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BIOLOGICAL CONTROL IN LATIN AMERICA

Heteropteran Bugs Assemblage Associated to Organic Tomato Farms: Knowledge for Pest Management

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Abstract

The suborder Heteroptera (Hemiptera) includes zoophagous and zoophytophagous species which conform diverse natural enemies' systems with potential to control several horticultural pests. In this study, we report the assemblage structure of heteropteran bugs species inhabiting open-field and greenhouse organic tomato crops and one common adjacent non-crop solanaceous plant, *Solanum sisymbriifolium*, in North Buenos Aires province, Argentina, aimed to select promissory biocontrol species. Biweekly direct inspection of selected plants was carried out during a 3-year period (2017–2019) to collect hemipteran nymphs and adults. As a result, nine species and morphospecies belonging to Berytidae (zoophytophagous), Lygaeidae (phytophagous), and Miridae (phytophagous and zoophytophagous) were found, with ≥ 75% of species belonging to the latter family. The zoophytophagous mirid *Tupiocoris cucurbitaceus* (Spinola) was the most frequent and dominant species in all sites studied. Among the phytophagous species, *Nysius simulans* Stål was mostly present in greenhouse crops. The community found in greenhouse tomato crops was more diverse than that registered in open-field crops. The characterization of the heteropteran complex in organic tomato farms provides basic knowledge necessary to design pest control strategies in the region studied.

Keywords Hemiptera · *Tuta absoluta* · *Solanum lycopersicum* · *Solanum sisymbriifolium* · Predatory bugs · Conservation biological control

Introduction

Community ecology provides the theoretical framework to study the mortality factors of insects of agricultural importance by analyzing the diversity and interspecific interactions occurring in an agroecosystem (Morin 2011). Exploring the structure of the ecological community, which involves crop and non-crop plants and the herbivorous and entomophagous insects associated, has been pointed out as useful to gather baseline knowledge for pest management, especially because it allows the identification of potential biocontrol agents, particularly for conservation biological control (DeBach 1964; Salas Gervassio et al. 2016a; López-Núñez et al. 2017). In this respect, the search for native or spontaneous natural enemies is considered a better strategy instead of using imported species as biological control agents, due to the environmental risks related to the introduction of exotic species in a new biogeographic area (van Lenteren 2012; Cédola et al. 2021).

Insect pests are a major constraint to horticultural production and many of them are common species of vegetable and fruits crops worldwide (Knapp et al. 2020). The greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae) and the South American tomato moth *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) are two main species of a complex of native insect pests of tomato crop, *Solanum lycopersicum* L. (Solanales: Solanaceae), in

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the Neotropical region (Desneux et al. 2010; López et al. 2019). The whitefly *T. vaporariorum*, a highly polyphagous species reported as pest of hundreds of crops, is a major pest in temperate regions causing direct crop damage due to nymphal and adult feeding on leaves and indirect damage by vectoring plant viruses. Regarding *T. absoluta*, this gelechiid has gained worldwide economic importance after its invasion into European, African, and Asian continents (Desneux et al. 2011; Biondi et al. 2018; Ferracini et al. 2019). Larvae mine leaves, stems, and fruits, yielding important tomato production losses (Desneux et al. 2021). *Tuta absoluta* feeds on tomato but it can develop using other solanaceous plant species, cultivated and wild, and among them, the sticky nightshade *Solanum sisymbriifolium* Lam. (Solanales: Solanaceae) has been reported as an alternative host plant for this pest (Salas Gervassio et al. 2016a). Control of these pests is difficult due to their population growth rates, their overlapping generations, and the rapid development of genetic resistance to insecticides (Knapp et al. 2020). Biological control is widely used for whitefly species management, being predatory heteropteran bugs, coccinellids and lacewings, and nymphal and adult parasitoids important natural enemies employed against this pest by means of augmentative and conservation strategies (López et al. 2012; van Lenteren et al. 2020). In relation to *T. absoluta* natural enemies, there have been reported over 100 entomophagous species worldwide, and among them, mirid bugs and egg and larval parasitoids show great potential as biocontrol agents (Desneux et al. 2010; Biondi et al. 2018; Salas Gervassio et al. 2019; Ferracini et al. 2019).

The suborder Heteroptera (Hemiptera) includes ca. 45,000 species recorded throughout the world, with a wide range of feeding habits (Henry 2017; Schuh and Weirauch 2020). Particularly, the species of agricultural importance vary from strictly phytophagous, phytozoophagous, zoophytophagous to strictly zoophagous (Schaefer and Panizzi 2000; Wheeler 2001). Phytophagous species that cause different degrees of damage in crops belong to several families, i.e., Pentatomidae, Coreidae, Lygaeidae, and some Miridae (Schuh and Weirauch 2020), meanwhile others, belonging to the Anthocoridae, Geocoridae, some genera of Miridae and Nabidae families, are important biocontrol agents of insect pests (van Lenteren et al. 2017). Indeed, mirid predators are used under conservation techniques or by releasing mass reared individuals in biofactories in Europe, Asia, New Zealand, and North and South America to control several horticultural pests, as whiteflies and *T. absoluta* (van Lenteren 2012; van Lenteren et al. 2017; 2020).

In the Mediterranean basin, several species of Heteroptera have been reported inhabiting tomato crops and feeding on eggs and small larvae of Lepidoptera, nymphs and adults of aphids, scales, and whiteflies (van Lenteren et al. 2017). In Brazil, studies on biocontrol of pests in greenhouses showed the potential of various heteropteran predators (Anthocoridae and Miridae) against them, especially to control *T. absoluta* (Bueno et al. 2012; 2020; van Lenteren et al. 2016; 2017; 2018). In Argentina, most of research was focused on parasitoid species of these pests (López et al. 2020; Luna et al. 2015; Salas Gervassio et al. 2019; Viscarret et al. 2000), and recently, a predatory species *Tupiocoris cucurbitaceus* (Spinola) (Hemiptera: Miridae) has gained attention as a biocontrol agent (Cagnotti et al. 2016; López et al. 2019). Progress has been made to study some biological traits of this heteropteran species and currently is commercially used to control whiteflies and *T. absoluta* in horticultural crops in Argentina and Uruguay (Polack et al. 2017; MGAP 2020).

Considering the economic importance of *T. vaporariorum* and *T. absoluta* for tomato production, the search for entomophagous insects associated with this crop, such as heteropteran species, deserves attention. Moreover, studying the co-occurrence of predators and prey in crops at plant level can help to understand the encountering opportunities among them, which is crucial to determine the potential of these natural enemies as biocontrol agents in field conditions. Our study hypothesis was that the complex of heteropteran species naturally present in tomato farms is more diverse than that currently known. Thus, we aimed to assess the assemblage of heteropteran bugs inhabiting tomato farms in a main horticultural region of Argentina with emphasis on those species that could have potential as biological control agents of *T. vaporariorum* and *T. absoluta*. We focused our study in organic farms since they rely on cropping practices which ban chemical inputs and promote crop and non-crop plant diversity, among others, increasing species richness and natural biocontrol services (Zalazar and Salvo 2007; Rouaux et al. 2020). The objectives were (1) to identify the heteropteran species present in tomato crops and in *S. sisymbriifolium*—a frequent non-crop solanaceous plant present in those farms—; (2) to analyze the community structure of heteropteran species in the organic tomato farms across the cropping cycle; and (3) to assess the co-occurrence between the main predators and the two main pest species, *T. vaporariorum* and *T. absoluta*, at plant level. The information of local diversity of natural enemies is relevant to design further augmentative and conservation biological control strategies in the region studied.

Materials and methods

The study was located at La Plata Horticultural Belt, NE Buenos Aires province, Argentina. In this important horticultural region, tomato crops are planted applying a two-cycles cropping scheme (spring and summer seasons) and cultivated under open-field and protected conditions (greenhouses). Although prevention and control of pests and diseases based on spraying with neurotoxic pesticides are conventional phytosanitary practices, organic farming, which relies on conservation biological control through habitat manipulation and botanical and *Bt*-based insecticides use, is increasing in the region.

Six organic farms were chosen to assess the assemblage structure of heteropteran species including both open-field and greenhouse tomato crops (each crop with ≈ 200 plants). Four of them were located at La Plata and the other two sites were one at Berazategui and one at Magdalena counties (Fig. 1). Biweekly samplings were carried out along both production cycles (from August to December and from January to May) and during three consecutive years (2017 to 2019) as follows: Guillermo Hudson and Lisandro Olmos 1 2017–2018; Gorina 2018–2019; Lisandro Olmos 3 2018; Lisandro Olmos 2 2017–2018–2019; and General Mansilla 2019. The number of samples taken in each season and field varied because of the dynamic farming activities, where the producers rotate crops according to economic and market conditions. All nymphs and adults of heteropteran bugs were captured by beating leaves, fruits, and stems of randomly selected plants over a white plastic tray (40 cm × 35 cm × 10 cm, length × width × depth), and the insects were collected from the tray with an aspirator. The number of revised plants per sample date ranged between 10 and 15, estimated according to heteropteran bug density and considering a standard error of 20% (Gotelli and Ellison 2004). Moreover, the presence of *T. absoluta* and *T. vaporariorum* were recorded in each sampled plant. Plants of the solanaceous *S. sisymbriifolium* were also revised in a similar manner when they were present in the surroundings of open-field tomato crops, since *T. absoluta* (Salas Gervassio et al. 2016a) and the mirids *T. cucurbitaceus* and *Campyloneuropsis cincticornis* (Stål) (Salas Gervassio and Rocca, unpublished data) have been recorded in that species. Because *S. sisymbriifolium* was not always found, only the heteropteran species collected are listed, but no statistical analyses were carried out.

The collected insects were transported to the laboratory and conditioned for further studies. All specimens were kept alive, individually placed in plastic Petri dishes (10 cm × 2 cm, diameter × height), and provided with tomato leaves and eggs of *Ephestia kuehniella* Zeller (Lepidoptera:

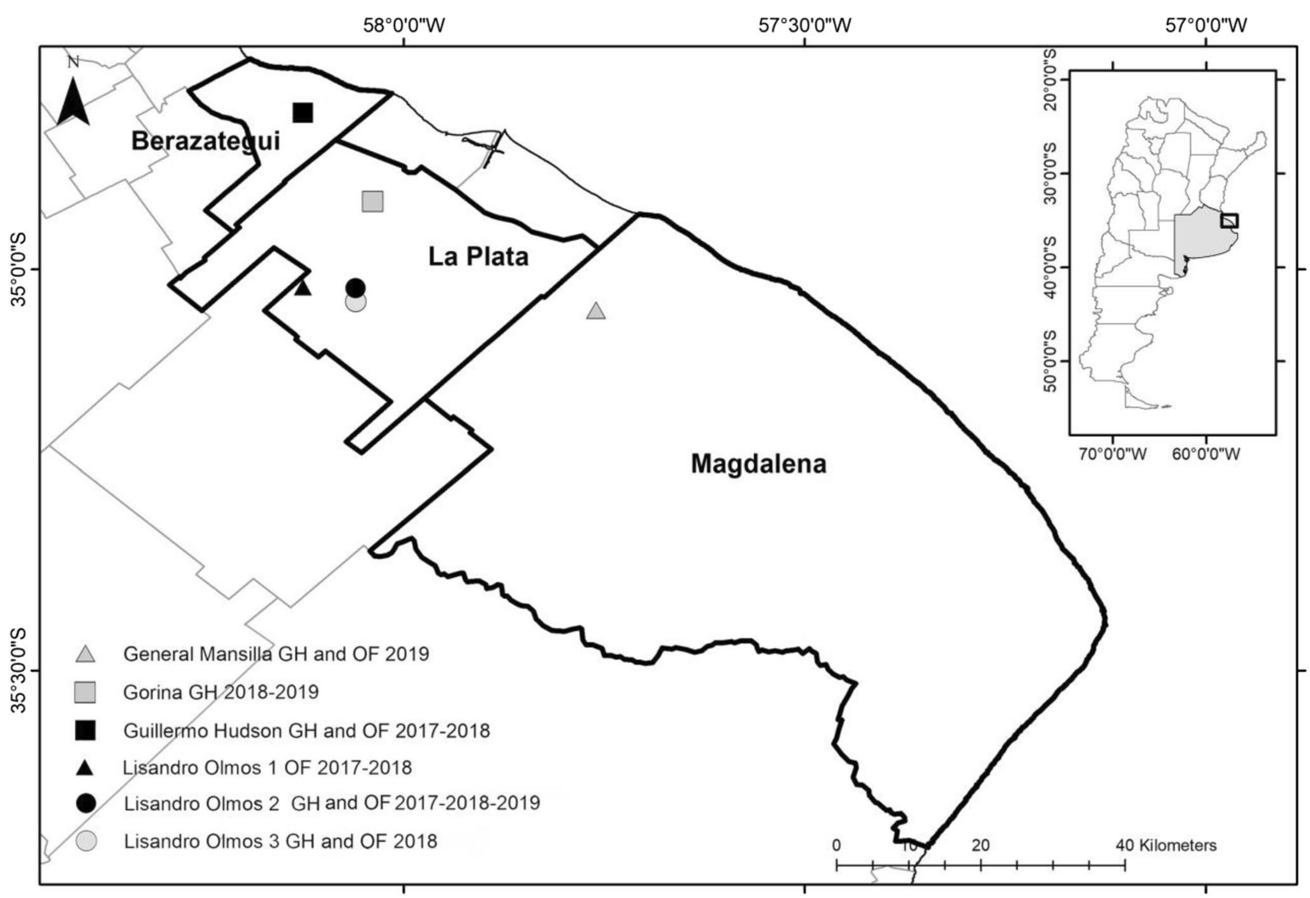

Fig. 1 Sampling sites to search for heteropteran species inhabiting horticultural crops located in NE Buenos Aires province, Argentina. GH, greenhouse; OP, open-field

Pyralidae) (Brometán S.R.L. Argentina SA) as food. Dishes were labelled with information regarding sampling site and date. Subsequently, they were maintained in a walk-in chamber under controlled environmental conditions (14:10 h L:D photoperiod, 25 ± 2 °C temperature, and 70% relative humidity).

Insect species identification

First separation in morphospecies was made in vivo based on visual morphological characteristics using a stereoscopic microscope (Nikon SMZ1270). Additionally, photographic images were taken with a video camera (Micrometrics 519CU CMOS, 5.0 megapixel), attached to the microscope. Dead specimens were stored in 70% ethanol for identification. Individuals were identified using literature and available keys by specialists (EM and PMD) and information about the food habits of the species was sought using literature and online catalogues (Henry et al. 2015; Wheeler and Krimmel 2015; Konstantinov et al. 2018; López et al. 2019; Nogueira et al. 2019; Dellapé and Henry 2021).

Characterization of the heteropteran species assemblage on tomato crop

The structure of the heteropteran species community present in open-field and greenhouse organic tomato crops in the NE of Buenos Aires province was assessed by means of Hill numbers (or the effective number of species). The purpose of this analysis was to standardize the variable number of samples, while extrapolation enabled to predict the real diversity by taking into account the expected number of species undetected by the sampling effort considered. This methodology measures the degree to which proportional abundances are distributed among the species and their units are species (Hill 1973). We first calculated for all sites and cropping techniques the sample coverage that indicates the proportion of the statistical population represented by the species sampled (Chao and Jost 2012). Additionally, we estimated, based on abundance data, the three most widely used members of the family of Hill numbers: $q = 0$ (species richness, ${}^{0}D$), which counts species equally without regard to their relative abundances, $q = 1$ (Shannon diversity, ${}^{1}D$) that can be interpreted as the effective number of common species in the assemblage, and $q = 2$ (Simpson diversity, ${}^{2}D$) that accounts for the effective number of dominant species in the assemblage (Chao et al. 2014).

We used the package iNEXT (iNterpolation/EXTrapolation), using R software, to compute and plot coverage-based rarefaction and extrapolation (R/E) sampling curve.

Co-occurrence analysis

To estimate the co-occurrence between the main heteropteran predators and *T. vaporariorum* and *T. absoluta* pest species in the same tomato plant (i.e., at plant level), at each farm, we first prepared a datasheet with information that included all sampled plants in which at least one predator and/or pest species (*T. absoluta* and *T. vaporariorum*) was present. Also, we considered the *T. absoluta*–*T. vaporariorum* combination to explore which is the probability that the predator could find both prey species together in the same plant. All analyses were performed using the R software (version 3.5.1) with the package Co-occur, which uses combinatory to determine the probability that the observed frequency of co-occurrence of a species pair is significantly equal to that expected (random association $\alpha = 0.05$), greater than expected: P (gt) ≤ 0.05 (association positive), or significantly lower than expected: P (lt) ≤ 0.05 (negative association) (Veech 2013).

Results

Insect species identification

A total of 40 samplings were carried out during the period studied: three in Gorina and four in General Mansilla (La Plata and Magdalena), five in Lisandro Olmos 1, 16 in Lisandro Olmos 2 and four in Lisandro Olmos 3 (all La Plata), and eight in Guillermo Hudson (Berazategui). We collected 2081 heteropteran bugs which were sorted out in nine species and morphospecies, belonging to three families (Table 1). Eight of the nine species/morphospecies were found in tomato crops, and only two species, *C. cincticornis* and *T. cucurbitaceus* (Fig. 2), were registered in *S. sisymbriifolium* plants (Table 1). *Tupiocoris cucurbitaceus* was present in all tomato farms and *Jalysus sobrinus* Stål was registered in five out of six farms.

Based on information of feeding habits reported for hemiptera bugs, most of species/morphospecies registered have been described as zoophytophagous, except for *Nysius simulans* Stål and *Collaria scenica* Stål which are phytophagous. The food habit of the morphospecies Dyciphini 1 could not be corroborated since species of this tribe have various feeding habits.

In relation to the common pest species present in the tomato crops sampled, besides *T. absoluta*, whiteflies *T. vaporariorum* were recorded in all farms.

Characterization of the heteropteran species assemblage on tomato crop

The highest relative abundance was observed for the mirid predatory bug *T. cucurbitaceus* (90.43%) in the tomato farms sampled, followed by *N. simulans* (6.15%), *J. sobrinus*

Table 1 Taxonomic list of Heteroptera (Hemiptera) species found on organic farms in NE of Buenos Aires province for 3 years (2017 to 2019)

Family	Subfamily	Tribe	Species	Food habits	Host plant
Berytidae	Metacanthinae	Metacanthini	*Jalysus sobrinus* Stål	Zoophytophagous	Tomato
Lygaeidae	Orsillinae	Nysiini	*Nysius simulans* Stål	Phytophagous	Tomato
Miridae	Mirinae	Stenodemini	*Collaria scenica* Stål	Phytophagous	Tomato
	Bryocorinae	Dyciphini	Dyciphini 1	Unknown	Tomato
			Dyciphus sp. 1	Zoophytophagous	Tomato
			Dyciphus sp. 2	Zoophytophagous	Tomato
			Tupiocoris curcubitaceus Spinola	Zoophytophagous	Tomato and *S. sisymbriifolium*
			Campyloneuropsis cincticornis Stål	Zoophytophagous	*S. sisymbriifolium*
			Nesidiocoris sp.	Zoophytophagous	Tomato

Fig. 2 Dorsal view of adults of **a** *Tupiocoris cucurbitaceus* (Spinola) and **b** *Campiloneuropsis cincticornis* (Stål), two main predatory mirids registered in organic tomato farms at La Plata Horticultural Belt (Buenos Aires province, Argentina)

(2.35%), and *C. scenica* (0.38%); meanwhile, the rest of mirids were rare (0.67%).

Tupiocoris cucurbitaceus was ubiquitous in all farms and recorded almost in all sampled dates, in which it generally presented the highest relative abundance. The phytophagous bug *N. simulans* was collected mainly from October to December during 2017, and it presented the highest relative abundance in most of these sampling dates. *Jalysus sobrinus* showed variable abundances in most of the sites; meanwhile, individuals of *Dicyphus* sp. 1 and *Dicyphus* sp. 2 and *Nesidiocoris* sp. (considered together as "other mirids") were rarely found during the study being present only at General Mansilla site (Fig. 3).

Regarding the characterization of the community structure of heteropteran bugs, Table 2 summarizes the values of the effective number of species calculated for both different sites and cropping techniques. The curve of sample completeness vs. sample size for each of the six sites showed that for any sample size $\geq$ 25 individuals, $\geq$ 97% sample coverage was obtained (Fig. 4a). Considering greenhouse and open-field cropping techniques, for sample size $\geq$ than 100 individuals, the curves showed almost 100% sample coverage (Fig. 4b).

In relation to Hill numbers, the heteropteran species richness (^{0}D) for tomato crops varied from 1 to 4 in all sites, being Olmos 3 the community with the lower number of species (Fig. 5a). Furthermore, General Mansilla and Guillermo Hudson sites yielded the highest number of common species (^{1}D) and very abundant species (^{2}D) than the other sites (Fig. 5b and c). Considering the cropping techniques, richness values observed in greenhouse crops does not differ

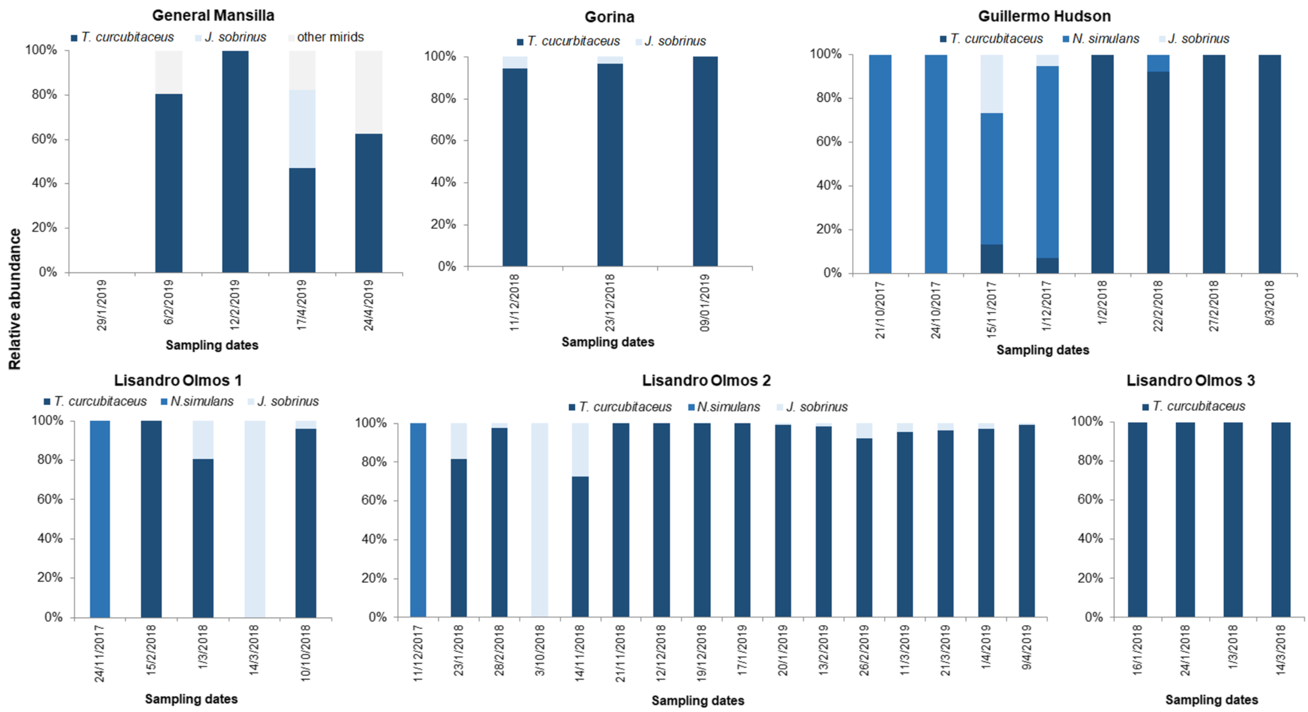

Fig. 3 Phenological variation of the relative abundances (%) of the heteropteran bug species found in six organic tomato farms at La Plata Horticultural Belt (Buenos Aires province, Argentina)

significantly from those observed in the open-field crops at abundances ≥ 100 individuals, i.e., the CI curves overlap 95% (Fig. 5d). When comparing the other Hill numbers, protected crops showed higher number of common species (^{1}D) and greatest "very abundant" species (^{2}D) than non-protected crops (Fig. 5e and f).

Co-occurrence analysis

This analysis was performed for the predatory species *T. cucurbitaceous* because it was the most frequent and abundant heteropteran species in all farms. As a result, the presence of the predatory bug was independent (at random) of the presence of either of the two pest species on the same plant (Table 3), except in Olmos 1, where the *T. cucurbitaceus–T. vaporariorum* and *T. absoluta–T. vaporariorum* combinations were segregated at plant level with a low probability of co-occurrence, lower than 35%, while *T. cucurbitaceus–T. absoluta* combination was positively associated, with a higher probability of co-occurrence. In Olmos 2, prey combinations were also segregated at plant level (Table 3).

Discussion

The use of predatory biocontrol agents has been largely underestimated in augmentative releasing programs compared to parasitoids and entomopathogenic microorganisms because of their potential negative effects on other species in the agroecosystem, due to polyphagia or omnivory, preying on non-target species, and interspecific competition and intraguild predation (Labbé 2005; van Lenteren 2012). In spite of that, predatory species can play an important role in reducing pest populations, and those with a narrower diet range or oligophagous have been subject of various conservation biological control tactics and are currently gaining importance for augmentative biocontrol programs (Snyder 2019). In the last decade, several successful biocontrol programs based on predatory arthropods (mites and heteropteran bugs) have been reported in European countries to control thrips and whiteflies in sweet pepper and tomato crops (Calvo et al. 2012; Urbaneja et al. 2012). In Latin American countries, this biotechnology is considered promissory and some native predatory biocontrol agents are being evaluated (van Lenteren et al. 2020).

In this study, we found a heteropteran species assemblage inhabiting organic tomato farms in NE Buenos Aires province composed of nine species and morphospecies, seven belonging to the family Miridae, and one to Lygaeidae and Berytidae each, with various feeding habits. The finding of a greater number of mirid species in the community agrees with the taxonomic diversity of this family, represented by ca. 11,300 species worldwide (Schuh and Weirauch 2020), and > 520 described for Argentina (Ferreira et al. 2015). Species of this family have been pointed out as early colonizers

Table 2 Results of Hill numbers (species richness: $q=0$, Shannon diversity: $q=1$, and Simpson diversity: $q=2$) for the six sites and both greenhouse and open-field cropping techniques sampled. SE Standard error, *LCI*, lower confidence interval; *UCI*, upper confidence interval

Indexes	Sites/cropping techniques	Values observed	Estimator	SE	LCI	UCI
Species richness ^0D	Greenhouse	4	4	0.002	4	4.01
	Open-field	4	4.5	1.32	4.03	12.43
Shannon diversity ^1D	Greenhouse	1.55	1.55	0.04	1.55	1.63
	Open-field	1.21	1.21	0.04	1.21	1.3
Simpson diversity ^2D	Greenhouse	1.26	1.26	0.02	1.26	1.3
	Open-field	1.08	1.08	0.02	1.08	1.13
Species richness ^0D	General Mansilla	3	3	0.05	3	3.1
	Gorina	2	2	0.34	2	2.86
	Guillermo Hudson	3	3	0.01	3	3.02
	Lisandro Olmos 1	3	3	0.34	3	3.84
	Lisandro Olmos 2	4	4	0.48	4	5.45
	Lisandro Olmos 3	1	1	0	1	1
Shannon diversity ^1D	General Mansilla	1.87	1.89	0.15	1.87	2.18
	Gorina	1.19	1.20	0.11	1.19	1.41
	Guillermo Hudson	1.88	1.88	0.06	1.88	2.01
	Lisandro Olmos 1	1.32	1.32	0.07	1.32	1.47
	Lisandro Olmos 2	1.23	1.239	0.03	1.23	1.28
	Lisandro Olmos 3	1	1	0	1	1
Simpson diversity ^2D	General Mansilla	1.51	1.52	0.13	1.51	1.78
	Gorina	1.08	1.09	0.06	1.08	1.21
	Guillermo Hudson	1.62	1.62	0.05	1.62	1.73
	Lisandro Olmos 1	1.15	1.15	0.04	1.15	1.22
	Lisandro Olmos 2	1.09	1.09	0.01	1.09	1.11
	Lisandro Olmos 3	1	1	0	1	1
Species richness ^0D	Greenhouse	4	4	0.002	4	4.01
	Open-field	4	4.5	1.32	4.03	12.43
Shannon diversity ^1D	Greenhouse	1.55	1.55	0.04	1.55	1.63
	Open-field	1.21	1.21	0.04	1.21	1.3
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	Open-field	1.08	1.08	0.02	1.08	1.13

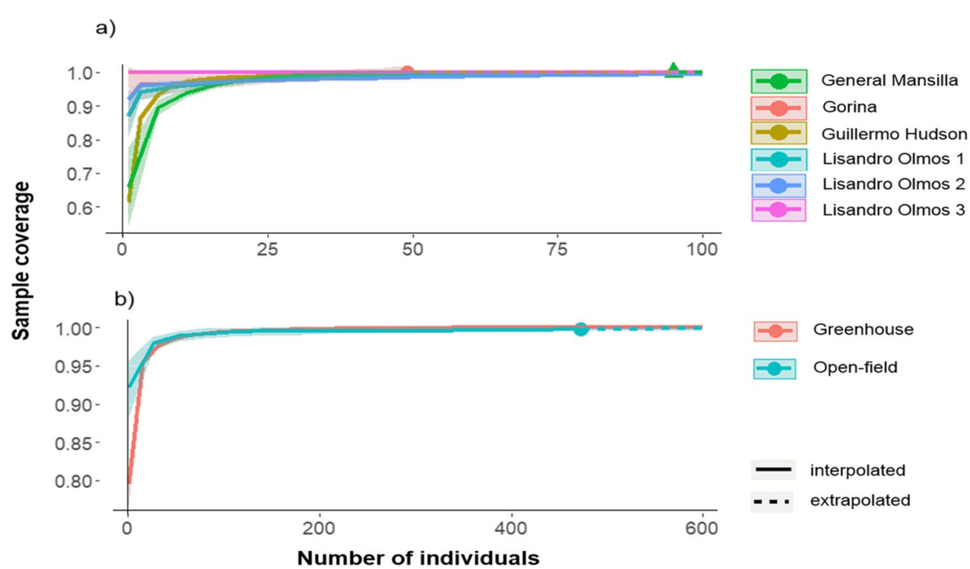

Fig. 4 Plots of sample coverage for samples as a function of sample size estimated for heteropteran communities associated to organic tomato farms in NE of Buenos Aires province for 3 years (2017 to 2019). **a** Independent six farms and **b** farms sorted out as greenhouse and open-field. Shaded regions show the 95% confidence intervals obtained by a bootstrap method. Reference samples are denoted by solid dots

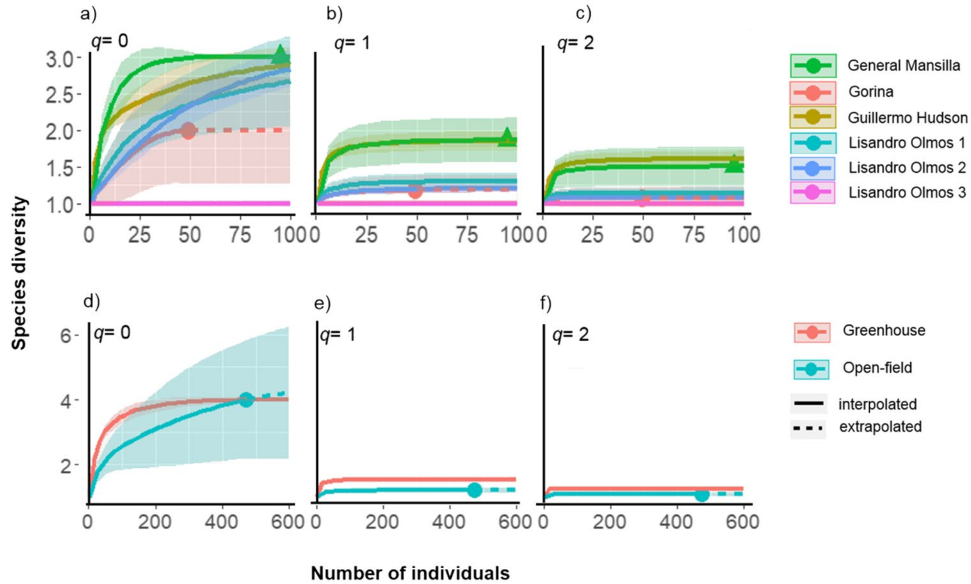

Fig. 5 Sample-size-based rarefaction (solid lines) and extrapolation (dashed lines, up to double the reference sample size) of heteropteran communities associated to organic tomato farms in NE of Buenos Aires province for 3 years (2017 to 2019) based on the Hill numbers: **a**–**c** independent six farms and **d**–**f** farms sorted out as greenhouse and open-field. **a** and **d** ^{0}D: $q=0$, **b** and **e** ^{1}D: $q=1$, and **c** and **f** ^{2}D: $q=2$. Shaded regions show the 95% confidence intervals obtained by a bootstrap method. Reference samples are denoted by solid dots

Table 3 Results of the probabilistic model of co-occurrence among *Tupiocoris cucurbitaceus*, *Trialeurodes vaporariorum*, and *Tuta absoluta* in the same tomato plant. *P* (lt) = probability of co-occurrence at a frequency lower than expected if it was random (*P* (lt) < 0.01 negative association) and *P* (gt) = probability of co-occurrence at a frequency greater than the observed frequency (*P* (gt) < 0.01 positive association)

Farms	# Sample units	Species combinations	Probability of co-ocurrence %	*P* (lt)	*P* (gt)	Association
General Mansilla	59	*T. absoluta–T. vaporariorum*	8.3	1	0.91	Random
		T. absoluta–T. cucurbitaceus	46.7	0.47	1	Random
		T. vaporariorum–T. cucurbitaceus	4	0.21	0.97	Random
Gorina	39	*T. absoluta–T. vaporariorum*	55	0.56	1	Random
		T. absoluta–T. cucurbitaceus	40	1	0.59	Random
		T. vaporariorum–T. cucurbitaceus	23.1	0.62	0.63	Random
Guillermo Hudson	77	*T. absoluta–T. vaporariorum*	25.8	0.79	0.38	Random
		T. absoluta–T. cucurbitaceus	39.6	0.07	0.97	Random
		T. vaporariorum–T. cucurbitaceus	23.3	0.6	0.58	Random
Lisandro Olmos 1	43	*T. absoluta–T. vaporariorum*	35	< 0.001	1	Negative
		T. absoluta–T. cucurbitaceus	56.5	1	< 0.001	Positive
		T. vaporariorum–T. cucurbitaceus	28.2	0.008	0.99	Negative
Lisandro Olmos 2	179	*T. absoluta–T. vaporariorum*	46.3	< 0.001	1	Negative
		T. absoluta–T. cucurbitaceus	59.6	0.78	0.36	Random
		T. vaporariorum–T. cucurbitaceus	52.3	0.48	0.67	Random
Lisandro Olmos 3	38	*T. absoluta–T. vaporariorum*	62.3	0.95	0.2	Random
		T. absoluta–T. cucurbitaceus	55.8	0.61	0.73	Random
		T. vaporariorum–T. cucurbitaceus	52.2	0.71	0.6	Random

into new habitats, showing that their inherent high dispersal capacity and the zoophytophagous feeding habit could allow them to exploit a variety of food resources and to rapidly increase their populations (Becker 1992). Notably, one of the phytophagous mirid species found, *C. scenica*, has been reported of economic importance as a pest of fodder crops (Barreto et al. 2012). For this reason, its presence in organic tomato crops in NE Buenos Aires province is worth studying. *Tupiocoris cucurbitaceus*, *C. cincticornis*, *Dicyphus* sp. 1 and *Dicyphus* sp. 2, and *Nesidiocoris* spp. are well-known zoophytophagous species/genera. These taxa have been reported in South America and Europe as predators of eggs and nymphs of whiteflies, and eggs and larvae of *T. absoluta* (Urbaneja et al. 2009; Bueno et al. 2012; Calvo et al. 2012; van Lenteren 2012; Ingegno et al. 2013; Baños-Díaz et al. 2017; López et al. 2019; Montiel Cáceres

2021). Among them, *T. cucurbitaceus* was a very frequent and abundant species in the heteropteran bugs assemblage, both in open-field and greenhouse tomato crops, and also found in *S. sisymbriifolium* plants adjacent to crops. Other mirid species, *C. cincticornis*, was found exclusively on the latter solanaceous species, which also hosts *T. absoluta* (Salas Gervassio et al. 2016a). A better understanding of the biology of *C. cincticornis* is necessary to determine its potential as a biocontrol agent in horticultural crops through conservation or augmentative tactics.

Both *T. cucurbitaceus* and *C. cincticornis* have been reported previously in northern Buenos Aires province by Carpintero et al. (2014). This author mentioned other eight mirid species in the region, and among them, another species of the genus *Campyloneuropsis*, *C. infumatus* Carvalho, which was not found in the present study. This species, together with *Engytatus varians* (Distant), and *Macrolophus basicornis* (Stål) are zoophytophagous bugs that have been evaluated in Brazil and were considered suitable *T. absoluta* control agents in tomato crops in that country (Bueno et al. 2012; 2018; Silva et al. 2016).

The species belonging to *Dicyphus* and *Nesidiocoris* have presumably great potential as natural enemies in tomato farms in NE Buenos Aires province, since other species of these genera are being commercialized as biocontrol agents (e.g., several bioproducts based on the predatory bug *Nesidiocoris tenuis* Reuter) (Urbaneja et al. 2009; Salas Gervassio et al. 2016b). Because of the low numbers recorded of these mirids, complementary prospections are recommended to be able to identify the species.

The greater abundance of mirid species in tomato crops, especially of *T. cucurbitaceus*, from the beginning of the cropping cycle (August to December) is probably related to the availability of prey (numerical response). *Tupiocoris cucurbitaceus* is the only species from the assemblage that has been reported as a natural enemy of *T. vaporariorum* and *T. absoluta* in Argentina (Cagnotti et al. 2020; López et al. 2019; Montiel Cáceres 2021). A decade ago, the company Brometán S.R.L. Argentina S.A. started its commercial production (Polack et al. 2017); however, it is noteworthy to mention that in this study, the co-occurrence of the predatory bug with these pests in field conditions was found mainly as independent. This result is relevant when considering augmentative releases of this biological control agent, since its effectiveness will depend, to some extent, on the encounter rates between the predator and the prey.

In relation to the other two families of heteropteran bugs recorded, the lygaeid *N. simulans* is a phytophagous species which was reported damaging several crops in Argentina (Dellapé 2014), and its pest status has been cited for soybean crops since it damages early vegetative crop stages (Aragón and Flores 2006). Populations of *Nysius* can increase in presence of its preferred host plant and eventually move to colonize new plant species, often of agricultural importance (Henry et al. 2015).

Conversely, despite most berytids appear to be predominantly phytophagous, many species exhibit predatory tendencies, especially on insects entrapped on the sticky stems of glandular plants (Henry 1997). There are no reports about predatory activity as a biocontrol agent of the berytid bug *J. sobrinus*; consequently, more studies are required to determine the feeding habits of this species in tomato crops.

At least other four species/morphospecies that conform the heteropteran bugs assemblage, i.e., *C. cincticornis*, *Dicyphus* sp. 1 and *Dicyphus* sp. 2, and *Nesidiocoris* sp., reported as zoophytophagous, could be also potential biocontrol candidates to manage horticultural pests — particularly *T. absoluta* — in Argentina. Preliminary studies showed that *C. cincticornis* nymphs and adults preyed on *T. absoluta* (Montiel Cáceres 2021). Regarding the other three taxa, as we mentioned above, species of the same genus are being used successfully in augmentative biocontrol programs (Calvo et al. 2012; Giorgini et al. 2019). Besides, it is well-known that habitat manipulation in an agroecosystem promotes biological diversity of natural enemies through differing patterns of crop colonization and niche partition (Snyder 2019).

Organic horticultural farms in NE Buenos Aires can support a diverse and abundant spontaneous heteropteran bug community, being some of them predatory species well-adapted to open-field and greenhouse tomato crops, and to spontaneous solanaceous species, such as *S. sisymbriifolium*. This study showed also that protected crops probably provide better conditions for the establishment of their populations, as is the case for *T. cucurbitaceus*, which becomes dominant in greenhouses. This constitutes an evidence that producers that reduce or eliminate applications of chemical pesticides at their farms could profit through conserving these natural enemies' populations in crop and non-crop vegetation to maximize pest control (van Driesche et al. 2008). An exception can be observed at Gorina site where only two species were found although most of individuals belonged to *T. cucurbitaceus*, a result reflected by the wider confidence interval observed (Fig. 5a).

In Argentina, there is important progress in the evaluation of other natural enemies of *T. vaporariorum* and *T. absoluta*. López and Botto (1995) and López et al. (2005) have studied various biological features of the parasitoid *Encarsia formosa* (Hymenoptera: Aphelinidae) that attacks *T. vaporariorum*. In relation to *T. absoluta*, the larval parasitoids *Dineulophus phthorimaeae* de Santis (Hymenoptera: Eulophidae) and *Pseudapanteles dignus* Muesebeck (Hymenoptera: Braconidae), which are spontaneously present in conventional and organic tomato farms, are also under assessment as biocontrol agents of this pest (Savino et al. 2012; Nieves et al. 2015; Salas Gervassio et al. 2016a; 2018;

2019). Thus, the combined action of these parasitoids, added to the mortality inflicted by predatory species that remain to be studied, could help to maintain these pests under the threshold action. Nonetheless, it is important to consider that predatory species can engage in competitive or intraguild predation interactions with other entomophagous species, which could affect biocontrol (Symondson et al. 2002). Hence, we propose to deepen biological and ecological studies of the natural enemies' complex of *T. vaporariorum* and *T. absoluta*, with the aim of synergizing their action in augmentative and conservation biological control programs and integrated pest management in Argentinian tomato crops.

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Author contribution RMC carried out the samplings, performed the analysis of data, and the interpretation and discussion of results. NGSG collaborated in the interpretation and discussion of results, prepared the draft of the manuscript, and participated in the final version of the manuscript. EM and PMD carried out the identification of all insects collected and participated in the edition of the final version of the manuscript. MGL participated in the planning of the assays, interpretation, and discussion of results, as well as in the writing of the final version of the manuscript. She also obtained the funds to carry out the investigation. MR participated in the planning of the assays, collaborated in the analysis of data, interpretation, and discussion of results, and in the writing of the final version of the manuscript, and also obtained the funds to carry out the investigation.

Declarations

Conflict of interest The authors declare no competing interests.

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