

Article

Forest Regeneration Following Emerald Ash Borer (*Agrilus planipennis* Fairemaire) Enhances Mesophication in Eastern Hardwood Forests

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Abstract: Emerald ash borer (EAB, *Agrilus planipennis* Fairemaire) is a phloem-feeding beetle that was introduced into North America in the late 20th century and is causing widespread mortality of native ash (*Fraxinus*) species. The loss of an entire genus from the forest flora is a substantial disturbance, but effects vary because of differences in *Fraxinus* dominance and remaining vegetation. At three sites near the center of the North American EAB range, we investigated the impacts of *Fraxinus* mortality on recruitment of woody and non-native vegetation in 14 permanent plots from 2012 to 2017. We used the change in relative *Fraxinus* basal area to determine the impact of EAB on density of woody species and non-native vegetation less than 2.5 cm diameter at breast height (dbh). Changes in canopy cover were not correlated with loss of *Fraxinus* from the overstory, and only the density of shade-tolerant shrubs and saplings increased with *Fraxinus* mortality. Both native and non-native shrub species increased in density at sites where they were present before EAB, but no new invasions were detected following *Fraxinus* mortality. These shifts in understory vegetation indicate that *Fraxinus* mortality enhances the rate of succession to shade-tolerant species.

Keywords: *Fraxinus*; *Agrilus planipennis* Fairemaire; mesophication; forest regeneration; disturbance

1. Introduction

In the nearly two decades since emerald ash borer (EAB, *Agrilus planipennis* Fairemaire) was first detected in North America [1], the response has evolved from preventing or mitigating damage to *Fraxinus* [2–4] to understanding how the introduced insect might impact other species and ecosystem function in forest communities [5–7]. Forest plant communities of eastern North America, like any system, are dynamic and subject to change, and EAB's impact on *Fraxinus* is not exceptional. By inducing *Fraxinus* mortality, EAB immediately reduces forest stand basal area and releases resources, which subsequently become available to other species [8–10].

As a component of mesophytic forests of eastern North America, particularly those within Eastern US Lowland Forest Region—Upland Forest Types [11], *Fraxinus* species might well be considered a minor component of the system, represented primarily by *F. americana* L. and *F. pennsylvanica* Marshall [12]. But these species have a wide distribution, and despite their relatively low abundance in this forest type [12], the loss of *Fraxinus* by EAB has the potential to drive changes in plant communities throughout the region, similar in respect to previous introductions that changed forest composition on a broad scale. Chestnut blight (*Cryphonectria parasitica* (Murrill) Barr) led to the widespread loss of *Castanea dentata* (Marshall) Borkh. throughout its native North American range, particularly in the Appalachian region [13], and Dutch elm disease (*Ophiostoma ulmi* Buisman (Melin

and Nannf.), *O. novo-ulmi* Brasier) reduced *Ulmus* species to minor understory tree species in mesophytic forests across the continent [14]. More recently, the exotic insects hemlock woolly adelgid (*Adelges tsugae* Annand) and beech scale (*Cryptococcus fagisuga* Lindinger) are influencing the structure and composition of eastern North American forests [15]. In all instances, the change in canopy structure associated with the loss of individual trees has been marked by a shift to increasing dominance of shade-tolerant species in the understory and overstory layers [15–20].

Because the loss of *Fraxinus* from the canopy is similar to that of these species, we might expect similar responses in the understory. Indeed, in regard to changes already described in Ohio and Michigan, where EAB was initially detected and where *Fraxinus* is a relatively important component of the forest ecosystem, the loss of *Fraxinus* from the canopy induced growth of intermediate canopy trees, especially shade-tolerant *Acer* and *Ulmus* [8]. Trees from these genera existed in the canopy prior to EAB and were better able to utilize resources in EAB-induced gaps than trees from other genera, including *Quercus* and *Carya* [8,21–23]. Even in wetter sites, preinvasion surveys indicate that co-dominant shade-tolerant trees are predicted to replace *F. nigra* (Marshall) in Ohio, Michigan, and Minnesota [24–26].

This pattern of change after pest-induced canopy loss generally follows predicted plant community succession from shade-intolerant and intermediate-tolerant species to dominance by shade-tolerant species. This continued process of transition in eastern North American forests has been termed “mesophication” [27], and these changes in canopy composition come with cascade effects and positive feedback on ecosystems, including changes to flammability, soil moisture, nutrient dynamics, decomposition, and forest regeneration [28–30]. EAB-induced *Fraxinus* mortality is likely hastening the process.

Since *Fraxinus* received scant attention prior to EAB, little is known about the long-term response of woody species at the ground level to the release of resources following the loss of *Fraxinus* trees. Initial descriptions of the seedling layer in EAB-impacted forests primarily show shade-tolerant species, including *Acer rubrum* L., *A. saccharum* Marshall., *Ulmus americana* L., *Prunus serotina* Ehrh., and *Quercus rubra* L. [9,23,24,31], but evidence of their persistence over time is lacking, and interactions between native woody seedlings and exotic invasive plants may further influence the composition of forests. Recent evidence suggests that existing invasive plants will increase in size following the release of resources by EAB-induced *Fraxinus* mortality [9].

We seek to understand the changes in richness and abundance of woody species, including their invasive competitors, in the years following EAB invasion. Specifically, we examine forest regeneration at the seedling and sapling layers, including the recruitment of seedlings into the sapling layer over a 5-year period following infestation. In addition, we are investigating shifts in the abundance of woody invasive species, especially those that compete with woody seedlings and saplings and have the potential to alter successional trajectories. We hypothesize that EAB indirectly increases the prevalence of shade-tolerant species in the understory, thus enhancing the process of mesophication.

2. Materials and Methods

2.1. Study Sites

Our 4 study sites are located in the deciduous forests of eastern North America and are associated with 3 colleges and universities: Baldwin-Wallace University (BW; Ohio), University of Findlay (UF; Ohio), and Washington & Jefferson College (WJ; Pennsylvania; Figure 1). All sites contain *Fraxinus* spp. but are generally dominated by other deciduous tree species (Table 1). Total basal area by plot ranges from 18 to 54 m²·ha^{−1}, including substantial differences in relative contributions of *Fraxinus* (Figure 2). Year of EAB detection was determined by decline of the *Fraxinus* canopy and confirmed by the presence of EAB exit holes. Only 1 site at UF is located in a floodplain; the rest are upland sites. Across these 4 sites, mean growing season length varies from 159 to 173 days, mean precipitation varies

from 847 to 1132 mm, and mean annual temperature varies from 9.6 to 11.8 °C (Table 1). Soils are predominantly finer textured, from silty loam to silty clay loam [32].

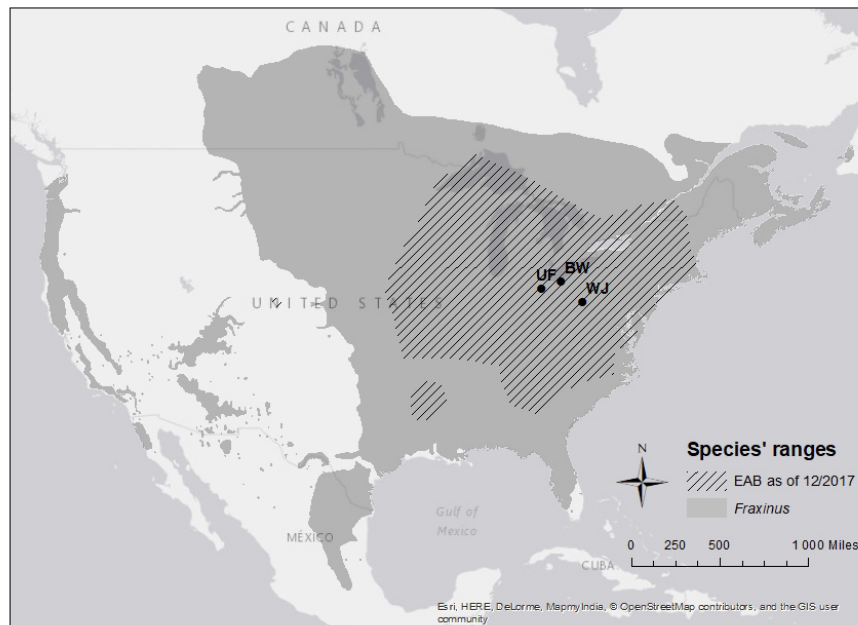


Figure 1. Current distribution of *Fraxinus* spp. (shaded region) and emerald ash borer (EAB, *Agrilus planipennis*, hatched region) in North America. Study sites are indicated on the map: UF, University of Findlay, Findlay, Ohio; BW, Baldwin-Wallace University, Berea, Ohio; and WJ, Washington & Jefferson College, Washington, Pennsylvania. Known EAB distribution as of 1 December 2017 [33].

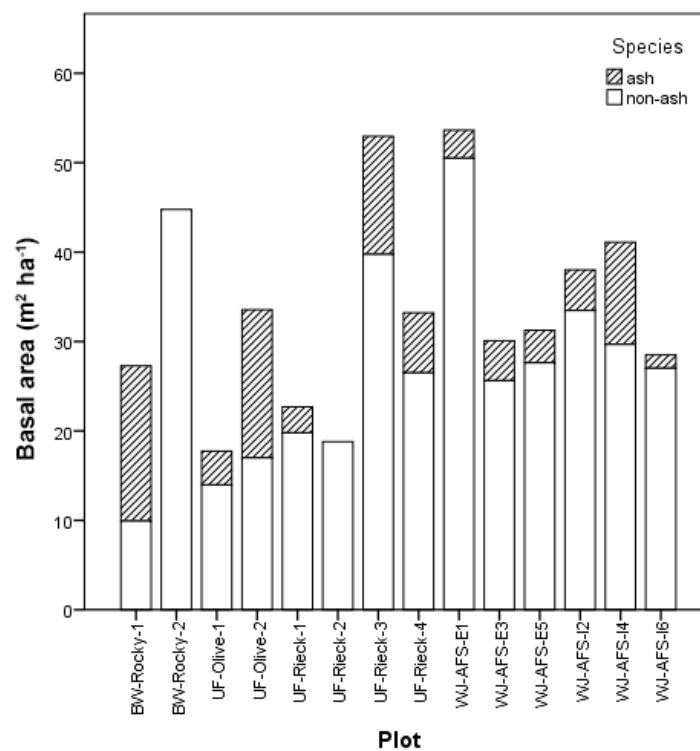


Figure 2. Cumulative basal area of trees by *Fraxinus* spp. (hatched) and non-*Fraxinus* (open) across plots at year of EAB detection at Baldwin-Wallace University (BW, 2015), University of Findlay (UF, 2010), and Washington & Jefferson College (WJ, 2012) sites.

Table 1. Physical characteristics, dominant vegetation, and year of detected emerald ash borer (EAB) infestation by site. Mean growing season, annual precipitation, temperature, elevation, and predominant soil texture were determined following standard Permanent Forest Plot Project (PFPP) methods [34]. MGS: mean growing season length; MAP: mean annual precipitation; MAT: mean annual temperature.

Site	Institution	County	State	MGS (days)	MAP (mm)	MAT (°C)	Mean Elevation (m·asl)	Predominant Soil Texture	Dominant Tree Species (in Order of Dominance)	Mean Plot Basal Area (m ² ·ha ^{−1})	Year of Detected EAB
Rocky River 41.411217° N, 81.881817° W	Baldwin-Wallace University (BW)	Cuyahoga	OH	173	1132	11.67	233	Silty loam	<i>Fraxinus americana</i> L., <i>Ulmus rubra</i> Muhl., <i>Quercus rubra</i> L., <i>Carya glabra</i> Miller, <i>Acer saccharum</i> Marshall	36.0	2012
Olive Street 41.002292° N, 83.642219° W	University of Findlay (UF)	Hancock	OH	159	847	10.81	240	Silty clay loam	<i>Celtis occidentalis</i> L., <i>Acer saccharum</i> , <i>Fraxinus pennsylvanica</i> Marshall, <i>Carya cordiformis</i> (Wangenh.) K.Koch, <i>Juglans nigra</i> L., <i>Ulmus americana</i> L.	25.7	2010
Rieck Center 40.950716° N, 83.549870° W	University of Findlay (UF)	Hancock	OH	159	857	10.81	250	Silty loam	<i>Acer saccharum</i> , <i>Fraxinus pennsylvanica</i> , <i>Fagus grandifolia</i> Ehrh., <i>Ulmus americana</i>	31.9	2010
Abernathy Field Station (AFS) 40.134110° N, 80.183625° W	Washington & Jefferson College (WJ)	Washington	PA	169	970	9.6	367	Silty loam	<i>Prunus serotina</i> Ehrh., <i>Acer saccharum</i> , <i>Fraxinus americana</i> , <i>Carya ovata</i> (Mill.) K.Koch	37.1	2014

2.2. Data Collection

We used the existing infrastructure of the Permanent Forest Plot Project (PFPP), one of the projects associated with the Ecological Research as Education Network (EREN; <http://erenweb.org/>). This project was launched in 2012 to establish a set of permanent research plots to address questions related to tree biomass, carbon accumulation, invasive species, and disturbance patterns across a range of sites and ecoregions [34]. Participants establish at least 1 permanent 400-m² plot in a forested area, identify and measure the diameter of all trees (>2.5 cm diameter at breast height (dbh), or 1.37 m above the ground), identify and tally all saplings (0–2.5 cm dbh, but at least 1.37 m tall) in 3 randomly selected subplots (25 m²), and characterize their site and plot using a standard protocol [34]. PFPP data are entered in a secure online database accessible to all PFPP participants.

We also scaffolded 4 variables onto PFPP to evaluate the impact of EAB on *Fraxinus* trees. Tree damage indicates whether the tree is broken, uprooted, or leaned on by another tree (including *Fraxinus*); this variable was incorporated into the PFPP protocol [34]. Ash rating [35] and ash tree breakup [36] indicate the level of decline, mortality, and breaking down of *Fraxinus* trees. We also counted the number of EAB exit holes observed between 1.25 and 1.75 m above the ground as a physical indicator that EAB is associated with the *Fraxinus* decline. These 3 variables are specific to the EAB Impacts Study [37], another EREN project.

To address questions related to the successional dynamics of forests, we built variables to characterize the understory plant community in the Complementary Vegetation (cVeg) Survey [38]. Canopy cover was measured using a concave spherical densiometer (Model C, Robert E. Lemmon, Rapid City, SD, USA), while all woody plants between 0.3 and 1.37 m tall (i.e., shrubs and saplings) were identified and tallied within each of the three 25-m² subplots used in the PFPP. In addition, all woody seedlings (<0.3 m tall) and non-woody plants were identified and tallied within 1-m² miniplots in each of the subplots. Woody species were classified according to their shade tolerance [39,40].

For our study, we used 2 plots from Rocky River (BW; 2016–2017), 2 plots from the Olive Street site (UF; 2012, 2014–2017), 4 plots from the Rieck Center (UF; 2012, 2014–2017), and 6 plots from Abernathy Field Station (AFS, WJ; 2012, 2014–2017). All of the PFPP, EAB, and cVeg variables were measured at each of the sampling years by site.

2.3. Analyses

Given our hypothesis that the loss of *Fraxinus* is driving a shift in community composition toward more mesophytic, or shade-tolerant, species, as well as increasing the prevalence of invasive plant species, we used the preinvasion relative basal area of *Fraxinus* as the independent variable. This variable was calculated as the proportion of cumulative basal area ($BA = \pi \times (0.5 \times dbh)^2$) of 3 *Fraxinus* species (*F. americana*, *F. pennsylvanica*, *F. quadrangulata* Michx.) relative to all other trees prior to (BW and WJ sites) or at (UF sites) the time of EAB detection. The variables of interest, such as annual changes in woody seedling density, invasive plant density, and sapling and shrub density, partitioned by shade tolerance [39,40], were calculated as the annual change in density from the first to last sampling year and divided by the number of years of sampling, whether we had 2 (BW) or 5 (UF, WJ) years of data. Data from miniplots (woody seedling and forb) and subplots (shrubs and saplings) were pooled by plot, thus plot became the observational unit. Each of these dependent variables was then linearly regressed onto the relative basal area of *Fraxinus*. All analyses were conducted using IBM SPSS Statistics v.24 (IBM Corp., North Castle, NY, USA).

3. Results

To determine whether we could detect changes in light resources at the forest floor, we regressed change in canopy cover on relative *Fraxinus* basal area prior to EAB invasion. Across all four sites, we found no significant relationship between canopy cover and relative *Fraxinus* dominance ($p = 0.46$),

thus no evidence that light resources increased more in sites with greater dominance of *Fraxinus* (Figure 3).

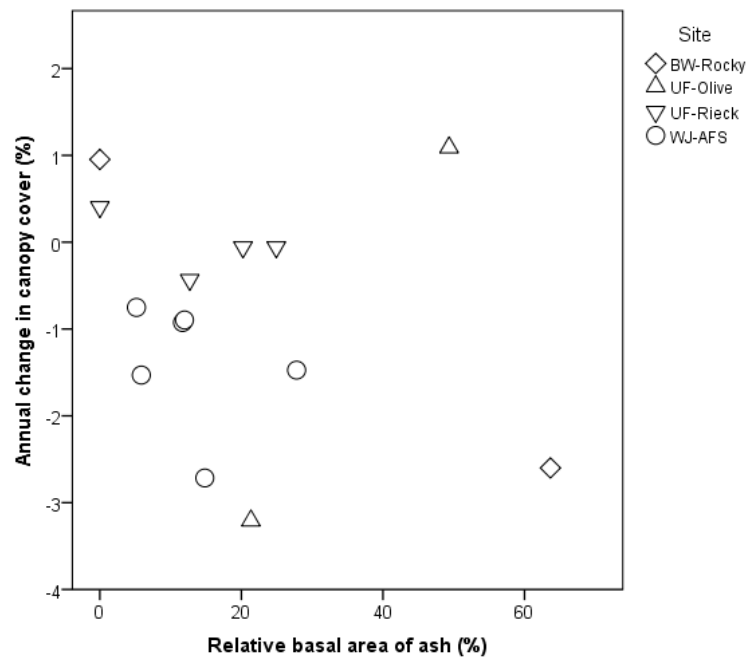


Figure 3. Mean annual change in canopy cover as a function of relative basal area of *Fraxinus* spp. prior to EAB invasion across four sites ($r^2 = 0.048$, $p = 0.450$). AFS: Abernathy Field Station.

The relative basal area of *Fraxinus* has not significantly affected the density of woody seedlings across sites ($p > 0.18$), whether with combined species or when partitioned by shade tolerance (Figure 4), yet some patterns are emerging. For example, shade-tolerant species increased in density at a higher rate in sites with more *Fraxinus* trees. Seedling density for *F. americana* generally declined across all sites, yet *F. pennsylvanica* seedlings generally increased in density at both UF sites (in supplementary file Table S1). Across UF and WJ sites, the density of *Parthenocissus quinquefolia* (L.) Planch. seedlings increased since EAB invasion. Other species, including the non-native *Rosa multiflora* Thunb. experienced both increased and decreased density within sites (Table S1).

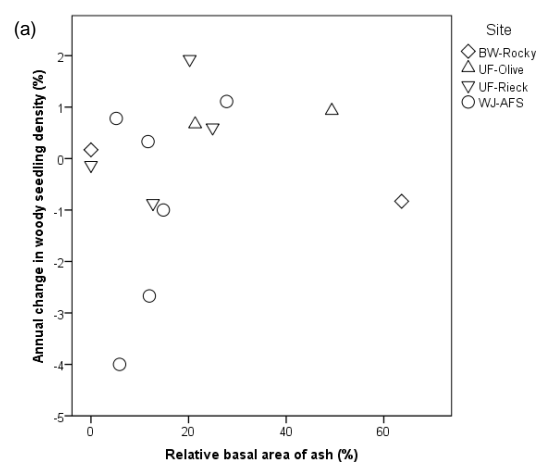


Figure 4. Cont.

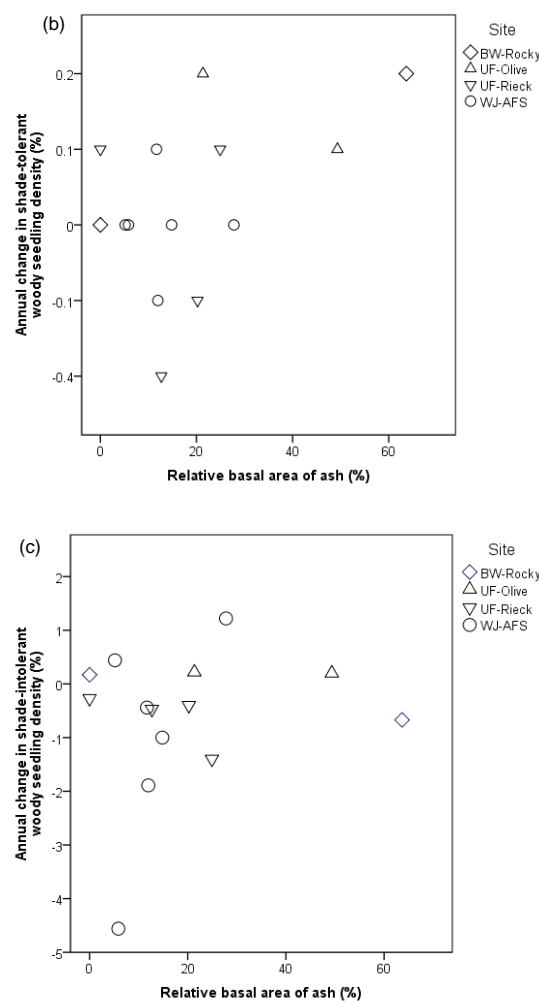


Figure 4. Effects of relative *Fraxinus* basal area on change in density of (a) woody seedlings of all species ($r^2 = 0.04$, $p = 0.482$), (b) shade-tolerant species ($r^2 = 0.14$, $p = 0.184$), and (c) shade-intolerant species ($r^2 = 0.03$, $p = 0.526$).

While total shrub density (Figure 5a), including shade-intolerant species (Figure 5c), did not respond to changes in relative basal area of *Fraxinus*, shade-tolerant shrubs significantly ($p = 0.005$) increased in density (Figure 5b). This response appears to be driven by individual plots at the BW (Rocky-1) and UF (Olive-2) sites, both of which had higher losses of *Fraxinus* than other plots (Figure 2); two native shrubs, *Lindera benzoin* L. and *Asimina triloba* (L.) Dunal, respectively, substantially increased in density in these plots, but the non-native *Rosa multiflora* also increased in density over this same period at UF (Olive-2) (in supplementary file Table S2). Saplings of *Fraxinus* spp. generally increased at UF (Rieck) and WJ (AFS), as did the native *Celtis occidentalis* at UF (Rieck) and non-native *Celastrus orbiculatus* Thunb. and native *Rubus* spp. at WJ (AFS). However, *Lindera benzoin* generally decreased in density at WJ (AFS), while the non-native *Lonicera* spp. and *Rosa multiflora* Thunb. increased in the UF (Olive-1) plot that experienced widespread canopy tree loss from the June 2012 North American derecho (Table S2).

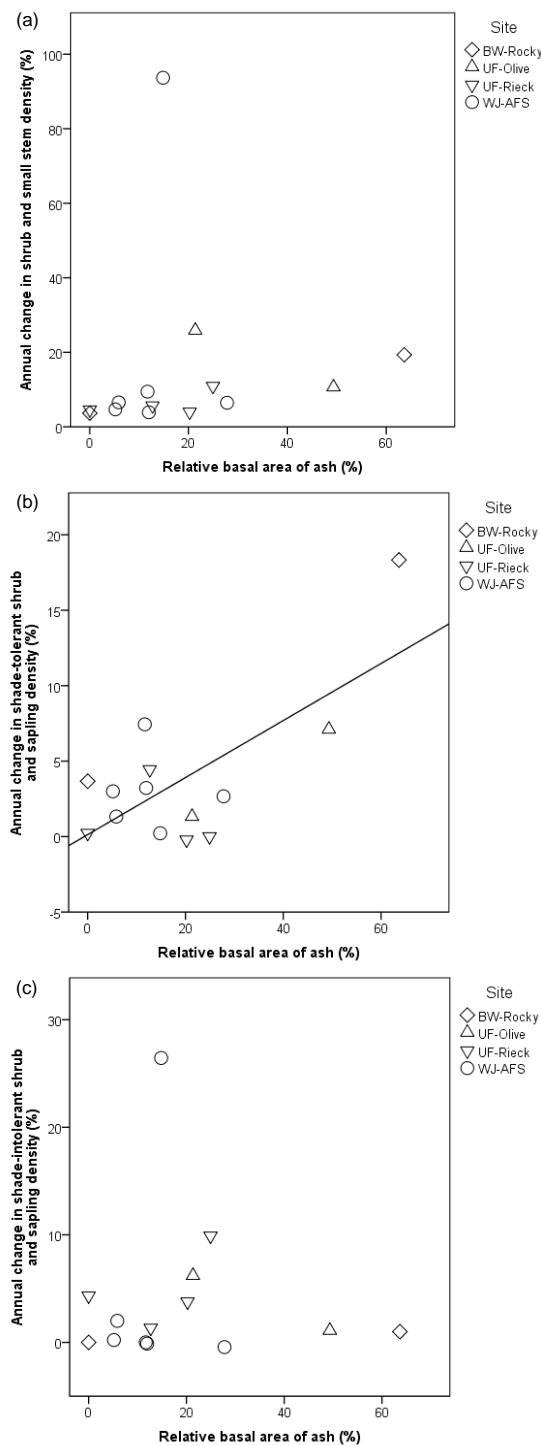


Figure 5. Effects of loss of *Fraxinus* on change in density of (a) shrubs and saplings of all species ($r^2 = 0.01$, $p = 0.764$), (b) shade-tolerant species ($r^2 = 0.50$, $p = 0.005$), and (c) shade-intolerant species ($r^2 = 0.003$, $p = 0.853$).

Relative basal area of *Fraxinus* was not a significant predictor of density of non-native vegetation in the ground layer or the shrub and sapling layer in 2017 (Figure 6). Only two plots, one each at WJ (AFS) and UF (Olive), saw above-average increases in non-native species density, yet both sites had relatively low relative amounts of *Fraxinus* basal area. And though three non-native species, *Celastrus orbiculatus* Thunb., *Lonicera maackii* (Rupr.) Maxim. and *Rosa multiflora*, increased in density in the

shrub layer within sites during the period of study (Table S2), the overall change in non-native species density does not show a relationship to the decrease in relative *Fraxinus* basal area.

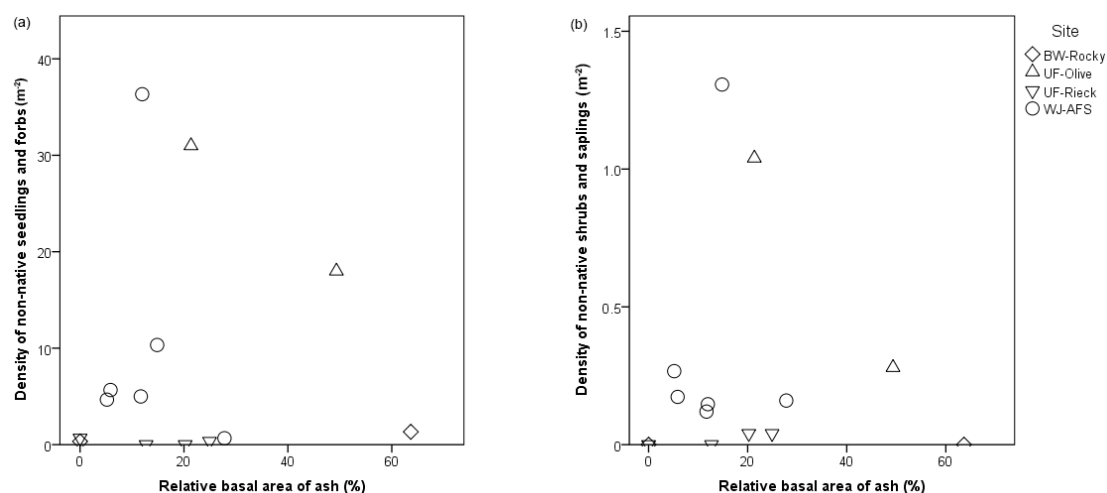


Figure 6. Effects of relative *Fraxinus* basal area on density of non-native vegetation, including (a) woody seedlings and forbs in 2017 ($r^2 = 0.003$, $p = 0.843$) and (b) shrubs and saplings ($r^2 = 0.001$, $p = 0.955$) in 2017.

4. Discussion

The loss of *Fraxinus* from mesophytic North American hardwood forests and the subsequent release of resources appear to have little influence on the distribution and abundance of forest regeneration at the seedling and sapling level. Furthermore, we found no evidence that this loss alters the process of mesophication in the same manner as acute, severe disturbances that typically impact canopy cover.

4.1. Canopy Cover

Light is the primary resource expected to change at the ground layer as a result of the death of large overstory *Fraxinus* trees [41], yet our evidence suggests that the protracted decline and ultimate death of *Fraxinus* individuals does not create conditions that substantially alter the light regime on the forest floor, as measured by our canopy cover index. Although canopy cover decreased at a rate of 0%–3% annually, there was no detectable relationship to *Fraxinus* mortality (Figure 3). In order to meet the physiological demands of shade-intolerant species, like *Quercus* and *Carya*, light levels need to reach 25%–50% full sunlight [42], which is often reached with more severe disturbances, like shelterwood harvesting [43].

Research on canopy trees in response to EAB-induced *Fraxinus* mortality shows that existing canopy trees respond positively. Gaps concurrently fill with non-*Fraxinus* species [23], likely influencing the lack of substantial change in annual canopy cover over time. Recent evidence using LIDAR (Light Detection and Ranging) indicates that single-tree death in northern hardwood forests is not sufficient to generate canopy gaps where the subcanopy is well developed [44], suggesting that the gradual canopy opening that occurs with EAB-induced *Fraxinus* mortality is less likely to enrich the ground layer with light than it is to promote the growth of existing subcanopy trees.

Indeed, in northwest Ohio, the relative growth rates of the shade-tolerant species *Acer saccharum* and *Ulmus americana* were faster than other species in the forest canopy following *Fraxinus* mortality [8], and smaller trees exhibited faster growth rates than larger ones, suggesting that subcanopy individuals benefit more than the co-dominant overstory trees. Trees remaining in the canopy of our forest sites include mesophytic species, typically from *Acer*, *Prunus*, *Ulmus*, and *Celtis* (Table 1), which supports

our hypothesis that *Fraxinus* loss will increase the speed at which forests are dominated by more shade-tolerant species.

4.2. Understory Composition and Density

The composition of woody species in the seedling layer is relatively stable following the loss of *Fraxinus* to EAB. We detected no statistically significant relationship between the loss of *Fraxinus* and the change in seedling density (Figure 4). In regard to individual species, there is a large amount of variability among sites and plots. Species with the largest, most consistent increases over time include the native vine *Parthenocissus quinquefolia*, while the non-native shrub *Rosa multiflora* increased or decreased across sites, indicating a lack of relationship with *Fraxinus* loss. Interestingly, the number of *Fraxinus* seedlings increased at both UF (Olive) plots, where overstory *Fraxinus* trees had succumbed to EAB beginning in 2012 (Table S1). Recent evidence suggests that *Fraxinus* seedbanks do not persist beyond the life of the tree [45], indicating that an off-site seed source persists for this site.

The shrub and sapling layer was more responsive to *Fraxinus* mortality than the seedling layer. As the amount of *Fraxinus* basal area increased in plots, the density of shade-tolerant species increased ($r^2 = 0.50$, $p = 0.005$). This was in contrast to the lack of association detected between *Fraxinus* basal area and the change in shade-intolerant species density ($r^2 = 0.003$, $p = 0.853$). The increase in shade-tolerant species density coincides with evidence of established trees in the mid-canopy responding to the resources made available through the mortality of *Fraxinus* individuals. The response of individual species varied across sites, but those with increases at more than one site include shade-tolerant *Lindera benzoin* and *Asimina triloba*, both native understory species.

Our findings are not unusual, as shrub and sapling density has been shown to increase in response to species-specific canopy dieback elsewhere. In Europe, fungal-induced *Fraxinus excelsior* L. dieback promoted the growth of widely distributed shade-tolerant shrubs and understory trees, including *Corylus avellana* L., *Prunus padus* L., and *Lonicera xylosterum* L. [46]. In North America, after Dutch elm disease induced *Ulmus* decline, the intermediate- and shade-tolerant shrubs *Alnus rugosa* (L.) Moench, *Viburnum recognitum* Fern., and *Cornus stolonifera* L. in wetland habitats responded more positively in gaps created by the death of *Ulmus* stems in the overstory than seedlings of other canopy trees [47]. In southeastern Wisconsin, species composition and density of woody seedlings were not associated with density of dead *Ulmus*, yet the density of shrubs, especially *Ribes* spp., *Rubus* spp., and *Cornus racemosa* Lam., was associated with *Ulmus* mortality [48].

4.3. Invasive Species

No new invasive species were detected in the research plots. For plots with existing invasive plants, some became more numerous, including *Lonicera maackii*, *Rosa multiflora*, and *Celastrus orbiculatus*, but because of variability among plots, we were unable to identify *Fraxinus* mortality as the primary cause of the increase at our sites. Prior to EAB invasion, one plot at the UF (Olive) site had large numbers of *L. maackii* and *R. multiflora*; these species increased in density over time. This particular site, however, was also strongly influenced by a storm that caused significant loss of the overstory in 2012. The confounding disturbances of storm damage and EAB-induced *Fraxinus* mortality cannot be distinguished. Recent evidence suggests that the amount of *Fraxinus*, and thus the amount of light increasing beneath the canopy, influences the response of existing *L. maackii*; in a comprehensive study of population-level responses to EAB, existing *L. maackii* individuals had increased stem diameter following *Fraxinus* mortality, while the number of individual plants, amount of fruiting, and height of the shrubs were not impacted [9].

Additionally, in three plots in Pennsylvania, *Celastrus orbiculatus* had higher annual increases in density than other species following EAB, but because of losses to this species in other plots at the same site and an overall lack of relationship between *Fraxinus* basal area and shrub and sapling density (Figure 6b; $r^2 = 0.001$, $p = 0.955$), the increase in this species was not likely caused by the loss of *Fraxinus*.

5. Conclusions

Our evidence shows that the resources released through *Fraxinus* mortality are insufficient to modify the process of mesophication in mesophytic forests, but instead generate changes that resemble those observed with small gaps. The primary beneficiaries of released resources include individuals already existing in the understory canopy, among them small shade-tolerant trees, saplings, and shrubs typical of mature mesophytic forests, conforming to what is observed in forest gap dynamics [8,49–52]. This enhanced mesophication resulting from the loss of *Fraxinus* has allowed shade-tolerant species, including those restricted to understory canopy positions, like *Asimina triloba* (L.) Dunal and *Lindera benzoin* L., to increase in the shrub and sapling layer at faster rates than shade-intolerant species (Figure 5). As mesophication has been noted throughout much of the eastern North American forest complex [28,53–55], we would expect to see similar patterns throughout the region where *F. pennsylvanica* and *F. americana* are the primary *Fraxinus* species represented in the canopy.

Importantly, some of our sites are in regions with relatively high amounts of *Fraxinus* compared to other mesophytic forest regions of eastern North America [11]. Our research primarily includes sites with relative *Fraxinus* basal area within the range of 5–25%, and we find no compelling evidence that the loss of trees at our sites impacts regeneration and recruitment. Where *Fraxinus* is a smaller component of the forest tree community, we expect that, like our sites, these areas will not see dramatic shifts in seedling and shrub composition resulting from the loss of *Fraxinus* in the overstory.

With the exception of *Fraxinus*, EAB is not a disturbance that influences the abundance of woody species regeneration and subsequent recruitment in sites where *Fraxinus* is a minor component of the canopy vegetation. The five species of *Fraxinus* most common to eastern hardwood forests, *F. americana*, *F. pennsylvanica*, *F. nigra*, *F. profunda* Bush, and *F. quadrangulata*, have been classified as critically endangered and on the brink of extinction by the International Union for Conservation of Nature (IUCN) [56–60]. Conservation of the genus is important, but the consequence of losing the species has little influence on immediate future successional pathways of woody vegetation in the forests where *Fraxinus* is a minor component.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1999-4907/9/6/353/s1>: Table S1. Annual change in density (ha⁻¹) of woody seedlings (<0.30 m tall) by plot after EAB invasion. Empty cells indicate species absence. Table S2. Annual change in density (ha⁻¹) of shrubs and saplings (woody plants, 0.30–1.37 m tall) by plot after EAB invasion. Empty cells indicate species absence.

Author Contributions: B.J.D. and J.S.K. developed the research questions, conceived the design for the EAB Impacts Study and Complementary Vegetation (cVeg) Survey, collected the data, performed the analyses, and wrote the manuscript. Both B.J.D. and J.S.K. provided edits and comments during the drafting of the paper.

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Conflicts of Interest: The authors declare no conflict of interest.

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