Combining Banker Plants To Achieve High Pest Control Efficiency In Multi-Pest, Multi-Natural Enemy Cropping Systems

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Research Article

Keywords: alternative resource, Bemisia tabaci, biocontrol agent, competition, Encarsia formosa, functional plant, Myzus persicae, Propylea japonica, secondary pest

DOI: https://doi.org/10.21203/rs.3.rs-503399/v1

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Abstract

Banker plants increase biological pest control by supporting populations of non-pest arthropod species used as alternative hosts or prey by natural enemies. Due to the specificity of trophic interactions, banker plants may not efficiently promote natural enemies with different ecologies. Yet in most cropping systems different pest species are present together and require different biocontrol agents to efficiently control them. In the present study, we tested the combined use of two banker plants and their associated prey / host to enhance populations of the specialist parasitoid Encarsia formosa targeting the main tomato pest Bemisia tabaci, and a polyphagous ladybird Propylea japonica targeting the secondary pest Myzus persicae in tomato crops. In a laboratory and a greenhouse experiment, we measured the abundances of these four species using the Ricinus communis – Trialeurodes ricini banker plant system alone, in combination with the Glycines max – Megoura japonica system, or in absence of banker plants. We found that the first banker plant system enhanced populations of E. formosa, resulting in higher control of B. tabaci populations and the suppression of their outbreak in both our laboratory and greenhouse experiment. Conversely, abundances of P. japonica were not affected by this first system, but were significantly increased when the second was present. This resulted in high control of M. persicae populations and the suppression of their early and late outbreaks. Our study demonstrates the potential for combined banker plants to provide long-term, sustainable control of multiple pests by their target natural enemies in complex agroecosystems.

Key Message

- Multiple pest species are present simultaneously in cropping systems, requiring multiple natural enemies.
- Multiple banker plants are needed to support populations of biocontrol agents with contrasted ecologies.
- We tested the combined use of two banker plants, targeting two biocontrol agents to control two tomato pests.
- Combined banker plants enhanced the control of both main and secondary pests in laboratory and greenhouse.
- Pest outbreaks were suppressed on the long term only when banker plants were present.

Introduction

With the rise of integrated pest management (IPM), practical applications of biological control agents releases have become increasingly complex to improve pest control with reduced used of chemical pesticides (Kogan 1998; Stiling & Cornelissen 2005; Desneux et al. 2007; Naranjo et al. 2015; Huang et al. 2020; Zang et al. 2021). Starting from simple pairs with one natural enemy species targeting one pest species, applications have been progressively improved in releasing combinations of multiple species of biocontrol agents to achieve sustainable control of multiple pest populations simultaneously and
throughout the cropping season (Barbosa 1998; Heimpel & Mills 2008). Such efficacy is achieved notably through the precise monitoring of pest population dynamics *in situ* (Tan et al. 2016). Multi-species releases should also involve natural enemy species with limited niche competition (Liu et al. 2012; Chailleux et al. 2014b; Liang et al. 2021; Sanchez-Hernandez et al. 2021), but with complementary ecologies allowing the regulation of pest populations over different time periods and spatial scales (Hall 2011; Chailleux et al. 2017). Most often, a specialist natural enemy (e.g., a parasitoid wasp) is combined with a generalist natural enemy in multi-species releases (Tan et al. 2016; Perez-Valencia et al. 2019): this way the specialist, targeting the dominant pest species, prevents its outbreaks, while the generalist regulates pest populations of secondary pest species (Chailleux et al. 2013; 2017; Dainese et al. 2017; Aparicio et al. 2020).

Yet such systems are intrinsically complex to develop since many factors may influence species interactions and the efficacy of pest control, including biocontrol agent fitness, their relative proportion, introducing times and developmental stages (Huffaker et al. 1971). The successful colonization of crop systems, and the establishment of stable populations by released biocontrol agents is even more challenging and may heavily rely on means to support populations (Bianchi et al. 2006). This is especially true since biocontrol agents are most often released before pest populations reach high densities to prevent pest outbreak (Albajes et al. 2000). Therefore the development of strategies supporting biocontrol agent populations could be useful in extending the adoption of multi-species releases.

The use of banker plants has been increasingly investigated and developed in the context of conservation biological control (Frank 2010; Gurr et al. 2017). Banker plants are non-crop plants supporting populations of herbivorous species which do not attack adjacent crops (Parolin et al. 2012), and which may be used as alternative prey or hosts by natural enemies targeting the main pest species in cropping systems. Hence, banker plants can be used in combination with crops and serve as entry points for the inoculative release of biocontrol agents. By providing shelter and alternative prey / hosts, banker plants can enable the early colonization of adjacent crops by natural enemies (Li et al., 2013) and the establishment of their populations when main prey are scarce (Yano et al. 2018). Plant species supporting populations of alternative prey / hosts in the same family or functional group than the main pest species are well suited to be used as banker plants (Laurenz & Meyhofer 2021). For instance, the non-crop oat species *Avena sativa* supporting populations of the alternative aphid species *Metopolophium dirhodum* resulted in an increased suppression of the main pest *Myzus persicae* by its parasitoid *Aphidoletes aphidimyza* in chilly crop (*Capsium annuum*; Hansen 1983). Similarly, the non-crop papaya plant *Carica papaya* supporting populations of the alternative whitefly species *Trialeurodes variabilis* successfully increased the suppression of the main pest *Bemisia tabaci* by the ladybird *Delphastus pusillus* in many vegetable crops (Osborne et al. 1991). These non-crop plants and alternative prey could also supply sufficient food resources and space to help biocontrol agents maintain their populations after the suppression of the main pest species and thereby avoid their escape from the target agroecosystem, which is common in practical biological control application and may cause severe loss
Such effect could in turn increase the suppression of secondary outbreaks of pest populations (Zheng et al. 2017).

Unlike other functional plants providing alternative food (floral) resources or attracting natural enemies (Gurr et al. 2017; Zhao et al. 2017; Perović et al. 2018; Jaworski et al. 2019), one key aspect in assessing the suitability of a plant species as a banker plant is the high fitness of the alternative herbivorous prey / host developing on the banker plant, versus a low fitness on crop plants (Huang et al. 2011; Damien et al. 2020; Wang et al. 2020). Theoretically, the alternative prey / host on banker plants and the target prey / host on crops form an apparent competition system by sharing a natural enemy (van Veen et al. 2006; Chailleux et al. 2014b; Jaworski et al. 2015; Desneux et al. 2019; Monticelli et al. 2021). Hence, the density of banker plants and alternative host / prey could severely impact the balance between the target agroecosystem and the banker plant system (Orrock et al. 2010). Most studies investigating the suitability of species as banker plants focused on a single plant species supporting a single alternative herbivorous prey species (Andorno & Lopez, 2014). Conversely in practical applications relying on multi-species releases of biocontrol agents, many functional non-crop plants have been studied for their potential to provide alternative food resources and shelter to these multiple natural enemies, but they have seldom been evaluated as constituents of a banker plant system (Avery et al. 2014; Jandricic et al. 2014). The use of a single functional plant species providing alternative food resources is likely to support populations of natural enemy species with similar ecological niches (Xu et al. 2020). Still, some functional plants may jointly provide alternative food resources such as nectar and pollen resources (Wäckers & van Rijn 2012) and support alternative host / prey populations, thereby potentially targeting natural enemy species with very different ecologies. Alternatively, combining various banker plant species to enhance populations of multiple natural enemy species could help achieve long-term sustainable pest control in multi-pest cropping systems.

Tomato is a major vegetable greenhouse crop in China (Li et al. 2021), attacked by several major insect pest species including the whitefly Bemisia tabaci Gennadius, 1889 (Hemiptera: Aleyrodidae) and the aphid Myzus persicae Sulzer, 1777 (Hemiptera: Aphididae), often present simultaneously (Lange & Bronson 1981 ; Czosnek & Ghanim 2011; Li 2013; Hullé et al. 2020). Encarsia formosa Gahan, 1924 (Hymenoptera: Aphelinidae) is a parasitoid wasp specialized on whiteflies and commonly used as a biocontrol agent to suppress B. tabaci whitefly populations (Enkegaard 2011; Tao et al. 2018). In particular, E. formosa can prey and develop on Trialeurodes ricini Misra, 1924 (Hemiptera: Aleyrodidae), a whitefly mainly using the castor bean host plant Ricinus communis Linnaeus, 1753 (Wang et al. 2016): it prefers R. communis over other host plants (Huang et al. 2014) and cannot survive on tomato (Shishehbor & Brennan 1996). Propylea japonica Thunberg, 1780 (Coleoptera: Coccinellidae) is a predatory ladybird attacking a variety of prey species and often used in biocontrol programmes especially to control aphids (Vuong et al. 2001; Kuroda & Miura 2003; Yang et al. 2014). In particular, P. japonica preys and develops on the aphid Megoura japonica Matsumura (Hemiptera: Aphididae) (Li et al. 2011). This aphid species develops well on soybean Glycines max Merr, 1917 or Vicia faba Linnaeus, 1753 (Wang et al. 2013) but has a reduced fitness on tomato crops (Liang Y, unpublished data). Besides, both R. communis – T. ricini and G. max – M. japonica have been used as banker plant systems in
commercial greenhouses, most often introduced as infested potted plants between cropped plants (Liang Y, unpublished data). Predatory ladybirds often engage in intraguild predation (Michaud 2010; Ovchinnikov et al. 2019; Liang et al. 2021) and may especially prey on parasitoid wasps developing inside their host (Chacón & Heimpel 2010; Tan et al. 2016; Aparicio et al. 2020). Therefore, the use of distinct banker plant systems supporting *E. formosa* and *P. japonica* could reduce the risk for intraguild predation and help enhance the control of the *B. tabaci – M. persicae* pest complex in greenhouse tomato crops.

In the present study, we tested the role of combined banker plant applications in enhancing pest control in a multi-pest, multi-biocontrol agent system in a laboratory and a greenhouse experiments. Using tomato crops, we measured the abundance of the pest species *B. tabaci* as main tomato pest and *M. persicae* as secondary pest, and of the introduced biocontrol agents *E. formosa* and *P. japonica*. We evaluated the potential of the two banker plant systems in combination: (i) *R. communis* supporting populations of the whitefly *T. ricini*, itself parasitized by *E. formosa* and (ii) *G. max* supporting populations of the aphid *M. japonica*, itself preyed upon by *P. japonica* (Table 1). We asked: How efficient is the long-term control of the two pest populations by the two natural enemies (1) In absence of banker plants? (2) When one banker plant system is provided? And (3) When two banker plant systems in combination are provided?

**Material And Methods**

**2.1. Plants and insects**

**Plants**

Tomato *Solanum lycopersicum* cv. Baofeng and soybean *Glycine max* cv. YY-1 plants were provided by the Noah Organic Farm (Ping’gu, Beijing, China, N40°09’, E116°99’), while castor bean *R. communis* cv. ZB plants were provided by the Jingnan Horticulture Company, Beijing, China, all free of pesticides. All plants were grown in pots (diameter 10 cm, height 10 cm) with a mixed nutrition soil (miracle-gro, Scotts, Miracle-GRO, Ohio, USA) and a hydroponic nutrient solution in a nursery garden free of pathogens and pests at the Institute of Plant and Environment Protection (IPEP), Beijing Academy of Agricultural and Forestry Sciences (BAAFS), Beijing, China, until they developed five true leaves (tomato and castor bean) or 20–25 cm height (soybean) to be used for insect rearing or in the laboratory and greenhouse experiments.

**Pest species**

All insects were reared in the insectary of the IPEP. Environmental conditions were automatically regulated (L-100, Suntech, Beijing, China; 25 ± 1 °C, 65 ± 5 % RH, photoperiod: 16 h L : 8 h D and a light intensity of 650 lux). Over tobacco *B. tabaci* adults were collected in tomato greenhouses in the Noah Organic Farm and 730 *T. ricini* adults were collected from horticultural castor bean plants in the nursery garden of the Jingnan Horticulture Company during May 2019. The *B. tabaci* strain was identified to be MEAM1 from 100 collected individuals randomly selected, and based on molecular tests (Zhang et al.
Both whitefly species were reared in separate cages with a 100 pairs of whiteflies per cage (40 × 40 × 35 cm, made of aluminium frames and 40-mesh fabric net walls). Four tomato plants and four castor bean plants were provided as host plants in every cage of *B. tabaci* and *T. ricini* whiteflies, respectively. We produced over 30,000 adults of *B. tabaci* and *T. ricini* each for the experiments.

Over 1,000 nymphs of *M. persicae* and 1,200 nymphs of *M. japonica* were collected in tomato greenhouses and soybean fields, respectively, in the Noah Organic Farm during May 2019. Up to 300 *M. persicae* or *M. japonica* aphids were placed in a separate cage similar to those for whiteflies above along with five tomato plants or soybean plants, respectively. Over 30,000 aphids of each species were produced for the experiments.

All colonies were maintained for a year (from May 2019 to June 2020) and had a mixed population structure with both adults and nymphs present simultaneously. Plants were replaced every 5–7 days when needed. About 3–4 and 12–15 generations completed before the 2019 laboratory experiment and the 2020 greenhouse experiment, respectively.

**Natural Enemies**

*Encarsia formosa* and *P. japonica* were bought from Hengshui Tianyi Biocontrol Co., Ltd, Hengshui, Hebei, China. Commercial *E. formosa* were provided at the pupal stage parasitizing *B. tabaci* whiteflies at the 3rd-4th nymphal stage and with a single parasitoid wasp per nymph, as evidenced by a visible black dot inside the nymph. Whiteflies were packaged in groups of 1,000 nymphs on one tomato leaf. The newly emerged viable *E. formosa* females were collected with a vacuum pipe and maintained in Petri dishes at 10–15 wasps per dish, in which honey (Baihua 75%; Beijing Aojinda Honey Co., Ltd.) was provided for feeding. Wasps were used in the experiments about 1–2 days later. Commercial *P. japonica* were provided as 4th instar larvae, packaged in groups of 30 larvae in a tetrahedron shape paper container filled with sawdust to reduce cannibalism. The larvae were kept in plastic boxes (30 per box, 15 × 15 × 20 cm) in the insectary and fed with daily supplied artificial diet microcapsules (Tan et al. 2015) for the experiments.

### 2.2. Laboratory experiment

In 2019 in a laboratory experiment, we evaluated the potential for the combined use of the *R. communis* – *B. tabaci* and the *G. max* – *M. japonica* banker plant systems to enhance pest control by the combination of the specialist *E. formosa* and the generalist *P. japonica* biocontrol agents (Table 1). We tested four treatments: (a) control with pest species *B. tabaci* and *M. persicae* on tomato plants, but no biocontrol agents and no banker plant systems; (b) control with the two pest species and the two biocontrol agents but no banker plant systems; (c) one-banker plant system with the two pest species and the two biocontrol agents and with the *R. communis* – *B. tabaci* banker plant system; and (d) two-banker plant system with the two pest species, the two biocontrol agents, and the two banker plant systems (*R. communis* – *B. tabacis* and *G. max* – *M. japonica*).

In a cage in the insectary (made of hollow aluminium pipes of diameter 1.5 cm and 40-mesh fabric net walls; 1.8 × 1.2 × 1.5 m; Fig. 1), we placed 15 tomato plants and four banker plants infested with their
respective alternative host / prey beforehand. In each cage, two *R. communis* banker plants were placed in A and C. In the two-banker plant system cages, two *G. max* plants were also added in B and D (Fig. 1), while in control cages no banker plant was provided. Ten days prior to the start of the experiment, tomato and *R. communis* plants were infested with *B. tabaci* and *T. ricini* whiteflies, respectively: 10 pairs of adults were enclosed on each of the five plant leaves with a 40-mesh net. The adults were removed after they had laid eggs two days later. Then, eight days later the number of 3rd-4th instar nymphs was adjusted to a 100 per tomato plant and 200 hundreds per *R. communis* plant by gently removing excess nymphs with a brush. Tomato plants were further infested with 30 *M. persicae* 3rd-4th instar aphid nymphs per tomato plant (taken directly from rearing cages) while *G. max* were infested with 250 *M. japonica* aphid nymphs each. Finally, one day after aphid infestations, 20 parasitoid female adults were introduced on each *R. communis* plant and five ladybird 4th instar larvae on each *G. max* plant if present, or per cage if the banker plants were absent and except in the control – no natural enemy treatment. Ten replicates per treatment (control, no biocontrol agent / control with biocontrol agents / one-banker plant system / two-banker plant system) were produced, with a total of 40 cages. The densities of insects were chosen based on a pilot experiment. We visually observed and counted the number of individuals of each species (*B. tabaci*, *M. japonica*, *E. formosa* and *P. japonica*) of all developmental stages (except eggs) on six randomly selected tomato plants per cage starting one week after the release of biocontrol agents and every Monday from June 3rd to September 30th 2019. We calculated the total number of insects of each species per six plants by summing numbers counted in each of the six plants so as to obtain one value per cage and per week.

### 2.3. Greenhouse experiment

In 2020 we performed a greenhouse experiment to estimate the potential for the combined banker plant systems to be used in practical biocontrol greenhouse applications involving multiple pest and biocontrol agent species. We tested the same four treatments as in our 2019 laboratory experiment (control, no biocontrol agent / control with biocontrol agents / one-banker plant system / two-banker plant system). We used four glass greenhouses located in the Noah Organic Farm (100 × 14 m, height 4.2 m). Each greenhouse was composed of ten independent chambers (12 × 12 m) isolated with plastic membranes preventing arthropod movement between chambers. In each chamber, we transplanted 56 tomato plants in seven rows with eight plants per row (Fig. 2). We transplanted two *R. communis* plants in each of four random points among the nine blue points shown in Fig. 2 in each chamber. In the two-banker plant system chambers, we also added two *G. max* plants in each of four other randomly selected points. In the control chambers, no banker plant nor associated alternative prey / host was provided. Two days after transplantation, 14 tomato plants randomly selected in each chamber were infested with *B. tabaci* adults and the *R. communis* banker plants were infested with *T. ricini* adults, following the same method as in the laboratory experiment. After three days – whiteflies nymphs had emerged by then – another 14 randomly selected tomato plants were infested with 30 3rd-4th *M. persicae* aphid nymphs per plant, and *G. max* plants were infested with 250 *M. japonica* aphid nymphs each. After two more days, 20 parasitoid female adults were released on each of the eight *R. communis* plants, and five ladybird 4th instar larvae
were released on each of the eight *G. max* plants per cage if the banker plants were present, or in four of the nine blue points randomly selected if the banker plants were absent. In the control – no natural enemy treatment, no biocontrol agents were released. Each treatment was replicated in ten chambers, randomly selected across the four greenhouses. The insect densities in greenhouses were chosen based on authors’ preliminary surveys.

We monitored population dynamics of the two targeted pest species (*B. tabaci* and *M. persicae*) and of the two introduced biocontrol agents (*E. formosa* and *P. japonica*) starting one week after biocontrol agent releases and every Monday from June 1st to September 28th 2020. At each sampling date, we selected randomly eight plants per chamber and we inspected all plant parts and counted all insect individuals (except eggs). We calculated the total number of insects of each species per eight plants by summing numbers counted in each of the eight plants, so as to obtain one value per greenhouse chamber and per week. The environmental conditions inside greenhouses followed seasonal trends (June: 26.9 ± 0.4°C, 32.2 ± 1.9 % RH; July: 26.3 ± 0.4°C, 41.6 ± 1.6 % RH; August: 26.2 ± 0.4°C, 36.5 ± 1.9 % RH; September: 21.4 ± 0.5°C, 24.8 ± 1.5 % RH).

2.5. Statistical analyses

All statistical analysis were performed with R Core Team (2020) version 3.6.3. We analysed the impact of the treatment (control – no natural enemy / control – with natural enemies / one-banker plant system / two-banker plant system) on the number of insects per six plants in the laboratory experiment independently for each insect pest (*B. tabaci* vs. *M. persicae*) and natural enemy (*E. formosa* vs. *P. japonica*) species because of large differences in densities and population dynamics (Fig. 3). We used Generalized Linear Models (GLMMs) with a negative binomial distribution recommended for count data with overdispersion (function ‘glmer.nb’, library ‘lme4’; Bates et al. 2015). The treatment was used as fixed effect, while the cage and the week were used as random effects to account for repeated measures through time, and patterns of insect population dynamics, respectively. The significance of the treatment was tested with an anova based on a $\chi^2$ test. Model validity was verified a posteriori (functions ‘simulateResiduals’ and testDispersion’, library ‘DHARMa’; Hartig 2020). To assess whether means across treatments were significantly different, we performed a post hoc comparison of means by computing estimated marginal means (function ‘emmeans’, library ‘emmeans’; Lenth 2021). Statistical tests used for the greenhouse experiment were identical to those described for the laboratory experiment.

Results

3.1. Laboratory experiment

The presence of natural enemies and of banker plants significantly affected the population densities of all four species (Table 2, Fig. 3). The presence of natural enemies prevented the early pest outbreaks of *B. tabaci* (populations 1.6 times lower in average: mean ± SE of individuals per six plants: control – no natural enemy 777 ± 29, control – with natural enemies 485 ± 7; Table 3, Fig. 3A) and of *M. persicae* (populations 1.4 times lower in average: control – no natural enemy 368 ± 10, control – with natural
enemies 257 ± 7; Table 3, Fig. 3B) in Weeks 2-8. Adding one banker plant type (\textit{R. communis} – \textit{T. ricini}) caused a further significant reduction in \textit{B. tabaci} numbers (297 ± 6, 0.6 times lower) compared with the control – with natural enemies systems, but this was not true for \textit{M. persicae} (256 ± 7). Finally, adding a second banker plant type (\textit{G. max} – \textit{M. japonica}) caused a further significant reduction in \textit{M. persicae} numbers (169 ± 5, 1.5 times lower) compared with the control – with natural enemies systems or the one-banker plant systems, and thanks to the suppression of the second aphid population outbreak in Weeks 10-14. Conversely in \textit{B. tabaci}, no second outbreak was observed, and numbers were not different between the two-banker plant systems (293 ± 9) and the one-banker plant systems.

Populations of \textit{E. formosa} were enhanced by the presence of the \textit{R. communis} – \textit{T. ricini} banker plant systems with a marked increase in numbers per six plants at Week 5 (Fig. 3C) resulting in a 1.2 times increase in average in the one-banker plant systems (35 ± 1) compared with the control – with natural enemies systems (21 ± 1; Table 3, Fig. 3C). However, adding a second banker plant type had no significant effect on \textit{E. formosa} numbers compared (37 ± 2) with one banker plant type only. Finally, \textit{P. japonica} numbers per six plants were not significantly different in presence (5.2 ± 0.2) or in absence of one banker plant type (5.0 ± 0.2) but they were 3.2 times higher in the two-banker plant systems (16 ± 1; Fig. 3D, Table 3).

### 3.2. Greenhouse experiment

Similar to the laboratory experiment, the presence of banker plant systems in the greenhouse experiment significantly impacted the population densities of all four species (Fig. 4; Table 2). Like in the laboratory experiment, the presence of natural enemies prevented the first pest outbreak in Weeks 2-8, with \textit{B. tabaci} numbers per eight plants 1.6 times lower in the control – with natural enemies systems (672 ± 11) compared with the control – no natural enemy systems (1,068 ± 22; Fig. 4A, Table 4), and \textit{M. persicae} numbers 1.3 times lower in the control – with natural enemies systems (182 ± 6) compared with the control – no natural enemy systems (250 ± 6; Fig. 4B, Table 4). Also, adding one banker plant system (\textit{R. communis} – \textit{T. ricini}) caused a further significant reduction in \textit{B. tabaci} numbers (428 ± 6, 1.6 times lower) compared with the control – with natural enemies systems, but this was not true in \textit{M. persicae} (180 ± 6). Finally, adding a second banker plant system (\textit{G. max} – \textit{M. japonica}) resulted in a further decrease in \textit{M. persicae} numbers (105 ± 3, 1.7 times lower) compared with the control – with natural enemies systems, again thanks to the suppression of the second aphid population outbreak in Weeks 10-14. Conversely and consistent with the laboratory experiment, there was no second population outbreak in \textit{B. tabaci} populations, and their numbers in the two-banker plant systems (406 ± 7) were not different than in the one-banker plant systems.

Consistent with the laboratory experiment, \textit{E. formosa} populations were enhanced by the presence of the \textit{R. communis} – \textit{T. ricini} banker plant system, with populations increasing from Week 3 and 2.1 times higher in average in the one-banker plant systems (mean ± Se of individuals per eight plants: 145 ± 7) compared with the control – with natural enemies systems (67 ± 3; Fig. 4C, Table 4). However, their numbers were not different in the two-banker plant systems (142 ± 6) compared with the one-banker

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plant systems. Finally, *P. japonica* numbers per eight plants were not different between the one-banker plant systems (41 ± 2) and the control – with natural enemies systems (42 ± 2) but they were significantly increased and 2.2 times higher in the two-banker plant systems (92 ± 4) compared with the one-banker plant systems, thanks to a continuous increase in population densities from Week 3 to 13 (Fig. 4D, Table 4).

**Discussion**

Conservation biological control has been widely proposed as the solution to increase biodiversity and the colonization and fitness of natural enemies within cropping systems notably via the introduction of non-crop functional plants (Naranjo et al. 2015). These solutions could decrease the input costs of biocontrol agent releases, increase pest control effectiveness and limit non-target impact risks during biological control processes (Stiling & Simberloff 2000). In particular, the use of banker plants could be an economically sustainable solution to enhance the populations of natural enemies via banker plants supporting alternative arthropod prey or host populations (Huang et al. 2011). Yet with the increased complexity in biocontrol application systems, the use of single banker plant systems in such complex cropping systems may not be efficient to support multiple released biocontrol agent species. In the present study, we tested the potential for a combination of two banker plant systems to promote the simultaneous control of two major tomato pests by two biocontrol agents, in a laboratory and a greenhouse experiment. We showed that combined banker plant systems increased the control of both the main tomato pest *Bemisia tabaci* by *Encarsia formosa* and the secondary pest *Myzus persicae* by *Propylea japonica* in both laboratory and greenhouse settings. Notably, adding the *Ricinus communis* – *Trialeurodes ricini* banker plant system allowed the suppression of the early population outbreak in *B. tabaci*, while adding the *Glycines max* – *Megoura japonica* system allowed the suppression of the two population outbreaks in *M. persicae*.

As expected, we found that the *R. communis* – *T. ricini* banker plant system promoted the populations of *E. formosa*, resulting in an increased control of *B. tabaci* populations, while only the use of the *G. max* – *M. japonica* system promoted *P. japonica* populations and resulted in an increased control of the secondary pest *M. persicae*. This proves the efficacy of the chosen banker plant systems to promote these target biocontrol agent species, but also their strong specificity to the target biocontrol agents. This is because *E. formosa* is specialized on whiteflies, and hence cannot use aphids as alternative hosts (Tao et al. 2018). Similarly, the predatory ladybird *P. japonica*, although polyphagous (Yang et al. 2014), primarily feeds on aphids and has a reduced fitness when fed on *B. tabaci* (Liu et al. 2008). This would explain that the *R. communis* – *T. ricini* system did not enhance *P. japonica* populations resulting in poor control of *M persicae*. Indeed the densities of *P. japonica* populations were too low to prevent the late population outbreak of *M. persicae*, suppressed in the two-banker plant systems only, in which *P. japonica* populations reached twice as high densities. The limited overlap between natural enemies supported by distinct banker plant systems could be beneficial to avoid the disruption of pest control. Such disruption could occur if natural enemies compete for the same pest resource and this could notably cause population outbreaks of secondary pest species (Bhattacharyya & Sinha, 2009).
Both in the laboratory and greenhouse experiments, we observed niche partitioning between the main tomato pest *B. tabaci* and the secondary tomato pest *M. persicae* in absence of natural enemies. Aphid populations rose rapidly in Weeks 2–6 and then decreased in Weeks 7–10 under high summer temperatures, while *B. tabaci* populations rose slower to peak in Week 10. However once *B. tabaci* populations decreased in late summer, aphid populations broke out again. Such dynamics are common in tomato cropping systems (Lu et al. 2004; Ap et al. 2019). In the banker plant systems, the alternative host *T. ricini* and prey *M. japonica* did not occupy the niche left empty by the control of *B. tabaci* and *M. persicae* populations as they preferred their primary host plants *R. communis* and *G. max*, respectively. Therefore they did not damage tomato crops, showing their suitability as banker plant systems for pest control in commercial greenhouse crops.

In the present study, we deliberately released *E. formosa* at higher densities than *P. japonica*, and proportionally to the densities of their respective target pests *B. tabaci* and *M. persicae*. These pest densities simulated real conditions commonly found in commercial greenhouse cropping systems, and in response multi-species releases of biocontrol agents are often asymmetric (Liu et al., 2013; Ma et al., 2018). The specialist natural enemy is released at higher densities to control the main pest species, while the generalist natural enemy is released at lower density to provide the suppression of the populations of secondary pest species throughout the cropping season (Garey & Ruffié 1987; Fonseca et al. 2020).

One key aspect in the industrial development of banker plant systems is to adjust the balance between the densities of the main and alternative hosts / prey (Frank 2010). Since they are targeted by a shared natural enemy, the main and alternative host / prey are under apparent competition in cropping systems enriched with banker plant systems (van Veen et al. 2006; Jaworski et al. 2015). Hence, adding too many banker plant units may cause natural enemies to reduce pressure on main pests and resulting in poor control. Conversely, adding too few banker plant units may be insufficient to enhance natural enemy populations, resulting in too low densities and poor establishment of their populations and therefore a poor pest control in the long term. Future research in banker plant systems should focus on developing flexible systems to accurately adjust the density of alternative prey / hosts and improve the sustainable control of arthropod complex by using multi-species biocontrol agent releases. Finally, it could be useful to investigate the potential for dual functions of banker plants, such as supporting populations of alternative prey / hosts and providing alternative floral resources (Wäckers & van Rijn 2012). This would allow the design of IPM strategies via the support of populations of specialist and generalist biocontrol agent species in multi-species systems providing pest control over the short-term and the long-term.

In conclusion, our study showed that the combined use of multiple banker plant systems targeting distinct biocontrol agents significantly increased the control of both main and secondary pest populations. Banker plants were necessary to avoid pest outbreaks and to provide long-term pest control via the establishment of natural enemy populations at high densities.

**Declarations**
5. Acknowledgments

The study was funded by the project 32072479 supported by National Natural Science Foundation of China, the National Key Research and Development Programme of China (2017YFD0201000; 2018YFD0200402), the Beijing Key Laboratory of Environment Friendly Management of Fruit Diseases and Pests in North China (BZ0432), the Beijing Science and Technology Project (z201100008020014), the Key Research and Development Programme of the Jiangxi Province (202002BBF62006), and the Key Research and Development Programme of Shandong (Public Welfare; 2019GSF109118).

Funding see acknowledgment section

Conflicts of interest/Competing interests Authors declare they have no competing interests.

Availability of data and material Not applicable

Code availability Not applicable

Authors' contributions

SW, ND, CCJ, YL and XG designed the study; CX and JW performed the experiments; CX, HDJ and CCJ analysed the data; YL, CX, CCJ, LSZ and SW wrote the manuscript. All authors read and approved the manuscript for submission.

References

1. Albajes R, Ghullino ML, van Lenteren JC, Elad Y (2000) Integrated pest and disease management in greenhouse crops. Dordrecht, Netherlands: Luwer Academic Publishers.
2. Andorno AV, López SN (2014) Biological control of Myzus persicae (Hemiptera: Aphididae) Through banker plant system in protected crops. Biological Control 78:9-14.
3. Ap H, Dk S, Devee A (2019) Population dynamics and management of whitefly, Bemisia tabaci in tomato ecosystem, Solanum lycopersicum L. Journal of Entomological and Zoological Studies 7:1232-1235.
4. Aparicio Y, Gabarra R, Arno J (2020) Interactions among Myzus persicae, predators and parasitoids may hamper biological control in Mediterranean peach orchards. Entomologia Generalis 40:217-228.
5. Avery, PB, Kumar V, Xiao Y, Powell CA, Osborne LS (2014) Selecting an ornamental pepper banker plant for Amblyseius swirskii in floriculture crops. Arthropod-Plant Interactions 8:49-56.
6. Barbosa P (1998) Conservation Biological Control. Academy Press, London, UK.
7. Bates D, Maechler N, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1-48.
8. Bhattacharyya S, Sinha S (2009) Ecological Networks: Structure, Interaction Strength, and Stability. In: Ganguly N, Deutsch A, Mukherjee A (Eds). Dynamics On and Of Complex Networks. Modeling and
9. Bianchi FJJ, Booij CJH, Tscharntke T (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings in Biological Sciences* 273:1715-1727.

10. Chacón JM, Heimpel GE (2010) Density-dependent intraguild predation of an aphid parasitoid. *Oecologia* 164:213-22.

11. Chailleux A, Biondi A, Han P, Tabone E, Desneux N (2013) Suitability of the pest-plant system *Tuta absoluta* (Lepidoptera: Gelechiidae) tomato for *Trichogramma* (Hymenoptera: Trichogrammatidae) parasitoids and insights for biological control. *Economic Entomology* 106:2310-2321.

12. Chailleux A, Wajnberg E, Zhou Y et al (2014a) New parasitoid-predator associations: female parasitoids do not avoid competition with generalist predators when sharing invasive prey. *Naturwissenschaften* 101:1075-1083.

13. Chailleux A, Mohl EK, Teixeira Alves M, Messelink GJ, Desneux N (2014b) Natural enemy-mediated indirect interactions among prey species: potential for enhancing biocontrol services in agroecosystems. *Pest Management Science* 70:1769-1779.

14. Chailleux A, Droui A, Bearez P, Desneux N (2017) Survival of a specialist natural enemy experiencing resource competition with an omnivorous predator when sharing the invasive prey *Tuta absoluta*. *Ecology & Evolution* 7:8329-8337.

15. Czosnek H, Ghanim M (2011) *Bemisia tabaci* – Tomato Yellow Leaf Curl Virus Interaction Causing Worldwide Epidemics. Springer Netherlands.

16. Dainese M, Schneider G, Krauss J, Steffan-Dewenter I (2017) Complementarity among natural enemies enhances pest suppression. *Scientific Reports* 7:8172.

17. Damien M, Llopis S, Desneux N, van Baaren J, Le Lann C (2020) How does floral nectar quality affect life history strategies in parasitic wasps? *Entomologia Generalis* 40:147-156.

18. Desneux N, Decourtye A, Delpuech JM (2007) The sublethal effects of pesticides on beneficial arthropods. *Annual Review of Entomology* 52:81-106.

19. Desneux N, Kaplan I, Yoo HJS, Wang S, O'Neil RJ (2019) Temporal synchrony mediates the outcome of indirect effects between prey via a shared predator. *Entomologia Generalis* 39:127-136.

20. Enkegaard A (2011) Temperature dependent functional response of *Encarsia formosa* parasitizing the Poinsettia-strain of the cotton whitefly, *Bemisia tabaci*, on Poinsettia. *Entomologia Experimentalis Et Applicata*, 73:19-29.

21. Fonseca MM, Pallini A, Nascimento PHMG, Lima E, Janssen A (2020) Compatibility of two predator species for biological control of the two-spotted spider mite. *Experimental and Applied Acarology* 80:409-422.

22. Frank SD (2010) Biological control of arthropod pests using banker plant systems: Past progress and future directions. *Biological Control* 52:8-16.
23. Garey L, Ruffié J (1987) The Population Alternative: A New Look at Competition and the Species. Penguin Books, UK.
24. Gurr GM, Wratten SD, Landis DA, You MS (2017) Habitat management to suppress pest populations: progress and prospects. Annual Review of Entomology 62:91-109.
25. Hall RJ (2011) Intraguild predation in the presence of a shared natural enemy. Ecology 92:352-361.
26. Hansen LS (1983) Introduction of *Aphidoletes aphidium* (Rond) (Diptera: Cecidomyiidae) from an open rearing unit for control of aphids in glasshouses. Bulletin SROP 6:146-150.
27. Hartig (2020) DHARMa: Residual Diagnostics for Hierarchical (Multi-level / Mixed) Regression Models. R package version 0.3.3.0. https://CRAN.R-project.org/package=DHARMa.
28. Heimpel GE, Mills N (2008) Biological Control: Ecology and Applications. Cambridge University Press, Cambridge, UK.
29. Huang NX, Enkegaard A, Osborne LS, Ramakers PMJ, Messelink GJ, Pijnakker J, Murphy G (2011) The banker plant method in biological control. Critical Reviews in Plant Sciences 30:259-278.
30. Huang H, Zhao H, Zhang Y-M, Zhang S-Z, Liu T-X (2014) Influence of selected host plants on biology of castor whitefly, *Trialeurodes ricini* (Hemiptera: Aleyrodidae). Journal of Asia-Pacific Entomology 17:745-751.
31. Huang NX, Jaworski CC, Desneux N, Zhang F, Yang PY, Wang S (2020) Long-term and large-scale releases of *Trichogramma* promote pesticide decrease in maize in northeastern China. Entomologia Generalis 40:331-335.
32. Huffaker CB, Messenger PS, DeBach P (1971) The Natural Enemy Component in Natural Control and the Theory of Biological Control. In: Huffaker CB (Eds) Biological Control. Springer, Boston, MA.
33. Hullé M, Chaubet B, Turpeau E, Simon JC (2020) Encyclop’Aphid: a website on aphids and their natural enemies. Entomologia Generalis 40:97-101.
34. Jandricic SE, Dale AG, Bader A, Frank SD (2014) The effect of banker plant species on the fitness of *Aphidius colemani* Viereck and its aphid host (*Rhopalosiphum padi* L.). Biological Control, 76:28-35.
35. Jaworski CC, Chailleux A, Bearez P, Desneux N (2015) Apparent competition between major pests reduces pest population densities on tomato crop, but not yield loss. Journal of Pest Science 88:793-803.
36. Jaworski CC, Xiao D, Xu QX, Ramirez-Romero R, Guo XJ, Wang S, Desneux N (2019) Varying the spatial arrangement of synthetic herbivore-induced plant volatiles and companion plants to improve conservation biological control. Journal of Applied Ecology 56:1176-1188.
37. Kogan M (1998) Integrated pest management: historical perspectives and contemporary developments. Annual Review of Entomology 43:243-270.
38. Kuroda T & Miura K (2003) Comparison of the effectiveness of two methods for releasing *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) against *Aphis gossypii* Glover (Homoptera: Aphididae) on cucumbers in a greenhouse. Applied Entomology & Zoology 38:271-274.
39. Lange WH Bronson L (1981) Insect Pest of Tomatoes. Annual Review of Entomology 26: 45-71.
40. Laurenz S, Meyhofer R (2021) Banker plants promote functional biodiversity and decrease populations of the cabbage whitefly *Aleyrodes proletella*. *Journal of Applied Entomology* 145:36-45.
41. Lenth RV (2021) emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.5.4. [https://CRAN.R-project.org/package=emmeans](https://CRAN.R-project.org/package=emmeans).
42. Li WD, Zhang SZ, Liu TX (2011) Effect of temperature on development and growth of *Propylea japonica* and *Harmonia axyridis* reared on *Megoura japonica*. *Proceedings of International Symposium on Mass Production and Commercialization of Arthropod Biological Control Agents*, pp44.
43. Li MT (2013) Biological characteristics and control method of *Myzus persicae* (Sulzer). *Journal of Agricultural Catastrophology* 3:1-4.
44. Li XW, Pan MZ, Liu TX (2013) The theory and practice of using banker plant system for biological control of pests. *Chinese Journal of Applied Entomology* 50:890-896.
45. Li JM, Xiang CY, Wang XX, Guo YM, Huang ZJ, Liu L, Li X, Du YC (2021) Current situation of tomato industry in China during “the Thirteenth Five-year Plan” period and future prospect. *China Vegetables* 2:13-20.
46. Liang Y, Xu C, Dai H, Wang J, Guo X, Wang S, Jaworski CC (2021) Flower provision helps reduce intraguild predation among predatory ladybirds and increases biological control of aphids in a greenhouse crop. *Journal of Pest Science*. Accepted with revisions.
47. Liu WX, Zhang YB, Wan FH (2008) Preference and fitness of *Propylea japonica* (Thunberg) feeding cotton aphid, *Aphis gossypii* Glover, and cotton whitefly, *Bemisia tabaci* (Gennadius). *China Journal of Biological Control* 24:293-297.
48. Liu YJ, Yu JX, Zhou G, Dai LX, Yang ZQ, Zhang LN (2012) Evaluation of biological control of *Monochamus alternatus* by releasing *Scleroderma sichuanensis* and *Dastarus helophoroides*. *Hunan Forestry Science and Technology* 39:20-23.
49. Liu LZ, Dai P, Lv B, Zang LS, Du WM, Wan FH (2013) Interspecific competition between *Encarsia sophia* and *E. formosa* and their impacts on suppression of *Trialeurodes vaporariorum*. *Scientia Agricultura Sinica* 46:4837-4841.
50. Lu CY, Yang DF, Shen GQ, Shen MX, Ma HM, Wu TD, Liu FJ (2004) Preliminary survey of aphids outbreaks on greenhouse tomato. *Shanghai Agricultural Technology* 6:84-85.
51. Ma LJ, Zhang SZ, Liu TX (2018) Influences of interspecific competition between ladybeetle *Serangium japonicum* and parasitoid *Encarsia formosa* on predation of tobacco whitefly *Bemisia tabaci*. *Journal of Plant Protection* 45:1289-1295.
52. Michaud JP (2010) A comparative study of larval cannibalism in three species of ladybird. *Ecological Entomology* 28:92-101.
53. Mirande L, Desneux N, Hamboure M, Schneider MI (2015) Intraguild predation between an exotic and a native coccinellid in Argentina: the role of prey density. *Journal of Pest Science* 88:155-162.
54. Monticelli LS, Desneux N, Heimpel GE (2021) Parasitoid-mediated indirect interactions between unsuitable and suitable hosts generate apparent predation in microcosm and modeling studies.
55. Naranjo SE, Ellsworth PC, Frisvold GB (2015) Economic value of biological control in integrated pest management of managed plant systems. *Annual Review of Entomology* 60:621-645.

56. Orrock JL, Holt RD, Baskett ML (2010) Refuge-mediated apparent competition in plant-consumer interactions. *Ecology Letters* 13:11-20.

57. Osborne LS, Hoelmer K, Gerling D (1991) Prospects for biological control of sweet potato whitefly. Research Report Bedding Plant Foundation Inc., 306.

58. Ovchinnikov AN, Belyakova NA, Ovchinnikova AA, Reznik SY (2019) Factors determining larval cannibalistic behavior in invasive and native populations of the multicolored Asian ladybird, *Harmonia axyridis*. *Entomologia Generalis* 38:243-254.

59. Parolin P, Bresch C, Poncet C, Desneux N (2012) Functional characteristics of secondary plants for increased pest management. *International Journal of Pest Management* 58:369-377.

60. Pérez-Valencia LI, Camorlinga-Cortés P, Carrillo-Arámbula LC, Palmeros-Suárez PA, Ramirez-Romero R (2019) Why can a predator increase its consumption of prey when it is released along with a parasitoid? *Entomologia Generalis* 39:205-219.

61. Perović DJ, Gámez-Virués S, Landis DA et al. (2018) Managing biological control services through multi-trophic trait interactions: review and guidelines for implementation at local and landscape scales. *Biological Reviews* 93:306-321.

62. Sanchez-Hernandez CV, Desneux N, Bao-Fundora L, Ramirez-Romero R (2021) Alternative extraguild prey modifies focal extraguild prey consumption and parasitism but not intraguild predation intensity. *Biological Control* 153:104475.

63. R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

64. Shishehbor P, Brennan PA (1996) Life history traits of castor whitefly, *Trialeurodes ricini* Misra (Hom., Aleyrodidae), on eight host plant species. *Journal of Applied Entomology* 120:519-522.

65. Stiling P, Simberloff D (2000). Nontarget effects of biological control. In: Follett PA & Duan JJ (Eds.). The frequency and strength of nontarget effects of invertebrate biological control agents of plant pests and weeds. Springer, Boston, MA, U.S.A., pp 31-43.

66. Stiling P, Cornelissen T (2005) What makes a successful biocontrol agent? A meta-analysis of biological control agent performance. *Biological Control* 34:236-246.

67. Tan XL, Zhao J, Wang S, Zhang F (2015) Optimization and evaluation of microencapsulated artificial diet for mass rearing the predatory ladybird *Propylea japonica* (Coleoptera: Coccinellidae). *Insect Science* 22:111-120.

68. Tan XL, Hu NN, Zhang F, Ramirez-Romero R, Desneux N, Wang S, Ge F (2016) Mixed release of two parasitoids and a polyphagous ladybird as a potential strategy to control the tobacco whitefly *Bemisia tabaci*. *Scientific Reports* 6:28245.
69. Tao X, Zhang CY, Fu WY, Xu Y, Liu TX (2018) Control efficacy of tomato *Bemisia tabaci* by using *Encarsia formosa* Gahan in greenhouse. *Journal of Changjiang Vegetables* 6:78-82.

70. van Veen FJF, Memmott J, Godfray HCJ (2006) Indirect effects, apparent competition and biological control. In Brodeur J, Boivin G (Eds). *Trophic and Guild in Biological Interactions Control*. Springer Netherlands.

71. Vuong PT, Kim J & Song Y (2001) The seasonal occurrence of the two aphid species, *Myzus persicae* and *Aphis gossypii*, and their natural enemies on vegetable crops in Chinju, Korea *Journal of Asia-Pacific Entomology* 4:41-44.

72. Wäckers FL, van Rijn PCJ (2012) Pick and mix: Selecting flowering plants to meet the requirements of target biological control insects. In Gurr G, Wratten S, Snyder W & Read D (Eds.). *Biodiversity and Insect Pests*. John Wiley & Sons, Ltd, pp. 139-165.

73. Wang S, Tan, X-L, Guo, X-J, Zhang F (2013) Effect of temperature and photoperiod on the development, reproduction, and predation of the predatory ladybird *Cheilomenes sexmaculata* (Coleoptera: Coccinellidae). *Journal of Economic Entomology* 106:2621-2629.

74. Wang XS, Chen QZ, Zhang SZ, Liu TX (2016) Parasitism, host feeding and immature development of *Encarsia formosa* reared from *Trialeurodes vaporariorum* and *Bemisia tabaci* on *Trialeurodes ricini*. *Journal of Applied Entomology* 140:346-352.

75. Wang YS, Yao FL, Soares MA, Amiens-Desneux E, et al. (2020) Effects of four non-crop plants on life history traits of the lady beetle *Harmonia axyridis*. *Entomologia Generalis* 40:243-252.

76. Xu QX, Wang S, Li S, Hatt S (2020) Conservation biological control in organic greenhouse vegetables. In: Gao Y, Hokkanen HM, Menzler-Hokkanen I (Eds). *Integrative Biological Control. Progress in Biological Control*, vol 20. Springer, Cham.

77. Yang NW, Zang LS, Wang S, Guo JY, Xu HX, Zhang F, Wan FH (2014) Biological pest management by predators and parasitoids in the greenhouse vegetables in China. *Biological Control* 68:92-102.

78. Yano E, Abe J, Hemerik L (2018) Evaluation of pest control efficiencies for different banker plant systems with a simple predator–prey model. *Population Ecology* 60:389-396.

79. Zang LS, Wang S, Zhang F, Desneux N (2021) Biological control with *Trichogramma* in China: history, present status and perspectives. *Annual Review of Entomology* 66:463-484.

80. Zhang GF, Wu X, Zhou ZX, Meng XQ, Wan FH (2013) A one-step, single tube, duplex PCR to detect predation by native predators on invasive *Bemisia tabaci* meam1 and *Frankliniella occidentalis*. *Entomologia Experimentalis Et Applicata* 150:66-73.

81. Zhao J, Guo XJ, Tan XL, Desneux N, Lucia Z, Zhang F, Wang S (2017) Using *Calendula officinalis* as floral resource to enhance aphid and thrips suppression by the flower bug *Orius sauteri* (Hemiptera: Anthocoridae). *Pest Management Science* 73:515-520.

82. Zheng X, Lu Y, Zhu P, Zhang F, Tian J, Xu H, Chen G, Nansen C, Lv Z (2017) Use of banker plant system for sustainable management of the most important insect pest in rice field in China. *Scientific Reports* 7:45581.
Tables

Table 1. The banker plant systems used in present study and their targeted natural enemy and apparent pest competitor.

| Banker plant system | Banker plant            | Target tomato pest | Alternative prey / host | Natural enemy       |
|---------------------|-------------------------|--------------------|-------------------------|---------------------|
| BPS1                | *Ricinus communis*      | *Bemisia tabaci*   | *Trialeurodes ricini*   | *Encarsia formosa*  |
| BPS2                | *Glycines max*          | *Myzus persicae*   | *Megoura japonica*      | *Propylea japonica* |

Table 2. Impact of the treatment (control – no natural enemy / control – with natural enemies / one-banker plant system / two-banker plant system) on the abundances of the two pest species *B. tabaci* and *M. persicae* and of their respective biocontrol agents *E. formosa* and *P. japonica* in the laboratory and the greenhouse experiments.

|                | $\chi^2$ | d.f. | $P$  |
|----------------|----------|------|------|
| **Laboratory experiment** |          |      |      |
| *B. tabaci*    | 143      | 3    | $<0.001$ *** |
| *M. persicae*  | 120      | 3    | $<0.001$ *** |
| *E. formosa*   | 69.7     | 2    | $<0.001$ *** |
| *P. japonica*  | 84.6     | 2    | $<0.001$ *** |
| **Greenhouse experiment** |        |      |      |
| *B. tabaci*    | 194      | 3    | $<0.001$ *** |
| *M. persicae*  | 118      | 3    | $<0.001$ *** |
| *E. formosa*   | 71.0     | 2    | $<0.001$ *** |
| *P. japonica*  | 66.1     | 2    | $<0.001$ *** |

‘***’: $P < 0.001$...

Table 3. Comparisons of means between treatments in the number of individuals per six plants for each insect species in the laboratory experiment (emmeans: contrast estimates $\pm$ SE and associated $P$-value).
|                | Estimate ± SE |   P    |
|----------------|--------------|--------|
| **B. tabaci**  |              |        |
| 1BP – 2BP      | 0.0109 ± 0.032 | 0.99   |
| 1BP – Control (no NE) | -0.950 ± 0.032 | < 0.001 *** |
| 1BP – Control (with NE) | -0.501 ± 0.032 | < 0.001 *** |
| 2BP – Control (no NE) | -0.961 ± 0.032 | < 0.001 *** |
| 2BP – Control (with NE) | -0.512 ± 0.032 | < 0.001 *** |
| Control (no NE) – Control (with NE) | 0.450 ± 0.032 | < 0.001 *** |
| **M. persicae** |              |        |
| 1BP – 2BP      | 0.361 ± 0.037 | < 0.001 *** |
| 1BP – Control (no NE) | -0.361 ± 0.037 | < 0.001 *** |
| 1BP – Control (with NE) | -0.00732 ± 0.037 | 0.99   |
| 2BP – Control (no NE) | -0.722 ± 0.037 | < 0.001 *** |
| 2BP – Control (with NE) | -0.369 ± 0.037 | < 0.001 *** |
| Control (no NE) – Control (with NE) | 0.353 ± 0.037 | < 0.001 *** |
| **E. formosa**  |              |        |
| 1BP – 2BP      | -0.0373 ± 0.042 | 0.64   |
| 1BP – Control (with NE) | 0.457 ± 0.044 | < 0.001 *** |
| 2BP – Control (with NE) | 0.494 ± 0.044 | < 0.001 *** |
| **P. japonica** |              |        |
| 1BP – 2BP      | -1.11 ± 0.06  | < 0.001 *** |
| 1BP – Control (with NE) | 0.0385 ± 0.0712 | 0.85   |
| 2BP – Control (with NE) | 1.15 ± 0.06  | < 0.001 *** |

***: \( P < 0.001 \).

**Table 4.** Comparisons of means between treatments in the number of individuals per six plants for each insect species in the greenhouse experiment (emmeans: contrast estimates ± SE and associated \( P \)-value).
|                | Estimate ± SE |   P   |
|----------------|--------------|------|
| **B. tabaci**  |              |      |
| 1BP – 2BP      | 0.0530 ± 0.0211 | 0.058 |
| 1BP – Control (no NE) | -0.902 ± 0.021 | <0.001 *** |
| 1BP – Control (with NE) | -0.444 ± 0.021 | <0.001 *** |
| 2BP – Control (no NE) | -0.955 ± 0.021 | <0.001 *** |
| 2BP – Control (with NE) | -0.497 ± 0.021 | <0.001 *** |
| Control (no NE) – Control (with NE) | 0.459 ± 0.021 | <0.001 *** |

| **M. persicoae** |         |      |
| 1BP – 2BP        | 0.489 ± 0.040 | <0.001 *** |
| 1BP – Control (no NE) | -0.331 ± 0.039 | <0.001 *** |
| 1BP – Control (with NE) | -0.0162 ± 0.0393 | 0.98 |
| 2BP – Control (no NE) | -0.820 ± 0.040 | <0.001 *** |
| 2BP – Control (with NE) | -0.506 ± 0.040 | <0.001 *** |
| Control (no NE) – Control (with NE) | 0.314 ± 0.039 | <0.001 *** |

| **E. formosa**  |         |      |
| 1BP – 2BP       | 0.0273 ± 0.054 | 0.90  |
| 1BP – Control (with NE) | 0.660 ± 0.056 | <0.001 *** |
| 2BP – Control (with NE) | 0.636 ± 0.056 | <0.001 *** |

| **P. japonica** |         |      |
| 1BP – 2BP       | -0.813 ± 0.067 | <0.001 *** |
| 1BP – Control (with NE) | -0.0299 ± 0.0671 | 0.90  |
| 2BP – Control (with NE) | 0.783 ± 0.067 | <0.001 *** |

‘***’: P < 0.001.

**Figures**
Figure 1

Description of the laboratory experiment. Green dots: position of the potted tomato plants. Blue dots: position of the infested potted banker plants.

Figure 2

* The height of the chamber is 1.5 m
Description of the greenhouse experiment. Green dots: position of tomato plants. Blue dots: position of infested banker plants. In each chamber, only four positions were used for each banker plant system.

Figure 3

Insect population dynamics in laboratory cages in the one-banker plant systems (dashed, light grey), two-banker plant systems (solid, dark grey), or without banker plants and with natural enemies (solid, orange) or without natural enemies (dashed, blue). Mean ± SE per week of individuals per six tomato plants (adults and juveniles) of pests: (A) B. tabaci, (B) M. persicae; and of natural enemies: (C) E. formosa, (D) P. japonica (N = 10 cages per treatment). NE: natural enemy; 1 BP: one-banker plant system; 2 BP: two-banker plant system.