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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)

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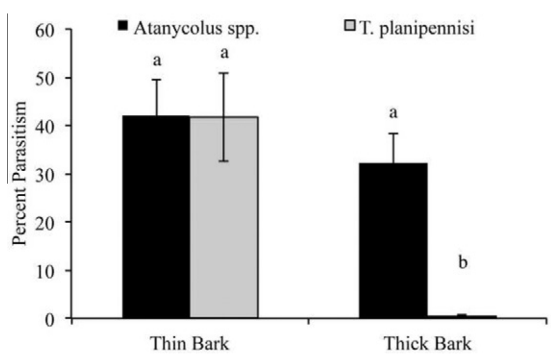
HIGHLIGHTS

- ▶ Parasitoid ovipositor length limits bark thickness that can be penetrated.
- ▶ *Tetrastichus planipennisi* did not parasitize EAB in trees with bark thicker than 3.2 mm.
- ▶ *Atanycolus* spp. parasitized EAB in trees with bark up to 8.8 mm thick.
- ▶ *T. planipennisi* is unlikely to establish or be effective in medium to mature aged ash.
- ▶ *T. planipennisi* should be released in young or regenerating ash stands.

GRAPHICAL ABSTRACT



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ABSTRACT

Parasitoids have recently been introduced from Asia to aid in biological control in the United States of the invasive, highly damaging, emerald ash borer, *Agrilus planipennis*. Three introduced parasitoids have established and field biological studies are underway to improve our understanding of niche partitioning among them. Here we report one such investigation, a field experiment conducted to determine how outer bark thickness of ash trees might affect parasitism by one introduced (*Tetrastichus planipennisi*) and one native parasitoid (*Atanycolus* spp.). We found that *T. planipennisi* was unable to parasitize EAB larvae in trees with outer bark thicker than 3.2 mm (>11.2-cm DBH) whereas *Atanycolus* spp. parasitized EAB larvae in ash trees with outer bark up to 8.8 mm thick (>57.4-cm DBH). These results suggest that establishment of, and control by *T. planipennisi* at release sites with only large diameter trees is less likely, and that *T. planipennisi* will be more effective in stands with younger trees (<12-cm DBH). Releasing *T. planipennisi* near the leading edge of EAB invasion may have little impact on EAB populations if many ash trees are too large. We recommend releasing *T. planipennisi* in stands dominated by small, early successional or regenerating ash trees. This may maximize the establishment and effectiveness of this species. This limitation of *T. planipennisi* for biological control of emerald ash borer suggests that other EAB parasitoids from its native range with longer ovipositors, such as *Spathius galinae* (Hymenoptera: Braconidae), should be sought and evaluated for possible use as EAB biocontrol agents in the US. The results of this study also suggest the importance of parasitoid guild introduction for biological control in general, and hint at possible broader implications relating to resource partitioning among native and introduced parasitoids.

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1. Introduction

Emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), is an invasive wood-boring beetle native to Asia responsible for the death of tens of millions of ash trees (*Fraxinus* spp.) in North America (Haack et al., 2002; MacFarlane and Meyer, 2005; Poland and McCullough, 2006; Kovacs et al., 2010). Although EAB arrived in southeast Michigan from China in solid-wood packing materials during the 1990s, it was not discovered until 2002 (Bray et al., 2011; Siegert et al., 2008). After extensive research on EAB natural enemies in both North America and China, limited environmental release of three EAB parasitoid species native to China began in Michigan in 2007, launching the USDA EAB biological control program (Bauer et al., 2004, 2005, 2008, 2009, 2011; Liu et al., 2003, 2007; Yang et al., 2005, 2006; USDA APHIS, 2007; Wang et al., 2008; Duan et al., 2009; Kula et al., 2010).

The larval endoparasitoid, *Tetrastichus planipennisi* Yang (Hymenoptera: Eulophidae), is one of the three parasitoid species being introduced in the US for EAB biocontrol (USDA APHIS, 2007). The results of recent studies in Michigan show establishment and dispersal of *T. planipennisi* is occurring in southern Michigan, although prevalence remains lower than in areas of China and Russia where it is native (Liu et al., 2003, 2007; Duan et al., 2010; Duan et al., 2011, 2012a,b). At our Michigan biocontrol release sites, these findings are to be expected since relatively few *T. planipennisi* were released and only recently (2007–2009). Parasitism of EAB by native larval ectoparasitoids in the genus *Atanycolus* (Hymenoptera: Braconidae), however, has shown a sharp and unexpected increase over a two-year sampling period at these and other Michigan study sites (Cappaert and McCullough, 2009; Duan et al., 2011, 2012a). Apparently some or all species of *Atanycolus* have a relatively broad host range within the genus *Agrilus*, and can utilize the abundant host resource found in Michigan's EAB-infested ash trees (Taylor et al., 2012).

At our Michigan EAB biocontrol release sites, we recently found larval parasitism by *T. planipennisi* was more common in smaller ash trees, whereas parasitism by *Atanycolus* spp. was not, suggesting bark thickness as a factor in host partitioning as *T. planipennisi*'s ovipositor ranges in length from 2.0 to 2.5 mm (Duan and Oppel, 2012) and *Atanycolus* spp. range from 4 to 6 mm (Marsh et al., 2009). Since parasitoids of wood-boring beetle larvae must oviposit through the outer bark of trees to reach their hosts, trees with thicker outer bark may reduce or prevent parasitism by certain species, particularly when bark thickness exceeds ovipositor length. Several studies have demonstrated host partitioning mediated by bark thickness for other parasitoids of wood and bark-boring insects (Ryan and Rudinsky, 1962; Ball and Dahlsten, 1973; Goyer and Finger, 1980; Gargiullo and Berisford, 1981; Urano and Hijii, 1995; Hanks et al., 2001; Wang et al., 2007). Similarly, Wang et al. (2007) found that another EAB larval parasitoid, *Spathius agrili* Yang (Hymenoptera: Braconidae), was unable to parasitize EAB in trees with bark thickness greater than 6.5 mm, and that 92% of all parasitism took place at bark thickness between 1 and 4 mm. Ulyshen et al. (2010) speculated that *T. planipennisi* would be restricted to EAB larvae in thin-barked trees, but to date this has not been demonstrated.

To understand successional changes in parasitoid diversity observed during EAB outbreaks in Michigan, we evaluated ovipositor length as a factor in host partitioning between *T. planipennisi*, an introduced parasitoid, and *Atanycolus* spp., a species complex of native parasitoids by caging each on ash trees of varying bark thickness. We hypothesized that *T. planipennisi* would be unable to parasitize emerald ash borer in larger trees where outer bark thickness exceeds ovipositor length and further that *Atanycolus* spp. will be able to successfully parasitize emerald ash borer unreachable by *T. planipennisi.*

2. Methods

2.1. Field trials

In May of 2011, ten thin barked and ten thick barked healthy green ash trees, *Fraxinus pennsylvanica* Marshall, were selected in Maple River State Game Area in Ionia Co., Michigan (43.03N 84.87W) where EAB density was very low based on visual inspection for symptoms of EAB infestation (bark splitting, wood pecker holes, and canopy condition). Trees were selected based on diameter breast height (DBH), with thin barked trees ranging from 5- to 15-cm DBH and thick barked trees ranging from 33- to 53-cm DBH. From June 1 to 9, laboratory-reared EAB eggs were placed around the trunk of each tree at three heights: 1, 2, and 3 m. Eggs were placed at a density of 0.67 per cm DBH (ranging from 6 to 32 eggs) at each height on the tree to create equivalent densities of EAB larvae.

The laboratory-reared EAB eggs were obtained by placing field-captured gravid EAB adults and some males in 473 ml plastic cups whose mouths were covered with screen mesh that was then overlaid with coffee filter paper. Eggs were laid by EAB on the coffee filter paper that was then cut into pieces, each with one to five eggs. Eggs were held in growth chambers at 24 °C and 16:8 h (L:D) photoperiod for 14 days. Small drops of Elmer's glue were placed at the edges of the coffee filter pieces to glue them onto the tree such that the paper was between the eggs and the bark surface. The eggs were covered with tufts of cotton and attached to the trees with tree wrap (Jobe's Tree Wrap, Easy Gardener Products Inc., Waco, TX), which held the eggs flush against the bark surface, facilitating EAB neonate entry into the trunks. The tuft of cotton acted as a cushion and distributed pressure from the tree wrap evenly. On thick-barked trees, where the bark surface was extremely irregular, small squares of outer bark were removed with a chisel to create a flat surface on which to apply each egg.

Eggs were left in place for five weeks, after which the cotton and tree wrap were removed. A 1-m tall cage of organdy cloth was then constructed around the trunk where a group of eggs had been applied. There were three cages per tree, for a total of 60 cages in the experiment. Each cage was constructed by first running a bead of silicone around the tree where the top and bottom of the cage would be, and then placing a strip of foam (Owens Corning Foam Seal-R) over the silicone. The foam and silicone acted to fill in cracks and crevices in the bark to effectively seal each cage to the trunk. Lengths of 12-gauge galvanized bailing wire were then bent into D-shapes and were stapled onto the tree at the center points of each cage to hold the cage material away from the tree surface. Organdy cloth was then wrapped around the tree and cinched tight at the top and bottom with cord over the strips of silicone and foam. Development of EAB larvae was monitored by periodically peeling off the bark of a separate set of trees at the same site inoculated in the same manner and the same time as the experimental trees.

On Aug 15, when the EAB larvae were late 3rd to early 4th instar, adult parasitoids were introduced to each cage. Each cage received either *T. planipennisi* or *Atanycolus* spp. resulting in 15 thick bark tree cages and 15 thin bark tree cages containing each parasitoid species (total of 60 cages). Thin bark tree cages received either approximately 50 *T. planipennisi* or five *Atanycolus* spp., and thick bark tree cages 100 *T. planipennisi* or ten *Atanycolus* spp. A ten-fold difference between the number of *T. planipennisi* and *Atanycolus* spp. used was based on general laboratory observations that parasitism by *T. planipennisi* increases as its density increases and parasitism by *Atanycolus* spp. decreases as its density increases (Duan and Lelito). The F:M sex ratio was 5:1 for these *T. planipennisi* and 1.5:1 for these *Atanycolus* spp. Honey was streaked on each cage once a week as a food source to keep the parasitoids alive as long as possible. The *Atanycolus* spp. used were likely a mixture of *A. cappaerti* Marsh (Hymenoptera: Braconidae) and *A. hicoriae* Shenefelt, which are nearly identical and difficult to distinguish (Marsh et al., 2009). These adult *Atanycolus* spp. were reared from EAB-infested logs collected in southern Lower Michigan. Upon emergence, the *Atanycolus* adults were placed in ventilated cups, provided honey and water, and held in growth chambers at 23 ± 2 °C and 16:8 h (L:D) photoperiod. They ranged in age from one- to six-weeks old when introduced into the field cages. The *T. planipennisi* adults were provided by USDA APHIS-PPQ Emerald Ash Borer Biocontrol Facility (Brighton, MI). *T. planipennisi* were reared in walk-in growth chambers under a 16:8 h (L:D) photoperiod at 26.5 ± 1 °C (day), 22.5 ± 1 °C (night) from on 3rd- and 4th-instar EAB larvae grown inside of green ash bolts. Adult *T. planipennisi* were collected upon emergence from rearing bolts and placed in groups of 50–100 individuals in ventilated cups, and provided honey and water. Adult *T. planipennisi* were between two to three weeks old when placed in the field cages.

In order to allow adequate time for parasitoids to locate and sting EAB larvae, parasitoids were left in cages until September 12 at which time cages were removed. From September 12 to 23, the area under each cage was debarked to recover EAB larvae and determine their fate (alive, dead, or parasitized). All EAB larvae were collected and examined visually in the lab for the presence of parasitoids. EAB larvae that did not initially show signs of parasitism were held and monitored for four weeks for the presence of parasitism. Samples of outer bark were collected from the middle of each cage (3 samples for thick barked trees and 2 for thin barked ones) using a hammer and chisel and were returned to the lab for measurement. Although the thickness of both the ridges and valleys on each outer bark sample was measured using calipers (once at the top and bottom of the cut edge), our resulting analyses and figures used the mean outer bark thickness measured in the valleys only. This mean bark thickness value for each cage was correlated to DBH in order to provide a more practical measure for determination of ash tree suitability for *T. planipennisi*.

2.2. Field surveys of T. planipennisi in North America

The data on percent parasitism by *T. planipennisi* at release sites in Michigan were taken from Duan et al. (2012a), and survey methods are described therein. These data allowed us to determine the DBH of all sampled trees and, as a subset, the DBH of all trees in which broods of *T. planipennisi* were found on green ash trees (*Fraxinus pennsylvanica*). These data of naturally occurring *T. planipennisi* in the wild allowed for a comparison to our findings from the caging experiment to investigate possible caging effects.

2.3. Field surveys of T. planipennisi in its native range

The data on percent parasitism by *T. planipennisi* at study sites near Vladivostok in the Russian Far East and northeast China (Jilin and Liaoning provinces) were taken from Duan et al. (2012b) and Liu et al. (2003), respectively; survey methods are described therein. These data allowed us to determine the DBH of all sampled trees and, as subset, the DBH of all trees in which broods of *T. planipennisi* were found on both green (*F. pennsylvanica*) and Manchurian ash (*F. mandschurica*). This then allowed for a comparison of maximum tree size in which *T. planipennisi* is found where it is native to where it has been introduced (MI).

2.4. Data analysis

A *t*-test was used to determine if there was a significant difference in percent parasitism between *T. planipennisi* and *Atanycolus* spp. in the trees categorized as thin and thick barked. A *P* value of less than 0.05 was considered significant. All analyses were done using SAS Version 9.1 (SAS, 2003).

3. Results

Parasitism by *T. planipennisi* in these EAB-inoculated ash trees did not occur in trees with bark thickness greater than 3.2 mm (Fig. 1) or DBH greater than 11.2 cm (Fig. 4). In contrast, *Atanycolus* spp., in the same experiment, were able to parasitize EAB larvae at all bark thicknesses tested, up to 8.8 mm thick (Fig. 2) and DBH = 57.4 cm (Fig. 4). There was no significant difference ($t = 0.06$, df = 28 $P = 0.9559$) in percent parasitism between *T. planipennisi* and *Atanycolus* spp. in the thin bark treatment; however, in the thick bark treatment *Atanycolus* spp. parasitism rate was significantly higher ($t = 5.15$, df = 28, $P < 0.0001$) than *T. planipennisi* (Fig. 3). Only one EAB larva in the thick bark treatment was parasitized by *T. planipennisi,* and that occurred because the larva had tunneled towards the surface of the bark. There was a strong correlation between outer bark thickness and DBH ($R^2 = 0.86784$) (Fig. 4), although outer bark thickness was more variable as DBH increased.

Experimental results from our Michigan field test were similar to the relationship between parasitism and bark thickness (as tree diameter) seen in surveys in *T. planipennisi*'s native range where it was not recovered in trees greater than 10-cm DBH, although the sample size for larger trees was smaller due to tight restrictions on felling trees in China (Fig. 5). Similarly, recoveries of *T. planipennisi* broods at release sites in Michigan from locations where

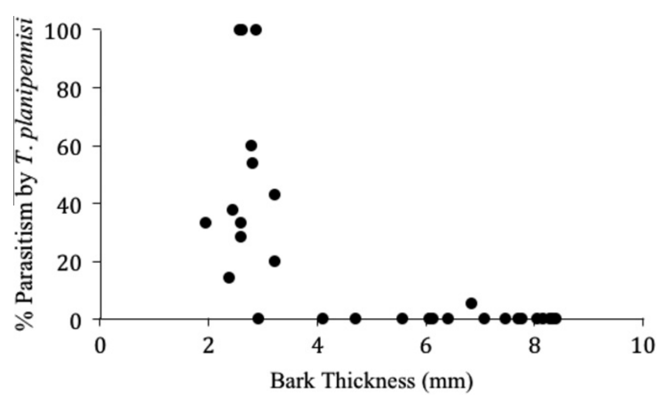

Fig. 1. Relationship between bark thickness and percent parasitism of EAB by *T. planipennisi* in experimental inoculations in Michigan in 2011.

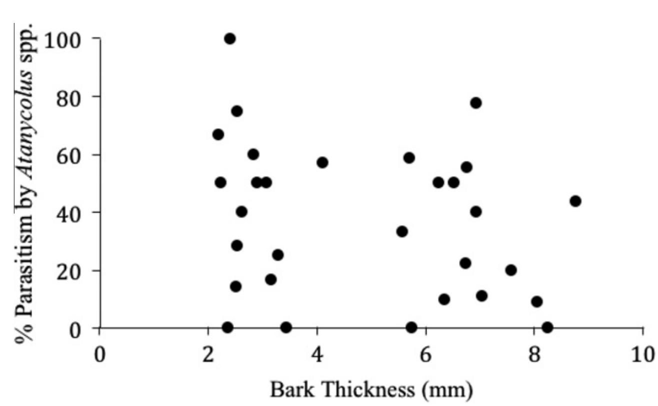

Fig. 2. Relationship between bark thickness and percent parasitism of EAB by *Atanycolus* spp. in experimental inoculations in Michigan in 2011.

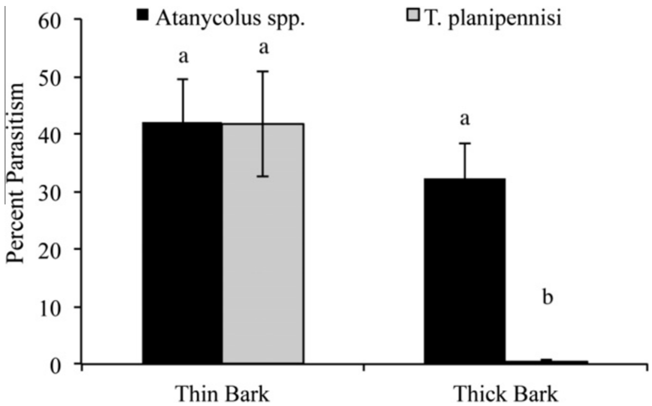

Fig. 3. Percent parasitism of EAB by *Atanycolus* spp. and *T. planipennisi* on thin-barked (2–5 mm) and thick-barked (6–9 mm) ash trees, data from experimental inoculations in Michigan in 2011.

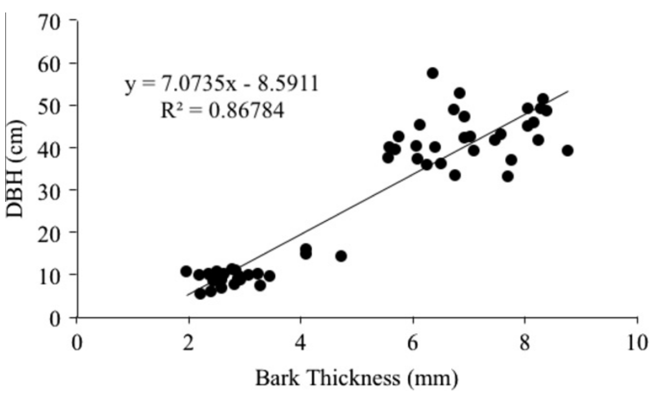

Fig. 4. Relationship between DBH and bark thickness in *Fraxinus pennsylvanica.*

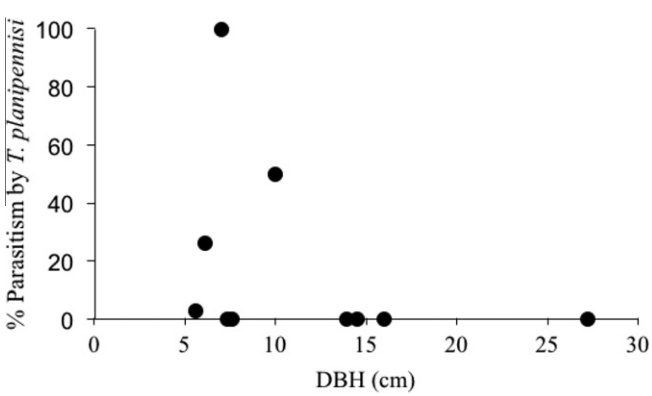

Fig. 5. Relationship between DBH of ash trees and percent parasitism of EAB by *T. planipennisi* from field surveys in China (2003) and Russia (2008).

the parasitoid was released found the same relationship, with all recoveries in trees with DBH less than 15-cm DBH (Fig. 6).

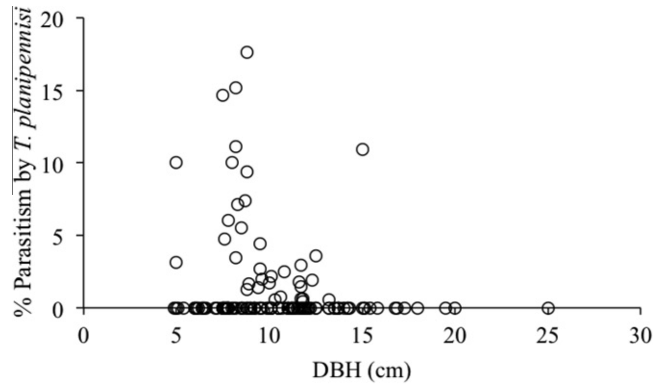

Fig. 6. Relationship between DBH of ash trees and percent parasitism of EAB by *T. planipennisi* from field surveys around Lansing, Michigan from 2009–2011.

4. Discussion

T. planipennisi failed to parasitize EAB larvae in large, thick barked trees except for a single larva that was likely excavating its pupation chamber in the outer bark. This behavior is typical of EAB larvae developing in thick barked, large diameter trees, whereas EAB in smaller diameter trees or tree section tunnel inward as they excavate pupation chambers in the outer sapwood (Bauer, personal communication). It is interesting to note that *T. planipennisi* were able to parasitize EAB larvae in trees with mean bark thickness greater than their ovipositor length; the greatest difference observed was 0.7 mm. This most likely is due to an ability to find areas in the bark that were less thick than the mean value. Regardless, there is clearly a maximum bark thickness that *T. planipennisi* can penetrate and reach EAB larvae. This may prevent *T. planipennisi* from being an effective biological control agent in moderate to mature aged green ash. For this reason, we now recommend selecting EAB-biocontrol release sites where the majority of ash trees are less than 12-cm DBH. Above this size, *T. planipennisi* will be less likely to successfully establish, because in forest landscapes the majority of EAB larvae occur in the middle and lower sections of the bole (Duan et al. unpublished data from our field research sites in MI). While some parasitoids may find suitable hosts in branches of thick barked trees, such hosts would be less common than if sites were dominated by smaller trees. This finding is corroborated by surveys of *T. planipennisi* in its native range (Liu et al., 2003; Duan et al., 2012a) in which researchers did not find the parasitoid in trees greater than 10-cm DBH, and by extensive surveys in North America at sites where *T. planipennisi* was released, which did not find the parasitoid's brood in trees greater than 15-cm DBH (Duan et al., 2012a). As a biological control agent, *T planipennisi* may be most effective in regenerating stands of ash several years after larger trees have died.

In contrast, even the thickest outer bark measured during the course of this study (8.75 mm) contained EAB larvae parasitized by *Atanycolus* spp. As with *T. planipennisi*, this bark thickness was thicker than the longest typical ovipositor length for *Atanycolus* spp. (6 mm). While *Atanycolus* spp. may also locate areas of bark thinner than the mean, two other reasons may have contributed to their ability to parasitize EAB larvae seemingly out of reach. First, while it was not common, a number of EAB larvae were observed to tunnel towards the surface of the bark in thick-barked trees. Second, since exact determination of living *Atanycolus* species is extremely difficult, it is possible that some individuals in this study were different species and may have had slightly longer ovipositors. Regardless of the exact reasons, it is clear that native *Atanycolus* spp. are capable of and readily parasitize EAB larvae in trees as large as 57.4 cm DBH. Parasitism rates by *Atanycolus* spp. have increased at EAB biocontrol study sites in Michigan since 2009 (Duan et al., 2011), and this appears to be a numerical response to high densities of EAB populations on infested trees.

The current value of native *Atanycolus* spp. as biological control agents of EAB is increasing in some areas (Michigan) with relatively high densities of EAB populations (Cappaert and McCullough, 2009; Duan et al., 2011). However, it is not yet known how these native parasitoid species will respond to low EAB densities in newly infested areas or as EAB densities in long-infested areas fall. Clearly, this must be the subject of continued research at these and other field sites. The finding, however, that *T. planipennisi* is limited in its ability to reach EAB larvae in older trees, suggests two important conclusions. First, it is likely that this parasitoid will be very important in protecting smaller diameter trees that are growing up in forested areas devastated by EAB. Second, it is clear that species such as *Atanycolus* and *Spathius* with longer ovipositors are needed (e.g., Duan et al., 2012b). Since the *Spathius* species (*S. agrili*) imported from China (USDA APHIS, 2007; Wang et al., 2007) has so far not shown a strong ability to establish and spread in Michigan and other northern areas (Duan et al., 2011; Gould et al., 2011), new species in these groups from the native range should be considered for release. Most promising among these is *S. galinae* Belokobylskij-Strazanac from the Russian Far East (Belokobylskij et al., 2012; Duan et al., 2012b), now being evaluated in USDA quarantine laboratories for possible use as an EAB biocontrol agent in the US. This species was the dominant parasitoid in the Vladivostok area in far eastern Russia, approximately 800 miles north of locations from which *S. agrili* from China was collected. *Spathius galinae*, approximately the same size as *S. agrili*, with a 4–5 mm long ovipositor, may fill an essential role in the biological control of EAB in the US.

The results of this study demonstrate that bark thickness provides a refuge for EAB larvae from *T. planipennisi*, a parasitoid introduced to control EAB. Given this result, it is unlikely that *T. planipennisi* alone will be effective in controlling EAB to prevent ash tree mortality, particularly in large ash trees. In contrast, native *Atanycolus* spp. parasitoids with their longer ovipositors were able to reach and readily parasitize EAB larvae in even very large thick barked trees. These results demonstrate that a guild of parasitoids, not just a single species, is often required to regulate host populations due to various biological and ecological constraints. This is a fact particularly salient to biological control efforts. In addition to thick barked trees, *Atanycolus* spp. readily parasitized EAB larvae in thin barked trees. With this result in mind, it is interesting to speculate how the interaction between *Atanycolus* spp. and *T. planipennisi* utilizing EAB hosts in thin barked trees will result. If *T. planipennisi* outcompete *Atanycolus* spp. for hosts in thin barked trees, then this may be a strong example of newly formed host partitioning of an invasive host between a native and introduced parasitoid based on a morphological trait (ovipositor length). This may prove a fruitful area of future research.

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