Journal of Pest Science (2023) 96:711–721
https://doi.org/10.1007/s10340-022-01570-9

ORIGINAL PAPER

Companion plants and alternative prey improve biological control by *Orius laevigatus* on strawberry

Mnqobi Zuma[1] · Cliven Njekete[1] · Kouassi A. J. Konan[2,3] · Philippe Bearez[1] · Edwige Amiens-Desneux[1] · Nicolas Desneux[1] · Anne-Violette Lavoir[1]

Received: 18 May 2022 / Revised: 19 September 2022 / Accepted: 23 September 2022 / Published online: 7 November 2022
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2022

Abstract

Macrosiphum euphorbiae (aphid) is an important economic pest because it causes significant damage to several crops, notably on strawberry. The use of natural enemies, especially predators, is an alternative that is being explored to protect strawberry crops against this pest, notably the species *Orius laevigatus* is a promising predator for biological control. However, the lack of suitable habitats and/or food is a constraint to the growth and/or the establishment of the predator populations, reducing their effectiveness as control agent against *M. euphorbiae*. Using additional food resources such as companion plants or alternative food sources may support predator population and associated biocontrol services they provide. The objective of this study was to evaluate the efficacy of *O. laevigatus* as biological control agent against *M. euphorbiae*, mediated by the presence of companion plants and alternative prey. We evaluated under greenhouse conditions the effect of *Lobularia maritima* (alyssum) as possible companion plant, as well as *Ephestia kuehniella* eggs as alternative prey, on *O. laevigatus* populations and biocontrol service in strawberry cropping system. Predators were placed in the presence or absence of alyssum and/or *E. kuehniella* eggs on strawberry plants previously infested with aphids. We showed that the presence of alyssum and/or *E. kuehniella* eggs enhanced *O. laevigatus* population growth (when compared to a control group). Furthermore, we observed a steady reduction of *M. euphorbiae* populations when the companion plant was present alone or when it was associated with the alternative prey. Finally, the treatment with the combination of alyssum and alternative prey resulted in the highest yield (number of fruits per plant). Our study demonstrated that combining alyssum, as a companion plant, and *E. kuehniella* eggs, as an alternative prey, could be an effective option for establishing *O. laevigatus* populations and for controlling aphids in strawberry cropping systems.

Keywords Alternative food sources · Non-prey food · Mixed diets · Predator · *Macrosiphum euphorbiae* · Biological control

Introduction

The development of synthetic insecticides in the mid-twentieth century made the controlling of herbivorous pests quite adequate, and these chemicals are still widely used in modern agriculture (Lu et al. 2012; Goulson 2019). However, long-term and over-dosage applications of chemical pesticides lead to food safety concerns, insect pest resistance, and adverse effects on non-target organisms (e.g., see Menail et al. 2020; Palma-Onetto et al. 2021; Passos et al. 2022 and Desneux et al. 2007 for a thorough review). Due to these critical limitations, biological control of arthropod pest populations by natural enemies has become an essential pest management method (Ragsdale et al. 2011; Heimpel and Mills 2017; Michaud 2018; Zang et al. 2021) notably in

Communicated by Alberto Urbaneja.

✉ Nicolas Desneux
nicolas.desneux@inrae.fr

[1] Université Côte d'Azur, INRAE, CNRS, UMR ISA, 06000 Nice, France

[2] Felix Houphouet Boigny University of Cocody, Abidjan, Côte d'Ivoire

[3] National Center for Agricultural Research (CNRA), Bouaké, Côte d'Ivoire

Integrated Pest Management (IPM) packages (Desneux et al. 2022). Biological control is an environmentally friendly technique of using organisms to reduce pests and their effects on crops (Heimpel and Mills 2017). Augmentative biological control—inundation type—involves the release of mass-reared natural enemies, such as predators, in large numbers to obtain immediate pest control (Collier and Van Steenwyck 2004; Perez-Alvarez et al. 2019; Huang et al. 2020). Although augmentative biological control is effective, natural enemies tend to rapidly disappear from crops once pest prey resources are mostly consumed, requiring frequent and costly reintroductions (Bennison et al. 2011; Messelink et al. 2014; Oveja et al. 2016; Labbé et al. 2018). To avoid these challenges, providing alternative diets such as alternative prey and/or companion plants showed great potential for sustaining biocontrol agents and thus to support the biocontrol services they provide (Lundgren et al. 2009; Messelink et al. 2014; Damien et al. 2020; Li et al. 2021). Indeed, food resources from companion plants (e.g., nectar or pollen) and alternative prey (e.g., *Ephestia kuehniella* eggs) are used as supplemental food to support beneficial arthropods in crops (Messelink et al. 2014).

Companion plants are secondary plants (considering the crop plant as the primary one in the agroecosystem) purposely established directly next to individual crop plants in order to offer an additional service. For instance, whereas crop plants provide food or fiber provision, companion plants provide pest regulation (Parolin et al. 2012a, b; Parker et al. 2013). Several strategies can provide predatory insects with the resources they need (so-called non-prey food or banker plants): food sources (e.g., nectar or pollen) and/or shelter (refuges, habitats, mating or oviposition sites) (Lundgren et al. 2009; Wäckers and Van Rijn 2012; Gurr et al. 2016; Lu et al. 2014; Ramsden et al. 2015; Chen et al. 2022). Then, companion plants allow natural enemies to survive and reproduce within a cropping system which can increase their abundance and their capacity to regulate pest populations (Begum et al. 2006; Frank 2010; Huang et al. 2011; Parolin et al. 2012a, b; Parker et al. 2013; Han et al. 2022). The flowering plant alyssum *Lobularia maritima* (Brassicaceae) shows several characteristics that could make it an excellent candidate as companion plant. For instance, this plant has a long flowering period (about 10 months) which means it can provide pollen and floral nectar for extended periods (Picó and Retana 2000). It attracts several natural enemies and enhances their fitness, thus having the potential to be an efficient companion plant in various contexts (e.g., Berndt and Wratten 2005; Hogg et al. 2011; Pumariño and Alomar 2012; Tiwari et al. 2020); this flowering plant may sustain natural enemies even when pest populations are low (Messelink et al. 2014).

Artificial food sources are foods produced from one or more ingredients, that are provided to replace natural food (prey or host), and that that are more convenient from a technical and/or economic perspectives (Pascacio-Villafán et al. 2017). Many artificial food sources, such as alternative prey, have the potential for enhancing establishment of natural enemies (Riddick 2009; Messelink et al. 2014). Due to their high percentage of amino acids and lipids, lepidopteran eggs, such as those of moth *E. kuehniella* (Lepidoptera: Pyralidae), are commonly used for mass rearing of various natural enemies, including predatory heteropterans (e.g., *Orius* spp., *Macrolophus pygmaeus* Wagner), coccinellid beetles (e.g., *Harmonia axyridis* Pallas, *Adalia bipunctata* L.), lacewings (*Chrysoperla* spp.), and egg-parasitoids belonging to the *Trichogramma* genus (Specty et al. 2003; Bonte and De Clercq 2008, 2011; Riddick 2009; St-Onge et al. 2014; Pehlïvan 2021; Zang et al. 2021; Zhang et al. 2021). Cocuzza et al. (1997) proposed *E. kuehniella* eggs as the most important food source, which resulted in positive effects for *O. laevigatus* fitness parameters such as fecundity, oviposition period, and female longevity.

The simultaneous use of various alternative food resources has been proposed to induce synergistic positive effects on predator population growth (Pekas and Wäckers 2017); combination of multiple resources for mutualistic arthropods can be better than the sum of each reward provided individually. Likewise, the combination of the companion plant *L. maritima* (alyssum thereafter) together with the alternative prey *Ephestia* eggs may have an additive, or even so a synergistic, enhancing effect(s) on predator population growth.

In this context we aimed to characterize the effects of supplemental food resources on establishing *O. laevigatus* populations in strawberry cropping systems. The study was designed to (i) determine whether a strawberry crop alone can support *O. laevigatus* population growth, (ii) test if the addition of alyssum as an intercrop to strawberry can enhance *O. laevigatus* population growth, (iii) determine if adding *Ephestia* eggs can enhance *O. laevigatus* population growth, (iv) assess if alyssum combined with *Ephestia* eggs can support increased *O. laevigatus* population growth, owing to an additive or synergistic effect, (v) analyze the effects of these different treatments on the regulation of aphid population on strawberry, and (vi) evaluate the potential impact on crop yield.

These objectives were tested on the cultivated strawberry *Fragaria x ananassa*, an important fruit crop. It has grown in popularity in recent decades, as more emphasis is placed on the health benefits of eating fruits and berries (Aaby and Remberg 2015). Nevertheless, Western Flower Thrips (*Frankliniella occidentalis*) and aphids (e.g., *Macrosiphum euphorbiae*) are the two major pests in greenhouse strawberry production systems (Solomon et al. 2001; Hulle et al. 2020). The minute pirate bug *O. laevigatus* (Fieber) (Hemiptera: Anthocoridae) is the most successful biocontrol species in strawberry cropping systems and it is used in augmentative release programs (Bouagga et al. 2018). Its prey is diverse, with a clear preference for pests, including aphids, mites, and thrips (Venzon et al. 2002).

Material and methods

Biological material

Strawberry plants (three-month old seedlings, < 7 cm height), variety 'Amandine' (Pépinières Martaillac, Saint Marthe, France) were planted in 14-cm-diameter pots with potting mix (Sphagnum peat moss, Softwood bark compost, Brown peat, Horse manure, Sea algae, Earthworm Compost) and pine bark. They were placed in a greenhouse for three weeks and supplied with water three times a week (due to high water retention of the potting mix). In addition, a nutrient solution was supplied through capillary systems before and during the experiment.

Lobularia maritima (L.) Desv. 1815 (alyssum) seeds were planted in 7 × 7 × 6.5 cm pots and placed in a growth chamber (25 ± 1 °C, 65 ± 5% RH, and 14:10 L:D). After 20 days, they were transferred to the greenhouse. They were watered and acclimatized for 7 days before being transplanted to larger plastic pots (diameter 10 cm, height 9 cm). The plants had all reached the flowering stage before their use in the experiment.

Orius laevigatus colony originated from Biobest, France, and was reared in plexiglass cages and fed with *E. kuehniella* eggs on strawberry and alyssum plants. The rearing cages were kept in growth chambers (25 ± 1 °C, 65 ± 5% RH, and 14:10 L:D). The *M. euphorbiae* colony was initiated using individuals naturally infecting tomato plants in the INRAE Sophia Antipolis experimental station. The aphid colony was reared on tomato plants in greenhouse cages covered with mesh. *E. kuehniella* eggs used as alternative prey were refrigerated at 8–10 °C for conservation.

Experimental design

Experiments were conducted in an environment-controlled greenhouse (T=25 °C and RH=60%) at INRAE Sophia Antipolis experimental station in Spring 2021. The experimental design was a randomized block design within four compartments comprising four treatments in each compartment (Fig. 1; Suppl. 1). Each of the four distinct compartments in the greenhouse was 40 m^2. Treatments in a given compartment were isolated from one another by fine mesh nylon, which formed tunnels (height: 2 m, width: 1 m, length: 5 m) and prevented insect transfer (Jaworski et al. 2015; Campos et al. 2020). Each tunnel contained one row (4.84 m long and 30 cm wide for one row) on which all the potted plants were placed about 20 cm from the soil (Suppl. 1).

The four treatments (A–control; B–alyssum; C–*Ephestia* eggs and D–alyssum + *Ephestia* eggs) were arranged in a randomized complete block design and repeated once in each compartment (*n* = 4; Fig. 1). The strawberry plants were selected to obtain the same number of flowers in each treatment. Treatments without alyssum had 16 strawberry plants with 30 cm between plants, while treatments with alyssum had 16 strawberry plants and 8 alyssums, i.e., one alyssum between 2 strawberry plants. The spacing between strawberry and alyssum plants was 15 cm as recommended by Brennan (2016). *Ephestia* eggs (1 g/plant) were introduced once a week through sprinkling by hand over strawberry leaves on treatments containing *Ephestia* eggs.

The predator *O. laevigatus* and the aphid *M. euphorbiae* were introduced in all treatments. Before inoculation, aphid

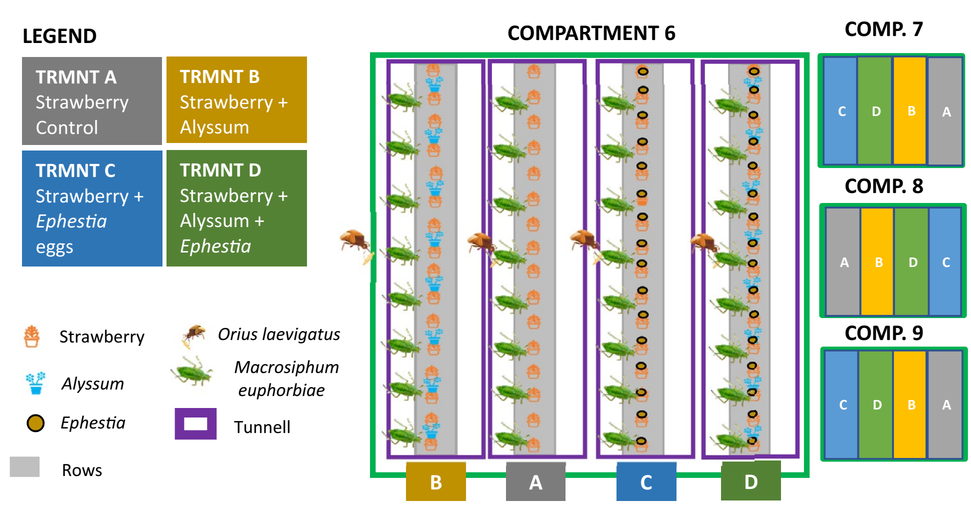

Fig. 1 Greenhouse experimental setup

individuals were collected from the colony on fresh tomato leaves. Then, 5 randomly selected individuals were placed in every second strawberry plant throughout the four treatments in all compartments (Fig. 1). Aphids were released 1 week before predators. Four *O. laevigatus* adults (1 male for 3 females) were released 3 times (once a week for the first three weeks) in each replicate for all the treatments in the middle of each row to ensure a homogeneous distribution.

Data recording

Population dynamic of both insect species (*O. laevigatus* and *M. euphorbiae*) was monitored weekly during 8 weeks following the first release of predators. The number of individuals was counted in the morning (7:00 to 10:00 a.m.) on each replicate. For each counting, numbers of *O. laevigatus* (adults and nymphs), and *M. euphorbiae* (adults and nymphs) per plant (both strawberry and alyssum) were assessed in situ by examining the stems, leaves, and flowers of plants. In addition, strawberry flowers were examined in situ for *O. laevigatus* nymphs, particularly between the receptacle and the calyx. The number of fruits per strawberry plant was also recorded and used as a proxy for strawberry yield at the end of the experiment.

Statistical analysis

In order to compare the effect of our four treatments on the population dynamic of both the predators and pests, we completed a generalized estimating equation (GEE, package "geepack") and a Poisson distributed response. The GEE was used to account for the effect of time and data interdependence, as well as the option of including the plant's identity number in the formula to specify the presence of autocorrelation on the data over time. When significant effects were found, the Least Square Means ("lsmeans") R package was used to perform Tukey's HSD tests for post hoc pairwise comparisons. This model enabled us to compare the tendency of the complete temporal set of data between treatments.

The effect of treatments on fruit mean number per treatment was evaluated using ANOVA, associated with the Tukey's HSD tests for post hoc pairwise comparisons.

All statistical analyses were performed using version 3.4.2 of the R software program (R core Team, 2013).

Results

Impact of treatments on predator population dynamics

The average number of *O. laevigatus* (nymphs and adults) per plant varied over time and according to the treatments applied (Table 1, Fig. 2). The evolution of the number of predators (nymphs and adults) was almost stable until day 28 before increasing exponentially for the treatments in which alyssum and/or *E. kuehniella* eggs were included except for the control treatment where the population remained very low (less than 0.5 individuals/plant) from the beginning to the end of the experiment. The presence of alyssum alone and its association with the addition of the eggs seemed to influence the fluctuation of the predator population in a similar way. The number of nymphs was higher when eggs were provided as alternative prey on strawberry plants from day 42.

Impact of treatments on pest population dynamics

Both treatment and time (and their interaction) have effects on the number of *M. euphorbiae* individual per plant (Table 1, Fig. 3). The presence of companion plant (alyssum) and alternative prey (*E. kuehniella* eggs) significantly decrease the number of pest individuals per plant. Without alyssum and *E. kuehniella* eggs (control treatment), this number increased rapidly from less than 1 individual/plant to more than 7 individuals/plant. The impact of *E. kuehniella* eggs on *M. euphorbiae* population was observed only from day 21, with a significant and rapid decrease in *M. euphorbiae* populations until day 56. On the other hand, in the presence of alyssum (with or without eggs), *M. euphorbiae* numbers remained consistently low (<2 individuals/plant).

Impact of treatments on fruit production

The average number of fruits produced per plant was influenced by the various treatments applied, i.e., the presence or not of alyssum, the presence or not of *E. kuehniella* eggs, or the simultaneous presence of both (alyssum + *E. kuehniella* eggs) (Fig. 4). Analysis of variance indicated significant differences between the number of fruits obtained per plant according to treatments ($df = 3$, $F = 150$, $P < 0.001$). The highest number was obtained when alyssum was associated with the alternative prey, followed, respectively, by the treatments with the presence of alyssum and *E. kuehniella* eggs only, and the lowest number of fruits was obtained in the control treatment.

Table 1 Number of *Orius laevigatus* adults and nymphs, as well as *Macrosiphum euphorbiae (adults + nymphs),* per plant (means and SE), according to the treatments and the times (days) as well as all the pairwise interaction (a - GEE: generalized estimating equation, b - Tukey's HSD post hoc test). For a given group (i.e. *O. laevigatus* nymphs, *O. laevigatus* adults, and *M. euphorbiae*) letters indicate significant differences among treatments and among sampling days (at P < 0.05).

(a)

Explanatory variables	Number of *Orius laevigatus* adults			Number of *Orius laevigatus* nymphs			Number of *Macrosiphum euphorbiae*		
	df	χ^2	*P* value	df	χ^2	*P* value	df	χ^2	*P* value
Treatment	3	153	**< 0.001**	3	103	**< 0.001**	3	269.8	**< 0.001**
Time	7	1335	**< 0.001**	7	909	**< 0.001**	7	6.3	**0.012**
Treatment: Time	3	8	**0.049**	3	9	**0.034**	3	74.1	**< 0.001**

(b)

Species	Days	Nb of individuals per plant			
		Strawberry	Strawberry + Alyssum	Strawberry + *Ephestia*	Strawberry + Alyssum + *Ephestia* eggs
Orius laevigatus (nymphs)	7	0.00 ± 0.00 d	0.00 ± 0.00 d	0.00 ± 0.00 d	0.00 ± 0.00 d
	14	0.00 ± 0.00 d	0.00 ± 0.00 d	0.00 ± 0.00 d	0.00 ± 0.00 d
	21	0.03 ± 0.03 d	0.03 ± 0.03 d	0.06 ± 0.04 d	0.13 ± 0.06 d
	28	0.02 ± 0.02 d	0.13 ± 0.06 d	0.11 ± 0.05 d	0.13 ± 0.04 d
	35	0.00 ± 0.00 d	0.14 ± 0.04 d	0.45 ± 0.11 cd	0.23 ± 0.08 d
	42	0.02 ± 0.02 d	0.58 ± 0.16 cd	2.58 ± 0.35 ab	1.02 ± 0.15 c
	49	0.39 ± 0.14 cd	2.15 ± 0.30 b	2.53 ± 0.35 ab	2.30 ± 0.30 b
	56	0.17 ± 0.04 cd	2.23 ± 0.22 b	3.19 ± 0.31 a	3.13 ± 0.31 a
Orius laevigatus (adults)	7	0.00 ± 0.00 g	0.00 ± 0.00 g	0.00 ± 0.00 g	0.00 ± 0.00 g
	14	0.08 ± 0.04 g	0.06 ± 0.03 g	0.11 ± 0.05 g	0.10 ± 0.03 g
	21	0.14 ± 0.06 g	0.17 ± 0.53 g	0.25 ± 0.12 g	0.18 ± 0.06 g
	28	0.11 ± 0.04 g	0.45 ± 0.09 fg	0.38 ± 0.08 fg	0.59 ± 0.09 fg
	35	0.20 ± 0.08 g	0.69 ± 0.12 efg	1.44 ± 0.18 def	1.39 ± 0.18 def
	42	0.20 ± 0.78 g	1.57 ± 0.19 de	1.72 ± 0.24 de	1.69 ± 0.22 d
	49	0.67 ± 0.17 defg	3.09 ± 0.30 bc	4.72 ± 0.53 a	3.26 ± 0.39 bc
	56	0.45 ± 0.13 fg	2.80 ± 0.26 c	4.03 ± 0.35 ab	3.54 ± 0.32 bc
Macrosiphum euphorbiae	7	0.00 ± 0.00 g	0.00 ± 0.00 g	0.00 ± 0.00 g	0.00 ± 0.00 g
	14	3.11 ± 0.71 def	1.05 ± 0.33 fg	2.63 ± 0.63defg	1.29 ± 0.51 fg
	21	5.02 ± 0.83 bcd	1.75 ± 0.51 fg	6.05 ± 1.06 abc	1.56 ± 0.45 fg
	28	5.00 ± 0.85 bcd	1.83 ± 0.40 efg	5.00 ± 0.83 bcd	1.34 ± 0.33 fg
	35	7.33 ± 0.92 ab	1.45 ± 0.34 fg	4.44 ± 0.71 cde	1.28 ± 0.29 fg
	42	7.92 ± 1.08 a	1.89 ± 0.37 efg	1.91 ± 0.42 efg	0.71 ± 0.22 fg
	49	5.09 ± 0.49 abcd	0.03 ± 0.03 g	0.09 ± 0.07 g	0.04 ± 0.03 g
	56	7.32 ± 1.04 ab	0.08 ± 0.04 g	1.06 ± 0.34f g	0.08 ± 0.05 g

Discussion

Our study evaluated the importance of providing additional and diversified food sources for the establishment of the predator *O. laevigatus* population using alternative prey and/or companion plants to control population of *M. euphorbiae*.

O. laevigatus population was not able to establish on strawberry alone (control); such low level observed could be explained by the fact that the presence of prey (aphids) only on strawberry is not qualitatively and/or quantitatively sufficient to allow the predator establishment and growth (Desneux et al. 2019). This could also be due to this species' difficulty or slowness in establishing and multiplying on strawberry. Indeed, Bennison et al. (2011) asserted that *O. laevigatus* established slowly on strawberry, especially when flowers are scarce. Regarding *M. euphorbiae* (aphid) population dynamic in the control treatment, the rapid and continuous increase in aphid number per plant could be related to the low number of predators in this treatment. Indeed, the establishment and very slow growth of predators

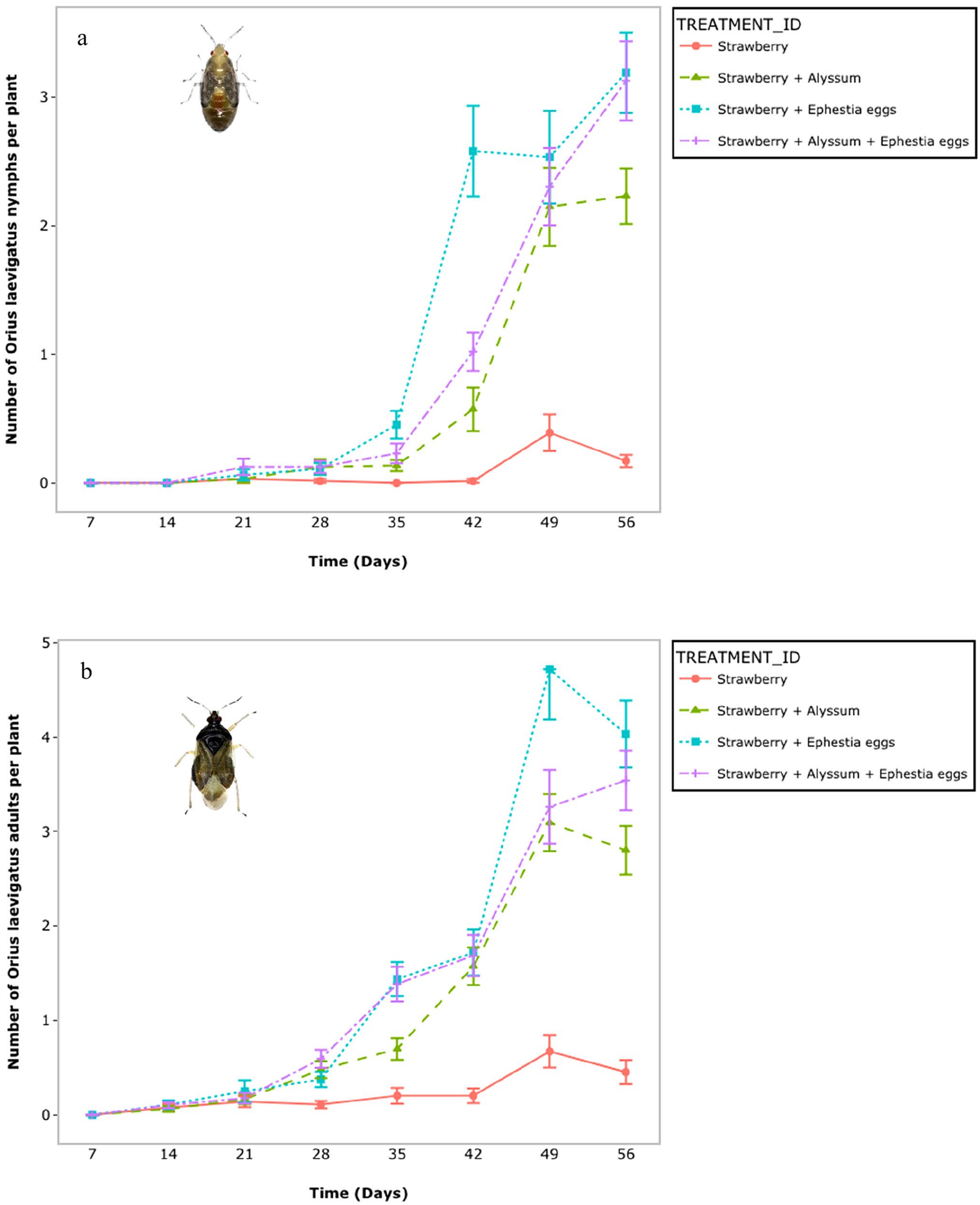

Fig. 2 Evolution of *O. laevigatus* nymphs (**a**) and adults (**b**) populations (means and SE) according to the treatments and the times (days)

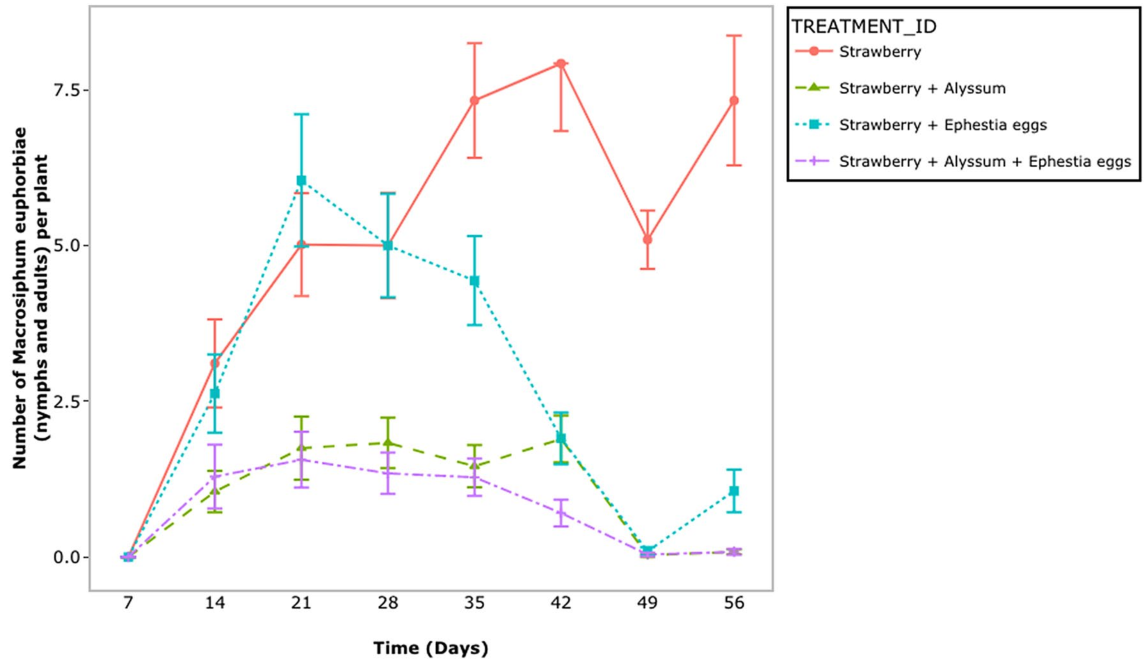

Fig. 3 Evolution of *M. euphorbiae* (adults + nymphs; mean ± SE) population according to the treatments and the time (days)

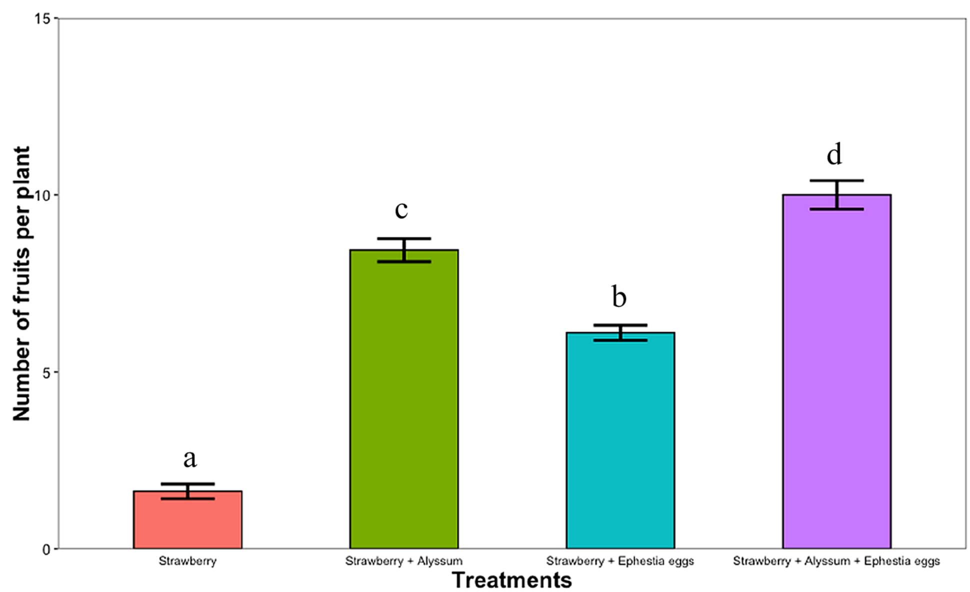

Fig. 4 The average number of fruits per strawberry plant (mean ± SE) according to the treatments. Different letters indicate significant difference at $P < 0.05$ (ANOVA followed by Tukey's HSD post hoc test)

on strawberry in the absence of alyssum and *E. kuehniella* eggs could favor the development of aphid populations. Finally, our study's evolution of the number of fruits per plant was inversely related to the number of aphids. When there are more aphids per plant, there are fewer fruits per plant. This result is in line with Paranjpe et al. (2003) where the cultivar with the highest number of fruits showed the lowest number of aphids. Indeed, aphids are known to affect crop yield through the transmission of viruses and/or by sucking out plant sap (Rabasse et al. 2001; Martin and Tzanetakis 2006). However, it should be noted that the conditions for fruit development are not optimal in this experimental design because the strawberry plants were inserted in tunnels closed off by insect-proof nets preventing the monitored insects from getting out but also the external insects, thus the pollinators, from getting in.

The supplementation with *Ephestia* eggs (Strawberry + *Ephestia* eggs) increased fecundity and established the highest *O. laevigatus* population which is in line with a previous laboratory experiment, where we reported an increased number of *O. laevigatus* nymphs on strawberry supplemented with *Ephestia* eggs (Suppl. 2). Pumarino and Alomar (2012) also observed a strong positive effect of *Ephestia* eggs input to another *Orius* species in laboratory conditions. Providing diets of only plant parts to omnivorous predators is insufficient to maintain a good fitness and the presence of a prey (targeted pest or others) is a necessity for predator fecundity (Vacante et al. 1997; Cocuzza et al. 1997; Pumariño and Alomar 2012; Suppl. 2). *Ephestia* eggs are also successfully used for mass rearing of *O. laevigatus* as they have been shown to be nutritionally superior to other natural and artificial foods increasing longevity, especially for the genus *Orius* (Cocuzza et al. 1997; Pehlïvan 2021; Gallego et al. 2022). Specty et al. (2003) also showed that the predator *Harmonia axyridis* had a good developmental capacity when fed with *E. kuehniella* eggs than with aphids as prey but Sylla et al. (2016) showed equivalent effect of both *Ephestia* and aphid prey on several traits (including fertility) of the mirid predator *Macrolophus pygmaeus*. On the other hand, the number of aphids in the presence of *E. kuehniella* eggs dropped later, compared to the control treatment, probably due to the preference of predators to feed first on *E. kuehniella* eggs which is a better food source (Pehlïvan 2021) before attacking aphids. In a similar experiment on pepper plants, Messelink et al. (2015) also showed that the most efficient control of the aphid population was achieved with *Macrolophus pygmaeus* as predator in combination with a weekly application of supplemental food including *E. kuehniella* eggs.

Alyssum could be considered a companion plant of choice in maintaining and growing *O. laevigatus* populations because it flowers prolifically and continuously provides pollen and nectar for predators, then *O. laevigatus* could reproduce, even without prey (Bennison et al. 2011; Ribeiro and Gontijo 2017). Alyssum might provide resource subsidies during times of prey scarcity as omnivorous predators may profit from a combination of plant components (particularly pollen; Vacante et al. 1997; Pumariño and Alomar 2012). Furthermore, the reduction of pests over time in the presence of alyssum only or alyssum + *E. kuehniella* eggs would thus be explained by the negative impact of predator population growth on their growth. In other words, the more *O. laevigatus* multiplies, the less the number of aphids increases. In effect, once established on alyssum, predators would then disperse on strawberry plants to attack the pests reducing the number of pests, as Bennison et al. (2011) observed in their study on western flower thrips.

A synergistic impact of multiple resources on the population dynamics of predatory mites for better pest control has been demonstrated in citrus (Pekas and Wäckers 2017). In the present study, we expected the treatment [strawberry + alyssum + *Ephestia* eggs] would provide a more well-balanced and nutrient-rich diet to support *Orius* populations, as suggested by Vacante et al. (1997) or Pumarino and Alomar (2012) results in laboratory conditions. In addition to benefit from the presence of prey (aphids and/or *E. kuehniella* eggs), predators also benefit from the presence of pollen from strawberry and alyssum flowers. However the presence of multiple resources was not synergistic even so additive in establishing *Orius* population when compared to the treatment with alyssum only. Also, as the number of offspring is limited by the initial number of individuals introduced, it is possible that synergistic and/or additional effects of nutrient resources cannot be observed in our conditions. Then to confirm the absence/presence of a synergistic effect, we should redo the experiments by testing higher initial predator density. Interestingly, the highest fruit number was reached in the treatment [strawberry + alyssum + *Ephestia* eggs] suggesting that pest control could improve strawberry yield, even though this experiment does not demonstrate the effects of aphids on fruit quality (Van Oystaeyen et al. 2022). Indeed, the increase in *O. laevigatus* populations due to alyssum and *E. kuehniella* eggs would have reduced aphid damages on strawberry plants by reducing their populations.

The establishment of *O. laevigatus* populations appears to be a critical factor in their practical use as a biological control agent in strawberry crops. The use of alternative prey and/or companion plant in IPM is being increasingly studied (Letourneau et al. 2011; Biondi et al. 2016; Konan et al. 2021). Moreover, our study provided evidence of the beneficial effects of their use on *O. laevigatus* and the biological control of *M. euphorbiae*. Thus, alyssum plants used alone or combined with *E. kuehniella* eggs-maintained predator populations and reduced *M. euphorbiae* damage on strawberry plants. These resources, besides providing quality food sources, did not interfere with the control of *M. euphorbiae* by *O. laevigatus* and could therefore be considered essential elements in implementing IPM systems for strawberry. Furthermore, the use of alyssum could provide an additional service to the agrosystem, by also attracting pollinators and thus promoting the pollination of strawberry plants (Hodgkiss et al. 2019). With the establishment of the predator population achieved, it is now necessary to question the possibility of maintaining the predator in the system, especially after the collapse of the pest population (Symondson et al. 2002; Messelink et al. 2014). Are these proposed alternative feeds sufficient to maintain the predator population, even in the complete absence of prey?

Author contributions

MZ, CN, AVL, and ND conceived and designed research. MZ, CN, KAJKL, EAD, and PB carried out the experiments.

MZ and AVL analyzed data. MZ, CN and AVL wrote the manuscript. All authors reviewed the manuscript.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10340-022-01570-9.

Acknowledgements We thank the project Hab'Alim (Casdar) and Campus France for funding.

Funding This work was funded by a CASDAR grant (project Hab'Alim, grant number: 19AIP5901).

Declarations

Competing interests All authors declare that they have no conflict of interest. Author ND is Editor-in-Chief of Journal of Pest Science and was not involved in the review process and decisions related to this manuscript.

Consent for publication All authors approved submission.

Ethics approval and consent to participate Not applicable.

References

Aaby K, Remberg SF (2015) Chapter 19 – Strawberry phenolics and impact of ripening. In: By Preedy V (ed) Processing and impact on active components in food. Academic Press, San Diego, pp 157–164

Begum M, Gurr GM, Wratten SD, Hedberg PR, Nicol HI (2006) Using selective food plants to maximize biological control of vineyard pests. J Appl Ecol 43:547–554. https://doi.org/10.1111/j.1365-2664.2006.01168.x

Bennison J, Pope T, Maulden K (2011) The potential use of flowering alyssum as a "banker" plant to support the establishment of *Orius laevigatus* in ever bearer strawberry for improved biological control of western flower thrips. IOBCWPRS Bull 68:15–18

Berndt LA, Wratten SD (2005) Effects of alyssum flowers on the longevity, fecundity, and sex ratio of the leafroller parasitoid *Dolichogenidea tasmanica*. Biol Control 32:65–69. https://doi.org/10.1016/j.biocontrol.2004.07.014

Biondi A, Zappalà L, Di Mauro A et al (2016) Can alternative host plant and prey affect phytophagy and biological control by the zoophytophagous mirid *Nesidiocoris tenuis*? Biocontrol 61:79–90. https://doi.org/10.1007/s10526-015-9700-5

Bonte M, De Clercq P (2008) Developmental and reproductive fitness of *Orius laevigatus* (Hemiptera: Anthocoridae) reared on factitious and artificial diets. J Econ Entomol 101(4):1127–1133. https://doi.org/10.1093/jee/101.4.1127

Bonte M, De Clercq P (2011) Influence of predator density, diet and living substrate on developmental fitness of *Orius laevigatus*. J Appl Entomol 135(5):343–350. https://doi.org/10.1111/j.1439-0418.2010.01554.x

Bouagga S, Urbaneja A, Rambla JL, Granell A, Pérez-Hedo M (2018) *Orius laevigatus* strengthens its role as a biological control agent by inducing plant defenses. J Pest Sci 91:55–64. https://doi.org/10.1007/s10340-017-0886-4

Brennan EB (2016) Agronomy of strip intercropping broccoli with alyssum for biological control of aphids. Biol Control 97:109–119. https://doi.org/10.1016/j.biocontrol.2016.02.015

Campos MR, Monticelli LS, Bearez P, Amiens-Desneux E, Wang YS et al (2020) Impact of a shared sugar food source on biological control of Tuta absoluta by the parasitoid Necremnus tutae. J Pest Sci 93:207–218

Chen X, Jaworski CC, Dai H, Liang YY, Guo XJ, Wang S, Zang LS, Desneux N (2022) Combining banker plants to achieve long-term pest control in multi-pest and multi-natural enemy cropping systems. J Pest Sci 95:685–697. https://doi.org/10.1007/s10340-021-01428-6

Cocuzza GE, Clercq PD, de Veire MV, Cock AD, Degheele D, Vacante V (1997) Reproduction of *Orius laevigatus* and *Orius albidipennis* on pollen and *Ephestia kuehniella* eggs. Entomol Exp Appl 82:101–104. https://doi.org/10.1046/j.1570-7458.1997.00118.x

Collier T, Van Steenwyk R (2004) A critical evaluation of augmentative biological control. Biol Control 31(2):245–256. https://doi.org/10.1016/j.biocontrol.2004.05.001

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? Entomol Gen 40:147–156. https://doi.org/10.1127/entomologia/2020/0906

Desneux N, Decourtye A, Delpuech JM (2007) The sublethal effects of pesticides on beneficial arthropods. Annu Rev Entomol 52:81–106. https://doi.org/10.1146/annurev.ento.52.110405.091440

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. Entomol Gen 39:127–136. https://doi.org/10.1127/entomologia/2019/0824

Desneux N, Han P, Mansour R et al (2022) Integrated pest management of *Tuta absoluta*: practical implementations across different world regions. J Pest Sci 95:17–39. https://doi.org/10.1007/s10340-021-01442-8

Frank SD (2010) Biological control of arthropod pests using banker plant systems: past progress and future directions. Biol Control 52:8–16. https://doi.org/10.1016/j.biocontrol.2009.09.011

Gallego FJ, Rodríguez-Gómez A, del Reche MC, Balanza V, Bielza P (2022) Effect of the amount of *Ephestia kuehniella* eggs for rearing on development, survival, and reproduction of *Orius laevigatus*. Insects 13:250. https://doi.org/10.3390/insects13030250

Goulson D (2019) The insect apocalypse, and why it matters. Curr Biol 29(19):R967–R971. https://doi.org/10.1016/j.cub.2019.06.069

Gurr G, Wratten S, Landis D, You M (2016) Habitat management to suppress pest populations: progress and prospects. Annu Rev Entomol. https://doi.org/10.1146/annurev-ento-031616-035050

Han P, Lavoir AV, Rodriguez-Saona C, Desneux N (2022) Bottom-up forces in agroecosystems and their potential impact on arthropod pest management. Ann Rev Entomol 67:239–259. https://doi.org/10.1146/annurev-ento-060121-060505

Heimpel GE, Mills N (2017) Biological control: ecology and applications. Cambridge University Press, Cambridge, UK

Hernández-Herrero MM, Roig-Sagués AX, López-Sabater EI, Rodríguez-Jerez JJ, Mora-Ventura MT (1999) Influence of storage temperature on the quality of beef liver; pH as a reliable indicator of beef liver spoilage. J Sci Food Agric 79:2035–2039. https://doi.org/10.1002/(SICI)1097-0010(199911)79:14%3c2035::AID-JSFA481%3e3.0.CO;2-I

Hodgkiss D, Brown MJ, Fountain MT (2019) The effect of within-crop floral resources on pollination, aphid control and fruit quality in commercial strawberry. Agr Ecosyst Environ 275:112–122. https://doi.org/10.1016/j.agee.2019.02.006

Hogg BN, Bugg RL, Daane KM (2011) Attractiveness of common insectary and harvestable floral resources to beneficial insects. Biol Control 56:76–84. https://doi.org/10.1016/j.biocontrol.2010.09.007

Huang N, Enkegaard A, Osborne L, Ramakers P, Messelink G, Pijnakker J et al (2011) The Banker Plant Method in biological control.

Crit Rev Plant Sci 30:259–278. https://doi.org/10.1080/07352689.2011.572055
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. Entomol Gen 40:331–335. https://doi.org/10.1127/entomologia/2020/0994
Hulle M, Chaubet B, Turpeau E, Simon JC (2020) Encyclop'Aphid : a website on aphids and their natural enemies. Entomol Gen 40:97–101. https://doi.org/10.1127/entomologia/2019/0867
Jaworski CC, Chailleux A, Bearez P et al (2015) Apparent competition between major pests reduces pest population densities on tomato crop, but not yield loss. J Pest Sci 88:793–803. https://doi.org/10.1007/s10340-015-0698-3
Konan KAJ, Monticelli LS, Ouali-N'goran S-WM et al (2021) Combination of generalist predators, *Nesidiocoris tenuis* and *Macrolophus pygmaeus*, with a companion plant, Sesamum indicum: What benefit for biological control of *Tuta absoluta*? PLoS ONE 16:e0257925. https://doi.org/10.1371/journal.pone.0257925
Labbé RM, Gagnier D, Kostic A, Shipp L (2018) The function of supplemental foods for improved crop establishment of generalist predators *Orius insidiosus* and *Dicyphus esperus*. Sci Rep 8:17790. https://doi.org/10.1038/s41598-018-36100-0
Letourneau DK, Armbrecht I, Rivera BS, Lerma JM, Carmona EJ, Daza MC et al (2011) Does plant diversity benefit agroecosystems? A Synthetic Review. Ecol Appl 21:9–21. https://doi.org/10.1890/09-2026.1
Li S, Jaworski CC, Hatt S, Zhang F, Desneux N, Wang S (2021) Flower strips adjacent to greenhouses help reduce pest populations and insecticide applications inside organic commercial greenhouses. J Pest Sci 94:679–689. https://doi.org/10.1007/s10340-020-01285-9
Lu YH, Wu KM, Jiang YY, Guo YY, Desneux N (2012) Widespread adoption of Bt cotton and insecticide decrease promotes biocontrol services. Nature 487:362–365. https://doi.org/10.1038/nature11153
Lu ZX, Zhu PY, Gurr GM, Zheng XS, Read DMY, Heong KL, Yang YJ, Xu HX (2014) Mechanisms for flowering plants to benefit arthropod natural enemies of insect pests: prospects for enhanced use in agriculture. Insect Sci 21:1–12. https://doi.org/10.1111/1744-7917.12000
Lundgren JG, Wyckhuys KAG, Desneux N (2009) Population responses by *Orius insidiosus* to vegetational diversity. Biocontrol 54:135–142. https://doi.org/10.1007/s10526-008-9165-x
Martin RR, Tzanetakis IE (2006) Characterization and recent advances in detection of strawberry viruses. Plant Dis 90(4):384–396. https://doi.org/10.1094/PD-90-0384
Menail AH, Boutefnouchet-Bouchema WF, Haddad N et al (2020) Effects of thiamethoxam and spinosad on the survival and hypopharyngeal glands of the African honey bee (*Apis mellifera intermissa*). Entomol Gen 40:207–215. https://doi.org/10.1127/entomologia/2020/0796
Messelink GJ, Bennison J, Alomar O, Ingegno BL, Tavella L, Shipp L, Palevsky E, Wackers FL (2014) Approaches to conserving natural enemy populations in greenhouse crops: current methods and future prospects. Biocontrol 59:377–393. https://doi.org/10.1007/s10526-014-9579-6
Messelink GJ, Bloemhard CMJ, Hoogerbrugge H, Van Schelt J, Ingegno BL, Tavella L (2015) Evaluation of mirid predatory bugs and release strategy for aphid control in sweet pepper. J Appl Entomol 139(5):333–341. https://doi.org/10.1111/jen.12170
Michaud JP (2018) Challenges to conservation biological control on the High Plains: 150 years of evolutionary rescue. Biol Control 125:65–73. https://doi.org/10.1016/j.biocontrol.2018.07.001
Oveja MF, Riudavets J, Arnó J, Gabarra R (2016) Does a supplemental food improve the effectiveness of predatory bugs on cucumber? Bio Control 61:47–56. https://doi.org/10.1007/s10526-015-9690-3
Palma-Onetto V, Oliva D, Gonzalez-Teuber M (2021) Lethal and oxidative stress side effects of organic and synthetic pesticides on the insect scale predator *Rhyzobius lophanthae*. Entomol Gen 41:345–355. https://doi.org/10.1127/entomologia/2021/1045
Paranjpe AV, Cantliffe DJ, Rondon SILVIA, Chandler CK, Brecht J et al (2003) Trends in fruit yield and quality, susceptibility to powdery mildew (*Sphaerotheca macularis*), and aphid (*Aphis gossypii*) infestation for seven strawberry cultivars grown without pesticides in a passively ventilated greenhouse using pine bark as soilless substrate. In Proc Fla State Hort Soc, vol 116, pp 740–755
Parker JE, Snyder WE, Hamilton GC, Rodriguez-Saona C (2013) Companion planting and insect pest control. Weed Pest Control-Conv New Chall 10:55044. https://doi.org/10.5772/55044
Parolin P, Bresch C, Desneux N, Brun R, Bout A, Boll R, Poncet C (2012a) Secondary plants used in biological control: a review. Int J Pest Manag 58:91–100. https://doi.org/10.1080/09670874.2012.659229
Parolin P, Bresch C, Poncet C, Desneux N (2012b) Functional characteristics of secondary plants for increased pest management. Int J Pest Manag 58:369–377. https://doi.org/10.1080/09670874.2012.734869
Pascacio-Villafán C, Birke A, Williams T, Aluja M (2017) Modeling the cost-effectiveness of insect rearing on artificial diets: a test with a tephritid fly used in the sterile insect technique. PLoS ONE 12:e0173205. https://doi.org/10.1371/journal.pone.0173205
Passos LC, Ricupero M, Gugliuzzo A, Soares MA, Desneux N, Carvalho GA, Biondi A (2022) Does the dose make the poison? Neurotoxic insecticides impair predator orientation and reproduction even at low concentrations. Pest Manag Sci 78(4):1698–1706. https://doi.org/10.1002/ps.6789
Pehlivan S (2021) Influence of the eggs of Ephestia kuehniella (Lepidoptera: Pyralidae) reared on different diets on the performance of the predatory bug *Orius laevigatus* (Hemiptera: Anthocoridae). EJE 118:51–56. https://doi.org/10.14411/eje.2021.006
Pekas A, Wäckers FL (2017) Multiple resource supplements synergistically enhance predatory mite populations. Oecologia 184:479–484. https://doi.org/10.1007/s00442-017-3877-5
Perez-Alvarez R, Nault BA, Poveda K (2019) Effectiveness of augmentative biological control depends on landscape context. Sci Rep 9:8664. https://doi.org/10.1038/s41598-019-45041-1
Picó FX, Retana J (2000) Temporal variation in the female components of reproductive success over the extended flowering season of a Mediterranean perennial herb. Oikos 89:485–492. https://doi.org/10.1034/j.1600-0706.2000.890307.x
Pumariño L, Alomar O (2012) The role of omnivory in the conservation of predators: *Orius majusculus* (Heteroptera: Anthocoridae) on sweet alyssum. Biol Control 62(1):24–28. https://doi.org/10.1016/j.biocontrol.2012.03.007
Rabasse JM, Trouve C, Geria A, Quignou A (2001) Aphid pests of strawberry crops and their parasitoids in France. Meded Rijksuniv Gent Fak Landbouwkd Toegep Biol Wet 66(2a):293–301
Ramsden MW, Menendez R, Leather SR, Wäckers F (2015) Optimizing field margins for biocontrol services: the relative role of aphid abundance, annual floral resources, and overwinter habitat in enhancing aphid natural enemies. Agric Ecosyst Environ 199:94–104. https://doi.org/10.1016/j.agee.2014.08.024
Ragsdale DW, Landis DA, Brodeur J, Heimpel GE, Desneux N (2011) Ecology and management of the soybean aphid in North America. Annu Rev Entomol 56:375–399. https://doi.org/10.1146/annurev-ento-120709-144755
R core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical computing, Vienna, Austria. URL http://www.R-project.org/

Ribeiro AL, Gontijo LM (2017) Alyssum flowers promote biological control of collard pests. Bio Control 62:185–196. https://doi.org/10.1007/s10526-016-9783-7

Riddick EW (2009) Benefits and limitations of factitious prey and artificial diets on life parameters of predatory beetles, bugs, and lacewings: a mini-review. Biocontrol 54(3):325–339. https://doi.org/10.1007/s10526-008-9171-z

Solomon MG, Jay CN, Innocenzi PJ, Fitzgerald JD, Crook D, Crook AM et al (2001) Review: natural enemies and biocontrol of pests of strawberry in Northern and Central Europe. Biocontrol Sci Technol 11:165–216. https://doi.org/10.1080/09583150120035639

Specty O, Febvay G, Grenier S, Delobel B, Piotte C, Pageaux JF, Ferran A, Guillaud J (2003) Nutritional plasticity of the predatory ladybeetle *Harmonia axyridis* (Coleoptera: Coccinellidae): comparison between natural and substitution prey. Archiv Insect Biochem Physiol: Publ Collab Entomol Soc Am 52(2):81–91. https://doi.org/10.1002/arch.10070

St-Onge M, Cormier D, Todorova S, Lucas É (2014) Comparison of Ephestia kuehniella eggs sterilization methods for Trichogramma rearing. Biol Control 70:73–77. https://doi.org/10.1002/arch.10070

Sylla S, Brévault T, Diarra K, Bearez P, Desneux N (2016) Life-history traits of *Macrolophus pygmaeus* with different prey foods. PLoS ONE 11(11):e0166610. https://doi.org/10.1371/journal.pone.0166610

Symondson WOC, Sunderland KD, Greenstone MH (2002) Can generalist predators be effective biocontrol agents? Annu Rev Entomol 47:561–594. https://doi.org/10.1146/annurev.ento.47.091201.145240

Tiwari S, Sharma S, Wratten SD (2020) Flowering alyssum (Lobularia maritima) promote arthropod diversity and biological control of *Myzus persicae*. J Asia-Pac Entomol 23(3):634–640. https://doi.org/10.1016/j.aspen.2020.05.002

Vacante V, Cocuzza GE, De Clercq P, Van De Veire M, Tirry L (1997) Development and survival of *Orius albidipennis* and *O. laevigatus* (He.: Anthocoridae) on various diets. Entomophaga 42(4):493–498. https://doi.org/10.1007/BF02769809

Van Oystaeyen A, Tuyttens E, Boonen S et al (2022) Dual purpose: predatory hoverflies pollinate strawberry crops and protect them against the strawberry aphid, *Chaetospihon fragaefolii*. Pest Manag Sci 78:3051–3060. https://doi.org/10.1002/ps.6931

Venzon M, Janssen A, Sabelis MW (2002) Prey preference and reproductive success of the generalist predator *Orius laevigatus*. Oikos 97:116–124. https://doi.org/10.1034/j.1600-0706.2002.970112.x

Wäckers FL, Van Rijn PC (2012) Pick and mix: selecting flowering plants to meet the requirements of target biological control insects. Biodiv Insect Pests: Key Issues Sustain Manag 9:139–165. https://doi.org/10.1002/9781118231838.ch9

Zang LS, Wang S, Zhang F, Desneux N (2021) Biological control with Trichogramma in China: history, present status, and perspectives. Annu Rev Entomol 66:463–484. https://doi.org/10.1146/annurev-ento-060120-091620

Zhang X, Wang HC, Du WM, Zang LS, Ruan CC, Zhang JJ et al (2021) Multiparasitism: a promising approach to simultaneously produce *Trichogramma chilonis* and *T. dendrolimi* on eggs of *Antheraea pernyi*. Entomol Gen 41:627–636. https://doi.org/10.1127/entomologia/2021/1360

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.