Potential Forest Regeneration in Western New York State Green Ash Stands Depleted by Emerald Ash Borer Invasion

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ABSTRACT

Since the discovery of the emerald ash borer (*Agrilus planipennis,* Coleoptera: Buprestidae) in 2002, it has caused near 100% mortality of North American ash trees (genus *Fraxinus*). Moreover, uncertainties remain regarding the future of the forest regeneration dynamics after the introduction this prolific forest pathogen. The objectives of this study were to: 1) Assess regeneration potential of green ash (*Fraxinus pennsylavnica* Marsh.) on the Lake Erie and Lake Tonawanda plains in Western New York State where it was formerly one of the dominant trees; 2) Identify other native tree species that could repopulate depleted ash stands; and 3) Assess factors constraining regeneration like invasive shrub cover and deer browsing pressure. In 32 plots (400 – 3600 m^2), proportion of ash trees in c. 2010 pre-ash-borer stands was catalogued (including dead or fallen stems), and all ash trees were assigned into health categories ranging from dead to unimpacted. Stump sprout and seedling recruits were recorded. Canopy and understory stems of all other trees were identified and measured (diameter at breast height). Identity and coverage of invasive shrubs were recorded. Data were analyzed and interpreted along gradients in two important independent variables: 1) stand age at ash borer invasion (from increment counts of fallen dead ash trees, or estimated from aerial imagery), and 2) % of ash in pre-ash-borer stands. Most adult ashes within plots were dead, and with no association with stand age or pre-ash-borer ash dominance. However, 11% of ash trees were completely un-impacted, but were <5 cm diameter and concentrated in young (<60 y) ash-dominated (>80%) stands. Stump sprouting was present in 78% of plots, and ash seedlings were noted at most sites, again primarily in young ash-dominated stands. Red and/or silver maples and American elms were the most common native trees and were most important in older less ash-dominated stands. Unfortunately, invasive shrubs were often very abundant, and deer browsing was evident in the majority of plots. This study suggests that green ash within the lake plains of Western New York may be able to regenerate, especially within younger stands, and that other native trees may replenish older stands. However, invasive shrubs and excessive deer browsing may hinder recovery.

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TABLE OF CONTENTS

Potential Forest Regeneration in Western New York State Green Ash Stands Depleted by Emerald Ash Borer Invasion

Abagail LaVin Coupland

ABSTRACT III

ACKNOWLEDGMENTS V

TABLE OF CONTENTS VI

LIST OF TABLES VIII

LIST OF FIGURES IX

CHAPTER PAGE

I. INTRODUCTION 1

Study Goals……………………………………………………………………..2

Specific Objectives…………………………………………………………..…3

Testable Hypothesis…………………………………………………………….3

Genus Fraxinus (The Ashes)……………………………………………………4

Green Ash……………………………………………………………………….5

Emerald Ash Borer……………………………………………………………...8

Emerald Ash Borer Invasion…………………………………………………..11

II. METHODS 14

Study Area……………………………………………………………………..14

Stand Selection and Surveying…………………………………………...………17

Stand Age……………………………………………………………………...18
Stump Sprouts and Seedlings……………..………………………………………22

Invasive Shrubs…………………………………………………………………..22

III. RESULTS 23

IV. DISCUSSION 40

Patterns of EAB-Induced Ash Mortality…………………………………………40
Stump Sprouts………………………………………………………………………41
Seedling Recruitment……………………………………………………………….41
Presence of Other Native Trees…………………………………………………….41
Presence and Impact of Invasive Shrubs………….…………………………………..42
Presence and Impact of Deer Herbivory…………...…………….………………...43
Similar Trends Seen in Other Research……………..……………………………43
Future Research…………………………………………………………………..…45

REFERENCES 47

APPENDIX 55

LIST OF TABLES

Table 1: Scientific and common name for the tree species associated with the four letter code used in Table 1 and 2………………………………………………………...28

Table 2: Counts of non-ash tree species contributing to survey plot canopies. These are counts per plot and are not converted to density per ha…………………………………29

Table 3: Counts of non-ash tree species contributing to survey plot understories. These are counts per plot and are not converted to density per ha……………………………...32

Appendix 1: GPS coordinates for each site. If coordinates are not present for a site, it was due to a lack of accessibility to the corner…………………………………….…54

LIST OF FIGURES

Figure 1: A map prepared by the U.S. Department of Agriculture, Forest Service of the native distribution of Green Ash (*Fraxinus pennsylvanica* Marsh.) in North America…..7

Figure 2: Map created by the United States Department of Agriculture (USDA) indicating the approximate distribution of native *Fraxinus* species in green, with positive cases of Emerald Ash Borer being detected in state counties denoted by a red dot…..…10

Figure 3: Map prepared by the United States Geological Survey (USGS) of the range of prehistoric Lake Tonawanda in western New York, USA, in relation to prehistoric Lake Iroquois, the Niagara River, and Early Lake Erie………………………………..……15

Figure 4: A map of Western New York state with red dots indicating public lands where data was collected. Going from South to North, the sites are as follows: Lake Erie State Park, Evangola State Park, Wendt Beach, and the SUNY at Buffalo Campus…………16

Figure 5 (previous page): An example of aerial and satellite image series (areas east of SUNY at Buffalo campus where the Ellicott Nike Trail provides public access to woodlands) revealing land cover changes and allowing estimates of stand ages of study plots. Note the development of the SUNY campus and Audubon Parkway starting in 1978 image, creation of Ellicott Creek flood-control spillway (grassy strip first appearing in 1995), and installation of Audubon Golf Course since 1995. Also, note stands wooded stands along Ellicott Creek in 1926 and patchy woodland in upper center of 1926 image (likely a shaded pasture), which are still present today…………………………………20

Figure 6: Percentage of green ash trees dead (represented by bubble diameters) in survey quadrats plotted on the two independent variables: stand age (years) and percentage of ash in the canopy pre-EAB…………………………………………………………………25

Figure 7: Number of decent (>1/3 foliage intact) and unimpacted ash per ha in survey quadrats plotted on the two independent variables: stand age (years) and percentage of ash in the canopy pre-EAB. ……………………………………………………………..26

Figure 8: Number of stump sprouting ash per ha in survey quadrats plotted on the two independent variables: stand age (years) and percentage of ash in the canopy pre-EAB..27

Figure 9: Number of canopy and understory *Acer rubrum/saccharinum* per ha in survey quadrats plotted on the two independent variables: stand age (years) and percentage of ash in the canopy pre-EAB. These two species are not easily distinguished without seed samaras, although the geographic range and non-flooded habitat suggest *A. rubrum* would be more common……………………………………………………………….36

Figure 10: Number of canopy and understory *Ulmus* spp. per ha in survey quadrats plotted on the two independent variables: stand age (years) and percentage of ash in the canopy pre-EAB. Elm species are likewise not easily distinguished without seed samaras, although habitat, growth form, and bark characteristics suggest *Ulmus americana* would be dominant…………………………………………………………………………37

Figure 11: Number of *Craetegus* sp. (hawthorns, which are exceptionally difficult to identify to species) per ha in survey quadrats plotted on the two independent variables: stand age (years) and percentage of ash in the canopy pre-EAB. Hawthorns never attained canopy status in terms of tree height, even when stems were >20 cm DBH……………38

Figure 12: Percentage of survey quadrats covered by invasive shrubs plotted on the two independent variables: stand age (years) and percentage of ash in the canopy pre-EAB. Solid bubble outlines indicate % ground coverage by shrubs and thickets. Dotted bubble outlines indicate two plots in Lake Erie State Park completely filled by understory tree-sized Glossy Buckthorn (*Frangula alnus*) and one plot near SUNY at Buffalo completely filled by understory tree-sized Common Buckthorn (*Rhamnus cathartica*). However, other vegetation occurred in these three plots……………………………………………39

I. INTRODUCTION

The Eastern Deciduous Forest biome of North America has been subject to numerous ecological threats since the early 20^{th} century, which have greatly altered the plant composition of forests on all layers, from the herbaceous ground layer up through the canopy (Bradshaw & Waller, 2016; Brunet et al., 2014; Lindbladh & Foster, 2010; Schulz et al., 2014;). Terbourgh et al., 2008; Tomback & Achuff, 2010). One of the most problematic is the introduction of forest pathogens, including insects and fungi that attack canopy trees. These typically infect adult plants, killing or severely stressing them over multiple seasons and compromise a tree's ability to reproduce (Anderson et al., 2004; Misra & Chaturvedi, 2015). Under the worst of pathogen invasions, large percentages of adults will die, taking with them the potential for new generations to recruit. Some of the best-known pathogens of eastern USA forests include the chestnut blight (attacking *Castanea dentata*), Dutch elm disease (*Ulmus* sp.), hemlock wooly adelgid (*Tsuga* sp.), beech bark and beech leaf diseases (*Fagus grandifolia*), and, the subject of this thesis, the emerald ash borer (Brasier & Gibbs, 1973; Brasier, 1991; Gluck-Thaler et al., 2015).

The emerald ash borer (*Agrilus planipennis* Fairmaire., henceforth "EAB") was first noted in North America near Detroit MI in 2002 and identified as the reason behind a regional decline in ash trees (Cappaert et al., 2005; Poland & McCullough, 2006). EAB is a boring beetle native to Asia that specifically targets the genus *Fraxinus* (ashes) as its host (Cappaert et al., 2005; Liu et al., 2003; McCullough et al., 2009; Siegert et al., 2015; Wei et al., 2004). EAB was likely transported to North America from Asia in infected shipping pallet wood. As of 2023, EAB has been discovered in 35 US states and five Canadian provinces.

Adult EAB lay eggs onto the bark of ash trees, after which larvae burrow inside and consume cambium and vascular tissue for up to 300 days. Over only a few seasons a tree loses its ability to move water and nutrients around to its tissues and will inevitably die (Wang et al. 2010). The mortality rate for EAB-infected ash trees is up to 99%, depending on *Fraxinus* species, accounting for billions of ash trees that have died or will die through this invasion (Knight et al., 2013; Tanis & McCullough, 2015).

As often typifies early stages of biological invasions, much prior and ongoing research on EAB focuses on either the pathogen itself, or on the directly targeted species. The EAB invasion of North America is still relatively recent, and gaps remain in the knowledge of how invaded *ecosystems* are responding, especially regarding potential or lack thereof for recovery.

Being that this is still a relatively new biological invasion, there are many research projects that have been, or are currently being generated in the aftermath. There is a large gap in knowledge of how forests are regenerating in response to the invasion, especially forests dominated by green ash (*Fraxinus pennsylvanica* Marsh.), which is common in bottomland hardwood forests.

Study Goals

The objectives of this research were to assess the impact of EAB induced mortality on green ash (*Fraxinus pennsylvanica* Marsh.) stands 10 – 15 years post-invasion, and to evaluate potential for recovery. Multiple responses to EAB invasion are likely possible, including post-invasion recovery of stands to pre-invasion conditions, development of altered but functional post-invasion stands, and collapse to degraded systems dominated by undesirable species. The last and most concerning possibility could yield near total dominance by invasive shrub species with no further recruitment of ash or other native tree species.

This project was conducted in western New York State, where extensive stands of Green Ash have developed on pro-glacial lake plains (flat and semi-hydric) since periods of logging and farming during the 20th century. These stands were invaded by EAB post-2010 and have suffered severe mortality.

Specific Objectives

1. Evaluate two primary independent variables that would have characterized stands prior to EAB invasion: 1) Predominance of ash stems in pre-invasion canopy, and 2) Maturity of stands.
2. Estimate survivorship and health condition amongst ash trees in present-day stands, assessing the potential for ash recovery.
3. Catalogue abundance of other native tree species in stands, representing potential for replacement by native-dominated alternate states.
4. Identify sources of regeneration (sprouts, seedlings) of ash and other native trees.
5. Establish extent of invasive shrub species within stands, which could yield highly undesirable and degraded post-EAB-invasion communities.

Testable Hypotheses

Regarding pre-EAB-invasion prevalence of ash trees, we logically hypothesize that higher ash dominance should yield greater impact from EAB simply because a higher proportion of the canopy would be dying out. However, we suggest several indirect corollaries to this premise that may have important effects on recovery potential. First, there is likely a pre-EAB ash canopy dominance above which high mortality produces an effective removal of the canopy, rather than just an increase in canopy gap area. Such a profound change could be followed by other deleterious impacts (e.g. takeover by invasive shrubs) that could hinder any native recovery. Conversely, at low ash prevalence, it is possible stands may have attracted fewer EAB during the invasion, perhaps yielding a refuge for ash trees in stands where they were less dominant.

We also surmise stand age (at time of EAB invasion) may be linked to patterns of impact severity. Stands young enough that many trees were not attacked by EAB may have a greater present-day abundance of non-impacted trees maturing into a post-invasion stand. Conversely, older stands, although perhaps more likely suffering high ash mortality, may represent more diverse canopy species richness, with possibly greater resilience to the sudden loss of a major canopy component. This higher resilience is due to the potential for other species present in the canopy to fill in the niche left by green ash.

Genus Fraxinus (The Ashes)

The genus *Fraxinus* (the ashes) is in the family Oleaceae and is distributed throughout North America and Asia (Wallander & Albert, 2000). The most common species in central and northeastern North America are *F. pennsylvanica* (Green ash), *F. americana* (White ash), *F. nigra* (Black ash), *F. profunda* (Pumpkin ash), and *F. quandrangulata* (Blue ash). White ash represents 36% of the ash distribution in the continental United States, with green ash 34% and black ash 28% (Hanberry, 2014).

Ashes are recognized by pinnately compound leaves and one-seeded "winged" samaras as fruit (Wallander & Albert, 2000). Most ashes grow as trees, including the North American species listed above, but there are some that are primarily shrubs. Most ashes are deciduous, but the subtropical species can be evergreen. Some species of *Fraxinus* (e.g. the Melioides clade that includes *F. pennsylvanica*) are dioecious (separate male and female plants), but this trait is restricted to North America (Wallander, 2008). Others are monoecious and have flowers of both sexes on the same plant.

Green Ash

Fraxinus pennsylvanica is most commonly called green ash, but is also known as red ash, swamp ash, or water ash. Green ash is the most widely distributed of the North American *Fraxinus* species, extending from Alberta, Canada, to southeastern Texas and to Northern Florida (Figure 1). It can reach 30 meters tall and exceed 60 centimeters in diameter, and occasionally liv/e to 200 years. Green Ash thrives in moist but well-drained soils of floodplains and other bottomland sites, but it can grow well in a range of soil types, including sandy, silty, and clay soils. (Burns & Honkala, 1990), Green ash can tolerate flooding for up to 40% of the growing season, although it is not as fully associated with swamps as is Black ash (Burns & Honkala, 1990).

Green ash can be a major canopy species in the forests it occupies, representing e.g., 18% to 73% of the canopy cover where studied in eastern Montana (Lesica, 2001). Other canopy trees commonly associated with green ash across its broad geographic range include boxelder (*Acer negundo*), red maple (*Acer rubrum*), pecan (*Carya illinoensis*), sugarberry (*Celtis laevigata*), sweetgum (*Liquidambar styraciflua*), American sycamore (*Platanus occidentalis*), eastern cottonwood (*Populus deltoides*), quaking aspen (*Populus tremuloides*), black willow (*Salix nigra)*, willow oak (*Quercus phellos*), and American elm (*Ulmus americana*) (Burns & Honkala, 1990).

Green ash has long been an important timber resource (along with White Ash, the other major North American *Fraxinus* timber product), with a historic value in the Unites States of US $280 billion prior to the discovery of EAB in Michigan. (USDA Forest Service Northern Research Station, 2019). Green and white ash have attractive grains, high shock resistance, and excellent durability. Common uses for ash lumber are hardwood floors, interior furniture, tool handles, baseball bats, and guitar bodies (McConnell et al., 2019). Ash also provides high quality firewood because it burns easily with a high heat content. Fast-growing *Fraxinus*, especially white ash, has been used extensively in landscaping, providing ample shade and beautiful fall colors.

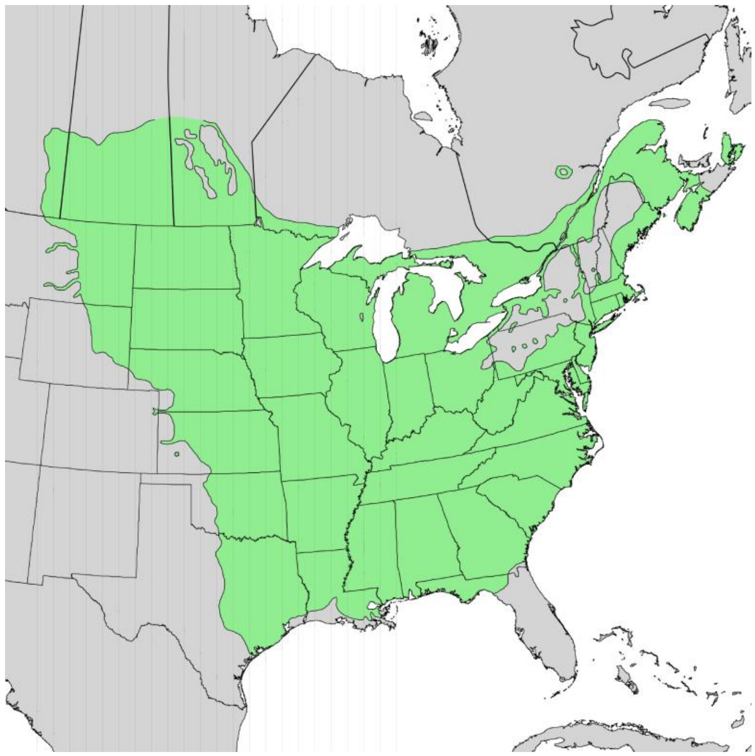

Figure 1: A map prepared by the U.S. Department of Agriculture, Forest Service of the native distribution of green ash (*Fraxinus pennsylvanica* Marsh.) in North America.

Green ash flowers are produced in spring at roughly the same time new leaves appear. The compact panicles are rather inconspicuous because they lack petals. Seeds are primarily wind-borne, to which the winged samara is well adapted (Tackenberg et al, 2003; Hintze et al., 2013). However, with green ash often growing along river corridors, long-distance seed transport by flowing water, especially during floods, may also drive its dispersal (Merritt & Wohl, 2002). An alternative reproductive strategy of the green ash is vegetative propagation through basal trunk sprouts (Uresk & Boldt, 1986). Lesica (2001) showed that ~30% of new green ash saplings in eastern Montana had arisen due to vegetative reproduction.

Emerald Ash Borer

The emerald ash borer (EAB) is a member of the family Buprestidae in the order Coleoptera. Buprestidae is often called the metallic wood-boring beetle family, as its members bore into tree species and consume the phloem inside. The EAB is native to East Asia, including parts of Russia, Mongolia, Japan, China, and Taiwan. In its native range, EAB functions as a *secondary* pest, in that it can colonize and kill *Fraxinus* trees that are already stressed and declining (Cappaert et al., 2005; Liu et al., 2003; McCullough et al., 2009; Siegert et al., 2015; Wei et al., 2004). In North America EAB will also land on non-*Fraxinus* species, such as *Ulmus americana* (American elm) and *Juglans nigra* (black walnut), to deposit eggs. However, eggs appear to develop and hatch only on *Fraxinus* sp. (Anulewicz et al., 2008).

Adult EAB have an average lifespan of 20.5 and 22.8 days for females and males, respectively. Adults grow to ~8.5mm in length. Females deposit eggs into bark furrows of ash trees from early-May until mid-July (Wang et al., 2010). EAB lay between 40 and 53 eggs, typically one per tree, although a maximum of seven per female on a single tree has been observed (Rutledge & Keena, 2012, Wang et al., 2010). Larvae emerge after 12 – 19 days, when they bore into the trees and consume the cambium and phloem. The larval stage is the longest life stage, 300 days and four instars, during which they cause extreme damage to host trees. EAB larvae create distinctive S-shaped tunnels (galleries) under the bark as they burrow and feed (Wang et al., 2010).

Larvae are full grown by late July, after which they burrow into the sapwood to construct an overwintering chamber, completed by late October to early November. In the overwintering chamber larvae enter the prepupal stage in mid-March, and the pupal stage from early-April to mid-May (Wang et al. 2010). Adults emerge in May to mate and oviposit. Emerging adults leave characteristic 3 – 4-mm D-shaped holes in the trunk, providing evidence of a tree’s infestation (Wang et al., 2010).

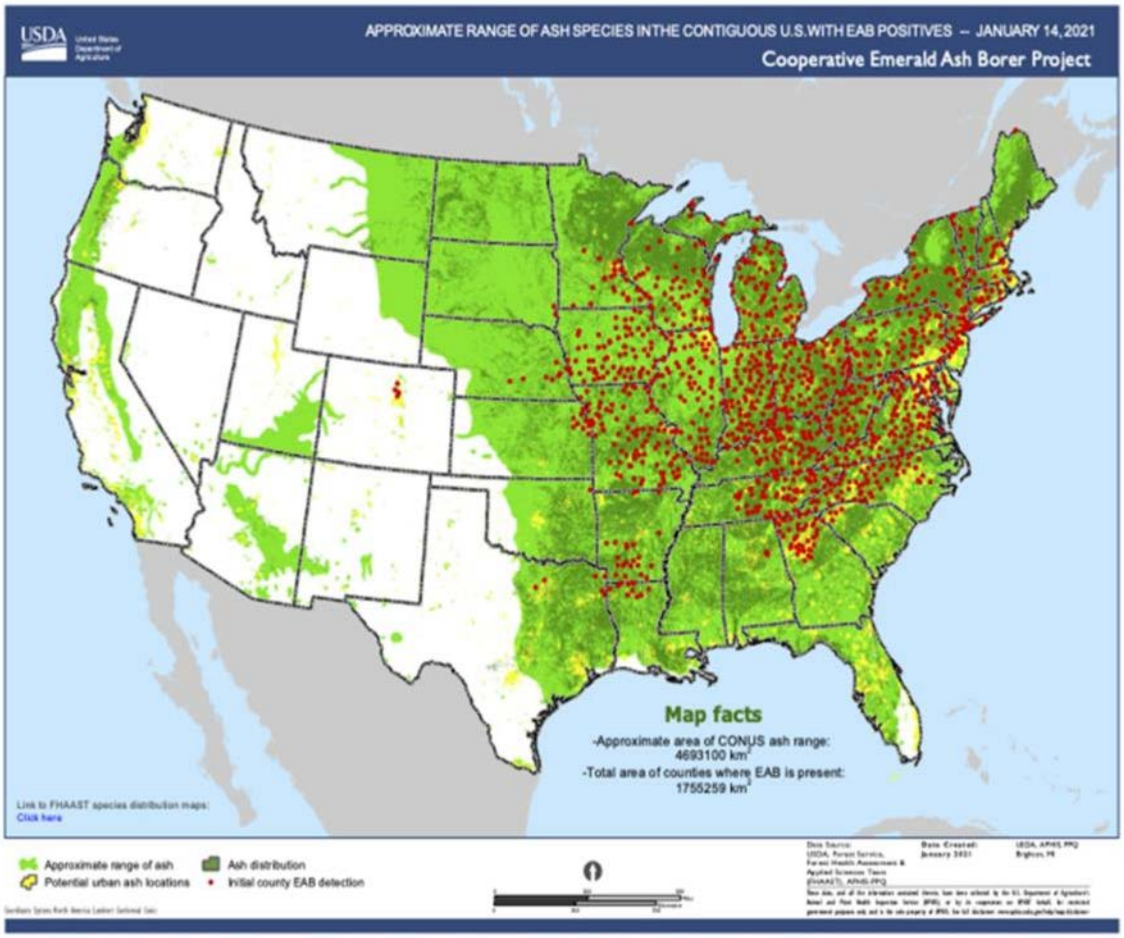

Figure 2. Map created by the United States Department of Agriculture (USDA) indicating the approximate distribution of native *Fraxinus* species in green, with positive cases of Emerald Ash Borer being detected in state counties denoted by a red dot.

Emerald Ash Borer Invasion

In 2002, the emerald ash borer was identified as the cause of mortality in ash trees in the greater Detroit MI metropolitan area. Shortly thereafter, the same finding was reported from Windsor, Ontario, Canada (Cappaert et al., 2005; Poland & McCullough, 2006). Tree ring cores from ash trees in the Detroit area suggest the earliest evidence of EAB infestation goes back as far as 1997 (Siegert et al., 2014). The mortality rate for infected adult ash trees is near 100%, with green ash being the most heavily impacted in terms of proportion of impacted individuals within the population, followed closely by white ash and black ash, respectively (Tanis & McCullough, 2015; Knight et al., 2013). The only North American species of ash that has so far displayed a degree of resistance to EAB is blue ash (Tanis & McCullough, 2012, 2015).

The invasion of such a prolific pathogen as EAB has had drastic consequences, both ecologic and economic. EAB has clearly had negative effects on *Fraxinus*, but there are other components of the ecosystem that have also suffered indirectly. The removal of an important canopy tree from a forest ecosystem can have cascading effects, including changes in species composition, understory light, temperature, and moisture conditions, and alteration of carbon and nutrient cycling (Lovett et al., 2006; Gandhi & Herms, 2010).

A tree can be infested by EAB larvae for several seasons before any outside evidence is present. The most obvious sign is the serpentine galleries left by the larvae as they burrow through the cambium and vascular tissue of at least 3 centimeters in diameter, but these are not readily noticeable when the bark is still on the tree (Lyons et al., 2004). The bark will readily fall off standing dead trees and can be peeled off live trees, but this sign of infection is often one of the last ones that will present itself. The most obvious sign is dieback of the crown of the tree as the tree is unable to circulate water and essential nutrients throughout (Flower et al., 2010). Larger, more mature trees will typically take longer to kill due to having more vascular tissue to eat through before a pronounced effect is seen (Flower et al., 2010). A mature ash tree can be killed by the EAB in as little as three to five years (McCullough & Katovich, 2004). Other signs of infection are the D-shaped emergence holes in the bark, and the presence of epicormic sprouts on the trunk (Lyons et al., 2004; Cappaert et al., 2005).

EAB damage can also negatively impact resident fauna. For example, North American ash species are important to amphibian larvae, such as those of the wood frog (*Lithobates sylvaticus)* (Stephens et al., 2013). Overstory trees shade ephemeral woodland ponds where amphibians develop, and their fallen leaves can serve as a food source (Maerz et al, 2005; Earl et al., 2012). Ash leaves have low tannin content compared to other native canopy species (e.g. oaks and red maples), and their loss after EAB invasion could hinder larval growth and subsequent fitness of adult frogs (Herrera-Silviera & Ramirez-Ramirez, 1996; Temmink et al., 1989). Also, Hodorff and Sieg (1986), in a study pre-dating the pathogen-generated loss of North American ash canopies, similarly concluded that intact and contiguous canopies of Green Ash supported a richer avian fauna than open stands in declining health.

Economic impacts of EAB are likewise daunting, especially considering the widespread timber and landscaping uses of the North American ashes. Modeling of economic losses from invasive insect pathogens (also including hemlock woolly adelgid [*Adelges tsugae*] and Asian gypsy moth [*Lymantria spp.*]) suggests EAB is causing the greatest economic losses among these (McConnell et al., 2019). An example in Louisiana shows that an estimated $1.7 billion has been lost from local government expenditures, with $380 million lost in residential property value per year since the EAB invasion began affecting the state. Much of the economic damage from EAB has not in fact come from direct timber losses, but from costs of tree removal, treatment, or replacement, often borne by private property owners (McConnell et al. 2019).

II. METHODS

Study Area

Lake Erie was formed at the end of the Wisconsin glaciation period roughly 17,500 years ago, when the Laurentide ice sheet was retreating and carved out a large lowland area. Its current form is less than 4,000 years old, making it a relatively new lake, but the lake went through several different stages in its formation, existing as several previous glacial lakes (Stothers & Abel, 2001). Current Lake Erie began as the proglacial Lake Maumee and evolved over the course of roughly 10,000 years into its current form due to rising and lowering water levels with the retreat of the Laurentide Ice Sheet.

Lake Tonawanda was a prehistoric lake that was present in western New York at the end of the last ice age roughly 10,000 years ago. It was present in between Early Lake Erie, located to the south, and Glacial Lake Iroquois to the north, which was ancestral to the current Lake Ontario (Muller, 1977). The lake was present during the high lake levels present during glacial retreat and was an overflow of Early Lake Erie but had subsequently dried up after the water levels in Early Lake Erie had dropped (Muller, 1977). While there are no longer any lacustrine features left behind of Lake Tonawanda, the lake plain is still present, with exceptionally flat topography in the area that had previously been the lakebed. The very fertile sediments in this area led to a large farming presence in this area of New York, which has now given way to suburban areas.

Figure 3: Map prepared by the United States Geological Survey (USGS) of the range of prehistoric Lake Tonawanda in western New York, USA, in relation to prehistoric Lake Iroquois, the Niagara River, and Early Lake Erie.

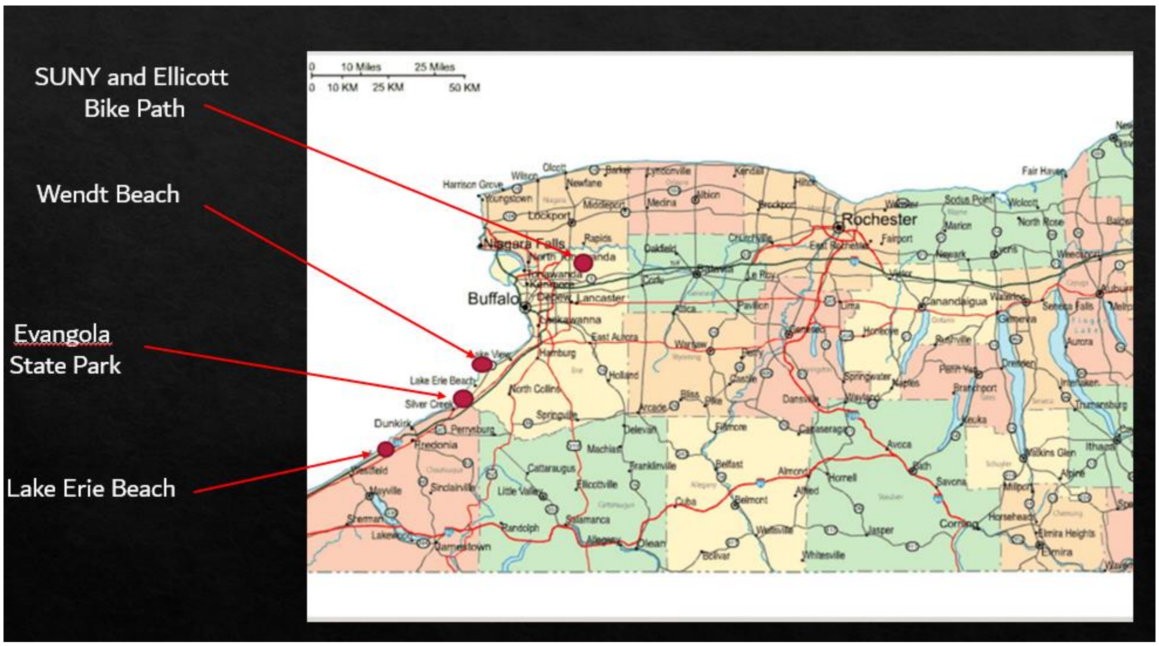

Figure 4: A map of Western New York state with red dots indicating public lands where data was collected. Going from South to North, the sites are as follows: Lake Erie State Park, Evangola State Park, Wendt Beach, and the SUNY at Buffalo Campus.

Stand Selection and Surveying

In the Lake Erie and Lake Tonawanda lake plains, green ash became extremely abundant, and was often the most common tree. We surveyed 32 stands of green ash at the following public lands: Lake Erie and Evangola State Parks, and Wendt Beach County Park (Erie) on the Lake Erie Plain, and the SUNY at Buffalo campus and adjacent Ellicott Bikeway on the Lake Tonawanda Plain.

We chose forest stands to represent a broad range of ash dominance and stand age. Although the entire study area exhibits much human influence in terms of prior (19^{th} thru early 20^{th} centuries) logging and often agriculture, we steadfastly avoided obvious human-derived stand composition such as landscaping and gardening, or plantation timber management. Perhaps not surprisingly, we initially gravitated to stands dominated by ash trees (mostly dead) because they were so identifiable from a distance. As the study progressed, we made efforts to survey stands with fewer ash trees to better represent the full gradient of this independent variable. There is always a debate regarding whether canopy survey plots in forests are truly independent of each other, but we minimized such concerns by selecting stands widely separated (by 100s of meters, with intervening roads, lawns, fields, etc., wherever possible), and never surveying multiple quadrats in any one locale of similar stand age and ash dominance. We haphazardly and without prior bias established survey quadrats with sides ranging from 20 – 80 m, according to stand characteristics and access. This yielded surveying efforts as similar as possible among stands. Quadrat corners were GPS pinned and temporarily marked with flags.

Adult green ash trees were identified, counted, and their condition assessed. Ash trees were placed in five health/condition categories (see also: Knight et al., 2012): 1)

Dead (although allowing for stump or root collar sprouts), 2) Sparse (estimate of <1/3 foliage remaining), 3) Medium, 4) Decent (>2/3 foliage remaining), and 5) Unimpacted. It was unlikely that more finely discriminated categories could have been based on these semi-qualitative assessments. Dead stems included those fallen. Ash stems >20 cm diameter at breast height (DBH), including fallen stems, were presumed to have represented the pre-EAB canopy.

The DBHs of all Decent and Unimpacted ash stems were measured and recorded. These tree-health categories correspond to a widely reported condition of "lingering ash" (see Knight et al., 2012) that may represent post-EAB persistence of the genus. Other native trees were identified and their DBHs were measured. While we specifically targeted sites without deliberately planted trees, non-native trees were occasionally encountered, and identified and measured. A 20-cm DBH threshold was always used to estimate pre-EAB canopy position. *Craetegus* sp. (the Hawthorns) were an exception to this protocol, because they never occupied canopy positions even when their DBH exceeded 20 cm.

Stand Age

With increment core dating an unlikely prospect in multiple parks and preserves, and with many stands dominated by long dead and rotting ash stems, stand age needed to be estimated indirectly. Where present, we were able to count growth rings on broken-off trunks of one or more fallen ash trees. Stand ages could also be estimated by examining aerial and satellite imagery, which is some cases extends all the way back to the 1920s, for visual evidence of stand initiation. Stand history on the Lake Tonawanda Plain

(SUNY campus and Ellicott Bikeway) were reconstructed from an especially complete image history (see Figure 5).

1926

1951

1978

1995

2008

2022

Figure 5 (previous page): An example of aerial and satellite image series (areas east of SUNY at Buffalo campus where the Ellicott Nike Trail provides public access to woodlands) revealing land cover changes and allowing estimates of stand ages of study plots. Note the development of the SUNY campus and Audubon Parkway starting in 1978 image, installation of Ellicott Creek flood-control spillway (grassy strip first appearing in 1995), and creation of Audubon Golf Course since 1995. Also, note wooded stands along Ellicott Creek in 1926, and patchy large-tree woodland in upper center of 1926 image (likely a shaded pasture), which are still present today.

Stump Sprouts and Seedlings

In each plot we recorded the number of ash stems (usually dead) producing stump sprouts. We estimated the height of both stump sprouts and seedlings and made qualitative notes of deer browse intensity (i.e., light, moderate, heavy). We also estimated the density of the seedlings present. Although we were focused on ash seedlings as a potential source of regeneration, we also recorded the presence of seedlings of other tree species.

Invasive Shrubs

We identified and catalogued invasive shrubs in all survey plots. Where these occurred as scattered clumps, we assigned their size as combinations of 1-, 2-, or 3-m length and width dimensions. Larger extents of invasive shrub cover were measured individually. We then converted invasive shrub coverage to percentage of each plot. Within several plots, Glossy Buckthorn or Common Buckthorn had completely covered the understory layer.

III. RESULTS

Twenty-four out of 32 plots surveyed had suffered >75% mortality of pre-EAB canopy ash trees, with no trend associated with either pre-EAB ash canopy percentage or stand age (Figure 6). Conversely, 9 out of 32 plots had more than 15% of ash trees currently present classified as either decent (less than ~1/3 leaf loss) or unimpacted (no leaf loss), offering potential for recovery. The average DBH of the decent and unimpacted ash trees was 4.8 and 4.1 cm, respectively.

Figure 7 shows that the unimpacted and decent ash trees tend to cluster within plots that are of a young stand age (<60 y) and have a high percentage of ash (>80%). There was a site of moderate stand age (70 y) and a low pre-EAB percentage of ash (< 25%) that had a moderately high number of healthy ash trees, but this was the only such case.

Figure 8 shows that the stump sprouts also dominate sites of young age and high percentage of ash. It is notable that stump sprouting is not present in any stands older than 80 years. Stump sprouts were present in 26 of 32 plots, 20 of which had experienced deer browsing. Ash seedlings were present in 29 plots, with deer browsing of the seedlings at 23 of these. Seedlings varied in size from less than 20 centimeters to 1 meter in height. While we were primarily focused on presence of ash seedlings, there were some seedlings of non-ash tree species (7 of 32 plots), such as red oak and tulip tree. These seedlings were consistently <20 centimeters in height.

Within all survey plots there were 34 native non-ash trees and shrubs encountered, and three non-native trees encountered. There were 21 species that contributed to the canopy and 31 species that contributed to the understory (Tables 2 and

3), with some species being both canopy and understory trees. The most prevalent non-ash canopy tree was *Acer rubrum/saccharinum*, with the two (red vs. silver maple) difficult to separate without seed samaras (see Fgiure 9). The two most common types of understory tree (Figures 9 and 10) were the *Acer rubrum/saccharinum* assemblage and the elms (*Ulmus* spp.), which appeared to be predominantly American elm (*Ulmus americana*). *Craetagus* spp. (exceptionally difficult to identify to species) were also commonly found within the understories of the plots surveyed (Figure 11). Other native tree species commonly encountered included *Prunus serotina* and *Populus deltoides*. Canopy and understory *Acer* spp. were uncommon in high pre-EAB ash density plots, but were instead concentrated in older, lower ash density stands (Figure 9). There was a site of moderate stand age and high percentage of ash in the canopy where *Ulmus* spp. was extremely prevalent. *Craetegus* spp. was very abundant in one site of young stand age and high percentage of ash in the canopy.

Invasive shrubs occurred in 26 of the 32 plots surveyed. Major species included multiflora rose (*Rosa multiflora*), Chinese privet (*Ligustrum sinense*), glossy buckthorn (*Frangula alnus*), European buckthorn (*Rhamnus cathartica*), Japanese barberry (*Berberis thunbergii*) and Morrow's honeysuckle (*Lonicera morrowii*). Invasive shrubs were the most prevalent in plots that were of a young stand age and high prevalence of ash in the canopy pre-EAB (Figure 12).

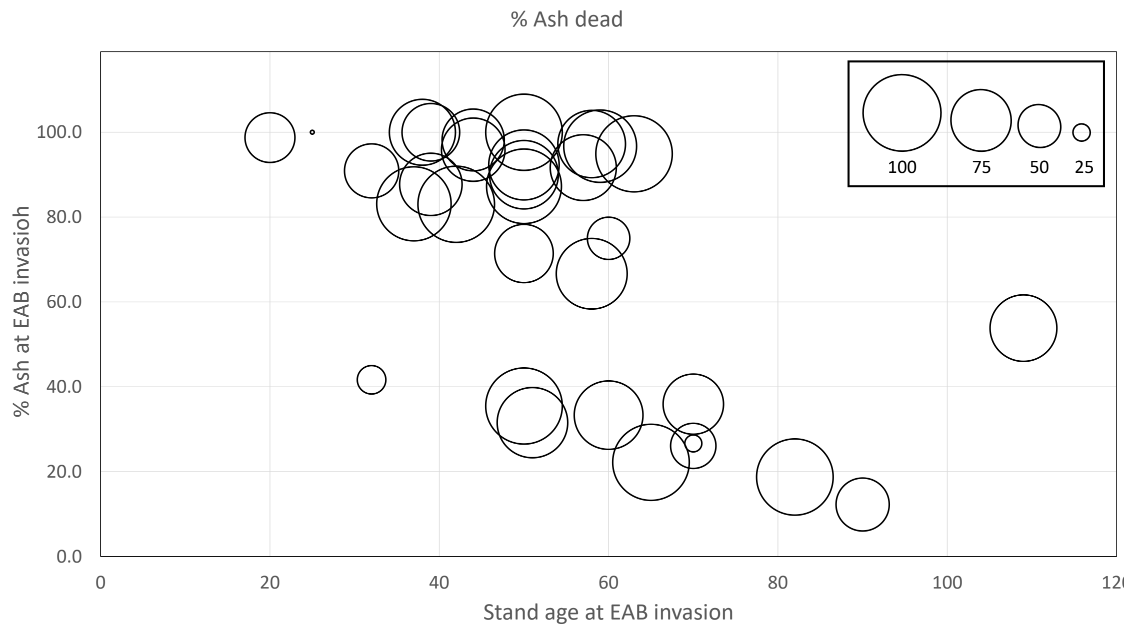

Figure 6: Percentage of green ash trees dead (represented by bubble diameters) in survey quadrats plotted on the two independent variables: stand age (years) and percentage of ash in the canopy pre-EAB.

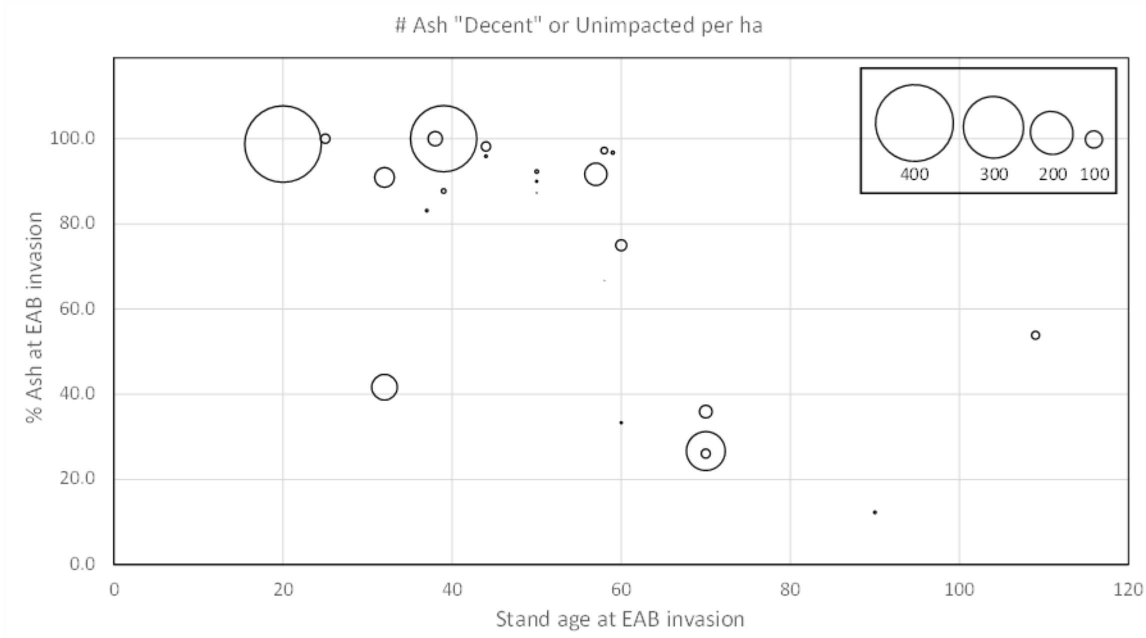

Figure 7: Number of decent (>1/3 foliage intact) and unimpacted ash per ha in survey quadrats plotted on the two independent variables: stand age (years) and percentage of ash in the canopy pre-EAB.

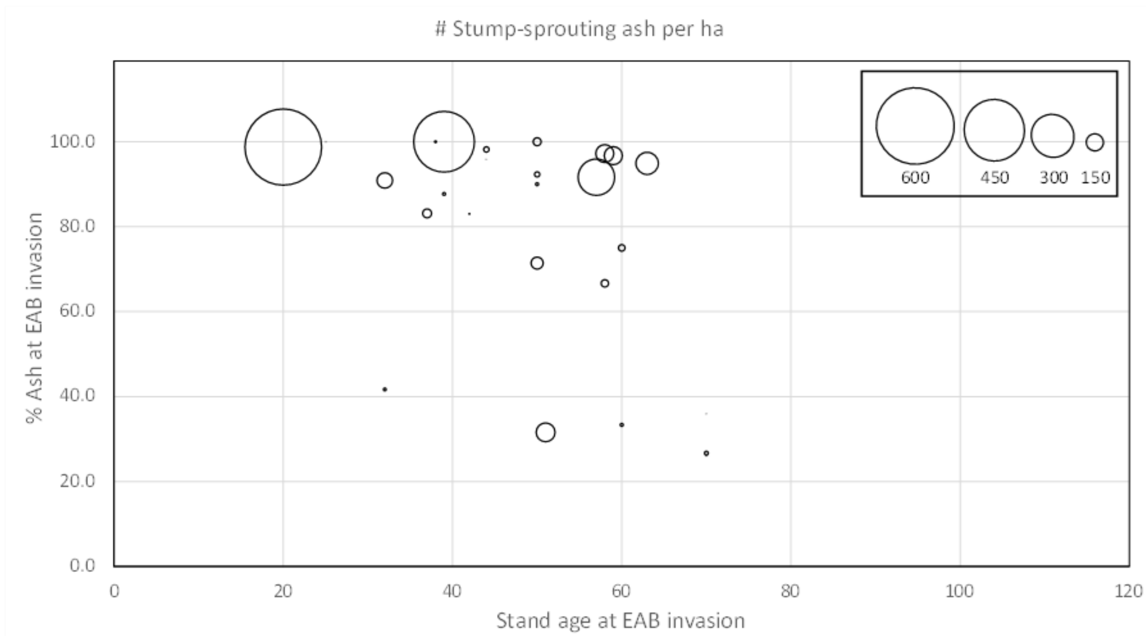

Figure 8: Number of stump sprouting ash per ha in survey quadrats plotted on the two independent variables: stand age (years) and percentage of ash in the canopy pre-EAB.

Table 1: Scientific and common name for the tree species associated with the four letter code used in Table 1 and 2.

4 Letter Code	Scientific Name	Common Name
ACNE	*Acer negundo*	Boxelder
ACRU	*Acer rubrum/saccharinum*	Red/Silver Maple
ACSA	*Acer saccharum*	Sugar Maple
BEAL	*Betula alleghaniensis*	Yellow Birch
CACA	*Carpinus caroliniana*	Musclewood
CAGL	*Carya glabra*	Pignut Hickory
CAOV	*Carya ovata*	Shagbark Hickory
CEOC	*Cephalanthus occidentalis*	Buttonbush
COFL	*Cornus florida*	Flowering Dogwood
FAGR	*Fagus grandifolia*	American Beech
GLTR	*Gleditsia triacanthos*	Honey Locust
HAVA	*Hamamelis virginiana*	Witch Hazel
ILVE	*Ilex verticillata*	Winterberry Holly
JUNI	*Juglans nigra*	Black Walnut
LITU	*Liriodendron tulipifera*	Tulip Tree
NYSY	*Nyssa sylvatica*	Black Tupelo
PISY	*Pinus sylvestris*	Scott's Pine
PODE	*Populus deltoides*	Eastern Cottonwood
POTR	*Populus tremuloides*	Quaking Aspen
PRPE	*Prunus pennsylvanica*	Pin Cherry
PRSE	*Prunus serotina*	Black Cherry
QUAL	*Quercus alba*	White Oak
QUBI	*Quercus bicolor*	Swamp White Oak
QUMA	*Quercus macrocarpa*	Bur Oak
QUPA	*Quercus palustris*	Pin Oak
QURU	*Quercus rubra*	Red Oak
SANI	*Salix nigra*	Black Willow
TIAM	*Tilia americana*	American Basswood
ULAM	*Ulmus americana*	American Elm

Table 2: Counts of non-ash tree species contributing to survey plot canopies. These are counts per plot and are not converted to density per ha. (Plot codes: WE = Wendt Beach, EV = Evangola, EB = Ellicott Bikeway, LE = Lake Erie State Park, SU = SUNY campus).

Non-ASH canopy stems							
	Native (counts)						
Plot	Acer (NOT sugar)	ACSA	ACNE	CAOV	Carya sp.	FAGR	JUNI
WE1	2						
EV1	8						
EV2	1						
SU1	2						
LE1	1						
LE2	8						
EV3							
EV4	3						
EB1	10						
WE2	5			2			
WE3							
EB2							3
EB3							
EB4							
EB5	7						
SU2	17					6	
SU3	1						
EV5	12						
US20.1							
SU4							
SU5	11						
LE3							
LE4					1		
EB7	1		9				4
EB8	44			3			
EB9	18						
SU6	7						
SU7	26	1					
SU8	24						
WE4	23			1			
WE5	22						
EV6	16						

Table 2 (cont.):

LITU	NYSY	PODE	POTR	PRSE	QUAL	QUBI
	1					
		5				
						1
				1		
						3
						1
		3				
1		2		6	1	1
	2					
		1				
			5			
				1		
		10				
1	3			5		
	7			3		

Table 2 (cont.):

					Non-Native (counts)		
QUMA	QUPA	QURU	SANI	TIAM	Ulmus sp.	PISY	
			1				
					3		
						1	
				2			
					1		
	2				1		
1		1			1		
			8		4		
		1		1	1		
					2		
					1		
					2		
		9			1		

Table 3: Counts of non-ash tree species contributing to survey plot understories. These are counts per plot and are not converted to density per ha.

	Native (counts)								
Plot	**ACNE**	**ACRU**	**ACSA**	**Amelanchier**	**BEAL**	**CACA**	**CAGL**	**CAOV**	**Carya sp**
WE1									
EV1		1							
EV2									
SU1		7							
LE1									
LE2		1							
EV3									
EV4		5							
EB1		1		1					
WE2		6				2		4	
WE3									
EB2									
EB3									
EB4									1
EB5		1						1	
SU2		7							
SU3									
EV5		9							
US20.1									
SU4				1					
SU5		11		1					
LE3									
LE4					4				3
EB7	6								
EB8		9		1		1		3	
EB9		49							
SU6		12	3				1		
SU7		12							
SU8		2							
WE4		11	1						
WE5		16						1	
EV6		2							

Table 3 (cont.):

CEOC	COFL	Crategus	FAGR	GLTR	HAVA	ILVE	JUNI
	1						
		6					
1						1	
		3		1			
		3					
		3					
		9					2
		1					
			2		18		
		54					
		2					
			1				
		9					
			1				

Table 3 (cont.):

NYSY	PRPE	PRSE	Prunus	QUPA	QURU	Rhus	SANI
		1					
							1
						1	
	1			1			
							1
				5			
2							
		2					
					1		1
		2					
			4				
2		7			1		
12		17					

Table 3 (cont.):

				Non-native		
TIAM	ULAM	Viburnum	Malus	PISY	Pyrus	Rhamnus
	1					
	1					
			1			14
	55					
			1			10
	1		1			1
						7
						1
	4					
	3	1				
			1			10
						5
						10
			1		1	
	4					
	15					6
	3					
			2	1		9
	1					
	2					
	21					
1	1					
	2					
	1					
	10					
	2					
	2					

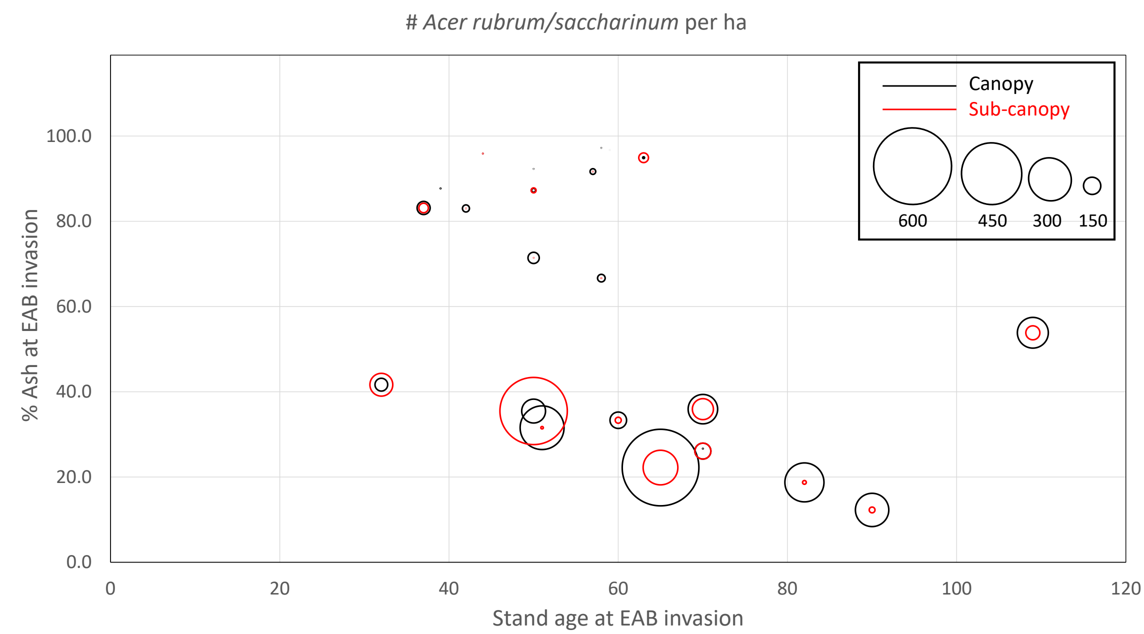

Figure 9: Number of canopy and understory *Acer rubrum/saccharinum* per ha in survey quadrats plotted on the two independent variables: stand age (years) and percentage of ash in the canopy pre-EAB. These two species are not easily distinguished without seed samaras, although the geographic range and non-flooded habitat suggest *A. rubrum* would be more common.

Figure 10: Number of canopy and understory *Ulmus* spp. per ha in survey quadrats plotted on the two independent variables: stand age (years) and percentage of ash in the canopy pre-EAB. Elm species are likewise not easily distinguished without seed samaras, although habitat, growth form, and bark characteristics suggest *Ulmus americana* would be dominant.

Figure 11: Number of *Craetegus* sp. (hawthorns, which are exceptionally difficult to identify to species) per ha in survey quadrats plotted on the two independent variables: stand age (years) and percentage of ash in the canopy pre-EAB. Hawthorns never attained canopy status in terms of tree height, even when stems were >20 cm DBH.

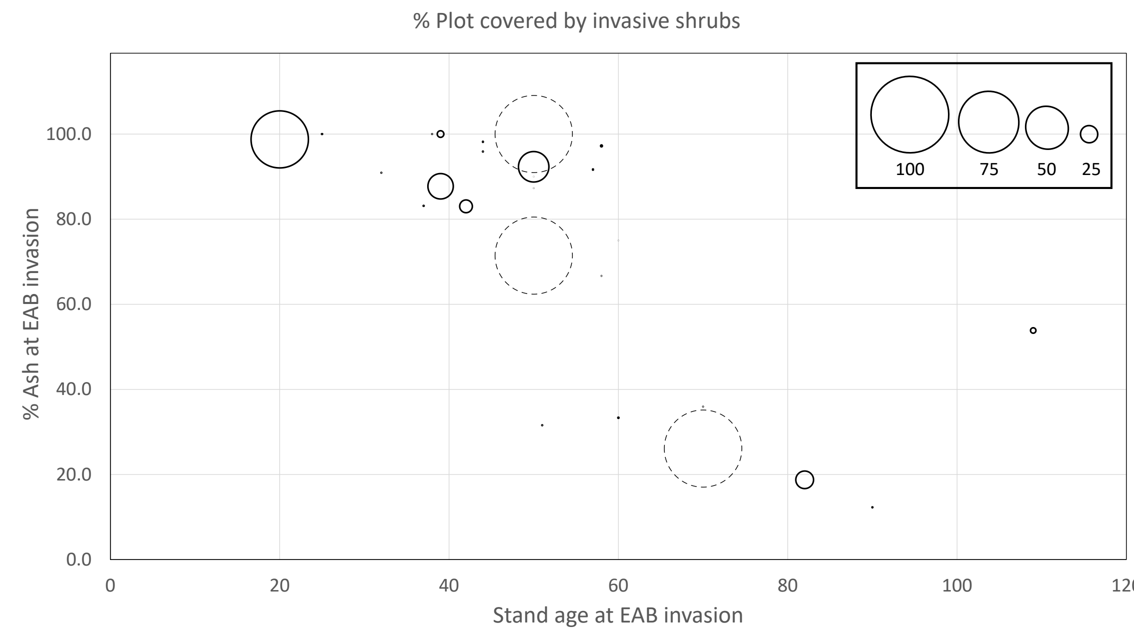

Figure 12: Percentage of survey quadrats covered by invasive shrubs plotted on the two independent variables: stand age (years) and percentage of ash in the canopy pre-EAB. Solid bubble outlines indicate % ground coverage by shrubs and thickets. Dotted bubble outlines indicate two plots in Lake Erie State Park completely filled by understory tree-sized Glossy Buckthorn (*Frangula alnus*) and one plot near SUNY at Buffalo completely filled by understory tree-sized Common Buckthorn (*Rhamnus cathartica*). However, other vegetation occurred in these three plots.

IV. DISCUSSION

Patterns of EAB-Induced Ash Mortality

It appears that neither stand age nor the percentage of ash within the pre-EAB canopy had an impact on green ash mortality. Mortality was high across the entire gradient of both of these independent variables. This counters one *a priori* hypothesis of ours, that mortality might be lower in stands with fewer ash in the canopy These trees might not be as easy for the EAB to find compared to trees in stands dominated by green ash (Root, 1973; Rand & Louda, 2006). The uniformly high mortality in this study could reflect unavoidable lethality once a tree is infected by the EAB.

Stand age also did not impact the total number of dead trees within a stand, although data are still being sought from any stands younger than 20 years. However, we speculate that younger stands would not suffer as high mortality, because decent and unimpacted trees were concentrated within younger stands. These decent and unimpacted ash trees, which offer potential for recovery, were most prevalent in stands with a high percentage of ash and young to moderate stand ages. Because these are very young trees (< 5 cm DBH), they were most likely either too small to have been impacted by the EAB when the invasion passed through, or they have regenerated since the invasion (Knight et al., 2013). Decent and unimpacted ash were very uncommon in stands with low pre-EAB ash percentage, which, at least in terms of regeneration, might reflect the light regime. Green ash is shade intolerant, so it is possible that it could recruit in stands that lost most of their canopies, as opposed to in the isolated gaps in stands with lower ash dominance.

Stump Sprouts

Stump sprouts were also prevalent in high-ash-dominance younger stands. Otherwise, they were relatively rare. Stump sprouting may likewise be a response to the higher light incidence after loss of ash-dominated canopies to EAB. Stump sprouting was absent in stands older than 80 years old, which may indicate an upper age limit to stump sprouting. Curiously, recruitment through stump or root collar sprouting was common in mid-aged (40-60 y) ash trees with a dead primary shoot. Stump sprouting appears to offer a large recovery potential, but these recruits will have the same genome as the parent trees originally killed by EAB, and thus may not be resistant if a further invasion occurs.

Seedling Recruitment

It was promising to discover that ash seedlings were present in 91% of all plots surveyed, suggesting high recruitment potential. In contrast, seedlings of non-ash species such as red oak and tulip tree were much less common. This is troublesome, because these are important native trees with potential to establish if ash is unable to do so. Also, there were very few, if any recruits of any species between seedling and sapling size classes. This could reflect deer herbivory preventing seedlings surviving on to become full sized trees (i.e. growing through the “deer filter”).

Presence of Other Native Trees

While plots differed in species composition, most included the red/silver maple assemblage, and many others had American elm present. It was perhaps not surprising to encounter abundant red/silver maples and American elm at our study sites, because they prefer the same general hydric conditions as green ash. It is a distinct possibility that depleted ash stands could transition to native red/silver maple and elm stands. In stands with lower pre-EAB ash dominance, there would be more opportunities for other native species to recruit within the canopy gaps. Conversely, in higher ash-dominance stands sources of new non-ash recruits may be limited. Further, recruitment into EAB-depleted stands may ultimately be hindered by invasive shrub presence and by deer browsing.

Presence & Impact of Invasive Shrubs

The highest density of invasive shrubs was observed in sites with high percentages of ash in the canopy. This is not a surprising finding, because invasive shrubs tend to grow in areas of high disturbance, high nutrient availability, and increased levels of sunlight (Tyser & Worley, 1992; Parendes & Jones, 2000; Trombulak & Frissell, 2000; Gelbard & Harrison, 2003; Watkins at al., 2003). Ash stands that have had their canopies removed now have much higher light levels than prior to the EAB invasion, which may promote shrub invasion. Also, invasive shrubs may have already been present at study sites (perhaps at lower densities), and EAB-induced canopy removal generated a growth release.

Another troubling finding is that decent and unimpacted ash trees are also likely to be in the same types of stands (younger, higher percentage of ash) as invasive shrubs. Thus, the invasive shrubs may hinder the recovery of ash within these sites where regeneration appears most possible. For some of the highly shrub-invaded stands to have a chance at recovering into healthier *native* stands, invasive shrub removal may be necessary.

Presence & Impact of Deer Herbivory

Although we did not quantify deer herbivory at ash survey plots, the intensity of the browse was estimated because white-tailed deer could be a major factor hindering recovery within the stands. Extreme levels of deer browsing can change the plant species composition in such a way that plant species favored by the deer can fail to regenerate, which can then cause other species that depend on these plants to be negatively impacted (Russell et al., 2001; Rooney & Waller, 2003; Casey & Hein, 1983; de Calesta, 2006). In extreme cases, sometimes the only plants left within a forest ecosystem are the ones unpalatable to deer, which can then dominate the forest ecosystem and create a recalcitrant understory layer where the plant coverage is so dense that no other plant species can grow through it (Royo & Carson, 2006).

Browsing by deer on stump sprouts and seedlings was observed in 77% and 79% of plots, respectively. Our publically accessible sites included parklands that prohibit deer hunting, which could be a potential reason for such a high amount of deer browsing. For some of the stands with heavy deer browsing present, it may be necessary to establish deer exclosure fences or even cull the deer.

Similar Trends Seen in Other Research

Potential for regeneration has been studied for white ash and black ash, even though they occupy different habitat types. White ash occupies the same geographic range as green ash but is an upland species that prefers well-drained soils. Black ash is a more northerly species found in swamps and wetlands. Robinett and McCollough (2018) studied white ash regeneration in central Michigan and found the average percentage of white ash alive in plots was 75%, which is much higher than that in our study of green ash. Interestingly, however, the authors noted most of the surviving white ash fit into their smallest size class of 30 centimeters DBH. Also most live white ash had signs of previous EAB colonization. (Robinett & McCullough, 2019).

Marshall (2020) studied ash regeneration in forests of Indiana, Michigan, and Ohio (which contained green, white, and black ash) and found that green ash was the most abundant seedling and midstory tree in surveyed stands. The authors also concluded that overstory composition did not change due to the EAB invasion, but instead simply transitioned from live green ash to standing dead ash (Marshall, 2020). Our research in Western New York also suggests that, despite near total ash canopy loss, there have yet to be clear compositional changes in different forest strata. This suggests that either the stands are not successfully recruiting enough to change the species composition, or perhaps there is a lag time in the response. Marshall (2020) even reported similar non-ash species to ours in their study stands, with the three most abundant non-ash trees being silver maple, black cherry, and American elm.

Black ash stands are often nearly monocultures due to the perennial flooding and low soil pH of their swamp habitats (Burns & Honkala, 1990). This is especially worrisome in response to EAB invasion, because there are few other non-ash trees that can tolerate these environmental conditions under which black ash thrives. Springer & Dech (2021) reported that EAB mortality in black ash swamps is being replaced entirely by black ash recruits, apparently with no input by any other tree species. Even though green ash is not so completely restricted to and dominant in swamp habitats, some of the stands surveyed in the present study were nearly 100% ash pre-EAB, and suffered near total mortality. There may also be few other trees here to recruit post-EAB.

Future Research

Due to many unknowns about how the future of the EAB invasion will pan out, there is much need for further and long-term studies of the regeneration of green ash stands. Deer exclosures and invasive shrub removals could be coupled to quantify the impacts of these confounding factors on regeneration in depleted stands. While the present study focused on green ash, these types of studies can be conducted regarding white and black ash as well.

Factors that can promote regeneration of ash trees will be greatly challenged if the emerald ash borer does reemerge within the study area. Most green ash trees of varying condition, from sparse to decent, have likely already been attacked by the borer, and could become infected again in the future. Even if a tree only suffered modest damage, there is a chance that further ash borer attack could ultimately kill it. The unimpacted green ash trees seen in the sites have been uniformly young, leading to the speculation that they were not present during the initial invasion. If that is the case, then it is possible that these trees have no special resistance to the ash borer and may die if infected during any EAB reemergence.

However, there is the possibility that some of the trees that are unimpacted may have had some measure of resistance against the ash borer. If that is the case then perhaps a new generation of EAB-resistant green ash trees may become more widespread in the population. It could be speculated that if the ash borer was to return to the area, it may not be as dramatic of a wave as the first time. There is less of the ash borer's food source present, and at least in the western New York area the post-EAB density of green ash is now low. A slower and less dramatic invasion front could also offer the opportunity for potential predators, such as woodpeckers, to capitalize on the emerald ash borer as a food source.

Combining the research conducted in this project along with known literature on ash species regeneration post-EAB invasion, it is evident that the three major ash species (green, white, and black) have the potential to regenerate within the forests. Ash is mostly a shade-intolerant species, so perhaps it is not entirely surprising that the species is regenerating so quickly and numerously. Even though ash is recruiting within the forests, it has many challenges that could hamper its successful return, including invasive shrub presence, high amounts of deer herbivory, and the potential for the invasion front to return. However, despite all the challenges, one can counter that due to some of the characteristics of the genus *Fraxinus*, such as being shade intolerant and a prolific seeder, there are valid reasons to be optimistic about the return of ash to the canopies of eastern forests in the decades to come as current studies conducted are showing some recruitment and persistance of the genus. (Robinett & McCullough, 2019; Marshall, 2020; Springer & Dech, 2021).

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APPENDIX

Appendix 1: GPS coordinates for each survey plot. If coordinates are not present for a point, it was due to a lack of accessibility to the corner.

Number	Site Code	GPS Coordinates			
1	WE1	42.6757125, -79.0432915	42.6758733, -79.0436831	42.6752736, -79.0437897	42.6756593, -79.0433059
2	EV1	42.611816, -79.107995	42.6117116, -79.1073346	42.611560, -79.107510	
3	EV2	42.6055068, -79.1075562	42.6056338, -79.1070731	42.6052827, -79.1074848	42.6054068, -79.1070191
4	SU1	43.0040128, -78.7933720	43.0043625, -78.7929177	43.0043205, -78.7931366	43.0040177, -78.7929636
5	LE1	42.4247054, -79.4275116	42.4247088, -79.4273242	42.4247900, -79.4273295	42.4242656, -79.4271267
6	LE2	42.4260918, -79.4310005			
7	EV3	42.6070718, -79.0975670	43.6072065, -79.097133	42.607098, -79.0617319	42.6071683, -79.0972042
8	EV4	42.6053212, -79.0984102	42.6051107, -79.0988800	42.604978, -79.098680	42.6053932, -79.0988007
9	EB1	43.0051343, -78.77165592	43.0049916, -78.7710738	43.0050426, -78.7716729	43.0050890, -78.7711154
10	WE2	42.6790981, -79.0447020	42.6789931, -79.0451473	42.6787957, -79.0451486	
11	WE3	42.6775972, -79.0386412	42.6773584, -79.0384977	42.677530, -79.038422	42.6774822, -79.0389591
12	EB2	42.9960645, -78.7630976	42.9959728, -78.7627449	42.9957504, -78.762805	42.9957680, -78.7631297
13	EB3	42.9973284, -78.7644980	42.9972791, -78.7649070	42.9968622, -78.7649771	42.9969306, -78.7645449
14	EB4	43.0007684, -78.772878	43.0007404, -78.7718862	43.0010011, -78.7717504	43.009467, -78.7724675
15	EB5	43.0038655, -78.7707771	43.0040011, -78.7703952	43.004357, -78.770714	43.0041678, -78.7709464
16	SU2	43.6057939, -78.7907850	43.0060336, -78.7908457	43.0058500, -78.7916892	43.0060039, -78.7915685
17	SU3	43.0030666, -78.8014035	43.0031895, -78.8016577	43.002779, -78.801648	43.0028362, -78.8016469
18	EV5	42.608452, -79.102615	42.6083021, -79.1022776	42.608614, -79.102423	42.6085635, -79.1020755
19	US20.1	42.558405, -79.122645	42.5584334, -79.1220941	42.5584719, -79.1224435	42.5583067, -79.1224361
20	SU4	43.0190065, -78.7908879	43.0192855, -78.7900826	43.0193095, -78.7906848	43.018934, -78.790280
21	SU5	43.0058704, -78.7823065	43.0059061, -78.7822881	43.005736, -78.782728	43.005589, -78.782466
22	LE3	42.4214708, -79.43172	42.4215142, -79.43170	42.4217678, -79.4317260	42.4217537, -79.4318524
23	LE4	42.4205137, -79.4282499	42.4203467, -79.4279367	42.4203855, -79.4280681	42.4203435, -79.4382774
24	EB7	43.0056443, -78.7675598	43.005848, -78.767670	43.005683, -78.768845	43.005826, -78.768798
25	EB8	43.005063, -78.768254	43.0047052, -78.7690900	43.004648, -78.768406	43.004955, -78.769100
26	EB9	43.004336, -78.768011	43.004097, -78.767830	43.004118, -78.767588	43.004107, -78.767848
27	SU6	43.0082856, -78.7923715	43.008404, -78.792376	43.008337, -78.792385	43.008290, -78.792095
28	SU7	43.008103, -78.788653	43.008207, -78.788622	43.008278, -78.788745	43.007991, -78.788655
29	SU8	43.020347, -78.791413	43.020712, -78.791792	43.020575, -78.791819	43.020518, -78.791352
30	WE4	42.675893, -79.052711	42.675473, -79.052837	42.675287, -79.052136	42.675753, -79.052083
31	WE5	42.677914, -79.045231	42.678436, -79.045297	42.678144, -79.045814	42.677927, -79.045874
32	EV6	42.608480, -79.104316	42.608822, -79.103814	42.608863, -79.104289	42.608762, -79.104643