



Invasive brown marmorated stink bug (Hemiptera: Pentatomidae) facilitates feeding of European wasps and ants (Hymenoptera: Vespidae, Formicidae) on plant exudates

DAVIDE SCACCINI and ALBERTO POZZEBON

Department of Agronomy, Food, Natural Resources, Animals and Environment, University of Padova, Viale dell'Università 16, 35020, Legnaro, Padova, Italy; e-mails: davide.scaccini@phd.unipd.it, alberto.pozzebon@unipd.it
ORCID: Davide Scaccini: 0000-0002-6850-7911; Alberto Pozzebon: 0000-0002-2445-7211

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Abstract. The brown marmorated stink bug, *Halyomorpha halys*, is a polyphagous species from eastern Asia, which has spread to America and Europe where it damages many crops. In recently colonized areas, facilitative interactions between *H. halys* and native insects are poorly investigated. In this study, we report for the first time facilitation of native wasp and ant feeding by *H. halys* in Europe. The facilitation was related to the outflow of plant exudates caused by *H. halys* feeding on manna ash trees, where they have aggregated in response to an aggregation pheromone, which then attracted species of Hymenoptera to the infested trees. Trees other than manna ash were not involved in the facilitation between these two taxa. The species that frequently visited infested manna ash were *Polistes dominula*, *Vespa crabro*, *Formica (Serviformica) cunicularia* and *Lasius emarginatus*, while *Polistes* cf. *nimpha*, *Vespula germanica*, *Crematogaster scutellaris* and *Tapinoma subboreale* were occasional visitors. The numbers of wasps and ants feeding on plant exudates differed at different times in a day, with more Hymenoptera foraging in the afternoon, when more *H. halys* individuals were actively feeding. Facilitative interactions, such as those recorded in this study, are important for furthering our understanding of the ecology of invasive species in terms of creating sources of food for native organisms.

INTRODUCTION

When phytophagous stink bugs (Hemiptera: Pentatomidae) feed, they insert their stylets into plant tissue and suck up nutrients, which causes wounding and abortion of fruit and seeds (Panizzi, 1997; Panizzi et al., 2000). Their feeding may affect both the phloem and the xylem of a tree (Torres et al., 2010; Lucini & Panizzi, 2016).

Brown marmorated stink bug, *Halyomorpha halys* (Stål), is an invasive species of Pentatomidae native to eastern Asia that was first detected in the United States in the 1990s and Europe in the mid-2000s and now considered one of the most damaging agricultural pests worldwide (Kriticos et al., 2017; Leskey & Nielsen, 2018). On a wide spectrum of host plants, *H. halys* mainly feeds on phloem (Ghosh et al., 2017), and potentially also on xylem and mesophyll/parenchyma (Serteyn et al., 2020). The damage to crops is usually due to the feeding of both immature and adult stages (Leskey & Nielsen, 2018). In some crops, *H. halys* infestations can result in an increase in the incidence of plant diseases (e.g. Kamminga et al., 2014; Rice et al., 2014; Paltrinieri et al., 2016; Moore et al., 2019). In the USA, *H. halys* is reported to feed through the bark of some species of trees, causing the outflow of tree

exudates, and this sugary food source was attractive for native species of wasps (Hymenoptera: Vespidae) and ants (Formicidae) (Martinson et al., 2013). Thus, feeding by *H. halys* provides a source of food, facilitating some native species of Hymenoptera, thus making a positive interaction that benefits at least one species and causes harm to neither (sensu Stachowicz, 2001). To our knowledge, facilitative interactions involving plant exudates induced by *H. halys* and native species of insects have not yet been reported in invaded regions other than the USA.

Other examples of facilitation occurring between non native and native species of insects are: the Japanese beetle *Popillia japonica* Newman (Coleoptera: Scarabaeidae) and the native green June beetle *Cotinis nitida* (Linnaeus) (Coleoptera: Scarabaeidae) on grapes in the USA (Hammons et al., 2009), and the non native moth *Epiblema sugii* Kawabe (Lepidoptera: Tortricidae) that induces galls on *Ambrosia trifida* L. (Asterales: Asteraceae) and native beetles and ants in Japan (Yamazaki & Sugiura, 2016). Facilitation between invasive and native species, however, is often poorly documented.

Here we report, for the first time in Europe, facilitation of the feeding of native species of Hymenoptera (wasps and

ants) on manna ash trees by invasive *H. halys*. To study this phenomenon, we artificially induced a long-lasting infestation of *H. halys* in which this pest fed on trunks of trees for months, which resulted in the outflow of plant exudates. We investigated if the presence of wasp and ant foragers was associated with the presence of *H. halys* feeding on trunks of trees and if their abundance differed at different times of day.

MATERIAL AND METHODS

Site surveyed and methodology

The experiment was conducted in 2017 at the experimental farm of the Department of Agronomy, Food, Natural resources, Animals and Environment – University of Padua in Legnaro, Padua (north-eastern Italy, 45.344124 N, 11.954504 E, 8 m a.s.l.). On a group of trees of different species (Table 1) all growing close together and located within an area of about 500 m², *H. halys* infestations were induced from June until September by using *H. halys* aggregation pheromone lures (Trécé Inc., Adair, OK, USA), which were installed on 5 June 2017. Lures were loaded with a synthetic analog of the aggregation pheromone, i.e. a pheromone that is known to be attractive to both sexes, including nymphs (*sensu* Millar, 2005) of *H. halys* (Weber et al., 2017). Eight pheromone lures were evenly distributed (every 5 m, maximum three lures per tree; Table 1) by hanging them in the canopies of trees three meters above the ground and renewed every three weeks in the same position. We assessed the abundance of *H. halys* on all the trees in the area every week (5 June – 31 August 2017) by beat sampling (beating sheet, 1 m × 1 m, UM01 – Clap Net, Omnes Artes s.a.s., Bergamo, Italy) after 5.30 p.m. In addition, visual inspections of the trunk of each tree were made from 21 July to 31 August 2017 to quantify the number of *H. halys* feeding and the presence of other insects. Trees with pheromone lures were not included in order to avoid bias. Inspections, each lasting 15 min, were carried out at 11:00 a.m., 2:00 p.m. and 5:00 p.m. (GMT + 1) local time, every 2–4 days (13 observation days and 39 surveys in total); surveys were not carried out on rainy days. Immediately before recording the number of wasps and ants present, two minutes were spent counting the number of bark-feeding *H. halys* on each tree. The number of Hymenoptera observed feeding on trunks was recorded on a 1-m section of trunk 1.5 m from the ground on five randomly selected trees per species. Each 1-m section was inspected, and wasps and ants actively feeding on plant exudates were counted. For ant species, the abundance was ranked in five classes: 0 = absent, 1 = less than 10, 2 = 11–25, 3 = 26–40, 4 = more than 40 workers. Wasp abundance was recorded as absolute numbers. Wasps were identified using Dvořák & Roberts (2006) and ants initially using a guide (Lebas et al., 2016) followed by confirmation using mtDNA analysis, cytochrome

c oxidase subunit I (coxI) as described by Hebert et al. (2003). Additional observations were made in September and October 2017, and in the following two years (not included in statistical analyses).

Statistical analyses

Data on the abundance of *H. halys* recorded by beat sampling and visual estimates of trunk feeding activity on different species of trees were analyzed using a one-way analysis of variance (ANOVA) through the GLM procedure in SAS (ver. 9.4; SAS Institute, 2016). In this analysis, the number of *H. halys* recorded on different trees by beat sampling and the number observed feeding on the trunks were dependent variables, in two separate analyses in which species of tree were explanatory variables, and their effect was tested using an F test ($\alpha = 0.05$). Differences among tree species were evaluated using a post hoc Tukey's test ($\alpha = 0.05$). Before the analyses, data were checked for ANOVA assumptions and transformed to $\log(x + 1)$.

We assessed the relationship between the numbers of *H. halys* feeding on the trunks of trees and of the most common species of wasps and ants feeding on the associated exudates using linear regression. In this analysis, the mean number of *H. halys* feeding on trunks was the independent variable, and the number of most common species of wasps and ants the dependent variables resulting from the visual inspections of five plants.

The variation in the abundance of *H. halys* and wasps and ants during the course of a day was assessed using the generalized linear mixed model with the MIXED procedure in SAS (ver. 9.4; SAS Institute, 2016). The different times in a day (i.e. 11:00 a.m., 2:00 p.m., and 5:00 p.m.) were the independent variable, while the dependent variables in separate analyses were the number of feeding *H. halys* and the presence of wasps (number of individuals) and ants (classes of abundance) feeding on plant exudates. The effect of the time of day was tested using an F test ($\alpha = 0.05$) followed by post hoc Tukey's test ($\alpha = 0.05$). The factor “tree” ($n = 5$) was included as a random effect. In this analysis, untransformed data were used.

RESULTS

In 2017, *H. halys* collected by beat sampling was more abundant on *Fraxinus ornus* L. (Scrophulariales: Oleaceae) than on the other species of trees ($F_{4,320} = 619.67$, $p < 0.001$; Table 1). On the other trees, *H. halys* infestation level was lower on *Paulownia tomentosa* Steud. (Lamiales: Paulowniaceae) than on *Ficus carica* L. (Urticales: Moraceae), and the lowest numbers on *Juglans regia* L. (Juglandales: Juglandaceae) and *Olea europaea* L. (Scrophulariales: Oleaceae) (Table 1). In addition, the number of *H. halys* recorded feeding on the trunks of *F. ornus* was higher than

Table 1. List of the species of trees at the site studied (listed alphabetically by the order). The abundance of *Halyomorpha halys* was evaluated by beat sampling (no. of stink bugs per plant; weekly sample from all plants from 5 June to 31 August 2017) and visual records of individuals feeding on the trunks of five randomly chosen plants (from 21 July to 31 August 2017; 13 days, every two to four days). Data are presented as total individuals per plant and per trunk (\pm st. err.), respectively. Different letters indicate significant differences using Tukey's test ($\alpha = 0.05$).

Order	Family	Species	Total no. of trees (no. with pheromone lure)	<i>Halyomorpha halys</i> abundance (mean no./plant)		<i>Halyomorpha halys</i> feeding individuals/trunk	
Juglandales	Juglandaceae	<i>Juglans regia</i> L.	6 (1)	6.6 (\pm 3.0)	d	0.4 (\pm 0.2)	b
Lamiales	Paulowniaceae	<i>Paulownia tomentosa</i> Steud.	15 (2)	30.2 (\pm 2.3)	c	1.2 (\pm 0.5)	b
Scrophulariales	Oleaceae	<i>Fraxinus ornus</i> L.	54 (3)	1946.0 (\pm 94.9)	a	51.1 (\pm 2.3)	a
		<i>Olea europaea</i> L.	8 (1)	0.8 (\pm 0.6)	d	0.0 (\pm 0.0)	b
Urticales	Moraceae	<i>Ficus carica</i> L.	7 (1)	77.8 (\pm 9.2)	b	1.8 (\pm 1.0)	b

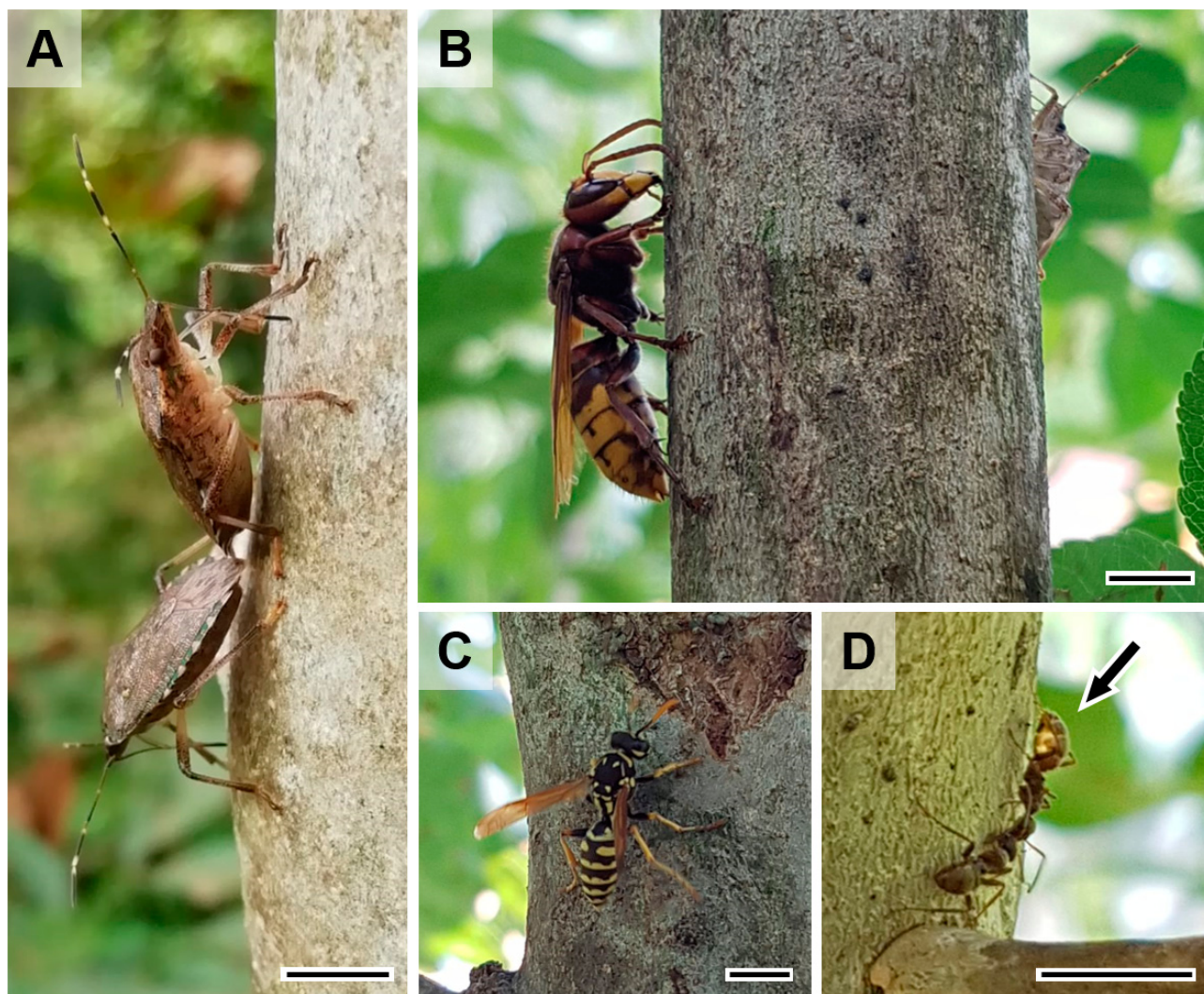


Fig. 1. *Halyomorpha halys* adults feeding on trunk of *Fraxinus ornus* (A). The European hornet, *Vespa crabro* (B) and the paper wasp, *Polistes dominula* (C) foraging for plant exudates induced by the feeding of *H. halys*. *Formica cunicularia* workers (D); the arrow indicates the abdomen of a worker containing *F. ornus* exudates. Scale bar: 5 mm.

on other trees ($F_{4,320} = 596.43$, $p < 0.001$; Table 1; Fig. 1A). On *F. ornus*, their feeding caused the outflow of tree exudates from the feeding wounds, whereas no exudates were detected on other tree species.

Even though some Hymenoptera were recorded on trees other than *F. ornus*, they were not actively feeding on trunks. The European hornet, *Vespa crabro* Linnaeus (Fig. 1B), the paper wasp *Polistes dominula* (Christ) (Fig. 1C) and *Formica (Serviformica) cunicularia* Latreille (Figs 1D and S1B; on all 13 days sampled) regularly visited *F. ornus* trunks to collect exudates. *Lasius emarginatus* (Olivier) workers were often recorded on *F. ornus* trunks feeding on exudates (on a total of eight days). In August, *Polistes* cf. *nimpha* (Christ) and *Tapinoma subboreale* Seifert were recorded on two and four occasions, respectively. Following this, the results for the most common wasp and ant species that fed on *F. ornus* (*P. dominula*, *V. crabro*, *F. cunicularia* and *L. emarginatus*) were analysed statistically.

Abundance of *P. dominula* ($F_{1,193} = 16.66$, $p < 0.001$, $R^2 = 0.212$) and *F. cunicularia* ($F_{1,193} = 12.25$, $p < 0.001$, $R^2 = 0.214$) actively feeding on *F. ornus* exudates were as-

sociated with the presence of bark-feeding *H. halys*. No significant trends were detected between bark-feeding *H. halys* and exudate-feeding foragers of *V. crabro* ($F_{1,193} = 0.60$, $p = 0.440$, $R^2 = 0.140$) or *L. emarginatus* ($F_{1,193} = 0.57$, $p = 0.450$, $R^2 = 0.004$).

Foragers of the German yellowjacket, *Vespula germanica* (Fabricius) (Fig. S1A) were recorded feeding on *F. ornus* exudates from September to the beginning of October 2017. While all the aforementioned species were recorded in all three years, *Crematogaster scutellaris* (Olivier) foragers were only recorded feeding on *F. ornus* exudates in 2019 (Fig. S1C).

More individuals of *H. halys* were recorded feeding on the trunks of *F. ornus* in the afternoon than late in the morning ($F_{2,132.5} = 23.18$, $p < 0.001$; Fig. 2A). Similarly, more foragers of *P. dominula* ($F_{2,128.1} = 40.98$, $p < 0.001$; Fig. 2B), *V. crabro* ($F_{2,48} = 120.43$, $p < 0.001$), *F. cunicularia* ($F_{2,132.7} = 103.55$, $p < 0.001$) and *L. emarginatus* ($F_{2,129.4} = 21.01$, $p < 0.001$; Fig. 2C) were recorded feeding on plant exudates in the afternoon than in the morning. *Vespa crabro* was never observed in the morning, and more individu-

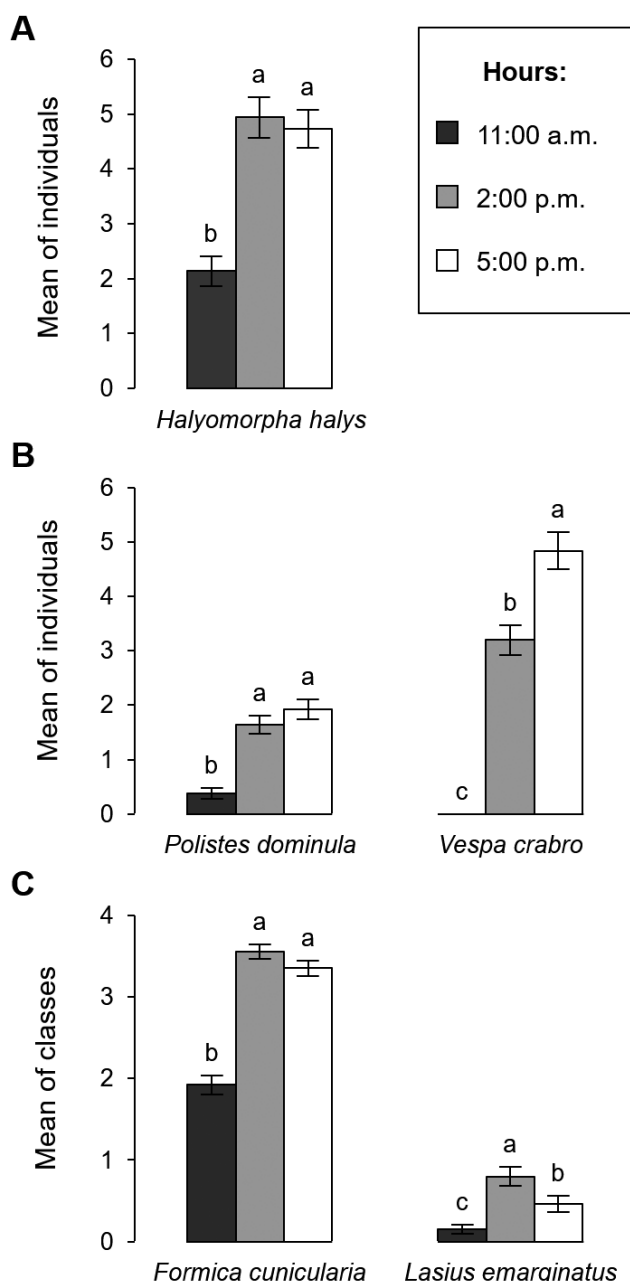


Fig. 2. Presence of *Halyomorpha halys*, wasps and ants feeding on *Fraxinus ornus* trunks at different times of a day (from 21 July to 31 August 2017). *Halyomorpha halys* (A). *Polistes dominula* and *Vespa crabro* (B). *Formica cunicularia* and *Lasius emarginatus* (C); for ant species, abundance classes are: 0 = absent, 1 = less than 10, 2 = 11–25, 3 = 26–40, 4 = more than 40 workers). Bars indicate standard errors. Different letters indicate significant differences based on Tukey's test ($\alpha = 0.05$).

als visited *F. ornus* trunks at 5:00 p.m. than at 2:00 p.m. (Fig. 2B). In contrast, *L. emarginatus* foragers were more abundant at 2:00 p.m. than at 5:00 p.m., and at 11:00 a.m. they were less abundant than at other times (Fig. 2C).

Furthermore, *P. dominula*, *V. crabro* and *V. germanica* were recorded disturbing and removing *H. halys* in order to collect fresh exudates from the trunk (Fig. S2), but this aggressive behaviour was only recorded on a few occasions.

DISCUSSION

Here we report, for the first time in Europe, facilitation of native wasp and ant feeding by invasive *H. halys*. These interactions are associated with the outflow of exudates from feeding punctures of *H. halys* on the trunks of *F. ornus*. In the USA, *Fraxinus americana* L. is considered to be an important host plant of stink bugs and hosts high densities of *H. halys* (Nielsen & Hamilton, 2009). Feeding on trunks or twigs is uncommon in stink bugs (Panizzi, 1997), but is reported for *H. halys* in the USA by Martinson et al. (2013) and also confirmed in Europe.

In the area studied, the induced-massive feeding on the trunks of manna ash trees by *H. halys* resulted in exudate outflow from their feeding punctures, which attracted eight species of native wasps and ants. No wasps or ants, however, were observed feeding on the liquid faeces produced by *H. halys*. Despite *H. halys* fed on species of trees other than *F. ornus*, we did not observe exudate outflow from the feeding punctures, possibly due to specific features of those trees and the low stink bug numbers recorded feeding on them. In this study, high infestation levels were artificially induced by using pheromone lures, so that the results do not reflect the true extent of the interaction between *H. halys* and other insects brought about by their feeding on the trunks of manna ash. Outbreaks of *H. halys*, however, are reported in invaded areas in Europe (e.g. Costi et al., 2017; Leskey & Nielsen, 2018; Maistrello et al., 2018). In addition, bark-feeding by *H. halys* is reported at other sites where attraction of *V. germanica* and *Formica* sp. on *F. ornus* and, with a less extent, on *Acer* sp. exudates following natural outbreaks of *H. halys* was observed in 2017 and 2019 (D. Scaccini, unpubl.). These observations indicate that facilitation of European wasp and ant feeding by *H. halys* may occur naturally in other areas. Similarly, the interactions between *H. halys* and native Hymenoptera reported in Maryland and West Virginia indicate that at least five species of native wasps and ants and two cosmopolitan ants are attracted by the carbohydrate rich source exuding from the feeding wounds made by this stink bug (Martinson et al., 2013).

Nutrient requirements of wasps and ants include carbohydrates, usually obtained from (extra)floral nectaries, honeydew, fruit, plant sap and other products, as well as anthropogenic compounds. Sugars are used as an energy source by wasps (Raveret Richter, 2000) and in metabolism and sperm production by ants (Wäckers et al., 2005; Blüthgen & Feldhaar, 2010).

Phloem sap is a food rich in sugars (Douglas, 2006) and, as reported for Oleaceae in general (Wäckers et al., 2005), *Fraxinus* exudates contain mannitol, fructose, glucose and other monosaccharides, together with oligosaccharides such as mannotriose and stachyose (Caligiani et al., 2013). *Vespa crabro* is known to feed on tree sap (Yoshimoto & Nishida, 2009) and Archer (2014) states that *V. crabro* actively wounds twigs of ash and lilac trees in order to cause an outflow of sap. Ants foraging activity on manna ash tree exudates is not surprising because sugar is a common part of the diet of Formicinae such as *F. cunicularia* (Akyürek

et al., 2016; Novgorodova & Ryabinin, 2018) and *Lasius* species (Madsen et al., 2017), in which the workers have receptors that possibly perceive carbohydrates (Tinti & Nofre, 2001). *Crematogaster scutellaris* is omnivorous and may attack and eat *H. halys* (Castracani et al., 2017), but in this study, it was only recorded foraging for plant exudates.

Halyomorpha halys feeding activity varied during the course of a day being higher in the afternoon than late in the morning. Indeed, *H. halys* activity increases with increase in temperature, but probing activity stops above 26.5–29.6°C (Wiman et al., 2014), development ceases at 35°C and it dies at higher temperatures (Haye et al., 2014; Aigner & Kuhar, 2016; Scaccini et al., 2019).

More wasps and ants were recorded feeding on *F. ornus* exudates in the afternoon than in the morning. Indeed, when it is warm, the rate of delivery of sugars by wasp foragers to their nest is higher than at lower temperatures, as reported for *V. germanica* (Jandt et al., 2010). Similarly, ant foraging activity is affected by environmental factors such as temperature, light intensity and other physical and biotic factors (Traniello, 1989), and at least in boreal forests, it generally increases in warm periods (Domisch et al., 2009).

Furthermore, on manna ash trees Vespidae disturbed *H. halys* feeding on the trunks. In fact, the aggressive behaviour of wasps toward other insects feeding on plant exudates was quoted by Wilson (1926) and, more recently, by Yoshimoto & Nishida (2009) and it dominates the hierarchies of insects feeding on plant exudates. Further investigations on aggressive behaviour, however, are needed for a better understanding of the plant exudate-feeding insect community.

The outflow of plant exudates that result from the feeding of phytophagous insects is known to attract different species of Hymenoptera in other regions (Yamazaki, 2007; Martinson et al., 2013), hence considered herbivores under an ecological point of view (Jones, 1994; Raveret Richter, 2000; Yoshimoto & Nishida, 2009; Iakovlev et al., 2017). Non native species can increase the availability of this sugary food source and create a novel feeding niche for native organisms (Rodriguez, 2006) that feed on tree exudates induced by phytophagous species. The positive interactions reported here are important for further understanding the ecology of invasive non native organisms, which induce plants to liberate exudates that are as attractive for native Hymenoptera as other sources of sugar from plants.

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Supplementary Figs S1–S2 follow on next page.

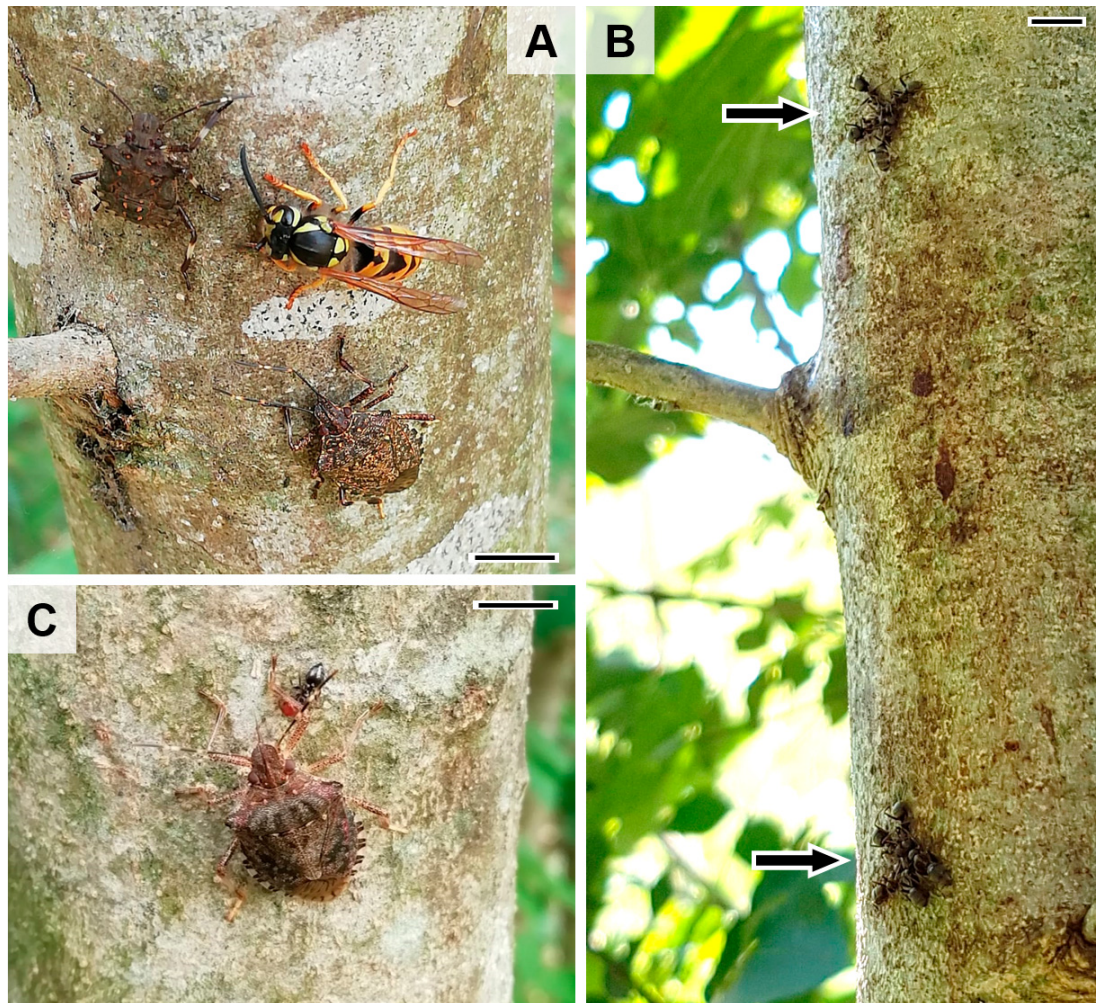


Fig. S1. *Vespa germanica* foraging for *Fraxinus ornus* exudates, with two *Halyomorpha halys* individuals (A). *Formica cunicularia* workers (indicated by arrows) grouped on plant exudates in the afternoon (B). A worker of *Crematogaster scutellaris* foraging for exudates, with a *H. halys* adult (C). Scale bar: 5 mm.

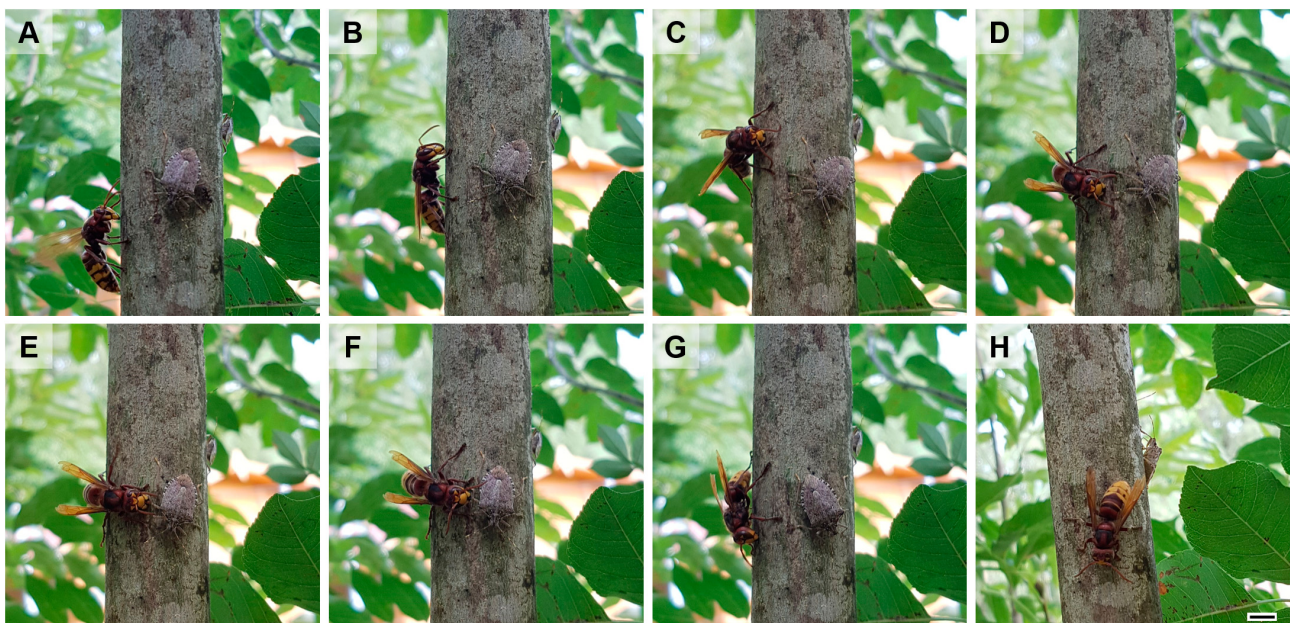


Fig. S2. Sequence of pictures of *Vespa crabro* disturbing and driving away *Halyomorpha halys* feeding on the trunk of *Fraxinus ornus*. European hornet landing on the trunk of manna ash close to an adult of *H. halys* (A) and searching for plant exudates (B). Movement to the adult *H. halys* (C). First approach to *H. halys* (D) followed by biting its leg (E, F). Movement of the *H. halys* disturbed by the hornet (G). Hornet searching for plant exudates in the area where *H. halys* was feeding (H). Scale bar: 5 mm.