Biological Control 160 (2021) 104698

Contents lists available at ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

Niche partitioning and coexistence of parasitoids of the same feeding guild introduced for biological control of an invasive forest pest

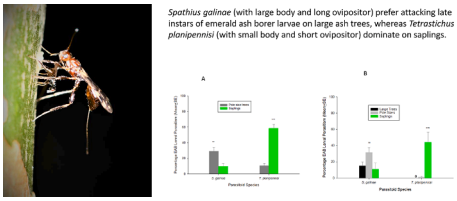
Jian J. Duan [a,*], Roy G. Van Driesche [b], Jonathan M. Schmude [a], Nicole F. Quinn [b], Toby R. Petrice [c], Claire E. Rutledge [d], Therese M. Poland [c], Leah S. Bauer [c], Joseph S. Elkinton [b]

[a] U.S. Department of Agriculture, Agricultural Research Service, Beneficial Insects Introduction Research Unit, Newark, DE 19713, USA
[b] Department of Environmental Conservation, University of Massachusetts, Amherst, MA 01003, USA
[c] U.S. Forest Service, Northern Research Station, Lansing, MI 48910, USA
[d] Connecticut Agricultural Experiment Station, New Haven, CT 06511, USA

HIGHLIGHTS

- Emerald ash borer (EAB) is a serious invasive pest of ash trees in North America.
- *Spathius galinae* (SG) and *Tetrastichus planipennisi* (TP) are EAB larval parasitoids.
- SG and TP were introduced from Asia to U.S. for EAB biocontrol 2007 and 2015, respectively.
- SG is more frequent in larger trees whereas TP dominates in saplings.
- These two parasitoids complement one another in biocontrol of EAB because of niche partitioning. .

GRAPHICAL ABSTRACT



ARTICLE INFO

Keywords:
Niche partition
Interspecific competition
Koinobiont endoparasitoid
Idiobiont ectoparasitoid
Tetrastichus planipennisi
Spathius galinae
Agrilus planipennis

ABSTRACT

When multiple species of host-specific natural enemies from the same feeding guild are introduced to areas against a target pest, strong interspecific competition is likely and may compromise biocontrol unless the agents effectively partition available resources. Here, we evaluate if two parasitoids (*Spathius galinae* and *Tetrastichus planipennisi*), introduced for biocontrol of the invasive emerald ash borer (EAB), *Agrilus planipennis,* into North America have established niche-partitioning, co-existing populations following their sequential or simultaneous field releases to 12 hard-wood forests located in Midwest and Northeast regions of the United States. We found the two recently introduced EAB larval parasitoids, *S. galinae* and *T. planipennisi,* established niche-partitioning, co-existing populations in all release areas. Presence, abundance, and/or host attack (parasitism) rates of the two parasitoid species differed significantly among ash tree-size classes, with *S. galinae* parasitism more abundant in larger diameter and pole-size trees, while *T. planipennisi* dominated in saplings. We also found the abundance of EAB larvae declined significantly with height in both ash saplings and pole-size trees, whereas the abundance of *S. galinae* and *T. planipennisi* broods was unaffected. However, the abundance of both larval parasitoid species was strongly and positively correlated with EAB larval abundance in sampled sections of their preferred tree-size classes. Our findings suggest that the two introduced specialist parasitoids, *S. galinae* and *T. planipennisi*, complement one another in protecting trees of different size classes against EAB.

* Corresponding author.
E-mail address: jian.duan@usda.gov (J.J. Duan).

https://doi.org/10.1016/j.biocontrol.2021.104698
Received 7 March 2021; Received in revised form 20 June 2021; Accepted 24 June 2021
Available online 26 June 2021
1049-9644/Published by Elsevier Inc.

1. Introduction

Ecological principles concerning interspecific competition suggest that species sharing identical niches cannot coexist unless they diverge in resource use, ultimately leading to niche separation (Hardin, 1960; DeBach, 1966; Tilman, 1982; Bonsall et al., 2002). Biological control introductions against invasive arthropod pests have generated some classic examples of competitive exclusion or habitat displacement among introduced natural enemies, including parasitoids (e.g., Bess et al., 1961; Turnbull and Chant, 1961; Watt, 1965; Turnbull, 1967; Ehler, 1985, 1990; Murdoch and Briggs, 1996; Murdoch et al., 1996) and predators (e.g., Alyokhin and Sewell, 2004; Evans, 2004). Because parasitoids are generally host species- and stage-specific, multiple species of parasitoids, particularly those from the same feeding guild (i.e., attacking the same host species and stage) have the potential to be in intense competition with each other that may lead to failures in successful biological control of the targeted pest. In nature, however, an insect pest is often attacked by multiple species of potentially competing parasitoids or predators that can co-occur due to various mechanisms leading to their niche partitioning (e.g., Bonsall et al., 2002; Pekas et al., 2016). Therefore, understanding of mechanisms or factors that facilitate the co-existence of competing parasitoid species is critical for developing and implementing biological control programs that involve multiple natural enemy introductions against an invasive agricultural or forest insect pest (Mills, 2003; Pedersen and Mills, 2004).

Following the invasion of North American forests by the emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), a highly destructive pest of ash (*Fraxinus* spp.) trees (Poland and McCullough, 2006; Herms and McCullough, 2014), three species of parasitoids were simultaneously introduced in 2007 from the region of the pest's origin (Northeast China) to the United States for biological control of this invasive pest (Federal Register, 2007). These parasitoids of Chinese origin were the egg parasitoid *Oobius agrili* Zhang & Huang (Hymenoptera: Encyrtidae) and the two larval parasitoids *Tetrastichus planipennisi* Yang (Hymenoptera: Eulophidae) and *Spathius agrili* Yang (Hymenoptera: Braconidae). Successful establishment and impact of *O. agrili* and *T. planipennisi* on EAB have been documented in most release areas in the northern United States (Duan et al., 2013, 2015, 2017; Abell et al., 2014; Jennings et al., 2016). However, the braconid larval parasitoid *S. agrili* failed to establish self-sustaining populations in nearly all these same release areas (Bauer et al., 2015; Duan et al., 2018). Failure of *S. agrili* establishment in northern U.S. may be due to the asynchrony with EAB phenology or climatic conditions (Jones et al., 2020; but see Ragozzino et al., 2020). However, because both *T. planipennisi* and *S. agrili* attack the same late instars of EAB larvae, interspecific competition may also limit their co-existence when released in the same habitat (Ulyshen et al., 2010; Yang et al., 2013).

More recently, *Spathius galinae* Belokobylskij & Strazenac, from the Russian Far East, was approved in 2015 for releases in the U.S. for biocontrol of EAB (Federal Register, 2015). Laboratory studies have demonstrated the occurrence of intrinsic competition between larval stages of *S. galinae* and *T. planipennisi* (Yang et al., 2012) but suggest that differences in the rate of host attack (parasitism) and progeny brood (clutch) size between the two species may potentially mediate their co-existence in nature (Wang et al., 2015). In addition, laboratory studies showed that the abilities of *T. planipennisi* and *S. galinae* to locate and attack EAB larvae feeding in the phloem tissues are differentially limited by the thickness of ash bark (Abell et al., 2012; Murphy et al., 2017), suggesting that host attack by *T. planipennisi* in large thick-barked trees is limited because of its short ovipositor (1.9–2.6 mm) whereas *S. galinae*, with its considerably longer ovipositor (3.5–5.3 mm), could attack EAB larvae not only in small trees but also in larger diameter trees with thicker bark.

In its native range in the Russian Far East, *S. galinae* is the dominant EAB larval parasitoid. While it does co-exist naturally with *T. planipennisi* in some locations (Duan et al., 2012), the natural distribution of *S. galinae* doesn't extend southward into Northeast China, where *T. planipennis* is the dominant EAB larval parasitoid (Wang et al., 2016). Currently, little is known about the ecological mechanisms or factors that would affect the co-existence and distributions of these two EAB natural enemies in the pest's native range.

When both *T. planipennisi* and *S. galinae* were released in several ash-containing forests in the Northeast U.S. from 2015 to 2017, both parasitoids established self-sustaining populations, but the rate of parasitism by *S. galinae* in relatively large (pole-size) ash trees is several times higher than is parasitism by *T. planipennisi* (Duan et al., 2019). Similar patterns of establishment and parasitism by *S. galinae* in relatively large ash trees were also observed in forests in central Michigan, where *T. planipennisi* was released between 2007 and 2010, establishing dense populations before *S. galinae* was released between 2015 and 2017 (Duan et al., 2015, 2017, 2020). These earlier field studies suggest that both parasitoids may co-exist across the northern U.S. either when released simultaneously or sequentially for biocontrol of EAB. Based on findings from these previous studies, we hypothesize that *S. galinae* and *T. planipennisi* may partition their host resources based on the size of EAB's host ash trees. This occurs because tree size is positively related to bark thickness, which in turn mediates the degree of exposure of EAB larvae to parasitoid attack due to differences in ovipositor lengths of the two parasitoids. In the present study, we tested this hypothesis by measuring the presence or absence of immature parasitoid brood(s), parasitoid brood density, and rates of EAB larval parasitism by these two introduced parasitoids on trees of different size classes in 12 ash-containing forests located in the Midwest and Northeast U.S., where both parasitoids were released either sequentially or simultaneously >2 years earlier. We also evaluated the host distribution and attack rates by both introduced parasitoids in relation to sections of sampled trees or saplings at different heights above ground with the aim at detecting any evidence of niche partitioning and co-existence of the two parasitoids within the host-infested trees.

2. Materials and methods

2.1. Study sites

The study was conducted in two northern regions of the U.S.: 1) Michigan, where EAB was first detected in 2002, and 2) the Northeast states (Connecticut, Massachusetts, and New York), where EAB was first detected between 2010 and 2012. In Michigan, the study sites consisted of six, secondary mixed-hardwood bottomland forests containing both green ash (*Fraxinus pennsylvanica* Marshall) and white ash (*F. americana* L.), where *T. planipennisi* was released from 2008 to 2010 (Duan et al., 2013), followed by *S. galinae* from 2015 and to 2017 (Duan et al., 2020). In the Northeast region, the study sites consisted of six, secondary mixed-hardwood forests containing green and white ash trees located in three states: Connecticut (three sites), New York (two sites), and Massachusetts (one site), where the two parasitoids were released simultaneously from 2015 to 2017 (Duan et al., 2019). Regional and study site maps are provided in the Supplementary Data (SF1). Published studies by Duan et al. (2013, 2015, 2019, 2020) provide site details including GPS coordinates, background on EAB-invasion history, number and time of parasitoid releases, and general site characteristics such as ash (*Fraxinus* spp.) tree species composition and abundance at each site in both regions. As noted in previous studies (Duan et al., 2015, 2019), there were notable differences in non-ash tree species composition, abundance, both ash and non-ash tree basal area, and average tree DBH (diameter at breast height) among the different study sites both within and between regions. For this study, we collected data on the post-release abundance and host attacks of these two introduced EAB larval parasitoids from these study sites in 2019, approximately 2–5 years after *S. galinae* was released in these sites.

2.2. Sampling procedures

In both study regions, we sampled overwintering EAB larvae and associated immature parasitoid broods of *S. galinae* and/or *T. planipennisi* in host galleries under the tree bark either in early spring of 2019 (Michigan) or late fall of 2019 (Northeast states), by felling and debarking EAB-infested ash trees of different sizes, as measured by diameter at breast height (DBH). The number of sampled ash trees or saplings of different size classes varied with the study region and across different sites, depending on the abundance of host trees of different sizes at a given study region or site, due to mainly differences in the EAB-invasion history between the two study regions. In Michigan, where virtually all large ash trees had been killed off by EAB, we sampled 8 living pole-size trees (DBH = 8–19 cm) and 20 saplings (DBH = 2.8–5.8 cm) with signs and symptoms of EAB infestation (e.g., fresh woodpecker feeding signs, D-shaped EAB exit holes, bark splits, epicormic shoots). In the Northeast states, we sampled 4–5 ash trees of each of three groups: large trees (DBH 22.0–37.0 cm), pole size trees (DBH 8.0–20.0 cm), and saplings (DBH 3.7–6.0 cm) at each site. Ash trees and saplings sampled in the Northeast also showed signs and symptoms of EAB infestation.

For sampling, each sample tree or sapling was felled using a chain saw and debarked using a draw knife. While we debarked the entirety of all sampled pole-size trees and saplings (including main trunks and branches >2.5 cm in diameter), there was an exception made for large trees in the Northeast states. We debarked only the first 2 m above ground of the sampled large trees in the Northeast sites because of the logistical difficulty of felling them. Therefore, for the Northeast states, we considered only the first two meters (above the ground) for all three tree size classes, so that data could be compared among them. In both regions, all data were collected and recorded by meter-long sections of the sampled tree or sapling trunks.

During debarking, immature parasitoid broods (larvae or pupae) in host trees, as well as healthy EAB larvae, prepupae, and pupae were recorded and then collected into a culture plate for laboratory rearing to confirm parasitoid identity and detect further parasitism of young larval stages not visible in the field. Fresh (same year or generation) D-shaped EAB exit holes were also recorded on each sampled tree or sapling, which represented successful development and emergence of EAB adults. These fresh D-shaped exit holes were distinguished from the old ones (if present) based on the absence of tree callus tissues surrounding the exit holes and/or associated galleries. In addition, we observed and recorded the EAB larval mortality due to other factors such as woodpecker predation (i.e., identified by the avian feeding cavity made to the larval galleries), putative host tree resistance (EAB cadaver encapsulated by host tree callus), and pathogens (cadaver dried, liquefied, or sporulated) but excluded those data from analyses in this study. During the study, we also observed low levels (<3%) of EAB larval parasitism by native or vagrant parasitoids, including primarily *Atanycolus* spp., *Phasgnophora sulcata* Westwood, and *Balcha indica* Mani and Kaul in both regions. Because of their low prevalence, we did not analyse their potential interactions with *S. galinae* or *T. planipennisi* but included those parasitized EAB larvae in the total sample size (i.e., the denominator used to calculate EAB larval parasitism rates by *S. galinae* or *T. planipennisi*).

2.3. Data analyses

For analyses, we assigned trees to different DBH classes (sapling- or pole-size trees in Michigan; sapling-, pole- or large-size trees in northeast states). To estimate the phloem area (Y in m^2) of a sampled pole size tree or sapling (in Michigan) based om DBH (X in cm), we used the mean of two estimates for the surface area (m^2) from two different models developed McCullough and Siegert (2007). We averaged estimates from the two models because the linear model ($Y = 0.38*X - 1.76$) tends to underestimate the surface area of smaller trees, whereas the first-order polynomial model ($Y = 0.024*X^2 - 0.307*X + 2.63$) tends to overestimate the surface area of smaller trees (McCullough and Siegert 2007). For the sampled section of the main trunk of a tree or sapling from the base to 2 m above the ground in the Northeast, we estimated the total sampled phloem surface area (S in m^2) using the trapezoid formula $S = ½ \pi*(D1 + D2)*H$, where D1 is the diameter (converted to m) of the trunk at the ground level, D2 is the diameter (converted to m) of the trunk at the 2 m above the ground, and H is the height of the main trunk section sampled (=2 m).

We used nominal logistic regression model to test the null hypotheses that the probability of each tree containing one or more broods of either parasitoid species or both has no significant relationship with the tree size (DBH) categories (Sall et al., 2017). The density of *S. galinae* or *T. planipennisi* broods in a sampled tree in Michigan or a sampled 2 m section of the tree trunk in northeast states was calculated as the number of parasitoid broods per m^2 of sampled phloem area and first analysed using a linear regression model for ANOVA, which included parasitoid species, tree size and study site as main factors as well as their interactions. These preliminary analyses detected highly significant interactions between parasitoid species and tree size (all P-values <0.0001) for both datasets from Michigan and Northeast states. Therefore, separate ANOVA tests were then conducted for each parasitoid species to test the null hypothesis that both tree size and study site have no significant effects on the density of *S. galinae* or *T. planipennisi* broods. The rate of EAB larval parasitism by *S. galinae* or *T. planipennisi* in a sampled tree or section of a sampled tree was calculated as the proportion of the EAB larvae parasitized by either parasitoid relative to total number of EAB larvae that had advanced to or beyond the parasitoid-susceptible stage (from third instar to adults), and then analysed using a logistic regression via a generalized linear model (GLM) fitted to a binomial distribution. The GLM procedure also tested overdispersion of the data and chose appropriate (e.g., beta-binomial) distributions if the Pearson Chi-square tests for overdispersion were highly significant ($P < 0.001$) (SAS Institute, 2020). As with previous analyses on parasitoid brood density, highly significant interactions between parasitoid species and tree size were detected (all P-values <0.001) when parasitoid species, tree size and study site as main factors as well as their interactions were included in the full general linear models. Separate GLM analyses of parasitism rates were thus conducted for each parasitoid species for both datasets from Michigan and Northeast states. The separate GLM tests the null hypothesis that rate of EAB larval parasitism by *S. galinae* or *T. planipennisi* is not significantly related to the sample section (or height) of the tree.

Using the data collected from each meter section of debarked pole size trees or saplings in the six Michigan study sites, we conducted simple linear regression analyses of the abundance of host larvae and associated *S. galinae* and/or *T. planipennisi* broods (as measured by the total numbers observed in each meter section of tree or sapling) versus height of the sample above the ground level. The same logistic regression procedures (via generalized linear model) were used to test the null hypothesis that there is no significant relationship between parasitism (host attack) rates at each meter section of sampled pole size tree or saplings and the height of the sample above the ground level. Using the same simple linear regression model, we also tested the null hypothesis that the abundance of *S. galinae* or *T. planipennisi* broods observed in the meter sections of sampled pole size trees or saplings is not significantly related to the EAB abundance in those same sample sections. All statistical analyses were carried out with JMP Pro 15.10 (SAS Institute, 2020) and JMP scripts and outputs provided in the Supplementary Data.

3. Results

3.1. Probability of parasitoid presence in trees of different size classes

Among all pole size trees (n = 48) pooled across all sites in Michigan (Fig. 1**A**), similar proportions of trees contained either *S. galinae* (23.0%), *T. planipennisi* (19.0%) or both parasitoid species (21.0%). In contrast, among all sampled saplings (n = 120) in Michigan, a higher proportion contained only *T. planipennisi* (33.3%) than contained *S. galinae* alone (3.3%) or both species (4.2%). Nominal logistic regression analysis indicated a highly significant effect of tree size class (pole size vs. saplings) on the probability of either parasitoid species or both being present in a pole size tree or sapling (log likelihood ratio χ^2 = 21.67, df = 2, P < 0.0001).

Similar patterns of parasitoid occurrence were observed in the northeast states, based on the 2-meter basal sections of the main trunks of sample trees or saplings (Fig. 1**B**). In very large trees, 60% of the 2-m basal sections contained only *S. galinae*, and this proportion dropped to 45.0% in pole size trees. This proportion of pole size trees (basal 2-m sections) with *S. galinae* only, however, was still 3 times greater than the proportion containing both *S. galinae* and *T. planipennisi* (12.0%), and no sampled 2-m basal section of pole size trees contained only *T. planipennisi*. In contrast, 50% of the 2-m basal sections from saplings contained only *T. planipennisi*, compared to 16.7% of the sections with both *S. galinae* and *T. planipennisi*. In saplings, no 2-m basal sections contained only *S. galinae*. Nominal logistic regression analysis again indicated a highly significant effect of the tree size class on the proportion of either parasitoid species or both being present on a 2-m section of a large tree, pole size tree, or sapling (log likelihood ratio χ^2 = 28.25, df = 6, P < 0.001).

3.2. Parasitoid densities in trees of different size classes

In Michigan, mean *S. galinae* density (no. broods per m^2 of phloem area) was approximately 5 times higher in pole size trees (2.49) than in saplings (0.48). Conversely, mean *T. planipennisi* densities were nearly 8 times higher in saplings (3.33) than in pole size trees (0.46) (Fig. 2**A**). Tree size class (pole size trees vs. saplings) had a highly significant effect on parasitoid density of both *S. galinae* (F = 14.83; df = 1, 67, P = 0.0003) and *T. planipennisi* (F = 16.85, df = 1, 67; P < 0.0001). There were no significant differences among the different Michigan study sites in EAB larval parasitism rates for either *S. galinae* (F = 1.89; df = 5, 67; P = 0.1081) or *T. planipennisi* (F = 1.03; df = 5, P = 0.4801).

In the Northeast, the pattern of parasitoid densities among tree-size classes was similar to those found in Michigan, with mean *S. galinae* density in pole size trees 4–5 times higher (11.4) than in large-size trees (3.4) or saplings (2.1) **(**Fig. 2**B)**. While no broods of *T. planipennisi* were observed in the 2-m basal sections of large trees, *T. planipennisi* density in saplings (4.7) was approximately 10 times higher than in the pole-size trees (0.3). Overall, tree-size class had a highly significant effect on densities of both *S. galinae* (F = 3.87, df = 2, 23, P = 0.0411) and *T. planipennisi* (F = 23.93, df = 2, 23, P < 0.0001). As observed in Michigan, there were no significant differences detected among study sites in parasitoid densities for either *S. galinae* (F = 1.13, df = 4, 23; P = 0.370) or *T. planipennisi* (F = 0.10, df = 4, 23; P = 0.9845).

3.3. Rates of host parasitism

In Michigan (Fig. 3**A**), the mean EAB larval parasitism rate by *S. galinae* in pole-size trees was 29.1%, which was significantly higher than in saplings (9.9%). In contrast, the mean EAB larval parasitism rate by *T. planipennisi* was significantly higher in saplings (58.4%) than in pole-size trees (10.5%). Tree-size class (pole-size trees vs. saplings) had a highly significant effect on EAB larval parasitism rates by both *S. galinae* (log likelihood ratio χ^2 = 17.91, df = 1, P < 0.001) and *T. planipennisi* (log likelihood ratio χ^2 = 87.13, df = 1, P < 0.0001), whereas study site also had a significant effect for *S. galinae* (log likelihood ratio χ^2 = 16.46, df = 1, P = 0.0056) but not for *T. planipennisi* (log likelihood ratio χ^2 = 5.40, df = 1, P = 0.3686).

In the Northeast (Fig. 3**B**), tree-size class also had a significant effect on EAB larval parasitism rate by *S. galinae* (log likelihood ratio χ^2 = 5.80, df = 2, P = 0.0550) and *T. planipennisi* (log likelihood ratio χ^2 = 55.62, df = 2, P < 0.0001), whereas there were significant differences among study sites for parasitism rates by *S. galinae* (log-likelihood ratio χ^2 =

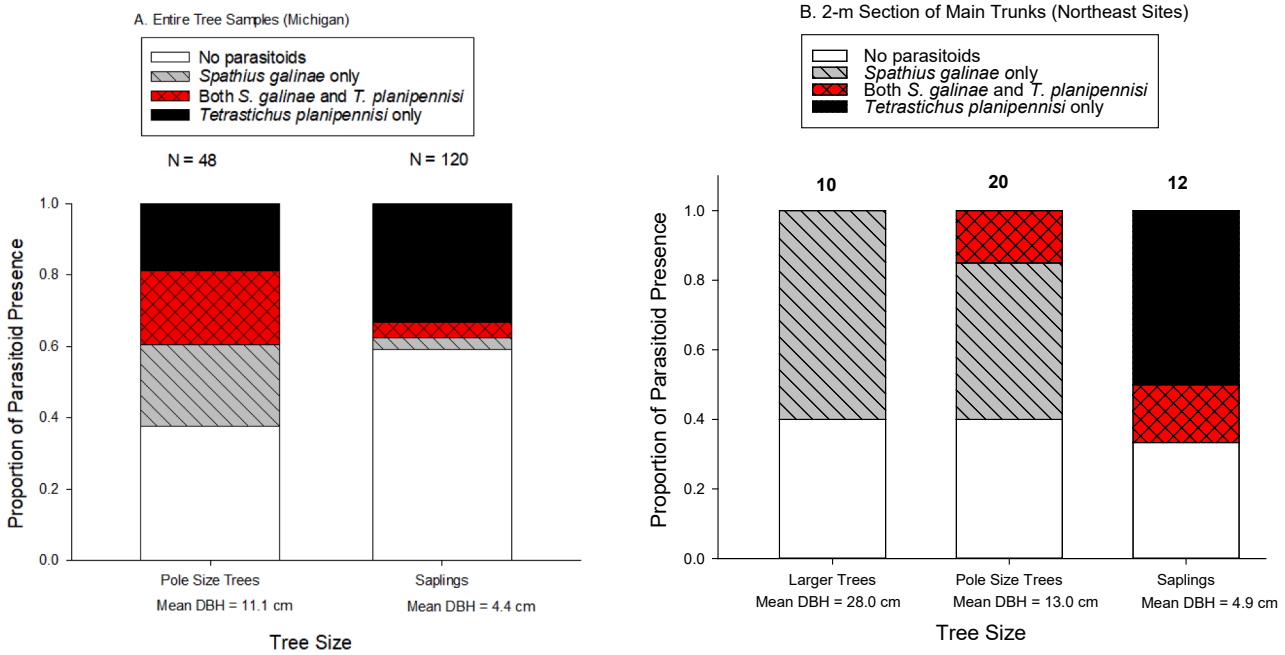


Fig. 1. Proportion of trees that contained at least one parasitoid brood (presence) of either *Spathius galinae* alone, *Tetrastichus planipennisi* alone, both species together, or neither species (absence) in sampled entire trees in Michigan (A) or sections of main trunks from the basal 2-m sections in the Northeast (B). Numbers at the top of bars are the sample size (number of sampled trees or saplings).

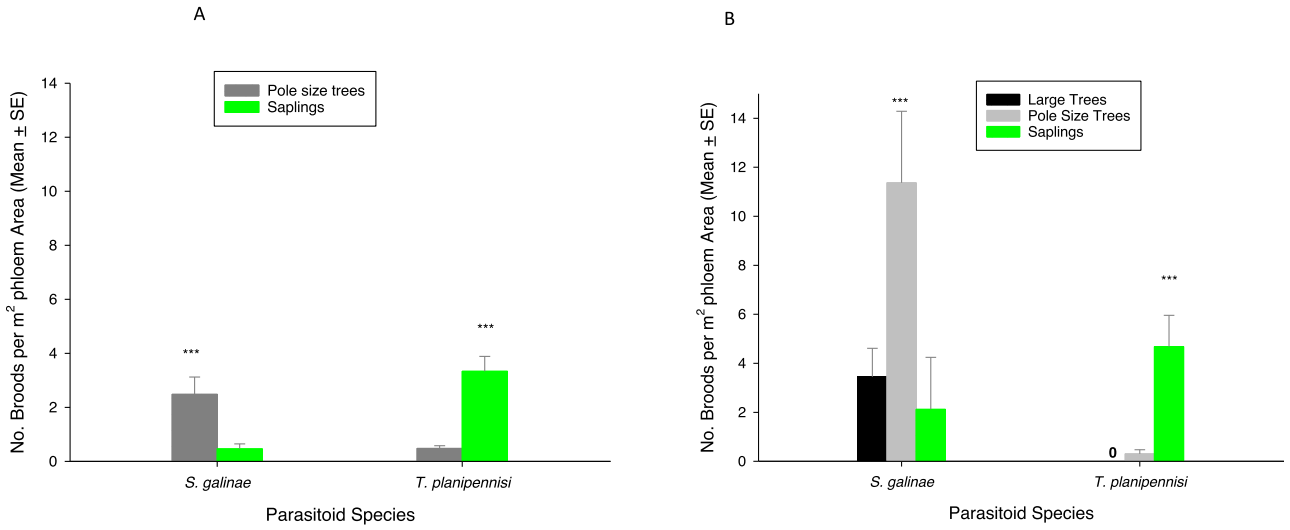


Fig. 2. Mean parasitoid density (no. broods per m^2 of sampled phloem area) in trees of different size classes in Michigan (A) and in the basal 2-m sections of trees in the Northeast (B). Triple asterisks indicate highly significant difference at $\alpha = 0.001$ error rate (ANOVA and lest square student t-tests).

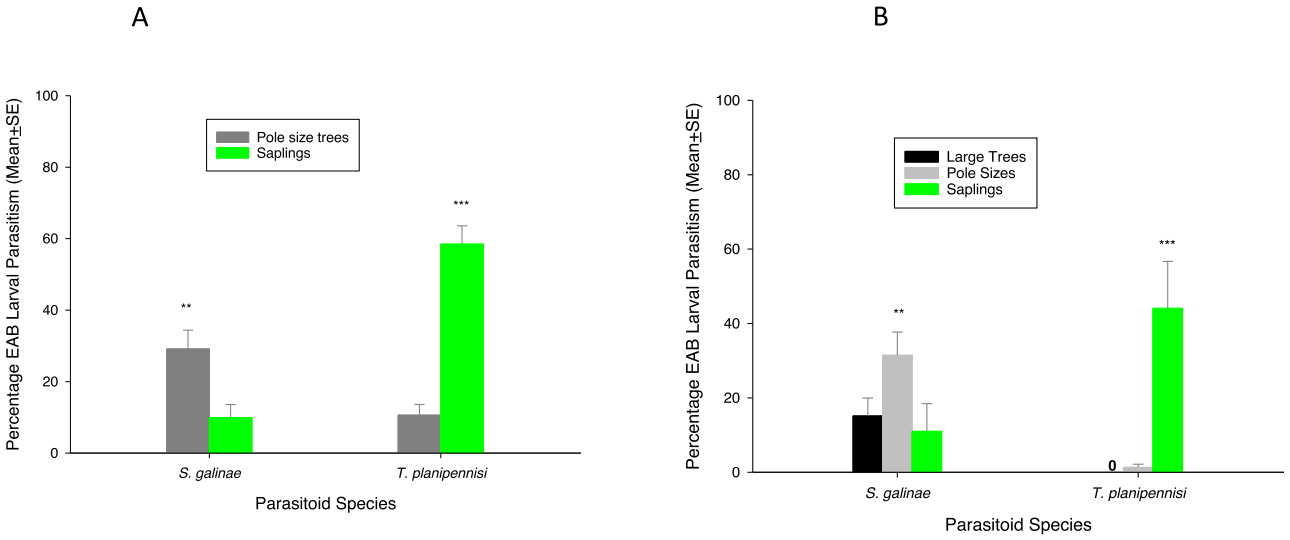


Fig. 3. Mean (%) rates of EAB larval parasitism by *S. galinae* and *T. planipennisi* in different size classes of trees in Michigan (A) and in the basal 2-m sections of trees in the Northeast (B). Within each parasitoid species, a single asterisk indicates a significant difference among tree-size classes at $\alpha \leq 0.05$ error rate; double asterisks indicate moderate significant difference at $\alpha \leq 0.01$ error rate; Triple asterisks indicate highly significant difference at $\alpha \leq 0.001$ error rate (Log-likelihood ratio Chi-square tests based on generalized linear model for logistic regression analysis).

14.31, df = 4, P = 0.0064) but not by *T. planipennisi* (log-likelihood ratio $\chi^2 = 3.74$, df = 4, P = 0.4418). EAB larval parasitism in the 2-m basal sections followed a similar pattern among different tree-size classes as in Michigan for both parasitoid species. Mean EAB larval parasitism rates by *S. galinae* across the study sites were significantly higher in the 2-m basal sections of pole-size trees (31.4%) than in either large-size trees (15.1%) or saplings (11.1%). While no EAB larval parasitism by *T. planipennisi* was observed in 2-m basal sections of large trees, EAB larval parasitism in saplings (44.6%) was 34 times higher than in pole size trees (1.31%).

3.4. Distribution of host larvae, parasitoids, and parasitism rates in different sections of sampled trees

In Michigan, the number of EAB larvae per 1-m section of pole-size tree or sapling decreased significantly with increasing height above the ground (Fig. 4**A**: slope = −0.51; t = −4.69, P < 0.0001) while the number of *S. galinae* broods per 1-m section decreased only slightly with height in sampled trees (Fig. 4**B**: slope = −0.13, t = −1.67; P = 0.0972). Similarly, the number of *T. planipennisi* broods showed little change in relation to height of sample section (Fig. 4**C**: slope = −0.02, t = −1.19, P = 0.2373). In saplings, as in pole-sized trees, EAB larval abundance also decreased significantly with increased height above ground (Fig. 4**D**: slope = −0.6620225, t = −2.48, P = 0.0149); however, there were no significant reductions in the number of *S. galinae* (Fig. 4**E**: slope = −0.0994382, t = −1.25, P = 0.2513) or *T. planipennisi* (Fig. 4F: slope = −0.23, t = −1.38, P = 0.1699) parasitoid broods at greater heights above ground. Nor were there any significantly relationships detected for host attack (parasitism) rates at each 1-meter section with the height of samples in either pole size trees (Fig. 5**AB**) or saplings (Fig. 5**CD**) by both *S. galinae* (Fig. 5**A**: log likelihood ratio $\chi^2 = 1.54$, df = 1, P = 0.2124; Fig. 5**C**: log likelihood ratio $\chi^2 = 0.63$, df = 1; P = 0.4281) and *T. planipennisi* (Fig. 5**B**: log likelihood ratio $\chi^2 = 0.30$, df = 1; P = 0.5834; Fig. 5**D**: log likelihood ratio $\chi^2 = 0.73$, df = 1; P = 0.3943).

Further linear regression analyses showed that the abundance of *S. galinae* broods (=number of hosts attacked) in pole size trees had a

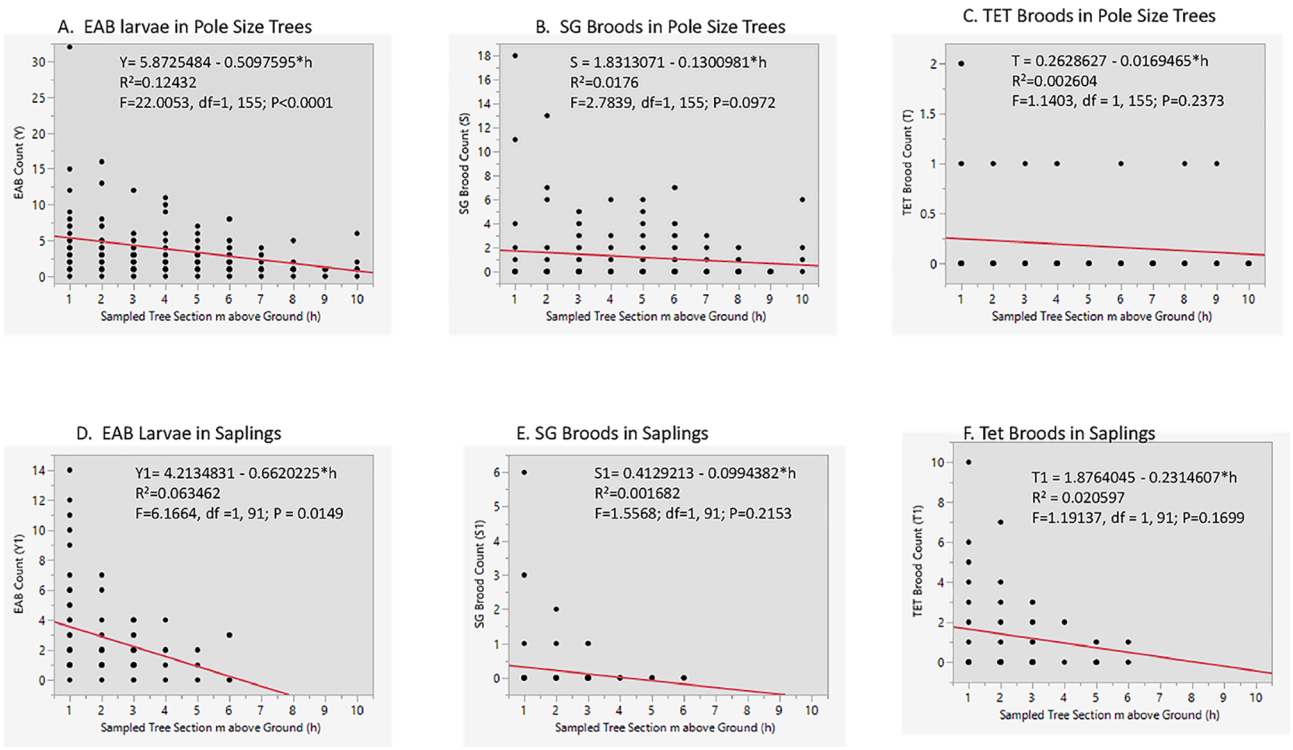


Fig. 4. Relationship between abundance (count) of EAB larvae and broods of *S. galinae* (SG) or *T. planipennisi* (TET) and height above the ground observed in each 1-m section from pole-size trees (A, B, C) and saplings (D, E, F) sampled in Michigan.

highly significant, positive relationship with EAB larval abundance in the sampled tree section (Fig. 6**A**: slope = 0.54418, t = 16.79, P < 0.0001), indicating that the abundance of *S. galinae* broods is related to host larval abundance in a given 1-m section sample of pole size trees. However, for *T. planipennisi* in pole-sized trees, there was no significant, positive relationship between parasitoid abundance (=number of hosts attacked) and EAB larval abundance (Fig. 6**B:** slope = 0.00081, t = 0.08, P = 0.9353). In saplings, conversely, there was no strong relationship between *S. galinae* abundance and EAB larval abundance (Fig. 6**C**: slope = 0.0298; t = 0.98, P = 0.3304); however, for *T. planipennisi* in saplings, there was a highly significant, positive relationship of parasitoid abundance and EAB larval abundance (Fig. 6**D**, slope = 0.3939; t = 7.98, P < 0.0001), indicating strong dependence of *T. planipennisi* abundance on EAB larval abundance in a given 1-m section sample of saplings.

4. Discussion

Our study provides strong field evidence for niche partitioning and coexistence of two specialist parasitoids, in the same feeding guild, *S. galinae* and *T. planipennisi*, recently introduced for biological control of the invasive tree pest *A. planipennis* in 12 hardwood forests in the Midwest and the Northeast U.S., where they were either sequentially or simultaneously released 2–5 years earlier. Results show that the two recently introduced EAB larval parasitoids, *S. galinae* and *T. planipennisi*, have established coexisting populations at all release sites. Their ability to partition the niche is demonstrated by the strong differentiation in their probability of presence, abundance, and/or host attack rates in ash trees of different size classes, with *S. galinae* parasitism being more frequent in larger diameter and pole size trees and *T. planipennisi* being dominant in saplings. Although host larval abundance (per 1 m section sample) appears to decrease with the height of a sampled tree or sapling, possibly because of the reduction in the tree phloem area (Timms et al., 2006), host attack rates and abundance of the parasitoid broods for both *S. galinae* and *T. planipennisi* are not significantly affected by the height of sampled trees or saplings. Instead, the abundance of the parasitoid broods in a given 1 m section sample in a tree or saplings is strongly correlated to the EAB larval abundance in that sample section of their preferred tree-size classes (pole size trees for *S. galinae* and saplings for *T. planipennisi*). These findings strongly suggest that *S. galinae* and *T. planipennisi* specialize on seeking EAB-larval hosts within different tree-size classes, and thus complement each other in providing additive rather than antagonistic control of EAB populations in North America.

It is well documented that host habitat heterogeneity influences the competition and coexistence of competing insect predators and parasitoids (e.g., Palmer, 2003; Vanbergen et al., 2006; Paranhos et al., 2013; Harvey et al., 2013). Abell et al. (2012) showed that EAB larval parasitism rates by *T. planipennisi* in both Northeast Asia and Michigan decreased significantly with the increases in DBH of EAB-infested ash trees, reaching nearly zero in trees of 15 cm or greater in DBH. Simplified laboratory studies also showed that parasitism rates by *T. planipennisi* were affected by the size of host-infested logs used in the experiments (Abell et al., 2012; Wang et al., 2015), with significantly higher rates of host attacks in small (3–5 cm in diameter) ash logs than in larger (8–10 cm) ones. However, no significant differences in host attack rates by *S. galinae* were observed in this laboratory study between small (3–5 cm in diameter) and large (8–10 cm in diameter) ash logs infested with late instars of EAB larvae (Wang et al., 2015). Divergent patterns of host attack between *S. galinae* and *T. planipennisi* have been attributed to differences in ovipositor length (Abell et al., 2012; Wang et al., 2015;). The length of the ovipositor in *T. planipennisi* ranges from 1.9 to 2.6 mm (Duan and Oppel, 2012), and thus this short length prevents female wasps from reaching EAB larvae infesting ash trees > 15 cm DBH (Abell et al., 2012). In contrast, the length of the ovipositor in *S. galinae* females ranges from 3.5 to 5.3 mm (Belokobylskij et al., 2012; Watt and Duan, 2014), and this length allows the females of *S. galinae* to attack host larvae in much larger infested trees, even those >36 cm DBH (Murphy et al., 2017). Although our field data confirm the inverse relationship of host attack rates with the size category of host-infested trees by *T. planipennisi*, our results showed that the host attack rates by *S. galinae* had a positive relationship with tree size, with higher parasitism rates in

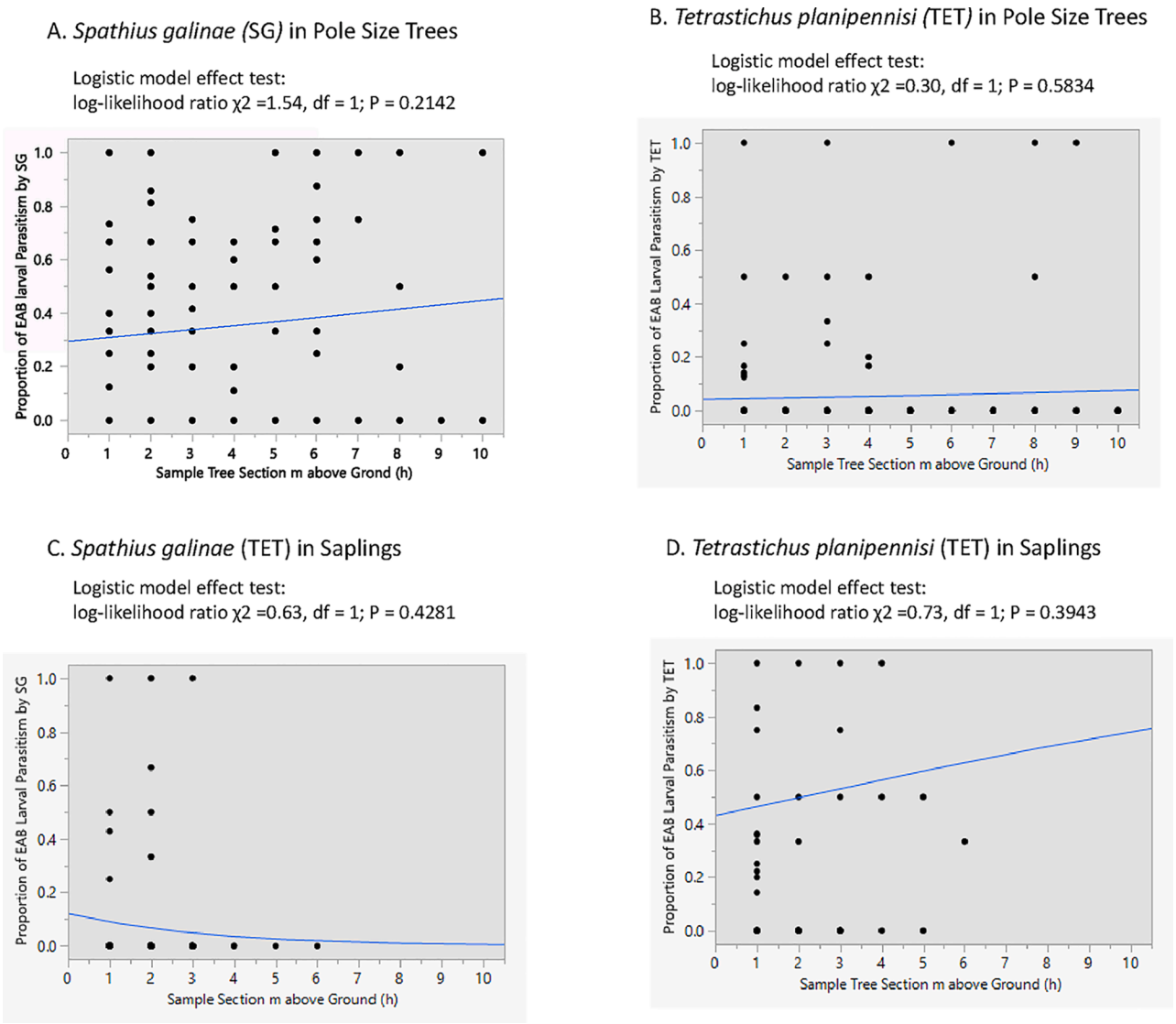


Fig. 5. Relationship between parasitism (host attack) rates by *S. galinae* or *T. planipennisi* at each 1-m section and the height of entire pole-size trees (A, B) and saplings (C, D) sampled in Michigan.

large or pole-size trees than in saplings. This is a bit surprising because the length of ovipositor in *S. galinae* should have allowed adult wasps to reach EAB larvae infesting saplings (with thinner bark) as well as those infesting large or pole size trees. However, this also reinforces the hypothesis that both parasitoid species have distinct niche partitioning among different sizes of ash trees. The reduced host attack rates by *S. galinae* in saplings may have resulted from the contemporary competition with *T. planipennisi* following their field releases at the same sites or simply represents the product of evolutionary processes that had ready shaped the host utilization pattern of *S. galinae* (i.e., preferring to forage on large, host-infested trees) in its native range (Northeast Asia) before the species' introduction to North America for EAB biocontrol.

Data collected within each meter section of an entire pole size tree or a sapling showed significant reductions in EAB larval abundance with increased height in the tree of the samples, but no significantly strong relationships between the abundance of parasitoid broods or EAB larval parasitism with the height of the samples for either *S. galinae* or *T. planipennisi*. Even though bark thickness decreases in meter sections higher above the ground (Abell et al., 2012; Murphy et al., 2017), which should facilitate parasitoid attack, our data showed that height above the ground did not significantly affect parasitoid brood abundance or number of host attacks by either *S. galinae* or *T. planipennisi.* These observations suggest that host niche differentiation between *S. galinae* and *T. planipennisi* may not occur within sections of a given EAB-infested tree or sapling, rather among trees of different size classes. Mechanisms leading to selection of host-infested trees of different size (DBH) classes by these two larval parasitoids for niche differentiations remain unknown and require further investigation.

Previous laboratory studies demonstrated low levels (≤3.6%) of multi-parasitism of EAB larvae by *S. galinae* and *T. planipennisi* when 16 gravid females of each parasitoid species were confined together with low densities of four EAB larvae infesting a small ash log in a small (30 × 30 × 30 cm) rearing containers (Wang et al., 2015). Although exploitative competition between *S. galinae* and *T. planipennisi* progeny from multiple parasitism of the same host larva leads to the failure of the successful development of both species, such competitive interactions in nature seem to be rare because adults of both parasitoids can discriminate healthy larvae from previously parasitized ones, greatly reducing the chance of intrinsic competition (Yang et al., 2012; Wang et al., 2015). Moreover, both *S. galinae* and *T. planipennisi* were collected from EAB-infested green ash trees (Mean DBH = 7.4–10.5) in the Vladivostok area of the Russian Far East (Duan et al. 2012), indicating that these two EAB larval parasitoids overlap in their native range (Northeast Asia). Niche differentiation of *S. galinae* and *T. planipennisi*, as evidenced by

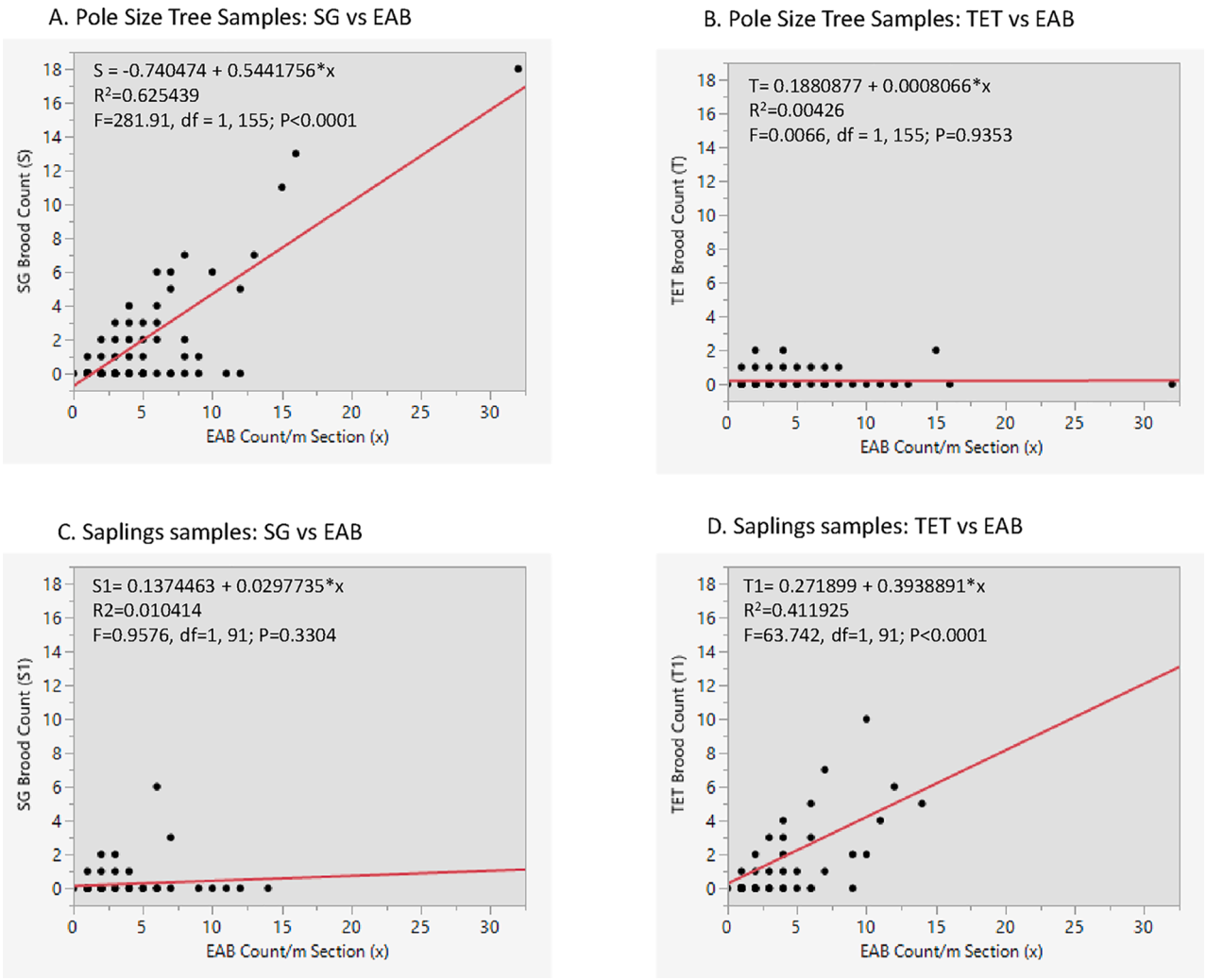


Fig. 6. Relationship between *S. galinae* or *T. planipennisi* brood abundance (number of broods) and EAB larvae (number) observed at each 1-m section of pole-size trees (A, B) and saplings (C, D) sampled in Michigan. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

their presence, abundance, and host attack rates among different tree size classes in the forests where both species co-occur, further indicates that the competitive interactions between them, if any, are reduced by the size heterogeneity of EAB-infested trees.

Niche partitioning patterns in natural communities can result from local competition (e.g., competitive displacement) within a contemporary time frame, or they may represent the end products of evolutionary (or historical) processes acting over longer time frames (Reitz and Tumble, 2002; Palmer, 2003; Finke and Snyder, 2008; Augustyn et al., 2016). Despite the potential for competition among specialist parasitoids sharing the same feeding guild in simplified laboratory experiments (e.g., Yang et al., 2012, 2013; Wang et al., 2015), opportunity or timeframe for *T. planipennisi* and *S. galinae* to interact in the field in both Midwest and Northeast U.S. has been rather short, approximately 2–5 years post field releases that were made either sequentially (in Michigan) or simultaneously (northeast states). Earlier field studies conducted in the same sites in Michigan prior to releases of *S. galinae* documented much higher levels of EAB parasitism rates by *T. planipennisi* on saplings than on pole-size trees (Duan et al., 2015, 2017), suggesting that *T. planipennisi's* preference for attacking hosts on saplings occurred before the later releases of *S. galinae* in those sites. In addition, the two parasitoid species have drastic differences in the length of their ovipositors, clutch size, mode of host parasitism (eternal vs. internal) and other behavioural or biological attributes that facilitate their differentiations in host attack and utilization (Duan and Oppel, 2012; Abell et al., 2012; Duan et al., 2011, 2014; Murphy et al., 2017). Thus, we postulate that the success in niche partitioning within such a short time period following their sequential releases in Michigan or simultaneous releases in northeast U.S. (Connecticut, Massachusetts, New York) likely represents the end product of their historical interactions in their native range. Assuming that candidate parasitoids have already evolved sufficient differences in morphology, biology and behaviour from their long historical interactions that promote host niche partitioning and coexistence in newly introduced regions, as suggested by theoretical models (Pedersen and Mills, 2004), our field study demonstrates that multiple species of specialist parasitoids of the same feeding guild may potentially be introduced, could co-exist, and complement each other for classical biological control of an invasive pest.

Acknowledgments

U.S. Department of Agriculture (USDA) is an equal opportunity provider and employer. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture. We thank Jennifer Chandler (University of Massachusetts), Amanda Stout (USDA ARS BIIRU) for assistance in field work in Michigan, Connecticut, Massachusetts and New York. We also

thank, Massachusetts Department of Conservation, Connecticut Department of Agriculture, Michigan Department of Natural Resource and Donald Dubac and his family members in New York for permission to work in their forests for our study. Dan Gruner (University of Maryland) and Kim Hoelmer (USDA Agricultural Research Service) provided helpful comments on an early version of this manuscript. This work was partly supported by the USDA Farm Bill Program through Interagency Agreement with USDA ARS (IRA# 60-8010-9-001) and partly supported by Agricultural Research Service Appropriated Base-Funds (CRIS # 8010-22000-028D).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2021.104698.

References

Alyokhin, A., Sewell, G., 2004. Changes in a ladybeetle community following the establishment of three alien species. Biol. Invasions 6 (4), 463–471.

Abell, K.J., Duan, J.J., Bauer, L., Lelito, J.P., Van Driesche, R.G., 2012. The effect of bark thickness on host partitioning between *Tetrastichus planipennisi* (Hymen.: Eulophidae) and *Atanycolus* spp. (Hymen.: Braconidae), two parasitoids of emerald ash borer (Coleop.: Buprestidae). Biol. Control 63 (3), 320–325.

Abell, K.J., Bauer, L.S., Duan, J.J., Van Driesche, R., 2014. Long-term monitoring of the introduced emerald ash borer (Coleoptera: Buprestidae) egg parasitoid, *Oobius agrili* (Hymenoptera: Encyrtidae), in Michigan, USA and evaluation of a newly developed monitoring technique. Biol. Control 79, 36–42.

Augustyn, W.J., Anderson, B., Ellis, A.G., Hambäck, P., 2016. Experimental evidence for fundamental, and not realized, niche partitioning in a plant–herbivore community interaction network. J. Anim. Ecol. 85 (4), 994–1003.

Bess, H.A., van den Bosch, R., Haramoto, F.H., 1961. Fruit fly parasites and their activities in Hawaii. Proc. Hawaiian Entomol. Soc. 17, 367–378.

Belokobylskij, S.A., Yurchenko, G.I., Strazanac, J.S., Zaldívar-Riverón, A., Mastro, V., 2012. A new emerald ash borer (Coleoptera: Buprestidae) parasitoid species of *Spathius* Nees (Hymenoptera: Braconidae: Doryctinae) from the Russian Far East and South Korea. Ann. Entomol. Soc. Am. 105, 165–178.

Bonsall, M.B., Hassell, M.P., Asefa, G., 2002. Ecological trade-offs, resource partitioning, and coexistence in a host–parasitoid assemblage. Ecology 83, 925–934.

Bauer, L.S., Duan, J.J., Gould, J.G., Van Driesche, R.G., 2015. Progress in the classical biological control of *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) in North America. Can. Entomol. 147, 300–317.

DeBach, P., 1966. The competitive displacement and coexistence principles. Annu. Rev. Entomol. 11, 183–212.

Duan, J.J., Oppel, C.B., 2012. Critical rearing parameters of *Tetrastichus planipennisi* (Hymenoptera: Eulophidae) as affected by host-plant substrate and host-parasitoid group structure. J. Econ. Entomol. 105, 792–801.

Duan, J.J., Oppel, C.B., Ulyshen, M.D., Bauer, L.S., Lelito, J.P., 2011. Biology and life history of *Tetrastichus planipennisi* (Hymenoptera: Eulophidae), a larval endoparasitoid of the emerald ash borer (Coleoptera: Buprestidae). Florida Entomol. 94, 933–940.

Duan, J.J., Yurchenko, G., Fuester, R., 2012. Occurrence of emerald ash borer (Coleoptera: Buprestidae) and biotic factors affecting its immature stages in the Russian Far East. Environ. Entomol. 41 (2), 245–254.

Duan, J.J., Bauer, L.S., Abell, K.J., Lelito, J.P., van Driesche, R.G., 2013. Establishment and abundance of *Tetrastichus planipennisi* (Hymenoptera: Eulophidae) in Michigan: potential for success in classical biocontrol of the invasive emerald ash borer (Coleoptera: Buprestidae). J. Econ. Entomol. 106, 1145–1154.

Duan, J.J., Watt, T.J., Larson, K., 2014. Biology, life history, and laboratory rearing of *Spathius galinae* (Hymenoptera: Braconidae), a larval parasitoid of the invasive emerald ash borer (Coleoptera: Buprestidae). J. Econ. Entomol. 107, 939–946.

Duan, J.J., Bauer, L.S., Driesche, R.G.V., 2017. Emerald ash borer biocontrol in ash saplings: The potential for early stage recovery of North American ash trees. For. Ecol. Manage. 394, 64–72.

Duan, J.J., Bauer, L.S., Abell, K.J., Ulyshen, M., Driesche, R.G.V., 2015. Population dynamics of an invasive forest insect and associated natural enemies in the aftermath of invasion: implications for biological control. J. Appl. Ecol. 52, 1246–1253.

Duan, J.J., Bauer, L.S., Driesche, R.G.V., Gould, J.R., 2018. Progress and challenges of protecting North American ash yrees from the emerald ash borer using biological control. Forests 9, 14. https://doi:10.3390/f9030142.

Duan, J.J., Driesche, R.G.V., Crandall, R.S., Schmude, J.M., Rutledge, C.E., Slager, B.H., Gould, J.R., Elkinton, J.S., 2019. Establishment and early impact of *Spathius galinae* (Hymenoptera: Braconidae) on emerald ash borer (Coleoptera: Buprestidae) in the Northeastern United States. J. Econ. Entomol. 112, 2121–2130.

Duan, J.J., Bauer, L.S. Driesche, R.G.V, Schmude, J.M., Petrice, T., Chandler, J.L., Elkinton, J. 2020. Effects of extreme low winter temperatures on the overwintering survival of the introduced larval parasitoids Spathius galinae and Tetrastichus planipennisi: Implications for biological control of emerald ash borer in North America. J. Econ. Entomol. 113, 1145–1151. https://doi.org/10.1093/jee/toaa048.

Evans E.W., 2004. Habitat displacement of North American ladybirds by an introduced species. Ecology, 85, 637–647.

Ehler, L.E., 1985. Species-dependent mortality in a parasite guild and its relevance to biological control. Environmental Entomology 14, 1–6.

Ehler, L.E., 1990. Introduction strategies in biological control of insects. In: Mackauer, M., Ehler, L.E., Roland, J. (Eds.), Critical Issues in Biological Control. Andover, UK, Intercept, pp. 111–134.

Federal Register, 2007. Availability of an environmental assessment for the proposed release of three parasitoids for the biological control of the emerald ash borer Agrilus planipennis in the Continental United States. Federal Register 2007, 72, 28947–28948. https://www.regulations.gov/docket?D=APHIS-2007-0060 (Accessed 28 December 2020).

Federal Register, 2015. Field release of the parasitoid Spathius galinae for the biological control of the emerald ash borer (Agrilus planipennis) in the contiguous United States: environmental assessment. Federal Register 2015, 80, 7827–7828. https://www.regulations.gov/docket?D=APHIS-2014-0094 (Accessed 28 December 2020).

Finke, D.L., Snyder, W.E., 2008. Niche partitioning increases resource exploitation by diverse communities. Science 321, 1488–1490.

Hardin, G., 1960. The competitive exclusion principle. Science 131, 1292–1297.

Harvey, J.A., Poelman, E.H., Tanaka, T., 2013. Intrinsic inter- and intraspecific competition in parasitoid wasps. Annu. Rev. Entomol. 58, 333–351.

Herms, D.A., McCullough, D.G., 2014. Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Annu. Rev. Entomol. 59, 13–30.

Jennings, D.E., Duan, J.J., Bean, D., Gould, J.R., Rice, K.A., Shrewsbury, P.M., 2016. Monitoring the establishment and abundance of introduced parasitoids of emerald ash borer larvae in Maryland. Biol. Control 101, 138–144.

Jones, M.I., Gould, J.R., Mahon, H.J., Fierke, M.K., 2020. Phenology of emerald ash borer (Coleoptera: Buprestidae) and its introduced larval parasitoids in the Northeastern United States. J. Econ. Entomol. 113, 622–632.

McCullough, D.G., Siegert, N.W., 2007. Estimating potential emerald ash borer (Coleoptera: Buprestidae) populations using ash inventory data. J. Econ. Entomol. 100, 1577–1586.

Mills, N.J., 2003. Parasitoid interactions and biological control. In: R. G. van Driesche ed. Proceedings of the 1st International Symposium on Biological Control of Arthropods. pp. 108–113. U.S. Dep. Agric., Forest Service, Washington, DC.

Murdoch, W.W., Briggs, C.J., 1996. Theory for biological control: recent development. Ecology 77, 2001–2013.

Murdoch, W.W., Briggs, C.J., Nisbet, R.M., 1996. Competitive displacement and biological control in parasitoids: A model. Am. Nat. 148, 807–826.

Murphy, T.C., Driesche, R.G.V., Gould, J.R., Elkinton, J.S., 2017. Can *Spathius galinae* attack emerald ash borer larvae feeding in large ash trees? Biol. Control 114, 8–13.

Pedersen B.S., Mills, N.J., 2004. Single vs. multiple introduction in biological control: the roles of parasitoid efficiency, antagonism and niche overlap. J. Appl. Ecol.ss 41, 973–984.

Palmer, T.M., 2003. Spatial habitat heterogeneity influences competition and consistence in an African acacia ant guild. Ecology 84, 2843–2855.

Pekas, A., Tena, A., Harvey, J.A., Garcia-Marí, F., Frag, F., 2016. Host size and spatiotemporal patterns mediate the coexistence of specialist parasitoids. Ecology 97, 1345–1356.

Poland, T.M., McCullough, D.G., 2006. Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. J. Forest. 104, 118–124.

Paranhos, B.J., Sivinski, J., Stuhl, C., Holler, T., Aluja, M., 2013. Intrinsic competition and competitor-free-space influence the coexistence of parasitoids (Hymenoptera: Braconidae: Opiinae) of neotropical Tephritidae (Diptera). Environ. Entomol. 42 (4), 717–723.

Reitz, S.R., Trumble, J.T., 2002. Competitive displacement among insects and arachnids. Annu. Rev. Entomol. 47, 435–465.

Ragozzino, M, Meyer, R. Duan, J. J. Slager, B. Salom S. 2020. Differences in early season emergence and reproductive activity between Spathius agrili (Hymenoptera: Braconidae) and Spathius galinae, larval parasitoids of the invasive emerald ash borer (Coleoptera: Buprestidae). Environ. Entomol. 49, 334–341.

Sall, J., Lehman, A., Stephens, M, Loring S. 2017. JMP® Start Statistics: A Guide to Statistics and Data Analysis Using JMP®, Sixth Edition. SAS Institute Inc., SAS Campus Drive, Gary NC 2751, USA.

SAS Institute 2020. JMP®, Pro 15.10. SAS Institute Inc., Cary, NC, USA.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ.

Timms, L.L., Smith, S.M., de Groot, P., 2006. Patterns in the within-tree distribution of the emerald ash borer *Agrilus planipennis* (Fairmaire) in young, green ash plantations of south-western Ontario, Canada. Agric. For. Entomol. 8 (4), 313–321.

Turnbull, A.L., 1967. Population dynamics of exotic insects. Bull. Entomol. Soc. Am. 13, 333–337.

Turnbull, A.L., Chant, D.A., 1961. The practice and theory of biological control of insects in Canada. Can. J. Zool. 39 (5), 697–753.

Ulyshen, M.D., Duan, J.J., Bauer, L.S., 2010. Interactions between *Spathius agrili* (Hymenoptera: Braconidae) and *Tetrastichus planipennisi* (Hymenoptera: Eulophidae), larval parasitoids of *Agrilus planipennis* (Coleoptera: Buprestidae). Biol. Control 52 (2), 188–193.

Vanbergen, A.J., Hails, R.S., Watt, A.D., Jones, T.H., 2006. Consequences for host–parasitoid interactions of grazing-dependent habitat heterogeneity. J. Anim. Ecol. 75 (3), 789–801.

Watt, K.E.F., 1965. Community stability and the strategy of biological control. Can. Entomol. 97, 887–895.

Watt, T.J., Duan, J.J., 2014. Influence of host age on critical fitness parameters of *Spathius galinae* (Hymenoptera: Braconidae), a new parasitoid of the emerald ash borer (Coleoptera: Buprestidae). J. Econ. Entomol. 107, 1320–1329.

Wang, X.-Y., Jennings, D.E., Duan, J.J., 2015. Trade-offs in parasitism efficiency and brood size mediate parasitoid coexistence, with implications for biological control of the invasive emerald ash borer. J. Appl. Ecol. 52, 1255–1263.
Wang, X.Y., Cao, L.M., Yang, Z.Q., Duan, J.J., Gould, J.R., Bauer, L.S., 2016. Natural enemies and their impacts on emerald ash borer populations in its native range, with new records of parasitism by two species of beetles. Can. Entomol. 148, 329–342.
Yang, S., Duan, J.J., Watt, T., Abell, K.J., van Driesche, R.G., 2012. Responses of an idiobiont ectoparasitoid, *Spathius galinae* (Hymen.: Braconidae), to host larvae parasitized by the koinobiont endoparasitoid *Tetrastichus planipennisi* (Hymen.: Eulophidae): implications for biological control of emerald ash borer (Coleop.: Buprestidae). Environ. Entomol. 41, 925–932.
Yang, S., Duan, J.J., Lelito, J., Van Driesche, R., 2013. Multiparasitism by *Tetrastichus planipennisi* (Hymenoptera: Eulophidae) and *Spathius agrili* (Hymenoptera: Braconidae): Implication for Biological Control of the Emerald Ash Borer (Coleoptera: Buprestidae). Biol. Control 65 (1), 118–123.