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2 **Perennial woodlands benefit parasitoid diversity, but annual flowering fallows enhance**
3 **parasitism of wheat aphids in an agricultural landscape**

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13 **Abstract**

14 Agriculture intensification poses serious threats to natural enemy biodiversity and associated
15 ecological services. The conservation or reestablishment of semi-natural habitats is used to
16 counteract negative effects of agriculture intensification on natural enemies. Understanding
17 specific functions of different habitats for natural enemies from a landscape perspective is an
18 important step needed for the development of sustainable agriculture. Here, focusing on
19 parasitoids of wheat aphids, we examined effects of the proportion and connectivity of two
20 main semi-natural habitats (woodlands and fallows) present in landscapes, measured within
21 circular buffer radii of 0.5, 1.0, 1.5, and 2.0 km around sampling sites, on parasitoid
22 (mummy) density, biodiversity (Shannon diversity) and associated services (parasitism rate)
23 in 35 wheat fields. We also compared local vegetation communities of these two semi-natural
24 habitats to test whether plant characteristics can shed light on the potential mechanisms
25 driving parasitoids responses to different landscape habitats. We found that the parasitoid
26 diversity was much higher in landscapes dominated by woodlands, while fallows in the
27 landscape promoted parasitoid density and parasitism. Woodlands connectivity at larger scales
28 (such as 1.5 or 2.0 km) displayed positive effects on parasitoid activities, fallows connectivity
29 at the smaller scale (0.5 km) had a positive effect on the hyperparasitism rate. In terms of
30 vegetation characteristics, fallows provided more flowering plants and floral resources, while
31 woodlands suffered less disturbance across years. Local vegetation composition of the semi-
32 natural habitats indeed help explain their different effects on parasitoids at larger landscape
33 scales. We suggested that future research should investigate the role of different types of
34 semi-natural habitats. Conservation management should combine different habitats, such as

35 perennial and annual habitats, to promote the functional complementarity for beneficial
36 organisms. Based on results from local vegetation survey, we also suggested native flowering
37 plants such as *Capsella bursa-pastoris* L., *Lagopsis supina* Steph., and *Calystegia hederacea*
38 Wall. in fallows could be used as functional plants to conserve wheat aphid parasitoids.

39

40 **Keywords**

41 Parasitoids; biodiversity conservation; ecosystem services; landscape; functional
42 complementarity; habitat characteristics

1. Introduction

The agricultural landscape in many areas is a mosaic of crops and semi-natural habitats such as perennial woodlands, hedgerows and fallow fields (Haan et al., 2021). Movement of natural enemies between different habitats is a common phenomenon in agricultural landscapes, as beneficial insects require resources (shelter, nectar, alternative prey/hosts, and pollen) to complete their life cycles (Schellhorn et al., 2014). As a result, the ecological processes of beneficial insect populations in a given crop field are influenced by the surrounding landscape (Ortiz-Martínez and Lavandero, 2017; Plečáš et al., 2014; Yang et al., 2018a). In general, a heterogeneous landscape that is characterized by a large amount or high connectivity of semi-natural habitat helps natural enemies gain access to additional resources and then promotes diversity and biocontrol activity (Chaplin-Kramer et al., 2011; Haan et al., 2019; Hatt et al., 2018), because the higher stable semi-natural habitats may provide more complementary resources for natural enemies compared with crop fields (Martin et al., 2019; Tscharrntke et al., 2012; Zhang et al., 2020).

Conservation or reestablishment of semi-natural habitats near agricultural areas is needed to counteract the loss of natural enemy diversity and the associated pest control services (Grass et al., 2021). However, different kinds of semi-natural habitats in agricultural landscapes differ greatly in their vegetational traits (e.g., vegetation constructure, floral abundance, floral morphology, nectar quality, duration of floral resources, etc.) and their conservation impact on natural enemies (Vattala et al., 2006). For example, Bartual et al. (2019) showed that the importance of different semi-natural habitats types and associated vegetation traits for natural enemies were distinct in European agricultural landscapes.

65 Perennial semi-natural habitats, such as woodlands and grasslands, are less disturbed over
66 time and usually provide both refuges and food for populations of overwintering natural
67 enemies, while annual fallows with concentrations of seasonal flowering plants tend to
68 support natural enemy populations only during the specific flowering period of the dominant
69 flowering species (Nilsson et al., 2021). Detecting habitats that enhance pest suppression at
70 specific spatial and temporal scales, identifying the plants that support natural enemies in
71 such habitats, and then planting or conserving these plants in the agricultural landscape may
72 provide a novel pathway for conservation biological control at the landscape scale.
73 Unfortunately, most studies of landscape effects on natural enemies and pest control have
74 pooled different types of semi-natural habitats simplistically, which may have caused some
75 valuable information to be lost.

76 Parasitoids are important biocontrol agents in wheat fields, exerting a significant
77 suppressive effect on the population growth of wheat aphids (Ali et al., 2018; Qiao et al.,
78 2021; Thies et al., 2011). Adult parasitoids, of most species, can disperse widely, leading to
79 spillover between crop and semi-natural habitats. Consequently, the diversity and magnitude
80 of the community and associated ecosystem services of parasitoids can be influenced by the
81 surrounding landscape context (Elliott et al., 2018; Hawro et al., 2015; Zhao et al., 2013). In
82 northern China, establishing appropriate semi-natural habitats at the local field scale to
83 enhance the biocontrol effectiveness of parasitoids of wheat aphids has been well studied (Xu
84 et al., 2018; Zhou et al., 2009), however, the effects of existing semi-natural habitats on these
85 parasitoids have rarely been investigated at the landscape scale.

86 Perennial woodlands and annual fallows make up the majority of semi-natural habitats in

northern China, where farmers commonly use a double-cropping system of wheat in spring and maize in summer. Fallows occur mainly because some maize fields are left fallow after the autumn harvest, and are held as fallow land until plant maize in the following summer. In this study, we investigated the effects of landscape composition and configuration on the diversity (Shannon diversity) of parasitoids and on the level of resulting biological control (parasitism rate) of aphids in wheat fields. We used the percentage of woodlands, fallows, and of other crops (i.e., vegetables, fruit trees, peas, and spring maize) as indicators of landscape composition, and we calculated the connectivity of woodlands and fallows, respectively, as indicators of landscape configuration. Additionally, we compared the plant communities of woodlands and fallows to shed light on the explain of potential different effects contributed by these two semi-natural habitats. We tested three hypotheses: (1) that higher proportion of woodlands and fallows would have positive impacts on parasitoids and on biological control of wheat aphids because of the resources these habitats provide for parasitoids; (2) that the connectivity of woodlands or fallows would also have positive effects on parasitoid activities through facilitating the movement of parasitoids between habitat patches; (3) that the plant communities of woodlands and fallows are different, and so would be the magnitude of their effects on parasitoids.

2. Materials and Methods

2.1. Study area and sites selection

The study was carried out in Hebei Province, Beijing and Tianjin Cites, in the North China Plain, a major wheat-growing region in China (Figure S1). In the study area, the landscape is

a mosaic of wheat, woodlands, fallows and some other crops (i.e., vegetables, fruit trees, peas, and spring maize) during the spring-summer season. We selected 35 winter wheat fields, spread over three consecutive years, as sampling sites (17 sites in 2015, 7 in 2016 and 11 in 2017). The selected wheat fields were located along compositional and configurational landscape gradients. In this study, landscape composition was classified in terms of the proportion of the two dominant semi-natural habitats (i.e., woodlands and fallows) and the other crops. We treated fallows as a semi-natural habitat because they covered by wild vegetation in the spring (Figure 1a). The landscape configuration was assessed by the connectivity of woodlands and the connectivity of fallows. The size of each sampled field was more than 0.5 ha, and the minimum distance between any of two wheat fields was more than 4 km, and none of the fields were treated with insecticides before the survey after sowing the crop.

2.2. Field survey and parasitoid identification

Aphid and mummy densities were sampled during the wheat flowering period, when wheat aphids are normally most abundant (Yang et al., 2017). Sampling was done from May 7 to May 13 in 2015, May 16 to May 18 in 2016, and May 15 to May 17 in 2017. At each site, inside the wheat field, we laid out three plots (20 × 30 m), with 10 m between adjacent plots. In each plot, we measured the density of aphids and mummies by visual observation at each of five randomly selected points. At each point, we chose 10 tillers haphazardly, provided that each tiller to be sampled was at least 10 m from the field edge. To estimate aphid and mummy density in each plot, we calculated values as the number of individuals per 100 tillers (the

total number per 50 tillers multiply by 2).

In addition, we randomly collected 50-200 mummies per field at the same time that aphids were sampled, in 2015 and 2016. The exact number of mummies collected in each study year was determined by availability of time and labor during our field survey. Mummies were placed individually in 1.5 mL centrifuge tubes and brought to the laboratory. Newly emerged parasitoids were stored in 1.5 mL centrifuge tubes filled with ethanol (95%) for identification. Parasitoids were identified most frequently based on morphological characteristics, but for some species the mitochondrial cytochrome c oxidase subunit one (COI) and the 16 S gene DNA were sequenced to confirm the species identification according to a protocol provided by Yang et al. (2017).

2.3. Landscape characterization

Land use cover types within a 2.0 km radius of each sampled wheat field (site) were identified in May each year. We firstly collected the geographical coordinates of each wheat field, and obtained open-access satellite imagery for the surrounding areas to a radius of 2.0 km for each site from Google Earth maps using these coordinates, printed the maps and marked the types of land cover on the maps with ground verification to eliminate inaccuracies caused by changes in land use between the image date and study period, and then digitized the maps in ArcGIS 10.5 (Yang et al., 2018b). We chose a 2.0 km radius as the maximum distance examined because previous studies have found a more significant response of wheat aphid parasitoids to landscape characteristics within this or a smaller scale (Chaplin-Kramer et al., 2011). Vegetation cover was divided into four categories: wheat, woodlands, fallows and

other crops. The proportion of each category within circular buffer radii of 0.5, 1.0, 1.5, and 2.0 km around sampling wheat fields was calculated and considered as the landscape composition parameter. Woodlands connectivity and fallows connectivity were calculated using the landscape class-level metric, Connectance Index (*CONNECT*), with a 100 m search radius, this threshold distance was recognized as the mean foraging flight capabilities of parasitoids (Zhang et al., 2020). These functional connectedness values (reported as a percentage) for woodland or fallow habitats represent, among all possible pairs of woodlands or fallows, the percentage of those less than 100 m apart (McGarigal et al., 2012). All metrics were calculated at four spatial scales in FRAGSTATS 4.2.

2.4. Plant surveys in woodland and fallow habitats

Vegetation surveys were conducted in 29 woodlands and 30 fallow areas (the area of each sampled area was at least 30 × 30 m), within in the study region. **Fallow and woodland habitats were selected randomly, some of them adjacent to central wheat fields, some in the same landscapes within a 2.0 km radius of central fields, and some just located in the same counties that our wheat field surveys performed (Figure S1).** In our study region the woodland habitats are mainly lands replanted as tree plantations. These perennial, semi-natural habitats usually consisted of a single tree species, and most often that tree was a poplar species (*Populus* L.) (Figure 1b). Consequently, our vegetation surveys only sampled the herbaceous layer, in both the woodland and fallow habitats. Five 1 × 1 m quadrats were randomly placed inside each habitat for vegetation sampling. In each sample quadrat, we estimated the total vegetation cover, as well as the percent coverage and the number of each

plant species. Additionally, the floral resource conditions for each flowering plant were estimated as the area of flowering units divided by the total coverage of that plant.

2.5. Statistical analyses

The responses of parasitoid density, parasitism and hyperparasitism rates, and diversity of parasitoids to the landscape context at four spatial scales were investigated, respectively. We used mummy density as the measure of parasitoid density. Parasitism rate was used to measure biological regulation services, which was calculated as the number of mummies divided by the sum of aphid and mummy density. Hyperparasitism rate was calculated as proportion of hyperparasitoids to all emerged parasitoids, and used to measure ecosystem disservices. Parasitoid diversity (of specimens reared from mummies) was calculated as Shannon diversity index, which accounts for evenness of species present and is less sensitive to sampling effects than species richness (Jost, 2006; Senapathi et al., 2021).

Generalized linear mixed models (GLMMs) with a negative binomial error distribution (to account for overdispersion in the data) were used to explain the variation in parasitoid density. The landscape compositional factors (i.e., the proportion of land in woodlands, fallows, and other crops within the landscape), and configurational indexes (i.e., woodlands connectivity, fallows connectivity) were treated as the fixed predictors. We also added $\log_{10}(x+1)$ transformed aphid density as a fixed factor, since the density of natural enemies usually depends on the number of prey or hosts present. Study site nested within year as a random factor. The proportion of land in wheat was excluded from analyses due to collinearity (Table S1). Parasitism and hyperparasitism rates were fitted with GLMM with

binomial error distribution, where the fixed factors were the landscape variables (woodlands %, fallows %, other crops %, woodlands connectivity, and fallows connectivity), the random factor was study site nested within year for parasitism rate and was year for hyperparasitism rate. Linear mixed models (LMMs) were used to test the effects of landscape context on the Shannon diversity index of parasitoids, with landscape variables included as fixed factors and year as a random factor. All explanatory variables were scale-centered to facilitate interpretation of coefficients, and were considered in an additive way. Variance inflation factor (VIF) values for the predictors except wheat cover in each global model were calculated and were found to be < 5 (Table S2), indicating that covariation between predictors was not a problem. For each response variable, a multi-model inference procedure based on the bias-corrected, Akaike's Information Criterion (AICc, corrected for small sample sizes) was performed to avoid redundant models and spurious results. We calculated all potential models that nested in the global model as candidate models, and then ranked the models according to their AICc. Models with $\Delta\text{AICc} < 2$ were selected as the top model set in the model averaging approach, from which we derived the importance values and coefficient estimates for each variable (Grueber et al., 2011). In some cases, we selected the best model (with the minimum AICc value) to test the effects of landscape context if there was only one model with $\Delta\text{AICc} < 2$ in the candidate model set. In addition, models were systematically tested for normality and homoscedasticity of the residuals. The residuals of all models were also used to test for spatial autocorrelation, and we found no evidence of autocorrelation.

Data from the five sample quadrats taken for vegetation composition were summed for each habitat to analyze vegetation composition data in the woodland and fallow habitats. The

overall cover, density, and frequency values were calculated for each plant species from the combined data set. To determine the proportion of each species in the total plant community, we calculated the relative cover, relative density, and relative frequency values for each species. To measure plant species dominance in fallow and woodland habitats, the Importance Value Index (IVI) was used, which was calculated as $IVI = \text{relative cover (\%)} + \text{relative density (\%)} + \text{relative frequency (\%)}$ (Haile et al., 2016). The Shannon diversity and species evenness values for the plant community of each habitat were calculated using the following equation:

$$\text{Shannon diversity} = \sum_{i=1}^S p_i \ln p_i ,$$

$$\text{Species evenness} = \frac{\text{Shannon diversity index}}{\ln (S)} ,$$

where $p_i = \frac{N_i}{N}$, N is the sum of the IVI in a habitat, N_i is the IVI for plant i , and S is the total number of plant species in the habitat. T-tests or nonparametric tests (Mann-Whitney U test) were used to compare vegetation characteristics of fallow and woodland habitats.

All statistical analyses were carried out in R 4.0.3 for Windows (R Core Team, 2019), using the ‘lme4’ package for fitting models (Bates et al., 2015), the ‘vif’ function in the ‘car’ package to calculate the variance inflation factor values (Fox and Weisberg, 2019), the functions ‘dredge’ and ‘model.avg’ in the MuMIn package for multi-model inference (Bartoń, 2017).

3. Results

3.1. Overview of system changes

There were four common wheat aphid species, i.e., *Rhopalosiphum padi* (L.), *Sitobion avenae*

(Fabricius), *Schizaphis graminum* (Rondani), and *Metopolophium dirhodum* (Walker), in wheat fields. The density of the wheat aphids changed dramatically over the three consecutive years of our study, being 3423.11 ± 247.68 (mean \pm SE) individuals per 100 tillers in 2015, 865.37 ± 124.68 in 2016, and 782.58 ± 129.06 in 2017. Parasitoid density (mummies) per 100 tillers was 21.16 ± 1.94 , 65.26 ± 10.66 and 4.00 ± 0.91 in 2015, 2016, and 2017, while parasitism rates were $0.75 \pm 0.10\%$, $7.12 \pm 0.78\%$ and $0.72 \pm 0.17\%$ in 2015, 2016 and 2017, respectively. In 2015, 979 parasitoids of 16 species (3 primary parasitoid species and 13 hyperparasitoid species) were collected, with primary parasitoids accounting for 59% of the community. In 2016, 506 parasitoids emerged from the field collected mummies and 79% of them were primary parasitoids (Table S3). The Shannon diversity index for the parasitoid community was 2.36 ± 0.12 and 1.4 ± 0.26 in 2015 and 2016, respectively.

3.2. *Effects of landscape on parasitoid density*

Across all four spatial scales, models at the smaller scales had lower AICc values than models at larger ones (Table S4), indicating that landscape variables within smaller buffers were more important for parasitoid density than landscape variables at larger spatial scales. At these smaller scales (such as, 0.5 and 1.0 km), the percentage of variance explained was 53-58% for models with $\Delta AICc$ less than 2 (Table S4). Results of model averaging procedures showed that the proportion of fallows and aphid abundance had the strongest effects on parasitoid density, with the highest averaged coefficients and relative importance values (Table 1). Wheat fields with high aphid density and surrounded by large proportion of fallows had higher parasitoid density (Figure 2a, b). For habitat connectivity, only the connectivity of

woodlands at the 2.0 km scale had a significant effect on parasitoid density (Table 1),
increased woodlands connectivity positively influenced parasitoid density (Figure 2c).

3.3. Effects of landscape on parasitism and hyperparasitism rates

The smaller radii that we examined were more effective for predicting parasitism rate, the
AICc values for models based on these scales were lower (Table S5). Both the proportion of
land in fallows and other crops within 0.5, 1.0 and 2.0 km had significant effects on the
parasitism rate of wheat aphids (Table 2), the parasitism rate increased with increasing
proportion of fallows (Figure 3a). The connectivity of woodlands at the 2.0 km scale had a
positive effect on the parasitism rate (significant at 0.1 level, $P = 0.0615$) (Table 2, Figure 3b).
The variance of hyperparasitism rate was also better explained by landscape factors within
smaller scales, models at 0.5 and 1.0 km had lower AICc values than models at 1.5 and 2.0
km (Table S5). The proportion of woodlands within 0.5 and 1.0 km had significant positive
effects on the hyperparasitism rate (Table 2), the hyperparasitism rate increased with
increasing proportion of woodlands (Figure 4a). Increasing fallows connectivity at the 0.5 km
scale, and woodlands connectivity at 1.5 and 2.0 km scales positively affected
hyperparasitism rate (Table 2, Figure 4b, c).

3.4. Effects of landscape on parasitoid diversity

For Shannon diversity of the parasitoid, models with woodlands alone were best for
predicting diversity of the parasitoid at 0.5 and 1.0 km scales, and models with woodlands
connectivity were the best models at the larger scales (Table S6). The percentage of woodland

habitats within smaller spatial scales (i.e., 0.5 to 1.0 km), and the connectivity of woodlands at larger scales (i.e., 1.0 to 2.0 km) significantly enhanced parasitoid diversity (Table 3). Parasitoid Shannon diversity was greater in the landscape with larger proportion of woodlands cover (Figure 5a), and with higher woodlands connectivity (Figure 5b).

3.5. Vegetation characteristics in woodlands and fallows

These two types of semi-natural habitats had similar herbaceous plant species, but there was more variability in the vegetation composition among woodland habitats (Whittaker β -diversity index: 3.32 for fallows and 5.06 for woodlands) (Table S7). Compared to the woodland areas, vegetation cover in the herb layer was much higher in the fallow habitats ($U = 49.5$, $P < 0.0001$) (Figure 6a). In addition, species richness and Shannon diversity values were both much higher for fallows (species richness: $t = 2.9$, $df = 57$, $P = 0.0053$; Shannon diversity: $t = 2.9$, $df = 57$, $P = 0.0053$) (Figure 6b, c).

A large difference was found for species dominance between fallow and woodland habitats (Table S7). *Capsella bursa-pastoris* L. had an importance value index of 53.62 and was the most herbaceous plant encountered in fallows. *Lagopsis supina* Steph., *Calystegia hederacea* Wall., *Hemistepta lyrata* Bunge, *Trigonotis peduncularis* Trev. and *Ixeris denticulata* Houtt. also had high importance values and were common in fallows (Table 4). In woodland habitats, *Salsola collina* Pall. was the most common plant species, with the highest importance value (35.37), followed by *Chenopodium album* L., *Humulus scandens* Lour., *Chenopodium glaucum* L., *Kochia scoparia* L., *C. bursa-pastoris* L., *L. supina* Steph. (Table 4). During the survey period, the flowering plant species and floral abundance was much

higher for fallows than that for woodlands, in terms of the top ten most common plant species (Table 4).

4. Discussion

Parasitoids can be very effective in reducing aphid populations. For wheat aphids, a threshold of 20-30% has been found to cause aphid populations to decline (Plečáš et al., 2014; Thies et al., 2011). The efficiency of against pests, however, largely depends on the availability of additional food resources (i.e., nectar and pollen), which enhance the survival, fecundity, and host foraging capacity of parasitoids (Benelli et al., 2017). Here, uncultivated fallows support fast growing, annual ruderal species such as *C. bursa-pastoris*, *L. supina*, *C. hederacea*, *H. lyrata*, *T. peduncularis*, and *I. denticulata* that flower in the spring. These plants are usually attractive to parasitoids that visit the flowers for nectar and pollen, and may move into adjacent crop fields. As a result, an increase in the proportion of fallows in the landscape can increase parasitoid activity in nearby wheat fields. In contrast, in woodlands, there is a smaller herbaceous coverage, dominated by *S. collina*, *C. album*, *H. scandens*, and *C. glaucum*, which rarely bloom in spring. This mismatch between the plants' flowering time and parasitoid occurrence results in woodlands making an insignificant contribution to parasitoid density in wheat. Although some spring-blooming flowering plants (like *C. bursa-pastoris*, *L. supina* and *I. denticulata*) occur in woodland habitats, there floral abundance in our study was low due to the shade. Therefore, annual flowering plants such as *C. bursa-pastoris* and *L. supina* could be used as functional plants to promote parasitoid natural enemies for wheat aphids in the early spring. Here, the study region is characterized by a

smallholder agriculture system, frequency and timing of pesticide applications are mainly decided by farmers, who are used to spraying insecticides to management wheat aphids around the wheat flowering stage (Yang et al., 2018b). In order to avoid the effects of insecticides, field surveys were conducted before the parasitism rates reaching up to threshold value. Although parasitism rates during the study period were lower than the threshold value, parasitism rates typically exceed 20% about two weeks later in our study region (Yang et al., 2017). The occurrence of parasitoids in the later period has a high correlation with that in the earlier time, and therefore our results could provide guidance for agricultural practices.

Landscapes rich in semi-natural habitats frequently have a greater abundance of natural enemies because such non-crop vegetation could provide resource continuity for beneficial insects (Iuliano and Gratton, 2020; Schellhorn et al., 2014, 2015). In some cases, however, insect pests may also benefit from semi-natural habitats (Santoemma et al., 2018; Tamburini et al., 2020). Thus, studying the response of populations of natural enemy alone to landscape context may not be sufficient to comprehensively assess the positive or negative impacts of landscapes on agricultural production. We quantified the impact of parasitoids on wheat aphid population using percentage parasitism as our measure of impact, and we found that fallows enhanced the parasitism rate during our study period, even though fallows were also positively correlated with wheat aphid abundance in the elongating stage (Yang et al., 2019). These results suggested that annual fallows do help suppress aphid populations during the wheat flowering stage, and that this positive service of fallows cover outweighs any disservices. In contrast, the presence of other crops (such as vegetables, fruit trees and spring maize) was negatively associated with the level of aphid parasitism in wheat which may be

because other crops attract parasitoids, reducing the number migrating into wheat fields.

Similarly, Yang et al. (2018a) found that landscapes with a higher proportion of other crops lowered ladybeetle numbers in wheat fields, likely for the same reason.

In northern China, a dramatic change in the parasitoid community of wheat aphids across the growing season, with primary parasitoids being the predominant species in the early growing season and hyperparasitoid dominating in the late season (Yang et al., 2017). Our sampling period coincided with the reproductive period of the primary parasitoids, which made up the majority of the population that we sampled. We also observed the colonization of the hyperparasitoids, but not their dominance. During this period, however, it was the number of hyperparasitoid species and their relative density that determined parasitoid Shannon diversity in our samples. Before becoming dominant in wheat fields, hyperparasitoids need time to build up their populations on other primary parasitoids, which are mainly available in early spring in perennial woodlands. Tender stems, buds, and leaves of trees that are infested with various aphids lead to an increase in both mummy densities and hyperparasitoids (Jiao et al., 2015; L.Y., personal observation). In addition, the undisturbed environmental conditions in woodlands may provide overwinter shelter for hyperparasitoids from the previous year, and thus woodlands can enhance the density of hyperparasitoid immigrants into wheat fields in the following year. Consistently, the proportion of hyperparasitoids (hyperparasitism rate) in wheat fields also correlated with the area of woodlands in the landscape positively. In contrast, in fallow habitats, annual plants are not yet established very early in spring and so provide fewer hosts for hyperparasitoids in this early period.

Conserving biodiversity and supporting ecosystem services are goals of programs to

373 restore or expand semi-natural habitats, but these two goals may mismatch in some cases. A
374 positive relationship is supported between a diverse community and ecosystem services
375 according to the functional complementarity arising from species trait diversity (Vanbergen et
376 al., 2020). In other cases, however, ecosystem services may be provided by a few dominant
377 species of beneficial insects (Nicholson et al., 2020). In this study, we illustrated that the
378 perennial woodlands benefit parasitoid diversity, but the ephemeral flowering of fallows
379 enhances the parasitism rate in wheat. This mismatch between biodiversity and biocontrol
380 services might be caused by the differences in vegetation characteristics as well as their
381 functional value to parasitoids between woodland and fallow habitats. High diversity of the
382 parasitoid may imply functional redundancy, but which tends to be more stable and resilient
383 to environmental changes (Damien et al., 2017; Feit et al., 2019). Consequently, we
384 recommend that perennial woodlands and fallows should be combined to promote
385 biodiversity and enhance associated ecosystem services in a compatible manner for habitat
386 management in northern China.

387 Habitat functional connectivity considers how accessible the same class patches are to
388 natural enemies, according to dispersal capacities of these beneficial organisms (McGarigal et
389 al., 2012). Increasing semi-natural habitat connectivity can sometimes promote natural
390 enemies to access different land cover types and diverse food resources because these habitats
391 usually act as ‘corridors’ or ‘stepping stones’. For example, the connectivity of forest areas
392 and grassy embankments was found to benefit population abundance and species richness of
393 pollinators or natural enemies (Dominik et al., 2018; Montagnama et al., 2021). Here, our
394 results also suggested that the connectivity of semi-natural patches (fallow or woodlands)

had a positive effect on the activities of primary parasitoids or hyperparasitoids. We suppose that the connectivity of annual flowering fallows may allow hyperparasitoids access to floral resources, while the connectivity of perennial woodlands may facilitate different kinds of parasitoid species immigration into wheat fields and give rise to a more diverse metapopulation.

Spatial scale in our study did affect parasitoid density, diversity, and parasitism (and hyperparasitism) rates, and these effects were better explained by landscape variables at smaller scales (0.5 or 1.0 km). Chaplin-Kramer et al. (2011)'s global meta-analysis found that specialist enemies showed a strong sensitivity to landscape scale and were usually most strongly affected by landscape composition at smaller scales (less than 1.0 km). To increase the diversity of parasitoids and their suppressive effects on wheat aphids, agri-environmental measures that aiming to improve biodiversity implemented at smaller scales are likely to be more effective. For example, establishing annual flower strips adjacent to wheat fields, using native flower plants that adapted to fallow lands, could provide supplementary resources for primary parasitoids during outbreaks of wheat aphids. Perennial woodlands, in contrast, may be more valuable if disjunctively distribute within greater radii (such as 1.0 to 2.0 km) around wheat fields, so that woodlands can support parasitoid biodiversity but do not promote the immigration of hyperparasitoids into wheat fields.

Taking a proportion of the field area out of agricultural production is an important component of the land-sharing strategy for the conservation of biodiversity and ecosystem services (Grass et al., 2021). Rotational fallows have been demonstrated to improve nutrient cycling, soil physical properties, pest control, and crop pollination services (Schmidt et al.,

2008; Toivonen et al., 2013, 2015). In the North China Plain, a fallow lands management strategy has been promoted by the government to conserve water and soil. Previous studies have suggested that fallows within agricultural landscapes can enhance the occurrence of predatory ladybeetles, suppress aphid population growth, and mitigate the negative effects of insecticides sprays in wheat fields (Yang et al., 2018a, 2018b). In our study, fallows increased the density of parasitoids and parasitism rate during the peak period of wheat aphids, with primary parasitoid are dominant species. We speculated that the presence of flowering plants in fallows may benefit hyperparasitoid species after the seasonal peak of aphid abundance (with hyperparasitoids accounting for most of the community), which may disrupt the suppressive effects of the primary parasitoids in the later growing season. Therefore, plants within fallows are ploughed under and used as green manure in the later part of the season may reduce resources available for hyperparasitoids. Herbicide use in fallows or the previous maize crop fields should be reduced because herbicide residues may change the plant species composition and reduced the diversity of plant community in fallows (Qi et al., 2020).

5. Conclusion

Our results confirmed that semi-natural habitats in agricultural landscapes are beneficial for parasitoid diversity and biological control services, although there was great variation in their specific functions on parasitoids. Specifically, fallows increased the density of parasitoids and enhanced their parasitism rate on wheat aphids, while woodlands benefited parasitoid diversity in general. The effects of fallows and woodlands on parasitoid diversity and associated services were not compatible, which may be due to the fundamental vegetation

characteristics of these two types of semi-natural habitats. Based on our results, we emphasized that future research needs to investigate the role of semi-natural habitats more specifically rather than simplistically grouping all semi-natural habitats together.

Adding annual flower strips is relatively easy for farmer to create and do not take land out of agriculture production (Nilsson et al., 2021). We found the annual flowering plants in fallows did not increase the overall diversity of parasitoids, but did increase pest control in wheat by raising the parasitism rate on wheat aphids. We believed that habitat management in our study region should combine both annual and perennial plants to promote functional complementarity of these habitats for beneficial insects, allowing a balanced approach to provide for both increases in overall parasitoids biodiversity and specifically in the level of ecosystem services from aphid parasitoids in wheat fields. We also suggested flowering native plants in fallows such as *C. bursa-pastoris*, *L. supina*, *C. hederacea*, *H. lyrata*, *T. peduncularis*, and *I. denticulata* could be used as functional plants that enhance the services of wheat aphid parasitoids.

Author contributions

Y. L. conceived and designed the study. L. Y., L. X., Y. Z. and M. L. performed the field surveys, L. X. contributed to the identification of parasitoids. L. Y. analyzed the data and wrote the first draft of the manuscript, H. W. analyzed the data, L. Y., Y. Z. and Y. L. critically revised it. All authors read and approved the manuscript.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

- Ali, A., Desneux, N., Lu, Y., Wu, K., 2018. Key aphid natural enemies showing positive effects on wheat yield through biocontrol services in northern China. *Agric. Ecosyst. Environ.* 266, 1-9.
- Bartoń, K., 2017. MuMIn: Multi-Model Inference. R package version 1.40.0. <https://CRAN.R-project.org/package=MuMIn>.
- Bartual, A.M., Sutter, L., Bocci, G., Moonen, A.-C., Cresswell, J., Entling, M., et al., 2019. The potential of different semi-natural habitats to sustain pollinators and natural enemies in European agricultural landscapes. *Agric. Ecosyst. Environ.* 279, 43-52.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* 67, 1-48. doi:10.18637/jss.v067.i01.
- Benelli, G., Giunti, G., Tena, A., Desneux, N., Caselli, A., Canale, A., 2017. The impact of adult diet on parasitoid reproductive performance. *J. Pest. Sci.* 90, 807-823.
- Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J., Kremen, C., 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecol. Lett.* 14, 922-932.

483 Damien, M., Le Lann, C., Desneux, N., Alford, L., Al Hassan, D., Georges, R., et al., 2017.
 484 Flowering cover crops in winter increase pest control but not trophic link diversity. *Agric.*
 485 *Ecosyst. Environ.* 247, 418-425.
 486 Dominik, C., Seppelt, R., Horgan, F.G., Settele, J., Vaclavik, T., 2018. Landscape
 487 composition, configuration, and trophic interactions shape arthropod communities in rice
 488 agroecosystems. *J. Appl. Ecol.* 55, 2461-2472.
 489 Elliott, N.C., Brewer, M.J., Giles, K.L., 2018. Landscape Context Affects Aphid Parasitism by
 490 *Lysiphlebus testaceipes* (Hymenoptera: Aphidiinae) in Wheat Fields. *Environ. Entomol.*
 491 47, 803-811.
 492 Feit, B., Blüthgen, N., Traugott, M., Jonsson, M., 2019. Resilience of ecosystem processes: a
 493 new approach shows that functional redundancy of biological control services is reduced
 494 by landscape simplification. *Ecol. Lett.* 22, 1568-1577.
 495 Fox, J., Weisberg, S., 2019. An {R} Companion to Applied Regression. Sage Pub., Thousand
 496 Oaks, California, USA.
 497 Grass, I., Batáry, P., Tschamtkke, T., 2021. Combining land-sparing and land-sharing in
 498 European landscapes. *Adv. Ecol. Res.* 64, 251-303.
 499 Grueber, C., Nakagawa, S., Laws, R., Jamieson, I., 2011. Multimodel inference in ecology
 500 and evolution: challenges and solutions. *J. Evol. Biol.* 24, 699-711.
 501 Haan, N.L., Iuliano, B.G., Gratton, C., Landis, D.A., 2021. Designing agricultural landscapes
 502 for arthropod-based ecosystem services in North America. *Adv. Ecol. Res.* 64, 191-250.
 503 Haan, N.L., Zhang, Y., Landis, D.A., 2019. Predicting landscape configuration effects on
 504 agricultural pest suppression. *Trends Ecol. Evol.* 35, 175-186.

505 Haile, G., Lemenih, M., Senbeta, F., Itanna, F., 2016. Plant diversity and determinant factors
506 across smallholder agricultural management units in central Ethiopia. *Agroforest. Syst.*
507 91, 677-695.

508 Hatt, S., Boeraeve, F., Artru, S., Dufrêne, M., Francis, F., 2018. Spatial diversification of
509 agroecosystems to enhance biological control and other regulating services: An
510 agroecological perspective. *Sci. Total Environ.* 621, 600-611.

511 Hawro, V., Ceryngier, P., Tschamtkke, T., Thies, C., Gagic, V., Bengtsson, J., et al., 2015.
512 Landscape complexity is not a major trigger of species richness and food web structure
513 of European cereal aphid parasitoids. *Biocontrol* 60, 451-461.

514 Iuliano, B., Gratton, C., 2020. Temporal resource (dis)continuity for conservation biological
515 control: From field to landscape scales. *Front. Sustain. Food S.* 4, 127.

516 Jiao, L., Li, X., Cai, H., Suo, X., 2015. The survey on major species of aphids on garden plant
517 and control measures in Shijiazhuang city. *J. Hebei Agric. Sci.* 19, 33-35.

518 Jost, L., 2006. Entropy and diversity. *Oikos*. 113, 363-375.

519 Martin, E.A., Dainese, M., Clough, Y., Baldi, A., Bommarco, R., Gagic, V., et al., 2019. The
520 interplay of landscape composition and configuration: new pathways to manage
521 functional biodiversity and agroecosystem services across Europe. *Ecol. Lett.* 22, 1083-
522 1094.

523 McGarigal, K., Cushman, S.A., Ene, E., 2012. FRAGSTATS v4: spatial pattern analysis
524 program for categorical and continuous maps. Computer software program produced by
525 the authors at the University of Massachusetts, Amherst. Available at the following web
526 site <http://www.umass.edu/landeco/research/fragstats/fragstats.html>.

527 Montagnana, P.C., Alves, R.S.C., Garófalo, C.A., Ribeiro, M.C., 2021. Landscape

528 heterogeneity and forest cover shape cavity-nesting hymenopteran communities in a
529 multi-scale perspective. *Basic Appl. Ecol.* 56, 239-249.

530 Nicholson, C.C., Ward, K.L., Williams, N.M., Isaacs, R., Mason, K.S., Wilson, J.K., et al.,
531 2020. Mismatched outcomes for biodiversity and ecosystem services: testing the
532 responses of crop pollinators and wild bee biodiversity to habitat enhancement. *Ecol.*
533 *Lett.* 23, 326-335.

534 Nilsson, L., Klatt, B.K., Smith, H.G., 2021. Effects of flower-enriched ecological focus areas
535 on functional diversity across scales. *Front. Ecol. Evol.* 9, 629124.

536 Ortiz-Martínez, S.A., Lavandero, B., 2017. The effect of landscape context on the biological
537 control of *Sitobion avenae*: temporal partitioning response of natural enemy guilds. *J.*
538 *Pest. Sci.* 91, 41-53.

539 Plećaš, M., Gagić, V., Janković, M., Petrović-Obradović, O., Kavallieratos, N., Tomanović,
540 Ž., et al., 2014. Landscape composition and configuration influence cereal aphid-
541 parasitoid-hyperparasitoid interactions and biological control differentially across years.
542 *Agric. Ecosyst. Environ.* 183, 1-10.

543 Qi, Y., Li, J., Guan, X., Yan, B., Fu, G., He, J., et al., 2020. Effects of herbicides on non-target
544 plant species diversity and the community composition of fallow fields in northern
545 China. *Sci. Rep.* 10, 9967.

546 Qiao, F., Yang, Q., Hou, R., Zhang, K., Li, J., Ge, F., et al., 2021. Moderately decreasing
547 fertilizer in fields does not reduce populations of cereal aphids but maximizes fitness of
548 parasitoids. *Sci. Rep.* 11, 2517.

549 R Core Team, 2019. R: A language and environment for statistical computing. Vienna,

550 Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>

551 [ct.org/](https://www.R-project.org/)

552 Santoiemma, G., Mori, N., Tonina, L., Marini, L., 2018. Semi-natural habitats boost

553 *Drosophila suzukii* populations and crop damage in sweet cherry. Agric. Ecosyst.

554 Environ. 257, 152-158.

555 Senapathi, D., Frund, J., Albrecht, M., Garratt, M.P.D., Kleijn, D., Pickles, B.J., et al., 2021.

556 Wild insect diversity increases inter-annual stability in global crop pollinator

557 communities. Proc. Biol. Sci. 288, 20210212.

558 Schellhorn, N., Bianchi, F., Hsu, C., 2014. Movement of entomophagous arthropods in

559 agricultural landscapes: links to pest suppression. Annu. Rev. Entomol. 59, 559-581.

560 Schellhorn, N.A., Gagic, V., Bommarco, R., 2015. Time will tell: resource continuity bolsters

561 ecosystem services. Trends Ecol. Evol. 30, 524-530.

562 Schmidt, M.H., Rucker, S., HanaW, J., Gigon, A., 2008. Rotational fallows as overwintering

563 habitat for grassland arthropods: the case of spiders in fen meadows. Biodivers. Conserv.

564 17, 3003-3012.

565 Tamburini, G., Santoiemma, G., M, E.O.R., Bommarco, R., Chaplin-Kramer, R., Dainese, M.,

566 et al., 2020. Species traits elucidate crop pest response to landscape composition: a

567 global analysis. Proc. Biol. Sci. 287, 20202116.

568 Thies, C., Haenke, S., Scherber, C., Bengtsson, J., Bommarco, R., Clement, L.W., et al., 2011.

569 The relationship between agricultural intensification and biological control: experimental

570 tests across Europe. Ecol. Appl. 21, 2187-2196.

571 Toivonen, M., Herzon, I., Helenius, J., 2013. Environmental fallows as a new policy tool to

572 safeguard farmland biodiversity in Finland. *Biol. Conserv.* 159, 55-366.

573 Toivonen, M., Herzon, I., Kuussaari, M., 2015. Differing effects of fallow type and landscape
574 structure on the occurrence of plants, pollinators and birds on environmental fallows in
575 Finland. *Biol. Conserv.* 18, 36-43.

576 Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., et al., 2012.
577 Landscape moderation of biodiversity patterns and processes-eight hypotheses. *Biol.*
578 *Rev.* 87, 661-685.

579 Vanbergen, A.J., Aizen, M.A., Cordeau, S., Garibaldi, L.A., Garratt, M.P.D., Kovács-
580 Hostyánszki, A., et al., 2020. Transformation of agricultural landscapes in the
581 anthropocene: nature's contributions to people, agriculture and food security. *Adv. Ecol.*
582 *Res.* 63, 193-253.

583 Vattala, H.D., Wratten, S.D., Phillips, C.B., Wäckers, F.L., 2006. The influence of flower
584 morphology and nectar quality on the longevity of a parasitoid biological control agent.
585 *Biol. Control.* 39, 179-185.

586 Xu, Q., Hatt, S., Han, Z., Francis, F., Chen, J., 2018. Combining E- β -farnesene and methyl
587 salicylate release with wheat-pea intercropping enhances biological control of aphids in
588 North China. *Biocontrol Sci. Techn.* 28, 883-894.

589 Yang, F., Xu, L., Wu, Y., Wang, Q., Yao, Z., Zikic, V., et al., 2017. Species composition and
590 seasonal dynamics of aphid parasitoids and hyperparasitoids in wheat fields in northern
591 China. *Sci. Rep.* 7, 13989.

592 Yang, L., Liu, B., Zhang, Q., Zeng, Y., Pan, Y., Li, M., et al., 2019. Landscape structure alters
593 the abundance and species composition of early-season aphid populations in wheat

594 fields. Agric. Ecosyst. Environ. 269, 167-173.

595 Yang, L., Zeng, Y., Xu, L., Liu, B., Zhang, Q., Lu, Y., 2018a. Change in ladybeetle abundance
 596 and biological control of wheat aphids over time in agricultural landscape. Agric.
 597 Ecosyst. Environ. 255, 102-110.

598 Yang, L., Zhang, Q., Liu, B., Zeng, Y., Pan, Y., Li, M., et al., 2018b. Mixed effects of
 599 landscape complexity and insecticide use on ladybeetle abundance in wheat fields. Pest
 600 Manag. Sci. 75, 1638-1645.

601 Zhang, Y., Haan, N.L., Landis, D.A., 2020. Landscape composition and configuration have
 602 scale-dependent effects on agricultural pest suppression. Agric. Ecosyst. Environ. 302,
 603 107085.

604 Zhang, Q., Yang, L., Li, M., Liu, Y., Lu, Y., 2020. Stable isotope analysis for assessing the
 605 intercrop movement of *Microplitis mediator*, a larval endoparasitoid of *Helicoverpa*
 606 *armigera*. Entomol. Exp. Appl. 168, 381-386.

607 Zhao, Z., Liu, J., He, D., Guan, X., Liu, W., 2013. Species composition and diversity of
 608 parasitoids and hyper-parasitoids in different wheat agro-farming systems. J. Insect Sci.
 609 13, 162.

610 Zhou, H., Chen, J., Cheng, D., Yong, L., Sun, J., 2009. Effects of wheat-pea intercropping on
 611 the population dynamics of *Sitobion avenae* (Homoptera: Aphididae) and its main natural
 612 enemies. Acta. Entomol. Sinica. 52, 775-782.

Table 1 Results of multi-model inference analysis to determine the effects of landscape context on parasitoid (mummy) density across four scales. For each scale, the averaged model was taken from the best models with $\Delta AICc$ values < 2 (see Table S4). **Z value is the estimate of each coefficient divided by its standard error**; Relative importance is the sum of the Akaike weight associated with each variable in models in the top model set.

Scales (km)	Variables	Estimate	Z value	Pr(> Z)	Relative importance
0.5	Intercept	2.86	4.31	< 0.0001	
	Aphids	0.67	3.51	0.0004	1.00
	Fallows	0.41	3.12	0.0018	1.00
	Other crops	-0.21	1.75	0.0801	0.67
	Woodlands connectivity	-0.13	1.03	0.3054	0.26
	Fallows connectivity	-0.14	0.96	0.3393	0.14
	Woodlands	0.11	0.73	0.4671	0.11
1.0	Intercept	2.85	4.47	< 0.0001	
	Aphids	0.68	3.53	0.0004	1.00
	Fallows	0.38	3.23	0.0012	1.00
	Woodlands connectivity	0.13	0.89	0.3711	0.21
	Other crops	-0.10	0.76	0.4489	0.18
	Woodlands	0.10	0.62	0.5349	0.17
1.5	Intercept	2.87	4.42	< 0.0001	
	Aphids	0.71	3.69	0.0002	1.00
	Woodlands connectivity	0.19	1.46	0.1444	0.33
	Fallows	0.30	2.47	0.0134	1.00
	Other crops	-0.22	1.65	0.0984	0.51
	Woodlands	0.19	1.25	0.2110	0.24
	Fallows connectivity	0.13	0.90	0.3682	0.09
2.0	Intercept	2.84	4.34	< 0.0001	
	Aphids	0.70	3.78	0.0002	1.00
	Woodlands connectivity	0.26	1.98	0.0477	1.00
	Fallows	0.32	2.66	0.0079	1.00
	Other crops	-0.23	1.89	0.0584	0.65

619 **Table 2** Results of multi-model inference analysis to determine the effects of landscape context on the parasitism and hyperparasitism rates of wheat aphids
620 across four scales. For each scale, the averaged model was taken from the best models with $\Delta AICc$ values < 2 (see Table S5).

Response variables	Scales (km)	Variables	Estimate	Z value	Pr ($> Z $)	Relative importance
Parasitism rate	0.5	Intercept	-4.34	5.61	< 0.0001	
		Fallows	0.33	2.67	0.0075	1.00
		Other crops	-0.26	2.28	0.0229	1.00
		Fallows connectivity	-0.18	1.25	0.2114	0.32
		Woodlands connectivity	-0.10	0.80	0.4256	0.21
	1.0	Intercept	-4.34	5.73	< 0.0001	
		Fallows	0.29	2.69	0.0072	1.00
		Other crops	-0.24	2.15	0.0317	1.00
		Woodlands connectivity	0.10	0.71	0.4768	0.29
	1.5	Intercept	-4.36	5.91	< 0.0001	
		Fallows	0.23	1.88	0.0604	0.68
		Other crops	-0.28	2.41	0.0161	1.00
		Fallows connectivity	0.21	1.55	0.1210	0.70
		Woodlands connectivity	0.13	1.14	0.2541	0.15
		Woodlands	0.15	1.10	0.2720	0.14
	2.0	Intercept	-4.37	6.05	< 0.0001	
		Woodlands connectivity	0.29	1.87	0.0615	0.80

Hyperparasitism rate		Fallows	0.26	2.22	0.0264	1.00
		Other crops	-0.28	2.38	0.0174	1.00
		Woodlands	-0.19	1.02	0.3080	0.28
	0.5	Intercept	-0.91	2.02	0.0439	
		Fallows connectivity	0.29	4.30	< 0.0001	1.00
		Other crops	0.21	2.85	0.0044	1.00
		Woodlands	0.38	5.38	< 0.0001	1.00
		Fallows	-0.11	1.63	0.1027	0.43
	1.0	Intercept	-0.86	2.36	0.0181	
		Other crops	0.15	2.22	0.0263	1.00
		Woodlands	0.36	5.14	< 0.0001	1.00
		Fallows connectivity	-0.05	1.14	0.2565	0.30
	1.5	Intercept	-0.84	2.20	0.0279	
		Woodlands connectivity	0.28	2.72	0.0065	1.00
		Woodlands	0.14	1.38	0.1674	0.41
	2.0	Intercept	-0.87	2.13	0.0332	
		Woodlands connectivity	0.39	6.30	< 0.0001	

Table 3 Results of multi-model inference analysis to determine the effects of landscape context on parasitoid diversity across four scales. For each scale, the averaged model was taken from the best models with $\Delta AICc$ values < 2 (see Table S6).

Scales (km)	Variables	Estimate	Z value	Pr(> Z)	Relative importance
0.5	Intercept	1.90	3.93	< 0.0001	0.66
	Woodlands	0.29	2.62	0.0087	
1.0	Intercept	1.91	4.11	< 0.0001	0.40
	Woodlands	0.27	2.31	0.0209	
	Woodlands connectivity	0.25	2.01	0.0440	
1.5	Intercept	1.8897	3.673	0.0002	0.58
	Woodlands connectivity	0.2762	2.469	0.0135	
2.0	Intercept	1.87	3.51	< 0.0001	
	Woodlands connectivity	0.33	3.28	0.0011	

626 **Table 4** The top ten most common plant species in terms of importance value index in woodlands and fallows. ‘/’ means the plant was not flowering during
627 survey period, ‘+’ means the floral plant percentage is 0-25%, ‘++’, ‘+++’ and ‘++++’ for 25-50%, 50-75% and 75-100% respectively

	Woodlands			Fallows		
	Species	Floral coverage	Importance value	Species	Floral coverage	Importance value
1	<i>Salsola collina</i> Pall.	/	35.37	<i>Capsella bursa-pastoris</i> L.	++++	53.62
2	<i>Chenopodium album</i> L.	+	26.84	<i>Lagopsis supina</i> Steph.	++++	28.13
3	<i>Humulus scandens</i> Lour.	/	26.66	<i>Calystegia hederacea</i> Wall.	++++	23.35
4	<i>Chenopodium glaucum</i> L.	+	24.26	<i>Hemistepta lyrata</i> Bunge	++++	16.99
5	<i>Kochia scoparia</i> L.	+	17.59	<i>Trigonotis peduncularis</i> Trev.	++++	16.56
6	<i>Capsella bursa-pastoris</i> L.	++	17.43	<i>Ixeris denticulata</i> Houtt.	++++	14.99
7	<i>Lagopsis supina</i> Steph.	++	16.06	<i>Chenopodium serotinum</i> L.	+++	13.42
8	<i>Ixeris denticulata</i> Houtt.	+	12.20	<i>Chenopodium glaucum</i> L.	+++	13.06
9	<i>Carex phacota</i> Spr.	/	9.90	<i>Descurainia sophia</i> L.	++++	10.84
10	<i>Trigonotis peduncularis</i> Trev.	++	8.88	<i>Salsola collina</i> Pall.	/	10.65

628

Figure Captions

Figure 1 The two main categories of semi-natural habitats in northern China: (a) fallow, and (b) woodland.

Figure 2 Response of parasitoid density to landscape variables. Parasitoid density increased with increasing (a) aphid abundance, (b) the fallows proportion within a 0.5 km radius, and (c) woodlands connectivity within a 2.0 km radius.

Figure 3 Response of parasitism rate to landscape variables. Parasitism rate increased with increasing (a) proportion of fallows within a 0.5 km radius and (b) woodlands connectivity within a 2.0 km radius.

Figure 4 Response of hyperparasitism rate to landscape variables. Hyperparasitism rate increased with increasing (a) proportion of woodlands and (b) fallows connectivity within a 0.5 km radius, and (c) woodlands connectivity within a 2.0 km radius.

Figure 5 Response of parasitoid diversity to landscape variables. Parasitoid Shannon diversity increased with increasing (a) proportion of woodlands within a 0.5 km radius and (b) woodlands connectivity within a 2.0 km radius.

Figure 6 Vegetation coverage, plant species richness and Shannon diversity in fallow and woodland habitats. * p -value < 0.05; ** p -value < 0.01; *** p -value < 0.001.

Figure 1



Figure 2

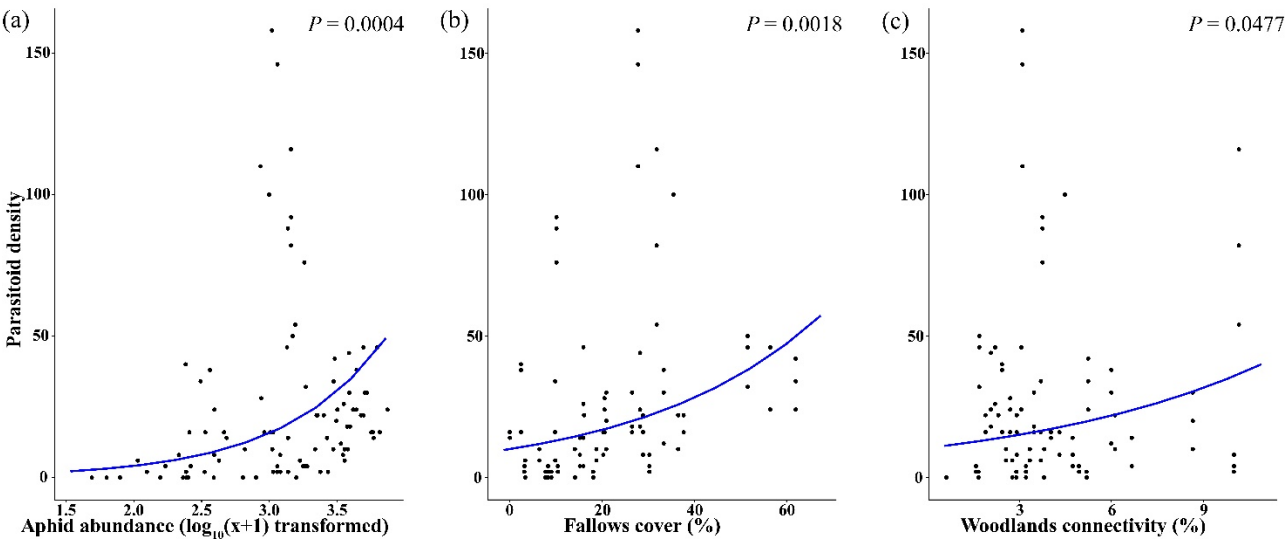


Figure 3

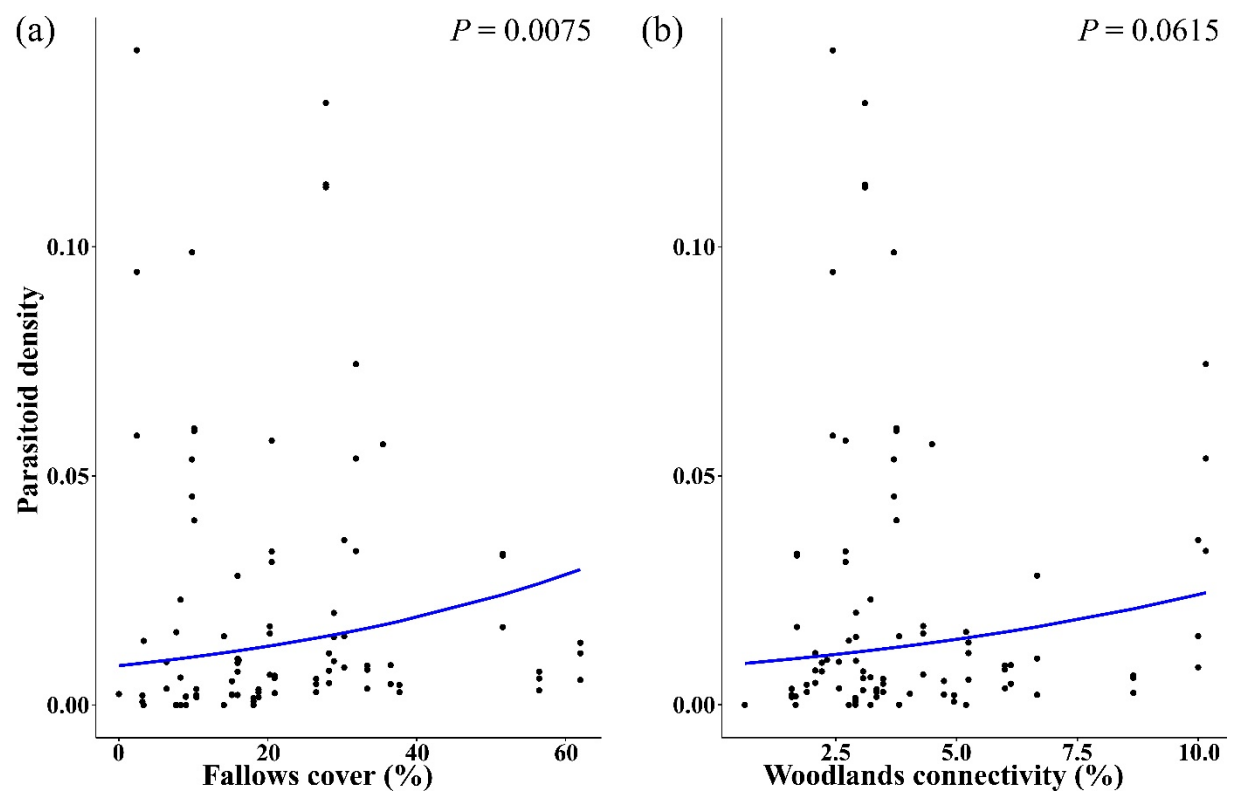


Figure 4

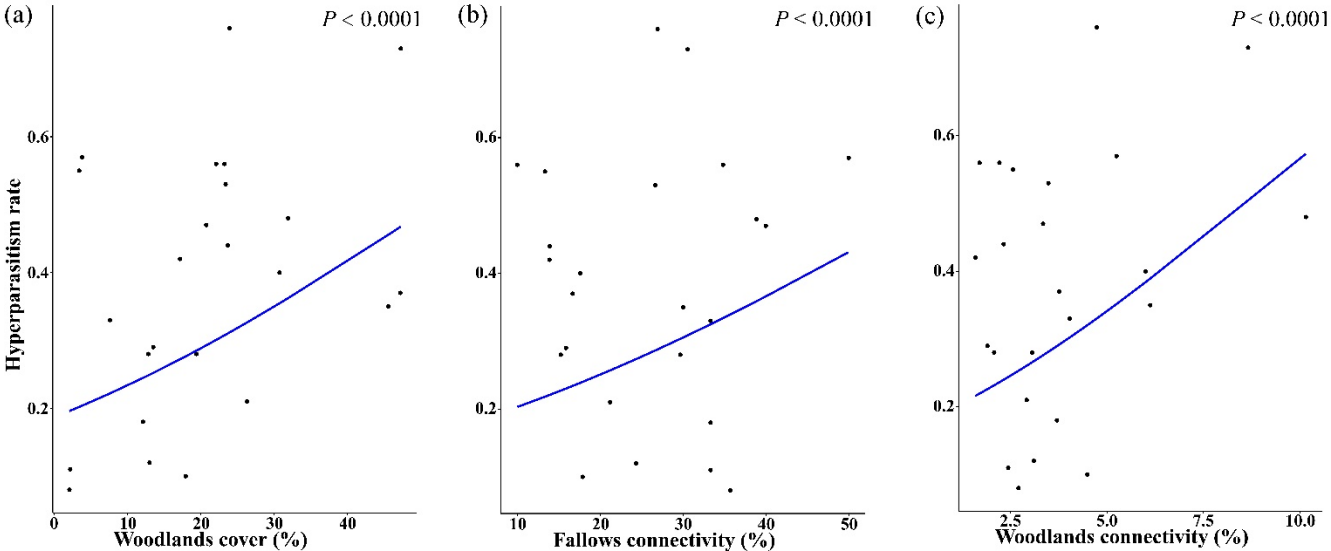


Figure 5

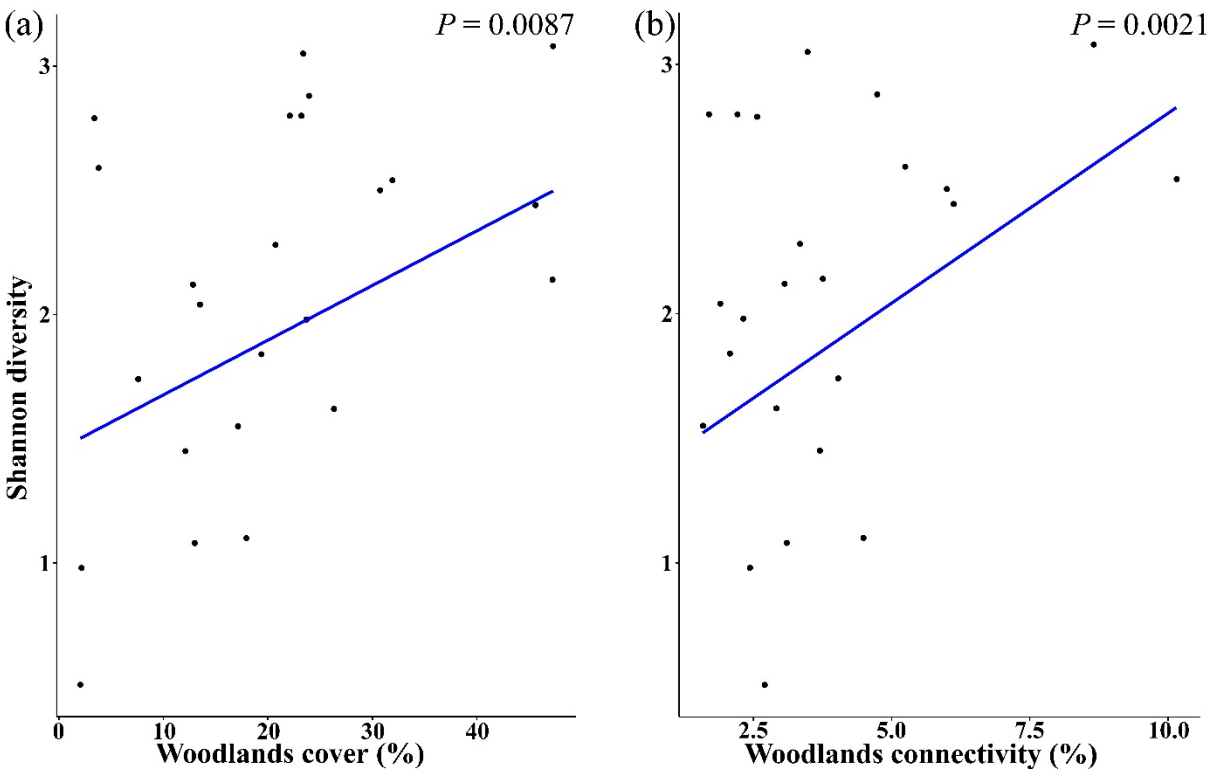


Figure 6

