enemy abundances in each subplot using independent Generalized Linear Models (GLMMs) with a negative binomial distribution (R library 'lme4', function 'glmer.nb') [61] using the crop diversity in interaction with the crop as fixed effect each year independently. In 2018, we also added pest diet breadth in the interaction since we had pest identification to the species level (Table S1). Pest diet (specialist vs. generalist) was categorized from the literature. We expected single-crop plots to attract significantly more specialist pests compared to multi-crop plots (H1.2.; resource concentration hypothesis) [62,63].

Second, we investigated how crop diversity affected the relative abundances of functional groups (H1.2.; Table S1) using the total number of individuals in each functional group counted per subplot throughout the weeks considered. Only groups with >5 individuals counted were included. We performed a constrained correspondence analysis (R function 'cca', library 'vegan') [64] separately for each year, followed by an ANOVA test. We implemented the crop (maize, tomato, or cabbage in 2017 and maize, cabbage, wheat, and cotton in 2018), the treatment (one-crop, four-crop, or six-crop in 2017 or single vs. multi in 2018) and the interaction between the two as fixed effects. This analysis also showed the correlations between the different natural enemy and pest functional groups.

Third, we analyzed species richness in 2018 (for which we had species identification) calculated as the total number of species over the time period considered but discarding specimens identified to the genus only, except *Neoscona* sp., *Anyphae* sp., *Enoplognatha* sp. and *Dictyni* sp. for which only one individual was found. We performed a LMM with the crop diversity in interaction with the crop as fixed effects.

Finally, we tested if crop diversity affected the response—and hence the control efficacy—of natural enemies to the abundance of their target pest functional groups (hypothesis H1.3.). We focused on aphids because of their major economic importance [65] and because, of the crops sampled, we used data from 2018 only, when aphids were abundant. The main natural enemies of aphids (and also most used biocontrol agents) are ladybirds and parasitoids [66–68]. Ladybirds have a diverse diet, preying upon diverse prey (although preferring aphids) [69–72] but also using plant resources [73,74]. Hence, this functional group could typically be enhanced by crop diversity. Conversely, aphid parasitoids are specialists and restricted to the distribution of their aphid hosts [75], and hosts could be typically easier to locate in large populations in low crop diversity [76]. Therefore, we analyzed separately the relationships between ladybirds and aphids and between aphid parasitoids and aphids, in crops in which they were found at least 30% of the time (maize and wheat for ladybirds; cabbage, cotton, and wheat for parasitoids). We performed two GLMMs with the crop diversity in interaction with the crop and the scaled aphid abundance as fixed effects.

2.3.2. Effect of Crop Diversity on Natural Enemy Spillover

The second question (Q2) of our study was to assess the effect of cultivated diversity on the spillover of natural enemies. Only data from the 2018 experiment were analyzed here, since it was designed to obtain spatio-temporal crop succession following agricultural practices (Figures S1B and S2B). We focused on ladybird and aphid populations, on 17 May 2018 and 4 October 2018 (Julian week: 20–40). These dates coincided with wheat plant decline and harvest (on 5 July 2018; Figure S2B) but also with a rapid ladybird population growth in maize following high aphid abundances in maize. We therefore hypothesized (H2.1.) that ladybirds could spillover from wheat to maize and from wheat and maize to cotton. If such spillover allowed ladybird abundances to build up, we expected to see a faster decline of aphid populations in corresponding crops in single-crop plots compared with multi-crop plots (H2.2.). We did not test spillover to cabbage because of low ladybird abundances in cabbage. We performed independent GLMMs for ladybirds and aphids and each crop with a negative binomial distribution, using crop diversity as a fixed effect and the plot as a random effect (only one sampled subplot per plot in each crop). For ladybirds, we also added aphid abundance as a co-variable.

2.3.3. Influence of the Spatial Scale of Crop Diversity

We expanded our analysis of the impact of crop diversity on pest and natural enemy abundances and diversity at a larger spatial scale, to test if they responded to larger crop diversity spatial scales than that tested in our two-year experiment (Q3). We compared aphid and ladybird abundances in cotton in our experimental plots (0.3 or 0.2 ha) to those measured in 2-ha fields. We used GLMMs with a negative binomial distribution and the plot/field size as a fixed factorial effect (2017: pooling subplots from four-crop and six-crop plots, two levels: 0.025 ha vs. 2 ha; 2018: three levels: 0.025 ha = four-crop plots/0.2 ha = one-crop plots/2 ha). To obtain similar numbers of replicates in each treatment, we used data from all sampling dates in large fields in 2017, and only data from half the dates in 2018 (that is, 14 June, 19 June, 9 July, 14 July, 24 July, 29 July, 3 August, 8 August and 7 September), removing the last sampling date in the crop diversity experiment (4 October). We used the plot or large field as random effect each year.

3. Results

3.1. Effect of Crop Diversity on Pest and Natural Enemy Abundances and Diversity

Contrary to our expectation (H1.1.), total pest and natural enemy abundances were not affected by the increase in crop diversity in either year, and were not different between crops (Table 1; Figure 1). The pest diet (cereal specialist vs. generalist) tested in 2018 did not affect either kind's total pest abundance. The community composition (i.e., the relative abundances of the pest and natural enemy functional groups, expected to be affected by crop diversity due to different ecologies and movement capacities; H1.2.) was only affected by the crop but not crop diversity in either year (Table 2; Figure 2). However, aphids were negatively correlated with ladybirds both years, and aphid parasitoids were positively correlated with aphids and Lepidoptera in 2018 (Figure 2B). We also found that species richness was not affected by the interaction between crop diversity and crop (χ^2 = 0.825, df = 3, p = 0.84) nor by the crop diversity (χ^2 = 0.808, df = 1, p = 0.37); it only responded to crop (χ^2 = 52.2, df = 3, p < 0.001), with cabbage hosting the highest arthropod diversity, wheat and maize hosting intermediate diversity, and cotton hosting the lowest diversity (Table S2).

Table 1. Impact of crop diversity on total pest and natural enemy abundances in 2017 and 2018. Diet tested in 2018 refers to diet breadth of pests (cereal specialists vs. generalists).

	χ^2	**d.f.**	***p***
2017			
Pests			
Diversity:Crop	6.41	4	0.17
Diversity	0.683	2	0.71
Natural enemies			
Diversity:Crop	2.78	4	0.86
Diversity	0.199	2	0.69
2018			
Pests			
Diversity:Crop:Diet	0.674	3	0.88
Diversity:Crop	1.54	3	0.67
Diversity:Diet	1.61	1	0.20
Natural enemies			
Diversity:Crop	0.575	3	0.90
Diversity	0.236	1	0.63

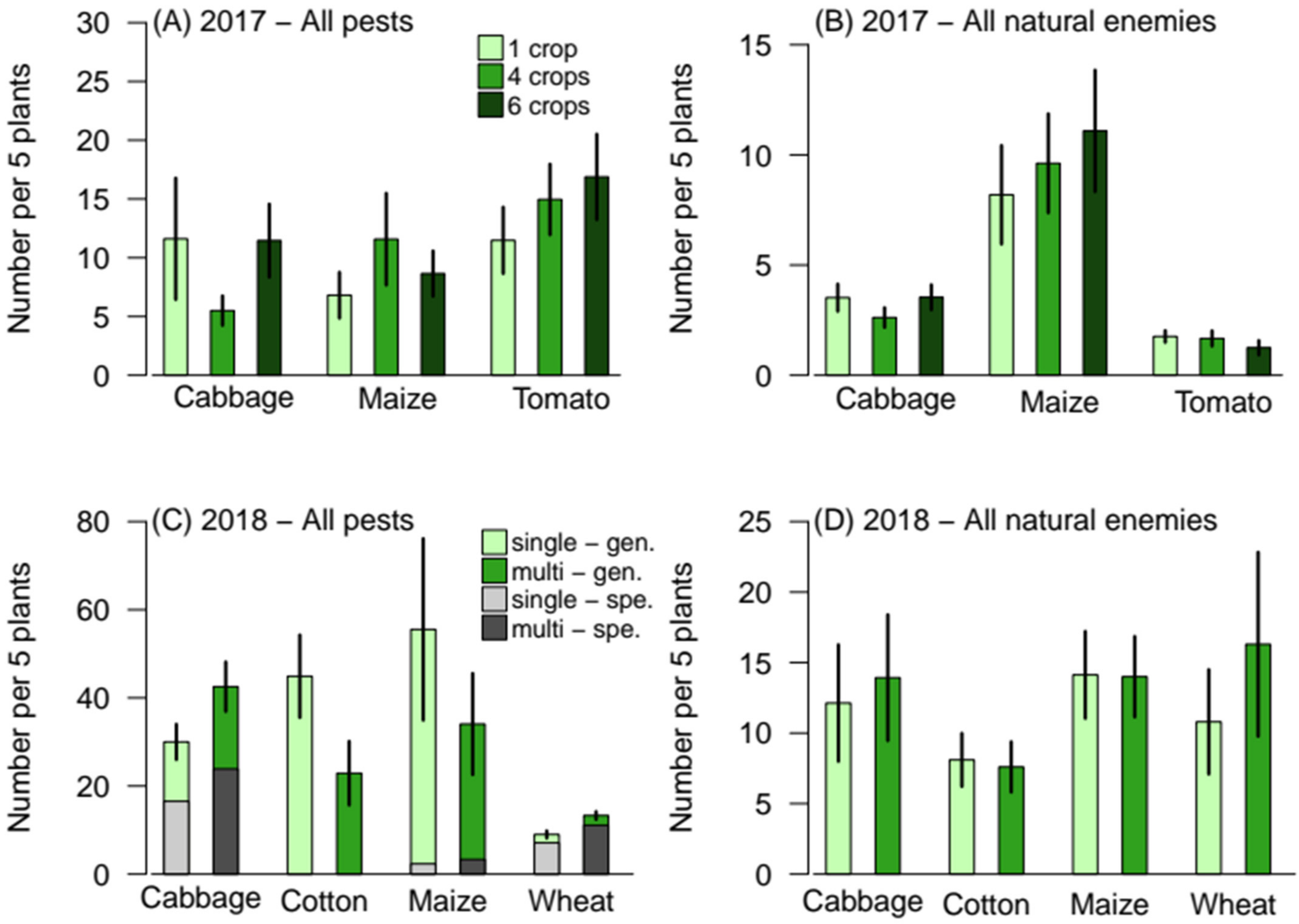

Figure 1. Mean total abundance (mean total number per five plant ± SEM over time) of pests (**A**,**C**) and natural enemies (**B**,**D**) in the different crops and crop diversity treatments in 2017 (**A**,**B**) and 2018 (**B**,**D**). The proportions of cereal specialists ("spe.") and generalists ("gen.") pests in 2018 are shown with grey and green bars, respectively. Neither crop diversity nor crop (or pest diet breadth in 2018) significantly affected total abundance (Table 1).

Table 2. Impact of crop diversity and crop type on community composition (relative abundances of functional groups: total number of individuals counted over time in each subplot).

	F	**d.f.**	***p***
2017			
Pests			
Diversity:Crop	1.49	4, 22	0.067
Diversity	1.17	4, 24	0.30
Crop	8.88	2, 26	<0.001
2018			
Diversity:Crop	0.368	3, 35	0.99
Diversity	0.303	1, 36	0.96
Crop	22.5	3, 36	<0.001

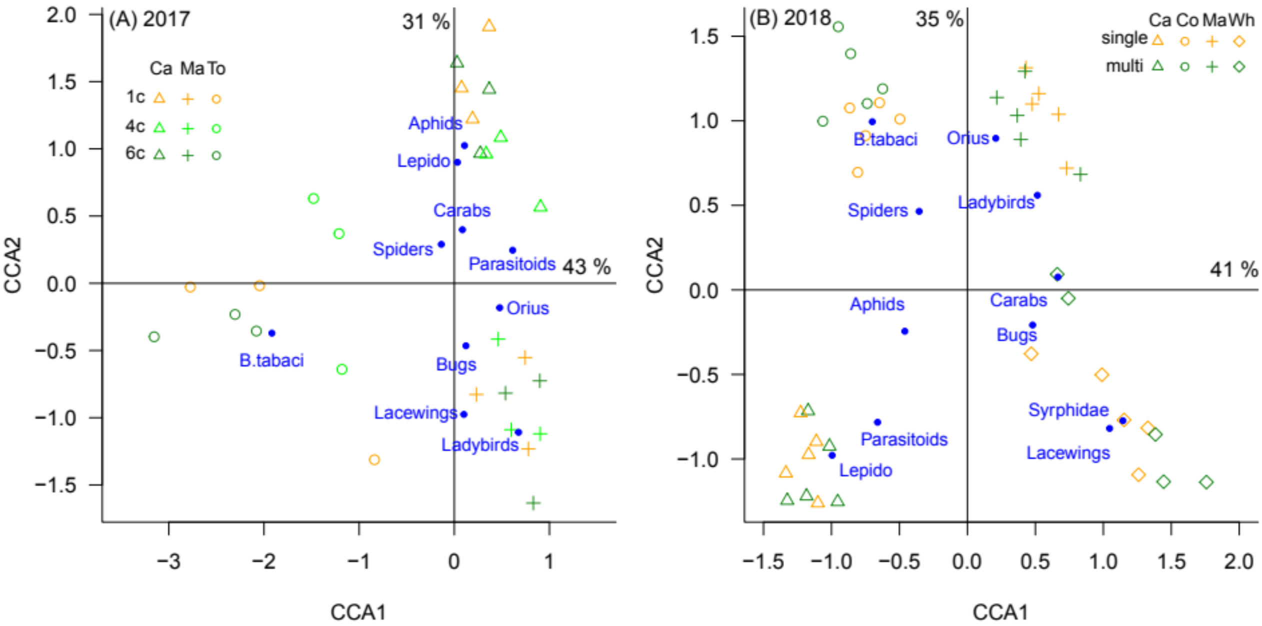

Figure 2. Communities of arthropod visitors (both pests and natural enemies) sampled over the 2017 (**A**) and 2018 (**B**) sampling seasons in each subplot: relative abundances of functional groups (total number of individual of each functional group sampled per subplot over time). Constrained correspondence analyses across crop-diversity treatments, crop types and arthropod functional groups. Only crop type (2017: Ca: cabbage, Ma: maize, To: tomato; 2018: Ca: cabbage, Co: cotton, Ma: maize, Wh: wheat) significantly affected the community composition as shown by the separation in distinct clouds of points in the two-dimensional space (Table 2).

We then investigated how the response of different functional groups to the abundance of their target pest was affected by crop diversity (H1.3.). Crop diversity had a marginally significant positive effect on ladybirds' response to aphid abundance in wheat (Table 3; Figure 3): there was a negative relationship between ladybird abundance and aphid abundance in wheat single-crop plots (negative regression coefficient), but not in wheat multi-crop plots (regression coefficient not different from zero). In maize however, crop diversity had no impact on the response of ladybirds to aphid abundance, and the negative relationship was true in both maize single-crop and multi-crop plots (negative regression coefficients with largely overlapping 95% confidence intervals). Increased aphid abundance led to increased parasitoid abundance, but this relationship was not affected by crop or crop diversity (Table 3, Figure 3; positive regression coefficient).

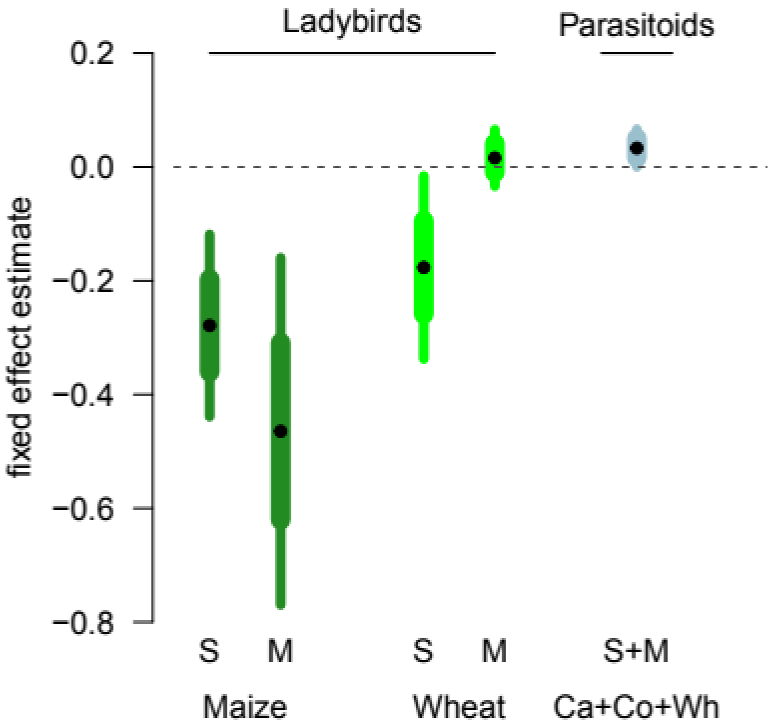

Figure 3. Regression coefficient estimates ± SE (thick bars) ± 95% confidence interval (thin bars) between ladybird and aphid abundances in maize (dark green) and wheat (light green) and between aphid parasitoid and aphid abundances in all crops (blue: 'Ca+Co+Wh': cabbage, cotton, and wheat), in single-crop plots (S) and multi-crop plots (M) (or all plots 'S+M'). An estimate significantly above zero shows a positive correlation between aphids and its natural enemies, while an estimate significantly below zero shows a negative correlation between aphids and its natural enemies. A significant impact of crop diversity would cause estimate ranges to not overlap (here, only the estimates for ladybirds in wheat show a marginally significant impact of crop diversity with disjunct SE ranges). The crop diversity and crop did not affect the correlation between aphid parasitoids and aphids (Table 3), hence only one regression coefficient is shown.

3.2. *Effect of Crop Diversity on Natural Enemy Spillover*

We then investigated whether spatio-temporal crop succession enhanced pest and natural enemy spillover (H2.1.) and consequently early pest control (H2.2.). Ladybird abundances were higher in multi-crop plots in cotton crops compared with single-crop plots soon after the establishment of cotton plots (Figure 4B; $\chi^2 = 7.56$, df = 1, $p = 0.0059$; mean number ± SE of ladybirds per five plants: multi-crop 0.80 ± 0.42, single-crop: 0). However, this had only a marginally significant impact on aphid abundances (Figure 4D; $\chi^2 = 3.08$, df = 1, $p = 0.079$; mean number ± SE of aphids per five plants: multi-crop: 9 ± 4, single-crop: 23 ± 7). In maize, neither ladybird nor aphid abundances were affected by crop diversity at these dates (Figure 4A,C; ladybirds: $\chi^2 = 0.0385$, df = 1, $p = 0.84$; aphids: $\chi^2 = 0.281$, df = 1, $p = 0.60$).

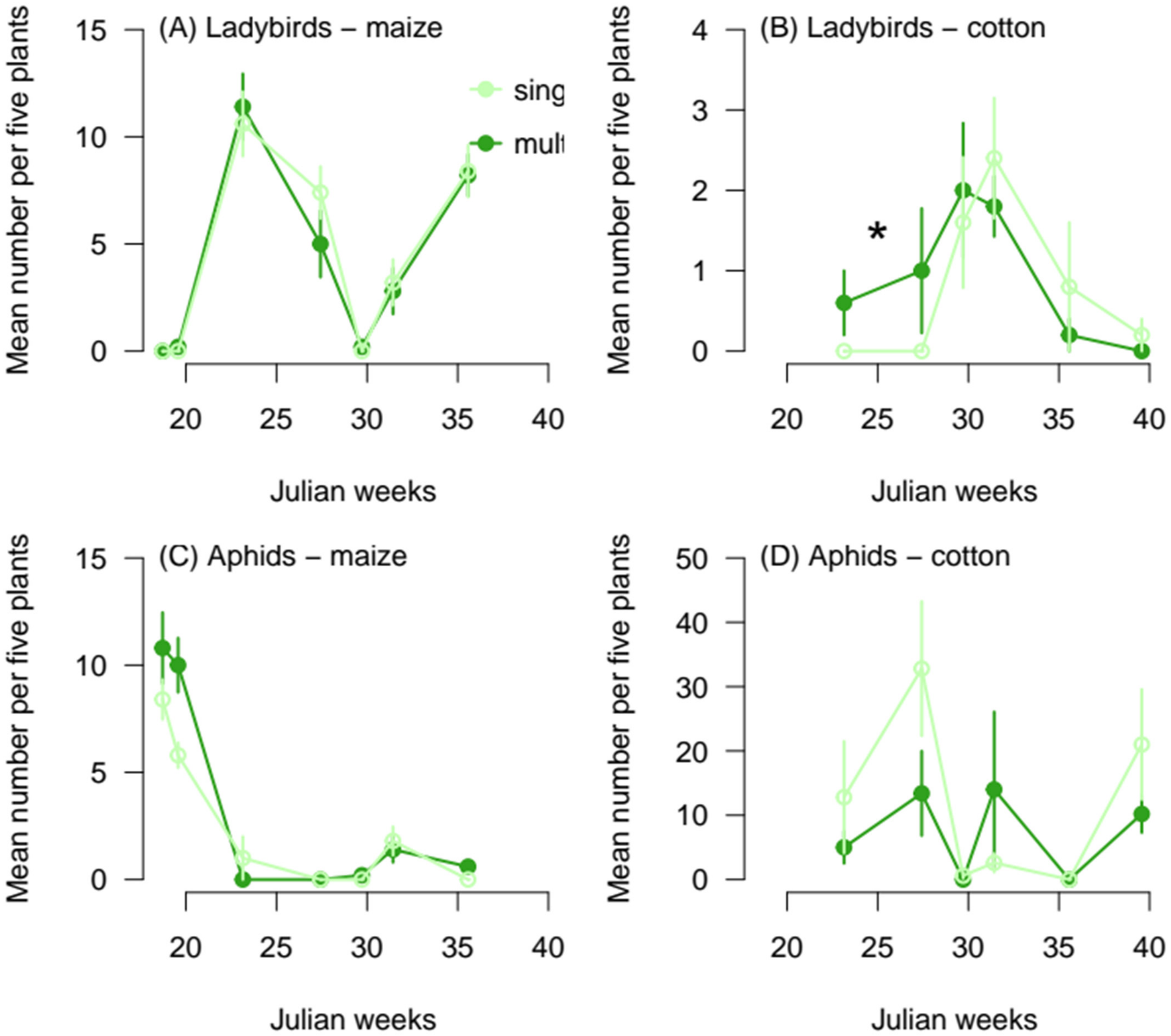

Figure 4. Mean ladybird (**A**,**B**) and aphid (**C**,**D**) abundances (number per five plants ± SEM) in maize (**A**,**C**) and cotton (**B**,**D**) subplots through time in each crop diversity treatment in 2018 (N = 5 for each date). The star shows a significant difference in the abundance of ladybirds in cotton subplots in single- vs. multi-crop plots during the first two weeks ($\chi^2{}_1 = 7.56$, $p = 0.0059$, GLMM with negative binomial distribution).

3.3. Influence of the Spatial Scale on Crop Diversity Effects

We finally explored whether crop diversity could be beneficial to natural enemies at a larger spatial scale than tested in our field experiments (H3.1.) by comparing ladybird and aphid abundances in cotton plots with that of large neighboring cotton fields. Ladybird abundances were not significantly different between the experimental plots and the larger fields either year (Figure 5A; 2017: $\chi^2 = 1.69$, df = 1, $p = 0.19$; 2018: $\chi^2 = 1.06$, df =2, $p = 0.59$), although they tended to be higher in multi- than in single-crop plots and in single-crop plots than in large fields in 2018. On the contrary, and consistent with H3.2. (enhanced pest control), aphid abundances were lower both years in the small experimental plots compared with the larger fields (Figure 5B; 2017: $\chi^2 = 11.6$, df = 1, $p < 0.001$; 2018: $\chi^2 = 24.4$, df = 2, $p < 0.001$, emmeans: multi~single < BIG, $p < 0.001$).

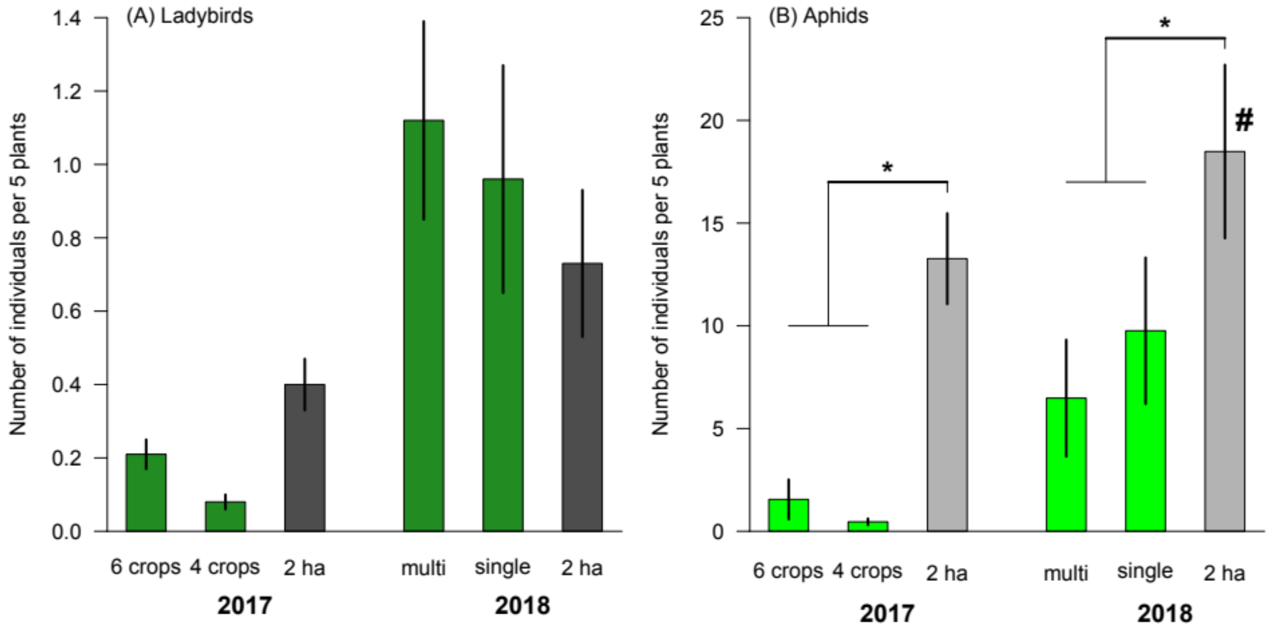

Figure 5. Impact of the spatial scale of crop diversity in our experiments versus nearby 2 ha fields on the abundance of (**A**) ladybirds and (**B**) aphids; '6 crops'/'4 crops': 2017 crop-diversity treatments (subplot size 0.025 ha); 'multi'/'single': 2018 crop-diversity treatments ('multi': 0.025 ha; 'single': 0.2 ha); '2 ha': large cotton fields nearby. '*' shows significant differences ($p < 0.001$). '#' Mean abundance ± SE of aphids in large fields in 2018 was divided by 10 for graphical aesthetics and clarity.

Table 3. Impact of crop diversity on the response of natural enemy functional groups to the abundance of their target pest functional groups. The regression coefficient estimates are shown in Figure 5. Significant effects of crop diversity are shown in bold.

	χ^2	d.f.	p
Ladybirds to aphids [1]			
Diversity:Crop:Pest	4.95	2	**0.026** *
Aphid parasitoids to aphids [2]			
Diversity:Crop:Pest	1.37	2	0.51
Crop:Pest	2.67	2	0.26
Diversity:Crop	5.41	2	0.067
Diversity:Pest	1.68	1	0.20
Diversity	0.195	1	0.66
Pest	4.43	1	**0.031** *

[1] maize and wheat only; [2] cabbage, cotton and wheat only; *: $p < 0.05$.

4. Discussion

In the present study, we assessed the impact of cultivated crop diversity within 0.2–0.3 ha plots on the abundance of arthropods and the movement of natural enemies (Q1). Contrary to our expectations, we did not detect an impact of increased crop diversity at the plot scale on the total abundance of pests and natural enemies in either 2017 or 2018 (H1.1.). Community composition at the functional group scale was determined by the crop type, not crop diversity (H1.2.). However, we found that (tested in 2018) the numeric response of ladybirds to aphid abundances was influenced by crop diversity in wheat (but not in maize): ladybird abundances were negatively affected by higher aphid abundances (suggesting predation) in single-crop wheat plots but not in multi-crop wheat plots, where their abundance might have been favored by alternative resources (H1.3.). In addition, and consistent with our expectation, crop diversity enhanced the spillover of ladybirds from cotton to maize (H2.1.), although this did not result in significantly lower aphid abundances

(H2.2.). Finally, we found that the spatial scale at which crop diversity was tested in our experiments may have been too small (H3.1.), since the abundance of aphids in either low or high crop diversity experimental plots was significantly lower than that in nearby large cotton fields (2 ha; H3.2.).

Overall, the effects of crop diversity on pests and natural enemies were limited at the scale tested (0.025 ha vs. 0.2–0.3 ha). This was unexpected, since other studies have shown that increased crop diversity enhances the diversity and abundance of natural enemies, resulting in increased pest biological control and reduced pest abundances (H1.1.; [27,29,77,78]. One reason why we did not see such impact is that the scale at which crop diversity effectively enhances natural enemy populations may be larger than 0.2 ha (H3.1.). Indeed, we found aphid abundances more than ten higher in large (2 ha) nearby cotton plots than in our 0.2–0.3 ha cotton plots (Figure 5B). This would be expected if pest control is lower in the large fields than at the plot scale. For natural enemies, the entire experiment, including single-crop and multi-crop plots, may have been perceived as just one large multi-crop field. This is quite possible, in regards to the movement capacities of the natural enemies considered: most of them were large predators with high movement capacity: ~10 km per day for ladybirds [38], ~125 m for small parasitoids [39], and over 40 km per night for lacewings [79]. Therefore, it is possible that neither the 5 m-distance of bare soil between plots nor plot size (0. 2–0.3 ha) represented a strong barrier to natural enemy movement, contrary to large-scale cotton fields (2 ha). Most aphids in wheat were also specialists (Figure 1C), and the much higher abundances in large fields than at the plot scale could also be a response to the high density of plant resources in single-crop, large fields (H3.2., resource concentration hypothesis) [62,63].

Despite a marked impact of crop diversity on aphid abundances at this larger spatial scale (0.2 vs. 2 ha), we did not find significant differences in ladybird abundances between our experimental plots and the large nearby cotton fields (H3.1.; Figure 5A). The high variability in abundances within plots and within fields in 2018 could have reduced the probability of detecting such an effect. Additionally, ladybirds mainly feed on aphids [65,70] and lay eggs in large aphid colonies such as those measured in the large fields (2 ha). This could have increased their abundance near large aphid populations in the large fields. More generalist predators, such as spiders and ground beetles might be more sensitive to crop and resource diversity at these scale. However, we did not find significant changes in the community composition at the functional group level, and spiders and carabids were always rare and contributed little to the dissimilarities in community composition between crops and crop-diversity treatments (Figure 2).

We expected pest diet to modulate the impact of crop diversity on pest abundance (H1.2.): the resource-concentration hypothesis predicts that specialist pests will aggregate in single-crop plots where food resources are abundant, while generalist pests may instead be favored by the diversity of food resources in multi-crop plots [62,63]. However, we could not find such a pattern in total pest abundance (tested in 2018; Figure 1C). Again, this could be because the small crop-diversity scale tested (0.025 vs. 0.2 ha) resulted in the entire experiment being perceived as a single crop-diverse field, favoring generalist pest populations in both single- and multi-crop plots, and diluting the perceived host resource densities for specialist pests.

The numeric response of ladybirds to aphid abundances was influenced by crop diversity (H1.3.; Figure 3): ladybird abundances were lower where aphid abundances were higher in wheat single-crop plots but not multi-crop plots. The negative relationship could be a consequence of high predation: ladybirds tend to lay eggs in large aphid colonies [18,70,80], and ladybird juveniles could then very rapidly deplete the colonies, causing the negative relationship between aphid and ladybird abundances found here. Our results also show that in maize, ladybird abundances were lower where aphid abundances were higher in both multi- and single-plots, which may be due to the high ladybird abundances (possibly through the delivery of additional alternative resources by maize, such as ears on which many ladybirds were observed) having heavily preyed upon aphid populations. The loss of the negative relationship between aphid and ladybird abundances in multi-crop wheat fields suggests that ladybirds did not exclusively or essentially rely on aphid resources in these plots, and could have benefited from alternative food resources (e.g., alternative prey enhanced by high crop diversity, or plant resources) [73]. Finally, unlike ladybird abundances, aphid parasitoid abundances were positively correlated to aphid abundances, but independently of the crop or crop diversity. This could be a simple consequence of the sampling method, since aphid parasitoids were counted based on the number of aphid nymphs parasitized (presence of a parasitoid larva in their body). Aphid parasitoids are known to be specialists and restricted to the distribution of their aphid hosts [75], and hosts could be typically easier to locate in large host populations at low crop diversity [76].

In areas of high crop diversity, crop succession along the growing season (through differential planting and harvest times following agricultural practices; Figure S2) may favor spillover of natural enemies between crops (H2.1.). This would result in the early establishment of natural enemy populations, as suggested by the higher ladybird abundances in multi-crop cotton subplots compared to single-crop cotton subplots measured early in the season (Figure 4B). The proximity of maize subplots in multi-crop plots, in which ladybirds were found at high densities early in the season (Figure 4A), could have been a source crop for ladybirds into neighboring cotton subplots. Ouyang et al. [81] found that maize was a source crop highly appreciated by ladybirds from which they moved towards neighboring cotton fields and in which they actively regulated aphid populations. Ladybirds were predicted to actively spillover from maize to cotton and inversely to find complementing food sources in both crops, maize acting as a shelter crop and cotton as a prey-resource crop [82]. Our finding suggests that placing maize crops in proximity to other types of crops might enhance the early presence of ladybirds in adjacent crops. In our experiment, however, the high ladybird abundance early in the season in multi-crop cotton subplots did not result in significantly lower aphid populations compared to single-crop cotton subplots, although they tended to be lower (H2.2.). The potential for crop diversity to enhance early pest control should be properly investigated in the future, by measuring the movement of natural enemies (e.g., through mark-recapture, carbon isotopic signature, or gut content) [83,84].

5. Conclusion

Our two-year experiment shows that arthropod abundances and movements are difficult to predict in real field conditions, even when predictions have been confirmed in small, controlled experiments [18,85]. We suggest that the effects of crop diversity should be investigated through a range of spatial scales relevant to the ecology of target natural enemies and pests, as well as to the eco-region. Here, the characteristics of northern Chinese landscapes and of their natural enemy communities may have influenced the results. The effective scale promoting pest control through increased crop diversity is likely to be lower than natural enemies' dispersal capacity but larger than tested here, and specific to each targeted functional group [29]. Future studies should test effects of crop diversity at appropriate scales based on the ecology of the targeted natural enemies and landscape specifically, and aim to directly measure arthropod movement.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/agronomy12081973/s1, Figure S1: experimental design and disposition of crop plots and subplots; Figure S2: schedule of experiments' planting, sampling and harvest of the different crops; Figure S3: crops grown in the 2017 experiment and apparent canopy density; Table S1: number, identity and functional group of arthropod specimens observed and identified in the experiments; Table S2. Post hoc comparison of means in species richness between crops in 2018.

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