EXPLORING THE POPULATION VIABILITY OF GREEN ASH (FRAXINUS PENNSYLVANICA) WITH A STAGE BASED MODEL

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ABSTRACT

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The invasive emerald ash borer beetle (*Agrilus planipennis*, EAB) has caused significant ash tree (*Fraxinus* spp.) declines and forest changes, which include loss of canopy cover and increased numbers of invasive plant species (Hausman et al. 2010). My focus was to assess ash population dynamics and environmental factors that could play a role in ash survival. My research used a population viability analysis (PVA) approach that combined literature review, targeted field studies, and greenhouse experiments to examine green ash trees (*F. pennsylvanica*) in the post-EAB peak infestation (aftermath) forest. Aftermath forests dynamics between ash and EAB are likely different from the initial infestation. I developed historic and worst case stochastic stage based ash population models as part of a PVA; these scenarios reflect time periods before and after EAB invaded Northwest Ohio. The ash population growth rates were estimated as 0.76 and 1.03, respectively, in worst case versus historic scenarios. Results indicated that population changes were more sensitive to survival and growth of the smallest stage class in the worst case scenario, where ash populations became locally extinct within 41 years. I examined ash parameters with little known information, such as germination, seedling survival and their environmental conditions, and mature ash tree neighbors. My germination experiments from the lab and the field resulted in a very low germination rate from the local population. Seedling survival was high and they were affected by leaf litter, bare ground and dead coarse woody debris. The number of ash neighbors within 6 m was significantly lower for the healthiest ash canopy class compared to declining health classes ($p = 0.02$). I modeled changes that could occur to the green ash aftermath forest (2010-2017) by introducing EAB periodically as a catastrophe that lowered ash survival and simulated a slow ash survival recovery. Management scenarios included, 1) reduced EAB catastrophes, 2) increase ash survival and growth, 3) individual ash size classes survival increased, and 4) planted EAB-resistant ash trees. Reduced EAB catastrophes, protecting the largest and smallest ash size class, and increase survival and growth provided an improvement for the population. Planting EAB-resistant trees allowed for a partial recovery, where saplings performed better than seedlings. While conservative, these green ash models indicated that increased tree survival improved population recovery, and EAB population fluxes have a large influence on ash population persistence. PVA, as this research demonstrates, allows us to quickly identify factors that influence the population viability of threatened species, allowing for the development of strategies that promote recovery.

This is dedicated to my family, and all the friends that I consider family.

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INTRODUCTION

The invasive emerald ash borer beetle *(Agrilus planipennis*, EAB), has caused significant ash tree declines and precipitated dramatic changes in North American forests. EAB is native to Asia, was introduced near Detroit, MI, and is a specialist beetle that feeds and reproduces on *Fraxinus* species (Herms & McCullough 2014). After nearly 100% mortality of ash canopy trees, EAB infested Michigan floodplain forests had greatly reduced densities of ash seedlings 1-2 years old or under 0.5 m tall, (93% and 78%, respectively; Klooster et al. 2014). In Ohio, forested ash stands had almost complete mortality within 6 years of initial EAB symptoms (Knight et al. 2013). Lingering ash remained, this term refers to healthy ash trees, with a diameter at breast height (DBH) >10 cm, that have survived for at least two years after the initial ash mortality rate reached 95% from EAB (Knight et al. 2012). Lingering ash can still be infested by the EAB but are dying at a slower rate. Lingering ash are individuals interspersed within other ash cohorts in the EAB aftermath ash forest.

The area where lingering ash trees were first discovered was the Oak Openings Region of Northwest Ohio. The Oak Openings Region is a mixed disturbance landscape containing rare natural ecosystems in a mosaic of small to large remnant habitat patches surrounded by a matrix of agriculture and urban development. Prior to human settlement the area was composed of oak savanna, oak woodland, oak barrens, wet prairie, floodplain forests, and surrounded by the black swamp forest (Brewer and Vankat 2004). Composition of floodplain forests includes American elm, ash species, maple species, basswood, sycamore, oak species, hackberry, honey locust, cottonwood, and Ohio buckeye. This region is a unique biodiversity hotspot that has undergone large changes from the EAB invasion. It holds a remnant population of ash trees within its floodplain forests where EAB is still present. This area is an ideal study system to better understand the impacts and recovery from EAB, as well as how management might influence these processes. My focus was to assess ash population dynamics and environmental factors that could play a role in ash survival post-EAB impact. A plethora of data on environmental factors can be collected and analyzed statistically to identify which affect ash survival. I investigated environmental factors that could influence this ash population, such as soil nutrients, vegetation composition, and neighboring tree species composition; these localized factors may influence long term ash persistence (Zhang et al. 2014, Canham et al. 2004, Rubert-Nason et al. 2015). Population models were modified to reflect the potential influence of these factors and revealed potential outcomes of management activities. The aftermath ash forest in this unique region offered an opportunity to research surviving post invasion trees.

Research Objectives

My research used a population viability analysis (PVA) approach that combined literature review, targeted field studies, and greenhouse experiments with mathematical models to examine population dynamics of green ash trees over time. For my dissertation research, I addressed questions related to the probability of future green ash tree (*Fraxinus pennsylvanica*) persistence in a floodplain setting of Northwest Ohio. Specifically, I studied the Oak Openings Region population at Oak Openings Preserve Metropark. I focused on the differences between pre and post emerald ash borer infestation, to help assess current and future impacts in these forests. This assessment was also used to evaluate potential adaptive land management plans and serves as a model for understanding ecological recovery following a catastrophic or extreme invasion event.

My research questions included: What was the viability of ash tree populations with EAB present within the Oak Openings Preserve Metropark (OOPM)? How did that compare to historic ash population dynamics? What environmental variables and management techniques were important for ash persistence? These questions will be answered within the following sections of my dissertation:

Chapter I

- Green ash population dynamics analysis, including survival, growth, and fecundity information from the literature before and after EAB invasion.

Chapter II

- Stage based stochastic model of green ash in the OOMP with comparisons among scenarios based on historic conditions and worst case EAB population persistence.
- Evaluating ash stages that were considered sensitive to changes in the models.

Chapter III

- Exploring natural germination of lingering ash seeds and environmental predictors of seedling establishment.
- Assessing effects of environmental variables on ash seedling/sapling survival.

Chapter IV

- Nearest neighbor and soil nutrient analysis of surviving ash trees in NW Ohio.

Chapter V

- Stage based stochastic models of green ash in OOMP with comparisons of hypothetical management scenarios.

References

Brewer, L. G., & Vankat, J. L. (2004). Description of Vegetation of the Oak Openings of Northwestern Ohio at the Time of Euro-American Settlement 1. *Ohio Journal of Science*, *104*(4), 76–85.

Burton, P. J., & Bazzaz, F. A. (1991). Tree seedling emergence on interactive temperature and moisture gradients and in patches of old-field vegetation. *American Journal of Botany*, *78*(1), 131–149. https://doi.org/10.2307/2445236

Canham, C. D., LePage, P. T., & Coates, K. D. (2004). A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research*, *34*(4), 778–787. https://doi.org/10.1139/x03-232

Herms, D. A., & McCullough, D. G. (2014). Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. *Annual Review of Entomology*, *59*, 13-30.

Klooster, W. S., Herms, D. A., Knight, K. S., Herms, C. P., McCullough, D. G., Smith, A., … Cardina, J. (2014). Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). *Biological Invasions, 16*(4), 859–873.

Knight, K.S., Herms, D., Plumb, R., Sawyer, E., Spalink, D., Pisarczyk, E., Wiggin, B., Kappler, R., Menard, K. (2012). Dynamics of surviving ash (*Fraxinus* spp.) populations in areas long infested by emerald ash borer (*Agrilus planipennis*). In: Sniezko, R.A., Yanchuk, A.D., Kliejunas, J.T., Palmieri, K.M., Alexander, J.M., Frankel S.J., tech. coords. Proceedings of the 4th international workshop on the genetics of host-parasite interactions in forestry: disease and insect resistance in forest trees; 2011 July 31-August 5; Eugene, OR. Gen. Tech. Rep. PSW-240. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 143-152.

Knight, K.S., Brown, J.P., Long, R.P. (2013). Factors affecting the survival of ash (*Fraxinus spp.*) trees infested by emerald ash borer (*Agrilus planipennis*). *Biological Invasions, 15*(2), 371–383.

Rubert-Nason, K. F., Couture, J. J., Major, I. T., Constabel, C. P., & Lindroth, R. L. (2015). Influence of Genotype, environment, and gypsy moth herbivory on local and systemic chemical defenses in trembling aspen (*Populus tremuloides*). *Journal of Chemical Ecology*, *41*, 651-661.

Zhang, C., Zhao, X., Gao, L., & Gadow, K. (2009). Gender, neighboring competition and habitat effects on the stem growth in dioecious *Fraxinus mandshurica* trees in a northern temperate forest. *Annals of Forest Science*, *66*(8), 812.

CHAPTER I. GREEN ASH TREE DEMOGRAPHY BEFORE AND AFTER EMERALD ASH BORER INVASION

Abstract

The invasive emerald ash borer beetle has caused significant ash tree declines and cascading forest changes in the United States. Major changes to ash tree populations in natural systems resulting from emerald ash borer include the loss of canopy cover and increased numbers of invasive plant species (Hausman et al. 2010). The size and effect of such changes must be understood to plan mitigation and management in these affected forests. This review summarizes the historical data on ash (*Fraxinus* spp.) population demographics and compares it to changes associated with emerald ash borer beetle (*Agrilus planipennis*, EAB) invasion. The seed bank longevity of ash is much shorter than previously thought, only up to 4 years. Seedling survival was linked to soil moisture condition in two different studies. Mortality from EAB was size dependent, with larger trees the target of infestations. The parameters summarized in this literature review can be used in population models that include information on survival, growth, and fecundity.

Introduction

Forests with higher tree species richness have a positive relationship with many ecosystem services, yet multiple tree species have been lost from natural areas as a result of pests and diseases (Gamfeldt et al. 2013). The invasive emerald ash borer beetle (*Agrilus planipennis*, EAB) is one of these pests that has devastated the N. American ash species populations and precipitated dramatic changes in North American forests. EAB is native to Asia and was introduced near Detroit, MI; it is a specialist beetle that feeds and reproduces on all *Fraxinus* species (Macfarlane & Meyer 2005, Herms & McCullough 2014).

EAB may be a continuing presence in the United States but has not yet expanded through the entire ash range in North America. As of spring 2018 EAB have been detected in Michigan, Wisconsin, Ontario, Quebec, and parts of Minnesota, Vermont and New Hampshire in the north of its range. It has spread south down the East Coast to North Carolina, with parts of South Carolina, Georgia, Tennessee, Arkansas and Louisiana invaded. Westward it had been found in Missouri and Iowa, with a very small part of Kansas, Nebraska, and Colorado invaded (Matsouki, C. 2018 www.emeraldashborer.info) (Figure 1.1).

Each time a female EAB mates it can lay up to 60 eggs in ash tree bark crevices, then after hatching the larvae burrow under the bark into the phloem layer of the tree. They continuously feed on the phloem layer allowing the larvae to grow through four instars, which causes girdling of the tree. The larval stage will transform into an adult and chew its way out of the bark leaving a D-shaped hole. EAB survive the winter by increasing the concentration of glycerol and antifreeze agents in their body fluids while remaining in their larval stage under ash bark (Crosthwaite et al. 2011). The estimated cost of removal, replacement, or treatment of ash trees within U.S. developed areas is 10.7 billion dollars for 17 million trees (Kovacs et al. 2010). Tree loss assessments of ecosystem services for free flowing rivers have been discussed in the literature; theoretically these services may be lost and then some but not all could return in a full or reduced form (Boyd et al. 2013). However, ash tree dams in floodplains alter the river’s natural flow regime and increases the risk of irreversible loss of other species and potential community collapse (Auerbach et al. 2014). The overall outcome of EAB and ash tree interactions depends on the resilience of the surrounding habitat and ecological conditions, which is dependent on the stabilizing effects of biodiversity (Hector and Wilby 2009).

Green ash (*Fraxinus pennsylvanica*) is a valuable commodity, which is grown for landscape trees or harvested for lumber to make furniture, tool handles, and baseball bats (Kennedy 1990). Green ash is a deciduous tree that can grow up to 20 m (70 ft) tall (Brakie 2013). In nature, green ash is typically found in bottomland areas, but is adapted to a variety of areas across the Eastern United States and Canada to the Gulf of Mexico and west to the Rocky Mountains (MacFarlane & Meyer 2005, Stewart & Krajicek 1973). The species is tolerant of several environmental stressors including high salinity, flooding, drought, and high alkalinity (MacFarlane & Meyer 2005). Ash are susceptible to four different boring insects, as well as leaf and root fungus, and the ash seed weevil (Brakie 2013). Green ash is dioecious where both male and female form small flowers, although females flower only 2-3 years out of every 5 years, females bear small (50 mm x 6 mm or 1 inch x 0.25 inch) winged seeds (samaras) that are wind dispersed (Franklin 1981, Brakie 2013). Wind disseminated pollen has been shown to travel 120 m from its source, but pollen count decreased rapidly beyond 46 m (Franklin 1981). Green ash seeds can disperse 120-250 m from the tree, float in water for up to 2 days, and show increased germination rates with increased inundation time in water (Schmiedel & Tackenberg 2013). In this chapter, we synthesize published ash demographic information from multiple natural habitats before EAB was a problem and summarize what is known thus far about ash demography during and after peak EAB infestation.

To assess the changes that have occurred we compare historical and current population dynamics found from the literature. Relevant search terms (i.e. green ash, survival, fecundity, population dynamics, etc.) were entered in science-based search engines, including Treesearch, a US Forest Service (USFS) search engine. All documents were based on research of North American green ash species unless information on a size class was not found, in which case white ash (*Fraxinus americana*) information was reviewed since the two species share similar habitat. Size classes were categorized to assess population demographics of the trees different life stages. We separated size classes by diameter at breast height (DBH, 1.37m). Size classes were: trees shorter than 1.37 m or < 1 cm, 1 - 9.9 cm, 10 - 19.9 cm, and > 20 cm DBH. Data were also gathered on information regarding seed production and germination. We separated literature so any references after EAB was officially recorded in a state (www.emeraldashborer.info) were considered current information on ash population dynamics after EAB infestation. We expected to find ample literature on ash tree life dynamics since it is a fast-growing tree used in horticulture. Much of the literature are likely to be white papers and scientific research articles that are highly focused on ash tree health and forest composition.

Ash Seedlings

Historical Demography

We identified literature on ash seedlings defined as first year individuals (emergent ash) up to those that were less than 1.0 cm DBH from time periods prior to EAB impact, to estimate historical demographic rates. In the literature information on this size class was found from reforestation experiments and forest surveys. In a Southern Quebec old growth maple-ash-beech forest, emergent white ash seedlings had a mean probability of survival of 0.22 (SD = 0.4) over their first summer, but the results were highly heterogeneous (Messaoud & Houle 2006). Seedling density in these forests varied by season with a spring emergence of 0.55 per m^2 (SE = 0.1) and a fall density of 0.09 per m^2 (SE = 0.03) (Messaoud & Houle 2006). They found that seedling emergence was positively correlated with soil nitrogen, soil moisture, and ash tree basal area (Messaoud & Houle 2006). White ash tree basal area was 6.2 m^2/ha (SE = 2.0) and density was 128 trees/ha (SE = 28) in this area of S. Quebec. In a central Ohio forested area research surveyed for emergent seedlings from 1984-1993 in both upland and lowland forests where white, green and black ash (*Fraxinus nigra*) were found more often in lowland forest wet depressions (Boerner & Brinkman 1996). In the Ohio forest they found on average 241 ± 21 new ash seedlings per 100 m^2 per year, with two high producing years (1988 and 1990) of approximately 800 - 1000 new ash seedlings per 100 m^2 (Boerner & Brinkman 1996). When following the 1990 cohort of new seedlings they reported 66.7% dead by October, and 96.6% dead by the next year (Boerner & Brinkman 1996). In former agricultural sites a reforestation experiment planted 1 year old bare-root green ash in Mississippi Alluvial Valley clay soils, and had 95% survival after 3 years, with initial root collar diameter having no effect on survival (Gardiner et al. 2009). In a river restoration project, several years after a nuclear power plant was shut down where reactor coolant water had been discharged only early successional vegetation was present (Kolka et al. 1998). Green ash seedlings were planted and after 2 years survival varied by location along the river, with 42% survival in the upper corridor, 9% survival in the lower corridor, and 18% survival in the delta (Kolka et al. 1998). Naturally regenerated seedlings experience harsher conditions, resulting in a lower survival than planted trees, which are larger with established root and shoot system that stores more resources.

Current Demography

Literature on ash seedlings after the introduction of EAB were primarily carried out in conjunction with the USFS. Since 2005, the USFS has used a protocol for monitoring changes in ash habitat throughout the EAB invasion. This protocol for monitoring included plots spread across Michigan and Ohio in natural areas. Each plot was 400 m^2 with 4 m^2 microplots at cardinal directions, 6 m from plot center (Knight et al. 2014). Ash seedlings were counted, and percent cover was recorded in each microplot, with seedlings separated into new and established categories (Klooster et al. 2014). New ash still had cotyledons attached to the stalk. With this information, Klooster et al. (2014) found yearly comparisons of mean densities per hectare of new and established seedlings for hydric, mesic, and xeric sites at a time when all Michigan sites and some Ohio sites had been infested by EAB. In Michigan, new seedlings decreased 99% from 2008 to 2010 and seedlings in Ohio increased 97% in response to a large seed mast (Klooster et al. 2014). For established seedlings (> 25 cm tall), there was a 35% decrease in Michigan, while Ohio had a 50% increase in mean density. There was no difference in number of established ash seedlings, but in Michigan they were more often found in mesic sites when compared to hydric or xeric sites, and in Ohio more were found in xeric sites than hydric or mesic (Klooster et al. 2014). Established ash seedlings resided in Michigan mesic sites with densities ranging from 4,583 – 4,753 per ha, and Ohio xeric sites with densities ranging from 6,801 – 19,120 per ha (Klooster et al. 2014). During the initial infestation in Southeastern Michigan (86% infested), ash seedling densities were higher in mesic stands than in hydric stands and were the most common seedling in all stands surveyed (Smith 2006). Other work has shown that the ash seed bank deteriorates within 3 years of adult ash death with a similar decline in germination and new seedlings, which revealed that the seed bank lifespan was shorter than previously thought (Klooster et al. 2014). EAB infested Michigan floodplain forests had greatly reduced densities of emerging ash seedling species 1-2 years old and those under 0.5 m tall (93% and 78%, respectively), while densities of intermediate sized seedling (0.5 - 1.0 m and >1.0 m tall) reduced by 11% on average (Kashian and Witter 2011). Explicit consideration of what is occurring in the younger generation of ash in the area can assist in future population predictions.

Changes to ash seedlings from the introduction of EAB had a greater impact on new and small seedlings than larger, older seedling. The invasion of EAB had an impact on ash seed banks, therefore reducing new seedling densities. At the time of the Klooster et al. (2014) study, only Northern Ohio had indications of EAB ash tree decline. Therefore, Ohio ash trees could respond to good seed mast conditions and proliferate greatly one last time before the EAB invasion worsened. Seedlings were found more often in mesic and xeric sites, whereas hydric sites may hinder seedling growth if inundated with water for too long.

Ash Saplings

Historical Demography

We identified literature on ash saplings, defined as individuals that are 1.0 - 9.9 cm DBH. In a long term study at the Delta Experimental Forest in Mississippi (Kennedy 1981), tree plantations were started in 1971 with six different species each in its own subplots for two treatments, either disking or mowing between trees, as well as a control with no management. After 4 years, green ash survived best in mowed or control plots, and grew taller and wider in disk plots (Kennedy 1981). At Year 5 green ash was thinned to 25% of its original density in mowed plots and disked plots. After ten years, green ash showed no difference in growth between mowed or disked plots (Krinard & Kennedy 1997). At Year 15 green ash in these plots had a survival of 45% and average DBH of 11.75 cm, with most mortality due to boring insect damage (Lilac borer, banded ash borer, carpenter-worm) (Krinard 1989). At Year 16 in the control plots green ash had a survival of 96% with an average DBH of 7.5 cm (Krinard & Kennedy 1997). These ash plots with high survival had a canopy structure consisting of 3% dominant, 44% codominant, 44% intermediate, and 9% suppressed trees, with DBHs ranging from 4.5 cm to 10 cm (Krinard & Kennedy 1997). Without management intervention in the control plots green ash grew slower and were smaller, but they had a greater chance of survival.

In other plantation studies on green ash, an area with Bowdre and Tunica series soil, had ash survival of 96.8% during the first three years after planting, and 94% over 11 years (Krinard & Johnson 1981). This area also had issues with flooding and beaver damage, which reduced survival of ash on average by 32% (Krinard & Johnson 1981). In an area with Commerce-silt-loam soil ash survival was 85% over 13 years (Krinard 1989). Variations among survival rates in these studies is attributed to environmental damage of trees rather than land management practices. When an individual is harvested it can re-sprout at the base, basal sprouts on live trees can also occur when they are damaged (Kennedy 1990, Del Tredici 2001). In a natural growth experiment where land management removed oak overstory trees once between year 1 and year 4, ash in the management unit grew up to 8.75 cm DBH in 14 years, although many were sprouts from stumps of cut trees (Johnson 1975). Green ash tolerance of shade is dependent on its location and age but it responds very well to competitive release and openings in the canopy (Kennedy 1990). These studies reveal the ability for ash saplings to survive under varying environmental stressors.

Current Demography

Ash saplings are less likely to be EAB targets if larger trees are near, but EAB can damage trees at least 2.5 cm DBH (McCullough et al. 2008). In a study in Michigan, the density of saplings < 2.5 cm DBH was least in xeric sites and ranged from 9 – 486 per ha (Klooster et al. 2014). With the changes occurring in Michigan, Klooster et al. (2014) concluded that the future ash population would be based on those individuals less than 2.5 cm DBH and without future seeds to establish new individuals this population has been labeled the “orphan cohort”. In another Michigan study which contained plots with high/medium/low ash mortality from EAB, the estimated average density of saplings 3-10 cm DBH was not significantly different (120-353 per hectare) (Burr & McCullough 2014). In a separate 3-year ash sapling study in Michigan where half of the study sites had parasitic wasps, an EAB biocontrol, released and 80% of saplings size 1-5 cm DBH survived (Duan et al. 2017). Sites were estimated to have 4-16 small saplings (1-5 cm DBH) and 2-9 large saplings (5.1-10.1 cm DBH) per 100 m^2 (Duan et al. 2017). While these results give us a good idea of green ash density, there are knowledge gaps in survival and growth.

Mature Ash Trees

Historical Demography

Here we identified mature ash trees as individuals larger than 10 cm DBH. Ash in full light may start to bloom when they are 10 cm DBH, although complete canopy flowering usually happens when the tree is 20 cm DBH (Franklin 1981). Green ash lifespan in natural stands is as high as 65 years, with 106 years as the oldest recorded individual (Kennedy 1990, Kaandorp 2010). Even though ash is dioecious, white ash had a sex ratio of 1:1 in the wild (Franklin 1981). Forest inventory analysis (FIA) data reported on mature ash trees (mostly white ash trees) in the past have been provided by the USFS, in which states would periodically review plots to assess state-wide tree dynamics. For Ohio information summarizing previous years is available for 1952, 1968, 1979, and 1991; in 2000 there was a change in the protocol which involved a more rigorous schedule that was applied to all states. The 1952 and 1968 reports describe the elm-ash-maple-cottonwood forest as comprising 24% (±2) of Ohio's commercial forests, which equates to roughly 546 hectares (Hutchinson & Morgan 1956, Kingley 1970). Net cubic-foot volume of white ash growing stock increased from 1956 to 1991 from 213.5 - 766.5 million, with the size classes (> 5 cm DBH) having a rather normal distribution over time (Hutchinson & Morgan 1956, Kingley 1970, Dennis 1983, Griffith 1993). Specific data was not reported for green ash until 1991, where in Ohio there were 39,669 saw timber stems (> 23 cm DBH) and 28,968 pole timber stems (11 – 23 cm DBH) counted, compared to white ash, which has 1.9 million saw timber and 841,188 pole timber stems counted (Griffith 1993). In a review on ash tree species characteristics and distributions prior to EAB, studies suggest that ash trees are found in greater numbers in newly disturbed areas, with fewer, large ash in secondary growth forests (MacFarlane & Meyer 2005).

Other information on mature ash was scarce, but urban records were found which included white ash. An urban growth study in Westminster, Colorado from 1992-2008, where EAB did not infest until 2013, found that ash grew on average 1.05 cm DBH per year (Wood 2010). This area of Colorado is part of the high plains ecosystem, a semi-arid climate with poor soil condition, although these trees were on private urban property and may have been treated to improve health. In all, fewer publications were found for historic mature ash than any other searched category.

Current Demography

Midwest states have continued data collection after nearly complete mortality of ash canopy trees. At the peak of infestation forests of the Huron River watershed in Michigan had 99.7% of its trees (> 2.5 cm DBH) die by 2009, with relative plot density of all ash > 12.5 cm DBH varying from 18% - 36 % ash stems/ha (Klooster et al. 2014). In Ohio, forested ash stands had 50% mortality in four years and almost complete mortality (> 99%) within 6 years of initial EAB symptoms (Knight et al. 2013). A survival analysis showed that mortality occurred faster if the tree was in the mid to lower canopy (intermediate or suppressed) or was found in lower density stands (Knight et al. 2012). Crocker and Meneguzzo (2010) found a 50% reduction in live ash from 2003 to 2009 from Indiana's FIA dataset. Forest service summaries of white and green ash over time since 2005 has shown a decrease in net volume, as expected from the introduction of EAB to Ohio in 2003 (Table 1.1). Growing stock volume of live white ash trees went down 3% between 1991 and 2006, while average annual mortality went up from 1.3% in the 2006 report to 2.1% in the 2011 report (Widmann et al. 2009, Widmann et al. 2013). For Northwest Ohio from 2006-2011 the average annual white ash mortality was 5.9% (Widmann et al. 2013). The ash group is ranked 7th overall in Ohio by volume, while white ash makes up 77% of Ohio's ash species, green ash makes up 20% (Widmann et al. 2013), but these numbers will likely change as EAB sweeps through the state. Over the entire state of Ohio, the number of green ash (> 2.5 cm DBH) counted in FIA plots decreased over time, with only 33% of the state population surviving in 2016 (Figure 1.2). Similar effects are expected throughout the rest of the ash range.

In locations where mature ash stands have been decimated, EAB persists at low numbers surviving on young trees (K.S. Knight, pers. comm.). Lingering ash are individual ash trees that survived the initial onslaught of EAB infestation even though they were large enough to be infected by the beetle (Knight et al. 2012). Lingering ash can still be infested by EAB but are dying at a slower rate. The area where lingering ash trees were first discovered was the Oak Openings Region of Northwest Ohio. The Oak Openings Region is a mixed disturbance landscape containing rare natural ecosystems in a mosaic of small to large remnant habitat patches surrounded by a matrix of agriculture and urban development.

Discussion

Dramatic changes have occurred from the EAB invasion. Ash seedling survival was highly heterogeneous before EAB was present, and positively correlated with ash tree basal area and soil moisture. Since the EAB invasion the lack of ash seeds and short-lived seed bank storage suggests a great reduction in future ash seedling density. Saplings had a survival of > 80% in non-managed plots in the past, and when EAB invaded only those < 2.5 cm DBH were too small to be infested. Mature green ash had more than 50,000 stems counted in Ohio's commercial forests in 1991. When EAB invaded nearly 100% of ash > 2.5 cm DBH would eventually die, usually occurring within the first 6 years of initial EAB symptoms. These changes are likely to have long term consequences for the forests and the other areas affected by EAB, such as increases in invasive plant species and changes in avian communities (Hausman et al. 2010, Koening et al. 2013).

The overall community effects from the loss of the majority of ash in areas where EAB has invaded are immense. There is the loss of ecosystem services to assess, as no single tree species can provide all services (Gamfeldt et al. 2013), and green ash can survive in specialized locations due to their tolerance of several environmental stressors where other trees could not (MacFarlan & Meyer 2005). Ash stands live for more than 50 years, a relatively long time to produce ecosystem services (Kennedy 1990). There is also the human value to consider, which is put on ash species as a commodity and landscape tree (Kennedy 1990). Urban ash loss to EAB has been shown to impact human health as well, urban areas that were infested with EAB had an increase in human mortality related to cardiac and lower respiratory tract illnesses (Donovan et al. 2013). The cost of removal and replacement is high for urban areas, $450-1500 per tree, and many private and public entities do not have the resources for implementation of this process (Kovacs et al. 2010). The loss of ash species may have great effects on ecosystem services.

The effects of EAB may be mitigated as options for management are created. Management with restoration may improve forest community dynamics and a number of different options are currently in development (e.g., EAB-resistant ash trees, pesticides, biological control). Researchers are searching for ash phenotypes that have resistance to

EAB (Koch et al. 2015). EAB egg assays showed that one ash tree was able to kill larvae similar to an EAB-resistant native ash host tree *F. mandschurica* selection, with other local trees obtaining a higher percentage of larval kills or slower larval growth than susceptible controls (Koch et al. 2015). Confirming and breeding EAB resistance in ash is the first step towards restoration with ash hybrids or resistant individuals.

Young ash trees still survive in EAB infested areas and are likely to become infested with EAB as they grow larger. Hypothetically, a lower infestation rate than the previous generations will occur since the next cohort of ash will be infested at a smaller size than the initial cohort. EAB may not have enough resources (ash bark cambium) to increase their population at the same rate and to the same population size as the initial invasion. This doesn't mean that the next wave of EAB population increase will not cause similar devastating effects, but it may take longer to do so, especially given the management and restoration efforts underway. EAB showed a boom and bust cycle in its initial population dynamics (Knight pers comm.), which is typical for invasive species (Williams 1996). Invasive species population information can be used to estimate how catastrophic infestation events may impact the future. Population modeling can provide insight into the recovery and possible effects of future infestations.

The older literature on ash is focused more on harvesting and landscaping, and less on natural populations, germination and younger stages. Based on our extensive searches, we suspect information on seed viability, germination rate and young seedling stage growth rates may have been documented but have not been turned into published material, i.e. inter-agency or horticultural data sets. In future studies forest research on growth should also address survival and fecundity of individuals under varying conditions, such as plantations, urban and natural areas. While a great number of trees are cared for by foresters for future harvesting, knowledge of populations in other locations could help us understand ecosystem services more completely.

References

Auerbach, D.A., Deisenroth, D. B., McShane, R. R., McCluney, K. E., & LeRoy Poff, N. (2014). Beyond the concrete: Accounting for ecosystem services from free-flowing rivers. *Ecosystem Services*, *10*, 1–5. https://doi.org/10.1016/j.ecoser.2014.07.005

Brakie, M. (2013). Plant Guide for green ash (*Fraxinus pennsylvanica*). USDA-Natural Resources Conservation Service, East Texas Plant Materials Center. Nacogdoches, Texas. 75964.

Boerner, Ralph E. J.; Brinkman, Jennifer A. (1996). Ten years of tree seedling establishment and mortality in an Ohio deciduous forest complex. *Bulletin of the Torrey Botanical Club*, *123*(4), 309-317.

Bonner, F. T., & Karrfalt, R. P. (2008). The Woody Plant Seed Manual. USDA FS Agriculture Handbook 727, p. 537-543.

Boyd, I. L., Freer-Smith, P. H., Gilligan, C. A., & Godfray, H. C. J. (2013). The consequence of tree pests and diseases for ecosystem services. *Science (New York, N.Y.)*, *342*(6160), 1235773. https://doi.org/10.1126/science.1235773

Burr, S. J., & McCullough, D. G. (2014). Condition of green ash *(Fraxinus pennsylvanica*) overstory and regeneration at three stages of the emerald ash borer invasion wave. *Canadian Journal of Forest Research*, *44*(7). https://doi.org/10.1139/cjfr-2013-0415

Crocker, S. J., & Meneguzzo, D. M. (2010). Quantifying change in riparian ash forest following the introduction of EAB in MI and IN. In *Joint Meeting of the Forest Inventory and Analysis (FIA) Symposium and the Southern Mensurationists* (pp. 105–107).

Crosthwaite, J. C., Sobek, S., Lyons, D. B., Bernards, M. A., & Sinclair, B. J. (2011). The overwintering physiology of the emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae). *Journal of Insect Physiology*, *57*(1), 166–173. https://doi.org/10.1016/j.jinsphys.2010.11.003

Del Tredici, P. (2001). Sprouting in temperate trees: A morphological and ecological review. *Botanical Review*, *67*(2), 121–140. https://doi.org/10.1007/BF02858075

Dennis, D. F. (1983). An Analysis of Ohio's Forest Resources. Northeast Forest Experiment Station. Broomall, PA, USA p 1-52. (USDA Forest Service Resource Bulletin NE-75).

Donovan, G. H., Butry, D. T., Michael, Y. L., Prestemon, J. P., Liebhold, A. M., Gatziolis, D., & Mao, M. Y. (2013). The relationship between trees and human health: Evidence from the spread of the emerald ash borer. *American Journal of Preventive Medicine*, *44*(2), 139–145. https://doi.org/10.1016/j.amepre.2012.09.066

Duan, J.J., Bauer, L.S., Van Driesche, R.G. (2017). Emerald ash borer biocontrol in ash saplings: The potential for early stage recovery of North American ash trees. *Forest Ecology Management, 394*, 64–72.

Franklin, E.C. (1981). Pollen management handbook. Agricultural Handbook 587. Washington, D. C. U.S. Dep. Agric. p 1-98.

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., … Bengtsson, J. (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications*, *4*, 1340. https://doi.org/10.1038/ncomms2328

Gardiner, E.S., Jacobs, D.F., Overton, R.P., Hernandez, G. (2009). Root-collar diameter and third-year survival of three bottomland hardwoods planted on former agricultural fields in the lower Mississippi Alluvial Valley. In: Dumroese, R.K., Riley, L.E., tech. coords. 2009. National Proceedings: Forest and Conservation Nursery Associations—2008. Proc. RMRS-P-58. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 85–89. Online: http://www.fs.fed.us/ rm/pubs/rmrs_p058.html.

Griffith, D. M. (1993). Forest statistics for Ohio, 1991. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, PA. (USDA Forest Service Resource Bulletin NE-128).

Hausman, C. E., Jaeger, J. F., & Rocha, O. J. (2010). Impacts of the emerald ash borer (EAB) eradication and tree mortality: Potential for a secondary spread of invasive plant species. *Biological Invasions*, *12*(7), 2013–2023. https://doi.org/10.1007/s10530-009-9604-3

Hector, A. & A. Wilby (2009). Biodiversity and Ecosystem Functioning In Levin, S., Carpenter, S., Godfray, H., Kinzig, A., Loreau, M., Losos, J., . . . Morris, C. (Eds.). *The Princeton Guide to Ecology*. Princeton University Press.

Herms, D. A., & McCullough, D. G. (2014). Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. *Annual Review of Entomology*, *59*, 13-30.

Hutchinson, O. K., Morgan, J. T. (1956). Ohio's Forests and Wood-Using Industries. Central States Forest Experiment Station, Columbus, Ohio, 40 p. (USDA Forest Service Survey Release NO. 19).

Johnson, Robert L. (1975). Natural regeneration and development of Nuttall oak and associated species. Southern Forest Experiment Station, New Orleans, La. 12 p. (USDA Forest Service Research Paper SO-104)

Kaandorp, Nardo. (2010 March 7). Green ash in the Stadspark (Standswandelpark). Retrieved 9-17-16 from http://www.monumentaltrees.com/en/trees/fraxinuspennsylvanica/records/.

Kashian, D. M., & Witter, J. A. (2011). Assessing the potential for ash canopy tree replacement via current regeneration following emerald ash borer-caused mortality on southeastern Michigan landscapes. *Forest Ecology and Management, 261*(3), 480–488. http://doi.org/10.1016/j.foreco.2010.10.033

Kennedy, H. E. (1981). Foliar nutrient concentrations and hardwood growth influenced by cultural treatments. *Plant and Soil*, *63*(3), 307–316. https://doi.org/10.1007/BF02370032

Kennedy, H. E., & Krinard, R. M. (1988). Coppice Growth and Development of three Bottomland Hardwoods through four years. (USDA Forest Service). Auburn, AL.

Kennedy, H. E. J. (1990). *Fraxinus pennsylvanica* Marsh. Green Ash. In *Silvics of North America: 2. Hardwoods* (p. 877). Washington, D.C.: Agriculture Handbook 654, U.S. Dept. of Agriculture, Forest Service. Retrieved from https://www.srs.fs.usda.gov/pubs/misc/ag_654/volume_2/fraxinus/pennsylvanica.htm

Kingsley, N. P., & Mayer, C. E. (1970). The Timber Resources of Ohio. Northeastern Forest Experiment Station, Upper Darby, PA. (USDA Forest Service Resource Bulletin NE-19).

Klooster, W. S., Herms, D. A., Knight, K. S., Herms, C. P., McCullough, D. G., Smith, A., … Cardina, J. (2014). Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). *Biological Invasions, 16*(4), 859–873. http://doi.org/10.1007/s10530-013-0543-7

Knight, K.S., Herms, D., Plumb, R., Sawyer, E., Spalink, D., Pisarczyk, E., Wiggin, B., Kappler, R., Menard, K. (2012). Dynamics of surviving ash (*Fraxinus* spp.) populations in areas long infested by emerald ash borer (*Agrilus planipennis*). In: Sniezko, R.A., Yanchuk, A.D., Kliejunas, J.T., Palmieri, K.M., Alexander, J.M., Frankel S.J., tech. coords. Proceedings of the 4th international workshop on the genetics of host-parasite interactions in forestry: disease and insect resistance in forest trees; 2011 July 31-August 5; Eugene, OR. Gen. Tech. Rep. PSW-240. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 143-152.

Knight, K. S., Brown, J. P., & Long, R. P. (2013). Factors affecting the survival of ash (*Fraxinus* spp.) trees infested by emerald ash borer (*Agrilus planipennis*). *Biological Invasions, 15*(2), 371–383.

Knight, K.S.; Flash, B.P.; Kappler, R.H.; Throckmorton, J.A.; Grafton, B.; Flower, C. E. (2014). Monitoring Ash (*Fraxinus* spp.) Decline and Emerald Ash Borer (*Agrilus planipennis*) Symptoms in Infested Areas. United States Department of Agriculture Forest Service General Technical Report NRS-139 Northern Research Station, Delaware, Ohio.

Koch, J. L., Carey, D. W., Mason, M. E., Poland, T. M., & Knight, K. S. (2015). Intraspecific variation in *Fraxinus pennsylvanica* responses to emerald ash borer (*Agrilus planipennis*). *New Forests, 46*(5-6), 995-1011.

Koenig, W. D., Liebhold, A. M., Bonter, D. N., Hochachka, W. M., & Dickinson, J. L. (2013). Effects of the emerald ash borer invasion on four species of birds. *Biological Invasions*, *15*(9), 2095–2103. https://doi.org/10.1007/s10530-013-0435-x

Kolka, Randall K., Trettin, Carl C., Nelson, E.A., Conner, W.H. (1998). Tree seedling establishment across a hydrologic gradient in a bottomland restoration. Proceedings of the twenty fifth annual conference on ecosystems restoration and creation, May 1998, Patrick J. Cannizzaro (ed.)

Kovacs, K. F., Haight, R. G., McCullough, D. G., Mercader, R. J., Siegert, N. W., & Liebhold, A. M. (2010). Cost of potential emerald ash borer damage in U.S. communities, 2009–2019. *Ecological Economics*, *69*(3), 569–578. https://doi.org/10.1016/j.ecolecon.2009.09.004

Krinard, R. M., & Kennedy, H. E. Jr. (1997). Planted Hardwood Development on Clay Soil Without Weed Control Through 16 Years. Southern Forest Experiment Station, New Orleans, LA, USDA Forest Service SO-343, 4p.

Krinard, R. M., & Johnson, R. L. (1981). Flooding, beavers, and hardwood seedling survival. Research Note, Southern Forest Experiment Station, USDA Forest Service, No. SO-270, 6 p.

Krinard, R. M. (1989). Stand Parameters of 11 to 15-year old green ash plantings. USDA Forest Service Research Paper. New Orleans, La. (No. SO-352), 4 p.

Marshall, P. E. (1981). Methods for Stimulating Green Ash. *Tree Planters' Notes*, 9–11.

Matsouki, C. (2018). Emerald Ash Borer detection map by county and year. Retrieved from http://www.emeraldashborer.info/timeline/by_county/index.html

McCullough, D. G., Schneeberger, N. F., Katovich, S. A. (2008) Emerald ash borer pest alert. USDA Forest Service, NA-PR-02-04.

MacFarlane, D. W., & Meyer, S. P. (2005). Characteristics and distribution of potential ash tree hosts for emerald ash borer. *Forest Ecology and Management*, *213*(1-3), 15–24.

Messaoud, Y., & Houle, G. (2006). Spatial patterns of tree seedling establishment and their relationship to environmental variables in a cold-temperate deciduous forest of eastern North America. *Plant Ecology, 185*, 319–331. http://doi.org/10.1007/s11258-006-9106-7

Schmiedel, D., Huth, F., & Wagner, S. (2013). Using data from seed-dispersal modelling to manage invasive tree species: The example of *Fraxinus pennsylvanica* Marshall in Europe. *Environmental Management*, *52*(4), 851–860. http://doi.org/10.1007/s00267-013-0135-4

Schmiedel, D., & Tackenberg, O. (2013). Hydrochory and water induced germination enhance invasion of *Fraxinus pennsylvanica*. *Forest Ecology and Management, 304*, 437–443. http://doi.org/10.1016/j.foreco.2013.04.027

Smith, A. (2006). Effects of Community Structure on Forest Suceptibility and Responce to the Emerald Ash Borer Invasion of the Huron River Watershed in Southeast Michigan. Ohio State University.

Stewart, H. A., & Krajicek, J. E. (1973). Ash, an American wood. American Woods Series FS216. USDA Forest Service. Washington, DC. 7 p.

Widmann, R. H., Balser, D., Barnett, C., Butler, B. J., Griffith, D. M., … Woodall, C. W. (2009). Ohio Forests. Northern Research Station, Newtown Square, PA. USDA Forest Service Resource Bulletin NRS-36.

Widmann, R. H., Randall, C. K., Butler, B. J., Domke, G. M., Griffith, D. M., … Woodall, C. W. (2013). Ohio's Forests 2011. Northern Research Station, Newtown Square, PA. USDA Forest Service Resource Bulletin NRS-90.

Williams, M. (1996). *Biological Invasions*. (pp. 43). Chapman & Hall Publishing.

Wood, K. (2010). Growth Rates of Common Tree Species in Westminster, CO. Colorado State Forest Service, 6p.

Tables

Table 1.1.

The net volume (cubic feet) of living ash (at least 12.5 cm DBH) in Ohio averaged over 2005-2010 and 2011-2016, with the sampling error given in percentage (FIA EVALIDator database).

	2005-2010		2011-2016	
Species	Total	Sampling error %	Total	Sampling error %
F. americana	973060157	6.12	783188019	6.8
F. pennsylvanica	292389755	11.87	200075914	15.51

Figures

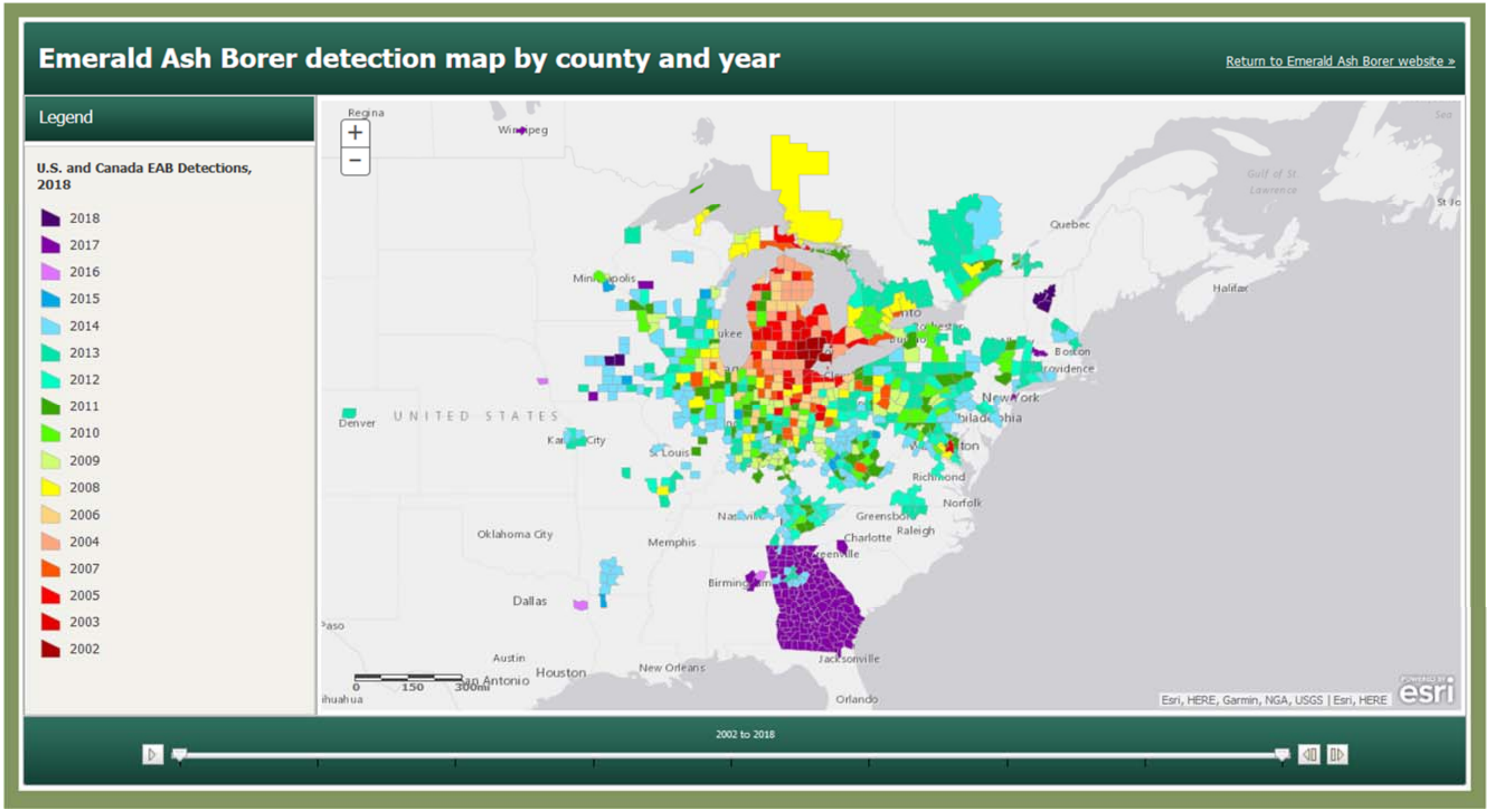


Figure 1.1. Map of EAB detections by county over time (years), replicated with permission, received April 29th, 2018 from

http://www.emeraldashborer.info/timeline/by_county/index.html

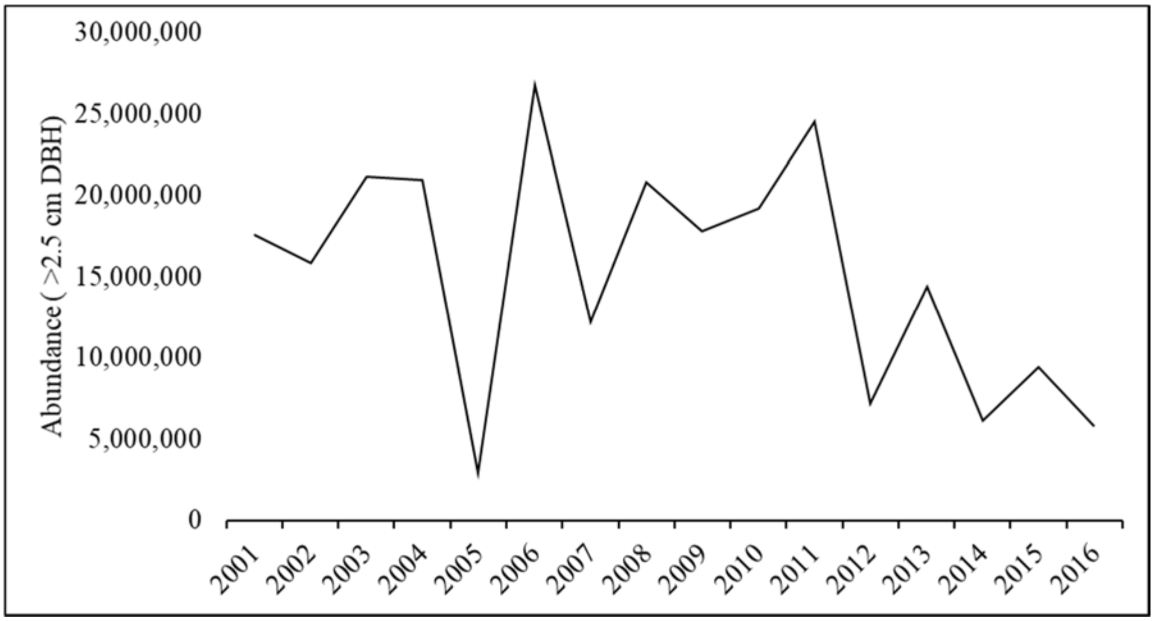


Figure 1.2. The number of green ash (> 2.5 cm DBH) counted in Ohio FIA plots decreased over time, with only 33% of the state population surviving in 2016.

CHAPTER II. EVALUATING THE POPULATION VIABILITY OF GREEN ASH TREES BEFORE AND AFTER THE EMERALD ASH BORER INVASION USING STAGE-BASED MODELS

Abstract

The invasive emerald ash borer beetle (*Agrilus planipennis*, EAB) has caused significant ash tree (*Fraxinus* spp.) mortality and cascading forest changes in the United States. The size and effect of such changes must be understood to plan mitigation and management. We quantitatively estimated the viability of a local green ash tree (*F. pennsylvanica*) population to evaluate the magnitude of change caused by EAB. Stage-based modeling is increasingly used with herbaceous plants, but rarely used for tree species. We developed historic and worst case stochastic stage based population models to explore changes in viability for a natural stand of green ash trees. Historic parameters were based on the literature before 2002, and worst case parameters were based on field data and literature from 2005 - 2008; these dates reflect time periods before and after EAB invaded our focal population in Northwest Ohio, respectively. The worst case model scenario assumed that parameters remained the same as under the initial EAB attack when many of the adult trees died after a few years. The ash population growth rate was estimated as 0.76 and 1.03, respectively, in worst case versus historic scenarios. Under the worst case scenario, ash populations became locally extinct within 41 years. Our results indicated that population changes in the worst case scenario were more sensitive to survival and growth of the < 1 cm diameter at breast height stage class. The worst case scenario trajectory did predict extinction, but caution is warranted given the high variability and stochasticity within the system, and the trajectory can change if human intervention occurs. The historic scenario had a population trajectory that decreased slightly at first, and then remained steady over time, and

under a stable stage distribution there were fewer larger individuals in final abundance estimates. The slight decrease in the population abundance was not unexpected since we included stochasticity in plant survival and reproduction, but it showed that ash tree populations can sustain themselves in forests under favorable conditions. PVA allows us to quickly identify factors that influence the population viability of species, allowing for the development of strategies that prevent further species endangerment.

Introduction

Population parameters can be utilized to build predictive models (Akcakaya et al. 1999) that connect environmental and species interactions to population dynamics (Boyce 1992). Population viability analysis (PVA) is a method that uses a variety of data to quantitatively estimate the population viability of a species and evaluate potential threats with a goal of determining the likelihood of future persistence under a variety of conditions (Akcakaya & Sjorgren-Gulve 2000). This type of method is especially useful in situations where species conservation is time sensitive. A population model can be built using different approaches, including individual based models, structured, unstructured or metapopulation models (Morris & Doak 2002). These approaches relate intrinsic and extrinsic factors to changes in survival, fecundity, and/or dispersal to estimate the population abundance over time (Morris & Doak 2002). The model parameters in a structured population model include abundance, survival, and fecundity at each age or life stage, as well as parameters for known factors that could change survival and fecundity. The parameters of each life stage are used to simulate a change in the population over time through matrix projections (Caswell 2001). Additional supplemental data from longer term studies or from the literature is used to estimate model parameters. For parameters with little or no information available, research methods are utilized to collect parameter estimates or assumptions are made to estimate certain parameters. From building matrix models we can also understand the degree of influence the environment and unknown parameters have on the accuracy of the model projections.

PVA's importance in conservation efforts means it should be adjustable in its design for different species. There are a variety of ways to design PVA models, from simple to complex, depending on data availability and the purpose of the model. Baseline models contain data that are helpful to compare with population outcomes under varying conditions. Models often produce results of minimum viable population size, probability of extinction or population reduction, and population trajectories (Akcakaya & Raphael 1998, Menges 1990, Zeigler et al. 2013). Challenges in developing models for plants include species that have seed/plant dormancy, periodic recruitment, and clonal growth; but benefits include the ability to add stochasticity, spatially explicit populations, and create a range of scenarios (Menges 2000). These benefits allow for increased model reliability and a greater understanding of environmental drivers of population dynamics and stochasticity that influence the population's persistence (Crone et al. 2011). PVA is increasingly used with herbaceous plants but has been rarely used for tree species. Menges (1990) used models to estimate the viability of the endangered Furbish's lousewort (*Pedicularis furbishiae*), by incorporating demographic stochasticity and catastrophes. In a review by Crone et al. (2011), half of all plant PVAs contained research focused on life history and population ecology, while the other half focused on management implications, such as harvested and invasive plants, and impacts of fire and grazing.

There are few viability models developed for tree species; most research is focused on growth models since trees are a harvested resource. For the endangered English Yew tree (*Taxus* *baccata*), models have explored management alternatives to create population viability risk management scenarios that assess which management strategy is most beneficial for species viability (Dhar et al. 2008). In the case of Big-leaf mahogany (*Swietenia macrophylla*), which is listed under the Convention on International Trade in Endangered Species (CITES), an individual based model was developed to examine whether harvesting was detrimental to the population (Grogan et al. 2014). For both trees there is a plethora of data available, yet models were not included in analyses until after species were listed. Non-endangered trees with pests and disease issues, like whitebark pine (*Pinus albicaulis*), are also evaluated with PVA (Jules et al. 2016). Analyses, such as PVA, are especially important to identify critical factors that influence long-term viability of vulnerable species in a timely enough manner to develop strategies that prevent further endangerment.

One such vulnerable species is the green ash tree (*Fraxinus pennsylvanica,* ash). This ash species typically grows in bottomland areas, survives up to 65 years, and is adapted to a variety of areas across the Eastern United States (Kennedy 1990, MacFarlan & Meyer 2005, Stewart & Krajicek 1973). The invasive emerald ash borer beetle (*Agrilus planipennis,* EAB) has caused significant declines for all ash species and precipitated dramatic changes in North American forests. EAB was introduced near Detroit, Michigan, and is a specialist beetle from Asia that feeds and reproduces on *Fraxinus* species (Herms & McCullough 2014). EAB adults feed on ash leaves, while EAB larvae feed on ash cambium underneath the bark. EAB can damage trees at least 2.5 cm DBH (McCullough et al. 2008). We have observed that EAB larvae can kill trees as small as 3 cm in diameter at breast height (DBH). After infestation, nearly 100% mortality of adult ash trees occurs within 6 years (Knight et al. 2013). EAB Michigan floodplain forests infested for at least 5 years had greatly reduced densities of ash seedlings 1-2 years old and under

0.5 m tall, while densities of seedlings 0.5-1 m tall remained the same, and seed banks dwindled to nearly zero (Kashian and Witter 2011, Klooster et al. 2014). During the initial infestation in Southeastern Michigan, ash seedling densities were greater in mesic stands than in hydric stands and were the most common seedling in all stands surveyed (Smith 2006). A survival analysis showed that the rate of mortality increased if the tree was in the mid to lower canopy (intermediate or suppressed) or was found in lower density stands (Knight et al. 2013). Crocker and Meneguzzo (2010) found a 50% reduction in live ash from 2003-2009 EAB evaluations in Indiana. Similar effects are expected throughout the rest of the ash species range, prompting the International Union for Conservation of Nature to apply the critically endangered status to many *Fraxinus* species, including green ash (Westwood et al. 2017).

After EAB has killed the majority of the ash trees in an area, a small number of surviving ash trees may remain. The future dynamics of these remnant populations are key to the persistence of the species. Surviving ash trees were first discovered in the Oak Openings Region of Northwest Ohio, which consisted of mostly green ash, subsequently surviving ash trees were discovered elsewhere in Ohio and Michigan (Knight et al. 2012). The Oak Openings Region is a mixed disturbance landscape containing rare natural ecosystems in a mosaic of small to large remnant habitat patches surrounded by a matrix of agriculture and urban development. Prior to human settlement the area was composed of oak savanna, oak woodland, oak barrens, wet prairie, floodplain forests, and surrounded by the black swamp forest (Brewer and Vankat 2004). The floodplain forest is primarily composed of green ash, maple (*Acer*), elm (*Ulmus*), sycamore (*Platanus*), and cottonwood (*Populus*) species (Knight et al. 2012). This region is a unique biodiversity hotspot (Abella et al. 2004) that is undergoing large changes from EAB invasion. It holds a remnant population of ash trees within its floodplain forests where EAB is still present.

The goal of this study was to compare historic and worst case ash population dynamics. We expected to find that when faced with persistent EAB populations and increased stochastic events, ash populations quickly decreased to extinction. Differences between models allowed us to assess parameters for best and worst case scenarios, and determine which ash life stage was most sensitive to changes.

Methods

We developed stage-based population models for green ash in the Oak Openings Preserve Metropark of Northwest Ohio to compare historic versus worst case (i.e., post-EAB invasion) conditions. The models included ash abundance, survival, and fecundity at multiple life stages, and were developed in RAMAS® Metapop (Setakaut, NY, USA). Each model scenario used a 50-year simulation based on 1 year time intervals with 10,000 replications. We used stage-based models to avoid estimating the age of each individual tree for parameter estimates. Aging trees adds more complexity to the matrix than needed, trees shorter than 1 m tall are difficult to age and larger trees would be damaged, as they need to be cored to examine growth rings.

Fecundity, survival, and the probability of growth to the next stage were needed for the model, with each stage based on ash size (Figure 2.1). Size classes were categorized to assess population demographics of the different life stages. We separated size classes by diameter at breast height (DBH, 1.37 m). Size classes included first year seedlings, trees < 1 cm DBH, 1 - 9.9 cm DBH, 10 - 19.9 cm DBH, and > 20 cm DBH. Size classes included first year seedlings since they tend to have high mortality. Full reproduction capabilities had been noted to start after trees have reached 20 cm DBH (Franklin 1981), and so only those > 20 cm reproduce. The stages 1-9.9 cm and 10-19.9 cm were created for an even distribution of sizes between 1-20 cm.

Seedlings between year two and 1 cm DBH were not separated further as our survival information was similar for separate sizes within that size class.

Ash trees are a sexually dimorphic species, so we utilized a female only model for simplification. As the sex ratio is typically 1:1, males would not significantly change the population trajectory (Franklin 1981, Zhang et al. 2009). Fecundity (F) was estimated as the number of seeds per tree surviving to spring germination that were female. Our best estimate of seeds surviving to germination was found in literature that counted newly emergent ash on the forest floor, which reported the mean number of seedlings per 100 m^2 (Boerner & Brinkman 1996). We assumed this value represented the number of seedlings produced from one female tree. The probability of remaining in a stage was based on yearly survival parameters (P) which were estimated from the literature and 11 years of US Forest Service survey data were used for the worst case scenario model. The probability of growth (G) or transition from one stage to another was based on average growth and ability to survive the number of years needed for growth into the next stage; these data were gathered from the literature and US Forest Service survey data. The vital rates were used to create a Leslie matrix that was multiplied by the number of individuals in each stage at each time step $N_x(t)$ to estimate how many would transition between each stage (Caswell 2001) (Equation 1).

$$\begin{array}{c} \textbf{Abundance} \\ \left\{ \begin{array}{c} N(1) \\ N(2) \\ N(3) \\ N(4) \\ N(5) \end{array} \right\} \end{array} \quad \text{X} \quad \left\{ \begin{array}{ccccc} \begin{array}{c}\textbf{Emergent}\\ \textbf{Seedling}\end{array} & \textbf{S (< 1)} & \begin{array}{c}\textbf{S}\\ \textbf{(1 – 9.9 cm)}\end{array} & \begin{array}{c}\textbf{S}\\ \textbf{(10 – 19.9 cm)}\end{array} & \textbf{S (20+ cm)} \\ 0 & 0 & 0 & 0 & \textbf{F5} \\ \textbf{G1} & \textbf{P2} & 0 & 0 & 0 \\ 0 & \textbf{G2} & \textbf{P3} & 0 & 0 \\ 0 & 0 & \textbf{G3} & \textbf{P4} & 0 \\ 0 & 0 & 0 & \textbf{G4} & \textbf{P5} \end{array} \right\}$$

Equation 1.

We searched the literature for estimates of green ash population demographic parameters throughout time. Relevant search terms (e.g., green ash, survival, fecundity, population dynamics, etc.) were entered in science-based search engines, including Treesearch, a US Forest Service search engine. All estimates were based on research of green ash unless data on a size class were not available. For example, for our largest size class we utilized white ash (*Fraxinus americana*) data since green and white ash can hybridize and there were no specific data on green ash of that size. We used research based documents to complete life stage matrices for PVA models (Table 2.1). For the worst case model, local population demographics were based on literature published from 2005-2008 and previously collected data by the US Forest Service from 2005-2008 (Kathleen Knight, pers communication), which represents the peak of EAB populations and ash mortality in this area. If a survival parameter had more than one estimate the geometric mean and its standard deviation were used for the vital rates in the models (Table 2.2). Emergent seedlings had a probability to grow into the next < 1 cm stage (G1), which was based on emergent seedling first year survival research. We assumed that growth from established seedling to 1.37 m tall would take 5 years (Bonner & Karrfalt 2008, Conner et al. 2000), and with our data on average it took 2 years for trees to grow from 0.1 – 1.0 cm DBH; therefore, in the models' trees stayed in life stage < 1 cm for 7 years. Growth rates into new stages for trees larger than 1 cm DBH were based on average growth of even aged green ash stands from natural silty bottomland flats, which was, on average, 2.5 cm per 4 years (Fitzgerald et al. 1975). Estimates from the literature showed decreases for survival in all size classes in the worst case scenario (Figure 2.2).

Other model elements included initial abundance, initial stage structure, density dependence, and stochasticity. Historic scenario initial abundance was calculated from Knight et al. (2012) for the entire floodplain area, where they estimated 11,894-24,375 ash trees >10 cm DBH within 50 m of Swan Creek. The historic scenario's initial population started with 12,933 female individuals in stable stage distribution based on the stage matrix, with 46% yearlings, 41% seedlings, 12.5% saplings, 0.4% small adults, and 0.01% reproducing adults. Initial abundance of the worst case scenario was kept the same as the historic scenarios, as well as starting with stable stage distribution. The worst case scenario's initial stable stage structure distribution was; 0% yearlings, 79% seedlings (< 1 cm DBH), 21% saplings (1 - 9.9 cm DBH), 0% small adults (10 - 19.9 cm DBH), and 0% were reproducing adults (> 20 cm DBH). A ceiling-type density dependence was included into the model for the entire population. Ceiling density dependence allows the populations to vary independently of the density until it reaches carrying capacity. Carrying capacity was set to 25,000, the maximum surveyed abundance, to examine a realistic trajectory (Knight et al. 2012). Stochasticity was added to the models as both demographic and environmentally related variation. Demographic stochasticity was modeled as the number of survivors from one year to the next sampled from a binomial distribution, and the number of offspring and young sampled from a Poisson distribution (Akcakaya 1991). Demographic stochasticity had a negligible effect on survival since the population abundance was not small, nor did it effect the fecundity distribution since fecundity was largely influenced by the environment rather than individual differences. Environmental stochasticity was modeled as a random sample from a lognormal distribution based on the average vital rates and standard deviation matrix (Akcakaya 1991). In creating a model based on the Oak Openings Preserve ash population, we assumed a closed population.

These model scenarios serve as baseline models, which represent the best (historic) and worst case scenarios applicable to the natural green ash population. Using elasticity analyses we assessed which parameters in the models were most influential when changed, which indicated the size class that had the greatest impact on population growth. Elasticity measures the proportional contribution of each demographic parameter in the model to the growth rate, and all values calculated sum to one (Caswell 2001). Population growth rates, population trajectories, and final abundances for both scenarios were estimated and reported. A Kolmogorov-Smirnov test was used to assess whether extinction risk curves among models were significantly different. We estimated the time to quasi-extinction as when the population fell below 10 individual female trees. Quasi-extinction assumed that once the population of female trees fell below 10 the population would likely become extinct.

Results

In the worst case scenario the ash population elasticities showed that only seedling (< 1 cm DBH) survival contributed to changes that occur in the population growth rate, whereas for the historic model adult (20+ cm DBH) survival contributed the most to the change in population growth rate (Table 2.3). The population growth rate varied from 0.76 – 1.03, respectively, in worst case versus historic scenarios where EAB was present or absent over the next 50 years. Variation in the abundance was higher for the worst case scenario than the historic scenario. There was a significant difference in interval extinction risk between the historic (30.1%) and worst case (99.6%) scenarios ($P < 0.001$, $D = 0.98$), with the difference in minimum tree abundance between the two scenarios equaling 2327. The population abundance steadily declined and was likely to crash under worst case conditions, while the abundance declined until Year 5 then remained relatively stable under historic conditions (Figure 2.2). The population under the worst case scenario had a 99.6% probability of extinction, reaching on average < 1 individual by Year 41 and had a 50% probability of quasi-extinction by Year 19 (Figure 2.3).

Average initial and final stage abundances for the historic scenario were unevenly distributed, with more individuals in smaller size classes. The final historic population had an average of 7888 individuals at Year 50; 55.5% yearlings, 23.6% for < 1 cm, 17.8% for 1-9.9 cm, 2.8% for 10-19.9 cm, and 0.23% for >20 cm DBH.

Discussion

The population models met our expectations, where historic and worst case data predicted opposite trajectories. The worst case trajectory predicted extinction within 50 years, but caution is warranted given the high variability and stochasticity within this system, as seen in the standard deviations around the curves (Figure 2.2). The historic trajectory indicated that natural ash populations performed well, although we did not explicitly account for other potential influences such as plant competition and habitat restrictions beyond what was inherent in the demographic estimates.

In the worst case population scenario EAB continued to have a major effect on tree survivorship over time, and this was the major factor that lead to a quasi-extinction of the population by Year 41. This scenario extrapolated the impact of EAB during high ash mortality to show us a worst case scenario, one in which no human intervention takes place and vital rates remain at peak ash mortality levels.

We hypothesize that current young ash trees will grow up having a lower infestation rate than the previous generation since the future cohort of ash will be infested when they are a smaller size. In contrast, the initial infestation impacted all available ash > 2.5 cm DBH, which allowed for a rapid increase of the EAB population (Knight et al. 2010). Currently, EAB may not have enough food resources (ash leaves and cambium) to increase their population to the same size in the future as they had at the initial peak invasion, especially with local and introduced predators adjusting to their presence (Lyons 2015). This does not mean that the next wave of EAB population increase will not cause similar devastating effects, but it may take longer to do so. EAB showed a boom and bust cycle in its initial population dynamics (Knight et al. unpublished data), which is typical for invasive species (Williams 1996). Invasive species population information can be used to estimate how often catastrophic infestation events may occur in the future, which we plan to incorporate into further model exploration. Future models that include variation in EAB impacts will likely reveal the potential sensitivity to frequency and intensity of invasion, and the vulnerability of ash populations in various stages of recovery.

The historic scenario had a population trajectory that decreased slightly at first, and then remained steady over time. Under stable stage distribution there were fewer larger individuals in final abundance estimates. The slight decrease in the population abundance was not unexpected since we included stochasticity in plant survival and reproduction, but it showed that ash tree populations can sustain themselves in forests under favorable conditions. Historically the floodplain forest was dominated by green ash, American elm, and red maple, but also contained cottonwood, silver maple, black willow, and sycamore (Brewer and Vankat 2004). It currently contains the same dominant species with a severe reduction in American elm due to Dutch elm disease and ash due to EAB (Dennis 1983; Brewer and Vankat 2004).

Literature on ash, and other economically important tree species, are more prevalent than other plant species since humans are interested in them for harvesting and landscaping. Our human interest in ash focuses the research on best greenhouse rearing practices, floodplain restoration with young, and harvesting practices (see Chapter I.). We found less literature focused on natural ash germination, seedlings and the oldest ash stage of growth, especially for historic parameters (see Chapter I.). A lack information on life history parameters limits the predictive power of the PVA from which we may derive an understanding of potential future outcomes and species recovery. We assumed that there were seeds available at the beginning of the worst case scenario based on our observation of seed producing trees in a post-EAB floodplain forest. There was no information about the predation rate or germination rate on these local seeds, so this parameter may vary more than we predicted. Our model scenarios were based on green ash in a floodplain or bottomland habitat and would likely have slightly different outcomes for green ash in other habitat types. These baseline models will allow for comparisons to future models with different possible viability estimates of future ash generations under varying conditions, e.g., continued EAB presence, additional disease or pests, weather extremes, land management changes and habitat limitations on carrying capacity.

Of the utmost importance is understanding what could occur with the EAB invasion over time. EAB has currently been found in many other areas within the Eastern N. America ash tree range. EAB are often found initially in human dominated landscapes but move to natural forested areas easily since they can fly, on average, 2.8 km/day in lab settings (Taylor et al. 2007). Management has continually increased its power to combat EAB, and improvements are still being made (McCullough et al. 2016; Jones et al. 2016). There are multiple Hymenoptera parasitoids that use EAB larvae as hosts for their eggs. *Leluthia astigma, Oobius agrili, Spathius agrili, Spathius galinae,* and *Tetrastichus planipennisi* have been documented parasitoids, of which, all but one, are reared and released to help control EAB populations (Gould et al. 2012). Natural control factors include intraspecific competition, woodpeckers and bark foraging bird predation, and environmental factors that limit EAB dispersal (Fahrner et al. 2015). *B. bassiana* is a fungal species that has been effective in controlling EAB populations (Castrillo et al. 2010).

Human management and natural factors will change the EAB population and thus the impact they have on ash survival.

PVA is very useful for organizing information, assessing vulnerabilities, and addressing specific questions about a species (Akcakaya & Sjorgren-Gulve 2000). Yet plant physiological traits, such as their ability to reproduce clonally and disperse in multiple ways, can limit plant population studies (Menges 2000, Silvertown 1982). These traits make it potentially difficult to identify individuals versus populations. While identifying individuals in our study was possible, challenges in tree models include their long life span, reproductive biology and ability to re-sprout after the original trunk's death. Ash are dioecious, while other trees are often monoecious. We assumed that the proportion of males was equal to females and that this would have no influence on the population growth rate. Further study is needed to account for negative impacts on model parameters from different proportions of males and females.

While plant species population models can be difficult to build, trees can effectively be modeled with a stage structure matrix (Davelos and Jarosz 2004). Models can explore the long term influence of rapid impacts such as pest infestation or harvesting. In harvesting scenarios for Big-leaf mahogany, yields were found to be severely depleted after 2-3, 30 y harvest cycles, and a tree density minimum was reported for sustainability (Grogan et al. 2014). Critical knowledge gaps can be identified with models, and thus shed light on productive research avenues. For example, models of the whitebark pine revealed that pine beetle attacks had larger impacts on population growth than the whitebark pine disease blister rust (Jules et al. 2016). Like ash, whitebark pine populations will improve with better pest management. Management options can be improved by first testing their potential outcomes in population models. In the case of the English yew, many management strategies were modelled to assess their impact on risk of extinction and population viability to then assess which combination of management strategies best improved the yew’s outcome in the next 20 years (Dhar et al. 2008). We will be able to apply our ash results towards future models that assist in adaptive management planning to improve ash community dynamics. This research reveals how natural green ash tree population dynamics change in the face of an invasive pest outbreak and adds to the few population viability analyses developed for tree species.

References

Abella, S. R., Jaeger, J. F., & Brewer, L. G. (2004). Fifteen years of plant community dynamics during a northwest Ohio oak savanna restoration. *The Michigan Botanist*, *43*(2), 117-127.

Akçakaya, H. R. (1991). A method for simulating demographic stochasticity. *Ecological Modelling*, *54*(1–2), 133–136. https://doi.org/10.1016/0304-3800(91)90103-8

Akçakaya, H. R., & Raphael, M. G. (1998). Assessing human impact despite uncertainty: viability of the northern spotted owl metapopulation in the northwestern USA. *Biodiversity and Conservation*, *7*(7), 875–894.

Akçakaya, H.R., Burgman, M.A., & Ginzburg, L.R. (1999). *Applied Population Ecology: Principles and Computer Exercises Using Ramas® EcoLab 2.0.* 2nd ed. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts, 285 p.

Akçakaya, H. R., & Sjögren-Gulve, P. (2000). Population viability analyses in conservation planning: an overview. *Ecological Bulletins*, 9-21.

Barger, J. H., & Davidson, R. H. (1967). A Life history study of the ash seed weevils, *Thysanocnemis bischoffi blatchley* and *T. helvola leconte* (Coleoptera: Curculionidae). *The Ohio Journal of Science*. *67*(2), 123-127.

Boerner, R. E. J., & Brinkman, J. A. (1996). Ten years of tree seedling establishment and mortality in an Ohio deciduous forest complex. *Bulletin of the Torrey Botanical Club*, *123*(4), 309-317.

Bonner, F. T., & Karrfalt, R. P. (2008). The Woody Plant Seed Manual. USDA FS Agriculture Handbook 727, p. 537-543.

Boyce, M.S. (1992) Population Viability Analysis. *Annual Review of Ecological Systems.* 23, 481-06.

Brewer, L. G., & Vankat, J. L. (2004). Description of Vegetation of the Oak Openings of Northwestern Ohio at the Time of Euro-American Settlement 1. *Ohio Journal of Science*, *104*(4), 76–85.

Castrillo, L. A., Bauer, L. S., Liu, H., Griggs, M. H., & Vandenberg, J. D. (2010). Characterization of *Beauveria bassiana* (Ascomycota: Hypocreales) isolates associated with *Agrilus planipennis* (Coleoptera: Buprestidae) populations in Michigan. *Biological Control*, *54*(2), 135–140.

Caswell, H. (2001). *Matrix population models: construction, analysis, and interpretation*. Second Edition, Sinauer Associates, Inc. Sunderland, MA, 01375 USA

Conner, W. H., Inabinette, L. W., & Brantley, E. F. (2000). The use of tree shelters in restoring forest species to a floodplain delta: 5-year results. *Ecological Engineering, 15,* 47-56.

Crocker, S. J., & Meneguzzo, D. M. (2010). Quantifying change in riparian ash forest following the introduction of EAB in MI and IN. In *Joint Meeting of the Forest Inventory and Analysis (FIA) Symposium and the Southern Mensurationists* (p. 105–107).

Crone, E. E., Menges, E. S., Ellis, M. M., Bell, T., Bierzychudek, P., Ehrlén, J., … Williams, J. L. (2011). How do plant ecologists use matrix population models? *Ecology Letters*, *14*(1), 1–8.

Davelos, A. L., & Jarosz, A. M. (2004). Demography of American Chestnut Populations: Effects of a Pathogen and a Hyperparasite. *Journal of Ecology*, *92*(4), 675-685.

Dennis, D. F. (1983). An Analysis of Ohio's Forest Resources. Northeast Forest Experiment Station. Broomall, PA, USA p 1-52. (USDA Forest Service Resource Bulletin NE-75).

Dhar, A., Ruprecht, H., & Vacik, H. (2008). Population viability risk management (PVRM) for in situ management of endangered tree species—A case study on a *Taxus baccata* L. population. *Forest Ecology and Management*, *255*(7), 2835-2845.

Fahrner, S. J., Lelito, J. P., & Aukema, B. H. (2015). The influence of temperature on the flight capacity of emerald ash borer *Agrilus planipennis* and its parasitoid, *Tetrastichus planipennisi*: implications to biological control. *BioControl*, 437–449.

Fitzgerald, C. F., Belanger, R. P., & Lester, W. W. (1975). Characteristics and growth of natural green ash stands. *Journal of Forestry, 73*(8):486-488.

Franklin, E.C. (1981). Pollen management handbook. Agricultural Handbook 587. Washington, D. C. U.S. Dep. Agric. p 1-98.

Gardiner, E.S., Jacobs, D.F., Overton, R.P., & Hernandez, G. (2009). Root-collar diameter and third-year survival of three bottomland hardwoods planted on former agricultural fields in the lower Mississippi Alluvial Valley. In: Dumroese, R.K.; Riley, L.E., tech. coords. 2009. National Proceedings: Forest and Conservation Nursery Associations—2008. Proc. RMRS-P-58. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 85–89.

Gould, J., Bauer, L., Lelito, J., & Duan, J. (2012). Emerald ash borer biological control release and recovery guidelines. United States Department of Agriculture, Forest Service (USDA–APHIS/ARS/FS). Retrieved http://treesearch.fs.fed.us/pubs/40545

Grogan, J., Landis, R. M., Free, C. M., Schulze, M. D., Lentini, M., & Ashton, M. S. (2014). Big-leaf mahogany *Swietenia macrophylla* population dynamics and implications for sustainable management. *Journal of Applied Ecology*, *51*(3), 664–674.

Herms, D. A., & McCullough, D. G. (2014). Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. *Annual Review of Entomology*, *59*, 13-30.

Johnson, R. L. (1975). Natural regeneration and development of Nuttall oak and associated species. South. For. Exp. Stn., New Orleans, La. 12 p. (USDA For. Servo Res. Pap. SO-104).

Jones, B. A., McDermott, S. M., & Chermak, J. M. (2016). PLAN or get SLAM'ed: Optimal management of invasive species in the presence of indirect health externalities. *Journal of Environmental Management, 180*, 538. doi:10.1016/j.jenvman.2016.05.026

Jules, E. S., Jackson, J. I., Van Mantgem, P. J., Beck, J. S., Murray, M. P., & Sahara, E. A. (2016). The relative contributions of disease and insects in the decline of a long-lived tree: a stochastic demographic model of whitebark pine (*Pinus albicaulis*). *Forest Ecology and Management*, *381*, 144–156.

Kashian, D. M., & Witter, J. A. (2011). Assessing the potential for ash canopy tree replacement via current regeneration following emerald ash borer-caused mortality on southeastern Michigan landscapes. *Forest Ecology and Management*, *261*(3), 480–488.

Kennedy, H. E., & Krinard, R. M. (1988). Coppice Growth and Development of three Bottomland Hardwoods through four years. (USDA Forest Service). Auburn, AL.

Kennedy, H. E. J. (1990). *Fraxinus pennsylvanica* Marsh. Green Ash. In *Silvics of North America: 2. Hardwoods* (p. 877). Washington, D.C.: Agriculture Handbook 654, U.S. Dept. of Agriculture, Forest Service. Retrieved from https://www.srs.fs.usda.gov/pubs/misc/ag_654/volume_2/fraxinus/pennsylvanica.htm

Klooster, W. S., Herms, D. A., Knight, K. S., Herms, C. P., McCullough, D. G., Smith, A., … Cardina, J. (2014). Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). *Biological Invasions, 16*(4), 859–873.

Knight, K.S., Herms, D.A., Cardina, J., Long, R.P., Rebbeck, J., Gandhi, K.J.K., Smith, A., Klooster, W.S., & Herms, C.P. (2010). Emerald ash borer aftermath forests: the dynamics of ash mortality and the responses of other plant species. In: Michler, C.H., Ginzel, M. D., eds. Proceedings of symposium on ash in North America. Gen. Tech. Rep. NRS-P-72. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station: 11.

Knight, K.S., Herms, D., Plumb, R., Sawyer, E., Spalink, D., Pisarczyk, E., Wiggin, B., Kappler, R. & Menard, K. (2012). Dynamics of surviving ash (*Fraxinus* spp.) populations in areas long infested by emerald ash borer (*Agrilus planipennis*). In: Sniezko, R.A., Yanchuk, A.D., Kliejunas, J.T., Palmieri, K.M., Alexander, J.M., Frankel S.J., tech. coords. Proceedings of the 4th international workshop on the genetics of host-parasite interactions in forestry: disease and insect resistance in forest trees; 2011 July 31-August 5; Eugene, OR. Gen. Tech. Rep. PSW-240. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 143-152.

Knight, K. S., Brown, J. P., & Long, R. P. (2013). Factors affecting the survival of ash (*Fraxinus* spp.) trees infested by emerald ash borer (*Agrilus planipennis*). *Biological Invasions, 15*(2), 371–383.

Kolka, R. K., Trettin, C. C., Nelson, E.A., & Conner, W.H. (1998). Tree seedling establishment across a hydrologic gradient in a bottomland restoration. Proceedings of the twenty fifth annual conference on ecosystems restoration and creation, May 1998, Patrick J. Cannizzaro (ed.)

Koch, J. L., Carey, D. W., Mason, M. E., Poland, T. M., & Knight, K. S. (2015). Intraspecific variation in *Fraxinus pennsylvanica* responses to emerald ash borer (*Agrilus planipennis*). *New Forests, 46*(5-6), 995-1011.

Krinard, R. M., & Johnson, R. L. (1981). Flooding, beavers, and hardwood seedling survival. Research Note, Southern Forest Experiment Station, USDA Forest Service, No. SO-270, 6.

Krinard, R. M. (1989). Stand Parameters of 11 to 15-year old green ash plantings (No. SO-352). USDA For. Servo Res. Paper. New Orleans, La.

Lyons, D. B. (2015). What's killing the green menace: mortality factors affecting the emerald ash borer (Coleoptera: Buprestidae) in North America? *The Canadian Entomologist*, *147*(3). https://doi.org/10.4039/tce.2014.62

MacFarlane, D. W., & Meyer, S. P. (2005). Characteristics and distribution of potential ash tree hosts for emerald ash borer. *Forest Ecology and Management*, *213*(1-3), 15–24.

Marshall, P. E. (1981). Methods for Stimulating Green Ash. *Tree Planters' Notes*, 9–11.

McCullough, D. G., Schneeberger, N. F., & Katovich, S. A. (2008). Emerald ash borer pest alert. NA-PR-02-04. USDA Forest Service.

McCullough, D. G., Poland, T. M., & Lewis, P. A. (2016). Lethal trap trees: A potential option for emerald ash borer (*Agrilus planipennis* Fairmaire) management. *Pest Management Science*, *72*(5), 1023–1030.

Menges, E. S. (1990). Population viability analysis for an endangered plant. *Conservation Biology*, *4*(1), 52-62.

Menges, E. S. (2000). Population viability analysis in plants: challenges and opportunities. *Tree*, *15*(2), 51-56.

Morris, W. F., & Doak, F. D. (2002). *Quantitative Conservation Biology; Theory and Practice of Population Viability Analysis*. Sunderland, MA: Sinauer Associates, Inc. Publishers.

Schmiedel, D., Huth, F., & Wagner, S. (2013). Using data from seed-dispersal modelling to manage invasive tree species: The example of *Fraxinus pennsylvanica* Marshall in Europe. *Environmental Management*, *52*(4), 851–860.

Schmiedel, D., & Tackenberg, O. (2013). Hydrochory and water induced germination enhance invasion of *Fraxinus pennsylvanica*. *Forest Ecology and Management*, *304*, 437–443.

Silvertown, J. W. (1982). *Introduction to plant population ecology*. Logman Group Limited.

Smith, A. (2006). Effects of Community Structure on Forest Susceptibility and Response to the Emerald Ash Borer Invasion of the Huron River Watershed in Southeast Michigan. (Thesis). Ohio State University, Ohio, USA.

Stewart, H. A., & Krajicek, J. E. (1973). Ash, an American wood. American Woods Series FS216. USDA Forest Service. Washington, DC. 7p.

Taylor, R. A. J., Poland, T. M., Bauer, L. S., Windel, K. N., & Kautz, J. L. (2007). Emerald Ash borer flight estimates revised. In: Mastro, V., Reardon, R., Parra, G. (eds) *Proceedings of the emerald ash borer/Asian longhorned beetle research and technical meeting.* FHTET-2007-04. US Department of Agriculture Forest Service, Forest Health Technology Enterprise Team, Morgantown. 10p.

Van Uytvanck, J., Milotic, T., & Hoffmann, M. (2010). Interaction between large herbivore activities, vegetation structure, and flooding affects tree seedling emergence. *Plant Ecology*, *206*, 173-184.

Westwood, M., Oldfield, S., Jerome, D. & Romero-Severson, J. (2017). *Fraxinus pennsylvanica*. The IUCN Red List of Threatened Species 2017: e.T61918934A61919002. http://dx.doi.org/10.2305/IUCN.UK.2017-2.RLTS.T61918934A61919002.en. (Accessed on October 9, 2017).

Williams, M. (1996). *Biological Invasions*. (pp. 43). Chapman & Hall Publishing.

Zeigler, S. L., Che-Castaldo, J. P., & Neel, M. C. (2013). Actual and Potential Use of Population Viability Analyses in Recovery of Plant Species Listed under the U.S. Endangered Species Act. *Conservation Biology*, *27*(6), 1265–1278.

Zhang, C., Zhao, X., Gao, L., & Gadow, K. (2009). Gender, neighboring competition and habitat effects on the stem growth in dioecious *Fraxinus mandshurica* trees in a northern temperate forest. *Annals of Forest Science*, *66*(8), 812.

Tables

Table 2.1. Details about the historic and worst case models. The model scenarios, parameters, data and standard deviation (S.D.), citations and details about the source.

Model	Parameter	Data Average (S.D.)	Citation	Details
Historic				
	G1	0.04 (NA)	Boerner & Brinkman 1996	Average survival of new seedlings over 1 year
	G1	0.22 (0.4)	Messaoud & Houle 2006	Average new seedling survival from May to Sept.
	P2	0.76 (0.12)	Kappler, R.H. 2018	2015-2017 survival Oak Openings Preserve seedlings < 1 cm
	P3	0.95 (0.0)	Gardiner et al. 2009	Green ash 3rd year survival, floodplain planting
	P3	0.91 (0.12)	Krinard & Johnson 1981	Survival for 3 years after planting
	P3	0.42 (NA)	Kolka et al. 1998	Survival for 3 years of growth, floodplain planting
	P3	0.78 (0.12)	Kennedy & Krinard 1998	Survival of 2 & 4 yr old planted floodplain trees
	P4	0.78 (0.23)	Krinard 1989	Survival, growth, density (tree/acre (planted trees))
	P4	0.76 (0.22)	Kennedy & Krinard 1998	Survival of 16 yr old planted floodplain trees
	P5	0.9 (0.1)	Marchin 2010	Survival of common garden white ash over 30 years
	F5	241 (65)	Boerner & Brinkman 1996	Average new seedling per year over ten years for ash spp.
Worst case				
	G1	0.04 (NA)	Boerner & Brinkman 1996	Average survival of new seedlings over 1 year
	G1	0.22 (0.4)	Messaoud & Houle 2006	Average new seedling survival from May to Sept.
	P2	0.76 (0.12)	Kappler, R.H.	Oak Openings Preserve seedlings < 1 cm 2015-2017 survival
	P3	0.19 (NA)	Kappler, R.H.	Oak Openings Preserve 1-9.9 cm DBH survival in plots
	P4	0.02 (0.02)	Kappler, R.H.	Oak Openings Preserve 10-19.9 cm DBH survival in plots
	P4, P5	0.03 (NA)	Klooster, et al. 2014	Michigan survival post EAB for trees > 2.5 cm DBH
	P5	0.07 (0.05)	Kappler, R.H.	Oak Openings Preserve adult 20+ cm DBH survival in plots
	P5	0.22 (NA)	Smith 2006	Survival, differences in stands and ash species
	F5	241 (65)	Boerner & Brinkman 1996	Average new seedling per year over ten years for ash spp.

Table 2.2. The parameter estimates and their standard deviations for both the historic and worst case scenarios.

Parameter	**Historic Mean**	**Historic S.D.+/-**	**Worst case Mean**	**Worst case S.D.+/-**
G1	0.13	0.45	0.13	0.45
P2	0.76	0.12	0.76	0.12
G2	0.15	0	0.15	0
P3	0.82	0.16	0.19	0.30
G3	0.04	0	1 x 10^-7	0
P4	0.75	0.20	0.025	0.01
G4	0.01	0	1 x 10^-7	0
P5	0.9	0.10	0.10	0.10
F5	241	65	241	65

Table 2.3. The elasticities for the (2.3a) worst case and (2.3b) historic scenarios. Numbers highlighted in bold represent the largest parameter(s) (survival, growth, fecundity), where the higher the number the larger the influence that parameter has on the population trajectory.

2.3a**.** Worst case scenario

	(yearling)	(<*1*)	(1-9.9)	(*10-19.9)*	(>20)
(yearling)	0	0	0	0	0
(<1)	0	**1**	0	0	0
(1-9.9)	0	0	0	0	0
(10-19.9)	0	0	0	0	0
(>20)	0	0	0	0	0

2.3b. Historic Scenario

	(yearling)	(<*1*)	(1-9.9)	(*10-19.9)*	(>20)
(yearling)	0	0	0	0	0.046
(<1)	0.046	0.132	0	0	0
(1-9.9)	0	0.046	0.183	0	0
(10-19.9)	0	0	0.046	0.125	0
(>20)	0	0	0	0.046	**0.329**

Figures

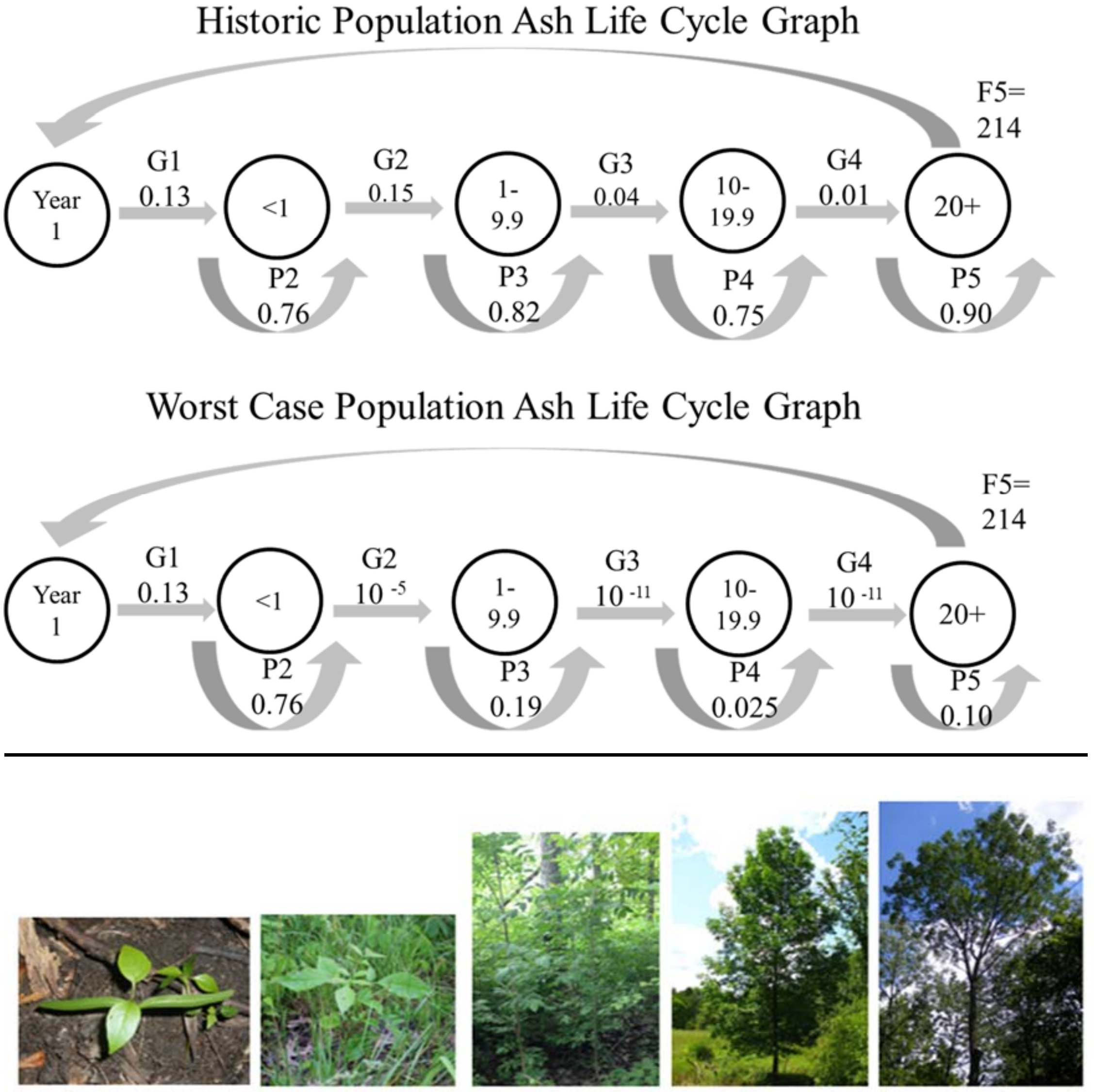


Figure 2.1. The life cycle graphics, based on stages of the green ash tree, for the historic and worst case population scenarios. Each circle represents a life stage based on diameter size at breast height. Transition arrows are probabilities of survival for each stage (P2-P5), and probability of growing into the next stage (G1-G5). F5 represents the fecundity of the adult ash stage. P, G, and F parameters are used to calculate population projections. Below are photographs representing each ash tree life stage.

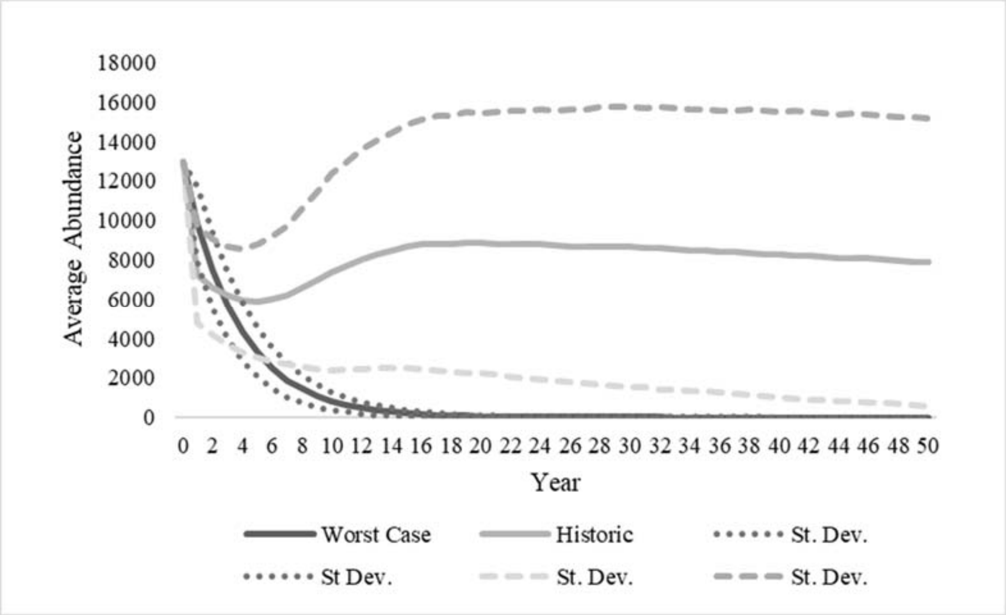


Figure 2.2. The average population abundances and standard deviations (St. Dev.) for the worst case and historic population scenarios. Worst case standard deviations are in dots, while historic standard deviations are dashed.

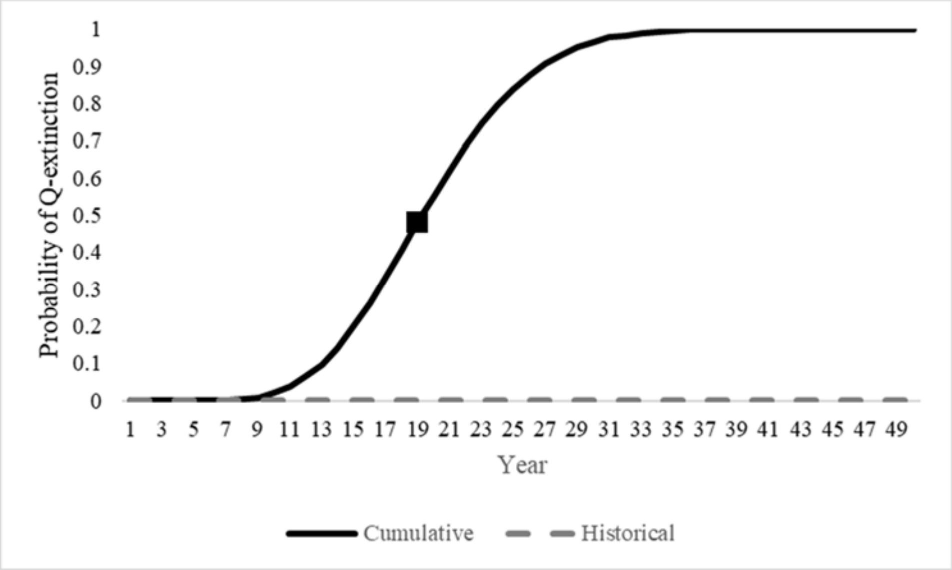


Figure 2.3. The probability that the population of the worst case and historic scenario will fall below 10 individuals (Q-extinction). There is a 50% probability of quasi extinction within 19 years, denoted by the square, and 0% probability for the historic scenario.

CHAPTER III. EXPLORING UNKNOWN DEMOGRAPHIC PARAMETERS OF GREEN ASH TREE EARLY LIFE STAGES

Abstract

There is a lack of available data from natural green ash tree (*Fraxinus pennsylvanica*) populations on regeneration, especially under stress from the emerald ash borer beetle (*Agrilus planipennis*). Such a lack of knowledge on natural regeneration can hamper our understanding of the impact invasive pests have on population dynamics following an outbreak. We monitored younger trees in Northwest Ohio preserves within surviving ash populations to fill this knowledge gap, identifying abundance, survival, growth and environmental factors that increased ash persistence at these small life stages. We also sought to examine the germination rate of our surviving ash focal population at Swan Creek, Swanton, Ohio. This population had 379 ash saplings that were 0.5 cm – 6 cm diameter at breast height, with an average survival rate of 87.5% and average growth of 0.84 cm at their base from 2015-2017. We found more established seedlings in locations with higher amounts of leaf litter within the Swan Creek population. All populations across NW Ohio had a stable average abundance of established seedlings from 2008-2017. The germination rate was little to none (0.05%) for ash trees after their population was impacted by EAB. These results indicated that there was an orphaned cohort of ash that have to survive to reproduction to support population survival since current adults were not producing enough offspring. This type of demographic information can be applied to population models to increase their accuracy.

Introduction

Populations of North American ash (*Fraxinus* spp.) have been affected by an invasive insect, the emerald ash borer beetle (*Agrilus planipennis*, EAB), which has caused escalating depletion of ash in forests where it is one of the dominant species. Any ash trees that were > 10 cm diameter at breast height (DBH) and had survived for at least two years after initial ash mortality reached 95% from EAB are defined as lingering ash; they may either be the last to be infested or have rare phenotypes which increase their resistance to EAB (Koch et al. 2015). Lingering ash trees were first discovered in the Oak Openings Region of Northwest Ohio, which consisted of mostly green ash (*Fraxinus pennsylvanica*), subsequently lingering green ash trees were discovered elsewhere in Ohio and Michigan (Knight et al. 2012).

There is a lack of available data on natural ash tree population regeneration, especially under stress from EAB. This gap in knowledge on natural regeneration can hamper our understanding of the impact invasive pests have on targeted species following an outbreak. Typically, reduction in targeted species survival occurs after an established invasive species has a population outbreak, however invasive species typically follow a boom and bust cycle in their population dynamics (Blackburn et al. 2011, Williams 1996). Emerald ash borer outbreaks start once ash tree resistance has failed, and initial urban outbreaks are only suppressed by density-independent factors, i.e. loss of food source (MacQuarrie and Scharbach 2015), whereas forest outbreaks may be suppressed by density-independent and density-dependent factors. The invasive species boom-bust cycle kills many large trees rapidly and impairs the native population's ability to rebound, especially for trees with low seed production or germination rates, making them more susceptible to future demographic and genetic stochastic changes. This is especially important for plants that do not have a long-lived seed bank. From recent research, ash seed numbers may be very low as there are fewer seeds surviving in the seed bank post EAB infestation (Klooster et al. 2014).

Ash seedling and germination data can be used in a population model with their respective life stage's survival and growth parameters, and their standard deviations applied towards stochasticity to evaluate future viability. In previous population model's young ash stages have been shown to be influential on population growth rate, so changes in the vital rates of these stages will have a disproportionately large impact on the population (Chapter II.). This sensitivity highlights the need for additional data to better estimate these parameters. Additional data will help fill in data gaps and help prioritize areas for future research. In a study on maple *(Acer miyabei),* proportion of viable tree seeds decreased with the reduction in adult trees (Nagamitsu et al. 2014). Tree seed emergence, leaf-out date, and survival changed significantly depending on if leaf litter was present in a multi-taxa analysis of North American species (Fisichelli et al. 2014).

Our objectives were to collect data on the smaller life stages of ash in floodplain forests. To do this we monitored younger trees within the surviving ash populations, estimated abundance and growth and identified environmental factors that increased ash persistence at these small life stages. We predicted environmental factors, such as leaf litter and soil moisture, would influence the long-term health of ash seedlings. We also sought to examine the germination rate of our lingering ash focal population. We expected that there would be a drop in the number of healthy seeds leading to lower abundances and germination rates.

Methods

Study Area

Our focal population was in Northwest Ohio, in the floodplain forest of Swan Creek, located in the Oak Openings Preserve Metropark (Swanton, Ohio, USA). This area has been infested with EAB for at least a decade. It holds a remnant population of green ash trees where EAB is still present in low numbers. It contains adult lingering ash trees that are either the last to be infested or have rare phenotypes which increase their resistance to EAB (Koch et al. 2015). The Oak Openings Region is a mixed disturbance landscape containing rare natural ecosystems in a mosaic of small to large remnant habitat patches surrounded by a matrix of agriculture and urban development. Prior to human settlement the area was composed of oak savanna, oak woodland, oak barrens, wet prairie, floodplain forests, and surrounded by the black swamp forest (Brewer and Vankat 2004). The floodplain forest was primarily composed of green ash, maple (*Acer*), elm (*Ulmus*), sycamore (*Platanus*), and cottonwood (*Populus*) species (Knight et al. 2012). This region is a unique biodiversity hotspot (Abella et al. 2004) that is undergoing large changes from EAB invasion and other anthropogenic influences. It holds a remnant population of ash trees within its floodplain forests where EAB is still present.

Small Ash Survey

Since 2010 the Forest Service (FS) has monitored lingering adult ash tree survivors. All ash trees were marked with silver aluminum tags and GPS locations were recorded. Diameter at breast height (DBH) in cm was recorded, as well as canopy health rating, canopy class (dominant, codominant, intermediate, suppressed), crown ratio (the ratio of crown length to total tree height), presence of flowers or seeds, and signs of EAB. Signs of EAB included bark splitting, EAB exit holes, woodpecker holes, presence of basal and epicormic branching. Number of EAB exit holes and woodpecker holes were counted between 1.25 and 1.75 m height around the trunk of the tree. Canopy health class was categorized from 1-5 based on thinning and dieback; with 1 having a full/healthy canopy, 2 having thinning of leaves but no dieback, 3 having a canopy with < 50% dieback, 4 having a canopy with > 50% dieback, and 5 having no canopy leaves, but epicormic sprouts may be present (Figure 3.1) (Knight et al. 2014, Smith 2006). In addition to the lingering ash tree survey, in summer of 2015 - 2017 we visually surveyed for ash trees that were at least 1.37 m tall within 50 m of the east side of the Swan Creek edge. We summarized the number of individuals found within different size classes, plus survival and growth over time.

Ash Seedlings in Microplots

Since 2005, the FS has been monitoring changes in ash habitat throughout the EAB invasion. These changes were monitored at locations spread across Ohio in natural areas; sites had three plots spaced at least 50 m apart. Each plot was 400 m^2 with 4 m^2 microplots at cardinal directions, 6 m from plot center (Knight et al. 2014). Ash seedlings were counted and recorded for each microplot. Seedlings were categorized as new or established; new ash seedlings still had cotyledons attached to the stalk. To keep track of survival of individuals we flagged seedlings in some microplots and in 2015 we attached an aluminum tree tag with twist ties at the base of each seedling at all microplots in the NW Ohio area. The natural areas surveyed included three sites at Oak Openings Preserve, three sites at Pearson Metropark, three sites at Fallen Timbers Battlefield Metropark, one site at Goll Woods State Nature Preserve, three sites at Maumee Bay State Park, and two sites at Maumee State Forest (Table 3.1). Once ash seedlings were identified by tag number, their height (cm) and base diameter (mm) were recorded. These individuals were surveyed between June – August yearly until 2017. We estimated the average survival and growth of tagged individuals. With information from seedling counts in previous years (2008-2014) we compared yearly site averages of new and established seedlings. A forward stepwise multiple regression was used to examine the relationship between environmental variables measured at each plot over time and with the average number of seedlings (both new and established). Continuous variables were log transformed to adjust for normality. The environmental variables evaluated were number of adult ash per plot, soil hydrology categories (mesic, xeric, hydric) based on presence of spring ephemeral pools and soil condition, and canopy openness at microplots measured with a densitometer.

Seedling Microhabitat Assessment

Five seeding ash trees were selected for placing seedling microhabitat assessment sites. The location of these seeding ash trees was along the outer edge of an oxbow in the creek where there was a portion of the large ash trees for this population that produced seeds. Choosing the seeding ash trees, we assumed that there was a higher chance of finding seedlings in the oxbow area. For each adult seeding tree, one microhabitat site was placed in the floodplain and one was at the edge of the floodplain (Figure 3.2). Floodplain sites were chosen in a random direction 6 m away from the adult seeding tree to remove any direct effects from that tree. Edge of floodplain sites were selected based on the closest location between the seeding tree and the floodplain edge, where elevation increased and habitat started to change from floodplain to upland forest. Edge sites were situated on the initial increasing slope of the soil. Each microhabitat site contained three 1 m^2 plots placed left, right, and center to where data collectors stood. Ash seedlings in these plots were counted and their height measured.

Soil samples were taken once per month in the spring (Feb.-May), approximately 1 m away from each site (10 samples), with the sample containing ~ 237ml (1 cup) of the top 6 cm of soil. These samples were used to find percent soil moisture (grams) via oven drying. A nonparametric Wilcoxon Rank Sum test was performed to assess if there was a difference between the floodplain and the edge of the floodplain.

Sites were visited once every 3-4 weeks to record environmental data. Canopy openness was measured with a densitometer at the center of each site. Pictures were taken of each plot's ground vegetation overlaid with a 1 m^2 grid during each visit to compare vegetation changes over time. For each photo we calculated number of sections in the grid that were leaf litter, bare ground, coarse woody debris, plant vegetation, and seedling vegetation**.** We looked for correlations between sites, differences between edge vs. floodplain, and differences between sites with vs. without ash seedlings. A stepwise logistic regression was used to assess influences on seedling presence.

Ash Germination Experiment

Ash seeds were collected at the end of September with either a pole pruner to trim small branches with seeds to shake off or with a BigShot slingshot to sling a rope over taller branches and shake the branch to remove seeds, with a tarp underneath to catch seeds (Knight et al. 2010). All seeds were kept separate based on parent tree in paper bags at 70°F/21°C in dry storage (~ 20% humidity) until they could be sorted, which may not have an impact on germination in this species (Brakie 2013). Seeds with damage or weevil holes visible to the naked eye were quantified but not selected for the germination experiment. Three parent trees were used for the experiment with seeds placed in outdoor treatments to mimic floodplain environments. Seeds were rehydrated in distilled water for 2-5 days, rinsed with distilled water for 5 minutes before set up in mid-November outdoors at BGSU Environmental Research Center, based on green ash research indicating inundation in water increased germination rate (Schmiedel & Tackenberg

2013). Seeds were kept in a mesh wire bag with an 20 cm diameter base that was pinned into bare ground with wire hooks. A layer of topsoil, (top 2.5 cm) collected from the Swan Creek floodplain, was sifted, then added to each bag. Soil collection sites were > 10 m away from any lingering ash tree to remove any direct effects and were all clay-based soil. In each of the treatments there were 16 bags with a single trees seeds, two trays with a mixed of the three trees seeds, and two trays of a single control tree seeds (green ash controlled cross of an Oak Openings Preserve male ash with a female ash from Chippewa National Forest, Minnesota collected before EAB exposure), and two trays with only soil for a negative control. Each seed tray contained 20 ash seeds placed under a fine layer of soil from the floodplain. Trays were visited once a month to record observations. Ground temperature and lux/canopy openness was recorded by a HOBO monitor (Onset Computer Corp., Bourne, MA, USA) attached to the ground near the seed bags. Secondary weather data was acquired from the Toledo Express Airport National Weather Service records.

A second indoor germination treatment was set up with a separate set (1/3 of the total) collected seeds from the same three trees (360 seeds) and control (40 seeds). Seeds were soaked in distilled water for 2-5 days, rinsed with distilled water for 5 minutes similar to outdoor seeds, then were immediately sown into sphagnum that had been treated with a fungicide (D. Carey, pers comm). Containers were 1 gallon plastic bags that can seal in the moisture added to the sphagnum. They were put into stable conditions with an average temperature of 72° F for 3 months. They were then moved to refrigeration to be kept at 38° F for 3 months. When removed from cooling they were kept moist in the bags under florescent lighting in average temperatures of 75° F, higher than the recommended 68° F due to circumstances out of our control, to germinate (Brakie 2013). Seeds were left intact during the entire process to mimic natural conditions.

Germination date was defined in either treatment as when the first shoot emerged from the seed. Data were recorded for the number of days it took germination to occur and percentage of seeds that germinated. Data were also obtained from the FS on ash seed germination rate of seeds from the same individual trees in their greenhouse conditions.

Results

Small Ash Survey

We found a total of 251 green ash saplings within 50 m of the east side of Swan Creek of size 0.3 – 10 cm DBH. Between 2015 and 2016 there was 98% survival, and from 2016 to 2017 there was 89% survival, leaving 218 individuals, 5 of which grew larger than 10 cm DBH. The average growth for all those who survived from 2015-2017 was 0.85 cm DBH. Most of the saplings found were very healthy and rated a canopy health of 1, but each year a few more individuals showed signs of distress (Table 3.2). Splitting was the most common sign of EAB or other stress on these trees, followed by basal sprouts.

Ash Seedlings in Microplots

In 2017, we had a total of 290 established ash seedlings tagged in microplots across NW Ohio. We started with 379 in 2015; survival from 2015-2016 was 89.7% and survival from 2016-2017 was 85.3%. The average growth in height for all individuals who survived from 2015 - 2017 was 7.6 cm. The average growth in base diameter for individuals who survived from 2015-2017 was 1.08 mm. From 2008 to 2017 in NW Ohio the average number of established seedlings per year was between 20 to 45 individuals with a large range (Figure 3.3). As shown in Figure 3.4, the number of new seedlings over time showed an increase in 2009 when adult ash trees were in a seed mast year (Klooster et al. 2014), but very few new seedlings were found after 2009.

For the forward stepwise multiple regression on the average number of seedlings per plot, the best model had an r^2 of 0.48 and included canopy openness, year, mesic habitat, and sum of adult ash. Listed in Table 3.3 are the model effects, the p-values and coefficients, all model effects were significant ($p < 0.05$). This model indicated that seedling numbers depended on more canopy cover and yearly variation in weather/environment. Sites that were slightly dryer mesic habitat had more seedlings than sites that were hydric or xeric. Ash seedling numbers were higher in areas with more adult ash trees. Mean canopy openness for plots was low overall, 1.19 % ± 3.011 (S.D.). Mean number of adult ash present was 10 ± 8, and there was total of 16 hydric habitats, 15 mesic habitats, and 24 xeric habitats.

Seedling Microhabitat Assessment

Soil moisture readings for these sites along Swan Creek ranged from 13 – 80 % over time (Figure 3.5). March data was not used because several sites were flooded and unreachable. The average soil moisture was significantly different ($p < 0.001$, $r^2 = 18.1$) between the floodplain and the edge of the floodplain by ~10%.

Variables gathered from vegetation pictures were rarely correlated with a few exceptions. Those exceptions included: vegetation and leaf litter were negatively correlated ($p < 0.0001$, $\rho = -0.79$), vegetation and dead wood were negatively correlated ($p < 0.0001$, $\rho = -0.55$), saplings and vegetation were negatively correlated ($p < 0.0001$, $\rho = -0.46$). There was a significant difference between the amount of vegetation in edge and floodplain sites ($p < 0.001$, $r^2 = 59.9$), with more vegetation found in the floodplain. There was a significant difference in total leaf litter between sites with and without ash seedlings ($p < 0.0001$, $r^2 = 9.01$), with more leaf litter in locations with ash seedlings. Our stepwise logistic regression on ash seedling presence ($p < 0.0001$, $r^2 = 0.26$, intercept = -1.75) predicted a positive relationship with leaf litter and dead wood, and a negative relationship with bare ground (Table 3.4).

Ash Germination Experiment

During indoor seed germination, a fungal infection was present in 1 seed bag after it was removed from cold storage, and only 13/130 seeds were recovered but they did not germinate. Seeds from the other three trees also had fungal infections, but much less and the affected seeds were removed from the group. The indoor control group had five seeds germinate after 10 days, 7/40 seeds (17.5%) in total germinated. The only lingering ash tree that had seeds germinate, had 2/77 seeds germinate (0.03%) indoors 20 days after being removed from cold storage. The US Forest Service had similarly low germination rates for these lingering ash seeds, 4/25 and 2/713 germinated (D. Carey, pers. comm.). The Forest Service used similar methods as our indoor treatment, but once removed from cold storage the seeds were put into a flat of soil and cared for in greenhouse conditions.

During the outdoor germination four bags lost seeds (80 seeds total from one tree source) from wind damage in March. No Oak Opening Preserve ash tree seeds germinated in our outdoor conditions. The outdoor control group had the first two seeds germinate on April 4th, with 14/40 total germinated (35%) by the end of April (4-30-17) when the experiment was stopped. HOBO temperature and light monitor recordings had technical issues and only data from 2-9-17 to 5-1-17 was recorded. The daily lux max ranged for February from 38,578 - 82,667 lux, 4,305 - 132,267 lux for March, and 6,544 - 154,312 lux for April. The mean temperature for that time was 10.2º C for February, 6.6º C for March, and 14.6º C for April. The HOBO ground and Toledo Express Airport temperatures had a mean difference of 17 degrees F, with the ground temperature being cooler. The weather from the Toledo Express Airport, OH from September 2016 to May 2017 had no major variations from average, temperature departure from normal was 0 - 4.9 degrees F and precipitation departure from normal was 0.075 - 7.1 cm.

Discussion

Understanding what is happening to the younger generation of ash in the area can assist in understanding the impact invasive pests have on targeted species following an outbreak. This research can also help us understand the possibility of ecological recovery in long-lived plant species. We expected to find that the key to ash seedling survival and germination would consist of a complex arrangement of environmental variables. We found that for abundance of ash seedlings, complex site characteristics were influential. The presence of seedlings was also influenced by local conditions such as increased leaf litter and decreased bare ground. We also found that lingering ash germination was rare (0.03%) and were unable to replicate it in semi-natural conditions.

Ash seedling establishment abundance had a complex model indicating light availability, mesic soil conditions, ash abundance, and time were important (Table 4). Other ash research has also found that ash seedlings are found in areas with mesic soil conditions and more ash basal area (Klooster et al. 2014, Smith 2006). Our seedlings in Swan Creek floodplain had a negative correlation with vegetation, and a positive interaction with leaf litter (Table 3.5). Floodplain inundation allows for the release of C, N, and P from leaf litter, increasing nutrient loads for plant uptake (Baldwin & Mitchell 2000). This would aid seedlings in growth, while un-degraded leaf litter would keep vegetation amounts low by blocking light. Another study of multiple N. American tree taxa found that leaf litter presence delayed seed emergence, leaf-out date, and increased survival (Fisichelli et al. 2014). Leaf litter is not only an important nutrient source for seedlings, but protection from the elements. In an increased CO_2 glasshouse experiment where light and nutrient amounts were altered, ash seedlings were more influenced by nutrient amounts than amount of light (Bazzaz and Miao 1993). Our results correspond with this and had a negative coefficient for canopy openness, leading us to think we may have overlooked soil nutrients, a major driving factor, and their effect on seedling establishment and survival. Future studies should include a more in depth analyses of soil nutrient amounts.

Germination in our study was rare, reduced viable seed production with decreasing adult populations has also occurred in the endangered Japanese maple (*Acer miyabei*), where viable seed proportions per sector ranged from 0.0 - 0.36 in a 700 ha urban-rural mixed area (Nagamitsu et al. 2014). We also see in other cases of pollinating plants that there are pollination limitations for small, fragmented populations, where there are issues with gene flow and pollination reaching its destination (Ghazoul 2005, Young et al. 1993). Ash seed weevils (*Thysanocnemis* spp.) are also a major pest of ash seeds in the Northeast US (Bonner & Karrfalt 2008). It is possible that these issues are influencing the germination rate of ash more than the stress of EAB presence. We cannot be sure as we could not find any literature reporting green ash germination rates in the field. In other germination studies of green ash, percent germination ranged from 30% - 80% depending on the methods used (time inundated in water, stratification or not) (DuBerry 1963, Walls et al. 2005, Bonner & Karrfalt 2008, Taylor 1972).

We expect that the younger ash cohorts will grow large enough to be infected by EAB and they may die before reproduction. EAB demographics at Oak Openings Preserve revealed a drop in numbers over the last five years (Knight et al. unpublished). We expect the number of EAB to remain relatively low with fewer large adult ash left for EAB to infest, and with local and introduced predators adjusting to their presence (Lyons 2015). Numbers of EAB may never get as high as they originally were at the peak of infestation even though EAB are able to pupate from small, non-reproductive ash. However, ash may sustain EAB at low population abundance in this manner for a number of years. As this research illustrates we can assess green ash seedling habitats, survival, and abundances to help us better understand the conditions needed for successful population recovery. Although, we found a lack of published data on young ash trees in scientific literature to help us indicate the size of change that has occurred in the wake of EAB infestations. Identifying the key life history stages and the conditions that foster population persistence will be critical for long-term management and restoration of affected forests.

References

Abella, S. R., Jaeger, J. F., & Brewer, L. G. (2004). Fifteen years of plant community dynamics during a northwest Ohio oak savanna restoration. *The Michigan Botanist*, *43*(2), 117-127.

Bacher, S., Carlton, J. T., Blackburn, T. M., Pys, P., Wilson, J. R. U., Duncan, R. P., & Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology and Evolution*, *26*(7), 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Baldwin, D. S., & Mitchell, A. M. (2000). The effects of drying and re-flooding on the sediment and soil nutrient dynamics of lowland river-floodplain systems: A synthesis. *Regulated Rivers: Restoration Management*, *16*(5), 457–467.

Bazzaz, F. A., & Miao, S. L. (1993). Successional status, seed size, and responses of tree seedlings to CO2, light, and nutrients. *Ecology*, *74*(1), 104-112. https://doi.org/10.2307/1939505

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., … Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology and Evolution*, *26*(7), 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Bonner, F. T., & Karrfalt, R. P. (2008). The Woody Plant Seed Manual. USDA FS Agriculture Handbook 727, 537-543p.

Brakie, M. (2013). Plant Guide for green ash (*Fraxinus pennsylvanica*). USDA-Natural Resources Conservation Service, East Texas Plant Materials Center. Nacogdoches, Texas. 75964.

Brewer, L. G., & Vankat, J. L. (2004). Description of Vegetation of the Oak Openings of Northwestern Ohio at the Time of Euro-American Settlement 1. *Ohio Journal of Science*, *104*(4), 76–85.

DuBarry Jr., A.P. (1963). Germination of bottomland tree seed while immersed in water. *Journal of Forestry, 61*, 225–226.

Fisichelli, N., Wright, A., Rice, K., Mau, A., Buschena, C., & Reich, P. (2014). First-year seedlings and climate change: species specific responses of 15 North American tree species. *Oikos, 123*, 1331-1340.

Ghazoul, J. (2005). Pollen and seed dispersal among dispersed plants. *Biological Review*, *80*, 413–443.

Klooster, W. S., Herms, D. A., Knight, K. S., Herms, C. P., McCullough, D. G., Smith, A., … Cardina, J. (2014). Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). *Biological Invasions, 16*(4), 859–873. http://doi.org/10.1007/s10530-013-0543-7

Knight, K.S., Herms, D., Plumb, R., Sawyer, E., Spalink, D., Pisarczyk, E., Wiggin, B., Kappler, R. & Menard, K. (2012). Dynamics of surviving ash (*Fraxinus* spp.) populations in areas long infested by emerald ash borer (*Agrilus planipennis*). In: Sniezko, R.A., Yanchuk, A.D., Kliejunas, J.T., Palmieri, K.M., Alexander, J.M., Frankel S.J., tech. coords. Proceedings of the 4th international workshop on the genetics of host-parasite interactions in forestry: disease and insect resistance in forest trees; 2011 July 31-August 5; Eugene, OR. Gen. Tech. Rep. PSW-240. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 143-152.

Knight, K. S., Flash, B. P., Kappler, R. H., Throckmorton, J. A., Grafton, B., & Flower, C. E. (2014). Monitoring ash (*Fraxinus* spp.) decline and emerald ash borer (*Agrilus planipennis*) symptoms in infested areas. Gen. Tech. Rep. NRS-139. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 18 p.

Koch, J. L., Carey, D. W., Mason, M. E., Poland, T. M., & Knight, K. S. (2015). Intraspecific variation in *Fraxinus pennsylvanica* responses to emerald ash borer (*Agrilus planipennis*). *New Forests, 46*(5-6), 995–1011. http://doi.org/10.1007/s11056-015-9494-4

Lyons, D. B. (2015). What's killing the green menace: mortality factors affecting the emerald ash borer (Coleoptera: Buprestidae) in North America? *The Canadian Entomologist*, *147*(3). https://doi.org/10.4039/tce.2014.62

Macquarrie, C. J. K., & Scharbach, R. (2015). Influence of mortality factors and host resistance on the population dynamics of emerald ash borer (Coleoptera: Buprestidae) in urban forests. *Environmental Entomology, 44(1),* 160–173. https://doi.org/10.1093/ee/nvu011

Nagamitsu, T., Kikuchi, S., Hotta, M., Kenta, T., & Hiura, T. (2014). Effects of Population Size, Forest Fragmentation, and Urbanization on Seed Production and Gene Flow in an Endangered Maple (*Acer miyabei*). *The American Midland Naturalist*, *172*(2), 303–316. https://doi.org/10.1674/0003-0031-172.2.303

Schmiedel, D., & Tackenberg, O. (2013). Hydrochory and water induced germination enhance invasion of *Fraxinus pennsylvanica*. *Forest Ecology and Management, 304*, 437–443. http://doi.org/10.1016/j.foreco.2013.04.027

Smith, A. (2006). Effects of Community Structure on Forest Susceptibility and Response to the Emerald Ash Borer Invasion of the Huron River Watershed in Southeast Michigan. (Thesis). Ohio State University, Ohio, USA.

Taylor, S.M.O. (1972). Ecological and genetic isolation of *Fraxinus americana* and *Fraxinus pennsylvanica*. University of Michigan, Dissertation.

Walls, R.L., Wardrop, D.H., & Brooks, R.P. (2005). The impact of experimental sedimentation and flooding on the growth and germination of floodplain trees. *Plant Ecology, 176*, 203–213.

Williams, M. (1996). *Biological Invasions*. (pp. 43). Chapman & Hall Publishing.

Young, A. G., H. G. Merriam, & Warwick, S. I. (1993). The effects of forest fragmentation on genetic variation in *Acer saccharum* Marsh. (sugar maple) populations. *Heredity, 71*, 277–289.

Tables

Table 3.1. Locations of ash sampling plot natural areas in Northwest Ohio. Area in hectares (ha) represents the entire property within each entity.

Name	Area (ha)	General Location
Fallen Timbers Battlefield Metropark	75	41.551818, -83.696087
Oak Openings Preserve Metropark	2023	41.565914, -83.853809
Pearson Metropark	252.5	41.640783, -83.438548
Maumee State Forest	1255	41.530746, -83.929126
Goll State Nature Preserve	130	41.553482, -83.361195
Maumee Bay State Park	540.5	41.678434. -83.374441

Table 3.2. The Swan Creek survey of ash saplings by their ash canopy rating over time. The canopy rating of 5 indicates that there is no canopy and they are dead.

Ash Canopy Rating	2015	2016	2017
1	239	203	154
2	12	32	43
3	0	8	11
4	0	3	16
5	0	5	27

Table 3.3. Results from the stepwise multiple regression on NW Ohio ash seedling abundance, (AICc of 120.42, r^2 of 0.48), including the predicted effects, p-value and coefficients.

Effect	**P-value**	**Coefficients**
Canopy Openness	0.0001	-0.85
Year	0.0008	-0.14
Mesic Habitat	0.017	-0.27
Sum of Adult Ash	0.002	0.39

Table 3.4. Stepwise Logistic regression results for seedling presence in Oak Opening Preserve, with explanatory variables representing the total amount of each found within vegetation sampling squares, including p-values and coefficients.

Variable	**P-value**	**Coefficient**
Leaf litter	0.0001	0.15
Dead wood	0.0001	0.16
Bare ground	0.2173	-0.06

Figures

Figure 3.1. The canopy rating scale used to assess the degree of dieback of ash trees in Swan Creek. 1 indicated a healthy canopy; 2 a declining canopy with leaves thinning; 3 a canopy with 25-50% leaf dieback; 4 a canopy with less than 50% leaf cover; 5 is a dead canopy with no leaves.

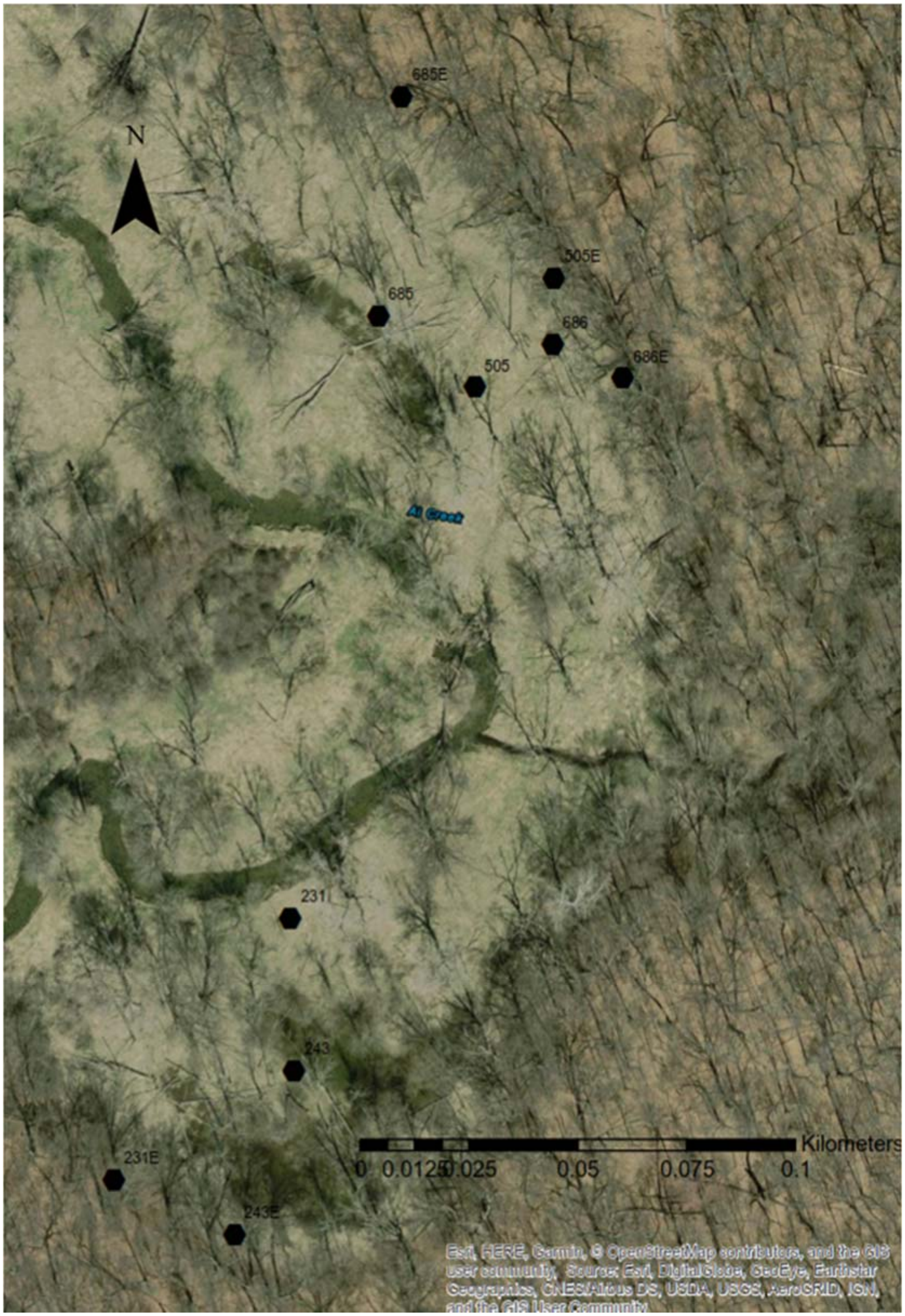


Figure 3.2. Map of Swan Creek layout of microhabitat sites (black dots). Locations ending in an E are edge sites.

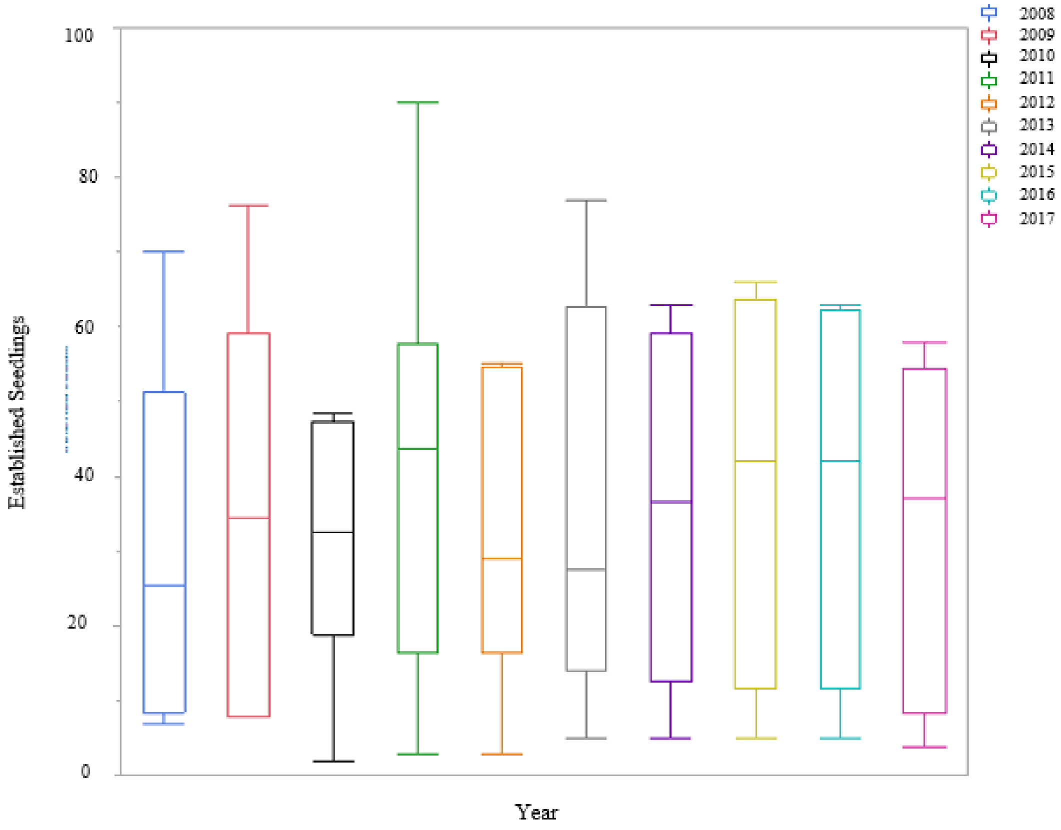


Figure 3.3. Established ash seedlings in NW Ohio sites over time from 2008-2017. Each year is represented as a box plot of the weighted averages.

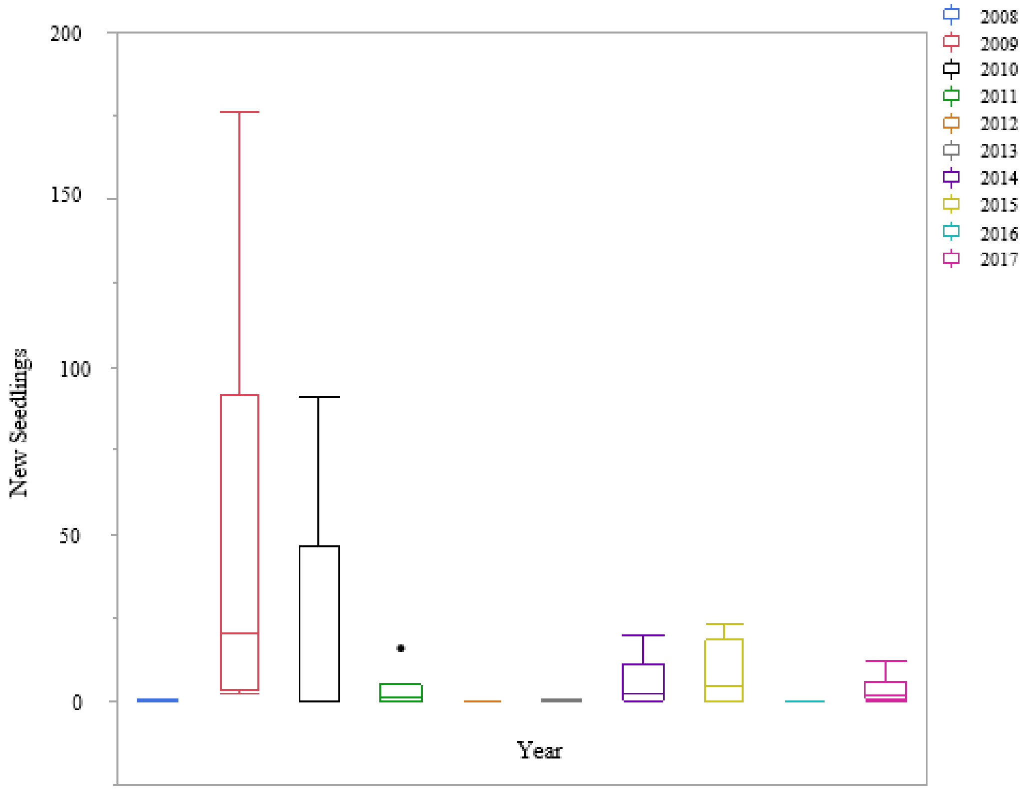


Figure 3.4. New ash seedlings in NW Ohio sites over time from 2008-2017. Each year is represented as a box plot of the weighted averages.

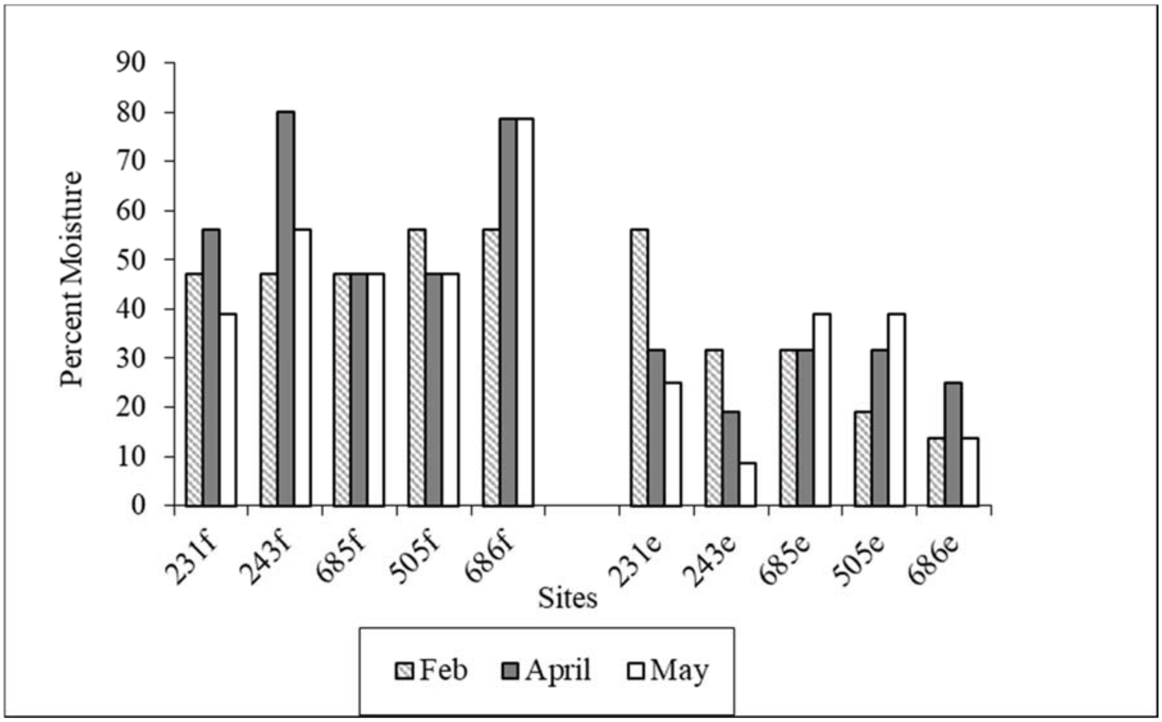


Figure 3.5. The percent soil moisture at microhabitat sites for seedlings over three months in the spring. Site numbers refer to the adult tree associated with the site, f is for floodplain sites, and e is for edge sites.

CHAPTER IV. NEIGHBORING TREE EFFECTS AND SOIL NUTRIENT ASSOCIATIONS WITH SURVIVING GREEN ASH IN AN EMERALD ASH BORER INFESTED FLOODPLAIN FOREST

Abstract

Few ash trees (*Fraxinus spp.*) have survived the initial devastation that emerald ash borer beetle (EAB) (*Agrilus planipennis*) has caused in natural populations. We studied green ash (*Fraxinus planipennis*) trees in a floodplain population after > 90% of ash had died from EAB infestation. We examined the relationship among the canopy health classes of surviving ash trees and their nearest neighboring trees (within 6 m) and available soil nutrients. A subset of focal ash trees was randomly selected within health classes ranging from healthy to recently deceased. Focal trees with the healthiest canopy class had significantly fewer ash neighbors compared to declining health classes. Other species of tree neighbors did not have a significant impact on surviving ash tree canopy health. Soil nutrients in soils immediately surrounding focal trees were compared among health classes. Samples from treeless areas were also used for comparison. There was a significantly greater amount of sulfur (ppm) and phosphorous (mg/kg) in ash tree soil compared to treeless area soil. The relationships between these soil nutrient differences may be from nutrient effects on trees, tree effects on nutrients, or microsite variation in flooded areas. Our data do not directly assess whether these ash trees with healthier canopies have increased resistance to EAB but does indicate that at neighborhood scales in EAB aftermath forests, the surviving ash trees have healthier canopies when separated at least 6 m from other ash trees. This research highlights scale dependent neighborhood composition drivers of tree susceptibility to pests and suggests that drivers during initial infestation differ from drivers in aftermath forests.

Introduction

The impacts made by the loss of tree species to forest pests and diseases highlight the need to understand the drivers of tree susceptibility to these threats. Two potential drivers of tree susceptibility to pests and diseases are tree neighborhood composition and soil nutrient availability. Tree neighborhood composition is influenced by tree interactions, such as competition, facilitation, and spread of pests and diseases. Plant composition is hypothesized to be based on a tradeoff between plants competing at high quality soil nutrient sites and tolerating poor quality soil nutrient sites (Grime 1977). Tree composition can change rapidly with the introduction or increase in tree pests and diseases. Insects that differ in their biology may exhibit different relationships with the density of their host. Some insects have greater impacts on host trees when host density is high, a phenomenon called the Resource Concentration Hypothesis (Root 1973). Others have lower impact at high host density, supporting the Resource Dilution Hypothesis (Otway et al. 2005). Emerald ash borer, (EAB) (*Agrilus planipennis*) has shown patterns in accordance with the resource dilution hypothesis during the initial outbreak; causing more rapid mortality in natural tree stands with low ash densities (Knight et al. 2013). Therefore, tree composition of an area can influence ash survival, and the spatial distribution of ash may be related to the influence of soil nutrient availability and tree composition.

Soil nutrient availability may influence tree survival of pests and diseases. Some have hypothesized that trees fend off and/or survive pests and disease better in resource limited environments because in those conditions plants put more energy into creating chemical defenses (Herms & Mattson 1992). However, research results on effects of soil nutrients on defenses have varied, as the degree of defense trees exhibit can be attributed to multiple factors, both environmental and genetic. Research results from pine weevil (*Hylobius abietis*) studies that added soil nutrients to trees for protection show no difference in pest damage (Wallertz & Petersson 2011) or an increase in pest damage (Zas et al. 2008). In another study, addition of soil nutrients to aspen seedlings showed varying changes in three foliar defense chemicals (Rubert-Nason et al. 2015). Variations in the degree of defense that trees exhibit can be attributed to multiple factors, including both genetic and environmental variation as well as interaction between the two. Unfortunately, tree defenses are usually not adapted to non-native diseases or pests.

The invasive EAB beetle has devastated populations of North American ash species. EAB is a specialist beetle from Asia that feeds and reproduces on all *Fraxinus* species, and was introduced near Detroit, MI (Mcfarlane & Meyer 2005, Herms & McCullough 2014). EAB spreads by flight and had been estimated to have a maximum cumulative flight distance of 9.8 km over a female beetle's life span (Taylor et al. 2010). EAB seeks out ash using both visual and olfactory cues (Poland et al. 2015). EAB scale of dispersal from host trees has been estimated as 100 to 200 m, dependent on ash phloem abundance, indicating that the scale of dispersal may be different in an aftermath forest which contains a different amount of ash phloem abundance (Siegert et al. 2015). There are multiple indicators of EAB damage including development of basal or epicormics sprouts, woodpecker holes, and EAB exit holes; although EAB exit holes are usually the last indicator to be seen on the tree trunk (Herms & McCullough 2014). The damage EAB create usually starts in the upper canopy, and research has shown that ash canopy health is highly indicative of the amount of EAB damage done (Flower et al. 2013).

Green ash (*Fraxinus pennsylvanica*) is a deciduous tree that can grow up to 20 m tall and has small (50 mm x 6 mm) winged seeds that are wind and water dispersed (Brakie 2013). The lifespan of green ash in natural stands averages 65 years (Kennedy 1990). In natural areas, green ash is typically found in bottomland forests, but is adapted to a variety of areas across the Eastern United States (MacFarlane & Meyer 2005, Stewart & Krajicek 1973). This species is tolerant of several environmental stressors including high salinity, flooding, drought, and high alkalinity (MacFarlane & Meyer 2005).

While EAB typically kills most of the mature ash trees in forest settings (Knight et al. 2013), a small number of surviving ash remain. The term lingering ash refers to healthy ash trees with a diameter at breast height (DBH) >10 cm that have survived for at least two years after the initial ash mortality rate reached 95% from EAB. Although some lingering ash trees may simply be the last to be infested, others have been shown to have rare phenotypes that increase their resistance (Koch et al. 2015). Despite the ability of lingering ash to remain healthy longer, they are still vulnerable to infestation by EAB. Lingering ash trees were first identified in the Oak Openings Preserve Metropark of Northwest Ohio and Indian Springs Metropark of Southeast Michigan in 2009 (Knight et al. 2012).

The Oak Openings Region is a mixed disturbance landscape containing natural ecosystems in a mosaic of small to large remnant habitat patches, surrounded by a matrix of agriculture and urban development. Prior to human settlement the area was composed of oak savanna, oak woodland, oak barrens, wet prairie, floodplain forests, and surrounded by black swamp forest (Brewer & Vankat 2004). Composition of Oak Openings Preserve Metropark floodplain includes sections that are considered silver maple - elm - cottonwood forest and maple - ash - elm forest (Faber-Langendoen 2001). Multiple studies have included this ash population in investigations related to EAB (Koch et al. 2015, Flower et al 2013, Knight et al. 2012, Knight et al. 20122013). EAB is still present in the floodplain which contains a remnant cohort of lingering green ash within other smaller size classes of green ash that may not have been infested when the initial infestation occurred. Floodplain forest soil types consist of loam and sandy variations, which was found using the USDA Natural Resource Conservation Service's Web Soil Survey website (https://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx). This region is a biodiversity hotspot that is undergoing large changes from the EAB invasion and other factors.

The objectives of this study were to determine if neighboring tree composition and/or soil nutrient variables differed among ash canopy health classes. Specifically, we compared the effects of ash tree neighbors, other tree species neighbors, and soil nutrients within the A horizon of ash tree root area on ash canopy health. We expected that healthier ash would be in locations with fewer tree competitors in soils with more available limiting nutrients important for growth, such as phosphorus. Investigation of this study site will help us better understand changes in a natural forest after the initial EAB decline in ash trees and may provide insights into potential restoration and land management options that could improve natural ash remnants.

Methods

An ash survey was conducted in the summer yearly from 2010-2017 at the Oak Openings Preserve Metropark Swan Creek floodplain, which is approximately 1.23 km^2 (41" 32-34'N x 83" 50-51'W). For each ash the following data were recorded: DBH (cm), canopy health class, crown ratio (the ratio of crown length to total tree height), presence of flowers or seeds, and signs of EAB. Signs of EAB included bark splitting, EAB exit holes and woodpecker feeding holes on the trunk between 1.25-1.75 cm from the ground, and the presence of basal and epicormic branching. Bark splitting and presence of basal and epicormic branching indicate tree response to stress and damage, while woodpecker holes and EAB holes indicate EAB presence. Woodpecker holes and EAB exit holes higher in the tree may appear earlier in the infestation of the tree but were not visible from the ground and thus were not counted. Therefore, the lack of exit holes or woodpecker holes on the lower trunk does not mean the tree was uninfested. Canopy health class was categorized from 1-5 based on thinning and dieback; with 1 having a full/healthy canopy, 2 having thinning of leaves but no dieback, 3 having a canopy with < 50% dieback, 4 having a canopy with > 50% dieback, and 5 having no canopy leaves, but epicormics sprouts may be present (Knight et al. 2014, Smith 2006).

A subset of focal ash trees was chosen using stratified random sampling of ash trees surveyed in 2016, stratified based on their canopy health class. With trees rated 5, we only kept those most recently deceased (2016) and removed others rated 5. We checked that the selected trees were at least 50 m from each other (checked in ArcGIS with their GPS points) to reduce spatial autocorrelation. When checking for spatial autocorrelation if one tree had to be removed we preferentially kept trees with more years of data. We included up to 10 trees within each canopy health class, but the spatial rule constrained some canopy health class categories to fewer trees. Thus, each ash canopy health class included seven to ten trees (n = 44; class 1 = 9, class 2 = 10, class 3 = 7, class 4 = 10, class 5 = 8).

Distance to nearest living neighbor trees and their species identity was recorded. Nearest neighbor trees were defined as any tree or woody bush over 1.37 m tall within a 6 m radius of the focal ash tree. The neighborhood of each ash tree was set at a radius of 6 m since effects from other trees have been shown to occur at smaller spatial scales (Zhang et al. 2009, Canham et al 2004).

To assess available nutrients, soil samples were taken once during June 2016 at each selected focal ash tree (n = 44). A galvanized 1 inch diameter soil corer was used to collect samples from the first 6 inches of the soil, removing surface organic material. Soil samples taken at each focal ash tree consisted of 4 sub-sampling points found 2 m from the tree trunk at cardinal directions. Soil samples from treeless floodplain sites were taken as a comparison (n = 8). Treeless samples had 4 sub-sampling points at cardinal directions 4 m from the center of an 8 m diameter circular area where no trees were present. The 4 sub-samples from one tree were homogenized in one plastic bag and kept cool till it could later be air dried. The soil corer was cleaned with distilled water and wiped dry after each sample collected. Standard analyses of soils were performed (Brookside Laboratories, New Breman, OH, USA) included: pH in water, base saturation of Cations (%), organic matter (%, based on the loss on ignition method), estimated nitrogen release (#'s N/acre, estimate of amount released annually through organic matter decomposition, based on the loss on ignition method), Bray II phosphorous (mg/kg), and total exchange capacity (meq/100g). Percentage of the following nutrients found on the soils total exchange capacity were analyzed: potassium, calcium, magnesium, sodium, hydrogen, other bases. Mehlich III extractables analyzed included: potassium (mg/kg), phosphorous (mg/kg), calcium (mg/kg), magnesium (mg/kg), sodium (mg/kg), zinc (mg/kg), copper (mg/kg), manganese (mg/kg), iron (mg/kg), aluminum (mg/kg), sulfur (ppm), and boron (mg/kg). The type of soil present at each tree site was identified from Lucas County soil survey data (2003) created by the United States Department of Agriculture, Natural Resources Conservation Service viewed in ArcMap 10.2 (ESRI, Redlands, California, USA).

Data collected was not normally distributed; therefore, we used a nonparametric Wilcoxon rank sum test in JMP (SAS Institute, Cary, NC, USA) to examine the relationship between measured variables and focal ash canopy health classes. These variables were total number of nearest neighbors (all species), number of nearest living ash trees, and select uncorrelated individual soil nutrients. A post-hoc paired Wilcoxon test was performed among ash canopy health classes and significant variables. A Spearman's correlation was used to compare the nutrient variables with each other and those highly correlated ($\rho > 0.70$) with another nutrient were removed. The ones that were removed were chosen because they correlated with estimated nitrogen or phosphorous, which is identified as an important nutrient in the literature. A Spearman's correlation test was also used to assess relationships between the ten select nutrient variables (pH, estimated nitrogen release, sulfur, phosphorous, Brays II phosphorous, sodium, boron, magnesium, copper, aluminum), number of ash neighbors, and total number of neighbors to check for strong correlations. To assess if tree presence alone had any effect on select soil nutrients a Wilcoxon rank sum test was used to compare between ash tree sites and treeless sites. We used a Bonferroni correction for multiple comparisons to establish a cut-off for statistical significance.

Results

In the floodplain forest, the most prominent nearest neighbor tree species found (from most to least numerous) were: green ash, Eastern cottonwood (*Populus deltoides*), boxelder (*Acer negundo*), willow (*Salix spp*.), American elm (*Ulmus americana*), buttonbush (*Cephalantis occidentalis*), hawthorn (*Crataegus sps.*), silver maple (*Acer saccharinum*), and oak (*Quercus spp.)* (Table 4.1). For the neighbor analysis, the highest number of neighbors any one ash tree had in the 6 m radius was seven. Over all the 44 focal trees, 54% of the neighboring trees were green ash.

The distribution of total living ash tree neighbors differed significantly among the ash canopy health classes ($p = 0.02$) (Figure 4.1). Ash with healthier canopies were usually found with no ash neighbors within a 6 m radius, while other ash health classes had on average one or two neighbors. No difference was found when comparing total number of neighboring trees at each ash canopy health class. Total number of neighbors was positively correlated with number of ash neighbors ($\rho = 0.78$, $p < 0.001$).

Focal ash trees were typically 15-25 cm DBH (Table 4.2), much larger than the susceptible size of 2 cm for EAB attack. The number of EAB holes and woodpecker holes generally increased with canopy health classes. Many of the healthy trees exhibited a very large crown ratio averaging 81% for the trees with a canopy health class rating of 1, typical of trees growing in open conditions. Presence of basal sprouts, epicormic sprouts and splitting increased with canopy health classes, although sprouts decreased from category 4 to 5 with the death of the trees.

While the Oak Openings contains sloan loam, udorthents loam, granby loam, Oakville fine sand, Ottokee fine sand, Dixboro fine sand, Tedrow fine sand, the floodplain soil was made up of saturated loam (So) for all the sampled ash trees. No significant correlations were found between canopy health classes and soil nutrients or neighboring tree abundance. The soil samples had relatively neutral pH and only sulfur and phosphorous varied in abundance between treeless sites and ash samples (Table 4.3). Sulfur ($p < 0.0001$) and phosphorous (mg/kg) ($p < 0.0001$) were found to be higher in soil sampled near ash trees compared to treeless sites (Figure 4.2). We also found two general trends in correlations between ash tree soil nutrients and tree neighbor variables. There was a positive correlation between Bray II phosphorous and total number of all neighbors ($\rho = 0.38$, $p = 0.03$), and a negative correlation between copper and number of ash neighbors ($\rho = -0.42$, $p = 0.01$).

Discussion

This study tested the relationship between neighboring tree composition, soil nutrients and canopy health class of ash after peak EAB infestation. We expected that healthier ash would be in locations with fewer tree competitors and more available nutrients important for growth, such as phosphorous. We found that the healthiest ash trees, in ash canopy health class 1, had few or no neighboring ash trees within a 6 m radius (Figure 4.1). Nutrient composition in the floodplain did not differ between ash canopy health classes but differed between ash tree and treeless sites in the amount of phosphorus and sulfur (Figure 4.2). General trends were found between copper and fewer ash neighbors, as well as phosphorous and an increase in all neighbor species. These results suggest that specific tree neighborhood composition in an EAB aftermath forest may drive ash tree susceptibility to pests.

There may be multiple reasons for the difference in phosphorus and sulfur in the soil between ash and treeless sites. Treeless sites could have anoxic conditions for a portion of the year from flooding inundation, these sites were only partially dry when samples were taken. Partial drying of previously inundated sediments will result in increased sediment affinity for phosphorous and may have resulted in the observed reduction in phosphorous at treeless sites (Baldwin & Mitchell 2000). In addition, phosphorus in areas where it is limited can be up to 50% immobilized by microbes, further limiting availability to plants (Cross & Schlesinger 1995). The amount of sulfate adsorption into the soil also increases with the amount of clay content, and sites with higher clay content are more inclined to flood, like our treeless sites (Neller 1959). Organic sulfur has been shown to be highly soluble in adjacent stream slopes, leaving on average < 5% unabsorbed after 24 hours in a mobilization experiment (Dail & Fitzgerald 1999). Trees may not be able to establish at these soil sites as a result of increased soil attachment to nutrients. Ash trees with fewer ash neighbors had slightly more copper in their samples, which is an important micronutrient for photosynthesis, metabolism, and potentially nitrogen fixation (Brady & Weil 2000). Ash with fewer neighbors were shown to have a healthier canopy, but the correlation with copper may not be the driver as variation in copper was small. The differences found in nutrients may be driven by a number of factors. With no difference in soil nutrients (Table 4.3) between the ash canopy health classes, we suspect the differences found may simply be related to whether trees were present or not, and site heterogeneity.

Despite increased likelihood of EAB attacks due to ash neighbor proximity, the impact of these attacks and the degree of tolerance to them could have varied depending on various environmental factors and the specific genotype of each separate lingering ash tree, which would also contribute to variation in the number of trunk exit holes. There were exit holes in all canopy classes except class 1 (Table 4.2). The small number of exit holes indicated trees across most canopy classes are still being attacked but may also reflect the current low level EAB population. It is possible that the number of EAB exit holes on the lower trunk do not reflect the number in the canopy, which were not counted. For example, one study has shown locations for larvae development increased on stems/branches up to 13 cm in diameter and occur at certain bark thickness (1.5 - 5 mm) (Timms et al. 2006). Another study revealed that two mid-canopy branches (sampling two 25 cm sections each) were 18 times more likely to allow detection of low density EAB larvae than a trunk window (25 cm wide by 25% circumference of trunk bark removal above 1.3 m) (Ryall et al. 2011). The number of exit holes may not be representative of the amount of EAB feeding damage within the tree because in lingering ash trees, host defenses may have prevented larvae from becoming adults. Even if a higher proportion of larvae were killed, larval feeding prior to death still caused damage impacting canopy development.

We found that the number of neighboring ash trees was related to ash canopy health (Figure 4.1). One potential explanation for this finding includes intraspecific competition. This floodplain was dominated by ash, leaving less chance for other tree species interactions. Local conspecifics can also have effects on pests or pathogens, with EAB the most likely culprit. According to the resource concentration theory live ash near each other are more likely to encounter EAB (Root 1973). In our case, this theory works in that ash with few or no neighbors are healthier. However, low density ash tree stands, which presumably would have had fewer ash neighbors, died from EAB faster than ash in high density stands, supporting the resource dilution theory (Knight et al. 2013). There are two possible explanations for this discrepancy, which may be interconnected: that the relationship between ash neighbors and ash health is: 1) scale-dependent, with resource concentration theory operating at neighborhood scales and resource dilution theory operating at stand scales or 2) invasion phase dependent, with resource dilution theory operating during the initial invasion of EAB and resource concentration theory operating during the aftermath phase.

There are examples of scale-dependence in tree density and pest density. Observing the neighborhood composition at a small scale surrounding individual ash has revealed a specific distance at which ash experience conspecific interactions. Female and male Asian ash trees (*F. manshurica*) have been shown to have negative effects on same sex ash trees at distances under 10 m, suggesting intrasexual competition in ash at a small spatial scale (Zhang et al. 2009). In insect studies, a honeylocust tree (*Gleditsia tricanthos*) study showed pest susceptibility varied at different scales. Density of honeylocust had effects on three pest species (honeylocust plant bug, honeylocust spider mite, mimosa webworm) abundances at the largest scale (100 m), whereas only one pest (non-native mimosa webworm) had a slightly reduced abundance from increased honeylocust density at the smallest scale (10 m) (Sperry et al. 2001). Scale of response to forest cover by native long horn beetle species had a wide range that varied by species, indicating beetle spatial response should not be assumed based on similar species (Holland et al. 2004).

EAB scale of dispersal from host trees has been shown to be mostly within 100 m, and up to 200 m, dependent on ash phloem abundance (Siegert et al. 2015). These studies show how both tree density and pest density have scale-dependent interactions. Additional studies in multiple spatial scales would be needed to fully understand the scale-dependence of EAB-ash interactions in an aftermath forest.

It is also possible that different processes operate during different phases: the initial phase is characterized by high EAB populations, highly susceptible ash populations, and rapid ash mortality. Although female EAB are efficient at locating healthy green ash, they prefer stressed, but not dying trees (Tanis et al. 2012). During the initial invasion of EAB the majority of ash trees were stressed. The aftermath phase is characterized by low EAB populations, small ash seedlings and saplings, and lingering ash populations that may exhibit various defense mechanisms and levels of resistance to EAB infestation. In an aftermath forest a major selection event has occurred where susceptible trees have been killed by EAB, and the remaining trees are likely to possess genetic variations that may favor their survival of EAB. Research has shown that some lingering ash genotypes (~5 % of the initial ones tested) had some type of measurable defense response including killing a high proportion of larvae and reduced feeding preference by adult EAB (Koch et al. 2015). At the time this study was initiated, the lingering ash trees had survived 3 years longer than when the Koch et al. studies were performed (Koch et al. 2015). During these additional years, some of the ash trees continued to decline and die, so additional selection for trees with defenses against EAB occurred, making it likely that a higher percentage of the surviving trees included in our study have some level of defense against EAB. Therefore, the surviving ash trees in our study may lack cues that attract females to them, thus the mechanism by which EAB females choose to feed and lay eggs may now be more dependent on proximity to ash neighbor trees that have such cues. This also appears to be playing a role in the extended survival reported in blue ash (Tanis et al. 2012). Feeding bioassays have shown blue ash is less preferred by adult beetles than green and white ash (Puraswaran et al. 2009). Recent egg bioassay experiments conducted on mature blue and green ash trees growing in natural forests, found that when eggs were placed directly onto the trees, larvae developed equally well in both species, leading the authors to conclude that extended survival of blue ash was due to adult beetle preference (feeding, oviposition or both) (Peterson et al. 2015). Taken together, these results provide support for the hypothesis that the discrepancy between the results in our current study (that support the resource concentration theory) and the results reported by Knight et al. (2013) that support the resource dilution theory, may be due to an EAB invasion phase dependent relationship between ash health and ash neighbors. Additional studies conducted during these different phases are necessary to further evaluate and confirm this relationship.

Our findings indicated that neighboring conspecific trees have an influence on individual ash tree canopy health. Regardless of the mechanism responsible, this result provides the first suggestion that silvicultural interventions could potentially play a role in ash conservation. For example, thinning other ash trees (perhaps less healthy or smaller trees) around a healthy surviving ash tree may be beneficial. Experimental studies are needed to determine whether this management strategy would have the desired result. This research suggests that consideration of the tree neighborhood can be important for projects seeking tree resistance to forest pests. It also suggests that the remaining ash are different than those in the pre-EAB population, supporting the idea that selection and breeding of these trees to further improve EAB-resistance is important for projects seeking to increase resistance. Continued monitoring and field experiments are needed to better understand the drivers of ash tree survival in EAB aftermath landscapes, to inform management and tree resistance breeding strategies, and to ultimately ensure the future of ash species in natural areas.

References

Baldwin, D. S., Mitchell, A. M. (2000). The effects of drying and re-flooding on the sediment and soil nutrient dynamics of lowland river-floodplain systems: A synthesis. *Regulatory Rivers: Restoration Management*, *16(5),* 457–467.

Brakie, M. (2013). Plant Guide for green ash (*Fraxinus pennsylvanica*). USDA-Natural Resources Conservation Service, East Texas Plant Materials Center. Nacogdoches, Texas. 75964.

Brady, N. C., & Weil, R. R. (1999). Soil phosphorus, potassium, and micronutrients. In: *Elements of the Nature and Properties of Soils*. (pp. 421-422). Upper Saddle River, N.J.: Prentice-Hall.

Brewer, L. G., & Vankat, J. L. (2004). Description of Vegetation of the Oak Openings of Northwestern Ohio at the Time of Euro-American Settlement 1. *Ohio Journal of Science*, *104*(4), 76–85.

Canham, C. D., LePage, P. T., & Coates, K. D. (2004). A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research*, *34*(4), 778–787. https://doi.org/10.1139/x03-232

Cross, A. F., & Schlesinger, W.H. (1995). A literature review and evaluation of the Hedly fractionation: Applications to the biogeochemical cycle of soil phosphorus in natural ecosystems. *Geoderma*, *64*, 197–214.

Dail, D. B., & Fitzgerald, J. W. (1999). S Cycling in soil and stream sediment: Influence of season and in situ concentrations of carbon, nitrogen and sulfur. *Soil Biology and Biochemistry*, *31(10),* 1395–1404.

Faber-Langendoen, D. (2001). Plant Communities of the Midwest. Classification in an Ecological Context. Association for Biodiversity Information. Arlington, VA, p. 5, 40, appendix pp. 172, 180.

Flower, C. E., Knight, K. S., & Gonzalez-Meler, M. A. (2013). Impacts of the emerald ash borer (*Agrilus planipennis* Fairmaire) induced ash (*Fraxinus* spp.) mortality on forest carbon cycling and successional dynamics in the eastern United States. *Biological Invasions*, *15(4),* 931-944.

Grime, J. P. (1977). Evidence for the existence of three primary strategies in plant and its relevance to ecological and evolutionary theory. *American Naturalist*, *111,* 1169–1194.

Herms, D. A., & Mattson, W. J. (1992). The dilemma of plants: to grow or defend. *The Quarterly Review of Biology*, *67(3)*, 283-335.

Herms, D. A., & McCullough, D. G. (2014). Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. *Annual Review of Entomology*, *59*, 13-30.

Holland, J. D., Bert, D. G. & Fahrig, L. (2004). Determining the spatial scale of species response to habitat. *BioScience*, *54(3),* 227-233

Kennedy, H. E. J. (1990). *Fraxinus pennsylvanica* Marsh. Green Ash. In *Silvics of North America: 2. Hardwoods* (pp. 877). Washington, D.C.: Agriculture Handbook 654, U.S. Dept. of Agriculture, Forest Service. Retrieved from https://www.srs.fs.usda.gov/pubs/misc/ag_654/volume_2/fraxinus/pennsylvanica.htm

Knight, K. S., Brown, J. P., & Long, R. P. (2013). Factors affecting the survival of ash (*Fraxinus spp.*) trees infested by emerald ash borer (*Agrilus planipennis*). *Biological Invasions, 15*(2), 371–383.

Knight, K.S.; Flash, B.P.; Kappler, R.H.; Throckmorton, J.A.; Grafton, B.; Flower, C. E. (2014). Monitoring Ash (*Fraxinus* spp.) Decline and Emerald Ash Borer (*Agrilus planipennis*) Symptoms in Infested Areas, United States Department of Agriculture Forest Service General Technical Report NRS-139 Northern Research Station.

Knight, K.S., Herms, D., Plumb, R., Sawyer, E., Spalink, D., Pisarczyk, E., Wiggin, B., Kappler, R. & Menard, K. (2012). Dynamics of surviving ash (*Fraxinus* spp.) populations in areas long infested by emerald ash borer (*Agrilus planipennis*). In: Sniezko, R.A., Yanchuk, A.D., Kliejunas, J.T., Palmieri, K.M., Alexander, J.M., Frankel S.J., tech. coords. Proceedings of the 4th international workshop on the genetics of host-parasite interactions in forestry: disease and insect resistance in forest trees; 2011 July 31-August 5; Eugene, OR. Gen. Tech. Rep. PSW-240. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 143-152.

Koch, J. L., Carey, D. W., Mason, M. E., Poland, T. M., & Knight, K. S. (2015). Intraspecific variation in *Fraxinus pennsylvanica* responses to emerald ash borer (*Agrilus planipennis*). *New Forests, 46*(5-6), 995-1011.

MacFarlane, D. W., & Meyer, S. P. (2005). Characteristics and distribution of potential ash tree hosts for emerald ash borer. *Forest Ecology and Management*, *213*(1-3), 15–24.

Neller, J. R. (1959). Extractable Sulfate-Sulfur in Soils of Florida in Relation to Amount of Clay in the Profile. *Soil Science Society of America Journal, 23(5)*, 346–348.

Otway, S. J., Hector, A. & Lawton, J. H. (2005). Resource dilution effects on specialist herbivores in a grassland biodiversity experiment. *Journal of Animal Ecology*, *74*, 234–240.

Peterson, D., Duan, J. J., Yaninek, J. S., Ginzel, M., & Sadof, C. (2015). Growth of larval *Agrilus planipennis* (Coleoptera: Buprestidae) and fitness of *Tetrastichus planipennisi*

(Hymenoptera: Eulophidae) in blue ash (*Fraxinus quadrangulate)* and green ash (*F. pennsylvanica*), *Environmental Entomology*, *44(6),* 1-10.

Poland, T. M., Chen, Y., Koch, J. & Pureswaran, D. (2015). Review of the emerald ash borer (Coleoptera: Buprestidae), life history, mating behaviours, host plant selection, and host resistance. *Canadian Entomology*, *147(3),* 252-262.

Puraswaran, D. S., & Poland, T. M. (2009). Host selection and feeding preference of *Agrilus planipennis* (Coleoptera: Buprestidae) on ash (*Fraxinus* spp.). *Environmental Entomology, 38*, 757–765.

Root, R. B. (1973). Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monograph, 43*, 95–124.

Rubert-Nason, K. F., Couture, J. J., Major, I.T., Constabel, C. P., & Lindroth, R. L. (2015). Influence of Genotype, environment, and gypsy moth herbivory on local and systemic chemical defenses in trembling aspen (*Populus tremuloides*). *Journal of Chemical Ecology*, *41*, 651-661.

Ryall, K. L., Fidgen, J. G., & Turgeon, J. J. (2011). Detectability of the emerald ash borer (Coleoptera: Buprestidae) in asymptomatic urban trees by using branch samples. *Environmental Entomology*, *40(3),* 679-688.

Siegert, N. W., Mercader, R. J., & McCullough, D. G. (2015). Spread and dispersal of emerald ash borer (Coleoptera: Buprestidae): estimating the spatial dynamics of a difficult-to-detect invasive forest pest. *Canadian Entomologist*, *147*, 338-348.

Smith, A. (2006). Effects of Community Structure on Forest Susceptibility and Response to the Emerald Ash Borer Invasion of the Huron River Watershed in Southeast Michigan. (Thesis). Ohio State University, Ohio, USA.

Sperry, C. E., Chaney, W. R., Shago, G. & Sadof, C. S. (2001). Effects of tree density, tree species diversity and percentage of hardscape on tree insect pests of honeylocust. *Journal of Arachnology*, *27(5),* 263–271.

Stewart, H. A., & Krajicek, J. E. (1973). Ash, an American wood. American Woods Series FS216. USDA Forest Service. Washington, DC. 7 p.

Tanis, S. R., & McCullough, D. G. (2012). Differential persistence of blue ash and white ash following emerald ash borer invasion. *Canadian Journal of Forest Research*, *42*, 1542–1550.

Taylor, R. A. J., Poland, T. M., Bauer, L. S., Windel, K. N., & Kautz, J. L. (2007). Emerald Ash borer flight estimates revised. In: Mastro, V., Reardon, R., Parra, G. (eds) Proceedings of the emerald ash borer/Asian longhorned beetle research and technical meeting. FHTET-2007-04. US Department of Agriculture Forest Service, Forest Health Technology Enterprise Team, Morgantown. P10.

Timms, L. L., Smith, S. M. & DeGroot, P. (2006). Patterns in the within-tree distribution of the emerald ash borer *Agrilus planipennis* (Fairmaire) in young, green-ash plantations of south-western Ontario, Canada. *Agriculture and Forest Entomology, 8*, 313-321.

United States Department of Agriculture Natural Resource Conservation Service Web Soil Survey. (2017). Home Page. Retrieved June 1, 2017, https://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx

Wallertz, K. & Petersson, M. (2011). Pine weevil damage to Norway spruce seedlings: effects of nutrient loading, soil inversion and physical protection during seedling establishment. *Agriculture and Forest Entomology, 13*, 413-421.

Zas, R., Sampredo, L., Moreira, X., & Martíns, P. (2008). Effect of fertilization and genetic variation on susceptibility of *Pinus radiata* seedlings to *Hylobius abietis* damage. *Canadian Journal of Forest Research*, *38*, 63–72.

Zhang, C., Zhao, X., Gao, L., & Gadow, K. (2009). Gender, neighboring competition and habitat effects on the stem growth in dioecious *Fraxinus mandshurica* trees in a northern temperate forest. *Annals of Forest Science*, *66*(8), 812.

Tables

Table 4.1. The total abundance of each neighboring tree species around our sampled ash trees (N = 44, 6 m radius), in order from most to least numerous.

All Neighboring Species	**Total Abundance**
Green Ash	39
Eastern cottonwood	10
Boxelder	10
Hawthorne	4
Spicebush laurel	4
Willow Spp.	1
Maple spp.	1
American elm	1
Black Walnut	1
Oak Spp.	1

Table 4.2. Measured variables for focal ash trees in five canopy health classes, range of values are given as well as average in parenthesis for DBH, number of EAB and woodpecker holes, and crown ratio (%). Basal sprouts, epicromic sprouts, and splitting were presence/absence data, therefore percent of trees with the variable present is reported.

Ash Variable	**Canopy Class 1**	**Canopy Class 2**	**Canopy Class 3**	**Canopy Class 4**	**Canopy Class 5**
DBH (cm)	13.5-30.2 (19.7)	13.0-24.7 (19.5)	14.2-21.3 (16.7)	17.2-26.6 (21.3)	13.5-23.8 (16)
# EAB holes	0	0-7 (0.7)	0-2 (0.67)	0-11 (3.4)	0-9 (2)
# Woodpecker holes	0	0-1 (0.3)	0-11 (4.34)	0-30 (15.8)	6-20 (17.1)
Crown Ratio %	70-90 (81)	65-80 (72.5)	50-70 (58)	10-50 (31)	0
Basal sprouts % present	22	22	83	80	75
Epicormic sprouts % present	22	10	67	90	75
Splitting % present	44	70	100	100	100

Table 4.3. The nutrient amounts in soil samples from treeless sites and ash tree samples (N=52), mean, minimum (min) and maximum (max) are reported. Ash tree soil samples were taken from all health classes, including recently dead individuals. Nutrients denoted with † were used in statistical analyses. Nutrients denoted with * are Mehlich III extractable elements, and ** represents the percent of a given element found on the soils total exchange capacity and are reported as received by the Brookside Laboratory.

	Treeless			Ash		
Nutrient	**Min**	**Mean**	**Max**	**Min**	**Mean**	**Max**
S*† (ppm)	10	13	17	15	28	67
P*† (mg/kg)	19	31	45	18	68	115
Bray II P† (mg/kg)	50	59	81	45	76	127
Cu*† (mg/kg)	3.60	5.75	9.32	3.08	7.05	10.24
Mn*† (mg/kg)	37	49	82	21	58	99
Al*† (mg/kg)	394	482	650	265	470	588
Na† (mg/kg)	16	25	40	25	44	84
Estimated Nitrogen Release† (#'s N/acre)	89	97	107	86	108	126
pH†	7.0	7.4	7.8	6.8	7.6	7.9
B*† (mg/kg)	0.90	1.09	1.27	0.77	1.19	1.67
Total Exchange Capacity (meq/100 g)	12.62	16.96	24.88	14.23	24.73	30.61
Ca** (%)	72.04	77.19	83.1	72.98	81.95	87.66
Other Bases** (%)	3.60	3.99	4.40	3.50	3.83	4.60
H** (%)	0	0	0	0	0.07	3
K** (%)	0.92	1.23	1.51	0.64	1.17	1.61
Mg** (%)	11.69	16.96	22.05	7.14	12.21	20.12
Na** (%)	0.47	0.62	0.80	0.55	0.77	1.30
Ca* (mg/kg)	1900	2636	4135	2239	4059	5065
K* (mg/kg)	56	82	128	38	115	170
Fe* (mg/kg)	225	284	357	199	355	484
Mg* (mg/kg)	273	335	421	152	359	585
Zn* (mg/kg)	5.28	6.51	8.89	6.21	10.51	16.00
Organic Matter (%)	3.90	4.83	6.32	3.61	6.67	11.65

Figures

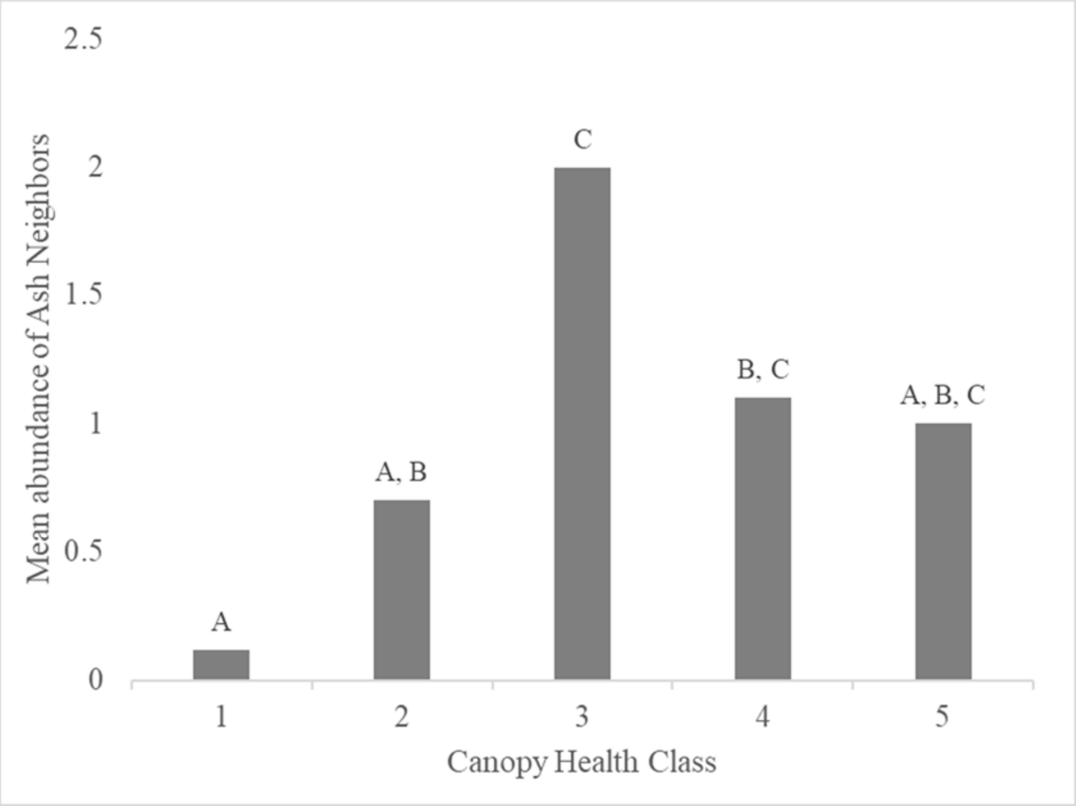
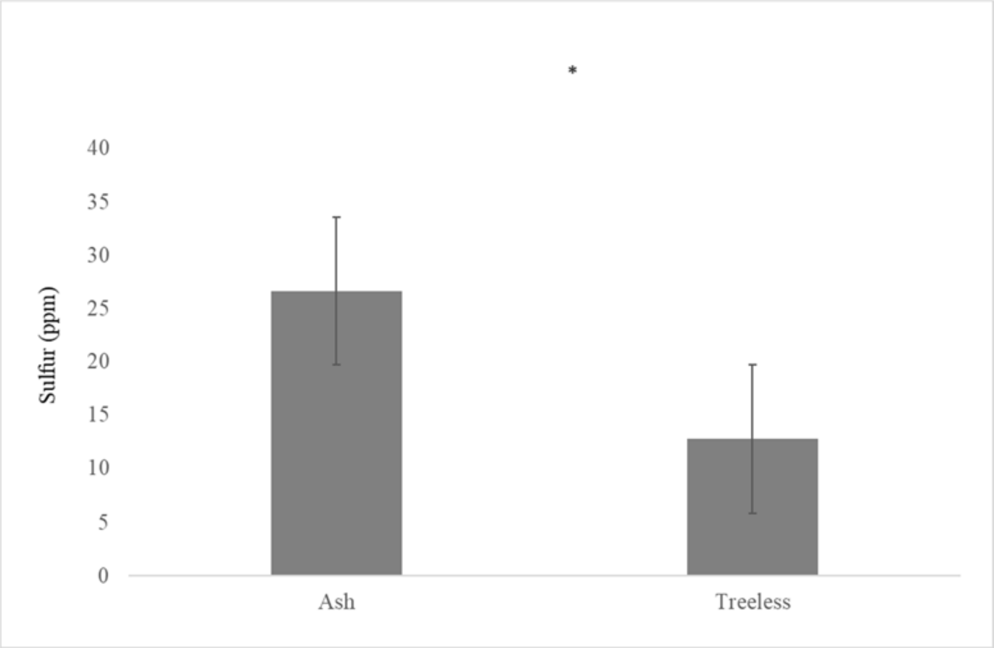
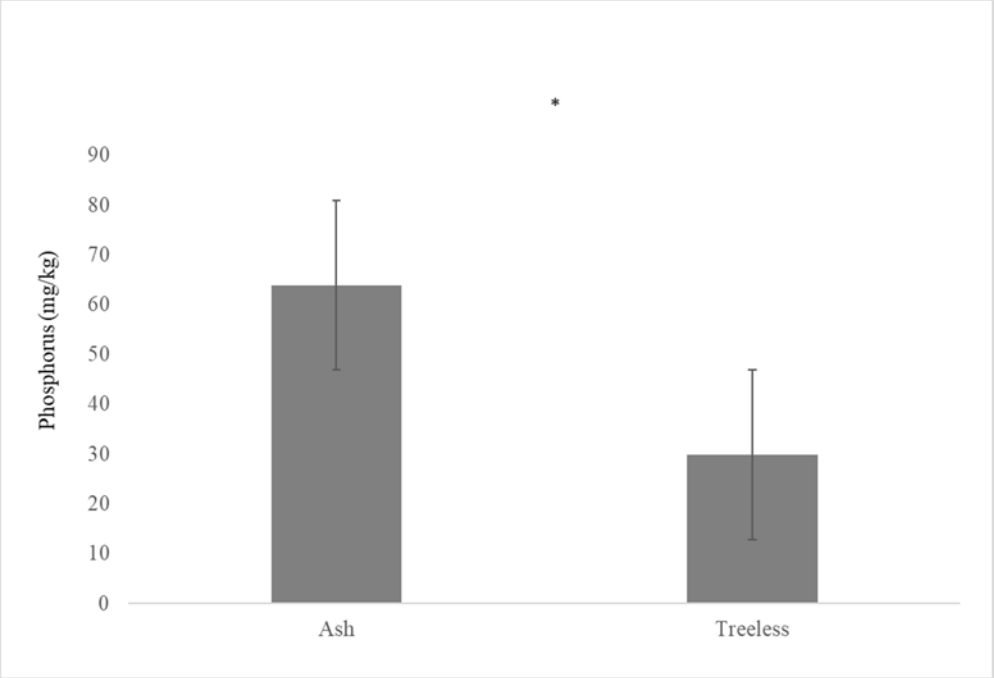


Figure 4.1. The mean number of ash neighbors per ash canopy health class within 6 m. Letters denote statistically significant differences between canopy condition classes in post-hoc tests. Ash canopy health class ratings are 1-5, where 1 is a full healthy crown to class 5 which is a dead crown.



A.



B.

Figure 4.2. Differences in soil sulfur and phosphorus between ash tree soil samples and treeless soil samples were found to be significantly different ($p < 0.0001$) for: (a) Sulfur (ppm) and; (b) Phosphorus (mg/kg).

CHAPTER V. GREEN ASH POPULATION MODELS WITH EMERALD ASH BORER MANAGEMENT SCENARIOS FOR A FLOODPLAIN FOREST

Abstract

Management actions have been improving over time in response to the invasive emerald ash borer beetle (*Agrilus planipennis*, EAB). There are multiple strategies to remove EAB from an area and improve tree persistence, but most work has focused on the urban environment. Adaptive management is important in this situation as new information is gathered on this invasion crisis. Here we extrapolate changes that could occur in a Northwest Ohio floodplain population of green ash (*Fraxinus pennsylvanica*) after EAB peak mortality occurred (2010-2017). Models were created to examine baseline conditions and catastrophe conditions where EAB populations had an increasing probability over ten years to reach levels that highly impacted ash forests. The catastrophe model also had EAB impacts reduced gradually over the following 9 years. We explored potential management scenarios that included, 1) the reduction of future EAB induced mortality events through introduced parasitic wasps; 2) increased survival and growth for large trees by removal of ash competitors; 3) increased survival for only one size class using management protection; and 4) restoration by planting EAB-resistant ash trees. Scenarios were compared to assess if outcomes were significantly different. Results indicated that scenarios 1 and 2 were an improvement for the population, reducing probability of extinction and decline. Scenario 3 did improve population abundances over time, but only when increasing survival for adults and seedlings. Scenario 4 allowed for a partial population recovery. These scenarios contained assumptions on how the population would react to management treatments, but we aimed for conservative models. The models also showed how important size class 1-9.9 cm diameter at breast height was to the persistence of future populations. Our PVA

has revealed potential outcomes of alternative management practices and can increase our understanding of ash populations remaining after EAB introduction.

Introduction

Populations of North American ash (*Fraxinus* spp.) have been affected by an invasive insect, the emerald ash borer beetle (*Agrilus planipennis*, EAB), which has caused escalating depletion of ash in forests where it is one of the dominant species. EAB was first discovered in the Detroit, MI area and was imported via wood crates from Asia. The beetle is known to feed and reproduce on all species of ash, which ultimately leads to their death (Herms and McCullough 2014). The entire EAB life cycle is carried out on ash trees, where adult female EAB deposit eggs within the bark of an ash tree. Upon hatching the pupae tunnel in and feed on the phloem layer of the tree, creating galleries. This continues until the pupae become larger larvae, which means additional consumption of the phloem layer until they emerge as adults. Adult EAB leave D-shaped exit holes in the tree upon maturation. Adult EAB eat ash foliage, find mates on ash trees, and respond to ash volatile cues (Herms & McCullough 2014). In areas where adult ash died off, our continued data collection reveals that EAB are still present feeding off of younger trees, though in fewer numbers.

Ash species range within the Eastern United States and Canada, and green ash has adapted to live in multiple habitats, as it is able to tolerate a variety of environmental stressors, e.g., high salinity, flooding, drought, and high alkalinity (Kennedy 1990, MacFarlan & Meyer 2005, Stewart & Krajicek 1973). As of 2010, the damage EAB has caused to ash has cost the US 10.7 billion dollars (Kovacs et al. 2010). The estimated cost of removal, replacement, or treatment of about 38 million ash trees in urban and residential settings across 25 states, however, is projected to be around 25 billion dollars (Gould et al. 2012). Costs vary from state to state, depending on ash abundance and selected management options for urban and natural areas. For costs, land managers can use the PURDUE calculator, which provides projected expenses based on input of factors like management plans, the number and size of existing ash trees, rough estimates of removing and insecticide treatment of affected trees based on size and estimates of replacement costs (http://int.entm.purdue.edu/ext/treecomputer/). Management options for EAB infested areas include but are not limited to: girdling, insecticide injections, parasitic wasp use, and tree restoration.

Insecticide usage for EAB reduction is very effective, although it has to be repeatedly applied and impacts other insects. There are two ways for insecticides to be applied: direct injection and basal soil drenches (water mixed root application); however, these are commonly used in urban settings. In order to reduce the amount of contamination and exposure, an insecticide can also be injected directly into the base of the tree, moving into the xylem tissue, and consequently, upwards into the canopy area (McCullough et al. 2016); the tree can readily absorb the injected insecticide with basal soil drenches through the root system after initial application (Smitley et al. 2015). Insecticides can also be paired with girdling of individual trees (McCullough et al. 2016). Girdling a tree creates volatile cues that cause EAB to aggregate and lay eggs in the tree before using insecticides on the girdled tree to kill the EAB. While these are used in urban settings, wasp parasitoids are more commonly used in natural settings.

Understanding wasp parasitoids (herein called parasitoids), which impact EAB directly, is important. The species that provide biological controls include non-native *Oobius agrili, Spathius agrili,* and *Tetrasichus planipennisi* (Gould et al. 2012); although there is a North American species, *Spathius floridanus* (Johnson et al. 2014). Exotic and native parasitoids respond to ash volatile cues differently (Johnson et al. 2014). It is important to know what specifically the parasitoids are attracted to in order to utilize biocontrol agents effectively. Parasitoid release is currently a government funded program so there is no cost to the user, but requirements must be met in order to carry out the application (Ben Slager, personal communication, 9/12/17). Effectiveness of parasitoids varies based on ash signals and the parasitoids ability to reproduce, reducing the need to have parasitoids re-released. If the population of ash and EAB are unable to support parasitoids, other measures may have to be taken to ensure the natural areas stability.

Restoration strategies for ash-dominated forested areas are an option in locations where the majority of ash have died; it usually involves planting young trees. Adding young trees (tree augmentation) to an area can increase population viability for that species. There are currently research projects underway that are examining the ability of individual ash trees to resist EAB damage and ways to improve resistance (Koch et al. 2015). This approach was utilized with American elm, where Dutch elm disease resistant individuals were refined so as to be planted for reforestation (Slavicek & Knight 2012). Population changes resulting from tree augmentation can be explored experimentally in the field or modeled in software. Currently, there are only examples of harvest reductions in population viability analysis models (Dhar et al. 2008, Grogan et al. 2014); most augmentation predictions are modelled in forest vegetation simulator (FVS), where forest stand growth and development are applied to ecosystem management (Dixon 2002). The FVS program has successfully predicted short term changes (2 years) of reduced stem density and basal area for ash with EAB infestation (Levin-Neilson & Rieske 2015). With population viability analysis models the predictions can be projected for a longer period of time in a dynamic environment.

Population viability analysis (PVA) is a method that uses a variety of data to quantitatively estimate the population viability of a species and evaluate potential threats with a goal of determining the likelihood of future persistence under a variety of conditions (Akcakaya & Sjorgren-Gulve 2000, Morris & Doak 2002, Caswell 2001). Analyses, such as PVA, are especially important to identify critical factors that influence long-term viability of vulnerable species in a timely enough manner to develop strategies that prevent further endangerment. Trees with pests and disease issues, like whitebark pine (*Pinus albicaulis*), have been evaluated with population models to help reveal that the pests impacted the trees more than the disease (Jules et al. 2016). Baseline models contain data that are helpful in understanding population dynamics and can be compared with scenarios containing varying conditions. Management actions are best done under circumstances where the species in duress is heavily studied, but this is not always feasible.

The potential changes from management can be incorporated into the models and evaluated for overall effectiveness in increasing population viability. For example, an individual based model was developed to examine how much harvesting was detrimental to the Big-leaf mahogany (*Swietenia macrophylla*) population, which is listed under the Convention on International Trade in Endangered Species (Grogan et al. 2014). For the endangered English Yew tree (*Taxus baccata*) management alternatives were modeled to create a population viability risk management assessment to identify which management strategy was most beneficial (Dhar et al. 2008). EAB deterrents are continuously improving and will, therefore, influence ash survival once implemented by land management units. Model variations based on management changes can reveal boundaries between successful and detrimental results. By creating models for species in danger of decline we can better assess future scenarios, and potentially understand the underlying mechanism driving the populations change.

The aim of this study was to compare, using PVA, the effects of EAB, with and without management interventions, on the population persistence of our focal green ash (*Fraxinus pennsylvanica*) population. We created a baseline model and baseline catastrophe model and added management scenarios to the catastrophe model. Management actions that we focused on were (1) reduced catastrophe, where release of a biocontrol parasitoid improved ash survival by reducing catastrophe impacts; (2) competition management, where removal of competitors was assumed to improve ash survival and growth; (3) save a size class management, where only one size class is focused on by management; and (4) ash restoration, where the population had added EAB-resistant ash individuals. We expected that the persistence of green ash in a natural floodplain would depend on ash survival and the establishment of EAB-resistant ash. Over time we have observed the death of many adult trees, leaving behind an orphaned cohort that may succumb to EAB before producing enough viable seed (Klooster et al. 2014), raising concern that this focal population will be functionally extinct if they do not reproduce successfully. Using population models we can evaluate the alternatives for management of this highly impacted population, which is a representative of many natural locations that EAB has infested.

Methods

Survey Site

Our focal population was in Northwest Ohio, in the floodplain forest of Swan creek, located in the Oak Openings Preserve Metropark (Swanton, Ohio, USA). This area has been infested with EAB for at least a decade. It holds a remnant population of green ash trees where EAB are still present in low numbers. It contains adult trees that are either the last to be infested or have rare phenotypes which increased their resistance to EAB (Koch et al. 2015). The Oak Openings Preserve is in the Oak Openings Region, a mixed disturbance landscape containing a mosaic of rare natural ecosystems surrounded by agriculture and urban development. The floodplain forest of Swan creek is primarily composed of green ash, maple (*Acer*), elm (*Ulmus*), sycamore (*Platanus*), and cottonwood (*Populus*) species (Knight et al. 2012a). This region is a unique biodiversity hotspot (Abella et al. 2004) that has undergone large changes from an EAB invasion which peaked from 2004-2010 (Knight et al. 2010).

EAB Traps

Purple panel sticky traps have been set up yearly since 2008 to survey for EAB presence in Ohio (Knight et al. 2014). Each year traps are set up in ash trees before EAB emergence and number of EAB caught are counted at the middle and end of summer. Trends in these data showed a decrease in EAB once large ash trees died, with a persistent low presence continuing over time. We may see a future increase of EAB numbers in response to the maturation of ash saplings, but not enough time has passed to examine a complete maturation of this next generation.

Population Models

We constructed stage-based, stochastic population models to explore a variety of scenarios. The baseline model was used as a starting point and included data after peak EAB outbreak (2010-2017) to model the aftermath forest. The aftermath forest data was used to assess what would happen to the forest in the future if EAB outbreaks continue to occur. We used peak infestation ash data in creating our EAB catastrophe impact parameters. For each stage the baseline model included ash abundance, survival, fecundity, and the probability of growth to the next stage, where stage was based on ash size (Figure 5.1). All models were developed in

RAMAS® Metapop (Setakaut, NY, USA), and each scenario was a 50-year simulation based on 1 year time intervals with 10,000 replications. Size classes were categorized to assess population demographics of the trees different life stages. We separated size classes by diameter at breast height (DBH, 1.37 m). Size classes included first year seedlings, trees < 1 cm DBH, 1 - 9.9 cm DBH, 10 - 19.9 cm DBH, and > 20 cm DBH. Full reproduction capabilities had been noted after trees have reached 20 cm DBH (Franklin 1981), so only those > 20 cm reproduced in the model. The stages 1-9.9 cm and 10-19.9 cm were created for an even distribution of sizes between 1-20 cm. Seedlings between year two and 1 cm DBH were not separated further as our survival information was similar for separate sizes within that size class.

Ash trees are a sexually dimorphic species, so we utilized female only models for simplification. As the sex ratio is typically 1:1, males were assumed to not significantly change the population trajectory (Zhang et al. 2009). Fecundity was estimated as the number of seeds per tree surviving to germination that were female. Our best estimate of seeds surviving to germination was found in literature that counted newly emergent ash on the forest floor, which reported the mean number of seedlings per 100 m^2 (Boerner & Brinkman 1996) (Table 5.1). We assumed this value represented the number of seedlings produced from one female tree. There was more than one estimate of some survival parameters, so the geometric mean and its standard deviation were used for the vital rates in the models search engines, including treesearch.org, a US Forest Service search engine. All estimates were based on research of American ash species. For larger stage classes, estimates were based on averages from 7 years (2010-2017) of US Forest Service survey data on our focal ash population (Knight, K.S.K., personal communication, 9-17-17) (Table 5.1). For the first year of life seedlings that survived grew into the next < 1 cm stage. For trees < 1 cm the growth rate was estimated based on a best-case scenario from the literature (Bonner & Karrfalt 2008, Conner et al. 2000). Growth rates for trees larger than 1 cm DBH were based on average growth of green ash from our focal population, which was on average 10 cm per 10 years.

Other model elements included in the baseline model were initial abundance, initial stage structure, density dependence, and stochasticity. Initial abundance of the population was estimated from field survey data for the baseline scenario. All living ash at least 1.37 m tall within 50 m of the creeks east side floodplain were recorded, as well as all ash > 10 cm DBH on both sides of the creek. This estimate was then halved and we estimated 857 individuals were female. The baseline scenario's initial stage structure abundances were arranged by the actual distribution, except for yearlings which was assumed; 58% yearlings, 2% seedlings (< 1 cm DBH), 14% saplings (1 - 9.9 cm DBH), 17% small adults (10 - 19.9 cm DBH), and 0.09% were reproducing adults (> 20 cm DBH). Density dependence was limited by a ceiling abundance of 25,000, which is the maximum estimate from a Swan Creek floodplain survey, in which both living and dead trees were counted (Knight et al. 2012a). Stochasticity was added as both demographic and environmentally related variation. In creating a model based on the Swan Creek ash population, we assumed a closed population. Demographic stochasticity was modeled as the number of survivors from one year to the next sampled from a binomial distribution, and the number of offspring and young sampled from a Poisson distribution (Akcakaya 1991). Environmental stochasticity was modeled as a random sample from a lognormal distribution based on the average vital rates and standard deviation matrix (Akcakaya 1991). The baseline model represents the population during 2010-2017, after the peak emergence of EAB, when the abundance of EAB had dropped significantly, but persisted, after killing > 90% of the ash trees.

To represent the probability of EAB increasing in abundance and impacting the survival of ash in the future as it did during its initial peak infestation, we introduced a catastrophe event into the baseline model for the catastrophe model. The probability of catastrophe occurrence increased linearly to 99% over 10 years, after an initial catastrophe occurred the probability of occurrence restarted at zero. Ten years was chosen based on aftermath forest growth rates, assuming that increased years in forest growth increases the probability of EAB catastrophically impacting the forest. We estimated that it takes seedlings at the minimum 7 years to grown into a tree > 1 cm DBH, and growth rates for trees larger than 1 cm DBH was on average 10 cm per 10 years. Therefore, 10 years would allow for the forest to accommodate enough EAB to cause a catastrophe. The EAB catastrophe reduced the survival rate of ash trees > 1 cm DBH by 90%, similar to survival rates during peak EAB infestation. In the initial peak infestation all saplings > 1 cm DBH did not survive in our location and others have shown that ash > 2.5 cm DBH are damaged by EAB (McCullough et al. 2008). We added a gradual reduction in the impact of the catastrophe over the following 9 years of the timeline after the catastrophe had occurred, reducing the impact to survival by 10% as each year past. This was done to simulate the documented slow recovery of our focal population from the initial EAB infestation, which we expected to occur every time the population grows large enough to initiate a EAB catastrophe. We decided to replicate this potential future oscillation of abundance in ash via EAB as a catastrophe because it allows to simulate the potential infestation oscillations before actually witnessing these oscillations in the field.

Management Scenarios

Potential effects of land management can be simulated in our catastrophe model. We modeled the potential effects of four management scenarios on the catastrophe model based on the following assumptions. (1) We reduced the impact of the EAB catastrophe on the survival of the population by half. This was done to simulate a successful introduction of parasitoids to the ash population with EAB, or a future where EAB do not impact ash as they did during the first peak infestation. We will refer to this scenario as the reduced catastrophe scenario.

(2) We created a scenario with an increase in survival and growth parameters for large trees. The changes made included faster growth of stage 10-19.9 cm, and a 10% increase in survival for young adults and adults (10-19.9 cm & 20+ cm). This was done to investigate potential changes that only impact large trees such as removal of competing large tree neighbors. We will refer to this scenario as the competition scenario.

(3) Next, we increased the survival of one particular stage in the catastrophe model to simulate tree management that focused on one stage only over time. We manually increased the survival to 99% one at a time for each individual stage with all other parameters remaining unchanged, creating four different scenarios (sizes < 1 cm, 1-9.9 cm, 10-19.9 cm, and 20+ cm, respectively). Survival was maximized to create extremes that clearly show if there would be population differences if management focused on a particular stage. We will refer to these scenarios as the save a stage scenarios, which includes adult save a stage (20 + cm), young adult save a stage (10-19.9 cm), sapling save a stage (1-9.9 cm), and seedling save a stage (< 1 cm) scenarios.

(4) To simulate a restoration event in our PVA we added an additional population of EAB resistant ash trees to the catastrophe model. The EAB resistant population had improved survival rates in their matrix which represented historic population dynamics (Chapter II.), and an initial population of 400, where all individuals were in the stage class size 1-9.9 cm. Restoration trees would likely be 1-2 cm in size, but we assumed with added care they would have the same

survival chance from size 1-9.9 cm. A second scenario was created where the initial population was 400 individuals of stage size class < 1 cm. These scenarios represented an introduction of 400 saplings (size 1-9.9 cm) or seedlings (< 1 cm), respectively. We will refer to these scenarios as the sapling restoration and seedling restoration scenarios.

For each model and scenario, we report the growth rate, average of the 10,000 replications for abundances to the nearest whole number over time, total final abundance, and expected minimum abundance, and mean time to fall below 10 individuals. Interval extinction risk results, or the probability that the population abundance will fall below *x* over the 50 year interval at least once, were tested for significant differences between scenarios with the Kolmogorov-Smirnov nonparametric test. We also report the Kolmogorov-Smirnov D statistic, which represents the maximum vertical deviation in the plotted probability curves.

Results

We found significant differences ($p < 0.001$) in the population's interval extinction risks between a number of the model variants. Final average total abundances varied, but in all models were heavily skewed towards smaller rather than larger individuals within the population. For the baseline model, the population growth rate was 1.05, there was no extinction risk, and the population trajectory varied within the first 10 years before leveling and slightly increasing (Figure 5.2). This trajectory pattern also occurred in our other simulations. With the catastrophe model, the probability of a 50% decline was 99% and the probability of extinction was 78% (Table 5.2). This model also had a 50% probability of quasi-extinction at Year 38 (Table 5.2). The average abundance over time for the management scenarios reflected their expected performance, with seedling save a stage, competition, and adult save a stage having improved abundance the most over the catastrophe model, respectively, followed by reduced catastrophe, young adult save a stage, and sapling save a stage scenario (Figure 5.3). Restoration scenarios did not improve the population abundance very much, although using saplings instead of seedlings was an improvement (Figure 5.4).

We found a significant difference in the interval extinction risk between the baseline model and the catastrophe model ($p < 0.001$; $D = 0.91$) and the baseline model and the reduced catastrophe scenario ($p < 0.001$; $D = 0.67$) (Table 5.3). When comparing the catastrophe model to the management scenarios the populations interval extinction risks were significantly different ($p < 0.0001$) (catastrophe vs. reduced catastrophe $D = 0.27$; catastrophe vs. competition $D = 0.32$; catastrophe vs. adult save a stage $D = 0.17$; catastrophe vs. young adult save a stage $D = 0.02$; catastrophe vs. sapling save a stage $D = 0.06$; catastrophe vs. seedling save a stage $D = 0.88$; catastrophe vs. sapling restoration $D = 0.25$; catastrophe vs. seedling restoration $D = 0.17$) (Table 3). When comparing sapling restoration to seedling restoration there was also a significant difference, but small deviations ($p < 0.0001$, $D = 0.07$). There was no clear pattern in distributional differences (D) (Table 5.3).

The final average total abundances for all models and scenarios were variable, from 2 – 8771 individuals, with 8771 for the baseline model and save a stage seedling scenario the next highest reaching 6167 individuals (Table 5.2). Those scenarios with lower final average total abundances were save a stage sapling (2 individuals), restoration saplings (30 individuals) and seedlings (37 individuals), and the catastrophe model (38 individuals) (Table 5.2).

The management options produced a variety of effects on the final population abundance and the risks of a decline. Reducing the catastrophe with the addition of a biocontrol (parasitic wasp) had a final average total abundance of 563, the same growth rate as the baseline, the probability of a 50% decline was 89% and the risk of extinction was 30% (Table 5.2). The competition scenario had a final average total abundance slightly higher than other scenarios (1340 individuals), the growth rate was 1.18, a lower probability of 50% decline than other scenarios (82%), and the extinction probability was 36% (Table 5.2). Adding EAB resistant ash trees to the current population produced about a 50% recovery of the population. There was no major difference in final average total abundance whether we added resistant seedlings of saplings (Table 5.2). The growth rates of the catastrophe model and the restoration scenario were an average of 1.04. The probability of a 50% decline was higher for the addition of seedlings (95%) than saplings (91%), therefore the addition of saplings improved the population abundance faster (Table 5.3).

When we protected only one stage of the population, results were significantly different from the catastrophe model, except for protection of the sapling stage (Table 5.4). There were very high probabilities of 50% decline, except for the save a seedling stage. The save the seedling stage (< 1 cm) scenario did not go extinct, had a small probability of 50% decline (26%), and had a high average final total abundance of 6167 (Table 5.2). Protecting the seedling stage had a positive impact on the population, but this scenario would still result in larger trees dying from EAB and a constant replenishment of seedlings from outside the population. The other save-a-stage size scenarios had growth rates that varied (1.01 – 1.15), in order from smallest to largest was saplings, seedlings, young adults, and adult scenarios (Table 5.2). Extinction rates ranging from 1-91%, in order from smallest to largest, seedlings (1%), adults (50%), young adults (72%), and saplings (91%) (Table 5.2). The average final total abundances only reached the double digits, except for the adult save a stage (626 individuals) (Table 5.2).

Discussion

Our baseline model results show that if current population vital rates remain the same without any further EAB damage, the population could recover. When EAB was a recurring catastrophe at least once every 10 years, then the extinction risk was 78% but could decrease to 30% if the catastrophe was reduced by half. The stage that was most sensitive to changes was the 1.0 - 9.9 cm stage, which represented established trees that focus their energy on growth rather than reproduction (Kennedy 1990). Management scenarios had varying effects on the catastrophe model. Efforts to keep a specific size class of trees alive improved chances of reducing extinction when increasing the survival of adults or seedlings. These size class specific scenarios can also be viewed as a sensitivity analysis and suggests that the success of reproductive efforts is very important to population survival.

In the baseline scenario, there was an initial increase in the population for the first year before the population decreased for 11 years, then started to gradually increase. This increase of the first year happened since the initial population had adult trees that were then removed by EAB. The initial stage distribution was based on recent survey information from a floodplain forest in Northwest Ohio. This stage structure and our estimated seed production heavily influenced the initial increase in the population. Once trees were large enough in size to be infested, the ash population was affected by EAB and declined.

A reduced catastrophe simulated an additional parasitoid biocontrol for the population and created conditions that were midway between the baseline and catastrophe scenario. With continual presence of EAB in our study area another EAB outbreak is likely and parasitoid use could be a productive solution. Many locations are already using the parasitic wasp species that specialize on EAB (USDA APHIS 2018). Some parasitoids are slightly susceptible to a fungus that kills EAB, whereas others are more affected by different environmental factors which reduce their numbers (Dean et al. 2012). When measuring the parasitism of these wasps, bark collecting, sifting, and sorting were shown to be more effective in estimating the rate of parasitism, as well as determining the relative percentage of trees in a stand where parasitized eggs occurred (Abell et al. 2014). This method was more time consuming than the other option; timed visual searches of standing ash tree bark. As such, these issues with establishing a population of parasitic wasps creates doubt that an increase in survival for ash trees with parasitoid use will work successfully. However, other areas have had success with biocontrol *T. planipennisi* killing 36-85% of EAB larvae in ash saplings of southern Michigan forests where EAB had already caused major population damage (Duan et al. 2017). If concerns are that the parasitoid would not work, a more specific age structured model for the parasitoids could be developed to assess which species may perform better, as others have done for the parasitoids of mango mealy bugs (*Rastrococcus invadens*) (Godfray & Waage 1991). Other natural factors may reduce the EAB catastrophe in half for our future scenario, such as increased EAB predators, reduced habitat for EAB, and higher fragmentation of ash forest stands.

Probability of survival and growth may increase under certain land management practices, such as in our competition scenario, where a reduction in tree neighbors was assumed to increase large ash survival and growth. Previous research on this population of green ash indicated an increase in ash health occurred when ash neighbors are at least 6 m away from each other (Kappler et al. 2018). Silvicultural thinning could be one method of increasing survival and growth of surviving ash trees. In a 35 year-long thinning experiment at slightly higher latitude (53°-56° N), European ash (*Fraxinus excelsior*) had a highly enhanced crown area and DBH with thinning, especially with younger stands (10-30 years-old), that lasted 3-8 years (Juodvalkis et al.

2005). With the focal population a remnant of what it once was, an aftermath forest, this difference in canopy openness may be an advantage to the remaining ash trees. Thinning out the remaining ash trees has its uncertainties, especially since ash are dioecious, reproduction will suffer if thinning unbalances the male: female ratio of trees.

When restoring areas by introducing EAB-resistant ash trees, adding resistant individuals of stage 1 - 9.9 cm had the best chance for re-establishing the population. When replanting resistant trees, it is important to learn from previous efforts, and use these successful interventions as a model for the introduction of EAB resistant ash trees. For example, elm trees were affected by Dutch Elm Disease (DED), and the process of controlled breeding in select individuals with resistance/tolerance proved to be beneficial in reducing DED symptoms (Slavicek & Knight, 2012). The use of DED resistant elm trees did well in native floodplain restoration experiments when using larger trees with tree cages to prevent deer browse (Knight et al. 2012b, Knight et al. 2017). Other diseases like the Chestnut Blight also required the reintroduction of resistant trees, where crosses of Chinese chestnut and American chestnut then backcrossed multiple times with American chestnut selected for resistance characteristics (Jacobs 2007). These resistant trees were able to thrive in areas with slow growing species like oaks and hickories (Schlarbaum et al. 1997). Different species of ash may be less susceptible to EAB, such as blue ash (Nisbet et al. 2015), and crossing with these species may be beneficial. Applying these methods for ash trees would not only increase overall survival of the species, but also incorporate increased resistance and promote a healthier ecosystem. Our models indicated that the stage of life most susceptible to changes in the environment are those 1-9.9 cm, and the saplings and seedling restoration scenarios had different impacts, with resistant saplings producing higher abundance values. This indicated that there is a higher probability of success for the population when planting resistant seedlings at least 1 cm DBH for restoration management.

Management options for dealing with ash damage from the invasive EAB include methods such as girdling the ash trees, utilizing insecticides, implementing the use of parasitoids, as well as various methods for tree restoration. Estimated costs of the overall damage due to the EAB were at about 11 - 25 billion dollars across 25 states in the U.S. (Kovacs et al. 2010, Gould et al. 2012). Each of the management plans associated with our management scenarios would have varying costs and benefits dependent on multiple variables. For some of the options, like using parasitoids, the costs are absorbed by government programs. Others, however, are not and require individual assessment for feasibility. In forested locations, not all trees can be saved due to overall cost from the quantity of trees in need of saving. Of course, these management options presented have other ecosystem and biological costs associated with them. Without the use of any of these options, there is a lower chance for overall ecosystem recovery. However, management options should still be considered even if most ash have already been a victim of EAB; the few remaining trees could show partial EAB resistance.

Management practices have been carried out on other invasive insect species, usually without prior predictive modeling, including the gypsy moth (*Lymantria dispar*). This species was brought over to North America via egg masses located on Russian ships, and eventually spread from the Atlantic Coast to Michigan by 1990, with the development of pheromone specific traps used for population detection and removal (Wallner 1996). Similar pheromone traps are also being developed for EAB (Ryall et al. 2013). Outbreak cycles can be paralleled between EAB and the gypsy moth. The gypsy moth can have population fluctuations that cycle either every 4-5 years, or 9-10 years (Bjornstad et al. 2010). EAB cycles of population fluxes are expected to be seen over a period of 10 years, as our estimate predicts that it takes seedlings 10 years to grown into a tree > 3 cm DBH. The gypsy moth is still a problem pest, and other management alternatives continue to be explored. With information on how these management alternatives have worked, population modeling could help with identifying the underlying issue in decimating the gypsy moth, or any invasive pests, population.

Green ash trees are an important species in floodplain forests, as they are tolerant of floods and help reduce erosion (Kennedy 1990). Their importance in native areas has become more apparent after losing a majority of them from EAB introductions, with our focal forest reverted to a more prairie or savanna-like state. Land managers need to know what may occur, and models such as the ones described here report testable predictions. With continued monitoring during management, new data would allow for further validation and refinement of the models (Boyce 1992). Adaptive management could be applied to this and other ash populations with the continued use of PVA, to keep ash from the brink of extirpation.

References

Abell, K. J., Bauer, L. S., Duan, J. J., & Van Driesche, R. (2014). Long-term monitoring of the introduced emerald ash borer (Coleoptera: Buprestidae) egg parasitoid, *Oobius agrili* (Hymenoptera: Encyrtidae), in Michigan, USA and evaluation of a newly developed monitoring technique. *Biological control*, *79*, 36-42.

Abella, S. R., Jaeger, J. F., & Brewer, L. G. (2004). Fifteen Years of Plant Community Dynamics during a Northwest Ohio Oak Savanna Restoration. *The Michigan Botanist*, *43*, 117–127.

Akçakaya, H. R. (1991). A method for simulating demographic stochasticity. *Ecological Modelling*, *54*(1–2), 133–136. https://doi.org/10.1016/0304-3800(91)90103-8

Akçakaya, H. R., & Sjögren-Gulve, P. (2000). Population viability analyses in conservation planning: an overview. *Ecological Bulletins*, 9-21.

United States Department of Agriculture Animal and Plant Health Inspection Service (USDA APHIS) (2018). *Emerald Ash Borer*. Retrieved June 4, 2018, from https://www.aphis.usda.gov/aphis/ourfocus/planthealth/plant-pest-and-disease-programs/pests-and-diseases/emerald-ash-borer/ct_emerald_ash_borer

Barger, J. H., & Davidson, R. H. (1967). A Life History Study of the Ash Seed Weevils, *Thysanocnemis Bischoffi* Blatchley and *T. Helvola* Leconte (Coleoptera: Curculionidae). *The Ohio Journal of Science*, *67*(2), 123–127.

Bjørnstad, O. N., Robinet, C., & Liebhold, A. M. (2010). Geographic variation in North American gypsy moth cycles: subharmonics, generalist predators, and spatial coupling. Ecology, *91*(1), 106-118.

Boerner, R. E. J., & Brinkman, J. A. (1996). Ten years of tree seedling establishment and mortality in an Ohio deciduous forest complex. *Bulletin of the Torrey Botanical Club*, *123*(4), 309-317.

Bonner, F. T., & Karrfalt, R. P. (2008). The Woody Plant Seed Manual. USDA FS Agriculture Handbook 727, p. 537-543.

Boyce, M. S. (1992). Population Viability Analysis. *Annual Review of Ecology Systems*, *23*, 481–506. https://doi.org/10.1002/9780470057339.vnn149

Caswell, H. (2001). Matrix population models: construction, analysis, and interpretation. Second Edition, Sinauer Associates, Inc. Sunderland, MA, 01375 USA

Conner, W. H., Inabinette, L. W., & Brantley, E. F. (2000). The use of tree shelters in restoring forest species to a floodplain delta: 5-year results. *Ecological Engineering, 15,* 47-56.

Dean, K. M., Vandenberg, J. D., Griggs, M. H., Bauer, L. S., & Fierke, M. K. (2012). Susceptibility of two hymenopteran parasitoids of *Agrilus planipennis* (Coleoptera: Buprestidae) to the entomopathogenic fungus *Beauveria bassiana* (Ascomycota: Hypocreales). *Journal of invertebrate pathology*, *109*(3), 303-306.

Dhar, A., Ruprecht, H., & Vacik, H. (2008). Population viability risk management (PVRM) for in situ management of endangered tree species-A case study on a *Taxus baccata* L. population. *Forest Ecology and Management*, *225*, 2835-2845. https://doi.org/10.1016/j.foreco.2008.01.059

Dixon, G. E. (2002). Essential FVS: A User's Guide to the Forest Vegetation Simulator. Internal Rep. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Forest Management Service Center. p. 266. (Revised: June 13, 2017).

Duan, J. J., Bauer, L. S., & Van Driesche, R. G. (2017). Emerald ash borer biocontrol in ash saplings: The potential for early stage recovery of North American ash trees. *Forest Ecology and Management*, *394*, 64–72.

Godfray, H. C. J., & Waage, J. K. (1991). Predictive modelling in biological control: the mango mealy bug (*Rastrococcus invadens*) and its parasitoids. *Journal of Applied Ecology*, *28*, 434-453.

Gould, J., Bauer, L., Lelito, J., & Duan, J. (2012). Emerald Ash Borer, *Agrilus planipennis* (Fairmaire), Biological Control Release and Recovery Guidelines. USDA-APHIS-ARS-FS, Riverdale, Maryland, p. 39. Retrieved from http://treesearch.fs.fed.us/pubs/40545

Grogan, J., Landis, R. M., Free, C. M., Schulze, M. D., Lentini, M., & Ashton, M. S. (2014). Big-leaf mahogany *Swietenia macrophylla* population dynamics and implications for sustainable management. *Journal of Applied Ecology*, *51*(3), 664–674. https://doi.org/10.1111/1365-2664.12210

Herms, D. A., & McCullough, D. G. (2014). Emerald Ash Borer Invasion of North America: History, Biology, Ecology, Impacts, and Management. *Annual Review of Entomology*, *59*(1), 13–30. https://doi.org/10.1146/annurev-ento-011613-162051

Hoffmann, M., Milotic, T., & Van Uytvanck, J. (2009). Interaction between large herbivore activities, vegetation structure, and flooding affects tree seedling emergence, *Plant Ecology, 206,* 173–184. https://doi.org/10.1007/s11258-009-9632-1

Jacobs, D. F. (2007). Toward development of silvical strategies for forest restoration of American chestnut (*Castanea dentata*) using blight-resistant hybrids. *Biological Conservation, 137*, 497-506.

Johnson, T. D., Lelito, J. P., & Raffa, K. F. (2014). Responses of two parasitoids, the exotic *Spathius agrili* Yang and the native *Spathius floridanus* Ashmead, to volatile cues associated with the emerald ash borer, *Agrilus planipennis* Fairmaire. *Biological Control*, *79*, 110–117. https://doi.org/10.1016/j.biocontrol.2014.05.004

Jules, E. S., Jackson, J. I., van Mantgem, P. J., Beck, J. S., Murray, M. P., & Sahara, E. A. (2016). The relative contributions of disease and insects in the decline of a long-lived tree: a stochastic demographic model of whitebark pine (*Pinus albicaulis*). *Forest Ecology and Management*, *381*, 144–156.

Juodvalkis, A., Kairiukstis, L., & Vasiliauskas, R. (2005). Effects of thinning on growth of six tree species in north-temperate forests of Lithuania. *European Journal of Forest Research*, *124*(3), 187–192. https://doi.org/10.1007/s10342-005-0070-x

Kappler, R. H., Knight, K.S., Koch, J., & Root, K. (2018). Neighboring tree affects and soil nutrient associations with surviving green ash (*Fraxinus pennsylvanica*) in an emerald ash borer (*Agrilus planipennis*) infested floodplain forest. *Forests*, *9*, 183.

Kennedy, H. E. J. (1990). *Fraxinus pennsylvanica* Marsh. Green Ash. In *Silvics of North America: 2. Hardwoods* (p. 877). Washington, D.C.: Agriculture Handbook 654, U.S. Dept. of Agriculture, Forest Service. Retrieved from https://www.srs.fs.usda.gov/pubs/misc/ag_654/volume_2/fraxinus/pennsylvanica.htm

Klooster, W. S., Herms, D. a., Knight, K. S., Herms, C. P., McCullough, D. G., Smith, A., … Cardina, J. (2014). Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). *Biological Invasions*, *16*(4), 859–873. https://doi.org/10.1007/s10530-013-0543-7

Knight, K.S.; Herms, D.A.; Cardina, J.; Long, R.P.; Rebbeck, J.; Gandhi, K.J.K.; Smith, A.; Klooster, W.S.; Herms, C.P. (2010). Emerald ash borer aftermath forests: the dynamics of ash mortality and the responses of other plant species. In: Michler, C.H.; Ginzel, M. D., eds. Proceedings of symposium on ash in North America. Gen. Tech. Rep. NRS-P-72. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station: 11.

Knight, Kathleen S.; Herms, Daniel; Plumb, Reid; Sawyer, Eileen; Spalink, Daniel; Pisarczyk, Elizabeth; Wiggin, Bernadette; Kappler, Rachel; Ziegler, Emily; Menard, Karen. (2012a). Dynamics of surviving ash (*Fraxinus* spp.) populations in areas long infested by emerald ash borer (*Agrilus planipennis*). In: Sniezko, Richard A.; Yanchuk, Alvin D.; Kliejunas, John T.; Palmieri, Katharine M.; Alexander, Janice M.; Frankel, Susan J., tech. coords. *Proceedings of the fourth international workshop on the genetics of host-parasite interactions in forestry: Disease and insect resistance in forest trees*. Gen. Tech. Rep. PSW-GTR-240. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. pp. 143-152.

Knight, K. S., Slavicek, J. M., Kappler, R., Pisarczyk, E., Wiggin, B., & Menard, K. (2012b). Using Dutch elm disease-tolerant elm to restore floodplains impacted by emerald ash borer. In: Sniezko, Richard A.; Yanchuk, Alvin D.; Kliejunas, John T.; Palmieri, Katharine M.; Alexander, Janice M.; Frankel, Susan J., tech. coords. *Proceedings of the fourth international workshop on the genetics of host-parasite interactions in forestry: Disease and insect resistance in forest trees*. Gen. Tech. Rep. PSW-GTR-240. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. pp. 317-323.

Knight, K.S.; Flash, B.P.; Kappler, R.H.; Throckmorton, J.A.; Grafton, B.; Flower, C. E. (2014). Monitoring Ash (*Fraxinus* spp.) Decline and Emerald Ash Borer (*Agrilus planipennis*)

Symptoms in Infested Areas. United States Department of Agriculture Forest Service General Technical Report NRS-139 Northern Research Station, Delaware, Ohio.

Knight, Kathleen S.; Haugen, Linda M.; Pinchot, Cornelia C.; Schaberg, Paul G.; Slavicek, James M. (2017). American elm (*Ulmus americana*) in restoration plantings: a review. In: Pinchot, Cornelia C.; Knight, Kathleen S.; Haugen, Linda M.; Flower, Charles E.; Slavicek, James M., eds. *Proceedings of the American elm restoration workshop 2016*; 2016 October 25-27; Lewis Center, OH. Gen. Tech. Rep. NRS-P-174. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station: 133-140.

Koch, J. L., Carey, D. W., Mason, M. E., Poland, T. M., & Knight, K. S. (2015). Intraspecific variation in Fraxinus pennsylvanica responses to emerald ash borer (Agrilus planipennis). *New Forests*, *46*(5-6), 995-1011.

Kovacs, K. F., Haight, R. G., McCullough, D. G., Mercader, R. J., Siegert, N. W., & Liebhold, A. M. (2010). Cost of potential emerald ash borer damage in U.S. communities, 2009–2019. *Ecological Economics*, *69*(3), 569–578. https://doi.org/10.1016/j.ecolecon.2009.09.004

Levin-Nielsen, a, & Rieske, L. (2015). Evaluating short term simulations of a forest stand invaded by emerald ash borer. *iForest - Biogeosciences and Forestry*, *8*(1), 19–24. https://doi.org/10.3832/ifor1163-007

MacFarlane, D. W., & Meyer, S. P. (2005). Characteristics and distribution of potential ash tree hosts for emerald ash borer. *Forest Ecology and Management*, *213*(1–3), 15–24. https://doi.org/10.1016/j.foreco.2005.03.013

McCullough, D. G., Poland, T. M., & Lewis, P. A. (2016). Lethal trap trees: A potential option for emerald ash borer (Agrilus planipennis Fairmaire) management. *Pest Management Science*, *72*(5), 1023–1030. https://doi.org/10.1002/ps.4083

Morris, William F., Doak, F. D. (2002). *Quantitative Conservation Biology; Theory and Practice of Population Viability Analysis*. Sunderland, MA: Sinauer Associates, Inc. Publishers.

Nisbet, D., Kreutzweiser, D., Sibley, P., & Scarr, T. (2015). Ecological risks posed by emerald ash borer to riparian forest habitats: A review and problem formulation with management implications. *Forest Ecology and Management*. https://doi.org/10.1016/j.foreco.2015.08.030

Purdue University Entomology Extension Emerald Ash Borer Cost Calculator. http://int.entm.purdue.edu/ext/treecomputer/ (Accessed 20 October 2017).

Ryall, K. L., Fidgen, J. G., Silk, P. J., & Scarr, T. A. (2013). Efficacy of the pheromone (3Z)-lactone and the host kairomone (3Z)-hexenol at detecting early infestation of the emerald ash borer, Agrilus planipennis. *Entomologia Experimentalis et Applicata*, *147*, 126–131. https://doi.org/10.1111/eea.12052

Schlarbaum, S. E., Hebard, F., Spaine, P. C., & Kamalay, J. C. (1997). Three American tragedies: chestnut blight, butternut canker, and Dutch elm disease. *Exotic pests of eastern forests. USDA Forest Service, Southeastern Research Station, Asheville, NC. Tennessee Exotic Pest Council*, 8-10.

Schmiedel, D., Huth, F., & Wagner, S. (2013). Using data from seed-dispersal modelling to manage invasive tree species: The example of *Fraxinus pennsylvanica* Marshall in Europe. *Environmental Management*, *52*(4), 851–860. https://doi.org/10.1007/s00267-013-0135-4

Slavicek, James M.; and Knight, Kathleen S. (2012). Generation of American elm trees with tolerance to Dutch elm disease through controlled crosses and selection. In: Sniezko, Richard A.; Yanchuk, Alvin D.; Kliejunas, John T.; Palmieri, Katharine M.; Alexander, Janice M.; Frankel, Susan J., tech. coords. *Proceedings of the fourth international workshop on the genetics of host-parasite interactions in forestry: Disease and insect resistance in forest* *trees.* Gen. Tech. Rep. PSW-GTR-240. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. pp. 342-346.

Smitley, D. R., Herms, D. A., & Davis, T. W. (2015). Efficacy of soil-applied neonicotinoid insecticides for long-term protection against emerald ash borer (Coleoptera: Buprestidae). *Journal of Economic Entomology*, *108*(5), 2344–2353. https://doi.org/10.1093/jee/tov205

Stewart, H. A., & Krajicek, J. E. (1973). Ash, an American wood. American Woods Series FS216. USDA Forest Service. Washington, DC. 7 p.

Wallner, W. E. (1996). Invasive pests ('biological pollutants') and US forests: whose problem, who pays?. *EPPO Bulletin*, *26*(1), 167-180.

Zhang, C., Zhao, X., Gao, L., & Gadow, K. (2009). Gender, neighboring competition and habitat effects on the stem growth in dioecious *Fraxinus mandshurica* trees in a northern temperate forest. *Annals of Forest Science*, *66*(8), 812. https://doi.org/10.1051/forest/2009068

Tables

Table 5.1 - Survival, growth, and fecundity parameters for the baseline model. Survival parameters had more than one estimate from the literature and data, so the geometric mean and its standard deviation (in parentheses) are listed.

Parameter	Data Average (S.D.)	Citation	Details
G1	0.04 (NA)	Boerner & Brinkman 1996	Average survival of new seedlings over 1 year
G1	0.22 (0.4)	Messaoud & Houle 2006	Average new seedling survival from May to Sept.
P2	0.76 (0.12)	Kappler, R.H. 2018	2015-2017 survival Oak Openings Preserve seedlings < 1 cm
G2	0.76^12	Kappler, R.H. 2018	7 year average to grow into next stage
P3	0.93 (0.06)	Kappler, R.H. 2018	Oak Opening Preserve data
G3	0.07	Kappler, R.H. 2018	10 year average to grow into next stage, 0.93^10 too high so P+G=1
P4	0.68	Kappler, R.H. 2018	Oak Opening Preserve data
G4	0.68^10	Kappler, R.H. 2018	10 year average to grow into next stage
P5	0.53	Kappler, R.H. 2018	Oak Opening Preserve data
F5	241 (65)	Boerner & Brinkman 1996	Average new seedling per year over ten years for ash spp.

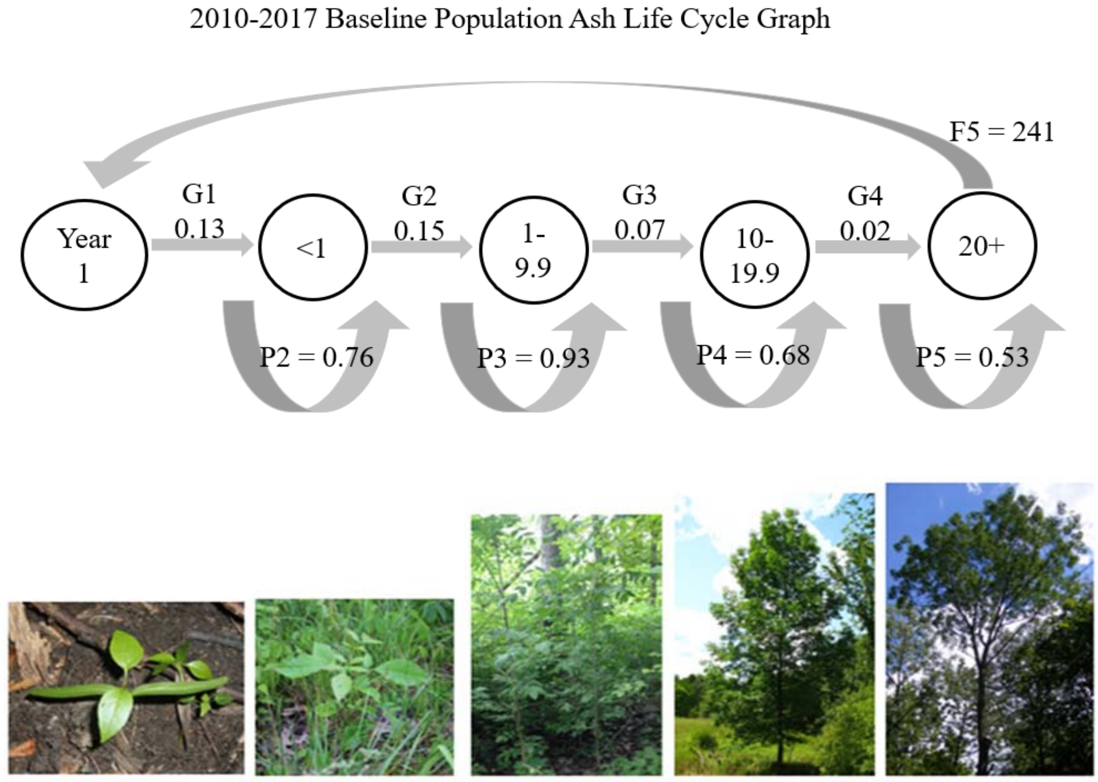
Table 5.2 - The results for models and scenarios, for each of the scenarios we report the growth rate, final (Year 50) average total abundance, probability of a 50% decline in abundance, number of year till a 50% probability of quasi(Q) extinction, and overall probability of extinction.

Scenario	**Growth Rate**	**Final Average Total Abundance**	**Probability of 50% decline**	**Years till 50% Probability of Q-extinction**	**Probability of extinction**
Baseline	1.05	8771	26%	> 50 y	0%
Catastrophe	1.05	38	99%	38 y	78%
Reduced Catastrophe	1.05	563	89%	> 50 y	30%
Competition	1.18	1340	82%	> 50 y	36%
Save adults	1.15	626	91%	50 y	50%
Save young adults	1.09	80	99%	40 y	72%
Save saplings	1.01	2	99%	35 y	91%
Save seedlings	1.09	6167	26%	> 50 y	1%
Restoration saplings	1.04	30	91%	> 50 y	41%
Restoration seedlings	1.04	37	95%	> 50 y	48%

Table 5.3. The results of the Kolmogorov-Smirnov test between models and scenarios. The D statistic represents the distribution difference between the two variables plotted curves. * denotes p < 0.0001.

Scenario Comparisons	**D statistic**
baseline vs. catastrophe	0.91*
baseline vs. reduced catastrophe	0.67*
catastrophe vs. reduced catastrophe	0.27*
catastrophe vs. competition	0.32*
catastrophe vs. adult save a stage	0.17*
catastrophe vs. young adult save a stage	0.02
catastrophe vs. sapling save a stage	0.06*
catastrophe vs. seedling save a stage	0.88*
catastrophe vs. sapling restoration	0.25*
catastrophe vs. seedling restoration	0.17*
sapling restoration vs. seedling restoration	0.07*

Figures



2010-2017 Baseline Population Ash Life Cycle Graph

Figure 5.1. The life cycle graphics, based on stages of the green ash tree, for the baseline population model. Each circle represents a life stage based on diameter size at breast height. Transition arrows are probabilities of survival for each stage (P2-P5), and probability of growing into the next stage (G1-G5). F represents the fecundity of the adult ash stage. P, G, and F parameters are used to calculate population projections. Below are photographic representations of each ash tree life stage.

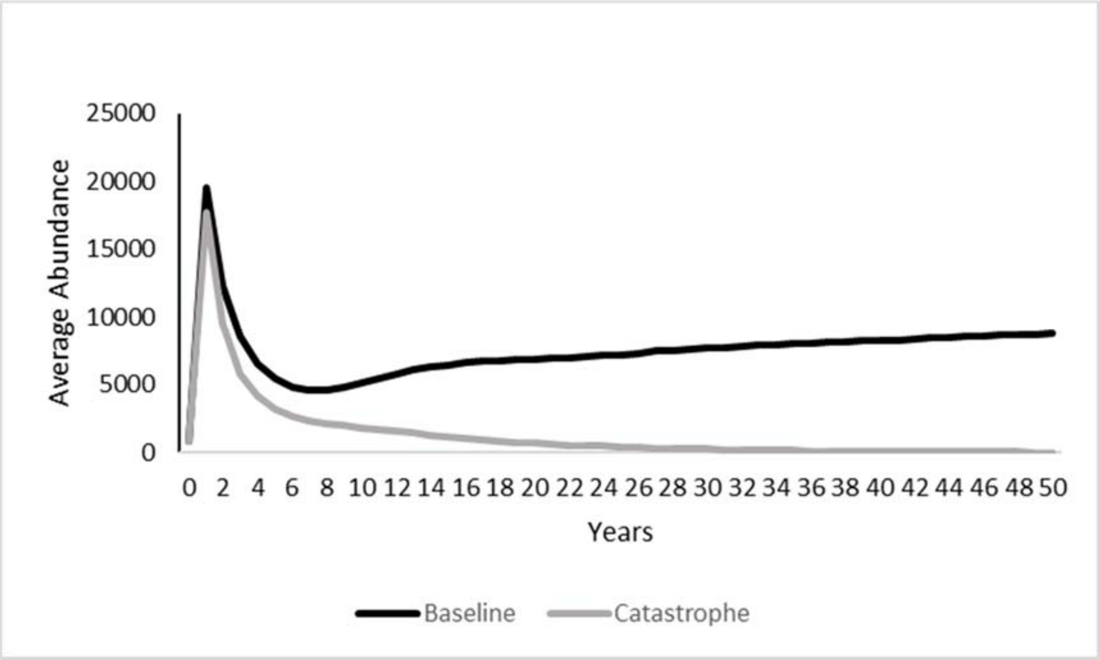


Figure 5.2. The average abundance trajectory over time for the baseline versus catastrophe models.

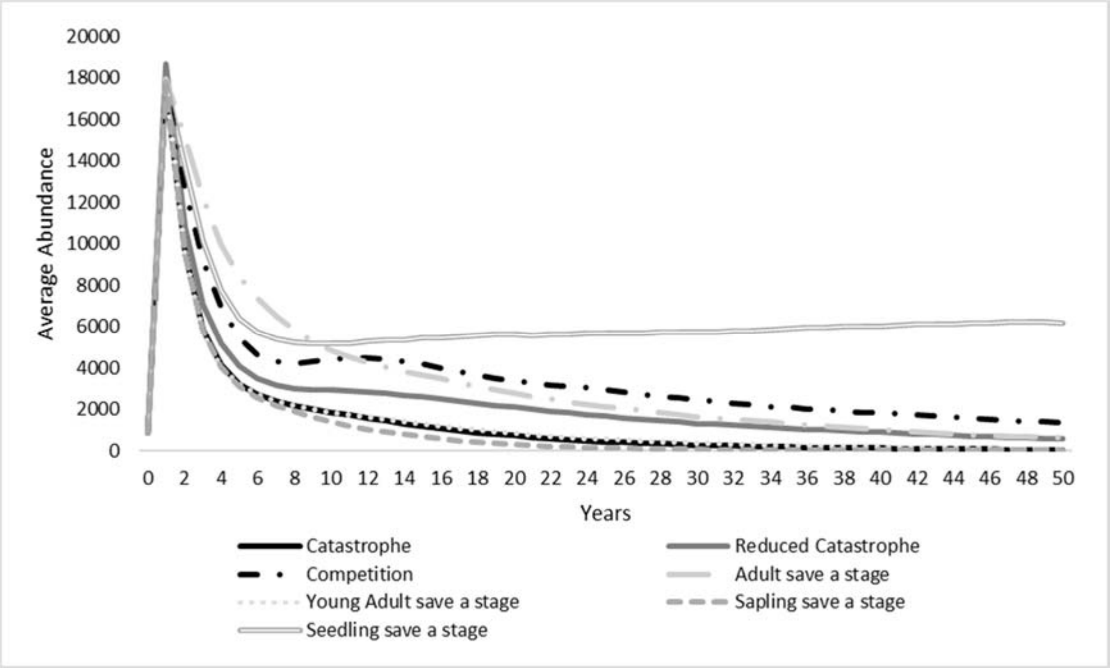


Figure 5.3. The average abundance trajectory for the management scenarios compared to the catastrophe model.

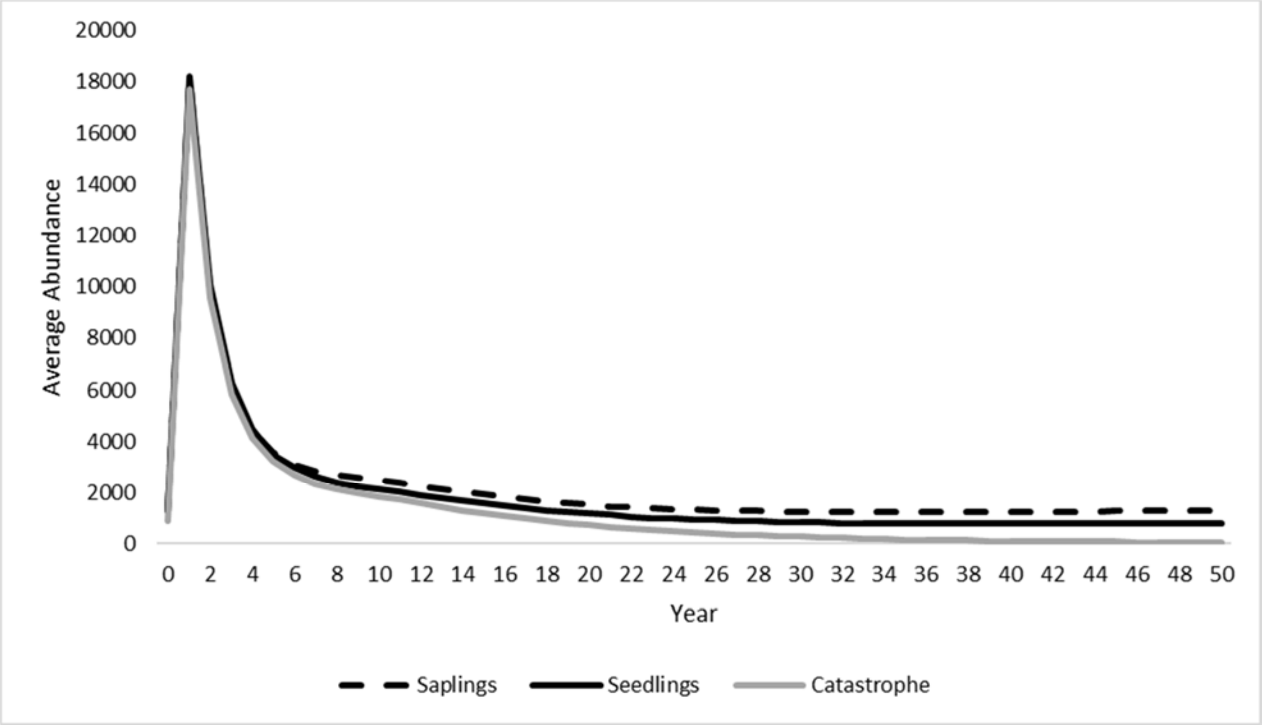


Figure 5.4. The average abundance trajectories for the restoration scenarios, comparing sapling to seedlings over time to the catastrophe model.