

Article

Buying Time: Preliminary Assessment of Biocontrol in the Recovery of Native Forest Vegetation in the Aftermath of the Invasive Emerald Ash Borer

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Received: 27 August 2017; Accepted: 25 September 2017; Published: 28 September 2017

Abstract: Introduced forest pests have become one of the major threats to forests, and biological control is one of the few environmentally acceptable management practices. Assessing the impacts of a biocontrol program includes evaluating the establishment of biocontrol agents, the control of target pest, the impact on the affected organism, and the indirect impacts that the biocontrol agent may have on the whole community. We assessed the recovery of forest vegetation following the mortality of ash trees caused by the invasive emerald ash borer (EAB) pest in forest stands where biocontrol agents were released or not. We used a multilevel framework to evaluate potential indirect effects of the biocontrol agents on native forest seedlings. Our results showed a higher number of ash saplings where increasing numbers of the dominant EAB biocontrol agent were released, while the number of invasive and weedy saplings was negatively associated with the number of ash saplings, and the density of native seedlings was negatively associated with invasive and weedy saplings. The protection of ash saplings by the biocontrol agent may help native recruitment during forest transition by supporting the growth of native hardwood seedlings over invasive and weedy species. These results show that research on the efficacy of EAB biocontrol should include all ash size classes and the community dynamics of co-occurring species.

Keywords: *Agrilus planipennis*; *Fraxinus* spp.; gap dynamics; invasive species; *Oobius agrili*; southeastern Michigan; *Spathius agrili*; temperate forests; *Tetrastichus planipennisi*

1. Introduction

Some of the major challenges facing North American forests are invasions of non-native pests [1–3]. In recent decades, the increase in new species introductions, associated primarily with increasing global trade, has exacerbated the frequency and impact of these invasive pest outbreaks [4]. Outbreaks decimate forests and, in some instances, result in the local elimination of tree species [5,6] substantially changing forest ecosystems [1,7]. Among North American forests, the northeastern region is being particularly affected by these introductions [8,9], and one of the most recent pests arriving to this area is the emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) [10].

The emerald ash borer (EAB) is an invasive wood-boring beetle from Asia that threatens North American ash species (*Fraxinus* spp.) [11,12]. Emerald ash borer was first discovered near Detroit, Michigan in 2002 [13,14]. Despite early eradication programs and ongoing quarantines by U.S. and Canadian regulatory agencies, EAB continues to spread and is now known in 30 states, Washington D.C. and two provinces [15]. While Asian species of ash are relatively resistant to EAB [16–18], most North American ash species show little resistance to this pest and most overstory ash trees die within three to

six years of initial infestation [19–21]. This is relevant because ash species are widespread in North American eastern forests amounting to ~2.5% of the above-ground biomass [22], and ash trees have been widely planted in urban settings [23]. The potential cost of EAB to non-urban forests was estimated at more than \$282 billion [24], and the undiscounted value of ash trees in the urban forests in the United States was estimated at \$20–60 billion [25], making EAB, among those quantified, the most economically devastating insect pest in North American history [26].

Soon after EAB was discovered in North America, researchers began studying the role that natural enemies play in regulating EAB densities. Results from early studies revealed a low diversity and prevalence of parasitoids attacking EAB compared to those attacking native *Agrilus* species [27,28]. Furthermore, in regions of Asia where EAB is native, several specialized hymenopteran parasitoids that co-evolved with EAB, suppress EAB densities below a tolerance threshold for survival of native and some exotic ash species [16,29,30]. Several of these parasitoids became the basis of a biological control program aimed at reducing the density of EAB populations in North America [31].

Following extensive decline and mortality among the mature overstory ash trees, in 2007, EAB biocontrol began in southern Michigan. Three EAB parasitoid species from China were introduced: the egg parasitoid *Oobius agrili* (*O. agrili*) Zhang and Huang (Hymenoptera: Encyrtidae), the larval endoparasitoid *Tetrastichus planipennisi* (*T. planipennisi*) Yang (Hymenoptera: Eulophidae), and the larval ectoparasitoid *Spathius agrili* (*S. agrili*) Yang (Hymenoptera: Braconidae) [31,32]. To date, the establishment of both *T. planipennisi* and *O. agrili* have been confirmed at several release sites in Michigan and several other states [33]. Parasitism rates are not yet as high as in China [16,34], and it is too early to know the full extent to which these two biocontrol agents can protect the surviving ash saplings and trees as they mature into large-diameter size classes [31,35].

After the death of mature overstory trees, the ash seedling, sapling, and basal sprout bank became an important transitional resource for forest recovery [36,37]. In particular, seedlings of white ash, *Fraxinus Americana* (*F. Americana*), a common species in many North American eastern forests [12], can tolerate very low light conditions [38], allowing for the establishment of a robust seedling bank of up to 10,000–20,000 seedlings per hectare pre-EAB [39]. The high mortality rates due to EAB for mature ash is not paralleled among seedlings and saplings (<2.5 cm diameter at breast height, DBH) [39], as these size classes are too small to support EAB larval feeding. Researchers working in southern Michigan, where EAB biocontrol began, found that *T. planipennisi* had higher parasitism in thin-barked, small-diameter ash trees [40], which is likely correlated with its relatively short ovipositor [41]. Thus, when these seedlings and saplings grow in response to the death of mature trees, they are temporally protected by this biocontrol agent [37].

The EAB invasion also affects the entire plant community, as gaps and other disturbances caused by death of canopy trees set up the process of succession. Forest succession will then reflect the composition of the advance regeneration layer and of the seeds available for germination [42–44]. In forest ecosystems, most seeds originate locally [45,46] and their abundances are correlated with the basal area of nearby trees [47], while off-site propagules often come from the neighboring landscape [48]. If the surrounding areas are largely intact, native species will account for the majority of the seeds reaching a site [7,49]. However, as the surrounding landscape becomes more human-altered, weedy and invasive propagules could constitute a large proportion of those seeds [50,51].

Besides propagule availability, successful establishment of invasive and weedy plant species in a new location often depends on the higher level of resources, e.g., light [50,52,53]. Moreover, disturbance is frequently necessary for these plant species to penetrate interior forest communities [49,54,55], and it is often in disturbed habitats when invasive plants can outcompete native species [56,57]. In particular, researchers have observed that forests with simulated EAB damage were more susceptible to invasive plants [58]. And, early EAB quarantine efforts that cut mature ash trees, which caused the creation of forest gaps and higher light levels, showed an increased in the likelihood of plant invasions [59]. However, if an abundant ash seedling bank exists and it rapidly responds to the canopy opening [38],

the resulting ash sapling layer, if protected from EAB, will then shade the stand and potentially curtail the success of the invasion (Figure 1a).

In our study, we investigated the impacts of recently introduced EAB biocontrol agents on ash sapling densities and forest vegetation, native and introduced, in the vicinity of the EAB-invasion epicenter in southeast Michigan, USA [60]. We collected data on the forest structure and composition of stands in this region and analyzed the data as a function of biocontrol release levels (Figure 1b). To understand the relationship between the release of biocontrol and native tree seedling populations, we investigated three dynamics: (i) does parasitoid release affect ash sapling density? (ii) What are the variable driving the establishment of invasive and weedy saplings in this system? And, (iii) is the density of invasive and weedy species associated with native seedling density? Our expectation was that with the protection from the biocontrol agents, the ash sapling layer would prevent the colonization of EAB-disturbed areas by invasive and weedy species, thereby buying time for other native, and more shade tolerant, species to establish and recruit (Figure 1a).

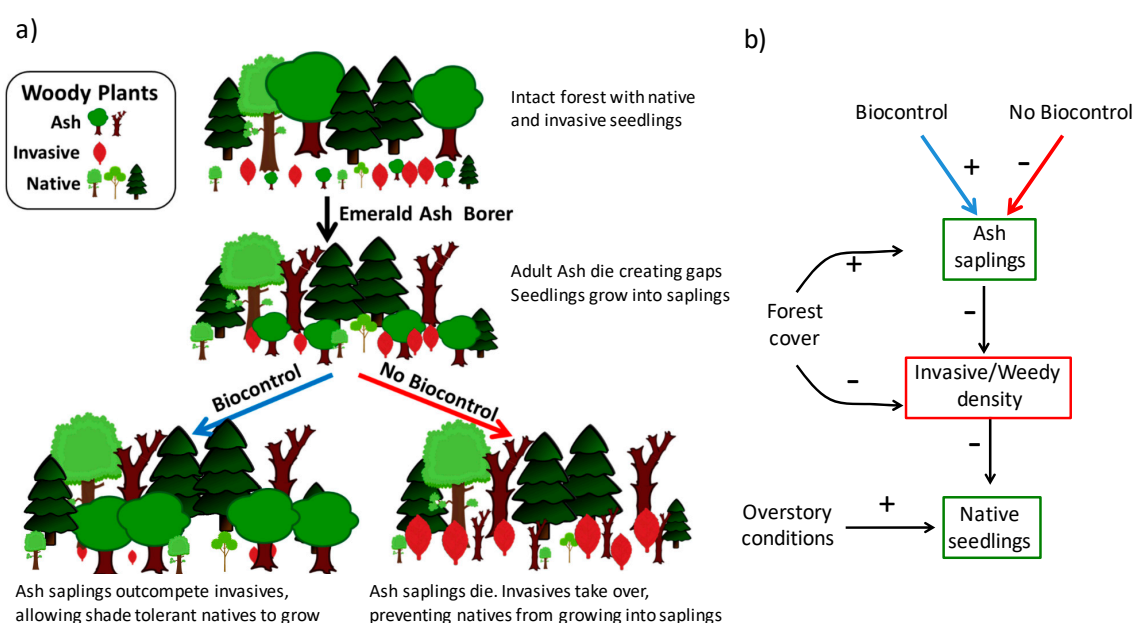


Figure 1. (a) Visual representation of the forest transition with and without biocontrol. This graphic outlines the hypothesis that as gaps are created from the loss of mature ash trees, EAB biocontrol agents, mainly *T. planipennisi* an introduced EAB natural enemy, can protect ash saplings, buying time for native seedlings to grow and fill gaps (left pathway). Without the influence of the EAB biocontrol program, ash do not survive long enough to allow the native community to recruit, resulting in invasive and weedy species taking over (right pathway); (b) Graphical representation of analysis testing the hypothesis, with positive and negative signs indicating our original expectations.

2. Materials and Methods

2.1. Study Sites

In the summer of 2014, we sampled forest composition at sites of varying distance from parasitoid release locations in southeastern Michigan, USA. A total of 21 sites were selected and surveyed (Figure 2). The sites were classified as a release site if parasitoids were released <1 km away (Supplementary Material 1). Seven release sites were chosen at random from the 22 parasitoid release locations within the counties of Ingham, Jackson, Livingston, Oakland and Washtenaw in 2014 [61]. The parasitoids were released in wooded stands larger than 16 ha, that were >100 m from a road and that would not be harvested or developed for at least five years after release. The 14 control sites were selected in the general area of the release plots to reflect similar vegetation types. Control sites

were between 4.1 km and 20.5 km to the nearest release location (Figure 2, Supplementary Material 1). The climate in the area is characterized by cold winters (average minimum temperature in January is $-8.8\text{ }^{\circ}\text{C}$) and warm summers (average maximum temperature in July is $28.8\text{ }^{\circ}\text{C}$) with a total annual precipitation of 953 mm evenly distributed along the year. Most soils of the region derive from end-moraine ridges and ground moraines, and from alluvial deposits along river valleys.

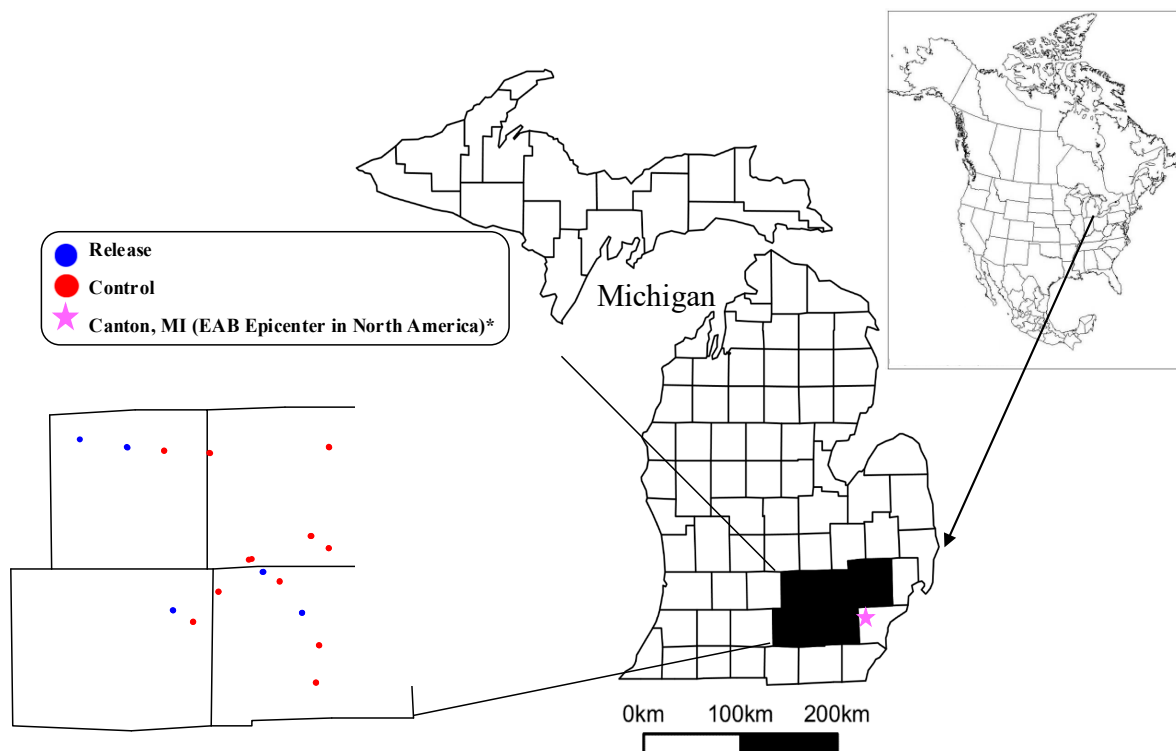


Figure 2. Map of Michigan showing the location of our 21 vegetative study sites (Lambert projection). Insert shows the five Michigan counties where the release and control vegetation plots were located (colored dots in the map).

2.2. Biocontrol Releases

The EAB parasitoid release data was obtained at mapbiocontrol.org, a geospatial framework for biocontrol information [59]. At the seven biocontrol sites, there were 44 discrete release events with a sum of 14,065 individual releases that took place between the years of 2007 and 2012 (Supplementary Material 2). At the release sites, the relative release proportions for *O. agrili*, *T. planipennisi*, and *S. agrili* were 19%, 68% and 13% respectively. Both *O. agrili* and *T. planipennisi* were confirmed established at one of the seven parasitoid-release plots, whereas establishment of *T. planipennisi* was confirmed at two other release plots; establishment of *S. agrili* has not been confirmed [61–63].

2.3. Vegetation Sampling

To investigate the succession process at both the control and release study sites, two 20×20 m plots were set up at each site. Plots were centered around a dead standing canopy tree, an ash tree if possible. All living woody species >10 cm DBH were classified as trees and identified to species level in the 400 m^2 plot. We measured the DBH of all the trees in the plot to calculate the plot's basal area. We established four 2×10 m sampling transects, totaling 80 m^2 per plot where native, invasive and weedy saplings (>1 m in height and <10 cm DBH) were counted. We also set up four 1×10 m groundcover (all vegetation <1 m in height) and seedling transects, totaling 40 m^2 per plot. Within each 1 m^2 , we quantified percent groundcover by invasive and weedy species. Plants were characterized as weedy species if they are native, not typically growing in closed canopy forests but rather in more

open, higher-light environments. Plants were characterized as invasive if they are not native to North America. The seedlings of woody plants (<1 m in height) were counted and identified to species within the same groundcover transects. All plot measures were estimated per m² unit area, and plot-level averages and standard deviations were used in the analyses. See Supplementary Materials 3 and 4 for data summaries.

2.4. Environmental and Land Cover Data

To account for resource availability, we measured the light and moisture levels at each plot when vegetation was surveyed (Supplementary Material 5). Photosynthetically active radiation (PAR) was measured as an indicator of light availability in every meter radiating along the cardinal axes from the central dead tree. This was repeated 3×, totaling 120 readings per plot using a LightScout Quantum Light 6 Sensor Bar and the LightScout Light Sensor Reader from Spectrum Technologies, Plainfield, IL, USA. Volumetric water content (VMC) was used as an indicator of soil moisture, it was measured every meter radiating along the cardinal axes from the central dead tree, with a total of 40 moisture readings per plot. VMC was measured in the top 15 cm using Fieldscout-TDR 300 Soil Moisture Meter from Spectrum Technologies, Plainfield, IL, USA. To determine the percent forested area surrounding each plot, we used available land cover data from 2002, using ArcGIS 10.3 (ESRI, Redlands, CA, USA) we estimated the percent of forested land within 1 km of the study sites [64]. Total land area was calculated by subtracting the area covered by water from the total area. See Supplementary Material 5 for light, soil moisture and forest cover data.

2.5. Statistical Analysis

To evaluate the relationship between native seedlings and the release of parasitoids, we first carried out extensive exploratory data analysis and then developed a multilevel, or hierarchical, model where estimates from a submodel were used as predictors in subsequent models (Figure 1b). First, parasitoid release information (number of released *T. planipennisi*, as this was the most successful parasitoid establishing and spreading [37,62]) was used to analyze ash sapling density, then invasive and weedy species density was analyzed as a function of the estimated ash sapling densities, and we finished by using estimates of invasive and weedy species densities to analyze the native tree seedling data (Figure 1b). This multilevel approach allowed sharing of information across the data sets [65], potentially better informing the dynamics taking place in these plots. Following this hierarchical approach, we ran variants of this basic model that included some additional explanatory variables (e.g., forest cover around the plots, basal area in the plots, ground cover, soil moisture, light, total releases, distance to release), we describe below the model best supported by the data (based on goodness of fit and deviance information criterion, DIC; [66]).

We first estimated the abundance of ash saplings, *AshSaplings*, as a function of the percent of forest cover (*Forest cover*) around the plots within 1 km radius. We used forest cover as a proxy for source of propagules determining the strength of the seedling bank growing into saplings. We also estimated ash sapling density as a function of the number of parasitoids released (*T. planipennisi*). Because these two variables were correlated, $r: 0.66$, we orthogonalized the number of released parasitoids with respect to forest cover, and used the residuals ($\epsilon_{\text{release}}$) in the analysis. This approach allowed us a better assessment of the independent effect of the biocontrol treatment on ash sapling density once the strength of the source of propagules, the major driver of sapling density, was accounted for. The likelihood for the average density of ash saplings in plot i , was:

$$\text{AshSaplings}_i \sim \text{Poisson}(\text{Ash}_i) \quad (1)$$

and process model:

$$\ln(\text{Ash}_i) = \alpha_1 + \alpha_2 \text{Forest Cover}_i + \alpha_3 \epsilon_{\text{release } i} \quad (2)$$

The density of invasive and weedy saplings, *InvWeedyS*, was analyzed as a function of the estimated density of ash saplings (*Ash*), the main native competitor after disturbance, and of the percentage of forest cover within 1 km, used here again as a proxy for sources of propagules [67,68], but in this case assuming that areas with higher forest cover are likely to have fewer invasive and weedy species, likelihood:

$$InvWeedyS_i \sim \text{Poisson}(IW_i) \quad (3)$$

and process model:

$$\ln(IW_i) = \beta_1 + \beta_2 Ash_i + \beta_3 Forest\ Cover_i \quad (4)$$

The average density of native woody seedlings, *NativeSeedlings_i*, was then analyzed as a function of the basal area of the stand (*BA* in units of m²/m²) to reflect sources of seeds [69], and of the estimated density of invasive and weedy saplings (*IW*) that could be competing with the native vegetation, likelihood:

$$NativeSeedlings_i \sim \text{Normal}(Native_i, NSvar_i) \quad (5)$$

and process model:

$$Native_i = \gamma_1 + \gamma_2 BA_i + \alpha \gamma_3 IW_i \quad (6)$$

The variances associated with each plot, *NSvar_i*, were estimates from our data. Due to the multilevel structure of the model we followed a Bayesian approach in the estimation of the parameters [70]. Parameters were estimated from non-informative distributions, $\alpha^*, \beta^*, \gamma^* \sim \text{Normal}(0, 10,000)$. The analysis was run in OpenBugs [71] (see Supplementary Material 6 for code), and three chains were run simultaneously to assess convergence. Parameter posterior means, variances and 95% credible intervals, were calculated after convergence, thinning every 100th iteration. Parameters associated with the covariates were considered statistically significant if the 95% credible interval (CI) around their means did not overlap with zero.

3. Results

In total, we surveyed 41 plots at 21 sites, which included 688 trees, 3,826 saplings, 19,583 seedlings, and 12,961 distinct recordings for groundcover (see Supplementary Material 3 for detailed data of each plot). The most common tree species was *Prunus serotina*, found in 58% of the plots, followed by *Ulmus americana* and *F. americana* (this last one included dead stems) growing in 44% of the sampled plots. Other common species were *Acer rubrum*, 48%, *Quercus rubra*, 36.5%, *A. saccharum* 30% and *Q. alba* 26.8% (Supplementary Material 3). Among the invasive and weedy saplings the most common species were *Elaeagnus umbellata* found in 44% of the plots, *Rubus* spp. in 31.7% of the plots, *Rosa multiflora* and *Lonicera maackii* in 26%, and *L. tatarica* in 24.4% of the plots (Supplementary Material 4). Of the additional variables included only forest cover around the plots (ash and invasive and weedy species submodels) and basal area in the plot (native seedlings submodel) improved the fit of the models, other variables (ground cover, soil moisture, light, total releases, distance to release) when included did not improve the fit of the model and we opted to exclude them in our final analysis. The hierarchical structure of the analysis greatly improved the fit of the model (see Supplementary Material 7 for alternative model comparisons). All parameter estimates from the analysis are reported in Table 1.

3.1. Results from the Ash Sapling Submodel

Increase in percent forest cover around the plots was associated with a higher number of ash saplings (α_2 parameter was positive and statistically significant; Table 1), this variable had the strongest impact on ash sapling densities (Figure 3a). The number of released parasitoids (*T. planipennisi*) was also statistically significant and positively associated with higher densities of ash saplings (α_3 parameter; Table 1, Figure 3).

Table 1. Posterior means, standard deviations (SD) and 95% credible intervals (CI) for all the parameters included in the analysis. Coefficients associated with the explanatory variables that were statistically significant (95% CI did not include zero) are shown in bold.

Parameter		Mean \pm SD	95% CI	
<i>Ash saplings submodel:</i>				
α_1	intercept	-0.382 ± 0.002	-0.385	-0.377
α_2	forest cover	0.406 ± 0.003	0.398	0.412
α_3	number of <i>T. planipennesis</i> released	0.001736 ± 0.0000019	0.001734	0.001737
<i>Invasive and weedy species submodel:</i>				
β_1	intercept	0.8999 ± 0.00015	0.8996	0.9002
β_2	ash saplings	-1.506 ± 0.005	-1.512	-1.492
β_3	forest cover	0.2737 ± 0.0015	0.2715	0.2753
<i>Native seedlings submodel:</i>				
γ_1	intercept	1.97 ± 0.19	-2.31	-1.64
γ_2	basal area	3830 ± 3.62	3822	3835
γ_3	invasive and weedy saplings	-4.95 ± 0.05	-5.04	-4.86

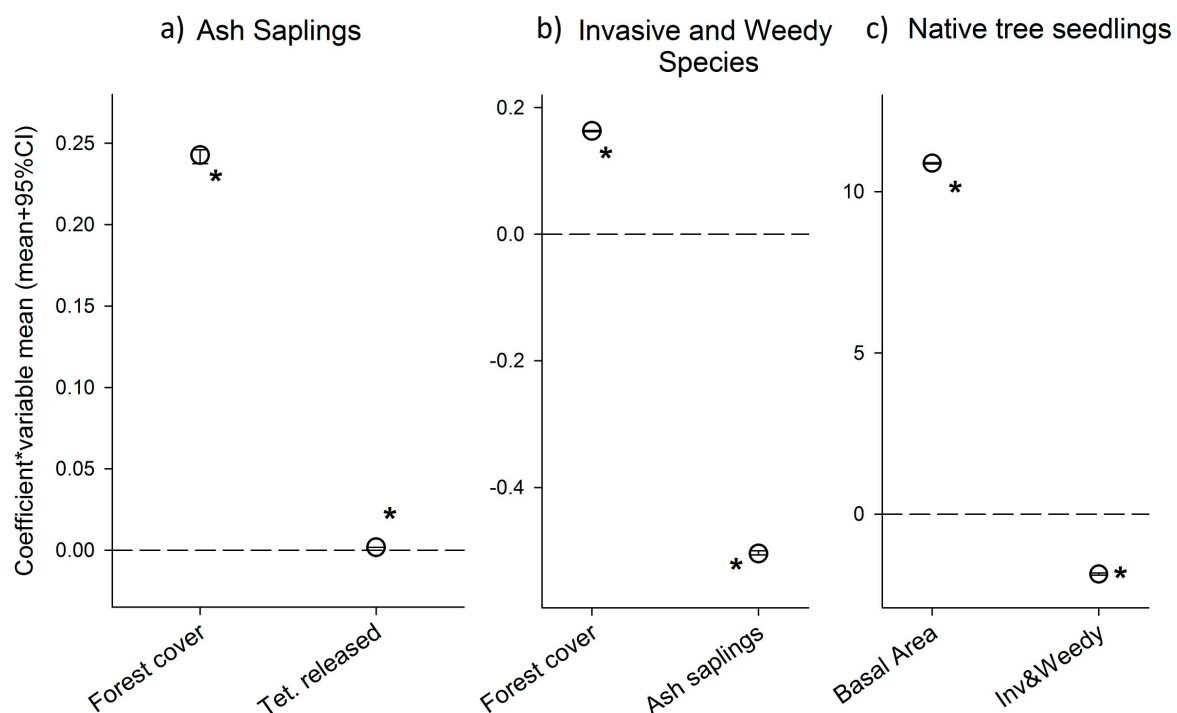


Figure 3. Posterior parameter means (+95% CI) of each of the parameters included in the analyses for each submodel, ash saplings (a); invasive and weedy species (b); and native tree seedlings (c). Parameters have been standardized (i.e., multiplied by the covariate mean, except for *T. planipennisi* releases where we used the orthogonalized variable which is centered around zero) to assess their influence. Coefficients that were statistically significant (95% CI did not overlap with zero) are indicated by an asterisk. Note: symbols are larger than the 95% CIs.

3.2. Results from the Invasive and Weedy Species Submodel

The abundance of invasive and weedy species was negatively associated with increasing number of ash saplings, which had the strongest effect, and was positively associated with increasing forest cover around the plots (parameters β_2 and β_3 were statistically significant; Table 1, Figure 3b).

3.3. Results from the Native Seedlings Submodel

Increase in plot basal area was significantly associated with a higher number of native seedlings (parameter γ_2 ; Table 1, Figure 3) and had the largest effect. The density of invasive and weedy species was associated with lower number of native seedlings, and the effect was statistically significant (parameter γ_3 ; Table 1, Figure 3c).

4. Discussion

Most biocontrol evaluation research focuses on the establishment and spread of introduced biocontrol agents, their impacts on the target pest or invasive species, and their potential interactions with non-target organisms and other natural enemies [72–74]. However, it may take several years before the impacts or recovery of affected species and communities can be assessed. In the case of trees, which have a long-life cycle, a comparatively long lag time may be needed before the impacts of biocontrol can be realized. In our system, the biocontrol program for EAB is still in the early phases (for a review see [31]). Nevertheless, researchers have found that one species of introduced parasitoid, *T. planipennisi*, is now the dominant natural enemy of EAB larvae in young ash trees and saplings, which are growing in large numbers in forest gaps after EAB decimated the overstory ash trees [37,62,75]. To evaluate the delayed impacts of EAB biocontrol on the entire woody community, we carried out an analysis that linked biocontrol with tree recruitment dynamics taking place since death of overstory ash trees. Our analyses showed a positive association between the release numbers of the parasitoid, *T. planipennisi*, and the density of ash saplings, the EAB tree host. We also documented negative associations between ash saplings and invasive plant species, and between invasive species and native seedlings. Our results indicate that even if *T. planipennisi* does not protect larger ash trees from EAB, it can still protect ash saplings which are likely out-shading invasive species, and thus, buying time for slower growing native species to recruit into these sites. This illustrates that there is a secondary positive community-level benefit of EAB biocontrol in these forests.

4.1. Do Biocontrol Agents Affect Ash Sapling Density?

Emerald ash borer biocontrol releases began in Michigan in 2007 and >14,000 parasitoids were released at our seven release plots during a six-year period [61] (Supplementary Material 2). Although parasitoid prevalence in some ash trees is as high as 35% for *O. agrili* and >90% for *T. planipennisi* at some study sites, the mature ash trees still experienced high mortality as they were already dead or dying when parasitoid releases began [31,37]. In areas not treated with biocontrol, up to 19% of the stems in the regenerating sapling layer can also be infected [76]. However, younger, thin barked ash trees and saplings growing at these release sites seem to be protected by the dominant biocontrol agent *T. planipennisi*, a small parasitoid with a short ovipositor that successfully parasitizes EAB larvae in ash trees <10 cm DBH [37,40,77,78]. Our results illustrate that this is likely the case at our study sites where a higher density of ash saplings was associated with higher release numbers of *T. planipennisi* (Figure 3).

This relationship was maintained after we controlled for the percent of forest cover around the plots, our proxy for the source of pre-EAB ash propagules that would subsequently grow into the seedling layer. And, as we sampled in areas with a canopy opening, we were able to document the seedling transition into a sapling layer in response to this disturbance. It would have been at this stage that the biocontrol agent, *T. planipennisi*, became most effective in protecting ash, as saplings have relatively thin barks. Previous work in this system have shown biocontrol can reduce EAB infestation in saplings (2.5–8 cm DBH) by >50% [37], ensuring a healthy sapling layer. Moreover, ash can reproduce at small sizes (8 cm DBH; [38]) and produce large number of seeds during mast years [36]. This could ensure that under the influence of the biocontrol agents ash populations will not entirely disappear because of EAB.

4.2. What Are the Variables Driving the Establishment of Invasive and Weedy Saplings in This System?

The sites in our study had experienced overstory tree dieback and were surrounded by agricultural, developed and other forested areas. Therefore, the likelihood of invasive plant species rapidly colonizing an area after a disturbance was relatively high. Still, one of the woody species that can rapidly take over after an opening in the forest canopy is *F. americana*, white ash. White ash seedling and basal sprouts densities have been observed as high as 20,000 per hectare [36,39]. Thus, even if adult trees succumb to the EAB, seedlings can rapidly grow into the sapling layer and, if protected by biocontrol, shade the ground vegetation. Our results revealed that this is likely the case at our study sites, where we found a negative association between ash saplings and the abundance of invasive and weedy species, unveiling an indirect beneficial effect of EAB biocontrol on the entire community.

Unexpectedly, we also documented a positive association of forest cover around the study sites and the incidence of invasive and weedy species. However, when we included other variables, e.g., light, we did not find an association with density of invasive and weedy species [79]. We had hypothesized that higher forest percent cover around our sites, which ranged from 25 to 90%, would be linked to a decrease in invasive species propagules. Invasive plant species are not common in forest interiors [7,80,81], and under natural disturbances the native vegetation, including both fast and slow growing species, can recover [82–84]. However, our results illustrate an opposite trend emphasizing the importance of assessing the risk of plant invasion not only at the site, habitat characteristics level, but also within the context of the historical landscape [85]. In our study area, forests have been under considerable human influence for almost two centuries, being highly fragmented and having a large edge to area ratio [86] where invasive and weedy species thrive, i.e., showing fast growing and reproductive rates [85]. As a result, the availability of propagules from introduced species is likely to be widespread in the region.

4.3. Is the Density of Invasive and Weedy Species Associated with Native Seedling Density?

One of the indirect effects a pest outbreak may have is the creation of optimal conditions for the establishment of harmful species. The conditions created by closed canopy forests and the lack of propagules are thought to buffer mature native forests from invasive plants [87,88]. It is mostly after disturbance events that invasive species are able to establish populations large enough to negatively affect the native community [54,89,90]. Our study supports this trend, as we observed a negative association between invasive and weedy saplings and native seedlings. This is due to some of the traits that prevail among the observed invasive and weedy species, i.e., fast growth rates and/or prolific seed production when resources are plentiful, which confer greater competitive ability to these species over natives, mostly non-ash seedlings in our sites, in disturbed forest areas where light is not limiting [91,92].

The understory vegetation response to disturbance mostly follows the direct regeneration hypothesis (DRH), which posits that tree communities will regenerate from existing seedlings to pre-disturbance levels within decades [93]. The resiliency of the DRH is based on the regeneration capacity of trees, which is proportional to basal area [69]. Since the degree of disturbance was similar among sites (one dead canopy tree), our analysis supports this hypothesis, we found a very strong effect of basal area on the density of seedlings from woody species (Figure 3). However, under highly modified contemporary landscapes, the availability of propagules from introduced harmful species increases with the level of development and roads around remnant vegetation patches [85]. Thus, after a disturbance event, a site with a high basal area may still be threatened by the establishment of invasive plant species.

5. Conclusions

In summary, this study provides a linkage between post disturbance vegetation recovery and an invasive insect biocontrol program. We found that biocontrol protection on ash saplings has

secondary effects that protect native seedling recovery from invasive and weedy saplings. Our results also indicate that after a disturbance event, biocontrol efforts can help forest recovery by buying time for the native community recruitment by reducing the threat of invasive and weedy species. We found that the efficacy of the ash biocontrol program could not be solely evaluated using the effect it had on parasitism levels or protecting mature ash trees, but should also include other ash size classes and the community dynamics of the adjacent species.

Supplementary Materials: The following are available online at www.mdpi.com/1999-4907/8/10/369/s1, Supplementary Material 1: Information on vegetation study sites. Supplementary Material 2: Parasitoid release information. Supplementary Material 3: Vegetation information. Supplementary Material 4: List of invasive and weedy species. Supplementary Material 5: Environmental data. Supplementary Material 6: Model code. Supplementary Material 7: Model comparisons.

Acknowledgments: This work is/was supported by the USDA National Institute of Food and Agriculture, McIntire Stennis project [2012-32100-06099]. We also appreciate the ongoing support provided for this research by USDA Forest Service, Northern Research Station, Lansing, MI, USA; USDA Agricultural Research Service, Beneficial Insects Introduction Research Unit, Newark, DE, USA; USDA Animal and Plant Health Inspection Service, Brighton, MI, USA and Buzzards Bay, MA, USA; and the Department of Entomology, Michigan State University, East Lansing, MI, USA.

Author Contributions: E.M., L.B. and I.I. conceived and designed the study; E.M. collected the data; I.I. analyzed the data; E.M., L.B. and I.I. wrote the paper.

Conflicts of Interest: The authors declare no conflict of interest. The founding sponsors had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, and in the decision to publish the results.

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