




Article

Complex Habitats Boost Predator Co-Occurrence, Enhancing Pest Control in Sweet Pepper Greenhouses

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Abstract: Sweet pepper is a crop that benefits from phytosanitary treatments with low environmental impact, especially the successful control of pests through the introduction of biological control agents in greenhouses. However, predators that naturally occur in these surroundings often enter greenhouses. The precise roles of these natural predators and their interactions with the introduced predatory insects and mites are often unknown. This study investigated the relationships between *Nesidiocoris tenuis*, which is naturally present, and *Amblyseius swirskii* and *Orius laevigatus*, which are two species of generalist predators released for the control of multiple pests. This study was conducted for two years on 13 commercial sweet pepper crops in various types of greenhouses (tunnels and traditional greenhouses) in Sicily. The environmental complexity value (ECV) for each site was estimated based on 18 points detected around the site according to the different habitats that occurred at each coordinate. The results showed that the occurrence of *N. tenuis* in greenhouses, independently of their typology (tunnel or traditional greenhouse), was mainly promoted by the greater diversification of habitats immediately surrounding the pepper crops (in a circular area with a diameter of 500 mt), with an increase in its density during the crop season. Moreover, *N. tenuis*–*O. laevigatus*'s co-occurrence in flowers suggested that they were not impacted by each other's presence and that their co-occurrence had a significant effect on pest reduction, although their co-occurrence was density-dependent. As an intraguild predator, *N. tenuis* competed with *O. laevigatus* for *Frankliniella occidentalis* when many predators were present. In addition, *N. tenuis* also competed with *A. swirskii* when they both occurred in flowers at a higher density. This study highlights the importance of pepper plant flowers in promoting a higher occurrence of juvenile forms of *N. tenuis* within flowers. *Amblyseius swirskii* colonized the plants in 3 weeks, distributing itself almost uniformly over the leaves with a clear control action against not only *Bemisia tabaci* but also *F. occidentalis* when present on the flowers. Thus, this concurrent analysis of several commercial pepper sites within the same production area suggests that, even with similar pest control plans, the diverse variability in the presence of natural enemies must be considered when selecting control strategies for pepper crop pests and that *N. tenuis*, favored by complex surrounding habitats, contributes actively to pest reduction.

Keywords: *Nesidiocoris tenuis*; *Orius laevigatus*; *Amblyseius swirskii*; landscape; *Frankliniella occidentalis*; predator completion; biological control; greenhouse; tunnel; pepper



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1. Introduction

Sustainable production is a significant goal in agriculture sectors at both local and global levels [1–5]. Current control strategies are mainly oriented toward reducing inputs, such as fertilizers and pesticides, for healthier crop production with a lower environmental impact. The environmentally friendly control of insects and mites harmful to crops is a priority across all crops, and in protected environments, such as greenhouses, it has

had some success. The key pests of sweet pepper (*Capsicum annuum* L.) are the western flower thrip (WFT) *Frankliniella occidentalis* (Thysanoptera: Thripidae) and the silverleaf whitefly *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae) [6]. In addition, mites, such as *Tetranychus urticae* Koch (Acari: Tetranychidae) and *Polyphagotarsonemus latus* Banks (Acari: Tarsonemidae), and aphids are secondary pests, which can all cause direct injury as a result of sap removal and honeydew build-up, resulting in sooty mold, physiological disorders, and the transmission of plant viruses [7,8].

The management of the WFT and silverleaf whitefly in greenhouse-grown pepper crops by the inoculative release of predatory insects and mites has been successful in many countries [9]. Biotic control strategies are based on the release of generalist biocontrol agents, such as the predatory mite *Amblyseius swirskii* Athias-Henriot (Acari: Phytoseiidae) and the minute pirate bug *Orius laevigatus* Fieber (Hemiptera: Anthocoridae) [9–11]. The use of other predatory species varies, such as *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) and *Neoseiulus californicus* McGregor, 1954, for the control of *T. urticae*, as does the use of traditional approaches through phytosanitary interventions with active ingredients that safeguard useful species [12]. Particularly widespread in recent years is the use of *A. swirskii* as an efficient biological control agent for whiteflies and, secondarily, thrips and spider mites, which are economically damaging pests of ornamental plants and vegetable crops grown in greenhouses and fields worldwide. *Amblyseius swirskii* has become one of the most successful external biocontrol agents in protected agriculture since its introduction into the market in 2005 [11,13,14].

Mirid bugs (Hemiptera: Miridae) are generalist predators widely known for their predatory actions, with different successes against various pests, especially in horticultural and vegetable crops [15–19]. Several studies, under both laboratory and field conditions [15], have shown that allotropy (variation in the trophic regime) is common in different species of mirids and involves a change from a phytophagous diet to a zoophagous diet or vice versa [20]. Under particular plant host and temperature conditions [21], these characteristics result in different mirids becoming pests, with phytophagy increasing, especially at low prey densities [22,23]. Such phytophagy raises many concerns in areas of recent spread, as seen, for example, for the species *Nesidiocoris tenuis* Reuter [24], which is considered a biocontrol agent in Italy. In contrast, it is considered a major phytophagous pest in areas like the South of France [25]. This species is being studied through the aid of traps with the aim of introducing monitoring as an indication of population levels [26] or to identify alternative plant hosts to crops capable of reducing or diluting the damage caused by their phytophagy [27]. In Mediterranean environments, *N. tenuis* has wide potential for use in the biological control of Aleyrodidae in various crops [28]. This species is widespread in southern Italy and is among the most frequent in vegetable production environments. They are abundant in habitats surrounding greenhouses and are known to enter them naturally, for example, those containing sweet pepper crops. It often predominates among mirids and is reported as a biotic agent in protected growing environments for tomatoes, eggplants, peppers, and beans, among others [21,29–32]. Although *N. tenuis* in the Mediterranean is considered to be a generalist predator [17,33], it does not always exert the desired control action against herbivores. This is related to uncertainties associated with its variability in geographical occurrence and abundance, even following its augmentative release [15]. The impacts of habitat-level environmental complexity on *N. tenuis* remain largely understudied, and there is a significant gap in our understanding of the potential seasonal incursions of the species into greenhouses or other protected environments. Therefore, further research is warranted to explore these aspects comprehensively. The data obtained would also be able to provide direct indications for the possible conservation of habitats or the need to increase complexity around protected environments, such as greenhouses or tunnels, especially in conditions in which many producers suspect that the mirid *N. tenuis* can also be considered a pest for pepper crops (personal communication, September–December 2020).

In operational practice, even less is known about the competitive action of this species with other species used in biological control, such as *O. laevigatus* and *A. swirskii*. In the current study area, pepper plants have a brief period of cultivation, and the short-term effects of shared predation, such as apparent mutualism [34,35], can determine the dynamics of the pests and predators involved. Therefore, in terms of effective biological control, it is important to assess whether the effects of shared predation on pest levels are positive or negative.

Here, our primary questions were as follows: How does the complexity of the habitat surrounding greenhouses impact the distribution of *N. tenuis* and its effects on the predatory insects (*O. laevigatus*) and mites (*A. swirskii*) introduced into greenhouses? And how does the naturally co-occurring predator interact with the predatory species *O. laevigatus* and *A. swirskii*, especially in floral structures? We explored these questions in a pepper crop area where *N. tenuis* is widespread and is among the most frequent species in greenhouses and other vegetable production environments.

2. Materials and Methods

2.1. Study Systems

This study was conducted on 13 sweet pepper crops (hereafter, sites) in Sicily, southern Italy, in 2020 and 2021 (Figure 1) (latitude 38°4', longitude 15°41'). The coastal area of this study borders the Mediterranean Sea (Agrigento district), at altitudes between 10 and 50 m a.s.l. next to SiteCode: ITA040010-Natura 2000. The investigated area is of a meso- and thermo-Mediterranean xerophile type, being mainly open, short-grass annual grasslands rich in therophytes growing on oligotrophic soils on base-rich, often calcareous substrates. The average temperature in the study area (1971–2000) is ~17.4 °C, with an average rainfall of 500 mm per year (concentrated in the autumn) and a dry summer period of ~5 months [36]. This habitat consists of Mediterranean grasslands characterized by a perennial vegetation community known as Thero-Brachypodietea and Thero-Brachypodietalia: Thero-Brachypodion. Poetea bulbosae is a plant community consisting of two main associations: Astragalo-Poion bulbosae (basiphile) and Trifolio periballion (silicolous) (see details in Supplementary Data). Grasslands that have been degraded or abandoned because of fire, grazing, and agricultural activities are relatively widespread. Several study sites were located near other horticultural areas, with protected cultivation, seedlings, olive groves, and vineyards (winemaking and table grapes). In contrast, others were located in the vicinity of private buildings with gardens, and some were located close to the sea (Figure 1). Crop sites were selected to promote the independence of observations. The average distance between sites was ~1 km; thus, it was assumed that the predator presence at each site was independent of other sites.

2.2. Sites of Study and Pest Control Plans

The 13 monitored sites were of different sizes and types (Table 1). In this study, pepper crops comprised tunnels (ten sites), big tunnels (one site), and greenhouses (two sites), all formed of iron frames and plastic covers. Tunnels (Ts) or high tunnels (HTs) are a type of hemicylindrical-protected environment similar to plastic houses, from 2 m to 2.5 m in height and 3 to 5 m wide. At all sites, pepper cultivation followed melon cultivation (*Cucumis melo*) and was repeated in each site for more than 3 years during the summer-winter period. The plants (Altea F1, Seoul, and Ciccior F1 cultivated varieties) were transplanted above all in August and irrigated once or twice a week. Phytosanitary control was followed as a precaution for all phytophagous and fungi species generally present before natural enemies were introduced, and, for specific cases, particular phytosanitary treatments limited to a single group of plants or tunnels were carried out among the pepper sites monitored. For example, the control of broad mites *Polyphagotarsonemus latus* Banks (Acari: Tarsonemidae) was conducted through powdered or wettable sulfur distributed on infested and neighboring plants. Pyrimor® (Pirimicarb) was used for aphid attacks detected in the tunnels. Overall, the pesticide treatment plans and strategies were

also determined through discussion with specialists in Koppert products, including those reduced side effects toward the natural enemies introduced: www.Koppert.en (accessed on 1 September 2020). In three monitored pepper sites, pheromone traps were inserted to detect the presence of *Spodoptera littoralis* (Boisduval, 1833) (Lepidoptera: Noctuidae), the flights of which were also monitored through the detection of larval attack. For the latter pest, treatments were carried out with different formulations of *Bacillus thuringiensis* Berliner, 1915, Kurstaki (B.t.). Generally, insecticide soil drenches using Minecto alpha® [9.14% (100 g/L) (Cyantraniliprole + Acibenzolar-S-methyl)] were installed 8–10 days after planting and then activated 7 days later. Before the release of natural enemies and in consideration of the harmful effects on introduced species, pesticides with abamectin (A.I.) and spinosad (A.I.) were applied fifteen and seven days before, respectively.

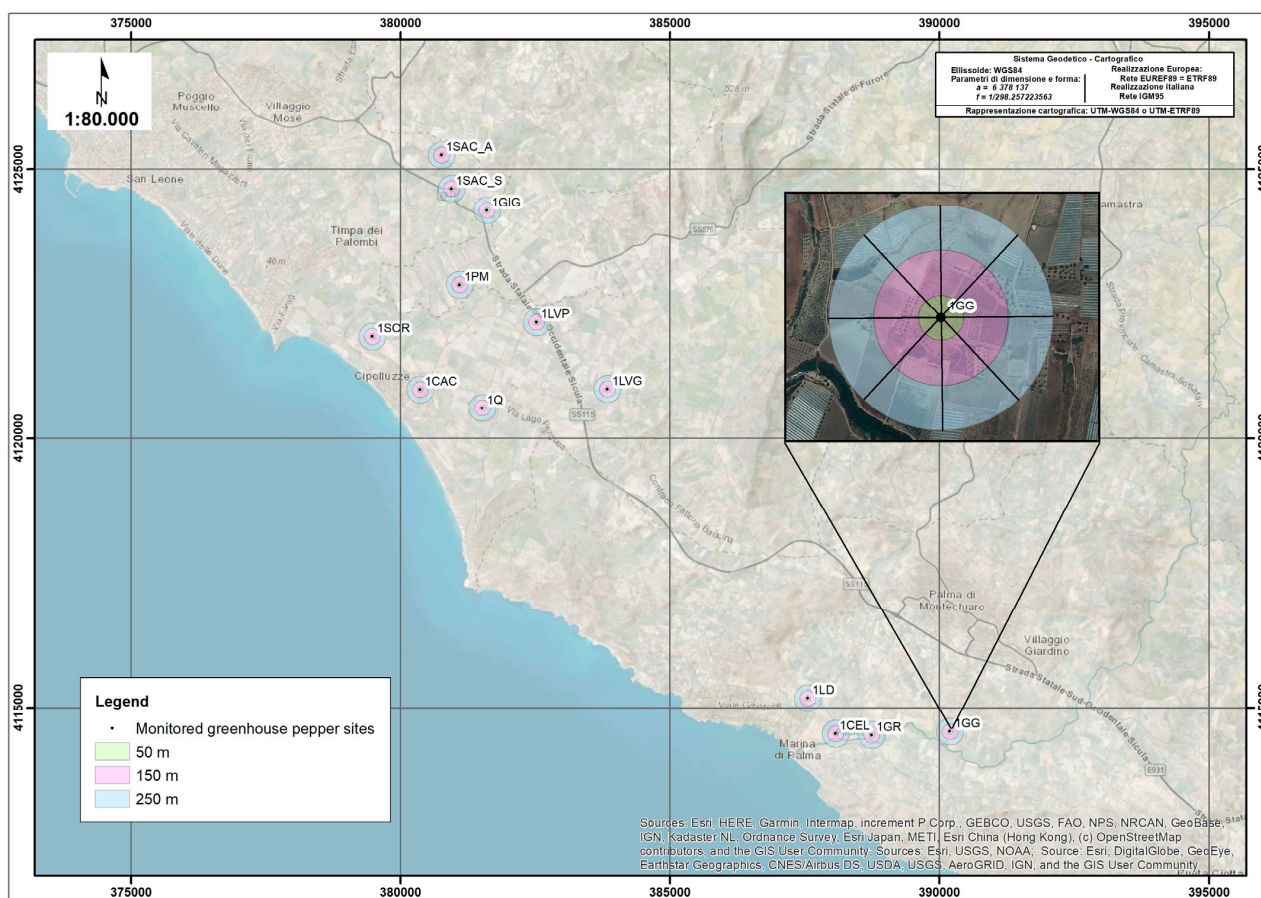


Figure 1. Map showing the study sites and how the area surrounding each pepper crop was monitored at 50, 150, and 250 m from the crop to estimate the environmental complexity value (ECV).

2.3. Introduction of Natural Enemies for the Control of Pepper Pests

The plant starts as a single stem, trained into two or more stems as soon as the first vigorous lateral stems appear. The release of predators took place at the first bifurcation of the three-branched plants. The predatory mites and insects used were *A. swirskii* (Swirski Ulti-Mite) and *O. laevigatus* (Thripor-L®) and were obtained from Koppert Biological Systems (Berkel en Rodenrijs, The Netherlands), with a density per square meter according to the manufacturer's instructions. The mite predator *A. swirskii* was inserted with the help of bags distributed on all the rows of peppers. Each bag of Swirski Ulti-Mite (approximately 250 mites per bag) was hung on every 5 or 6 pepper plants, while *O. laevigatus* was distributed at a dose of one individual per square meter. No pollen or additional food sources were provided. The possible presence of natural enemies was unknown for each site before starting the trials.

Table 1. Thirteen sweet pepper sites were surveyed (2020 and 2021), including the typology of the greenhouse environment (T = tunnel, HT = high tunnel, G = greenhouse), size (number of plants), and geographical position.

Company Code and Year of Monitoring	N° of Plants	Typology of Greenhouse	Lat.	Long
1LD (2020)	58,000	T	37°10'34.53" N	13°44'0.16" E
1CEL (2020)	33,000	T	37°10'13.36" N	13°44'21.55" E
1GR (2020)	13,000	HT	37°10'12.81" N	13°44'48.70" E
1GG (2020-21)	22,000	T	37°10'15.44" N	13°45'47.53" E
1LVP (2020-21)	12,000	T	37°14'19.10" N	13°40'32.46" E
1LVG (2020-21)	33,000	T	37°13'39.22" N	13°41'26.26" E
1PM (2020-21)	50,000	G	37°14'40.58" N	13°39'33.88" E
1Q (2020-21)	28,000	T	37°13'26.67" N	13°39'52.24" E
1SOR (2020-21)	28,000	T	37°14'8.49" N	13°38'28.65" E
1CAC (2020-21)	48,000	T	37°13'37.26" N	13°39'5.34" E
1GIG (2020-21)	15,000	G	37°15'25.47" N	13°39'53.74" E
1SAC_A (2020-21)	12,000	T	37°15'58.51" N	13°39'18.94" E
1SAC_S (2020-21)	20,000	T	37°15'38.31" N	13°39'26.79" E
1COS (2021)	23,000	T	37°10'34.93" N	13°45'0.60" E
1MANB (2021)	15,000	T	37°14'40.58" N	13°39'33.88" E
1MANP (2021)	22,000	T	37°9'57.24" N	13°46'39.38" E

2.4. Data Collection

2.4.1. In Situ Monitoring of Species

Weekly monitoring occurred from a week before the introduction of beneficial insects (approximately the first weeks of September) to December. All counts to estimate pest and predator density for each site were performed in situ on the same day, 2 or 3 days a week. The succession of monitored sites was random. The sampling included each pepper site (Table 1). Pepper plants bloom constantly, and one flower for every 1000 pepper plants was randomly sampled in both tunnel and greenhouse settings, counting, in addition, WFTs (neanids and adults), *O. laevigatus* (neanids and adults), *N. tenuis* (neanids and adults), and *A. swirskii*. The presence or absence of aphids or other species in the flowers was recorded. Counting *B. tabaci* involved determining the number of adults on a single leaf collected randomly at three-quarters of the height of the plants per 1000 plants. Finally, to assess the presence of *N. tenuis* and predatory mites, pepper leaves at three-quarters of the height of the plants were collected, and the presence or absence of *N. tenuis* and *A. swirskii* was evaluated. In total, 4700 and 4347 flowers and leaves were sampled for 2020 and 2021, respectively. Each flower and leaf were examined by a hand-held magnification lens (20×; Eschenbach®, Nürnberg, Germany).

2.4.2. Determining the Environment Surrounding Each Study Site

To quantify the landscape-level environmental complexity at each study site, the surroundings of each site were monitored in terms of the presence of natural enemies. A 0.5 km buffer was marked around each study site. Then, six coordinates were established, three each at 50, 150, and 250 m from the center of the buffer zone, with a weight attributed to each ($\pi = 1.5, 1.0, \text{ and } 0.5$ for 50, 150, and 50 m, respectively). The different habitats that occurred at each coordinate were recorded as (a) a greenhouse or tunnel, (b) arable land, (c) uncultivated, (d) private gardens, (d) orchards, (e) olive groves, or (f) river courses or drainage valleys. For each habitat detected, its complexity was determined in terms of the number of herbaceous, shrub, and tree species, the presence of walls and uncultivated areas, windbreaks, and so on; a value from 1 to 7 was then assigned, with 1 being the least complex (a) and 7 (f) being the most complex. This resulted in a complexity value (CV) for each point. The environmental CV (ECV) for each site was estimated based on the

weighted average of the 18 points detected by the site (Figure S1). The average obtained was used to calculate the ECV per site using Equation (1):

$$ECV_{site} = \sum_{n=1}^{18} (CV\ value_n \times p_i) / \sum_{n=1}^{18} (p_i) \quad (1)$$

2.5. Data Analysis

To analyze the presence or absence of *N. tenuis* and co-occurrence with *O. laevigatus* in each flower, we used generalized linear mixed models (GLMMs) with a log link function [37]. To analyze *N. tenuis* presence, the random factor was the site surveyed, and the independent variables included in the model were the ECV, number of WFTs, number of *O. laevigatus*, size (number of pepper plants in the site), and the week of monitoring, the latter being a discrete variable. For the co-occurrence of *O. laevigatus*–*N. tenuis* data (presence or absence of both species in the same flower), the random factor was the sites surveyed, and the predictor variables included in the model were the number of WFTs, *O. laevigatus*, *N. tenuis*, size (number of pepper plants in the site), the week of monitoring, and the presence or absence of *A. swirskii* in each flower. To highlight if the WFT populations in flowers differ in the presence or absence of *N. tenuis*, *A. swirskii*, and *O. laevigatus*, Welch's unequal variances t-test was performed each year. To evaluate the relationship for all pairs of variables in each site, a scatter plot matrix and Pearson correlation matrix for monitored sites were drawn to visualize the bivariate relationships between combinations of variables. In addition, the association between *B. tabaci* and *A. swirskii* on leaves was tested using a Spearman rank correlation test. The association between *N. tenuis* on each flower and the presence or absence of *N. tenuis* on leaves for each site and week was tested using a Spearman rank correlation test. All data are expressed as untransformed values (\pm SE). SPSS v.23 [38] was used for all data analyses, and SigmaPlot 13.0 [39] was used to produce all graphs.

3. Results

The linear model highlighted that ECV and WFTs had a major effect on predicting the presence of *N. tenuis* in each year surveyed (Table 2a, F values). The site's size and the monitoring week also affected the presence of *N. tenuis*. According to the fixed coefficients, an increasing ECV value was more likely to predict the presence of *N. tenuis* (2020: coefficient value = 1.77 ± 0.139 ; T-value = 12.74; $p < 0.001$; 2021: coefficient value = 0.767 ; T-value = 10.96; $p < 0.001$) and a slightly negative relationship with WFT and *O. laevigatus* in 2020 (Table 2b). This study's minimum estimated ECV value was 1.44, whereas the maximum was 3.

The predictive model used to verify the *N. tenuis*–*O. laevigatus* association in flowers highlights that the simultaneous presence of the two predators in one flower was mainly connected to the density of these predators and is not influenced by the presence of mites and aphids across different years, except for the size of pepper sites in 2021 (Table 3a). The *N. tenuis*–*O. laevigatus* association was determined by the variation in the density of each species (coefficient value for *N. tenuis* = 1.12 and 1.49, $p < 0.001$; *O. laevigatus* = 0.99 and 1.50, $p < 0.001$, respectively, for 2020 and 2021) (Table 3b).

The abundance of *N. tenuis* in flowers was 0.12 ± 0.06 ; $N = 4782$ and 0.17 ± 0.079 ; $N = 4348$ in each year, mainly being juveniles rather than adults (2020: mean = 0.11 ± 0.005 versus 0.02 ± 0.002 , 2021: mean = 0.15 ± 0.008 versus 0.02 ± 0.002 , respectively). The maximum number of individuals found per flower was six. Each year, of the 13 sites monitored over the growing season, *N. tenuis* was found at almost all sites, with clear differences between sites (Table S1). The seasonal abundance of *N. tenuis* changed weekly and showed a clear increase with predator *O. laevigatus* abundance during the pepper season (Figure 2). In both 2020 and 2021, there were significantly less WFTs in flowers with *N. tenuis* than in flowers where this predator was absent (Figure 3). The correlation with WFT points to an inverse relationship with *N. tenuis* in pepper flowers confirmed by correlation (2020: $r = -0.107$, $p < 0.001$; $N = 4782$; 2021: $r = -0.087$,

$p < 0.001$; $N = 4341$) (Table S2). The relationship between the mean number of *N. tenuis* on the leaves and flowers was positively related to the *N. tenuis* population on pepper plants (2020: $r = 0.326$, $p < 0.001$, $N = 168$; 2021: $r = 0.785$, $p < 0.001$, $N = 172$, Figure S2).

Table 2. The results of the generalized linear mixed model used to predict *Nesidiocoris tenuis* presence with a log link function (a,b).

(a) Summary of GLMM fit for the model of the presence of <i>Nesidiocoris tenuis</i> .								
Source	F (2020)	Df1	Df2	Sign	F (2021)	Df1	Df2	Sign
Corrected model	16.68	17	4761	<0.001	16.32	21	4312	<0.001
Week of monitoring	4.90	13	4761	<0.001	4.314	17	4312	<0.001
ECV	162.25	1	4772	<0.001	120.13	1	4312	<0.001
n. plants	28.12	1	4772	<0.001	101.53	1	4312	<0.001
WFT	37.17	1	4772	<0.001	20.43	1	4312	<0.001
<i>O. laevigatus</i>	16.51	1	4772	<0.001	2.493	1	4312	0.114

(b) The fixed coefficient for the generalized linear mixed model used to predict <i>Nesidiocoris tenuis</i> .								
	Model term	Coefficient	Std. Error	T	Sig.	95% Confidence Interval		
						Lower	Upper	
2020	Intercept	−6.07	0.424	−14.309	<0.01	6.90	5.24	
	Week of monitoring	0.801	0.245	3.273	0.01	0.321	1.281	
	ECV	1.77	0.139	12.74	<0.01	1.50	2.04	
	n. plants	−0.015	0.003	−5.30	<0.01	−0.02	−0.009	
	WFT	−0.279	0.046	−6.1	<0.01	−0.397	−0.189	
	<i>O. laevigatus</i>	−0.396	0.091	−4.06	<0.01	−0.548	−0.191	
2021	Intercept	−3.55	0.370	−9.60	<0.01	−4.28	−2.83	
	Week of monitoring	1.337	0.323	1.135	<0.01	0.703	1.970	
	ECV	0.767	0.070	10.96	<0.01	0.63	0.904	
	n. plants	−0.047	0.005	10.08	<0.01	−0.056	−0.037	
	WFT	−0.214	0.047	−4.52	<0.01	−0.308	−0.121	

Table 3. The generalized linear mixed model results were used to predict the presence of *Nesidiocoris tenuis*–*Orius laevigatus* association in flowers with a log link function (a,b).

(a) Summary of GLMM fit for the <i>Nesidiocoris tenuis</i> – <i>Orius laevigatus</i> model;								
Source	F (2020)	Df1	Df2	Sign	F (2021)	Df1	Df2	Sign
Corrected model	202.80	5	4772	<0.001	30.69	6	4320	<0.001
<i>N. tenuis</i> (tot)	634.80	1	4772	<0.001	43.80	1	4320	<0.001
<i>O. laevigatus</i> (tot)	373.03	1	4772	<0.001	142.78	1	4320	<0.001
WFT	16.67	1	4772	0.001	3.06	1	4320	0.08
n. plants	12.82	1	4772	0.001	2.22	1	4320	0.137
Mites in flower	0.878	1	4772	0.198	3.81	1	4320	0.51
Aphids in flower					0.71	1	4320	0.40

(b) The fixed coefficient for the generalized linear mixed model used to predict <i>Nesidiocoris tenuis</i> – <i>Orius laevigatus</i> . Display coefficients with sig. values less than 0.05.								
	Model term	Coefficient	Std. Error	T	Sig.	95% Confidence Interval		
						Lower	Upper	
2020	Intercept	−5.294	0.204	−26.00	<0.001	−5.69	−4.89	
	<i>N. tenuis</i> (tot)	1.12	0.044	25.19	<0.001	1.03	1.21	
	<i>O. laevigatus</i> (tot)	0.99	0.048	19.31	<0.001	0.83	1.02	
	WFT	−0.36	0.088	−4.08	0.001	−0.54	−0.19	
	n. plants	0.016	0.004	3.58	0.001	0.007	0.024	
	2021	Intercept	−4.73	0.604	−13.46	<0.001	−5.42	−4.042
<i>N. tenuis</i> (tot)		1.49	0.226	6.62	<0.001	1.05	1.93	
<i>O. laevigatus</i> (tot)		1.50	0.125	11.95	<0.001	1.25	1.74	

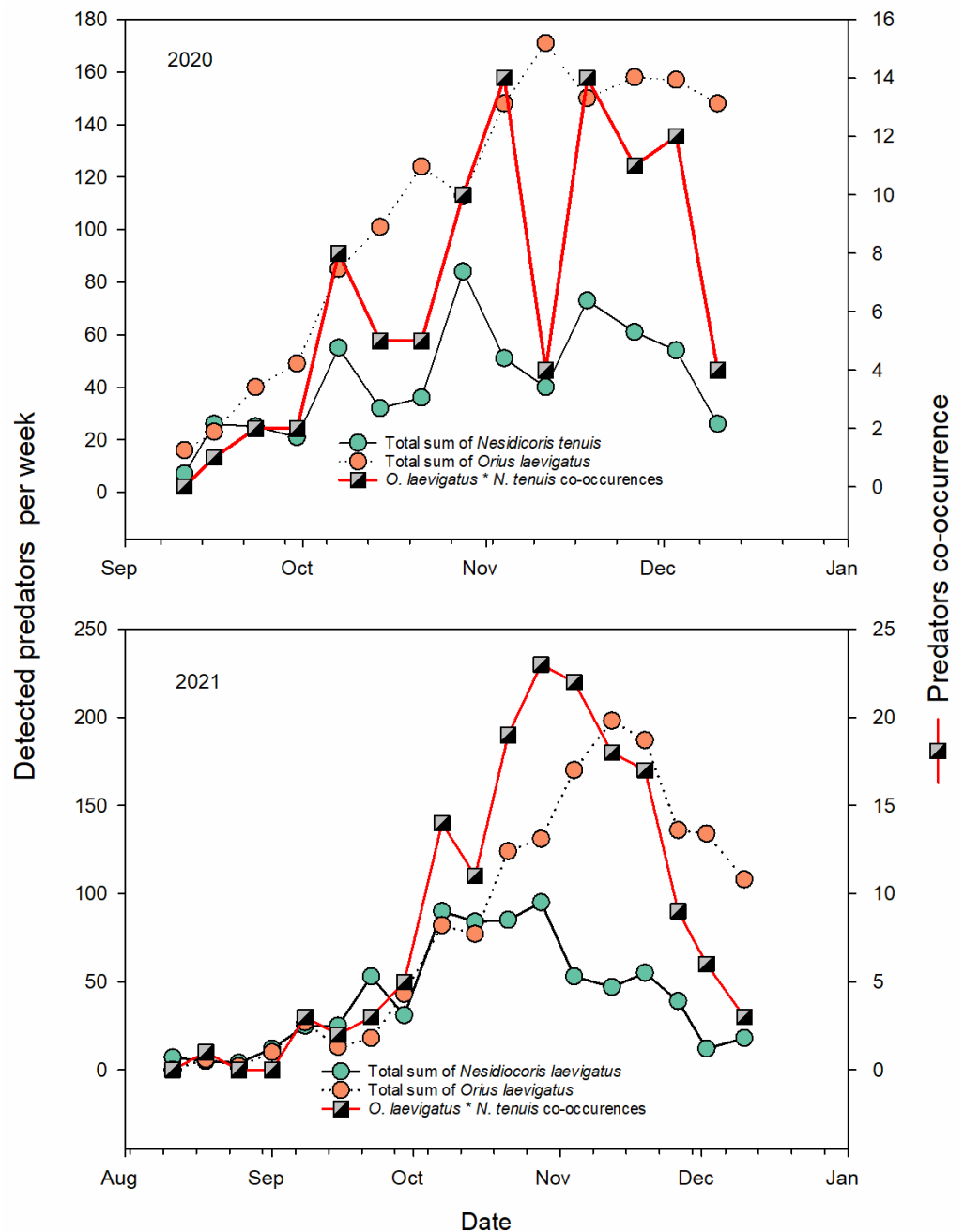


Figure 2. Weekly variation in the abundance of predatory bugs (adults and nymphs) and their co-occurrence on flowers for all monitored pepper sites.

The abundance of *O. laevigatus* per flower for all sites was 0.31 ± 0.009 and 0.338 ± 0.088 (average \pm SE for each year), with more juveniles than adult forms (2020: 0.234 ± 0.076 versus 0.08 ± 0.04 , 2021: mean = 0.24 ± 0.008 versus 0.10 ± 0.005 , respectively) (Table S1). In the pepper flowers, there was a negative relationship between WFTs and *O. laevigatus* ($r = -0.185$, $N = 4781$; $p < 0.001$ and $r = -0.251$, $N = 4336$; $p < 0.001$ for 2020 and 2021, respectively) (Figure 4). There was a slight negative relationship between *O. laevigatus* and *N. tenuis* for all sites only for 2021 (2020: $r = -0.027$, $p = 0.066$, $N = 4782$; 2021: $r = -0.036$, $p = 0.018$, $N = 4329$), but this competition had no negative effect on pest regulation (see Table S1, Figure 4). In both years, there were significantly less WFTs in flowers with *O. laevigatus* than in flowers where this predator was absent (Figure 3).

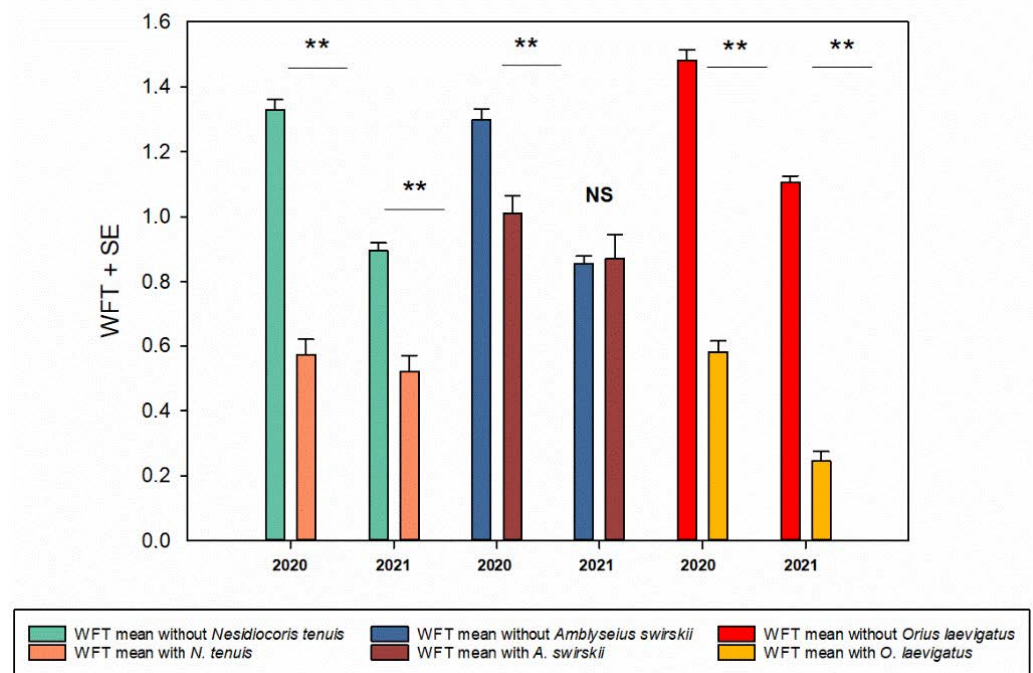


Figure 3. Western flower thrip (WFT) mean abundance in pepper flowers with or without presence of its natural enemies (2020, 2021). T statistic value (*Nesidiocoris tenuis*): 13.16, df = 1, 925; $p < 0.001$ (2020) and 47.42, df = 1, 700; $p < 0.001$ (2021). *Amblyseius swirskii*: 4.49, df = 1, 1321; $p < 0.001$ (2020) and -0.206 , df = 1, 720; $p = 0.84$ (2021). *Orius laevigatus*: 18.35, df = 1, 3695; $p < 0.001$ (2020) and 24.79, df = 1, 4334; $p < 0.001$ (2021). Asterisks show significant differences at $p < 0.001$ and NS = Not significant.

The presence of *A. swirskii* in flowers varied between sites, with this species detected in 16% of the sampled flowers, with an overall mean of 0.93 ± 0.041 ($N = 4782$) in 2020 and 8.4% and 0.33 ± 0.021 ($N = 4348$) in 2021. The mean per flower was highly variable between sites (Table S1). The number of *A. swirskii* in the pepper flowers also varied, from a minimum of 1 to a maximum of 35. There was a negative relationship in 2020 among *A. swirskii*, WFTs, and *O. laevigatus* in the flowers ($r = -0.074$, $N = 4782$; $p < 0.001$ for WFT and $r = -0.086$, $N = 4782$; $p < 0.001$ for *O. laevigatus*). The same negative relationship was confirmed in 2021 (Table S2, Figure 3). Aphids occurred in only 2.52% and 2% of flowers (2020: $N = 4783$, 2021: $N = 4346$). However, in 2020, there were significantly less WFTs in flowers with *A. swirskii* than in flowers where this predator was absent (Figure 3).

In some sites and each year, species of springtails were found in the pepper flowers (see Supplementary Data, Figure S3).

In the leaves, *A. swirskii* was nearly uniformly distributed from the fifth week of sampling in all sites for each year and from the third week of sampling in a few sites; the percentage of leaves sampled on which *A. swirskii* was found exceeded 50%. The presence of the predatory mite remained constant (>85% of leaves) until the end of the sampling period (Figure 5). The relationship with the number of adults of *B. tabaci* on the leaves showed that the presence of this predator limits the development of the whitefly population (2020: $r_s = -0.074$, $p < 0.001$, $N = 4783$; 2021: $r_s = -0.049$, $p = 0.001$, $N = 4341$). The seasonal abundance of *B. tabaci* changed weekly and showed a clear decrement during the season (Figure 6).

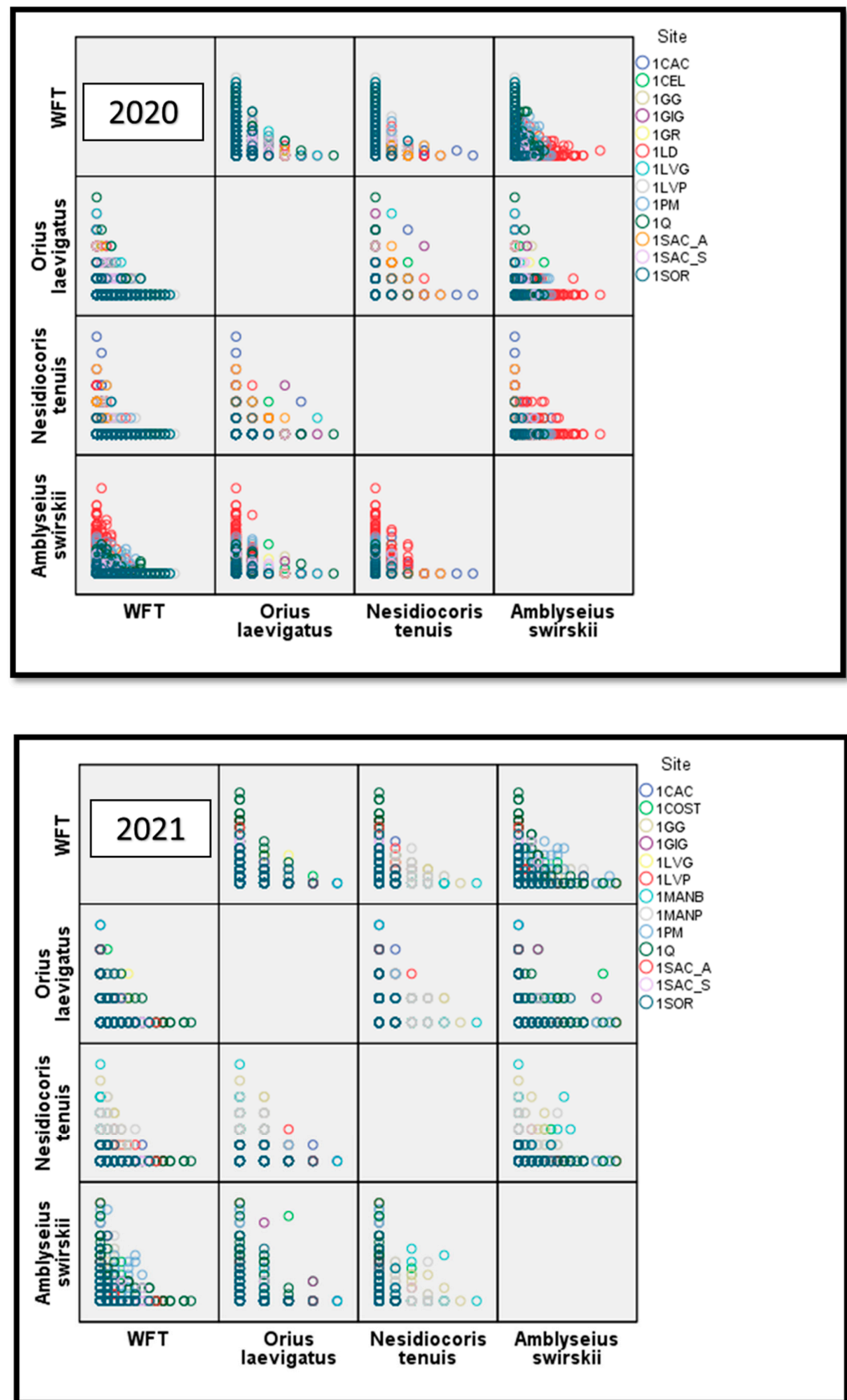


Figure 4. Scatter plot matrix indicating the correlation between white flower thrips (WFTs) and the predators *Orius laevigatus*, *Nesidiocoris tenuis*, and *Amblyseius swirskii* (2020 above, 2021 below). The figures represent the number of juveniles and predators in each flower for each species.

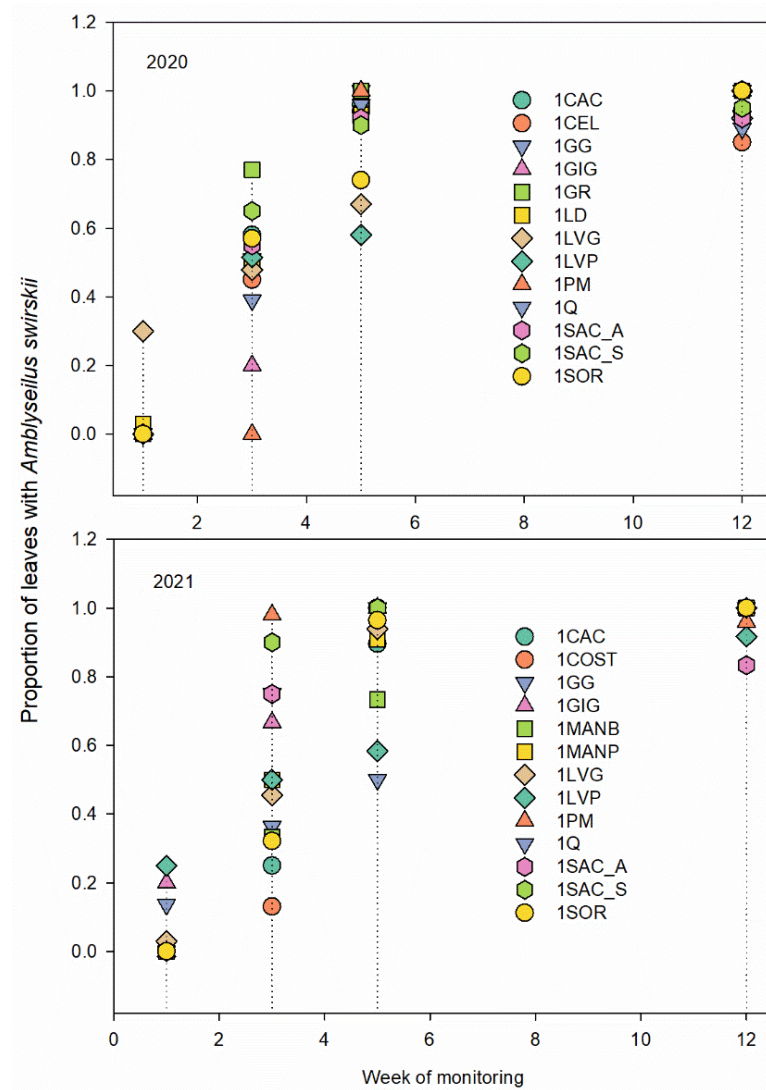


Figure 5. *Amblyseius swirskii*'s presence on pepper leaves variation during different monitoring weeks (weeks 1, 3, 5, and 12) at different pepper sites.

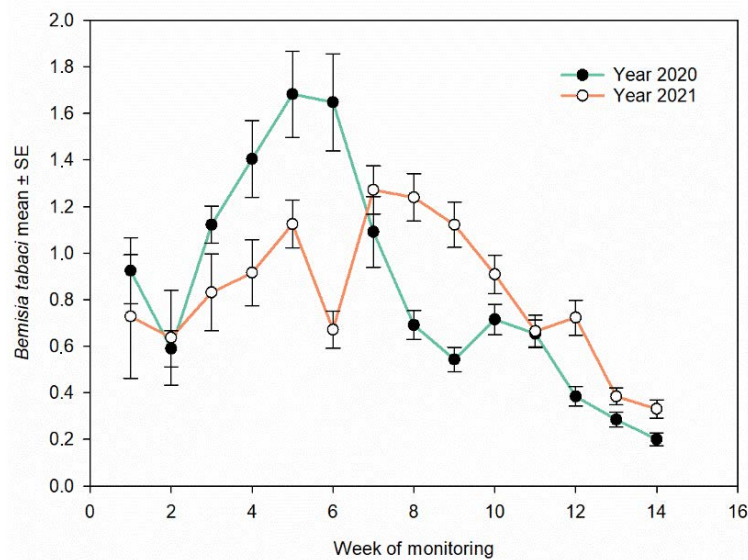


Figure 6. Weekly variation in the abundance of *Bemisia tabaci* on pepper leaves at all sites.

4. Discussion

Pepper plants in the study area are cultivated in autumn–winter, and the short-term effects of shared predation, such as apparent mutualism, could determine the pest–predator dynamics, especially in sites where natural predators occur, such as *N. tenuis*. Therefore, for biological control programs, it is important to assess whether the effects of shared predation on pest levels are positive or negative.

This study provides evidence that the dispersal of *N. tenuis* is not uniform in the same climatic area, as it is more likely to occur in a pepper crop located close to biodiversity-rich habitats compared with more uniform and biodiversity-poor sites. Parolin et al. [40] identify a fundamental role of secondary plants in improving pest management in crops, and the results of the current study confirm the importance of the interaction between the crop area and its immediate surrounding environment. The different types of uncultivated habitats and protected environments near greenhouses and tunnels may support distinct communities of plants, herbivores, and natural enemies. Therefore, diversified landscapes may represent the greatest potential for conserving biodiversity and maintaining pest control services.

Several studies confirm the important role of secondary plants in surrounding and nearby crops and greenhouses' habitats [41–45]. Generally, mirid bugs in the Mediterranean area move in greenhouses commonly at the end of the spring cycle [46,47], whereas little information is available for the autumn–winter season, particularly where this study was performed. Saulich and Musolin [48] highlighted that *N. tenuis* has homodynamic seasonal development and that its autumn and winter generations are related to food availability and temperature [49–51]. The presence of, and increase in, natural mirid predators within the crop increases the probability of the co-occurrence of *O. laevigatus* with *N. tenuis*, explaining, in part, their competitive relationship with pepper flowers. Although associations among different species are also known among mirids, it is essential to understand how such interactions affect the distribution preference of individual predatory species within the plant [52,53]. The co-occurrence of several predators on the plant, especially in the flower, is positive overall, but the introduction of more predators for the control of WFTs and *B. tabaci* would not necessarily result in the same effect for the different predators' distribution patterns on the plants [54]; however, previous research highlighted the efficiency of predatory mirids against WFT on different hosts and under controlled climatic conditions [52]. Pepper flowers were attractive for juveniles of *N. tenuis* feeding, and their preponderant presence highlighted how the flower of pepper plants could favor the establishment of crop species. Pepper plant injury in this study was not investigated, but it is not an issue in these pepper crops for which no damage has been detected.

The constant and uniform occurrence of *A. swirskii* on pepper plants in this study also highlighted their predatory action on WFTs when they co-occur in flowers, although the high density of *O. laevigatus* significantly reduced the abundance of the predatory mite. Bouagga et al. [55] reported the competitive action of *O. laevigatus* against *A. swirskii* [54]; however, the established presence of *A. swirskii* on flowers for the growing season in one site (1PM-2020) meant that WFTs could not increase above a certain threshold even in the absence or reduced presence of *O. laevigatus*.

Future investigations are needed to understand other factors that can play a role in the relationships between the abundance of *N. tenuis* and introduced natural enemies in protected pepper crops and sites. It might be that, in some sites, the abundance of *N. tenuis* could also be influenced by the production of pollen by host plants or by the effects of fires on the immediate surrounding areas, which negatively impacted the flora that hosts this species. Another unresolved issue to investigate is the understanding of the mechanisms by which landscape composition drives natural enemy–herbivore interactions or explore alternative specific host plants in the crop area such as the widespread *Dittrichia viscosa* L. Future efforts are necessary to develop tools that inform farmers when habitat conservation would be beneficial in terms of providing an increased understanding of how landscape effects are modulated by local farm management and the biology of pests and their enemies.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/horticulturae10060614/s1>, Figure S1. For example, calculate the environmental complexity values (ECVs) in the various coordinates analyzed for each site. The ECV values ranged from a minimum of 0.5 to a maximum of 10.5. Figure S2. Weekly mean of *Nesidiocoris tenuis* on leaf and flower (2020 left, 2021 right). Figures represent juveniles and adults in leaves or flowers. Figure S3. (a) Entomobrya sp (Fam. Entomobryidae: Entomobryinae); (b) springtails Entomobrya sp. on pepper flower; (c) *Seira* sp. (Fam. Entomobryidae: Seirinae); (d) lateral view of *Seira* sp. Table S1. The mean and standard deviation at different sites. At different sites, *Orius laevigatus*, *Nesidiocoris tenuis*, *Amblyseius swirskii*, and WFTs are the total of juveniles and adults for each flower. Table S2. Pearson correlation matrix of juveniles and adults of western fly thrips (WFTs), *Orius laevigatus*, *Amblyseius swirskii*, and *Nesidiocoris tenuis* on pepper flowers from each study site.

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