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Article

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Abstract: Banker plant systems have the advantages of introducing natural enemies preventively and maintaining by providing alternative prey, thus controlling the pests sustainably. Banker plant systems are usually composed of three factors: a banker (secondary) plant, an alternative prey, and a shared predator (attacking an alternative prey on the secondary plant, and the targeted pest on the crop). However, for most banker plant systems, there is a lack of understanding regarding the dynamic relationship among these elements, with detrimental effects on practical applications. Therefore, in this study, the control of *Myzus persicae* on *Capsicum annum* by the *Coccinella septempunctata*–*Megoura japonica*–*Vicia faba* banker plant system was used as the research system. The effects of different release time of predators, different initial numbers of alternative prey (*Me. japonica*) and different initial ratios of target pests/alternative prey on the indirect interaction of two aphids and the biological control effect of shared predators were tested. The occurrence of indirect interactions between the two aphid preys, the impact on population dynamics, and biological control effectiveness of the shared predator *C. septempunctata* were investigated. When the initial numbers of both species of aphids were equal (200 each), the delay between aphid and *C. septempunctata* introduction in the cage had no effect on *My. persicae*, but *Me. japonica* showed lower numbers when testing the least time between predatory introductions. When the numbers of the two aphids were manipulated, the *My. persicae* population was significantly reduced by the predator only at a ratio of *My. persicae* to *Me. japonica* < 1, while initial ratios ≥ 1 enabled *My. persicae* population growth. In 1–6 days, the control effect of *C. septempunctata* was the best. Principal component analysis showed that the experimental time, initial numbers of *Me. japonica*, and relative numbers of *Me. japonica* affected the predation of *My. persicae* by *C. septempunctata*. In addition, when the initial aphid ratio was greater than 1/4, *C. septempunctata* was able to effectively control *My. persicae*. Overall, our study confirmed the number-mediated indirect interaction (apparent competition) relationship and its impact on prey population dynamics. We provide useful information for optimizing banker plant systems, to boost biocontrol of aphid pests.

Keywords: biological control; *Coccinella septempunctata*; predation; *Myzus persicae*; apparent competition; pepper

1. Introduction

The aim of Integrated Pest Management (IPM) is to keep pests below the economic threshold level [1–3]. Within IPM, biological control is a key lever via the release of natural enemies, as well as through methods promoting them in fields [4–6]. In addition, the mass release of natural enemies can effectively control pests, but this approach can be costly and not applicable in all agroecosystems [7–9]. Conservation biological control (CBC) provides natural enemy populations with increased availability of food supplements

and habitats, thereby boosting sustainable pest control [4,10–13]. Compared with other biological control strategies, such as inoculative and inundatory biological control needing multiple natural enemy releases over time, CBC relying on banker plant systems may be effective in pest control by allowing the maintenance of natural enemy populations in cropping systems [14].

The banker plant system indirectly provides substitute hosts, preys, nutrients, and habitats for biological control agents (BCA) through the presence of non-crop plants that provide nutrients for alternative preys and hosts, allowing the reproduction and survival of natural enemies, thereby inhibiting the growth of pest populations in greenhouses or fields for a medium-to-long periods [15,16]. This CBC tool combines BCA protection and supplementation [17–19]. The banker plant system includes beneficial organisms (predators or parasitoids), one or more alternative preys, and their banker plants [4,15,16,20]. In the absence of pests in the early stage, a banker plant can improve the survival rate of natural enemies, helps to establish stable populations in agroecosystems, and favorably enhances biological control success [14].

However, most of the research on this topic has focused on the design of banker plant systems through screening constituent factors, performing suitability evaluations [18], and establishing quantitative effects on beneficial organisms [12,19,21,22]. Of note, the initial numbers of pests and alternative preys in banker plant systems can also have an impact on pest control. There are few studies on the optimization of various factors in banker plant systems; due to the lack of understanding regarding the dynamic relationship between alternative preys, target pests, and natural enemies, the need for quantitative regulation in practical applications has not been met [20]. When two prey populations that do not directly compete for resources have a shared predator, predator-mediated indirect interactions between the two preys could be influential factors on prey population growth [23–25]. The initial population of a species affects the interaction between the others [25]. Whether there is an indirect relationship between the shared predator-mediated captured prey species in banker plant systems (Figure 1) needs to be further explored, especially the different numbers of target pests and alternative preys.
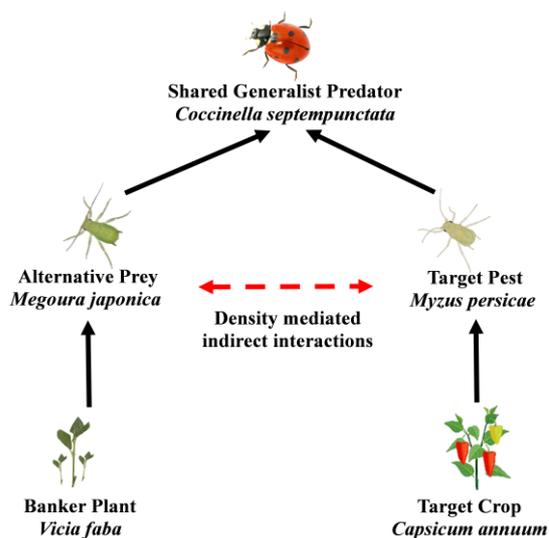
Figure 1. A schematic illustration of the indirect interactions existing between species in the *Coccinella septempunctata*–*Megoura japonica*–*Vicia faba* banker plant system. Solid arrows indicate the trophic relations among host plants, preys, and the predator; dotted arrows show the indirect interaction between the numbers of the alternative prey *Me. japonica* and the target pest *Myzus persicae*, mediated by the shared predator *C. septempunctata*.

In a complex food web structure, a species mediates an indirect interaction between two prey species. For example, the presence of a substitute prey can enhance or disperse

the predation of another prey by shared predators (apparent mutualism or apparent competition), and the apparent relationship can be a positive interaction (apparent mutualism) or a negative interaction (apparent competition) [23,26–28]. Research has shown that the indirect effects of apparent mutualism and apparent competition are a continuum of change: in simple food chain systems, population changes can be mediated by frequent changes in the instantaneous dynamics of predators and prey populations [29]. Apparent competition is a phenomenon where a certain prey population indirectly leads to the decline of another prey population by maintaining a common predator [30,31]. Therefore, clarifying the indirect-role relationship in the banker plant system is conducive to better manage the prey species in a sustainable CBC scenario.

The aim of this study was to evaluate the initial numbers of two prey species in a *C. septempunctata*–*Me. japonica*–*V. faba* banker plant system to simulate the population dynamics of *C. septempunctata* feeding on two prey species under different predation pressures (Figure 1). The biocontrol efficacy of *C. septempunctata* on *My. persicae* was determined, providing a theoretical basis for the short-term indirect correlation between shared predators and captured prey species.

2. Materials and Methods

2.1. Tested Insects

(1) The initial *C. septempunctata* population was obtained from the laboratory of the Institute of Plant Protection, Beijing Academy of Agriculture and Forestry Sciences. Fifty male and 50 female adult lady bugs were reared, one per mesh cage (100 cages). There was an expanded female ladybird population for all cage trials. Broad bean seedlings infested with many *Me. japonica* were continuously provided as a food source and as oviposition sites for the ladybirds.

(2) The *My. persicae* population originated from peppers in the greenhouse of Beijing Noah Agricultural Development Co., Ltd. (Beijing, China). Rearing was conducted using pepper seedlings as host plants.

(3) *Me. japonica* was obtained from a long-term breeding population of the Institute of Plant Protection, Beijing Academy of Agriculture and Forestry Sciences. Inoculation was carried out on 1-year-old broad bean seedlings for population propagation in 100 mesh insect cages. Synonymy of *Megoura crassicauda* Mordvilko, 1919 with *Megoura japonica* (Matsumura,1918) [32].

All the insect rearing conditions were regulated by a fully automatic room environment control system (LT-100, Suntech, Beijing), at $25 \pm 1\,°C$, $70 \pm 5\%$ R.H., 16:8 (L:D) photoperiod, and light intensity of 1100 lux. These conditions applied to alternative prey, banker plant and all experiments.

2.2. Tested Plants

Vicia faba seeds were purchased from a market and soaked in water indoors until the seeds absorbed enough water. After the germination of the broad bean seeds, five germinated broad bean seeds were planted in vermiculite in plastic pots (length × width × height: $30 \times 17 \times 6$ cm). Plants were placed under the conditions reported above for 14 days, and regularly checked for their growth status; experiments started when they reached the 5- to 6-leaf stage.

Capsicum annuum seedlings (variety Zhongjiao 105) were obtained from Beijing Noah Agricultural Development Co., Ltd. A single plant was planted in a flowerpot with a height of 20 cm and a diameter of 13 cm. The matrix components of the flowerpot were vermiculite, perlite, and peat soil mixed in a ratio of 1:1:4 in a pot (diameter × height: 13×10 cm). The bottom of the tray was filled with water until the soil had absorbed it and was slightly wet. The experiment started when the plants reached the 5- to 8-leaf stage. The cultivation environment conditions were as mentioned above.

2.3. Experimental Methods

2.3.1. Effects of Different Release Times of *C. septempunctata* on the Population Dynamics of *My. persicae* and *Me. japonica*

In each of the 100 insect mesh cages (length × width × height of 35 × 35 × 55 cm) that were held at 25 ± 1 °C, 70 ± 5% R.H., and LD 16:8 h, we placed a pot of broad bean seedlings and a pot of pepper seedlings. Before the experiment, we introduced separately 200 *My. persicae* and 200 *Me. japonica* of the same proportion into pepper and broad bean plants. The next day, aphids were removed or added to ensure the population were exactly 200. If not up to 200 aphids initially, they would be added to reach 200 aphids. The newly emerged and mated female adults of *C. septempunctata* were introduced to plants using a brush. The different release times of *C. septempunctata* were set up, which consisted of two treatments, i.e., 12 h and 24 h, with 0 h as the control treatment, in which the numbered *C. septempunctata* were released in their respective cages. Populations of *My. persicae* on whole pepper plants and *Me. japonica* on whole broad bean plants were investigated in this experiment. Each treatment was repeated 15 times.

2.3.2. Temporal Dynamic Effects of *C. septempunctata* on *My. persicae* and *Me. japonica* in Banker Plant Systems with Different Initial Ratios

To clarify the population preference of *C. septempunctata* regarding the two aphid species, we designed a banker plant system with different initial ratios of the target pest to the alternative prey, i.e., *My. persicae*: *Me. japonica* ratios of 100:300, 200:200, and 300:100. Pepper seedlings (1 plant/pot) and broad bean seedlings (5 plants/pot) were placed diagonally in the insect cage. Flowerpots containing pepper plants and flowerpots containing broad bean plants were placed diagonally in a cage. We infested seedlings with aphids using different initial ratios. Each survey was conducted from 8:00 a.m. to 10:00 a.m. for 15 consecutive days. The survival of *C. septempunctata* was observed on the 1st, 3rd, 6th, and 9th day. The populations of *My. persicae* and *Me. japonica* were recorded. Each treatment was repeated 15 times.

2.3.3. The Effect of *C. septempunctata* on the Population of *My. persicae* in Alternative-Prey Banker Plant Systems with Different Initial Numbers

Healthy and well-developed broad bean plants were infested with *Me. japonica* nymphs at different initial numbers (i.e., 0, 50, 100, 200, and 400 individuals); 100 *My. persicae*-infested pepper plants were planted diagonally above the cage. The number of aphids in each treatment was confirmed the next day. At the beginning of each experiment, a female *C. septempunctata* was released into each cage. These were mated (without spawning) and starved for 24 h prior to release.

2.4. Statistical Analyses

The populations of *My. persicae* and *Me. japonica* were subjected to one-way ANOVA using SPSS 22.0, and Duncan's test was selected for the significance of differences ($p < 0.05$). All data were plotted using Origin Pro and R. To better understand our initial results, we performed principal component analysis (PCA) on data of the relative abundance of *Me. japonica* and *My. persicae* for different initial numbers of *Me. japonica* and initial numbers of *My. persicae*: 100 aphids/plant. We tested the relationship between the experimental day (t), initial numbers of *Me. japonica* (Me. j_0), relative numbers of *Me. japonica* (Me. j_t), relative numbers of *My. persicae* (My. p_t), and the ratio of *My. persicae*/*Me. japonica* (My. p_t/Me. j_t), where Me. j_t or My. p_t is the number of aphids at an experimental time, Me. j_0 is the initial numbers of aphids, and t is days interval between Me. j_t and Me. j_0. Prior to PCA, the abundance data were transformed by log10 (x + 1) to decrease the model error estimated. PCA was fitted with the function "procomp" of the R 4.2.1 software.

3. Results

3.1. Effects of Different Release Times of C. septempunctata on My. persicae and Me. japonica Populations in the Banker Plant System

When the initial numbers of *My. persicae* and *Me. japonica* were equal, *C. septempunctata* releases at different times showed no significant effects on *My. persicae* population over time. For the day 6 and 9 time points, the increase in *Me. japonica* has been added to Figure 2 to make it easier to view. The populations of *My. persicae* and *Me. japonica* were comparable on day 3 in 12 h and 24 h release treatments. The predation of the target pest, *My. persicae*, was not affected by the predation pressure generated by the release of *C. septempunctata* at 12 h and 24 h during the first 9 days, while the *Me. japonica* population was affected. Concerning the control release (0 h delay), the population increased between the 12 h and 24 h delay, while that in the 0 h delay assay firstly decreased and then increased (Figure 2A). The *My. persicae* population was significantly higher at the 6 and 9 day time points for both 12 and 24 h delay treatments compared to the 0 h control *Me. japonica* ($F_{6,44} = 6.029$, $p = 0.05$; $F_{9,44} = 3.998$, $p = 0.026$) (Figure 2B). *Me. japonica* showed lower numbers in the 0 h delay treatment.
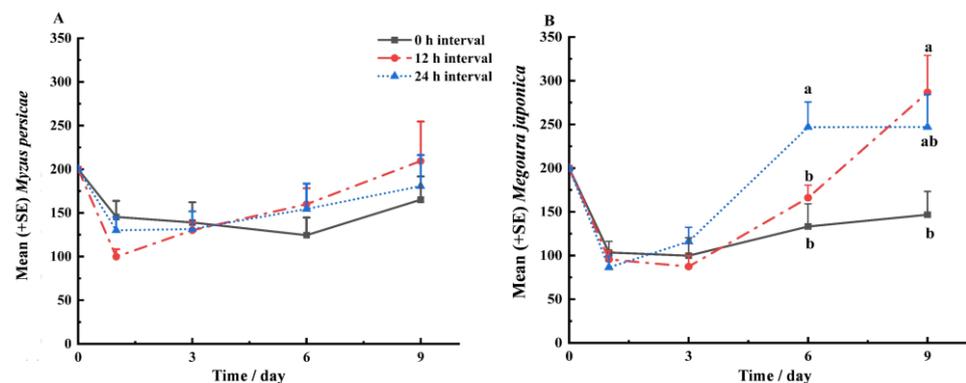

Figure 2. *Myzus persicae* (**A**) and *Megoura japonica* (**B**) numbers at different times after the release of *Coccinella septempunctata* with different release intervals. Different lowercase letters within the same sampling date indicate significant differences ($p < 0.05$).

3.2. Effects of Different Initial Prey Ratios on the Temporal Dynamics of My. persicae and Me. japonica in a Banker Plant System with C. septempunctata

When the total and initial numbers of coccinellids and aphids, respectively, in each cage were the same, increasing the initial ratio of *My. persicae* to *Me. japonica*, *C. septempunctata* released at different times had an asymmetrical indirect interaction with the two aphid species. On the first day, the indirect interactions between the three initial ratios were all biased toward *My. persicae* (Figure 3A); within 3–9 days, in the treatment with an initial ratio of *My. persicae* to *Me. japonica* ≥ 1, the indirect interaction was biased toward *My. persicae*; the treatment with an initial ratio < 1 caused the indirect interaction between the two aphids to be significantly biased toward *Me. japonica* (Figure 3B–D, $F_{3,44} = 4.035$, $P_3 = 0.025$). This means that in the short term (0–9 days), when the initial ratio of *My. persicae* and *Me. japonica* was 1/3–3, the initial ratio of the two prey species was ≥ 1, and the negative effect of *C. septempunctata* on *My. persicae* was stronger than that of *Me. japonica*. Thus, *C. septempunctata* was able to control the target pest *My. persicae* through direct and/or indirect interaction under the influence of the initial prey ratio.
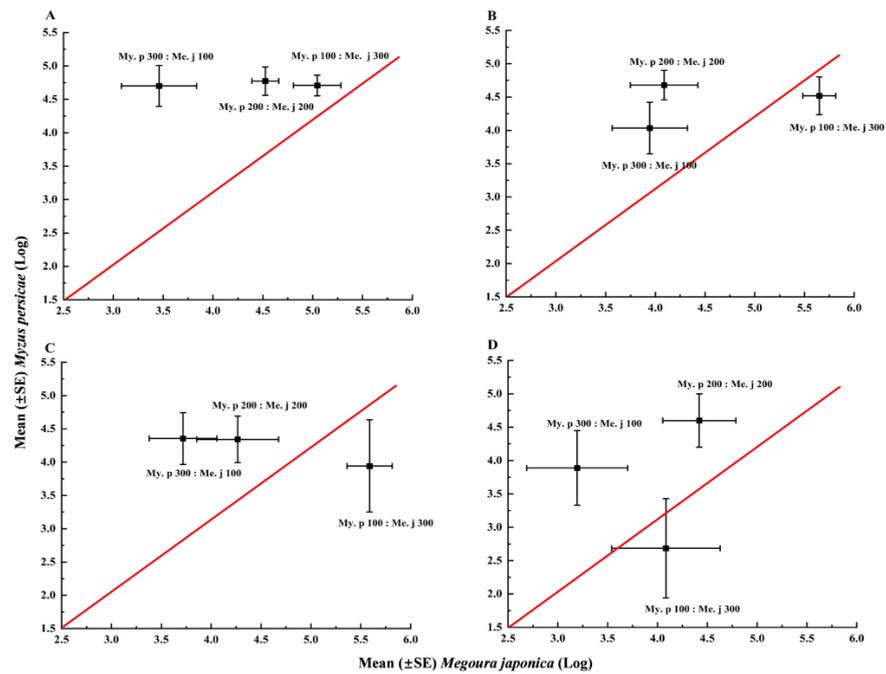
Figure 3. The relationship between *Myzus persicae* and *Megoura japonica* under different initial ratios on the 1st (**A**), 3rd (**B**), 6th (**C**), and 9th day (**D**). My. p represents *My. persicae*, and Me. j represents *Me. japonica*.

With the increase in the alternative prey initial numbers, the population of *My. persicae* decreased, but its own population increased nonlinearly (Figure 4A,B). In the banker plant system with different initial numbers of *My. persicae* and *Me. japonica*, when the ratio of the initial numbers of *My. persicae* to the numbers of *Me. japonica* was ≥1, we observed a growth in *My. persicae* population. When the initial ratio was <1, *My. persicae* population showed a decline and reached the maximum on the 6th day; there was a significant difference in the net growth of the *My. persicae* populations among the three treatments (Figure 5).
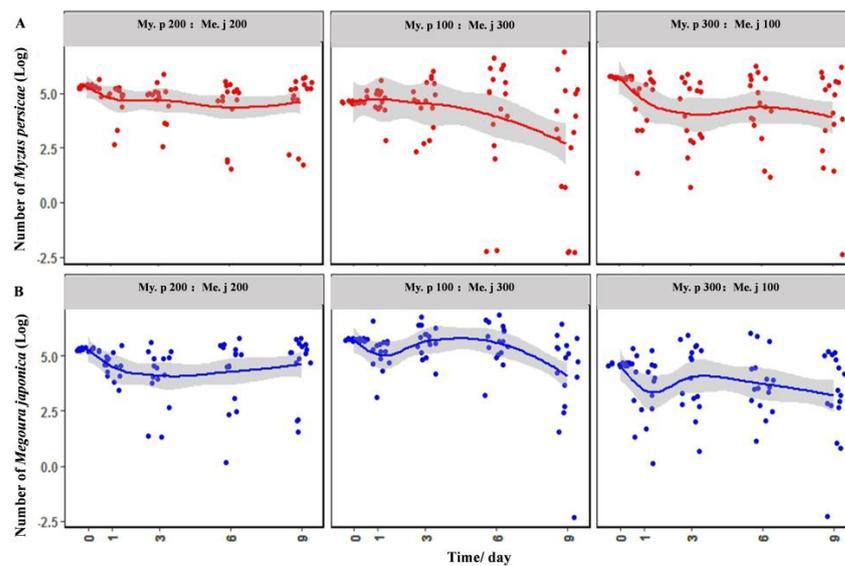

Figure 4. The population dynamics of *Myzus persicae* (**A**) and *Megoura japonica* (**B**) at different initial ratios. My. p represents *My. persicae*, and Me. j represents *Me. japonica*.
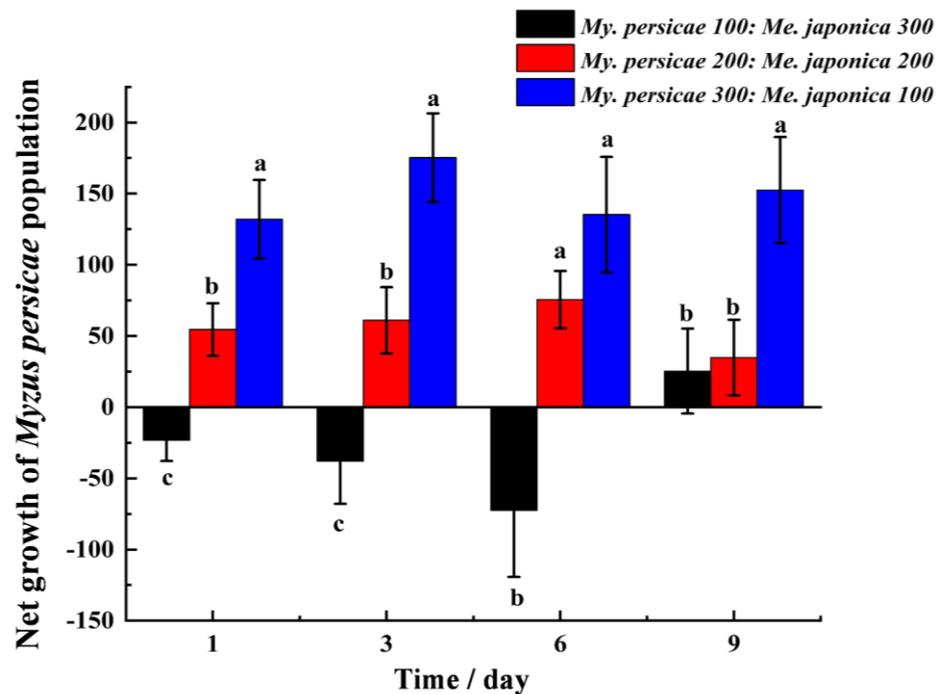
Figure 5. Net growth dynamics of *Myzus persicae* populations seedlings infested with pepper plants with *My. persicae* and *Megoura japonica* at different initial ratios. Different lowercase letters within the same sampling date indicate significant differences ($p < 0.05$).

3.3. Temporal Dynamic Effects of C. septempunctata on My. persicae in the Banker Plant System with Different Initial Numbers of the Alternative Prey

As shown in Figure 6, when the population of the target pest *My. persicae* was 100, the population of *My. persicae* and *Me. japonica* differed significantly in the *C. septempunctata* banker plant system constructed by replacing the *My. persicae* with different initial numbers (Figure 6A). On the 9th day, *My. persicae* population in the treatment with an initial population of 400 individuals was significantly higher than that in the other treatments ($p < 0.05$), so the control effect of the target pest was the best when the initial numbers of the two aphids exceeded 1/4.

To further analyze the difference between the factors that influenced the composition of the *My. persicae* population, a principal component analysis (PCA) was performed on the experimental time (t), initial numbers of *Me. japonica* (Me. j_0), relative numbers of *Me. japonica* (Me. j_t), relative numbers of *My. persicae* (My. p_t), and the *My. persicae*/*Me. japonica* ratio (My. p_t/Me. j_t) (Figure 6B). The first principal component had a value of 82.6%, and the second principal component had a value of 12.14%. There were overlaps in the spatial distribution of the other four treatments, except for the treatment with *Me. japonica* in terms of initial numbers. The similarity between the *My. persicae* populations was very high when the initial numbers of the alternative prey were 50, 100, and 200. The time on PCA1 mainly reflects the information regarding the *My. persicae* population in different treatments over different times. Time on PCA2 mainly reflected the initial and relative numbers of *Me. japonica* and the information regarding the *My. persicae* populations in different treatments, including the interaction of time, the initial numbers, and the relative numbers of alternative prey; these factors significantly affected *My. persicae* populations ($F_{t,213} = 44.79$; $F_{Me. j0,213} = 534.91$; $F_{Me. jt,213} = 238.59$; $p < 0.001$).
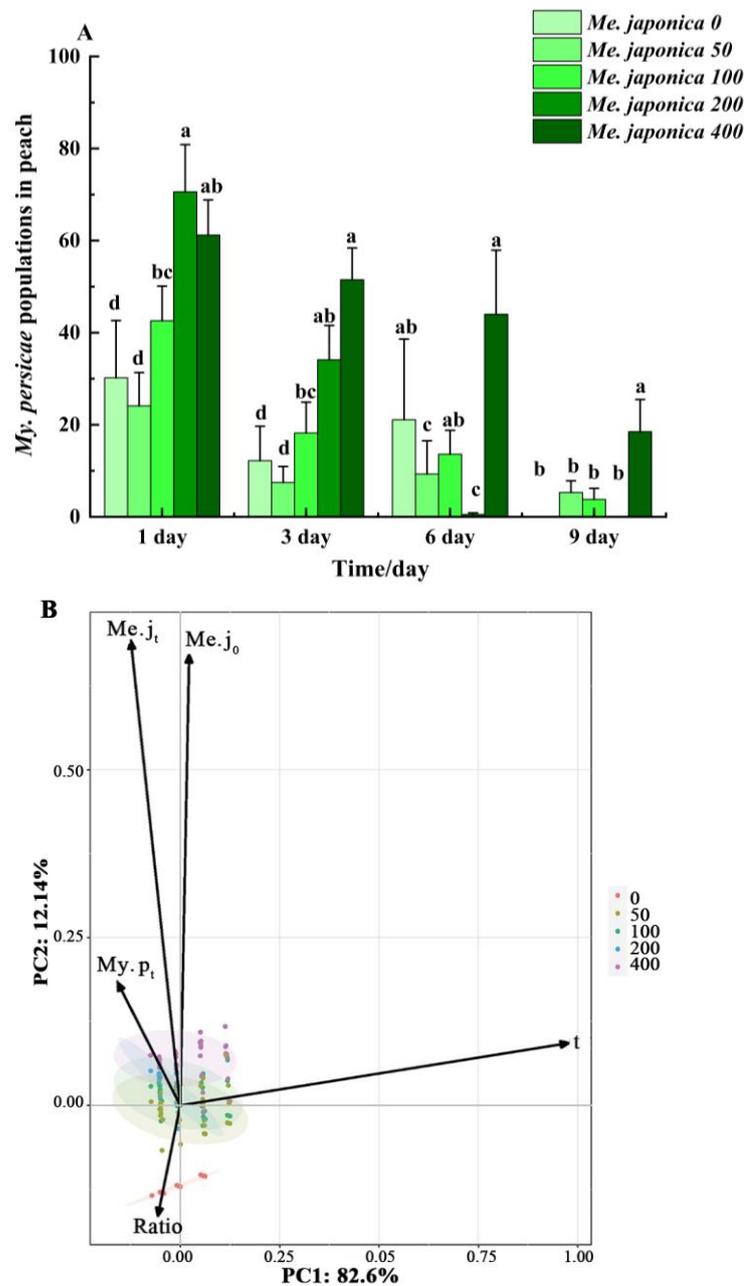
Figure 6. (**A**) *Myzus persicae* population in presence of *Megoura japonica* different initial numbers at different times (initial numbers of *My. persicae*: 100 aphids/plant). (**B**) Principal component analysis performed on the experimental day (t), initial numbers of *Me. japonica* (Me. j_0), relative numbers of *Me. japonica* (Me. j_t), relative numbers of *My. persicae* (My. p_t), and the ratio of *My. persicae*/*Me. japonica* (My. p_t/Me. j_t). Different lowercase letters within the same sampling date indicate significant differences ($p < 0.05$).

4. Discussion

In our experiments, we quantitatively manipulated the relative numbers of the target pest, *My. persicae*, and the alternative prey, *Me. japonica*, in the *C. septempunctata* banker plant system to clarify the instantaneous dynamic relationship between two aphid species with a common predator. The initial ratio of the two aphids was in the region of 1/3–3. The presence of more alternative prey led to an indirect asymmetric interaction between *My. persicae* and *Me. japonica*. Over time, this asymmetric effect shifted from favoring *My. persicae* to being biased toward *Me. japonica*. Although the target pest's population was

unaffected at spatially induced predation pressure, the time of investigation and relative numbers of *Me. japonica* had a direct impact on the population of *My. persicae*. Determining the quantity of prey in a banker plant system is crucial. The control effect on target pests may be impacted by an excessive number of alternative preys in the system, which may result in concentrated feeding of natural enemy insects. A lack of available alternative prey will encourage the spread of natural enemies to target crops.

In ecosystems, insect communities can be constructed through time and space [31,33,34]; space–time conversion can predict changes in population dynamics, and this can only solve the problem of ecological experiments having low repeatability or false repetitions on a large scale, and also help face the challenge of ecological experiments dealing with a narrow distribution of research objects, small spatial scale, and long-term observation data [35–37]. Herein, a release–retrieve–release experiment with *C. septempunctata* was conducted in a banker plant system. The time-for-space method was used to examine the effects of *C. septempunctata* under various predation pressures on the populations of *My. persicae* and *Me. japonica*. Our results showed that the length of the recovery–release time interval of *C. septempunctata* caused predation pressure, but this had no appreciable impact on the *My. persicae* populations. However, it had a significant impact on the alternative prey, *Me. japonica*. The predation pressure produced by exchanging time for space had no effect on the target pest populations due to the short-term indirect interaction between the two prey species mediated by BCA. Natural enemies can successfully suppress pest numbers to some extent when their populations coincide in both space and time [38].

Studies focusing on the apparent competition between predators and prey have shown that the prey numbers frequently influence the aggregation reaction of the predators, creating an apparent competition [39,40]. This was discovered through observations of the predation behavior in a particular space and/or patch. In our banker plant system, when *My. persicae* and *Me. japonica* shared the BCA *C. septempunctata*, at various initial numbers of alternative prey, the negative impact on aphids gradually diminished as the alternative prey numbers increased. In the short term, the reduction in alternative prey significantly promoted the reproduction of *My. persicae*. This is consistent with Leman's test on thrips [41], where the supplementation of alternative food boosted thrips' reproduction. Although such indirect interactions cannot be measured explicitly, our study directly supports them. *C. septempunctata* is a co-predator of *My. persicae* and *Me. japonica*. The indirect interaction between the two prey species might alter quickly, which is beneficial for the prey population changes [27,42–44]. Nevertheless, when the initial numbers of *Me. japonica* expanded, the impact on the population of *My. persicae* increased gradually, demonstrating that number-mediated apparent competition occurred. In the predator–prey system *Lachnus niger–Lachnus tropicalis–Myzocallis kuricola*, increasing the population of *L. tropicalis* decreased the population of *L. tropicalis*. This increase in prey numbers also increased the predation pressure of co-predators, which had an asymmetric negative effect on the population of other prey species [45].

Indirect interaction mediated by natural enemy numbers was verified in an apparent competition model. Research showed that changes in alternative prey numbers may alter the population balance in a basic ecosystem with predator–alternative prey–target pests [46]. The initial numbers affected species coexistence, and the numbers and species coexistence mediated apparent competition with natural enemies. For example, *Eotetranychus pruni* significantly raised the predator population and indirectly reduced the population of *Tetranychus urticae* when it was introduced into apple orchards with an alternative prey and its natural enemy, *Euseius finlandicus* [46,47]. In addition, intraspecies interactions of predatory coccinellids have an influence on population establishment and pest control in banker plant systems [48–50], and this may impact the strength and direction of indirectly mediated interactions.

The timing of the banker plant system's installation, the method of releasing natural enemies, and the relative numbers of the prey all have a role in how effective natural enemies are at controlling pests. These factors directly affect the results of pest management,

and the most critical factor is the number of preys [51,52]. The competitive relationship between the number of substitute prey and target pests in the short term was examined here by maintaining the initial numbers of the target pests and changing the initial numbers of the alternative prey, *Me. japonica*. Different initial populations of the alternative prey, *Me. japonica*, significantly affected the population dynamics of the target pest, *My. persicae*, and the control effect of the target pest was the best when the initial numbers of the two aphids exceeded 1/4. Both population and trait regulation (behavioral or life history) influence the interaction between two prey species mediated by a third species, and numbers-mediated indirect interactions can alter ecosystem structures and population dynamics [53–55]. This has been widely used for studying predation behavior to identify midgut prey detection using molecular marker techniques [56,57]. This method may help to quantitatively and qualitatively characterize the strength and direction of indirect interactions mediated by predators at molecular level in the future.

The focus of this research was to advance our understanding about indirect interactions in food webs and the potential benefits of increased biodiversity in the CBC of crop pests [51,58–60]. Further research on phenological synchronicity in other systems will help to shed light on the presence and relevance of such mechanisms and their predictive capacity for ecosystem management in crops [61]. The current quantitative regulatory experiment, which was conducted under controlled environmental conditions, carefully monitored the dynamics of the interactions between two prey species sharing the same predator through time and in various numbers. It can help to clarify how and when indirect interactions prey may change under different parameters in a banker plant system, and the findings may enable improvement of banker plant systems and biocontrol services offered. This work may provide information for optimizing IPM packages relying on *C. septempunctata* banker plant-based systems [4], and more broadly may help in the goal of reducing insecticides [62–65] in IPM packages [66] in various agricultural settings.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The datasets generated during the study are available from the corresponding author upon reasonable request.

Conflicts of Interest: The authors declare that there are no conflicts of interest.

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