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Evaluating the population viability of green ash trees (*Fraxinus pennsylvanica*) before and after the emerald ash borer beetle (*Agrilus planipennis*) invasion

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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. We quantitatively estimated the viability of a local green ash tree (*F. pennsylvanica*) population to evaluate the magnitude of change caused by EAB. We developed historic and worst case stochastic stage based population scenarios to model changes in viability for a natural stand of green ash trees. Historic parameters were based on the literature, and worst case parameters were based on field data and the literature during dates that reflect time periods before and after EAB impacted the focal population in Northwest Ohio. The worst case scenario assumed that parameters remained the same as the initial EAB attack, when many of the adult trees died after a few years. The ash annual population growth rates were estimated as 0.99 and0.76, respectively, in historic versus worst case scenarios. The historic scenario had a population trajectory that dipped slightly at first and then reduced slowly over time. This was not unexpected since we included stochasticity in plant survival and reproduction, but it showed that the model may not account for ecological variation that stabilizes ash tree populations in forests under favorable conditions. In the worst case scenario ash populations became locally extinct within 34 years, and changes in the population growth rate were more sensitive to changes in the survival of the < 1 cm diameter at breast height stage class. Caution is warranted given the high variability and stochasticity within the system, and the trajectory can change if post-EAB population dynamics differ from initial EAB invasion dynamics or if human intervention occurs. The use of 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.

1. Introduction

Population parameters can be utilized to build predictive models (Akçakaya 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 (Akçakaya and 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 and 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 and Doak, 2002). The model parameters in a 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). Data from longer term studies or from the literature are used to refine model parameter estimates. For parameters for which there is 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 uncertainty in the parameters have on the accuracy of the model projections.

PVAs importance in conservation efforts means it should be adjustable in its design for different species, and there are a variety of

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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 (Akçakaya and 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 65 years on average, and is adapted to a variety of areas across the eastern United States (Kennedy, 1990; MacFarlan and Meyer, 2005; Stewart and 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 (Herms and McCullough, 2014; Kashian and Witter, 2011; Klooster et al., 2014; Knight et al., 2013). EAB was introduced near Detroit, Michigan, and is a specialist beetle from Asia that feeds and reproduces on *Fraxinus* species (Herms and McCullough, 2014). EAB adults feed on ash leaves, while EAB larvae feed on ash cambium underneath the bark. EAB can damage trees with a diameter at breast height (DBH, 1.37 m) of 2.5 cm or larger (Cappaert et al., 2005). After infestation, the trees in the mid to lower canopy (intermediate or suppressed) or in lower ash density stands died the fastest; and nearly 100% mortality of adult ash trees occurred within 6 years (Knight et al., 2013). Michigan floodplain forests infested by EAB had greatly reduced densities of ash seedlings and seed banks (Kashian and Witter, 2011; Klooster et al., 2014). 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 kills 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). These surviving ash trees are called lingering ash when they remain healthy for > 2 years after the area's ash mortality has reached 95% from EAB, and they have a diameter at breast height > 10 cm (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.

The goal of this study was to compare historic and worst case ash population dynamics within the floodplain forest. 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 degree of influence on long-term viability. In the face of large episodic changes, like invasive pests, that tree populations are likely to face in the future, population viability analysis can provide critical insight into the dynamics of catastrophes and recovery.

2. Methods

We developed stage-based population models for green ash in the Oak Openings Preserve Metropark of Northwest Ohio (41″ 32–34′N x 83″ 50–51′W) to compare historic versus worst case (i.e., peak-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. Ash trees are a sexually dimorphic species, so we utilized a female only model for simplification. As the ash sex ratio is typically 1:1 (Franklin, 1981; Zhang et al., 2009), therefore males would not significantly change the population trajectory. We used stage-based models to avoid the need to estimate the age of each individual tree for parameter estimates. Aging trees adds more complexity to the matrix; 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. Moreover, ash tree susceptibility to EAB appears to be size-based rather than age-based.

2.1. Model stages

Fecundity, survival, and the probability of growth to the next stage were needed for the model, with each stage based on ash size (Fig. 1). Size classes were categorized to assess population demographics of the different life stages. We separated size classes by trunk 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 variability in mortality. Full reproduction capabilities start after trees have reached 20 cm DBH (Franklin, 1981), and so only those > 20 cm reproduce in our models. The stages 1–9.9 cm and 10–19.9 cm were created for an even distribution of sizes between 1–20 cm. Seedlings < 1 cm DBH were not separated further as our survival information was similar for sizes within that size class.

2.2. Model parameters

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

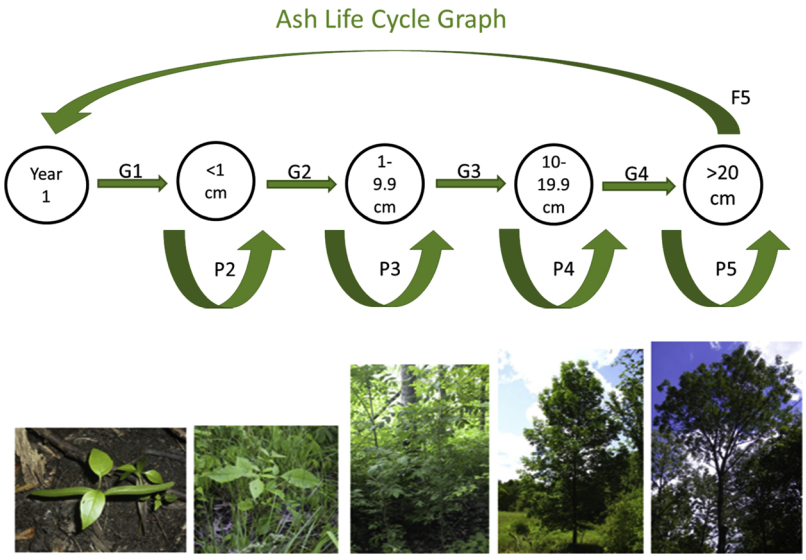

Fig. 1. The life cycle graphics, based on stages of the green ash tree, for the historic and worst case population scenarios. Each circle represents a life stage based on diameter size at breast height. Transition arrows are probabilities of survival for each stage (P2-P5), and probability of growing 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.

Table 1
The model scenarios, parameters, data and standard deviation (S.D.), citations and demographic parameters about the use in the historic and worst case models.

Model	Parameter	Average (S.D.)	Citation	Demographic parameters
Historic				
	G1	0.04 (NA)	Boerner and Brinkman, 1996	Average survival of new seedlings over 1 year
	G1	0.22 (0.4)	Messaoud and Houle, 2006	Average new seedling survival from May to Sept.
	P2	0.76 (0.12)	Kappler, 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 and 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 and Krinard, 1988	Survival of 2 and 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 and Krinard, 1988	Survival of 16 yr old planted floodplain trees
	P5	0.9 (0.1)	Marchin et al., 2008	Survival of common garden white ash over 30 years
	F5	241 (643)	Boerner and Brinkman, 1996	Average new seedling per year over ten years for ash spp.
Worst case				
	G1	0.04 (NA)	Boerner and Brinkman, 1996	Average survival of new seedlings over 1 year
	G1	0.22 (0.4)	Messaoud and Houle, 2006	Average new seedling survival from May to Sept.
	P2	0.76 (0.12)	Kappler, 2018	Oak Openings Preserve seedlings < 1 cm survival
	P3	0.19 (NA)	Kappler, 2018	Oak Openings Preserve 1-9.9 cm DBH survival in plots
	P4	0.02 (0.02)	Kappler, 2018	Oak Openings Preserve 10-19.9 cm DBH survival in plots
	P4, P5	0.03 (NA)	Kappler, 2018	Michigan survival post EAB for trees > 2.5 cm DBH
	P5	0.07 (0.05)	Kappler, 2018	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 (643)	Boerner and Brinkman, 1996	Average new seedling per year over ten years for ash spp.

Table 2
The parameter estimates and their standard deviations (± S.D.) for both the historic and worst case scenarios. Parameter mean estimates were used for growth (G), survival (P), and fecundity (F) at the appropriate stages (1–5, see Fig. 1.).

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	1×10^{-7}	0
P4	0.75	0.20	0.025	0.01
G4	0.01	0	1×10^{-7}	0
P5	0.9	0.10	0.10	0.10
F5	120	320	120	320

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 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 1). For the worst case model, local population demographics were based on literature published from 2005 to 2008 and previously collected data by the US Forest Service from 2005 to 2008 (Kappler, 2018), which represents the peak of EAB populations and ash mortality in this area. If a survival parameter had more than one estimate, we used the geometric mean and its standard deviation for the vital rates in the models (Table 2).

Fecundity 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, identified by presence of cotyledons (Boerner and Brinkman, 1996). We assumed this value represented the number of seedlings produced from one female tree, although only half of the seedlings would be female, so the number of seedlings and its standard deviation were divided in half for our fecundity parameter. The probability of remaining in a stage was based on yearly survival parameters, which were estimated from the literature, and with 3 years of US Forest Service survey data for the worst case scenario model. The

probability of growth 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 to estimate how many would transition between each stage (Caswell, 2001).

Emergent seedlings had a probability to grow into the next < 1 cm stage, which was based on emergent seedling first year survival research (Boerner and Brinkman, 1996; Messaoud and Houle, 2006). We assumed that growth from established seedling to 1.37 m tall would take a minimum of 5 years (Bonner and Karrfalt, 2008; Conner et al., 2000), and with our post-EAB outbreak data, on average, it took 2 years for trees to grow from 0.1 to 1.0 cm DBH. Therefore, in the model's 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 (Fig. 1).

2.3. Model specifications

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 half of the median value of the estimated abundance to represent female individuals in stages > 10 cm DBH. In the stable stage distribution based on the stage matrix, there were 46% yearlings, 41% seedlings, 12.5% saplings, 0.4% small adults, and 0.01% reproducing adults. We used the percentage per class and the estimated abundance of those > 10 cm to estimate the initial abundance of 213,013 individuals (101,105 yearlings, 55,637 seedlings, 47,355 saplings, 8077 young adults, and 839 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 allowed the populations to vary independently of the density until they reached carrying capacity and was set to 214,000). 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 (Akçakaya, 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 (Akçakaya, 1991). In creating a model based on the Oak Openings Preserve ash population, we assumed a closed population without immigration or emigration of ash trees.

2.4. Model analyses

These model scenarios serve as baseline models, which represent the 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 the population growth rate. 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 based on the minimum density required for successful pollination based on pollen dispersal characteristics (Beatty et al., 2015). Quasi-extinction assumed that once the population of female trees fell below 10 the population would become extinct. The predictions of the historic scenario were not only compared to the predictions of the worst case scenario, but also to the estimated population abundance of ash trees in 2010 and 2015. Data for the population estimates came from two data collection methods done in 2010 and 2015: trees > 10 cm were surveyed in the entire floodplain, and smaller size classes were surveyed in sampling plots (Knight et al., 2012; Kappler, 2018). Yearlings were estimated as the fecundity multiplied by number of > 20 cm trees, and size class 1–9.9 cm DBH were extrapolated from the plots sampled to the area of the floodplain. Total abundance was used for trees 10–19.9 cm and > 20 cm DBH.

3. Results

The ash annual population growth rates were estimated as 0.99 and 0.76, respectively, in historic versus worst case scenarios where EAB was absent or present over the next 50 years. The population abundance declined slowly under historic conditions, while the abundance steadily declined and was likely to crash under worst case conditions (Fig. 2). In the historic model it was the adult (> 20 cm DBH) survival that contributed the most, whereas for the worst case scenario the ash population elasticities showed that only seedling (< 1 cm DBH) survival contributed to changes that could occur in the population growth rate (Table 3). There was a significant difference in interval extinction risk between the historic and worst case scenarios ($P < 0.001$, $D = 0.99$); the difference in the final minimum tree abundance between the two scenarios was 17,563 individuals. The population under the worst case scenario had a 99.6% probability of extinction, reaching on average < 1 individual by Year 45, and had a 50% probability of quasi-extinction by Year 34 (Fig. 3). Average initial and final stage abundances for the historic scenario were similarly distributed, with more individuals in the 10–19.9 cm size class at the end of the simulation. The final historic population had an average of 50% yearlings, 24% for < 1 cm, 21.4% for 1–9.9 cm, 3.8% for 10–19.9 cm, and 0.4% for > 20 cm DBH.

The projected trajectory of the worst case scenarios seems to mimic the field estimates from 2010 and 2015. From our surveys we estimated that there were 82,395 ash trees in the floodplain in 2010. In 2010,

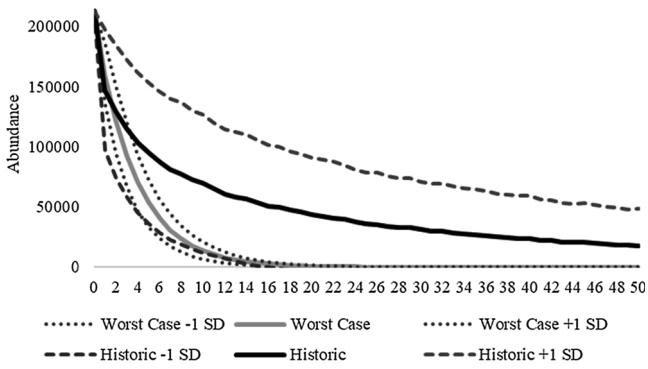

Fig. 2. The average population abundances and standard deviations (SD) for the worst case and historic population scenarios. Worst case standard deviations are in dots, while historic standard deviations are dashed.

Table 3
The elasticities for the (3a) historic and (3b) worst case 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.

3a. Historic Scenario

Stages (cm)	(yearling)	(< 1)	(1-9.9)	(10-19.9)	(> 20)
(yearling)	0	0	0	0	0.040
(< 1)	0.040	0.127	0	0	0
(1-9.9)	0	0.040	0.184	0	0
(10-19.9)	0	0	0.040	0.120	0
(> 20)	0	0	0	0.040	**0.370**

3b. Worst case Scenario

Stages (cm)	(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

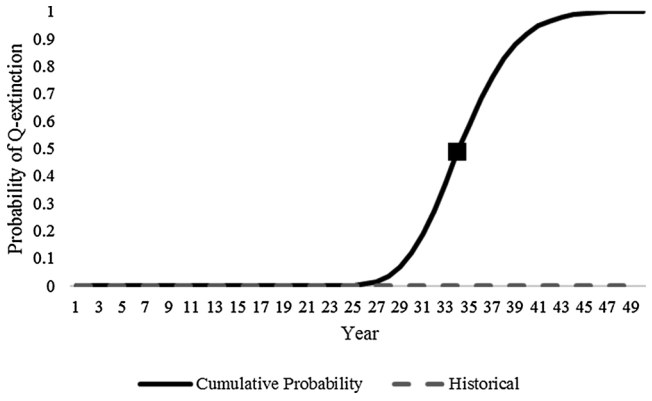

Fig. 3. The probability that the population of the worst case and historic scenario will fall below 10 individuals (Q-extinction). There is a 50% probability of quasi extinction within 34 years, denoted by the square, and 0% probability for the historic scenario.

abundance estimates were 6600 for yearling, with 74,478 individuals < 1 cm, and 2050 trees size 1–9.9 cm; we found 212 trees size 10–19.9 cm and there were 55 trees > 20 cm. When comparing worst case scenario abundance to the estimated ash population abundance from 2010 survey data, they were relatively similar at Year 4 of the simulation (70,167 ± 23,280) or 4 years post peak infestation. In 2015, the floodplain had an estimated 15,539 individual ash trees present. There were an estimated 8640 yearlings, 6150 trees < 1 cm, and 470 trees 1–9.9 cm; we found 207 trees size 10–19.9 cm and 72 trees > 20 cm. The worst case scenario abundance estimates at Year 9 were similar to 2015 data at 17,661 ± 8660 individuals.

4. Discussion

The population models met our expectations, where historic and worst case scenarios predicted different outcomes, a 23% decline in population growth rate under invasion, indicates the degree of overall population change. The historic trajectory slowly decreased over time, which indicates that the natural ash population was very close to, but not completely stable. The worst case trajectory predicted extinction, likely within 34–41 years, but caution is warranted given the high variability and stochasticity within this system, as seen in the standard deviations around the curves (Fig. 2) from each scenarios 10,000 replications. We found that large adult trees were important to the population growth rate of the historic scenario, e.g., had the greatest influence on population growth, and that importance switched to seedlings (< 1 cm DBH) in the worst case scenario.

The overall the population growth rate of the historical scenario was most sensitive to change in the survival of the adult ash size class (> 20 cm DBH), which is likely from their contribution to the population via reproduction. In comparison, population growth rate in the worst case scenario was most sensitive to change in the survival of the seedling size class (< 1 cm DBH). Since this size class is not impacted by EAB (ash > 2.5 cm DBH are damaged by EAB) they are a critical stage in the ash life cycle (Cappaert et al., 2005). This differentiation between scenarios emphasizes the impact EAB has on varying stages of ash life cycle and that recovery will be dependent on the stage structure of the population following invasion. The younger stage could be the focus of future exploration into ash forest management. Research at the same location had shown leaf litter and ash basal area as important indicators of ash seedling presence (Kappler, 2018). Useful insights from PVA results are important to any species management plan.

In the worst case scenario EAB continued to have a major effect on tree survivorship over time, and this was the factor that lead to a quasi-extinction of the population by Year 34. This scenario extrapolated the impact of EAB during high ash mortality, one in which no human intervention takes place, and vital rates remain at peak ash mortality levels. We expect our worst case scenario will not come to fruition, but allows us to extrapolate the intensity of the change which occurred with the EAB outbreak. We hypothesize that current ash trees will grow over time with a lower EAB infestation rate than the previous generation since we have witnessed the next cohort of ash infested when they are a smaller size (Kappler, 2018). 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 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 local population dynamics (unpublished data), which is typical for invasive species (Williams, 1996). Invasive species population information can be used in models to estimate how often catastrophic infestation events may occur in the future, which we plan to incorporate in 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 (Kappler, 2018).

The worst case scenario 4th year was comparable to the 2010 survey abundance estimate, as well as the 9th year comparison to the 2015 abundance estimate. In 2010 our location had experienced a 99% loss of ash trees > 10 cm which had occurred over 6 years (Knight et al., 2013). Therefore, the modelled scenario closely mimics the actual events. As such, our model's quasi-extinction of 34 years indicates that our location extinction would be around the year 2040 if high ash mortality conditions remain prevalent. These results should be viewed with caution though, as our 2010 survey data was extrapolated for the smaller size classes, including yearlings, which were found to have high variability in survival (Boerner and Brinkman, 1996; Messaoud and Houle, 2006). These comparisons suggest that worst case model has captured much of the trend in ash abundance that was first observed, which highlights the benefit in considering PVA to facilitate understanding of these natural populations.

Management has also 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 also been proven 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 and the longevity of the population.

The historic scenario had a population trajectory that dipped slightly at first, and then decrease slowly over time. The decrease in the population abundance was not unexpected since we included stochasticity in plant survival and reproduction. The trajectory showed that the ash tree population was unlikely to be sustainable forever under the conditions we initiated. In subsequent analyses with longer time periods used, our historic scenario had a quasi-extinction at Year 132, and when standard deviations were removed the population did not go extinct, which indicates the variation in our parameters maybe too large to produce a stable ash population over time. It is also possible that over 50–100 years habitat changes would influence ash parameters towards a different growth rate. We did not explicitly account for other potential influences beyond what was inherent in the demographic estimates. For our estimates we were able to find literature on adult ash survival in horticultural gardens, which may or may not be accurately reflected in natural settings. 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. We found less literature, though, focused on natural ash germination, seedlings and the oldest ash stage of growth, especially for historic parameters. 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.

Our model scenarios were based on green ash in a floodplain or bottomland habitat and would likely have slightly different outcomes for ash species in different 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. In addition, this stage-based modeling approach is readily adaptable to other locations, other species, and other habitat types. PVA is very useful for organizing information, assessing vulnerabilities, and addressing specific questions about a species (Akçakaya and 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 and seperate 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 also 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. However, as adult ash tree populations fall to low densities, it is possible that lack of pollination will limit the reproduction success of female trees. Further study is needed to account for impacts on model parameters from different proportions of males and females and increasing distance between trees as the number of trees decreases.

While plant species population models can be difficult to build, trees can effectively be modeled with a stage structure matrix (Davelos and Jarosz, 2004). Our model adds to the few population viability analyses developed for tree species. Other tree models have explored the long term influence of rapid impacts such as pest infestation or harvest. In harvest scenarios for big-leaf mahogany, yields were severely depleted after 2–3, 30-year 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 (*Pinus albicaulis*) 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). Of the utmost importance is understanding what did and could occur with the EAB invasion over time, and PVA can help accomplish this.

EAB has been found in many other areas within the eastern N. America ash tree range. This research reveals how natural green ash tree population dynamics change in the face of an invasive pest outbreak. We will be able to apply our results to future models that assist in adaptive management planning to improve natural ash population dynamics which may be applicable to other areas across the species range.

Declaration of interest

None.

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