



Strategic removal of host trees in isolated, satellite infestations of emerald ash borer can reduce population growth



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ABSTRACT

Emerald ash borer is an invasive beetle causing significant mortality of ash trees (*Fraxinus* spp.) in North America and western Russia. The invasive range has expanded to more than half of the states in the United States since the initial detection in Michigan, USA in 2002. Emerald ash borer is typically managed with a combination of techniques including surveys/trapping, insecticide treatments, host tree removal, biological control, and public education/outreach. The insect's rapid spread rate and cryptic life history and a lack of resistance among most North American *Fraxinus* spp. have limited opportunities to gather empirical data on how aggressive tree removal may slow population growth in isolated, satellite infestations if detected early. An early detection of an isolated population of emerald ash borer in 2009 in Minnesota, USA was managed by using a selective host-tree removal program (i.e., sanitation). Trees were preferentially removed based on the assumption that evidence of woodpecker foraging (i.e., pecking) was a good indicator of infestation by emerald ash borer. Extensive sampling and survey data on larval densities and the presence/absence of pecking on ash trees in a 6-km² area for the Twin Cities, Minnesota were used to parameterize a model of population growth over the next four years. We found that removing ~63% of the total trees across four years reduced the cumulative number of beetles produced in the core infested area by ~54%. However, we also found that increases in efficacy, i.e., larger decreases in beetle production per removed tree, could be achieved by preferentially removing trees with pecking. The invasive range of emerald ash borer in North America and western Russia continues to expand via natural and human-aided dispersal. While silvicultural control tactics alone will not be an adequate management strategy, tree removal is an important component of both a broader pest management program and the systematic replacement of ash canopies in urban forests. Increasing understanding of the efficacy of different management techniques in slowing population growth of emerald ash borer will be useful to support decision-making by land managers.

1. Introduction

Invasions and range expansions by alien or native species create global challenges. Invasive alien species cause severe ecological and evolutionary impacts across a range of ecosystems with economic impacts totaling \$150 billion in damages and losses in the United States alone per annum (Mooney and Cleland 2001; Pimentel et al., 2005; Pejchar and Mooney, 2009). Increases in international trade and globalization have been positively correlated with establishment rates of non-native species in North America (Levine and D'Antonio, 2003; Hulme, 2009; Aukema et al., 2010; Huang et al., 2011). Within invaders from the class Insecta, over half of new insects detected in the United States from 1980 to 2006 were classified as phloem- or wood-boring

(Aukema et al., 2010). Between 1985–2005, for example, at least 25 new species of phloem or wood-boring beetles became established in the United States (Haack, 2006). Several *Agrilus* spp. (Coleoptera: Buprestidae), referred to as flat-headed borers, have emerged as destructive native and alien pests of hardwoods in both the United States and Europe (e.g., Coleman et al., 2012; Brown et al., 2014; Herms and McCullough, 2014).

The emerald ash borer *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) is an invasive pest native to eastern Russia and China that was discovered causing widespread mortality of ash trees (Oleaceae: *Fraxinus* spp.) near Detroit, MI, USA in 2002 (Haack et al., 2002; Poland and McCullough, 2006; Herms and McCullough, 2014). The initial introduction near Detroit likely occurred in the early to mid 1990s

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(Siegert et al., 2014). The discovery of emerald ash borer in North America was followed by the detection of another invasion by this insect in Moscow, Russia in 2003 (Baranchikov et al., 2008). The invasive range of emerald ash borer in North America has since expanded to include two Canadian provinces and more than twenty states in the central and eastern half of the contiguous United States (Herms and McCullough, 2014). The expansion of the invasive range is due in part to natural dispersal via the strong-flying adults (Mercader et al., 2009; Siegert et al., 2010; Taylor et al., 2010; Fahrner et al., 2015), whereas long range dispersal is primarily driven by the human-mediated movement of firewood (BenDor et al., 2006; Herms and McCullough, 2014). Most species of ash appear highly susceptible to infestation by emerald ash borer (Herms and McCullough, 2014) and most of the North American continent where *Fraxinus* spp. occur remains at risk.

Following a new detection of an invasive phloem or wood-boring insect, there are several management options available (Brockerhoff et al., 2006; El-Sayed et al., 2006; Brockerhoff et al., 2010; Suckling et al., 2012). If the invader is detected soon after establishment and the area infested is sufficiently confined, eradication may be attempted via a combination of insecticides, trapping/surveys, host plant removal, and public outreach (Haack et al., 2010; Suckling et al., 2012). For example, Asian long-horned beetle has been successfully eradicated from urban sites in Japan and Chicago, IL, USA using a combination of these methods (Haack et al., 2010; Liebhold et al., 2016). However, similar concerted attempts to eradicate emerald ash borer from the site of initial establishment failed (Herms and McCullough, 2014). No successful eradications of emerald ash borer have ever been reported, likely due to its endophytic larval life history and difficulties in detecting low-density infestations (Tobin et al., 2014; Herms and McCullough, 2014).

When eradication fails, efforts shift to reducing populations of the pest below ecologically and/or economically damaging levels. A pilot project called SLAM (SLOW Ash Mortality) was initiated as a management strategy in 2008 against emerald ash borer, for example (McCullough and Mercader, 2012). The program integrates the application of systemic insecticides, girdling and removing trees, and reducing phloem resources on the landscape via the removal of at-risk and infested host trees (Herms and McCullough, 2014). Indeed, host plant removal may be a useful technique in decreasing population growth and spread of emerald ash borer, despite social challenges and difficult logistics of removing and destroying large host plants (Suckling et al., 2012). Computer simulations have suggested, however, that host removal may exacerbate dispersal of emerald ash borers if individuals disperse farther to procure resources (Mercader et al., 2011b). Elucidation of the impacts of removing host trees on the population dynamics of emerald ash borer will bolster comparisons between management options and, potentially, aid decision-making by resource managers.

The aim of our study was to develop a simulation model from empirical data and apply it to determine if the removal of at-risk or infested trees in a recently-established satellite infestation of emerald ash borer could significantly influence population growth. In May 2009, emerald ash borer was discovered in Saint Paul, Minnesota, USA. The Minneapolis-Saint Paul region is an urban center of approximately 4 million people with the urban forest comprised of ~14% ash (> 11 million ash trees). Dendrochronological analyses showed a lag time of approximately 3–4 years between introduction and detection (N.W. Siegert, personal communication), and no trees were visibly dead at time of detection. After detection and an extensive delimitation survey, an aggressive tree removal program was undertaken in which trees with evidence of woodpecker foraging were targeted during annual removals. Log sections were sampled from standard areas of removed trees to characterize emerald ash borer populations. Specifically, larval densities and instar distribution were recorded, from which the proportion of the population emerging in the current vs. subsequent years was estimated.

Here, we analyze the effects of four years of host tree removal on the population growth of emerald ash borer from 2009 to 2013 in the Minneapolis-Saint Paul Metropolitan Area. We aimed to (1) quantify the effects of host tree removal on the cumulative number of beetles produced across four years, (2) determine if preferentially removing trees with woodpecking influenced cumulative beetle production, and (3) determine how voltinism may have moderated the efficacy of tree removal. Quantification of efficacy was achieved by comparing the actual management scenario to hypothetical management scenarios using a model parameterized with these data collected in Minnesota. We hope that conclusions from this study will improve decision making by municipalities and state governments in the management of newly-established satellite infestations of emerald ash borer as well as other invasive endophytic insect pests of trees.

2. Materials and methods

2.1. Core infested area

In 2009, the Minnesota Department of Agriculture (MDA) initiated a survey program throughout the Minneapolis-Saint Paul Metropolitan Area to delimit a recently established infestation of emerald ash borer. The delimitation survey used purple prism traps and external symptoms (e.g., evidence of woodpecker foraging, epicormic shoots, crown thinning) to identify trees that were potentially infested. A rhombus, the “core infested area,” of approximately 6 km² was identified (Fig. 1). Ensuing management efforts between 2009 and 2013 were aimed at reducing emerald ash borer populations and phloem resources via the removal of ash trees. This study focused on 2370 ash trees in the core infested area at the start of our study in 2009. The primary goal of the study was to determine the impact of sanitation on emerald ash borer population growth. Consequently, we excluded 260 trees that were either treated with insecticides or girdled before removal during the course of the study because emerald ash borer numbers might be expected to be lower than average in treated trees and higher than average in girdled trees. Thus, there were 2370 ash trees in the core infested area at the start of our study in 2009 in addition to the 260 trees that had been subjected to girdling or treatment with insecticides. The *Fraxinus* component of the core infested area and removed trees were mostly *Fraxinus pennsylvanica* (Marshall) with a small portion of white ash *Fraxinus americana* (L.).

2.2. Tree surveys and removal

As part of ongoing surveys from 2009 to 2013 following the discovery of emerald ash borer in Saint Paul, the MDA recorded diameter at breast height (DBH; approximately 1.4 m above ground) and presence/absence of foraging damage by woodpeckers (referred to henceforth as “pecked or pecking”/“unpecked”, respectively) on every tree in the core infested area. In emerald ash borer infestations, pecking appears relatively early compared to other symptoms such as epicormic shoots and thinning of the crown (Baranchikov et al., 2008; Lindell et al., 2008; McCullough and Mercader, 2012) and woodpecker predation is positively associated with densities of emerald ash borer (Lindell et al., 2008; Jennings et al., 2013, 2016). Thus, trees with pecking were targeted for removal. Surveyors were equipped with binoculars to increase detectability of pecking on branches in the upper crown. Surveys typically occurred during winter when leaves were absent and pecking was easier to detect.

Despite preferential removal of trees with pecking, both pecked and unpecked trees were removed during the study and removals occurred year-round (Table 1). For analyses, trees were assigned to a given removal year such that trees removed in Spring 2009 through Spring 2010 were recorded as removed in 2010, with similar patterns followed for 2011, 2012, and 2013. Over four years of removal, from 2010 to 2013, 1497 trees were removed (Table 1). In our data, 71 of the 2370



Fig. 1. Map of core infested area, Minneapolis-Saint Paul, MN, USA. Core infested area enclosed by a 6 km² polygon delimited via surveys by the Minnesota Department of Agriculture (MDA). First detection of emerald ash borer in Minnesota was near Hampden Park by an arborist in 2009, well before any tree mortality was observed.

Table 1
Summary statistics of the tree removal program by year from 2010 to 2013 in the core infested area in the Minneapolis-Saint Paul, MN, USA.

Status	Year	Trees	DBH (± SE) cm	Proportion pecked ^a
Removed	2010	197	31.8 (1.21)	0.87
Removed	2011	377	31.6 (0.84)	0.74
Removed	2012	641	18.1 (0.54)	0.32
Removed	2013	282	37.1 (1.06)	0.53
Removed	2010–2013	1497	26.7 (0.45)	0.54
Standing	2009	2370	27.6 (0.36)	
Standing	2014 ^b	873	29.1 (0.59)	

^a Proportion of removed trees that had evidence of woodpecker foraging at time of removal. Thus, 13% of trees removed in 2010 did not have pecking.

^b Reduction in trees was due to management. Most trees were removed preemptively and < 1% of trees were killed by emerald ash borer.

trees in the core infested area (3%) were missing DBH measurements. Ten of these trees were removed during management. Analyses required a measurement of tree size (see below), so each tree with a missing diameter record was assigned a randomly sampled value from a log-normal distribution fit to the values of diameters of all trees in the core infested area. This distribution was fit using maximum likelihood estimation (Fig. S1) via the fitdistrplus package in R (Delignette-Muller and Dutang, 2015). The maximum likelihood estimates for the log-normal distribution (± SE) were $\bar{x} = 3.14$ (0.01) and $s = 0.68$ (0.01).

2.3. Population growth

A population growth model for beetle production was developed to

assess the efficacy of the management program implemented in the core infested area from 2010 to 2013. This model was built from empirical data and run for 200 simulations. Following is a detailed description of model construction and a summary is included in Table 2.

A portion of the trees removed between September and May were selected each year for subsampling to estimate the number of larvae per square meter of phloem in host trees. To determine larval densities, the bark was completely removed from a branch section or section of the main stem (i.e., a sample log). There were 894 sample logs ranging from 2.54–50.8 cm (mean = 12.6 cm) in diameter and 12.7–304.8 cm (mean = 90.6 cm) in length. The average diameter of a log, which are typically conical, was estimated by averaging the diameter measurements taken from both ends of the log. Number of logs sampled per tree ranged from 1 to 10 with a mean (± SE) of 3.43 (0.10) samples per tree. A total of 261 different trees were sampled. Larvae were recorded by developmental stage (i.e. instars one through four, j-larvae, and pre-pupae). Overwintering larvae in a j-shape were recorded as j-larvae whereas as all larvae that appeared straight, shortened, and broadened were recorded as pre-pupae (Wang et al., 2010). The total number per square meter of phloem was then calculated [= number of larvae in all stages/(average diameter of sample in meters × π × length of sample in meters)]. A summary of log sampling data and associated larvae are included in Tables 3 and 4, respectively. Log sampling data was aggregated to the tree level (i.e. total number of larvae found per total area of phloem examined per tree) such that each sampled tree had a single estimate for larval density. Given that presence/absence of pecking was recorded for each tree, the resulting data set of larval densities and trees was split into pecked and unpecked trees, producing two subsets of data. A linear mixed-effects model with a term for “sample year” fit as a random intercept was used to determine if the

Table 2

Summary of population growth model for larval emerald ash borers from 2010 to 2014 in the core infested area in Minneapolis-Saint Paul, MN, USA with statistical distribution and parameters.

Step	Procedure
1.	If tree does not have a recorded diameter, randomly assign a value from a log-normal distribution ($\bar{x} = 3.14$ cm, $s = 0.68$ cm)
2.	Estimate surface area of each tree based on its diameter at breast height (Eqs. (2) and (3) in text).
3.	Define the carrying capacity for larvae per square meter of phloem for each tree.
4a.	If a tree is pecked, determine if that tree will contain larvae using a random sample from a binomial distribution ($p = 0.82$). If the draw is equal to 1, randomly draw a value for larval density from a log-normal distribution ($\bar{x} = 1.70$ larvae per square meter of phloem, $s = 1.05$). If the draw is equal to 0, then the tree will not contain larvae.
4b.	If a tree is not pecked, determine if that tree will contain larvae using a random sample from a binomial distribution ($p = 0.53$). If the draw is equal to 1, randomly draw a value for larval density from a log-normal distribution ($\bar{x} = 0.59$ larvae per square meter of phloem, $s = 0.90$). If the draw is equal to 0, then the tree will not contain larvae.
5.	Scale the number of larvae per square meter of phloem to the number of larvae per surface area of the entire tree. These larval densities equal the estimated beetle population emerging in spring 2010 (year 1).
6.	Take a random draw to obtain a simulation-specific growth rate, Gaussian($\bar{x} = 1.90$, $s = 1.01$).
7.	Grow beetles produced by each tree for “3–X” steps, where X = the number of years before 2013 that a tree was removed. That is, trees removed in 2010 would be grown for 3–3 = 0 time steps, as these trees would be removed before beetles could emerge from them in spring 2010. For the <i>no removal</i> scenario, X = 0 for each year. For scenarios with mixed voltinism, number of adults emerging from a given pecked tree or unpecked trees was multiplied by 0.61 and 0.42, respectively. The remaining proportions (0.39 and 0.58) emerged the following year if the tree was not removed.
8.	Record yearly number of beetles produced for each year in each management scenario.
9.	Repeat steps 1–8 for 200 iterations. An additional 600 simulations were run, 200 with $R \sim \text{Gaussian}(\bar{x} = 5.18, s = 1.51)$, 200 with $R \sim \text{Gaussian}(\bar{x} = 10.35, s = 3.02)$, and 200 with $R \sim \text{Gaussian}(\bar{x} = 10.35, s = 0)$

larvae per square meter of phloem differed between pecked and unpecked trees ($\alpha = 0.05$). The variable for larval density was log-transformed ($\log_e(y + 0.01)$) to meet assumptions of homoscedasticity of the errors.

To run simulations, every tree in the data set required a value for larval density in 2010 (at the start of management). For trees that were directly sampled, we calculated larval densities in 2010 as follows:

$$N_{1,i} = \frac{N_{y,i}}{R^{y-1}} \quad (1)$$

where $N_{1,i}$ is the number of larvae per square meter of phloem in tree i in year 1 (2011), $N_{y,i}$ is the number of larvae per square meter of phloem in tree i in year y , and R is the population growth rate. Thus, if a tree was directly sampled, that empirical estimate for larval density was used. The growth rate, R , was the same for each tree within a simulation and was randomly drawn from a Gaussian distribution with $\bar{x} = 1.90$ and $s = 1.01$ at the start of each simulation. The mean and standard deviation of the statistical distribution were calculated from the 3 ratios of larvae per square meter of phloem in unpecked trees in successive years (e.g., 2012 larval density/2011 larval density in unpecked trees = 1.42, 2013/2012 = 3.05, and 2014/2013 = 1.21). Ratios of larval densities across years were used to obtain a growth rate applicable to the satellite infestation under investigation. The growth rates we estimated were within but on the lower end of growth rates reported in the primary literature (Mercader et al., 2011a; Duan et al., 2014, 2015). The growth rate was sampled at the start of each simulation. Larval densities for each year (2010–2013) were necessary to estimate the number of beetles emerging from each tree in each year.

We used our empirical data to estimate larval densities in trees that

Table 3

Summary of 894 log samples aggregated to the tree level for trees removed from 2010 to 2013 in the core infested area in Minneapolis-Saint Paul, MN, USA.

Year	Trees sampled	Proportion pecked	Proportion infested ^a		EAB density ^b (± SE)	
			Pecked	Unpecked	Pecked	Unpecked
2010	91	0.87	0.82	0.53	7.52 (1.13)	1.36 (0.52)
2011	139	0.74	0.70	0.44	5.77 (0.81)	2.62 (0.99)
2012	16	0.32	0.78	0.57	6.20 (1.68)	5.92 (2.59)
2013	12	0.53	0.43	0.60	10.9 (9.10)	3.57 (2.02)
Total	258	0.54	0.74	0.49	6.65 (0.69)	2.76 (0.67)

^a Values do not sum to 1, as proportions reported refer to the percent of pecked and unpecked trees that contained larvae, respectively (e.g., 82% of trees with pecking in 2010 were infested compared to unpecked trees in 2010 of which only 53% were infested).

^b Larvae per square meter of phloem.

Table 4

Summary of larval data from sample logs taken from trees removed between 2010 and 2013 in the core infested area in Minneapolis-Saint Paul, MN, USA. Data were used to estimate number of larvae requiring an extra year to complete development.

Year	Larvae detected	Proportion in pecked samples ^a	Proportion of larvae expected to emerge in current year from pecked samples ^b	Proportion of larvae expected to emerge in current-year from unpecked samples ^b
2010	706	0.62	0.65	0.25
2011	752	0.64	0.58	0.55
2012	97	0.67	0.55	0.47
2013	52	0.67	0.69	0.88

^a Proportion of larvae within a given year that were found in a pecked log sample.

^b Current-year larvae = larvae in the 4th instar or any subsequent immature stage. Current-year larvae are expected to emerge within 1 year from time of observation.

were not directly sampled. Using all trees that were removed in 2011, the proportion of both pecked and unpecked trees containing emerald ash borer was quantified ($p = 0.82$ for pecked trees and $p = 0.53$ for unpecked trees). For trees that were positive for emerald ash borer, a log-normal distribution was fit to the larval density of both pecked and unpecked trees using maximum likelihood estimation via the fitdistrplus package in R (Delignette-Muller and Dutang, 2015). The maximum likelihood estimates for the mean (± SE) and standard deviation (± SE), respectively, were 1.70 (0.13) and 1.05 (0.09) larvae per square meter of phloem for pecked trees compared to 0.59 (0.32) and 0.90 (0.22) for unpecked trees (Fig. S1). Each tree that was not sampled directly was then assigned a larval density (larvae/m² phloem) based on two random draws from either pecked-specific or unpecked-specific

Table 5
Definitions for the tree removal scenarios that were simulated for the core infested area in Minneapolis-Saint Paul, MN, USA.

Management scenario ^a	Type of scenario	Description
<i>Actual</i>	Actual	Actual management scenario for core infested area in which trees were selectively removed from the landscape.
<i>No removal</i>	Hypothetical	No trees removed from the core infested area.
<i>Delayed</i>	Hypothetical	Removed same number of trees as <i>actual</i> , except all removals occurred at a single time point in winter 2013.
<i>Pecked-only</i>	Hypothetical	Removed only the pecked trees out of trees removed under <i>actual</i> .
<i>Random</i>	Hypothetical	Removed same number of trees per year as <i>actual</i> , except removals were done randomly.
<i>Adjusted-random</i>	Hypothetical	Removed same trees as <i>random</i> , except trees were standardized for surface area so that phloem removed was equivalent to <i>actual</i> .
<i>Voltinism</i>	Actual	Equivalent to <i>actual</i> except accounted for delayed beetle emergence between pecked and unpecked trees
<i>No removal-voltinism</i>	Hypothetical	Equivalent to <i>no removal</i> except accounted for delayed beetle emergence between pecked and unpecked trees

^a All emerald ash borer populations were assumed to be univoltine for all management scenarios except for *voltinism* and *no removal-voltinism*, in which a proportion of the populations were assumed to require an extra year to complete development.

distributions. The first draw was from a binomial distribution and, if the draw was equal to 1 (indicating presence of emerald ash borer), a second draw from a log-normal distribution was assigned as the larval density. For pecked and unpecked trees, the binomial distributions were parameterized with $p = 0.82$ and $p = 0.53$ whereas the log-normal distributions were parameterized with $\bar{x} = 1.70$ and $s = 1.05$ and $\bar{x} = 0.59$ and $s = 0.90$, respectively. Thus, every tree in the data set that was not directly sampled was randomly assigned a larval density based on statistical distributions parameterized using data collected in 2011 from pecked and unpecked trees in the core infested area.

Each tree in the data set was also assigned a carrying capacity for larvae per square meter of phloem. The carrying capacity of larvae per tree, K , was randomly assigned based on published estimates of maximum number of exit holes per square meter of phloem: 105 (± 5.7 SE) estimated from 39 large trees (> 13 cm in DBH) and 69 (± 5.9 SE) estimated from 32 small trees (≤ 13 cm in DBH) (McCullough and Siegert, 2007). To permit variation in maximum beetle production per square meter of phloem, two Gaussian distributions were parameterized with $\bar{x} = 105$ and $s = (5.7 \times)$ for large trees and $\bar{x} = 69$ and $s = (5.9 \times)$ for small trees. The larval density per square meter of phloem for each tree was capped at this randomly assigned carrying capacity to protect against randomly assigning impossibly high larval densities.

Larval densities were then scaled from larvae per square meter of phloem to larvae residing in the entire tree. To achieve this, the surface area of trees (i.e. amount of phloem available to developing larvae) was estimated using two regression equations published by McCullough and Siegert (2007) that relate diameter at breast height to surface area for ash trees. Using data from green ash (*F. pennsylvanica*) and white ash (*F. americana*) trees, McCullough and Siegert (2007) developed separate equations for large trees (> 13 cm in DBH; Eq. (2)) and small trees (≤ 13 cm in DBH; Eq. (3)):

$$\text{phloem}_i = 2.630(\pm 0.881) - \text{dbh}_i \times 0.307(\pm 0.081) + \text{dbh}_i^2 \times 0.024(\pm 0.001) \quad (2)$$

$$\text{phloem}_i = -1.759(\pm 0.274) + \text{dbh}_i \times 0.380(\pm 0.027) \quad (3)$$

where phloem_i is the amount of suitable phloem for emerald ash borer development in tree i and dbh_i is the diameter (cm) at breast height of tree i . Numbers in parentheses are standard errors of regression coefficients. For each tree, regression coefficients were randomly drawn from a Gaussian distribution with means and variances equal to slope coefficients and standard errors. On rare occasions where a random draw resulted in a negative number, the value was resampled.

The estimates of phloem area and larvae per square meter of phloem were multiplied to obtain the number of larvae in each tree in fall 2009 (before the first removal). For simplicity and given the relatively low densities of larvae per square meter of phloem observed in our empirical data (max = 65.03, mean = 5.73, SE = 0.56) relative to expected carrying capacities for a square meter of phloem (Hermes and McCullough, 2014), all larvae were assumed to emerge if the host

tree was not removed. This procedure resulted in a cohort of emerged beetles per tree in spring 2010 that was propagated for three time steps (2010–2013) on a per tree basis according to the following discrete time model:

$$N_{t,i} = N_{t-1,i} - R \quad (4)$$

where $N_{t,i}$ is the number of beetles produced by tree i in year t , $N_{t-1,i}$ is the number of beetles produced by tree i in the previous year, and R is the population growth rate.

Model progression began with a bout of tree removal followed by beetle emergence. The number of beetles emerging each year was stored to enable calculation of cumulative emergence by spring 2013. The growth rate was defined as in Eq. (1). We elected to use a model without a carrying capacity for total beetles produced on the landscape because we are interested in estimating beetle pressure, or the total number of beetles resulting (not necessarily emerging) from each tree per year. Therefore, the model included beetles produced by a tree that potentially dispersed to and reproduced in another tree the following year. This assumes that, during our four-year study, emerald ash borer did not consume all available phloem resources, which we deemed appropriate as trees in the surrounding area were not exhibiting mortality as of 2015. All steps involving randomization were simulated anew for each iteration of the model.

2.4. Management scenarios

Cumulative number of beetles produced across four years was estimated for eight different management scenarios in which trees were or were not removed. A summary of each removal scenario is provided in Table 5. The *actual* scenario represented the actual tree removal program whereas *no removal* represented a scenario in which no trees were removed from the core infested area. In the *delayed* scenario, the same trees were removed as under the *actual* removal scenario except that tree removal occurred at a single time point in winter 2013, the last year of the study. The *delayed* scenario was used to quantify the benefits of early detection and removal compared to a significant time lag between establishment and detection. Under the scenario *pecked-only*, the same trees were targeted for removal as under the *actual* scenario except that trees without pecking were left standing. Under the *random* scenario, the same numbers of trees were removed per year as *actual* but removals were done randomly. Thus, the trees that were removed could have been removed during the actual management, or may still be present in the core infested area. The *adjusted-random* scenario was equivalent to *random* scenario except that the surface area of trees in *adjusted-random* were randomly sampled, without replacement, from the *actual* scenario trees to account for differences in phloem resources between removals. The *adjusted-random* scenario was included to quantify the benefits of targeting pecked trees while holding phloem resources constant.

The *actual*, *no removal*, *delayed*, *pecked-only*, *random*, and *adjusted-random* scenarios assumed that beetle populations were completely

univoltine. However, it is well documented that populations of emerald ash borer developing in the same tree can develop through either a semivoltine or univoltine life cycle (Wei et al., 2007; Tluczek et al., 2011). If pecked trees have higher proportions of larvae that complete development in a single year compared to unpecked trees, then preferentially removing them may increase efficacy as an extra year could be afforded to managers to remove the unpecked trees with higher proportions of larvae with delayed emergence. We use the terms “current-year larvae” and “delayed larvae” instead of univoltine and semivoltine, as 4th instar larvae may be semivoltine individuals but in their second year of development. Current-year larvae refer to insects that are expected to emerge in the following spring, whereas delayed larvae refers to insects expected to emerge a year from the following spring. To estimate if the probability of an individual emerging the following spring was associated with pecking, we classified all larvae found during empirical sampling in instars one through three as “delayed larvae” and otherwise as “current-year larvae.” We tested whether the probability of current-year emergence was associated with woodpecking status of the sample using a generalized linear mixed-effects model with random intercepts for tree and log nested within tree. A binomial error structure and logit link were used. After concluding that emergence was more likely to occur in the present year from pecked logs (see Results), the additional selective removal scenario, *voltinism*, and associated no management scenario, *no removal-voltinism*, were simulated. In both scenarios, a proportion of the insects within each tree were assumed to require two years to complete development. The proportion of current-year larvae observed in log samples was 61% and 42% in pecked and unpecked samples, respectively. We incorporated delayed emergence into the model by multiplying the number of emerging beetles per year in either pecked or unpecked logs by the proportion that are current-year larvae (i.e. 0.61 for beetles emerging from pecked trees, 0.42 for beetles emerging from unpecked trees). The remaining proportion of beetles (i.e., delayed larvae) would emerge the following year if their host tree was not removed. The *voltinism* scenario resulted in the removal of the same exact trees as removed under *actual* above.

For each scenario, beetle production was estimated for each year and the model was run for 200 simulations, totaling 1600 simulations and 6400 values of beetle production. That is, a value was recorded for each year (2010–2013) in each scenario (8) and for each simulation (200). To quantify efficacy, we compared cumulative beetle production under the actual removal program with univoltine development (*actual*) to the other management scenarios that assumed completely univoltine populations (*no removal*, *delayed*, *pecked-only*, *random*, and *adjusted-random*). Next, to understand the importance of *voltinism* in beetle production and management efficacy, the *voltinism* scenario was compared to *no removal* and *no removal-voltinism*. In addition to comparisons after four years of management, a comparison between *actual* and *no removal* within each year of management was conducted to compare temporal patterns in efficacy.

2.5. Sensitivity analyses

To test sensitivity of our results to population growth rates, we ran 1200 additional simulations using three different distributions of growth rates. For each of the *actual* and *no removal* scenarios, 200 simulations were ran with R sampled from a Gaussian distribution with $\bar{x} = 5.18$ and $s = 1.51$, $\bar{x} = 10.35$ and $s = 3.02$, and $\bar{x} = 10.35$ and $s = 0$. The first two distributions were used to evaluate how efficacy shifted with changes in mean growth rate whereas as the third distribution was used to evaluate how efficacy shifted with variance in growth rate. These growth rates reflect published growth rates of emerald ash borer in other regions of the United States (Mercader et al., 2011a; Duan et al., 2014, 2015). Percent reduction in beetle production when implementing the *actual* vs. *no removal* scenario was calculated after 4 years for each distribution of R , producing 600 values.

2.6. Statistical analyses

Formal statistical comparisons between management scenarios were conducted by calculating the percent reduction in cumulative beetle production at the end of each year in each simulation as follows:

$$\%reduction_t = \left(1 - \frac{scenario_{0,t}}{scenario_{r,t}} \right) \times 100 \quad (5)$$

where *% reduction* is the reduction in cumulative number of beetles produced after t years of management as a result of removing trees via *scenario_i* compared to *scenario_r*, *scenario_i* is the number of beetles produced in scenario i after t years of management, and *scenario_r* is the number of beetles produced in the reference scenario after t years of management. Management scenarios were considered statistically different if the 95% confidence interval for percent reduction in larvae (i.e. the middle 95% of simulation values) excluded zero. We conducted yearly comparisons of the *no removal* scenario (*scenario_r* in Eq. (5)) to *actual*, *random*, and *pecked-only* scenarios (*scenario_{i=1,2,3}* in Eq. (5)) to determine if the relationship between percent reduction in cumulative number of beetles produced and cumulative percent of trees removed changed across time. Otherwise, all comparisons between management programs were conducted for cumulative beetle production cross all four years ($t = 4$). All analyses were completed using R (R Core Team, 2016). All mixed-effects models were fit using the lme4 package (Bates et al., 2013) and P -values were obtained using Satterthwaite’s approximation for the degrees of freedom via the lmerTest package (Kuznetsova et al., 2014).

3. Results

Removing trees with evidence of woodpecker foraging significantly decreased the cumulative number of emerald ash borer adults produced in the core infested area across four years of management. Trees with pecking had an average of 2.4 more larvae per square meter of phloem, significantly more than unpecked trees ($F_{1,255} = 17.28$, $P < 0.0001$). Under the *actual* scenario, the median cumulative number of adults produced in the core infested area was 1.6 million (M) (95% CI: 0.6–5.8; Fig. 2A) compared with 3.4 M adults that would have been produced if no trees had been removed (95% CI: 1.1–13.9; *no removal* scenario in Fig. 2B). Under *delayed* removal, cumulative beetle production was 2.2 M (95% CI: 0.9–7.4; Fig. 2C). Under a *pecked-only* scenario, where only pecked trees within the *actual* scenario were removed (reducing percent of trees removed from 63.2% to 33.8%), a median of 1.7 M (95% CI: 0.6–6.5; Fig. 2D) adults were produced in the core infested area across four years of management. Thus, focusing on removal of trees with woodpecker damage allowed removal of approximately half as many trees as the actual management strategy undertaken, while resulting in only slightly greater beetle production.

Under a *random* removal scenario, the median estimated number of beetles produced in the core infested area was 1.6 M (95% CI: 0.6–6.1; Fig. 2E). Under an *adjusted-random* scenario, in which randomly removed trees were adjusted for surface area to match the *actual* scenario, there was a median of 1.7 M (95% CI: 0.6–6.4; Fig. 2F) beetles produced in the core infested area. The adjustment for surface area resulted in more larvae on the landscape because the trees removed under selective management were smaller by 4.4 cm on average compared to trees left standing ($t = 6.16$, $df = 1786$, $P < 0.0001$). Thus, the *random* scenario resulted in an increased probability of removing a larger tree than those removed under the *actual* scenario. Under the *voltinism* scenario, in which delayed emergence was included in the model and the same number of trees were removed as in the *actual* scenario, cumulative beetle production was 1.2 M (95% CI: 0.5–3.9; Fig. 2G). Under the *no removal-voltinism* scenario, cumulative beetle production was much higher than the *voltinism* scenario at 2.6 M beetles (95% CI: 0.9–9.6; Fig. 2H).

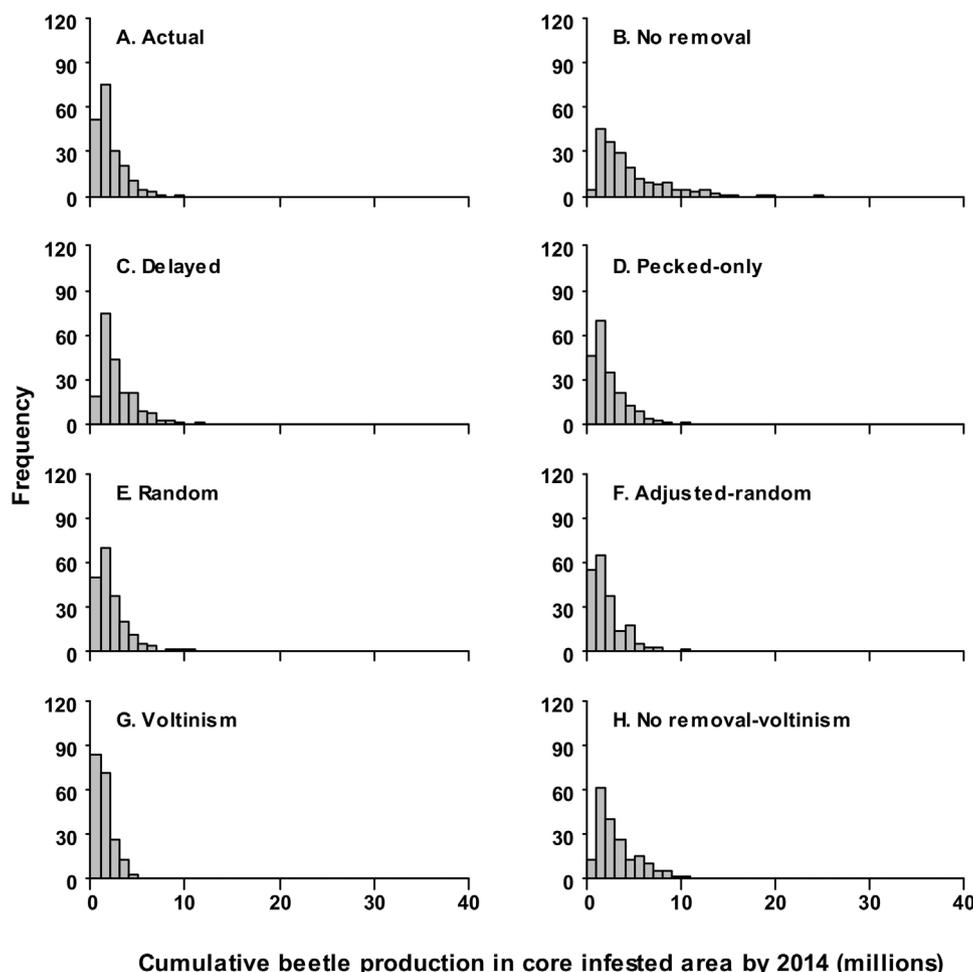


Fig. 2. Estimates of cumulative number of beetles produced in the core infested area across four years of tree removal programs in the core infested area in Minneapolis-Saint Paul, MN, USA. See Table 5 for explanation of removal scenarios.

Each of the hypothetical removal scenarios that assumed beetle populations were univoltine was then compared to the *actual* scenario (i.e., *actual* was set to *scenario*, and each hypothetical scenario was set to *scenario*, in Eq. (5)) (Fig. 3). If there was a positive difference between scenarios and the 95% confidence interval did not include “0”, this provided strong evidence that the *actual* management scheme was superior to the scenario under comparison in terms of reducing cumulative beetle production. The percent reduction in cumulative beetle production under *actual* compared to *no removal* was significant, as removing 63.2% of the total trees across four years reduced beetle numbers by a median of 54.1% (95% CI: 42.4–61.2%; Figs. 3A, 4C) in the core infested area. Moving from *delayed* to *actual* removal highlighted the importance of early detection and management, as beetle production was reduced by 27.1% (95% CI: 20.2–32.8%; Fig. 3B) across four years. A change to *actual* removal from *pecked-only*, in which 33.8% of the trees were removed from the core infested area, resulted in an estimated median reduction of 8.6% of insects (95% CI: 5.7–12.9%; Fig. 3C) after four years. Targeting pecked trees appeared to be slightly more advantageous than simply removing the same number of trees at random, as a change from *random* to *actual* reduced the number of larvae after four years by an additional 4.4% (95% CI: –11.0–16.7%; Fig. 3D). This finding did not appear to be moderated by the fact that trees removed under the *actual* scenario were smaller by an average of 4.4 cm than trees left standing, as a change to *actual* from *adjusted-random* resulted in a 3.0% (95% CI: –22.1–23.5%; Fig. 3E) reduction in beetles produced.

Accounting for extended development in a fraction of the population appeared to have merit, as pecked branch samples contained

higher proportions of current-year larvae on average. For example, if sampling from a pecked versus unpecked branch, the odds of finding a current-year larva increase by 2.49 ($Z = 4.11$, $P < 0.0001$). Simulations using delayed emergence suggested that, in addition to removing more larvae per square meter of phloem, targeting pecked trees removed higher proportions of current-year larvae and afforded managers an extra year to remove the delayed larvae. Comparing *voltinism* to *no removal-voltinism* resulted in an estimated percent change in cumulative beetle reduction of 55.4% (95% CI: 44.7–62.3%; Fig. 4A). When *voltinism* was compared to *no removal* (i.e. completely univoltine populations), cumulative beetle production was decreased by 63.6% (95% CI: 50.3–71.5%; Fig. 4B).

Comparisons across years between *actual* and *no removal* suggest that, across the first four years of tree removal, a selective removal program can delay population growth by 1–2 years (Fig. 5). Annual comparisons of *actual*, *random*, and *pecked-only* scenarios to *no removal* demonstrated that a drop in efficacy occurred in 2012 (year 3 of management) due to a change in tree removal strategy (Fig. 6). In this year, a large number of relatively small trees were removed from a wooded park in an effort to manage towards non-ash species. Indeed, there were 641 trees removed in 2012, or 1.7 times the next highest number. Trees removed in 2012 had a mean DBH of 18 cm, more than 13 cm smaller on average than the next smallest cohort of removed trees. Moreover, a smaller percent (32%) of the trees were pecked, compared to the next smallest percentage of 53% observed in 2013 (Table 1). We compared the ratio of median percent reduction in cumulative beetle production to cumulative percent tree removal. A ratio greater than 1 suggests that removal of trees had a disproportional

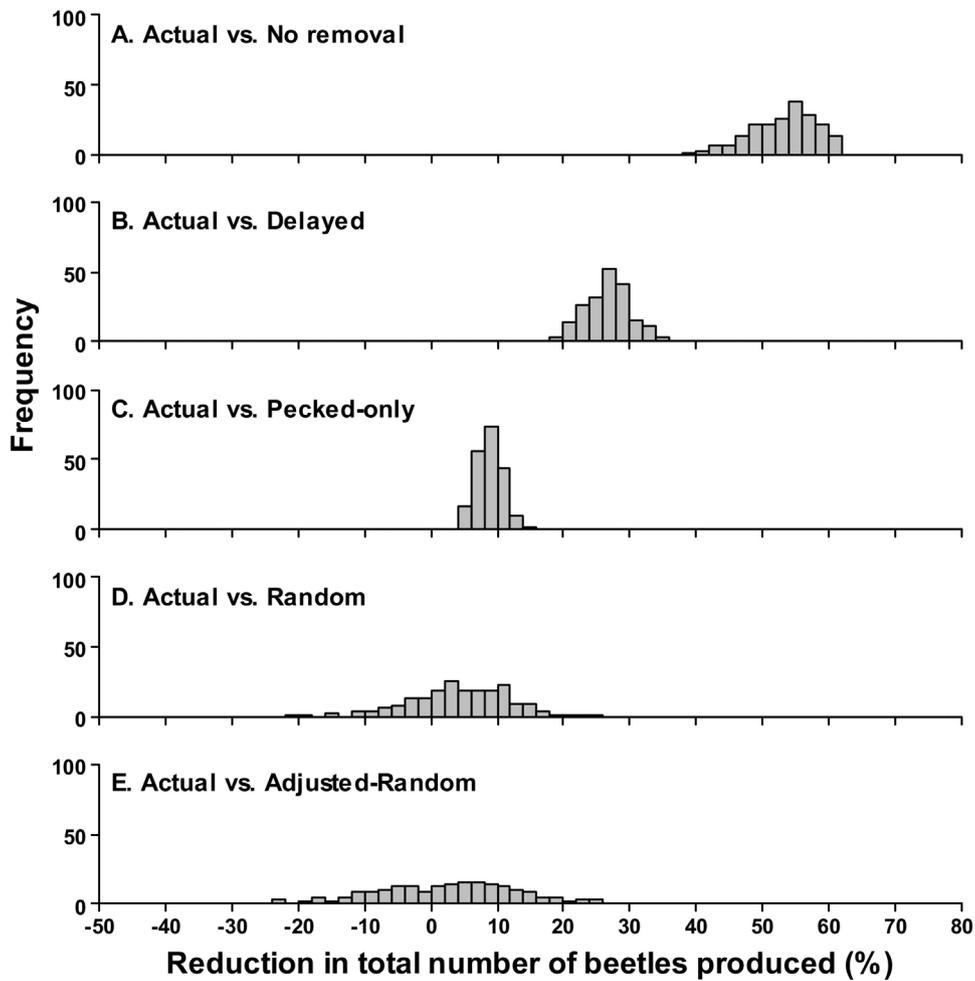


Fig. 3. Percent reduction in cumulative number of beetles produced after four years (2010–2013) of tree removal in the core infested area in Minneapolis-Saint Paul, MN, USA. Negative numbers indicate that there would have been more insects resulting than under the removal regime pursued.

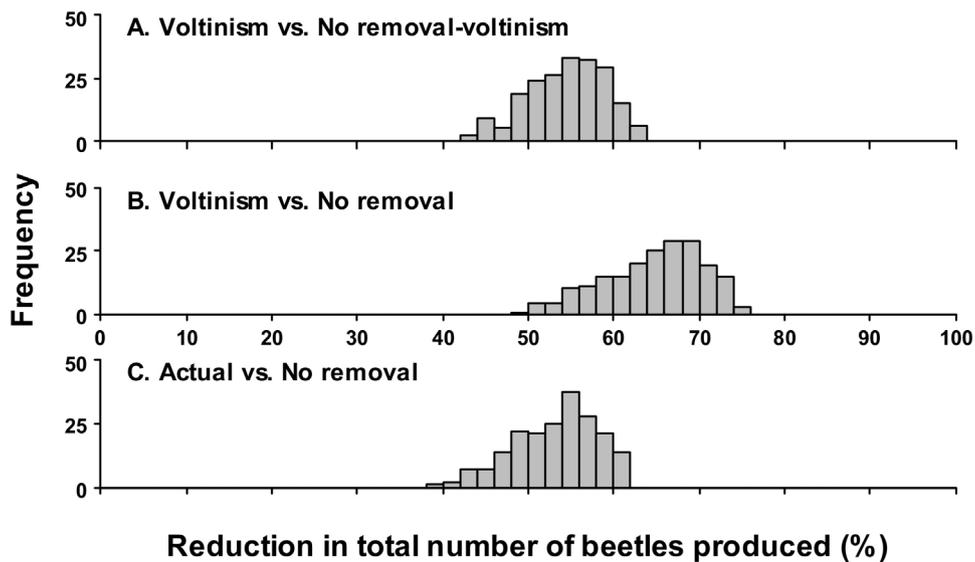


Fig. 4. Percent reduction in cumulative number of beetles produced after four years (2010–2013) of tree removal in the core infested area in Minneapolis-Saint Paul, MN, USA. Figure shows comparisons of A) *voltinism* to *no removal-voltinism* (i.e., both scenarios with mixed voltinism) and B) *voltinism* (mixed voltinism) to *no removal* (completely univoltine) C) *actual* to *no removal* (i.e., both scenarios with completely univoltine populations). Panel C is similar to Fig. 3A but reproduced here for ease of comparison.

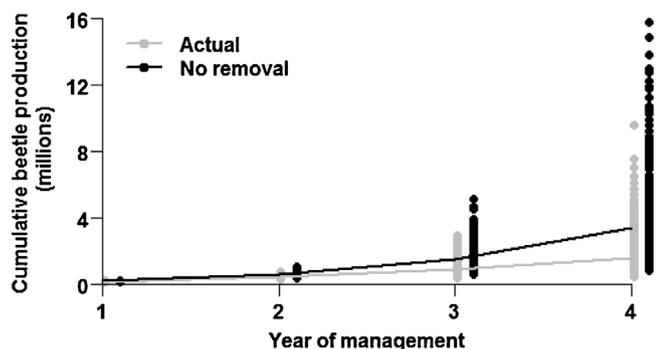


Fig. 5. Cumulative beetle production under *actual* versus *no removal* scenarios across four years (2010–2013) of management in Minneapolis-Saint Paul, MN, USA.

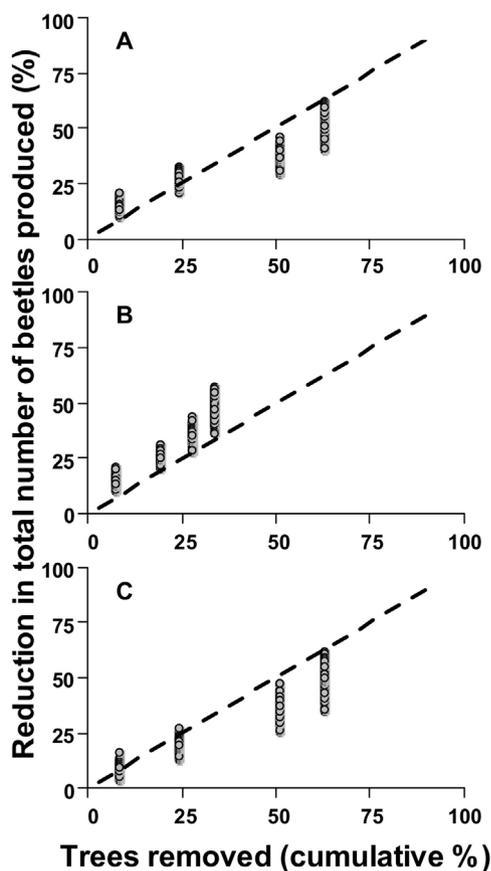


Fig. 6. Efficacy of A) *actual* B) *pecked-only* and C) *random* scenarios versus *no removal* across four years (2010–2013) of management in Minneapolis-Saint Paul, MN, USA. Figure shows association of percent reduction in cumulative beetle production with cumulative percentage of trees removed. Each dot represents within-year values for a single simulation. A ratio greater than 1 (i.e. a point above the dashed line) suggests that removal of a percentage of the trees had a disproportionate, advantageous impact on the reduction of beetles (i.e. greater percentage reduction).

tionate, advantageous impact on the reduction of beetles (e.g., removal of 5% of trees resulted in > 5% reduction in beetles). This ratio was greater than one until year 3 for the *actual* scenario (1.89, 1.12, 0.75, and 0.86; Fig. 6A). Under the *pecked-only* scenario all years had a ratio greater than 1 (2.15, 1.37, 1.33 and 1.46; Fig. 6B) compared to the *random* scenario under which no year had a ratio greater than 1 (0.99, 0.79, 0.74, and 0.82; Fig. 6C).

Sensitivity analyses suggested that reductions in population growth increased with mean growth rate until R reached approximately 5, at which point efficacy plateaued (Fig. 7A). Comparisons between percent reduction between the *actual* and *no removal* scenarios where growth rate was allowed to vary in one scenario ($R = 10.35 \pm 3.02$ SD) but

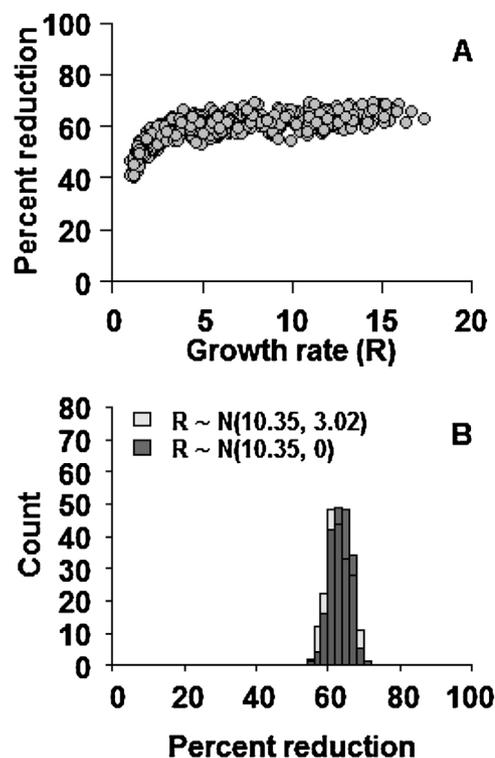


Fig. 7. Sensitivity analysis depicting the effect of growth rates on percent reduction of beetles due to *actual* removal scenario in the core infested area in Minneapolis-Saint Paul, MN, USA. Figure depicts effects of A) mean growth rate on percent reduction and B) variance in growth rates on percent reduction.

held constant in another ($R = 10.35$) demonstrated that estimates of percent reduction were not heavily influenced by variance in growth rates (Fig. 7B).

4. Discussion

Our results demonstrate that aggressive sanitation of a satellite population of emerald ash borer, if detected early, can slow population increase by approximately 54% versus doing nothing. The suppression was achieved by preferentially removing ash trees with evidence of woodpecker feeding from within the satellite infestation across four years. These results are likely conservative, as our sampling methods may have overestimated the densities of emerald ash borer in unpecked trees. Unpecked trees that were sampled were generally in close proximity to pecked trees and more likely to be infested than unpecked trees in other parts of the core infested area. The effectiveness of concentrating on pecked trees was clear, as the total number of beetles produced in the *pecked-only* scenario (1.7 M) was comparable to the *actual* scenario (1.6 M) but only 34% of the trees were removed in the *pecked-only* simulation compared to 63% in *actual*.

The eradication of emerald ash borer is not a feasible management goal even in satellite infestations, although tree removal within a few years following establishment (before mortality becomes apparent) can result in up to a two-year delay in population growth (Fig. 5). Given the rapid rate at which almost complete mortality of the mature ash component can occur following infestation of emerald ash borer (e.g., 99% in less than 6 years in forested areas; Knight et al., 2013), a two-year delay will benefit managers by increasing time for the implementation of other management strategies. Prior simulation studies have found that treating trees with stem injections of emamectin benzoate or using girdled trees as population sinks rank among the most effective management options to reduce population growth, for example (Mercader et al., 2011a,b; McCullough and Mercader, 2012; McCullough et al., 2015). We expect that girdling and removing trees

enhanced emerald ash borer control efforts in the Twin Cities metropolitan area, although we do not believe that excluding the 260 treated/girdled trees from the present analyses accentuated our conclusions as the sensitivity analyses were robust to variability in growth rates (Fig. 7).

The strategy of proactively removing ash in advance of emerald ash borer arrival to slow the ultimate mortality of ash, which lacks empirical support (Knight et al., 2013; Smith et al., 2015), is distinct from our emphasis to remove infested trees to reduce the number of insects and “buy time.” Systematic replacements of ash trees in urban areas or ash-dominated forest stands do accomplish important goals of diversification and buffering impacts on ecosystem function (Iverson et al., 2016). Resource managers should interface budgetary constraints and geographic extent and severity of the infestation with current and future goals as they pertain to the composition of the urban forest. Management efforts and goals should be employed and developed, respectively, on a site-specific basis and select from the several integrated pest management techniques that have been developed to date to combat this pest (Vannatta et al., 2012; Kovacs et al., 2014; Herms and McCullough, 2014; Sadof et al., 2017).

In some instances, guidelines are still developing. To guide decision-making by land managers and private property owners regarding when a tree should be removed versus treated with insecticides, for example, a relationship between larval density and efficacy of insecticides is necessary. Given the difficult logistics of sampling trees directly to obtain an estimate of larval density, crown ratings are often used as a proxy for both larval density (Flower et al., 2013) and the potential efficacy of emamectin benzoate (Flower et al., 2015). Thus, deciding whether or not to remove a tree should depend on that tree’s expected lifespan following application of an insecticide, balancing the percent of phloem remaining with the tree’s monetary, aesthetic, and cultural values. Indeed, in simulations by McCullough and Mercader (2012), trees were only considered for removal when greater than 60% of the phloem was consumed.

Our results show that a two-year life cycle for emerald ash borer can afford managers an extra year to treat or remove trees and results in a decrease in cumulative beetle production. Comparisons of *voltinism* to *no removal* scenarios suggest that significant increases in percent reduction of ~64% may occur if removing trees helps maintain the proportion of the population that requires an extra year to complete development. Warmer climates and stressed trees are predicted to have higher proportions of univoltine (current-year) beetles (Wei et al., 2007; Tluczek et al., 2011). The failure to remove trees will increase beetle production and lead to additional weakened trees on the landscape in the early stages of an infestation. If more stressed trees increases the proportion of the population that is univoltine, then the benefits of removing trees could be compounded. The *voltinism* to *no removal* comparison may be considered an extreme case in which, under no management, all insects are univoltine.

In examining the beetle production through time, it was clear that a marked decrease in efficacy was associated with the removal of trees in 2012 (year 3 of management; Fig. 6A). The decrease in efficacy was likely driven by the removal of smaller trees on average and the decrease in the proportion of removed trees that had pecking for 2012 (Table 1). In comparing temporal trends of *actual* to *pecked-only* scenarios, it was clear that higher percent reductions per tree were achieved by targeted removal, despite that greater absolute percent reductions were achieved by simply removing more trees.

It is difficult to empirically determine whether tree removal could affect spread, especially in situations where new introductions may occur with high frequency. Simulation studies have suggested that host tree removal may lead to an increase in dispersal distances by emerald ash borer as emerging beetles search for oviposition sites on a landscape depleted of ash by management efforts (Mercader et al., 2011a,b). Studies of tethered flight show that emerald ash borer can fly several kilometers (Taylor et al., 2010; Fahrner et al., 2015). Indeed, during

initial attempts to prevent the spread of emerald ash borer in Essex County, Ontario, Canada, the beetle likely dispersed across a 10 km wide buffer zone from which all ash trees had been removed (Taylor et al., 2010). Given the flight and dispersal capacity of emerald ash borer, and the response of dispersal by emerald ash borer to phloem resources (Siegert et al., 2010), it is almost certain that emerald ash borer spread beyond the core infested area during this study. Yet, despite these projected dispersal patterns, several trees remain in the core infested area and appear healthy.

Another potentially important factor in the management of emerald ash borer are Allee effects in population growth and spread (Liebhold and Tobin, 2008; Tobin et al., 2011). A positive correlation between spread rates and initial population density of emerald ash borer were found in cellular automata models developed by Mercader et al. (2011b), for example. Estimates for growth and spread of populations of emerald ash borer that account for potential challenges in mate finding in low density infestations, however, have not yet been achieved (Mercader et al., 2011a,b). Studies on European gypsy moth *Lymantria dispar dispar* (L.) (Lepidoptera: Erebididae), for example, show that reduction of gypsy moth populations to low densities leads to decreases in mate finding ability and thus slower population growth and expansion (Johnson et al., 2006; Tobin et al., 2007; Tobin et al., 2007). Models of spread that incorporate Allee effects will improve predictions of the role of dispersion of phloem resources, both in managed and un-managed landscapes, in population growth and spread of emerald ash borer.

Our study demonstrates the importance of efficient and early detection as well as the potential roles of regional differences in population density, growth rates, and voltinism in managing endophytic herbivores via host tree removal. As an endophytic herbivore with no identified long-distance sex pheromone (Herms and McCullough, 2014) and the presence of a long lag time between infestation and easily-detectable tree symptoms (Cappaert et al., 2005), emerald ash borer remains a challenging invader to manage (Herms and McCullough, 2014). Following the early discovery of a satellite infestation of emerald ash borer in an urban area, tree removal may be a useful management tool to reduce populations of emerald ash borer as part of a broader, integrated pest management program. Larger diameter trees with pecking will likely contain the most larvae (McCullough and Siegert, 2007; Lindell et al., 2008; Jennings et al., 2013, 2016). Within tree removal strategies, preferentially removing large trees will be most effective in reducing beetle production.

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Appendix A. Supplementary material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ufug.2017.03.017>.

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