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INVASION NOTE

Attack dynamics and impacts of emerald ash borer on wild white fringetree populations

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Abstract North American forests have been heavily impacted from the loss of ash trees (*Fraxinus* spp.) due to emerald ash borer (EAB, *Agrilus planipennis*) invasion. Recently, white fringetree (*Chionanthus virginicus*), an ash relative, has been found to support the development of EAB in ornamental plantings, but interactions between EAB and this plant have never been examined in wild populations. We monitored two wild white fringetree populations in Ohio throughout the invasion wave of EAB to examine its impacts and factors that increased the likelihood of attack. Within 2 years of study initiation, the majority of white ash (*F. americana*) were attacked by EAB in these areas, in contrast to a few individual fringetrees. By the end of 5 years, however, EAB attacked up to 30% of white fringetrees and caused branch mortality in several individual plants. The percentage of white fringetrees attacked was significantly lower than in white ash trees, the majority of ash died due to EAB. Those fringetrees that were attacked displayed signs of stress, including epicormic branching and canopy thinning, both symptoms of larval damage by EAB. Our results provide the first reported findings of the dynamics and impact of EAB on wild white fringetree populations.

Keywords *Agrilus planipennis* · Attack wave · Novel host · White fringetree · *Chionanthus virginicus*

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Introduction

Invasive herbivores cost billions of dollars each year in economic damage (Pimentel et al. 2005), with forest pests causing an estimated 1.7 billion dollars annually (Aukema et al. 2011). Wood-boring buprestid beetles can be particularly problematic for evolutionarily naive plant hosts (Coleman and Seybold 2008; Muilenburg and Herms 2012; Herms and McCullough 2014). In particular, emerald ash borer (*Agrilus planipennis* (Fairmaire) Coleoptera: Buprestidae) is one of the most devastating North American invaders causing high mortality rates of ash wherever they grow naturally or were planted (*Fraxinus* spp. Lamiales: Oleaceae) (Aukema et al. 2011; Herms and McCullough 2014). The impact of EAB and other invaders can be perpetuated by the expansion of their host range to encompass novel plant species that can occur by ecological fitting (Janzen 1985; Agosta 2006; Cipollini and Peterson 2018). This process occurs where organisms colonize and survive in novel environments, resources, or associations with other taxa from the use of traits they currently possess in the novel environment (Janzen 1985; Agosta 2006).

Recently, EAB was found developing on a new host, white fringetree (*Chionanthus virginicus* (L.) Lamiales: Oleaceae), a close relative of ash trees (Wallander and Albert 2000), and the first confirmed non-ash host for EAB (Cipollini 2015). White fringetree is a large shrub or small tree native to the southeastern U.S. that is planted ornamentally across the eastern U.S. (Cipollini and Peterson 2018; Ellison et al. 2020). The extent to which these beetles will damage white fringetree is of concern because EAB kills the majority of susceptible ash trees in North America (Rebek et al. 2008; Herms 2014; Klooster et al. 2014). Examinations made at the height of the invasion wave of EAB revealed that about a quarter of the white fringetrees may be attacked on average at a given ornamental site (Cipollini 2015; Cipollini and Rigsby 2015; Peterson and Cipollini 2017; Ellison et al. 2020). Larval feeding mostly causes canopy thinning or branch mortality, but some individual trees can be killed (Peterson and Cipollini 2017; Ellison et al. 2020). Previous studies of the interaction of EAB with white fringetree in the field were limited to ornamentally planted trees, which grow in relatively optimal conditions, including open and sunny conditions with little to no competition, and with some management via pruning, mulching, or watering. In wild populations of white fringetrees, conditions are less optimal with trees growing in denser groupings in the understory in competition for light, space, and nutrients. Such stressors can influence plant susceptibility to attack (e.g. Folgarait et al. 1995; Peterson and Cipollini 2020), suggesting that white fringetrees in wild populations may be more impacted by EAB than those in ornamental settings.

Like on ash trees, signs of EAB attack in white fringetree include D-shaped adult exit holes, presence of larvae and/or adults, and serpentine larval feeding galleries containing larval frass, while symptoms of EAB attack include canopy dieback, epicormic branching, bark splits, and woodpecker holes (Cipollini 2015; Cipollini and Rigsby 2015; Peterson and Cipollini 2017). Epicormic branching, a shoot that arises from a dormant bud along the bark or branches, and canopy dieback are plant responses that can be caused by various agents, such as insects, pathogens, or abiotic stress (e.g. drought) (Matusick et al. 2012). Previous studies have associated symptoms like epicormic branching and canopy dieback with EAB attack in white fringetree, but in retrospective studies it is unclear if these symptoms were present before attack or were primarily a response to attack (Peterson and Cipollini 2017).

The goal of this research was to understand the dynamics of EAB attack on wild populations of white fringetrees where growing conditions are less optimal than in managed, ornamental plantings. In addition, we examined tree health characteristics before, during, and after the main invasion wave of EAB to examine which tree factors increased the likelihood of attack and which are primarily responses to attack. Two sites in southern Ohio with large populations of white fringetrees were monitored alongside white ash (*F. americana* (L.) Lamiales: Oleaceae) for 5 years. Plants were examined yearly for signs and symptoms of EAB attack and the results were related to tree health characteristics.

Materials and methods

White fringetree sites

We monitored two wild populations of white fringetree in southeastern Ohio from 2015 to 2019. At Vinton Furnace State Experimental Forest ("Vinton", GPS coordinates 39.202414, − 82.390920), owned by the Ohio Division of Forestry and co-managed by the US Forest Service Northern Research Station, 33 white fringetrees were marked along with 16 white ash trees growing nearby. On a private property near Jackson ("Jackson", GPS coordinates 39.084863, − 82.621561), another 31 white fringetrees with four white ash trees growing nearby were marked. No visual signs of EAB were detected on any of our study trees at these sites in 2015, but in 2016, we captured 27 EAB on prism traps baited with Manuka oil (SI Fig. 1). This indicates that beetles were in the area by 2015 but had not yet visibly affected any of our study trees. Thus, our monitoring of study trees started prior to or just at the start of EAB impacts in the area and progressed through the main invasion wave.

Field examinations

White fringetrees and white ash trees were examined for signs and symptoms of EAB infestation once each year from 2015 to 2019 in early August, except in 2015 when examinations occurred in September. Signs of EAB were determined by searching trees for D-shaped exit holes or apparent serpentine galleries (indicated by characteristic bark swellings over galleries, Cipollini 2015) during the 2015–2018 seasons. These passive methods of searching for EAB were used initially because debarking the plants for more thorough examinations could stress the trees and likely influence attack rates and damage by any potential feeding larvae (Peterson and Cipollini 2020). In 2019, the final year of monitoring, we expanded our search on white fringetrees for signs of EAB by removing small areas of bark tissue with wood chisels to reveal feeding larvae or galleries in the bark over suspected areas (see Thiemann et al. 2016; Peterson and Cipollini 2017). Thus, signs of EAB on plants that we observed were conservative, qualitative measurements and not quantitative within individual trees since we were unable to destructively harvest and/or debark entire trees to quantify galleries. In addition to measures of EAB attack, tree diameter was measured at 1.3 m above ground for white ash trees, while the largest stem of white fringetree was measured at 10 cm above the soil line, since this plant has multiple main stems and branches divide several times at or below 1.3 m. Canopy health was rated on the amount of dieback that trees exhibited based on the ash tree rating system (see Smith 2006; Gould et al. 2015 for details), 1 = 0–12% dieback; 2 = ~ 13–37% dieback, 3 = ~ 38–62% dieback, 4 = ~ 63–87% dieback, and 5 = ~ 88–100%. Purple prism traps with manuka oil lure were placed at each site and year in a white ash and white fringetree to observe for the presence of EAB. For white fringetrees, presence or absence of epicormic sprouts was also recorded.

Statistical analysis

Data were analyzed using SAS (SAS Studio, SAS Institute Inc., Cary, NC). Fisher's Exact tests (PROC FREQ) were used to compare EAB attack (presence or absence) of white ash and white fringetrees within sites, among sites, and among overstory and understory ash at Vinton. PROC LOGISTIC was used to run a binary regression of the relationships of epicormic sprouting (present or absent), basal diameter of the largest stem (proxy for plant size), crown dieback, site, and with EAB attack of white fringetrees by EAB (yes or no). All models were run from the full model to those with only select variables and the model with the lowest Akaike information criterion (AIC) was selected and presented. PROC GLM was used to compare canopy dieback and epicormic branching over sampling years between attacked and unattacked white fringetrees. Data were normal except for the comparison using a T-test, (PROC TTEST) to compare canopy dieback among attacked white fringetrees with EAB exit holes and those without exit holes. Welch's T-test was used since sample sizes were unequal and data were non-normal.

Results

Attack by EAB on white ash was significantly higher through time than that on white fringetree at both the Vinton (Fig. 1; $\chi^2 = 67.65$; $df = 1$; $p \leq 0.001$) and Jackson sites ($\chi^2 = 23.66$; $df = 1$; $p \leq 0.001$). White ash showed signs of attack by 2016, which was at least a year earlier than shown by white fringetree at both sites, and cumulative EAB attack by the end of 2019 on white ash was substantially higher than on white fringetrees across sites (Fig. 1; $\chi^2 = 18.90$; $df = 1$; $p < 0.001$). The first indication of attack on white

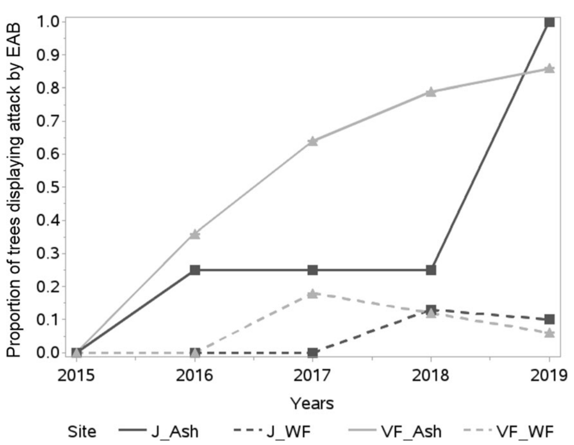

Fig. 1 Proportion of white fringetrees (WF; *Chionanthus virginicus*) and white ash (Ash; *Fraxinus americana*) present at each site that displayed attack by emerald ash borer (*Agrilus planipennis*) from 2015 to 2019 at two sites in southeastern Ohio, USA: Jackson (J) and Vinton Furnace (VF)

fringetree was found in 2017 at Vinton and in 2018 at Jackson. EAB attacked a similar cumulative percentage of white fringetrees at Vinton (33.3%) and Jackson (22.6%) (χ^2 = 0.91; *df* = 1; *p* = 0.410). White ash trees were more abundant at the Vinton site, including both larger, overstory trees (n = 9) and smaller understory trees (n = 5). There, the smaller ash trees in the understory were attacked at similar rates (n = 2/5, 40%) as similarly-sized white fringetrees (n = 11/33, 33.3%) (χ^2 = 1.33; *df* = 1; *p* = 0.337). Traps captured EAB each year with more observed in white ash then white fringetrees (SI Fig. 1) and overall more were captured at Vinton than Jackson. By the end of the study, all of the overstory white ash at Vinton were attacked and killed by EAB, a significantly higher rate than the one understory white ash that was killed (χ^2 = 10.08; *df* = 1; *p* = 0.005). We monitored four ash trees at Jackson; all were attacked by 2019 with one overstory ash being killed by EAB and a second one displayed a high degree of dieback (50%) caused by EAB damage. No white fringetrees were killed at either site during the course of this study.

The binary regression model with the lowest AIC contained the variables of sample year, stem diameter, canopy dieback, and epicormic branching. Epicormic branching was significant (χ^2 = 7.83, *p* = 0.005) with fringetrees showing this symptom being 4.63 times more likely to be infested with EAB than trees with no epicormic branching. Dieback on white fringetrees was also significant (χ^2 = 5.30, *p* = 0.021) with plants being 12.62 times more likely to be infested with EAB for each 25% loss of canopy.

Overall, the proportion of white fringetrees showing epicormic branching was significantly different among attacked and unattacked trees through time (Fig. 2; F = 8.44; *df* = 9, 376; $p \leq 0.001$), with a higher proportion of attacked white fringetrees displaying epicormic branching than unattacked trees (F = 58.77; *df* = 1; $p \leq 0.001$). This proportion varied among years (F = 3.23; *df* = 4; *p* = 0.013), but there was no interaction between years and attack status (F = 1.00; *df* = 4; *p* = 0.407). A similar pattern was observed for canopy dieback over the years (Fig. 3; F = 14.97; *df* = 9, 376; $p \leq 0.001$), with canopy dieback being significantly higher in attacked than in unattacked white fringetrees (F = 20.53; *df* = 1; $p \leq 0.001$). There was variation among years in this trait as well (F = 19,68; *df* = 4; $p \leq 0.001$), but there was no interaction between year and attack status

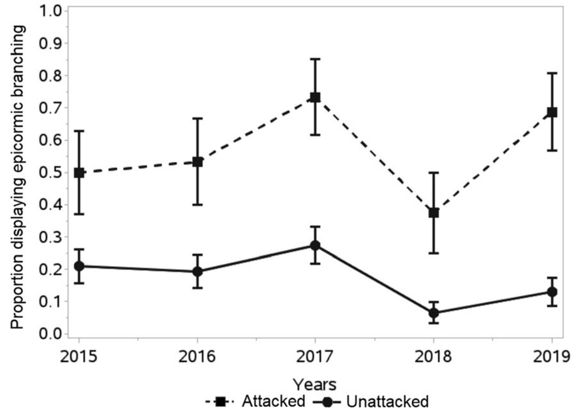

Fig. 2 Average (± SE) proportion of white fringetrees (*Chionanthus virginicus*) displaying epicormic branching overtime (2015–2019) that were attacked or unattacked by emerald ash borer (*Agrilus planipennis*) by end of survey study at two field sites in southeastern Ohio, USA

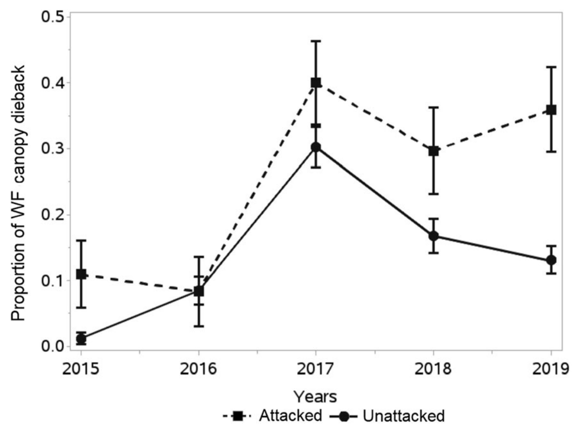

Fig. 3 Average (± SE) proportion of canopy dieback of white fringetrees (WF, *Chionanthus virginicus*) that were attacked or unattacked by emerald ash borer (*Agrilus planipennis*) by end of survey at two field sites in southeastern Ohio, USA

(F = 2.28; *df* = 4; *p* = 0.060). Among attacked white fringetrees, those that were found to have exit holes displayed a higher proportion of canopy dieback, 0.46 ± 0.08 (t = 2.22; *df* = 17; *p* = 0.040) in contrast with 0.18 ± 0.08 in those that had EAB galleries, but no exit holes.

Discussion

Emerald ash borer is a destructive pest of North American ash tree species (Herms and McCullough 2014). When EAB was found attacking white fringetree in 2014 (Cipollini 2015), the potential impact was concerning since another North American tree could face extinction. White fringetrees in ornamental landscapes are attacked by EAB across their co-occurring ranges in the U.S. (Peterson and Cipollini 2017; Ellison et al. 2020), yet attack rates are lower than those on susceptible ash tree species (Rebek et al. 2008; Herms 2014). Additionally, while most susceptible ash are killed by EAB, white fringetrees show signs of recovery after the beetle invasion wave passes and attack declines (Ellison et al. 2020). These studies suggest that EAB is less destructive to fringetree than susceptible ash trees, at least in ornamental sites. But, these studies were retrospective, leaving questions unanswered such as when does EAB begin to attack white fringetrees in relation to ash trees, what tree or site factors increase the likelihood of attack, and how do attack dynamics change through time? Previous studies were also conducted on planted white fringetrees growing in managed landscapes, whereas the fate of wild trees in unmanaged systems was unstudied. To address these questions, we examined attack dynamics of two wild fringetree populations throughout the invasion wave of EAB.

Attack by EAB on white fringetrees is generally less frequent than on susceptible ash trees (Rebek et al. 2008; Herms 2014; Cipollini 2015; Peterson and Cipollini 2017). Our data supports this observation since EAB attacked and killed nearly all of the ash trees at both sites, while $\leq$ 30% of the white fringetrees were infested by EAB, with most evidence of attack occurring as observations of single exit holes or one or a few larval galleries. At the Vinton site, all of the overstory white ash were killed compared to only 20% of the smaller ash trees in the understory. When understory ash and white fringetree of similar size growing under the same conditions were compared, cumulative infestation rates were similar, suggesting that EAB attacks these hosts at similar levels when they are the same size. If true, the similarity in attack among white ash and white fringetree could be associated with adult attraction via volatiles since females appear to find host volatiles of white fringetree (Peterson et al. 2020) as attractive as a highly preferred ash species, green ash (*F. pennsylvanica*; Pureswaran and Poland 2009; Rigsby et al. 2014). We also found that EAB use of white fringetrees was observable within 1–2 years after observable attack on ash. This supports previous assertions from retrospective studies in ornamental settings (Cipollini 2015; Thiemann et al. 2016) that EAB starts to attack white fringetrees shortly after they are encountered, not only when ash hosts have been exhausted.

White fringetrees that are attacked by EAB are more likely to show signs of stress (Peterson and Cipollini 2017; Ellison et al. 2020). Epicormic branching and canopy dieback are both plant stress responses which can be caused by EAB, and these factors increased the likelihood of attack on white fringetrees in this study, as they were shown to do in earlier studies (e.g., Peterson and Cipollini 2017). Larval feeding could have produced these plant stress responses in white fringetree; alternatively, these indicators of stress may have already been present on white fringetree and led to increased attraction to adults and susceptibility to larvae (Liu et al. 2003; McCullough et al. 2009). In our study, white fringetrees that ended up being attacked at some point by EAB showed a higher proportion with epicormic sprouting, and a slightly higher percent canopy dieback, at the start of the study before beetles presumably impacted the plants. However, our study is limited to two sites in southern Ohio and the number of attacked white fringetrees was limited; thus, future studies are needed to expand upon the attack preference of EAB for healthy and stressed fringetrees. But, female fitness would benefit from the selection of stressed white fringetrees for oviposition since larval survival and performance can increase on stressed white fringetrees (Peterson and Cipollini 2020).

The presence of exit holes on several wild fringetrees in this study clearly demonstrates that beetles can succeed on this plant, as observed in ornamental settings (Cipollini 2015; Peterson and Cipollini 2017, 2020). The success of the larvae could have been facilitated by stress, and fringetrees with exit holes exhibited a higher degree of stress than fringetrees with only larval galleries. As seen in other studies (Peterson and Cipollini 2017; Ellison et al. 2020), the health impacts of EAB on white fringetree were lower than on susceptible ash species. No white fringetrees were killed by EAB during this study, although some mortality has been noted in studies of ornamental trees (Peterson and Cipollini 2017; Ellison et al. 2020). More often, individual stems and branches can be killed by EAB, which we observed in this study, along with canopy thinning. If attack declines as beetle density declines, as observed in ornamental settings

(Ellison et al. 2020), we would expect the health of previously attacked trees to improve through time.

Overall, our observations of attack dynamics and impacts of EAB on wild white fringetree largely support previous findings and assertions made in ornamental landscapes (Peterson and Cipollini 2017; Ellison et al. 2020). In addition, we confirmed that EAB attacks white fringetree shortly after it is encountered and not only after ash trees have been exhausted, at similar rates as ash trees when controlling for tree size, and that a higher proportion of trees showing signs of stress at the onset of invasion will get attacked. Fringetrees in this study were directly adjacent to ash trees, so proximity of hosts may have been one reason we observed attack on fringetree. But, fringetrees that are more distant to ash hosts are also attacked by EAB in ornamental settings (Peterson and Cipollini 2017; Ellison et al. 2020) so we anticipate that EAB would similarly have the capacity to find and select fringetrees that are far from ash hosts. While white fringetree in our study met a better fate than the susceptible white ash, investigation into other geographic regions where white fringetree grows naturally could reveal differing patterns where climate, genetics, or other factors could change the impact of EAB on this novel host.

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Author contribution Both authors contributed to the study conception and design. Material preparation, data collection, analysis and first draft writing were performed by Donnie Peterson. Both authors commented and edited previous draft and approved the final manuscript.

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Data availability The data generated from this study are available from the corresponding author on request.

Declarations

Conflict of interest The authors declare that they have no conflict interest.

Ethics approval Not applicable.

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