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RESEARCH ARTICLE

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Organic fertilisation enhances generalist predators and suppresses aphid growth in the absence of specialist predators

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Abstract

1. Biological control by natural enemies is a valuable ecosystem service. The predator community in a crop field is a combination of predators dwelling in the field and those moving into it from the surrounding landscape. The former is mainly affected by field management, the latter more by the composition of the surrounding landscape. Yet, separate and combined effects of local and landscape management on pest suppression have seldom been investigated.
2. We set-up mesocosms within an existing long-term agricultural field experiment to investigate the effects of local management of organic manure or inorganic mineral fertilisation, and simulated the spillover from the surrounding landscape of different predator types: no predators, generalist predators (wolf spiders) and specialist predators (ladybirds). We examined whether aphid density was driven by top-down or bottom-up processes under different fertilisation treatments, and how the magnitude of pest suppression was affected by predator community composition.
3. We found positive synergistic effects between manure fertilisation and predator spillover on the suppression of aphid growth. Top-down suppression of aphids was more effective under manure fertilisation and in presence of specialist predators (ladybirds). Bottom-up effects on the plant biomass growth dominated in inorganically fertilised plots.
4. Organic and inorganic fertilisation gave the same yield, but through different mechanisms. The abundance of locally emerging predators in the manure treatment increased top-down pest suppression yielding plant biomass levels comparable with inorganically fertilised plants, being the latter driven by bottom-up effects.
5. *Synthesis and applications*. Organic fertilisation enhanced local emergence of predators increasing top-down pest suppression. In contrast, local predator communities were unable to suppress aphid populations in inorganic and no fertilisation treatments. Here, predator inflow from outside the crop field was essential for lowering aphid population growth. Managing landscapes to promote

mobile predators emerges as particularly important for crop fields without manure amendments. We advise the active promotion of both local predators in the crop field and mobile predators in the landscape to secure the conservation of biological insect pest suppression.

KEYWORDS
agroecosystems, carabid beetles, ecosystem services, ladybird beetles, manure, pest control, soil management

1 | INTRODUCTION

Pest suppression by predatory arthropods, such as ground carabid beetles and spiders, provides a crucial basis for crop protection (Chaplin-Kramer & Kremen, 2012). Semi-natural habitats in the landscape enhance predator communities in crop fields (Hendrickx et al., 2007; Holland et al., 2017), but the variability around the trend is large (Karp et al., 2018). Divergences could arise because of differences in predator's habitat preference and dispersal abilities (Meyer et al., 2019; Schalkwyk et al., 2020). Additionally, there is increasing evidence that soil management in the crop field can determine predator community composition (Eyre et al., 2012; Hanson et al., 2016; Marrec et al., 2015; Palmu et al., 2014). Managing soils to increase soil carbon and biodiversity benefits predator biomass (Riggi et al., 2017; Tamburini et al., 2016), but this needs confirmation for other management practices such as fertilisation. Furthermore, interactive effects of local and landscape factors on predator communities have rarely been investigated (Concepción et al., 2012; Zhao et al., 2014).

The use of fertilisers is currently ubiquitous. Fertiliser type can affect natural pest suppression (Riggi & Bommarco, 2019). Organic fertilisers can increase soil diversity of several taxa (Liu et al., 2016; Lori et al., 2017) including potential pest regulators such as carabids (Birkhofer, Bezemer, et al., 2008; Birkhofer, Fließbach, et al., 2008; Holland & Luff, 2000; Idinger et al., 1996). By providing resources to the detritus-based soil community, manure fertilisation provides alternative food to generalist predators, increasing their abundance and, thus, enforcing pest suppression (Leroux & Loreau, 2008), but it could also divert predators from eating the crop pest (Jaworski et al., 2013). Inorganic mineral fertilisers, in contrast, provide more directly accessible nutrients to the plant increasing plant nitrogen content, biomass and which can boost the herbivore growth rate (De Bruyn et al., 2002; Herencia et al., 2007; Mäder et al., 2002). Despite these indications of significant fertiliser effects on natural pest suppression, most research on this topic lacks the connection between above-ground communities and fertilisation management. Few comprehensive examinations have found that manure fertilisation boosted top-down predator suppression of aphids in barley fields (Birkhofer, Bezemer, et al., 2008; Riggi & Bommarco, 2019) likely caused by manure subsidising the detrital compartment and boosting generalist predators early in the season.

Carabids, spiders and ladybirds are common predators that often immigrate into crop fields from nearby semi-natural habitats. However, several carabid species also overwinter within crop fields and their populations are known to be affected by crop type and management (Hanson et al., 2016; Holland et al., 2005; Palmu et al., 2014). Thus, predator communities in crop fields are assembled by locally emerging and seasonally immigrating predators, making it difficult to separate local and landscape effects on pest suppression, and their interaction (Concepción et al., 2012). The presence of more soil prey in organically fertilised fields could attract more predators from the surrounding landscape. However, if the enrichment of the soil fauna drives a switch in the predator diet from pest to soil fauna or increases intra-guild predation, then we might see interactions between organic fertilisation and the composition of the predator community which could reduce pest suppression (Roubinet et al., 2018).

We used 2 × 2 × 2 m mesocosms in an oat field, to examine interactive effects on natural pest suppression between experimentally simulated combinations of predator guilds (generalists and specialists) moving to the crop field from the surrounding landscape, and three fertilisation treatments (no fertilisation, organic manure and inorganic mineral fertilisation). We explored whether fertilisation boosted local predator fauna, and how this impacted pest suppression when combined with a spillover of predators from the surrounding landscape of either specialist (ladybirds) and/or generalist predators (spiders). We aimed to investigate (a) the combined effects of fertilisation and predator immigration on aphid population suppression; (b) whether the strength of top-down and bottom-up suppression of aphids is mainly regulated by the fertilisation type or by the predator immigration; and, finally, (c) whether yield is affected by interactions between fertilisation and the immigrating predator community. We expected manure fertilisation to boost local soil fauna, benefitting local predators and translating into more efficient suppression of aphid densities. We also expected positive interactions between manure fertilisation and the inflow of predators from the surrounding landscape in suppressing aphid populations and in determining yield, by an increased top-down suppression.

2 | MATERIALS AND METHODS

2.1 | Fertilisation experiment

To quantify the long-term effects of fertilisation treatments, we took advantage of an agricultural fertilisation experiment established in 1996 in the region of Västergötland, Sweden (58°20′38.0″N 13°06′13.5″E). The long-term field experiment (total size 8,200 m^2) was divided into four blocks. In each block, nine fertilisation treatments, including a no fertilisation control, had been applied every second year in the same plots, that is, block was the replication (see Appendix S1 in Supporting Information for more information about soil properties). The field has been sown with cereals every year since 1996. We carried out a mesocosm experiment in 2018, in which the entire experiment was sown with spring oats. We selected three out of the nine fertilisation treatments: manure (organic fertiliser), calcium nitrate (inorganic fertiliser) and a no fertilisation treatment (control; Appendix S1 in Supporting Information). In each experimental plot (6 × 18 m) within each block, that is, four replicates per treatment, we built three cages (2 × 2 × 2 m) covered by nylon net (0.6 × 1.6 mm mesh size), giving a total of 36 cages. Nets were placed on the frame and dug 20 cm providing complete exclusion and avoiding ground-dwelling predators entering from outside. The cages were established at the beginning of May and emptied of predators using pitfall traps for 48 hr after the set-up.

2.2 | Aphid inoculation

To establish a pest population, we introduced aphids *Rhopalosiphum padi* (L.), reared on oat plants within temperature-controlled facilities, to the treatment cages between the tillering and stem elongation oat stages (Zadoks et al., 1974; 11th–16th of June). We inoculated the cages with aphids for 5 consecutive days. For the inoculation, 100 reared aphids were placed into Petri dishes and left inside the cages. After 12 hr, plants were checked for aphid establishment. We repeated this step until reaching 100 successful aphid establishments per cage.

2.3 | Predator community treatment

Three predator community treatments were introduced to each plot, one per cage (+A+P), on 18th of June (Appendix S2 in Supporting Information), simulating three predator community assembly patterns:

Firstly, to simulate a landscape effect of generalist predators moving into the crop field from the surrounding landscape, we introduced 45 adult wolf spiders (*Pardosa* sp.; Roubinet et al., 2018).

Secondly, to simulate a landscape effect of generalist and specialised predators moving into the field, we introduced 45 adult wolf spiders and four adult ladybirds *Coccinella septempunctata* (L.). Ladybirds were chosen to represent specialised predators because they feed primarily on aphids and not on soil fauna as do carabids and spiders (Roubinet et al., 2018). We selected the density of wolf spiders based on *Pardosa agrestis* densities in alfalfa (Kiss & Samu, 2000); grass-clover (Birkhofer, Bezemer, et al., 2008; Birkhofer, Fließbach, et al., 2008) and barley (Riggi & Bommarco, 2019), and ladybird densities based on densities in cereal fields (Elliott & Kieckhefer, 2000).

Thirdly, we simulated a lack of predators moving from adjacent habitats and introduced no predators to 12 cages. However, all treatments were expected to contain local ground-dwelling predators, such as carabids emerging from the soil as affected by the fertilisation treatment.

To separate top-down and bottom-up effects, we used two smaller exclosures within each large cage. These exclosures consisted of a cylinder of 30 cm diameter dug 10 cm into the soil and a mesh net (mesh size smaller than 0.6 × 1.6 mm) preventing ground-dwelling predators from entering. Each small exclosure was 1.2 m high letting plants grow with minimum disturbance (Appendix S1 in Supporting Information). To measure plant performance without herbivore pressure, we established one exclosure with no aphids nor predators (−A−P). To measure the aphid population growth in the absence of predators, we established another small exclosure with aphids and no predators (+A−P; Appendix S2 in the Supporting Information). Each time we visited the cages, we checked the exclosures to ensure they were free from emerging predators.

We measured the temperature and humidity variation in cages (+A+P), exclosures (+A−P and −A−P) and outside the cages. We observed no cage effects in these aspects (Appendix S3 in Supporting Information). Light conditions might have been affected, especially by the double caging effect of the exclosures so we cannot extrapolate our absolute values to a real scenario. However, all comparisons among treatments were done with the same cage effects so the relative values and differences remain representative (i.e. we measured bottom-up effects on plants comparing −A−P exclosures).

Top-down suppression of predators on aphids and top-down effects on plant biomass were calculated by comparing aphid density and plant biomass in the presence and absence of predators (+A−P vs. large cages) respectively. Bottom-up effects of fertilisation on aphids were calculated by comparing aphid density in the predator exclosure (+A−P) in the fertilised and unfertilised treatments. See the Section 2.7.4 below.

2.4 | Measurement of aphid growth

We measured aphid population growth by counting aphids in each cage 12 times between the 16th of June and the 3rd of August. At each count, we randomly selected 10 consecutive plants at five crop rows. For each group of 10 plants, we noted the number of aphids. We also measured aphid the growth inside the predator exclosure (+A−P; total number of aphids/total number of plants) throughout the same period, but only six times minimising the risk of predators entering the exclosure.

2.5 | Local generalist predators and soil fauna

To examine the soil fauna community (i.e. collembolans, mites and dipterans), we extracted two core soil samples per cage (5 cm diameter and 18 cm depth) three times (8th of May, 15th of July and 4th of August). Fauna extractions from soil cores were performed with Tullgren funnels and individuals were counted as the total amount of specimens per soil core sample.

We assessed two aspects regarding the carabid community. First, we estimated the community composition of emerging carabids just after the cages +A+P were built, but before aphids were inoculated. After the cages +A+P were built, we removed all ground-dwelling predators using pitfall traps for 48 hr. These were not counted or re-introduced into the cages as the aim was to remove any predator from inside the cages before measuring 'true emergences' of soil predators. Once the cages +A+P were emptied, we quantified the ground beetle abundance emerging from the soil with three sampling rounds performed 2 weeks before aphid inoculation. Pitfall traps were kept open 24 hr and contained clay balls to provide the beetles with shelter and to keep them from escaping. Abundances of carabids were quantified in situ. All catches from the three rounds were released back into the respective cages.

We further estimated the density of ground-dwelling beetles during the rest of the experiment as a measurement of their activity. We opened pitfall traps for 2 hr, for minimal disturbance, at three sampling rounds (26th of June, 11th and 24th of July) after aphid inoculation and quantified the density of carabids in situ. All catches were released back to the cages.

2.6 | Yield

To obtain the total biomass of the grain (caryopses) and the straw in each large cage, we hand-harvested 0.5 × 0.5 m of the crop as well as the total crop in both (+A−P) and (−A−P) exclosures (0.07 m^2). We oven-dried the samples at 70°C over 48 hr and weighed them.

2.7 | Statistical analysis

All data analyses were performed in R (version 3.6.2, R Core Team, 2014) using linear mixed models (LME4 package, Bates et al., 2015) and removing non-significant interactions with backward stepwise removal. For analysing differences between levels at each factor, we used post hoc Tukey's tests.

2.7.1 | Soil fauna

To examine the effect of soil fertilisation and predator community treatments on the total abundance of soil fauna, we built a model with sampling round (May, July and August), fertilisation treatment, predator community treatments, the interactions between fertilisation treatment and predator community treatment interactions as fixed factors, and cage nested within the block as random factor.

To compare the emergence of carabids between fertilisation treatments before adding the spiders and ladybirds, we calculated the total number of individuals emerging per cage before the aphids were inoculated. Effects on the total emergence of carabids were tested in a model with fertilisation treatment and date (every 3rd day during 9 days before the aphids were inoculated) as fixed factors, and cage nested within block as random factor.

To compare carabid densities among treatments during the experiment, that is, after the aphids were inoculated, we used the catches per cage and sampling date after the aphid inoculation. We assumed that the density of carabids during the experiment could be affected by the introduced predators via interference. Therefore, for the carabid density analysis we included both the fertilisation treatments and predator community treatments, their interaction and the sampling round (26th of June, 11th and 24th of July) as fixed factors, and cage nested within block as random factor.

2.7.2 | Herbivore growth rates

To examine aphid population growth, we first calculated aphid density as the average number of aphids per plant (tiller) in each cage. To estimate aphid population growth during the exponential growth phase (Costamagna et al., 2007), we excluded the last two sampling days when aphid populations had begun to decrease. We tested the effect of the fertilisation treatment, predator community treatments and their interaction on the log-transformed aphid densities. For this model, we used day of sampling, and its interaction with fertiliser and predator community as a fixed factor, and cage nested within block as a random factor.

2.7.3 | Yield and plant biomass

To examine the effect of fertilisation and predator community treatments on crop yield, we first calculated grain (caryopsis) and straw biomass in each cage as weight per square metre. We then tested the effect of the fertilisation treatments and the predator community treatments on the total plant biomass and grain/ straw ratio using cage nested within block as random factor in the model.

2.7.4 | Top-down and bottom-up effects

To investigate differences between top-down and bottom-up effects on aphid densities and on plant biomass among the fertilisation and predator community treatments, we did the following calculations:

Log Top-Down effect size on aphids ($\mathrm{LTD}_{\mathrm{aphids}}$) is measured by comparing aphid densities at the aphid growth peak in cages (+A+P) and the corresponding predators' exclosure (+A−P) at aphid peak density using:

$$\mathrm{LTD}_{\mathrm{aphids}} = \ln\left[\frac{\text{Aphid density cage}(+\mathrm{A}+\mathrm{P})}{\text{Aphid density exclosure}(+\mathrm{A}-\mathrm{P})}\right].$$

Log Top-Down effect size on plant biomass ($\mathrm{LTD}_{\mathrm{plant}}$) is measured by comparing total plant biomass in cages (+A+P) and the corresponding predators' exclosure (+A−P) using:

$$\mathrm{LTD}_{\mathrm{plant}} = \ln\left[\frac{\text{Plant biomass cage}(+\mathrm{A}+\mathrm{P})}{\text{Plant biomass exclosure}(+\mathrm{A}-\mathrm{P})}\right].$$

Log Bottom-Up effect sizes on aphids ($\mathrm{LBU}_{\mathrm{aphids}}$) are calculated by comparing aphid densities at the aphid growth peak in exclosures with aphids, but not predators (+A−P), under manure (+A−P manure) or inorganic treatment (+A−P inorganic) with aphid densities in the no fertilisation treatments (+A−P control).

$$\mathrm{LBU}_{\mathrm{aphids}} = \ln\frac{\text{Aphid density exclosures}(+\mathrm{A}-\mathrm{P})\text{ manure(inorganic)}}{\text{Aphid density exclosures}(+\mathrm{A}-\mathrm{P})\text{ control}}.$$

Log Bottom-Up effect sizes on plant biomass ($\mathrm{LBU}_{\mathrm{plant}}$) are calculated by comparing plant biomass (straw + grain) after harvest in exclosures without aphid under manure (−A−P manure) and inorganic treatment (−A−P inorganic), with aphid densities in the no fertilisation treatments (−A−P control).

$$\mathrm{LBU}_{\mathrm{plant}} = \ln\frac{\text{Plant biomass exclosures}(-\mathrm{A}-\mathrm{P})\text{ manure(inorganic)}}{\text{Plant biomass exclosures}(-\mathrm{A}-\mathrm{P})\text{ control}}.$$

Using mixed models, we tested the effect of the fertilisation treatment, the predator community treatments and their interaction on the $\mathrm{LTD}_{\mathrm{aphid}}$ and $\mathrm{LTD}_{\mathrm{plant}}$, and the effect of the fertilisation treatment on $\mathrm{LBU}_{\mathrm{aphids}}$ and $\mathrm{LBU}_{\mathrm{plant}}$. Cage nested within block was included as random factor for LTD, while only block was used as random factor for modelling LBU as the fertilisation treatment was applied at the cage level.

3 | RESULTS

3.1 | Soil fauna

Fertilisation and predator community treatments did not affect the total amount of soil mesofauna (other than carabids). However, we found temporal variation (mean number of soil specimens per sample ± 95% confidence intervals; May = 3.77 ± 0.91, July = 2.00 ± 0.66, August = 5.47 ± 1.70; Table 1a; Appendix S4 in Supporting Information).

Total emergence of carabids (before aphid inoculation) was affected by fertilisation treatments (Figure 1; Table 1a), where plots fertilised with manure scored the highest numbers (post hoc: Inorganic-Manure, $p < 0.001$; Control-Manure, $p = 0.002$). The inorganic and control (no fertilisation) treatments did not differ in carabid emergence (post hoc tests, $p = 0.724$). The three dominant

TABLE 1 (a) Effect of fertilisation, natural enemy community and their interaction on the soil fauna, carabid emergence and carabid activity (number per cage); (b) Effect of fertilisation, natural enemy community and their interaction on the aphid density (log-number per plant); and (c) Effect of fertilisation, natural enemy community and their interaction on the top-down, bottom-up, plant biomass (g/m^2), grain yield (g/m^2) and grain/straw ratio. Significant *p*-values are in bold

	Fertilisation		Natural enemies		Time		Fertilisation × natural enemies	
(a)	F	p	F	p	F	p	F	p
Emerging carabids	12.09	**<0.000**			2.09	0.130		
Carabid density	2.87	0.073	0.64	0.53	3.58	**0.033**	1.03	0.393
Soil fauna	0.67	0.516	0.06	0.938	9.11	**<0.000**	0.33	0.860

	Fertilisation		Natural enemies		Time		Fertilisation × time		Natural enemies × time		Fertilisation × natural enemies	
(b)	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Aphid growth	0.16	0.850	1.53	0.23	7.66	**0.006**	12.85	**<0.000**	58.89	**<0.000**	2.93	**0.020**

	Fertilisation		Natural enemies		Fertilisation × natural enemies	
(c)	*F*	*p*	*F*	*p*	*F*	*p*
LTD aphids	3.82	**0.034**	5.17	**0.012**	0.88	0.486
LTD plant biomass	9.06	**<0.000**	0.24	0.785	0.98	0.438
LBU aphids	0.27	0.758				
LBU plants	1.06	0.357				
Plant biomass	10.94	**<0.000**	0.29	0.74	0.80	0.531
Grain biomass	5.27	**0.009**	0.25	0.77	0.52	0.717
Grain/straw ratio	0.53	0.590	1.25	0.299	1.36	0.273

carabid species captured were *Nebria brevicollis*, *Pterostichus melanarius* and *Poecilus cupreus*, which are known to overwinter in crop fields (Baranovská & Knapp, 2014; Noordhuis et al., 2001; Palmu et al., 2014).

Carabid density during the experiment differed marginally among fertilisation treatments (Table 1a). Manure-fertilised plots had higher densities (estimate = 3.92 ± 1.21) than inorganically fertilised (estimate = 2.19 ± 1.00; post hoc, $p = 0.142$) and unfertilised plots (estimate = 2.00 ± 0.95; post hoc, $p = 0.093$). There were no differences between unfertilised and inorganically fertilised plots in carabid density during the experiment (post hoc, $p = 0.973$). Carabid densities varied over time, with higher numbers of carabids caught in the second sampling round (26th of June = 3.08 ± 1.04; 11th of July = 3.30 ± 1.29; 24th of July = 1.72 ± 0.82; Table 1a).

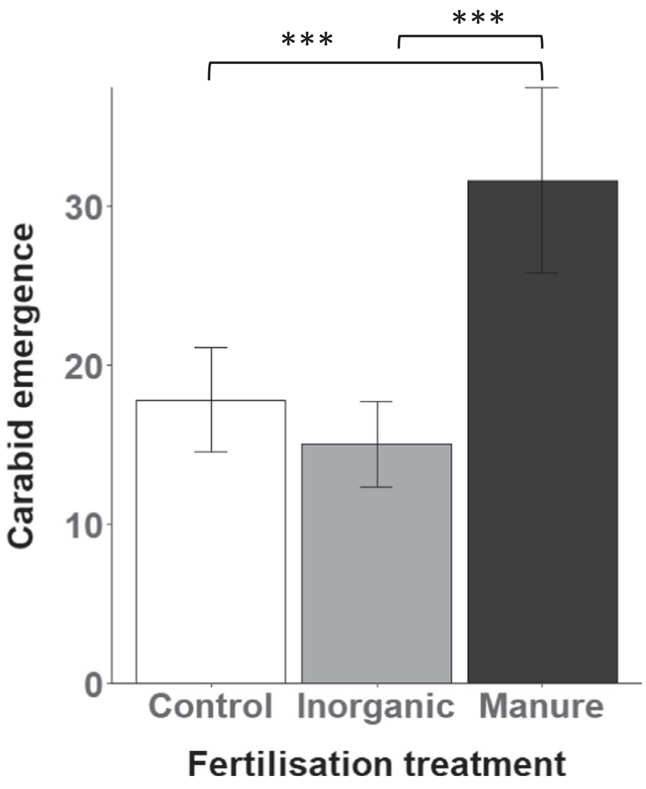

FIGURE 1 Mean number of carabids caught per cage (+A+P) before aphid inoculation by fertilisation treatment. Error bars show the 95% confidence intervals (***indicates a significant difference $p < 0.001$ between treatments after post hoc analysis; $n = 4$)

3.2 | Herbivore growth

Fertiliser type affected aphid population growth over time (Table 1b; Figure 2). Manure-fertilised plots had the slowest aphid growth (estimate = 0.26 ± 0.32) and inorganically fertilised plots the highest (estimate = 0.66 ± 0.32; post hoc tests inorganic-manure, $p = 0.031$). Adding immigrant specialists (ladybirds) to the predatory community had the highest impact on aphid density over time (Figure 2; Table 1b). Aphid densities decreased, that is, population growth was negative, in the ladybird and spider treatments (estimate=−0.02 ± 0.49). Additionally, there was an interactive effect between the fertiliser treatments and the predator community treatments over time mainly driven by a decreased difference of aphid growth among fertilisation treatments when adding ladybirds (Figure 2; Table 1b).

3.3 | Yield and plant biomass

Overall, fertilisation increased crop yield (Table 1c; Figure 3). Fertilisation increased total dry biomass (Table 1c) in the inorganically fertilised treatment compared to the unfertilised control (Figure 3, post hoc, $p > 0.001$) and to the manure treatment (Figure 3, post hoc, $p > 0.045$). Similarly, fertilisation increased grain weight (Table 1c) in the inorganic fertilised compared to the unfertilised treatment (Figure 3, post hoc, $p = 0.007$). Grain weight

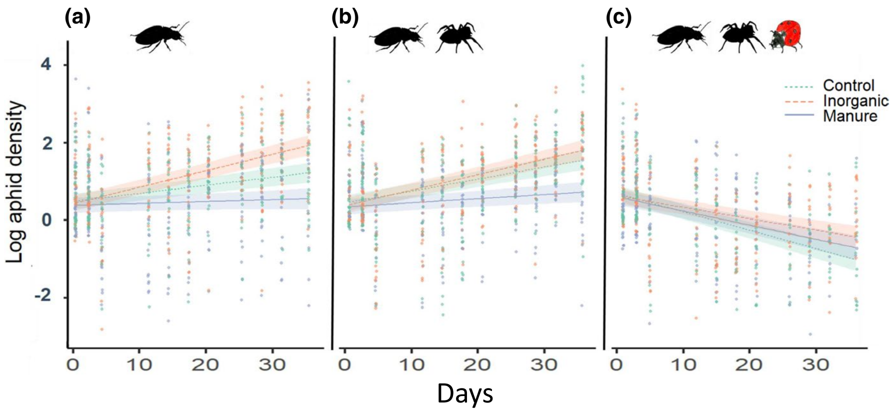

FIGURE 2 Interactive effect of the soil fertilisation treatments and predator community treatments on aphid density (log-aphids per plant) over time. The lines show the model estimates of average number of aphids per plant over time since inoculation. Grey areas show 95% confidence intervals for each fertilisation treatment and predator community treatment (a = local community; b = local community + spiders; c = local community + spiders + ladybirds; $n = 4$)

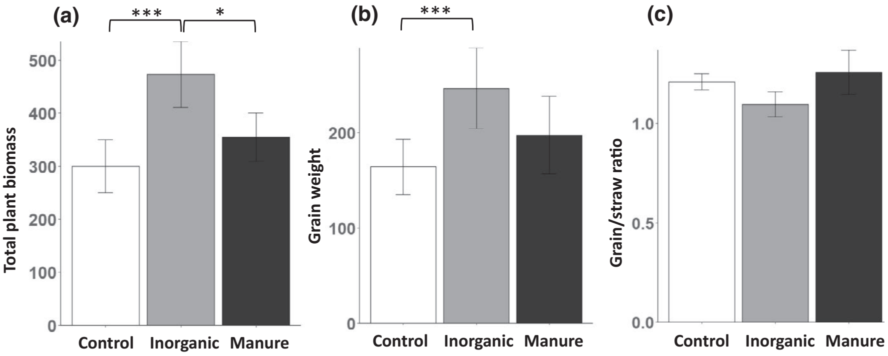

FIGURE 3 Fertiliser effect on (a) average total plant biomass (g/m^2); (b) average grain biomass (g/m^2); and (c) ratio of average grain over straw biomass (g/m^2) in the harvested area (cage) per fertilisation treatment ±95% confidence intervals. *indicates a significant difference ($p < 0.05$); ***indicates a significant difference ($p < 0.001$) between two treatments after post hoc analysis ($n = 4$)

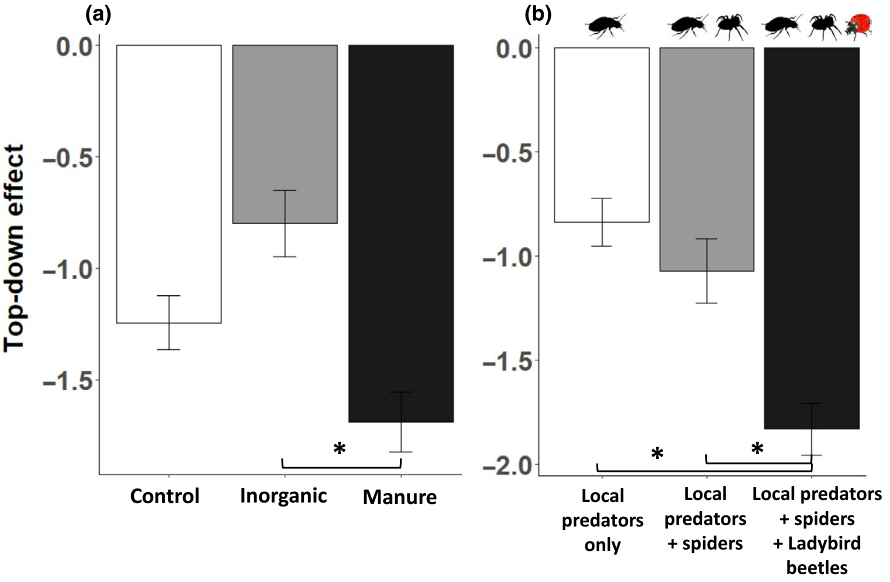

FIGURE 4 Mean top-down (predation) log-ratio effect size on aphids per (a) fertilisation treatment and (b) predator community treatment. Error bars show 95% confidence intervals on aphid density (*indicates a significant difference $p < 0.05$ between treatments after post hoc analysis; $n = 4$)

did not differ between the inorganically and the manure-fertilised treatments (Figure 3, post hoc, $p > 0.214$). For the grain/straw ratio analysis, we found no significant differences among the fertilisation treatments (Table 1c; Figure 3).

3.4 | Top-down and bottom-up effects

Top-down effect size on aphid densities (LTD$_{\text{aphids}}$) was affected by fertilisation (Table 1c; Figure 4a) and predator community (Table 1c; Figure 4b), but not by their interaction (Table 1c). We observed the largest top-down effect (log-ratio) on aphids (LTD$_{\text{aphids)}}$ in the manure-fertilised treatment (Figure 4a), and this effect was higher than in the inorganic fertilised (Figure 4a, post hoc, $p = 0.026$). Regarding the top-down effect of predators moving into the crop field on aphids, cages with added ladybirds (specialised predators) and spiders (generalist predators) showed a stronger response (log-ratio) when compared with treatments with no addition of predators (Figure 4b, post hoc, $p = 0.014$), and near-significant differences with treatments where only spiders had been added (Figure 4b, post hoc, $p = 0.07$). Regarding top-down effects on plant biomass, we found that inorganic fertilisation boosted the top-down effect size on total plant biomass (LTD$_{\text{plant}}$; 4.69 ± 0.18) compared with the manure-fertilised (4.32 ± 0.20) and compared with the control treatments (4.35 ± 0.17; Table 1c). Fertilisation treatments had no detectable bottom-up effect on the aphid population, that is, comparing

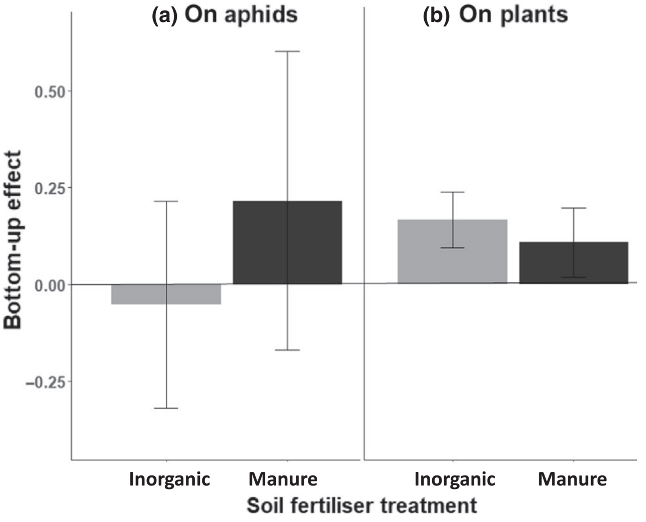

FIGURE 5 Mean bottom-up (fertilisation) log-ratio effect size per fertilisation treatment. Error bars show 95% confidence intervals for (a) aphid density (aphids per plant) and (b) plant biomass (g/m^2; $n = 4$)

+A−P between fertilised and control treatments, but affected plant biomass, that is, comparing -A-P between fertilised and control treatments (Table 1c; Figure 5).

4 | DISCUSSION

We show that fertiliser type and the composition of highly mobile predators moving into crop fields from the surrounding landscape can drastically reduce herbivorous pest populations. In particular, the combination of predators immigrating into the crop field from the surrounding landscape, and nutrient management with organic fertiliser enhance pest suppression via different mechanisms. Generally, predators drive top-down effects and fertilisation triggers bottom-up control. However, fertilisation with manure also mediated top-down control by benefiting local predators overwintering in the soil. Hence, local and landscape-level effects interplay in determining predator and herbivore abundances and crop yield.

The greatest aphid suppression occurred in plots fertilised with manure where specialist predators (ladybirds) were added. Overall, the aphid population growth was lower in the presence of predators (+A+P; locally emerging and immigrating from the landscape) than in their absence (+A−P), and this effect was independent of the fertilisation treatment. The suppression was particularly large for treatments supplemented with specialist predators (ladybirds) as compared with treatments with only locally emerging predators from the soil, or with locally emerging predators supplemented with spiders. This attests to a high suppressive capacity of ladybirds as a taxon that will typically emerge in large numbers after overwintering in refugia and immigrate to crop fields (Honek et al., 2017). Spiders played a smaller role in suppressing aphids. We found no differences in aphid population growth rates between treatments with predators emerging from the soil and treatments with spiders added. While spiders can provide efficient pest suppression (Michalko et al., 2019), their lack of influence in our experiment could be due to microhabitat mismatch between wolf spiders and the aphid species we studied. Wolf spiders are primarily ground-dwellers, while *R. padi* aphids are leaf-dwellers, resulting in low encounter rates.

Mineral and manure fertilisation strengthened bottom-up effects (LBU_{plant}). However, manure fertilisation also indirectly benefited top-down control of aphids by enhancing carabid beetle numbers emerging from the soil. Aphid population growth rates were lower in the manure-treated plots compared with mineral-treated and unfertilised plots. A likely explanation is that fertilisation with manure improves conditions for ground-dwelling predators by bolstering a diverse soil fauna, which provide alternate prey for carabids, and improves habitat structure in the soil (Riggi & Bommarco, 2019). Alternative preys are important for sustaining carabids when crop pest populations are low, and for larval stages of the beetles residing in the soil (Leroux & Loreau, 2008; Liu et al., 2016). Several ground-dwelling beetles are well-adapted to agricultural landscapes, and lay their eggs and overwinter in the crop field (Hanson et al., 2016; Kromp, 1999). Manure fertilisation might further improve soil texture or biochemistry benefitting the overwintering survival of adult carabids and their larvae (Lövei & Sunderland, 1996). Interestingly, we found that in manure-fertilised soils, ground-dwelling predators already present in the soil were, by themselves, able to control the aphid population growth (Figure 2).

Contrarily, we recorded the highest aphid densities and growth rates and the lowest top-down suppression in inorganically fertilised plots, consistent with the hypothesis that fast-growing plants are nutritious to herbivores and promote their population growth (Aqueel & Leather, 2011; De Bruyn et al., 2002). Overall, we also found the highest top-down effect on plant biomass (LTD_{plant}) in inorganically fertilised plots, meaning that the gain of plant biomass when comparing plants that were attacked by aphids and plants under pest suppression was higher in inorganically fertilised plots. These results suggest that organic fertilisers impact the crop in multiple ways due to complementary mechanisms by boosting the soil fauna as well as the plant quality, whereas inorganic fertilisers solely impact plant quality.

For an effective pest suppression, it is important to support both, predators immigrating into the crop fields from the surrounding landscape and the local predator fauna within the crop field. Generalist predators already present in the crop field were, in organically fertilised soils, able to control aphid abundances by themselves. However, if a crop field does not already contain high densities of local predators, management aiming to enhance immigration of specialist predators from the surrounding landscape becomes crucial for biological control. Ladybirds, such as *Coccinella septempunctata*, are habitat generalists and track food resources in the landscape. A management strategy to enhance ladybirds is to build a resource continuity in the landscape (Honek et al., 2017; Schellhorn et al., 2015). Heterogeneous landscapes can in this way support a wider range of generalist predators, potentially leading to enhanced levels of natural pest control (Feit et al., 2019). We also need to consider species traits to understand the predation efficiency of assembled predator communities (Schmitz, 2017). For example, in retrospect, selecting leaf-dwelling spiders instead of ground-dwelling ones might have rendered a stronger top-down suppression. Further, aphids are not high-quality food items for some spider species which might switch to more nutritious soil prey (Toft, 2013).

Higher efficiency of specialised predators in reducing pest densities was not translated to an increase in plant biomass. Top-down processes are the main mechanisms explaining pest suppression in crops (Bianchi et al., 2006). However, strong bottom-up effects can mask this relationship under some circumstances. In our experiment, plants that received inorganic fertiliser had higher infestation levels than the ones receiving manure, and at the same time, inorganically fertilised had the highest total plant and straw biomass. However, no differences in plant biomass were found between fertilisation treatments in the predator exclosures (+A−P) and in the total exclosures (−A−P; Appendix S5 in Supporting Information). These non-significant differences point at few interesting possibilities. First, the lack of detectable differences among +A−P exclosures implies that plants receiving fertiliser (manure or inorganic) compensated for the biomass loss by herbivory by growing more biomass. Second, the lack of detectable differences among −A−P exclosures demonstrates that fertilisation type did not affect yields of not attacked plants. An alternative is that inorganically fertilised plants are better able to compensate by growing more biomass when attacked by herbivores (Garratt et al., 2011; Mäder et al., 2002). Thus, it is plausible that both manure and inorganic fertilisation enhance plant biomass, but through two mechanisms: top-down and bottom-up respectively. If differences in top-down effects between manure and inorganic fertilisation are compensated with opposing differences in their bottom-up effects, we can expect similar outcomes in terms of final plant biomass. Plants in organically fertilised plots benefited from a stronger top-down suppression while plants in inorganic plots had higher straw biomass. However, there was no difference in final grain (caryopsis) weight. From the plant perspective, the use of manure fertiliser will boost both the herbivore top-down control and biomass bottom-up creation. From the farmer's perspective, and considering long-term effects, the use of manure as fertiliser is a well-founded management practice to reduce pest damage, improve soil fertility and increase yields. However, one must consider possible biases from the cage effects such as a lower plant biomass in the exclosures because of light conditions or a higher aphid feeding activity.

4.1 | Application and synthesis

We show that manure fertilisation increased local carabid emergence from the soil. This enhanced the top-down herbivore suppression reducing their population growth. Inorganic fertilisers promoted bottom-up forces by directly increasing plant biomass, thereby compensating for increased herbivore density. When the local predator community was not able to suppress the aphid population (in the inorganic and no fertilisation treatments), predators moving into the crop fields became essential for pest control. Overall, the most effective top-down suppression of herbivorous crop pests was attained by enhancing the local predator community by adding organic fertilisers and specialist predators moving from the surrounding landscape. Managing landscapes to promote mobile and specialist predators emerges as particularly important for crop fields receiving no manure amendments. We suggest the active promotion of both local predators within the crop field and mobile predators in landscapes to secure crop protection and yields.

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AUTHORS' CONTRIBUTIONS

G.A., L.R., K.M., T.M. and R.B. provided the ideas and designed the methodology; G.A. collected the data, analysed the data and led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.3n5tb2rgp (Aguilera et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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