

Effects of crop species richness on pest-natural enemy systems based on an experimental model system using a microlandscape

ZHAO ZiHua^{1†*}, SHI PeiJian^{1,2†}, MEN XingYuan^{3†}, OUYANG Fang¹ & GE Feng^{1*}

¹State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China;

²Laboratory of Stock Assessment and Ecosystem Management, Yellow Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Qingdao 266071, China;

³College of Plant Protection, Shandong Academy of Agricultural Sciences, Jinan 250100, China

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The relationship between crop richness and predator-prey interactions as they relate to pest-natural enemy systems is a very important topic in ecology and greatly affects biological control services. The effects of crop arrangement on predator-prey interactions have received much attention as the basis for pest population management. To explore the internal mechanisms and factors driving the relationship between crop richness and pest population management, we designed an experimental model system of a microlandscape that included 50 plots and five treatments. Each treatment had 10 repetitions in each year from 2007 to 2010. The results showed that the biomass of pests and their natural enemies increased with increasing crop biomass and decreased with decreasing crop biomass; however, the effects of plant biomass on the pest and natural enemy biomass were not significant. The relationship between adjacent trophic levels was significant (such as pests and their natural enemies or crops and pests), whereas non-adjacent trophic levels (crops and natural enemies) did not significantly interact with each other. The ratio of natural enemy/pest biomass was the highest in the areas of four crop species that had the best biological control service. Having either low or high crop species richness did not enhance the pest population management service and lead to loss of biological control. Although the resource concentration hypothesis was not well supported by our results, high crop species richness could suppress the pest population, indicating that crop species richness could enhance biological control services. These results could be applied in habitat management aimed at biological control, provide the theoretical basis for agricultural landscape design, and also suggest new methods for integrated pest management.

biological control service, biomass, habitat management, microlandscape, trophic level

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Agro-ecosystems are composed of a variety of cultured crops grown mostly for human consumption, and simultaneously supply multiple ecosystem services. In these ecosystems, tri-trophic level interactions (crop, pest, and natural enemy) are an important component and have evolved close relationships. Indeed, the effect of species composi-

tion and community structure on yields and ecosystem services is a very popular topic in ecology [1]. Some studies have reported that plant species richness directly affects species composition and the abundance of pests, which would influence the biological control services provided by natural enemies [2,3]. Indeed, a high level of plant diversity (e.g., intercropping, non-tillage, and weeds) could suppress pest populations and reduce yield losses caused by pest damage [4]. Root [5] proposed two hypotheses (the resource

†Contributed equally to this work

*Corresponding author (email: gef@ioz.ac.cn; zihuazhao@126.com)

concentration hypothesis and the natural enemy hypothesis) to interpret these phenomena. The resource concentration hypothesis suggests that pest populations will increase during periods of high host density and decrease with low host density. In contrast, the natural enemy hypothesis states that high plant species richness can provide abundant resources and refuge for natural enemies (predators and parasitoids), greatly enhancing the activity of natural enemies and suppressing pest populations [6]. However, Andow found that high plant species richness did not always facilitate the biological control of pests [7], and only 52%–53% of pest species can be affected by plant species richness [2]. In fact, no consensus has been reached based on this type of research to date. Therefore, the effect of plant species richness on biodiversity and the biological control service of natural enemies in agro-ecosystems is currently an important research topic [8].

Agro-ecosystems have experienced major landscape changes in the last few decades caused by agricultural intensification, including the expansion of arable lands and landscape simplification, both of which drive loss of biological control services in agricultural landscapes [7,8]. In China, approximate 10% of crop yields were estimated to be destroyed by pests before the harvest of various crops, despite the use of a variety of crop protection measures including the widespread use of chemical pesticides. These processes have led to serious environmental problems. However, previous studies have found that the intercropping of two crops could improve biological control services; however, the effects of multiple crop species (three or more species) on pest damage and natural enemies have rarely been reported. Recently, experimental model systems (EMSs) of microlandscapes have been used to analyze the relationship between plant species richness and the diversity of insects on grasslands [3,9]. Accordingly, this EMS method provides a promising tool that can be used to study the effects of crop composition on pest damage and the biological control services provided by natural enemies of crop species.

Agricultural landscapes and the local management of arable lands can influence the abundance and composition of pest species present in an area. In the last few decades, frequent outbreaks of pests believed to have been caused by landscape simplification and agricultural intensification have brought large risks for agricultural production and have endangered the ability of farmers to secure adequate food supplies [10,11]. Therefore, ecological research has focused on creating ways to design healthy agricultural landscapes and to renew the stability of agro-ecosystems by achieving biological control of pest species [12]. Nonetheless, a large number of pest and natural enemy species exist in any specific crop ecosystem. For example, cereal aphids are parasitized by more than 17 parasitoid species [12]; in

addition, more than 10 pest species exist in wheat fields. Similar situations exist in other crop ecosystems (e.g., cotton, rice, and corn), and this large number of species in a single ecosystem creates difficulties for community analysis. Fortunately, biomass analysis, a method that mainly considers material recycling and energy flow, provides an effective method which can be used to study predator-prey interactions related to agricultural plants, associated pest species and the natural enemy species of agricultural pests. Thus, we can place all species in one trophic level into a group and analyze the tri-trophic interactions (plant, pest, and natural enemy) [13,14].

The Huang-Huai-Hai Plain in North China is one of China's most important grain producing regions. In the last few decades, population growth and changes in agricultural management and planting patterns have caused landscape simplification and a loss of biodiversity in the region's agro-ecosystems [15–18]. In particular, the rapid expansion of the monoculturing of crops has led to serious outbreaks of agricultural pests and the loss of biological control agents. Crop species richness facilitates biological control through the use of natural enemies of plant pest species in annual arable systems. However, agricultural intensification has led to high levels of landscape simplification and a reduction of habitat heterogeneity. In the present experiment, we studied the relationships between crop species richness and the biomass of pests and natural enemies based on a microlandscape EMS. Two hypotheses were tested: (i) based on the resource concentration hypothesis, high crop species richness suppresses pest populations, whereas decreased crop species richness will result in increases in pest species populations [19]; (ii) based on the natural enemy hypothesis, high crop species richness would supply abundant resources and refuge for natural enemies, which would indirectly improve the biological control service they provide and suppress pest populations [20]. The aim of this experiment was to achieve multiple ecological services and to supply a theoretical basis for potential pest management [21].

1 Materials and methods

1.1 study region

The study region is located in the county of Yishui, Linyi City, Shandong Province, China (35°48'05"N, 118°37'11"E) and has a temperate maritime monsoon climate with an elevation of 101.1–916.1 m. The region receives an average 2421 h of sunshine annually and has an annual average temperature of 14.1°C. The value of effective accumulated temperatures above 10°C is 2390°C and the frost-free period is longer than 200 d. The average annual precipitation is 849 mm; the average annual evaporation capacity is 1773.5 mm. In the center of this agricultural region, grain is produced from several important crops (e.g., wheat, cotton, and corn) which grow mainly on Podzol E soil.

1.2 Study site

An experimental microlandscape (EMS) was implemented [17,18]. Twenty primary crop species commonly grown in North China were selected, including *Gossypium* spp., *Zea mays* L., *Triticum aestivum* L., *Glycine max* (L.) Merr., *Solanum lycopersicum* L., *Brassica oleracea* L., *Setaria italica* (L.) Beauv., *Sorghum bicolor* (L.) Moench, *Lolium perenne* L., *Vigna angularis* (Willd.) Ohwi et Ohashi, *Arachis hypogaea* L., *Vigna radiata* (L.) R. Wilczek, *Medicago sativa* L., *Solanum melongena* L., *Apium graveolens* L., *Trifolium repens* L., *Helianthus annuus* L., *Phaseolus vulgaris* L., *Brassica napus* L., and *Sesamum indicum* L. Five plant richness levels (1, 2, 4, 8, and 16) were designed, and we randomly selected 1, 2, 4, 8, and 16 species to achieve the five crop species richness levels. Every treatment was repeated 10 times. Fifty 9 m×9 m plots were used which were located 1 m apart; the entire experimental site covered 70 m×150 m (Figure 1). For a given plot, the crops were distributed in a matrix of 22 rows and 22 columns.

The crop density and amount of fertilizer use was the same in each plot so that the study sites were homogeneous. Herbicide was applied to the unplanted area between the plots to suppress weed growth. In this experiment, we only considered the effect of crop species richness on pests and natural enemies. No pesticides, herbicides, chemical fertilizers, or other agrichemicals were applied to any of the crops in any of the plots. Weeds were removed by hand. These management practices were expected to largely decrease the external disturbance to the insect community. The distance between the experimental site and surrounding landscape was 5 m. In addition, the corn fields in the landscape surrounding the study area provided homogeneous buffer habitat, which was expected to eliminate stochastic disturbance (Figure 1). Crop species richness (N) and crop arrangements in each plot remained the same during the

four-year study (2007–2010).

1.3 Study methods

1.3.1 Insect sampling

A cross-sectional sampling method was used in these experiments, which is similar to a parallel sampling method. We only sampled one row with 22 plants in the center line in each plot (Figure 1). This uniform collection method was designed to minimize edge effects caused by the surrounding habitat. All insect species and their abundance (pests and natural enemies) on the 22 plants (center line) were recorded. We collected insect samples five times in each year, or once a month in April, May, June, July, and August, during the crop growing season. The species composition and abundance of pest species and their natural enemies were carefully recorded. To reduce disturbance to the plants, insect populations on the abaxial and adaxial leaf surfaces were studied using a handheld mirror and by visual observation, respectively. Small insects were surveyed using an insect magnifier. These processes were expected to greatly decrease the human disturbance. Every plant was carefully surveyed for 10 min. The instars, state, and injury characteristics of pests were recorded at the same time; the investigations in each plot required an average of 220 min. The insect density was transformed to individuals/22 plants based on the cross-sectional sampling method (Figure 1).

1.3.2 Biomass determination

The total dry organic matter of plants and insects (pests and natural enemies) was determined. Below- and above-ground plant parts were transported to the lab and their biomasses were determined after 72 h of drying at 60°C. Large plants (e.g., corn) were cut into several sections, and we calculated the biomass by summing these several sections. Each test involved three repetitions for every crop species. The same

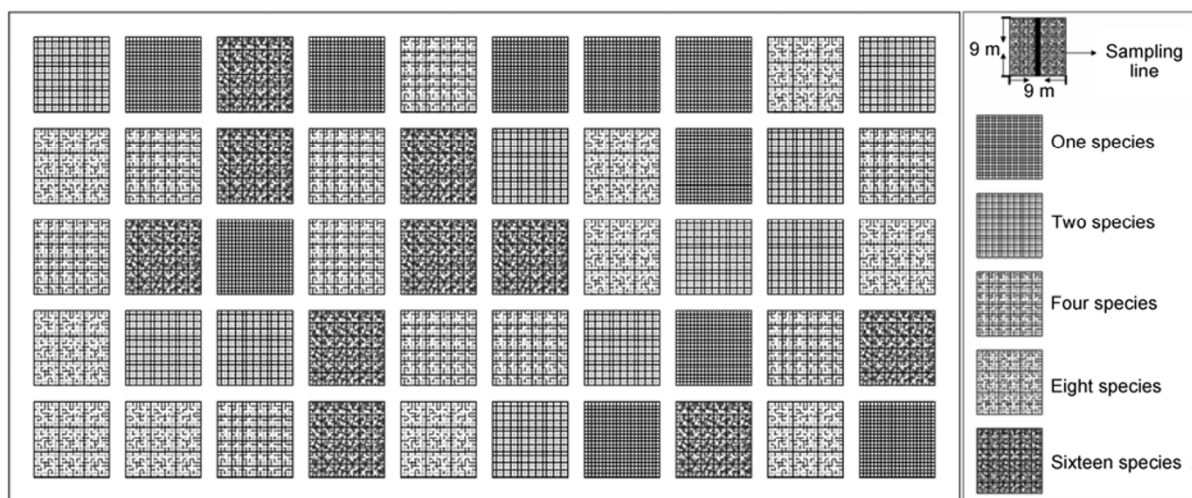


Figure 1 Crop arrangement and composition in an experimental model system (EMS) of a microlandscape.

methods were used to determine the biomass of pests and natural enemies (60°C drying for 72 h). Small insect biomass (aphids, aleyrodid, and thrips) was determined as g/100 individuals to calculate the mean value (g/individual); the biomass of other arthropods (spiders, carabid, and plant hoppers) was determined individually. Five repetitions were conducted for each insect species.

1.3.3 Transformation of insect population biomass

All insect species were divided into two groups (pests and natural enemies); neutral insects (honeybees, flies, and mosquitoes) were excluded from the analysis. The biomass of individual insect species was first determined; then the biomass of each pest and natural enemy species was calculated based on its population density. The crop biomass was obtained by the same method.

1.4 Statistical analysis

1.4.1 Biomass of tri-trophic levels (crop-pest-natural enemy)

The tri-trophic level interactions were determined by a correlation analysis, and the biomass of each of the three trophic levels (crop, pest, natural enemy or tri-trophic if considered as a group) was calculated. We did not consider interspecies relationships or specific species and only tested the correlation relationship at the tri-trophic level. The effects of crop species richness on biological control services were measured. Neutral insects that supply pollination and/or decomposition functions in agro-ecosystems were excluded from the analysis.

1.4.2 Biological control service

The ratio of biomass (natural enemy/pest) was established as an index of the biological control service [22], by investigating the insect populations on 22 different plants on the center line in the different experimental plots. Therefore, we

calculated the ratio of natural enemy biomass to pest biomass to represent the biological control service provided by each natural enemy species.

1.4.3 Generalized additive model

The generalized additive model (GAM) is a non-parametric method of local regression that explores the relationships between variables [23]. In this experiment, two generalized additive models were constructed. The first model aimed to analyze the effects of sampling time, pest biomass, and crop biomass on the natural enemy biomass (eq. (1)):

$$y = \alpha + s_1(x_1) + s_2(x_2) + s_3(x_3) + \varepsilon. \quad (1)$$

This model was composed by smoothing functions, which included three spline functions: s_1 , s_2 , and s_3 . x_1 represents sampling time, x_2 represents pest biomass, x_3 represents

crop biomass, ε represents the error term, and y represents natural enemy biomass. Parameter α was also added into the model. This GAM has been widely used in ecology, which was applied to analyze the non-linear relationship.

The second model could be constructed by the same method, which analyzed effects of sampling time, natural enemy biomass, and crop biomass on pest biomass (eq. (2)):

$$x_2 = \alpha + s_1(x_1) + s_4(y) + s_3(x_3) + \varepsilon. \quad (2)$$

These two generalized additive models were performed using R 2.11 (R Development Core Team, 2010) with package mgcv.

1.4.4 Linear regression model

The linear regression model was used to analyze the relationship of tri-trophic levels (crop, pest, and natural enemy). We first examined the relationship between pest biomass and natural enemy biomass. Then the other relationships (crop biomass and natural enemy biomass or crop biomass and pest biomass) were analyzed in a similar way. For checking the biological control services supplied by crop species richness, the analysis of variance was used to test whether the ratios of biomass (natural enemy/pest) at five crop species richness (i.e., 1, 2, 4, 8 and 16) were equal. The linear regression model was performed using R 2.11 (R Development Core Team, 2010).

2 Results

2.1 Effects of crop species richness on pest and natural enemy biomass

Crop species richness had major effects on the biomass of pests and natural enemies (Figure 2), with the pest biomass increasing with increasing crop species richness. However, the differences were not significant (Figure 2A, $F_{1,593}=1.464$, $P=0.227$). In addition, the natural enemy biomass also increased with increasing crop species richness, although the differences were not significant (Figure 2B, $F_{1,593}=0.682$, $P=0.409$). The mid-range value of the pest and natural enemy biomass peaked when the crop species richness was at a maximum ($N=16$); the mid-range value of biomass was 0.12 g/22 plants and 0.04 g/22 plants, respectively. When the crop species richness was at a minimum ($N=1$), the mid-range value of pest and natural enemy biomass was also low (pest, 0.04 g/22 plants; natural enemy, 0.03 g/22 plants).

2.2 Relationship at the tri-trophic level (crop-pest-natural enemy)

The relationship at the tri-trophic level was analyzed by generalized additive models. The effects of sampling time, pest biomass, and crop biomass on the natural enemy biomass were also analyzed (Figure 3). The sampling time had

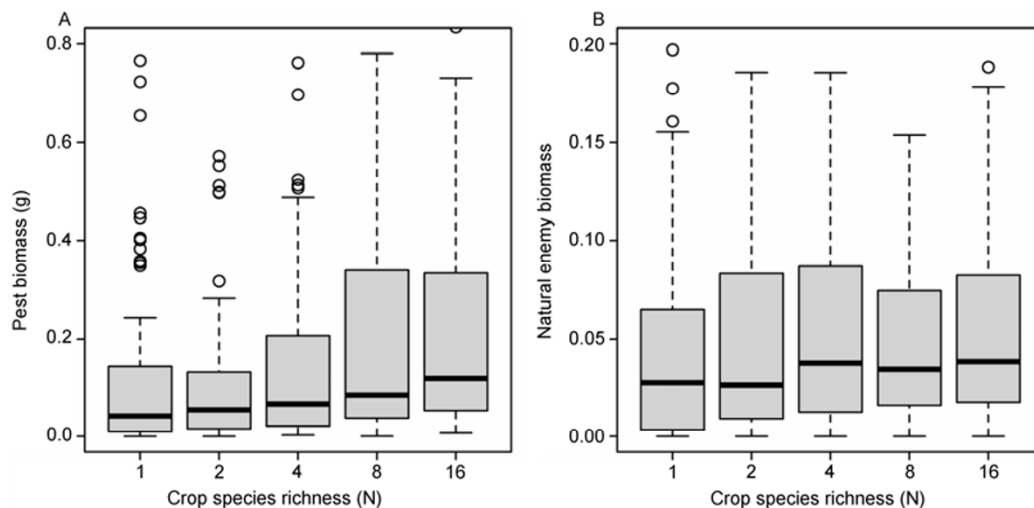


Figure 2 Relationship between crop richness and pest and natural enemy biomass.

significant effects on the biomass of natural enemies (Figure 3A, $F_{1,000}=4.007$, $P=0.046$). Although the crop biomass also had no significant effects on the natural enemy biomass (Figure 3E, $F_{1,044}=0.574$, $P=0.462$), the pest biomass did have significant effects (Figure 3C, $F_{8,846}=15.130$, $P<0.001$).

The sampling time had no significant effects on the pest biomass (Figure 3B, $F_{2,092}=1.908$, $P=0.136$), and the crop biomass also did (Figure 3F, $F_{1,893}=2.031$, $P=0.123$). In contrast, the natural enemy biomass did have significant effects on the pest biomass (Figure 3D, $F_{6,505}=9.478$, $P<0.001$).

2.3 Effects of crop species richness on pest damage and biological control service

The ratio of biomass (natural enemy/pest) was used to analyze the relationship between the biological control service and crop species richness. The results showed that the ratio of biomass (biological control service) first increased and then decreased with increasing crop species richness; the differences were significant (Figure 4A, $F_{4,593}=5.163$, $P=0.0234$). The biological control service peaked when the crop species richness was 4, with the median and mean of the natural enemy/pest ratio at the maximum (Figure 4A). In contrast, the median and mean of the natural enemy/pest ratio were both at a minimum when the crop species richness was 8 (Figure 4A).

The relationship between the pest and natural enemy biomass was positive and significant: the natural enemy biomass increased with increasing pest biomass (Figure 4B, $F_{1,593}=32.79$, $r=0.2289$, $P<0.01$). The relationship between the pest and crop biomass was also positive and significant: the pest biomass increased with increasing crop biomass (Figure 4D, $F_{1,593}=10.82$, $r=0.1338$, $P=0.0011$). However, no significant relationship existed between the crop and natural enemy biomasses (Figure 4C, $F_{1,593}=0.62$, $r=0.0323$, $P=0.4326$).

3 Discussion

3.1 Relationship between crop species richness and biomass of pests and natural enemies

In this experiment, we designed five crop species richness levels to analyze the effects of the crop species richness on the biomass of pests and natural enemies based on EMS at the microlandscape level. The biomass of pests and natural enemies increased with increasing crop species richness. Therefore, the resource concentration hypothesis was not well supported by our results. This may occur because agricultural pests are polyphagous. Accordingly, the plot with the highest crop species richness supplied the most abundant food resources for pests [24,25]. For example, the cotton bollworm (*Helicoverpa armigera* Hübner, Lepidoptera: Noctuidae), which can feed on several hosts, including wheat, corn, cotton, and vegetables, has a high level of biomass in plots with high crop species richness [26,27]. In addition, multiple crop species also supply an abundance of prey and food resources for natural enemies. Although the biomass of pests and natural enemies increased with increasing crop species richness, the differences were not significant. This biomass method could simplify community analyses of pests and natural enemies in agro-ecosystems, and the biomass method could be used to study energy flow of plants-pests-natural enemies based on multiple crop systems [14,28].

The diversity-yield relationship is an important aspect in biodiversity and ecological function and has received much attention [29]. Some studies report that high plant diversity can result in high yields [30–32]. However, Ge and Ding [7] found no relationship between species diversity and yield. In our experiments, we found that the adjacent trophic levels (pests and natural enemies and crop and pests) had significant linear correlations. The pest biomass increased with increasing crop biomass; similarly, the natural enemy bio-

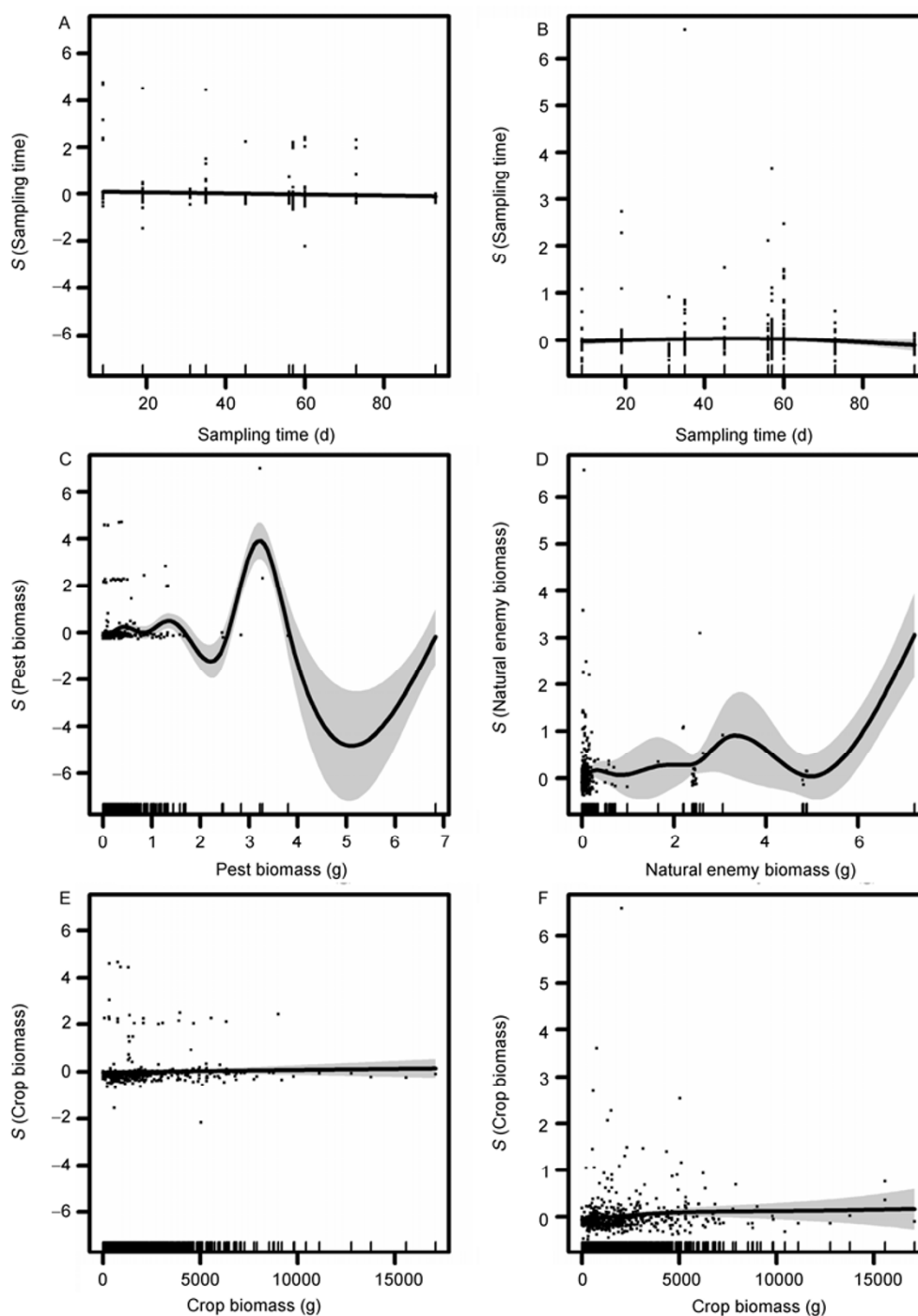


Figure 3 Relationships of sampling time and biomass in a generalized additive model (GAM). A, C, and E indicate the effects of sampling time, pest biomass, and crop biomass on natural enemies; B, D, and F indicate the effects of sampling time, natural enemy biomass, and crop biomass on pests.

mass increased with increasing pest biomass. Conversely, non-adjacent trophic levels (crop and natural enemies) showed no significant linear correlation. These results indicated that energy flow in agro-ecosystems might affect adjacent trophic levels; for non-adjacent trophic levels, energy flow and material recycling would show no significant effects.

3.2 Effects of crop species richness on biological control services in an agro-ecosystem

Biodiversity in an agro-ecosystem has large effects on integrated pest management [6]. However, previous studies mainly focused on the effects of the intercropping of two crops on biological control services; indeed, related studies are rare for multiple crops (three or more species). In our

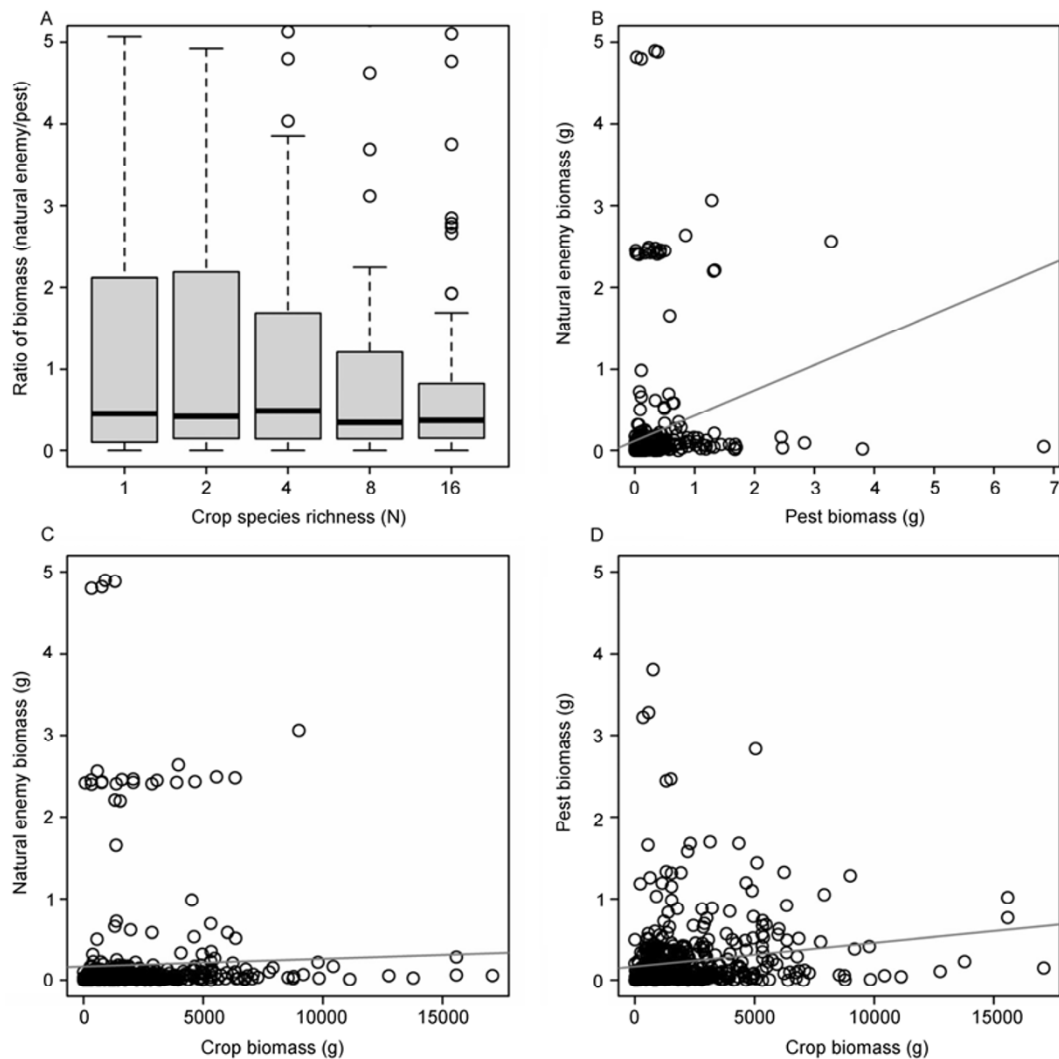


Figure 4 Tri-trophic level interactions of crop, pest, and natural enemy.

experiment, five crop species richness levels were designed to analyze the effects of the level of crop species richness on pests and natural enemies based on EMS at the micro-landscape level. The biological control services (the ratio of biomass) were significantly affected by the crop species richness, as based on biomass methods, decreasing with increasing crop species richness. In addition, the biological control services peaked when the crop species richness was four. Two possible mechanisms could be invoked to interpret these findings: (i) high crop species richness could disturb the host-searching behaviors of pests, leading to the inadequate identification of a plant host [33,34], or (ii) multiple crop species could supply alternative prey and refuge, enhancing the activity of natural enemies and improving the biological control service [35–37].

The relationships between crop arrangement and biological control services are among the most important issues in agro-ecosystems [38,39], and the methods used to manipulate habitat composition and agricultural management in

mosaic landscapes to achieve biological control services are important aspects of ecological research. Such landscape designs should consider the dynamics of pests and natural enemies at different spatial and temporal scales. Polyphagous pests complicate these processes more than oligophagous pests. The biological control services were optimal when the crop species richness was 4, showing that the biological control service could be improved through habitat manipulation and landscape design. Microlandscape EMS based on a small spatial scale provided a valuable tool which can be used to study the effects of crop arrangement and composition on biological control services. The plot in our experiments was 9 m×9 m; however, other researchers have conducted experiments on a larger scale (10 m×10 m and 30 m×30 m) [40,41] or using smaller plots (4.7 m×4.7 m and 2.4 m×2.4 m) [15,42]. Future research should analyze the tri-trophic level interactions on a large spatial scale, which could produce reliable results [20,43,44]. All of these results could be applied in habitat manipulation aimed at

pest biological control, provide a theoretical basic for agricultural landscape design, and also supply new methods for integrated pest management [44,45].

Our finding on the effect of crop species richness on biomass of pest and natural enemy species can be applied in integrated pest management strategies that aim to incorporate crop composition and arrangement into habitat management as they suggest that successful biological control would mainly be effective through the use of well-planned landscape design and the creation of habitat diversity. Combining agricultural landscape design with biological control services may effectively address the ecological function of natural enemies when integrated pest management strategies are used regionally and may provide multiple ecosystem services [46,47]. Far less attention has been paid to additional ecosystem services that agricultural landscapes could provide as managed landscapes. Our results not only address the biological control of insect pests but also address other ecological services received through landscape design and habitat manipulation [48].

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