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Simulated Emerald Ash Borer Induced Changes in Western New York Forests

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Table of Contents

Chapter 1

Shifts in Community Structure and Species Composition in Western New York Forests Impacted By Simulated Emerald Ash Borer

Chapter 2

Ecosystem Effects of Simulated Emerald Ash Borer in Western New York Forests

Chapter 3

A synthesis on Emerald Ash Borer

List of Tables

List of Figures

Comprehensive Abstract

Invasive pests and pathogens are among the biggest threats currently faced by Northeastern forests. The emerald ash borer (*Agrilus planipennis*) is one such pest and targets trees in the genus *Fraxinus*. The primary goal of this research was to determine the ecological effects of EAB on forests in Western New York, emphasizing forest composition, succession, and carbon cycling. Each ash-dominated site contained two 20 x 20 m plots, an experimental plot where ash trees were girdled to simulate the effects of EAB and a control plot with ash trees left intact and healthy. Forest composition was examined in each of the plots to examine how composition and succession would change as a result of EAB. The effect of EAB on carbon dynamics and microclimate was also determined by quantifying soil organic matter, decay rate, soil respiration, tree productivity, soil and air temperature, and soil moisture.

Ash was prevalent in all three woody strata (seedlings, saplings, and trees) at the examined sites; however, once these sites are impacted by EAB, ash will not be able to remain the dominant species. Although it remains unclear how different species will respond to the gaps left by ash, it is likely that invasive shrubs will benefit the most from EAB attack due to their current presence in examined sites. Ultimately, these invasive shrubs will likely alter the successional trajectories of the sites they invade. These changes in composition, as well as the loss of ash, will have an impact on ecosystem

functioning. Overall, the results of this study suggest that, in the short term (at least two years based on my results), sites impacted by EAB will become C sources as suggested by the slightly increased soil CO_2 efflux (one year after girdling) and decomposition rates that were observed in the girdled plots. Additionally, there is a loss of ash productivity in the girdled plots and this loss is not being fully compensated by other species. Based on the results of this study, EAB will have a substantial impact on the composition of the sites it impacts in Western New York, resulting in altered functioning and decreased C sink strength. However, it is important to note that these responses will be site-specific, and therefore, the response of sites will vary with environmental conditions. Finally, EAB will result in altered species composition and, consequently, ecosystem functioning over longer time scales as other species completely fill the gaps left by ash.

Chapter 1

Shifts in Community Structure and Species Composition in Western New York Forests Impacted By Simulated Emerald Ash Borer

Abstract

The emerald ash borer (EAB, *Agrilus planipennis*) is an invasive forest pest that targets trees in the *Fraxinus* genus. This pest is expected to have a large impact on the composition of impacted stands, especially those with high ash abundance. This project examined changes in successional status and invasive species in stands with relatively high ash abundance in Western New York. EAB infestations were simulated via girdling and compared to adjacent control forested stands with abundant ash (>50% of tree density). Ash was the prevalent species in the seedling, sapling, and canopy tree layers, and this dominance of ash contributed to the low diversity of examined sites. Despite this prevalence, it is unlikely that ash will be able to persist in sites impacted by EAB. With few seedlings and saplings of other species to replace ash, it is likely that an invasive shrub (e.g., common buckthorn *Rhamnus cathartica*) will benefit the most from ash loss in the short term until canopy trees can overtake them. However, this will differ by site due to site-specific differences in composition. Ultimately, EAB will effectively act as a canopy replacing disturbance in ash-dominated stands, favoring the few remaining species.

Introduction

Forests of the Northeastern U.S. face many threats, but invasive pests and pathogens currently present the greatest threat (Lovett *et al.* 2006). The destructive potential of these pests first became a concern in the U.S. in the early 1900s when the gypsy moth (*Lymantria dispar*) started to spread throughout the country, defoliating large areas of hardwood forests (Liebhold *et al.* 1992). The ever-increasing threat from these invasive pest and pathogen species is demonstrated by the exponential increase in the number of alien phytophagus insect species in North American forests over the last two centuries (Mattson *et al.* 1994, Liebhold *et al.* 1995, and Niemelä and Mattson 1996). At the present time, there is nearly one exotic insect species or pathogen for every genus of woody plant endemic to the eastern United States (Mattson *et al.* 1994, 2007). The problem with these pests is that they cause changes in forest composition, structure, and ecosystem processes by triggering widespread mortality of their hosts (Gandhi and Herms 2010a).

One of the many ways in which alien insects alter forests is through the formation of canopy gaps (Rabenold *et al.* 1998, Runkle 2005) and as such there is potentially a lot that learned about the effects of EAB from studies of gap dynamics. These gaps generally alter forest understory light availability, which in turn alters microclimate conditions such as temperature and soil moisture (Twery 1990, Stadler *et al.* 2006). These changes in microclimate can then lead to substantial changes in understory composition (Kasbohm *et* *al.* 1996) and can have important implications for forest successional trajectories (Gandhi and Herms 2010a), with large gaps often benefiting early successional species (Klooster 2012). Additionally, tree pests may facilitate the establishment and spread of alien plant species, as gaps tend to reduce interspecific competition for space and resources (Herms *et al.* 2008).

One of these invasive pests is the emerald ash borer (Buprestidae: *Agrilus planipennis*; EAB). This bark beetle is native to Asia (Poland and McCullough 2006; Yu 1992) and thought to have been introduced on solid packing material (Cappaert *et al.* 2005, Poland and McCullough 2006) in the 1990s (Haack et al. 2002; McCullough and Katovich, 2004; Cappaert et al., 2005). EAB was first discovered in North America in 2002 in Detroit, Michigan, United States and Windsor, Ontario, Canada (Siegert *et al.* 2007). U.S. Forest Service Forest Inventory and Analysis data indicate that widespread ash mortality does not become apparent until about five years after infestation (Liebhold *et al.* unpublished data obtained through Kovacs *et al.* 2011), suggesting that EAB is likely well-established before it is detected (Siegert *et al.* 2010).

EAB is capable of killing more than 85% of ash in a stand (*Fraxinus* spp.) within 3 to 5 years of infestation (Poland and McCullough 2006) via feeding on the phloem and thereby disrupting the transport of photosynthates between the roots and shoots (Haack and Benjamin 1982). Mortality rates of nearly 100% have been reported near the point of introduction in Michigan

(Gandhi *et al.* 2008). Small trees may even die after a single year of infestation (Poland and McCullough 2006). However, trees with a DBH (diameter at breast height) of less than 2.5 cm are too small for the larvae to develop and can temporarily escape attack (Mercader *et al.* 2011).

In the US, ash trees are the most abundant and reach their highest density in the Great Lakes region (MacFarlane and Meyer 2005, Flower *et al.* 2013a,b), with New York having the second highest ash abundance of any state other than Minnesota (DeSantis *et al.* 2013). Ash trees are very common in New York, with roughly 900 million ash trees (King 2011) of 15 *Fraxinus* species in the state (Williamson *et al.* 2011). EAB was first discovered in New York in 2009 in Randolph, Cattaraugus County; then just one year after its first detection, EAB infestations were found in six additional New York counties (King 2011). New York State authorities admit that one of the greatest threats to the state's trees and forests is attack by invasive exotic insects (Williamson *et al.* 2011).

EAB will cause a compositional change in infested stands because ash loss will alter patterns of succession. Ash will likely be replaced by early successional shrubs, which will be able to take advantage of increased light levels. Thus, EAB may represent an example of "invasional meltdown" where invasion by one species facilitates further invasion of other exotics (Simberloff and Von Holle 1999; Simberloff 2006). In this case, the invasive EAB leads to the spread of invasive plant species by creating a resource-releasing disturbance. The spread of invasive plants that I anticipate to occur following EAB-induced ash loss is a concern because non-native shrublands have been shown to inhibit the germination and establishment of trees changing species compositions (Fagan and Pert 2004). I reason that this will result in slowed succession, altered community composition to stands dominated by non-native species, and the creation of novel ecosystems (as the species assemblages present will be the result of human introduction of EAB and invasive plant species).

This project examined short-term aspects of simulated EAB infestations, including forest compositional changes. Specifically, it examined changes in successional status and invasive species in stands with relatively high ash abundance in Western New York. I hypothesized that EAB would likely turn back the successional clock of the affected sites by altering the compositional dynamics. I expect this to occur via the establishment of early successional and invasive species, such as shrubby invaders, with the loss of ash trees. This was studied by simulating EAB infestations and comparing experimental plots to adjacent control plots in forested stands with abundant ash (>50% tree stems).

Methods

Site Selection

To determine the impacts of Emerald Ash Borer (EAB) on ash dominated forests, six sites across western New York were chosen: three at

Iroquois National Wildlife Refuge (INWR), two at Montezuma National Wildlife Refuge (MNWR), and one at the Northern Montezuma State Wildlife Management Area (NMSWMA; Table 1, Figure 1). Sites were chosen so that three of them were dominated by white ash and the other three were dominated by green ash to investigate possible differences between these two common ash species. Sites chosen were ash-dominated and free from EAB, as EAB presence would impact ash health in the control plots where conditions should remain constant for comparison purposes. Chosen sites were at least eight kilometers from known EAB infestation areas at the time of plot establishment in the early spring of 2012 to reduce the likelihood of infestation in control plots.

As EAB is already present in the state, it was important to monitor experimental sites for EAB infestation. Visual surveys were used to look for D-shaped exit holes, longitudinal cracks (that result over EAB larval galleries), increased woodpecker activity, canopy dieback, and epicormic shoots (Poland and McCullough 2006). However, it is difficult to detect low-to-moderate EAB infestations using visual surveys because, at these infestation rates, D-shaped exit holes are likely the only symptom of infestation present (Poland and McCullough 2006) and they are likely to be high in the canopy (Cappaert *et al.* 2005). Additionally, at each of the three sites at Iroquois Wildlife Refuge, two purple sticky prism traps (one per plot) were set up in trees throughout the summer of 2013 due to the close proximity of known

EAB detections. Traps were placed in the plots on 17 May and removed on 8 and 9 September to capture the timeframe where adults would be emerged. Traps were bated with both Manuka oil (Synergy Semiochemicals Corp.) and leaf alcohol (Synergy Semiochemicals Corp.), which have been shown to attract adult EAB. Insects were removed from the traps at various times throughout the summer and returned to the lab for identification. No EAB were found in the traps.

Plot Selection and Preparation

At each site, two 20 x 20 m plots, including an experimental plot and a control were established within each site (Figure 2). The locations of the plots were established by reconnoitering the study areas once a general area at the site was determined with the help of refuge managers. Forest species composition and soil conditions were examined to find the best location to place the plots, ensuring that plots at each site would have few to no initial difference in general forest characteristics. Treatment and control plots were located 20 m from one another, the edge of forest, and from any trails to avoid forest edge effects.

The experimental plots differed from the control in that all ash trees >2.5 cm DBH were girdled to simulate the effects of EAB. EAB does not affect seedlings and sapling of less than 2.5 cm DBH because EAB larvae cannot develop in trees of this size (Mercader *et al.* 2011). Girdling was used as an analog to EAB larval feeding because they are functionally equivalent (Chen *et al.* 2011). For example, both cause crown dieback, and epicormic shoots interfere with the transfer of nutrients via wounding the phloem and cause mortality in 3-5 years (Chen *et al.* 2011). Trees were girdled via methods similar to those used by McCullough *et al.* (2009). In short, the bark and cambium encircling the tree from a 15 cm wide area (0.85-1.00 m above ground) were removed. Trees were girdled between 1 July and 16 September 2012 once permit-granting and site establishment were complete (Table 1).

Forest Composition

Concurrent with girdling, all trees ≥ 2.5 cm DBH within the 20 x 20 m plot (whole plot) were identified and measured (DBH) in order to determine species composition within the plots. Each tree (of all species) was also assigned a canopy class rating according to Knight (2012), based on canopy position and access to light: dominant trees received light on all sides of the canopy, co-dominant trees received light on more than one side of the canopy, intermediate trees only received light on the top of the canopy, and suppressed trees did not receive any direct sunlight. One year after treatment, these plots were once again sampled to see how loss of ash is affecting the forest tree structure with respect to species presence, forest diversity (Shannon-Wiener index: H’), productivity (chapter 2), and tree size (DBH). H’ was calculated for the experimental plots with all ash present and again with only the ash still alive one year after girdling. Trees in the experimental plot were also given a canopy loss rating modified from Griffin *et* *al.* (2003) as follows: 1- tree in good health with intact canopy; 2- tree in declining health with canopy 75 to 100% intact; 3- canopy between 25 and 75% intact; 4- canopy less than 25% intact; and 5- tree dead. An independent t-test was conducted on the diversity data in the experimental plots to compare the diversity of these plots with all ash and then again with the ash that had died due to girdling removed from the analysis.

A central 10 x 10 m plot (center plot) was established within each of the larger plots (Figure 2). This smaller inside plot was used to decrease edge effects that may result from the surrounding undisturbed forest. Within this central plot, all tree and shrub seedlings (< 1.37 m tall) and saplings (>1.37 m tall but < 2.5 cm DBH) were identified and measured (DBH for saplings, height for seedlings) both prior to and one year after girdling in both plots. These data were then used to examine how girdling affected the seedling and sapling layers by allowing comparison of both across years and between control and experimental plots. These data can be used to examine how the successional trajectory of the plot is changing due to the simulated EAB attack. Data from the subplots (see below) regarding understory composition, as well as seed bank data, were also used to examine how the EAB loss is affecting these layers and to predict future species composition.

Three randomly located $1m^2$ subplots were established inside the central 10 x 10 m plots (Figure 2), in which all vegetation (excluding sapling and tree) cover was estimated by functional group (woody, forbs, graminoid).

These data, once transformed to achieve normality, were examined using a two-way ANOVA on the effects of year and treatment to determine if simulated EAB attack caused a change in the understory one year post girdling. Additionally, by monitoring this aspect of the forest, I was able to determine if invasive species are benefiting from the simulated EAB disturbance and becoming established or spreading in the plots. Invasive species were surveyed via percent cover to determine their presence in both the entire 20 x 20 m plot and the center 10 x 10 m plot.

Canopy Loss

Increased understory light availability was expected to be the main driver of forest compositional change. Therefore, 20 densiometer readings at random locations in each center 10 x 10 m plot were used to examine canopy loss at the end of September 2012 (roughly two months after girdling at most sites). This was used to provide a sense of how fast the canopy was changing. Densiometer readings were again taken in August 2013 (roughly one year after girdling) to examine how girdling affected canopy cover. Independent t-tests were conducted on 2012 and 2013 data; 2012 data were transformed by taking the square root of a reflection (each data point was subtracted from the largest number plus one) of the data to achieve normality.

Seed Bank

The soil seed bank was examined to determine what species are present and likely to become established following ash loss. Three groups of five PVC soil cores (5 cm diameter) were collected to a depth of five centimeters per central 10 x 10 m subplot (similar to Gurnell *et al*. 2007). A total of 15 cores were taken with a volume of approximately 100 cm^3 each. These soil core samples were collected during the first week of April 2013. Samples were stored in a refrigerator until they could be spread into greenhouse flats. Prior to being spread, soil samples were sieved (4.0 mm mesh) to remove large organic debris and to mix the subsamples of each plot together thoroughly. Any seeds that were sieved out were added back to the soil. The 26 x 26 cm flats were prepared by placing 2.5 cm of sand on the bottom and covering the sand with roughly two centimeters of the soil sample (similar to Ashton *et al.* 1998). The seed bank study began on 19 April 2013. The soils were watered regularly and monitored throughout the growing season to examine seed bank composition. New plants were identified and removed as soon as possible. These data were used to determine which species are present in the seed bank and in what proportions.

A leaf litter seed-bank analysis was also conducted to examine species presence. Using the same date as for soil seed-bank sampling, in each 10 x 10 m subplot, three 10 x 10 cm leaf litter samples were taken. These samples were then air dried and hand-crushed. The leaf litter seed-bank samples were then placed in the same size flats as the soil seed bank; however, the 2.5 cm of sand was covered by an additional 1.5 cm of greenhouse mix (Pro-Mix BX, Premier Tech, Quebec, Canada) before the crushed leaf litter seed- bank sample was placed on top. Monitoring was done in the same manner as the soil seed bank until terminated on 13 October 2013.

Results

Girdling

Girdling successfully resulted in ash canopy loss and death and thus satisfactorily simulated EAB infestation. One year after girdling, approximately 1.8 % of girdled ash remained in good health, while 63.2% of girdled trees were dead, with the rest of the trees having some fraction of the canopy intact. Canopy cover corresponded with this pattern as well. The average 2012 percent canopy cover (taken in late September on average six weeks after girdling) was significantly greater at the control sites (76.67 ±9.8%) than at the experimental sites (45.83 ±11.58%; p=0.018). This same trend was even more pronounced in 2013 (control = 79.17 ±13.93%; experimental = 36.67 ±24.63%; p=0.004).

Canopy Layer

Ash was the dominant tree (≥2.5 cm DBH) species at all sites, and on average, ash (1356.25 ±187.47 stems/ha) outnumbered other species (262.50 ±87.01 stems/ha) by approximately 5 to 1 (Figure 3). The average basal area of ash (19.60 ±2.60 m^2/ha) was about four times that of non-ash species (5.58 ±1.83 m^2/ha; Figure 3). Non-ash tree species were present at five of the six experimental (girdled) plots, absent only at the TIBB site. Only five non-ash canopy species were encountered across all sites, and their composition and abundance varied considerably by site (Table 2). Two of these species are of special interest: American elm (*Ulmus americana*), which was decimated by Dutch elm disease (Holmes 1980), and common buckthorn (*Rhamnus cathartica*), an invasive species.

Canopy Diversity

In four of the six sites, diversity (H') increased as ash were lost via girdling and other species becomes more important (Table 3). At only one site (Unit) did diversity decrease due to the high density of buckthorn, which was the only non-ash species present at that site. While the loss of girdled ash generally resulted in increased diversity, this pattern was not significant across all sites (p=0.300).

Sapling Layer

Saplings (classified as trees and shrubs < 2.5 cm DBH but >137 cm in height) were present at four of the six sites (JACK, NMONT, TIBB, and UNIT). In every site that had saplings, ash saplings (of the same species as the canopy; 308.33 ± 106.93 stems/ha) were present and were slightly more abundant than other species (291.67 ± 153.97 stems/ha; Figure 4A). Across all sites, ash were the most dominant species in the sapling layer, followed by common buckthorn, silky dogwood (*Cornus amomum*), and swamp oak (*Quercus bicolor*).

Seedling Layer

Seedlings (classified as < 1.37 m tall) were present at all sites. The average density of ash was more than double that of non-ash seedlings, 2,116.67 (±884.62) /ha and 1,000.00 (±287.36)/ha, respectively (Figure 4B). Non-ash species were present at four of the experimental (girdled) plots and included elm, red maple (*Acer rubrum*), swamp oak, silky dogwood, and buckthorn (Table 4). Buckthorn was only present at one site, but it was notably the only species of seedling present in that plot.

Seed Bank

A total of 1,223 seeds from all sites germinated over the course of the seed-bank experiment, none of which were woody (Table 5). More than 77% of the seeds to germinate in the seed bank were sedges in the *Carex* and *Cyperus* genera (Table 5). Forbs were much less common than graminoid species, but several species were seen nonetheless. The most notable forb species encountered was purple loosestrife (*Lythrum salicaria*), which is invasive (Munger 2002). Finally, 44 individual plants senesced before they were able to be identified.

Understory Response

The average woody, graminoid, and forb percent cover deceased but not significantly (p>0.05) in each treatment from 2012 to 2013 (Figure 5). This decrease seemed less drastic in the experimental treatment than the control treatments in the graminoid and forb functional groups. In the woody functional group, this decrease was more drastic in the experimental treatment than in the control. However, treatments were not statistically different (p>0.05) from each other over time. Over all sites, graminoid species (approximately 30% cover) were most common, followed by forbs (~20%), and finally woody species (~5%) and followed a similar pattern as germinants in the seed-bank study with graminoids being the most commonly encountered functional group, followed by forbs and finally woody species.

Invasive Species

Invasive species were noted at five of the six sites prior to girdling and were present in both control and experimental plots. Buckthorn had the greatest densities and cover of any of the invasive species and was seen at three of the sites. Other invasive species encountered included Japanese barberry (*Berberis thunbergii,* patchy abundance at one site), honeysuckle (*Lonicera tatarica*, limited to patchy abundance at three sites), multiflora rose (*Rosa multiflora,* limited abundance at three sites*)*, and autumn olive (*Elaeagnus umbellate,* limited abundance at one site).

Discussion

Woody Strata Composition

Study sites were chosen where ash was the dominant canopy species (at least 50% of stem density, Figure 3). Locally high ash densities are not atypical of forests in Western New York (WNY), where ash is the most important genus, comprising, on average, 11.7% of all trees (Wang *et al.* 2009), and more than twenty percent of the basal area in several counties (Wilson and Lister in review). Therefore, these forests will be altered by EAB, which will likely act as a stand-replacing event in areas where ash is a dominant canopy species. This will likely have cascading community effects as environmental conditions are altered in effected stands and other species are forced to respond (such as higher concentrations of leaf litter arthropods and earthworms near inputs of ash wood on the forest floor (Ulyshen *et al.* 2011).

Due to this ash dominance (Figure 3), none of the studied forests were very diverse (low species richness) in spite of other tree species presence (Table 3). However, the results of this study indicate that, as ash trees are lost to EAB, diversity will increase, but these results may be misleading. The only reason for the increased diversity is the loss of the dominant species, which makes each of the other species proportionally more important. Long-term patterns in diversity will likely change as some species are better able to fill the canopy gaps than others and individual trees respond in different manners to the canopy gaps formed. For example, Flower *et al.* (2013a) found in northern Ohio that it is the small trees in the understory, as well as those in the maple and elm genres, that will likely become the dominant canopy species once ash is lost because of their faster relative growth rates.

As canopy ash are lost to EAB, light availability at the forest floor is expected to increase, likely benefiting plant growth and establishment (Klooster 2012), especially of the woody species that are currently in the seedling and sapling layers. The sapling layer was generally not very diverse, suggesting that the some forests may become dominated by the shrub species encountered in the sapling layer (e.g., silky dogwood and buckthorn) in the future.

Ash will not likely persist in sites impacted by EAB, despite its prominence in the seedling layer (Figure 4A). Klooster (2012) documented ash dominance in the seedling layer but found that, over time, these ash were not being replaced as they grew. The lack of ash replacement in the understory is likely because ash seeds do not form a viable seed-bank (Griffith 1991; Gucker 2005a, b; Klooster *et al.* 2013). Corresponding with this, no woody species, including ash, were found in my seed-bank study. It is unlikely that small ash trees (< 2.5 cm DBH) that initially escape EAB attack will ever reach reproductive maturity (which occurs at 20-25 cm DBH and can take up to 60 years, Kurmis and Kim 1989), as they will become susceptible to EAB once reaching the appropriate size (Klosser *et al.* 2013). Low densities of EAB have been reported in Michigan and Ohio stands with nearly 100% ash mortality (unpublished data cited by Klosser 2012). These low densities of EAB will eventually attack ash trees that survive the first wave of EAB.

Elm, which was common in the seedling layer of examined sites (Table 4), is also not likely to replace ash and persist in EAB impacted sites. American elm was decimated by Dutch elm disease in the United States over the course of the 20th century and now typically only exists in smaller size classes before succumbing to the disease (DeSantis *et al.* 2013).

Regardless of my results, individual forests will likely respond differently based on regional differences in the subcanopy and understory plant community prior to EAB-induced disturbance. Studies of gap dynamics demonstrate that the characteristics of the gaps formed, such as their size will also play a role in how individual forests respond (Brokaw and Busing 2000). For example, Klooster (2012) suggested that sugar maple has a strong potential to become a dominant canopy species in the absence of ash because it is already dominant in the seedling layer of many impacted eastern North American forests. Despite this, I do not expect sugar maple to become dominant in the investigated sites because it was not present in any of the sites examined. These differing results demonstrate that future species compositions and successional trajectories will vary by site and that regional differences in species compositions may play a part in how different forests respond. Finally, there are difficulties with predicting future species compositions based on seedlings because mortality is typically very high in the seedling layer and may not represent what are seen in future, larger size classes (Franklin *et al.* 2002).

Altered Succession

Altered successional trajectory as a result of tree mortality can occur through various mechanisms (Franklin *et al*. 1987; Lovett *et al*. 2006; Gandhi and Herms 2010b), such as disturbance. When a disturbance such as EAB impacts a forest, resources such as light, water, and nutrients increase in availability and can become exploited by other plants for growth and establishment (Tilman 2004). However, the changes in successional dynamics following invasion of exotic species are largely unknown (Ehrenfeld 2010).

One way that successional dynamics may be altered is if canopy gaps are large enough that light levels increase dramatically. The size of gaps formed is predominately a result of the number of trees impacted. Therefore the abundance of ash in a particular area will determine the number and/or size of gaps formed. The results of this study showed that experimental sites had significantly less canopy cover than control sites, suggesting that there is increased understory light availability in plots impacted by EAB nearly immediately. Increased light levels would allow more early successional species to colonize the gap (Klooster 2012) in the short term as more light becomes available to woody species in the understory. Moreover, others have noted that following large disturbances, the affected area may be colonized by a new suite of plants that have life-history traits more suitable to the new conditions (Peltzer *et al*. 2000; Selmants and Knight 2003) such as more early successional species. For these reasons, I anticipate that in sites with high relative ash abundance, such as those examined as a part of this analysis, EAB-infestation will rapidly shift forests from early successional ash forests to those dominated by even earlier successional species, as a result of large gap formation. This expected shift is supported by the high density of shrub species (four invasive species and one native across the six sites), especially those that are non-native, at many of the sites prior to girdling. Since these species are already present in the sites prior to infestation, they have an advantage over species that are not currently present and will likely fill the gaps left when ash succumb to EAB. In addition, invasive shrubs have an advantage over native trees that are present because shrubs have extensive lateral branching compared to trees, which allows them to capture additional light (Poulson and Platt 1996). Finally, since dense shrub understories can lead to reduced light levels reaching the forest floor, there will likely be lower tree seedling recruitment over time, as well as a slow shift toward more shade-tolerant species (Beckage *et al.* 2000).

Invasion

When the dominant species is lost, other species, including invasives, will be able to take advantage of the released resources and either become established or spread if already present in the disturbed area (Herms *et al.* 2008). Invasive species are able to outcompete many of their native competitors because of their fast growth and reproductive rates (Tilman 2004, Davis *et al.* 2005). Klooster (2012) found that the relative growth rate of invasive tree and shrub species was generally greater than that of native species in forests with varying ash densities. Many of the invasive species that Klooster (2012) examined were found in my study, including buckthorn, Japanese barberry, honeysuckle, multiflora rose, and autumn olive.

When canopy gaps caused by EAB are filled by an invasive species, it is an example of invasional meltdown (Simberloff and Von Holle 1999), where one invasive (i.e., EAB) facilitates other invasive species by altering the environmental conditions. This may cause additional cascading effects. For example, buckthorn was found in all three layers (seedling, sapling, and tree) of ash-dominated forests in this study and is an invasive species. Buckthorn increases decomposition rates due to the high N content of its litter (Heneghan *et* al. 2002, 2004), leading to less leaf litter cover over time. Many invasive plant species, including buckthorn, have enhanced germination and emergence rates in areas of lower leaf-litter cover (Klooster 2012).

Consequently, buckthorn may further contribute to an invasional meltdown by facilitating additional plant invasions (Klinosky *et al.* 2011; Klooster 2012).

Furthermore, buckthorn reproductive rates may be influenced by growing conditions, as buckthorn growing in a wetland is more likely to bear fruit when it is seedling size as well as produce more and larger fruit (Gourley 1985). Additionally, seedlings in higher moisture treatments had greater survival but lower growth than those in lower moisture treatments (Gourley 1985). Buckthorn’s enhanced fecundity in wetlands is a concern, as ash is common in wetlands and, as ash are lost to EAB, buckthorn will likely be able to invade or spread in these sites. A future study examining competition between buckthorn and a native shrub such as silky dogwood may provide more insight into how these species will react to the canopy gaps left behind by EAB. In this experiment, buckthorn and a native shrub would be planted in close proximity to one another, as well as a buckthorn next to buckthorn, and the native shrub next to a native shrub in EAB created gaps. This would allow us to examine how species growth is influenced by intra- and inter-specific competition in the environmental conditions created by EAB.

Understory Composition

In general, the percent cover of the understory functional groups decreased over time from 2012, when all sites were dry in early summer, to 2013, which was much wetter and several sites were flooded until August. These differences in moisture (due to differing precipitation patterns between the two years) make it difficult to determine if girdling caused changes in the understory community. Nonetheless, this decrease was less drastic in the experimental treatment for the graminoid and forb functional groups (Figure 5). In the absence of differing hydrology between the two years, I expected, based on my field survey and seed-bank-analysis results, that graminoids and forbs would have increased in the experimental plots from the increased light levels. It is possible that these herbaceous species would have shaded out woody species and caused them to have less of an increase than the herbaceous plants. A future seed-bank study examining how the seed bank responds differently in drawdown and flooded conditions may provide valuable insights into how the understory responds to different environmental conditions. Following up on the understory composition in future years at the examined sites may also lend insight into how girdling effected the understory by allowing us to examine additional relatively wet and dry years.

Conclusion

Despite the prevalence of ash in all three of the woody layers, it is not likely that ash will be able to sustain itself in forests impacted by EAB. Even small ash seedlings and saplings will not be able to persist, as EAB can infest trees as small as 2.5 cm DBH, and once trees reach this size, they will succumb to the pest. Once ash trees are lost, species already present in the sites will likely be the first able to fill the canopy gaps; thus, species replacements will be site-specific. Additionally, it remains unclear how different species will respond to the gaps and which species will benefit the most. Nonetheless, due to their ability to prosper in disturbed areas (Herms *et al.* 2008), as well as the fact that they are already present in many of the examined sites, it is likely that invasive shrubs will benefit the most from EAB attack at least initially until canopy species are able to overtake them. However, it is possible that the loss of ash itself could alter the environmental conditions in the effected sites enough (i.e., flooding as a result of loss of ash transpiration leading to reduced evapotranspiration rates) to inhibit shrubs. Nonetheless, these invasive shrubs are expected to change the environmental conditions enough that succession will be further altered. Ultimately, EAB-impacted sites will be pushed back from the early successional forests of ash to even earlier successional sites with patchy dominance by invasive shrubs such as buckthorn, honeysuckle, barberry, and others in the short term. This site-specific changing composition will, in turn, have cascading effects on ecosystem functioning (Chapter 2).

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Tables

Table 1. Site name (abbreviation), location, and girdle date of six study sites in Western New York. Dominant ash species also noted as either green (*Fraxinus pennsylvanica*) or white (*Fraxinus americana*).

Site Name	Location	Species	Girdle Date (2012)
Swallow Hallow (SH)	Iroquois National Wildlife Refuge	Green	1-Jul
Sour Springs (SS)	Iroquois National Wildlife Refuge	Green	10-Jul
Northern Montezuma (NMONT)	Northern Montezuma State Wildlife Management Area	Green	16-Sep
Tibbet (TIBB)	Iroquois National Wildlife Refuge	White	1-Jul
Unit 17 (UNIT)	Montezuma National Wildlife Refuge	White	6-Aug
Jackson (JACK)	Montezuma National Wildlife Refuge	White	2-Aug

Table 2. Non-ash tree species densities (#/ha) and basal areas (m^2/ha) in the experimental (girdled) plots; the percent of all non-ash is contained within parenthesis.

Site	Species	Density #/ha (%)	Basal Area m^2/ha (%)
Jack	Buckthorn (*Rhamnus cathartica*)	25 (14.3)	0.126 (0.9)
	Elm (*Ulmus americana*)	25 (14.3)	0.363 (2.6)
	Red Maple (*Acer rubrum*)	125 (71.4)	13.508 (96.5)
Nmont	Elm (*Ulmus americana*)	75 (50)	1.122 (20.2)
	Red Maple (*Acer rubrum*)	25 (16.7)	0.701 (12.6)
	Swamp Oak (*Quercus bicolor*)	50 (33.3)	3.732 (67.2)
SH	Cottonwood (*Populus deltoides*)	200 (100)	18.999 (100)
SS	Elm (*Ulmus americana*)	125 (83.3)	1.587 (90.9)
	Swamp Oak (*Quercus bicolor*)	25 (16.7)	0.159 (9.1)
Tibb	-	-	-
Unit	Buckthorn (*Rhamnus cathartica*)	975 (100)	1.476 (100)

Table 3. Shannon-Wiener Index (H') values for tree layer (≥2.5 cm DBH) representing the change in diversity one year after girdling in the experimental plots. H' was calculated for the experimental plots using all the ash present and alive prior to girdling (2012) and then again calculated excluding those dead one year after girdling (2013). Ash was the only tree species present in the experimental plot at TIBB.

	Jack	Nmont	SH	SS	Tibb	Unit	Average
2012 Pre-Girdling	0.366	0.297	0.554	0.616	0	0.692	0.421
2013 One Year Post-Girdling	1.01	0.432	0.683	0.943	0	0.659	0.621

Table 4. Non-ash seedling densities by species (#/ha) in the experimental (girdled plots). The percent of all non-ash is contained within parenthesis.

Site	Species	Density #/ha (%)
Nmont	Elm (*Ulmus americana*)	100 (5.26)
	Red Maple (*Acer rubrum*)	600 (31.58)
	Swamp Oak (*Quercus bicolor*)	600 (31.58)
	Dogwood (*Cornus amomum*)	600 (31.58)
SH	Elm (*Ulmus americana*)	200 (18.18)
	Red Maple (*Acer rubrum*)	900 (81.82)
Tibb	Elm (*Ulmus americana*)	200 (66.67)
	Dogwood (*Cornus amomum*)	100 (33.33)
Unit	Buckthorn (*Rhamnus cathartica*)	2500 (100)

Table 5. Results of the seed bank study with percent (%) of the 1,223 germinated seeds in each species or genus.

Species/Genus	**Percent of Germinated Seeds**
Carex spp	43.09
Cyperus spp	34.67
Canada blue joint (*Calamagrostis canadensis)*	6.30
Purple loosestrife (*Lythrum salicaria)*	5.89
False nettles (*Boehmeria cylindrical)*	2.45
Wild strawberry (*Fragaria virginiana)*	1.14
Creeping jenny (*Lysimachia nummularia)*	0.98
White snakeroot (*Ageratina altissima)*	0.74
Barnyard grass (*Echinochloa crus-gali)*	0.57
Rice cut grass (*Leersia oryzoides)*	0.41
Gill-over-the-ground (Glechoma hederacea)	0.08
Oxalis spp	0.08
Unidentified	3.60

Figures

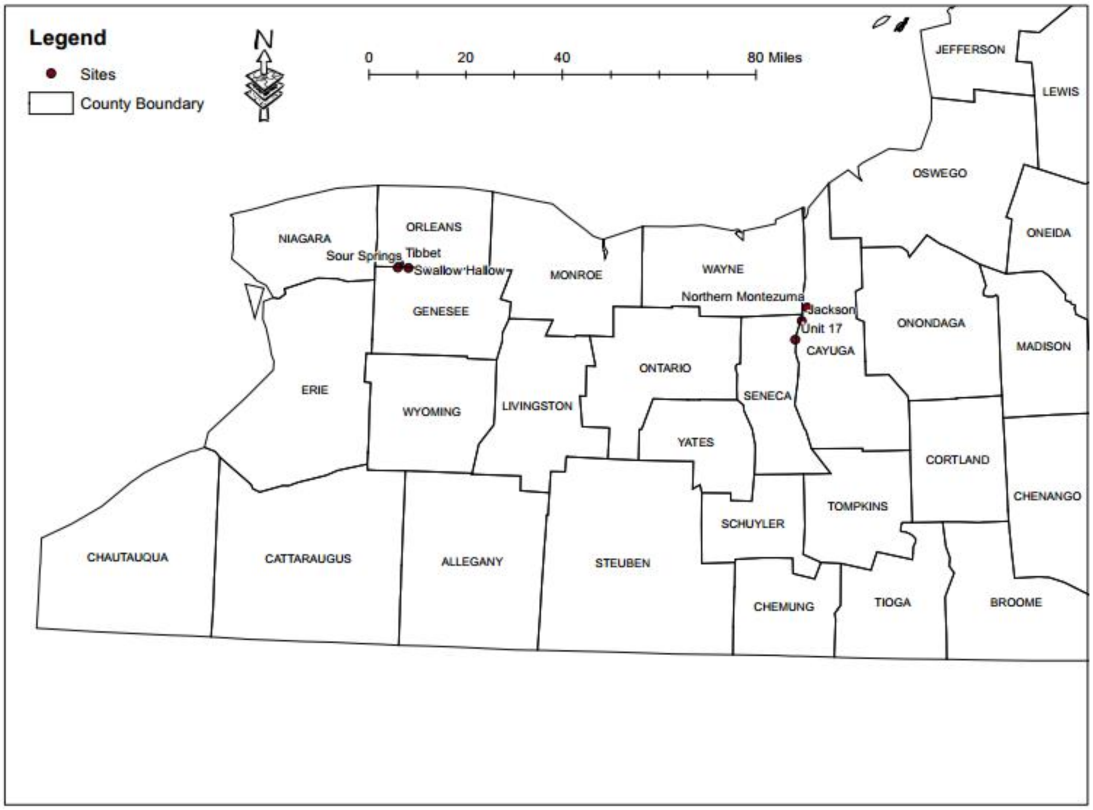

Figure 1. Site locations across Western New York.

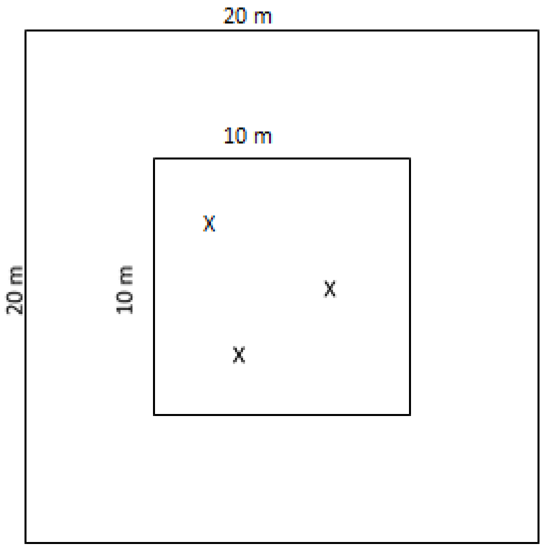

Figure 2. Diagram of plot layout at each of site. 20 x 20 m entire plot, center 10 x 10 m center plot, and three randomly located 1 x 1 m understory vegetation plots (X).

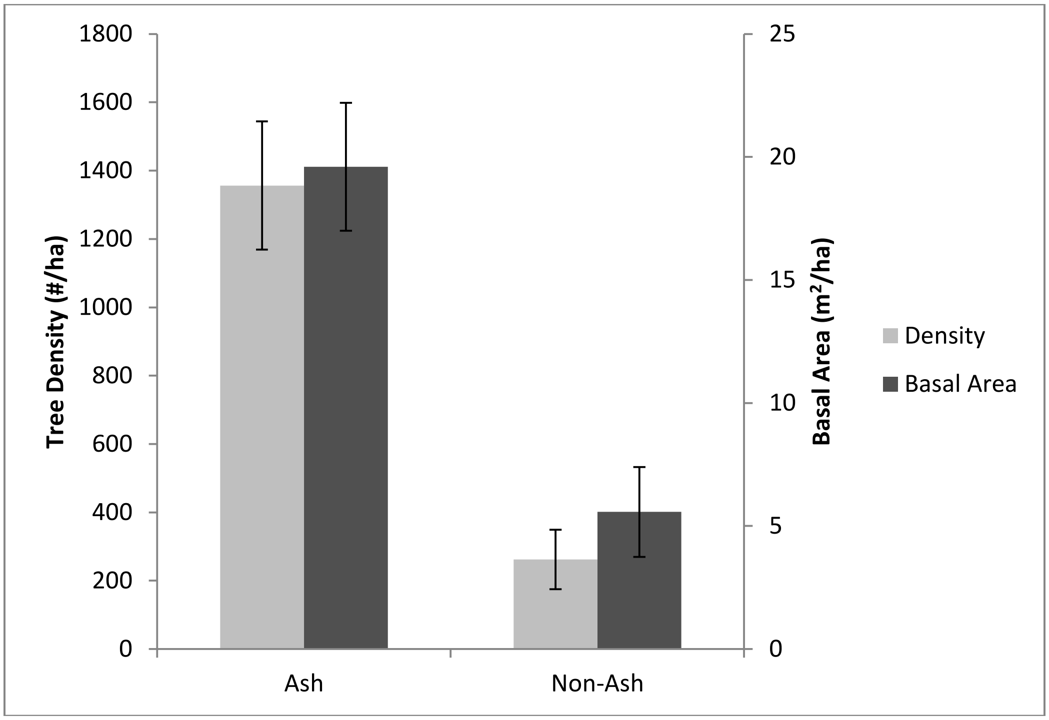

Figure 3. Average (mean ± standard error) 2013 canopy composition (trees ≥ 2.5 cm DBH), both density (#/ha) and basal area (m^2/ha) of all twelve plots (control and experimental plots at each site); dead ash due to girdling included.

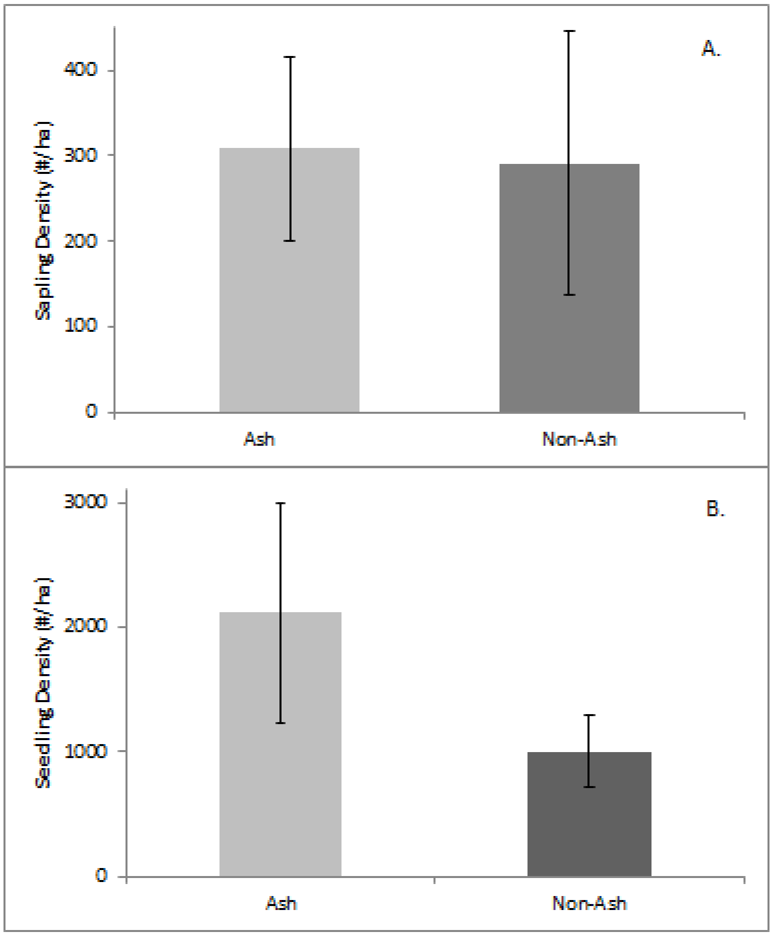

Figure 4. Average (mean ± standard error) 2013 sapling (A) and seedling layer (B) composition of all twelve plots (control and experimental plots at each site).

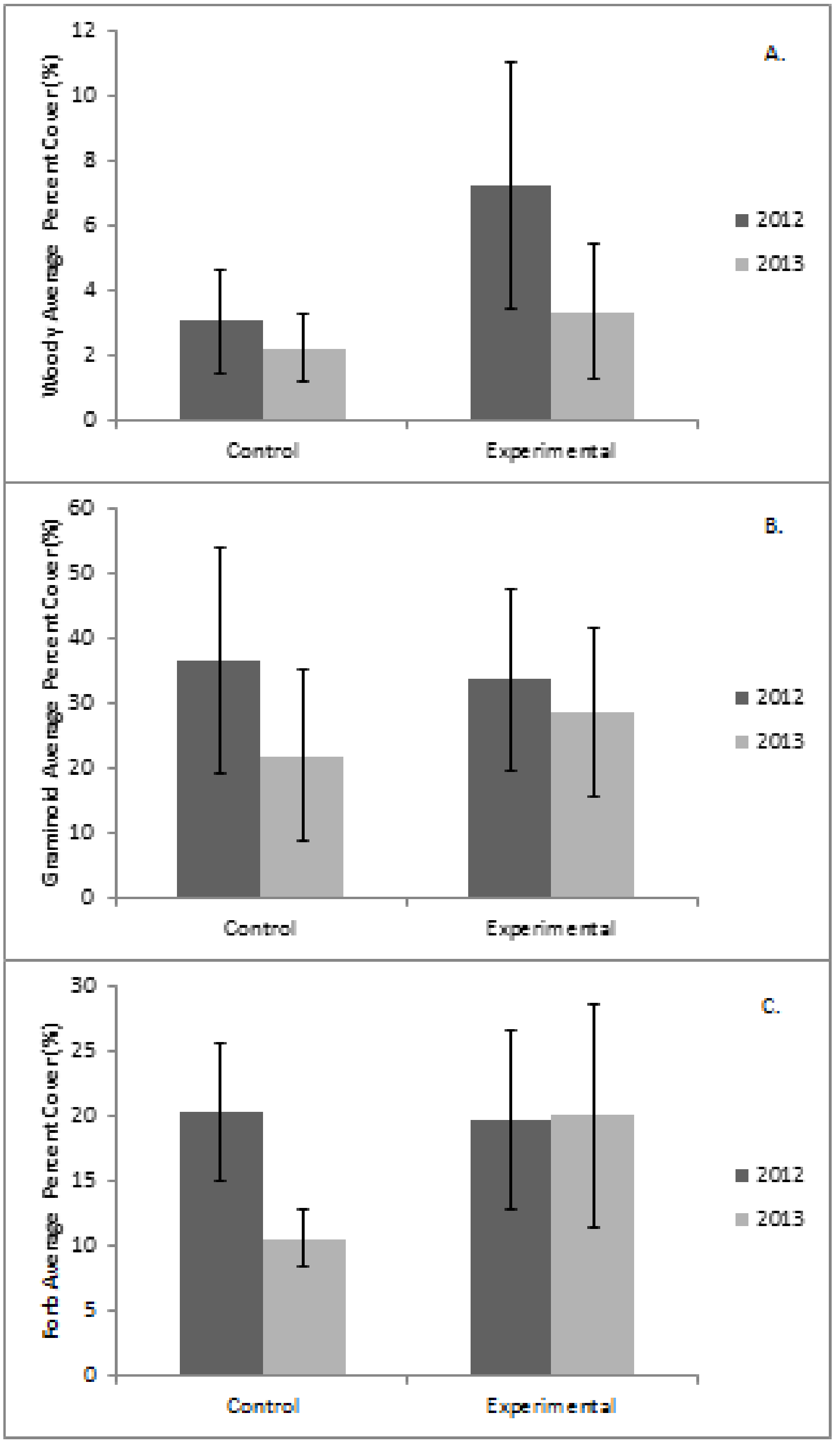

Figure 5. Average (mean ± standard error of six sites of each treatment) percent cover of woody (excluding saplings and trees; A), graminoid (B), and forb (C) in 1m^2 plots.

Chapter 2

Ecosystem Effects of Simulated Emerald Ash Borer in Western New York Forests

Abstract

As emerald ash borer (EAB, *Agrilus planipennis*) causes ash tree (*Fraxinus* species) death in impacted forested stands, there will likely be impacts on ecosystem functioning. For instance, in areas with high ash abundance, it is expected that stands will have substantially decreased net ecosystem productivity due to decreased tree production and increased carbon efflux, at least in the short term. EAB infestation was simulated in 20 x 20 m plots via girdling. Microclimate, soil CO_2 efflux, decomposition, and productivity were compared to adjacent control plots in Western New York forests where ash were prevalent (>50% of tree density).

Although treatment effects were variable temporally and across sites, soil CO_2 efflux generally decreased in the girdled plots relative to the control in the first year after girdling; however, it rebounded in the second year of the experiment as the experimental plots had higher efflux rates than the control plots. These changes in soil CO_2 efflux can largely be explained by changes in both autotrophic and heterotrophic respiration due to changes in microclimate and substrate. Decomposition rates were also subtly increased in experimental plots. Finally, girdling in the experimental plots decreased ash

productivity but the productivity of non-ash species increased to offset a portion of the ash loss. Results suggest that EAB will cause impacted stands to become C sources, at least in the short term, as soil CO_2 efflux increases and ash loss is not fully compensated by increased growth of other species. It is anticipated that impacted sites will continue to have decreased C storage until canopy species can fill the gaps left by ash loss, but longer term studies are needed to determine the carbon response more than two years after infestations.

Introduction

Invasive insect pests and pathogens seriously endanger Eastern forests by causing both long-and short-term effects on the forest ecosystems that they inhabit (Lovett *et al.* 2006). One such pest, the emerald ash borer (Buprestidae: *Agrilus planipennis*; EAB) threatens the survival of ash trees (*Fraxinus* species) and may have far-reaching effects on forest composition and function (DeSantis *et al.* 2013). EAB is an invasive bark beetle, native to Asia (Yu 1992; Poland and McCullough 2006), that was introduced into North America in the 1990s (Haack *et al.* 2002; McCullough and Katovich, 2004; Cappaert *et al*. 2005). Since its first detection near Detroit, Michigan, United States and Windsor, Ontario, Canada in 2002 (Siegert *et al.* 2007), EAB has spread extensively throughout the United States and was first detected in Western New York in 2009. EAB can kill ash trees quickly, with reported mortality rates exceeding 85% of a stand within 3-5 years of infestation (Poland and McCullough 2006). This is concerning because ash trees are one of the most common, fast-growing trees in the northeastern US (Poland and McCullough 2006) and are important in early successional forests (Wright 1959, Meiners and Gorchov 1998). The US Forest Service estimates that there are over 8 billion ash trees (FIA 2006) occurring in US forests, worth an estimated $300 billion (Poland and McCullough 2006). Ash are also a common urban tree, making up 5-20% of all street trees in the US (Du and Pijut 2008).

Studying the ecosystem-scale effects of EAB is important due to the lack of information surrounding this topic as well as the importance of this information in helping to predict and manage the long-term impacts of EAB in forested ecosystems. Most of the previous studies on EAB deal with its biology and dispersal, as well as the mortality that it causes in ash and the economic ramifications of its destruction (e.g., Timms *et al.* 2006, Homans and Horie 2011, Mercader *et al.* 2011, Sydnor *et al.* 2011). One portion of ecosystem functioning that is likely to be impacted by EAB is forest carbon cycling. Ash trees (*Fraxinus* species) are responsible for storing about 2.5% (varying from 0-24% per state) of the aboveground carbon mass of the contiguous US (Flower *et al.* 2013). The loss of this C sink may have implications for the global carbon cycle and therefore climate change through reductions in stored biomass C and soil organic matter C in infested stands in the short term. Over longer time scales, it is thought that these impacted forests will once again become C sinks as new canopy trees are able to fill the gaps left by ash, taking C out of the atmosphere and storing it in their biomass.

There is an increasing amount of evidence indicating that insect and disease outbreaks, such as EAB, can increase carbon efflux from forests (Kurz *et al.* 2008, Clark *et al.* 2010, Hicke *et al.* 2012, Weed *et al.* 2013). This is a concern because many temperate forests, including those where ash are dominant, act as net CO_2 sinks (Curtis *et al.* 2002). Both soils and vegetation play a critical role in the global carbon cycle and will likely be affected by EAB. EAB will likely decrease C gain due to reduced plant CO_2 uptake as ash are lost (at least until other species compensate for ash loss) and increased release of CO_2 from higher respiration rates (which mainly occurs through decomposition; Hicke *et al.* 2012). Therefore, EAB may cause temperate forests dominated by ash to transition from CO_2 sinks to CO_2 sources.

EAB results in high mortality of ash, which will lead to reduced photosynthetic carbon uptake, and will negatively influence net ecosystem production (Flower *et al.* 2013). Dead trees no longer take up carbon and store it as biomass; instead, their biomass C becomes available to the atmosphere as the tree decomposes. However, as ash are lost from the canopy, other species are expected to increase their growth rates to fill canopy gaps. These species will help to buffer some of the carbon losses occurring with EAB-induced ash death (Flower *et al.* 2013).

In addition to altering forest productivity, EAB will also likely alter soil carbon dynamics. Soil respiration is one of the largest fluxes in the global C cycle and consists of both root and heterotrophic respiration (Taneva and Gonzalez-Meler 2011). It is anticipated that tree death caused by EAB will decrease and eventually eliminate ash root respiration. At the same time, however, root growth and respiration of other species may increase. Additionally, heterotrophic respiration is expected to increase, at least in the short term, due to increased litterfall as ash die and from changes in microclimate, such as increased temperature and moisture, which will likely stimulate heterotroph activity (Bhupinderpal-Singh *et al.* 2003, Scott-Denton *et al.* 2006).

In this paper, a holistic view examining multiple components of forest carbon cycling is presented, referring to data collected in a field study. Each component examined provides valuable information concerning shifts in carbon pools associated with disturbance (Flower *et al.* 2013). The goal of this research was to examine the effects of EAB on the various aspects of ecosystem carbon cycling that are anticipated to be altered by this pest. This was achieved by comparing forested plots with a simulated EAB outbreak (girdled) to adjacent control plots over the course of two growing seasons. Nuckolls *et al.* (2009) found that soil CO_2 efflux, moisture, and temperature responded in statistically similar ways in both girdled and hemlock woolly adelgid infested sites, suggesting that girdling is a good simulator of pest-induced soil responses. The specific objectives and hypotheses of this experiment are fourfold:

1. Examine soil respiration. Soil CO_2 efflux is predicted to increase because enhanced growth of non-ash roots and a more favorable microclimate for heterotrophic respiration will likely offset the loss of respiration from ash roots. Predicted changes in microclimate include

increased temperature (due to increased light levels) and soil moisture (due to the loss of ash transpiration).

2. Evaluate changes in soil organic matter (SOM) associated with ash girdling to assess how much carbon is retained within the soils. I predicted that simulated EAB (girdling) will decrease SOM over time due to enhanced decomposition rates and reduced organic matter inputs until ash loss is fully compensated by other species.

3. Assess decomposition rates through the use of litter bags. Simulated EAB is expected to increase decomposition due to changes in litter fall and microclimate.

4. Assess changes in forest productivity in tree aboveground biomass (using allometric equations) and litter production. I hypothesized that simulated EAB will reduce production through ash death, although increased growth of non-ash species will buffer some, but not all, of this loss in the short term.

Methods

Site and Plot Selection and Preparation

The impacts of Emerald Ash Borer (EAB) on ecosystem functioning in ash-dominated forests were examined in six sites across western New York State (Table 1). These sites were split evenly between white and green ash to investigate any potential differences between the two species (Table 1). Chosen sites were free of EAB infestation and at least eight kilometers away from known EAB detections in the spring of 2012 to ensure that control sites were unaffected and remained reliable controls. At each site, two 20 x 20 m plots, one experimental plot with all ash ≥2.5 cm dbh girdled and the other a non-girdled control were established with a 20 m buffer between them. Each plot contained a center 10 x 10 m subplot (Figure 1). For a more complete review of site selection and plot selection and preparation, see chapter 1.

Temperature Data Loggers

To assess changes in microclimate that may influence ecosystem functioning, temperature measurements were taken continuously in each plot throughout the growing season. A HOBO Pendant temperature data logger (Onset Computer Corporation, Bourne, MA) was placed approximately 20 cm above the soil surface (or standing water if present) near the center of each plot. Data loggers were launched on 7 April and recorded temperature every hour. They were removed from the field on 28 and 30 October.

Budburst period (24 April - 15 May) was also examined to see if there was a difference in microclimate during budburst and leaf-out (i.e., did it warm up faster in experimental plots because they had less leaf cover). A fall senescence period (22 September - 27 October) was also examined to see if there were any differences in air temperature as the leaves were falling (i.e., did it get cooler sooner in experimental plots because they had less leaf cover). These time periods were chosen based on observations of budburst and leaf-out, and senescence time at the sites, as well as in Brockport, NY, centrally located between study sites.

Soil Measurements

Baseline measurements for soil organic matter (SOM), *in situ* soil respiration, soil moisture, and soil temperature were taken before girdling treatment. *In situ* soil respiration (LI-6400 infrared gas analyzer equipped with a LI-6400-09 soil CO_2 efflux chamber, LI-COR Biosciences, Lincoln, Nebraska) was not statistically different between control and experimental plots at each site before trees in the experimental plot were girdled (data not shown). Soil respiration and soil temperature measurements began with site establishment in summer 2012 and continued approximately every three weeks through the end of September. These readings were planned to be initiated once again in the spring of 2013; however, 2013 was an unusually wet year and several sites remained flooded until August. Therefore, measurements were made at SH and TIBB on 16 July to give a sense of soil CO_2 efflux in some of the drier sites. Then, in mid-August (10 Aug for JACK and UNIT, 11 August for SH), all of the sites that were free of standing water were sampled. All six sites were free of standing water at the next visit, and therefore, measurements were taken at all six sites between 20 and 21 August. Soil respiration measurements were taken roughly every three weeks until the end of September or until a site became flooded again, which affected half of the sites.

Soil samples were collected at the same sampling times. To examine gravimetric soil moisture, six 2.54 cm diameter, 20 cm deep soil cores were taken at random locations in each central 10 x 10 m subplot. These samples were mixed together, passed through a 2mm sieve, and used for analysis in the lab. Three replicate samples of approximately 50 g of the sieved soil were dried for 48 hours at 105°C and massed prior to and after oven-drying to determine soil moisture.

Soil organic matter (SOM) was determined using loss-on-ignition by combusting organic matter in a ~10g oven-dried soil subsample at 380°C in a muffle furnace for two hours (modified from Konen *et al.* 2002). SOM was determined in samples taken in each site prior to girdling (summer 2012) and then in the last sample for which all sites were sampled (September 2013).

Litter Bags

Decay rates of ash litter, using litter bags, were examined to determine the longer term effects of simulated EAB attack on ecosystem functioning. Decay rates were analyzed using freshly senesced *Fraxinus* litter collected near SH (green ash) and TIBB (white ash) for two weeks in October 2012. Ash leaves were air-dried and then 3.5 (±0.5) g were placed in 15 x 15 cm fiberglass mesh litterbags. The litter bags were placed in the 10 x 10 m center plots at each site (with each site having litter of the dominant species (Table 1) in the litterbags deployed there), with three replicates for each of the five collection dates. Litterbags were placed in all sites in mid-November 2012.

Litter bags were collected on five dates during the following summer, with progressively longer times between collections. Collections occurred on 5 and 6 April, 26 April, 15 and 17 June, 10 and 11 August, and finally on 28 and 30 October. The third collection at the SS site was delayed by one week due to flooding.

Once returned to the lab, litter bags were laid flat and air dried for at least 48 hours. Once dry, litter bags were opened and the contents removed, massed, and dried at 60°C for 48 hours. Care was taken to ensure that the contents used for analysis only contained the original sample; therefore, samples were cleaned of dirt and debris. In some cases, dirt was tightly bound to the leaf surface and was gently removed either by scraping the dry leaf or using a small amount of water to loosen the dirt and then scraping. Leaves that were wetted in the dirt removal process were re-air-dried before analysis continued. Corrected percent mass remaining was calculated using “traveler bags” (litter bags prepared exactly like those placed in the field but carried into the field and brought back to the lab) to determine how much mass was lost in transport and handling and therefore not due to decomposition.

A single exponential decay model was fit to the data following the formula: $X_t/X_0=e^{-kt}$, where X_t/X_0 represents the fraction of original mass remaining at time t in years and k is the annual decay constant (Olson 1963). A natural logarithum of the proportion of mass remaining over time (years) was regressed to fit a linear model. The annual decomposition rate, k, is equal to the slope of the regression line.

Seed and Leaf Litter Buckets

Leaf litter and ash seed production during fall 2013 senescence was assessed using buckets. Litter buckets with a 23 x 23 cm square opening were constructed by drilling holes into the bottom of buckets to allow for water drainage. Four buckets were placed randomly in the 10 x 10 m center plots at each site; however, several were flipped onto their sides before collection and were excluded from analysis. Buckets were placed in the field on 28 and 29 September 2013. Collections of the litter were planned to occur at two weeks and four weeks, but a federal government shutdown that resulted in prohibited access to federal sites (Iroquois National Wildlife Refuge (INWR) and Montezuma National Wildlife Refuge (MNWR)) resulted in only one collection at the these sites. Therefore, the contents of buckets at Northern Montezuma State Wildlife Management Area (NMSWMA) were collected on 15 October 2013 and 28 October 2013, at MNWR on 28 October 2013, and at INWR on 30 October 2013. On the date of final collection, buckets were removed from the sites.

Litter collected in the buckets was returned to the lab and placed in paper bags to air-dry. Once dry, the contents of the buckets were sorted into one of three categories: ash litter, other species litter, or ash seeds. Once separated, litter was oven-dried at 60°C for 48 hours. Average litter weight (kg) per ha was calculated using these data. In addition to weight, the count of ash seeds per bucket was also assessed.

Allometric Equations

Increment cores were taken from each site at the end of September 2013. In each control plot, five cores were taken from the representative ash species, and ten cores from the other species present, with the individual trees of each species sampled being randomly selected. These ten non-ash cores were proportionally representative of the species present in the plot (e.g., if a plot had 20 non-ash trees and 10 of them were cottonwood (*Populus deltoides*), five of the 10 non-ash cores would be from cottonwoods). In the experimental plots, no cores were taken from ash because growth was assumed to be zero, since these trees had been girdled and many of them were already dead. Ten non-ash cores were taken in the experimental plots in the same manner as in control plots.

Increment cores were brought back to the lab, and the last five easily recognizable growth rings were measured. This measurement was divided by five to determine the average growth per year and then multiplied by two to get the annual change in tree diameter. Growth per year was determined for each species of ash in control plots and averaged for non-ash species in each treatment. The growth per year was then subtracted from the 2013 tree survey data (see Chapter 1 for methods) to obtain an estimated DBH for each tree for the preceding year. These adjusted DBHs and the actual DBHs were used along with allometric equations (Jenkins *et al.* 2004, Table 2) to determine the productivity over one year. Jenkins *et al.* (2004) was used to determine the best allometric equations for each species, with the exception of buckthorn (*Rhamnus cathartica*), where Mascaro and Schnitzer (2011) was referenced (Table 2). If a species was absent from Jenkins *et al.* (2004), a species of the same genus was used (Table 2).

Statistical Analyses

For the temperature data-logger data, independent t-tests were used to examine differences between species (green vs. white ash dominated plots) and treatments for daily average, minimums, and maximums. Histograms revealed that the data were approximately normally distributed. The assumption of homogeneity of variances was assessed for each case using a Levene’s test and if it was violated, the Welch t-test was used.

Soil organic matter was assessed using a two-way ANOVA to determine if there were differences between control and experimental treatments or over time. Data met all of the assumptions of the test.

To determine if changes in soil CO_2 efflux were related to changes in microclimate, multiple regression was used to test if soil moisture and temperature significantly correlated 2012, 2013, and combined 2012/2013 soil CO_2 efflux. Data met all of the assumptions of multiple regression analysis.

Additionally, to test for differences in treatments over time, repeated measures ANOVAs were done using the combined 2012/2013 soil moisture and soil CO_2 efflux data. Although measurements were taken on ten different occasions for each of these variables, measurements could be taken at all six sites on only four occasions due to flooding. Therefore, only the four occasions when all six sites were measured were used in this analysis. Data that failed to meet the assumption of normality were reciprocal-transformed. Finally, soil moisture data failed Mauchly’s test of sphericity, and consequently a Greenhouse-Geisser correction was used.

The soil temperature probe broke in the summer of 2012; therefore, measurements were taken at all six sites on only two occasions. Since this precluded a repeated measures ANOVA, a two-way ANOVA was used to test for differences between treatments and time.

An independent sample t-test was used to assess differences between treatments in final corrected percent mass remaining and the decay constant (k). Data met all of the assumptions of the test.

One-way ANOVAs were used to assess litter bucket data for differences between treatments. All of the assumptions of this test were met once the variables of ash and other species leaf litter were square-root-transformed to meet normality.

For the productivity data, two-way ANOVAs were used to examine the data for differences between control and experimental treatments and between 2012 and 2013 productivity. Data were approximately normally distributed once they were square-root-transformed. Independent sample t-tests were conducted to examine for additional differences. Finally, difference between years was calculated and independent sample t-tests were used to look for differences between treatments.

Results

Air Temperature

Despite a lack of statistical difference, in most cases, average and maximum daily temperatures were modestly warmer in the experimental plots than in the control plots in each of the various time periods considered (Table 3). The experimental plots also had lower minimum daily temperatures compared to the control plots (Table 3). The only statistically significant difference was the experimental treatment averaging about half a degree higher in maximum daily temperature over the entire period (p=0.020; Table 3).

Soil Measurements:

Microclimate, CO_2 Efflux, and Organic Matter

When data from 2012 and 2013 were combined, 49.6% of the variance in soil CO_2 efflux was explained by soil moisture and temperature together (R^2 =0.496, F(2,66)=32.487, p=0.000), with each separately being significant predictors (p≤0.001, Figure 2). When these data were analyzed by year, the results varied slightly in that moisture was not a significant factor in 2012 but it was in 2013 (soil temperature remained statistically related in both years).

General trends were seen in soil CO_2 efflux and moisture between treatments despite a lack of significant statistical influence of treatment. In 2012, control plots generally had a higher CO_2 efflux than experimental plots, but this trend was reversed in 2013 (Figure 3C). A repeated measures ANOVA showed that although time had a significant effect on soil CO_2 efflux (p=0.000), there was not a significant difference between the control and experimental treatments (p=0.296, Figure 3C). Despite a lack of significant difference between treatments over time (p=0.882) and variation between sites, experimental plots tended to have higher soil moisture than control plots and time had a significant effect on soil moisture (p=0.000, Figure 3A). There was no effect of treatment for soil temperature (Figure 3B, p=0.803).

In 2012, around the time of girdling, control plots had an average of 13.5 (±6.7 standard error) % SOM, while the experimental plots had an average of 13.6 (±7.0) % SOM. In 2013, toward the end of the growing season, the control plots had an average 12.3 (±6.3) % SOM, whereas the experimental plots had an average of 12.8 (±7.3) % SOM. Therefore, SOM decreased more in the control plots than in the experimental plots over the course of a year, but there was still not a statistically significant difference between plots (p=0.938, Figure 4).

Decomposition

Trends reveal the rates of decomposition were subtly higher in the experimental plots (Figure 5). Girdling did not affect decay rates as both decay constants (control=1.11 vs. girdled=1.25) and final percent mass remaining (control=36.8 vs. girdled=31.9) did not differ statistically between treatments (p=0.723 and p=0.635, respectively, Figure 5).

Litter Production

Ash leaf litter production was consistently greater in control plots (mean ± standard error, 628.11 ±251.50 kg/ha) than in experimental plots (187.43 ±98.06 kg/ha), although this trend was not statistically significant (p=0.117, Figure 6A), presumably due to a large amount of variation, particularly across the control plots. Again, despite the lack of a statistically significant difference (p=0.531), all of the control plots (except Jackson) produced more non-ash litter (997.69 ±483.84 kg/ha) than their experimental plots (696.67 ±546.88 kg/ha, Figure 6B). For ash seeds, four of the six sites had a greater seed weight in the control plot (193.84 ±42.82 kg/ha) than the experimental site (164.38 ±50.80 kg/ha); however, this trend was not significant (p=0.716, Figure 6C). Contamination of litter in the litter buckets can probably be ruled out as the buckets were placed close to the center of the plots and examination of the litter did not reveal any species present that were not in the examined plot.

Tree Productivity

The control sites gained more ash biomass than the girdled sites from 2012 to 2013. However, there was not a significant interaction of ash productivity and year (p=0.920, Figure 7). The ash control sites gained an average of about 4,750 kg biomass/ha/yr, whereas the experimental sites were assumed to have no biomass gain since the trees in these plots were girdled and therefore died. The difference in ash productivity between 2012 and 2013 was significantly greater in control plots than in experimental plots (p=0.000).

A similar trend was observed for the non-ash productivity. Although there was a lack of a significant interaction of non-ash productivity and year (p=0.995), the experimental sites gained more non-ash biomass (around 1,400 kg biomass/ha/yr) than the control sites (around 900 kg biomass/ha/yr) from the 2012 to 2013 (Figure 7). Examining the difference in productivity between 2012 and 2013 did not reveal any significant differences between treatments (p=0.540).

Discussion

EAB-induced ash mortality is expected to have a large impact on the ecosystem functioning of the temperate forests where ash are present (Flower *et al.* 2013). This is particularly true in areas where ash are abundant, such as Western New York, as ash can make up more than twenty percent of the basal area in each county (Wilson and Lister in review) and be much more important locally (Chapter 1). Temperate forests, such as those where ash are prevalent, are often net C sinks (Brown and Schroeder 1999; Williams *et al.* 2012); however, this sink strength will almost certainly decrease as ash are lost to EAB. Therefore, the effect of EAB on the carbon cycle in impacted stands is of particular interest.

The effects of EAB on broad scale carbon cycling of impacted stands occur very rapidly (Flower *et al.* 2013) but can also have long-term effects. As ash trees become impacted by EAB, they will drop their leaves (which will likely eventually impact soil CO_2 efflux rates), and as they die, they will stop sequestering C. Over the longer time scale, these trees will begin to decompose and their biomass C will enter the atmosphere. Over time, other species will be able to fill the gaps resulting from EAB (Flower *et al*. 2013), and these subsequent changes in litter quality and quantity will also influence soil CO_2 efflux rates and soil carbon (Hancock *et al.* 2008).

Microclimate, Soil CO_2 Efflux, and Decomposition

Invasive pest species and girdling can both alter microclimate factors such as moisture and temperature regimes through gap formation (Stadler *et al.* 2006, Twery 1990).This is important, as soil temperature and moisture are perhaps two of the largest abiotic controls of soil CO_2 efflux (Oishi *et al.* 2013). Therefore, it is not surprising that, in my study, both soil temperature and moisture were generally significant predictors of soil CO_2 efflux (Figure 2). Both girdling and forest pest studies have found that soil temperature (Nuckolls *et al.* 2009, Levy-Varon *et al.* 2013) and moisture (Nuckolls *et al.* 2009) have a significant influence on soil CO_2 efflux. Nuckolls *et al.* (2009) found that soil moisture and temperature responded in a statistically similar manner between girdled and hemlock woolly adelgid infested sites, suggesting that girdling is a good simulator of pest-induced environmental responses. In my study, soil CO_2 efflux was statistically correlated to soil temperature (Figure 2) but not treatments due to inconsistent temperature-treatment patterns. Consequently, it is unlikely that soil temperature can help to explain the differences seen in soil CO_2 efflux between treatments due to the inconsistent temperature-treatment patterns. Despite the lack of soil temperature-treatment patterns, air temperature following girdling was generally warmer in experimental sites (Table 3). Experimental sites tended to be slightly wetter than the control sites over the course of the study (although not statistically so, Figure 3A) and, unlike soil temperature, may help to explain some of the difference between treatments in soil CO_2 efflux. In their oak-girdling experiment, Levy-Varon *et al.* (2013) found that girdled sites were wetter than control sites, likely due to the loss of transpiration associated with tree mortality (Morehouse *et al.* 2008, Clow *et al.* 2011).

Immediately after girdling, CO_2 efflux decreased insignificantly in the experimental plots relative to control plots (Figure 3C). The decrease observed in the first year of the experiment is likely primarily due to a decrease in microbial respiration. A decrease in root respiration can largely be ruled out as a cause of decreased soil respiration because an abundance of epicormic shoots was seen below the girdle location, suggesting that roots are still alive. These roots were likely still relying on carbohydrate stocks

(Levy-Varon *et al.* 2013) and may not be obtaining as many carbohydrates as they would in a tree with a full canopy, although some very fine roots may have begun to decay (Nuckolls *et al.* 2009). Despite root persistence, it is possible that roots were no longer releasing root exudates that the microbial community relied on, thus reducing microbial contribution to soil respiration (Nuckolls *et al.* 2009). A decrease in fine root inputs one to two years post girdling has been shown through isotopic analysis to reduce heterotrophic respiration (Bhupinderpal *et al.* 2003). Nuckolls *et al.* (2009) observed a similar reduction in soil CO_2 efflux the year after both girdling and hemlock woolly adelgid infestation in their experiment and also attributed this decrease to reductions in root respiration and exudation.

In the year following girdling (2013), soil CO_2 efflux rebounded, and the experimental plots had higher CO_2 efflux when compared to control plots (Figure 3C). This may be due to increased growth of non-ash roots into the area, which would increase the amount of roots respiring there. Ash root decomposition, from trees that had died due to girdling, may also have contributed to the increase in CO_2 efflux seen in 2013. Nuckolls *et al.* (2009) found that very fine root biomass in both girdled and hemlock woolly adelgid sites decreased by 20-40% within two years. This suggests that ash roots would begin decomposing in girdled sites once they deplete their carbohydrate stores (Nuckolls *et al*. 2009), and this decomposition would manifest as increased soil respiration. Additionally, subtle temperature shifts

(Table 3) may have made the environment more favorable for microbial respiration, perhaps explaining some of the increased soil CO_2 efflux.

Others have similarly noted rebounds in soil CO_2 efflux after initial decreases in sites that have either been girdled or affected by forest pests. Levy-Varon *et al.* (2013) attributed significantly lower soil respiration in oak sites soon after girdling to the autotrophic component (along with associated decrease of mycorrhizal fungi) of soil respiration. However, soil respiration quickly rebounded by the second year post-girdling, and they concluded that for a non-stand replacing disturbance, the response of soil CO_2 efflux is a short-lived reduction in soil respiration. Moore *et al.* (2013) also found a rebound in CO_2 efflux after an initial decrease in sites affected by the mountain pine beetle over a slightly longer time scale. They observed a strong decrease in CO_2 efflux for the first three years after disturbance, but after approximately six years, soil CO_2 efflux had almost completely recovered to pre-disturbance levels (Moore *et al.* 2013). However, this recovery was short-lived and corresponded with a pulse of fallen litter. Therefore, it is important to continue monitoring EAB impacted sites to see how soil CO_2 efflux responds over longer time scales.

Decomposition is another aspect of the carbon cycle that is likely to be altered by EAB. Trends suggest that decomposition may occur more rapidly in experimental plots (Figure 5) due to the subtle shifts in microclimate, a pattern also seen by Levy-Varon *et al.* (2013) in their oak girdling experiment.

Decay rates as well as the R^2 values were low in this experiment. It is thought that since the sites were flooded for much of the study period, decomposition was restricted due to low oxygen levels under the water and thus decomposition did occur as rapidly as expected. Future studies may lend insight into decomposition rates. Only ash litter decomposition was examined as part of my litter bag/decomposition study and litter quality is a big factor in determining decay patterns. The loss of ash trees due to EAB will likely cause changes in species composition. Hancock *et al.* (2008) reported that increasing sugar maple dominance along a beech bark disease gradient may lead to increased soil CO_2 efflux due to the change in litter quality or some other factor that covaries with differing species compositions. Therefore, decay rates will likely change as the dominant species changes as litter quality, along with climate and the decomposer community drive decomposition (Swift *et al.* 1979, Berg and McClaugherty 2007, Cornwell *et al.* 2008). In addition, examining belowground decomposition rates, especially of fine roots, may help to explain some of the observed differences in soil CO_2 efflux between treatments, warranting investigation. This could be accomplished by using the same litterbag method as used in the aboveground decomposition except these bags would be buried beneath the surface and filled with fine root litter.

Tree Productivity

The storage of carbon in woody biomass will also be altered by EAB. Flower *et al.* (2013) reported that, based on FIA inventory data, regional C budgets in the Great Lakes region could be dramatically influenced with the decay of 0.156 Pg C in existing ash biomass. This number underestimates the amount of carbon currently stored in Great Lakes region ash population because it excludes urban and suburban trees (Flower *et al.* 2013). When trees die, they are no longer growing and adding new biomass. Sites with healthy ash are likely taking more C out of the atmosphere and storing it in ash biomass than those with dead ash. As ash continue to die, fewer ash trees will be actively storing C in their biomass.

My hypothesis that ash in control sites would be more productive (kg biomass/ha) than experimental sites was somewhat supported by litter bucket data as control plots tended to produce more ash litter than girdled plots (Figure 6). Although these results were not statistically significant, if more area was covered by the litter buckets (and hence a greater amount of litter was collected), those additional data may have helped to better demonstrate the observed trend in ash litter collection.

The reduction in C storage associated with ash mortality is temporally dynamic and may be partially offset by increased growth of other species. Despite a lack of statistical significance, productivity of non-ash trees was marginally greater in experimental sites than in control sites (Figure 7).

Corresponding with these results, Flower *et al.* (2013) found that compensatory growth by non-ash trees was able to offset about one-fourth of the net primary production loss associated with ash mortality. This compensatory growth by other species likely resulted due to the release from competition for resources such as water, light, and nutrients (Flower *et al.* 2013).

The trend of increased non-ash productivity in experimental plots was not seen in litter production, as control sites tended to produce more non-ash litter than experimental sites, with these results being site-specific (Figure 6). Similarly, in their girdling experiment, Levy-Varon *et al.* (2013) found that by one year post girdling, litterfall did not vary statistically by treatments. However, they did find that the composition of the litter varied with treatment (Levy-Varon *et al.* 2013).

Changes in Species Compositions

Although EAB threatens all forests where ash are present, the level of influence on ecosystem patterns and processes such as C stocks will depend on local ash densities (Flower *et al.* 2013). This is directly due to the fact that stands with a higher proportion of ash will lose more of their biomass and indirectly due to the response of non-ash species. Although recovery from disturbance is usually associated with greater C storage (Odum 1969, Magnani *et al.* 2007), during the time of gap closure, it is important to consider the species involved with each stage of that transition. In forests infested with EAB, ash is usually an early successional tree and, according to my data, likely to be replaced by invasive shrubs such as common buckthorn, honeysuckle, and Japanese barberry (Chapter 1). This transition from trees to shrubs will have consequences for ecosystem C storage. For example, Mascaro and Scnitzer (2011) found that woody biomass was significantly less in forests that had a canopy dominated by buckthorn than in those with canopies dominated by native species (even when buckthorn was in the understories).

The replacement of ash by invasive shrubs will have cascading effects on ecosystem functioning. As an example, common buckthorn can cause multiple changes in its ecosystem and was commonly seen in each of the three woody layers (seedlings, saplings, and trees) at some of the examined sites. Therefore, it is expected that buckthorn will fill gaps left by ash, reducing aboveground carbon stocks as it becomes dominant by storing less C in its biomass than trees (Mascaro and Scnitzer 2011) and altering successional dynamics (Niering and Goodwin 1974). Buckthorn litter increased soil nitrogen content, altering the C:N ratio (Henegham *et al.* 2006) and often leading to faster decomposition rates (Henegham *et al.* 2007, Madritch and Lindroth 2009). Due to the prevalence of buckthorn at examined sites, a future study reciprocal litterbag experiment examining differences in decay rate between buckthorn litter and ash litter may be of interest to see how this change in species composition will alter decomposition rates.

Conclusion

EAB will affect ecosystem functioning and specifically the carbon stocks of stands that it impacts through various pathways. First, as ash trees die and the microclimate is altered through increased soil and air temperature and soil moisture, soil CO_2 efflux and decomposition rates will likely be increased. Soil CO_2 efflux showed a general pattern of a decrease immediately flowing girdling with a rebound by the following year, where the girdled sites had greater efflux than control sites. I anticipate soil CO_2 efflux to remain elevated in girdled sites as roots and other materials continue to decompose, but longer term studies will be needed to see how this aspect of soil carbon responds over time. Decomposition was subtly elevated in the experimental treatment, but future studies examining how the anticipated changes in species composition affect decomposition are needed. Finally, ash productivity likely decreased due to girdling, while the productivity of other species increased, albeit not significantly. This suggests that the growth of non-ash species was partially able to off-set the loss of productivity associated with ash loss. Future monitoring of productivity would help to indemnify when non-ash species are fully compensating for the loss of ash productivity.

This study illustrates the short-term carbon response to simulated EAB and helped to identify several areas where more research is needed. It suggests that, in the short term, EAB attack alters forest processes, although not always in a statistically significant way, nor in a consistent way depending on forest environment and/or composition. Nonetheless, these changes are meaningful, and it is possible that examining more sites would have helped to elucidate some of the forest response. Overall, these results suggest that sites impacted by EAB are becoming C sources due to increased soil CO_2 efflux and loss of ash productivity, which is not being fully compensated by other species at this time frame. Finally, longer term studies of all of these aspects of carbon cycling are needed to determine how carbon cycling responds beyond two years post-infestation. It is anticipated that soil CO_2 efflux and decomposition will remain elevated as dead ash trees decompose and that biomass C will remain reduced as ash are replaced by invasive shrubs that store less C by nature of their growth form. This would result in decreased C storage over longer time scales.

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Tables

Table 1. Site name (abbreviation) and location of six study sites in Western New York. Dominant ash species also noted as either green (*Fraxinus pennsylvanica*) or white (*Fraxinus americana*).

Site Name	Location	Ash Species
Swallow Hallow (SH)	Iroquois National Wildlife Refuge	Green
Sour Springs (SS)	Iroquois National Wildlife Refuge	Green
Northern Montezuma (NMONT)	Northern Montezuma State Wildlife Management Area	Green
Tibbet (TIBB)	Iroquois National Wildlife Refuge	White
Unit 17 (UNIT)	Montezuma National Wildlife Refuge	White
Jackson (JACK)	Montezuma National Wildlife Refuge	White

Table 2. Allometric Equation table adapted from Jenkins *et al.* 2004. *Also used for silver maple **used for swamp white oak. Sources for all species except buckthorn taken from Jenkins *et al.* 2014.

Species	**Component**	**Biomass Equation**	**a**	**b**	**c**	**d**	**dbh^2**	**Units Diameter**	**Units Biomass**	**Source**	**Source Location**
American Elm (*Ulms americana*)	Whole Tree (Above Stump)	a + b * dia + c * (dia ^ d)	0	0	0.08248	2.468	no	cm	kg	Perala and Alban 1994	North Central States
Buckthorn (*Rhamnus cathartica*)	Aboveground Biomass	a*dia^b x c	0.1692	2.2904	1.0074		no	cm	kg	Mascaro and Schnitzer 2011	Wisconsin
Cottonwood (*Populus deltoides*)	Whole Tree (Above Stump)	a + b * dia + c * (dia ^ d)	9.1583	-0.4291	0.005799	2	no	mm	kg	Monteith 1979	New York
Green Ash (*Fraxinus pennsylvanica*)	Whole Tree (Above Stump)	a + b * dia + c * (dia ^ d)	0	0	2.76583	1.15849	yes	in	lb	Clark *et al.* 1985	Gulf and Atlantic Coastal Plains
Red Maple (*Acer rubrum*)*	Whole Tree (Above Stump)	a + b * dia + c * (dia ^ d)	6.1147	-0.3598	0.006344	2	no	mm	kg	Monteith 1979	New York
White Ash (*Fraxinus americana*)	Whole Tree (Above Stump)	a + b * dia + c * (dia ^ d)	3.2031	-0.2337	0.006061	2	no	mm	kg	Monteith 1979	New York
White Oak (Quercus alba*)* **	Whole Tree (Above Stump)	a + b * dia + c * (dia ^ d)	0	0	2.17051	1.29463	yes	in	lb	Clark *et al.* 1986	Southeastern US

Table 3. Average daily mean, minimum, and maximum temperatures (°C) across six sites in each of the three periods (mean ± SE). * Indicates a statistically significant difference ($p < 0.05$). The entire growing period ranges from 7 April to 27 October, the budburst period from 24 April to 15 May, and the senescence period from 22 September until 27 October.

Entire Period		
	Control	**Experimental**
Avg	16.60 (±0.15)	16.85 (±0.16)
Min	11.57 (±0.18)	11.43 (±0.18)
Max	23.33 (±0.17)*	24.68 (±0.19)*
Budburst Period		
Avg	14.68 (±0.35)	14.90 (±0.36)
Min	7.11 (±0.34)	6.95 (±0.34)
Max	24.77 (±0.55)	25.63 (±0.55)
Senescence Period		
Avg	14.04 (±0.36)	13.96 (±0.38)
Min	9.11 (±0.42)	8.92 (±0.42)
Max	21.53 (±0.44)	21.78 (±0.43)

Figures

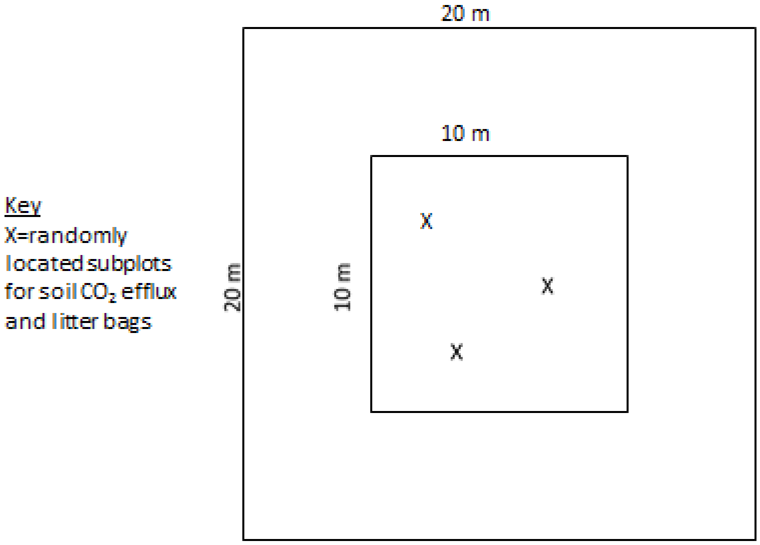


Figure 1. Diagram of 20 x 20 m plot layout at each of site. Each plot had a 10 x 10 m center subplot and three randomly located 1 x 1 m vegetation plots that which were also used to determine the location of the soil CO_2 efflux collars and the litterbags which were placed just outside the vegetation plots.

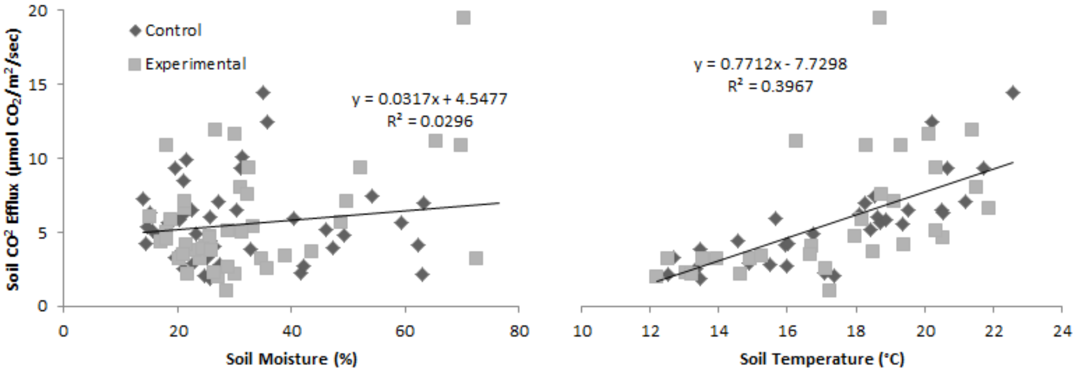


Figure 2. Relationship between soil CO_2 efflux and soil moisture and soil temperature in control and experimental plots. Each data point represents the average for 3-6 replicates of soil temperature CO_2 efflux measurements and six soil moisture samples that were combined prior to soil moisture determination. Includes all soil carbon flux data points for which soil moisture and soil temperature data available.

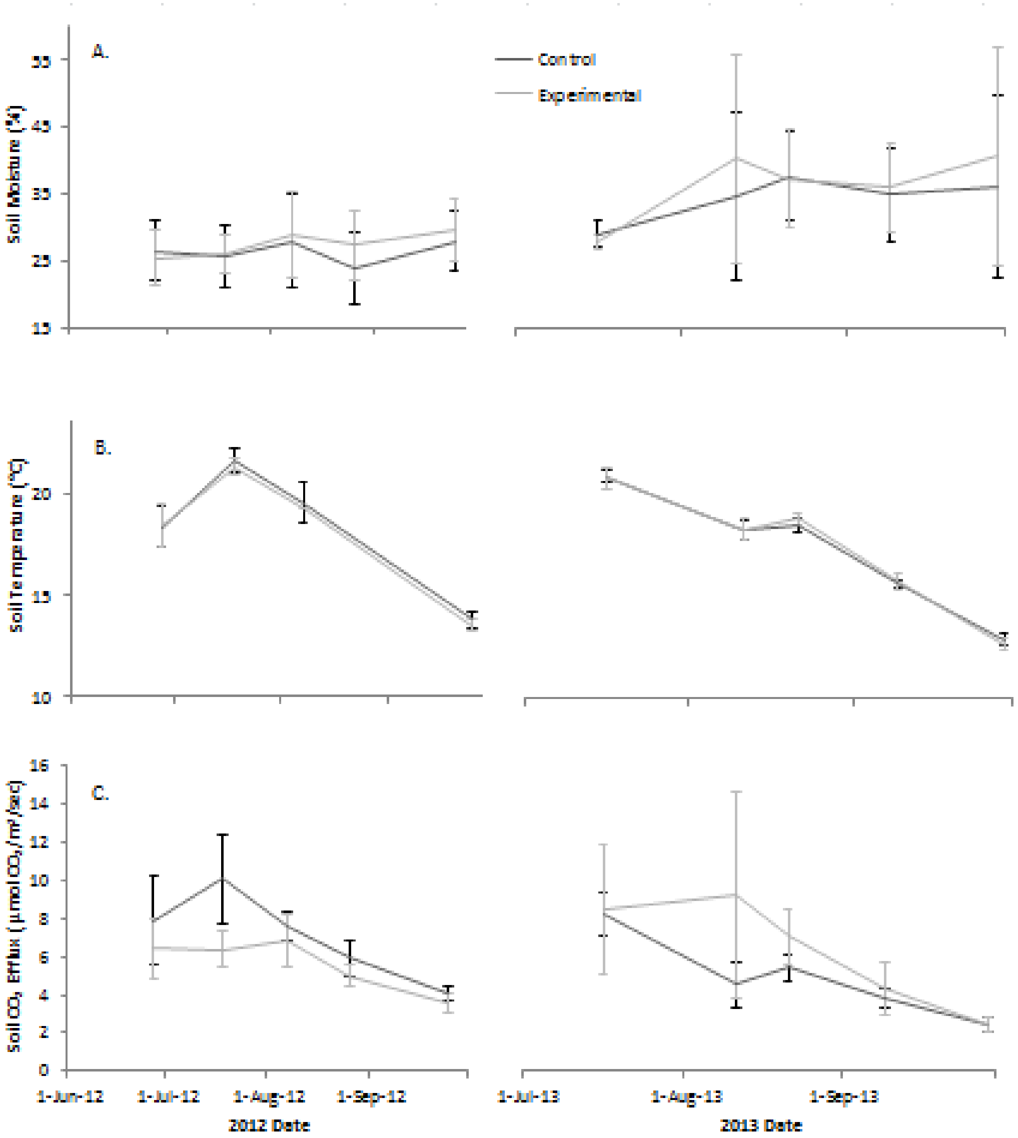


Figure 3.Average (±SE) 2012 and 2013 A.) soil moisture (%), B.) soil temperature (°C), and C.) soil CO$_2$ efflux (µmol CO$_2$/m^2/sec) in control and experimental plots.

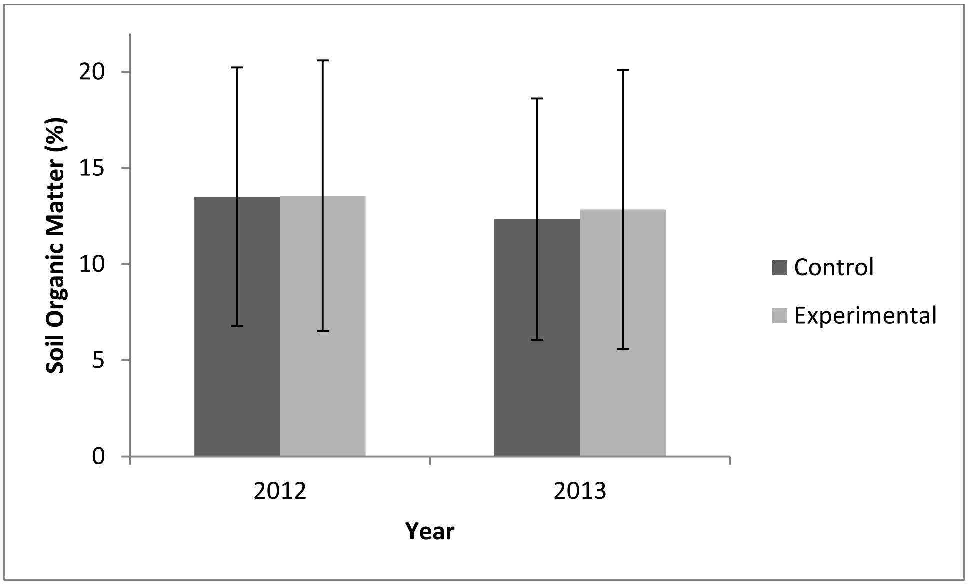
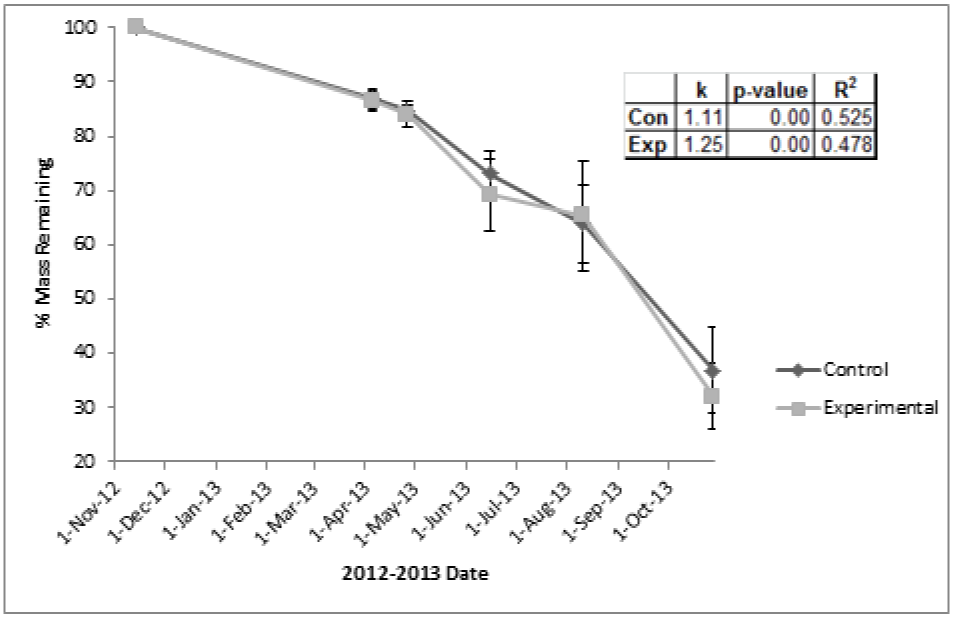


Figure 4. Average (±SE) percent soil organic matter in 2012 and 2013 (n=6 sites).



	k	p-value	R^2
Con	1.11	0.00	0.525
Exp	1.25	0.00	0.478

Figure 5. Average (±SE; six sites per treatment) percent mass remaining at each collection. Decay curves are fit to mass remaining data using the exponential decay model for each treatment with inset chart displaying decay constant (k), regression p-value and R^2 values for average control and experimental plots.

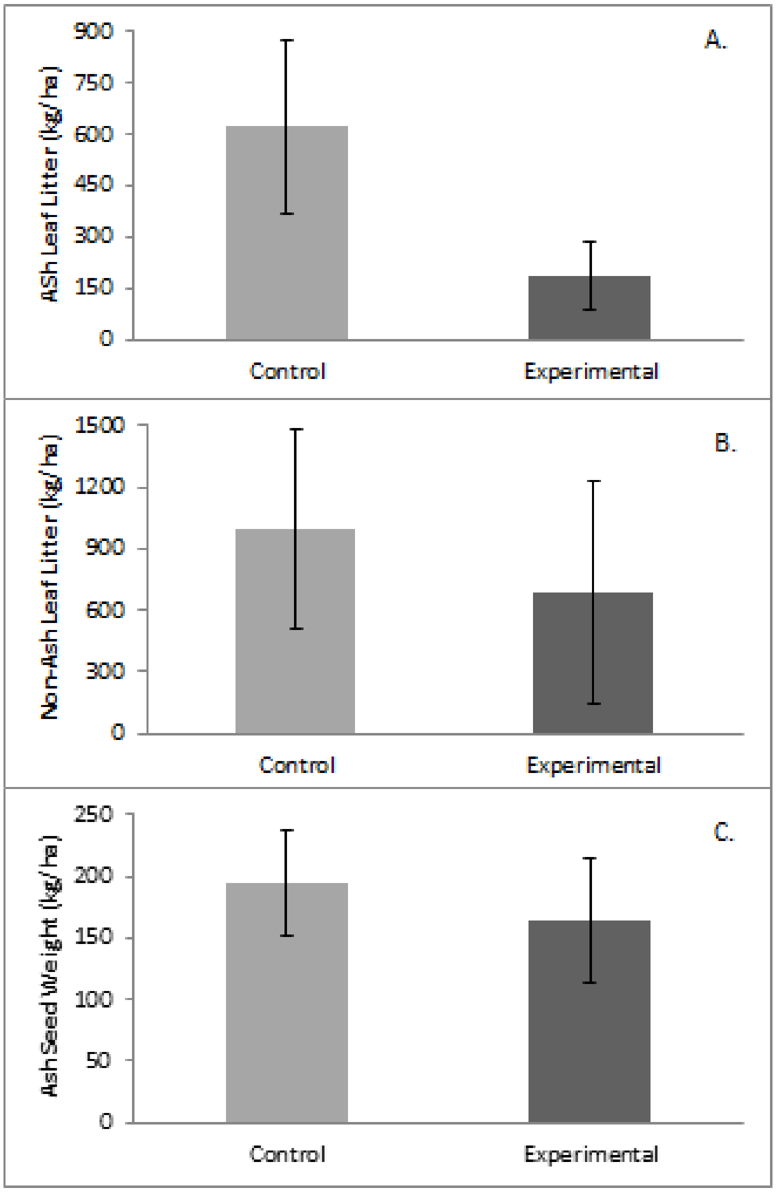


Figure 6. Litter production, showing mean ±SE, thought the month of October 2013. A. Average ash leaf litter weight (kg/ha). B. Average non-ash leaf (kg/ha). C. The average ash seed weight (kg/ha).

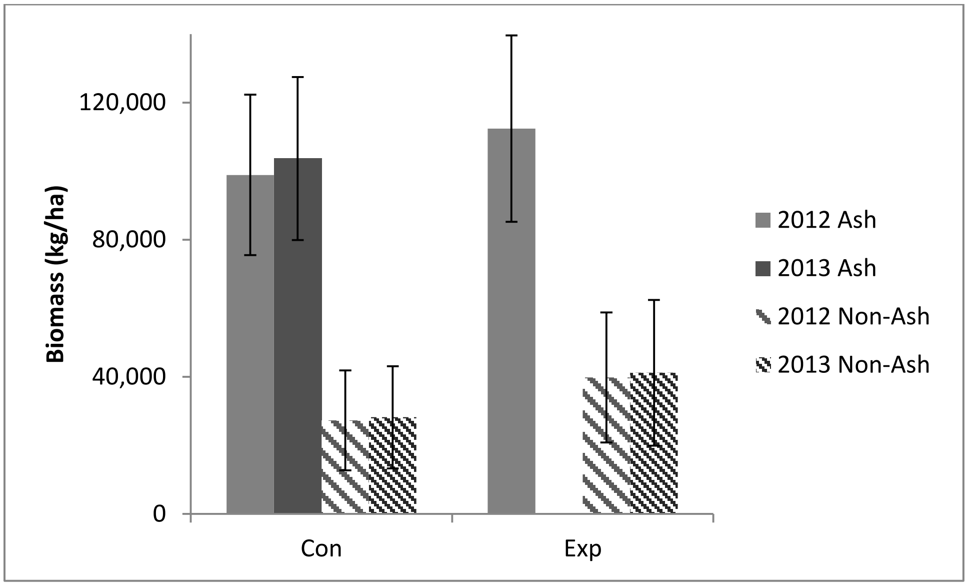


Figure 7. Ash and non-ash aboveground biomass (kg/ha) based on 2013 data and estimated 2012 biomass using increment bores and allometric equations. It was assumed that there was no ash biomass gain in the experimental plots as these trees were girdled and therefore dead or dying.

Chapter 3

A synthesis on Emerald Ash Borer

Summary

It is clear that the effects of emerald ash borer (EAB) will reach far beyond just the death of ash trees. In areas where ash is a dominant species, an EAB infestation may trigger a stand-replacing event. This will likely be the case in stands similar to those that were examined as a part of this study and are common in Western New York. In these stands, ash was generally the dominant species in all three woody layers (seedling, sapling, and canopy). Despite the prevalence of ash in the seedling and sapling layers, it is unlikely that any of these smaller ash trees will survive to reproductive maturity (Klooster 2012). This is due to both the long time scale before ash reach reproductive maturity and the high likelihood that ash will be infested with the pest once they reach 2.5 cm DBH (Klooster 2012). Other species will likely fill the gaps left by ash as they succumb to EAB, although which species will benefit most from these gaps remains uncertain on broad scales due the site-specific nature of these responses. Nonetheless, with sufficient information, it is possible to make predictions for specific sites. The results of this study show that invasive shrubs that are already present in the understory are likely to fill many of the gaps left in the wake of EAB. The shift in species composition from early successional ash forests to sites occupied by invasive shrubs represents an alteration of the successional trajectory of infested sites.

The impacts of EAB extend far beyond modifying succession, as ecosystem functions are likely to be altered as well. Since temperate forests such as those dominated by ash usually represent C sinks (Curtis *et al.* 2002) with potential feedbacks to the global C cycle, carbon cycling in EAB-infested stands is of interest.

Sites that are impacted by EAB will potentially sequester less carbon in biomass and release more C through soil CO_2 efflux and decomposition. This will likely reduce ecosystem C sink strength, if not shifting impacted sites to C sources. More specifically, in my simulated EAB outbreaks, girdling reduced the amount of ash aboveground productivity relative to control plots in the short term (< two years) by killing ash and causing them to stop growing. However, this was somewhat compensated by the productivity of non-ash species. Over longer time frames, there will be reduced C storage in biomass if ash trees are replaced by invasive shrubs that store less C in their biomass (McPherson *et al.* 1997). Secondly, soil CO_2 efflux initially decreased relative to the control in the same year as girdling and rebounded in the following year when efflux was greater in girdled plots. However, this response was not statistically significant and temporally variable as well as variable by sites. This increase in the CO_2 efflux is only expected to continue increasing in the long term as more of the dead ash begins to decay. Finally, the decay of ash litter was only subtly faster in girdled plots, but long-term changes in species composition associated with EAB will likely cause changes in decomposition rates (Hancock *et al*. 2008). The effects of EAB will go far beyond just ash deaths and will effect ecosystem functioning causing changes in species compositions and carbon cycling.

Trophic Cascades

As a species is lost from a community, a cascade of effects across other species and other tropic levels is expected (Orwig 2002, Gandhi and Herms 2010) as the species that depended on the lost species for food, survival, and reproduction respond. Furthermore, a disturbance such as EAB that alters food supply through increases in insects (EAB) and decreases in foliage will also cause effects through multiple trophic levels (Chan-McLeod 2006, Drever et al. 2009). Two groups that have been studied with respect to EAB are woodpeckers and arthropods.

Woodpeckers will be both positively and negatively affected as EAB infests the forests that they inhabit depending on the time period examined. When EAB becomes common in their area, there will be a substantial nutritional benefit to species that forage on EAB, and this will translate into high reproductive success (Koenig *et al.* 2013). Cavity-nesting woodpeckers are also expected to benefit from increased nest substrate as ash are lost to EAB (Cockle *et al.* 2011). Both of these benefits will likely only exist in the short term (likely less than a decade), as EAB levels are expected to decrease due to the loss of their host and ash tends to fall quickly after death, resulting in woodpecker habitat loss (Flower *et al.* 2014).

Gandhi and Herms (2010) assessed the risk that EAB poses to arthropods. There are currently 282 known species that are associated with ash species present in North America. Of these, 44 are monophagous and only associated with ash. An additional 17 species are only associated with ash and one other plant species (biphageous). The risk to each of these groups increases as they become increasingly dependent on ash, causing each of these groups to respond in a different manner to ash loss. As arthropods respond to EAB, Ghandhi and Herms (2010) expect there to be negative cascading effects such as decreased population sizes on species that are associated with arthropods, including fungi, bacteria, invertebrates, and vertebrates (Purrington and Nielsen 1987; Langor and Hergert 1993; Koh et al. 2004).

Management

Eradicating EAB is not a plausible goal due to outlier infestations (infestations that are separate from the main EAB infestation) and limited funding (GAO 2006); however, several methods have been employed to slow the spread of EAB as outlined by Mercader *et al.* (2011). The first is the harvest or removal of ash before EAB spreads to the area, with the goal of reducing the phloem available for larval development. While this method can reduce the number of EAB larvae developing in an area, it may not reduce the spread of EAB. The second method is to girdle trees, which attracts oviposting females and then destroy the tress before the progeny can develop, destroying those progeny. This method was found to both decrease EAB population size and the radial spread rate (Mercader *et al.* 2011), but the attraction radius of a girdled tree is largely unknown and influenced by site-specific characteristics (McCullough *et al.* 2009). Finally, injecting trees with insecticides can be used to protect living ash trees. To inject insecticides, such as TREE-age^{TM} holes are drilled into the bark and outer sapwood at the base of the tree and high pressure nozzles are used to inject the insecticide (Herms *et al.* 2014). Mercader *et al.* (2011) found that this third method created the strongest reduction in radial spread of EAB.

Chemical controls are currently used to control the pest in some urban areas via individual tree injections; however, this is both impractical and prohibitively costly for forest systems (Poland and McCullough 2006). Chemical control is also not environmentally desirable for use in forest systems due to non-target effects of the chemicals used on other species. It is hypothesized that insecticides will predominantly be used in urban areas, while girdled sink trees will be more widely used in forested areas (Mercader *et al.* 2011). It is important to note that care must be taken in application because the effectiveness of these tree injections varies depending upon several variables, such as the product and method used, timing, prior EAB injury, and tree size (McCullough *et al.* 2005). For example only trees up to 63.5 cm DBH can be protected by insecticide (Sadof *et al.* 2011) and treating in late spring is more effect than in mid-summer (McCullough *et al.* 2005).

Also, these insecticide treatments are a long-term expense, as they only remain effective for three years and then trees must be retreated (Sadof *et al.* 2011).

The drawbacks associated with chemical injections will likely prompt many communities to choose replacement over treatment for their urban trees. It will be important to plant new trees of a wide range of species and genera because planting just a single species or genus leaves the entire tree community vulnerable to another insect or disease (Ball *et al.* 2007). Santamour (1990) proposes 10-20-30 guidelines that no more than 10% of a community's trees should be of one species, 20% of one genus, and 30% of one family. This guideline will provide urban tree communities sufficient diversity to provide stability even in the wake of another insect pest or disease (Ball *et al.* 2007).

Another potential control method for EAB is bio-control. Two native parasitoids, *Balcha indica* and *Eupelmus pini*, have become associated with EAB. Nonetheless, together, they were found to have only parasitized 3.6% of sampled EAB hosts (Duan *et al.* 2009). Additionally, native eupelmid species of the *Atanycolus* genus attack EAB larvae (Bauer *et al.* 2004, 2005) and exhibit a numerical response to EAB densities, but the overall rates of predation are generally low (Duan *et al.* 2012). Three non-stinging parasitic wasps and a fungal pathogen from the EAB native range are also being evaluated (O'Brien and Suszkiw 2011). The wasps have been found to be able to successfully overwinter in Michigan, and one species, *Tetrastichus planipennisi*, is able to become established in some infested sites (O'Brien and Suszkiw 2011). *Tetrastichus planipennisi*, in particular, may eventually play an important role in suppressing EAB populations but will not likely be able to control EAB to the point of ash perseverance on its own (Duan *et al.* 2013).

Finally, native woodpeckers may be the most effective source of EAB mortality in the U.S. (Lindell *et al.* 2008) and have been able to remove up to 95% of EAB larvae in some trees (Cappaert *et al.* 2005). A 2008 study in Michigan documented that the downy woodpecker (*Picoides pubescens*), hairy woodpecker (*Picoides villosus*), and red-bellied woodpecker (*Melanerpes carolinus)* are likely to forage on EAB (Lindell *et al*. 2008). Nearly all woodpecker attacks on EAB occur in winter and spring and result in mortality for the prepupal larva (Lindell *et al.* 2008). Woodpeckers are taking advantage of the food (EAB) and spend roughly five-fold more time foraging on EAB-infected ash than on other species, with higher predation in white ash than in green (*Lindell et al.* 2008). By eating a large number of larvae, woodpeckers may be keeping the pest at low-to-moderate levels in some areas and may even help to slow the spread of EAB (Lindell *et al.* 2008). Still, the variables that may help to explain differing woodpecker predation on EAB require more research (Lindell *et al.* 2008). Although, most studies have focused on woodpeckers, other species in the bark-foraging guild have been documented to shift their foraging efforts on highly impacted EAB trees (Flower *et al.* 2014).

Protecting woodpecker habitat will be important to keep woodpeckers in the area as ash are lost (Flower *et al.* 2014). Managers need to consider retaining snags as woodpecker habitat (Flower *et al.* 2014), as snags have been shown to affect the abundance and diversity of woodpeckers (Raphael and White 1984, Zarnowitz and Manuwal 1985). However, dead ash tend to fall quickly, and mangers will need to supplement forests with high tree-fall rates with nest boxes (Flower *et al.* 2014).

Managing forests with EAB will be increasingly important as more forests are impacted. A major challenge for management is the difficulty in detecting low-density infestations (McCullough *et al.* 2009) and the limited research on the biology of EAB before infestations first broke out in the US and Canada (Herms and McCullough 2014). Even though there has been considerable progress in developing effective methods to protect urban and residential ash, there are very limited options to protect forest ash, and this resource remains threatened. It is hoped that the results of this study and those like it can further the knowledge about forest pest outbreaks and therefore aid in predicting forest response to future outbreaks to better protect them.

The results of this study indicated that invasive shrubs species may benefit substantially from the loss of ash. Consequently, management of the forests to reduce the prevalence of invasive shrubs and increase the success of native trees will become increasingly important in the wake of EAB. These actions will hopefully give native species an advantage so that they can fill the gaps left by EAB.

Two commonly used methods to remove invasive shrubs are mechanically through cutting or mowing and chemically through foliar applications and cut-stem treatments (Mattrick 2014). For example, when infestations of common buckthorn are small, they can but cut or pulled by hand, but when infestations get larger, herbicide is preferred, with the most common application methods being the cut stump method or basal bark applications (USDA Forest Service 2005). Nonetheless, the best strategy to remove invasive shrubs will likely depend on the site as well as the particular invasive species, and long-term monitoring should always be used to control seedlings and resprouts.

Once invasive shrubs have been removed from the area, native tree seedlings such as red (*Acer rubrum*) and silver maple (*Acer saccharinum*) and cottonwood (*Populus deltoides*) should be planted and protected from deer browse to ensure their success. Native plantings are preferred to exotics to ensure that these forests are as close to pre-EAB condition as possible and do not represent novel ecosystems with unknown consequences on ecosystem services. The overall aim of management in sites altered by EAB should be to facilitate native trees success to protect the integrity of ecosystem functioning. Therefore, if invasive shrubs are not present in sites impacted by EAB, restoration should not be attempted, and these sites should be allowed to grow without any intervention as they would from any natural disturbance. Adaptive management techniques should be used if the initial management is not successful.

EAB represents a large disturbance, and sites that are impacted by it will likely require some management due to the likelihood that invasive shrubs will thrive in the disturbed conditions left by EAB. Management plans will need to be site-specific, with the species of invader, its distribution, and native non-ash species currently in the canopy being major considerations. Therefore, individual land managers will need to determine the best course of action for managing EAB on their lands in each phase from control to restoration.

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