ABSTRACT

Title of Thesis:	ELUCIDATING FACTORS TO IMPROVE BIOLOGICAL CONTROL OF *HALYOMORPHA HALYS* BY EGG PARASITOIDS
	Madeline Elizabeth Potter, Master of Science, 2023
Thesis Directed By:	Professor, Paula M. Shrewsbury, and Assistant Professor, Karin T. Burghardt, Department of Entomology

Halyomorpha halys Stål (Hemiptera: Pentatomidae), also known as the brown marmorated stink bug, is an invasive species from Northeast Asia, which has now spread to 47 USA states and invaded several other countries. In the USA, *H. halys* is an economically important pest of fruit, vegetable, field, and nut crops, and it feeds on ornamental plants. A sustainable means of controlling this pest is needed. Here I focus on elucidating features from bottom-up forces (alternate host identity, host plant identity, and habitat type) which may influence top-down forces such as parasitism by *H. haly's* key natural enemies, Hymenoptera egg parasitoids. Naturally laid eggs of insects were collected from a tree nursery in 2020 and from diverse habitats throughout Maryland in 2021 to investigate *H. halys* parasitoids' alternate insect egg hosts, host plant and habitat associations, and which factor(s) (host plant identity and/or host egg identity) are important to egg mass discovery, or to egg parasitism rate. Effects of host insect feeding guild (herbivore vs predator) and host plant origin (native vs non-native)

on parasitism were also examined. One new overwintering insect host and four new in season hosts for *Anastatus* spp., and five new in season hosts for *Telenomus cristatus* were found. A diverse array of plant species, particularly native *Acer* and *Quercus* species, were found to support alternate host insects. *Halyomorpha halys* related parasitoids were reared from eggs collected in all habitat types. Host egg order and egg feeding guild affected *Anastatus* spp. egg unit discovery efficiency and egg parasitism rate. Host plant identity and plant origin affected egg unit discovery efficiency and egg parasitism rate by all *H. halys* parasitoids. These findings support the importance of having a diverse community of alternate prey and informed plant selections to support parasitoids and their biological control of *H. halys* and other insect pests.

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ELUCIDATING FACTORS TO IMPROVE BIOLOGICAL CONTROL OF *HALYOMORPHA HALYS* BY EGG PARASITOIDS

by

Madeline Elizabeth Potter

Thesis submitted to the Faculty of the Graduate School of the
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Advisory Committee:
Professor Paula M. Shrewsbury, Chair
Assistant Professor Karin T. Burghardt, Co-chair
Associate Professor Daniel S. Gruner

Dedication

This work is dedicated to all my family, friends, and loved ones who have supported me through the ups and downs of life and pursuit of this graduate degree. I could not have done this without their support, and I feel so lucky to have had such an amazing support system.

To my parents who are my biggest cheerleaders in life, particularly throughout my academic pursuits. I look up to them and I feel very fortunate to have them in my life. They remind me to stay curious and embrace adventure and new experiences. To my dad who introduced me to the world of arthropods at such a young age through our walks in the woods. These early experiences left a strong impression on me that I will forever be grateful for. His guidance into the field of sciences has given me the confidence to pursue a career in science while staying true to who I am. He taught me the importance and joy of sharing knowledge with others. To my mom who was and is my rock through thick and thin. She has taught me how to see the good in others and to lead with love and passion. Through her career pursuits and relationships, she taught me the importance of helping and supporting others to make positive changes in this world. My mom's never-ending creativity inspires me to think outside the box and find new ways to express myself and communicate science with the world. She helped me stay present and embrace the unexpected twists and turns life can bring.

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Introduction

Herbivorous insect pests cause significant economic damage to agricultural and ornamental plants throughout the world. Globally an estimated 20-32% of agricultural yields are lost to insect pests (Oerke, 2006) and 70 billion USD globally lost to invasive insect pest damage annually (Bradshaw et al., 2016; Conti et al., 2020). In addition, insect pests cost millions USD annually due to resulting damage or costs of management (Jetter and Godfrey, 2009; Zalucki et al., 2012; Zapata et al., 2017; Leskey and Nielsen, 2018; DiGiacomo et al., 2019). With climate change, market globalization, agricultural intensification, accelerating urbanization, and increasing occurrence of pesticide resistance, insect pest outbreaks are on the rise (Bass et al., 2015; Ju et al., 2015; Bradshaw et al., 2016; Lehmann et al., 2020; Raven and Wagner, 2021). Chemical control of insect pests can be unreliable, expensive, and harmful to the environment (Pimentel, 2005; Dutcher, 2007). Therefore, there is an increasing need for sustainable insect pest management to conserve our environment and to sustain and grow plant resources needed for present and future generations.

Biological control is a sustainable method of pest management utilizing insect pest natural enemies such as predators, parasitoids, and pathogens. Natural enemies keep pest populations below damaging levels over long periods of time (Losey and Vaughan, 2006). Natural enemy predators and parasitoids provide an estimated 4.5 billion USD service in the USA annually (Losey and Vaughan, 2006). Absence of natural enemies, often caused by broad-spectrum pesticide use, reduced vegetation diversity and complexity, lack of floral resources, and insufficient alternate

prey/hosts, can lead to pest outbreaks (Shrewsbury and Raupp, 2000; Shrewsbury and Raupp, 2006; Zytynska et al., 2021; Korányi et al., 2022). Invasive insects can quickly outbreak once they reach new regions that are devoid of natural enemies that have a shared evolutionary history with them (Keane and Crawley, 2002).

Halyomorpha halys Stål (Hemiptera: Pentatomidae), also known as the brown marmorated stink bug, is an invasive insect that has reached damaging levels in the USA, in part due to a lack of co-evolved natural enemies. *Halyomorpha halys* is native to China, Japan, Korean, and Taiwan and was first detected in the USA in 1996 in Allentown, Pennsylvania (Hoebeke and Carter, 2003). *Halyomorpha halys* quickly spread and is currently found in 47 USA states, four Canadian provinces (Hoebeke and Carter, 2003; Northeastern IPM Center, 2021), Chile (Faúndez and Rider, 2017), Africa (Algeria, Morocco) (Nouere et al., 2019; Van Der Heyden et al., 2021), Central and Eastern Europe (Haye et al., 2014), the Caucasus (Southern Russia, Georgia, Armenia) (Mityushev, 2016; Gapon, 2017; Kalashian, et al., 2022), and Guam (Moore, 2014). Depending on location and corresponding climate, *H. halys* can have one to six generations per year (Hoffman, 1931); one to two generations in the mid-Atlantic USA (Nielsen et al., 2008). *Halyomorpha halys* is polyphagous, feeding on over 170 host plants (in North America) from more than 12 plant families, including fruit, vegetable, field, and nut crops, as well as ornamental plants. Both nymphal and adult *H. halys* are known to cause feeding damage to fruit and leaf tissue (Acebes-Doria et al., 2016; Bergmann et al., 2016). In 2010, *H. halys* feeding damage cost 37 million USD to apples alone and some stone fruit growers lost over 90% of their crops (Leskey and Hamilton, 2012). *Halyomorpha halys* is also a

nuisance for homeowners, as *H. halys* aggregates on the outside and inside of buildings in late fall and winter, respectively.

Halyomorpha halys populations are likely to expand due to rising temperatures from global warming. Using climate models, Kistner (2017) found the number of *H. halys* generations per year are likely to increase and their suitable range is likely to expand northward in both North America and Europe, under possible future climate scenarios. Using maximum entropy models, Illán et al. (2022) predicted regions of high suitability where *H. halys* has not yet been detected, suggesting further spread and impact of *H. halys*, particularly in agricultural regions (e.g. southern California and Idaho). The ongoing scenario of *H. halys* and these predictions indicate an increasing need for sustainable *H. halys* control. Chemical control is currently the most widely used method for managing *H. halys*. Broad-spectrum insecticides generally used against *H. halys* can cause secondary pest outbreaks, increase insecticide resistance, and compromise existing integrated pest management programs (Leskey et al., 2012; Rice et al., 2014). Given these non-target effects of pesticides to control *H. halys*, there has been increased interest in natural enemies that attack *H. halys* and its biological control.

Several different chewing and piercing-sucking generalist predators are documented to feed on various *H. halys* life stages in the USA. These *H. halys* predators include members from Agelenidae, Pholcidae, Salticidae, Theridiidae, and Thomisidae (Arachnida: Araneae), Gastropoda, and Cantharidae, Carabidae, and Coccinellidae (*Coleomegilla maculate* De Geer, *Harmonia axyridis* Pallas) (Insecta: Coleoptera), Forficulidae (Dermaptera), Asilidae (Diptera), Anthocoridae (*Orius*

insidiosus Say), Geocoridae (*Geocoris punctipes* Say), Lygaeidae (*Geocoris punctipes* Say, *G. uliginosus* Say), Miridae, Nabidae (*Nabis* spp.), Pentatomidae (*Podisus maculiventris* Say), and Reduviidae (*Arilus cristatus* Linnaeus) (Hemiptera), Crabronidae (*Astata bicolor* Say), Formicidae (Hymenoptera), Mantidae (Mantodea), Chrysopidae (*Chrysoperla carnea* Stephens) (Neuroptera), and Acrididae (*Melanoplus femurrubrum* De Geer), Gryllidae (*Acheta domesticus* L., *Oecanthus* spp.), and Tettigoniidae (*Atlanticus testaceous* Scudder, *Conocephalus fasciatus* De Geer*, C. strictus* Scudder, and *Orchelimum* spp.) (Orthoptera), as well as insectivorous mammals, birds, and reptiles (reviewed in Lee et al., 2013; reviewed in Rice et al., 2014; Abram et al., 2015; Morrison et al., 2016; Ogburn et al., 2016; reviewed in Abram et al., 2017; Biddinger and Joshi, 2017; Morrison et al., 2017; Northeastern IPM Center, 2017; Pote and Nielsen, 2017; Poley et al., 2018; Tillman et al., 2020).

Currently, there are 18 species of Nearctic Hymenoptera endoparasitoids in the genera *Anastatus* Motschulsky (Eupelmidae), *Trissolcus* Ashmead, *Telenomus* Haliday, and *Gryon* Haliday (Scelionidae), and *Ooencyrtus* Ashmead (Encyrtidae) that have been reported to parasitize *H. halys* eggs in the USA (reviewed in Rice et al., 2014; reviewed in Abram et al., 2017; Jones et al., 2014; Cornelius et al. 2016a, b; Herlihy et al., 2016; Ogburn et al., 2016; Dieckhoff et al., 2017; Jones et al., 2017; Tillman et al., 2020).

In *H. halys's* native range, *Trissolcus japonicus* Ashmead (Hymenoptera: Scelionidae), is considered the primary *H. halys* egg parasitoid. *Trissolcus japonicus* can cause up to 80% parasitism in *H. halys* eggs in China (Yang Zhong-Qi, et. al.,

2009). *Trissolcus japonicus* is a pentatomid specialist (Talamas et al., 2015a) that prefers arboreal habitats (Herlihy et al., 2016). In 2014, *T. japonicus* was first detected in Beltsville, Maryland and believed to be accidentally introduced (Talamas et al., 2015a). Since 2014, *T. japonicus* is now found in 13 USA states and Washington D.C., mainly concentrated in the northeastern and western USA (Northeastern IPM Center, 2021; Quinn et al., 2021).

Concerns over the release and spread of *T. japoncius* in the USA have centered around potential non-target impacts on native stink bugs, particularly beneficial predatory stink bugs. Studies have found that *T. japonicus* can parasitize pentatomid species' eggs native to North America (Zhang et al., 2017) but generally prefers to parasitize *H. halys* eggs when given a choice (Hedstrom et al., 2017; Botch and Delfosse, 2018; Lara et al., 2019). A study by Conti et al. (2020) suggested exploring biological control using natural enemies native to the country of introduction. Native egg parasitoids are promising candidates for biological control of *H. halys* in the USA (Cornelius et al., 2016b; Jones et al., 2017; Tillman et al., 2020).

Anastatus reduvii Howard (Hymenoptera: Eupelmidae) is one such North American native egg parasitoid that successfully parasitizes, develops within, and emerges from *H. halys* eggs (Jones et al., 2014; Cornelius et al., 2016a, b; Dieckhoff et al., 2017; Jones et al., 2017). *Anastatus reduvii* has shown significantly higher egg emergence rates when compared to certain native Scelionidae parasitoids (*Telenomus podisi*, *Trissolcus euschisti*, and *T. brochymenae*) (Cornelius et al., 2016a; Jones et al., 2017). In Maryland nurseries in 2012 and 2013, *Anastatus reduvii* accounted for ~98% of all parasitoid species that emerged from, and ~40% parasitism of, naturally

laid *H. halys* eggs (Jones et al., 2017). *Anastatus reduvii* are generalist egg parasitoids across several insect orders (including Lepidoptera, Hemiptera, and Orthoptera) (Thompson, 1954; Peck, 1963; Burks, 1967, 1979; De Santis, 1979, 1980; Mitchell and Mitchell, 1986; Herlihy et al., 2016; Tillman and Cottrell, 2016; Jones et al., 2017), which prefer arboreal habitats (Cornelius et al., 2016a; Herlihy et al., 2016; Jones et al., 2017).

Anastatus reduvii also exhibits host egg feeding behavior, which is an important source of host egg mortality (Stahl et al., 2019). In the USA, *A. reduvii* is distributed in Washington D.C. and MD, the mid-Atlantic region and south to Florida, as well as west to Kansas and Texas (Burks, 1967; Jones et al., 2017; Ogburn and Walgenbach, 2019). *Anastatus reduvii* could potentially be utilized in augmentative or conservation biological control approaches against *H. halys*. However, little is known about *A. reduvii'*s life history including its species' specific host range, reproductive biology, phenology, and host plant associations. A better understanding of the biology and ecology of potential biological control agents, such as *A. reduvii*, is important for effective biological control programs (Stahl et al., 2019).

Despite the presence of *H. halys* natural enemies in the USA, *H. halys* predation and parasitism rates are relatively low in many areas (Morrison et al., 2016; Ogburn et al., 2016; Tillman et al., 2020; Cornelius et al., 2021). Recently reported native egg parasitism rates have been too low to reduce *H. halys* populations below economic thresholds (Dieckhoff et al., 2017; Abram et al., 2017). Ogburn et al. (2016) reported that the overall impact of predators and parasitoids on *H. halys* ranged from 7.9% to 10.4% in agricultural systems. Cornelius et al. (2021) reported

an average parasitism rate of 4.2% and an average predation rate of 2.3% of *H. halys* eggs in urban, ornamental landscapes. In nursery habitats, a higher average egg parasitism rate of approximately 30% and a predation rate of approximately 7% has been reported (Jones et al., 2017). There is a need to identify measures to increase biological control of *H. halys*. Several studies have found that the prevalence of *H. halys* parasitoids is primarily habitat specific (Okuda and Yeargan, 1988; Herlihy et al., 2016; Tillman, 2016; Abram et al., 2017; Tillman et al., 2020). The surrounding landscape has an impact on natural enemies and their resulting biological control service. Literature highlights habitat type and diversity, plant species composition, and the present fauna or alternate prey as important variables that influence biological control (Shrewsbury and Raupp, 2000, 2006; Martin et al., 2013; Xu et al., 2013; Dainese et al., 2017; Konopka et al., 2017; Perez-Alvarez et al., 2019).

Here I focus on elucidating features from bottom-up forces (alternate host identity, plant identity, and habitat type) which may influence top-down forces such as parasitism. Parasitoids are generally attracted to an area based upon the plant community and what that community can provide for the parasitoids' survival and reproduction. Certain plant groups or species can be selected for their nectar (Takasu and Lewis, 1995; Gurr et al., 2004), physical refugia (Halaj et al., 2000), alternate prey/hosts (Abou-Awad et al., 1998; Viggiana, 2003; Shrewsbury et al., 2004; Shrewsbury and Raupp, 2006), breeding sites (Sutherland et al., 2001), and/or overwintering sites (Pollard, 1968; Halaj et al., 2000). The presence of alternate prey allows generalist predators/parasitoids to colonize a habitat before a target pest population arrives or increases and later sustains the generalist natural enemy after the

target pest density decreases, promoting top-down control (Walde 1994). A study by Shrewsbury and Raupp (2006) found predator abundance was related to a greater abundance of alternate prey in urban landscapes with complex vegetation compared to simpler ones. Variations in the availability of prey and non-prey food (in the case of omnivorous natural enemies) can have a significant effect on natural enemy dispersal, survival, and population dynamics (Eubanks and Denno, 1999). Identifying attractive landscape features and alternate hosts for *H. halys* parasitoids can inform plant selection and arrangement within and around habitats to support parasitic wasp populations and enhance biological control.

To increase our knowledge of *H. halys* related parasitoids and variables that impact their biological control, the present study on Hymenoptera egg parasitoids was conducted to: 1) identify over-wintering and in season hosts of parasitoid species, 2) assess what host plant species and habitat types are associated with parasitoid species, and 3) elucidate which factor(s) (host plant identity and/or host egg identity) are important to whether an egg mass was discovered or not, or to parasitism rate. Effects of the feeding guild of host insects (herbivore vs predator) and plant origin (native vs non-native) on parasitism were also examined.

Materials and methods

Egg collection

Two different methods were used to collect insect eggs. The first method, called “standardized nursery sampling”, involved sampling the same set of trees, searching for and collecting any insect eggs found, at one Maryland tree nursery. The second method, called “diverse habitats survey”, involved randomly selecting plants

throughout Maryland and searching for and collecting any insect eggs found. After the eggs were collected the same processing of insect eggs and emerged parasitoids and insect egg and parasitoid identification methods were used for both collection methods.

Standardized nursery sampling

Sampling for naturally laid insect eggs was conducted on nursery trees on nine dates from July to September 2020 at Raemelton Farm (Adamstown, MD). Trees were field grown in an organic growing system and planted between spring 2015 – spring 2018. On each sampling date, five tree species (*Acer rubrum* 'Franksred', *A. saccharum* 'Legacy', *Quercus alba*, *Q. coccinea*, and *Q. rubra*) and ten trees per species (50 trees total), were searched. The same trees were searched at each sampling date. Each tree was searched until the searcher felt they had sufficiently searched the bark (trunk and branches) and the upper and lower sides of reachable leaves (approximately three minutes per tree). Each tree was assigned a unique tree code and a record was kept at each search event of what and how many egg units (individual eggs, egg clusters, egg masses or oothecas) were found on each tree or if no egg units were found. If an egg unit was found, the egg unit was assigned a unique code and a record was kept of the collection date, field and tree location, and the tree's identification and unique tree code. All eggs were collected from the field and placed in a labeled petri dish and then transported in a cooler to the Shrewsbury laboratory (University of Maryland, College Park) for further processing.

Diverse habitats survey (urban landscapes, nurseries, and other habitats)

Surveys to collect insect eggs were conducted throughout Maryland, USA, in 2020 and 2021. In 2020, surveyors randomly searched and collected eggs from commercial tree nurseries and urban woody landscapes (June through August). In 2021, fifty Community Scientist volunteers from the University of Maryland Extension Master Gardener Program were recruited from five Maryland counties (Allegany, Frederick, Garrett, Montgomery, and Washington) and trained to help survey for eggs. Community Scientists searched for and collected eggs from various habitat types (agricultural, urban herbaceous, urban vegetable garden, urban woody, and woods/wooded edge) from March through September. If an egg unit was found, the egg unit was assigned a unique code and a record was kept of the collection date, habitat type, plant identification and locality, and collector identification. All eggs were collected from the field and were naturally laid. Eggs were placed in a labeled petri dish, which were transported in a cooler to the Shrewsbury laboratory (University of Maryland) for further processing.

Processing of insect eggs and emerged parasitoids

Once in the laboratory, petri dishes were sealed with parafilm and placed into a growth chamber maintained at 23.3-25.4° C, 58-87% relative humidity (RH), and a 16L:8D photoperiod. The egg units were checked every one to six days for any emergence of nymphs, larvae, or parasitoid adults from June through October 2020 and March through September 2021. Monitoring of egg units was stopped once there was zero emergence from all the egg units for 30 days in a row. Emerged parasitoids were counted and placed in a labeled vial of 70% ethanol for later identification.

Emerged nymphs and larvae were identified, recorded, and then either released outside or disposed of.

Insect egg and parasitoid identification

Only egg parasitoids of interest to this study were recorded. These include those that have been documented as Hymenoptera egg parasitoids of Pentatomidae in North America. Parasitoids of interest will be referred to as "parasitoids" through the remainder of this paper. All emerged parasitoid adults were identified to genus, and species when possible. *Trissolcus* species were identified using a key by Talamas et al. (2015b); some difficult to identify specimens were confirmed by E. J. Talamas (Florida State Collection of Arthropods, Gainesville, FL). *Telenomus podisi* and *T. cristatus* were identified using the key by Johnson (1984); some difficult to identify specimens were confirmed by J.S. Bremer (Florida State Collection of Arthropods, Gainesville, FL), M. Moore (University of Florida, Gainesville, FL), and E.J. Talamas using Cytochrome c Oxidase Subunit I (COI) barcoding. *Anastatus* species were identified using a key by Dieckhoff et al. (2014a) and using voucher specimens provided by R. A. Waterworth (USDA EPA, Washington, D.C.). *Anastatus* males were not identified to species because there is no key due to extreme sexual dimorphism for Eupelminae (Gibson, 1986; 1995). All *Anastatus* males were labeled as *Anastatus* spp. male. *Ooencyrtus* were identified to genus (since they are difficult to identify to species) using voucher specimens provided by R. A. Waterworth and/or identified by J. L. Mottern (USDA APHIS, Beltsville, MD). Parasitoids that emerged from insect eggs collected in this study were categorized into one of five "parasitoid taxon groups": (1) *Anastatus* spp. (*Anastatus* male spp., *A. mirabilis* Walsh & Riley,

A. pearsalli Ashmead, and *A. reduvii*); (2) *Ooencyrtus* spp.; (3) *Telenomus* spp. (*Telenomus cristatus* Johnson and *T. podisi* Ashmead); (4) native *Trissolcus* spp. (*Trissolcus brochymenae* Ashmead, *T. euschisti* Ashmead, and *T. thyantae* Ashmead); (5) *Trissolcus japonicus* (non-native).

Pentatomidae eggs were identified using a book by Herbert et al. (2015), a guide by Dieckhoff (2014b), and voucher specimens provided by R. A. Waterworth. Other insect eggs were identified using voucher specimens provided by R. A. Waterworth and photos from credible online Extension sources (University of Illinois, Kansas State University, North Carolina State University, Michigan State University, and Ohio State University) and other educational websites (Cloyd, 2015; Frank and Dale, 2015; Baker, 2017; Boggs and Chatfield, 2020; Haag and Frillman, 2020; Walton, 2020; BugGuide.net; InsectImages.org; Roos, n.d.).

Insect egg host associations (all data)

An insect egg taxon group was labeled as a "host" if at least one parasitoid emerged from an egg of the insect species. Each insect host was categorized into one of two host groups: (1) overwintering host (a host species that overwinters in the egg stage and only has one generation per year); and (2) in season host (a host species that does not overwinter in the egg stage).

Parasitoid genera known to potentially overwinter inside a host egg include *Anastatus* spp., *Ooencyrtus* spp., and *Telenomus* spp. To my knowledge, the overwintering strategy of North American *Anastatus* species known to parasitize *H. halys* eggs (*A. mirabilis*, *A. pearsalli*, and *A. reduvii*), has not been described, but several *Anastatus* congeners are known to overwinter as mature larvae (pre-pupal

stage) inside host eggs including *A. bifasciatus* Geoffroy (Stahl et al., 2019), *A. madagascariensis* Risbec (Narasimham and Sankaran, 1982), *A. disparis* Ruschka, *A. japonicus* Ashmead (Sullivan et al., 1977) and *Anastatus* sp. (Huang et al., 1974). The overwintering strategy of *Ooencyrtus* species varies and there is evidence of both adult stage and larval stage overwintering strategies for the genus *Ooencyrtus* (Power, 2020). To my knowledge the overwintering strategy of *O. johnsoni* Howard, a species known to attack *H. halys* eggs, is unknown. *Telenomus* species overwinter primarily as adults but can sometimes overwinter as immatures inside host eggs (Legault et al. 2012). To my knowledge not much is known about the overwintering strategy of *Telenomus podisi*, the *Telenomus* species known to parasitize *H. halys* eggs, although Lahiri et al.'s (2017) study suggests *T. podisi* overwinter as adults in leaf-litter.

An insect egg taxon group was labeled as a "non-host" if no parasitoids emerged, and a sample size of five or more egg units were collected (less than 5 egg units were not categorized). Results for both hosts and non-hosts were pooled across egg collection method (diverse habitats survey and standardized nursery sampling); to include all of the data collected.

Host plant associations (all data)

Host plant taxon groups were considered associated with a parasitoid species if at least one parasitoid had emerged from an insect egg unit that was collected from that plant species. A host plant taxon group, groups plants that were identified to the same taxon (i.e. plants that could only be identified to *Acer* were grouped together as one taxon group, while plants identified as *Acer rubrum* were grouped together as a different taxon group). Results for host plant associations were pooled across

collection method (surveys of insect eggs in diverse habitats and nursery egg sampling).

Habitat associations (all data)

Habitat descriptions of where each insect egg unit was collected were categorized into one of seven "habitat categories": (1) agricultural; (2) tree nursery; (3) urban herbaceous; (4) urban vegetable garden; (5) urban woody; (6) urban all (urban herbaceous, urban vegetable garden, and urban woody pooled) (7) woods/wooded edge. A habitat category was associated with a parasitoid species if at least one parasitoid had emerged from an insect egg unit that was collected from the habitat category. Results for habitat associations were pooled across collection method (surveys of insect eggs in diverse habitats and nursery egg sampling).

Statistical analysis

All analyses were done in R (v.4.2.1) (R Development Core Team, 2022). Data for statistical analysis was separated by collection method (standardized nursery sampling data; diverse habitats survey data) and in the case of the diverse habitats survey data, also by year (2020; 2021), where only 2021 diverse habitats survey data was analyzed; there was not enough 2020 diverse habitats survey data to analyze.

The response variables, discovery efficiency and egg parasitism rate were examined by general linear mixed-effect models (GLMM) or by generalized linear models (GLM) with a logit-link and binomial distribution. The analyses were conducted using the glmer or glm function in the lme4 package in R (Bates et al., 2012). Discovery efficiency was expressed by the number of discovered egg units (discovered defined as at least one parasitoid emerged from said egg unit) over the

total number of egg units collected. Discovery efficiency was looked at to measure how many egg units were located by parasitoids. Egg parasitism rate was defined as the number of eggs from which a parasitoid emerged, out of the total number of individual eggs (those eggs laid individually and individuals in an egg mass). Egg parasitism rate was used to measure the level of parasitism.

The response variable, discovery efficiency, was modeled using a log-link transformation (fixed effect coefficients are presented on the logit [log-odds] scale). Drop1() performed a chi-squared likelihood ratio test (LRT) comparing an intercept only model to one containing the fixed effect. With more than two fixed effect levels, if the fixed effect was a significant predictor, I used emmeans() to perform post hoc pairwise tests comparing the fixed effect levels using Tukey adjustments for multiple comparisons (Russell, 2021). When analyzing the response variable egg parasitism rate, only data from parasitized egg units were used. When egg parasitism rate was used as a fixed effect the "weights" command weighted each egg unit based on the total number of eggs it contained.

Standardized nursery sampling data

Effect of host insect egg order on Anastatus spp. parasitism

To determine if the probability of egg unit discovery or egg parasitism rate by *Anastatus* spp. differed by host insect egg order, I built GLMMs with insect egg order as a fixed effect and tree species and egg collection date as random intercepts. There was not enough data to analyze parasitism differences by egg identity for parasitoids species other than *Anastatus* spp.

Effect of pentatomid species on parasitism

To determine if the probability of egg unit discovery or egg parasitism rate differed by pentatomid species, I built GLMMs with pentatomid egg species as a fixed effect and tree species and egg collection date as random intercepts. Due to low egg unit counts, all *Euschistus* species were pooled under the taxon group *Euschistus* spp. and all *Podisus* species were pooled under the taxon group *Podisus* spp.

Effect of tree genus and tree species on parasitism

To determine if the probability of egg unit discovery or egg parasitism rate differed by tree genus (*Acer* and *Quercus*) and/or species (*Acer rubrum*, *A. saccharum*, *Quercus alba*, *Q. coccinea*, and *Q. rubra*), I built GLMMs with tree genus or species as a fixed effect and egg collection date and egg mass species as random intercepts. Separate models were run for parasitism (discovery and rate) pooling all parasitoid species together and for parasitism just by *Anastatus* spp., since *Anastaus* is a key parasitoid genus of interest in this study. Additional GLMMs were run to determine if the probability of pentatomid egg unit discovery or egg parasitism rate differed by tree genus or tree species.

Relationship between plant genus and pentatomid egg species

To determine if egg parasitism rate of a pentatomid species depended on the tree genus the eggs were found on, I first built a GLMM with pentatomid species, tree genus, and an interaction between pentatomid species and tree genus as fixed effects, and unique tree code as a random intercept. Then, the *emmeans* function was used to compare pentatomid species and tree genus combinations and the results were plotted

using the *ggplot* function to visualize the predicted parasitism rate by pentatomid species and by tree genus (*Acer* and *Quercus*).

Diverse habitats survey data (2021)

Effect of host insect egg species' feeding guild on Anastatus spp. parasitism

To determine if the probability of egg unit discovery or egg parasitism rate differed by host insect egg species' feeding guild, I built GLMs with feeding guild (herbivore vs predator) as a fixed effect. The predator level included omnivorous insect species.

Effect of plant origin on parasitism

To determine if the probability of egg unit discovery or egg parasitism rate differed by plant origin (native vs non-native to North America), I built GLMs with plant origin as a fixed effect. Native plants were defined as plants endemic to North America and included native cultivars. Separate models were run for parasitism, pooling all parasitoid species together and for parasitism just by *Anastatus* spp.

Results

1. All data (pooled by collection method)

1.1. Summary of egg collections

A total of 949 egg units were collected (27,668 eggs and 141 mantis ootheca) from 44 different insect taxon groups (Table S1). The standardized nursery sampling resulted in a total of 165 egg units collected (4,562 eggs and two mantis ootheca) from 15 different insect taxon groups. The diverse habitats survey resulted in a total of 784 egg units collected (23,106 eggs and 139 mantis ootheca) from 39 different insect taxon groups.

1.2. Summary of emerged parasitoids

A total of 2,692 parasitoids were reared from collected eggs (Table 1; Table S2). The standardized nursery sampling resulted in a total of 445 parasitoids reared. The diverse habitats survey resulted in a total of 2,247 parasitoids reared.

1.3. Insect egg host associations

Of the 22 insect egg taxon groups (of 44) that supported parasitoids, three taxon groups were used as overwintering parasitoid hosts (Table 2) and 19 were used as in season parasitoid hosts (Table 3). Not all eggs collected emerged parasitoids. Twenty-two insect egg taxon groups did not rear any parasitoids (*H. halys* related parasitoids). Eighteen out of the 22 host taxon groups were categorized as "non-hosts" (Table S3).

1.3.a. Overwintering egg hosts

Of the parasitoids of interest in this study, only generalist parasitoids, *Anastatus* spp. and *Ooencyrtus* spp., emerged from overwintering egg hosts. The overwintering hosts included three taxon groups: *Arilus cristatus* (Linnaeus) (Hemiptera: Reduviidae), *Stagmomantis carolina* (Johansson) (Mantodea: Mantidae), and Tettigonidae spp. (Orthoptera). *Anastatus* spp. and *Ooencyrtus* spp. emerged from *A. cristatus* eggs. *Anastatus* spp. emerged from *S. carolina* ootheca (Table 2). Parasitoid composition of the 999 parasitoids reared from the total of 13,607 *A. cristatus* eggs included 65.36% *Anastatus* spp. and 34.63% *Ooencyrtus* spp. Parasitoid composition of the 49 parasitoids reared from the total of 59 *S. carolina* ootheca included 100% *Anastatus* spp. (Fig. 1). Only a single *Anastatus* male spp. parasitoid emerged from a Tettigoniidae sp. egg (Table 2; Table S2).

1.3.b. In season egg hosts

Of the parasitoids of interest in this study, both generalist and pentatomid specialist parasitoids emerged from a variety of insect egg taxon groups (Table 3). In season hosts include 19 taxon groups (Table 3). *Anastatus* spp. emerged from 15 insect egg taxon groups (across two orders, Hemiptera and Lepidoptera), *Ooencyrtus* spp. emerged from five taxon groups (across two orders, Coleoptera and Hemiptera), *Telenomus* spp. emerged from four Pentatomidae taxon groups, native *Trissolcus* spp. emerged from six Pentatomidae taxon groups, and *Trissolcus japonicus* emerged from two Pentatomidae taxon groups (Table 3).

Parasitoid composition was looked at for the two most collected insect egg taxon groups, *H. halys* (46 egg units, 1152 eggs) and *Euschistus* spp. (113 egg units, 2219 eggs). Out of the 255 parasitoids that were reared from *H. halys* eggs, 56.86% were *Trissolcus japonicus* spp., 39.61% were *Anastatus* spp., 1.96% were native *Trissolcus* spp., and 1.57% were *Telenomus* spp. Out of the 685 parasitoids that were reared from *Euschistus* spp. eggs, 43.07% were native *Trissolcus* spp., 41.75% were *Anastatus* spp., 14.89% were *Telenomus* spp., and 0.29% were *Trissolcus japonicus*. No *Ooencyrtus* spp. emerged from *H. halys* or *Euschistus* spp. eggs (Fig. 2).

1.4. Host plant associations

Insect egg hosts and parasitoids were associated with a diverse array of plant species (Table S4). Of the five tree species searched in the standardized nursery sampling and the additional 123 plant taxon groups that were searched in the diverse habitats survey, 52 plant taxon groups had at least one parasitoid species emerge from an egg unit on that plant. *Anastatus* spp. were associated with 38 plant taxon groups,

Ooencyrtus spp. were associated with 14 plant taxon groups, *Telenomus* spp. were associated with 10 plant taxon groups, native *Trissolcus* spp. were associated with 17 plant taxon groups, *Trissolcus japonicus* were associated with six plant taxon groups (Table 4). Plant taxon groups that supported four or more parasitoid taxon groups (of 5) included *Acer rubrum* (Sapindales: Sapindaceae), *Acer saccharum* (Sapindales: Sapindaceae), *Cercis canadensis* (Fabales: Fabaceae), *Quercus alba* (Fabales: Fabaceae), and *Quercus coccinea* (Fabales: Fabaceae) (Table 4).

1.5. Habitat associations

Of the six different habitat categories searched (agricultural, tree nursery, urban herbaceous, urban woody, urban vegetable garden, and woods/wooded edge), each setting had at least one parasitoid of interest emerge from an egg collected from the habitats (Fig. 3; Table 5). Egg unit parasitism rate ranged from 7.41 – 32.52% for all habitat categories (Fig. 3). *Anastatus* spp. emerged from five different habitat categories, *Ooencyrtus* spp. emerged from five habitat categories, *Telenomus* spp. emerged from four habitat categories, native *Trissolcus* spp. emerged from five habitat categories and *Trissolcus japonicus* emerged from three habitat categories (Table 5).

Parasitoid composition varied by habitat type (Fig. 4) Out of the 59 parasitoids collected in the agricultural habitat, 1.69% were *Anastatus* spp. and 98.3% were *Ooencyrtus* spp. Out of the 1078 parasitoids collected in the tree nursery habitat, 42.7% were *Anastatus* spp., 19.5% were *Ooencyrtus*, 6.1% were *Telenomus* spp., 20.2% were native *Trissolcus* spp., and 11.3% were *Trissolcus japonicus*. Out of the 1307 parasitoids collected in the urban all habitat, 56% were *Anastatus* spp., 13%

were *Ooencyrtus* spp., 6.8% were *Telenomus* spp., 21.9% were native *Trissolcus* spp., and 1.9% were *Trissolcus japonicus*. Out of the 124 parasitoids collected in the urban herbaceous habitat, 20.1% were *Telenomus* spp. and 79.8% were native *Trissolcus* spp. Out of the 121 parasitoids collected in the urban vegetable garden habitat, 13.2% were *Ooencyrtus* spp. and 86.7% were native *Trissolcus* spp. Out of the 1062 parasitoids collected in the urban woody habitat, 69.2% were *Anatstaus* spp., 14.5% were *Ooencyrtus* spp., 6.1% were *Telenomus* spp., 7.8% were native *Trissolcus* spp., and 2.3% were *Trissolcus japonicus*. Out of the 20 parasitoids collected in the woods/wooded edge habitat, 100% were *Anastatus* spp. (Fig. 4).

2. Standardized nursery sampling data

2.1. Effect of host insect egg order on Anastatus spp. parasitism

Insect egg order: Discovery efficiency. The probability of *Anastatus* spp. egg unit discovery differed by host insect egg order with higher probability of discovery for Lepidoptera then Hemiptera egg units (LRT: X^2=19.29, p<0.001; Hemiptera: coef=18.38, SE±316.96; Lepidoptera: coef=18.41, SE±316.96) (Table S5). Post hoc comparisons revealed no significant egg order comparisons.

Insect egg order: Egg parasitism rate. Using data from discovered egg units, egg parasitism rate differed by egg order with a higher predicted egg parasitism rate on Lepidoptera eggs compared to Hemiptera eggs (LRT: X^2=12.66, p<0.001; Lepidoptera: coef=2.05, SE±0.61; Hemiptera: coef=-1.14, SE±0.43) (Figure 5).

2.2. Effect of pentatomid egg species on parasitism

Discovery efficiency: The probability of egg unit discovery, by all parasitoid species, did not differ by pentatomid species (LRT: X^2=6.22, p=0.10) (Table S6).

Egg parasitism rate. Using data from discovered egg units, there was weak evidence that egg parasitism rate differed by pentatomid species (LRT: X^2=6.73, p=0.08) (Figure 6).

2.3. Effect of tree genus and tree species on parasitism by all parasitoid species

Tree genus: Discovery efficiency: There was weak evidence that the probability of discovery was higher for egg units laid on *Quercus* (LRT: X^2 = 2.91, p = 0.09; *Acer*: coef= -2.14, SE±1.04; *Quercus*: coef= 0.81, SE±0.48) (Table S7).

Tree genus: Egg parasitism rate. Using data from discovered egg units, egg parasitism rate diffed by tree genus, with a higher predicted egg parasitism rate for eggs laid on *Quercus* (LRT: X^2=25.74, p<0.001; *Acer*: coef=-0.93, SE±0.88; *Quercus*: coef=1.01, SE±0.20) (Figure 7a).

Tree species: Discovery efficiency. The probability of egg unit discovery differed by tree species (LRT: X^2=14.02, p=0.01) (Table S8).

Tree species: Egg parasitism rate. Using data from discovered egg units, egg parasitism rate differed by tree species (LRT: X^2 = 14.20, p = 0.01). Eggs laid on Q. *alba* had the highest predicted parasitism rate out of all the tree species (*Q. alba*: coef=1.44, SE±0.75) (Figure 7b).

2.4. Effect of tree genus and tree species on parasitism by Anastatus spp.

Tree genus: Discovery efficiency. The probability of egg unit discovery by *Anastatus* spp. did not differ by tree genus (LRT: X^2=1.54, p =0.22; *Acer*: coef=-2.55, SE±0.88; *Quercus*: coef=0.62, SE±0.51) (Table S9).

Tree genus: Egg parasitism rate. Using data from discovered egg units, there was weak evidence that *Anastatus* spp. egg parasitism rate differed by tree

genus (LRT: X^2=2.88, p=0.09; *Acer*: coef=-0.50, SE±0.84; *Quercus*: coef=0.57, SE±0.33) (Figure 8a).

Tree species: Discovery efficiency: The probability of egg unit discovery by *Anastatus* spp. did not differ by tree species (LRT: X^2=6.27, p=0.18) (Table S10).

Tree species: Egg parasitism rate: Using data from discovered egg units, predicted *Anastatus* spp. egg parasitism rate differed by tree species (LRT: X^2=22.67, p<0.001). Eggs laid on *Q. alba* had the highest predicted egg parasitism rate out of all the tree species (*Q. alba*: coef=2.23, SE±0.79) (Figure 8b).

2.5. Effect of plant genus and species on parasitism of pentatomid species eggs

Tree genus: Discovery efficiency. The probability of egg unit discovery did not differ by tree genus (LRT: X^2=1.82, p=0.18; *Acer*: coef=-1.22, SE±0.72; *Quercus*: coef=1.16, SE±0.85) (Table S11).

Tree genus: Egg parasitism rate. Using data from discovered egg units, egg parasitism rate did not differ by tree genus (LRT: X^2=1.49, p=0.22; *Acer*: coef=-1.72, SE±1.02; *Quercus*: coef=1.52, SE±1.16) (Figure 9a).

Tree species: Discovery efficiency. The probability of egg unit discovery differed by tree species (LRT: X^2=13.33, p=0.01). Post hoc comparisons demonstrated a significant difference in the probability of egg unit discovery between all the tree species (p<0.001) (Table S12).

Tree species: Egg parasitism rate. Using data from discovered egg units, egg parasitism rate differed by tree species (LRT: X^2=134.37, p<0.001). Eggs laid on *Q. alba* had the highest predicted egg parasitism rate out of all the tree species (*Q. alba*: coef=3.54, SE±0.61) (Figure 9b).

2.6. Relationship between plant genus and pentatomid egg species

Using data from discovered egg units, there was a significant interaction between tree genus and pentatomid egg species when looking at predicted egg parasitism rate (LRT: X^2=20.76, p<0.001). Post hoc comparisons found a significant difference in egg parasitism rate between *H. halys* eggs laid on *Acer* vs *Quercus*, with a higher predicted egg parasitism rate for *H. halys* eggs laid on *Quercus* (*H. halys*, *Acer-H. halys*, *Quercus*: coef=-2.19, SE±0.34, p<0.001) (Figure 10). A higher predicted egg parasitism rate was found for *Euschistus* spp. eggs laid on *Quercus*, but this comparison was not significant (*Euschistus* spp., *Acer-Euschistus* spp., *Quercus*: coef=-0.37, SE±0.25, p=0.90). Other pentatomid egg species collected (*Banasa* spp., and *Podisus* spp.), had discovered egg units that were only laid on either *Acer* or *Quercus* trees, not both tree genera, thus comparisons of egg parasitism rate by tree genus could not be analyzed for these pentatomid species (Table S13).

3. Diverse habitats survey (2021 data only)

3.1. Effect of host insect egg species' feeding guild on Anastatus spp. parasitism

Discovery efficiency. The probability of egg unit discovery by *Anastatus* spp. differed by egg species' feeding guild with higher probability of discovery for predaceous egg species (LRT: X^2=13.56, p<0.001; Herbivore: coef=-2.96, SE±0.24; Predator: coef=1.12, SE±0.31) (Table S14).

Egg parasitism rate. Using data from discovered egg units, egg parasitism rate differed by egg species' feeding guild with a slightly higher predicted egg parasitism rate for predaceous egg species (LRT: X^2=233.09, p<0.001; Herbivore: coef=-1.13, SE±0.05; Predator: coef=-1.07, SE±0.07).

3.2. Effect of plant origin on parasitism

All parasitoid species of interest: Discovery efficiency. The probability of discovery differed by host plant origin (LRT: X^2=21.30, p<0.001), with a higher probability of discovery for egg units laid on native plants (native: coef=-0.96, SE±0.17; non-native: coef=-1.09, SE±0.24) (Table S15).

All parasitoid species of interest: Egg parasitism rate. Using data from discovered egg units, predicted egg parasitism rate differed by plant origin (LRT: X^2=314.78, p<0.001), with a higher predicted egg parasitism rate for eggs laid on non-native plants (native: coef=-1.33, SE±0.04; non-native: coef=1.50, SE±0.08).

***Anastatus* spp.: Discovery efficiency.** The probability of egg unit discovery differed by host plant origin (LRT: X^2=61.20, p<0.001), with a higher probability of discovery for egg units laid on native plants (native: coef=-1.26, SE±0.18; non-native: coef=-2.79, SE±0.45) (Table S16).

***Anastatus* spp.: Egg parasitism rate.** Using data from discovered egg units, predicted egg parasitism rate differed by plant origin (LRT: X^2=8.95, p<0.01), with a higher predicted egg parasitism rate for eggs laid on non-native plants (native: coef=-1.85, SE±0.04; non-native: coef=-0.25, SE±0.09).

Discussion

When investigating biological control of *H. halys* by egg parasitoids, one must consider variables that affect parasitoids' foraging and host finding behavior. The host finding behavior of parasitoids is typically influenced sequentially by habitat, host plant, and host cues (Vinson, 1984). This study confirmed that the bottom-up forces of host plant identity (Cornelius et al., 2016a; Jones et al., 2017; Zapponi et al.,

2020) and host plant origin significantly affect parasitism by *H. halys* related parasitoids. Moreover, host egg identity and host egg species' feeding guild significantly affect parasitism by *Anastatus* spp. Elucidating these variables and understanding their impact on biological control is critical towards the development of effective biological control programs.

Alternate insect egg hosts

Overwintering hosts. Few studies have explored the host range and overwintering strategy of *H. halys* generalist parasitoids. To my knowledge this is the first study to investigate the overwintering hosts of the generalist egg parasitoids *A. mirabilis*, *A. pearsalli*, and *A. reduvii*. This study not only confirmed that *A. mirabilis*, *A. pearsalli*, and *A. reduvii* overwinter in host eggs, but also what egg species are used by *Anastatus* spp. as overwintering hosts. *Arilus cristatus*, *S. carolina*, and Tettigoniidae eggs were used by *Anastatus* spp. as overwintering hosts (Table 2). *Arilus cristatus* and *S. carolina* overwinter as eggs and have one generation per year (Rau and Rau, 1913; Readio, 1926), thus *Anastatus* spp. likely parasitized these hosts' eggs in the fall, in correspondence with the host egg species' life cycle and presence in the landscape. *Arilus cristatus* and Tettigoniidae are known hosts for *Anastatus* spp., but this study is the first to record *S. carolina* as a host for *A. mirabilis*, *A. pearsalli* and *A. reduvii*. Further research is needed to confirm the use of Tettigoniidae eggs and the specific Tettigoniidae species that are utilized by *Anastatus* spp, as only one *Anastatus* male spp. specimen was reared from a single Tettigoniidae egg. These findings are consistent with studied *Anastatus* congeners that were found overwintering as mature larvae (pre-pupal stage) inside a host egg

(Huang et al., 1974; Sullivan et al., 1977; Narasimham and Sankaran, 1982; Stahl et al., 2019).

The other generalist parasitoid of interest, *Ooencyrtus* spp., was reared from *A. cristatus* eggs (Fig. 1; Table 2), suggesting *Ooencyrtus* spp. may be utilizing *A. cristatus eggs* as an overwintering host. However, *A. cristatus* eggs that reared *Ooencyrtus* spp. were collected between April and June. *Arilus cristatus* eggs (11 egg units/masses) collected in March 2021, did not rear any *Ooencyrtus* spp., possibly indicating *Ooencyrtus* spp. overwinter as adults and laid eggs in the yet unhatched *A. cristatus* eggs in the spring. Other studies on *Ooencyrtus* spp. overwintering strategies found *O. kuvanae* and *O. nezzarae* overwinter as adult females, likely in leaf litter (Parker, 1933; Dowden, 1961; Teraoka and Numata, 2000). Not much is known about the overwintering strategies of other *Ooencyrtus* species, including North American native *O. johnsoni* Howard, a species known to attack *H. halys* eggs (Cornelius et al., 2016a). *Ooencyrtus* spp. are known to attack eggs of Hemiptera and there is a record of *O. clisiocampae* Ashmead emerging from *A. cristatus* eggs (Swadener and Yonke, 1973). Further research is needed to elucidate the overwintering strategy of *Ooencyrtus* species. Identifying overwintering hosts of parasitoids gives us information on what alternate insect hosts need to be within a landscape to support the presence of parasitic wasps.

Intraguild interactions. The overwintering hosts used by *Anastatus* spp., *A. cristatus* and *S. carolina*, are generalist predators that have been documented to attack *H. halys* (Jones, 2013; Rice et al., 2014; Morrison et al., 2016). I also found *Anastatus* spp. are more likely to parasitize and parasitize more eggs within an egg unit of

predaceous egg species compared to herbivorous egg species. These intraguild interactions inform our understanding of the overall biological control of a prey/host species in the field (Fig. 11). The average parasitism rate of *A. cristatus* eggs by both *Anastatus* spp. and *Ooencyrtus* spp. was 7.97% (SE±1.33). I predict given this low parasitism rate, parasitism would likely not have a significant biological affect *A. cristatus* or *S. carolina* populations, indicating augmentative and conservation biological control programs for *Anastatus* spp. should still be pursued, but monitored closely. In the field, *Anastatus* spp., *A. cristatus*, and *S. carolina* appear to be coexisting, as active populations of all these taxon groups were seen and collected. Future research should determine the threshold at which parasitism might significantly impact *A. cristatus* and/or *S. carolina* populations and under what conditions this threshold could be reached. *Anastatus* spp., *A. cristatus*, and *S. carolina* make up the diverse community of *H. halys* natural enemies that contribute effective and sustainable biological control.

Most studies that investigate intraguild interactions between a predator and parasitoid are typically cases where predators feed on the parasitized host, thus feeding on the parasitoid. Frago (2016) even goes on to state the parasitoid is always the subordinate species (i.e. the intraguild prey) as their larvae can be eaten by the intraguild predator (Polis et al., 1989; Hemptinne et al., 2012). I would challenge this statement as in my study system the parasitoid, *Anastatus* spp., parasitizes the predator, *A. cristatus* and *S. carolina* (Fig. 11). Besides the direct trophic effects of *Anastatus* spp. parasitizing intraguild hosts, there may also be trait-mediated indirect effects such as induced plant defenses and changes in behavior (Frago, 2016). Several

studies have shown that predator cues can reduce parasitoid efficacy, such as time spent foraging, handling the host, and/or laying eggs (parasitizing) (Martinou et al., 2010; Velasco-Hernández et al., 2013; Frago and Godfray, 2014;). Intraguild interactions can have major consequences for the control of pest species (Snyder and Ives, 2008; Letourneau et al., 2009; Tylianaki and Romo, 2010). Use of *Anastatus* spp. in augmentative biological control programs should be done with attentiveness and f research should continue to investigate the intraguild relationships between *Anastatus* spp., *A. cristatus* and *S. carolina*, before *Anastatus* spp. The coexistence of natural enemies does not imply zero negative natural enemy interactions, thus determining the level of coexistence or competition between species is important information when influencing a natural enemy community and facilitating a biological control program.

Non-host. Out of all the insect egg species collected in these studies, non-native *Tenodera sinensis* Saussure (Mantodea: Mantidae) is the only other species known to overwinter in the egg/ootheca stage, and thus was the only other potential overwintering host collected for *Anastatus* spp. or *Ooencyrtus* spp. Surprisingly, no *Anastatus* spp., *Ooencyrtus* spp., or any other *H. halys* related parasitoids emerged from *T. sinensis* ootheca (Table S3). Interestingly, I did find several *Pseudogaurax* spp. (Diptera: Chloropidae) specimens emerging from *T. sinensis* oothecae; keyed out by Dr. Kelly Hamby and Scott McCluen (Department of Entomology, University of Maryland) using a key by Sabrosky (1987). I also found *Pseudogaurax* spp. specimens emerging from *S. carolina* oothecae, *A. cristatus* eggs, and an unknown Lepidoptera cocoon. Some *Pseudogaurax* species, including the Nearctic and

Neotropical *P. signatus* Loew and Ethiopian *P. elachipteroides* Sabrosky, and *P. mantivorus* Séguy, are known to attack mantid oothecae (Hall, 1937; Breland, 1941; Sabrosky, 1945; Séguy, 1946; Sabrosky, 1951; Séguy, 1951). *Pseudogaurax* spp. larvae are also known predators of spider egg sacs, Lepidoptera eggs and cocoons, and Megaloptera eggs (Sabrosky, 1987; Barnes et al., 1992; Melo and Wheeler, 2009). Key (1970) suggests *Pseudogaurax* spp. are scavengers and not necessarily parasitoids, suggesting *Pseudogaurax* spp. may be utilizing this underused, non-native insect host, *T. sinensis*; as we did not find any other parasitoids emerging from *T. sinensis*, potentially due to the lack of North American native parasitoids adapting to exploit this non-native host. Further research needs to confirm my findings and explore the impact of *Pseudogaurax* spp. on *T. sinensis*, *S. carolina*, *A. cristatus*, and Lepidoptera populations and *Pseudogaurax* spp.'s interactions with other egg parasitoids.

New in season host records. In addition to identifying overwintering hosts of *H. halys* parasitoids, it is also important to determine the identity of in season host eggs. In this study I identified five new alternate in season hosts for *Anastatus* spp. (Table 3). Specifically, a new USA host record of *Acanthocephala* spp. (Hemiptera: Coreidae) for *A. reduvii*; *Euschistus variolarus* Palisot for *Anastatus spp.*; *Leptoglossus phyllopus* Linnaeus (Hemiptera: Coreidae) for *A. mirabilis*, *A. pearsalli*, and *A. reduvii*; *Antheraea polyphemus* Cramer (Lepidoptera: Saturniidae) for *A. pearsalli*; and *Dryocampa rubicunda* Fabricius (Lepidoptera: Saturniidae) for *A. reduvii*. These new in season host records for *Anastatus* spp. are not surprising as *Anastatus* spp. is a generalist across multiple orders and *Anastatus reduvii* have been

recorded emerging from *Anasa tristis* De Geer (Hemiptera: Coreidae) eggs (Burks, 1967). A study by Tillman and Cottrell (2016) recorded *A. reduvii* emerging from *Euschistus servus* eggs; a study by Mitchell and Mitchell (1986) recorded undescribed *Anastatus* spp. emerging from *L. phyllopus* eggs, and other saturniid species are recorded hosts for *A. reduvii*, including *Antheraea polyphemus* (Burks, 1967), *Anisota* sp. (Burks, 1967) and *Anisota senatoria* (Burks, 1979). Expanding upon *Anastatus* spp.'s described host range is a starting point for understanding its biology and ecology and adds to our knowledge of egg hosts that support *Anastatus* spp.

Five new in season pentatomid hosts were identified for the egg parasitoid pentatomid specialist, *Telenomus cristatus*, (Table 3) with the use of COI barcoding (Potter et al., unpubl.). The new USA host records for *T. cristatus* were *Banasa* sp., *Euschistus servus* Say, *E. tristigmus* Say, *E. variolarius*, and *H. halys* (Hemiptera: Pentatomidae) (Potter et al., unpubl.). This suggests that North American native pentatomid parasitoids may be adapting to *H. halys*, which is of interest since some North American native *Trissolcus* and *Telenomus* species (pentatomid specialists) have previously been shown to unsuccessfully emerge from *H. halys* eggs, thus acting as an evolutionary trap (Abram et al., 2014; Haye et al., 2015; Abram et al. 2017).

There are multiple hypotheses that may explain parasitoids adapting to new hosts. It may be that adapting parasitoids are likely 'acquiring' the ability to recognize kairomones for new hosts, such as *H. halys* (Conti and Colazza 2012, Blassioli-Moraes et al. 2016, Michereff et al. 2016). Another likely influence or explanation comes from the Hopkin' host selection principle (HHSP) (Hopkins, 1917): a species

'will prefer to continue to breed in the host to which it has become adapted.' As more *T. cristatus* successfully emerge from *H. halys* eggs, their progeny may be more likely and more adapted to parasitize *H. halys* eggs (Tognon et al., 2019). A study by Tognon et al. (2019) found that individual females of *Telenomus podisi*, which had been recorded as unsuccessfully emerging from *H. halys* eggs (Abram et al., 2014), could be conditioned to *H. halys* egg-surface aldehydes in Y-tube olfactometer experiments, and the positive memory lasted three to four days. They also found that conditioned *T. podisi* wasps successfully parasitized and emerged from fresh *H. halys* eggs in no choice tests and their progeny continued to successfully parasitize and emerge from fresh *H. halys* eggs for two to three more generations. Previous studies have hypothesized that failed development of some North American native parasitoids in *H. halys* eggs could be due to the absence of necessary developmental cues or nutritional resources (Lawrence, 1990; Vinson, 2009), hindered respiration due to the egg chorion (Nénon et al., 1995), or an innate immune response by the host egg (Abdel-latief and Hilker, 2008; Abram et al., 2014). Unknown epigenetic mechanisms are likely behind the successful development and emergence of *T. cristatus* and other North American native parasitoid species that have adapted to find/be attracted to *H. halys* eggs (Tognon et al., 2019).

Co-evolutionary relationships. Native *Euschistus* spp. and non-native *H. halys* were the two host egg species with the highest number of egg units collected in the standardized nursery sampling. Between these two pentatomid species we observed an interesting contrast in parasitoid species composition. *Euschistus* spp. eggs reared a higher proportion of native *Trissolcus* spp. compared to non-native

Trissolcus japonicus, while *H. halys* eggs reared a higher proportion of *T. japonicus* compared to native *Trissolcus* spp. (Fig. 2). The difference in parasitoid composition is likely due to the co-evolutionary history between *H. halys* and *T. japonicus* (both non-native) and the lack of a co-evolutionary history between *H. halys* and the North American native *Trissolcus* spp.; and the co-evolutionary history between native *Euschistus* spp. and North American native *Trissolcus* spp., and the lack of co-evolutionary history between *Euschistus* spp. and *T. japonicus*. *Anastatus* spp. emerged at similar rates from both *Euschistus* spp. and *H. halys* species indicating *Anastatus* spp. could be a successful biological control agent against native and non-native pentatomid species. *Telenomus* spp. (*T. cristatus* and *T. podisi*) emerged at a higher rate from *Euschistus* spp. compared to *H. halys* eggs. This is not surprising, as discussed earlier, North American *Telenomus* spp. are likely adapting to *H. halys* chemical cues, yet they have co-evolved with *Euschistus* spp. resulting in parasitism of both pentatomid species. Interestingly, no *Ooencyrtus* spp. emerged from either of these pentatomid species (in the standardized nursery sampling), but *Ooencyrtus* spp. was reared from *Euschistus* spp. and *Murgantia histrionica* eggs (Table 3) from the diverse habitats suvery, indicating some of the *Ooencyrtus* spp. collected in Maryland were capable of parasitizing and emerging from pentatomid eggs, and thus may be a viable biological control agent of *H. halys* in our landscapes. Future research using COI barcoding could further identify *Ooencyrtus* spp. specimens to species to identify which *Ooencyrtus* species are successfully parasitizing and emerging from *H. halys* and other hosts.

Host egg identity's impact on *Anastatus* spp. parasitism. Amongst the many insect egg host species described for *Anastatus* spp., I sought to determine if there was a significant difference in discovery efficiency and/or parasitism rate between the host egg orders. I found discovery efficiency differed by egg order, with the highest predicted egg unit discovery for the order Lepidoptera. The only Lepidoptera eggs that were discovered by *Anastatus* spp., in the standardized nursery sampling, belonged to the family Saturniidae, despite collecting egg units from three other Lepidoptera families (Lymantriinae, Noctuidae, and Tortricidae). These findings suggest Saturniidae eggs may be an important in season, alternate host for *Anastatus* spp. Out of the *Anastatus* spp. parasitized egg units, predicted parasitism rate also differed by egg order (Fig.5). This may indicate *Anastatus* spp. differentially parasitizes egg orders and further research needs to be conducted to confirm these findings and to explore any mechanisms behind *Anastatus* spp. host preference and host quality. Future research with more egg unit samples could elucidate if there are differences in *Anastatus* spp. parasitism between egg families, particularly families within the orders of Lepidoptera and Hemiptera.

Since many of the *H. halys* related parasitoid species are pentatomid specialists (*Telenomus* and *Trissolcus* species), I also sought to compare parasitism by all parasitoids of interest, between the penatatomid egg species. Egg unit discovery did not differ by pentatomid species (*Banasa* sp., *Euschistus* spp., *H. halys*, and *Podisus* spp.) and there was weak evidence that egg parasitism rate differed by pentatomid species (Fig.6). This suggests parasitoids may be similarly locating/discovering and exploiting pentatomid species' eggs.

Associated host plants

Interaction between tree genus and pentatomid species. The significant interaction between tree genus and pentatomid species suggests the importance of multitrophic studies. I found a significant difference in predicted parasitism rate between *H. halys* eggs laid on *Acer* vs *Quercus*, with a higher predicted parasitism rate on *Quercus* (Fig.10). This may suggest that there is a difference in attractiveness between *Acer* and *Quercus* for foraging parasitoids. There could be physical (differences in canopy density, leaf surface structure, etc.) and chemical differences between *Acer* and *Quercus* that impact plant volatiles (PVs). To date there have not been studies comparing *H. halys* parasitism between *Quercus* and *Acer*, but studies have found higher parasitism of *H. halys* eggs on *Prunus* when compared to *Acer* (Jones et al., 2017; Tillman et al., 2020). Further studies should consider parasitoid and pentatomid species-specific chemical mechanisms, as *H. halys* induced PVs can be unattractive to some North American native parasitoids and can even interfere with attractive native pentatomid induced PVs (Martorana et al., 2017, 2019). Chemo-ecological methods (direct and indirect manipulation of semiochemicals) should be considered when facilitating conservation biological control programs of *H. halys* and other pentatomid pests (Foti et al., 2017).

Determining host plant associations for not only the herbivore pest but also the natural enemies allow us to provide informed recommendations on plant selection, with the potential of enhancing both conservation and augmentation biological control programs. The egg species (herbivore/host) is an important link (and may be a critical driver) in parasitoid-host plant associations. Along with

herbivore induced PVs, parasitoids may also be attracted to a host plant based upon other cues and resources like extrafloral nectaries (EFNs) and flowers that provide valuable nectar. Herbivore hosts can vary in abundance and diversity between host plants affecting alternate prey resources (Shrewsbury and Raupp, 2006). I compared parasitism of egg units on *Acer* vs *Quercus* species from the 2020 standardized nursery study. None of the tree species searched contained EFNs, although all the tree species had the potential to bloom flowers. Plant biomass, plant architecture, and alternate prey can attract natural enemies when flowers are not in bloom (Langellotto and Denno 2004, Rebek et al. 2005, Shrewsbury and Raupp 2006).

Host plant identity's impact on parasitism. This study suggests tree genus may affect discovery efficiency and parasitism rate, although further research should compare additional *Acer* and *Quercus* species and collect more egg units to confirm this finding. However, I did find evidence that tree species affects discovery efficiency and parasitism rate. These results indicate there could be plant species-specific differences when it comes to host plant-parasitoid attraction. *Quercus alba* was found to be a key host plant species with the highest predicted parasitism rate. This isn't surprising because I collected the greatest number of egg units (36% of egg units in standardized nursery sampling) from *Q. alba* trees compared to the other tree species. *Quercus alba* was also one of five tree species (out of 128 total plant taxon groups searched) that was found to be associated with four or more parasitoid taxon groups in this study (data pooled by collection method). *Quercus alba* is native throughout eastern North America from Quebec, Canada south to Florida and Texas, USA (United States Department of Agriculture [USDA], 2018). North American

native oaks support hundreds of herbivorous species (Southwood, 1961), particularly hundreds of Lepidoptera species (Tallamy & Shropshire, 2009); a key insect order for prey of many parasitoid species, including *Anastatus* spp. These results represent a starting point for evaluating which plant species are most attractive to *Anastatus* spp. and other *H. halys* related parasitoids. Identifying attractive plants is a fundamental part of creating successful and sustainable biological control programs.

Plant origin. Native plants have become of great interest with studies highlighting their ecological benefits (Harper-Lore, 1996; Slattery et al., 2003; Vallejo et al., 2012; Bucharova and Krahulec, 2020). Plant origin has been studied for its influence on the natural enemy community and overall parasitism/predation of herbivores (Fiedler and Landis, 2007; Simao et al., 2010; Frank et al., 2019; Gibson et al., 2019; Cornelius et al., 2021). I found discovery efficiency and parasitism rate both differed by plant origin (native / non-native) for all parasitoids and just *Anastatus* spp. Interestingly, the probability of discovery was higher for egg units on native plants than non-native, but predicted parasitism rate was higher for egg units on non-native plants. Through further data analysis, the higher predicted parasitism rate on non-native plants appeared to be driven by Reduviidae egg units (log odds ratio Reduviidae-native: Reduviidae-non-native=-0.79, SE±0.19, 95% CI, $p<0.01$). *Anastatus* spp. and *Ooencyrtus* spp. were the only parasitoids that emerged from Reduviidae eggs in this study, indicating further research is needed to see if there is a preference for non-native plants in locating and exploiting their overwintering host, *A. cristatus*. *Arilus cristatus* is a generalist predator and thus is more likely to be found on a wide range of plant species compared to specialist predators. This may

explain why *A. cristatus* egg units were found on non-native plants, and then discovered by generalists *Anastatus* and *Ooencyrtus* species. The remaining pentatmoid specialist parasitoids of interest to this study were native to North America (except *T. japonicus*), and thus it isn't surprising they may be more adapted to native plants and their cues, possibly explaining the higher probability of egg unit discovery on native plants.

Associated habitat types

Habitat type influences the composition of *H. halys* related parasitoid species (Herlihy et al., 2016; Abram et al., 2017). This study is one of few that has examined pentatomid egg parasitoid species composition in urban landscapes (Cornelius et al., 2021). *Anastatus* spp. were predominantly reared from eggs collected in the tree nursery, urban woody, and woods/wooded edge habitat categories. *Anastatus* spp. were also reared from some egg units collected in the agricultural habitat, this may be due to nearby trees. *Telenomus* spp. were predominantly reared from eggs collected in the urban herbaceous habitat, but they were also found in the tree nursery, and urban woody habitats. Native *Trissolcus* spp. (*T. brochymenae*, *T. euschisti*, and *T. thyantae*) were predominantly reared from eggs collected in the urban herbaceous and urban vegetable garden habitats, but they were also collected from the tree nursery and urban woody habitats. *Trissolcus japonicus* were predominantly reared from eggs collected in the tree nursery habitat, but they were also collected from the urban woody habitat. *Ooencyrtus* spp. were predominantly reared from eggs collected in the agricultural habitat category, but they were also collected from the tree nursery, urban vegetable garden, and urban woody habitats (Fig.4). These results are consistent with

previous findings, *Anastatus* and *Trissolcus* species generally prefer wooded habitats, and *Telenomus* and *Ooencyrtus* species generally prefer herbaceous and/or agricultural habitats (Okuda and Yeargan 1998; Serrano and Foltz 2003; Qiu 2007; Hou et al. 2009; Maltese et al. 2012; Danne et al. 2013). Native *Trissolcus* spp. deviated from previous findings, with its high presence in urban herbaceous and urban vegetables garden habitats. This may be due to the patches of trees that are typically included in urban/suburban areas. Also, a majority of the native *Trissolcus* spp. were *Trissolcus brochymenae* (Table 1), where many were reared from their associated host, *Murgantia histronica* eggs (Morgan, 1897), laid on *M. histronica*'s preferred host plants, Brassicales species (cabbages, mustards, and allies) (McPherson and McPherson 2000), in urban vegetable gardens or urban herbaceous habitats. Previous studies investigating parasitoid composition in different habitats were not conducted in urban areas (except a study by Cornelius et al., 2016a), thus the urban habitats *Trissolcus* species were collected from may be novel habitats for the *H. halys* related parasitoid literature.

Urban habitats. The top three habitat categories with the highest egg unit discovery appear to be the tree nursery, urban herbaceous, and the urban woody habitat categories, respectively (Fig.4). These results along with the parasitoid-habitat association results, demonstrate that *H. halys* related parasitoids are present and providing biological control services in urban areas; every parasitoid taxon group of interest was recovered from at least one urban habitat category. With increasing urbanization, further research should investigate the impact of urban variables such as

habitat fragmentation and simplification, impervious surface cover, and heat island effects on parasitoid efficacy.

Conclusions

Host plant identity and host egg identity (bottom-up forces) significantly affect parasitism by *H. halys* related parasitoids (top-down forces). Both *Acer* and *Quercus* plants supported several insect host egg species, including *Anastatus* spp.'s overwintering hosts, *A. cristatus*, *S. carolina*, and Tettigoniidae eggs. The genera *Quercus* and *Acer* contain some of the most common tree species in urban landscapes (Raupp et al., 2006), and both tree genera have been shown to support other parasitoid families including Aphelinidae, Platygastridae, and Mymaridae, through the presence of several herbivorous insect host species (Frank et al., 2019). Further research should explore parasitism differences by host egg species, host plant species, and habitat type, utilizing molecular identification methods and large-scale insect egg collections, to inform biological control programs aimed at supporting egg parasitoids. Through integrating informed plant selection into *H. halys* biological control programs, we can bolster *H. halys* management by parasitoid species, and prepare for current and future invasions of *H. halys* and potentially other insect pests.

Practical implications for landscape practitioners

The results of this study indicate *Anastatus* species such as *A. reduvii*, could be effective biological control agents for *H. halys* and potentially other insect pests. To support and conserve parasitoid populations like *Anastatus* species, landscape practitioners should design landscapes with a diversity of plant species, such as native

Acer, *Cercis* and *Quercus*. Studies indicate plant species diversity provides diverse resources for natural enemies, including a diversity of alternate hosts (reviewed in Russell, 1989; Shrewsbury and Raupp, 2006; Raupp et al. 2010; Scherber et al., 2010; Schuldt et al., 2019; reviewed in Staab and Schuldt, 2020). Allowing non-outbreaking alternate hosts within an area can attract and sustain parasitoids and other natural enemies. Identify an insect and its threat before considering it a pest that requires control.

Only pesticides that have been shown to not be harmful to parasitoids and other beneficial arthropods should be utilized. A study by Ogburn and Walgenbach (2019) found negative impacts of Spinosad-based products on *A. reduvii* and *T. podisi* and recommend minimizing the use of these products, particularly during periods of stink bug oviposition activity. These findings are consistent with other studies reporting lethal and sublethal effects of Spinosads on Hymenoptera parasitoids (Biondi et al., 2012). If chemical control is needed, apply selective, well-times spot treatments with pesticides that have been shown to not be harmful to natural enemies.

In the case of augmentative biological control, *Anastatus* spp. should be released in areas where a diversity of alternate hosts (overwintering and in season hosts) and diverse plant species are present and where no harmful pesticides are being applied. To enhance natural enemy populations, we need to consider ways to provide natural enemy shelter and food resources through landscape design, conservation, and plant management practices.

Tables

Table 1. Total number of *H. halys* related parasitoids reared from collected insect eggs by parasitoid species and by parasitoid taxon group. Data pooled across collection method. All eggs were field collected and naturally laid.

Parasitoid species	Total number of parasitoids	Parasitoid taxon group	Total number of parasitoids
Anastatus mirabilis	9	*Anastatus* spp.	1434
Anastatus pearsalli	31		
Anastatus reduvii	760		
Anastatus spp. male	634		
Ooencyrtus spp.	450	*Ooencyrtus* spp.	450
Telenomus cristatus	34	*Telenomus* spp.	156
Telenomus podisi	121		
Trissolcus euschisti	97	*Trissolcus* spp.	505
Trissolcus brochymenae	393		
Trissolcus thyantae	15		
Trissolcus japonicus	147	*Trissolcus japonicus*	147
TOTAL			2692

Table 2. Overwintering hosts of *H. halys* related parasitoids. Table is organized by insect egg species (order, family, genus, species) and then by parasitoid species group. An "X" indicates at least one parasitoid from that species group emerged from that egg species. Data pooled across collection method.

Egg order	Egg family	Egg genus	Egg species	Egg common name	**Anastatus* male spp.	**Anastatus mirabilis*	**Anastatus pearsalli*	**Anastatus reduvii*	**Ooencyrtus* spp.
Hemiptera	Reduviidae	*Arilus*	*cristatus*	Wheel bug	X		X	X	X
Mantodea	Mantidae	*Stagmomantis*	*carolina*	Carolina mantis	X	X	X	X	
Orthoptera	Tettigoniidae			Bush cricket species	X				

* Generalist parasitoid taxon group.

Table 3. In season insect egg hosts of *H. halys* related parasitoids. Table is organized by insect egg species (order, family, genus, species) and then by parasitoid species group. An "X" indicates at least one parasitoid from that species group emerged from that egg species. Data pooled across collection method.

Egg order	Egg family	Egg genus	Egg species	Egg common name	**Anastatus* spp.	**Ooencyrtus* spp.	*Telenomus* spp.	Native *Trissolcus* spp.	*Trissolcus japonicus*	**TOTAL**
Coleoptera	Coccinellidae			Ladybird beetle species		X				1
Hemiptera	Coreidae	*Acanthocephala*		*Acanthocephala* species	X	X				2
Hemiptera	Coreidae	*Anasa*	*tristis*	Squash bug		X				1
Hemiptera	Coreidae	*Leptoglossus*	*phyllopus*	Eastern leaffooted bug	X					1
Hemiptera	Pentatomidae	*Banasa*		*Banasa* species			X			1
Hemiptera	Pentatomidae	*Brochymena*		*Brochymena* species	X					1
Hemiptera	Pentatomidae	*Chinavia*	*hilaris*	Green stink bug	X					1
Hemiptera	Pentatomidae	*Chinavia*		*Chinavia* species	X			X		1
Hemiptera	Pentatomidae	*Euschistus*	*servus*	Brown stink bug	X		X			2
Hemiptera	Pentatomidae	*Euschistus*	*tristigmus*	Dusky stink bug	X		X	X		3
Hemiptera	Pentatomidae	*Euschistus*	*variolarius*	One-spotted stink bug	X		X			2
Hemiptera	Pentatomidae	*Euschistus*		*Euschistus* species	X	X	X	X	X	5
Hemiptera	Pentatomidae	*Halyomorpha*	*halys*	Brown marmorated stink bug	X		X	X	X	4
Hemiptera	Pentatomidae	*Murgantia*	*histrionica*	Harlequin bug	X	X		X		3
Hemiptera	Pentatomidae	*Podisus*	*maculiventris*	Spined soldier bug	X			X		2
Hemiptera	Pentatomidae	*Podisus*		*Podisus* species			X	X		2
Hemiptera	Reduviidae	*Zelus*		*Zelus* species	X					1
Lepidoptera	Notodontidae	*Datana*	*ministra*	Yellownecked caterpillar	X					1
Lepidoptera	Saturniidae	*Anisota*	*senatoria*	Orange-tipped oakworm moth	X					1
Lepidoptera	Saturniidae	*Antheraea*	*polyphemus*	Polyphemus moth	X					1
Lepidoptera	Saturniidae	*Dryocampa*	*rubicunda*	Greenstriped mapleworm	X					1
Lepidoptera	Saturniidae	*Eacles*	*imperialis*	Imperial moth	X					1
TOTAL					15	5	4	6	2	

* Generalist parasitoid taxon group.

Table 4. Host plant species and *H. halys* related parasitoid associations. Table is organized by host plant species (order, family, genus, species, common name), then by columns of parasitoid species groups, an "X" indicating at least one parasitoid specimen emerged from that insect egg species on that plant species. Data pooled across collection method.

Plant order	Plant family	Plant genus	Plant species	Plant common name	*Anastatus* spp	*Ooencyrtus* spp	*Telenomus* spp	Native *Trissolcus* spp	*Trissolcus japonicus*	**TOTAL**
Aquifoliales	Aquifoliaceae	*Ilex*	.	*Ilex* species	X					1
Asterales	Asteraceae	*Calendula*	.	*Calendula* species				X		1
Asterales	Asteraceae	*Silphium*	*perfoliatum*	Cup plant			X			1
Brassicales	Brassicaceae	*Brassica*	*oleracea*	Kale				X		1
Brassicales	Brassicaceae	*Brassica*	*rapa*	Turnip	X	X				2
Brassicales	Cleomaceae	*Cleome*	*hasslerian a*	Spider flower				X		1
Caryophyllales	Amaranthaceae	*Amaranthus*	.	*Amaranthus* species			X			1
Cornales	Cornaceae	*Cornus*	*amomum*	Silky dogwood	X					1
Cucurbitales	Cucurbitaceae	*Cucurbita*	.	*Cucurbita* species		X				1
Cucurbitales	Cucurbitaceae	*Cucurbita*	*pepo*	Summer squash		X				1
Ericales	Ericaceae	*Rhododendron*	.	*Rhododendron* species	X					1
Fabales	Fabaceae	*Cercis*	*canadensis*	Eastern redbud	X	X	X	X	X	5
Fagales	Betulaceae	*Betula*	*nigra*	River birch	X	X		X		3
Fagales	Betulaceae	*Carpinus*	*carolinian a*	American hornbeam		X				1
Fagales	Fagaceae	*Fagus*	*sylvatica*	European beech	X					1
Fagales	Fagaceae	*Quercus*	*alba*	White oak	X		X	X	X	4
Fagales	Fagaceae	*Quercus*	*bicolor*	Swamp white oak	X					1
Fagales	Fagaceae	*Quercus*	*coccinea*	Scarlet oak	X		X	X	X	4
Fagales	Fagaceae	*Quercus*	*macrocarpa*	Burr oak	X	X				2
Fagales	Fagaceae	*Quercus*	*palustris*	Pin oak	X					1
Fagales	Fagaceae	*Quercus*	*phellos*	Willow oak	X					1
Fagales	Fagaceae	*Quercus*	*rubra*	Red oak	X			X	X	3
Fagales	Fagaceae	*Quercus*	*velutina*	Black oak	X					1
Fagales	Juglandaceae	*Juglans*	*nigra*	Black walnut	X	X		X		3
Lamiales	Oleaceae	*Fraxinus*	*nigra*	Black ash	X					1
Lamiales	Oleaceae	*Fraxinus*	*pennsylvanica*	Green ash	X					1
Lamiales	Oleaceae	*Syringa*	*pekinensis*	Pekin lilac	X	X				2
Magnoliales	Magnoliaceae	*Liriodendron*	*tulipifera*	Tulip poplar	X	X				2
Malpighiales	Salicaceae	*Salix*	*alba*	White willow			X	X		2
Malpighiales	Salicaceae	*Salix*	*matsudana*	Chinese willow				X		1
Malvales	Malvaceae	*Tilia*	.	*Tilia* species				X		1
Malvales	Malvaceae	*Tilia*	*tomentosa*	Silver linden				X		1
Myrtales	Lythraceae	*Lagerstroemia*	.	Crepe myrtle species	X					1

Pinales	Cupressaceae	*Chamaecyparis*	.	False cypress species			X			1
Proteales	Platanaceae	*Platanus*	.	London planetree	X					1
Proteales	Platanaceae	*Platanus*	*occidentalis*	American sycamore	X					1
Rosales	Cannabaceae	*Celtis*	*occidentalis*	Common hackberry	X		X	X		3
Rosales	Rosaceae	*Malus*	.	*Malus* species	X	X		X		3
Rosales	Rosaceae	*Prunus*	.	*Prunus* species	X	X				2
Rosales	Rosaceae	*Prunus*	*serotina*	Black cherry	X					1
Rosales	Rosaceae	*Prunus*	*serrulata*	Japanese cherry	X			X		2
Rosales	Rosaceae	*Pyrus*	.	*Pyrus* species	X					1
Rosales	Rosaceae	*Pyrus*	*calleryana*	Callery pear	X	X				2
Rosales	Ulmaceae	*Ulmus*	*parvifolia*	Chinese elm	X					1
Rosales	Ulmaceae	*Zelkova*	*serrata*	Japanese zelkova		X				1
Sapindales	Sapindaceae	*Acer*	*negundo*	Boxelder	X					1
Sapindales	Sapindaceae	*Acer*	*rubrum*	Red maple	X	X	X	X	X	5
Sapindales	Sapindaceae	*Acer*	*saccharinum*	Silver maple	X		X			2
Sapindales	Sapindaceae	*Acer*	*saccharum*	Sugar maple	X		X	X	X	4
Sapindales	Sapindaceae	*Aesculus*	*pavia*	Red Buckeye	X					1
Saxifragales	Altingiaceae	*Liquidambar*	*styraciflua*	Sweet gum	X					1
Saxifragales	Hamamelidaceae	*Hamamelis*	*virginiana*	Witch hazel	X					1
TOTAL					38	14	10	17	6	

Table 5. Habitat and *H. halys* related parasitoid associations. Table is organized by habitat category (agricultural, tree nursery, urban all- which includes urban herbaceous, urban woody, and urban vegetable garden, urban herbaceous, urban vegetable garden, urban woody, and woods/wooded edges) and then by parasitoid species group (*Anastatus* spp., *Ooencyrtus* spp., *Telenomus* spp., native *Trissoclus* spp., and *Trissolcus japonicus*). An "X" indicates at least one parasitoid from that species group emerged from that habitat category. Data pooled across collection method.

Habitat category	*Anastatus* spp.	*Ooencyrtus* spp.	*Telenomus* spp.	Native *Trissolcus* spp.	*Trissolcus japonicus*	**TOTAL**
Agricultural	X	X				2
Tree nursery	X	X	X	X	X	5
Urban all	X	X	X	X	X	5
Urban herbaceous			X	X		2
Urban vegetable garden		X		X		2
Urban woody	X	X	X	X	X	5
Woods/Wooded edge	X					1
TOTAL	5	5	4	5	3	

Figures

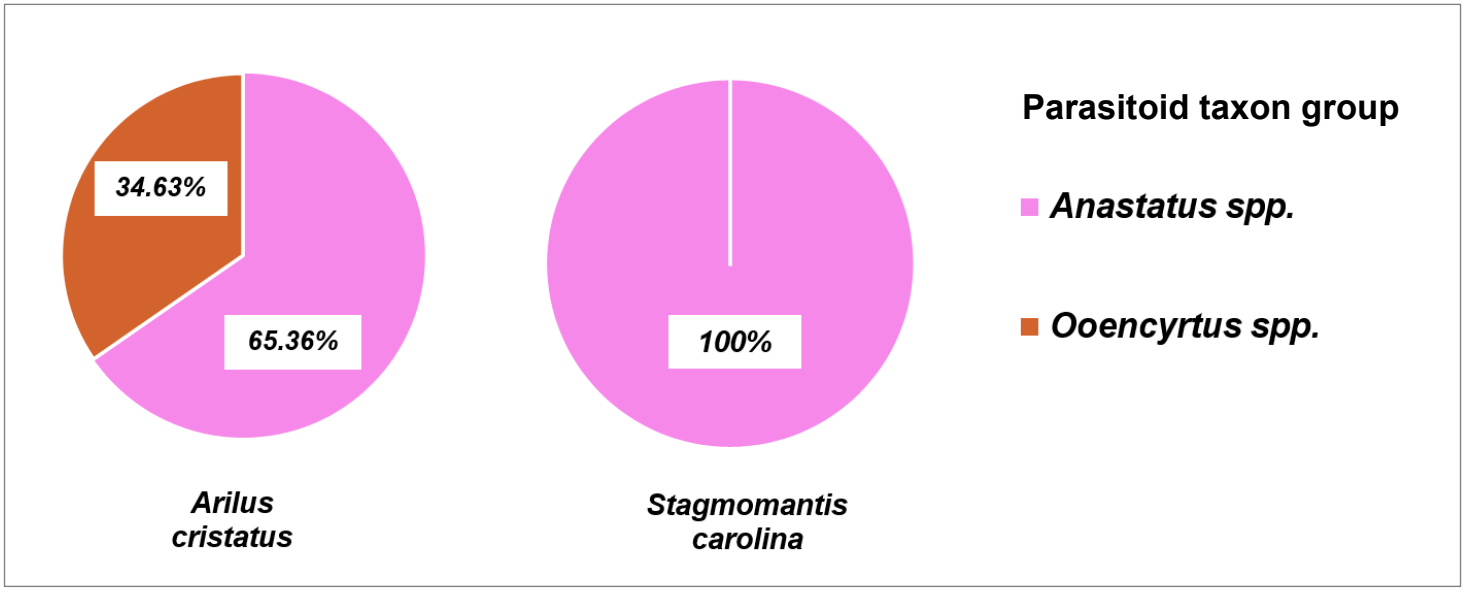

Figure 1. Composition of parasitoids (999 total) by parasitoid taxon groups that had emerged from 13,607 field collected, naturally laid *Arilus cristatus* eggs (left). Composition of parasitoids (49 total) by parasitoid taxon group that had emerged from 59 field collected, naturally laid *Stagmomantis carolina* ootheca (right). Data pooled across collection method.

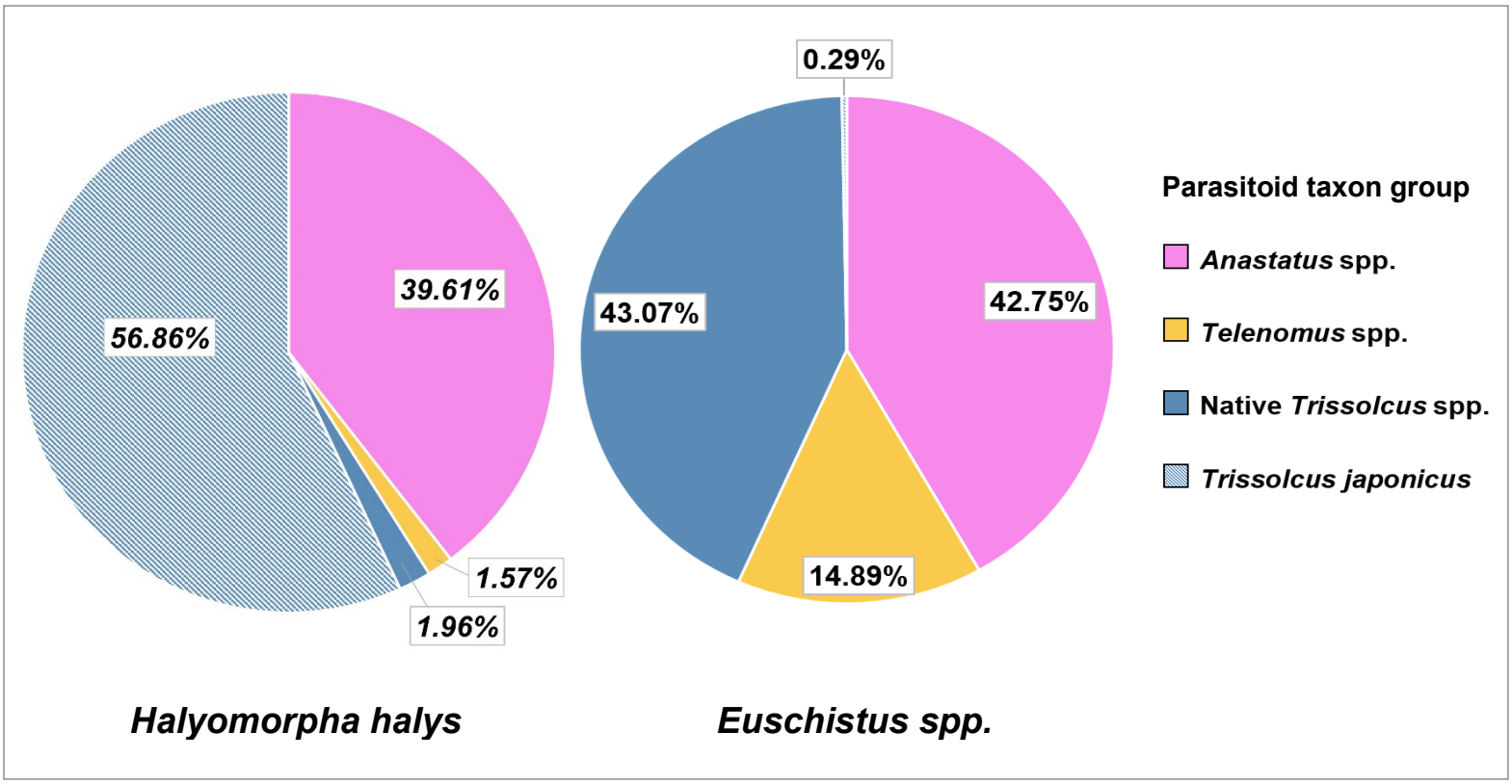

Figure 2. Composition of parasitoids by parasitoid taxon group (*Anastatus* spp., *Telenomus* spp., native *Trissoclus* spp., and *Trissolcus japonicus*) for the two most collected insect egg taxon groups *Halyomorpha halys* and *Euschistus* spp. Out of the 1,152 *Halyomorpha halys* eggs collected, 255 parasitoids were reared (left). Out of the 2,219 *Euschistus* spp. eggs collected, 685 parasitoids were reared (right). All eggs were field collected and naturally laid. Data pooled across collection method.

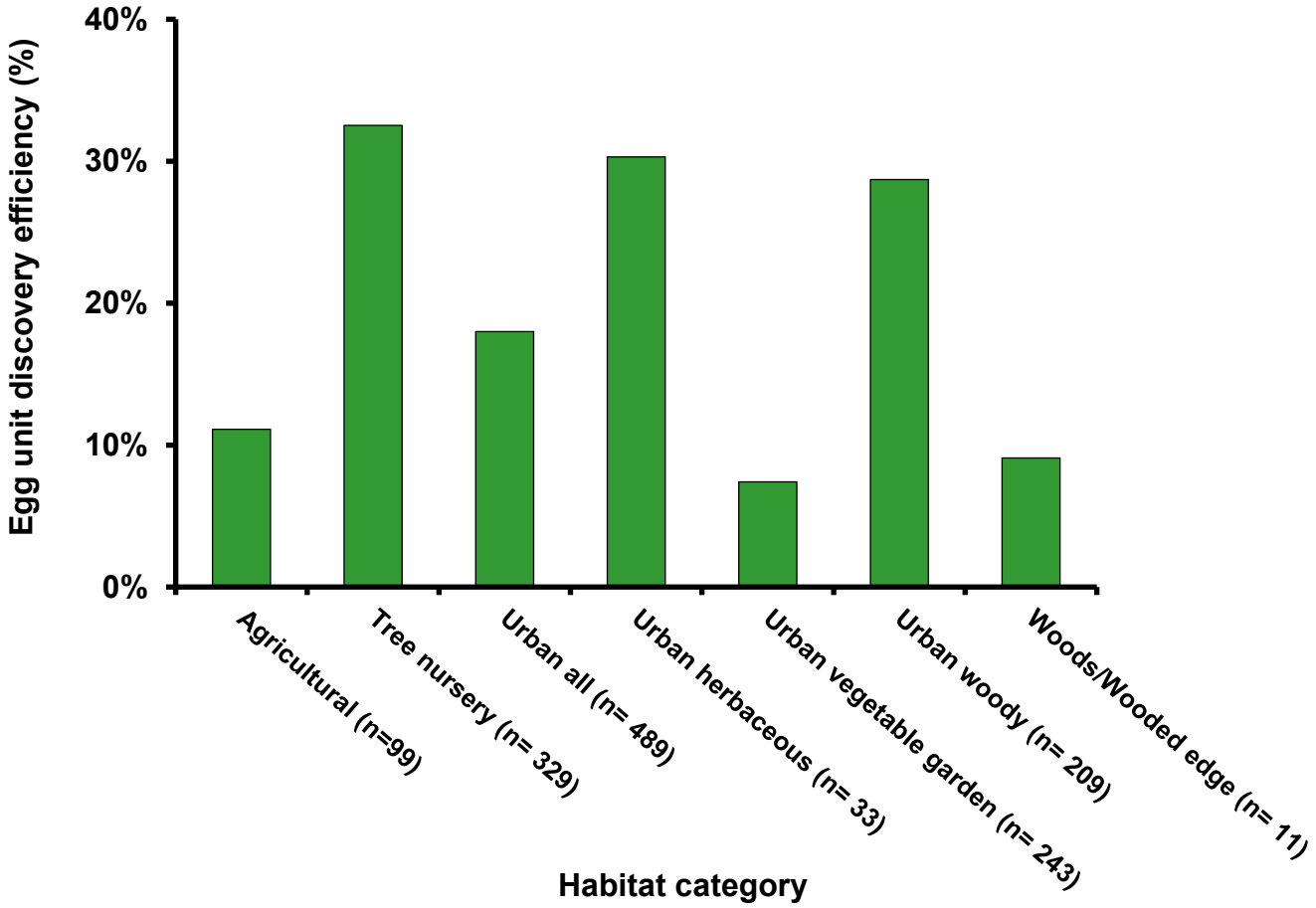

Figure 3. Egg unit discovery efficiency by habitat category; total number of discovered egg units divided by the total number of collected potential host insect egg units. "n" equals the total number of potential host egg units, which includes all potential insect egg host species for stink bug related egg parasitoids (*Anastatus* spp., *Ooencyrtus* spp., *Telenomus* spp., and *Trissolcus* spp.). Egg units represent either an individual egg or an individual egg mass from a particular insect species. If an egg unit had at least one stink bug related parasitoid emerge from it, then it was counted as discovered. Data pooled across collection method.

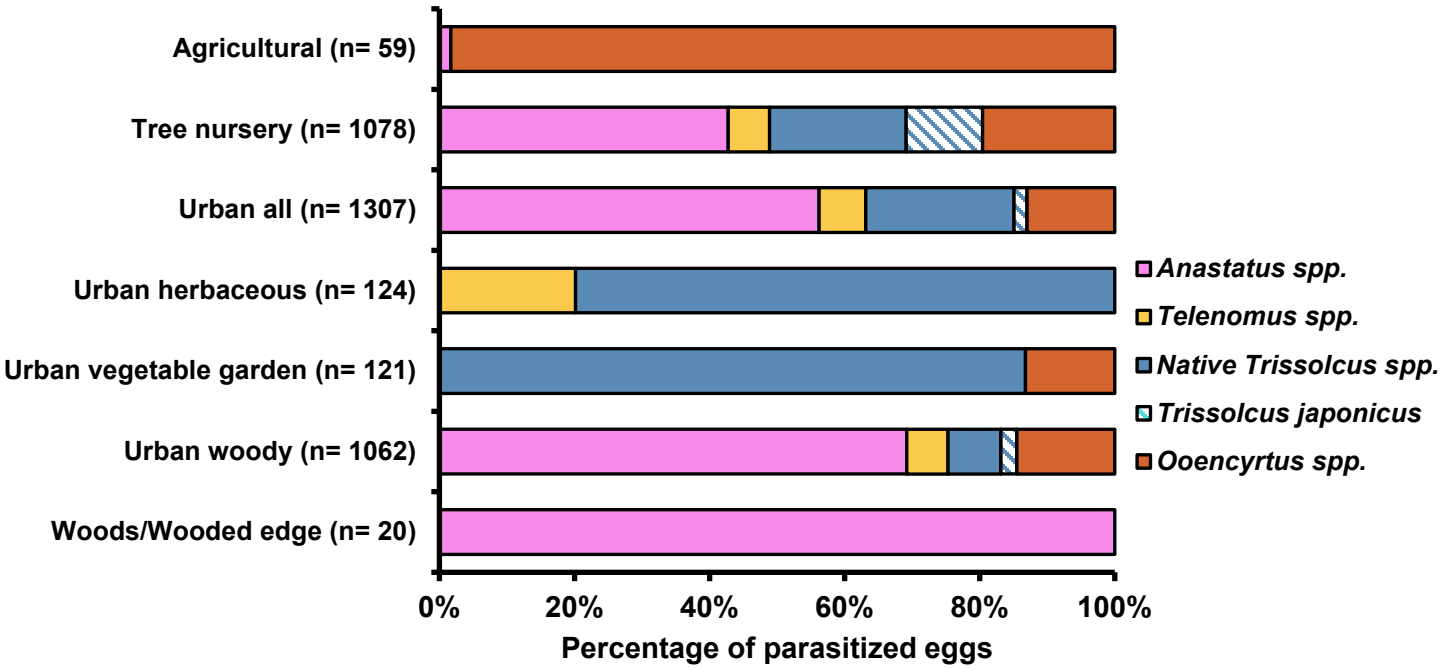

Figure 4. Composition of stink bug related egg parasitoid species groups (*Anastatus* spp., *Ooencyrtus* spp., *Telenomus* spp., native *Trissolcus* spp., and *Trissolcus japonicus*) that emerged from eggs from each habitat category. "n" equals the total number of stink bug related parasitoids collected from all the eggs in a particular habitat category (example: 59 parasitoids emerged from eggs in the agricultural habitat). Data pooled across collection method.

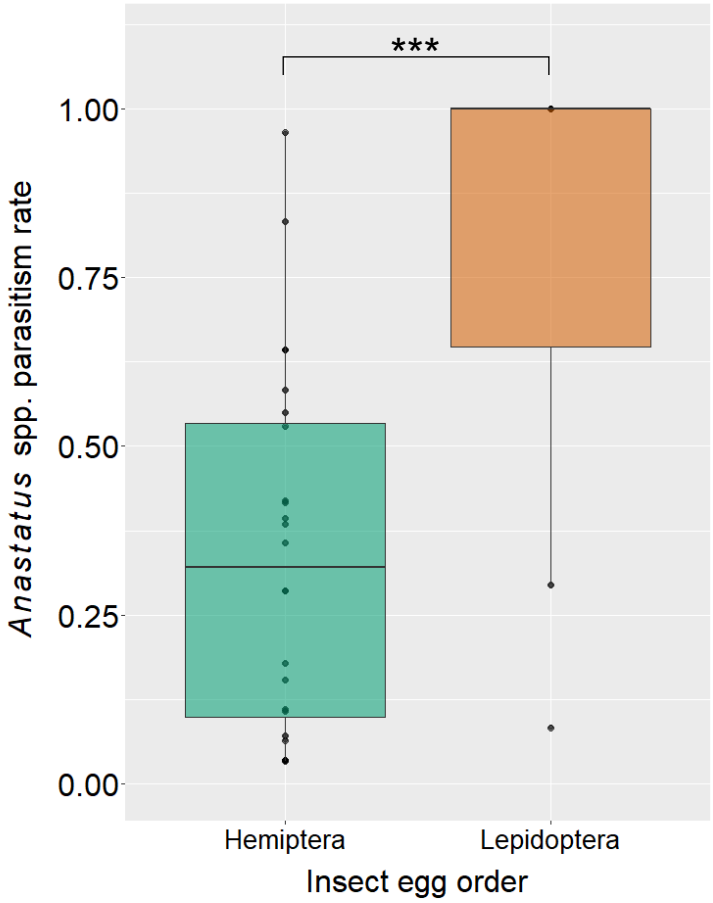

Figure 5. *Anastatus* spp. egg parasitism rate of field collected, naturally laid insect egg units by host egg order. Only egg units with parasitism incidence (parasitized by at least one parasitoid species of interest) are shown. Egg units were collected from organic trees in a Maryland tree nursery. Significant differences between host insect egg order are denoted by *** (p<0.001). Parasitism rate differed by egg order, with a higher predicted parasitism rate for Lepidoptera eggs. Data from the standardized nursery sampling.

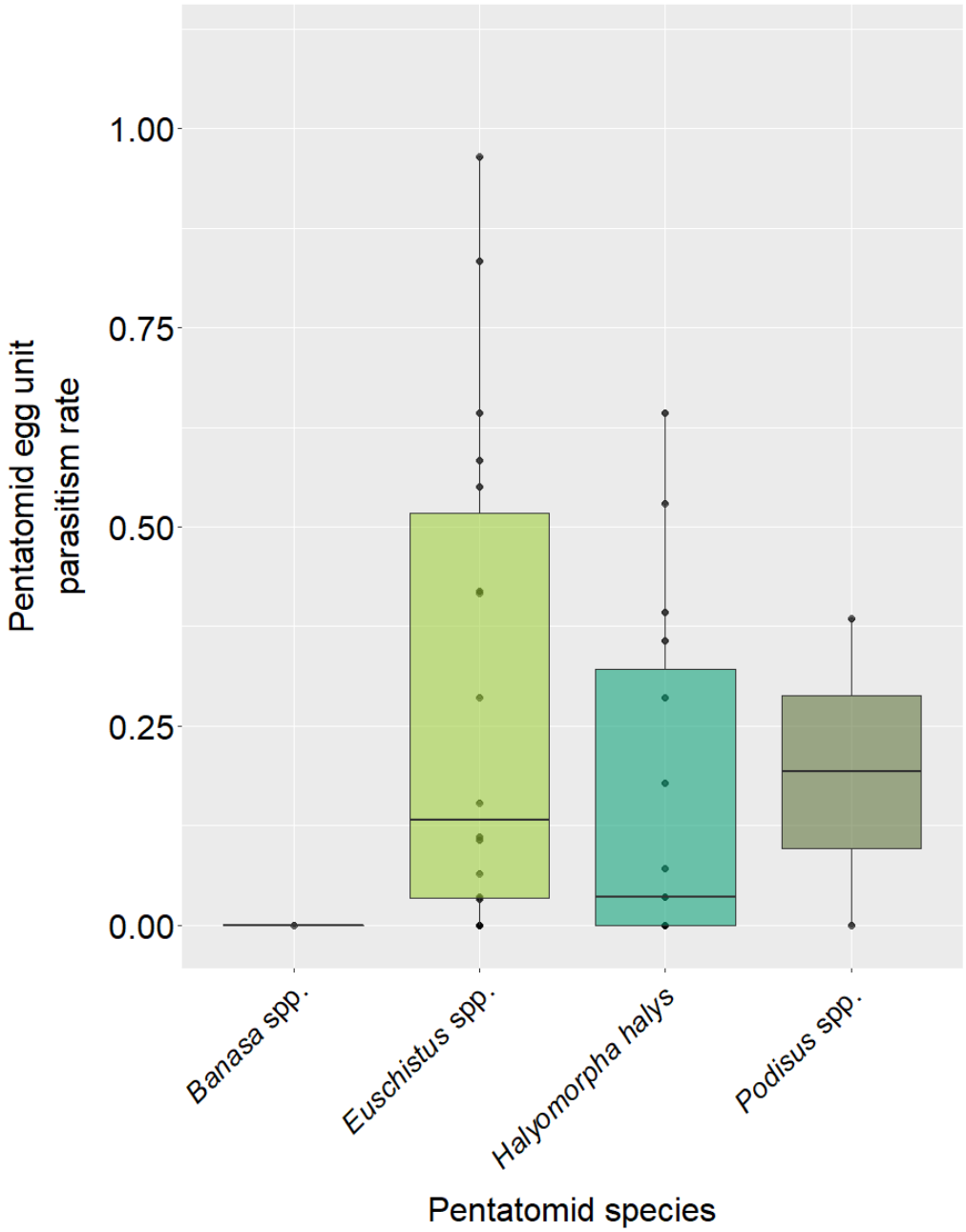

Figure 6. Parasitism rate of field collected, naturally laid pentatomid egg units. Only discovered egg units are shown. Pentatomid egg units were collected from organic trees in a Maryland tree nursery. Parasitism rate did not differ by pentatomid species. Data from the standardized nursery sampling.

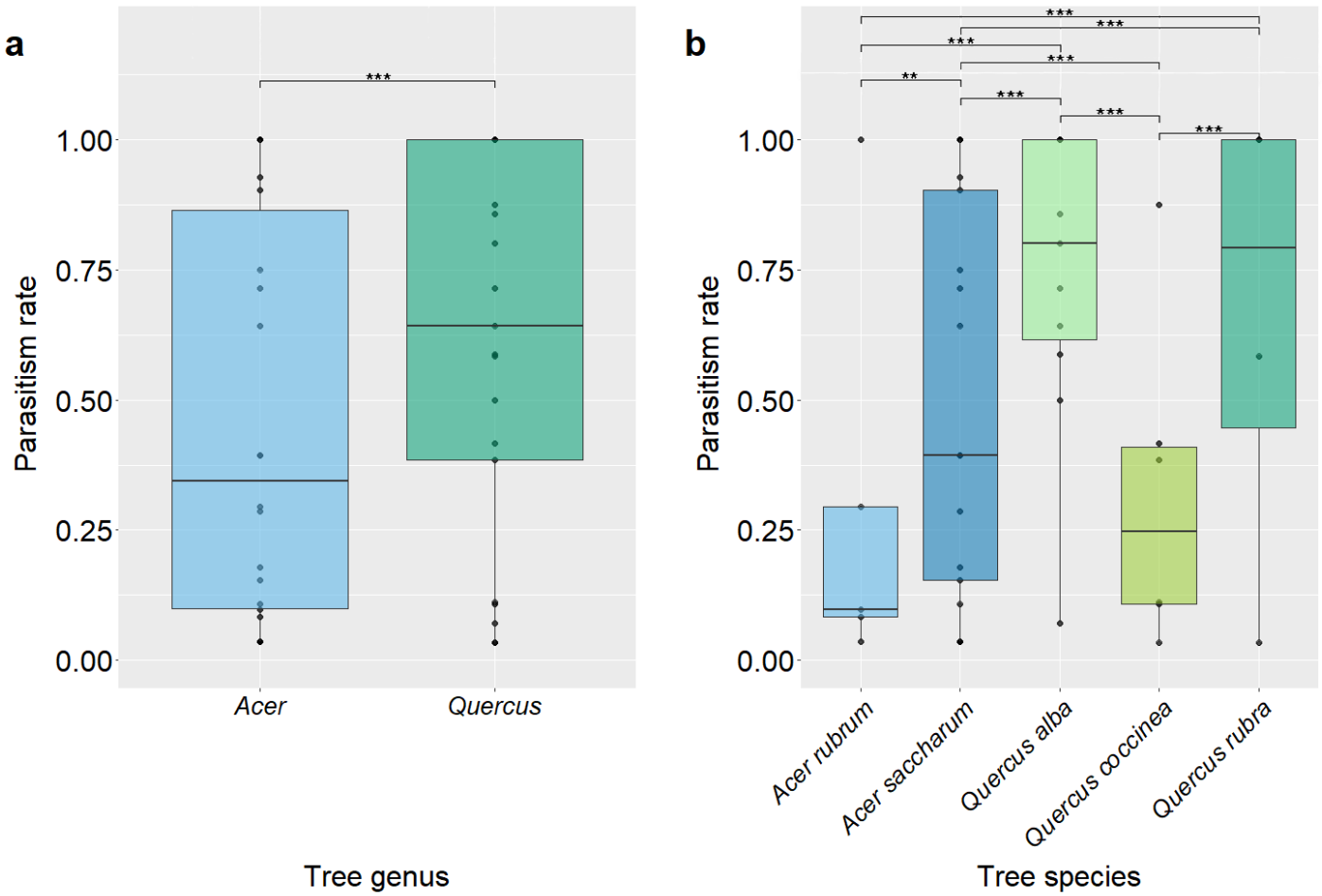

Figure 7. Egg parasitism rate of field collected, naturally laid insect egg units by tree identity by all parasitoids. Only egg units with parasitism incidence (parasitized by at least one parasitoid species of interest) are shown. Egg units were collected from organic trees in a Maryland tree nursery. Significant differences between tree genera/species are denoted by *** (p<0.001) or ** (p<0.01). (a) Parasitism rate by tree genus. Parasitism rate differed by tree genus, with a higher predicted parasitism rate for eggs laid on *Quercus*. (b) Parasitism rate by tree species. Parasitism rate differed by tree species. Post hoc pairwise comparisons found significant comparisons between all species except between *Acer rubrum* and *Quercus coccinea*, and between *Q. alba* and *Q. rubra*. Highest predicted egg parasitism was for eggs laid on *Q. alba*. Data from the standardized nursery sampling.

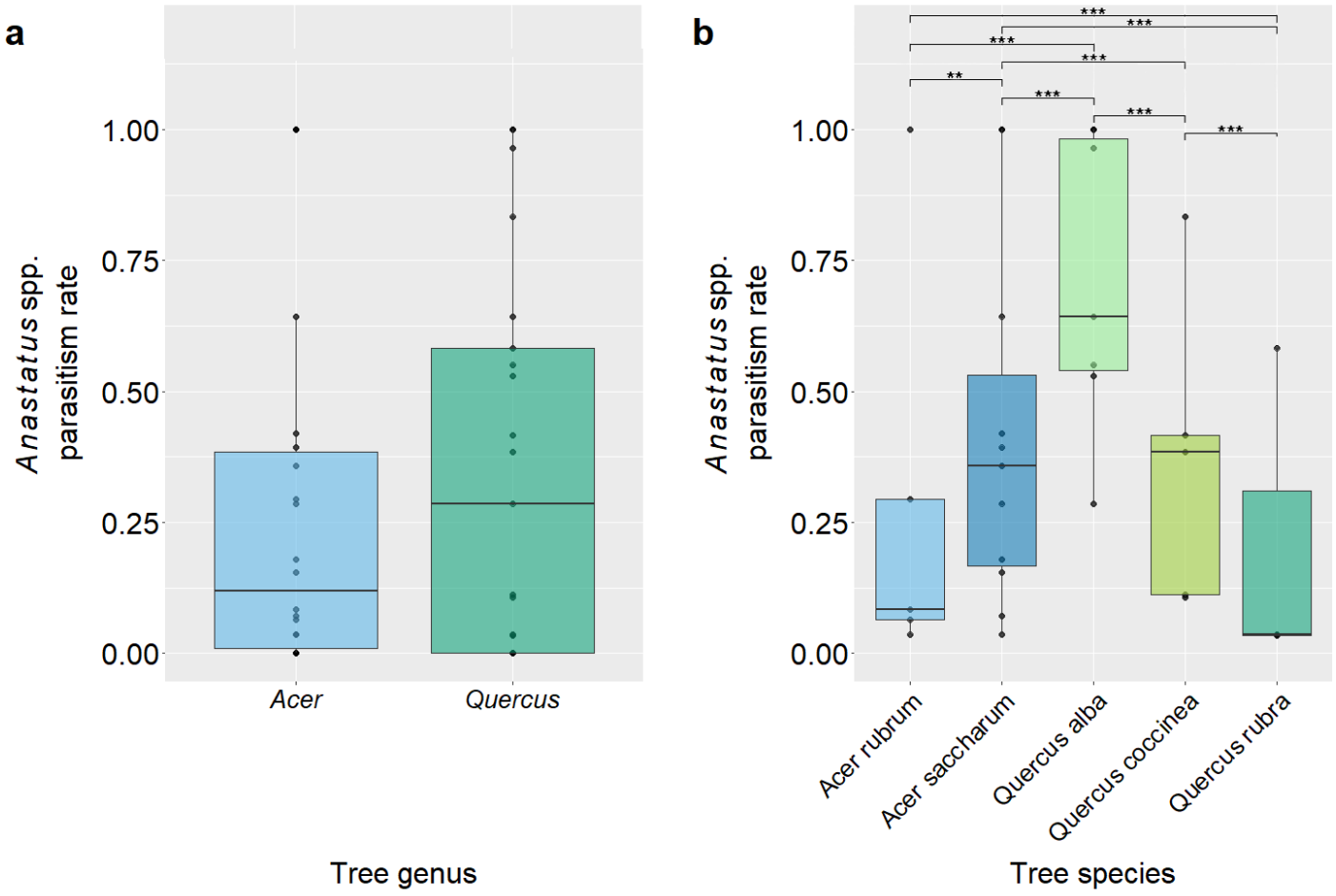

Figure 8. *Anastatus* spp. egg parasitism rate of field collected, naturally laid insect egg units by tree identity. Only egg units with egg unit parasitism incidence (parasitized by at least one *Anastatus* spp. parasitoid) are shown. Egg units were collected from organic trees in a Maryland tree nursery. (a) *Anastatus* spp. parasitism rate by tree genus. Parasitism rate did not differ by tree genus. (b) *Anastatus* spp. parasitism rate by tree species. *Anastatus* spp. parasitism rate differed by tree species. Post hoc pairwise comparisons found significant comparisons between all species except between *Acer rubrum* and *Quercus coccinea*, and between *Q. alba* and *Q. rubra*. Highest predicted egg parasitism was for eggs laid on *Q. alba*. Data from the standardized nursery sampling.

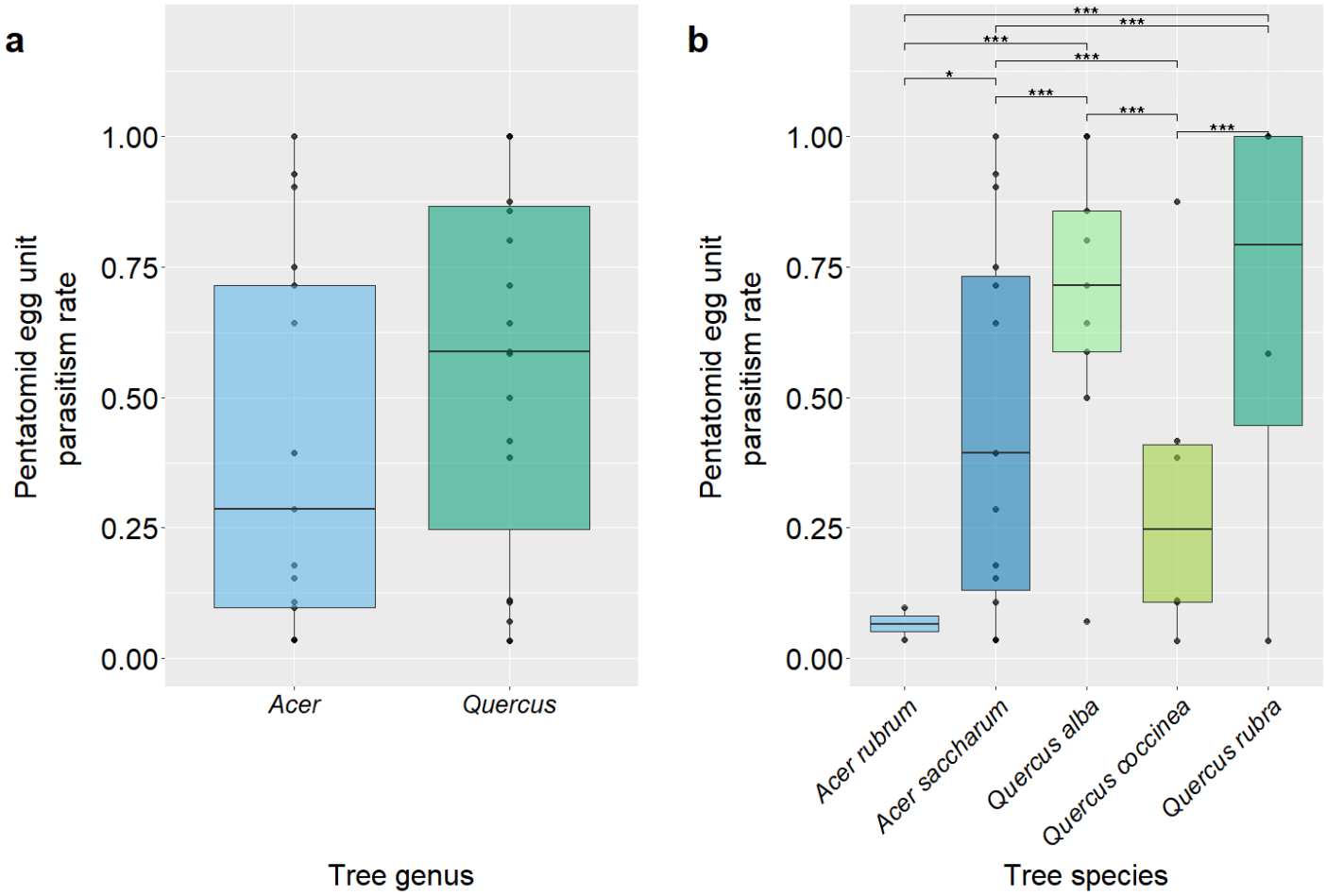

Figure 9. Egg parasitism rate of field collected, naturally laid pentatomid egg units by tree identity. Only egg units with parasitism incidence (parasitized by at least one parasitoid of interest) are shown. Pentatomid egg units were collected from organic trees in a Maryland tree nursery. Significant differences between tree genera/species are denoted by *** (p<0.001) or * (p<0.05). (a) Pentatomid egg parasitism rate (by all parasitoids of interest) by tree genus. Parasitism rate did not differ by tree genus. (b) Pentatomid egg parasitism rate by tree species. Parasitism rate differed by tree species. Post hoc pairwise comparisons found significant comparisons between all species except between *Acer rubrum* and *Quercus coccinea*, and between *Q. alba* and *Q. rubra*. Highest predicted parasitism was for eggs laid on *Q. alba*. Data from the standardized nursery sampling.

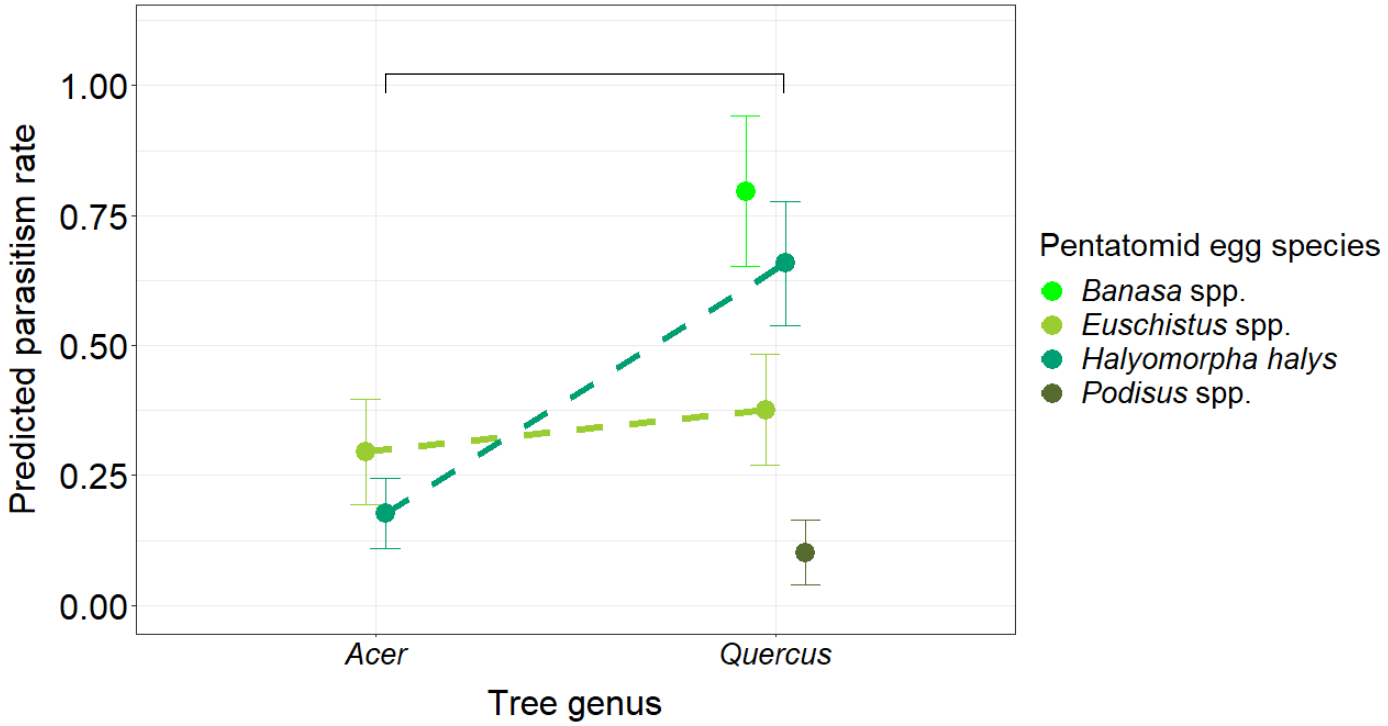

Figure 10. Predicted egg parasitism rate of egg units by pentatomid species and by tree genus based on a generalized linear mixed-effects model (GLM). Only discovered egg units were included in the model. Significant differences between tree genera by pentatomid species are denoted by *** (p<0.001). There was a significant interaction between pentatomid species and tree genus. Post hoc comparisons found a higher predicted parasitism rate for *Halyomorpha halys* eggs laid on *Quercus* compared to *H. halys* egg laid on *Acer*. Data from the standardized nursery sampling.

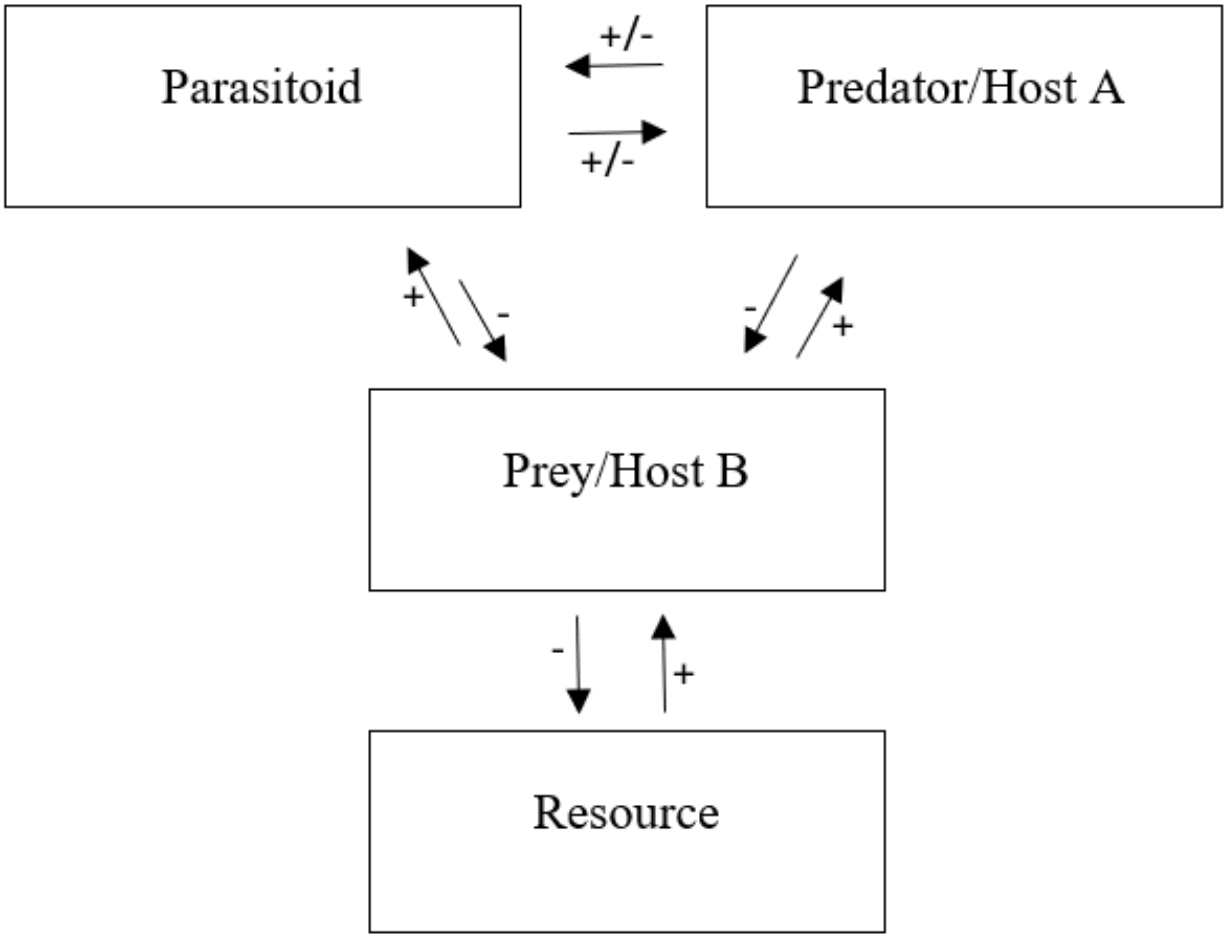

Figure 11. An interaction figure displaying the relationships between an *Anastatus* spp. parasitoid (Parasitoid), *Stagmomantis carolina*, *Arilus cristatus*, and/or *Podisus maculiventris* (Predator [of *H. halys*]/Host A [of *Anastatus* spp.]), *Halyomorpha halys* (Prey [of Predator/HostA]/Host B [of *Anastatus spp*.]), and host plant of *H. halys* (Resource). *Anastatus* spp. parasitizes eggs of both *H. halys* and *H. halys* predators such as *S. carolina*, *A. cristatus*, and *P. maculiventris*; an example of intraguild parasitism/predation (IGP). Figure based off Hatcher et al. (2006) interaction figures.

Appendix

Supplemental tables

Table S1. Summary of insect egg species collected regardless of if they supported parasitoids or not, by order, family, genus, species, common name, total number of egg units (egg, egg clusters, egg masses, ootheca), and by total number of [individual] eggs. Data pooled across collection method.

Order	Family	Genus	Species	Common name	Total number of egg units	Total number of eggs
Coleoptera				Coleoptera species	2	20
Coleoptera	Chrysomelidae			Chrysomelidae species	2	18
Coleoptera	Chrysomelidae	*Crioceris*		Asparagus beetle species	2	26
Coleoptera	Chrysomelidae	*Crioceris*	*asparagi*	Asparagus beetle	2	55
Coleoptera	Chrysomelidae	*Lema*	*daturaphila*	Three lined potato beetle	17	117
Coleoptera	Chrysomelidae	*Leptinotarsa*	*decemlineata*	Colorado potato beetle	17	115
Coleoptera	Chrysomelidae	*Xanthogaleruca*	*luteola*	Elm leaf beetle	7	143
Coleoptera	Coccinellidae			Ladybird beetle species	105	2070
Hemiptera	Coreidae	*Acanthocephala*		*Acanthocephala* species	12	12
Hemiptera	Coreidae	*Anasa*	*tristis*	Squash bug	139	2961
Hemiptera	Coreidae	*Leptoglossus*	*phyllopus*	Eastern leaffooted bug	7	179
Hemiptera	Membracidae			Treehopper species	3	26
Hemiptera	Membracidae	*Entylia*	*carinata*	Keeled treehopper	5	NA
Hemiptera	Pentatomidae	*Banasa*		Banasa species	1	14
Hemiptera	Pentatomidae	*Brochymena*		*Brochymena* species	1	14
Hemiptera	Pentatomidae	*Chinavia*		*Chinavia* species	3	70
Hemiptera	Pentatomidae	*Chinavia*	*hilaris*	Green stink bug	4	197
Hemiptera	Pentatomidae	*Euschistus*		*Euschistus* species	113	2219
Hemiptera	Pentatomidae	*Halyomorpha*	*halys*	Brown marmorated stink bug	46	1152
Hemiptera	Pentatomidae	*Murgantia*	*histrionica*	Harlequin bug	104	1237
Hemiptera	Pentatomidae	*Oebalus*	*pugnax*	Rice stink bug	1	9
Hemiptera	Pentatomidae	*Podisus*		Podisus species	9	134
Hemiptera	Pentatomidae	*Podisus*	*maculiventris*	Spined soldier bug	5	72
Hemiptera	Reduviidae			Reduviidae species	2	33
Hemiptera	Reduviidae	*Apiomerus*		Bee assassin bug species	1	6
Hemiptera	Reduviidae	*Arilus*	*cristatus*	Wheel bug	94	13607
Hemiptera	Reduviidae	*Zelus*		Zelus species	2	96
Hemiptera	Reduviidae	*Zelus*	*luridus*	Pale green assassin bug	1	47
Hemiptera	Tingidae			Lace bug species	3	NA
Lepidoptera				Lepidoptera species	1	1
Lepidoptera	Lymantriinae			Tussock moth species	1	121
Lepidoptera	Noctuidae			Owlet moth species	6	1204
Lepidoptera	Notodontidae	*Datana*	*ministra*	Yellownecked caterpillar	2	410
Lepidoptera	Pieridae	*Pieris*	*rapae*	Cabbage butterfly	9	11
Lepidoptera	Saturniidae	*Anisota*	*senatoria*	Orange-tipped oakworm moth	3	913
Lepidoptera	Saturniidae	*Antheraea*	*polyphemus*	Polyphemus moth	31	38

Lepidoptera	Saturniidae	*Dryocampa*	*rubicunda*	Greenstriped mapleworm	9	182
Lepidoptera	Saturniidae	*Eacles*	*imperialis*	Imperial moth	2	2
Lepidoptera	Tortricidae			Tortricidae species	7	87
Mantodea	Mantidae	*Stagmomantis*	*carolina*	Carolina mantis	59	NA
Mantodea	Mantidae	*Tenodera*	*sinensis*	Chinese mantis	82	NA
Neuroptera				Lacewing species	4	9
Orthoptera	Tettigoniidae			Bush cricket species	2	28
Psocodea				Barklice species	21	13

Table S2. Summary of the total number of parasitoids reared from eggs by insect taxon group and by parasitoid taxon group. Data pooled across collection method.

Egg Order	**Egg Family**	**Egg Genus**	**Egg Species**	**Egg Common Name**	***Anastatus* spp**	***Ooencyrtus* spp**	***Telenomus* spp**	**Native *Trissolcus* spp**	***Trissolcus japonicus***	**Total**
Coleoptera	Coccinellidae			Coccinellidae species		11				11
Hemiptera	Coreidae	*Acanthocephala*		*Acanthocephala* species	1	17				18
Hemiptera	Coreidae	*Anasa*	*tristis*	Squash bug		16				16
Hemiptera	Coreidae	*Leptoglossus*	*phyllopus*	Eastern leaffooted bug	32					32
Hemiptera	Pentatomidae	*Banasa*		*Banasa* species			12			12
Hemiptera	Pentatomidae	*Brochymena*		*Brochymena* species	3					3
Hemiptera	Pentatomidae	*Chinavia*		*Chinavia* species	21			14		35
Hemiptera	Pentatomidae	*Chinavia*	*hilaris*	Green stink bug	38					38
Hemiptera	Pentatomidae	*Euschistus*		*Euschistus* species	286	2	102	293	2	685
Hemiptera	Pentatomidae	*Halyomorpha*	*halys*	Brown marmorated stink bug	101		4	5	145	255
Hemiptera	Pentatomidae	*Murgantia*	*histrionica*	Harlequin bug	1	58		183		242
Hemiptera	Pentatomidae	*Podisus*		*Podisus* species			38	2		40
Hemiptera	Pentatomidae	*Podisus*	*maculiventris*	Spined soldier bug	7			8		15
Hemiptera	Reduviidae	*Arilus*	*cristatus*	Wheel bug	653	346				999
Hemiptera	Reduviidae	*Zelus*		*Zelus* species	5					5
Lepidoptera	Notodontidae	*Datana*	*ministra*	Yellownecked caterpillar	80					80
Lepidoptera	Saturniidae	*Anisota*	*senatoria*	Orange-tipped oakworm moth	123					123
Lepidoptera	Saturniidae	*Antheraea*	*polyphemus*	Polyphemus moth	7					7
Lepidoptera	Saturniidae	*Dryocampa*	*rubicunda*	Greenstriped mapleworm	25					25
Lepidoptera	Saturniidae	*Eacles*	*imperialis*	Imperial moth	1					1
Mantodea	Mantidae	*Stagmomantis*	*carolina*	Carolina mantis	49					49
Orthoptera	Tettigoniidae			Bush cricket species	1					1
Total				23	1434	450	156	505	147	

Table S3. Field collected, naturally laid insect egg species that did not have any parasitoids of interest emerge, “non-hosts”. Only insect egg taxa with a sample of five or more egg units were included. The table is organized by insect egg order, family, genus, species, and common name. Data pooled across collection method.

Egg Order	**Egg Family**	**Egg Genus**	**Egg Species**	**Egg Common Name**	**Total # of Egg Units**	**Total # of Eggs**
Coleoptera	Chrysomelidae	*Lema*	*daturaphila*	Three lined potato beetle	17	117
Coleoptera	Chrysomelidae	*Leptinotarsa*	*decemlineata*	Colorado potato beetle	17	115
Coleoptera	Chrysomelidae	*Xanthogaleruca*	*luteola*	Elm leaf beetle	7	143
Hemiptera	Membracidae	*Entylia*	*carinata*	Keeled treehopper	5	NA
Lepidoptera	Noctuidae			Owlet moth species	6	1204
Lepidoptera	Pieridae	*Pieris*	*rapae*	Cabbage butterfly	9	11
Lepidoptera	Tortricidae			Leaf roller species	7	87
Mantodea	Mantidae	*Tenodera*	*sinensis*	Chinese mantis	82	NA
Psocodea				Barklice species	21	NA

Table S4. Host plant species, insect host egg species, and parasitoid associations. Table is organized by host plant species (order, family, genus, species, common name), then by an insect egg species found on the plant species, followed by columns of parasitoid species groups, an "X" indicating at least one parasitoid specimen emerged from that insect egg species on that plant species. Data pooled across collection method.

Plant Order	Plant Family	Plant Genus	Plant Species	Plant Common Name	Egg Species	Anastatus spp	Ooencyrtus spp	Telenomus spp	Native Trissolcus spp	Trissolcus japonicus	Total
Aquifoliales	Aquifoliaceae	*Ilex*	.	*Ilex* species	*Stagmomantis carolina*	X					1
Asterales	Asteraceae	*Calendula*	.	*Calendula* species	*Euschistus* sp.				X		1
Asterales	Asteraceae	*Silphium*	*perfoliatum*	Cup plant	*Euschistus* sp.			X			1
Brassicales	Brassicaceae	*Brassica*	*oleracea*	Kale	*Murgantia histrionica*				X		1
Brassicales	Brassicaceae	*Brassica*	*rapa*	Turnip	*Murgantia histrionica*	X	X				2
Brassicales	Cleomaceae	*Cleome*	*hassleriana*	Spider flower	*Murgantia histrionica*				X		1
Caryophyllales	Amaranthaceae	*Amaranthus*	.	*Amaranthus* species	*Podisus* sp.			X			1
Cornales	Cornaceae	*Cornus*	*amomum*	Silky dogwood	*Arilus cristatus*	X					1
Cucurbitales	Cucurbitaceae	*Cucurbita*	.	*Cucurbita* species	*Anasa tristis*		X				1
Cucurbitales	Cucurbitaceae	*Cucurbita*	*pepo*	Summer squash	*Anasa tristis*		X				1
Ericales	Ericaceae	*Rhododendron*	.	*Rhododendron* species	*Stagmomantis carolina*	X					1
Fabales	Fabaceae	*Cercis*	*canadensis*	Eastern redbud	*Arilus cristatus*	X	X				2
Fabales	Fabaceae	*Cercis*	*canadensis*	Eastern redbud	*Euschistus* sp.	X		X	X		3
Fabales	Fabaceae	*Cercis*	*canadensis*	Eastern redbud	*Halyomorpha halys*					X	1
Fagales	Betulaceae	*Betula*	*nigra*	River birch	*Arilus cristatus*	X	X				2
Fagales	Betulaceae	*Betula*	*nigra*	River birch	*Coccinellidae spp.*		X				1
Fagales	Betulaceae	*Betula*	*nigra*	River birch	*Euschistus* sp.				X		1
Fagales	Betulaceae	*Carpinus*	*caroliniana*	American hornbeam	*Arilus cristatus*		X				1
Fagales	Fagaceae	*Fagus*	*sylvatica*	European beech	*Chinavia hilaris*	X					1
Fagales	Fagaceae	*Fagus*	*sylvatica*	European beech	*Datana ministra*	X					1
Fagales	Fagaceae	*Fagus*	*sylvatica*	European beech	*Zelus* sp.	X					1
Fagales	Fagaceae	*Quercus*	*alba*	White oak	*Antheraea polyphemus*	X					1
Fagales	Fagaceae	*Quercus*	*alba*	White oak	*Banasa* sp			X			1
Fagales	Fagaceae	*Quercus*	*alba*	White oak	*Eacles imperialis*	X					1
Fagales	Fagaceae	*Quercus*	*alba*	White oak	*Euschistus* spp.	X		X	X		3

Fagales	Fagaceae	*Quercus*	*alba*	White oak	*Halyomorpha halys*	X			X	X	3
Fagales	Fagaceae	*Quercus*	*alba*	White oak	*Podisus* sp.				X		1
Fagales	Fagaceae	*Quercus*	*bicolor*	Swamp white oak	*Anisota senatoria*	X					1
Fagales	Fagaceae	*Quercus*	*coccinea*	Scarlet oak	*Anisota senatoria*	X					1
Fagales	Fagaceae	*Quercus*	*coccinea*	Scarlet oak	*Antheraea polyphemus*	X					1
Fagales	Fagaceae	*Quercus*	*coccinea*	Scarlet oak	*Arilus cristatus*	X					1
Fagales	Fagaceae	*Quercus*	*coccinea*	Scarlet oak	*Chinavia* sp.	X					1
Fagales	Fagaceae	*Quercus*	*coccinea*	Scarlet oak	*Euschistus* spp.	X		X	X		3
Fagales	Fagaceae	*Quercus*	*coccinea*	Scarlet oak	*Halyomorpha halys*			X	X	X	3
Fagales	Fagaceae	*Quercus*	*coccinea*	Scarlet oak	*Podisus maculiventris*	X					1
Fagales	Fagaceae	*Quercus*	*coccinea*	Scarlet oak	*Stagmomantis carolina*	X					1
Fagales	Fagaceae	*Quercus*	*macrocarpa*	Burr oak	*Acanthocephala* sp.		X				1
Fagales	Fagaceae	*Quercus*	*macrocarpa*	Burr oak	*Datana ministra*	X					1
Fagales	Fagaceae	*Quercus*	*palustris*	Pin oak	*Anisota senatoria*	X					1
Fagales	Fagaceae	*Quercus*	*palustris*	Pin oak	*Leptoglossus phyllopus*	X					1
Fagales	Fagaceae	*Quercus*	*phellos*	Willow oak	*Podisus maculiventris*	X					1
Fagales	Fagaceae	*Quercus*	*phellos*	Willow oak	Tettigoniidae sp.	X					1
Fagales	Fagaceae	*Quercus*	*rubra*	Red oak	*Euschistus* spp.	X			X		2
Fagales	Fagaceae	*Quercus*	*rubra*	Red oak	*Halyomorpha halys*					X	1
Fagales	Fagaceae	*Quercus*	*velutina*	Black oak	*Stagmomantis carolina*	X					1
Fagales	Juglandaceae	*Juglans*	*nigra*	Black walnut	*Arilus cristatus*	X	X				2
Fagales	Juglandaceae	*Juglans*	*nigra*	Black walnut	*Euschistus* sp.				X		1
Lamiales	Oleaceae	*Fraxinus*	*nigra*	Black ash	*Acanthocephala* sp.	X					1
Lamiales	Oleaceae	*Fraxinus*	*pennsylvanica*	Green ash	*Arilus cristatus*	X					1
Lamiales	Oleaceae	*Syringa*	*pekinensis*	Pekin lilac	*Arilus cristatus*	X	X				2
Magnoliales	Magnoliaceae	*Liriodendron*	*tulipifera*	Tulip poplar	*Arilus cristatus*	X	X				2
Magnoliales	Magnoliaceae	*Liriodendron*	*tulipifera*	Tulip poplar	*Leptoglossus phyllopus*	X					1
Malpighiales	Salicaceae	*Salix*	*alba*	White willow	*Podisus* sp.			X	X		2
Malpighiales	Salicaceae	*Salix*	*matsudana*	Chinese willow	*Podisus maculiventris*				X		1
Malvales	Malvaceae	*Tilia*	.	*Tilia* species	*Euschistus* sp.				X		1
Malvales	Malvaceae	*Tilia*	*tomentosa*	Silver linden	*Halyomorpha halys*				X		1
Myrtales	Lythraceae	*Lagerstroemia*	.	Crepe myrtle species	*Stagmomantis carolina*	X					1
Pinales	Cupressaceae	*Chamaecyparis*	.	False cypress species	*Euschistus* sp.			X			1

Proteales	Platanaceae	*Platanus*	.	London planetree	*Antheraea polyphemus*	X					1
Proteales	Platanaceae	*Platanus*	*occidentalis*	American sycamore	*Arilus cristatus*	X					1
Proteales	Platanaceae	*Platanus*	*occidentalis*	American sycamore	*Leptoglossus phyllopus*	X					1
Rosales	Cannabaceae	*Celtis*	*occidentalis*	Common hackberry	*Euschistus* spp.	X		X	X		3
Rosales	Rosaceae	*Malus*	.	*Malus* species	*Arilus cristatus*	X					1
Rosales	Rosaceae	*Malus*	.	*Malus* species	*Chinavia* sp.				X		1
Rosales	Rosaceae	*Malus*	.	*Malus* species	*Euschistus* spp.	X					1
Rosales	Rosaceae	*Malus*	.	*Malus* species	*Stagmomantis carolina*	X					1
Rosales	Rosaceae	*Prunus*	.	*Prunus* species	*Arilus cristatus*	X	X				2
Rosales	Rosaceae	*Prunus*	.	*Prunus* species	*Stagmomantis carolina*	X					1
Rosales	Rosaceae	*Prunus*	*serotina*	Black cherry	*Arilus cristatus*	X					1
Rosales	Rosaceae	*Prunus*	*serrulata*	Japanese cherry	*Arilus cristatus*	X					1
Rosales	Rosaceae	*Prunus*	*serrulata*	Japanese cherry	*Euschistus* spp.	X			X		2
Rosales	Rosaceae	*Prunus*	*serrulata*	Japanese cherry	*Halyomorpha halys*	X					1
Rosales	Rosaceae	*Pyrus*	.	*Pyrus* species	*Chinavia* sp.	X					1
Rosales	Rosaceae	*Pyrus*	*calleryana*	Callery pear	*Arilus cristatus*	X	X				2
Rosales	Ulmaceae	*Ulmus*	*parvifolia*	Chinese elm	*Arilus cristatus*	X					1
Rosales	Ulmaceae	*Ulmus*	*parvifolia*	Chinese elm	*Stagmomantis carolina*	X					1
Rosales	Ulmaceae	*Zelkova*	*serrata*	Japanese zelkova	*Arilus cristatus*		X				1
Sapindales	Sapindaceae	*Acer*	*negundo*	Boxelder	*Arilus cristatus*	X					1
Sapindales	Sapindaceae	*Acer*	*rubrum*	Red maple	*Antheraea polyphemus*	X					1
Sapindales	Sapindaceae	*Acer*	*rubrum*	Red maple	*Euschistus* sp.	X		X	X		3
Sapindales	Sapindaceae	*Acer*	*rubrum*	Red maple	*Arilus cristatus*	X	X				2
Sapindales	Sapindaceae	*Acer*	*rubrum*	Red maple	*Dryocampa rubicunda*	X					1
Sapindales	Sapindaceae	*Acer*	*rubrum*	Red maple	*Halyomorpha halys*	X			X	X	3
Sapindales	Sapindaceae	*Acer*	*saccharinum*	Silver maple	*Dryocampa rubicunda*	X					1
Sapindales	Sapindaceae	*Acer*	*saccharinum*	Silver maple	*Euschistus* sp.			X			1
Sapindales	Sapindaceae	*Acer*	*saccharum*	Sugar maple	*Antheraea polyphemus*	X					1
Sapindales	Sapindaceae	*Acer*	*saccharum*	Sugar maple	*Arilus cristatus*	X					1
Sapindales	Sapindaceae	*Acer*	*saccharum*	Sugar maple	*Euschistus* spp.	X		X	X	X	4
Sapindales	Sapindaceae	*Acer*	*saccharum*	Sugar maple	*Halyomorpha halys*	X		X		X	3
Sapindales	Sapindaceae	*Aesculus*	*pavia*	Red Buckeye	*Brochymena* sp.	X					1

Saxifragales	Altingiaceae	*Liquidambar*	*styraciflua*	Sweet gum	*Leptoglossus phyllopus*	X					1
Saxifragales	Hamamelidaceae	*Hamamelis*	*virginiana*	Witch hazel	*Halyomorpha halys*	X					1
Total						67	15	14	22	7	

Table S5. Total number of field collected, naturally laid insect egg units by egg order and by *Anastatus* spp. discovery. Model probability of *Anastatus* spp. egg unit discovery differed by egg order, but post hoc comparisons revealed no significant order comparisons. Egg units were collected from organic trees in a Maryland tree nursery. Data from standardized nursery sampling.

Host insect egg order	Total number of discovered egg units	Total number of non-discovered egg units	Total number of collected egg units	Percentage of discovered egg units	Significant host insect egg order pairwise comparisons from model
Coleoptera	0	39	39	0%	No significant comparisons
Hemiptera	36	60	96	37.5%	
Lepidoptera	7	21	28	25%	
Mantodea	0	2	2	0%	
TOTAL	43	122	165	26.06%	

Table S6. Total number of field collected, naturally laid egg units by pentatomid species and by discovery by all parasitoid species of interest. Model probability of egg unit discovery marginally differed by pentatomid species, but post hoc comparisons revealed no significant pentatomid species comparisons. Egg units were collected from organic trees in a Maryland tree nursery. Data from the standardized nursery sampling.

Host pentatomid egg species	Total number of discovered egg units	Total number of un-discovered egg units	Total number of collected egg units	Percentage of discovered egg units	Significant host pentatomid egg species comparisons from model
Banasa spp.	1	0	1	100%	No significant comparisons
Euschistus spp.	18	39	57	31.58%	
Halyomorpha halys	15	12	27	55.56%	
Podisus spp.	2	3	5	40%	
TOTAL	36	54	90	40%	

Table S7. Total number of field collected, naturally laid insect egg units by host tree genus and by discovery by all parasitoid species of interest. Model probability of egg unit discovery marginally differed by tree genus, with a higher probability of discovery for egg units laid on *Quercus*. Egg units were collected from organic trees in a Maryland tree nursery. Data from the standardized nursery sampling.

Tree genus	Total number of discovered egg units	Total number of un-discovered egg units	Total number of collected egg units	Percentage of discovered egg units	Significant tree genus pairwise comparisons from model
Acer	22	54	76	28.95%	*Acer*-*Quercus*: p=0.08
Quercus	21	68	89	23.60%	
TOTAL	43	122	165	26.06%	

Table S8. Total number of field collected, naturally laid insect egg units by host tree species and by discovery by all parasitoid species of interest. Model probability of egg unit discovery differed by tree species. Post hoc comparisons found a higher probability of discovery for egg units laid on *Quercus alba* and *Q. coccinea* when both species were compared to *Acer rubrum*. Egg units were collected from organic trees in a Maryland tree nursery. Data from the standardized nursery sampling.

Tree species	Total number of discovered egg units	Total number of un-discovered egg units	Total number of collected egg units	Percentage of discovered egg units	Significant tree species pairwise comparisons from model
Acer rubrum	5	28	33	15.15%	*Acer rubrum*-*Quercus alba*: p=0.06 *A. rubrum*-*Q. coccinea*: p= 0.03
A. saccharum	17	26	43	39.53%	
Quercus alba	11	48	59	18.64%	
Q. coccinea	6	6	12	50%	
Q. rubra	4	14	18	22.22%	
TOTAL	43	122	165	26.06%	

Table S9. Total number of field collected, naturally laid insect egg units by host tree genus and by *Anastatus* spp. discovery. Model probability of *Anastatus* spp. egg unit discovery did not differ by tree genus. Egg units were collected from organic trees in a Maryland tree nursery. Data from the standardized nursery sampling.

Tree genus	Total number of discovered egg units	Total number of un-discovered egg units	Total number of collected egg units	Percentage of discovered egg units	Significant tree genus pairwise comparisons from model
Acer	16	60	76	21.05%	No significant comparison
Quercus	15	74	89	16.85%	
TOTAL	31	134	165	18.79%	

Table S10. Total number of field collected, naturally laid insect egg units by host tree species and by *Anastatus* spp. discovery. Model probability of *Anastatus* spp. egg unit discovery did not differ by tree species. Egg units were collected from organic trees in a Maryland tree nursery. Data from the standardized nursery sampling.

Tree species	Total number of discovered egg units	Total number of un-discovered egg units	Total number of collected egg units	Percentage of discovered egg units	Significant tree species pairwise comparisons from model
Acer rubrum	5	28	33	15.15%	No significant comparisons
A. saccharum	11	32	43	25.58%	
Quercus alba	7	52	59	11.86%	
Q. coccinea	5	7	12	41.67%	
Q. rubra	3	15	18	16.67%	
TOTAL	31	134	165	18.79%	

Table S11. Total number of field collected, naturally laid pentatomid egg units by host tree genus and by discovery by all parasitoid species of interest. Model probability of egg unit discovery did not differ by tree genus. Pentatomid egg units were collected from organic trees in a Maryland tree nursery and included the species *Banasa* sp., *Euschistus* spp., *Halyomorpha halys*, and *Podisus* spp. Data from the standardized nursery sampling.

Tree genus	Total number of discovered egg units	Total number of un-discovered egg units	Total number of collected egg units	Percentage of discovered egg units	Significant tree genus pairwise comparisons from model
Acer	17	37	54	31.48%	No significant comparison
Quercus	19	17	36	52.78%	
TOTAL	36	54	90	40%	

Table S12. Total number of field collected, naturally laid pentatomid egg units by host tree species and by discovery by all parasitoid species of interest. Model probability of egg unit discovery differed by tree species. Post hoc comparisons found a significant difference in the probability of egg unit discovery between all tree species. Pentatomid egg units were collected from organic trees in a Maryland tree nursery and included the species *Banasa* sp., *Euschistus* spp., *Halyomorpha halys*, and *Podisus* spp. Data from the standardized nursery sampling.

Tree species	Total number of discovered egg units	Total number of un-discovered egg units	Total number of collected egg units	Percentage of discovered egg units	Significant tree species pairwise comparisons from model
Acer rubrum	2	16	18	11.11%	*Acer rubrum-A. saccharum*: $p<0.001$ *A. rubrum-Quercus alba*: $p<0.001$ *A. rubrum-Q. coccinea*: $p<0.001$ *A. rubrum-Q. rubra*: $p<0.001$ *A. saccharum-Q. alba*: $p<0.001$ *A. saccharum-Q. coccinea*: $p<0.001$ *A. saccharum-Q. rubra*: $p<0.001$ *Q. alba-Q. coccinea*: $p<0.001$ *Q. alba-Q. rubra*: $p<0.001$ *Q. coccinea-Q. rubra*: $p<0.001$
A. saccharum	15	21	36	41.67%	
Quercus alba	9	6	15	60%	
Q. coccinea	6	3	9	66.67%	
Q. rubra	4	8	12	33.33%	
TOTAL	36	54	90	40%	

Table S13. Total number of field collected, naturally laid egg units by pentatomid species, by tree genus, and by discovery by all parasitoid species of interest. Egg units were collected from organic trees in a Maryland tree nursery. Data from the standardized nursery sampling.

Host pentatomid egg species	Tree genus							
		Acer			*Quercus*			
	Total number of discovered egg units	Total number of un-discovered egg units	Total number of collected egg units	Percentage of discovered egg units	Total number of discovered egg units	Total number of un-discovered egg units	Total number of collected egg units	Percentage of discovered egg units
Banasa spp.	0	0	0	NA	1	0	1	100%
Euschistus spp.	5	26	31	16.13%	13	13	26	50%
Halyomorpha halys	12	9	21	57.14%	3	3	6	50%
Podisus spp.	0	2	2	0%	2	1	3	67%
TOTAL	17	37	54	31%	19	17	36	52.78%

Table S14. Total number of field collected, naturally laid insect egg units by host insect egg species' feeding guild and by *Anastatus* spp. discovery. Model probability of *Anastatus* spp. egg unit discovery differed by feeding guild, with a higher probability of egg unit discovery for predaceous insect egg species. Predaceous insect egg species included omnivorous species. Egg units were collected from diverse habitats throughout Maryland. Data from the diverse habitats survey.

Host insect egg species' feeding guild	Total number of discovered egg units	Total number of un-discovered egg units	Total number of collected egg units	Percentage of discovered egg units	Significant insect egg species' feeding guild pairwise comparisons from model
Herbivore	19	368	387	4.91%	Herbivore-Predator: $p<0.001$
Predator	29	183	212	13.68%	
TOTAL	48	551	599	8.01%	

Table S15. Total number of field collected, naturally laid insect egg units by host plant origin and by discovery by all parasitoid species of interest. Model probability of egg unit discovery differed by plant origin, with a higher probability of discovery for egg units laid on native plants. Native plants were defined as plants endemic to North America and included native cultivars. Egg units were collected from diverse habitats throughout Maryland. Data from the diverse habitats survey.

Plant origin	Total number of discovered egg units	Total number of un-discovered egg units	Total number of collected egg units	Percentage of discovered egg units	Significant plant origin pairwise comparisons from model
Native	50	131	181	27.62%	Native-Non-native: $p<0.001$
Non-native	40	311	351	11.4%	
TOTAL	90	442	532	16.92%	

Table S16. Total number of field collected, naturally laid insect egg units by host plant origin and by *Anastatus* spp. discovery. Model probability of *Anastatus* spp. egg unit discovery differed by plant origin, with a higher probability of discovery for egg units laid on native plants. Native plants were defined as plants endemic to North America and included native cultivars. Egg units were collected from diverse habitats throughout Maryland. Data from the diverse habitats survey.

Plant origin	Total number of discovered egg units	Total number of un-discovered egg units	Total number of collected egg units	Percentage of discovered egg units	Significant plant origin pairwise comparison from model
Native	40	141	181	22.1%	Native-Non-native: $p<0.001$
Non-native	6	345	351	1.71%	
TOTAL	46	486	532	8.65%	

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