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White ash (*Fraxinus americana*) survival in the core of the emerald ash borer (*Agrilus planipennis*) invasion

Molly A. Robinett and Deborah G. McCullough

Abstract: Despite catastrophic ash (*Fraxinus* spp.) mortality observed by the mid-2000s in the epicenter of the emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire) invasion in southeast Michigan, we noticed numerous live white ash (*Fraxinus americana* L.) in some forests in this region. In 2015, we inventoried overstory trees and regeneration in 28 white ash sites spanning 11 counties. White ash survival ranged from 0% to 100% of stems. Overall, 75% of 821 white ash trees, ranging from 10.0 to 44.0 cm diameter at breast height, and 66% of the white ash basal area, ranging from 0.3 to 3.5 m²·ha⁻¹, were alive. Nearly all live white ash had signs of previous EAB colonization, but 83% had healthy canopies (≤10% canopy dieback). Green ash trees were recorded in 27 sites, but 92% were killed by EAB. Model selection indicated that variation in white ash survival was related to white ash abundance and distance of sites from the original EAB epicenter but not to green ash related variables or to the distance of sites from the Asian parasitoid release or recovery locations. Regeneration strata were dominated by white ash, suggesting that some white ash populations may persist in post-invasion areas.

Key words: invasive forest pest, *Agrilus planipennis*, EAB, *Fraxinus americana*, ash mortality.

Résumé : Malgré la mortalité catastrophique du frêne (*Fraxinus* spp.) observée depuis le milieu des années 2000 dans l'épicentre de l'invasion de l'agrile du frêne (AF) (*Agrilus planipennis* Fairmaire) dans le sud-est du Michigan, nous avons noté la présence de plusieurs frênes blancs (*Fraxinus americana* L.) vivants dans certaines des forêts de cette région. En 2015, nous avons inventorié les arbres de l'étage dominant et la régénération dans 28 frênaies à frêne blanc réparties dans 11 comtés. La survie du frêne blanc variait de 0 à 100 % des tiges. Globalement, 75 % des 821 frênes blancs de 10,0 à 44,0 cm au DHP et 66 % de la surface terrière en frêne blanc, variant de 0,3 à 3,5 m²·ha⁻¹, étaient vivants. Presque tous les frênes blancs vivants portaient des marques de colonisation antérieure par l'AF mais 83 % avaient une cime en santé (≤10 % de dépérissement du feuillage). Des frênes verts (*Fraxinus pennsylvanica* Marsh.) ont été recensés dans 27 frênaies, mais 92 % avaient été tués par l'AF. La sélection du modèle indiquait que la variation dans la survie du frêne blanc était reliée à son abondance et à la distance entre les frênaies et l'épicentre original de l'AF et non à des variables reliées au frêne verte, ni à la distance entre les frênaies et les endroits où le parasitoïde asiatique a été relâché ou les endroits où les arbres avaient récupéré. La strate composée de la régénération était dominée par le frêne blanc, indiquant que certaines populations de frêne blanc pourraient persister dans les zones où l'invasion est déjà passée. [Traduit par la Rédaction]

Mots-clés : ravageur forestier invasif, *Agrilus planipennis*, *Fraxinus americana*, mortalité du frêne.

Introduction

Emerald ash borer (EAB; *Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae), first discovered in 2002 in southeast Michigan, has become the most destructive and costly forest insect to invade North America (Aukema et al. 2011; Herms and McCullough 2014). To date, EAB populations are known to occur in 35 states and four Canadian provinces (Emerald Ash Borer Information Network 2018). Although EAB preferentially colonizes stressed ash (*Fraxinus* spp.) trees, it can also colonize and kill healthy ash trees in North America (Cappaert et al. 2005; Poland and McCullough 2006; McCullough et al. 2009a, 2009b). An extensive dendrochronological study showed that the North American EAB invasion likely originated in the Detroit suburbs of Westland and Canton, located in southeast Michigan, by the early 1990s (Siegert et al. 2014). Since then, this beetle, a native of Asia, has killed hundreds of millions of ash in forests and landscapes and threatens more than 8 billion trees in forests of the United States (US) (Poland and McCullough 2006; Pugh et al. 2011; Herms and

McCullough 2014; Morin et al. 2017). Recent estimates suggest that at least 10.7 billion US dollars will be spent by 2019 for removal or treatment of roughly half of the municipal ash landscape trees likely to be affected in the US (Kovacs et al. 2010). Ecological impacts associated with the EAB invasion in forested areas can include changes in species composition, light, temperature, and moisture availability, increased coarse woody material, and altered carbon and nitrogen cycling (Gandhi and Herms 2010; Flower et al. 2013a; Burr and McCullough 2014; Robertson et al. 2018; Wagner and Todd 2016).

Catastrophic levels of ash mortality, ranging from 80% to 99% of stems, have been recorded in forested sites dominated by green ash (*Fraxinus pennsylvanica* Marsh.) (Flower et al. 2013b; Burr and McCullough 2014), black ash (*Fraxinus nigra* Marsh.), and white ash (*Fraxinus americana* L.) in southeast Michigan and Ohio (Gandhi and Herms 2010; Knight et al. 2013; Klooster et al. 2014; Smith et al. 2015). Smith et al. (2015) evaluated an array of site- and stand-level variables from 2004–2007, but the only variable significantly re-

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lated to the rate of ash mortality was distance from individual sites in southeast Michigan to the core of the EAB invasion in the greater Detroit area. In sites where either green, black, or white ash trees were abundant, Klooster et al. (2014) reported ash mortality rates from 2005–2009 ranged from 40% to 99.7%. In a related study, Knight et al. (2013) noted that ash trees died somewhat more rapidly in stands with low ash densities than in stands with abundant ash, but overall, 25% of the ash trees were dead three years after the EAB infestation became apparent, and 99% of the ash trees were dead after six years.

Given the extent of ash mortality, particularly in forested areas, EAB parasitoids native to China have been imported into the US and Canada for classical biological control of EAB. Asian parasitoids were first released in sites in southeast Michigan in 2007 (Federal Register 2007; Bauer et al. 2008, 2015), and releases have continued in Michigan and other infested states and provinces (Duan et al. 2011, 2012b, 2013b; Gould et al. 2017; Abell et al. 2014; Bauer et al. 2015). Two species, the larval parasitoid *Tetrastichus planipennis* Yang (Eulophidae) and the egg parasitoid *Oobius agrili* Zhang and Huang (Encyrtidae) (Yang et al. 2006), have reportedly become established in some Michigan sites (Duan et al. 2013a, 2015; Bauer et al. 2015; Slager 2017). Parasitoid recovery or establishment information, however, is not available for many release sites.

While EAB can likely develop on all North American ash species (Herms and McCullough 2014), consistent interspecific differences in EAB host preference or host resistance have been observed. Green ash and black ash are consistently highly preferred and vulnerable hosts of EAB (Cappaert et al. 2005; Anulewicz et al. 2007, 2008; Rebek et al. 2008; Chen and Poland 2010), while healthy blue ash trees (*Fraxinus quadrangulata* Michx.) are less preferred (Tanis and McCullough 2012, 2015). White ash appears to be an intermediate host (Limback 2010; Tanis and McCullough 2015).

Although there is clearly substantial white ash mortality in areas of southeast Michigan (Gandhi and Herms 2010; Tanis and McCullough 2012; Knight et al. 2013, 2014; Klooster et al. 2014; Smith et al. 2015), interactions between white ash trees and EAB may be less consistent or perhaps more complex compared with those between green ash or black ash and EAB. In plantation studies, larval densities on green or black ash were two to five times higher than on similarly sized white ash trees (Limback 2010; Tanis and McCullough 2015). Similarly, Anulewicz et al. (2007) reported that green ash landscape trees were preferentially colonized over white ash trees in four residential areas where these species co-occurred in southeast Michigan.

Casual observations, along with scattered anecdotal reports, suggested that white ash trees in at least a few forested areas in the “core” of the EAB invasion in southeast and south central Michigan remained alive, despite at least 10–12 years of EAB presence (D.G. McCullough, personal observation). It was not clear, however, whether high rates of white ash survival occurred in other areas in this region or if this was limited to a few areas with an abundance of live white ash. We hypothesized that green ash, a preferred and highly vulnerable host of EAB, growing within or in close proximity to white ash dominated sites could affect white ash survival, either negatively or positively. For example, high numbers of beetles emerging from heavily infested green ash trees could subsequently colonize and kill white ash trees. Conversely, green ash trees could function as sinks by attracting most ovipositing EAB females, perhaps reducing pressure on less preferred white ash trees, particularly if intraspecific competition resulted in high mortality of larvae on the green ash. Distance to Asian parasitoid release and recovery sites or distance to the epicenter of the EAB invasion in the greater Detroit area could also influence white ash survival rates.

To address these questions, we identified and surveyed white ash in forested sites across much of the core area of the EAB invasion in southeast and south central Michigan. Our goals in-

cluded documenting the proportion of white ash alive, assessing the condition of the live trees within sites, and evaluating stand-related factors, including green ash presence or abundance, that could influence white ash survival. We also quantified regeneration in these sites to assess potential long-term species composition. Previous studies showed that in sites where nearly 100% of the overstory ash trees were killed by EAB, ash seed banks were rapidly depleted, and ash regeneration sharply declined (Burr and McCullough 2014; Klooster et al. 2014; Smith et al. 2015). Orphan cohorts, consisting of previously established seedlings and saplings too small to be colonized by EAB, remained, but competition with co-occurring species could limit recruitment of young ash to the overstory (Burr and McCullough 2014; Herms and McCullough 2014).

Methods

Site selection

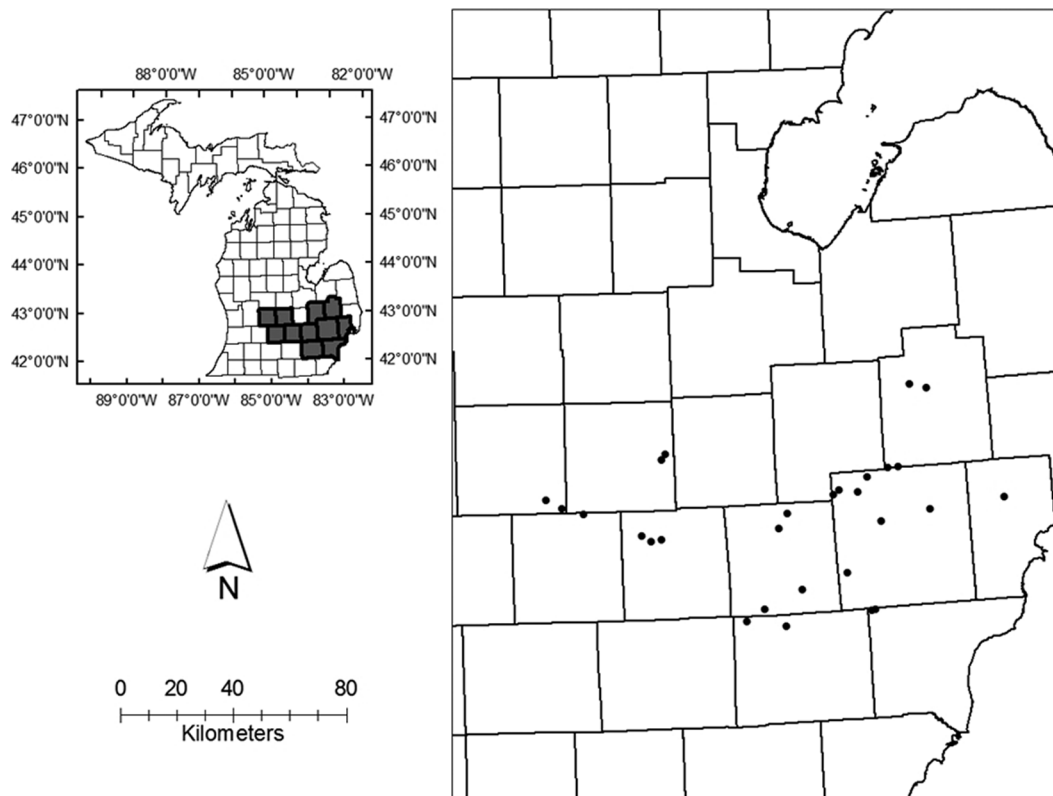
To avoid bias in site selection, we used an atlas to identify 70 areas of public forestland (state, county, or municipal property) spanning 11 counties in southeast and south central Michigan known to have been invaded by EAB at least 10–12 years earlier (Pugh et al. 2011; Siegert et al. 2014). Most areas were comprised of large state or county parks, recreation areas, or wildlife management areas with second-growth forests that had regenerated on abandoned agricultural land or following other disturbances. We queried area managers about the presence and distribution of white ash and excluded 30 areas where white ash was scarce or absent. In spring 2014, we scouted the remaining areas and selected 28 sites where white ash trees, live or dead, appeared to be relatively abundant (Fig. 1). There were no stumps or other evidence indicating that any ash or other tree species had been felled or removed in any of the sites. We then recorded coordinates of a center point established in the midst of the white ash trees in each site and delineated a rectangular 1 ha area around each center point. Four non-overlapping, circular macroplots with a fixed radius of 18 m were established in each cardinal direction from the center point within the 1 ha area using ArcMap 10.3.1 (Esri, Redlands, California, U.S.A., <https://www.esri.com/en-us/arcgis/about-arcgis/overview>). At the center of each macroplot, we established a subplot (7 m radius) to quantify recruits and saplings and a microplot (1.8 m radius) to survey seedlings.

Macroplots

Between late May and mid-August 2015, we recorded diameter at breast height (DBH) of all live and dead trees ≥ 10 cm DBH by species within each macroplot. Canopy dieback of live trees was visually assessed in increments of 10% in early to mid-summer after trees were fully flushed, where 10% indicated a nearly full, healthy canopy and 90% indicated a nearly dead canopy (Zarnoch et al. 2004). Standing dead ash were encountered in nearly all sites, but fallen ash trees and other forms of coarse woody material were scarce or non-existent within and beyond our plots. Counts of live and dead white ash trees overall and by DBH class in the four macroplots in each site were summed and standardized per hectare. Basal area ($\text{m}^2\text{-ha}^{-1}$) was calculated for live and dead trees for all overstory species, white ash trees, and green ash trees, when present. Relative importance values (RIV), which represent the sum of the frequency, dominance, and density of a species relative to all other species, was calculated for the five most abundant overstory species across sites and within each site following methods of Kent and Coker (1995).

Evidence of EAB colonization, including D-shaped exit holes left by emerging adults, larger holes left by woodpeckers preying on EAB larvae, and bark cracks over old larval galleries on tree trunks, were tallied. If callus tissue (i.e., wound periderm) or new xylem and bark were growing along the perimeter or over the top of old larval galleries, we categorized the galleries as “healing”.

Fig. 1. Location of 28 sites in southeast and south central Michigan surveyed in 2015 to assess white ash condition.



Asian parasitoid release and recovery data were acquired from the MapBioControl database, a geospatial framework established to monitor release, recovery, and spread of the introduced parasitoids (Gould et al. 2017; MapBioControl 2016). A total of 565 release sites and 107 recovery sites were identified in the Lower Peninsula of Michigan, including 103 release and 77 recovery sites in southeast and south central Michigan. Parasitoid recovery locations, however, were not necessarily locations where parasitoids were released, and the type and quality of data reported in MapBioControl varied considerably. Frequently, no information on parasitoid recovery was available for release sites, and conversely, recovery sites were not necessarily locations where parasitoids were released. Despite these limitations, we identified the parasitoid release and (or) recovery sites closest to each of the 28 sites that we surveyed.

Regeneration

Number and species of recruits (3.0–9.9 cm DBH) and saplings (DBH < 3.0 cm; height \geq 45.0 cm) were tallied by species in subplots (7 m radius), and number of seedlings (<45.0 cm height) were recorded by species in microplots (1.8 m radius) from May to August 2015. Ash and elm seedlings were recorded only to genus due to difficulty in distinguishing species. Recruit, sapling, and seedling counts from subplots and microplots were summed by species (or genus) and standardized per hectare for each site.

Statistical analysis

White ash trees were grouped into three DBH classes to assess survival rates of pole-sized trees (10.0–20.0 cm DBH), large and potentially merchantable trees (>30.1 cm DBH), and medium-sized trees (20.1–30.0 cm DBH). Severely declining overstory trees with \geq 80% canopy dieback appeared unlikely to recover and were classified as “dead” for analyses. Normality of residuals was evaluated using the Shapiro–Wilk test. A one-way ANOVA was used to determine if survival varied among size classes, and Tukey’s mul-

tiple comparison test was applied when ANOVA results were significant. Logistic regression was applied to further evaluate white ash survival in relation to tree size.

Stand-level variables and white ash survival

We conducted model selection to evaluate several stand-level variables as predictors of the percentage of white ash stems and white ash basal area alive in 2015. Potential predictor variables considered were basal area and stem density (stems per hectare) of white ash, green ash, and all overstory species combined (live and dead), and the distance from each site to the EAB origin near Westland, Michigan. Pearson’s correlation coefficients were calculated for potential predictors, and only variables with a correlation coefficient < 0.7 were included in the initial models to avoid multicollinearity. Generalized variance inflation factors (VIFs) were considered for the remaining predictor variables (Neter et al. 1996; Brunson et al. 2012), and competing variables with the highest VIF values were eliminated until all VIFs were <3.

We fit a set of competing models to our data and applied multimodel inference to assess the fit (Burnham and Anderson 2002). We used the Akaike information criterion corrected for small sample sizes (AICc; Shono 2000), as recommended when the ratio between n (the number of observations used to fit the model) and K (the number of parameters in the largest model) is <40 (Shono 2000; Burnham and Anderson 2002). To optimize model strength, we applied a multimodel dredging function (dredge) in the MuMIn package in R (available at <http://r-forge.r-project.org>) to assess valid combinations of variables to predict the percentages of white ash trees and basal area alive in the sites. We then included an exponentially distributed spatial autocorrelation term to evaluate the influence on parameter estimates of accounting for this term using the nlme package in R (available at <http://r-forge.r-project.org>). Diagnostics for the competing models were examined to check for normality of residuals and homoscedasticity by evaluating plots

Table 1. Total number and density of stems (≥ 10 cm diameter at breast height (DBH)), mean (\pm SE), minimum (min) and maximum (max) DBH, total basal area (live and dead), and mean (\pm standard error (SE)) total basal area of white ash and the five overstory species with the highest relative importance values (RIVs) recorded in macroplots in 28 sites surveyed in 2015 in southeast and south central Michigan.

Species	No. of trees			No. of trees-ha ⁻¹	DBH, mean \pm SE (cm); min, max	Total (live + dead) basal area (m ² ·ha ⁻¹)	Total (live + dead) basal area, mean \pm SE (m ² ·ha ⁻¹)	RIV
	Live	Dead	Total					
White ash	606	215	821	72	15.3 \pm 0.2; 10, 44	42.7	1.5 \pm 0.2	132.9
Green ash	21	352	373	33	17.8 \pm 0.4; 10, 53	27.9	1.0 \pm 0.2	88.7
Black cherry	301	32	333	29	18.6 \pm 0.5; 10, 65	26.9	1.0 \pm 0.2	79.5
American elm	220	76	296	26	17.1 \pm 0.5; 10, 77	20.4	0.8 \pm 0.2	75.4
Sugar maple	351	3	354	31	18.3 \pm 0.5; 10, 90	28.4	1.3 \pm 0.4	58.4
Red oak	212	3	215	19	26.1 \pm 0.4; 10, 92	35.8	2.0 \pm 0.5	52.7

^aRelative importance represents the sum of frequency, dominance, and density of a species relative to all other species (Kent and Coker 1995).

of fitted values vs. residuals, Q-Q plots, and Cook's distance plots. Model selection and residual diagnostics were conducted using the R statistical software (R Core Team 2017, <http://www.R-project.org>) at an α of $P < 0.05$.

To evaluate whether varying levels of white ash survival could be related to Asian parasitoid release or establishment, we used ArcMap 10.3.1 to measure the Euclidean distance between each of the 28 sites and the nearest parasitoid release or recovery site. Simple linear regression was applied to evaluate the relationship between white ash survival rates and distance to parasitoid release or recovery locations. All analyses were conducted using the R statistical software (R Core Team 2017, <http://www.R-project.org>) ($P < 0.05$).

Regeneration

We calculated stems per hectare by species and determined species richness within and across sites. We identified the five most frequently recorded species in each regeneration stratum (recruits, saplings, and seedlings) and then calculated total and mean (\pm standard error (SE)) density and relative frequency and density of these species. Number of recruit, sapling, and seedling species within sites were compared to overstory white ash survival rates and live white ash basal area using linear regression.

Additionally, we conducted a canonical correspondence analysis (CCA) to assess the relationship between stand-level variables and species composition of recruits, the regeneration class most likely to become overstory trees. The variables included were the percentage of white ash trees alive, white ash tree basal area (live + dead), green ash tree basal area (live + dead), and basal area of all live overstory species. We then conducted a Mantel test to evaluate the probability of a nonzero correlation between overstory species and recruit species assemblages using the *ade4* package in R (available at <http://r-forge.r-project.org>).

Results

Macroplots

We recorded 2856 live trees and 731 dead trees (DBH ≥ 10 cm) (total of 3587 trees), representing 44 different species across the 28 forested sites. This included 821 white ash, 373 green ash, and 2393 trees of other species. Trees that co-occurred with white ash averaged 20.7 \pm 2.0 cm DBH, and most (74%) were ≤ 25 cm DBH. Relatively abundant species co-occurring with white ash included green ash, black cherry (*Prunus serotina* Ehrh.), American elm (*Ulmus americana* L.), sugar maple (*Acer saccharum* Marsh.), and red oak (*Quercus rubra* L.) (Table 1). Green ash, found in 27 sites, and sugar maple, found in 22 sites, each accounted for approximately 10% of the total trees, but RIVs of the species were notably different (Table 1). Green ash was both frequently recorded and abundant in most sites, whereas sugar maple was less frequently encountered but abundant when it occurred. Black cherry, American elm, and red oak were recorded in 26, 26, and 18 sites, respectively, and

accounted for 9%, 8%, and 6% of the total stems, respectively (Table 1).

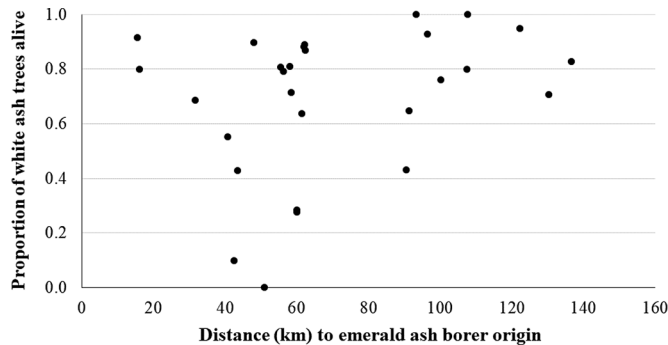
Dead trees co-occurring with white ash represented 18% of the total stems recorded but, with the exception of green ash, were generally scarce. We tallied 344, 76, and 30 dead green ash, American elm, and black cherry trees, respectively. Green ash accounted for 68% of all dead trees (mean DBH 17.9 \pm 0.46 cm). Dead American elm (mean DBH 19.0 \pm 1.1 cm) and black cherry trees (mean DBH 16.5 \pm 1.3 cm) were recorded in 18 and 9 sites, respectively, and accounted for 15% and 6% of the dead trees, respectively.

White ash survival rates varied substantially among sites, ranging from 0% to 100% of the stems recorded (Fig. 2), but across all sites, 75% of the white ash (≥ 10 cm DBH) were alive. At least 50% of the white ash were alive in 22 sites, and $\geq 80\%$ of the white ash trees were alive in 14 sites (Fig. 2). High white ash survival ($\geq 80\%$) was recorded in 5 of the 14 sites that were ≤ 60 km from the EAB origin near Westland, Michigan (Siegert et al. 2014), and in 9 of the 14 sites located 61 to 137 km from the EAB origin (Fig. 2). Most (83%), live white ash trees had $\leq 10\%$ dieback and 95% had $\leq 30\%$ canopy dieback (Fig. 3). Only 27 trees, representing $< 2\%$ of the white ash stems, were severely declining with $\geq 80\%$ canopy dieback (Fig. 3). These trees were heavily colonized by EAB, as evidenced by abundant adult EAB exits and bark cracks above old larval galleries on the trunk.

White ash survival varied with DBH, which ranged from 10.0 to 44.0 cm across the 28 sites. We recorded 685, 107, and 29 white ash trees in the pole-sized (10.0 to 20.0 cm DBH), medium (20.1 to 30.0 cm), and large (> 30.1 cm) DBH classes, respectively, which averaged (\pm SE) 13.1 \pm 0.1 cm, 24.1 \pm 0.2 cm, and 35.1 \pm 0.6 cm DBH, respectively. Overall, 77% of pole-sized trees and 63% of medium trees were alive. Only 45% of the large trees were alive, which was significantly lower than survival rates for trees in the two smaller DBH classes ($F_{[3,98]} = 6.42$; $P < 0.001$). Dead white ash trees averaged 17.2 \pm 0.5 cm DBH, which was slightly higher than the DBH of live white ash trees, which averaged 14.7 \pm 0.2 cm ($t = 4.61$, $df = 277.6$; $P < 0.0001$). Within sites, mean DBH of the white ash trees was negatively related to the proportion of those trees alive in 2015 ($F_{[1,26]} = 18.78$; $R^2 = 0.419$; $P = 0.0002$) (Fig. 4A). Results of logistic regression similarly indicated that larger trees had a lower probability of surviving EAB invasion than smaller trees ($P < 0.0001$) (Fig. 4B).

Total basal area of species co-occurring with white ash averaged 10.7 \pm 1.3 m²·ha⁻¹. White ash basal area (live and dead) averaged 1.5 \pm 0.2 m²·ha⁻¹ and ranged from 0.3 to 3.5 m²·ha⁻¹ within sites. Live white ash basal area averaged 1.0 \pm 0.2 m²·ha⁻¹ and comprised 66% of the total white ash basal area (live and dead) summed across all sites (42.7 m²·ha⁻¹). Green ash basal area (live and dead) averaged 1.0 \pm 0.2 m²·ha⁻¹ and ranged from 0 to 4.3 m²·ha⁻¹ within sites. Dead green ash basal area averaged 1.0 \pm 0.2 m²·ha⁻¹ and comprised 95% of the total green ash basal area recorded across all

Fig. 2. Proportion of white ash trees (≥ 10 cm DBH) alive in 2015 in 28 sites varying in distance (km) from the original epicenter of the emerald ash borer invasion.



sites ($27.9 \text{ m}^2 \cdot \text{ha}^{-1}$), while live green ash basal area averaged $0.2 \pm 0.05 \text{ m}^2 \cdot \text{ha}^{-1}$ across sites.

Signs of EAB colonization were apparent on all dead overstory white ash trees. Holes left by woodpeckers preying on late instar EAB larvae and small D-shaped exit holes left by EAB adults were readily apparent on >90% of the dead white ash trees, and bark cracks above old larval galleries were observed on 68% of the dead white ash. The dead green ash (344 trees) were also clearly killed by EAB; woodpecker holes, numerous EAB adult exit holes, and old larval galleries were present on all dead green ash.

Nearly all live white ash trees, however, had also been colonized at some point by EAB. Exit holes of adult EAB beetles, woodpecker holes, and old larval galleries beneath bark cracks were observed on the trunk of 37%, 53%, and 68% of the live white ash trees, respectively. Of the live white ash trees within individual sites, 8% to 81% had EAB exit holes, 35% to 100% had bark cracks above old larval galleries, and 6% to 67% had at least one visible woodpecker hole. We tallied a total of 418 old larval galleries on 616 of the 821 live white ash, including 69%, 64%, and 54% of trees in the pole-sized, medium, and large DBH classes, respectively. Similarly, 52%, 58%, and 69% of the live white ash in the pole-sized, medium, and large DBH classes had woodpecker holes, respectively. When we examined tree trunks, we could see that 62% of the live white ash in the pole-sized and medium DBH classes and 54% of the large DBH class trees had produced callus tissue (i.e., wound periderm) (Woodward and Pocock 1996) around the edges of galleries or were laying new xylem and bark over the top of old galleries. Overall, 91% of the old galleries visible on live white ash were classified as healing.

We tallied only 29 (17.2 ± 1.4 cm DBH; minimum = 11.4, maximum = 38.0 cm) live green ash trees across the 28 sites, and nearly all (93%) had at least five woodpecker holes visible on the trunk. Old larval galleries beneath bark cracks were present on 22 of the live green ash, but only two trees had produced callus tissue around one or more old galleries. A single live green ash tree (15 cm DBH) had no signs of EAB infestation. All live green ash trees had $\leq 50\%$ canopy dieback.

Models to predict white ash survival

White ash stems

We considered seven variables as potential predictors of survival rates for white ash stems, i.e., the proportion of white ash trees (≥ 10 cm DBH) in each site that were alive. Four variables were dropped because of multicollinearity, including basal area of dead green ash, total density of stems (live and dead) of all species, density of live stems of all species, and density of live green ash stems. The top model included two significant predictors: distance of the 28 sites to the EAB epicenter in Westland, Michigan, which was positively related to survival, and total basal area (live + dead) of all overstory species, which was negatively related to

survival (Table 2). Overall, the model explained 41% of the variability in the proportion of white ash trees alive in 2015 (Table 2). Including an exponentially distributed spatial autocorrelation term in our top model had relatively little influence on parameter estimates (Table 2).

White ash basal area

We considered 13 variables as potential predictors of the proportion of white ash basal area alive in the 2015 survey. Six variables were dropped because of multicollinearity, including basal area of dead green ash, density of live green ash stems, density of total stems (live and dead), density of total live stems, density of live white ash stems, and total (live and dead) white ash basal area. Two variables, density of total white ash stems, which was positively related to live white ash basal area, and density of dead white ash stems, which was negatively related to live white ash basal area, were included in the model, which explained 58% of the variability in the proportion of white ash basal area that was alive (Table 2). As before, the addition of an exponentially distributed spatial autocorrelation term to the model had little effect on model parameters.

We examined the relationship between white ash survival (percentage of stems alive) and distance between sites and the closest locations where Asian parasitoids of EAB were released and (or) recovered using simple linear regression. Distances between the white ash sites and the nearest parasitoid release or recovery site recorded in the MapBioControl database ranged from 0.09 to 47.70 km and from 0.04 to 47.90 km, respectively. Little variability in white ash survival rates could be explained by the distance of sites to locations where parasitoids were released ($y = -0.0007x + 0.714$; $F_{[1,26]} = 0.0291$; $R^2 = 0.001$; $P = 0.866$) or recovered ($y = 0.002x + 0.679$; $F_{[1,26]} = 0.244$; $R^2 = 0.009$; $P = 0.628$) (Fig. 5).

Regeneration

Recruits

Overall, 1601 recruits (DBH 3.0 to 9.9 cm) representing 25 species were recorded in the 28 subplots, but white ash dominated all three regeneration strata (Table 3). Density of white ash recruits was at least four to five times higher than densities of other species (Table 3), and white ash comprised 64% of all recruits tallied. Within sites, we recorded anywhere from 3 to 171 white ash recruits, all of which were alive. We recorded <10 white ash recruits in 5 of the 28 sites and >30 in 11 sites. In 18 sites, white ash recruits comprised $\geq 50\%$ of all recruits, while in one site, white ash comprised <20% of the recruits. This site also had the fewest white ash overstory trees and the lowest white ash basal area (live or dead). Results of linear regression, however, indicated that little variation in the density of white ash recruits in the subplots was explained by the percentage of white ash trees (≥ 10 cm DBH) alive in the macroplots ($y = 0.00005x + 0.677$, $F_{[1,26]} = 0.34$; $R^2 = 0.013$; $P = 0.56$) or by total white ash basal area (live and dead) ($y = -0.0003x + 1.686$; $F_{[1,26]} = 1.019$; $R^2 = 0.038$; $P = 0.32$).

Other species of recruits encountered in subplots generally reflected the presence of overstory tree species. American elm, hawthorn (*Crataegus* spp.), sugar maple, and black cherry, which were frequently tallied in the macroplots, collectively accounted for $\leq 8\%$ of the total recruits recorded. Green ash, an abundant, albeit mostly dead, overstory species, was nearly absent in the recruit stratum. A total of 21 live green ash recruits were recorded in 9 of the 28 sites. Seven sites had a single green ash recruit, while the two other sites had 14 recruits. No dead green ash recruits were encountered. Other species of recruits recorded in our plots included box elder (*Acer negundo* L.), black walnut (*Juglans nigra* L.), white oak (*Quercus alba* L.), and American beech (*Fagus grandifolia* Ehrh.), which collectively accounted for 12% of the recruits tallied. American elm recruits were recorded in 19 of the 28 sites, while none of the other species was recorded in more than 13 sites.

Fig. 3. Variability of live white ash tree (≥ 10 cm DBH) canopy dieback, recorded within 27 of the 28 sites in southeast and south central Michigan in 2015.

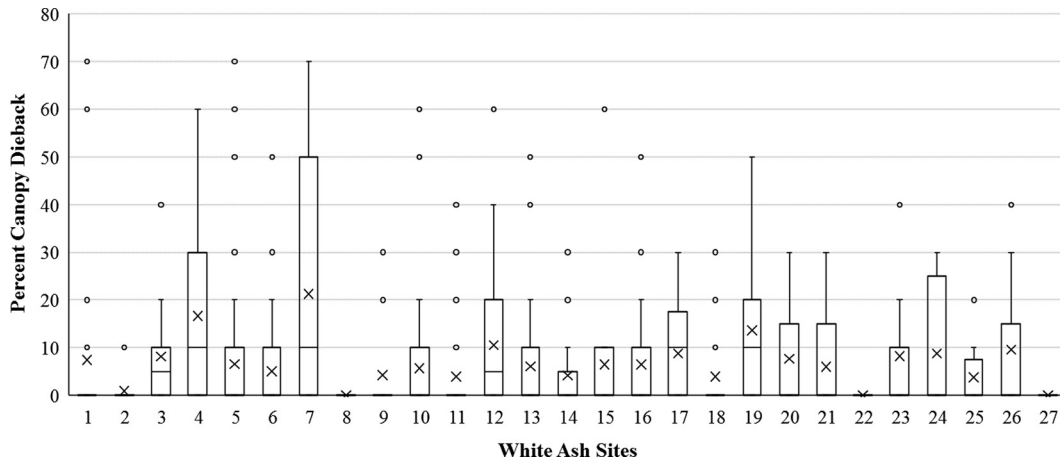
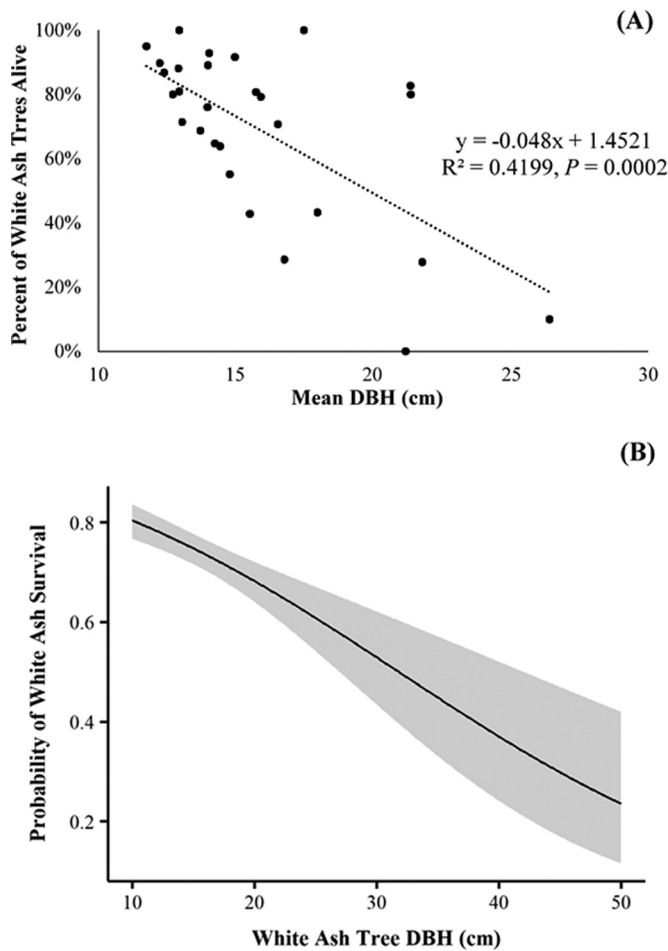


Fig. 4. Linear relationship (A) and logistic regression (B) between mean DBH (cm) of white ash trees and the proportion of white ash trees alive in 28 sites surveyed in 2015 in southeast and south central Michigan. The shaded area in the logistic regression (B) represents the 95% confidence interval around the predicted mean probability of white ash tree survival.



Saplings

A total of 2849 saplings (DBH < 3.0 cm; height ≥ 45.0 cm) representing 25 species were recorded in the subplots, but as with recruits, white ash accounted for 79% (2256) of the saplings and all

Table 2. Parameter estimates (\pm standard error (SE)), *t* values, and *P* values of stand-related variables in our top models to predict percentage of white ash stems ($F_{[2,25]} = 8.77$; $R^2 = 0.41$; $P = 0.001$) and white ash basal area ($F_{[2,25]} = 17.14$; $R^2 = 0.58$; $P < 0.001$) alive in 28 sites in Michigan surveyed in 2015 and with and without accounting for spatial autocorrelation.

Predictor variables	Estimate \pm SE	<i>t</i> value	<i>P</i> value
White ash survival – trees			
Without spatial autocorrelation			
Distance to EAB core (km)	0.003 \pm 0.115	6.52	0.022
Basal area of all species (m ² ·ha ⁻¹)	-0.021 \pm 0.005	-3.94	<0.001
With spatial autocorrelation			
Distance to EAB core (km)	0.003 \pm 0.001	1.84	0.077
Basal area of all species (m ² ·ha ⁻¹)	-0.020 \pm 0.006	-3.55	0.002
White ash survival – basal area			
Without spatial autocorrelation			
Dead white ash stems (ha ⁻¹)	-0.016 \pm 0.009	-1.85	0.077
White ash stems (ha ⁻¹)	0.017 \pm 0.003	5.82	<0.001
With spatial autocorrelation			
Dead white ash stems (ha ⁻¹)	-0.013 \pm 0.009	-1.51	0.144
White ash stems (ha ⁻¹)	0.017 \pm 0.003	6.02	<0.001

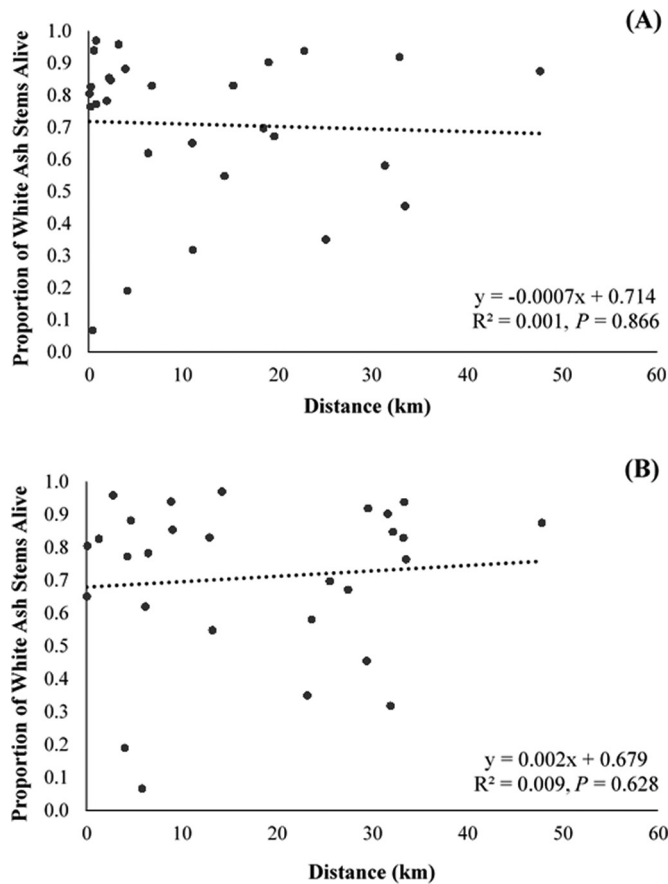
were alive. White ash saplings were present in all 28 sites, and average densities were at least four times higher than those of other species (Table 3). In 24 sites, white ash accounted for $\geq 50\%$ of all saplings, and in two sites, white ash accounted for 100% of the saplings. Little variation in the density of white ash saplings was explained by overstory white ash survival rates ($y = 0.001x + 0.591$; $F_{[1,26]} = 3.162$; $R^2 = 0.110$; $P = 0.08$) or white ash basal area (live and dead) ($y = 0.0002x + 1.236$; $F_{[1,26]} = 1.821$; $R^2 = 0.07$; $P = 0.189$).

Other sapling species tallied in the subplots included American elm, black cherry, sugar maple, and hawthorn (Table 3). As with recruits, green ash saplings were rare. A total of 10 live green ash saplings were present in four sites; no dead green ash saplings were recorded. American elm was encountered in 18 sites and represented 6% of saplings tallied. No other species accounted for more than 3% of the total saplings.

Seedlings

A total of 5973 seedlings (height < 45.0 cm) representing 24 species were tallied in the 28 microplots. Ash and elm seedlings were recorded only by genus due to the difficulty in differentiating species. Ash seedlings dominated all sites, accounting for 30% to 100% of seedlings within sites and 74% (4397) of all seedlings (Table 3). Survival rates of overstory white ash trees explained little of the variation in the density of ash seedlings ($y = -0.00001x +$

Fig. 5. Linear relationship between the distance (km) of 28 white ash sites surveyed in 2015 in southeast and south central Michigan to the nearest site where introduced EAB parasitoids were (A) released and (B) recovered.



0.717, $F_{[1,26]} = 0.032$; $R^2 = 0.001$, $P = 0.858$), but total white ash basal area (live and dead) did account for some of this variation ($y = 0.00001x + 0.963$; $F_{[1,26]} = 10.9$; $R^2 = 0.296$; $P = 0.003$). Other seedling species tallied in microplots included sugar maple, black cherry, hawthorn, and elm (Table 3). Sugar maple represented 8% of the total seedlings, and was present in 17 of the 28 sites. Elm represented ~2% of the seedlings and was present in 16 sites, black cherry and sugar maple seedlings were present in 17 sites, and hawthorn was recorded in 9 sites.

Discussion

A substantial number of white ash trees remain alive and healthy in forested areas in the core of the EAB invasion in southeast and south central Michigan, despite the relatively long history of EAB presence across this region. Although EAB was not discovered in North America until 2002, dendrochronological evidence showed that EAB was killing ash trees in the greater Detroit, Michigan, area by 1998 and ash mortality was widespread across southeast Michigan by 2003 (Siegert et al. 2014). Populations of EAB in the sites that we surveyed had ample time to build to densities capable of killing white ash trees, as evidenced by the nearly complete mortality of green ash trees encountered in the sites. Ten of the 11 counties encompassing our sites were quarantined for EAB by 2004, and the remaining county was quarantined in 2006 (Emerald Ash Borer Information Network 2018). We did encounter a site in which every white ash tree was dead, and in four other sites, more than half of the white ash trees had been killed by EAB, similar to the catastrophic ash mortality rates reported in other studies (Gandhi and Herms 2010; Tanis and

McCullough 2012; Knight et al. 2013; Burr and McCullough 2014; Klooster et al. 2014; Smith et al. 2015). Nevertheless, more than 65% of the white ash basal area and 75% of the white ash trees tallied across the 28 sites that we surveyed were alive, and nearly all of those trees (95%) had healthy canopies with less than 30% dieback.

We originally hypothesized that the presence of green ash, a highly preferred and vulnerable EAB host (Cappaert et al. 2005; Anulewicz et al. 2007, 2008; Rebek et al. 2008; Chen and Poland 2010; Limback 2010), could affect white ash survival, either positively or negatively. If green ash trees acted as a sink for EAB oviposition, the number of eggs laid on less attractive white ash might be reduced, particularly if larval survival on green ash trees was minimal because of intraspecific competition for phloem. Conversely, if high numbers of EAB adults emerged from green ash trees, nearby white ash trees could be heavily colonized as the green ash declined and succumbed, a pattern previously documented in plantations where green ash and white ash landscape trees co-occurred (Anulewicz et al. 2007). In addition, an abundance of green ash, which can grow in heavy, clay soils or in ephemeral flooded areas, could indicate that site conditions were less than optimal for white ash, which is more often found on upland mesic sites (Schlesinger 1990; USDA Natural Resource Conservation Service (NRCS) 2017). In our survey, more than 90% of the green ash trees, which were present in all but one site, were dead and had sloughing bark, discolored wood, and lacked fine twigs, indicating that they had been killed by EAB some years earlier. The 29 green ash trees that were alive were recorded in 10 of the 28 sites. While these live green ash trees had ≤50% canopy dieback, only one tree had no signs of EAB infestation. None of the green ash related variables tested in our model selection (total density of green ash stems, total green ash basal area, live green ash basal area), however, was a significant predictor of survival rates of white ash stems or basal area.

Differential survival of green ash and white ash trees in most of our sites is consistent with previous observations of interspecific variation in EAB host preference or host resistance. Both ash species appear to be highly suitable hosts for leaf-feeding by adult beetles and larval development in phloem and cambium (Cappaert et al. 2005; Anulewicz et al. 2008; Rebek et al. 2008; Pureswaran and Poland 2009; Chen and Poland 2010; Tanis and McCullough 2012, 2015). Although substantial research has been conducted on phenolic compounds, protein chemistry, and inducible responses of ash species that could affect EAB larval feeding (reviewed in Villari et al. 2015), host preferences of ovipositing female beetles appear to largely determine EAB larval densities and tree mortality rates. Field studies have shown that green ash is consistently colonized sooner and at higher densities than co-occurring white ash (Anulewicz et al. 2007; Limback 2010). For example, in a plantation study, 21 randomized blocks, each consisting of four ash species, were exposed to the local EAB population for a single season and then debarked in autumn (Tanis and McCullough 2015). All 21 green ash trees were heavily infested, with an average of 220 ± 40 larval galleries·m⁻². In comparison, larval densities on the 21 white ash averaged 41 ± 12 larvae·m⁻², and while three white ash trees were heavily infested, five white ash had no galleries.

Variation in white ash survival may be partially attributable to the size and density of the white ash trees, along with the basal area of co-occurring overstory species. Most white ash trees in the second-growth forests that we surveyed were ≤30 cm in DBH, and 75% of these small- and medium-sized trees were alive and healthy. Larger trees, which were not common, did not fare as well. Slightly less than half of the trees > 30 cm DBH were alive, and there was a negative relationship between average DBH and survival rates across sites. The underlying mechanisms driving this pattern are not clear. Although ash trees as small as 2.5 cm DBH can be colonized and killed by EAB (Cappaert et al. 2005;

Table 3. Mean (\pm standard error (SE)) density, frequency, and density relative to all species of the five most abundant recruit, sapling, and seedling species recorded in 28 sites surveyed in 2015 in southeast and south central Michigan.

Recruits	White ash	American elm	Hawthorn	Sugar maple	Black cherry
Mean (\pm SE) stems·ha ⁻¹	596 \pm 118.9	115 \pm 38.2	112 \pm 37.7	155 \pm 45.1	60 \pm 11.3
Mean relative frequency \pm SE	79 \pm 4.6	29 \pm 5.5	19 \pm 5.1	13 \pm 4.5	15 \pm 4.5
Mean relative density \pm SE	59 \pm 4.8	8 \pm 2.0	5 \pm 2.2	6 \pm 2.8	5 \pm 1.6
Saplings	White ash	American elm	Black cherry	Sugar maple	Hawthorn
Mean (\pm SE) stems·ha ⁻¹	458 \pm 34.3	97 \pm 22.5	74 \pm 22.2	81 \pm 22.4	66 \pm 16.3
Mean relative frequency \pm SE	90 \pm 3.5	35 \pm 6.5	22 \pm 5.4	16 \pm 5.6	16 \pm 5.0
Mean relative density \pm SE	74 \pm 4.4	6 \pm 2.4	3 \pm 1.2	2 \pm 0.8	1 \pm 0.7
Seedlings	Ash	Sugar maple	Black cherry	Hawthorn	Elm
Mean (\pm SE) stems·ha ⁻¹	10 186 \pm 1262.9	3495 \pm 1484.6	2153 \pm 329.4	2253 \pm 434.8	1112 \pm 279.8
Mean relative frequency \pm SE	93 \pm 3.0	30 \pm 5.9	37 \pm 7.0	15 \pm 4.9	27 \pm 5.0
Mean relative density \pm SE	69 \pm 4.4	6 \pm 2.5	9 \pm 2.7	2 \pm 1.2	2 \pm 1.0

Poland and McCullough 2006), some of the small trees that we tallied could have been too small for EAB to colonize during years when local EAB densities were peaking, i.e., as beetles emerged from declining and dying green ash trees (Knight et al. 2013; Burr and McCullough 2014; Klooster et al. 2014; Smith et al. 2015; Burr et al. 2018).

Captures of EAB adults on sticky bands or traps and EAB larval densities vary predictably between stressed and healthy trees (Marshall et al. 2009; Siegert et al. 2010; Mercader et al. 2013, 2015; Jennings et al. 2014; McCullough et al. 2015; Burr et al. 2018), open-grown and shaded trees (Anulewicz et al. 2007; McCullough et al. 2009a, 2009b), and among ash species (Anulewicz et al. 2007; Tanis and McCullough 2015), but relationships between tree size and either EAB adult captures or larval densities are less consistent. Further, at least 64%–9% of the live white ash trees in the pole-sized and medium DBH classes had clearly been colonized by EAB in previous years. Larger and presumably older white ash trees may have been less vigorous than smaller trees, perhaps attracting female EAB adults who preferentially oviposit on stressed ash trees (McCullough et al. 2009a, 2009b; Siegert et al. 2010; Tluczek et al. 2011; Mercader et al. 2013, 2015). Additionally, total basal area of all species was negatively related to white ash survival rates, which further suggests competition with other overstory species or less than ideal growing conditions for white ash corresponded to higher mortality.

Distance between sites and the epicenter of the EAB invasion in North America was also a significant variable included in our top model predicting the percentage of live white ash trees. Smith et al. (2015), who measured an array of stand-related variables in forested plots in southeast Michigan from 2004–2007, reported that distance to the EAB origin was the only variable significantly related to rates of ash decline and mortality. In a 2010–2011 study, green ash mortality decreased from sites in the EAB core in southeast Michigan, where an average of 79% of the ash were dead, to sites in southwest Michigan, where an average of 20% of the ash had died (Burr and McCullough 2014). In our study, the four sites where the lowest proportion of white ash were alive were approximately 40 to 60 km from the EAB epicenter, while three of the six sites where \geq 90% of the white ash stems and basal area were alive were \geq 100 km from the epicenter. Although EAB populations generally advanced outward from southeast Michigan, numerous satellite infestations were established in other regions of the state by human transport of infested ash firewood, nursery trees, and logs (Siegert et al. 2010, 2014). For example, one site where more than 30% of the white ash trees were dead, was 130 km west of the EAB origin.

While we did not attempt to directly assess parasitism rates by collecting bark to sample EAB eggs or debarking trees to expose EAB larvae, variability in white ash survival was not related to the distance between sites and locations where Asian parasitoids

were either released or recovered. Native parasitoids such as *Atanycolus* spp. as well as the introduced *Tetrastichus planipennis* can cause substantial larval mortality, particularly in heavily infested trees (Cappaert and McCullough 2009; Duan et al. 2011, 2013a; Bauer et al. 2015), but we are aware of no evidence that parasitoids have slowed ash mortality rates in North America (Abell et al. 2012; Bauer et al. 2015; Duan et al. 2015). Although *T. planipennis* is capable of dispersing a considerable distance, its short ovipositor (2.0–2.5 mm length) reportedly limits its ability to parasitize EAB larvae in branches and boles > 12 cm DBH (Liu et al. 2003; Abell et al. 2012; Duan et al. 2012a, 2013a). The quality of records in the MapBioControl database also varied considerably. Information on parasitoid recovery was lacking for many release sites, and recovery sites often did not correspond to locations where parasitoids were released. Although we found no evidence that EAB parasitism affected white ash survival, a limited amount of destructive sampling could be useful to evaluate parasitoid presence or parasitism rates in sites with high ash survival rates. Understanding how geographical features or forest structure may limit or enhance dispersal of the parasitoids introduced for EAB could also be helpful (Shigesada and Kawasaki 1997; Sharov and Liebhold 1998).

In previous studies, individual living ash trees in the midst of dead ash trees were occasionally observed in forested areas following EAB invasion (Knight et al. 2013). These “lingering” ash trees were assumed to exhibit at least some level of genetically based resistance to EAB (Koch et al. 2012, 2015; Knight et al. 2013, 2014). Efforts were undertaken to collect seeds or propagate tissue from these trees (Koch et al. 2012), although some of the lingering ash trees eventually succumbed (Knight et al. 2014). While the live green ash trees that we encountered in these sites may be consistent with the definition of “lingering” ash, we did not encounter individual lingering white ash trees, which were defined by Knight et al. (2014) as an individual healthy ash tree (>10 cm DBH) in a site where >95% of the ash were killed by EAB. In the four sites where 55%–80% of the white ash trees were dead, we still tallied four to seven live white ash trees in our plots. Moreover, on most live white ash, as well as the dead ash, we could readily observe evidence of past EAB colonization on the tree trunks, including holes left by woodpeckers preying on late instar EAB larvae, bark cracks over larval galleries, and exit holes left by emerged EAB adults. This indicates that while the trees are suitable EAB hosts, larval densities have not been high enough to cause mortality.

Ash trees, which are characterized by highly sectored xylem tissue (Zwieniecki et al. 2001; Tanis et al. 2012; Tanis and McCullough 2016), produced wound periderm (callus tissue) around the perimeter of longitudinal wounds on the trunk (McCullough et al. 2009a; Tanis and McCullough 2016) or laid new xylem over plastic plugs or wounds following trunk injections of insecticide (Herms and McCullough 2014; Tanis and McCullough 2016). In our study, ap-

proximately 90% of the live white ash trees had formed wound periderm around the perimeter of the old EAB larval galleries that were visible, re-establishing phellogen and cambial integrity (Mullick and Jensen 1973; Mullick 1977; Biggs et al. 1984). Whether this response, which presumably facilitates the ability of trees to recover from wounds such as EAB larval feeding, varies among ash species is not clear.

Whether white ash trees will continue to persist in areas of southeast and south central Michigan over the long term remains unknown. Nearly complete mortality of green ash trees in and near the sites that we surveyed suggest that the EAB carrying capacity and presumably the density of local EAB populations are substantially lower now than during the peak of the invasion. Nevertheless, EAB remains present in all of the sites that we surveyed (Robinett 2017), and densities could presumably build to damaging levels, particularly if trees are severely stressed by drought or other inciting factors such as severe defoliation.

White ash regeneration was abundant in all sites, indicating that these sites will retain a white ash component for some time. Mature white ash trees (≥ 20 years old) typically produce abundant seeds one out of every three years (Schlesinger 1990), and while seedlings are fairly shade tolerant, saplings and recruits require substantial sunlight (Wright 1965; Schlesinger 1990; Griffith 1991; NRCS 2017). White ash dominated not only the seedling and sapling strata, but also the recruits (3.0–9.9 cm DBH), which could potentially replace overstory trees that decline or die. In previous surveys in southeast Michigan and Ohio, nearly complete mortality of white ash, green ash, or black ash overstory trees corresponded to depletion of the relatively short-lived ash seeds in seed banks (Knight et al. 2013; Klooster et al. 2014; Smith et al. 2015), leaving only an “orphan cohort” of previously established ash seedlings and saplings. In contrast to the abundant white ash regeneration in our sites, green ash was not well-represented in any of the regeneration strata, despite often plentiful numbers of dead overstory green ash. While this partially reflects our plot locations, which were established in the midst of abundant white ash, the scarcity of live overstory or regenerating green ash suggests that this species could be effectively lost in these areas. Despite the somewhat bleak outlook for green ash in areas invaded by EAB, the generally healthy condition of most overstory white ash in most sites, along with the abundant white ash regeneration, is encouraging.

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