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Factors influencing short-term parasitoid establishment and efficacy for the biological control of *Halyomorpha halys* with the samurai wasp *Trissolcus japonicus*

Martina Falagiarda,[a] Veronica Carnio,[a,b] Serena Giorgia Chiesa,[c] Antonio Pignalosa,[a] Gianfranco Anfora,[d,e] Gino Angeli,[c] Claudio Ioriatti,[c] Valerio Mazzoni,[d] Silvia Schmidt[a] and Livia Zapponi[d,f*]

Abstract

BACKGROUND: Classical biological control has been identified as the most promising approach to limit the impact of the invasive pest species *Halyomorpha halys* (Heteroptera: Pentatomidae). This study investigated the parasitism rate at sites where the biocontrol agent *Trissolcus japonicus* (Hymenoptera: Scelionidae) was released and where its unintentional introduction took place, in the Trentino–South Tyrol region. The effect of land-use composition was studied to understand which factors favor the establishment of hosts and parasitoids, including native and exotic species.

RESULTS: The released *T. japonicus* were detected a year after the start of the program, with a significant parasitoid impact and discovery, compared to control sites. *Trissolcus japonicus* was the most abundant *H. halys* parasitoid, and *Trissolcus mitsukurii* and *Anastatus bifasciatus* were recorded also. The efficacy of *T. mitsukurii* was lower in sites where *T. japonicus* was successfully established, suggesting a possible competitive interaction. Parasitism level by *T. japonicus* at the release sites was 12.5% in 2020 and 16.4% in 2021. The combined effect of predation and parasitization increased *H. halys* mortality up to 50% at the release sites. Landscape composition analysis showed that both *H. halys* and *T. japonicus* were more likely to be found at sites with lower altitude and with permanent crops, whereas other hosts and parasitoids preferred different conditions.

CONCLUSION: *Trissolcus japonicus* showed a promising impact on *H. halys*, at release and adventive sites, with minor nontarget effects, mediated by landscape heterogeneity. The prevalence of *T. japonicus* in landscapes with permanent crops could support IPM in the future.

Supporting information may be found in the online version of this article.

Keywords: biocontrol; pest; BMSB; stink bug; alien species; landscape

1 INTRODUCTION

Even though herbivore stink bugs (Hemiptera: Pentatomoidaea) are not a common taxa of invasive insect species, their wide host-plant range enables them to cause extreme crop damage in invaded areas.[1] *Halyomorpha halys* (Stål, 1855) (Hemiptera: Pentatomidae) is a recent example of an unexpected impact that introduced stink bugs may have: native to East Asia, in a few decades it has become a key global agricultural pest. *Halyomorpha halys* was first recorded in the United States in the mid-1990s and in Europe almost 10 years later.[2] These introductions shared a few common steps: multiple arrivals probably associated with commercial trading;[3] population expansion often associated with urban areas;[4,5] and finally extensive crop damage, with a worrisome growing list of host plants.[6] In the invaded areas, *H. halys* reached high levels of population density and caused significant economic losses to farmers.[7–9]

* *Correspondence to: L Zapponi, Institute of BioEconomy, National Research Council of Italy, Via Francesco Biasi 75, 38098 S. Michele all'Adige (Trento), Italy. E-mail: livia.zapponi@cnr.it*

a *Institute for Plant Health, Entomology Group, Laimburg Research Centre, Auer, Bozen, Italy*

b *Faculty of Science and Technology, Free University of Bozen-Bolzano, Bozen, Italy*

c *Technology Transfer Centre, Fondazione Edmund Mach, S. Michele all'Adige, Trento, Italy*

d *Research and Innovation Centre, Fondazione Edmund Mach, S. Michele all'Adige, Trento, Italy*

e *Center for Agriculture, Food and Environment (C3A), University of Trento, S. Michele all'Adige, Trento, Italy*

f *Institute of BioEconomy, National Research Council of Italy, S. Michele all'Adige, Trento, Italy*

Integrated pest management (IPM) strategies for the management of *H. halys*, such as mass trapping, trap crops,[10] perimeter restructuring in apple orchards,[11–13] push–pull,[14] exclusion nets[15] and behavioral manipulation[16] alone had only reduced potential to significantly decrease the damage to fruits. Pest management utilizing insecticides has been investigated extensively,[17] however, as a result of the lack of effective monitoring tools, the resulting overuse of chemicals has contributed to disruption of low-impact IPM practices (traditionally employed for other pests) or caused secondary pest outbreaks.[18,19]

Stink bug invasions occurring in the last decades (e.g. *Bagrada hilaris* and *H. halys*) have revitalized the interest in classical biological control (CBC) as a sustainable management strategy.[20] CBC, with the release of antagonists native to the pest area of origin, has been advocated as the most promising approach to restore *H. halys* top-down control once introduced in newly invaded ranges.[21] *Trissolcus japonicus* (Ashmead) (Hymenoptera: Scelionidae) was identified as the most promising *H. halys* biocontrol agent (BCA),[22,23] considering both its specificity and high parasitization rate.[24,25] Adventive populations of *T. japonicus* have been recorded several times in the US since 2014[24,26,27] and in Europe since 2017.[28–30] To expand its distribution, a re-distribution program of individuals originated from adventive populations has been implemented in the US, placing *T. japonicas*-infested eggs[31] or releasing adults[32] in several states. Italy is the first country where a program with all key characteristics of classical biocontrol initiatives[33] has taken place: *T. japonicus* imported into quarantine facilities for host-range evaluation; obtention of release approval by the competent authorities (the Ministries for Agriculture and Environment and the National Institute of Health); experimental rearing of the BCA (no mass production in place); and inoculation of the individuals in the new area so that they could autonomously increase in response to pest populations.

A successful CBC program relies on the in-depth understanding of the traits underneath the interaction between the BCA, its target host, nontarget organisms and other parasitoids present in a particular environment. Nevertheless, the potential impact on nontarget species is fundamental to guiding policymakers in authorizing releases of exogenous organisms. Roland and Taylor[34] showed that landscape descriptors can be used to explain the different parasitism rate recorded for four parasitoids attacking the same host. Because the spatial scale at which species perceive the surrounding landscape, as well as the suitability of the different elements that form the land-use mosaic, influence trophic interactions, investigating how the landscape structure of the invaded range influences pest suppression may be critical.[35,36] Although previous studies showed that there is a significant edge effect on *H. halys* abundance[37] and feeding injury,[38] how landscape influences both its proliferation and suppression remains unexplored.

The goal of this study was to assess short-term BCA establishment and evaluate its efficacy. We aimed to investigate whether the parasitization rate increased with time; to evaluate the occurrence of nontarget effects; and to compare the efficacy of the BCA in comparison with other native and exotic parasitoids. Furthermore, we investigated the role of landscape elements in the establishment and spread of *H. halys* and its parasitoids. We evaluated the spatial scale, to understand whether pest infestation and parasitism rate could be favored by crop abundance and availability of semi-natural habitats.[39] Thus, we aimed to identify the most important landscape metrics and the most relevant spatial scale for a set of target species, which included *H. halys* and two native stink bugs, *Palomena prasina* and *Pentatoma rufipes* as parasitoid hosts[25,40] and three main stink bug parasitoids of the investigated area, *Anastatus bifasciatus, T. japonicus* and *T. mitsukurii*.[41]

2 MATERIALS AND METHODS

2.1 Study area

The study was carried out in northern Italy, in the Trentino–South Tyrol region [centroid: 46° 26′ N, 11° 17′ W; study area elevation: 75–635 m above sea level (a.s.l.)] (Fig. 1). Most of the regional territory is >1000 m a.s.l., and hence agricultural areas are concentrated in the valleys, where the main crops are vineyards (15 400 ha) and apple orchards (28 000 ha), the latter covering 15% of European production.[42] In this area, large populations of *H. halys* have been recorded since 2017.[43,44] From 2020 to 2022 the area has been involved in a national CBC program with the release of *T. japonicus* to manage *H. halys* populations.

The *T. japonicus* release sites (Supporting Information Tables S1 and S2) were selected after field inspections carried out 6–10 months before the initial release, where the presence of *H. halys* individuals and/or attractive host plant species was assessed. To improve the probability of establishment, only sites with absent or reduced chemical input were selected. A minimum distance of 1 km was ensured between neighboring release sites and areas where adventive populations of *T. japonicus* were documented.[41]

2.2 Rearing and release of *Trissolcus japonicus*

The parasitoids used for the releases were provided by CREA-DC (Italy), and they originated from the same population on which the risk assessment study was performed.[45] They were reared at the Fondazione Edmund Mach (Italy) and Research Centre Laimburg (Italy) on *H. halys* egg masses from specifically maintained colonies. Following a national protocol for *T. japonicus* release, the individuals were placed in plastic tubes (VWR 50-mL centrifuge tubes, 525–0611) with honey, maintained in climatic chambers at 24°C ± 1 °C, 60 ± 5% relative humidity (RH) and 16 h: 8 h photoperiod. All released individuals were 1–3 weeks old, to allow females to maximize ovary egg load,[46] without compromising their lifespan (reported at 1–3 months[47]). At each site, three releases of 100 females and 10 males each, were performed 3 weeks apart, from the end of June to mid-August in 2020 and 2021.

2.3 Sampling design

In order to address the dual purpose of this project, two sets of sampling sites were identified: Set 1, to compare the presence of *H. halys* parasitoids between release, adventive and control locations; and Set 2, to identify landscape factors potentially influencing parasitoid recovery after release.

Set 1 included three types of sites (Table S1). Establishment sites (a, $n = 9$) were where *T. japonicus* was found after its initial release in 2020 and no other releases were performed in 2021. In these sites, *T. japonicus* presence was not recorded before the first release.[41] The sites were sampled in both 2020 and 2021 in order to verify *T. japonicus* establishment, and accordingly they were named 'Establishment 2020' and 'Establishment 2021'. Adventive sites (b, $n = 2$) were where adventive

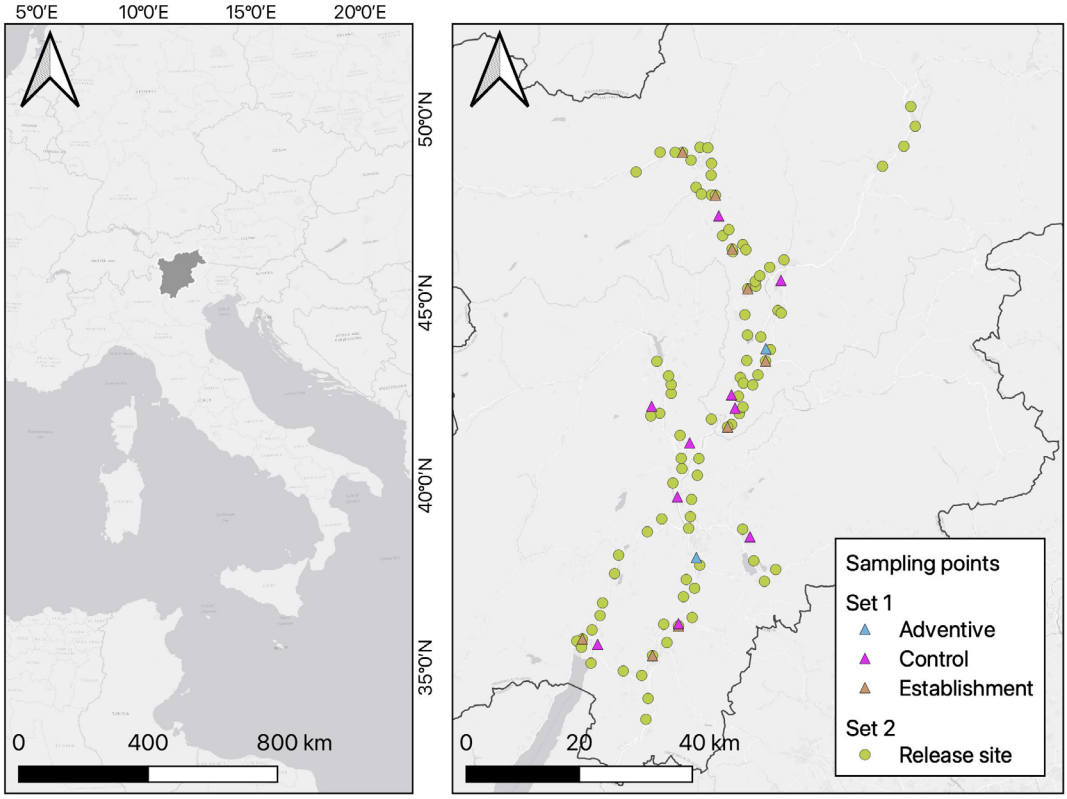

Figure 1. Study area location showing the distribution of the two sets of sampling points.

populations of *T. Japonicus* were found before the beginning of the biocontrol program, in 2019, after an extensive monitoring effort throughout the region.[41] These sites were sampled only in 2021. Control sites (c, $n = 10$) were where no releases were performed and no adventive populations were detected in 2019. Control sites were sampled only in 2021. All sites in Set 1 were surveyed four times every 4 weeks, from July (Week 27) to September (Week 39).

Set 2 included all the sites where *T. japonicus* was released in 2020 and 2021 (Table S2). These sites were selected according to *H. halys* presence (recorded in the previous years with traps and visual sampling) and availability of host plants[48] and were surveyed once before (June) and twice after (mid-August to mid-October) the releases with a minimum interval of 8 weeks between consecutive surveys.

The sampling protocol was the same for both sets and involved a visual inspection of all the vegetation (herbs, shrubs and trees), from the ground to 2 m height, in an area of 50 m radius for 1 h per session, searching for Acanthosomatidae and Pentatomidae egg masses. The leaves with egg masses were collected and stored in plastic tubes and brought to the laboratory for further analysis.

2.4 Morphological identification of Pentatomidae egg masses and parasitoid species

All egg masses were examined with a stereomicroscope and determined to species or genus level according to Derjanschi and Péricart,[49] Péricart[50] and Ribes & Pagola-Carte,[51] as well as a previously developed reference collection.[41] Single eggs were categorized in four groups: hatched, unhatched, predated[52] and parasitized (including parasitoids emerged before collection and in the laboratory). For *H. halys*, emergence holes were identified according to their shape and morphology of meconial[53] to species or family level. Emerged parasitoids were transferred in 70% ethanol and morphologically identified using a stereomicroscope and the taxonomic keys developed by Askew and Nieves-Aldrey[54] for Eupelmidae, Sabbatini Peverieri *et al.*[55] for *Acroclisoides*, and Talamas *et al.*[56] and Tortorici *et al.*[57] for *Trissolcus*.

2.5 Parasitoid efficacy

Two indices of parasitoid efficacy were obtained for the collected egg masses: 'Discovery efficiency' and 'Parasitoid impact'.[58] The discovery efficiency describes the parasitoid's ability to find the egg masses, calculated as the number of egg masses with at least one parasitized egg divided by the total number of egg masses found in a site. The parasitoid impact was calculated as the number of parasitized eggs divided by the total number of collected eggs. These analyses were performed for *H. halys* egg masses collected in Set 1. Only egg masses from which a single parasitoid species emerged were included, to avoid under-/overestimation related to intrinsic competition or hyperparasitism. Besides, the number of female and male emerged parasitoids for each species were recorded to calculate the proportion of emerged females.

2.6 Landscape structure

In order to determine the effect of landscape scale variation on the distribution of stink bug species (*H. halys*, *P. prasina*, *P. rifipes*) and parasitoids (*A. bifasciatus*, *T. japonicus*, *T. mitsukurii*), QGIS 3.22 (QGIS.org, 2022) was used to calculate

the amount of different land-cover types surrounding the release points. Land-cover maps were obtained from the open data portals of the provinces of Bolzano and Trento. We considered three nested circular buffers to compare the landscape composition at the longest investigated dispersal distance for *T. japonicus* (50 m[32]) with wider spatial scales (250 and 500 m). For each buffer, landscape data were gathered using five land-cover categories, where 33 land-cover types were

Table 1. Numbers of egg masses and eggs of each stink bug collected species, with the percentage of hatched, unhatched, predated and parasitized eggs, and emerged parasitoids, in the release sites of *T. japonicus* in 2020, in the control sites and the sites with adventive population of *T. japonicus* before 2020

		Egg masses		Eggs					
Type of site	Species	No.	Parasitized %	No.	Hatched %	Unhatched %	Predated %	Parasitized %	Species and number of parasitoids
Establishment	*Acanthosoma haemorrhoidale*	2	50.00	54	0	50.00	0	50.00	*A. bifasciatus* (22), *T. elasmuchae* (5)
	Acrosternum heegeri	1	0.00	14	100.0	0.00	0.00	0.00	-
	Eurydema ventralis	1	0.00	11	100.0	0.00	0.00	0.00	-
	Graphosoma lineatum	2	50.00	29	44.83	10.34	0.00	44.83	*T. japonicus* (13)
	Halyomorpha halys	93	53.76	2487	34.01	13.59	12.71	39.69	*A. sinicus* (10), *A. bifasciatus* (284), *T. japonicus* (666), *T. mitsukurii* (21), *Scelionidae indet.* (6)
	Palomena prasina	22	40.91	393	37.41	21.88	6.87	33.84	*A. sinicus* (12), *A. bifasciatus* (11), *Telenomus spp.* (106), *T. japonicus* (4)
	Pentatoma rufipes	6	66.67	83	16.87	1.2	19.28	62.65	*T. japonicus* (28), *Scelionidae indet.* (14)
	Rhaphigaster nebulosa	9	44.44	124	25.81	40.32	2.42	31.45	*A. bifasciatus* (14), *T. cultratus* (5), *Scelionidae indet.* (20)
Control	*Acanthosoma haemorrhoidale*	1	100.00	28	0.00	0.00	0.00	100.00	*Scelionidae indet.* (28)
	Acrosternum heegeri	4	75.00	60	53.33	16.67	0.00	30.00	*A. bifasciatus* (18)
	Graphosoma lineatum	1	0.00	12	50.00	16.67	33.33	0.00	-
	Halyomorpha halys	84	35.71	2215	55.26	12.87	10.38	21.49	*A. bifasciatus* (204), *T. japonicus* (54), *T. mitsukurii* (218)
	Nezara viridula	2	0.00	166	48.19	51.81	0.00	0.00	-
	Piezodorus lituratus	2	50.00	23	34.78	34.78	13.05	17.39	*Scelionidae indet.* (4)
	Palomena prasina	12	83.33	255	5.88	24.31	18.44	51.37	*A. bifasciatus* (39), *T. mitsukurii* (13), *Scelionidae indet.* (79)
	Pentatoma rufipes	6	33.33	84	50.00	3.57	17.86	28.57	*T. cultratus* (11), *Scelionidae indet.* (13)
	Rhaphigaster nebulosa	4	50.00	55	47.27	29.09	0.00	23.64	*Scelionidae indet.* (13)
Adventive	*Acanthosoma haemorrhoidale*	1	100.00	26	23.08	30.77	0.00	46.15	*A. bifasciautus* (12)
	Eurydema ventralis	1	0.00	14	100.00	0.00	0.00	0.00	-
	Halyomorpha halys	59	77.97	1525	21.31	20.79	3.21	54.69	*A. sinicus* (7), *A. bifasciatus* (293), *T. cultratus* (2), *T. japonicus* (425), *T. mitsukurii* (100), *Scelionidae indet.* (7)
	Nezara viridula	2	0.00	168	10.12	89.88	0.00	0.00	-
	Palomena prasina	4	75.00	106	14.15	27.36	3.77	54.72	*A. sinicus* (13), *Scelionidae indet.* (45)
	Pentatoma rufipes	2	50.00	28	50.00	0.00	10.71	39.29	*T. japonicus* (11)
	Rhaphigaster nebulosa	2	50.00	25	40.00	0.00	20.00	40.00	*Scelionidae indet.* (10)

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pooled: permanent crops (fruit trees, berry plantations, olive groves and vineyards), annual crops (arable land), semi-natural habitats (forest, shrub and herbaceous vegetation associations), human settlements (continuous and discontinuous urban fabric; industrial and commercial units) and transport (road and rail networks).

2.7 Statistical analysis

Data analysis and plotting were performed with R.[59] Because data were not normally distributed, a Kruskal–Wallis test followed by Dunn's *post hoc* test with Bonferroni correction was used to compare the impact, discovery efficiency and sex ratio for the different parasitoid species, recorded in Set 1 sites. Cohen–Friendly association plots, which indicate deviation from independence in 2D contingency tables, were used to detect significant differences and obtained with the VCD package.[60] Package CHISQ.POST.HOC'[61] was used to interpret chi-square contingency-table test results. Release sites were subdivided with *k*-means clustering according to the surrounding land cover, identifying a permanent crop–semi-natural habitats gradient. The number of parasitized, predated and hatched eggs collected in the two surveys was analyzed per week and year (Set 1) and per landscape cluster (Set 2).

In order to compare the parasitization rate recorded in control and adventive sites on the same year (2021), we used generalized linear mixed models (GLMMs) using package GLMMTMB,[62] to account for the repeated surveys performed in each site. Adventive sites were not included because of the

Table 2. Numbers of egg masses and eggs of each stink bug collected species, before and after the release of *T. japonicus* in 2021, showing the percentage of hatched, unhatched, predated and parasitized eggs, and emerged parasitoids

		Egg masses		Eggs					
Tim	Species	No.	Parasitized %	No.	Hatched %	Unhatched %	Predated %	Parasitized %	Species and number of parasitoids
Before release	*Acanthosoma haemorrhoidale*	9	66.67	241	16.18	29.46	6.22	48.13	*A. bifasciatus* (2), *T. elasmuchae* (78), *Scelionidae* (36)
	Acrosternum spp.	2	0.00	31	100.00	0.00	0.00	0.00	-
	Arma custos	2	0.00	25	100.00	0.00	0.00	0.00	-
	Dolycoris baccarum	2	100.00	54	0.00	16.67	1.85	81.48	*Telenomus spp.* (23), *T. belenus* (21)
	Eurydema ventralis	14	57.14	161	12.42	36.65	0.00	50.93	*T. viktorovi* (82)
	Halyomorpha halys	107	11.21	2854	78.03	12.68	3.22	6.10	*A. bifasciatus* (59), *Telenomus spp.* (1), *T. cultratus* (20), *T. japonicus* (71), *T. mitsukurii* (23)
	Nezara viridula	1	0.00	67	85.07	14.93	0.00	0.00	-
	Palomena prasina	50	66.00	1192	29.53	17.03	4.19	48.57	*A. sinicus* (86), *A. bifasciatus* (43), *Telenomus spp.* (188), *T. belenus* (8), *T. mitsukurii* (43), *Scelionidae indet.* (211)
	Piezodorus lituratus	4	25.00	69	14.49	5.80	40.58	39.13	*Telenomus spp.* (27)
	Rhaphigaster nebulosa	14	57.14	194	31.96	14.43	6.70	46.91	*A. bifasciatus* (29), *T. belenus* (14), *T. cultratus* (14), *Telenomus spp.* (20), *Scelionidae indet.* (14)
After release	*Aelia spp.*	1	0.00	13	0.00	0.00	100.00	0.00	-
	Dolycoris baccarum	2	50.00	28	50.00	0.00	0.00	50.00	*T. mitsukurii* (5)
	Graphosoma lineatum	2	100.00	28	10.71	21.43	28.57	39.29	*A. bifasciautus* (6), *T. japonicus* (5)
	Halyomorpha halys	237	51.48	6237	36.04	13.45	12.03	38.48	*A. bifasciatus* (525), *A. Sinicus* (223), *T. japonicus* (1022), *T. kozlovi* (1), *T. mitsukurii* (599), *Scelionidae indet.* (30)
	Nezara viridula	14	21.43	1218	57.80	37.52	0.66	4.02	*A. bifasciatus* (20), *Scelionidae indet.* (29)
	Palomena prasina	11	63.64	248	10.89	13.31	28.63	47.18	*A. sinicus* (2), *A. bifasciatus* (14), *T. mitsukurii* (4), *Scelionidae indet.* (97)
	Pentatoma rufipes	30	86.67	437	9.84	16.02	8.01	66.13	*A. sinicus* (54), *A. bifasciatus* (32), *T. cultratus* (40), *T. japonicus* (55), *T. kozlovi* (2), *T. mitsukurii* (51), *Scelionidae indet.* (56)
	Rhaphigaster nebulosa	3	66.67	42	33.33	2.38	50.00	14.29	*A. bifasciatus* (5)

reduced number of replicates. Because the collected data were skewed, we used Tweedie GLMMs with logit link, where site ID was used as random factor. The effect of the survey week as well as the altitude of the site (three categories: 0–200, 201–400, 401–650 m a.sl.) were considered also. The tested model was:

Parasitization rate (response variable) ~ Type of site (control/establishment) + Week number + Altitude The effect of landscape structure was analyzed with GLMs using package LME4.[63] To determine which spatial scale was more relevant for the target species, an *a priori* set of models was built and collinearity was checked, ensuring that it did not exceed 30% among variables in the same model.[64] For stink bugs (*H. halys*, *P. prasina* and *P. rufipes*) the tested models included:

Number of egg masses (response variable) ~ altitude (explanatory variable)

Number of egg masses ~ perennial crops

Number of egg masses ~ annual crops

Number of egg masses ~ semi-natural habitats + human settlements + transport

For parasitoids (*A. bifasciatus*, *T. japonicus* and *T. mitsukurii*) models included:

Presence/absence ~ altitude

Presence/absence ~ perennial crops

Presence/absence ~ annual crops

Presence/absence ~ semi-natural habitats + human settlements + transport

The same set of models was applied to each target species, considering each buffer separately.

This analysis was performed on Set 2 points ($n = 81$), considering only the data collected in 2021 after *T. japonicus* release. For parasitoids, we modelled species occurrence (presence/absence) with binomial GLMs with a cloglog-link function. For stink bugs, the response variable was the number of collected egg masses, because the analyses revealed that the data suffered from overdispersion, negative binomial GLMs with a log-link were used.

All variables were standardized before the analyses, model assumptions were verified following Zuur & Ieno[65] and with the package DHARMa.[66] Akaike's information criterion (AIC) and model performance indices[67,68] were used for model selection.[68] Predictor effect plots from the package EFFECTS'[69] were used to visualize the fitted coefficients.

3 RESULTS

3.1 Stink bug egg masses and parasitoid seasonal abundance

In 2020, total 991 stink bug egg masses (28 478 eggs) were collected, 84.0% belonging to *H. halys* and the rest to nine other stink bug species (Table S3). In 2021, a total of 1829 stink bug egg masses (49 699 eggs) were collected, 77.3% belonging to *H. halys* and the rest to 12 other stink bug species (Tables 1 and 2). From all these, 12 species of parasitoids emerged: the two exotic *Trissolcus* (*T japonicus* and *T. mitsukurii*) and 10 native species belonging to two families, Eupelmidae and Scelionidae (Tables 1 and 2). The hyperparasitoid *Acroclisoides sinicus* (Hymenoptera: Pteromalidae) emerged also. The highest number of *H. halys* parasitized egg masses were recovered from *Acer* spp., *Prunus* spp. and *Corylus avellana*, with the highest number of parasitized eggs being found on *Acer* spp. and *Prunus* spp. Overall, the recovery of the three parasitoid species of *H. halys* was similar

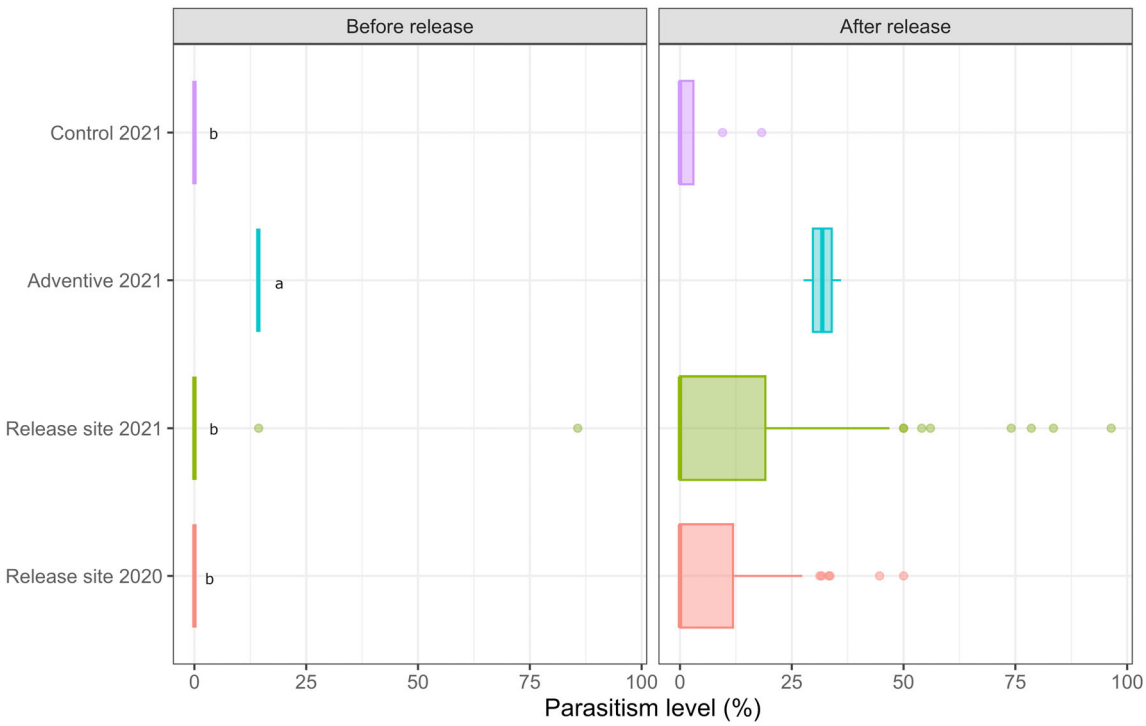

Figure 2. Proportion of *H. halys* eggs parasitized by *T. japonicus*, recorded in the release sites in 2020 and 2021, before release (Kruskal–Wallis, $H = 31.3$, df = 3, $P < 0.01$) and after release (Kruskal–Wallis, $H = 4.56$, df = 3, $P = 0.21$). Letters indicate significant differences ($P < 0.05$) after Dunn's *post hoc* test with Bonferroni correction.

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to the abundance trend of its egg masses, with an initial small peak during Week 24 and the highest peak during Week 36 (Fig. S1).

3.2 Release and establishment of *T. japonicus*

Trissolcus japonicus was released in Trentino–South Tyrol at 62 sites in 2020 (20 460 released individuals) and at 81 sites in

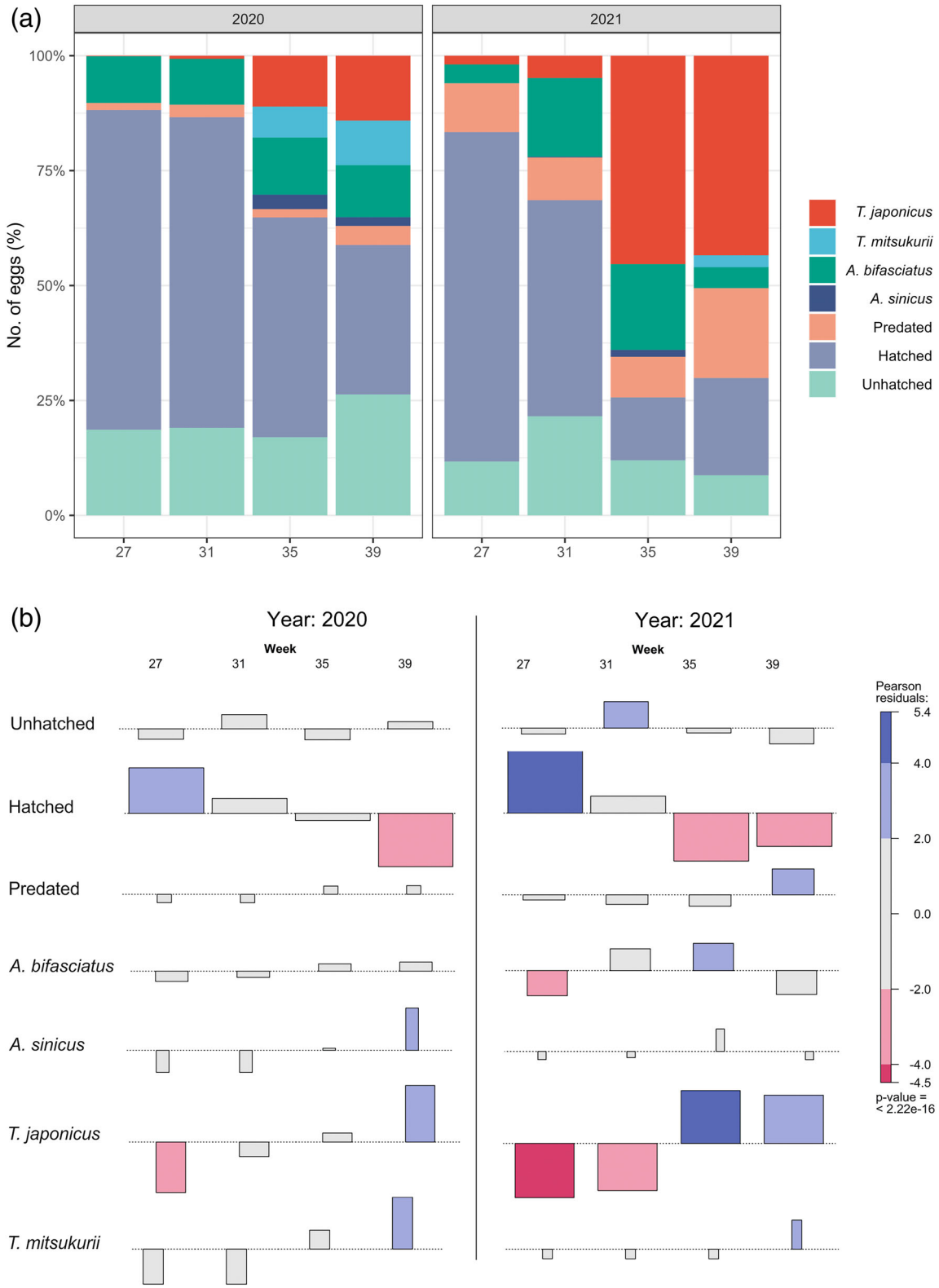

Figure 3. Number of *H. halys* hatched, unhatched, predated and parasitized in 2020 and 2021 in the establishment sites (Set 1): (a) bar plot and (b) association plot, where rectangle size is proportional to the amount of the chi-square Pearson residuals; color shading shows the magnitude and significance (red, significantly smaller than the expected frequencies; blue, significantly larger than the expected frequencies).

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2021 (26 730 released individuals). In 2020, it was recaptured at 26 of 62 sites (42%) while in 2021 at 29 sites out of 81 sites (36%).

Trissolcus japonicus parasitism rate (expressed as the proportion of parasitized eggs within an egg mass) recorded early in the season (before release) was higher in adventive sites than in the other sites, where it was almost null (Kruskal–Wallis, $H = 31.3$, df = 3, $P < 0.01$). After release, the parasitism rate in the release sites was 12.52% in 2020 and 16.39% in 2021, with a progressive numerical increase (Fig. 2).

At nine of the 26 sites where *T. japonicus* was recaptured in 2020, no further releases were performed (these nine sites were used to obtain the establishment data during 2020 and 2021). During the 2021 season starting from the beginning of July [Fig. 3(a)] the releases carried out in the previous year led to the recovery of several individuals in six of nine sites. At these sites, *T. japonicus* emerged from 27% of the collected eggs, whereas *A. bifasciatus* emerged from 11% and *T. mitsukurii* from 1% of the collected eggs. The percentage of *H. halys* eggs parasitized by *T. japonicus* was the highest in August 2021 (45.2%), whereas in the same period during the 2020 it was 17.4%. The number of eggs parasitized by *T. japonicus* was significantly higher for each week in 2021 compared to 2020, with a lower number of hatched eggs from the begging of August (Week 31) onwards (Table 3). The contribution of other parasitoids plus predators was lower in 2020 during the Week 31, yet it did not differ in other periods. In 2021, the observed significant decrease in hatched eggs from the end of August (weeks 35 and 39) corresponded to a significant increase in the number of emerged *T. japonicus* [Fig. 3(b)].

For the 2021 release sites, the subdivision of the sites in three clusters based on the surrounding vegetation (permanent crops and semi-natural habitats) emphasized the pre-release (June 2021) presence of *T. japonicus* only in the semi-natural habitats and intermediate sites [Fig. 4(a)]. After the release, the number of eggs parasitized by *T. japonicus* become higher in sites surrounded by perennial crops [Fig. 4(b)]. Conversely, egg predation and the occurrence of *A. bifasciatus* were more frequent in sites with high abundance of semi-natural habitats. In three control sites (which were <3 km distant from the closest release points) we recorded the presence of *T. japonicus*.

The parasitism rate recorded was significantly higher in establishment than in control sites (Table 4); the type of site was the strongest predictor, followed by a positive effect of week (Fig. 5), whereas altitude had a weaker negative effect.

3.3 Parasitoid impact

The performance of the three most abundant parasitoids demonstrated different trends at sites in Set 1 (establishment 2020 and 2021, adventive and control). Parasitization by *T. japonicus* was lower (Table 5; Fig. 6) at the control sites (mean impact = 5.62%; mean discovery = 4.17%), in comparison with establishment (mean impact = 32.98%; mean discovery = 30.62%) and adventive sites (mean impact = 41.55%; mean discovery = 41.66%). Conversely, the effectiveness of *T. mitsukurii* was lower (Table 4; Fig. 5) at the establishment sites in 2021 (mean impact = 0.40%; mean discovery = 0.40%) compared to control (mean impact = 16.88%; mean discovery = 18.07%). No significant differences were observed for *A. bifasciatus* (Table 5; Fig. 6).

The recorded sex-ratio was similar for *T. japonicus* and *T. mitsukurii*, with a higher proportion of females than in collected *A. bifasciatus* (Table S4).

3.4 *Trissolcus japonicus* impact on nontarget species

In 2020, *T. japonicus* emerged from 62 eggs of *Pentatoma rufipes* (16.2% of collected eggs). In 2021, it emerged from *P. rufipes* (94 eggs, 14.9% of collected eggs), *Palomena prasina* (4 eggs, 0.2% of collected eggs) and *Graphosoma lineatum* (18 eggs, 26.1% of collected eggs). Parasitization of *P. prasina* eggs was observed near the end of August, whereas parasitization was from September to the beginning of October for *P. rufipes* eggs and in September for *G. lineatum* eggs.

Table 3. Chi-square test and *post hoc* testing for significant differences in the number of *H. halys* in the categories: parasitized by *T. japonicus*, predated and parasitized by other species (other biocontrol), hatched and unhatched per week in 2020 and 2021 in the establishment sites (Set 1)

		Year		Chi-square test of independence			*Post hoc*	
Week	Category	2020	2021	χ^2	df	*P*-value	Residuals	*P*-value
27	*T. japonicus*	1	7	21.659	3	0.0001	3.515	0.004
	Other biocontrol	98	54				1.445	1
	Unhatched	156	43				−2.976	0.023
	Hatched	582	263				0.743	1
31	*T. japonicus*	3	34	60.783	3	<0.0001	3.879	0.001
	Other biocontrol	56	186				5.582	<0.001
	Unhatched	84	151				1.027	1
	Hatched	298	329				−6.802	<0.001
35	*T. japonicus*	307	272	487.973	3	<0.0001	20.191	<0.001
	Other biocontrol	669	174				2.51	0.097
	Unhatched	472	72				−3.026	0.02
	Hatched	1327	82				−15.383	<0.001
39	*T. japonicus*	112	353	209.934	3	<0.0001	12.956	<0.001
	Other biocontrol	215	217				−0.175	1
	Unhatched	209	71				−9.294	<0.001
	Hatched	258	172				−5.133	<0.001

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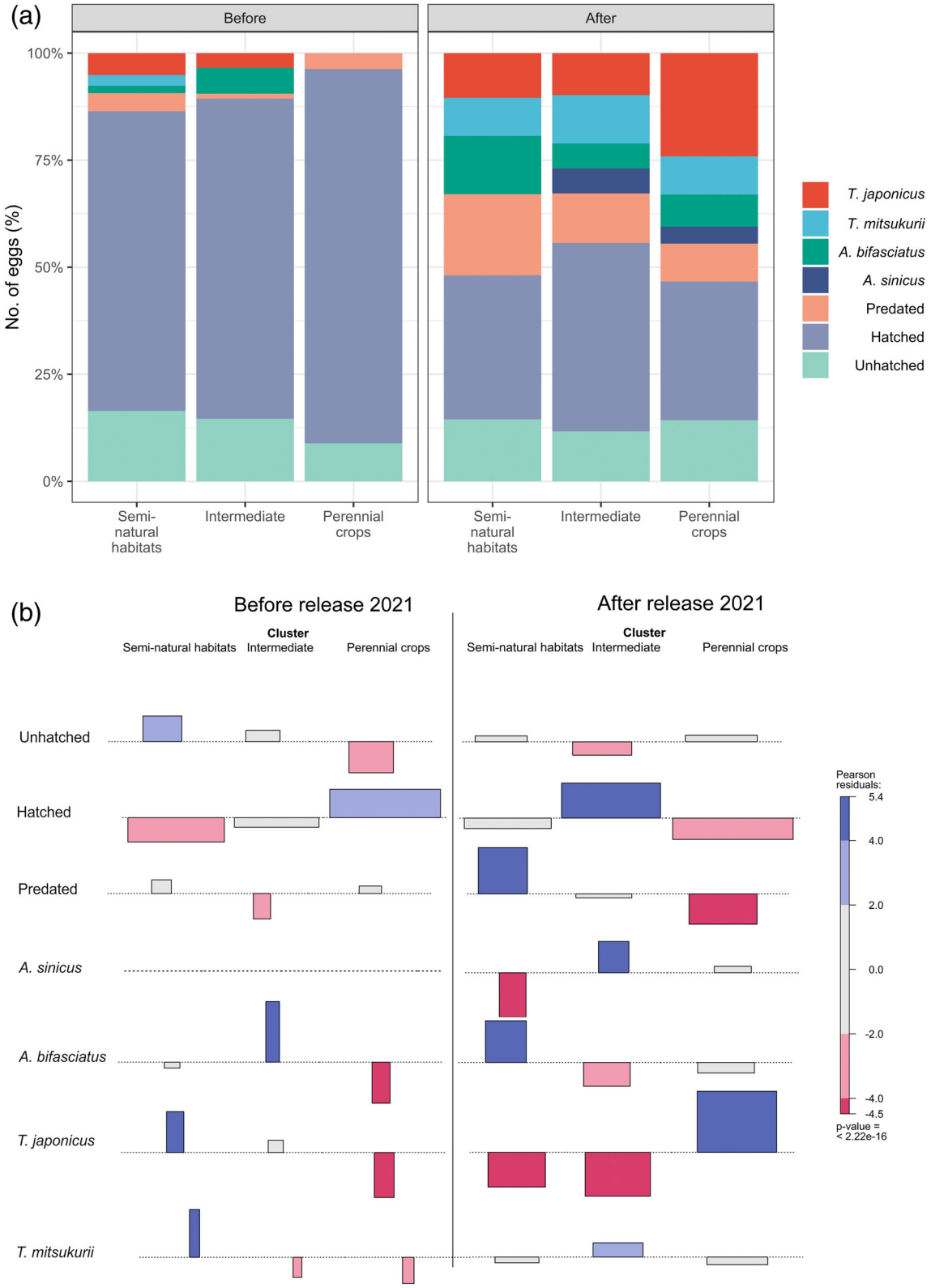

Figure 4. Association plot for the number of eggs collected before and after *T. japonicus* introduction in the release sites (Set 2), for each category per before and after release. Sites were grouped in three clusters corresponding to a semi-natural habitat to permanent crops gradient. Rectangle size is proportional to the amount of the chi-square Pearson residuals; color shading shows the magnitude and significance (red, significantly smaller than the expected frequencies, blue,- significantly larger than the expected frequencies).

3.5 Impact of landscape composition and spatial scale

Our validation process confirmed that the models complied with underlying assumptions. The GLM results revealed that target species responded neither to the same factors nor to the same spatial scale. The performance analysis on the species distribution as a function of land use disclosed that the best models for

Table 4. Estimated regression parameters, standard errors, z-values and *P*-values for the negative binomial GLMM model on the parasitization rate recorded in 2021 in establishment and control sites

	Estimate	SE	*z*-value	*P*-value
Intercept	−3.646	2.047	−1.781	0.075
Type: Establishment	2.003	0.724	2.766	0.006
Week	0.136	0.058	2.347	0.019
Altitude: 201–400 m	−0.269	0.798	−0.336	0.737
Altitude: 401–650 m	−26.490	8739.175	−0.003	0.998

H. halys and *T. japonicus* included the same factors: perennial crops and the combination of semi-natural habitats, transport and human settlements within the 500-m buffer (Tables 6, 7 and S5). For *T. japonicus*, we detected a negative effect of annual crops in the 500-m buffer (which were inversely correlated to perennial crops). Conversely, the most accurate models for *P. prasina* and *P. rufipes* included altitude and the combination of semi-natural habitats, transport and human settlements, within the 500- and 50-m buffers. None of the evaluated factors were significant for *A. bifasciatus* whereas *T. mitsukurii* responded only to altitude.

Plotting the effect of the most relevant factors included in the most accurate models (Figs 7 and 8) demonstrated that both *H. halys* and *T. japonicus* responded negatively to altitude and to semi-natural habitats (500-m buffer) and positively to perennial crops (500-m buffer). The occurrence of both *P. prasina* and *P. rufipes* egg masses was favored by altitude. For *P. prasina* the presence of semi-natural habitats (500-m buffer) had a positive effect whereas perennial crops (250-m buffer) had a negative impact. Landscape composition did not have a significant effect on *P. rufipes* (Fig. 7). Apart from a negative effect of altitude, the remaining factors had only a marginal effect on *A. bifasciatus* and for *T. mitsukurii*, all models had similar AIC (Table 7) values and the plots showed wide confidence intervals (Fig. 8).

4 DISCUSSION

A year after the initial release, *T. japonicus* was detected in numerous sites, proving successful overwintering by *T. japonicus* individuals. Redistributed *T. japonicus* survived average winter lows of −3 °C in Oregon (US),[32] and the recovery of several egg masses parasitized by *T. japonicus* in the establishment sites supports that they can survive at the local climatic conditions winter (with lows down to −5 °C; temperature recorded by local weather stations), largely exceeding laboratory-established lower lethal temperature values.[70] Despite the relatively small number of individuals introduced (330 yearly per site), our results are corroborated by a significantly higher presence of *T. japonicus* in the release sites compared to control sites, in terms of parasitism rate, impact and discovery. The latter indices had similar values in each group of sites, suggesting that the searching ability and the efficiency as biocontrol agent varied together. Comparable small inoculations of parasitoids were adopted in the last two CBC programs carried out in Italy.[71,72] Similar promising results were obtained within a few years after the first releases of the parasitoid *Torymus sinensis* (Kamijo) (Himenoptera: Torymidae) and *Neodryinus typhlocybae* (Ashmead) (Himenoptera: Dryinidae), to control the chestnut gall wasp *Dryocosmus kuriphilus* (Yasumatsu) (Himenoptera: Cynipidae)[73] and the planthopper *Metcalfa pruinosa* (Say) (Homoptera: Flatidae),[74,75] respectively.

The parasitoid effectiveness recorded at the establishment sites documented a positive trend with parasitization rates during the second year comparable to what was observed at sites where adventive *T. japonicus* populations have been recorded since 2019. However, such rates are still lower than what was recorded in its native range in northern China (36% of eggs parasitized by *T. japonicus*, 47% total parasitized eggs) by Zhang *et al.*,[22] suggesting a possible potential for increase in the future. From the 2020 to 2021 season, a considerable increase in egg predation also was observed. Unfortunately, these levels of biocontrol offered by native predators were insufficient to have an impact on *H. halys*, similar to the results recorded by Morrison *et al.*[52]

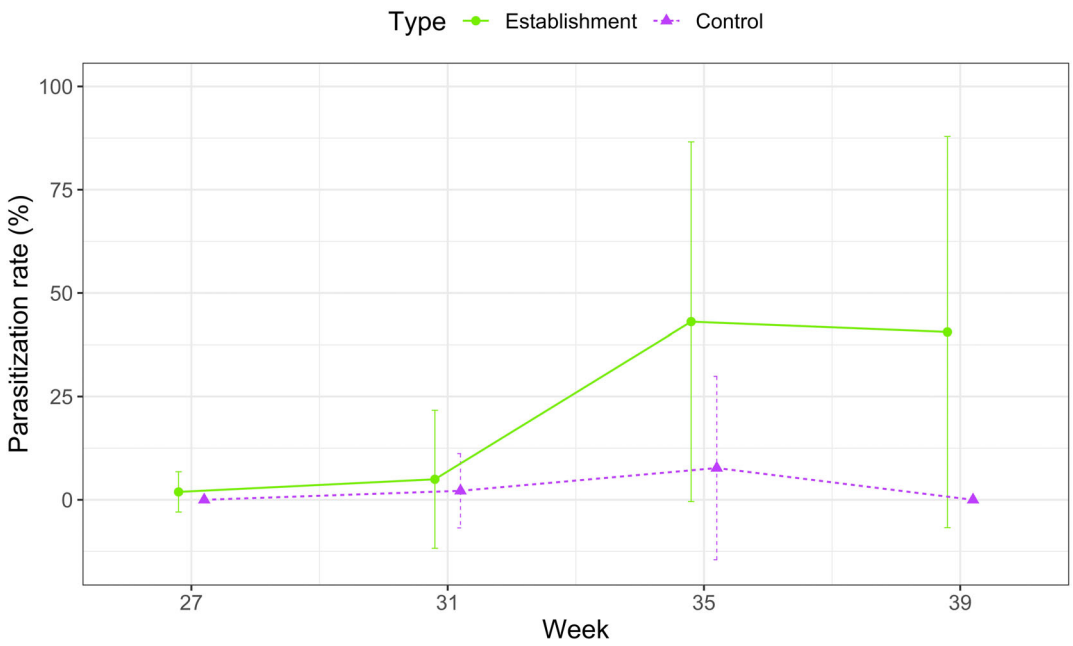

Figure 5. Parasitization rate recorded per survey week in 2021 in control and establishment sites.

Table 5. Comparison of the parasitoid efficacy recorded in the 2021 in the sites in Set 1: results of the Kruskal–Wallis test followed by Dunn's *post hoc* test with Bonferroni correction

Species	Index	*H*	df	*P*-value	Comparison	Z	*P*-value
Trissolcus japonicus	Parasitoid impact	10.46	3	0.02	Adventive–Control	2.32	0.06
					Adventive–Establishment 2020	1.08	0.42
					Control–Establishment 2020	−2.06	0.08
					Adventive–Establishment 2021	0.58	0.56
					Control–Establishment 2021	−2.78	0.03
					Establishment 2020–Establishment 2021	−0.78	0.52
	Parasitoid discovery	11.13	3	0.01	Adventive–Control	2.38	0.05
					Adventive–Establishment 2020	0.96	0.5
					Control–Establishment 2020	−2.35	0.04
					Adventive–Establishment 2021	0.64	0.63
					Control–Establishment 2021	−2.78	0.03
					Establishment 2020–Establishment 2021	−0.5	0.62
Trissolcus mitsukurii	Parasitoid impact	10.9	3	0.01	Adventive–Control	−0.15	0.88
					Adventive–Establishment 2020	0.79	0.51
					Control–Establishment 2020	1.57	0.18
					Adventive–Establishment 2021	1.81	0.21
					Control–Establishment 2021	3.19	0.01
					Establishment 2020–Establishment 2021	1.67	0.19
	Parasitoid discovery	11.78	3	0.01	Adventive–Control	−0.43	1
					Adventive–Establishment 2020	0.58	1
					Control–Establishment 2020	1.67	0.57
					Adventive–Establishment 2021	1.65	0.59
					Control–Establishment 2021	3.38	0
					Establishment 2020–Establishment 2021	1.76	0.48
Anastatus bifasciatus	Parasitoid impact	1.37	3	0.71	Adventive–Control	1.1	1
					Adventive–Establishment 2020	0.71	1
					Control–Establishment 2020	−0.65	0.62
					Adventive–Establishment 2021	0.68	0.99
					Control–Establishment 2021	−0.66	0.77
					Establishment 2020–Establishment 2021	−0.03	0.98
	Parasitoid discovery	2.17	3	0.54	Adventive–Control	1.24	1
					Adventive–Establishment 2020	0.84	1
					Control–Establishment 2020	−0.66	1
					Adventive–Establishment 2021	0.53	1
					Control–Establishment 2021	−1.13	1
					Establishment 2020–Establishment 2021	−0.48	1

However, combining the contributions of predators and parasitoids (plus the presence of unhatched eggs) the recorded mortality exceeded 50% in 2021 at the release sites. Traditionally, the parasitization rate and the impact on population density are considered proxies to assess the success of a CBC program.[76] However, in a field IPM context, the damage mitigation can be the result of combining multiple techniques, and therefore even a partial impact on the pest density can still indicate a potential for a long-term success.

In our study, the CBC program was preceded by the unintentional introduction of the exotic natural enemy, and thus the recorded individuals may represent a mixture of both introductions, as suggested for previous case studies.[77] Still, in the survey performed in the same region a year before the first release,[41] *T. japonicus* was recorded in only one site (one of the two adventive sites included in this study) with sentinel egg masses (parasitism rate 0.4%), whereas it did not emerge from any of the 585 egg masses collected in the same areas where the releases took place. This lends weight to the argument that the adventive populations were still only locally abundant when the CBC program was initiated and that the released individuals played a major role in the parasitism rates recorded. However, without a genetic characterization of the different strains (i.e. adventive and released) we cannot exclude the contribution of dispersing adventive populations.

In terms of seasonal phenology, we recorded the emergence of *T. japonicus* from the beginning of July, reaching its maximum at the end of August, following *H. halys* population dynamics and in a similar way to what has been observed in Japan.[78] The previously observed delay in the occurrence of exotic parasitoids compared to the native ones[48] was no longer noted, suggesting that the increased density of *T. japonicus* allowed monitoring of its life cycle with greater accuracy. We detected the emergence of *T. japonicus* from egg masses collected in three control sites, which could be related to the spread of both adventive and released individuals. As mentioned previously, adventive populations may be only locally abundant, suggesting the possibility that

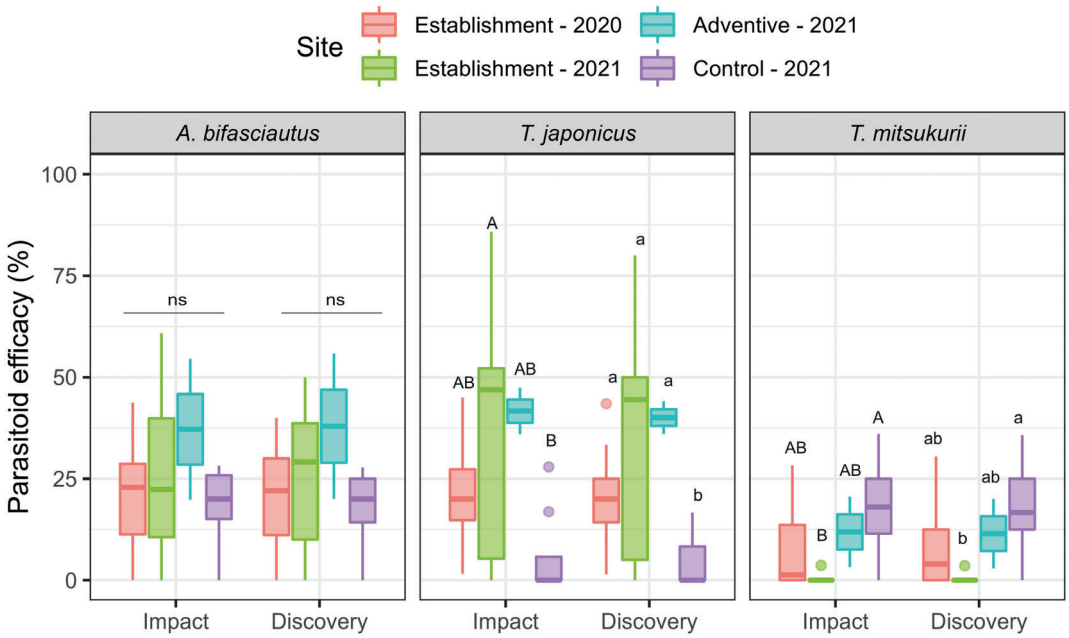

Figure 6. Boxplot showing the recorded efficacy for the three most abundant parasitoid species recorded in Set 1 sites. Kruskal–Wallis test and *post hoc* Dunn's test with Bonferroni correction; letters indicate significant differences ($P < 0.05$); ns, not significant.

Table 6. Performance indices for the set of models applied to the stink bug target species. Buffer sizes: B50 (50 m), B250 (250 m) and B500 (500 m). Variables included in the models: altitude (m a.s.l.), PC (surface of perennial crops), AC (surface of annual crops), SNH (surface of semi-natural habitats), TRN (surface of transport infrastructures) and HS (surface of human settlements)

Species	Model	Nagelkerke's R^2	AIC	Performance score
Halyomorpha halys	B500: SNH + TRN + HS	0.24	375.96	71.08%
	B500: PC	0.12	379.50	54.55%
	B250: SNH + TRN + HS	0.14	382.14	30.48%
	B250: PC	0.05	384.37	30.39%
	Altitude	0.02	385.97	25.93%
	B50: AC	0.01	386.75	24.83%
	B500: AC	<0.001	386.93	24.29%
	B250: AC	0.03	385.36	23.95%
	B50: PC	<0.001	387.13	23.74%
	B50: SNH + TRN + HS	0.05	387.89	19.55%
Palomena prasina	Altitude	0.16	198.58	74.33%
	B500: SNH + TRN + HS	0.21	199.22	53.10%
	B250: PC	0.11	200.95	37.35%
	B50: PC	0.07	202.87	29.75%
	B250: SNH + TRN + HS	0.14	203.59	27.78%
	B50: SNH + TRN + HS	0.09	205.82	22.69%
	B500: PC	0.01	206.01	21.99%
	B50: AC	<0.001	206.44	21.55%
	B250: AC	<0.001	206.67	21.20%
	B500: AC	0.02	205.75	20.75%
Pentatoma rufipes	Altitude	0.19	115.60	78.54%
	B50: SNH + TRN + HS	0.18	119.89	42.66%
	B50: PC	0.01	121.19	38.69%
	B500: PC	0.00	121.50	38.66%
	B250: PC	0.01	121.37	38.65%
	B50: AC	0.00	121.51	38.46%
	B250: SNH + TRN + HS	0.02	124.90	32.29%
	B500: SNH + TRN + HS	0.04	124.24	28.35%
	B250: AC	0.01	121.17	27.76%
	B500: AC	0.09	118.75	26.58%

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Table 7. Performance indices for the set of models applied to the parasitoid target species. Buffer sizes: B50 (50 m), B250 (250 m) and B500 (500 m). Variables included in the models: altitude (m a.s.l.), PC (surface of perennial crops), AC (surface of annual crops), SNH (surface of semi-natural habitats), TRN (surface of transport infrastructures) and HS (surface of human settlements)

Species	Model	Nagelkerke's R^2	AIC	Performance score
Anastatus bifasciatus	B50: AC	0.06	95.38	69.10%
	Altitude	0.04	95.80	63.44%
	B250: AC	0.04	96.44	50.36%
	B500: AC	0.03	96.96	44.43%
	B50: PC	<0.001	98.47	42.60%
	B250: PC	0.01	97.63	40.70%
	B500: PC	0.01	97.88	38.50%
	B250: SNH + TRN + HS	0.07	97.74	37.79%
	B50: SNH + TRN + HS	0.06	98.38	36.54%
	B500: SNH + TRN + HS	0.02	100.90	24.71%
Trissolcus japonicus	B500: SNH + TRN + HS	0.17	89.02	67.84%
	B500: PC	0.07	91.35	47.89%
	B500: AC	0.08	92.13	40.39%
	Altitude	0.04	92.74	37.15%
	B250: AC	0.06	92.88	32.98%
	B50: PC	0.01	94.09	35.70%
	B50: AC	0.01	95.64	33.05%
	B50: SNH + TRN + HS	0.09	95.76	31.54%
	B250: SNH + TRN + HS	0.09	95.86	31.36%
	B250: PC	0.01	95.94	29.63%
Trissolcus mitsukurii	Altitude	0.19	84.04	74.03%
	B50: SNH + TRN + HS	0.09	93.82	30.66%
	B250: AC	0.00	94.35	30.10%
	B50: AC	0.00	94.14	29.87%
	B250: PC	0.00	94.24	28.30%
	B500: PC	0.00	94.26	27.80%
	B500: SNH + TRN + HS	0.07	94.78	27.16%
	B50: PC	0.02	93.56	26.91%
	B250: SNH + TRN + HS	0.06	95.12	25.61%
	B500: AC	0.01	93.94	21.04%

individuals could disperse a few kilometers from the release sites, further than observed previously.[32] The survey confirmed that, besides *T. japonicus*, two other parasitoid species *A. bifasciatus* and *T. mitsukurii* were the most abundant parasitoids of *H. halys*. The much lower parasitoid efficacy of *T. mitsukurii* at sites with successfully established *T. japonicus*, compared to control sites, suggests a possible competition between the two species with a prevalence of the latter. For *T. mitsukurii* in the release, both efficacy index sites were approximately a tenth of what was recorded for other adventive populations of this species.[79] Female parasitoids from the family Scelionidae tend to exhibit aggressive behaviors to monopolize hosts when these are spatially aggregated, and several species perform brood guarding and fighting.[80] Laboratory experiments performed on *T. mitsukurii* and *T. japonicus* showed that both species can exhibit intrinsic competition (being able to oviposit on eggs previously parasitized by the other species) and interference competition, with chase-off events, more frequently shown by *T. mitsukurii*, when it arrived first on the egg mass.[81] Understanding these potential antagonistic interactions is fundamental to the clarification of whether or not competition is interfering or accelerating pest suppression.[82] Further studies are needed to better understand how such competitive interactions will influence the distribution of the two sympatric species.

Several concerns have been raised on the potential impact of *T. japonicus* on populations of native stink bugs. Surveys completed in northern China utilizing field-collected egg masses revealed that *T. japonicus* is an oligophagous species which can successfully parasitize other species [i.e. *Plautia crossota* Fabricius and *Dolycoris baccarum* (L.)], but results suggested that the habitat and/or resource partitioning influenced the lower levels of parasitism recorded for nontarget sympatric species compared to *H. halys*.[22] Studies performed in the US[24,83] and in Europe[25] confirmed a broad physiological host range. Under laboratory conditions, *T. japonicus* developed on several nontarget species, with host-acceptance rate correlated with egg morphology.[40] In our study we recorded the emergence of *T. japonicus* from three native Pentatomids, mostly in September, implying an increased parasitism after the oviposition period of *H. halys*, as suggested by Haye *et al.*[25] The proportion of eggs parasitized by *T. japonicus* was comparable to what was observed for *H. halys* at the release sites for *P. rufipes* and higher than that for *G. lineatum*. However, because the sampled habitats did not align with those preferred by mentioned native species, with deciduous and coniferous forests being preferred by the former and forest edges with flowering plants of the carrot family (Apiacee) for the latter,[84] these observed results may overestimate the actual

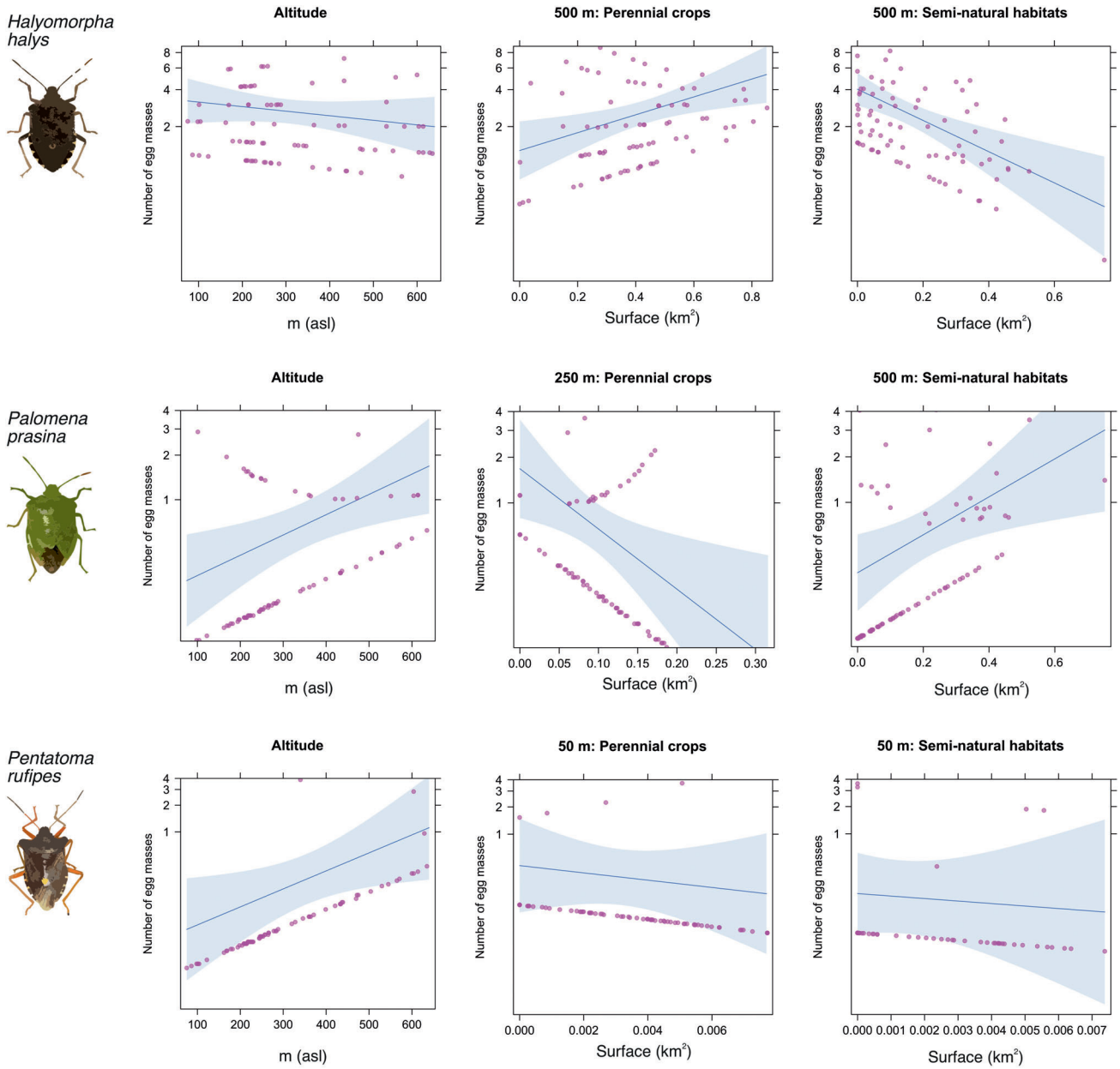

Figure 7. Plots of the best generalized linear models for the stink bug target species, showing the effect of the most relevant factors (model fit plus confidence intervals) and the partial residuals.

impact. In the current study we did not apply molecular methodologies,[85,86] and thus details of the host–parasitoid associations were not determined.

Field-based studies allow a better understanding how spatio-temporal ecological barriers (or 'ecological sieves') mitigate the actual risk posed to nontarget species by *T. japonicus*.[83] Our results showed that both *H. halys* and *T. japonicus* were more likely to be found in sites located at lower altitudes within landscapes with abundant perennial crops and scarce semi-natural habitats, whereas the presence of nontarget hosts increased with altitude and with the availability of semi-natural habitats (for *P. prasina*), indicating that landscape composition and elevation could act as 'ecological sieves'. As observed previously by Peterson *et al.*[70] in contrast with the occurrence data of native Scelionids, *T. japonicus* was detected more often in orchard than in forest habitats, in a similar distribution to that of its main host. High levels of *T. japonicus* parasitization on *H. halys* in agricultural areas were observed in their native area also.[22] In our study area, the observed distribution of *H. halys* was in accordance with the 'resource concentration hypothesis',[87] with increasing herbivore abundance in landscapes with higher availability of suitable crops. Such a result may be a consequence of the structure of Trentino–South Tyrol landscapes, where permanent crops account for <4% of the territory and conversely woodland covers ≈50% (data derived from land-cover maps). Thus, in a heterogenous context, with several orchards often divided by hedgerows, the total area of available crop surfaces in the landscape was a better predictor of presence of both the

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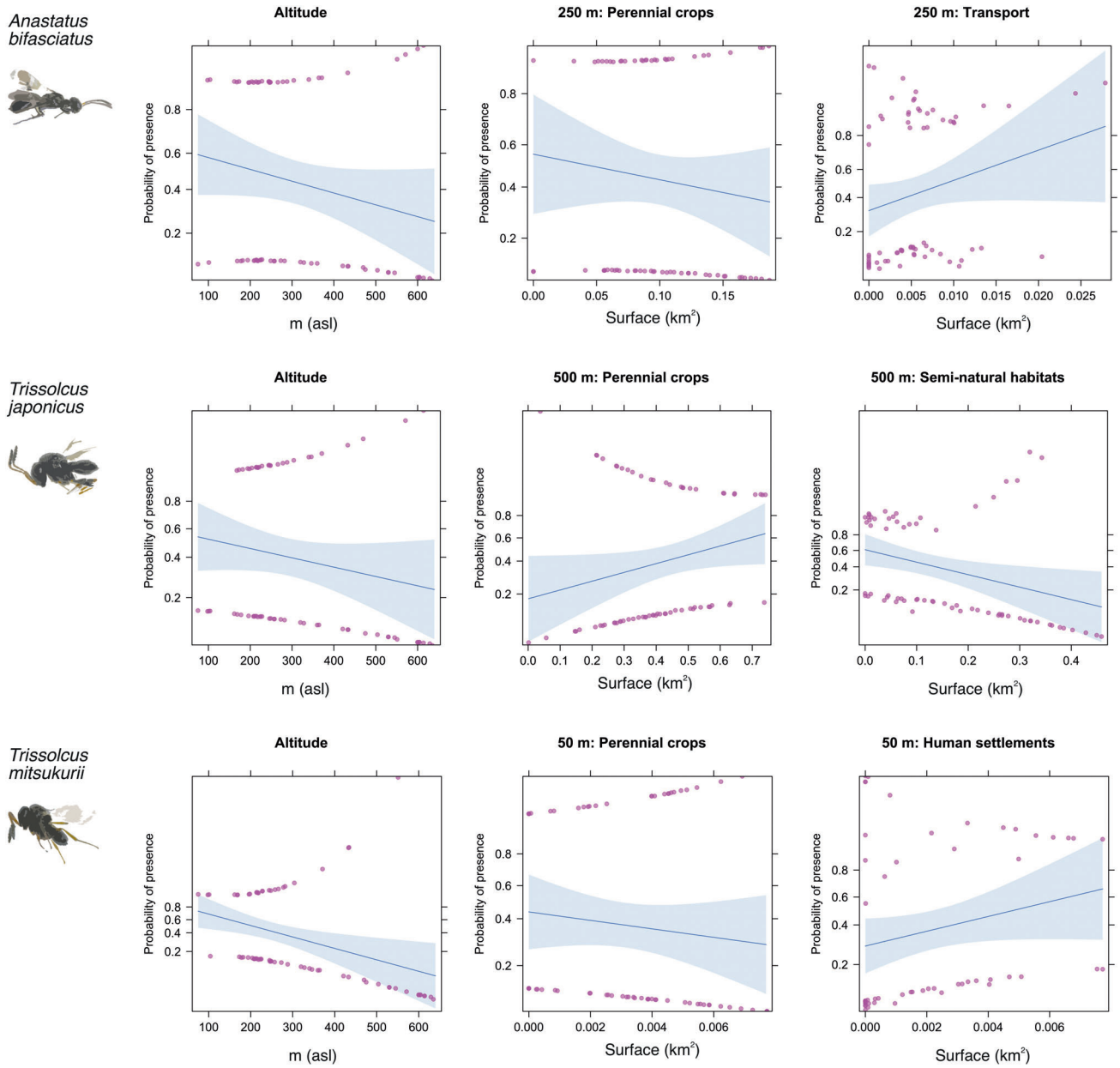

Figure 8. Plots of the best generalized linear models for the parasitoid target species, showing the effect of the most relevant factors (model fit plus confidence intervals) and the partial residuals.

polyphagous pest and its co-evolved parasitoid, than the availability of noncrop areas. In structurally complex landscapes (i.e. where noncrop habitats are >20%), such as in our study area, biodiversity and associated mechanisms, such as pest control, tend to be high.[88] We could argue that the multifunctional landscape that characterizes the area supports the spread of both a polyphagous species with high dispersal capabilities, such as *H. halys*, and its BCA. The wide spatial scale (500 m) to which both species responded could corroborate this view. The *T. mitsukurii* distribution pattern did not overlap with *H. halys* and *T. japonicus*, suggesting the relevance of different metrics, as suggested by Mele *et al*.[79] at a smaller spatial scale (50 m). When the realized host ranges coincide, as for *T. japonicus* and *T. mitsukurii*, the different abilities to deal with habitat complexity may mediate species interactions, reducing competition.[89] However, long-term studies are needed to confirm these hypotheses.

5 CONCLUSIONS

Even if the number of introduced insect BCA has decreased since the 1970s, the proportion of successful programs has increased, reflecting the important research efforts behind.[90] Petitions for the release of *T. japonicus* have been filed in several countries (e.g. Canada, USA), including, for New Zealand, the first approval of release preceding the establishment of the target pest.[91] The results of the current study showed, in the short term, a promising impact of the BCA both where it has been released intentionally and where adventive populations have established, with minor nontarget effects. Besides, this first attempt to analyze host–

parasitoid dynamics at the landscape scale has revealed that in a complex territory, the availability of permanent crops may be beneficial for *H. halys* and its BCA, suggesting a key role in the future for *T. japonicus* in supporting sustainable IPM.

Moreover, the prevalence of the BCA towards such landscapes also may have a further beneficial effect of limiting nontarget impact. On the level of control that can be achieved, recent CBC programs with the release of *T. sinensis* to control the chestnut gall wasp *D. kuriphilus* showed that even with small releases it was possible to observe a significant decrease in the target species abundance after 4 years.[92] A longer-term post-release survey is needed to corroborate our initial observations and verify how host–parasitoid dynamics will evolve.

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AUTHOR'S CONTRIBUTION

M.F. and L.Z. designed the study. M.F., V.C., S.G.C., A.P. and L.Z. collected the data. L.Z., M.F., V.C. and S.S. drafted the manuscript which was revised and edited by all authors.

CONFLICT OF INTEREST STATEMENT

The authors have no relevant financial or nonfinancial interests to disclose.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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