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ORIGINAL PAPER

Organic fertilizer amendment promotes wheat resistance to herbivory and biocontrol services via bottom-up effects in agroecosystems

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Abstract

Excessive mineral fertilizer input results in little extra yield but exacerbates insect herbivory and affects environmental health and ecosystem services. The use of organic fertilizer is considered to have promise for mitigating those impacts. How organic fertilizer amendment modifies crop resistance to insect herbivory and modulates biocontrol services on a landscape scale has not been well studied. We conducted a series of field experiments on a large spatial scale with three fertilization regimes (mineral fertilizer, mineral fertilizer amended with organic matter, and no fertilizer control) in Shandong Province, northern China. Soil nutrient content, wheat plant metabolism, cereal aphid abundance, parasitism rate, and wheat yield were quantified. Maize straw amendment combined with mineral fertilization significantly reduced cereal aphid abundance and promoted parasitism during the peak aphid period, compared with mineral fertilizer alone and the no fertilizer control. Modeling simulations showed increased biological pest control when a larger proportion of fields were additionally treated with maize straw amendment. Foliar chemical analyses revealed that the types and content of plant free amino acids, rather than plant defensive compounds, most likely accounted for the variation in aphid abundance and biological control efficiency. A mineral fertilization regime plus plant straw amendment may promote wheat resistance to herbivory and benefit biocontrol via bottom-up effects. Heterogeneity in fertilizer regimes between fields may be the key ecological force shaping pest control at a landscape scale.

Keywords Bottom-up effect · Ecological intensification · Landscape heterogeneity · Phytochemistry · Pest control services · Scaling up modeling

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Key Message

- How organic fertilizer benefits pest control is not well understood.
- Local field scale maize straw amendment aided wheat aphid suppression.
- Higher levels of free amino acid were associated with aphid abundance and parasitism rate.
- At a landscape scale, having more amendment treated fields resulted in higher biocontrol.
- Covariance between aphid and parasitoid density was key for biocontrol on large scales.

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Introduction

To meet the food demand of a continuously increasing global population, agricultural production has intensified and has in turn accelerated the deterioration of the global environment (Matson et al. 1997). Tilman et al. (2001) predicted that 1 billion hectares of natural habitat could be converted to agricultural production by 2050. As agricultural production has expanded and intensified, the long-term excessive use of mineral fertilizer has had adverse environmental impacts globally (Foley et al. 2011). A serious problem with soil mineral fertilizers is that redundant nutrition can benefit insect pests and thus increase their populations, while providing no gain in crop yield (Tittonell 2014; Zhao et al. 2015). Such an outcome runs counter to the goal of maintaining or improving yield by applying fertilizers.

Ecological intensification could reduce the undesirable consequences of widespread excessive fertilizer use (Cassman 1999). Soil organic matter provides functional ecological intensification benefits to arable systems by reducing the need for mineral fertilizer input, while optimizing stable productivity of crops and suppression of pest insects (Bommarco et al. 2013; Garratt et al. 2018). Soil organic fertilizers that improve soil quality (i.e., soil organic matter content) may increase biological control efficiency (Birkhofer et al. 2008) and could to some extent contribute to meeting the goals of sustainable pest management and crop yields (Muneret et al. 2018).

Fertilizer type (i.e., organic vs. mineral fertilizer) and the amounts applied may influence plant nutritional and defensive traits and consequently alter host plant palatability to insect herbivores as a “bottom-up” effect (Comadira et al. 2015; Han et al. 2016; Rashid et al. 2017). Such effects may cascade up to higher trophic levels and thus modify biocontrol services (Butler et al. 2012; Han et al. 2019a). For example, conventionally fertilized wheat fields have been shown to have larger numbers of *Metopolophium dirhodum* (Walker) (Aphididae) than organically grown fields (Altieri and Nicholls 2003; Lohaus et al. 2013). This pattern was attributed to the ratio of certain nonprotein to protein amino acids, which determined the palatability of wheat crops for aphids and thus the potential infestation levels (Altieri and Nicholls 2003). When coccinellid larvae were fed aphids that had been grown on organically fertilized Brassica, their mortality was reduced in comparison with larvae fed aphids exposed to the full synthetic fertilizer treatment (Banfield-Zanin et al. 2012). Compared with low or medium nitrogen (N) fertilizer input, high or excessive treatments were positively associated with plant growth, but they also favored pest colonization and development (Wale et al. 2006; Islam et al. 2017). In addition, higher N fertilizer increased herbivore abundance and had a negative effect on the natural enemy-to-prey ratio (Petermann et al. 2010), which had little benefit for crop yield (Rusch et al. 2017). Moreover, the response of aphids to organic fertilizer treatments was specific to the host plant. For example, higher aphid colonization occurred on cabbage treated with organic fertilizers (Karungi et al. 2006), but fewer aphids were found on maize that received an organic treatment (Morales et al. 2001). So far, field-scale evidence of organic fertilizers having a bottom-up effect on pest control is limited and the mechanisms underlying the observed patterns are not clear (Rusch et al. 2017).

Positive effects of organic fertilizers on pest control have been observed at the field scale (Muneret et al. 2018). Maintaining a certain level of soil organic matter content is not only important for crop productivity (Tsiafouli et al. 2015; Ghaley et al. 2018) but also provides a promising way to reduce pest pressure (Birkhofer et al. 2008; Garratt et al. 2018). A meta-analysis showed that organic fertilizers have positive effects on controlling natural enemies at a farm scale (Garratt et al. 2011), but direct evidence for such an effect at larger spatial scales is limited. The sustainability of both biological control and crop yields under future agro-ecological intensification needs to include a landscape-scale perspective (Bianchi et al. 2006) and consider the heterogeneity in plant nutrient levels in agroecosystems (Wetzel et al. 2016). However, the bottom-up effects on pest control over large spatial scales have not been widely studied (Tittonell 2014; Isbell et al. 2017; Han et al. 2019b).

In the current study, we used winter wheat (*Triticum aestivum* L.) fields, cereal aphids, and their parasitoids to explore the bottom-up effects of soil fertilizers on aphid control. Sucking herbivore–parasitoid relationships are sensitive to the use of fertilizers (Aqueel et al. 2015; Rusch et al. 2017; Garratt et al. 2018). The planting system in our study was a wheat–maize rotation, with maize straw amendment serving as the organic fertilizer treatment. Field-scale experiments and a landscape-scale investigation deployed different fertilizer treatments to determine the bottom-up effects on wheat aphid abundance, biological control efficacy of parasitoids, and wheat yield. In agricultural areas across the region, cropland patches included a series of fields, and the fertilizer treatment applied to each field was recorded. Insect assessments included the abundance of aphids and their parasitoids. We used a scaling-up approach (Melbourne and Chesson 2006) to predict bottom-up effects of fertilizers on variation in aphid abundance on a landscape scale due to field-scale processes. We also used this approach to assess how fertilization heterogeneity (i.e., changing proportions of crop fields with organic fertilizer in agricultural landscapes) influenced the spatial variance in terms of pest control. We tested three working hypotheses: (1) nitrogen fertilization with maize straw amendment reduces aphid abundance across spatial scales; (2) maize straw amendment alters how wheat plants allocate resources for metabolism of nutrients and/or defensive compounds to resist herbivory; and (3) the plant-mediated bottom-up effects on aphid population growth and the top-down control on aphids through parasitoids are equally important in explaining variation in aphid abundance at the landscape scale.

Materials and methods

Experimental design and investigation on field and landscape scales

A field-scale fertilizer experiment was conducted in 2018 at the Yucheng Integrated Experiment Station of the Chinese Academy of Sciences (36.8372°N; 116.5828°E) in Shandong Province, northern China. The annual mean temperature (± SD) was 14.2 ± 0.49 ℃ and precipitation (± SD) was 583 ± 157.5 mm. The long-term fertilizer treatments were established in 2012. To simulate general practices in fields with wheat–maize rotations, the field-scale experiment consisted of one control and two treatments in nine plots. Each treatment had three replicated plots (10.3 × 7.7 m per plot). The distance between plots was about 0.5 m. Concrete foundations (depth = 1.5 m) were built to separate possible below-ground soil-based transfer between them. The treatment plots were randomly distributed. Three treatments were set up: the control (without any mineral fertilizer or added organic matter), N (with 600 kg/ha of mineral fertilizer), and N + straw (with 600 kg/ha of mineral fertilizer plus 7700 kg/ha maize straw as the organic matter amendment). Nitrogen, phosphorus, and potassium composition of the mineral fertilizer (Summit Fertilizer [Qingdao] Co., Ltd) was at least 20% N, at least 9% P_2O_5, and at least 11% K_2O. For all plots, field tillage, irrigation, soil type, wheat variety, and planting patterns were consistent to enable detecting effects mainly from the fertilization treatment. Pesticides and fungicides were not used during the wheat season, and only one herbicide (containing the main functional components florasulam, MCPA-Na and flucarbazone-sodium) was sprayed during wheat stem elongation to control gramineous weeds, including *Bromus japonicus* Thunb. Ex Murr., *Alopecurus aequalis* Sobol., *Aegilops tauschii* Coss., *Sclerochloa dura* (L.) Beauv., *Avena fatua* L., and *Puccinellia distans* (L.) Parl., and broadleaf weeds, including *Descurainia sophia* (L.) Webb. ex Prantl, *Capsella bursa-pastoris* (L.) Medic., and *Galium* sp. (L.).

A large-scale field investigation across wheat planting areas was conducted in 2018 in Shandong Province, northern China. The information collected included wheat field location, mineral/mineral + organic (without/with maize straw amendment) fertilizer type and amounts applied, crop yield, wheat aphid abundance, and parasitism rate at the grain-filling stage. There were 45 sites (Fig. 1) throughout the main wheat cropping regions in Shandong province

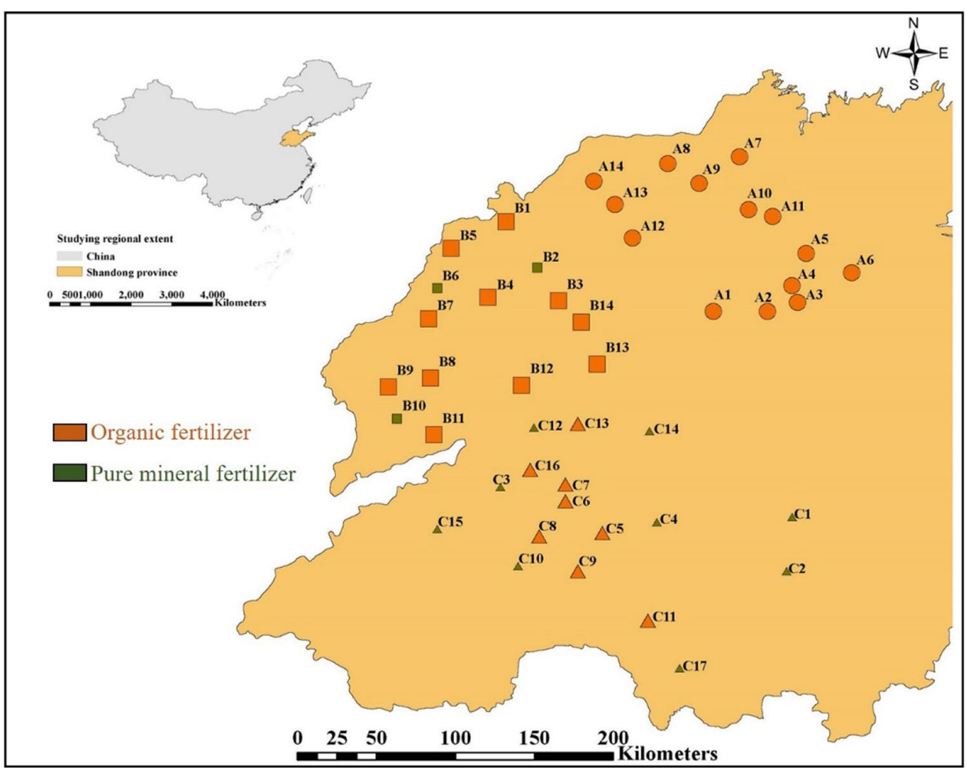

Fig. 1 Distribution of sampling locations over three regions in northern China. The different symbols (circle, square, triangle) indicate region A (locations where all fields had organic fertilizer), B (locations where 79% of fields had organic fertilizer), and C (locations where 47% of fields had organic fertilizer), respectively. (See more details of location information in Table S1.) Larger size and orange symbols were organic fertilizer fields. Smaller size and green symbols were pure mineral fertilizer fields

(Table S1). The sampling dates were around wheat grain-filling to enable comparison of fertilizer bottom-up effects between sites. Sites were located across a large geographic area that contained different types of climates. Meteorological data were sourced from the National Meteorological Information Center, China Meteorological Administration (NMIC, CMA). Since mean temperature or total precipitation were not found to affect aphid abundance or parasitism rate (Table S2), they were not included in further analyses. No pesticides were used at any sampled sites. The average field size of sample sites was 0.7 ha (range 0.1–2.0 ha). Each site represented a focal field in a specific agricultural landscape. The distance between any two sites was larger than 20 km, which helped to minimize possible spatial autocorrelation and provided contrasting types of fertilization management.

Soil sampling and nutrient level testing

For both field- and landscape-scale experiments, soil samples from 0- to 20-cm depth were collected during April and May in 2018. This period covered the wheat season from stem elongation to milk ripe stage. In each plot/site, five soil cores (3-cm diameter, 20-cm depth; one in the center and others in the four corners at least 2 m away from the field margin) were collected. Stones and plant residues were removed, and the five soil cores were then mixed to yield one composite soil sample from each site/plot. Each soil sample was passed through 2-mm mesh, air-dried, and passed through a grinder (2000 rpm, four cycles, 90 s/cycle) to homogenize the sample before testing. An Elemental Analyzer (Elementar Co., Ltd, vario MACRO cube CHNS) was used to test soil total C and total N content.

Plant sampling, nutrient and defense compounds, and yield

Plant tissue samples were collected from plants at the soil sampling points. Eight wheat flag leaves and heads were taken at each point in each field plot. All plant samples in each plot were equally divided into two parts. Each part contained a total of 20 flag leaves and 20 heads, respectively. One part was stored at −80 °C (the time from field sampling to store in the freezer was no more than 6 h), while the other was dried to constant weight at 80 °C and then ground into powder. Free amino acid composition and content were assayed by reverse phase high-performance liquid chromatography (HPLC) following our previous study (Gao et al. 2018). The detailed procedures, parameters, and setting of sample analysis performed for soluble sugars, nonprotein amino acids (L-3,4-dihydroxyphenylalanine [L-DOPA] and L-ornithine), and phenolic compounds are provided in Part 2 of the Supporting Information. Wheat plant yield was evaluated by standard measurement for grain yield as summarized by Bastos et al. (2020). Data including (1) number of heads per unit area (heads/m^2); (2) average number of kernels per head; and (3) 1000-kernel weight (kg) were collected and later used to evaluate the wheat yield (kg/ha). Three rows with similar wheat growth vigor in each plot were randomly selected, and the number of heads in 1 m per row was counted. In each wheat planting plot, the average row distance was about 35 cm, and this value was used to derive the head number per area (heads/m^2). The average kernel number per head was based on counts from 90 randomly selected heads in each plot. In the same plot, aboveground parts of unsampled plants in 1 m^2 were harvested and three replicates were randomly chosen to evaluate 1000-kernel weight. The kernels were weighed after drying at 105 °C for 30 min and drying at 80 °C to a constant weight.

Wheat aphid abundance

Aphid species in wheat fields in northern China include *Sitobion avenae* (Fabricius), *Schizaphis graminum* (Rondani), and *Rhopalosiphum padi* (Linnaeus). In our study, *S. avenae* and *R. padi* predominated, and we pooled the counts of the two dominant aphid species for subsequent analyses. At six time points with 7-day intervals, a field census of aphid populations was undertaken in the field-plot experiment. The counts started on April 19, 2018, and continued throughout the stem elongation phase. The aphid abundance in each plot was based on five sample points, as with soil and plant sampling. At each sample point, the abundance of each aphid species on 20 wheat plants (except at peak aphid abundance on May 10 when only 10 wheat plants were surveyed) were visually counted. Sample plants were at least 2 m away from the field edge. Landscape-scale investigation of aphid abundance was undertaken only during the wheat grain-filling stage. Again, at each sampling site, samples were taken at five points; one in the center and the others at least 2 m away from the field edge. The numbers of *S. avenae* and *R. padi* on 10 wheat plants were counted.

Natural enemy density and biological control efficiency evaluation

In both field- and landscape-scale experiments, a five-point sampling scheme was used to assess the density of natural enemies in each plot/site. Natural enemies considered were mainly parasitoids. The primary parasitoids were *Aphidius gifuensis* (Ashmead) and *A. avenae* (Haliday). Surveyed points overlapped with those for aphid abundance. The numbers of mummified aphids observed on the plants during aphid counts were recorded and used to evaluate parasitism. To evaluate the variation in mummified aphid parasitism across treatments, we standardized our method by only counting mummies on whole sample plants. The parasitism rate at each point (calculated as the number of mummified aphids divided by the sum of mummified aphids and live aphids on sampled plants) was used as an indicator of the biological control efficiency. Obviously, some live aphids were parasitized but not yet mummified and some mummies from earlier time points remained adhered to plants.

Scaling-up modeling and prediction of diversified fertilizer effects on a landscape scale

We used the scaling transition framework (Melbourne and Chesson 2006; Englund and Leonardsson 2008) to predict the relative key driver(s) that explained variation in aphid abundance as fertilizer treatment heterogeneity increased, from relative homogeneity at a field scale to heterogeneity at a landscape scale. We were especially interested in the pest control services as the proportion of organic fertilized fields varied in an agricultural landscape. The framework and details of the standardized modeling procedures used are provided in Supporting Information (Part 3). At the local (field) scale, different fertilizer treatments may have caused variation in aphid abundance, which reflected the field-scale conditions and was used to define a mean-field model. We predicted the larger-scale situation by using local-scale processes, that is, the mean-field model combined with scale transition terms (Englund and Leonardsson 2008). In the landscape-scale experiment, because distances between sites were large relative to the scale of parasitoid activities (Evans et al. 2015; Evans 2018), we assumed site conditions (fertilizer treatment, phytochemistry, aphid abundance, and parasitoid density) possibly acted at a relatively limited spatial scale. To evaluate the effects of fertilizer treatment on variation in wheat aphid abundance at a large spatial scale, the landscape-scale experimental dataset was used to fit a scaling-up model and to identify possible driver(s) (Part 3 in Supporting Information).

Statistical analyses

In the field-scale experiment, survey data from 7 days before peak aphid period and from the peak period were used for analyses. The sample sizes for specific variables (measured plant and soil samples) in various analyses differed due to missing values (i.e., due to failed sample assay processing in the laboratory). Even though each plot maintained a relatively homogeneous environment in terms of soil nutrients, aphid abundance varied over a large range within plots. Thus, to limit the effects of environmental heterogeneity on aphid and mummy abundance and parasitism rate per plot, we used averaged plot data to conduct comparisons (three treatments and nine sample plots, expected $df = 2,8$ in tests). For free amino acid testing, we averaged the five replicates tested in each plot covering the five sampling points; for all other plot data, three replicated laboratory assays from each plot were undertaken and averaged for comparisons.

For the investigation at a landscape scale across wheat planting areas, the mineral fertilization amount and production data were used to calculate the fertilization cost index (i.e., the ratio of the total amount of nitrogen fertilizer in tons to the total amount of wheat production in tons) for each sampled field. The normality of residuals of the response variables was checked using Shapiro–Wilk's test. The aphid abundance per 20 plants was scaled up to an abundance per 100 plants for aphid abundance analyses. Mummified aphid abundance was also transformed to the abundance per 100 plants for subsequent analyses. Aphid abundance and amino acid content were $\log(x+1)$ transformed, and the parasitism rate was transformed using an arcsine square-root before analysis. Comparisons between treatment groups were made using Fisher's LSD test, and the significance level was 0.05 in all analysis. Correlation analysis was used to detect relationships between plant chemical compounds, aphid abundance, and parasitism rate in the field-scale experiment. Before the correlation tests were run, the normality of residuals was confirmed to meet the statistical assumption for correlation analysis. Pearson's correlation coefficient (r) was calculated, and the significance level was set to 0.05 level. To explore how aphid abundance, mummified aphid abundance, and parasitism rate could be related to plant chemical compounds, redundancy analysis (RDA) was used (Peresneto et al. 2006). In RDA, the control, N, and N + straw were treatments and furnished the dataset for building two matrices. One matrix included response variables of aphid abundance, mummified aphid abundance, and parasitism rate, while the other contained plant free amino acid content.

A one-way repeated measures ANOVA was used to test differences in soil and plant nutrients, plant defense compounds, wheat yield, aphid and mummy abundances, and parasitism rate among treatments. Aphid abundance and the ID of sampling sites were used as covariates when analyzing mummified aphid abundance and parasitism rate with the treatment (i.e., fertilizers) as the main factor being tested. All data analysis and plotting were conducted in R version 3.5.1 (R Core Team 2018). Correlation analysis and RDA were performed using 'ggcorrplot' (Kassambara 2016) and 'vegan' (Oksanen et al. 2016) packages, respectively. Scatter regression, correlation, and RDA plots were further adjusted by the 'ggplot2′ package.

Results

Aphid abundance response to fertilizer regimes

In the field-scale experiment, two key periods of aphid population activity were considered, 7 days before the aphid abundance peak period and the peak period. Compared with the control, fertilizer treatments had no significant influence on aphid abundance before the aphid abundance peaked (F (2, 5) = 1.222, P = 0.370). There was no difference in aphid abundance between the two fertilizer treatments during this period (Fig. 2a). At the aphid abundance peak, the 600 kg/ha mineral fertilizer with maize straw amendment (N + straw) treatment negatively affected aphid abundance (F (2, 5) = 6.762, P = 0.038) (Fig. 2b) in comparison with the 600 kg/ha mineral fertilizer treatment (N).

Effects of fertilization on the third trophic level

There was no difference in mummified aphid abundance between the fertilizer treatments (N and N + straw), but both treatments were higher than the control before the aphid abundance peak (F (2, 4) = 11.470, P = 0.022, Fig. 2c). Before the peak, parasitism rates in the control, N, and N + straw treatments were similar (F (2, 4) = 1.178, P = 0.396, Fig. 2e). During the peak period, there was still no difference in mummified aphid abundance between the N and N + straw treatments, while the control had the highest abundance (F (2,4) = 23.446, P = 0.006, Fig. 2d). The parasitism rate for the control and N treatments was lower than that for the N + straw treatment (F (2, 4) = 9.333, P = 0.031, Fig. 2f), but only in the peak period. In a comparison of the N and N + straw treatments, which had similar amounts of mineral fertilizer, the maize straw amendment was found to benefit the parasitism rate only during the peak aphid period; however, the mummified aphid abundance did not differ in any period.

Contributions of soil and plant chemical compounds to variation in pest control

There was variation mainly in soil C and N, plant nutrients, and chemical defense compounds across fertilization regimes (Part 2 in Supporting Information, Table S3) but variation in total aphid abundance was not related to soil total N, total C, or the C/N ratio. Only the mummified aphid abundance was negatively related to soil total N, and it was positively related to the C/N ratio at the peak aphid time

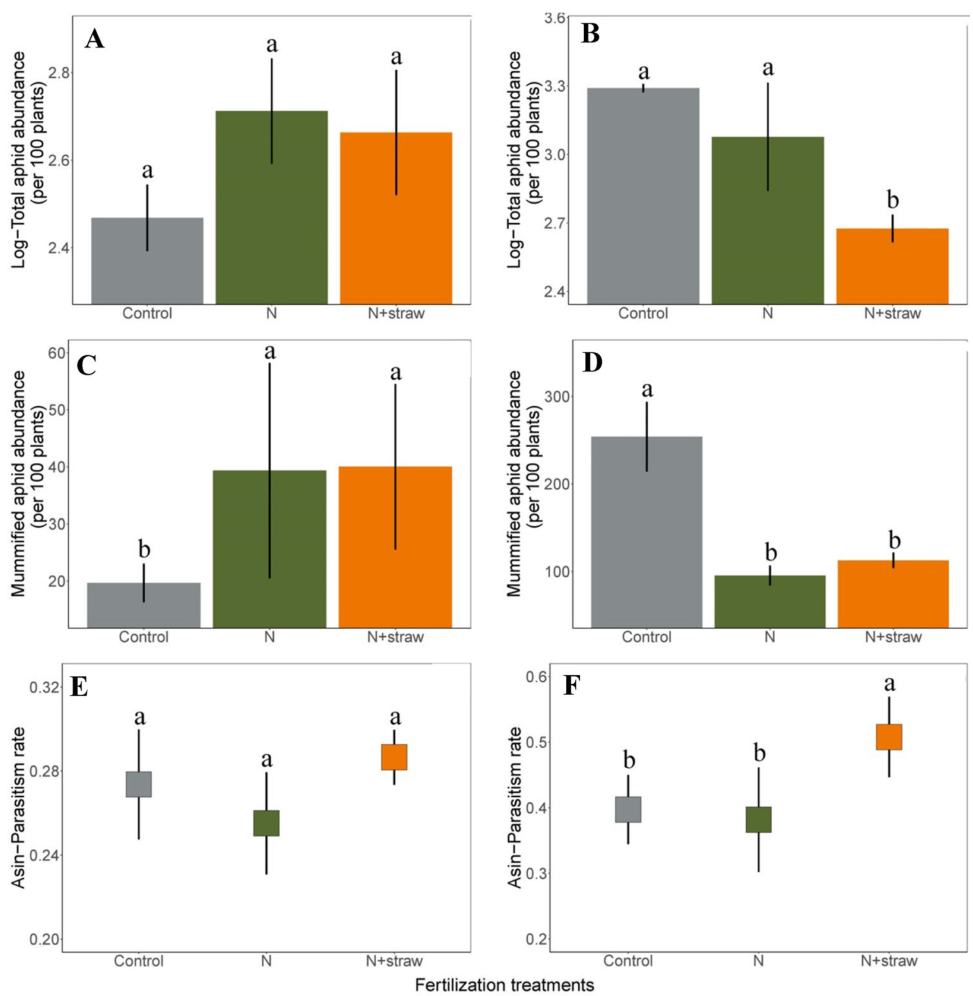

Fig. 2 Aphid abundance, mummified aphid abundance, and parasitism rate (mean ± SE) response to fertilizer treatments in a field-scale experiment. **a** Aphid abundance estimates 7 days before peak aphid period (May 3); **b** aphid estimates at peak abundance; **c**, **e** 7 days before peak aphid period (May 3); and **d**, **f**) at the peak period (May 10)

(Table 2). Plant soluble sugar content had a positive effect on aphid abundance but a negative effect on parasitism rate during the peak aphid period. Total free amino acid content was negatively related to aphid abundance ($r = -0.817$) but positively related to parasitism rate ($r = 0.691$) during the peak aphid period (Table 2). The assayed plant defense compounds, including L-DOPA, L-ornithine, and nonstructural phenolics, were not associated with total aphid abundance or parasitism rate. Mummified aphid abundance was negatively related to L-ornithine ($r = -0.825$) only at the peak aphid period (Tables 1 and 2).

Predicting effects of organic fertilizer on pest control service on a landscape scale

Over the three regions (A, B, and C, Fig. 1), when organic fertilizer (maize straw amendment) was used in more than 79% of fields within the cropland (regions A and B), aphid abundance was lower (F (2,41) = 4.931, $P = 0.012$, Fig. 3a). Where organic fertilizer was used in all fields (region A), there was no difference in aphid abundance compared with cropland in which 79% fields received organic fertilizer (region B). By comparison, mummified aphid abundance was different between regions (F (2, 41) = 5.287, $P = 0.009$, Fig. 3b), and cropland that had more than 47% of fields using only mineral fertilizer (region C) had the lowest level. The parasitism rate was similar between regions A and B, and rates in both were higher than in region C (F (2, 41) = 5.283, $P = 0.008$, Fig. 3c). In the scaling-up prediction after 100 iterations of model fits (Table S5), aphid population growth provided little explanation for aphid abundance compared with parasitism functional responses or spatial covariance of aphid and parasitoid density. The statistically relative key factor accounting for aphid abundance variation on a landscape scale was the covariance term (Fig. 3d).

Discussion

Maize straw amendment benefited suppression of aphid abundance and a higher parasitism rate during the peak aphid period. Free amino acid type and content were much more important than plant defense compounds in explaining pest suppression variance between fertilization measures and had a negative effect on aphid abundance. On a landscape scale, cropland with a higher proportion of fields with organic fertilizer had increased levels of biocontrol. Wheat yield also benefited on both a local and a landscape scale (Part 4 in supporting information). Therefore, from local to agri-landscape scales, combined organic and mineral fertilizer treatments resulted in spatial plant nutritional diversity, which we suggest is an important aspect in cropland management of pest control.

Table 1 Correlations among soil total C and N, C:N ratio, plant chemical compounds, aphid and mummified aphid abundance, and parasitism rate 7 days before peak aphid period in a field-scale experiment

	Soil total N (mg/kg)	Soil total C (mg/kg)	C:N ratio	Soluble sugars (mg/g)	Amino acids (mg/g)	L-DOPA (μg/g)	L-ornithine (μg/g)	Phenolic (μg/g)	Aphid/100 plants	Mummies/100 plants	Parasitism rate
Soil total N	1										
Soil total C	0.818**	1									
C:N ratio	−0.730*	−0.206	1								
Soluble sugars	−0.660	−0.514	0.517	1							
Amino acids	0.020	0.212	0.171	0.164	1						
L-DOPA	0.608	0.460	−0.488	−0.578	−0.452	1					
L-ornithine	0.839**	0.820**	−0.471	−0.816**	0.112	0.532	1				
phenolic	−0.745*	−0.335	0.876**	0.399	0.204	−0.529	−0.537	1			
Aphid	0.480	0.439	−0.261	−0.051	−0.071	0.368	0.367	−0.512	1		
Mummies	0.430	0.200	−0.479	0.046	0.082	0.170	0.290	−0.649	0.866**	1	
Parasitism rate	−0.061	−0.423	−0.409	0.204	0.057	−0.361	−0.082	−0.413	0.116	0.560	1

All correlation coefficients are shown in the table

**$P < 0.01$; *$P < 0.05$

Table 2 Correlations among soil total C and N, C:N ratio, plant chemical compounds, aphid and mummified aphid abundance, and parasitism rate at the peak abundance period in a field-scale experiment

	Soil total N (mg/kg)	Soil total C (mg/kg)	C:N ratio	Soluble sugars (mg/g)	Amino acids (mg/g)	L-DOPA (μg/g)	L-ornithine (μg/g)	Phenolic (μg/g)	Aphid/100 plants	Mummies/100 plants	Parasitism rate
Soil total N	1										
Soil total C	0.818**	1									
C:N ratio	−0.730*	−0.206	1								
Soluble sugars	−0.035	−0.511	−0.519	1							
Amino acids	0.356	0.541	0.050	−0.498	1						
L-DOPA	0.426	0.205	−0.485	0.133	0.536	1					
L-ornithine	0.893**	0.702*	−0.714*	−0.022	0.377	0.574	1				
phenolic	−0.148	−0.184	0.045	0.012	−0.573	−0.391	−0.433	1			
Aphid	−0.233	−0.466	−0.125	0.689*	−0.817**	−0.410	−0.402	0.554	1		
Mummies	−0.771*	−0.439	0.816**	0.008	−0.357	−0.622	−0.825**	0.200	0.402	1	
Parasitism rate	−0.218	0.227	0.608	−0.718*	0.691*	0.108	−0.003	−0.506	−0.828**	0.149	1

All correlation coefficients are shown in the table

** $P<0.01$; * $P<0.05$

Aphid responses to maize straw amendment and mineral fertilizers

Soil nitrogen fertilizer significantly influences aphid abundance (Butler et al. 2012), but the effects of plant composts-based organic fertilizer on herbivores are divergent and context dependent (Garratt et al. 2011). We found that the effect of maize straw amendment on aphid abundance was time specific. Seven days before the aphid population peak (May 3), aphid abundance did not change in response to maize straw amendment. However, significant differences in aphid abundance were observed during the peak aphid period between treatments with and without maize straw amendment (N vs. N + straw). It is possible that the organic fertilizer improved the ability of plants to adjust their nutrient and defense compounds to levels that adversely affected aphid feeding.

The amino acid content in plant phloem sap constitutes a key aspect of aphid nutrient acquisition and the effects are species specific (Douglas 2006). For example, *Myzus persicae* (Sulzer) preferred young leaves with high levels of free amino acids even though such leaves generally have higher contents of defense compounds such as glucosinolates (Cao et al. 2018). *Schizaphis graminum* (Rondani) and *Diuraphis noxia* (Kurdjumov) could significantly change the nutritional quality to benefit their feeding, but *R. padi* could not change host nutritional quality (Sandstrom et al. 2000). This finding suggests that *R. padi* is passively sensitive to the temporal nutrient quality of cereal plants (Garratt et al. 2010). Plants are known to regulate their primary metabolism in response to herbivory (Zhou et al. 2015; Jakobs et al. 2018). When sucking insect pests feed upon plants, the plants may transport amino acids via phloem to the attacked tissue to produce defense-related metabolic compounds and move amino acids away from insect feeding sites (Zhou et al. 2015). Tyrosine and phenylalanine are related to the biosynthesis of benzenic and aliphatic glucosinolates, which can reduce herbivory (Sønderby et al. 2010). Proline has been linked to oxidative burst and hypersensitive responses to herbivory via sucking (Zeier 2013). As found in our study, wheat grown with the N + straw treatment had high levels of tyrosine, isoleucine, and proline, but lower phenylalanine content, compared with wheat grown with the N treatment (Figure S1). Aphid abundance differences between treatments may largely result from bottom-up effects of fertilizer measures through variation in plant free amino acid content. The relationship between the specific types of free amino acids and aphid abundance was negative (Figure S2 and 3), but the content of plant defense compounds (L-DOPA, L-ornithine, or non-structural phenolics) was uncorrelated with aphid abundance across treatments (Tables 1 and 2). How the improved plant resistance to aphids by maize straw amendment was related to higher free amino acid requires further exploration.

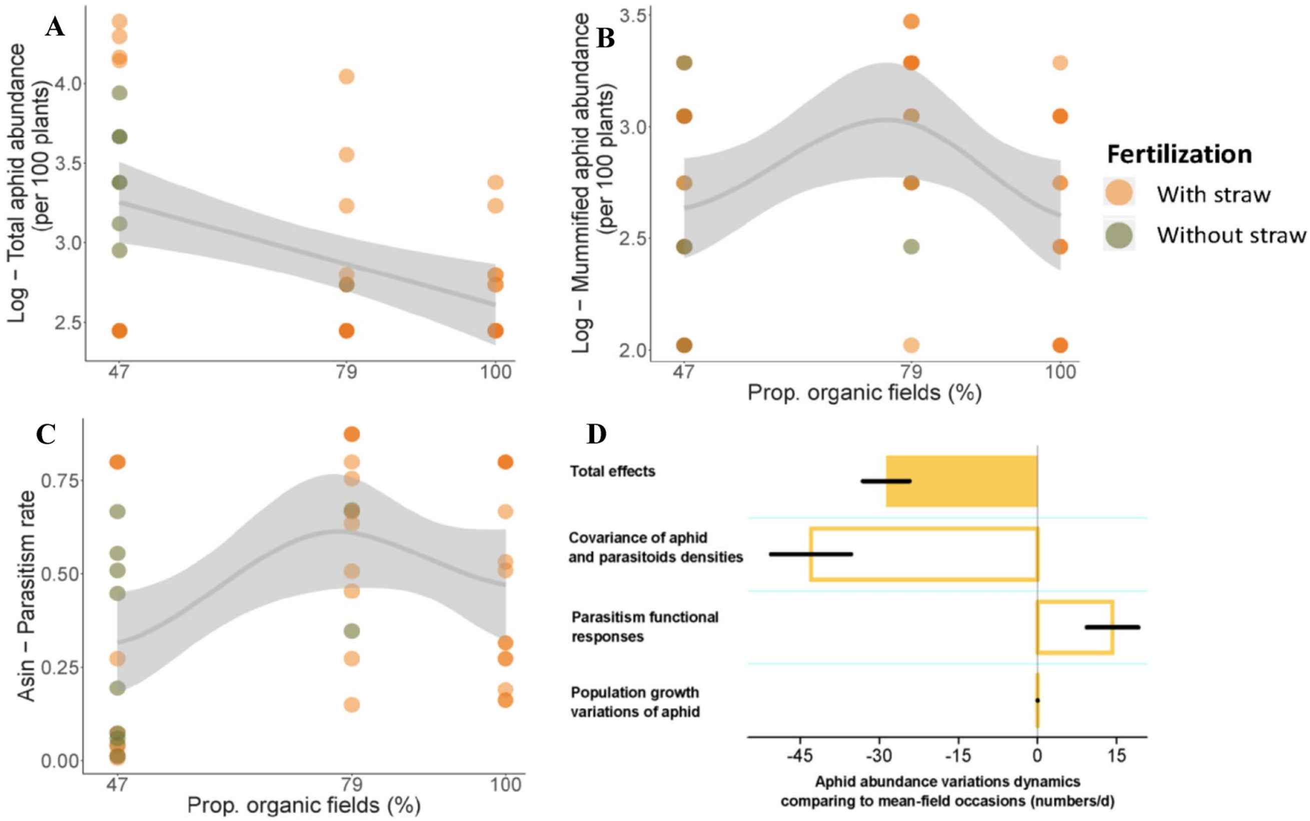

Fig. 3 Comparison and trend predications of aphid abundance and biological control efficiency by parasitoids across regions with different proportions of organic fertilizer fields and contributions of each scale transition term (mean ± SE) to aphid abundance from scaling up the model prediction. **a** Total aphid abundance, **b** mummified aphid abundance, and **c** parasitism rates were the average values of each region. Proportions of fields with straw amendment on a regional scale ranged from 47%, 79%, to 100% and pertains to regions **c**, **b**–**a** (see Fig. 1). **d** The x-axis indicates the estimated coefficient (mean ± SE) from fitting the scaling-up model. Total effect was given by the sum of values of the other three coefficients in this plot

Bottom-up effects of fertilizer on biological control by parasitoids

Parasitoids, as the third trophic level in the study, showed a significant response to fertilizer treatments. Plant residues, as a typical means of adding organic fertilizer, may be valuable for pest control under ecological intensification (Ramsden et al. 2016). Before or around the peak aphid abundance, mummified aphid abundance did not differ between the N and N + straw treatments. However, the parasitism rate was the highest in the N + straw treatment during the peak aphid period, suggesting the biological control by parasitoids benefited from the maize straw amendment.

Compared with no fertilizer, treatments of N and N + straw that applied mineral fertilizer had a negative effect on mummified aphid abundance in the peak aphid period. The added soil nitrogen fertilizer may have directly influenced the parasitoid responses to aphids (Aqueel et al. 2015). Sarfraz et al. (2009) found that *Plutella xylostella* (L.) that developed on canola (*Brassica napus* L.) treated with a high level of nitrogen fertilizer had lower *Diadegma insulare* (Cresson) parasitism.

We found that free amino acid type and content in plants were positively related to the mummified aphid abundance and parasitism rate (Figures S2 and S3). Since primary parasitoids are mostly specialists (Evans 2018), they rely on the herbivores for their fecundity and development (Cusumano et al. 2018). Herbivore-induced plant volatiles are related to amino acid metabolism (Zhou et al. 2015), and they attract parasitoids to sites with hosts (Islam et al. 2017). Weber et al. (2020) found that abundant amino acids in leaves supported higher success of aphid parasitoid development. These findings indicate that the three trophic levels are potentially linked through amino acid–mediated host orientation and nutrition delivery. In our study, despite similar mummified aphid abundance, aphid abundance was much lower for sites treated with fertilizer paired with maize straw amendment. We conclude that maize straw amendment hold promise for benefiting biological control by parasitoids.

Predicting organic fertilizer effects on pest control within an agricultural landscape

Cropland diversity and the level of intensification are important components of the agricultural landscape that shape pest and parasitoid responses (Tscharntke et al. 2016; Karp et al. 2018), such as differences associated with local mineral vs. organic fertilizer use (Comte et al. 2013). However, how biocontrol on larger spatial scales is influenced by fertilizers has not been widely studied. In our study, biological control of aphids benefited from croplands having a high proportion of fields treated with organic fertilizer. Spatial heterogeneity of crop planting configuration or species composition on agri-landscape scales contributes to pest control (Baillod et al. 2017; Karp et al. 2018). In addition, Wetzel et al. (2016) suggested that plant nutrient diversity over large spatial scales could also work to decrease herbivore fitness. Fields treated with organic and mineral fertilizer that are randomly distributed within cropland result in spatial nutrient diversity, which serves as a new aspect of landscape heterogeneity for pest control.

Scaling up modeling predictions suggested that, with an increase in spatial scale (from field-scale to landscape-scale fertilization differences), spatial covariance between aphid and parasitoid densities was the key factor explaining aphid abundance variation on a landscape scale. Parasitism functional responses was the second largest driving variable, and aphid growth variation was minimally important. Habitat effects on the abundance of pests and their natural enemies and the movements of both depend on the spatial scale (Bommarco and Banks 2003; Bianchi et al. 2010; Schellhorn et al. 2014, 2015; Tscharntke et al. 2016). Aphid population growth is influenced by local field factors such as host plant defensive compounds (Cao et al. 2018), nutrient availability (Sandstrom et al. 2000; Garratt et al. 2010), negative density dependence (Honek et al. 2006), and even interspecific or intraspecific competition (Petersen and Sandström 2001; Zytynska and Preziosi 2013). Parasitoids can disperse long distances (Evans et al. 2015; Evans 2018) and are more likely to be influenced on scales greater than a field (about 0.3 ha). Because parasitism functional responses in fields with organic fertilizers commonly resulted in a high parasitism rate, we assumed turnover (Beduschi et al. 2018; Winfree et al. 2018) of parasitoid communities between fields with organic fertilizer would be much higher than in fields with organic and mineral fertilizers. A high frequency of parasitoid movement between fields with organic fertilizer may have produced a similar community structure. Parasitoid turnover could be one potential mechanism in aphid abundance fluctuations in an agricultural landscape.

Conclusion

To enable further development of ecological intensification of agriculture, organic fertilization using plant straw amendment is a promising measure for sustainable pest control and environmental protection. In the current study, bottom-up effects of maize straw amendment were mainly attributed to increased concentrations of free amino acids suppressing aphid abundance and promoting biological control by parasitoids. Cropland dominated by the use of organic fertilizer had greater aphid suppression and a high parasitism rate. Scaling up the bottom-up effects from the field scale to the landscape scale showed that spatial covariance of aphid and parasitoid densities was the key driver in aphid abundance variation on a landscape scale. In addition, randomly distributed fields treated with organic or mineral fertilizer produced a nutrient-diversified cropland. This nutrient diversity could enable fluctuation of herbivore abundance over large spatial scales. Nutrient diversity has not been considered in previous studies (Wetzel et al. 2016), and it needs to be integrated in describing landscape heterogeneity, especially in agricultural landscape research.

Authors' contributions

The study was conceived by FO, FG, and SG. The field experiment was designed by JL and RH, and field work was carried out by SG. Large spatial scale investigation was conducted by XM and QZ, and the supplied dataset over space was compiled by QZ. The sample assays and scaling up modeling were done by SG and MPZ, and SG led the composition of the manuscript. All authors contributed to drafts of the manuscript and gave final approval for publication.

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Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

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