

RESEARCH ARTICLE

The effects of wheat-pea mixed intercropping on biocontrol potential of generalist predators in a long-term experimental trial

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Abstract

Arthropod generalist predators can be effective natural control agents of pests and weeds in agroecosystems. Their activity and contribution to biocontrol may increase in response to more complex agricultural habitats. In this study, we investigated the effects of winter wheat-pea mixed intercropping on the biocontrol potential of generalist predators compared with the respective mono-crops. We evaluated not only the effects during the intercropping season but also the pre-crop values of the mixture for the subsequent barley crop. Furthermore, we evaluated the influence of different long-term soil organic carbon and fertility management regimes on activity and biocontrol potential of predators. Field work was conducted over two seasons in a field experiment located in Gembloux, Belgium. A set of proxies for ecosystem functions were measured using the Rapid Ecosystem Function Assessment approach. We measured attack and predation rates of sentinel prey and weed seeds artificially placed in the field. Furthermore, we assessed activity density of the main groups of generalist predators during the exposure of the baits. Our results showed that crop type affected activity and biocontrol potential of predators. Predation rates were much lower in wheat than pea and wheat-pea. The mixture wheat-pea had a positive effect on predator activity density compared to wheat mono-crop, while pea supported an intermediate activity of epigeal predators. In the second season of the field work, we found the highest biocontrol potential by predators in barley plots cultivated after pea. Finally, our results failed to find any differences in biocontrol potential of predators between long-term soil organic carbon and fertilisation management strategies. These results suggest that crop type has a major relevance in influencing the activity of generalist predators, and the mixed intercropping wheat-pea may represent a valid strategy to enhance biological pest control in comparison to wheat cultivated as mono-crop. Furthermore, we show that the cultivation of pea as mono-crop may have an important pre-crop value within the rotation increasing the provision of ecosystem services such as biocontrol.

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KEYWORDS

biological control, crop diversification, generalist predators, intercropping, plant–insect interactions

1 | INTRODUCTION

Conservation of natural enemies in agroecosystems is considered to be fundamental to improve biological pest regulation services (Barbosa, 2003; Landis, Wratten, & Gurr, 2000). This may be achieved via habitat manipulation and by changing the cultural practices that will favour the development and survival of natural enemies (Altieri & Letourneau, 1982; Andow, 1991; Landis et al., 2000). Potential mechanisms include improving the availability of alternative foods such as nectar and pollen, providing shelter or a moderated microclimate in which natural enemies may overwinter or seek refuge from factors such as predation or pesticides, and providing habitat in which alternative hosts or prey are present (Landis et al., 2000). Agroecological structures that may boost such mechanisms, can be found nearby as well as within crop fields (Gontijo, 2019). Non-crop habitats outside the fields like hedgerow, field margins and grasslands may be used by natural enemies for shelter, breeding or dispersal (Holland & Luff, 2000). Such structures offer alternative food sources, suitable microclimate as well as protection from intraguild predation and direct contact with sprayed pesticides (Finke & Denno, 2002; Tixier, Dagneaux, Mollot, Vinatier, & Duyck, 2013; Tschardtke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). For instance, many species of ground beetles at times depend on non-crop habitats (Wamser, Dauber, Birkhofer, & Wolters, 2011), and it is shown that those may serve as important hibernation sites for them (Geiger, Wäckers, & Bianchi, 2009). Non-cropped habitats have been therefore considered crucial to improve biodiversity in farmland and they have been often the main focus of many agroecological schemes (Butler, Vickery, & Norris, 2007). Nevertheless, to increase the biodiversity value of agricultural fields, within fields diversification strategies by mixing crops (i.e., intercropping), crop with non-crop plants (i.e., cover cropping), trees (i.e., agroforestry) or wildflower strips can be implemented (Altieri & Nicholls, 2004; Hatt, Lopes, Boeraeve, Chen, & Francis, 2017). In a meta-analysis, Letourneau et al. (2011) showed that spatial diversification of both habitats (crop and non-crop) at the local scale allows reducing insect pests and damages to crops while increasing natural enemies. Such agroecosystems that support trophic and structural resources both nearby and within crop fields are likely to maintain robust natural enemy communities, having a greater potential for pest suppression (Iuliano & Gratton, 2020).

Intercropping is one of the agroecological strategies that promotes plant species diversity within crop fields, likely creating more favourable conditions for natural enemy populations (Gontijo, 2019; Zhou et al., 2013). Intercropping is defined as the cultivation of at least two plant species simultaneously in the same field, and it is categorised into four principal types based on the spatial and temporal overlap of plant species: mixed intercropping, row intercropping, strip

intercropping and relay intercropping. The mixed intercropping studied in the present paper is defined as the cultivation of two or more crops mixed with no distinct row arrangement (Andrews & Kassam, 1976). Several ecological functions of crop-associated biodiversity in terms of pest biocontrol have been demonstrated in diverse intercropping systems (Hummel et al., 2009; Xie et al., 2012). Although numerous studies have documented a more efficient pest population control in wheat-based intercropping systems compared to monocultures (Lopes, Bodson, & Francis, 2015; Wang et al., 2009; Zhou et al., 2013), a review showed that while pests are generally reduced, their natural enemies are not necessarily enhanced (Lopes et al., 2016). In such systems, epigeal generalist predators [i.e., ground beetles (Coleoptera: Carabidae), spiders (Arachnida: Araneae), rove beetles (Coleoptera: Staphylinidae)] and their potential contribution to the biological pest control still remains little investigated. Field studies have shown that generalist predators can be effective control agents, reducing pest numbers and in some case preventing crop damage (reviewed by Symondson, Sunderland, & Greenstone, 2002). They can contribute to reduce the populations of herbivorous insects during the growing season in wheat (Lang, 2003), and complementary effects of epigeal predators and parasitoids appear to be an important factor limiting the growth of aphid populations in cereal fields (Schmidt et al., 2003).

In developing more sustainable cropping systems, crop management practices that aim to reduce chemical inputs are also of major importance. Soil fertility management, for instance, can influence insect pests, natural enemies and their relation in agroecosystems (Eyre, Sanderson, Shotton, & Leifert, 2009; Rowen, Tooker, & Blubaugh, 2019). Amendment with animal manures, cultivation of cover crops and green manures increase the availability of soil organic matter (Watson, Atkinson, Gosling, Jackson, & Rayns, 2002), which in turn, can influence the soil-based food web increasing the quantity of alternative prey, thereby fostering generalist predator activity (Aldebron, Jones, Snyder, & Blubaugh, 2020; Rowen et al., 2019). Birkhofer, Fließbach, Wise, and Scheu (2008); Birkhofer, Wise, and Scheu (2008) found that detrital availability after organic fertiliser application influenced predators' activity, and several studies reported positive responses of ground-beetle and spider activity to treatments involving application of compost or manure (Brown & Tworokski, 2004; Mathews, Bottrell, & Brown, 2002; Purvis & Curry, 1984). Nevertheless, Eyre et al. (2009) showed that effects of fertility management mainly depend on crop type and arthropod taxa considered.

Therefore, given the importance of generalist predators as a fundamental component of the natural enemy spectrum for conservation biological control, and considering the general lack of scientific evidence coming from field studies in intercropping systems, experimental studies are necessary to assess their potential contribution to pest

control under different crop arrangements and management practices. In the present study, we investigated the effects of mixed intercropping winter wheat-winter pea on activity density and biocontrol potential of epigeal generalist predators. We applied the Rapid Ecosystem Function Assessment (REFA, Meyer, Koch, & Weisser, 2015) approach to measure a set of ecosystem function proxies relevant for biological pest and weed control. To adequately quantify the contribution to biological control of those predator groups, it is necessary not only to measure their activity, but also to quantify their predation. To obtain this information, the use of sentinel prey artificially placed in the field represents a useful and widely implemented method (Lövei & Ferrante, 2017). Furthermore, we aimed to investigate the effects of the wheat-pea association during the intercropping season, and to evaluate the pre-crop values for biocontrol services of the mixture and the mono-crops on the subsequent crop (i.e., winter barley). Finally, we tested the effects of different long-term regimes of soil organic carbon management on the potential contribution to biocontrol of generalist predators. We expected (a) a positive impact of the mixed intercropping wheat-pea on activity density and biocontrol potential of generalist predators during the growing season, (b) a positive impact of the mixed intercropping in the subsequent crop, as a result of a pre-crop effect and (c) a positive response of generalist predators to increase of soil organic carbon and soil fertility obtained through practices such as inclusion of manure and cover crops.

2 | MATERIALS AND METHODS

2.1 | Description of the field experiment

This study was conducted at an experimental site located in Gembloux, Belgium (50°33'37"N, 4°43'35"E). The site hosts a long-term experiment under conventional management established in 1959 to investigate the influence of different strategies of organic matter management on crop yield, soil organic carbon content and soil physical properties. Soil organic carbon is managed through crop residues incorporation (crop residues are incorporated in the soil through ploughing at the end of each cropping season), farmyard organic manure (pig slurry and cow manure) application and cultivation of cover crops. The experimental design includes six treatments with six replicates for a total of 36 rectangular plots (72 m long and 10 m wide), in a randomised complete block design (Buysse, Roisin, & Aubinet, 2013).

For the purpose of the project, four treatments among the six established were considered: (T1) without organic matter incorporation or importation, (T2) with crop residues incorporation, one pig slurry application and one winter cover crop in the rotation, (T4) without any incorporation and one cow manure application in the rotation, (T6) with crop residues incorporation and one winter cover crop in the rotation (Table 1). T1 represents an extreme system without any organic matter incorporation or external input, while T4 is the reference system, because it represents the classic management in the studied region under conventional agriculture. From 1991 to

2017, a 3-year rotation (sugar beet, winter wheat and winter barley) was implemented on the experimental site. In 2018, exceptionally, maize was cultivated in the whole field. The application of animal manure to the soil and the cultivation of cover crops is carried out every 3 years, with their last implementation prior this experiment during the season 2017–2018, when the cover crop was a mix of oat, vetch and clover. Crop residues were restored to the soil at the end of each cropping season, with the exception of 2018, when T2 and T6 did not receive any additional crop residue (apart from stubble) because the whole maize plants were harvested as silage. In the season 2018–2019, an additional crop diversification strategy was implemented: mixed intercropping winter wheat-winter pea was cultivated to evaluate the performance of the crop mixture in comparison to the pure stands of both crops. In this context, each plot was divided in three parts for each crop type cultivated during this season, resulting in subplots, each 24 m long and 10 m wide. Each long-term soil organic carbon treatment was applied to each crop in six complete replicates; however, four spatial replicates were used to perform our observations. Winter wheat (variety "Apostel") and winter pea (variety "Fresnel") were sowed on November 8, 2018. Wheat was sown with 325 seed/m² in the pure stand and 200 seed/m² in the mixture, while pea was sown with 80 seed/m² in the pure stand and 50 seed/m² in the mixture. In the season 2019–2020, all the subplots were sown with winter barley (variety "LG Veronika") on October 3, 2019 (225 seed/m²), and harvested on July 13, 2020. The trial received mineral nitrogen fertilisation every year. The rate of fertilisation is based on residual mineral nitrogen quantified in the soil from T4 (usually showing the highest level of residual N when compared to the other treatments) at the end of winter. During the first year, mineral nitrogen fertilisation was applied twice to wheat pure stand (80 kg N ha⁻¹ + 75 kg N ha⁻¹) and crop mixture (35 kg N ha⁻¹ + 55 kg N ha⁻¹) in April and May, 2019. During the barley growing season mineral nitrogen fertilisation was applied twice, in March (100 kg N ha⁻¹) and April 2020 (60 kg N ha⁻¹). In 2018–2019 season, herbicide was used in wheat and pea pure stand, while in the mixed intercropping weeds were managed mechanically, due to the lack of herbicides registered for the crop mixture. No pesticides were used during this season. In 2019–2020 season, three herbicide, one insecticide and one fungicide application occurred during the trial. Finally, the entire field was ploughed every season after harvest at 25 cm depth.

2.2 | Data collection

Data were collected over two periods of 48 hr from 13 to May 16, 2019 and from 18 to May 21, 2020. Temperature and rainfall during the sampling were taken from a meteorological station located 10 km from the experimental site (Sombreffe, Belgium; CRA-W/Réseau Pameseb). In 2019, mean temperature during the sampling was 10.3°C, with a minimum of 3.8°C and maximum of 16.1°C. In 2020, mean temperature was 16.6°C, with a minimum of 6.7°C and a maximum of 26.5°C (hourly measurements). No rainfall was measured in both years during the collection of the data.

TABLE 1 Overview of the long-term soil organic carbon management treatments and the crops cultivated during the period 2018–2020

Year	Long-term soil organic carbon management treatments			
	T1	T2	T4	T6
2018	No organic matter importation or incorporation	Pig slurry + crop residues + winter cover crop	Cow manure	Crop residues + winter cover crop
2018–2019	Maize Wheat Barley	Maize Wheat Barley	Maize Wheat Barley	Maize Wheat Barley
2019–2020	Crops Wheat Pea Barley	Wheat-pea Pea Barley	Wheat-pea Pea Barley	Wheat-pea Pea Barley

The ecosystem function proxies were measured following the REFA approach described by Meyer et al. (2015). In particular, we assessed invertebrate predation measuring the attack rates on artificial caterpillars and the predation rates of standardised prey, and weed seed predation calculating the removal rates of weed seeds. Furthermore, activity density of the main groups of generalist predators was assessed using pitfall traps. The detailed description of the methods used to measure the proxies follows.

Invertebrate predation was assessed measuring the attack rates on artificial caterpillars made from green plasticine. Dummies were 25 mm long and 5 mm wide (Low, Sam, McArthur, Posa, & Hochuli, 2014). They were glued on small pads of wood and fixed in 90 mm-diameter polystyrene Petri dishes, previously sprayed with an aerosol glue and covered with fine sand. Each dish, containing two dummies, was buried flush to the soil surface. After exposure dummies were collected and checked for attack marks, which were attributed to either arthropod or vertebrate predators based on the collection of images from Low et al. (2014). Attack rates were calculated as a binary variable, based on the presence/absence of predation marks attributed to different groups in each single dummy.

Invertebrate predation was also assessed measuring the predation rates of insect baits (fly pupae, *Lucilia* sp.). Ten pupae were placed into Petri dishes glued on finely sieved sand and buried flush to the ground. Vertebrates were excluded from the insect baits using a metal netting with 1.2 cm² mesh. Predation was calculated for each sampling point as the proportion of removed baits. Partially eaten pupae were considered predated.

To assess seed predation, the removal rates of different species of weed seeds were measured. Ten seeds of each of the weed species *Sinapis arvensis* L., *Capsella bursa-pastoris* (L.) Medik., and *Anthriscus sylvestris* (L.) Hoffm. were placed into Petri dishes on the surface of 80 grit sandpaper lightly sprayed with an aerosol glue and exposed on the ground (Westerman, Hofman, Vet, & van der Werf, 2003). For this assessment, vertebrates were excluded from seed cards using a metal netting with 1.2 cm² mesh. Predation rates were calculated for each seed species separately as the proportion of removed seeds in each sampling point.

At each sampling point, one pitfall trap (120 ml jars, 7 cm high with a diameter at the mouth of 5 cm; i.e., three traps per subplot) was used to measure the activity density of epigeal arthropods. Pitfall traps were buried in the ground flush with the soil surface and part-filled (one-third full) with saturated salt (NaCl) solution. Invertebrate specimens from each trap were preserved in alcohol and the predators collected were counted and classified into different taxa (ground beetles, spiders, rove beetles). Within subplots, activity density data from different sampling points were aggregated.

In both years, four replicates for each combination of four long-term organic carbon treatments (T1, T2, T4, T6) and three crop (and pre-crop) treatments (wheat, pea, wheat-pea) were sampled, for a total of 48 subplots. In each subplot, three sampling points were installed. Each sampling point had one item (Petri dish or pitfall trap) at every corner of a 50 cm × 50 cm square for the assessment of the four different ecosystem function proxies. In relation to the spatial

proximity of the exposed items it may need to be considered, that multiple encounters of more than one item by the same individual may occur, as generalist predators also show an opportunistic feeding behaviour catching prey based on the relative encounter rates.

2.3 | Statistical analysis

Statistical analysis was performed with R (R Core Team, 2018). To test the effects of crop type (wheat, pea, wheat-pea), long-term soil organic carbon treatment and year we fitted individual generalised linear mixed models (Schall, 1991) with the package “glmmTMB” (Brooks et al., 2017) for each proxy measured. Models always included crop type, long-term organic carbon treatment and year as explanatory variables. The interaction term crop type \times year was included to test the effects of different crops in 2019 and their pre-crop effects in 2020. The interaction term crop type \times treatment was also included and dropped from the final models if not significant ($p > .05$, Wald Chi-squared test). For predation and attack rates (proportional and binary data) models were fitted using a Binomial distribution with a logit link function. A Negative Binomial distribution with a log link function was used in order to account for overdispersion in the count data. Models included random effects in a nested structure (block:plot:subplot) to account for any block-, plot- and subplot-level random deviation. An additional random effect for sampling point was included for models of the predation data on insect prey and dummy caterpillars. The Wald Chi-squared test through the “ANOVA” function from the “car” package (Fox & Weisberg, 2011) was used to test if the explanatory variables were significant. The type III Chi-squared test was used in the models with significant ($p < .05$, Wald Chi-squared test) interaction terms. When significant ($p < .05$, Type III Chi-squared test) effects were present, the Estimated Marginal Means (EMMs) were calculated and post hoc comparisons of biological interest were performed using the “emmeans” package (Lenth, 2018).

To assess whether predation rates could be linked to ground-dwelling predators' activity density, we calculated separate generalised linear mixed models relating the predation rates calculated on insect prey to the activity density of predators. The models were fitted using the package “glmmTMB” including the same random error intercept structure as the predation model in the main analysis. A binomial distribution with a logit link function was used, and activity density was log transformed prior to the analysis. Significance levels of the explanatory variables were obtained using the “ANOVA” function from the package “car.”

3 | RESULTS

From 576 artificial caterpillars exposed in total, 99.6% of these could be retrieved from the field and assessed for attack marks. In 2019, 12.8% of the dummies showed attack marks, 43.2% of these were attacked by arthropods, and 62.1% by vertebrates. In 2020, 9.4% of the dummies were attacked, with 74.0% of them showing arthropod

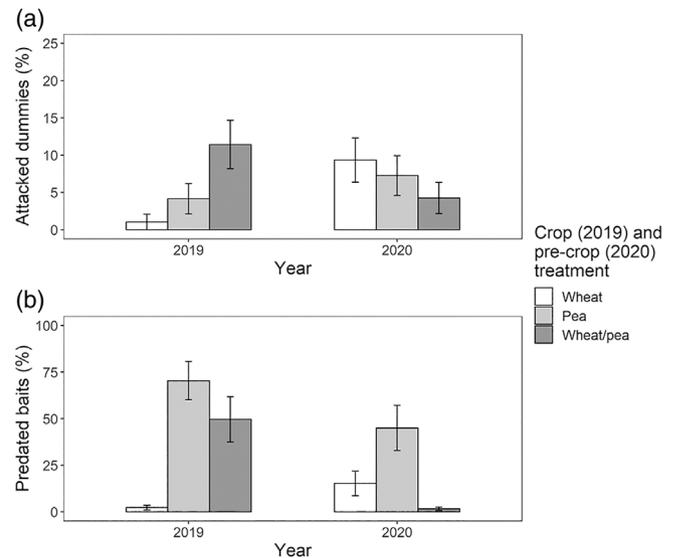


FIGURE 1 Arthropod attack rates on artificial caterpillars (a), and arthropod predation rates on insect baits (b) in 2019 and 2020 (estimated marginal mean \pm SE). For 2020, wheat, pea and wheat-pea represent the respective pre-crops cultivated in 2019.

attack marks, and 25.9% vertebrate attack marks. Invertebrate marks were caused by biting arthropods while vertebrate marks were caused by rodents. On average, arthropod attack rate on dummies was 5.0%. Arthropod predation rate on insect baits could be assessed in almost the totality of the exposed baits (99.6%), and it was on average 40.6% in 2019 and 28.3% in 2020, calculated as mean predation per Petri dish. Regarding the predation of weed seeds, *C. bursa-pastoris* was the most predated species compared to *S. arvensis* and *A. sylvestris*. Regardless of the species, predation rates were on average higher in 2019 (3.6%) than in 2020 (1.1%) (mean predation per Petri dish).

During the two sampling periods in 2019 and 2020, we sampled 1,629 predators. The predator community was dominated by ground beetles (43.5%), followed by spiders (42.6%), and rove beetles (13.9%). In 2019, 344 ground beetles (38.9%) and 361 spiders (40.8%) were collected, and rove beetles (180) accounted for 20.3% of the total of predators (885). In 2020, the total number of individuals collected was lower (744), with 364 ground beetles, 333 spiders and 47 rove beetles collected (Table S1).

3.1 | Attack and predation rates of predators

During the 2019 intercropping season, attack rates on artificial caterpillars were affected by the crop type. In particular, arthropod attack rates were higher in wheat-pea ($11.4 \pm 3.2\%$) compared to wheat pure stand ($1.0 \pm 1.0\%$) and pea ($4.1 \pm 2.0\%$) (Figure 1a), but only between the mixture and wheat this difference was significant ($p = .01$, Type III Chi-squared test). Including the vertebrate attack on dummies weakened the positive effect of the mixed intercropping, with no significant ($p > .05$, Wald Chi-squared test) effect of crop type on the total attack rates (Table S2).

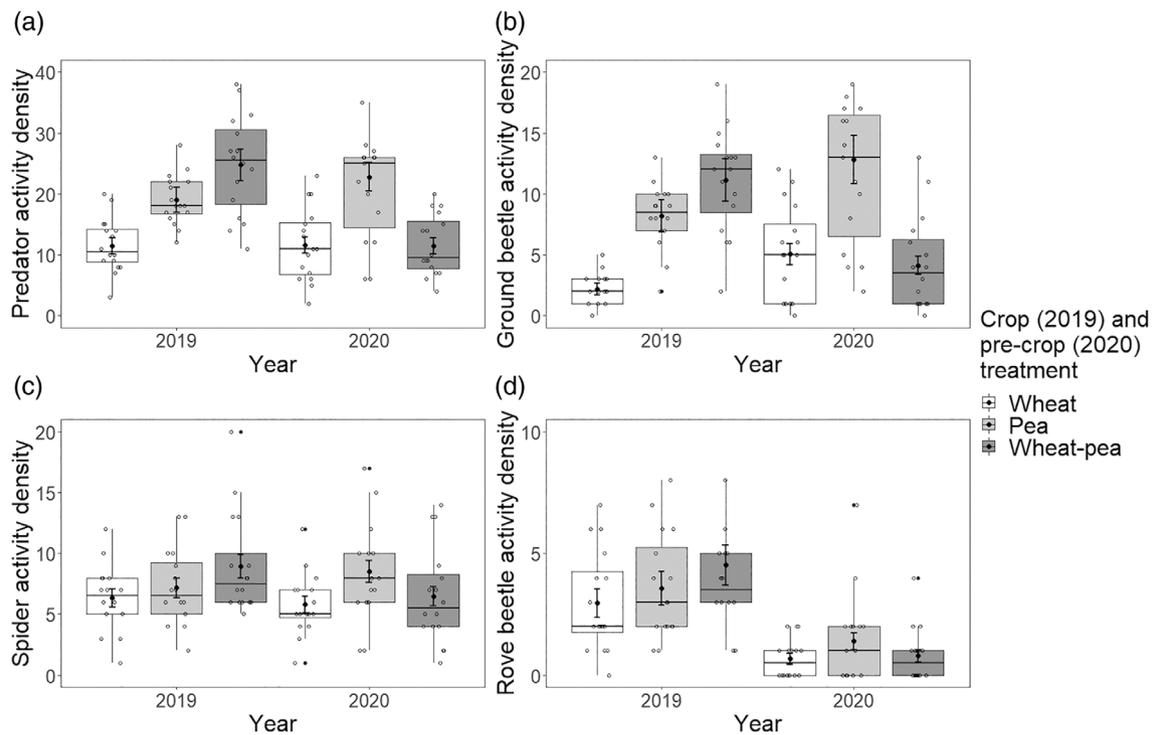


FIGURE 2 Activity density of all predators (a), ground beetles (b), spiders (c), and rove beetles (d) in 2019 and 2020. Boxplots with observations as jitter (grey) and standard error of the estimated marginal mean (black bars). For 2020, wheat, pea and wheat-pea represent the respective pre-crops cultivated in 2019.

Crop type affected the arthropod predation rates on insect baits (Table S2). Predation rates were significantly higher in pea ($70.4 \pm 10.2\%$, $p < .001$, Type III Chi-squared test) and wheat-pea ($49.6 \pm 12.1\%$, $p < .001$, Type III Chi-squared test) compared to wheat ($2.2 \pm 1.2\%$; Figure 1b).

In 2020, no significant ($p > .05$, Type III Chi-squared test) differences between barley grown after pea, wheat and wheat-pea were observed in terms of arthropod attack rates on artificial caterpillars. Attack rates were $7.2 \pm 2.6\%$ after pea, $9.3 \pm 2.9\%$ after wheat, and $4.2 \pm 2.0\%$ after the mixture (Figure 1a). On the contrary, predation rates on insect baits were strongly affected by the crop cultivated in the previous season (Figure 1b). Higher predation rates were measured in barley after pea ($44.9 \pm 12.1\%$), compared to barley after wheat ($15.2 \pm 6.5\%$), and after wheat-pea ($1.6 \pm 0.9\%$), with a significant difference between all three pre-crop treatments ($p < .001$, Type III Chi-squared test).

Predation rates on weed seeds were generally very low and were not affected by the crop type for any of the three seed species (Table S2). For *A. sylvestris* and *S. arvensis* predation rates around 1% were measured in both years. For *C. bursa-pastoris* predation rates were significantly ($p < .001$, Wald Chi-squared test) higher in 2019 ($7.4 \pm 0.6\%$) compared to 2020 ($1.6 \pm 0.3\%$), regardless of the crop type.

Long-term strategies of soil organic carbon management (i.e., treatments T1, T2, T4 and T6) had no significant ($p > .05$, Wald Chi-squared test) effects on the attack and predation rates of generalist predators (Table S4).

3.2 | Activity density of predators

The wheat-pea mixed intercropping had positive effects on the activity density of generalist predators during the REFA in 2019, although the respective species groups responded differently to crop type (Table S3). The activity density of all generalist predators was higher in wheat-pea (24.7 ± 2.5), followed by pure stand of pea (19.0 ± 2.0) and pure stand of wheat (11.4 ± 1.3 ; Figure 2a), with significant differences between wheat-pea and wheat and between pea and wheat ($p < .001$, Type III Chi-squared test). For ground beetles, activity density was significantly higher in the mixture (11.1 ± 1.7 , $p < .001$, Type III Chi-squared test) and pea (8.1 ± 1.3 , $p < .001$, Type III Chi-squared test) compared with wheat (2.1 ± 0.4 ; Figure 2b). Activity density of spiders was significantly higher in wheat-pea compared with wheat (8.9 ± 0.9 vs. 6.3 ± 0.7 , $p = .03$, Wald Chi-squared test; Figure 2c), while it was intermediate in pea (7.1 ± 0.8) with no significant ($p > .05$, Wald Chi-squared test) differences with the other two crop types. The activity density of rove beetles was higher in wheat-pea (4.5 ± 0.8) than pea (3.5 ± 0.6) and wheat (2.9 ± 0.5), but without any significant ($p > .05$, Wald Chi-squared test) differences between crop types (Figure 2d).

In 2020, the activity density of predators was significantly higher in barley grown after pea (22.7 ± 2.3) compared with barley after wheat (11.5 ± 1.3 , $p < .001$, Type III Chi-squared test) and after wheat-pea (11.4 ± 1.3 , $p < .001$, Type III Chi-squared test; Figure 2a). The activity density of ground beetles had a similar pattern (Figure 2b), with significant differences between the pea treatment

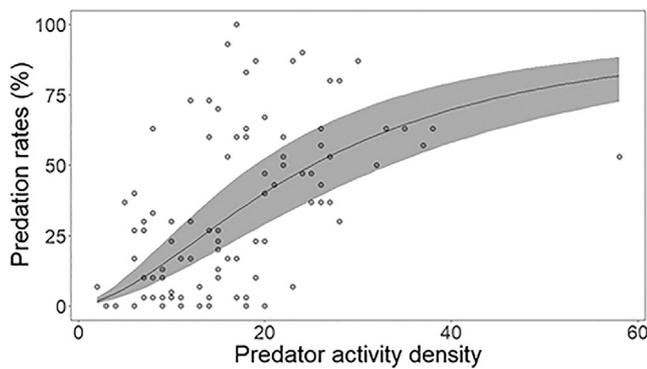


FIGURE 3 Relationship between predation rates of insect baits and predator activity density. Model predictions with 95% confidence interval.

(12.8 ± 1.9) and both wheat (5.0 ± 0.8 , $p < .001$, Type III Chi-squared test) and wheat-pea (4.1 ± 0.7 , $p < .001$, Type III Chi-squared test). For spiders, activity density was significantly higher in barley after pea (8.5 ± 0.9 , $p = .02$, Wald Chi-squared test) than after wheat (5.7 ± 0.7). In barley after wheat-pea the activity density was intermediate (6.4 ± 0.7 , Figure 2c). Finally, the activity density of rove beetles was not significantly ($p > .05$, Wald Chi-squared test) affected by the crop cultivated the previous season, with the highest and the lowest values observed after pea (1.3 ± 0.3) and after wheat (0.6 ± 0.2), respectively (Figure 2d).

Soil organic carbon treatments had no significant ($p > .05$, Wald Chi-squared test) effects on the activity density of generalist predators for any of the taxa investigated (Table S3). The lowest activity density of predators was found in T6 (14.6 ± 1.3), and the highest in T2 (17.6 ± 1.5) (Table S4).

3.3 | Relationship between predation rates and predator activity density

We found a positive effect of predator activity density on the predation rates of insect prey. Considering both years of observations and all predator taxa together, an increased number of predators collected corresponded to higher predation rates (Figure 3). The same results were found when analysing the effects of the activity density of ground beetles and spiders separately. Model results are summarised in Table S5.

4 | DISCUSSION

In our 2-year study we aimed to evaluate the effects of mixed intercropping winter wheat-winter pea on the potential contribution to biological pest control by predatory epigeal arthropods compared with the pure stands of the two crops. We tested whether the mixed intercropping has positive effects on predators' biocontrol potential during the intercropping season, and also whether these effects may be

carried over in whole or in part to the subsequent crop in the following season. Finally, we evaluated the effects of different long-term regimes of soil organic carbon and fertility management on the biocontrol potential of generalist predators.

4.1 | Effects of mixed intercropping

During the intercropping season (2019), we found that predators' activity density responded positively to the mixed intercropping. In terms of attack and predation rates, for both caterpillar dummies and insect baits, we found the lowest arthropod attack and predation rates in wheat pure stand. Concerning predation rates on weed seeds, no effects of crop type were observed and seed predation rates were overall particularly low compared to studies with similar method and exposure time (O'Rourke, Heggenstaller, Liebman, & Rice, 2006; Schumacher, Dieterich, & Gerhards, 2020). Seeds of *C. bursa-pastoris* were more predated, which can be attributed to the increased pool of predators that can feed on seeds of smaller dimension (Saska, Koprlová, Martinková, & Honěk, 2014). Generalist predators, especially ground beetles, are important seed predators and they may have a regulatory effect on the soil seedbank (Honek, Martinkova, & Jarosik, 2003). However, inconsistency of results between field studies seems to limit the estimation of this ecosystem service. The outcomes of these studies appear to be strongly influenced by the availability of alternative prey, the weed species composition and the spatio-temporal interactions between predator species (Bohan, Boursault, Brooks, & Petit, 2011; Carbonne et al., 2020). More specifically, in situations where alternative prey are abundant, this can have negative effects on seed predation, as omnivorous ground beetles may prefer alternative prey to weed seeds (Carbonne et al., 2020). A further classification of ground beetle species and their diet preferences would be necessary to evaluate those co-variations.

In general, more predators were collected in wheat-pea mixture than in pure stand of both crops, but with remarkable differences between predator groups. In particular, both ground beetles and spiders were found in higher number in wheat-pea than in wheat, while rove beetles were not affected at all by the crop type. Activity density of predators in pea was intermediate, and it was never statistically different from mixed intercropping. Langellotto and Denno (2004) have shown that modifications enhancing habitat structural complexity may not have the same effect on different guilds of beneficial arthropods. Our results are in line with the assumption that a more complex agricultural habitat may provide diverse benefits for natural enemies enhancing their presence and activity. Mechanisms that may drive such positive effects on different taxa may benefit from structurally rich crops that create a shady and dense canopy and hence provide more favourable microhabitat conditions (Carcamo & Spence, 1994; O'Rourke, Liebman, & Rice, 2008). Furthermore, such habitats may provide alternative prey or food resources, refuges and structural support (Birkhofer, Scheu, & Wise, 2007; Finke & Denno, 2002). All of these factors not only attract natural enemies, but also decrease the need to move in search of more suitable conditions (Sunderland &

Samu, 2000). For generalist predators, intraguild predation and cannibalism represent a common mortality source (Rosenheim, Kaya, Ehler, Marois, & Jaffee, 1995; Wagner & Wise, 1996), and there are evidences that refuges may offer important protection sites explaining their accumulation in complex-structured habitats (Finke & Denno, 2002; Langellotto & Denno, 2004). Complex habitats may be also important as structural support for web-building spiders, improving sites for web attachment (McNett & Rypstra, 2000).

Increased availability of alternative food resources may also explain why different guilds of natural enemies accumulate in complex structured habitats. Generalist predators, given their polyphagous feeding habits, may be able to sustain their population on alternative prey (Toft, 2005), especially on the early stage of the season (Harwood, Sunderland, & Symondson, 2001). The higher activity of spiders found in the mixed intercropping system in our study is in line with the results of Sunderland and Samu (2000), who found that their abundance increased when vegetation diversity and detrital structure were enhanced. Similarly, ground beetles appear to be positively affected by greater access to alternative prey resources in complex habitats (Zangger, Lys, & Nentwig, 1994). For many ground beetles that are omnivorous or herbivorous, also the presence of enhanced vegetational resources (e.g., weed seeds) in such habitats may represent an additional source of food (Lys, Zimmermann, & Nentwig, 1994). However, the effects of different resources on individual species of ground beetles may be very different, as it has been shown in previous studies (Eyre, Luff, Atlihan, & Leifert, 2012; Jowett et al., 2021).

In addition, also agronomic practices used to control weeds may directly and indirectly affect density of beneficial ground dwelling arthropods. In our field, while in pea and wheat weed management was performed chemically, in the mixed intercropping it was performed mechanically. Weed harrowing may cause a major disturbance for generalist predators, although it has been demonstrated that they are able to quickly recolonise the field, counteracting the negative effects of the mechanical operations (Thorbeck & Bilde, 2004). The small sub-plot sizes of this trial may have favoured their rapid recolonization. Negative effects due to the weed removal and deterioration of the habitat may appear later in the season (Thorbeck & Bilde, 2004). The use of herbicides can affect the habitat quality for arthropods, altering the occurrence of arable weeds and thus the resulting above-ground habitat. These indirect effects of herbicide application are considered to be more important than the direct effects for epigeal predators (Brust, 1990; Miñarro & Dapena, 2003; Pekár, 2012). However, a more specific study would be necessary to distinguish the effects caused by different weed management strategies.

4.2 | Pre-crop effects of mixed intercropping

In 2020, we found a clear positive effect of pea cultivated as previous crop on the activity density of generalist predators in the current crop (barley), although those effects were not the same for all predator groups. Statistically significant differences were found for ground

beetles and spiders, while rove beetles did not show any response to different previous crop treatments. The arthropod attack rates on artificial caterpillars did not differ between previous crop treatments, on the contrary, differences were observed for insect baits with the highest predation rates found in barley after pea. Meyer, Ott, Götze, Koch, and Scherber (2019) demonstrated that generalist predators may be influenced by a previous crop cultivated up to 2 years before the investigations, as a result of a crop “memory effect.” In our experiment, barley cultivated after pea had a substantially higher above-ground biomass than barley cultivated after wheat and wheat-pea at the end of the growing season. The difference in aboveground biomass, which was observed also during our measurements (Figure S1), can be explained by the higher availability of nitrogen in the soil after the pea cultivation. Measurements carried out post-harvest in 2019 indicated that the level of nitrogen in the soil was much higher in pure pea plots (Hellou & Jensen, 2020). Different vigour and quality of the plants in these plots may have created more favourable conditions in terms of habitat and microclimate for epigeal predators. Agronomic pre-crop benefits of grain legumes to cropping systems, including yield benefits, reductions in nitrogen fertiliser demand, and improvements of soil structure, are well known (Köpke & Nemecek, 2010; Preissel, Reckling, Schläfke, & Zander, 2015; Stagnari, Maggio, Galieni, & Pisante, 2017). Improved soil and plant quality may favour the presence of herbivores such as aphids, hence fostering the activity of natural enemies (Ekschmitt, Wolters, & Weber, 1997). Thus, it is possible that the capacity of legumes to influence characteristics of the following crop may indirectly affect its ecological function contributing to the conservation of those natural enemies capable to influence biological pest control services.

4.3 | Effects of organic carbon management treatments

In contrast with our third hypothesis, we did not find any differences for any of the variables investigated caused by different regimes of organic carbon and soil fertility management. Neither activity density of predators nor their predation rates showed statistically significant responses to soil organic carbon long-term treatments. There is evidence that crop type has greater influence on invertebrate activity than fertility management schemes (Eyre et al., 2012; Weibull & Östman, 2003). Nevertheless, the addition of organic fertiliser such as green manure and animal manure, may affect the soil decomposer community, increasing the availability of other alternative prey (Rowen et al., 2019). Collembola, for instance, which represent an important component of generalist predators' diet (Bilde, Axelsen, & Toft, 2000), may lead to an increase in epigeal predators if present in high densities (Birkhofer, Wise, & Scheu, 2008). In the present experiment, the annual ploughing of the plots had reduced the amount of residue in the top soil, most likely restricting the effects on alternative epigeal prey organisms. It is also important to note that in our field, the application of organic manure occurs once every 3 years on top of the conventional management, which may represent too low

frequency in order to observe the expected differences, especially when the measurements are not carried out during the same growing season. Hence, further investigations of the effects of long-term organic carbon management schemes on the decomposer community may be useful in order to determine if a cascade effect in the above-ground herbivore food web could be expected. Furthermore, it has been shown that differences in soil organic carbon content may be able to influence generalist predators and biocontrol potential when integrated within an organic crop management scheme (Aldebron et al., 2020). Our field experiment is run under conventional management, and both herbicides and pesticides are applied during the growing seasons, likely hampering possible benefits for natural enemies provided by the organic fertilisation.

5 | CONCLUSION

In conclusion, in our study we could link the predation rates measured with sentinel prey to the activity density of the main predator groups in the field. Previous studies found the same positive relationship (Boetzel, Konle, & Krauss, 2020; Menalled, Lee, & Landis, 1999), while other studies did not find these activity density effects (e.g., Rusch, Birkhofer, Bommarco, Smith, & Ekblom, 2015). However, differences in the predator species assemblages could determine inconsistent results between studies conducted in different geographical areas and habitats. Our results show that, under the situation studied here, predation rates increase at higher activity density of generalist predators. Thus, according to our first hypothesis, mixed intercropping wheat and pea may represent a valid strategy to favour generalist predators and support conservation biological control compared to wheat cultivated as mono-crop. Furthermore, we show that the cultivation of pea may have an important ecological pre-crop value within the rotation improving relevant biodiversity-related ecosystem services such as biological pest control. It is generally accepted that legumes may be important to improve biodiversity in agroecosystems (Everwand, Cass, Dauber, Williams, & Stout, 2017), therefore, further studies will be necessary in order to determine if the relevant potential contribution to biological control by generalist predators found in this experimental study may occur in commercial settings, thus being effective at reducing pest densities and preventing plant damage.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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