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Research

Sampling

Density of Emerald Ash Borer (Coleoptera: Buprestidae) Adults and Larvae at Three Stages of the Invasion Wave

Stephen J. Burr,[1,2] Deborah G. McCullough,[1,3,5] and Therese M. Poland[4]

[1]Department of Entomology, Michigan State University, 243 Natural Science Building, 288 Farm Lane, East Lansing, MI 48824, [2]Present Address: USDA Forest Service, Forest Health Protection Alaska Region, 3700 Airport Way, Fairbanks, AK 99709, [3]Department of Forestry, Michigan State University, 126 Natural Resources Building, 480 Wilson Road, East Lansing, MI 48824, [4]USDA Forest Service, Northern Research Station, 3101 technology Boulevard, Ste. F East Lansing, MI, 48910, and [5]Corresponding author, e-mail: mccullo6@msu.edu

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Abstract

Emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae), an invasive phloem-feeding buprestid, has killed hundreds of millions of ash (*Fraxinus* spp.) trees in the United States and two Canadian provinces. We evaluated EAB persistence in post-invasion sites and compared EAB adult captures and larval densities in 24 forested sites across an east–west gradient in southern Michigan representing the Core (post-invasion), Crest (high EAB populations), and Cusp (recently infested areas) of the EAB invasion wave. Condition of green ash (*Fraxinus pennsylvanica* Marsh) trees were recorded in fixed radius plots and linear transects in each site. Ash mortality was highest in Core sites in the southeast, moderate in Crest sites in central southern Michigan, and low in Cusp sites in the southwest. Traps and trap trees in Crest sites accounted for 75 and 60% of all EAB beetles captured in 2010 and 2011, respectively. Populations of EAB were present in all Core sites and traps in these sites captured 13% of all beetles each year. Beetle captures and larval densities at Cusp sites roughly doubled between 2010 and 2011, reflecting the increasing EAB populations. Sticky bands on girdled trees captured the highest density of EAB beetles per m^2 of area, while baited double-decker traps had the highest detection rates and captured the most beetles. Larval densities were higher on girdled ash than on similar ungirdled trees and small planted trees. Woodpecker predation and a native larval parasitoid were present in all three invasion regions but had minor effects on ash survival and EAB densities.

Key words: invasive forest pest, EAB, *Fraxinus pennsylvanica*, double-decker trap, girdled ash tree

Emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae), a phloem-feeding beetle native to Asia, became established in southeast Michigan at least 10 yr before it was identified in 2002 as the cause of declining ash (*Fraxinus* spp.) in Detroit, MI, USA and Windsor, Ontario, Canada (Cappaert et al. 2005, Siegert et al. 2014). In its native range, EAB is a secondary pest, colonizing severely stressed ash trees, similar to several North American congeners such as *Agrilus anxius* Gory (Coleoptera: Buprestidae) and *Agrilus bilineatus* (Weber) (Coleoptera: Buprestidae), (Balch and Prebble 1940, Barter 1965, Dunn et al. 1986, Muzika et al. 2000). In North America, EAB can successfully attack and develop in healthy ash but will preferentially colonize ash trees stressed by girdling or other problems (McCullough et al. 2009a, b; Poland and McCullough 2006; Siegert et al. 2010, 2017; Tluczek et al. 2011; Mercader et al. 2013). Several studies have also shown EAB host preference and host resistance varies among North American ash species. For example, green ash (*Fraxinus pennsylvanica* Marsh), the most widely distributed species of ash in North America (Wright et al. 1959, Kennedy 1990), is a highly preferred and vulnerable EAB host (Anulewicz et al. 2007, 2008; Rebek et al. 2008; Pureswaran and Poland 2009; Tanis and McCullough 2015).

Dendrochronological evidence showed transport of infested ash nursery trees, logs, and firewood before EAB was identified in 2002 resulted in establishment of satellite populations of EAB well beyond the original infestation, increasing the overall rate of expansion (Mercader et al. 2011, 2016; Siegert et al. 2014). Quarantines imposed to regulate transport of potentially infested ash material and increased public awareness have presumably minimized artificial transport of EAB in recent years (Cappaert et al. 2005). Nevertheless, EAB populations continue to spread as local ash resources are depleted and beetles disperse to find new hosts. Additionally, evidence suggests a small proportion of mature female EAB beetles engage in long distance dispersal flights, contributing to overall spread (Taylor et al. 2010; Mercader et al.

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2012, 2016). As of July 2017, EAB populations were known to be established in at least 30 states and two Canadian provinces (EAB.info 2017). Hundreds of millions of ash trees have been killed by EAB, which has become the most destructive and costly forest insect to invade North America (Aukema et al. 2011, Herms and McCullough 2014).

Detecting new EAB infestations remains notably difficult. Most larvae in newly infested, relatively healthy trees require 2 yr to complete development (Siegert et al. 2010, Tluczek et al. 2011), which slows population growth rates (Mercader et al. 2011), but also delays the ability of surveyors to identify recently infested trees. Small D-shaped holes in the bark left by emerging EAB adults or larger holes left by woodpeckers preying on late stage larvae are often the first evidence of EAB presence, but can be difficult to observe in the upper canopy of trees where most infestations begin (Cappaert et al. 2005, Poland and McCullough 2006). As EAB populations increase to moderate or high densities, bark cracks over larval galleries, canopy thinning or dieback, and epicormic sprouts become apparent (Cappaert et al. 2005, Anulewicz et al. 2007).

Girdling ash trees in spring and then debarking the trees in fall to locate EAB larvae remains the most effective means to detect or monitor low-density EAB infestations (McCullough et al. 2011b, Mercader et al. 2013). Locating suitable and accessible ash trees for girdling, however, can be problematic, especially for large-scale or long-term surveys (Mercader et al. 2013, 2015; McCullough et al. 2015). Artificial traps are more commonly used for EAB detection, especially for large-scale surveys. Beetles are attracted to specific shades of green or purple (Crook et al. 2009, Francese et al. 2010) and to lures containing volatiles present in ash leaves or bark (Crook et al. 2008; de Groot et al. 2008; Crook and Mastro 2010; Grant et al. 2010, 2011; Silk and Ryall 2015). A female-produced sex pheromone combined with host volatiles reportedly increased captures of EAB males in some studies when green prism traps were hung high in ash trees (Silk et al. 2011, Ryall et al. 2013, Silk and Ryall 2015). Green or purple traps baited with one or more host volatiles have been used widely in the United States and Canada for EAB detection and monitoring (CFIA 2017, USDA APHIS 2017).

We used a variety of methods to assess adult and larval EAB abundance in 2010 and 2011 in 24 forested sites distributed across an east–west gradient in Michigan representing three stages of the EAB invasion wave. Our major objectives included assessing persistence of EAB populations in Core sites in southeast Michigan that were invaded by EAB by the early 2000s. We were also interested in comparing EAB adult and larval densities in the Core sites with those in Crest sites in south central Michigan, where EAB populations were at or near peak densities, and recently infested Cusp sites in the southwest. Changes in EAB densities from 1 yr to the next were also of interest, particularly in the southwestern sites where there was little evidence of EAB at the onset of the study. Size and condition of green ash trees, which comprised a major portion of the overstory in the sites, were evaluated each year.

An additional objective focused on comparing detection rates and EAB adult captures on baited, artificial double-decker traps with those on three types of trap trees in the three invasion stages. We quantified larval densities on the trap trees, both to compare densities among the invasion stages, and to assess correlations with adult EAB captures. We also wanted to determine whether native parasitoids of EAB larvae were present in all sites. We predicted that native parasitoids would be attracted to volatiles produced by heavily infested and declining ash trees in the Crest sites (Paré and Tumlinson 1999), but whether EAB larvae in trees in the Core and Cusp sites would be parasitized was unknown.

Materials and Methods

In July and August 2009, we contacted land managers and scouted forested sites on public lands representing a temporal gradient of EAB infestation from southeast Michigan, near the origin of the EAB invasion (Siegert et al. 2014), to more recently invaded sites in southwest Michigan (Fig. 1). We ultimately selected 24 sites and centered a 1 ha plot in each site in areas where green ash comprised ≥20% of the overstory, based on inventory data provided by land managers and preliminary walk-through surveys (Burr and McCullough 2014). Six 'Core' sites were in southeast Michigan where dendrochronological data showed EAB was killing trees by the early 2000s (Siegert et al. 2014). Two areas further west thought to have resulted from early introductions of infested ash material were also designated as Core sites EAB (Fig. 1). Most ash trees in these Core areas had been killed by EAB, as evidenced by D-shaped exit holes, larger holes left by woodpeckers preying on EAB larvae, and abundant larval galleries beneath the bark. Eight 'Crest' sites in south central Michigan (Fig. 1) were characterized by ash trees in various stages of decline. Approximately half of the ash trees in the Crest sites were alive, but most live and all dead trees had obvious signs of EAB infestation, including holes left by woodpeckers or emerged EAB adults, larval galleries visible under bark cracks, epicormic shoots, and canopy thinning or dieback. In contrast, we observed little evidence of EAB infestation in the eight 'Cusp' sites in southwest Michigan, ~200–300 km from the EAB origin in the greater Detroit area (Fig. 1).

Adult EAB Captures

We used a variety of methods to assess adult EAB populations, including baited double-decker traps and sticky bands applied to girdled and non-girdled ash trees, and to newly planted ash trees

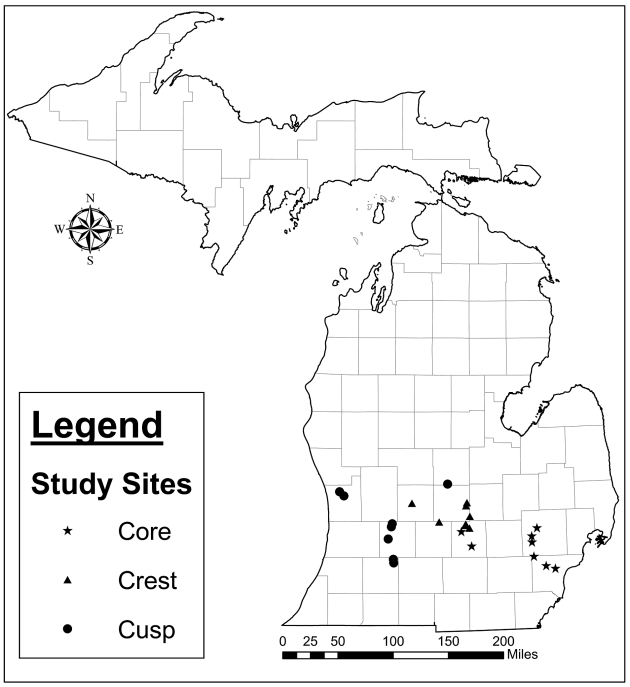

Fig. 1. Locations in southern Michigan of 24 green ash sites representing three stages of the EAB invasion wave in 2010 and 2011, including Core sites near the center of the initial invasion in southeast Michigan, Crest sites where EAB populations were at or near peak levels, and more recently infested Cusp sites in southwest Michigan.

acquired from a nursery. Traps and sticky bands were deployed at sites from 10–18 May 2010 and remained in place until mid-to-late August 2010, after beetle activity ceased.

Two double-decker traps were installed in each site. Each trap consisted of two purple 60 × 40 cm coroplast panels (Harbor Sales Inc., Sudlersville, MD) folded into a three-sided prism and attached to a 3.0 m tall polyvinyl chloride (PVC) pipe (10 cm diameter). The PVC pipe with the prisms was supported by sliding the pipe over a 1.7 m tall t-post set into the ground. One prism was attached to the top of the PVC pipe while the second prism was 60 cm beneath the upper prism. Double-decker traps were placed in locations where they would be exposed to full or nearly full sun whenever possible, either in openings within the stands or along the edge of wooded areas, 5–10 m from ash trees (Wang et al. 2010, McCullough et al. 2011b, Poland et al. 2011, McCullough and Poland 2017). Clear Pestick (Hummert International, Earth City, MO) was applied to the external surfaces of both prisms. The top prism was baited with two bubble caps of *cis*-3-hexenol (combined volatilized release rates of 7.4 mg/d, determined in the laboratory at 20°C, Contech Enterprises, Inc., Delta, BC, Canada). The lower prism was baited with an 80:20 blend of Manuka oil and Phoebe oil (release rate of 50 mg/d determined in the laboratory at 20°C, Synergy Semiochemicals Corp., Burnaby, BC, Canada). Manuka oil and Phoebe oil are natural tree oils derived from the New Zealand manuka tea tree, *Leptospermum scoparium* J. R. and G. Forst (Myrtaceae) and the Brazilian walnut tree, *Phoebe porosa* Mez. (Lauraceae), respectively. They contain high levels of bark sesquiterpenes present in green ash bark that elicit antennal responses by EAB (Cossé et al. 2008, Crook et al. 2012). Manuka oil contains five of the antenally active bark sesquiterpenes while Phoebe oil also includes a sixth compound, 7-*epi*-sesquithugene (Crook et al. 2012).

Three uninfested bare root green ash nursery trees, 3.8–6.4 cm DBH (Bailey Nursery, Newport, MN) were planted at each site, typically in full sun along edges or in gaps to optimize beetle captures (McCullough et al. 2009a, b). We assumed transplant stress would elicit changes in volatile profiles that would attract adult EAB. A sticky band, consisting of a 30 cm wide band of clear plastic wrap, was wrapped around the trunk of each planted tree, 1 m aboveground, and coated in Tanglefoot (Contech Enterprises, Inc., Delta BC, Canada) to capture EAB adults.

Four naturally regenerated ash growing in relatively sunny conditions and representative of trees in the respective sites were selected. Two trees were girdled using drawknives and handsaws to remove a 15 cm wide band of outer bark and phloem, 1 m above the base of the tree. The other two trees were not stressed or otherwise altered and were designated as 'control' trees. Sticky bands were wrapped around the trunk of each girdled and non-girdled tree, 1 m aboveground.

Planted, girdled, and control trap trees and the double-decker traps were at least 10 m apart. Trees and traps of the same type (i.e., the two control trees, or the two double-decker traps) were at least 20 m apart to avoid possible additive effects, particularly between girdled trees (Mercader et al. 2013). Traps were checked biweekly. Adult EAB were collected from each trap and returned to the laboratory, where beetles were soaked in Histo-Clear II (National Diagnostics, Atlanta, GA) to remove Pestick and Tanglefoot. Insects were examined to confirm identification. Numbers of EAB captured on the double-decker traps and the sticky bands on the trap trees were standardized per m^2 of trap surface area.

Trapping was repeated in 2011 with the following modifications. Traps and sticky bands were placed in sites beginning on 9 May and remained in place until 12 August. Double-decker traps and planted trap trees were placed in roughly the same locations as the previous year. Trees selected for girdling and controls were as near as possible to the location of trees in 2010. Bare root ash trees (3.8–6.5 cm DBH) planted in each site were acquired from Laws Nursery Inc. in Hastings, MN. The upper prism of double-decker traps was baited with the *cis*-3-hexenol lures as in the previous year, but the lower prisms were baited with lures containing only Manuka oil (Phoebe oil was unavailable in 2011).

Densities of EAB Larvae

Densities of EAB larvae were evaluated on trap trees between mid-October and mid-December in 2010. Trees <10 cm DBH, including planted trap trees and small control and girdled trees, were debarked from the base to roughly 2 m aboveground. Stem diameters and tree height were measured prior to debarking. Because stem diameter was smaller near the top than at the base of trap trees, the equation for a conical frustum was used to determine m^2 of exposed surface area. Larvae were tallied by tree and larval density expressed as larvae per m^2 of phloem surface. Trees ≥10 cm DBH were felled and bucked into 1 m logs beginning just above the sticky bands. An area equal to 0.5 m in length and half the circumference of the upper half of each log was measured then debarked on alternate logs to expose larvae in galleries. Surface area of exposed phloem and number of EAB larvae were summed for each tree and larval density was expressed as larvae per m^2 of phloem.

In 2011, larval density was surveyed much as in 2010, except that on the alternate 1 m long logs (trees ≥10 cm DBH), we debarked half the circumference of the log. All trap trees were felled and debarked in October and November in 2011.

Larval Parasitoids

Parasitoids found either as pupae in EAB larval galleries, or as small larvae attached to the larger EAB larvae, were recorded when trees or logs were debarked. We calculated the proportion of EAB larvae that were parasitized and parasitoid densities per m^2 of exposed surface area for each debarked tree. When parasitoids were observed, alternate logs with intact bark were returned to the laboratory and held in individual cardboard tubes, allowing parasitoids to develop and emerge as adults. Representative adult parasitoids from each site (where present) were submitted to and identified by Dr. John S. Strazanac from the University of West Virginia in Morgantown WV, as *Atanycolus cappaerti* Marsh and Strazanac (Hymenoptera: Braconidae). Voucher specimens of 10 EAB larvae, 10 male, and 10 female EAB adults, and 10 male and 10 female adult *A. cappaerti* were submitted to the Albert J. Cook Arthropod Research Collection at Michigan State University in East Lansing, MI in March 2012.

Ash Tree Condition

We tallied and measured DBH of live and dead ash trees (DBH ≥ 10 cm) in two belt-transects, each 150 m × 2 m, and four circular fixed radius plots (18 m radius) established in the 1 ha area delineated in each site (Burr and McCullough 2014). Belt-transects ran diagonally across each site in an X-formation, dividing sites into four quadrats. One circular plot was established in the center of each quadrat. Trees within 10 m of the belt-transect intersections were marked to ensure individual trees were not measured more than once. Dead ash trees, that is, trees with no live foliage, were assumed to be killed by EAB if evidence such as holes left from woodpecker predation of larvae or EAB exit holes were present. If no external signs of infestation were apparent, sections of bark were removed from dead ash trees to confirm presence of larval galleries. Dead

ash trees without EAB galleries were excluded from EAB mortality estimates. Detailed data from surveys of ash and other species in the overstory, along with seedling, sapling, and recruit strata, were reported in Burr and McCullough (2014).

Abundance of holes left by woodpeckers preying on EAB larvae and stump sprouts growing from the base of ash trees were qualitatively assessed by visually examining live and dead ash trees. Woodpecker holes were recorded as absent, low (1–6 woodpecker holes visible), and high (>6 woodpecker holes). Dates of woodpecker predation cannot be determined with visual surveys, so estimates represented cumulative woodpecker predation. Stump sprouts were recorded as absent, low (1–4 stump sprouts), and high (>4 stump sprouts).

On live trees, we also recorded abundance of epicormic shoots and canopy dieback. Epicormic shoots growing on the trunk or branches were tallied as absent, low (1–4 epicormic shoots), and high (>4 epicormic shoots). Canopy dieback was visually estimated in 10% increments, where 0% indicated a full canopy, and 90% indicated a nearly complete absence of leaves (Zarnoch et al. 2004). Canopy dieback was assessed from 21 June to 23 July in 2010, after trees were fully flushed but before current-year larvae began feeding, and from 18 June to 20 July in 2011.

Data Analysis

Data were tested for normality using the Shapiro–Wilk test (Shapiro and Wilk 1965) and residual plots. The two double-decker traps and seven trap trees with sticky bands in each site represented the sampling units for EAB adult captures, while the seven trap trees represented the sampling units for larval densities. Captures of EAB adults, larval densities, and basal area were normalized by $\log_{10}(x + 1)$ transformations. Adult captures and larval densities were tested as unplanned comparisons to assess differences among the three invasion stages. Tukey's honestly significant difference (HSD) multiple comparison procedure was applied if the overall analysis of variance (ANOVA) was significant ($P < 0.05$). Two-way ANOVA was used to evaluate main effects of trap type, invasion stage, and the interaction of the two factors on adult captures and larval densities (PROC GLM, SAS Institute 2012). Estimates of trap surface area, trap tree DBH, the surface area debarked, parasitoid densities, and canopy dieback could not be normalized by transformations. Friedman's two-way nonparametric test was, therefore, used to evaluate differences among the types of trap trees (i.e., control, girdled, and planted), the three invasion stages, and the interaction between the two factors (Friedman 1937; PROC RANK, SAS Institute 2012). Friedman's two-way nonparametric test was also used to evaluate effects of invasion stage on ash mortality, canopy dieback, and abundance of epicormic shoots, stump sprouts, and woodpecker holes (Friedman 1937; PROC RANK, SAS Institute 2012). When results for nonparametric tests were significant ($P < 0.05$), Tukey-type nonparametric multiple comparisons were applied (Zar 1984). Simple linear regression (PROC REG, SAS Institute 2012) was used to evaluate the relationship between larval density in trap trees and the density of EAB adults captured on double-decker traps or on sticky bands on the trap trees. Densities of EAB larvae per trap tree were related to densities of EAB adults captured on the same tree. For double-decker traps, the mean densities of larvae captured in all trap trees at the same site were related to densities of EAB adults captured on the traps. All analyses were conducted at $P < 0.05$ level of significance using SAS statistical software (SAS Institute 2012).

Results

Adult EAB Captures

In 2010, we captured 2,600 EAB adults on traps and the sticky bands on the trap trees, including 338 (13%), 1,960 (75%), and 302 (12%) beetles in the Core, Crest, and Cusp sites, respectively. Adults were captured in all 24 study sites. Beetle captures peaked from 21 June to 2 July, when 1,142 EAB were captured, representing 44% of the total. Adult EAB captures, standardized by total trapping surface area, were fivefold higher in Crest sites than in Core sites, and ninefold higher than in Cusp sites ($F = 47.94$; df = 2, 211; $P < 0.001$) (Fig. 2A). More EAB adults were captured in Core sites compared with Cusp sites, but the difference was not significant.

Number of EAB adult captures varied among the different trap types in 2010. Double-decker traps accounted for 75–80% of all beetles captured and at least one EAB adult was captured on traps in all sites. Surface area of the double-decker panels was greater than the surface area of sticky bands on girdled trees, control trees, and planted trees ($H = 28.38$; df = 3, 216; $P < 0.001$) (Table 1). When we standardized captures per m^2 of trapping surface, sticky bands on girdled trap trees captured more EAB adults per m^2 than all other trap types ($F = 12.69$; df = 3, 210; $P < 0.001$) (Table 1). Differences in EAB captures per m^2 between double-decker traps and the sticky bands on control and planted trees were not significant nor was the interaction between the invasion stages and trap type ($F = 1.4$; df = 6, 207; $P = 0.22$). Detection rates (i.e., at least one EAB captured) for sticky bands on trees in Core, Crest, and Cusp sites were 8, 21, and 21% for planted trees, 25, 37, and 25% for control trees, and 69, 94, and 56% for girdled trees, respectively. In comparison, detection rates for double-decker traps were 100% in Crest and Cusp sites and 94% in the Core sites.

In 2011, we captured 2,504 adults on traps and trap trees, including 319 (13%), 1,498 (60%), and 687 (27%) beetles in the Core, Crest, and Cusp sites, respectively. Beetle activity peaked from 5 July to 15 July when 1,116 EAB were collected, comprising 45% of the total captures. Captures of EAB adults in Crest sites were

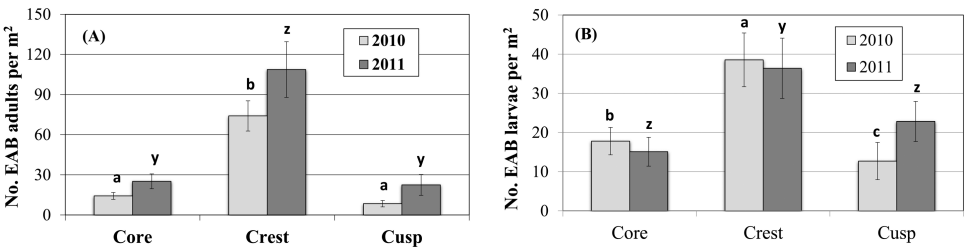

Fig. 2. (A) Mean (±SE) number of captured EAB adults per m^2 of trapping area in Core, Crest, and Cusp sites in 2010 and 2011 and (B) mean (± SE) number of EAB larvae per m^2 of exposed ash phloem in Core, Crest, and Cusp sites in 2010 and 2011. Means with different letters are significantly different (Tukey's protected HSD test, $P < 0.05$). (a, b, and c for 2010; y and z for 2011).

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Table 1. Mean (± SE) diameter at breast height (DBH) of green ash (*Fraxinus pennslyvanica*) trap trees, number, and density of captured EAB adults, trapping surface area of traps and trap trees, number and density of EAB larvae, and phloem area exposed on trap trees in 2010 and 2011 at 24 sites in Michigan

	Control trees	Girdled trees	Planted trees	Double-decker traps
2010				
Ash tree DBH (cm)	13.1 ± 1a	15.1 ± 1.1a	6.4 ± < 0.01b	–
Adult EAB beetles				
No. EAB adults captured	1.9 ± 0.5c	8.9 ± 2b	1.7 ± 0.5c	41.1 ± 9.7a
Trapping surface area (m^2)	0.1 ± 0.01b	0.1 ± 0.01b	0.1 ± < 0.01b	1.5 ± < 0.01a
Adult EAB per m^2	14.1 ± 3.2b	62.4 ± 13.9a	28.1 ± 7.7b	27.6 ± 6.6b
EAB Larvae				
No. larvae	12.2 ± 3.1b	30.9 ± 4.7a	2.3 ± 0.5c	–
Phloem area exposed per tree (m^2)	1.5 ± 0.3a	1.5 ± 0.4a	0.5 ± 0.01a	–
EAB larvae per m^2	28.2 ± 4.1b	57.7 ± 8.2a	5.1 ± 1.1c	–
2011				
Ash tree DBH (cm)	13.3 ± 0.8a	14.5 ± 0.7a	5.0 ± 0.1b	–
Adult EAB beetles				
No. EAB adults captured	3.5 ± 1.2c	17.3 ± 4.2b	2.0 ± 0.5c	28.5 ± 4.2a
Trapping surface area (m^2)	0.1 ± 0.01b	0.1 ± 0.01b	0.05 ± < 0.01c	1.5 ± < 0.01a
Adult EAB per m^2	25.5 ± 7.4bc	126.1 ± 28.3a	43.2 ± 12.4b	19.2 ± 2.8c
EAB Larvae				
No. larvae	9.2 ± 2.1b	44.0 ± 6.1a	5.0 ± 1b	–
Phloem area exposed per tree (m^2)	0.7 ± 0.04a	0.9 ± 0.07a	0.7 ± 0.03a	–
EAB larvae per m^2	14.0 ± 2.7b	63.3 ± 9.4a	6.7 ± 1.3b	–

Within rows, means followed by different letters are significantly different ($P < 0.05$).

fourfold higher than in Core and Cusp sites ($F = 17.8$; df = 2, 210; $P < 0.001$) (Fig. 2A), where captures did not differ.

As in 2010, trap type affected adult EAB captures in 2011. Double-decker traps accounted for 62, 44, and 75% of the adults captured in Core, Crest, and Cusp sites, respectively, and one or more EAB adults were captured in every site. Surface area of double-decker panels was again greater than other trap types, while the area of sticky bands on girdled and control trees were similar and sticky bands on planted trees had the least area ($H = 7.52$; df = 3, 212; $P < 0.001$) (Table 1). Sticky bands on girdled trees captured nearly threefold more EAB adults per m^2 than sticky bands on planted trees, fourfold more than sticky bands on control trees, and sixfold more than panels on double-decker traps. Sticky bands on the small planted trees captured twice as many adults per m^2 as the panels on double-decker traps ($F = 15.4$; df = 3, 209; $P < 0.001$) (Table 1). Differences in EAB adult captures per m^2 among other trap types were not significant nor was the interaction of invasion stage and trap type ($F = 2.01$; df = 6, 206; $P = 0.06$). Detection rates (i.e., at least one EAB captured) for sticky bands on trees in Core, Crest, and Cusp sites were 42, 71, and 12% for planted trees, 31, 62, and 67% for control trees, and 81, 100, and 79% for girdled trees, respectively. Detection rates for double-decker traps were 94, 100, and 94% in Core, Crest, and Cusp sites, respectively.

Densities of EAB Larvae

We debarked rectangular areas on the trunk and major branches of girdled, control, and planted trees in fall 2010 to assess EAB larval density (Table 1). Area of exposed phloem per tree averaged 0.6 ± 0.04, 0.6 ± 0.04, and 0.9 ± 0.20 m^2 in Core, Crest, and Cusp sites, respectively, and did not differ among invasion stages ($H = 0.05$; df = 2, 157; $P = 0.93$). Overall, 1,818 larvae were recorded in the debarked areas on trap trees in 2010, including 441, 902, and 475 larvae on trees in Core, Crest, and Cusp sites, respectively. Larvae were found on trees in 22 of the 24 study sites, but we did not find any larvae on trees in the two most westerly Cusp sites.

Larval densities in 2010 differed among all three invasion stages ($F = 17.03$; df = 2, 163; $P < 0.001$) (Fig. 2B). Girdled trap trees accounted for 68, 69, and 64% of all larvae recorded in Core, Crest, and Cusp sites, respectively. Average DBH of control and girdled trees was more than twice the DBH of planted trees ($H = 28.38$; df = 2, 163; $P < 0.001$) (Table 1), but did not differ between girdled and control trees. Densities of larvae on girdled trees were twice as high as on control trees, and 11-fold higher than on planted trees. Larval densities on control trees were fivefold higher than on the small planted trees ($F = 43.04$; df = 2, 163; $P < 0.001$) (Table 1). There was no significant interaction between trap tree type and invasion stage on larval density ($F = 0.74$; df = 4, 161; $P = 0.56$). Larvae were recorded in 2010 on 46, 62, and 12% of planted trees, 56, 87, and 44% of control trees, and 94, 100, and 62% of girdled trees in the Core, Crest, and Cusp sites, respectively.

In 2011, area of phloem exposed in bark windows to assess larval density averaged 0.8 ± 0.10, 0.7 ± 0.04, and 0.8 ± 0.03 m^2 per tree in Core, Crest, and Cusp sites, respectively, and was not affected by invasion stage ($H = 0.19$; df = 2, 162; $P = 0.82$). We recorded a total of 2,895 larvae in the 24 sites in 2011, including 584, 1,245, and 1,066 larvae on trees, in Core, Crest, and Cusp sites, respectively.

Trap trees in Crest sites had higher larval densities in 2011 than those in Core and Cusp sites ($F = 7.2$; df = 2, 162; $P = 0.001$) (Fig. 2B), where densities did not differ significantly. Girdled trees accounted for 71–75% of all larvae in all sites. The DBH of control and girdled trees in 2011 was more than twice that of planted trees ($H = 7.52$, df = 2, 162, $P < 0.001$) (Table 1), but did not differ between girdled and control trees. Larval density on girdled trees was fourfold greater than on control trees and 10-fold greater than on planted trees ($F = 39.7$; df = 2, 162; $P < 0.001$) (Table 1). More larvae were found on control trees than on planted trees but differences in larval densities were not significant nor was the interaction between trap tree type and invasion stage ($F = 1.61$; df = 4, 160; $P = 0.16$). Larvae were recorded in 2011 on 58, 6, and 18% of the planted trees, 75, 81, and 62% of control trees, and 87, 100, and 87% of girdled trees in the Core, Crest, and Cusp sites, respectively.

Relationship Between Adult Captures and EAB Larval Density

There was a significant and positive linear relationship between density of EAB larvae in trap trees and the density of adult EAB beetles captured on sticky bands on the same trap trees or on double-decker traps for all sites combined and all trap types combined in both 2010 and 2011 (Table 2). The slope and intercept parameters of the regression models for all sites and all trap types combined were significant and similar in both years. In 2010, there was a significant positive relationship between larval density and density of EAB adults captured on all trap types at Core and Crest sites, but not at Cusp sites. Considering the different trap types at all sites, the relationship between larval density and density of captured adults was positive and significant for double-decker traps and for girdled or planted trap trees, but not for control trap trees. Slope and intercept parameters in the models were substantially lower for planted trap trees than for girdled trap trees or double-decker traps (Table 2).

In 2011, the linear relationship between larval density and density of captured adults on all trap types was significant and positive at the Crest and Cusp sites, but not at the Core sites. Larval and adult densities were significantly and positively related for each of the different trap types at all sites (i.e., double-decker, control, girdled, and planted trap trees). As in 2010, the slope and intercept parameters in the regression models were substantially lower for planted trap trees than for the other types of traps (Table 3).

Larval Parasitism

In 2010, 283 EAB larvae were parasitized by *A. cappaerti*, including 57, 223, and 3 larvae in Core, Crest, and Cusp sites, respectively. Parasitism rates by *A. cappaerti* averaged 12 ± 4.0, 27 ± 6.0, and 1.3 ± 1.2% in Core, Crest, and Cusp sites, respectively. Parasitism rates in Crest sites were higher than in Cusp sites (H = 10.28, df = 2, 21, P = 0.005), but other differences were not significant. Densities of parasitoids averaged 1.4 ± 0.6, 7.2 ± 2.4, and 0.1 ± 0.1 parasitoids per m^2 of exposed phloem in Core, Crest, and Cusp sites, respectively. Average densities of parasitoids were higher in Crest sites than Core and Cusp sites (H = 20.42; df = 2, 163; P < 0.001), where densities did not differ.

Density of *A. cappaerti* in 2010 was higher on EAB larvae in girdled trees than on planted and control trees, and higher on control trees than on planted trees (H = 42.65; df = 2, 163; P < 0.001). Parasitoid density in girdled trees was lower in Cusp sites than in Core and Crest sites (Friedman's F = 9.99; df = 4, 160; P < 0.001), where densities did not differ. We recorded an average of 4.7 ± 1.8, 22.2 ± 7.3, and 0.3 ± 0.2 parasitoids per tree on girdled trees in Core, Crest, and Cusp sites, respectively, compared with 0.6 ± 0.4, 3.1 ± 1.3, and 0.2 ± 0.2 parasitoids per tree on control trees in Core, Crest, and Cusp sites, respectively. No parasitoids were observed on planted trap trees in 2010.

In 2011, we recorded 145 EAB larvae parasitized by *A. cappaerti*, including 28, 84, and 33 parasitoids in Core, Crest, and Cusp sites, respectively. Parasitism rates by *A. cappaerti* averaged 5.3 ± 1.2, 7.7 ± 3.5, and 2.3 ± 1.1% of EAB larvae in Core, Crest, and Cusp sites, respectively, and did not differ among invasion stages (F = 1.60; df = 2, 111; P = 0.21). Differences in parasitoid densities also did not differ among the three invasion stages (F = 2.77; df = 2, 162; P = 0.11), averaging 0.7 ± 0.2, 2.4 ± 1, 0.5 ± 0.3 parasitoids per m^2 in Core, Crest, and Cusp sites, respectively. Girdled trees had significantly higher average densities of parasitoids than control and planted trees (H = 17.66; df = 2, 161; P < 0.001). On average, there were 1.3 ± 0.9, 2.3 ± 0.8, and 0.4 ± 0.2 *A. cappaerti* parasitoids on control trap trees, girdled trap trees, and planted trap trees, respectively, in 2011. The interaction between trap type and invasion stage did not significantly affect parasitoid densities (F = 0.53; df = 4, 160; P = 0.71).

Condition of Ash Trees

In 2010, we recorded 1,035 green ash trees (DBH ≥ 10 cm) in the plots, including 216, 376, and 443 trees in Core, Crest, and Cusp sites, respectively. Most ash trees in the sites were <30 cm in DBH (88, 95, and 87% in Core, Crest, and Cusp sites, respectively). Ash

Table 2. Relationship between EAB larval density per m^2 in trap trees (y) and density of EAB adults captured per m^2 on sticky bands on trap trees or on double-decker traps (x) in 2010 and 2011 at 24 sites in Michigan

Sites and Trap Types	Linear Regression Model	N	R^2	P
2010				
All sites, all trap types	$y = 0.29\,x + 13.70$	214	0.27	<0.0001
Core sites, all trap types	$y = 0.53\,x + 10.41$	72	0.24	<0.0001
Crest sites, all trap types	$y = 0.25\,x + 19.75$	72	0.28	<0.0001
Cusp sites, all trap types	$y = 0.29\,x + 10.20$	70	0.03	0.1
All sites, control trap trees	$y = 0.29\,x + 13.19$	47	0.05	0.1
All sites, girdled trap trees	$y = 0.39\,x + 32.77$	47	0.43	<0.0001
All sites, planted trap trees	$y = 0.07\,x + 3.09$	72	0.211	<0.0001
All sites, double-decker traps	$y = 0.15\,x + 19.06$	48	0.119	0.02
2011				
All sites, all trap types	$y = 0.15\,x + 17.02$	213	0.21	<0.0001
Core sites, all trap types	$y = 0.06\,x + 13.73$	69	0.02	0.37
Crest sites, all trap types	$y = 0.13\,x + 22.19$	72	0.20	<0.0001
Cusp sites, all trap types	$y = 0.28\,x + 16.44$	72	0.29	<0.0001
All sites, control trap trees	$y = 0.17\,x + 10.03$	48	0.22	0.0008
All sites, girdled trap trees	$y = 0.14\,x + 41.95$	48	0.17	0.003
All sites, planted trap trees	$y = 0.05\,x + 5.18$	69	0.16	0.0006
All sites, double-decker traps	$y = 0.35\,x + 19.68$	48	0.09	0.04

Larval density in a trap tree was compared with density of adults captured on the same tree. For double-decker traps, mean larval density within all trap trees was compared with adults captured per trap at the same site.

Table 3. Mean (± SE) percentage of green ash (*Fraxinus pennsylvanica*) trees that were dead, visual estimates of canopy dieback and presence of epicormic shoots on live ash trees, and proportion of all ash trees (dead and live) with stump sprouts or holes left by woodpeckers recorded in plots in 2010 and 2011 in the Core, Crest, or Cusp sites in Michigan (24 total sites)[a]

	Ash mortality (%)	Canopy dieback (%)	Epicormic shoots (%)	Stump sprouts (%)	Woodpecker predation (%)
2010					
Core	67 ± 11a	40 ± 5a	38 ± 6a	39 ± 7a	76 ± 6a
Crest	27 ± 9b	34 ± 2a	44 ± 11a	37 ± 10a	52 ± 11ab
Cusp	11 ± 4c	11 ± 1b	22 ± 7b	11 ± 5b	20 ± 6b
2011					
Core	79 ± 10x	39 ± 6y	56 ± 14y	43 ± 9y	93 ± 4y
Crest	45 ± 11y	28 ± 3y	52 ± 12y	51 ± 10y	73 ± 13yz
Cusp	20 ± 7z	20 ± 2z	36 ± 8z	19 ± 6z	41 ± 10z

Within columns, means followed by different letters are significantly different (a, b, and c for 2010; x, y, and z for 2011) ($P < 0.05$).

[a]Detailed data on ash and other overstory species were reported in Burr and McCullough 2014.

mortality varied among the three invasion stages ($H = 290.8$; df = 2, 1032; $P < 0.001$) (Table 3). Ash killed by EAB were present in all eight Core sites, six Crest sites, and four Cusp sites. In three of the Core sites, 100% of the overstory ash had succumbed to EAB. The highest ash mortality rate recorded in the Crest sites was 70% in one site, while 34% of the ash in one Cusp site were dead. Nearly all dead ash trees remained standing; fallen trees and branches were scarce, even in Core sites. Detailed data on ash and other species in the overstory and regeneration strata in these sites were presented in Burr and McCullough (2014).

Canopy condition of live ash trees also varied among invasion stages. Ash trees in Cusp sites had healthier canopies than ash trees in Core and Crest sites ($H = 112.3$; df = 2, 713; $P < 0.001$) (Table 3), where canopy dieback did not differ significantly (Burr and McCullough 2014). Fewer ash trees had epicormic shoots in 2010 in Cusp sites than in Core and Crest sites ($H = 81.28$; df = 2, 710; $P < 0.001$) (Table 3), which did not differ. In Crest sites, 40% of trees had relatively abundant epicormic shoots (>4 shoots), compared to 29 and 11% of trees in Core and Cusp sites, respectively. Of the trees in Core, Crest, and Cusp sites, 11, 6, and 4% of the ash had 1–4 epicormic shoots, respectively.

A higher proportion of live and dead ash trees had stump sprouts in the Core and Crest sites than in Cusp sites ($H = 157.49$; df = 2, 958; $P < 0.001$) in 2010 (Table 3). Stump sprouts were relatively abundant (>4 sprouts per tree) on 38, 40, and 6% of trees in Core, Crest, and Cusp sites, respectively. Ash trees with 1–4 stumps sprouts comprised 6, 7, and 3 of trees in Core, Crest, and Cusp sites, respectively.

Live and dead ash trees with holes left by woodpeckers preying on EAB larvae were more abundant in Core sites compared with Cusp sites ($H = 259.61$; df = 2, 958; $P < 0.001$) (Table 3) in 2010, but other differences were not significant. Trees with >6 woodpecker attacks comprised 73, 56, and 13% of trees in Core, Crest, and Cusp sites, respectively. Trees with 1–6 woodpecker holes were rare, accounting for only 4, 6, and 3% of trees in Core, Crest, and Cusp sites, respectively.

In 2011, we recorded 1,054 ash trees in transects and plots, including 207, 404, and 443 trees in Core, Crest, and Cusp sites, respectively. As in 2010, 85–97% of the trees were <30 cm in DBH. Ash mortality again varied among the three invasion stages ($H = 259.55$; df = 2, 1,052; $P < 0.001$) (Table 3). All overstory ash trees were dead in three Core sites (the same sites with 100% mortality in 2010), while mortality rates of 85 and 50% were recorded in Crest and Cusp sites, respectively. Ash trees killed by EAB were present in all eight Core sites, seven Crest sites, and seven Cusp sites.

Canopies of live ash trees in 2011 were again healthier in Cusp sites than in Core and Crest sites ($H = 20.41$; df = 2, 581; $P < 0.001$) (Table 3), where canopy dieback did not differ significantly. The slight reversal in ash canopy decline between 2010 and 2011 in Core and Crest sites (Table 3) reflected increased ash mortality in these sites in 2011. A number of trees with relatively high canopy dieback in 2010 did not survive and were excluded from the 2011 estimates of canopy condition of live trees, leading to a slight decrease in the proportion of surviving trees with healthier canopies.

In 2011, the proportion of trees with epicormic shoots was again higher in Core and Crest sites than in Cusp sites ($H = 24.23$; df = 2, 581; $P < 0.001$) (Table 3). Trees with high numbers of stump sprouts comprised 58, 27, and 22% of the live ash trees in Core, Crest, and Cusp sites, respectively, while low numbers of epicormic shoots were recorded on 5, 9, and 6% of trees in Core, Crest, and Cusp sites, respectively.

A higher proportion of live and dead ash trees had stump sprouts in Core and Crest sites than in Cusp sites in 2011 ($H = 157.49$; df = 2, 977; $P < 0.001$) (Table 3). Trees with abundant stump sprouts (>4 sprouts) comprised 39, 53, and 12% of trees in Core, Crest, and Cusp sites, respectively, while 1–4 stump sprouts were present on 9, 8, and 6% of trees in Core, Crest, and Cusp sites, respectively.

Ash trees with woodpecker holes were also more common in all three invasion stages in 2011 than in 2010. Woodpecker attacks were higher in Core sites than Cusp sites ($H = 249.28$; df = 2, 977; $P < 0.001$) (Table 3), but other differences were not significant. Trees with >6 woodpecker holes comprised 88, 75, and 30% of trees in Core, Crest, and Cusp sites, respectively. Trees with 1–6 woodpecker holes represented 3, 6, and 7% of trees in Core, Crest, and Cusp sites, respectively.

Discussion

Captures of EAB adults, larval densities on the trap trees, and the condition of ash trees in our sites effectively represented three temporal stages of the EAB invasion process. Populations of EAB were building in Cusp sites, peaking in Crest sites and declining in the Core sites during the years of our study. Populations of EAB clearly persisted in all eight Core sites in southeast Michigan, although adult EAB captures and larval densities were dramatically lower than in the Crest sites. A dendrochronological study encompassing 1.5 million ha showed EAB-caused ash mortality was widespread across this region by 2003 (Siegert et al. 2014). Past studies reported a high proportion of ash trees in a local area died over a 4–7 yr period after external signs of EAB infestation became apparent (Knight et al. 2013, Smith et al. 2015). This pattern was also confirmed in simulations derived from additional empirical data (Mercader et al. 2011, McCullough and Mercader 2012). Ash mortality in our Core sites continued to accumulate as trees that were severely declining in 2010 succumbed in 2011. Overall, nearly 80% of the ash trees (DBH ≥ 10 cm) were dead in 2011 and canopy dieback exceeded 50% on nearly half of the live trees in Core sites.

The dramatic reduction in live ash phloem available for EAB larval development in Core sites indicates the carrying capacity for EAB

in these areas is orders of magnitude lower than it was pre-invasion. On average, approximately 89 EAB adults can potentially develop per m^2 of ash phloem (McCullough and Siegert 2007). Larval densities recorded on girdled trees in the Core sites approached this level. Densities on the control trees were lower, although previous generations of larvae had likely consumed some portion of the phloem on many ungirdled ash trees, as evidenced by declining canopies and other symptoms. Ash regeneration was abundant in some of the Core sites (Burr and McCullough 2014) and if recruits and saplings continue to grow, suitable phloem could sustain local EAB populations for years. Green ash seedlings are fairly shade tolerant and may persist in the understory for more than 15 yr, but exposure to full or nearly full sun is necessary for recruitment into the overstory (Johnson 1961, 1975; Kennedy 1990). In a related study, Burr and McCullough (2014) reported lateral in-growth by canopies of non-ash trees occupied many of the canopy gaps resulting from overstory ash mortality, substantially reducing light available to young ash regeneration. The long-term future of green ash following EAB invasion, therefore, appears to depend on the ability of young ash trees to compete with other species for light and the ability of trees to tolerate low densities of EAB larvae.

The Crest sites represented the peak of the EAB invasion wave and exemplify the rate at which the EAB 'death curve' noted by Knight et al. (2008, 2013) can progress. At least five times as many adult beetles were captured in Crest sites and larval densities on the trap trees were roughly twice as high as in Core and Cusp sites in both years. Ash mortality increased markedly from 2010 to 2011 in Crest sites as declining trees succumbed. The relative densities of EAB in the Crest sites have implications for efforts to manage EAB or protect valuable ash trees. For example, in field trials with systemic insecticides, annual application of neonicotinoid products reduced EAB larval densities by ~55–70% (McCullough et al. 2011a). Whether this level of EAB control can adequately protect valuable ash trees from some amount of injury and decline will presumably vary, depending on EAB pressure, for example, the numbers of EAB ovipositing on the treated trees. Strategies such as lethal trap trees, in which a few ash trees are treated with a highly effective systemic insecticide then girdled to attract ovipositing EAB adults away from other ash trees, could perhaps be employed to reduce local EAB densities or as a means to diminish the EAB pressure on more valuable trees (McCullough et al. 2015, 2016; Mercader et al. 2015). Moreover, the increase in ash mortality in the Crest sites between 2010 and 2011 indicates that as EAB populations approach peak densities, delaying insecticide applications by even a year can have serious consequences for the local ash resource.

Changes in EAB populations and ash condition in the Cusp sites between 2010 and 2011 are particularly relevant to municipalities and private landowners in areas where EAB has recently been detected. There was little or no evidence of EAB presence in 2009 when the Cusp sites were selected and most ash trees still appeared healthy in 2010. Ash mortality and the proportion of trees with EAB signs such as woodpecker holes or epicormic sprouts roughly doubled between 2010 and 2011, paralleling the upsurge in captures of EAB adults and larval densities in these sites. These data illustrate the inadequacy of visual surveys to assess local EAB presence, distribution, and infestation rates. Regulatory surveys to detect EAB typically end once a state or county is determined to be infested, but local residents or land managers often have little information about the proximity of EAB to their property. Employing either double-decker traps or girdled ash trees to monitor local EAB distribution and population levels could provide adequate time to secure funding and initiate efforts to protect ash trees and slow EAB population growth.

The double-decker traps and the various trap trees used in our study provided different information about the local EAB populations. Detection rates, which are critical for assessing EAB presence and distribution, were greatest for the double-decker traps. At least 15 of the 16 double-decker traps in each of the three regions captured one or more EAB adults in both years. Previous studies have demonstrated the efficacy of the double-decker trap design relative to other artificial traps, including single prisms or funnel traps hung from branches in ash trees (McCullough et al. 2011a, Poland et al. 2011, Poland and McCullough 2014, McCullough and Poland 2017, Wieferich et al. 2017). Double-decker traps are placed in full sun among or near ash trees, providing a readily identifiable source of olfactory and visual cues, as well as exploiting the preference of EAB adults for sunny conditions (Poland et al. 2011, Poland and McCullough 2014, McCullough and Poland 2017). Captures of EAB adults on double-decker traps were consistently lower in 2011 than in 2010, which may be at least partially attributed to differences in lures used to attract beetles to the traps. In both years, the upper prisms of the traps were baited with *cis*-3-hexanol, a compound associated with ash foliage (de Groot et al. 2008). In 2010, the lower prisms were baited with a blend of Manuka oil and Phoebe oil but in 2011, only Manuka oil was used because the blend was not available. While compounds in both Manuka oil and Phoebe oil are similar to those emitted by ash bark or wood, Phoebe oil contains the compound 7-*epi*-sesquithujene, which increased EAB captures compared with Manuka oil alone in a previous field trial (Crook et al. 2008). Large-scale EAB detection surveys in the United States have largely abandoned both natural oils because of difficulties in acquiring consistent supplies and now rely on *cis*-3-hexenol lures (USDA APHIS 2017).

Although double-decker traps captured the highest numbers of EAB adults, when the area of trapping surface was standardized, sticky bands on girdled trap trees captured more EAB adults per m^2 than either the traps or the other trap trees in both years. Other field studies have shown girdled ash trees were considerably more attractive to EAB than baited prism traps hung in ash trees (McCullough et al. 2011b, 2015; Mercader et al. 2013, 2015) or ash trees stressed by other injuries or baited with attractive volatiles (McCullough et al. 2009a, b; Tluczek et al. 2011. Girdling alters volatile profiles emitted by ash trees (Rodriguez-Sanoa et al. 2006; Crook et al. 2008) and hyperspectral imaging has suggested girdling may also alter visual cues used by EAB adults (Bartels et al. 2008; Pontius et al. 2008) when locating hosts. Number of EAB adults that can be captured on any type of ash trap tree, however, is limited by the area and position of the sticky band. This is especially true for large trees where EAB leaf-feeding and oviposition activity are typically concentrated on leaf-bearing branches in the canopy, while the sticky band is 1–2 m aboveground (Cappaert et al. 2005; McCullough et al. 2009a, b).

Debarking the trap trees provided valuable information on EAB densities within sites and across the three regions. As in many previous studies, EAB females strongly preferred ovipositing on girdled ash compared with the relatively healthy control trees (McCullough et al. 2009a, b, 2015; Mercader et al. 2013; Siegert et al. 2017). Detection rates for girdled trees, that is, the proportion of girdled trees with at least one EAB larva, ranged from 87 to 100% in Core and Crest sites but increased from 62 to 87% in Cusp sites between 2010 and 2011. Previous studies have indicated preferential oviposition on girdled trees is most notable in recently infested sites where EAB beetles can readily differentiate between girdled and healthy

trees (McCullough et al. 2009a, b; Mercader et al. 2013). However, even in the Crest sites where a high proportion of ash trees were declining, larval densities were higher on girdled trees than other trap trees. Girdling ash trees destined for eventual removal has been suggested both as a means to retain beetles in a local area and to decrease EAB population growth by eliminating a portion of larvae before they can emerge as adults (Mercader et al. 2011, 2015, 2016; Siegert et al. 2017). Data from the Core and Crest sites suggest such a strategy could be beneficial even at relatively high EAB densities.

We anticipated the small, bare root ash trees acquired from a nursery and planted in each site would also attract EAB adults because of transplant and water stress. Detection rates, however, were low for the planted trees relative to the double-decker traps and the other trap trees. In the Cusp sites, only 12 and 18% of the planted trees had EAB larvae in 2010 and 2011, respectively. In contrast, larvae were tallied on 44 and 62% of the control trees and 62 and 87% of the girdled trees in the Cusp sites in 2010 and 2011, respectively. Although the small trees were easy to debark, the low detection rates and larval densities associated with these trees indicate they would not be reliable indicators of EAB presence or population levels in an operational program. This problem is also reflected in the linear regression models derived for densities of captured adults and larvae. While this relationship was significant for the planted trap trees, the slope and intercept parameters were substantially lower than those derived for the other trap types, potentially yielding overly conservative estimates of local EAB population levels.

Overall, EAB larval density was significantly and positively related to the density of EAB adults in all trap types combined at all sites in both 2010 and 2011, indicating adult trap captures generally reflected EAB population levels. While the linear relationships were significant ($P < 0.0001$ for all sites and all traps in both 2010 and 2011), the amount of variation explained by the linear models was fairly low ($R^2 = 0.27$ and 0.21 in 2010 and 2011, respectively). This indicates that while density of captured adults on sticky bands or traps can partially explain trends in EAB larval density, attack densities can vary substantially within a site. Numerous factors may affect attack density on individual trees, including characteristics such as bark texture (Anulewicz et al. 2008), size (Marshall et al. 2009), canopy position and exposure to sunlight (McCullough et al. 2009a, b). Not surprisingly, densities of larvae and captured adults were not significantly related where EAB populations were very low and the linear range of density values was limited, such as in the Cusp sites in 2010 or the Core sites in 2011. Local distribution of EAB, as well as adult captures, can be particularly spotty and uneven in low-density sites, resulting in relatively high variation that obscures any relationship. In the Cusp sites, for example, there was little relationship between adult captures and larval densities in 2010, whereas in 2011, when EAB populations were higher, this relationship was significant. In contrast, adult captures and larval densities in the Crest sites were significantly related in both years.

In both 2010 and 2011, slope and intercept parameters of the regression models were substantially lower for planted trap trees than for other trap types. This reflects the very low densities of larvae and captured adults on the planted trees and indicates the small planted trees would not be reliable for detecting EAB infestations or indicating population levels.

At least 56 species of native parasitoids attack *Agrilus* spp. larvae in North America (Taylor et al. 2012), but *Atanycolus* spp. and particularly *A. cappaerti* have emerged as relatively common native parasitoids of EAB larvae (Cappaert and McCullough 2009; Duan et al. 2012, 2015; Davidson and Rieske 2015; Abell et al. 2016; Duan and Schmude 2016). Many parasitoids detect plant volatiles induced by herbivorous insect feeding (Stowe et al. 1995, Gols and Harvey 2009) and parasitoids often exhibit a density dependent response to their hosts (Girling et al. 2011, Cotes et al. 2015). In our sites, *A. cappaerti* parasitism rates and densities were higher on girdled trees than on other trap trees in both years and were higher in the Crest sites than in the other two regions in 2010. Nearly 80% of the parasitoids we collected in 2010 and 67% of the parasitoids in 2011 were from the girdled trees, indicating this native parasitoid is responding to volatiles emitted from stressed ash trees (Rodriguez-Saona et al. 2006, Crook et al. 2008, de Groot et al. 2008), high EAB larval densities, or both. In 2011, parasitism rates were again higher in girdled trees than in other trap trees, but overall, parasitoid numbers were substantially lower than in 2010. We suspect that collecting parasitoids in 2010 from the trap trees, especially the girdled trees, may have depleted the local *A. cappaerti* populations available to parasitize EAB larvae in 2011. Two species that parasitize EAB larvae in China, *Spathius agrili* (Braconidae) and *Tetrastichus planipennisi* (Eulophidae), were imported for biocontrol of EAB in North America. Releases began in 2007 in multiple sites in southeast Michigan (Bauer et al. 2011, Gould et al. 2015) and additional wasps were released annually in areas near our Core and Crest sites. We observed no evidence of either Asian parasitoid when we debarked the trap trees in 2010 and 2011.

Woodpeckers cause more mortality of EAB larvae in North America than any other factor (Cappaert et al. 2005, Lindell et al. 2008, Tluczek et al. 2011, Jennings et al. 2013, Flower et al. 2014) and evidence of woodpecker predation on previous larval cohorts was apparent in our sites. Lindell et al. (2008) observed three common woodpecker species preying on EAB larvae in southern Michigan forests, including the downy woodpecker, *Picoides pubescens*, the hairy woodpecker, *Picoides villosus*, and the red-bellied woodpecker, *Melanerpes carolinus*. All three species are year-round residents in wooded habitats in central and southern Michigan (Brewer et al. 1991, Shackelford et al. 2000, Jackson and Ouellet 2002, Jackson et al. 2002). These species exhibit flexible foraging patterns in terms of tree size and may respond to pest outbreaks or other disturbances (Kilham 1965, Jackson 1970, Fayt et al. 2005, Covert-Bratland et al. 2006, Barber et al. 2008, Lindell et al. 2008, Covert-Flower et al. 2014). We observed woodpecker holes on an average of 93 and 73% of the trees tallied in 2011 in Core and Crest sites, respectively, and most of those trees had at least seven visible woodpecker holes. Rates of woodpecker predation, although highly variable among trees, typically increase as EAB larval density builds or canopy condition of infested ash trees declines (Lindell et al. 2008, Jennings et al. 2013, Flower et al. 2014). Between 2010 and 2011, the proportion of ash trees with at least one woodpecker hole increased in all of our sites, but jumped most notably in the Cusp region, where woodpecker holes were observed on an average of 20% of trees in 2010 but 41% of trees in 2011. Our qualitative assessments represent the accumulation of woodpecker holes rather than predation rates in a specific year. Previous studies have shown woodpeckers typically prey on late instar EAB over the winter and early spring (Duan et al. 2010, 2014; Tluczek et al. 2011; Jennings et al. 2013). Our trap trees were felled and debarked in fall, which likely precluded woodpecker predation of the current-year larval cohort in those trees.

Understanding the population dynamics of pest invasions, and factors that may affect population density and growth, is critical to developing sound pest-management strategies. Our data illustrate how densities of EAB larvae and adults surged in the recently infested Cusp sites, peaked in the Crest sites, and persisted at low levels in the Core sites where most host trees had died. While native natural

enemies accounted for some amount of EAB mortality in all three invasion regions, their densities were overwhelmed by those of EAB, even in the Core and Cusp sites. Given the rate of EAB population growth and ash decline observed in this and other studies (Knight et al. 2008, Klooster et al. 2014, Smith et al. 2015) and the natural dispersal of EAB adults (Mercader et al. 2009, 2012; Siegert et al. 2010, 2014), it seems inevitable that the invasion process observed in our sites will be repeated across much of the green ash range.

An integrated approach is clearly needed to reduce the economic and ecological impacts associated with EAB invasion (Poland and McCullough 2006, Herms and McCullough 2014, Mercader et al. 2015). Such strategies could incorporate systemic insecticides, both to protect individual landscape trees and to slow EAB population growth (McCullough et al. 2015, 2016; Mercader et al. 2015; Sadof et al. 2017). Girdled ash trees attract and retain EAB (Mercader et al. 2016, Siegert et al. 2017) and if debarked, provide useful information on EAB densities, development, and larval parasitism. Combining highly effective systemic insecticides with girdling can produce lethal trap trees that attract ovipositing EAB females but preclude larval development (McCullough et al. 2016). Biological control, including augmentation of native natural enemies and release of introduced natural enemies, is compatible with systemic insecticides and if integrated with other tactics, could perhaps generate additive or even synergistic effects on local EAB populations (Suckling et al. 2012, McCullough et al. 2015). Comprehensive EAB management, along with ash seed collection and preservation, and research on ash resistance, will likely be needed if green ash is to persist as a functional component in some forests in North America.

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