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RESEARCH ARTICLE

Predators do not benefit from crop diversity but respond to configurational heterogeneity in wheat and cotton fields

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Abstract
Context Manipulating crop diversity in the landscape has been suggested as a promising management option to enhance biocontrol but how crop diversity independently of other important aspects of landscape structure affects predator and pest abundances remain largely unexplored.
Objectives Our study assessed the relative and interactive effects of crop composition and configuration on aphids and their generalist predators, i.e. ladybirds, spiders and lacewings.
Methods We sampled arthropods in 47 cotton fields and 21 wheat fields in Hebei, China, located along three landscape gradients: crop diversity (Shannon diversity of crops ranging from 0.27 to 1.32 corresponding to a crop richness varying from 2 to 7 different crops), crop configurational (crop edge density varying from 0.0012 m/ha to 0.066 m/ha) and proportion of semi-natural habitats (varying from 0.5% to 56%).
Results Crop diversity never had any effect on arthropod communities and we found no effect of the proportion of semi-natural habitats on natural enemies' abundances. Aphid abundance was positively correlated with the proportion of semi-natural habitats both in cotton and wheat fields. Lacewing abundance benefited from configurational heterogeneity as abundances increased with crop edge density.
Conclusions Our result provide evidence that crop diversity is probably not the best management option to enhance biocontrol of aphids in Chinese landscapes and confirms that the amount of semi-natural habitats in the landscape is a critical aspect shaping arthropod communities. It also indicates that manipulating crop edge density by promoting agricultural landscapes with small field size for instance can benefit natural enemies of crop pests.

Keywords Landscape diversity · Landscape composition · Landscape configuration · Generalist predator · Aphids

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Introduction

Agricultural productivity gains have been achieved at the expense of biodiversity, which is now seriously threatened (Dudley and Alexander 2017; Raven and Wagner 2021). Ecological intensification of agricultural systems, which consists in increasing the services delivered by biodiversity, offers a promising way to reduce environmental impacts of modern agriculture (Wratten et al. 2012; Bommarco et al. 2013). Among the key ecological processes embedded within ecological intensification, biological pest control, that consists in controlling pest populations by their natural enemies, is an important ecosystem service that can help in reducing crop damages and pesticide use (and multiple associated side effects e.g. see Desneux et al. 2007).

Evidences indicates that landscape simplification characterized by loss of semi-natural habitats, decrease in crop diversity or enlargement of field sizes have made crop fields more susceptible to pest outbreaks (Gagic et al. 2021). Pest populations benefit from landscape simplification as it directly limits the level of top-down control by natural enemies while increasing the level of food resources for the phytophagous species (Rand et al. 2014; Rusch et al. 2016). However, the optimal strategy for diversifying agricultural landscapes in order to maximize pest suppression remains poorly investigated and we lack clear guidelines on how to combine crop diversification with amount and spatial arrangement of semi-natural habitats to maximize natural pest control.

The key role of semi-natural habitats, such as grasslands, forests and hedgerows, on natural enemy abundances and biological pest control has long now been established (Bianchi et al. 2006; Veres et al. 2013; Rusch et al. 2016). These habitats are considered as sources of natural enemies in the landscape as they provide resources such as nectar, pollen as well as alternative preys or hosts and overwintering sites to natural enemies that are scarcer in crops (Bianchi et al. 2006; Veres et al. 2013). Crops can also offer key resource for natural enemies such as food and prey enabling populations to build up (Rand et al. 2006; Blitzer et al. 2012). Spillover of natural enemies through the crop-non-crop interface is mainly driven by spatio-temporal shifts in resource availability across the landscape (Rand et al. 2006; Schellhorn et al. 2015; Tscharntke et al. 2016; Thomine et al. 2020a, b). This suggests potential synergistic effects between maintaining semi-natural habitats and diversifying crop over space and time effect on biological control of pests in agricultural landscapes (Perovic et al. 2018). In addition to top-down processes shaping pest populations, landscape simplification may directly affect pest populations through bottom-up effects mediated by higher availability of crop resources or lower physical barrier to dispersion (Rusch et al. 2010; Han et al. 2022). However, the consequences of landscape-scale diversification through crop diversification in interaction with non-crop habitat management on natural enemy and pest communities remains poorly investigated (Thomine et al. 2021); but see Aguilera et al. 2020).

In this study we aim at assessing the relative and interactive effects of crop diversity, the proportion of semi-natural habitats and crop edge density on generalist predators and aphid abundances. First, we (H1) hypothesized that increasing crop diversity would enhance top-down control of pests through beneficial effects on natural enemies and increase bottom-up control resulting from resource dilution for pests. In addition, we also hypothesized (H2) an interactive effect between the amount of semi-natural habitats and crop diversity on natural enemies and pest abundance. We expected a lower effect size of crop diversity on natural enemies and pests in landscapes with higher amount of semi-natural habitats. This hypothesis relies on synergistic effects of having both semi-natural habitats and crop diversity if we assume that semi-natural habitats are sources of natural enemies able to colonize crop fields early in the season and that crop diversity promotes high resource availability for arthropods. Finally, we also hypothesized (H3) that crop configurational heterogeneity at the landscape scale would have a positive impact on predators with high dispersal capacity, this high dispersal capacity and high spillover capacity allowing to explore a complex environment with lower mean crop patch area or higher crop edge density. Increasing crop patch area would on the contrary increase aphid abundance due to resource concentration.

Materials and methods

Field sites

The field sites were located in the Heibei and Tianjin Province of China characterized by typical small-scale (in average 3 ha) multi-cropping fields (Pan et al. 2019). The study sites covered more than 600 km^2 in the main cotton producing regions of northern China (116°29′–117°37′E, 38°46′–39°36′N). Sites sampled the same year were separated by at least 4 km to avoid redundant effects between sites (Liu et al. 2018). The study design consisted of 47 cotton fields and 21 wheat fields (Fig. 1). The cotton fields were sampled during 4 years between 2013 and 2016 with 19 sites in 2013, 12 sites in 2014, 9 sites in 2015 and 7 sites in 2016. The wheat fields were sampled during 2 years between 2015 and 2016, with 14 fields in 2015 and 7 in 2016. Due to crop rotations, the sampled fields were different each year and the number of sampled sites differed because the farmers engaged in the experiment didn’t do exactly the same number of targeted crop fields every year.

Arthropods community assessment

In cotton crops, the sampling was done during the flower and boll stage from early to mid-August in 2013, late-July to early-August in 2014 and 2016 and mid to late-July in 2015, 3 times at 1 week interval. In wheat fields, the sampling was done during the flowering stage, from early to mid-August in 2013, from late July to early August in 2014, from mid to late July in 2015 and from late July to early August in 2016, 1 time each year (Liu et al. 2018). Because of these different plant phenology, the number of sampling rounds within a year differs between the two crops. In each sampled field, three quadrats of 300 m^2 (30 m x 10 m) were chosen in the center of the field to sample arthropods. The quadrats were at least 10 m from field edges in order to avoid border effects. In each quadrat, 50 plants randomly selected according to a Z sampling pattern were carefully inspected. Only the known dominant natural enemies and pests in each crop were recorded (Ali et al. 2018; Hulle et al. 2020; Yang et al. 2020). Therefore, on wheat crop, only ladybeetles and aphids were recorded whereas in cotton fields, lacewings, spiders, ladybeetles and aphids

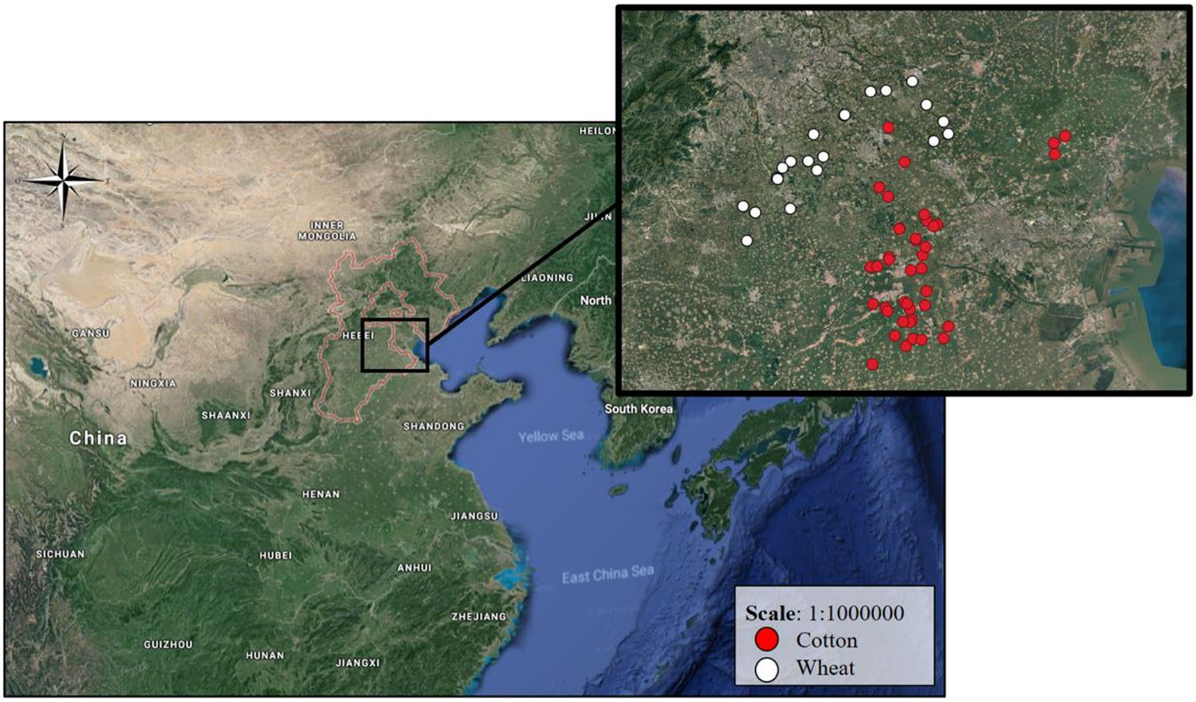

Fig. 1 Location of the sampling sites in China

were recorded (Liu et al. 2018). Both natural enemies (i.e. ladybirds, lacewings and spiders in cotton and ladybirds in wheat) and aphids were counted visually and identified to the family level.

Landscape analysis

Land-use types surrounding each study site were characterized at four different radii: 500 m, 1000 m, 1500 m and 2000 m. After analysing all the spatial extent, we only present here results from models with landscape variables calculated at the 500 m radii as models using explanatory variables at this spatial extent explained the largest proportion of variance in the response variables (Fig. S1). In our study, arable lands occupy around 80% of the landscapes. We considered a total of 18 different land-use types taking into account 15 cultivated crops (cotton, maize, peanut, soybean, rice, sweet potato, wheat, vegetables, fruit trees, pea, Chinese yam, oilseed rape, watermelon, sunflower, alfalfa), artificial land covers, semi-natural habitats (fallows, forests, greenbelts, shrub and grass pooled together) and water. The mapping was done with the QGis Desktop 3.4.1 software. For more details about the map construction, see Liu et al. (2018).

Three landscape variables were calculated at each radius to assess crop diversity, the proportion of semi-natural habitats as well as crop edge density. Crop diversity was calculated using the Shannon index applied to the several crop types. Crop edge density (ED) was calculated as the ratio between edge crop edge length and the total crop area (ED = edge length of a given crop species (m)/total crops area (ha)) (Martin et al. 2019). Crop edge density therefore reflects crop patchiness, and to which extent the landscape is divided into small patches of crops. All metrics were calculated with the Lecos Plugin on QGis (Jung 2016). All correlation matrixes are given in Fig. S2 for cotton and Fig. S3 for wheat and showed Pearson correlation value lower than 0.5.

Statistical analyses

The effects of crop diversity, crop edge density and the proportion of semi-natural habitats on abundance of natural enemies and aphids were examined using generalized linear mixed models [package lme4 (Bates et al. 2015)] with appropriate error distribution. Poisson, Negative Binomial or Gaussian error distribution was used for the number of arthropods, depending on the residual's distribution. All two-way interactions were considered in full models. We fitted separate models for cotton and wheat sites because the sampling design did not allow us to conduct all analyses in the same model (different time period and sites for each model). Sites was introduced in all models as a random effect to take into account repetitive samples in the same sites over time. In addition, the year effect was included in the models as a random factor (crossed with the site effect) for models explaining arthropod abundance in cotton. For models explaining abundance of arthropods sampled in wheat fields the year effect was not considered as a crossed random effect due to the too low number of levels within the year effect (ie, only 2 years) but we analyzed a potential bias of year on the residuals of this model and no problem was detected.

We then applied a multimodel inference approach to estimate the effects of our explanatory variables as well as all potential two-way interactions between them. Model averaging based on models with the lowest AICc (ΔAICc < 2) were kept for inference. Only results from the full averaging were kept for the interpretation of the results. All analyses were done using R 3.5.1. Multicollinearity between variables was investigated for each model with the variance inflation factor (VIF) and all the VIF were lower than 2. software (R Core team 2018). Residuals were inspected using the DHARMa package (Hartig 2018) and no issues were detected. The potential spatial autocorrelation in the residuals of the different models was examined using bubble plots and variograms. Multimodel inferences were done using the MuMIn package (Barton 2018) and the ggplot2 (Wikham 2016) and sjPlot (Lüdecke 2018) packages were used for data visualization.

Results

Cotton

The set of best models fitted to explain aphid abundance in cotton included the proportion of semi-natural habitats, crop edge density as well as crop diversity. The proportion of semi-natural habitats was the most important variable and had a significant positive effect on aphid abundance (Fig. 2, Table 1; estimate = 0.43, $P = 0.01$). All other variables had no significant effect on aphid abundance. None of the two-way interactions were retained in the set of best-fitting models. No significant effect of any landscape variables was detected by models explaining ladybird or spider abundances (Table 1). Lacewing abundance were found to be positively affected by crop edge density in the landscape (Fig. 3, Lines represent model predictions and grey area the 95% confidence intervals obtained by model averaging among the set of best-fitting models (Delta AICc < 2). 3; Table 1; estimate = 0.83, $P = 0.007$). Model with crop edge density was the only model selected in the set of best-fitting models (AICc < 2) (Table 1).

Wheat

The set of best models fitted to explain aphids abundance in wheat fields included the proportion of semi-natural habitats, crop edge density, crop diversity, the interactions between crop edge density and crop diversity, as well as the interactions between crop edge density with the proportion of semi-natural habitats. Among these variables, the proportion of semi-natural habitats was the most important variable with a significant positive effect on aphid abundance (Fig. 4, Table 1; estimate: 1.21, $P = 0.002$). All the other variables or their interactions selected in the set of best-fitting models had no significant effects on aphid abundance and had a lower relative importance (Table 1). We found no significant effect of any of the landscape variables nor their interactions selected in the set of best-fitting models to explain ladybirds abundance in wheat fields (Table 1).

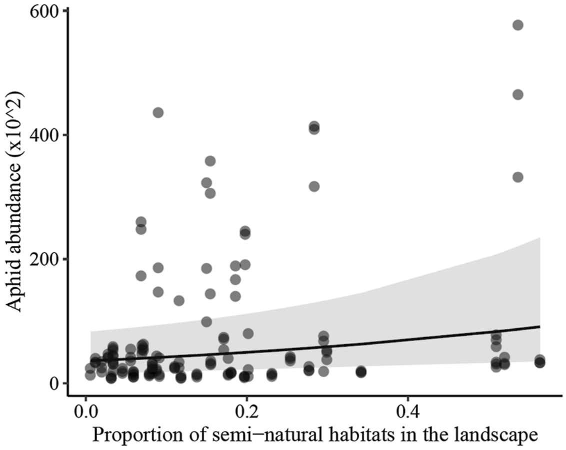

Fig. 2 Illustration of the effect of the proportion of semi-natural habitats in a 500 m radius on aphid abundance in cotton fields. Lines represent model predictions and grey area the 95% confidence intervals obtained by model averaging among the set of best-fitting models (Delta AICc < 2)

Discussion

The objective of our study was to assess the effect of landscape-scale diversification through crop and non-crop habitats on aphids and their natural enemies in agricultural landscapes. Contrary to our expectations, we did not find strong effects of crop diversity (alone or in interaction with the amount of semi-natural habitats) on abundance of aphids or natural enemies. Our results revealed a consistent positive effect of semi-natural habitats on aphid populations both in wheat and cotton while no effect was detected on natural enemies. However, crop edge density did not affect aphids but enhanced lacewing abundance suggesting that landscapes with low field-size are beneficial for such natural enemies.

We hypothesized that increasing crop compositional heterogeneity through crop diversity would increase the abundance of natural enemies by providing diversified food sources and consequently decrease the abundance of aphids through top-down control and bottom-up control resulting from the resource dilution for the pests (Rusch et al. 2010). Moreover, we expected an interactive effect between the amount of semi-natural habitats in the landscape and crop diversity on natural enemies due to complementation between habitats providing different resources across time. Our results do not confirm these hypotheses as we found that overall abundance of natural enemies did not benefit from higher crop diversity in the landscape (Shannon diversity of crops ranging from 0.27 to 1.32 which corresponds to a crop richness varying from 2 to 7 different crops) and that aphid populations responded positively to the amount of semi-natural habitats in the landscape. Such results indicate that there are no additive or synergistic effects between the amount of semi-natural habitats and crop diversity on aphid populations and their natural enemies.

Table 1 Statistical results of the multimodel inference applied to explain abundances of aphid, ladybird, lacewing and spider in cotton and wheat fields

Crop	Response variable	Explanatory variables	Estimate	Std.error	z-value	Pr(>|z|)		Variable importance
Cotton	Aphid abundance	Proportion of semi-natural habitats	0.43	0.186	2.34	0.01	*	1
		Crop edge density	– 0.03	0.11	0.27	0.78		0.23
		Crop diversity	0.02	0.1	0.24	0.8		0.22
	Ladybird abundance	Proportion of semi-natural habitats	0.14	0.27	0.53	0.59		0.36
		Crop edge density	– 0.03	0.15	0.21	0.83		0.18
	Lacewing abundance	Crop edge density	0.83	0.31	2.67	0.007	***	–
	Spider abundance	Proportion of semi-natural habitats	– 0.02	0.13	0.21	0.83		0.21
		Crop edge density	0.04	0.15	0.3	0.75		0.24
Wheat	Aphid abundance	Proportion of semi-natural habitats	1.21	0.39	2.99	0.002	***	1
		Crop edge density	0.15	0.31	0.47	0.63		0.77
		Crop diversity	0.24	0.38	0.61	0.53		0.77
		Crop edge density: crop diversity	1.64	1.08	1.5	0.13		0.77
		Crop edge density: proportion of semi-natural habitats	0.22	0.50	0.44	0.65		0.28
	Ladybird abundance	Proportion of semi-natural habitats	0.69	1.09	0.62	0.53		0.84
		Crop edge density	– 0.02	1.19	0.02	0.98		1
		Crop diversity	1.69	1.32	1.24	0.21		1
		Crop edge density: crop diversity	2.71	2.19	1.21	0.22		1
		Crop edge density: proportion of semi-natural habitats	0.02	2.20	0.01	0.99		0.63
		Crop diversity: proportion of semi-natural habitats	0.21	2.25	0.09	0.92		0.63

Model avergaing was applied on the full models considering the prorpotion of semi-natural habitats, crop edge density, and crop shannon diversity as well as all the two-way interactions as explanatory variables. Only the results of the "full" average were taken into consideration after performing the model averaging. Variable Importance correponds to the sum of model weights over all models including each explanatory variable

"–" corresponds to cases where only one best model was selected by the mutlimodel selection procedure

Factors marked with an asterisk have a significant effect on the variables to explain at $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

Contrary to our hypotheses, we found no effect of the proportion of semi-natural habitats on abundances of natural enemies and a significant positive effect on aphid abundance in cotton and wheat fields. The strong context-dependency and inconsistency in the effects of semi-natural habitats has been reported before (Holland et al. 2016; Karp et al. 2018) and can be due to the life-history traits of pests and their natural enemies (Martin et al. 2016, 2019), the type of semi-natural habitats considered and their quality in this rather vague classification (Badenhausser et al. 2020) or agricultural practices in the local fields or in the studied region that might have counteracted the potential beneficial effects of semi-natural habitats (Tscharntke et al. 2016; Etienne et al. 2022). The fact that semi-natural habitats may indeed be a greater source of pests than natural enemies appears credible given that the region studied in this paper, the Hebei Province, is a region with an intensive use of pesticides (Li et al. 2014). Additionally, many of the habitats characterized as semi-natural habitats in our study are quite low in plant diversity (forests of poplar mostly, personal obs.) and may be of low quality for natural enemies while acting as overwintering sites or sources of alternative food for pests (Delbac et al. 2020; Cornara et al. 2021). Future researches should now focus on fully understanding when and why semi-natural habitats can be a source of pest more than a source of natural enemies.

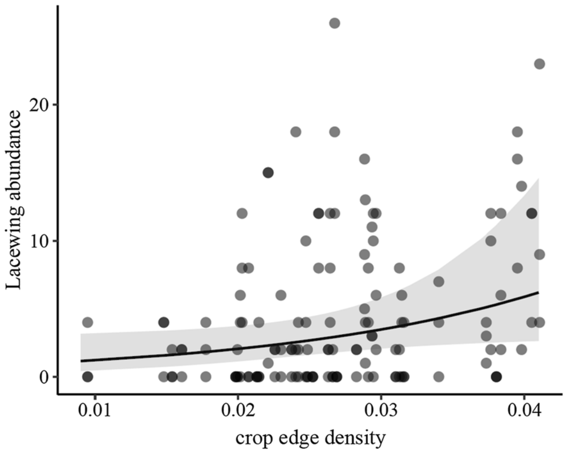

Fig. 3 Illustration of the effect of crop edge density in a 500 m radius on lacewing abundance in cotton fields. Lines represent model predictions and grey area the 95% confidence intervals obtained from the best-fitting model (only one model with Delta AICc < 2)

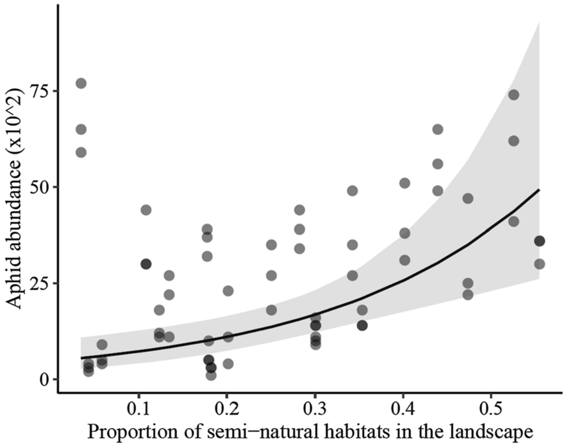

Fig. 4 Illustration of the effect of the proportion of semi-natural habitats in a 500 m radius on aphid abundance in wheat fields. Lines represent model predictions and grey area the 95% confidence intervals obtained by model averaging among the set of best-fitting models (Delta AICc < 2)

Contrary to our hypotheses, crop diversity had no impact on pest, nor on natural enemies. To date, only a few studies have addressed the question of landscape crop diversity impact on natural enemies and pests. While beneficial effect of crop diversity on pest control has been reported (Liu et al. 2016, 2018; Redlich et al. 2018; Kheirodin et al. 2020; Zhao et al. 2021) very few studies have quantified the relative and interactive effect of crop diversity in addition to the proportion of semi-natural habitats or crop configurational aspects (eg, crop edge density). Here again, farming practices and intensive use of pesticide in particular may have hinder our ability to detect any positive effect of crop diversity on natural enemies' population. In addition, we used a rather low range of variation in crop diversity (from 2 to 7 crop types per landscapes) and we used a taxonomic classification of crop types and not a functional one (ie, considering crop traits for instance). For instance, wheat and barley were counted as two different crops while these two species are very similar. Future studies should therefore use a functional classification of crop type in order to further investigate crop diversity effects on natural enemies (Fahrig et al. 2011).

In line with our hypothesis, we found that increasing crop configurational heterogeneity, i.e. crop edge density, enhanced lacewing abundance, an important functional groups for aphid biological control. This result suggests that increasing configurational heterogeneity through higher crop edge density (i.e., landscapes supporting more small patches of crops) benefit spillover across edges. This result also partly confirms our initial hypothesis about higher complementarity between food resources and higher spillover in landscapes with higher crop edge density. This result is in line with recent studies on natural enemies and pollinators finding a positive effect of landscape configuration mediated by mean crop patch area (Hass et al. 2018; Martin et al. 2019). However, our study also highlights that not all taxonomic group of natural enemies respond to crop configurational heterogeneity and strongly suggests that examining how life-history and species traits might provide explanations about these different responses of natural enemies to landscape context (Martin et al. 2019).

Conclusions

Our study investigated the effect of landscape-scale diversification through crop and non-crop habitats on aphids and their natural enemies in agricultural landscapes. Our study does not provide any evidence about a positive effect of crop diversification in the landscape on biological pest control while the proportion of semi-natural habitats benefitted aphid abundance in cotton and wheat fields. Interestingly, our study suggests that promoting agricultural landscapes with small field patches is beneficial for some natural enemies and not for pests. Future research should now examine more precisely the effect of the quality of semi-natural habitats and the major role of farming practices (eg, pesticide use) in the landscape to fully understand the inconsistent effects of semi-natural habitats on pests. In addition, expanding the analysis of crop diversity effects on biological pest control to other context and along larger range of crop diversity should help to draw robust conclusions about this management option in agricultural landscapes.

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Author contributions All authors contributed to the study conception and design. Data collection and analysis were performed by ET and AR. The first draft of the manuscript was written by ET and all authors contributed to the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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