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Effects of agricultural intensification on ability of natural enemies to control aphids

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Agricultural intensification through increasing fertilization input and cropland expansion has caused rapid loss of semi-natural habitats and the subsequent loss of natural enemies of agricultural pests. It is however extremely difficult to disentangle the effects of agricultural intensification on arthropod communities at multiple spatial scales. Based on a two-year study of seventeen 1500 m-radius sites, we analyzed the relative importance of nitrogen input and cropland expansion on cereal aphids and their natural enemies. Both the input of nitrogen fertilizer and cropland expansion benefited cereal aphids more than primary parasitoids and leaf-dwelling predators, while suppressing ground-dwelling predators, leading to an disturbance of the interspecific relationship. The responses of natural enemies to cropland expansion were asymmetric and species-specific, with an increase of primary parasitism but a decline of predator/pest ratio with the increasing nitrogen input. As such, agricultural intensification (increasing nitrogen fertilizer and cropland expansion) can destabilize the interspecific relationship and lead to biodiversity loss. To this end, sustainable pest management needs to balance the benefit and cost of agricultural intensification and restore biocontrol service through proliferating the role of natural enemies at multiple scales.

In an agroecosystem, arthropods provide important ecosystem services due to their abundance and diversity; such service can be sustained and even enhanced by conserving semi-natural and natural habitats within agricultural landscapes^{1,2}. This is because many arthropod species are very mobile and need to cross multiple habitats, including both crop and semi-natural habitats, for food and refuge^{3,4}. Indeed, heterogeneous landscapes with a high proportion of semi-natural habitats can sustain a high diversity of aphid natural enemies including specialists and generalists, a prerequisite for effective biocontrol^{5,6}. As such, the provision of arthropod ecosystem service in croplands is sensitive to resource availability in surrounding semi-natural habitats⁷.

Agricultural intensification, through increasing fertilization input within fields and cropland expansion at landscape scales, is considered a key driver of biodiversity loss and the decline of ecosystem services⁸. To this end, habitat management which optimizes the effect of agricultural landscape structure on the efficacy of biological control of agricultural pests has become a new paradigm for sustainable pest management^{7,9}. At the field scale, agrochemical inputs can have great impacts on arthropod communities through changing plant nutrition, resulting in a rapid biodiversity loss in agroecosystems^{10–12}. Increasing fertilizer input within fields affects insects differently due to the asymmetric responses of different species to changing host nutrition. Phytophagous insects, which have a relatively rapid developmental rate in high-nutrition plants, are more sensitive to changes in host nutrition than their natural enemies¹³. Changes in plant nitrogen availability could trigger a bottom-up effect on insect survival and the interaction between insect herbivores and pathogenic fungi^{14,15}. At the landscape scale, cropland expansion (increasing the proportion of cropland in agricultural landscapes) has been shown to negatively affect biocontrol efficacy by disproportionately harming the natural enemies of agricultural pests^{16,17}.

The effects of landscape structure on pest populations can vary with spatial scale; that is, habitat management should be prioritized at a specific spatial scale^{7,18,19}. The negative effect of agricultural intensification on biocontrol often peaks at a specific spatial scale²⁰. As such, habitat management is proven here to be most effective at the optimal spatial scale while making little contribution at other spatial scales²¹. Moreover, the response of arthro-



Pods to landscape structures could also be scale dependent due to species-specific dispersal ability. For species with strong dispersal ability (e.g. flying predators such as hover flies, lady beetles, and lacewings), habitat management should target large spatial scales, while improving local habitat quality can enhance the activity of species with weak dispersal ability (e.g. walking predators such as spiders and Carabid beetles). For example, the species diversity and abundance of ground-dwelling arthropods could increase after planting grass strips every 200 m, supplying alternative food resources and refuge for these natural enemies^{9,22}. These grass strips can act as banker plants which release the natural enemy when pest populations increase in crop fields and conserve them after harvest²³. Some field experiments have examined the effects of landscape complexity on predation and parasitism at either the field or landscape scales, but to date studies have not examined both scales concurrently²⁴.

Higher levels of ecosystem service provision are sometimes achieved through interactions of species from different functional groups²⁵, making assessing the effects of agricultural intensification rather challenging. Many arthropod species belong to different functional modules in the insect community of wheat fields (e.g. cereal aphid, predator, and parasitic wasp), forming complicated food webs¹¹. Therefore, landscape modification differentially benefits some species over others, complicating the biocontrol of cereal aphids by their natural enemies^{26,27}. To date, most research has been conducted for specific insect modules at one particular scale, emphasizing the need for experiments at multiple scales and targeting multiple functional modules¹¹.

Here, we conducted a field experiment of collecting cereal aphids and their natural enemies of different functional modules in Northwest China to elucidate the effects of agricultural intensification at both field and landscape scales. Based on empirical evidence and existing hypotheses in the literature, we specifically addressed two research questions: i) whether the effects of agricultural intensification on population and community structures differ at the field and landscape scale; ii) the potential mechanism behind the scale dependence of the effects of agricultural intensification (increasing fertilizer input and cropland expansion) on agricultural arthropods.

Results

Effect of nitrogen fertilizer. In the experiment, the amount of nitrogen fertilizer ranged from 115.8 kg/ha to 170.6 kg/ha while the proportion of cropland ranged from 63.73% to 90.25% (see supplementary Table S1). In total, we collected 24,672 individuals including 19,723 cereal aphids, 3,679 primary parasitoids, 843 leaf-ground predators, and 427 ground-dwelling predators.

All selected species (two species in each functional group) were significantly affected by the increasing input of nitrogen fertilizer within the sampled fields (Figure 1, see supplementary Table S2). Specifically, the increasing input of nitrogen fertilizer led to the increase of the population densities of cereal aphids, their primary parasitoids, and leaf-dwelling predators. The correlation coefficient between population density and nitrogen input ranged from 0.3365 (*Syrphus nitens*) to 0.8653 (*Aphidius gifuensis*), showing different sensitivity to applying nitrogen fertilizer within the field (e.g. a positive correlation for primary parasitoids, in contrast to a negative correlation for ground-dwelling predators; Figure 1, see supplementary Table S2). The abundance of cereal aphids increased more rapidly than their natural enemies in response to the increasing input of nitrogen fertilizer, followed by the primary parasitoids (Figure 1, see supplementary Table S2), indicating a weakening effect of biocontrol service from applying nitrogen fertilizer within the field in agroecosystems.

Effect of cropland expansion. At the population level, agricultural intensification (AI) caused by increasing proportion of cropland has a positive effect on the abundance of cereal aphids at all spatial scales

except when measured at the broadest scale (1500 m; Figure 2, see supplementary Table S3). The correlation coefficients between the proportion of cropland and the population densities of the two aphid species (*Sitobion avenae* and *Schizaphis graminum*) peaked at the scales of 800 m and 200 m, respectively. Furthermore, the correlation coefficients for primary parasitoids and leaf-dwelling predators were positive, which peaked at the scales of 200 m and 500 m. In contrast, the correlation coefficients became negative for ground-dwelling predators (see supplementary Table S3). Overall, at broad scales increasing proportion of cropland had a positive effect on cereal aphids, leaf-dwelling predators and primary parasitoids but had a negative effect on ground-dwelling predators (Figure 2, see supplementary Table S3). Moreover, the response of cereal aphids and their natural enemies to cropland expansion was species specific. The parasitic wasps were more sensitive than cereal aphids to cropland expansion across multiple scales, while even species within the same module (e.g. the two leaf-dwelling predators, *H. variegata* and *S. nitens*) responded differently (Figure 2, see supplementary Table S3).

Impact on biocontrol and diversity. At the community level, the increasing input of nitrogen fertilizer significantly enhanced the primary parasitism in wheat field ($F_{1,101} = 6.31$, $P = 0.013$, Figure 3A) but negatively affected the predator/pest ratio (Leaf-dwelling predator: $F_{1,101} = 4.29$, $P = 0.041$; Ground-dwelling predator: $F_{1,101} = 8.11$, $P = 0.005$, Figure 3B, C). The increasing input of nitrogen fertilizer was also detrimental to the species diversity of natural enemies in the wheat field ($F_{1,101} = 7.72$, $P = 0.006$, Figure 3D).

Moreover, we selected the scale of 500 m to examine the effects of the proportion of cropland on predation and parasitism, showing an insignificant effect on primary parasitism ($F_{1,101} = 2.36$, $P = 0.127$, Figure 4A) but a negative effect on the predator/pest ratio (Leaf-dwelling predators: $F_{1,101} = 5.58$, $P = 0.020$; Ground-dwelling predators: $F_{1,101} = 6.97$, $P = 0.010$, Figure 4B, C) and a negative effect on the species diversity of natural enemies ($F_{1,101} = 6.61$, $P = 0.012$, Figure 4D).

Discussion

Differential responses to agricultural intensification. Our results show that the input of nitrogen fertilizer facilitates the cereal aphid populations. Surprisingly, increasing nitrogen input did not suppress the activity of parasitic wasps; rather, it slightly increased the parasitism of cereal aphids, contrasting the result from Lohaus *et al.* (2013) that the parasitism of cereal aphids showed no difference between conventional and organic wheat fields²⁸. However, the density of cereal aphids still increased with the input of nitrogen fertilizer due perhaps to the rapid development of cereal aphids in high-nitrogen wheat fields²⁹. As such, cereal aphids were not controlled by the high parasitism driven by the high nitrogen input. Other possible reasons include that species at the higher trophic level (hyperparasitoids) may also gain benefits from nitrogen input and pose a top-down interference to the interaction between cereal aphids and their primary parasitoids^{27,30}. These results suggest that several modules (parasitoids, leaf- and ground-dwelling predators) can have strong complementary effects on the biological control of cereal aphids in wheat fields^{6,11,31}.

Landscape simplification (i.e. a high percentage of arable lands in agricultural landscapes or homogeneous landscape structure) can have a negative effect on biological control of cereal aphids^{32,33}. Here, the correlation between the percentage of arable lands in the agricultural landscape and parasitism decreased as the spatial scale increases, suggesting that parasitic wasps might respond to changes in landscape structure at small spatial scales²⁸. Additionally, agricultural intensification can facilitate the population growth of cereal aphids due to the abrupt decline of natural enemy/pest ratio³⁴. The

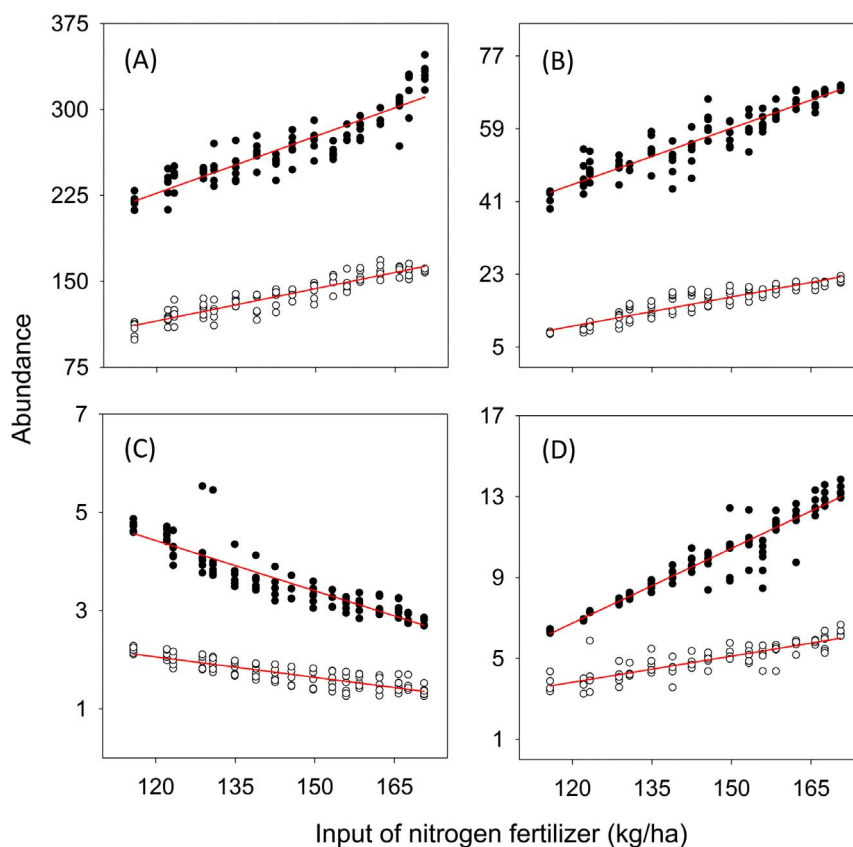


Figure 1 | The effects of input of nitrogen fertilizer on cereal aphids and their natural enemies in wheat fields ((A) cereal aphids: solid circular indicates *Sitobion avenae* (Fabricius), hollow circular indicates *Schizaphis graminum* (Rondani); (B) parasitic wasps: solid circular indicates *Aphidius avenae* Haliday, hollow circular indicates *Aphidius gifuensis* Ashmead; (C) leaf-ground predators: solid circular indicates *Hippodamia variegata* (Goeze), hollow circular indicates *Syrphus nitens* Zetterstedt; (D) ground-dwelling predators: solid circular indicates *Pardosa astrigena* L. Koch hollow circular indicates *Chlaenius spallipes* Geb).

abundance of ground-dwelling predators decreased significantly with increasing proportion of cropland at all spatial scales, suggesting that a homogenous landscape cannot stabilize the population density of natural enemies due to the importance of semi-natural habitats to the recruitment of natural enemies^{17,35,36}. Therefore, agricultural intensification, including increasing fertilizer input within fields and cropland expansion at the landscape scale, can disturb the interspecific relationship of arthropod community in wheat fields, which may have a negative effect on biocontrol of cereal aphids.

Strong evidence shows that species within a same functional module can respond differently to changes in landscape structure^{37,38}. For example, ladybirds and parasitic wasps differ greatly in their dispersal ability and thus respond differently to changes in landscape composition across spatial scales³⁹. Wheat crop is attacked by multiple pest species which are then attacked by multiple natural enemies that perceive/use the mosaic landscape differently at different spatial scales⁴⁰. Based on our results, the spatial range for analyzing the effect of landscape structures on insect communities varied depending on the particular functional groups¹¹.

Potential mechanism of differential responses. In agroecosystems, agricultural intensification is the most important driver for changing the land cover and soil structure^{6,23}. In particular, nitrogen deposition in China's agroecosystem has increased by about 60% in the past three decades⁴⁵, causing great disturbance to the food web of arthropods. On the one hand, although increasing nitrogen fertilizers has directly proliferated crop nutrition and yield, it also accelerates the development rate of herbivorous insects and their natural enemies to a different extent, with the outbreak of pests

causing serious damage to crops. Two hypotheses have been proposed so far to explain the effect of increasing nitrogen fertilizer input on insect performance, namely the plant vigor hypothesis and nitrogen limitation hypothesis¹⁵. These hypotheses argue that the nitrogen content in plants is an important limiting factor which dictates the developmental rate, breeding, behavior, and fecundity of insect herbivores. Contrast to their natural enemies, these insect pests could benefit more from increasing nitrogen fertilizer input due to the direct improvement of both food quantity and quality.

On the other hand, cropland expansion further provides more resources and habitats for insect pests (resource concentration hypothesis), while the decline of semi-natural habitats from the expansion eliminates alternative preys and refuges of natural enemies^{41,42}. Moreover, landscape simplification could cause the rearrangement of habitat patches and reallocation of plant resources. These changes could further affect the population dispersion and host searching. The asymmetric responses of cereal aphids and their natural enemies to cropland expansion could therefore cause the shifts observed in community structure, leading to biocontrol loss under agricultural intensification³⁰.

Conclusion. Global environmental changes have been occurring at multiple spatial scales and are an important driver of changes in biodiversity composition and population dynamics. Increasing nitrogen input can facilitate the population of parasitic wasps while suppressing the activity of ground-dwelling predators⁴³, all greatly affecting the community structure of natural enemies within fields. Cropland expansion in agricultural landscapes can

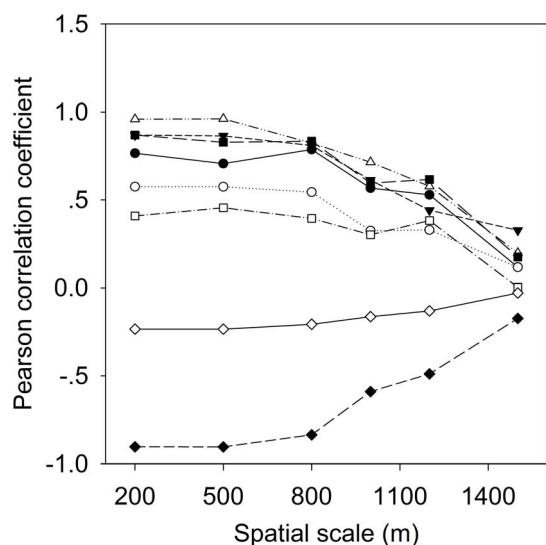


Figure 2 | Effect of spatial scales on the Pearson correlation between the proportion of cropland and the abundance of cereal aphids and their natural enemy in agricultural landscapes (cereal aphids (individuals/100 straws): solid circular indicates *S. avenae*, hollow circular indicates *S. graminum*; primary parasitoids (individuals/100 straws): solid triangle indicates *A. avenae*, hollow triangle indicates *A. gifuensis*; leaf-ground predators (individuals/100 nets): solid square indicates *H. variegata*, hollow square indicates *S. nitens*; ground-dwelling predators (individuals/traps): solid rhomb indicates *P. astrigena*, hollow rhomb indicates *C. spallipes*).

also shift the natural enemy community, causing the loss of biocontrol service and the outbreak of cereal aphids at landscape scale. Therefore, agricultural intensification at both the field and landscape scales can disturb the food web structure of arthropods

and destabilize the interaction between cereal aphids and their natural enemies^{21,35}. Habitat management for sustainable pest management should be conducted at multiple spatial scales including the field and landscape scales^{46,47}.

The marked changes of different species modules in response to agricultural intensification suggest that studies on isolated modules could be misleading, and that quantitative food web metrics need to be considered in future research^{37,44}. Future studies should compare functional groups or interspecific relationship of all species in landscapes with different levels of complexity in patch arrangement and spatial structure in order to distinguish between the intraguild effects of different biocontrol agents working at different spatial scales^{7,28,48}.

Methods

The study area. This experiment was conducted near the city of Yinchuan, Ningxia Hui Autonomous Region of Northwest China. This agricultural region (Yinchuan plateau, 1100–1200 m a.s.l) has a temperate continental climate and a long history of crop culture. The area has an average 3,000 h p.a. of sunshine and an annual mean temperature of 13.1°C. The type of soil is Chernozem, a typical type of the region. The area has experienced drastic land use changes from natural habitats to arable land, forming a gradient of landscape simplification through agricultural intensification in the past decades. The landscape mosaic consists of different habitat patches including crops, fallow land, grasslands, and woodlands. Agricultural management within crop fields has led to a gradual change of soil chemical composition through frequent use of nitrogen fertilizer for sustaining high crop yields. These changes could have affected the distribution and composition of arthropod communities in wheat fields at both local and regional scales.

Seventeen agricultural sites (see supplementary Table S1) were selected along a gradient of landscape simplification in a radius of 1500 m among sites, from intensive agricultural sites with a high percentage of arable land (maximum value = 83.26%) to sites with a low percentage of arable land (minimum value = 55.82%). Semi-natural habitats in these sites, including woodlands and fallow land, remained unchanged during the experiment period from 2010 to 2011⁴⁹. The nearest neighbor distances of these sites ranges from 3000 m to 5600 m.

The experimental region had an old planting history (>30 years) of wheat crop. Three wheat fields in the center of 1500 m radius were selected in each site. To simplify the experiment design, we chose the wheat fields with the same wheat variety and soil type. This has been shown to be an appropriate method for studying the effect

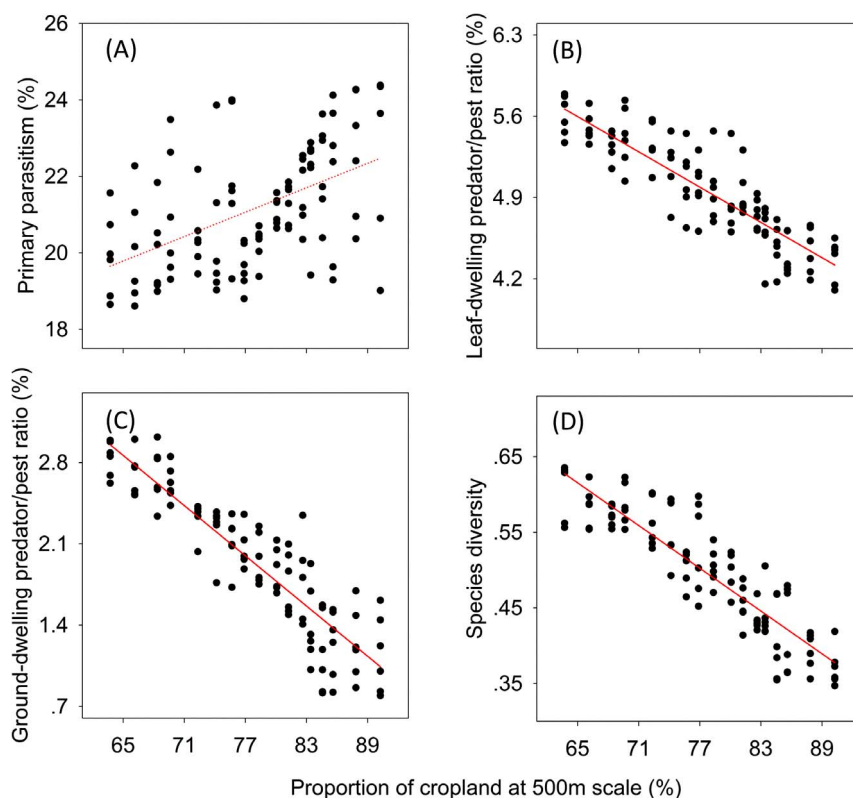


Figure 3 | The effects of nitrogen fertilizer input on parasitism, predator/pest ratio, and species diversity in wheat fields ((A) primary parasitism; (B) predator/pest ratio for leaf-ground predators; (C) predator/pest ratio for ground-dwelling predators; (D) species diversity).

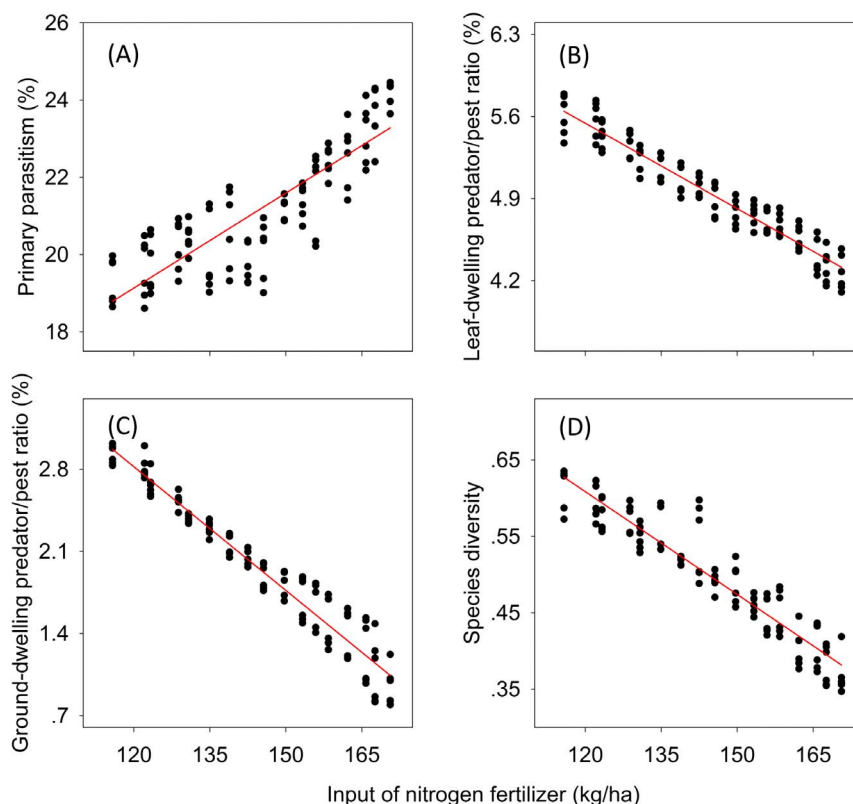


Figure 4 | The effects of the proportion of cropland at the 500 m scale on parasitism, predator/pest ratio, and species diversity in wheat fields ((A) primary parasitism; (B) predator/pest ratio for leaf-ground predators; (C) predator/pest ratio for ground-dwelling predators; (D) species diversity).

of landscape structure on arthropod communities^{7,17,50}. Wheat density was kept to about 400–450 plants per m², and the irrigation was kept nearly the same across all studied wheat fields, each year from March to June.

Insect sampling. Two dominant pests, *Sitobion avenae* (Fabricius) and *Schizaphis graminum* (Rondani), and their primary parasitoids, leaf- and ground-dwelling predators were investigated in the field experiment. As the primary parasitoids spend their whole larval stage in the mummies of cereal aphids, they can be investigated at the same time. In each field, five randomly-selected points were used to sample cereal aphids and their primary parasitoids by visual inspection and hand collection⁴⁹. In each point, 100 wheat tillers were selected for investigation (5 minutes for cereal aphid and 15 minutes for primary parasitoids). All fields were sampled within a two-day period (for diminishing potential stochasticity); three times per year (14th–15th, 19th–20th, and 24th–25th of May -when the population of cereal aphids peaks). All cereal aphids and their natural enemies were collected before pesticide application (30th May–5th July) to ignore the effect of pesticides on the experiment. All aphid mummies were taken back to the laboratory and reared in the gelatin capsules for 30 days. The hatched adults of primary parasitoids were collected and conserved in 90% ethyl alcohol.

The ground-dwelling predators (e.g. Carabid beetles and spiders) are important natural enemies of aphids⁵¹. We used pitfall traps for collecting ground-dwelling predators at the same five randomly-selected points. In each pitfall trap (6.5 cm in diameter and 11 cm high), 60 mL mixture of vinegar, sugar, propylene glycol and water at a ratio of 2 : 1 : 1 : 20 were filled in a 0.2-L plastic cup. An odorless detergent (0.3%) was added into the trap to break the surface tension of the mixture. Ground-dwelling predators were collected 3 times from 10th to 25th of May in each year. In every time, the trap was open for five days. Population density of ground-dwelling predators was calculated in individuals per 5 traps.

The same five randomly-selected points were also used to collect leaf-dwelling predators (coccinellids, syrphids and lacewings); we used a sweep net (200 meshes) for this purpose at the same period of pitfall trapping⁵¹. We sampled 10 times (nets) per point by sweeping and thus 50 times (nets) per wheat field. The leaf-dwelling predators collected in the sweeping were transferred into finger shaped bottles, with 80% ethyl alcohol added into each bottle to preserve the samples. Population density of leaf-dwelling predators was calculated in individuals per 10 nets. All adult primary parasitoids, ground- and leaf-dwelling predators were identified to species according to their morphological and taxonomic characteristics.

Field and landscape survey. Within each field scale, landowners were surveyed by questionnaires and data was collected regarding type of the fertilizer, insecticide, and yield. These three variables were obtained through two questions: 1) What is the

amount of fertilizer applied per hectare and its composition? 2) What is the average yield in sampled wheat fields? Because nitrogen fertilizer is the main limiting resource for wheat growing and breeding, we calculated the amount of nitrogen fertilizer applied based on the answers to question 1.

At the landscape scale, geostatistic methods were used for collecting information on agricultural intensification. Specifically, the spatial arrangement of habitat composition in each landscape was derived from the Cropland Data Layer, with a 30-m resolution, obtained from the Chinese Academy of Sciences. All landscape metrics were computed using the Patch Analyst extension of FRAGSTATS (ArcGIS 9.3, 2008). For further analysis, proportion of cropland (*PC*) was indicated by the percentage of arable lands in the selected site:

$$PC\% = \frac{AREA_{arable\ habitat}}{AREA_{total\ area}} \times 100\%,$$

where $AREA_{arable\ habitat}$ and $AREA_{total\ area}$ are the area sizes of arable habitats and total area in each landscape. The *PC* was obtained at six spatial scales from 200 to 1500 m based on the buffer circle method in agricultural landscape.

Statistical analysis. The abundance (Individuals per 5 traps for ground-dwelling predators; per 10 sweeps for leaf-dwelling predators; per 100 wheat tillers for primary parasitoids) were estimated for further analyses. At the population level, two dominant species (primary parasitoids: *Aphidius avenae* and *Aphidius gifuensis*; leaf-dwelling predators: *Hippodamia variegata* and *Syrphus nitens*; ground-dwelling predators: *Pardosa astrigena* and *Chlaenius spallipes*) were selected for the analysis in each module containing natural enemies. To prevent the interference of temporal trends in the analysis, we detrended population density by regressing population density against year before calculating standard deviation of detrended population density^{52,53}. The detrended data was used for examining the relationship between agricultural intensification and insect communities at the six spatial scales. At the community level, Simpson's diversity ($D = 1 - \sum_i (N_i/N)^2$) was used to calculate species diversity of natural enemies according to population density.

At the field scale the Pearson correlation was used to examine the relationship between fertilizer input and the abundance of cereal aphids and their natural enemies. As the amount of nitrogen fertilizer is strongly correlated with grain yield (covariance), it was removed from the analysis. At the landscape scale, the Pearson correlation was also used to examine the relationship between proportion of cropland (*PC*) and the abundance of cereal aphids and their natural enemies at multiple spatial scales.

To analyze the joint effects of nitrogen input within the field and the proportion of cropland at the landscape level on the distribution of cereal aphids and their natural



enemies, we applied a linear mixed-effect model (LMM) with the restricted maximum likelihood method⁵⁴. Species were lumped together into three modules (aphids, predators and parasitoids) for calculating the predator/prey ratio and primary parasitism in wheat fields. Nitrogen fertilizer input and the proportion of cropland were considered as fixed factors, and the landscape site and year as random factors. Wald tests were used to examine the significant level of fixed effects and twofold interactions between them. A backward stepwise procedure was used to examine the contribution of fixed factors and interactions; the fixed factors with $P < 0.05$ were left in the full model. Response factors were log-transformed to meet the Gaussian distribution requirement. Furthermore, the polynomial effects of landscape structure were tested by adding the fixed factors, (nitrogen input)² and (the proportion of cropland)², to the model. As none of these factors had noticeable additional explanatory power, we considered the relationships between landscape structure and log-transformed insect population density to be linear. R was used for conducting the statistical analysis (lme4, packages, R Development Core Team 2005). Sigma Plot 12.5 was used for drawing the graphs.

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Author contributions

Z.Z. and D.H. designed and conducted the field experiments. Z.Z. conducted the data analysis. Z.Z., H.C. and B.L. wrote the main manuscript text. All authors reviewed the manuscript.

Additional information

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