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Ecological dynamics of true bugs (Hemiptera: Pentatomidae, Acanthosomatidae, and Coreidae) and associated egg parasitoids (Hymenoptera) in an Alpine region of Italy

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Research Paper

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Abstract

True bugs (Hemiptera: Acanthosomatidae, Coreidae, and Pentatomidae) include harmful crop pests affecting global agriculture, with different species displaying distinct optimal conditions for development and using different habitats. Over a 2-year period, this research investigates how habitat variation and altitude can influence the species composition of true bugs and their egg parasitoids in South Tyrol (North Italy), unveiling different trends in their population and diversity across habitats: apple orchards, urban areas, and forests. A total of 25 true bug species were sampled. Urban environments hosted the highest bug abundance, predominantly driven by the invasive *Halyomorpha halys*, while forests showed a higher prevalence of native species such as *Pentatoma rufipes* and *Palomena prasina*. Altitude significantly influenced species composition, with *H. halys* and *P. rufipes* abundance negatively and positively correlated with altitude, respectively. A total of 12 parasitoid species (Hymenoptera: Eupelmidae, and Scelionidae) emerged from the field-collected bug eggs, including the exotic *Trissolcus japonicus*, predominantly associated with *H. halys* in urban areas. Native parasitoids exhibited higher parasitism rates on native bug species, indicating co-evolutionary relationships. The results give an insight into the ecological dynamics of local true bug species and their egg parasitoids, and highlight the value of natural and urban areas for conserving both hemipteran and parasitoid species richness and abundance.

Introduction

Leaf-footed bugs (Hemiptera: Coreidae), shield bugs (Hem: Acanthosomatidae), and stink bugs (Hem: Pentatomidae) are often phytophagous, polyphagous, and feed on cultivated, wild, and ornamental plants (Jones and Sullivan, 1982; Kriticos *et al.*, 2017; Panizzi, 2015). Some of them are pests that can cause significant crop damage and contribute to agricultural losses worldwide (Leskey and Nielsen, 2018; Panizzi, 1997; Schaefer and Panizzi, 2000). Understanding the factors influencing pest population dynamics is essential for targeting efficient and environmentally friendly pest management strategies. These strategies typically focus on the local field level; however, these bugs are generally highly mobile and use various habitat types throughout their life cycle (Tillman *et al.*, 2022; Venugopal *et al.*, 2014).

South Tyrol, a mountain region located in northeastern Italy, is known for its diverse habitats and unique ecosystems (Kuttner *et al.*, 2015). In this mountainous region, rich in woods, apple production (about 18,400 ha) covers the main valleys up to 1,100 m a.s.l. (Fischnaller *et al.*, 2022). In the context of apple production, most stink bugs can inflict damage to apple trees by piercing the fruit and sucking out plant fluids, leading to deformities and reduced fruit quality (Brown and Short, 2010). This results in significant economic losses for apple farmers and affect overall apple yields (Nielsen and Hamilton, 2009). The situation worsened even more after the arrival of the brown marmorated stink bug *Halyomorpha halys* (Stål) (Hem.: Pentatomidae) in 2016 (Fischnaller *et al.*, 2022). Therefore, efforts have been made to monitor and study this pest, as well as other true bugs whose occurrence in this region appear to have increased in recent years not only in cultivated areas but also in urban areas (Zapponi *et al.*, 2020).

The great diversity in environments, microclimates, and host plants in South Tyrol has an influence on the species composition of both true bugs and their egg parasitoids (Hymenoptera) (Falagiarda *et al.*, 2023; Zapponi *et al.*, 2020). In these environments, the presence of woodlands and inhabited areas bordering crops provides a wide variety of both wild and ornamental non-crop hosts for true bugs. It is known that these insects can move within and between crop and non-crop habitats throughout the season, depending on the suitability of host plants and food availability (Tillman *et al.*, 2014). For instance, Venugopal *et al.* (2014) observed that adjacent wooded, crop, and building habitats influenced the density of stink bugs in corn and soybean fields, with higher densities found at field edges. Moreover, specific wild plant species in woodlands could serve as a source of stink bugs dispersed into adjacent crops (Tillman, 2016).

In line with habitat type, elevation also represents a critical factor influencing various aspects of insect ecology, from species distribution and richness, to their abundance, biology, and behaviour, as well as interactions with plants and natural enemies, as evidenced by numerous studies (Corcos *et al.*, 2018; Hodkinson, 2005; Kozlov *et al.*, 2022). Moreover, climate change and rising temperatures in mountain regions will impact insect physiology and fitness, causing shifts in population distribution and composition of several insect species (Shah *et al.*, 2020). Many mountain insects are already shifting to higher elevations (McCain and Garfinkel, 2021). Climate change scenarios predict altitudinal range expansion also for *H. halys* (Stoeckli *et al.*, 2020). Other stink bug species, such as the coffee stink bug *Antestiopsis thunbergii* (Gmelin) (Hem.: Pentatomidae), already show higher population density at higher elevations due to immature stage susceptibility to extreme temperatures at lower altitudes (Azrag *et al.*, 2018). Knowledge of variation in communities of true bug and their egg parasitoids as altitude changes could serve as a starting point for future investigations to track changes in species composition, distribution, and interactions in response to climate change.

Understanding the natural biological control of true bugs in different habitats is necessary for the development of effective management strategies. Egg parasitoids are among the main natural enemies of true bugs, which, in some cases, can reach high levels of parasitism, contributing to the regulation of bug populations (Koppel *et al.*, 2009; Maltese *et al.*, 2012; Paz-Neto *et al.*, 2015). Research on parasitism has predominantly focused on agricultural systems, while investigations across other habitat types remain limited. Because stink bugs, such as *H. halys*, use urban structures for overwintering (Hancock *et al.*, 2018; Lee and Leskey, 2015), urban habitats were included in a large-scale monitoring programme of this pest's parasitoids in 2019 (Zapponi *et al.*, 2021). Interestingly, these environments hosted high numbers of parasitised egg masses on ornamental trees in gardens, parks, parking lots, and streets. Another study showed a higher presence of *H. halys* egg masses in urban areas than in apple orchards, and different patterns in parasitoid species distribution in these two habitats (Zapponi *et al.*, 2020). In fact, parasitoids can also disperse from woodlands to crops, and the extent of their dispersal is influenced by factors such as the presence of alternative flowering hosts (Tillman, 2016, 2017). For instance, *Anastatus* sp. (Hym.: Eupelmidae) parasitises the egg masses of *Euschistos servus* (Say) (Hem.: Pentatomidae) in corn crops, because of its proximity to a woodland habitat, where the parasitoid was mainly found on woody trees parasitising *Chinavia hilaris* (Say) eggs (Tillman, 2016).

In South Tyrol, monitoring of parasitoid species attacking *H. halys* and indigenous bugs resulted in the discovery of two exotic parasitoids: *Trissolcus japonicus* (Ashmead) and *Trissolcus mitsukurii* (Ashmead) (Hym.: Scelionidae) (Scaccini *et al.*, 2020; Zapponi *et al.*, 2020). Moreover, starting from 2020, releases of *T. japonicus* were performed according to a national programme of classical biological control of *H. halys* (MATTM, 2020). Since then, this parasitoid has spread and established in several areas of northern Italy, showing a promising impact as biocontrol agent against the target host (Falagiarda *et al.*, 2023). However, it is still too early to estimate its long-term regulating efficacy and non-target effects.

Despite existing knowledge, comprehensive studies on the distribution of true bugs and their egg parasitoids in a mountain agro-ecosystem are still lacking. As mentioned above, habitats located at different altitudes can offer various resources for insects (Hodkinson, 2005). Perennial crops can support stink bug populations by providing host plants during late spring and summer, while forests and urban areas are expected to primarily serve as overwintering sites, and provide alternative host plants and suitable environments for reproduction and development (Panizzi, 1997). Therefore, this study aimed to understand the influence of habitat type and altitude on true bug and parasitoid species composition. Two-year field surveys were carried out to assess species abundance and diversity across three distinct habitats within the study region – perennial crops (i.e., apple orchards), urban areas, and forests – covering an elevation gradient from 200 to 1000 m a.s.l.

Materials and methods

Study sites

Surveys were conducted over the 2-year period 2022–2023 in 27 sites in South Tyrol, selected across three different habitat types, including apple orchards, forest margins, and urban areas. These sites were located within distinct altitude ranges, spanning from 200 to 500 m, 501 to 800 m, and above 801 m a.s.l. (fig. 1, Supplementary Table 1). In total, three sites were monitored for each habitat in a specific altitude range. The surveyed apple orchards were managed according to integrated pest management guidelines (Beratungsring, 2022), except for the site 19, which was an organically managed apple orchard. The study sites were not involved in the *T. japonicus* release programme implemented in Italy starting in 2020.

Bug sampling and identification

In each site, monthly surveys were performed starting from early April, and extending through September in both 2022 and 2023, so as to capture seasonal variations in true bug populations. As in similar studies (e.g., Kawatsu *et al.*, 2021; Majeed *et al.*, 2022), sampling was conducted on a monthly basis as it could identify major seasonal trends and allow consistent comparisons between sites during the growing season. In the surveyed sites, true bug populations were monitored in an area with a radius of approximately 50 m using two methods: beat sheet and direct observation through visual inspection of host plants. Surveys were performed in the morning between 8 and 11 in all sites, to avoid high temperatures that usually make the insects more active and therefore more difficult to detect during sampling.

Plant species on which true bugs were monitored included shrubs and trees and changed from site to site, and even within the same site during the season. In both urban and woodland settings, beat sheet samples were taken on six different plant species with 15 beats per species, for a total of 90 beats per survey and site. In apple orchards, a total of 45 beats were carried out on three apple plants (15 per plant), changing rows in the successive samples. The beat sheet had an opening in the middle to which a plastic bag was attached to directly collect the insects. Plastic bags with samples were labelled and transported to the laboratory, where they were kept in a freezer at −30°C.

Visual inspection of vegetation was conducted for 1 person-hour per survey and site, at a standardised height of approximately 1.5 m. Bug species and their developmental stages were recorded

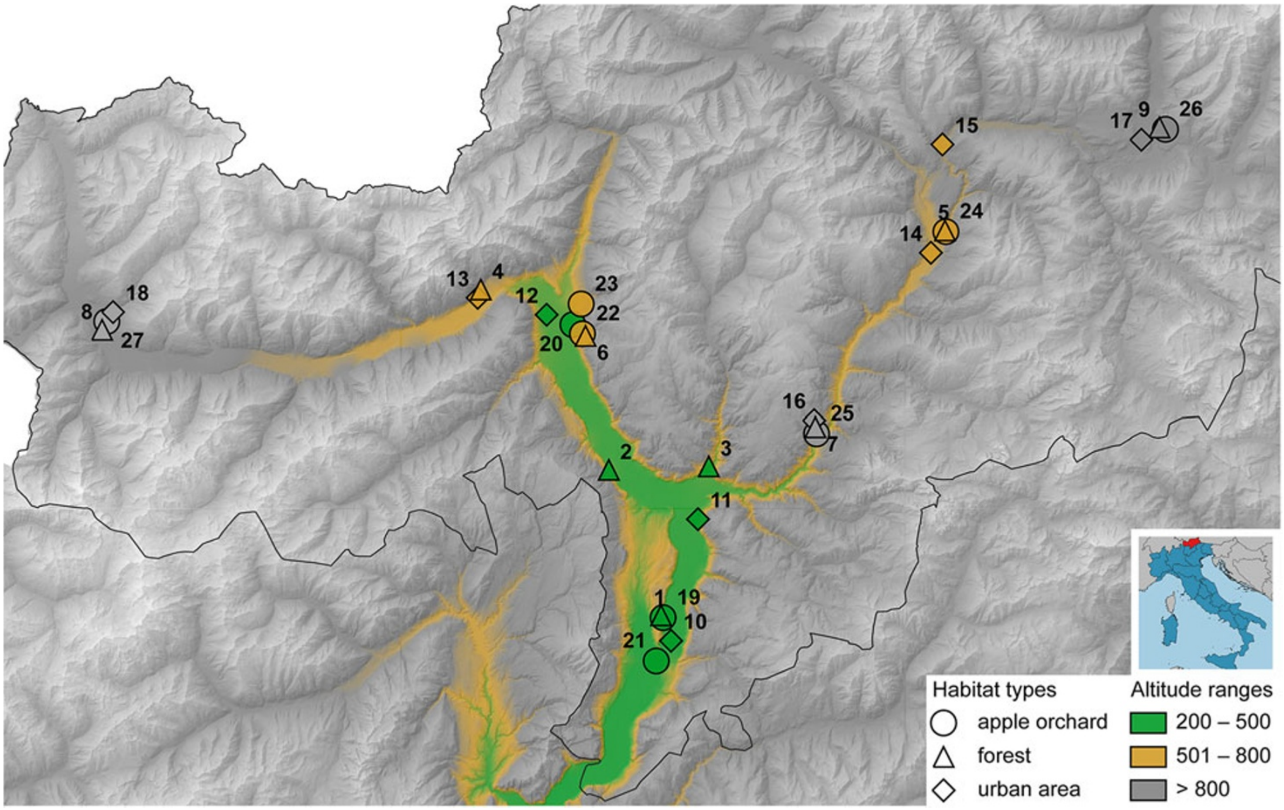

Figure 1. Study area location showing the distribution of the survey points, according to habitat type and altitude.

on site in case of the most common species. Only the least common species, or those of uncertain identification, were collected and brought to the laboratory.

In the laboratory, the field collected bugs were examined using a stereomicroscope and morphologically identified following the keys in Derjanschi and Péricart (2005), Péricart (2010), Ribes and Pagola-Carte (2013), and Tamanini (1989).

Egg collection and parasitoid identification

Egg sampling was performed by collecting all egg masses or single eggs observed by visual inspection during the surveys. Field collected egg masses and single eggs were placed in plastic Petri dishes (Ø 90 mm), labelled, brought to the laboratory, and held in a climatic chamber at 25 ± 1°C and 60 ± 5% relative humidity for emergence of bug nymphs or adult parasitoids. All egg masses and eggs were examined using a stereomicroscope and identified to the species or family level according to Derjanschi and Péricart (2005), Péricart (2010), and Ribes and Pagola-Carte (2013). Three to four weeks after collection, all eggs were categorised as hatched, unhatched, predated, or parasitised. Parasitoids emerged from true bug egg masses were stored in 1.5-mL Eppendorf® (Eppendorf SE, Germany) tubes with 70% ethanol. Hymenoptera specimens were morphologically identified under a stereomicroscope by using taxonomic keys provided by Moraglio *et al.* (2021a), Talamas *et al.* (2015, 2017), and Tortorici *et al.* (2019) for genus *Trissolcus* Ashmead, Tortorici *et al.* (2024) for genus *Telenomus* Haliday, and Kononova and Kozlov (2008) for genus *Hadronotus* Förster for Scelionidae, Askew and Nieves-Aldrey (2004) and Peng *et al.* (2020) for Eupelmidae, Sabbatini-Peverieri *et al.* (2019) for genus *Acroclisoides* Girault and Dodd, and Graham (1991) for Eulophidae.

All specimens used for morphological analysis were deposited in the Laimburg Research Centre, Institute for Plant Health, Laimburg, Italy, and Dipartimento di Scienze Agrarie, Forestali e Alimentari (DISAFA), University of Torino, Italy.

Data analysis

All analyses were performed using R software version 4.3.1 (R Core Team, 2023). The two sampling methods, beat sheet and visual inspection, were compared by Mann–Whitney–Wilcoxon test to assess if the number of individuals recorded during surveys was influenced by the monitoring method. For the comparison, raw data points from all dates and sites were aggregated into a unified dataset, with each observation representing an individual count from either beat sheet or visual inspection method. This approach allowed a direct comparison of the relative efficiency of each method across the entire study period and area, rather than comparing method performance at specific spatiotemporal points. As the two methods did not show any significant difference in the number of individuals counted ($W = 19{,}217$, $p = 0.091$), data were processed jointly for further analyses. To compare the composition of true bug assemblies according to habitat and altitude, permutation multivariate analysis of variance (PERMANOVA) was performed, using the *adonis2* function from the *vegan* package (Anderson, 2014). Principal Coordinate Analysis (PCoA) based on Bray-Curtis dissimilarity was applied to visualise the relationship between the variables. To identify the predominant species in each habitat and altitude range, rank-abundance curves were used.

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Table 1. Species richness, abundance, and individuals of Acanthosomatidae, Coreidae, and Pentatomidae collected according to habitat types and altitude ranges

	Orchard			Forest			Urban area		
	200–500	501–800	>801	200–500	501–800	>801	200–500	501–800	>801
No. of sites	3	3	3	3	3	3	3	3	3
Species richness	5	6	4	13	15	13	12	17	10
Abundance	28	23	9	125	197	104	188	307	258
Mean site species richness (±SE)	3.0 ± 0.6	3.3 ± 0.9	1.7 ± 0.3	8.3 ± 0.3	8 ± 1.2	6.3 ± 0.9	7.0 ± 2.3	10.7 ± 1.7	6.7 ± 0.3
Mean site abundance (± SE)	9.3 ± 3.8	7.7 ± 2.7	3 ± 0.6	41.7 ± 13.4	65.7 ± 4.4	34.7 ± 17.5	62.7 ± 13.4	102.3 ± 10.8	86.0 ± 3.0
Acanthosomatidae									
Acanthosoma haemorrhoidale	0	0	0	1	0	1	0	1	1
Elasmostethus interstinctus	0	0	0	1	0	0	0	0	0
Elasmucha grisea	0	0	0	0	0	3	8	11	44
Coreidae									
Ceraleptus gracilicorinis	0	0	0	1	0	0	0	0	0
Coreus marginatus	0	2	3	3	30	2	0	3	0
Gonocerus acuteangulatus	1	0	1	5	3	1	1	10	0
Leptoglossus occidentalis	0	0	0	0	2	0	0	1	0
Pentatomidae									
Acrosternum heegeri	0	0	0	0	0	2	4	1	0
Aelia sp.	0	0	0	0	0	0	0	1	0
Arma custos	0	0	0	0	2	1	1	0	7

(*Continued*)

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Table 1. (*Continued.*)

	Orchard			Forest			Urban area		
	200–500	501–800	>801	200–500	501–800	>801	200–500	501–800	>801
Carpocoris mediterraneus	0	0	0	0	0	0	0	1	0
Carpocoris purpureipennis	0	0	0	0	0	0	0	0	1
Dolycoris baccarum	0	0	0	0	2	2	0	2	1
Dyroderes umbraculatus	1	0	0	0	0	0	0	0	0
Eurydema oleracea	0	0	0	0	2	0	0	1	0
Graphosoma lineatum italicum	0	0	0	2	0	0	0	0	1
Holcostethus albipes	0	0	0	0	1	0	3	3	0
Halyomorpha halys	22	9	0	58	23	1	115	170	12
Nezara viridula	0	1	0	4	15	1	17	22	0
Palomena prasina	0	9	4	25	30	32	7	50	18
Peribalus strictus	0	0	0	4	1	1	4	0	0
Piezodorus lituratus	1	0	0	1	10	0	3	4	0
Pentatoma rufipes	0	1	0	16	47	53	9	19	168
Rhaphigaster nebulosa	3	1	1	4	7	4	16	7	5
Stagonomus venustissimus	0	0	0	0	22	0	0	0	0

Table 2. PERMANOVA results for habitat type and altitude range influencing true bug species composition

Source of variation	df	*F*	R^2	*p*
Habitat	2	7.664	0.305	0.001
Altitude	2	4.443	0.177	0.001
Habitat × Altitude	4	2.022	0.161	0.011
Residual	18		0.358	
Total	26		1	

This involved ranking species based on their relative abundance, calculated as the total number of individuals collected divided by the overall number of individuals. The analysis used the *rankabundance* function from the *Biodiversity R* package (Kindt and Coe, 2005). Linear regression was conducted to characterise the associations between altitude and the occurrence of stink bugs, focusing on the three prevalent species. Egg fate was calculated for each bug species as the percentage of hatched, unhatched, predated, and parasitised eggs.

Results

True bug species richness and diversity

A total of 1,239 true bug adults and nymphs belonging to three families were recorded during the survey period, among which 25 species were identified (table 1). In the superfamily Pentatomoidea, 3 species were found in the family Acanthosomatidae and 18 species in the family Pentatomidae, while in the superfamily Coreoidea 4 species belonging to the family Coreidae were collected. Notably, more phytophagous species (24 in total) were identified, in stark contrast to the only predatory species, *Arma custos* (F.) (Hem.: Pentatomidae).

Unless otherwise specified, abundance values refer to the total number of individuals collected in both sampling years and at all sites within the same habitat type or altitudinal range. Maximum relative abundance was found in urban areas (753 individuals), followed by forests (426) and orchards (60). Based on altitude range, the highest abundance was found between 501 and 800 m a.s.l. (527 individuals), while 371 and 341 individuals were recorded at higher and lower elevations, respectively. In urban areas and forests, 21 species were recorded, whereas only nine species were found in orchards. Six species were singletons. PERMANOVA results showed a significant influence of both habitat and altitude on species composition, and also the interaction of the two variables had an impact on species diversity and abundance (table 2). The PCoA plots obtained with the presence/absence data showed a clear distinction in the sorting space of the different habitats and the altitude ranges (fig. 2A, B).

Rank abundance curves for habitat type and altitude range showed that the most abundant species above 801 m and in woodland habitats was *Pentatoma rufipes* (L.) (Hem.: Pentatomidae), followed in both cases by *Palomena prasina* (L.) (Hem.: Pentatomidae). At lower altitudes and in urban areas and orchards, the predominant species was the invasive *H. halys* (fig. 3). In fact, altitude was found to be negatively correlated with *H. halys* abundance ($r = -0.44$; $R^2 = 0.19$; $p = 0.024$), while it was positively correlated with *P. rufipes* abundance ($r = 0.49$; $R^2 = 0.24$; $p = 0.010$). Moreover, altitude was not significantly correlated with *P. prasina* abundance ($r = 0.26$; $R^2 = 0.07$; $p = 0.183$) (fig. 4).

True bug egg fate and associated parasitoid species

Across years and sites, a total of 270 egg masses plus 43 single eggs were collected for a total of 6,626 eggs of 10 true bug species (table 3, Supplementary Table 2). Almost 80% of the collected egg masses belonged to the three most representative species for South Tyrol, *H. halys, P. rufipes,* and *P. prasina*. Egg fate varied greatly by species. For instance, the hatching rate for *H. halys* eggs exceeded 56%, while for the native *P. rufipes* and *P. prasina* it reached 41% and 31%, respectively. Furthermore, eggs of these two species recorded parasitism rates of almost 50%, while *H. halys* parasitism only reached 28.5%. For all species, predation rates were negligible.

Twelve species of parasitoids, including nine scelionids, one eupelmid, one pteromalid, and one eulophid, parasitised naturally occurring egg masses of true bugs (table 4). *Trissolcus japonicus* was the prevalent species in urban areas and mainly emerged from *H. halys* eggs. It was only sporadically found emerging from eggs of native bug species, mainly from *Rhaphigaster nebulosa* (Poda) and *P. prasina*, and rarely from *Acrosternum heegeri* (Fieber), *Nezara viridula* (L.), and *P. rufipes. Trissolcus cultratus* (Mayr) was mainly associated with *P. rufipes* in forests and urban areas, while *Telenomus truncatus* (Nees von Esenbeck) and *Telenomus turesis* Walker (Hym.: Scelionidae) emerged from *P. prasina* eggs in each of the three habitats, including apple orchards. Other scelionids, such as *Trissolcus kozlovi* (Rjachovskij), *Trissolcus semistriatus* (Nees von Esenbeck), and *Trissolcus belenus* (Walker), rarely emerged from *P. rufipes* and *P. prasina* eggs. *Hadronotus muscaeformis* (Nees von Esenbeck) and *Trissolcus elasmuchae* (Watanabe) specifically emerged from Coreidae spp. and *Elasmucha grisea* (L.) eggs, respectively. In forests, the generalist *Anastatus bifasciatus* (Geoffroy) (Hym.: Eupelmidae) was the most frequent parasitoid species and parasitised eggs of several bug species. The hyperparasitoid *Acroclisoides sinicus* (Huang and Liao) (Hym.: Pteromalidae) was found in both forests and urban areas, and emerged from egg masses of four stink bug species. Four individuals of *Baryscapus oophagus* (Otten) (Hym.: Eulophidae) emerged from a *H. halys* egg mass in one urban habitat.

Parasitism of *H. halys* eggs in urban areas reached almost 40%, while the percentage was highly reduced in orchards and woodlands (fig. 5). Eggs of the native *P. rufipes* and *P. prasina* showed high parasitism rates in both urban areas and forests, and the number of parasitised eggs of *P. prasina* also exceeded 30% in apple orchards. Predation was negligible in urban environments, while it reached 15% of *H. halys* eggs in forests and 20% of *P. prasina* eggs in orchards. In relation to altitudinal range, parasitoid activity appeared to be more strongly associated with host egg availability than with altitude. Higher parasitism rates generally corresponded to areas of higher egg abundance, consequently below 800 m for *H. halys*, and above 800 m for *P. prasina* and *P. rufipes*.

Discussion

In the 2-year field survey, 25 true bug species belonging to three families, almost all of them phytophagous, were collected. The species composition, with distinct patterns observed in PCoA plots, was significantly influenced by habitat type and altitude. The invasive *H. halys*, and the native *P. rufipes* and *P. prasina* were the three most common species. Among them, *P. rufipes* is commonly found in many parts of the Palaearctic region, and it is particularly associated with deciduous trees. Also known as forest bug, it can be found in woodlands all year-round, feeding on various species, including oak, beech, and hazel (Powell, 2020).

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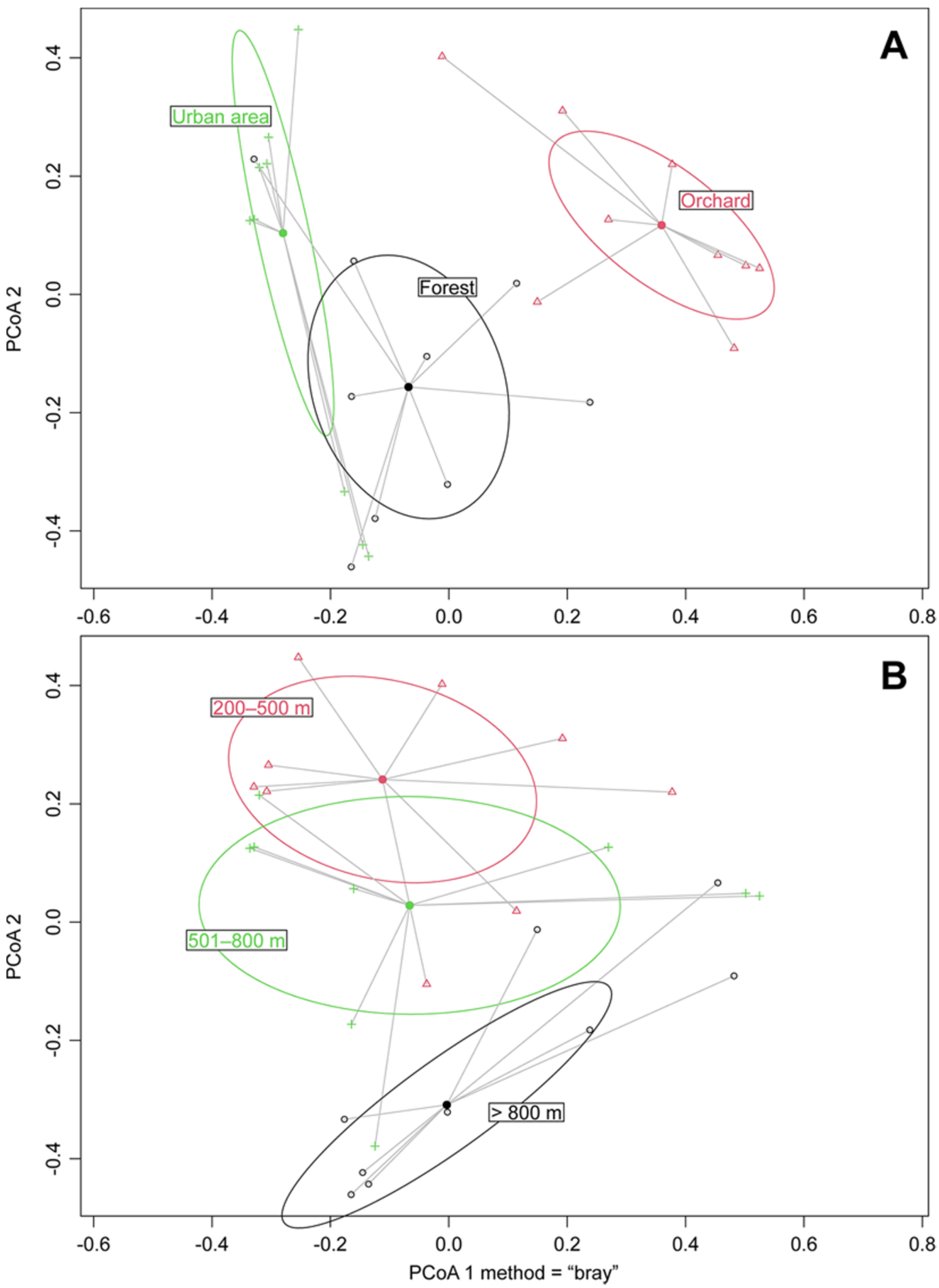

Figure 2. Ordination diagrams (PCoA) of the 27 sites based on site-to-site dissimilarity measures used in this study. The measures represent site-to-site dissimilarities in species composition according to habitat type (A) and altitude (B), respectively.

Palomena prasina has a broad distribution across the Eurosiberian region and is considered a harmful hazelnut pest in many regions (Driss *et al.*, 2024; Hamidi *et al.*, 2022). These two species were the most common in forests, and *P. rufipes* was also the prevalent species found in urban settlements above 800 m. The presence of this species at high elevations, up to 1500 m, has already been observed in the Italian and Austrian Alps (Alma *et al.*, 2009; König, 2015). Previous studies recorded populations of *P. rufipes* in apple and pear orchards in northern Europe, where it is considered as emerging pest of fruit trees (Alkarrat *et al.*, 2020; Powell, 2020). Nevertheless, no *P. rufipes* individuals were found in apple orchards in South Tyrol during the surveys.

Similarly, several true bug species found in forest and urban areas were not observed in apple orchards. Certainly, management practices, such as pesticide applications in apple orchards, may negatively affect true bug populations compared to undisturbed

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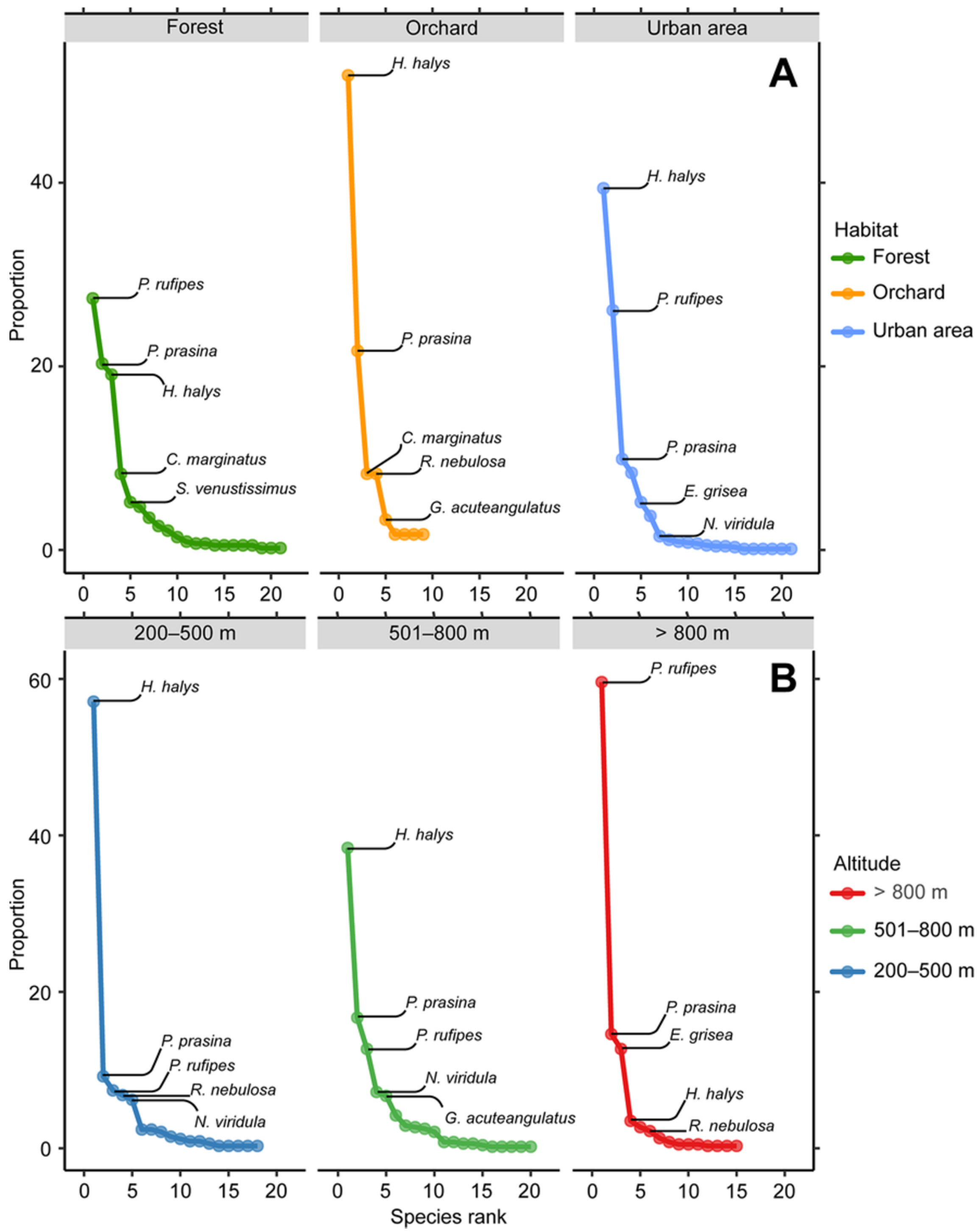

Figure 3. Rank abundance curves of true bug species collected in the surveyed sites in 2022 and 2023, according to habitat type (A) and altitude (B). Species names are shown for the first five species.

woodland sites. Most pentatomid species spend only a third of their lifespan feeding on spring/summer crops, while the rest is devoted to feeding and reproducing on wild hosts or using these plants as overwintering sites (Panizzi, 1997). This may explain the highest relative abundance of bugs observed in urban areas, followed by forests and orchards. This trend reflects the availability of various plant species, which serve as hosts for several species of Pentatomidae (Holthouse *et al.*, 2021; Palumbo *et al.*, 2016).

Likewise, the positive correlation between the abundance of the invasive *H. halys* and urbanised areas is consistent with earlier findings reported in the mid-Atlantic region in the United States (Venugopal *et al.*, 2016; Wallner *et al.*, 2014). Landscape characteristics are known to influence the distribution and dynamics of *H. halys* and its natural enemies. Although different studies reported high-density populations of *H. halys* in agricultural areas adjacent to forests (Acebes-Doria *et al.*, 2016; Quinn *et al.*, 2019;

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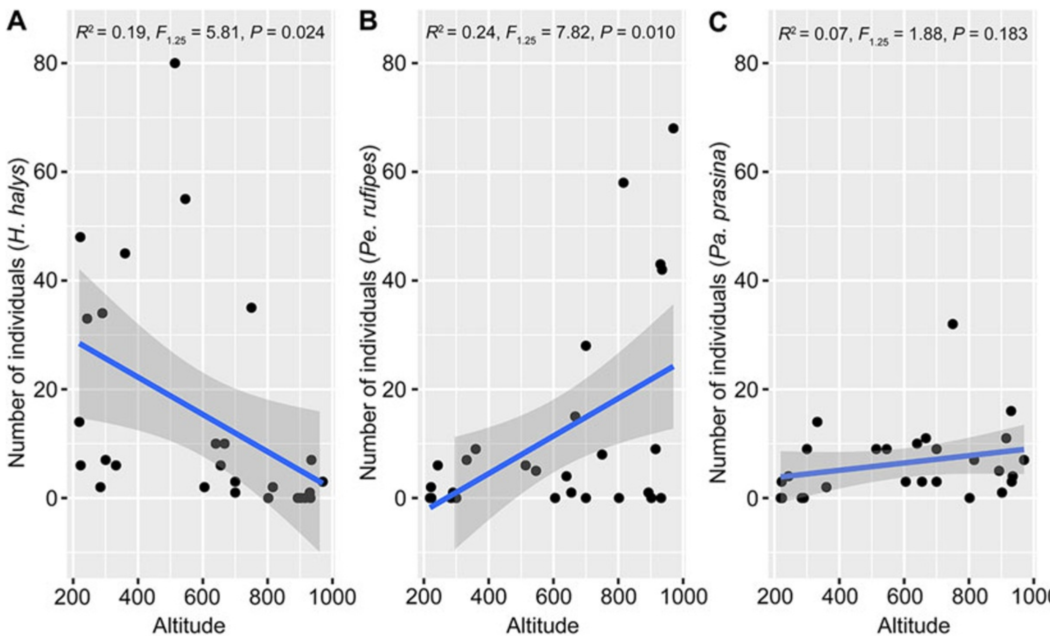

Figure 4. Correlation between altitude and number of individuals of the three main stink bug species found in South Tyrol, *Halyomorpha halys* (A), *Pentatoma rufipes* (B), and *Palomena prasina* (C).

Table 3. Fate of true bug egg masses and eggs in the surveyed sites in 2022 and 2023

Species	Egg masses no.	Eggs no.	Hatched %	Unhatched %	Predated %	Parasitised %
Pentatomidae						
H. halys	116	3091	56.32	10.38	4.79	28.50
P. rufipes	47	652	41.72	9.51	2.30	46.47
P. prasina	46	1179	31.98	13.99	6.79	47.24
R. nebulosa	18	250	62.40	5.60	4	28
A. custos	13	179	20.11	31.84	0	48.04
A. heegeri	9	160	46.25	30	3.13	20.63
N. viridula	5	456	51.75	44.96	0.44	2.85
D. baccarum	4	90	43.33	8.89	4.44	43.33
Acanthosomatidae						
E. grisea	12	526	51.52	13.50	0.19	34.79
Coreidae						
Coreidae spp.	–	43	60.47	20.93	0	18.60

Venugopal *et al.*, 2014), this pest shows high abundance in urban areas (Wallner *et al.*, 2014), probably because its host plants, such as *Ailanthus altissima* (Mill.) Swingle, *Paulownia tomentosa* (Thunb.) Steud., *Acer* spp., and *Prunus* spp. (Bergmann *et al.*, 2016; Holthouse *et al.*, 2021), are more prevalent in urban environments, such as parks and hedges, than in forest habitats. Furthermore, urban areas may support higher pest densities not only because of the availability of host plants, but also because of the presence of suitable overwintering structures and stable microclimatic conditions (Bergh *et al.*, 2017; Rice *et al.*, 2017). Conversely, agricultural landscapes bordering semi-natural habitats can enhance the activity of natural enemies, particularly egg parasitoids, through spillover effects and the presence of alternative hosts and floral resources (Abram *et al.*, 2020; Dieckhoff *et al.*, 2017). In our study, however, the high parasitism rate observed in urban areas is likely due to a higher concentration of host eggs in these environments, and a density-dependent response of parasitoids to increased host availability.

Concerning altitude range, the highest abundance of true bugs was observed between 500 and 800 m, where summer mean temperatures range approximately between 15°C and 25°C. Since plant community composition was relatively consistent at the studied sites, all located below 1000 m where substantial vegetation transitions do not typically occur, the observed altitudinal patterns in bug populations can be primarily attributed to climatic factors rather than vegetation changes (Zhao *et al.*, 2023). Variations in elevation lead to differences in temperature, which have an impact on the geographic distribution and prevalence of bug species. This

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Table 4. Egg parasitoid species emerged from true bug eggs collected in the surveyed sites in 2022 and 2023

Family	Species	Hosts[a]
Scelionidae	*Trissolcus japonicus*	Hh, Pp, Rn, Ah, Pr, Nv
	Trissolcus cultratus	Pr, Pp
	Trissolcus kozlovi	Pr
	Trissolcus belenus	Pp
	Trissolcus semistriatus	Pp
	Trissolcus elasmuchae	Eg
	*Telenomus truncatus**	Pp, Ac, Db, Rn
	*Telenomus turesis**	Pp, Db
	*Hadronotus muscaeformis**	C. sp.
Eupelmidae	*Anastatus bifasciatus*	Hh, Pp, Pr, Rn, Ac, Ah, C. sp.
Pteromalidae	*Acroclisoides sinicus*	Pr, Pp, Hh, Ah
Eulophidae	*Baryscapus oophagus**	Hh

[a]Hh, *Halyomorpha halys*; Pp, *Palomena prasina*; Pr, *Pentatoma rufipes*; Rn, *Rhaphigaster nebulosa*; Ah, *Acrosternum heegeri*; Nv, *Nezara viridula*; Eg, *Elasmucha grisea*; Ac, *Arma custos*; C. sp., Coreidae sp.
*These species are recorded for the first time in South Tyrol.

phenomenon is attributable to the temperature ranges and tolerances exhibited by different true bug species, especially by egg masses and early juvenile stages (Daane *et al.*, 2022; Venugopal *et al.*, 2016). For instance, laboratory studies indicate 25°C as *H. halys* optimal survival and developmental temperature (Haye *et al.*, 2014; Nielsen *et al.*, 2008), as well as for *N. viridula* (Ali and Ewiess, 1977; Chanthy *et al.*, 2015). Unfortunately, data on the developmental temperature thresholds for *P. rufipes* are currently lacking (Powell, 2020). Nonetheless, our findings indicate that this species is likely to have lower optimal temperatures compared to the invasive *H. halys*, as it was mostly found at higher altitudes. *Halyomorpha halys* was mainly recorded up to 800 m, which is consistent with the current known distribution patterns of this species recorded in Switzerland (Stoeckli *et al.*, 2020).

Twelve parasitoid species were identified in this study, of which the two *Telenomus* species, and *H. muscaeformis*, are recorded for the first time in South Tyrol. Generally, higher levels of parasitism were found in native bug species compared to the invasive *H. halys*. Notable parasitism rates of *P. prasina* and *P. rufipes* eggs in urban and forest habitats indicate effective host-parasitoid interactions for these autochthonous species in the studied environments. The main parasitoids of these two native species belonged to the family Scelionidae: five *Trissolcus* species, including *T. japonicus*, and two *Telenomus* species. Among them, *T. kozlovi* emerged only from *P. rufipes* eggs in urban areas above 500 m. Previous studies found this species sporadically parasitising *H. halys* in the field (Falagiarda *et al.*, 2023; Moraglio *et al.*, 2021b; Scaccini *et al.*, 2020), and investigated its potential as a biocontrol agent of the pest (Moraglio *et al.*, 2021a, 2021b). Nevertheless, its limited success as a biocontrol agent could be explained by the different habitat suitability compared to that of *H. halys*, as suggested by our study.

Trissolcus belenus and *T. semistriatus* emerged only from *P. prasina* eggs in our survey, but were recorded parasitising other hosts in previous studies (Falagiarda *et al.*, 2023; Moraglio *et al.*, 2021b). Both *Telenomus* species emerged from *P. prasina* eggs, consistent with observations from another study (Tortorici *et al.*, 2024). While *T. turesis* was present in all habitats, *T. truncatus* was observed only in urban areas, where it also emerged from eggs of *Dolycoris baccarum* (L.) (Hem.: Pentatomidae), *R. nebulosa*, and also of the predatory stink bug *A. custos*. Therefore, while high parasitism rates can be advantageous for the control of potential pests, they are undesirable in the case of predatory arthropods, as they may interfere with the control of other insects (Fei *et al.*, 2023). This is precisely the case of *A. custos*, on which high parasitism was recorded not only in this study, but also by Moraglio *et al.* (2021b).

The predatory bug *A. custos* was parasitised also by the generalist *A. bifasciatus*. Confirming its wide host range (Stahl *et al.*, 2018); this parasitoid emerged from the highest number of hosts among true bugs, and was found in all altitude ranges in both urban and forest habitats, and it was even the predominant species in the latter. Previous studies reported a predominance of *A. bifasciatus* as a parasitoid of bug species in urban and suburban areas (Rot *et al.*, 2021; Zapponi *et al.*, 2020). This might be due to higher biodiversity in forests, which represents a source of different hosts (e.g., lepidopterans, other hemipterans) for this parasitoid.

In our study, the exotic *T. japonicus* was prevalent in urban areas where its main host, *H. halys*, was the predominant species. In this environment, parasitism rates were higher than in the other habitats. This observation is in line with surveys conducted in Slovenia, where the urban areas showed the highest number of *H. halys* eggs and the highest parasitism rate (Rot *et al.*, 2021). The high abundance of *H. halys* in the apple orchard was not related to an equally high abundance of *T. japonicus*. Indeed, the percentage of hatched eggs was higher in apple orchards than in forest and urban areas. This suggests that pest management practices could have a significant impact on parasitoid development and establishment.

Analysis of parasitism rates at different elevations revealed that parasitoid activity was more strongly associated with host egg availability than with altitude *per se*. The correspondence of higher parasitism rates with areas of higher egg mass abundance suggests density-dependent parasitism dynamics. Following the distribution patterns of its main host *H. halys, T. japonicus* was mainly found up to 800 m. According to the geographic distribution model developed by Tortorici *et al.* (2023), the patterns of suitable habitats for *T. japonicus* across Europe resemble the core areas for *H. halys*. Several studies reported parasitism of *T. japonicus* on different pentatomid species (Falagiarda *et al.*, 2023; Haye *et al.*, 2024; Zapponi *et al.*, 2021), which can be considered both non-target hosts and at the same time support the increase of the parasitoid populations. However, in our study, the exotic parasitoid had minimal impact on native species, due to their different habitat preferences and phenology compared to its primary host, *H. halys. Trissolcus japonicus* occasionally emerged from the eggs of *A. heegeri, N. viridula, P. prasina, P. rufipes*, and *R. nebulosa,* and mainly in sites located up to 500 m. These species were successfully parasitised by *T. japonicus* under laboratory conditions, with the exception of *N. viridula*, which was attacked but not found to be suitable for parasitoid development (Haye *et al.*, 2020; Moraglio *et al.*, 2021b; Sabbatini-Peverieri *et al.*, 2021). Oviposition in this host resulted in significant non-reproductive mortality. Haye *et al.* (2024) found a high proportion of unemerged eggs from field-collected *N. viridula* egg masses containing *T. japonicus* DNA, confirming the parasitoid-induced non-reproductive mortality. This could explain the high percentage (45%) of unhatched *N. viridula* eggs recorded in our study. Further investigations on the seasonal dynamics of *T. japonicus* parasitism could help clarify the exploitation of other hosts rather than *H. halys*.

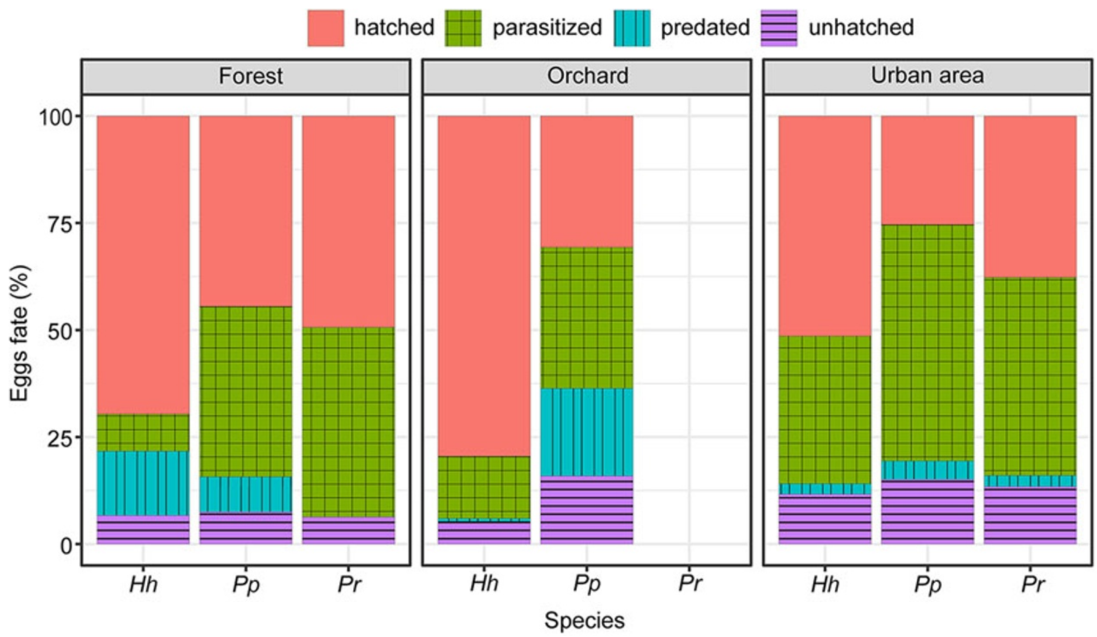

Figure 5. Fate of *H. halys* (*Hh*), *P. prasina* (*Pp*), and *P. rufipes* (*Pr*) eggs: percentage of hatched, unhatched, predated, and parasitised eggs in the three habitats.

Among the hymenopteran parasitoids obtained from the field-collected bug eggs, *B. oophagus* is recorded for the first time emerging from eggs of *H. halys*. Previously, this species has been reported attacking the common pine sawfly, *Diprion pini* (L.) (Hym.: Diprionidae) (Graham, 1991) and the lackey moth, *Malacosoma neustria* (L.) (Lepidoptera: Lasiocampidae) (Özbek and Coruh, 2010; Žikić *et al.*, 2017), while other species of *Baryscapus* Förster are hyperparasitoids that attack the primary parasitoids of caterpillars and other insect larvae (Marshall, 2023). It will therefore need to be verified whether this is an isolated case or not. On the contrary, the finding of the hyperparasitoid *A. sinicus* is definitely not an isolated case, as it was found in all habitats and altitude ranges, and emerged from the eggs of four stink bug species, in greater numbers from the native species in comparison with *H. halys*. This hyperparasitoid, whose taxonomic position has recently been clarified (Sabbatini-Peverieri *et al.*, 2019), was first reported in Europe during investigations of the indigenous parasitoid complex capable of adapting to the exotic *H. halys* (Moraglio *et al.*, 2020). Studies to date aimed to ascertain which conditions are most favourable and which species of exotic *Trissolcus* is most suitable for the development of the hyperparasitoid (Giovannini *et al.*, 2021; Mele *et al.*, 2021), while there are no studies on the relationships of this hyperparasitoid, with indigenous *Trissolcus* species. The fact that it emerged from the eggs of *P. prasina* and *P. rufipes*, even at altitudes that did not appear suitable for *T. japonicus*, prompts further research into the origin and distribution as well as the indigenous hosts of *A. sinicus*.

This study extends previous research by investigating a wider range of habitats and altitudes, providing a more comprehensive understanding of the ecology of true bugs and associated egg parasitoids in the region. Urban environments are particularly important for the biodiversity protection, because they provide habitat, support ecosystem services, and offer conservation opportunities through the management of urban green spaces (Dearborn and Kark, 2010; Goddard *et al.*, 2010). In our study, these areas were widely used for reproduction by true bugs, offering a wide variety of ornamental plants. Moreover, urban areas in South Tyrol are not as extensive as in other regions and are often located in proximity of forests, especially at higher elevations. Different studies underlined the importance of forest habitats for the overwintering of several true bug species (Laterza *et al.*, 2023; Musolin, 2012; Schaefer and Panizzi, 2000). Identifying areas in the agroecosystem, where pests consistently thrive, is crucial for effective pest management (Grabarczyk *et al.*, 2021; Panizzi and Lucini, 2024), enables the assessment of outbreak risks, and facilitates the implementation of precise control measures. For example, the infestation risk could be reduced by using wild hosts as trap plants to concentrate populations in limited areas, where they can be easily controlled eradicated, and by decreasing the presence of wild hosts in production zones (Hokkanen, 1991; Mizell *et al.*, 2008; Panizzi, 1997; Rea *et al.*, 2002). Designing habitats to encourage parasitoids is promising but has had limited success in reducing pest damage so far (Tillman, 2017). Parasitoids and predators of true bugs can exploit certain plant and flower resources. Therefore, incorporating these natural resources into the agricultural ecosystem could promote biological regulation and enhance biodiversity conservation (Landis *et al.*, 2000; Rusch *et al.*, 2013). However, further research is needed to understand how these are best compatible with local regulation strategies. Future efforts should focus on developing strategies to mitigate the economic damage caused by true bugs, maintaining populations of natural enemies in and around orchards, and promoting biodiversity in agricultural landscapes. Understanding these ecological dynamics is crucial for the preservation of different habitats that enhance both true bug and egg parasitoid abundance and diversity.

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