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Estimating local spread of recently established emerald ash borer, *Agrilus planipennis*, infestations and the potential to influence it with a systemic insecticide and girdled ash trees

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ABSTRACT

Information on the pattern and rate of spread for invasive wood- and phloem-feeding insects, including the emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire), is relatively limited, largely because of the difficulty of detecting subcortical insects at low densities. From 2008 to 2011, grids of girdled and subsequently debarked ash (*Fraxinus* spp.) detection trees were established across a >390 km^2 area encompassing two recently established EAB infestations in Michigan as part of the SLow Ash Mortality (SLAM) Pilot Project. Ash distribution and abundance were inventoried across the project area which included public and private forestland, a state park, and street trees in a small municipality. Spread rates of EAB from 2008 to 2011, based on larval presence in girdled detection trees, were estimated to be 1.2–1.7 km yr^{-1} in the larger, presumably older, infestation and 0.4–0.7 km yr^{-1} in the smaller infestation; suggesting a slower spread rate during the initial stages of population establishment. From 2009 to 2011, a total of 587 ash trees in the project area were trunk-injected with a highly effective, systemic emamectin benzoate insecticide. Potential effects of girdled ash trees and the systemic insecticide treatment on EAB spread were evaluated using a simulation model and a simple descriptive model of observed spread. Not surprisingly, density of trees treated with the insecticide was too low to exert a detectable effect on EAB spread. However, while the density of girdled trees was also relatively low, model results indicated a reduced spread of EAB out of areas containing girdled trees.

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1. Introduction

Invasive species pose significant risks to forest biodiversity and ecological functions (e.g., NRC, 2002; Ellison et al., 2005; Loo, 2009; Fei et al., 2014), result in substantial economic costs (Kovacs et al., 2010; Aukema et al., 2011), and may even affect human health (e.g., Etkind et al., 1982; Donovan et al., 2013, 2015). Not surprisingly, billions of dollars are spent in the U.S. annually to prevent the arrival, establishment, or spread of non-native and potentially invasive forest insects (Liebhold and Tobin, 2008; Aukema et al., 2011; Leung et al., 2014).

Unfortunately, many invasive forest insects remain unnoticed until they have become pests of economic or ecological significance because we lack basic information about their biology. This is exacerbated when organisms are difficult to detect or monitor, such as subcortical insects, which feed on phloem or wood beneath the bark of their hosts. Phloem- and wood-borers may be readily transported in wood packing material commonly used in containerized shipping (Haack, 2006) and are the most rapidly increasing guild of nonnative forest insects in the United States (Aukema et al., 2010). These species spend the majority of their life span hidden within their hosts and many either do not produce long

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distance pheromones or their pheromones have not been identified. Efforts to detect, delineate, or monitor infestations of these invasive pests must rely on visual surveys to identify symptomatic trees, felling and debarking host trees to assess pest presence, or traps baited with non-specific host volatiles.

These problems are exemplified by the emerald ash borer (EAB), *Agrilus planipennis* Fairmaire, a phloem-feeding beetle native to Asia that was first identified in Detroit, MI, USA and Windsor, ON, Canada in 2002 (Cappaert et al., 2005). Larvae feed in galleries in the phloem and cambium of ash (*Fraxinus* spp.) trees, often scoring the outer xylem. As larval densities build, nutrient and water translocation within the tree is disrupted, leading to mortality (Cappaert et al., 2005). To date, populations of EAB have been found in 25 U.S. states and two Canadian provinces (Emerald Ash Borer Information 2015). Interspecific differences in EAB host preference or host resistance have been documented (Anulewicz et al., 2007; Rebek et al., 2008; Whitehill et al., 2011; Tanis and McCullough, 2012, 2015), but all North American ash species can likely be colonized (Herms and McCullough, 2014). Emerald ash borer has become the most destructive and costly forest insect to invade North America (Aukema et al., 2011; Herms and McCullough, 2014).

Regional spread of EAB is characterized by stratified diffusion (Shigesada and Kawasaki, 1997; Siegert et al., 2014), with long distance dispersal events occurring via artificial transport of infested ash trees, logs, or firewood and short distance dispersal resulting from flight of adult beetles. Inadvertent artificial transport of EAB, sometimes across considerable distances, is facilitated by the difficulty of identifying trees with low to moderate densities of EAB larvae, which typically exhibit few external signs or symptoms of infestation (Crook and Mastro, 2010; Poland et al., 2011; Poland and McCullough, 2014; Herms and McCullough, 2014). Moreover, EAB larvae can complete development and emerge from logs or firewood a year or sometimes longer after trees are felled (Petrice and Haack, 2006). Siegert et al. (2014) used dendrochronological methods to document the year ash trees died across an >15,000 km^2 area in southeast Michigan during the initial phases of the EAB invasion in North America. They reported the spread of ash mortality from 1998 to 2001 averaged 3.84 km yr^{-1}, but the rate increased to 12.97 km yr^{-1} from 2001 to 2003 as nearby satellite colonies began to coalesce. Following identification of EAB in 2002, however, quarantines were imposed to regulate artificial transport of potentially infested ash material (Cappaert et al., 2005; Herms and McCullough, 2014).

Given the difficulty of accurately delineating EAB distributions (McCullough and Siegert, 2007; Siegert et al., 2010), particularly at low densities (Mercader et al., 2012, 2013), intensive sampling efforts to assess EAB dispersal have been fairly limited (e.g., Mercader et al., 2009; Siegert et al., 2010). Estimates from flight mill tests showed the median flight distance for mature female EAB over a four day period could exceed 3 km (Taylor et al., 2010), indicating a strong physiological potential for flight. Field studies, however, have shown that when hosts are readily available, EAB females lay the majority of their eggs within 100 m of their emergence point and lay over 90% of their eggs within 500 m (Mercader et al., 2009; Siegert et al., 2010). Nevertheless, at least a few females have been observed to lay some portion of their eggs on trees beyond 750 m from the point of origin (Mercader et al., 2009; Siegert et al., 2010). Mercader et al. (2011a) found that using observed EAB dispersal in a site with a continuous ash distribution to model EAB dispersal in a site with heterogeneous ash distribution provided a poor fit. Simulations also indicated that the influence of known, but unquantified, behaviors of adult EAB females have the potential to meaningfully alter the spread of a population (Mercader et al., 2011a). Specifically, EAB dispersal is likely to be affected by the distribution and condition of ash trees (Siegert et al., 2015). For example, female EAB are attracted to and preferentially oviposit on trees stressed by girdling, other injuries, or poor site conditions, and open-grown trees in sunny location are more likely to be colonized than shaded trees (McCullough et al., 2009a,b; Siegert et al., 2010; Tluczek et al., 2011). For these reasons, predicting natural spread of an EAB population based on data from small, albeit intensively sampled sites, may be tenuous at best. Therefore, our knowledge of unaided local spread of EAB adult beetles remains largely limited.

In autumn 2007, two isolated EAB infestations were identified in Mackinac Co., Michigan, USA and subsequently selected for the SL.ow A.sh M.ortality (SLAM) Pilot Project. This collaborative effort, which involved personnel from universities, and federal, state, and county agencies, focused on developing and implementing an integrated management approach for EAB (Poland and McCullough, 2010; McCullough et al., 2015; Mercader et al., 2015). Goals of the SLAM Pilot Project included evaluating area-wide effects of two treatments on EAB population growth and the subsequent progression of ash mortality. Treatments included the application of a highly effective systemic insecticide, emamectin benzoate, to selected ash trees, while other ash trees were girdled to attract egg-laying females, then destroyed before larvae could complete development (Poland and McCullough, 2010; McCullough et al., 2015; Mercader et al., 2015). As part of the SLAM Pilot Project, multiple years of data on EAB distribution were collected across the area encompassing the two sites. In addition, extensive surveys of ash distribution were undertaken across the heterogeneous project area that included portions of a national forest, private forests, residential and rural areas, and small municipalities. These data-sets provided a unique opportunity to evaluate the detectable spread rate of EAB across a sizeable area and to determine whether spread rates were affected by either the systemic insecticide applications or the girdled ash trees.

2. Methods

2.1. Site description and data collection

Two infestations near the towns of St. Ignace and Moran in Mackinac Co., MI were first detected in autumn 2007 when girdled ash detection trees were debarked (Poland and McCullough, 2010). The epicenters of the two infestations were approximately 25 km apart in 2007. As part of the SLAM Pilot Project, systematic inventories of ash were conducted at both sites and supplemented with U.S. Dept. of Agriculture Forest Service FIA (Forest Inventory and Analysis) data, St. Ignace street tree inventories, and surveys of ash within Straits State Park (Poland and McCullough, 2010; McCullough et al., 2015; Mercader et al., 2015).

Although baited artificial traps were also deployed, this and other field studies have shown girdled ash trees are substantially more likely to detect low density EAB populations than baited artificial traps (McCullough et al., 2011; Mercader et al., 2013). Distribution of EAB was, therefore, monitored using systematic grids of girdled ash trees (10–20 cm diameter at breast height) established annually from 2008 to 2011 at three densities: (1) dense grids (16 girdled trees per 2.6 km^2) were centered on areas where infested trees were identified; (2) standard grids (4 girdled trees per 2.6 km^2) surrounded the dense grids; and (3) coarse grids (1 girdled tree per 2.6 km^2) extended to the perimeter of the project areas (McCullough et al., 2015; Mercader et al., 2013, 2015). Some grid cells were excluded from the survey due to the absence of ash trees or in a few occasions, the inability to secure landowner permission for access. Each girdled ash tree was debarked in autumn

to assess EAB larval presence and numbers. A total of 444, 603, 748, and 855 girdled ash trees were established across the project areas in 2008, 2009, 2010, and 2011, respectively. Establishment and distribution of girdled ash trees was previously described (McCullough et al., 2015; Mercader et al., 2013, 2015) and is presented in Fig. A1 in Appendix A. In addition to serving as EAB detection tools, the girdled ash trees also functioned as EAB population "sinks" because larvae in the debarked trees died before completing development.

2.1.1. Insecticide treatment

A systemic insecticide with emamectin benzoate as the active ingredient (TREE-äge™, ArborJet, Inc., Woburn, MA) was applied to selected ash trees within the SLAM project areas in 2009, 2010 and 2011 to reduce local EAB population growth (McCullough et al., 2015). Large, replicated field studies have shown this product provides at least two years of nearly 100% protection from EAB (Smitley et al., 2010; McCullough et al., 2011). The insecticide is injected into the base of the trunk in spring, then is translocated in xylem to canopy branches and leaves (Mota-Sanchez et al., 2009; Tanis et al., 2012), controlling both adult and larval EAB. Between 2009 and 2011, a total of 587 ash trees were treated (229 trees in 2009 and 358 trees in 2010). Insecticide-treated trees were located on private land or rights-of-way accessible to contractors. Insecticide applications and distribution of treated trees were previously described (McCullough et al., 2015; Mercader et al., 2015) and locations of treated trees is illustrated in Fig. A1 in Appendix A.

2.2. Estimates of EAB spread with OLS regression

In an ideal situation, spread of an invasive organism is determined using data from evenly spaced points, each of which is monitored over time. However, given the operational nature of the SLAM Pilot Project and the extensive geographic area of the project, which encompassed >390 km^2 by 2011 (McCullough et al., 2015; Mercader et al., 2015), grids of girdled ash trees varied in size and density from year to year. In addition, new trees for girdling had to be located each year and in some grid cells, the only ash trees suitable for girdling were located near the edge of the cells rather than in the center of the cells. We circumvented this problem by overlaying a lattice of 200 × 200 m cells across the area encompassing the Moran and St. Ignace infestations. Ash inventory data from the extensive survey were used to estimate the area of ash phloem (m^2) in each cell in the lattice, following McCullough and Siegert (2007) (Fig. 1).

For all cells in the lattice where ash occurred, we calculated a proxy estimate of the expectation that a girdled ash tree would be detected as positive (e.g., infested) in 2008, 2009, 2010, and 2011 using data from the detection trees debarked each year. To accomplish this, we considered all positive detection trees to be 1 and negative detection trees to be 0, then estimated a distance-weighted average value of the detection trees present within 2000 m of the center of each grid cell. The average value was weighted by the inverse of the distance of each detection tree to the center of the grid cell. We used 2000 m as a cutoff, because most eggs are laid on trees within an 800 m radius of the emergence point of the adults and the vast majority of eggs will likely

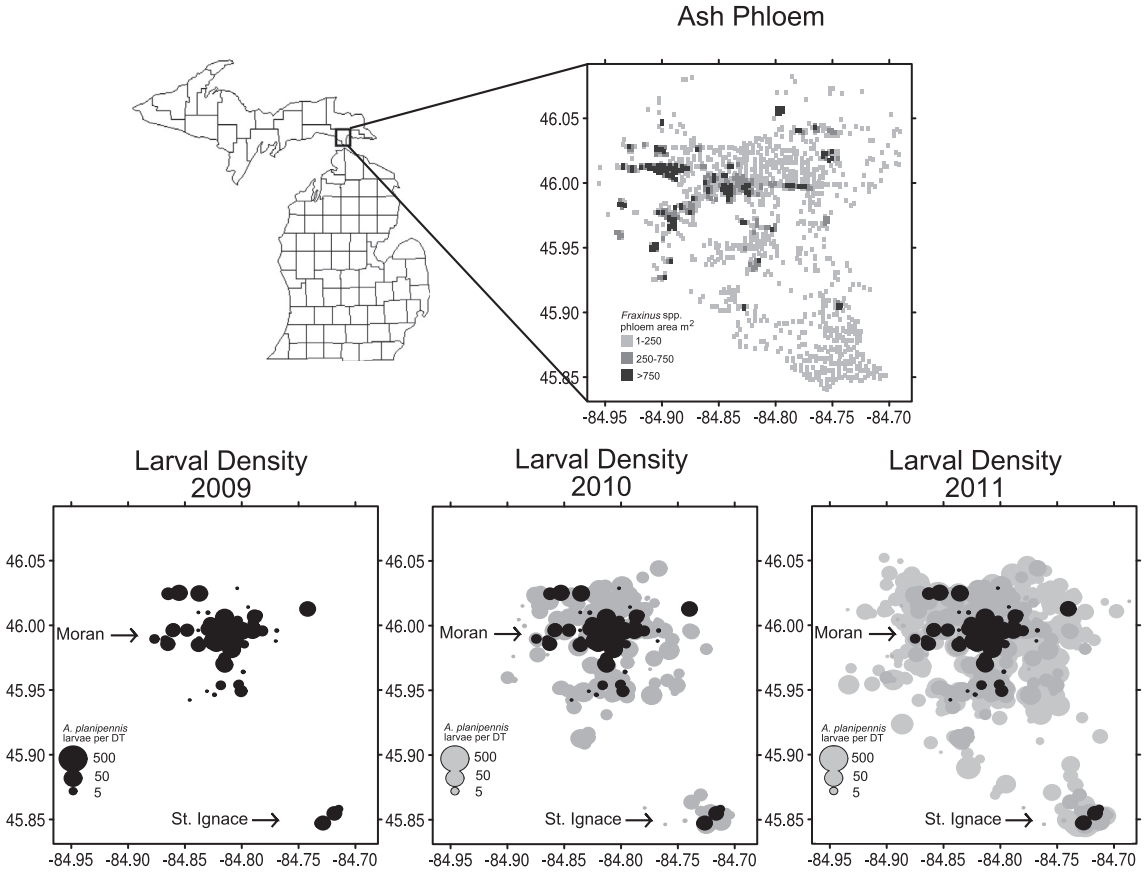

Fig. 1. Map of ash phloem area available for EAB larval development and number of EAB per girdled ash detection tree (DT) in 2009 (black), 2010 (gray), and 2011(light gray) in the Moran and St. Ignace areas.

be laid within 2000 m of the emergence point. Results were then used to estimate the expected detectable spread of EAB at both the Moran and St. Ignace sites using two methods. For the first method, we used 35%, 40%, and 45% as minimum thresholds to determine whether a cell was detected as positive. For each of these thresholds, we established the median distance of new detections in each year, and ran ordinary least squares (OLS) regressions between the distance from the origin and the date in which the cells were detected as positive to estimate the rate of spread. This process was performed using all infested trees in the project areas, then repeated but with satellite populations excluded. Satellite populations here refer to the infested trees located well beyond the primary Moran and St. Ignace infestations (Fig. 2).

Due to an absence of sufficiently high detection thresholds in 2008 and 2009 for the St. Ignace site (Fig. 2), OLS regressions for the St. Ignace infestation excluded 2008 and the detection distance for 2009 was set at 0. Bootstrapped standard deviations were calculated by resampling the data set 1000 times for each year, recalculating the median distances of newly discovered infested cells, running OLS regressions on each resampled dataset, and estimating the standard deviation for the adjusted r^2 and slope. The second method consisted of running a single Bernoulli trial for each cell each year using the probability of detection estimated for that year to establish the first year of detection for each cell. Subsequently, OLS regressions between the distance from the origin and the date in which the cells were detected as positive were used to estimate the rate of spread. This procedure was conducted 1000 times to estimate the average and standard deviation for the adjusted r^2 and slope.

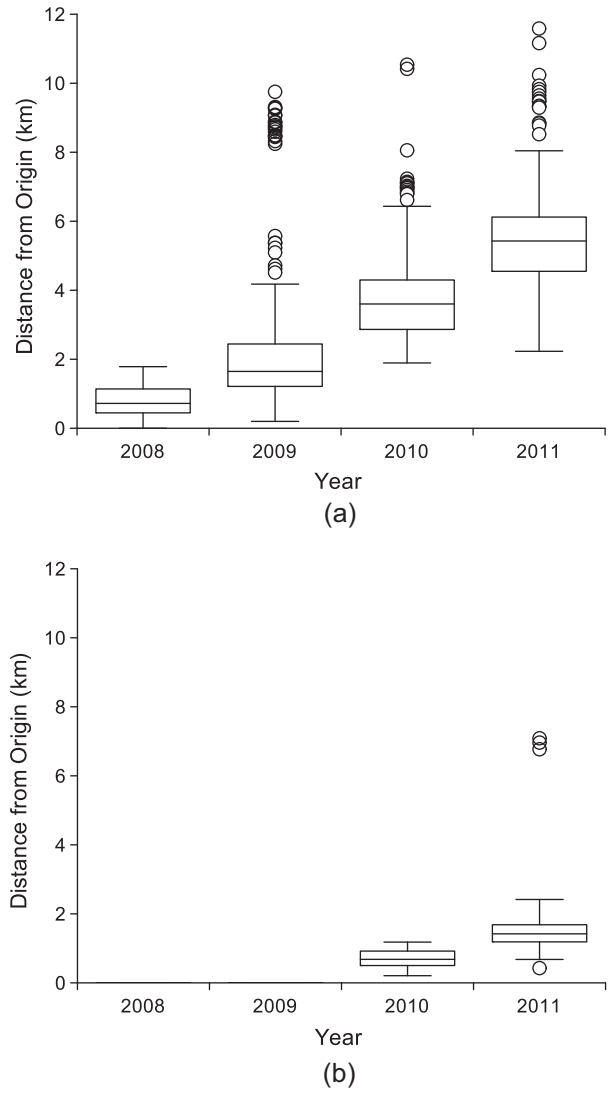

Fig. 2. Distance from the origin for EAB detections expected to occur with 40% or higher probability in 200 × 200 m cell lattices overlaid onto the (a) Moran and (b) St. Ignace project areas.

2.3. Mechanistic simulation model

The simulation model of EAB spread presented by Mercader et al. (2011a) was adjusted to better account for EAB population growth and dispersal. The model described in Mercader et al. (2011a) is a spatially explicit model that simulates the localized spread of EAB based on field collected data from numerous sites in Michigan. Briefly, the model couples population processes relevant to EAB spread onto matrices that track the quantity of ash phloem available for EAB larvae, the number of larvae that develop and emerge as adults in one year, and the larvae that require two years for development (Siegert et al., 2010; Tluczek et al., 2011). Population processes linking these matrices include (1) the number of adult beetles emerging in a specific year, (2) adult dispersal, (3) population growth, and (4) the loss of ash phloem consumed by developing EAB larvae. Variables for the model were determined and parameterized using data collected from multiple field sites (see Mercader et al., 2011a). Adult dispersal in the model is based on the dispersal function described by Mercader et al. (2009) and used to determine the proportion of adult beetles exiting a grid cell and entering other cells in the lattice.

Population growth in the model presented in Mercader et al. (2011a) relied primarily on a single site. Given the more extensive data collected across the SLAM project areas, we adjusted population growth by using data from four additional sites varying in EAB population levels. Specifically, population growth was estimated using the function described in Fig. A2 in Appendix A, with a maximum value of a 12-fold increase.

As previously described (Mercader et al., 2011a, 2012; Siegert et al., 2015), dispersal in the model described in Mercader et al. (2011a) did not accurately describe spread in larger areas. For this reason, expected detections estimated from the observed larval densities in this study were used to adjust the dispersal function that simulates EAB spread in the model. Evidence from the original detection trees examined in 2007 indicated the EAB infestation in Moran had originated 4–6 yrs earlier (Poland and McCullough, 2010). We assumed the initial infestation began when EAB was introduced into a single cell of the lattice in 2002. Simulations were run for six iterations (years) with an initial population of 100 adult beetles, varying the dispersal function used in the model and contrasting the fit to the estimated EAB distribution observed in 2008. Because the probability of detection is low when EAB populations are low, the estimated spread in 2008 was estimated simply as an 800 m boundary surrounding EAB-positive detection trees. Densities of EAB in the girdled detection trees at the edges of these boundaries were assumed to be 0.5 larvae per m^2 of phloem, indicative of an established but unlikely to be detected population (Mercader et al., 2012). In simulations, cells with at least 0.5 larvae per m^2 were thus considered as a cutoff to estimate the corresponding 800 m boundaries from the simulation runs. Subsequently, the mean square difference between the observed and simulated 2008 distributions was determined for each variation of the dispersal function. The dispersal function used to determine the proportion of beetles remaining or entering each cell, is described below for a cell j at time $t + 1$,

$$N_{t+1}^{j} = \sum_{k=1}^{n} N_t^k \frac{e^{-bD_{kj}}}{\sum_{k=1}^{n+1} e^{-bD_{kj}}} \quad (1)$$

where N_t^k is the number of individuals present in cell k at time t, k denotes all cells in the site including cell j (i.e., the number of beetles remaining in cell j), b represents the parameter that was varied to find the best fitting dispersal function, and D_{kj} is the distance between cell k and cell j. The best fitting parameter for b was 0.0017.

In 2010 and 2011, the EAB populations were substantially larger, providing more reliable estimates of EAB presence across the project areas (Mercader et al., 2012). For this reason, we contrasted the expected probability of detection for cells in 2010 and 2011 from the adjusted simulation model. The probability of detection for each cell was estimated following Mercader et al. (2012), assuming a single detection tree would be placed per cell and detection trees were 1.7 times more likely to detect an infestation than a non-girdled tree, a value derived from several field studies in other Michigan sites (Mercader et al., 2012; DGM and NWS, unpubl. data).

The code for the mechanistic simulation model written in the R programming language can be found in Appendix B.

2.4. Descriptive model

Intensive ash inventories, such as the data collected for the SLAM Pilot Project, are rarely available when EAB infestations are detected. Therefore, we developed a simplified model intended to run on lattices composed of 200 × 200 m cells, as above, but requiring only the presence/absence of ash and known positive detections at the start of the simulations. To accomplish this, we developed a simple model based on a negative exponential function to predict the expected detections present in 2011 from the results observed in 2010 for the St. Ignace and Moran project areas, as calculated above. The simple model calculates the expected detections for a specific cell in the grid as a function of the weighted mean of the detections observed in all cells the previous year and their distance to the cell in question as illustrated below,

$$E_{t+1}^{j} = \sum_{k=1}^{n} E_t^k \frac{ae^{-bD_{kj}}}{D_{kj}\sum_{k=1}^{n}\frac{1}{D_{kj}}} \quad (2)$$

where E_{t+1}^{j} is the expected detection in cell j at time $t+1$, k denotes all cells in the site within 2000 m of cell j and including cell j, a and b represent the parameters estimated via maximum likelihood, and D_{kj} is the distance between cell k and cell j.

An important aspect affecting EAB dispersal is the attraction of egg-laying females to stressed ash trees. Over time, EAB populations build, leading to an increase in the number of stressed ash trees, which should, in turn, attract or retain egg-laying females. Here we added a simple function to adjust EAB dispersal based on population density as described by Eq. (3) below,

$$p_k = \frac{1}{1 + uP_k} \quad (3)$$

$$E_{t+1}^{j} = \sum_{k=1}^{n} E_t^k \frac{p_k ae^{-bD_{kj}}}{D_{kj}\sum_{k=1}^{n}\frac{1}{D_{kj}}} \quad (4)$$

where p_k is the estimated population density in cell k and u is a parameter estimated via maximum likelihood to adjust for the effect of population density. Eq. (3) represents the reduction in the spread from cell k to cell j resulting from population density in cell k. Eq. (4) represents a modification of Eq. (2) to include the effects of population density. Densities of EAB populations in the Moran and St. Ignace infestations were estimated as larvae per m^2 of ash phloem, using the mean larval count from detection trees weighted by distance and divided by the ash phloem area present per cell.

Model parameters were fit using maximum likelihood as implemented in the bbmle package (Bolker, 2008) for the statistical package R (R core group, 2015). The fit of the base models developed for each site, as well as a model fit to the combined data, were contrasted using corrected Akaike's Information Crtiteria (AICc). Likewise, AICc was used to determine whether population density provided a substantially improved the fit of the model.

The code for the descriptive simulation model written in the R programming language can be found in Appendix C.

2.5. Effects of insecticide and girdled ash trees on EAB spread

2.5.1. Mechanistic simulation model approach

A potentially important influence on the spread observed in the SLAM Pilot Project is the location and number of trees treated with insecticide or girdled to reduce EAB population growth. To account for these treatments, we incorporated the effects of insecticide-treated trees and girdled "sink" trees as in Mercader et al. (2011b) with minor modifications. To simulate the impact of insecticide-treated trees we (1) adjusted population growth by subtracting the number of larvae expected to be present in insecticide treated trees and (2) prohibited the possibility of consumption of phloem present in insecticide treated trees. However, as the actual effect size of this treatment at the whole cell level is unknown, a scaling parameter to modify the effect of insecticides on population growth was added. The scaling parameter was simply multiplied by the expected reduction in population size caused by the mortality of larvae for each cell. Therefore, if the value providing the best fit for the scaling parameter is equal to zero, then the insecticide-treated trees did not have noticeable effect on EAB spread, while a value of 1 would represent the same effect as the one simulated effect by Mercader et al. (2011b), a value of 0.5 would represent 50% of the effect simulated, and a value of '2' would represent twice the effect simulated. To determine the best fitting parameter simulations were run allowing the scaling parameters value to range between 0 and 10, representing 0–1000% of the effect simulated by Mercader et al. (2011b), in intervals of 0.0001 and allowing the parameter 'b' in the dispersal kernel to also range from 0.001 to 0.003. Subsequently, the mean square difference between the actual expected detections and the predicted detections by distance class was determined for each model permutation and used to identify the best fitting parameters.

The effect of girdled ash trees on spread was then estimated with and without including the effect of insecticide treated trees. Here it is important to note that we tested the effect of girdled ash trees placed the year before on the current year's detections. In other words we tested the effect detection trees placed in 2010 had on the spread observed in 2011. As with insecticides, the potential effects of the girdled ash trees on population growth were modeled by subtracting the number of beetles expected to be present in those trees. The number of EAB present in the girdled sink trees was expected to be greater than in non-girdled trees, particularly when most of the nearby ash trees are not stressed. To account for this effect, a scaling parameter increased attraction of egg-laying EAB females to stressed trees as a function of EAB density, following Mercader et al. (2011b). Finally, because sink trees were debarked and removed each year, the phloem contained in sink trees was subsequently removed. In addition, because girdled trees can also influence the movement of adult EAB, a simple function was added to modify beetle dispersal. Specifically, the effect of girdled tress on dispersal was accounted for by multiplying the numerator in Eq. (1) by $1/(1 + S * PhloeminSinks)$, where

PhloeminSinks is the estimated quantity of ash phloem in the cell within the girdled trees and S is a modifier fit as for insecticide treatments.

2.5.2. Descriptive model approach

We considered the effect of the insecticide and girdled trees on EAB spread and observed increase in detections in 2011 compared to 2010 for the Moran and St. Ignace project areas. To accomplish this, we adjusted the exponential function to include the effects of treatments individually and together, and fit these again via maximum likelihood. These modifications adjusted the model by altering the increase in the expected detections in a specific cell by a treated cell as defined below,

$$i_k = \frac{1}{1 + uI_k} \tag{5}$$

$$S_k = \frac{1}{1 + vS_k} \tag{6}$$

$$E_{t+1}^{j} = \sum_{k=1}^{n} E_t^k \frac{I_k S_k a e^{-bD_{kj}}}{D_{kj} \sum_{k=1}^{n} \frac{1}{D_{kj}}} \tag{7}$$

where I_k is the estimated total area of ash phloem treated with the insecticide in cell k, S_k is the estimated total phloem area of girdled trees (i.e., sinks) in cell k, and u and v are parameters estimated via maximum likelihood to adjust treatment effects. Eqs. (5) and (6) represent the reduction in the spread from cell k to cell j caused by the treatments. Eq. (7) is a modification of Eq. (2) to include the effects of both treatments. To simulate the effect of only one treatment, the corresponding effect (I_k or S_k) was simply removed from Eq. (7).

The fit of the adjusted models to the base model was contrasted using corrected Akaike's Information Criteria (AICc) to determine whether treatments substantially improved the fit of the model. Maximum likelihood was implemented in the bbmle package (Bolker, 2008) for the statistical package R (R core group, 2015).

3. Results

3.1. Estimates of EAB spread

3.1.1. Estimates of EAB spread with OLS regression

By 2011, EAB had spread throughout much of the Moran and St. Ignace project areas. However, the spread was not evenly distributed across ash containing regions adjacent to previously detected populations (Fig. 1), indicative of stratified dispersal. The number of larvae in girdled detection trees increased considerably from 2010 to 2011 (Figs. 1 and 2) and in 2011, the St. Ignace and Moran infestations became blurred as the two infestations essentially began to coalesce. However, the rate of spread of the Moran EAB population was notably greater than the spread of the St. Ignace population (Figs. 1 and 2).

The approximate detectable spread rate from 2008 to 2011 observed from the girdled detection trees in the Moran infestation using the threshold method varied, depending on the detection threshold used. At detection thresholds of 0.35, 0.40 and 0.45, spread rates averaged (±SD) 1.69 ± 0.038 (r^2 = 0.98 ± 0.008), 1.46 ± 0.052 (r^2 = 0.95 ± 0.017) (Fig. 2) and 1.48 ± 0.053 (r^2 = 0.96 ± 0.016) km yr^{-1}, respectively. When satellite populations were not included, the approximate detectable spread rates over the same time period averaged (±SD) 1.77 ± 0.024 (r^2 = 0.99 ± 0.004), 1.56 ± 0.037 (r^2 = 0.97 ± 0.008), and 1.57 ± 0.034 (r^2 = 0.97 ± 0.007) km yr^{-1} when the detection threshold was 0.35, 0.40 (Fig. 2) and 0.45, respectively. Differences between spread rates observed with and without satellites illustrate the effect of the satellite populations on the spread of the population front. Specifically, when satellites were excluded from the analysis, the spread appears to occur faster because the increased spread of the infestation caused by the satellites is attributed to the main population front. In effect, the increased spread rate observed when outliers/satellites are not included in the population represents how the rate of spread can be overestimated when detection thresholds don't permit the detection of satellite populations.

The St. Ignace infestation, which was also detected in 2007, was considerably smaller than the Moran infestation, either because it was a more recent infestation or because fewer EAB were originally introduced into the St. Ignace area. The lack of expected detectability of EAB in 2008 and 2009 for cells in St. Ignace (40% likelihood) suggests the infestation was detected at an early stage of invasion. In addition, application of the systemic insecticide to numerous trees within a relatively recently established infestation may have had a stronger impact on subsequent spread of this EAB population. However, we cannot separate potential effects of the insecticide-treated trees from the apparently younger age and smaller size of the St. Ignace infestation relative to the Moran infestation. The outliers identified in 2011 in the area between the St. Ignace and Moran infestations (Fig. 2) were likely colonized by EAB dispersing from the nearby Moran population, rather than EAB originating from the St. Ignace infestation (Fig. 1). Therefore, the detectable spread in St. Ignace was only estimated excluding the outliers. Spread in the St. Ignace infestation averaged (±SD) 0.73 ± 0.038 (r^2 = 0. 99 ± 0.013), 0.70 ± 0.04 (r^2 = 0.99 ± 0.0712 SD) (Fig. 2), and 0.622 ± 0.04 (r^2 = 0.985 ± 0.025) km yr^{-1}, when the detection threshold was set at 0.35, 0.40 (Fig. 2) and 0.45, respectively.

The rate of spread estimated when simulating detections using Bernoulli trials was lower than rates generated by the threshold method. Spread rates for Moran were 1.103 ± 0.052 km yr^{-1} (r^2 = 0.23 ± 0.021) when including satellite infestations and 1.24 ± 0.047 km yr^{-1} (r^2 = 0.30 ± 0.021) when excluding satellites. For the St. Ignace site, however, spread could not be estimated with certainty using this method (0.405 ± 0.257 km yr^{-1}; r^2 = 0.38 ± 0.362).

3.1.2. Mechanistic simulation model

The observed and simulated EAB distributions in 2010 and 2011 by distance class indicated a strong fit of the simulation model with the observed spread (Figs. 3 and 4). However, the simulation model did not accurately reflect spread at the edges of the infestations. This effect likely reflects the lack of a long distance dispersal component in the model, as well as the merging of the Moran and St. Ignace infestations in 2011.

3.1.3. Descriptive model

The descriptive model fit to the combined Moran and St. Ignace project areas indicated a reasonable fit between the predicted probability of detecting an infestation and the observed estimate of the probability of detection (r^2 = 0.8) (determined using the weighted mean of EAB presence or absence in detection trees). However, as with the mechanistic model the descriptive model does not accurately predict detections observed far from the edge of the previous year's infestation (Fig. 5). Again, this is likely due to our inability to accurately predict the movement of long distance dispersers. When the base model was used to predict the 2010 infestation using the 2009 observed detections, the model fit reasonably well (r^2 = 0.64). Including the effect of EAB population density substantially increased the fit (ΔAICc = 11.97, Table 1), but did not have a large effect on the overall relationship between the predicted and observed spread (r^2 = 0.80). These results indicate EAB spread rates are likely to increase as populations build, an important consideration when developing management strategies for a given infestation (Mercader et al., 2011b).

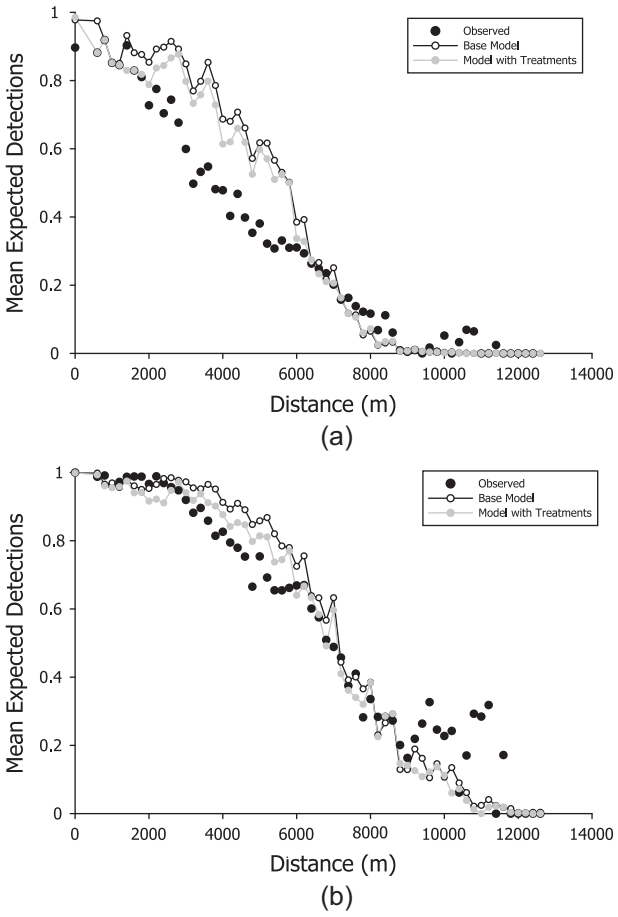

Fig. 3. Mean EAB detection probabilities per cell by distance from the origin of simulated infestations (mechanistic simulation model) with and without inclusion of treatment effects through a 200 × 200 m cell lattice overlaid onto the Moran and St. Ignace areas in (a) 2010 and (b) 2011. Simulated mean detection probabilities were estimated based on EAB larval densities predicted using a simulation model and observed mean detection probabilities for each cell were estimated as distance-weighted means of detection trees.

3.2. Effects of treatments on EAB spread

3.2.1. Mechanistic simulation model approach

Incorporating the effect of insecticide-treated trees and girdled ash "sink" trees in the updated model did not increase the fit of the model. The best fitting scaling parameter to modify the treatment effect was 0, indicating the treatments had no detectable effect on EAB spread rates. Simulations to assess effects of the girdled sink trees included two modifiers; the first for the reduction in EAB population growth attributable to larval mortality when trees were debarked and the second for adult EAB attraction to girdled trees. Both were positive (3.92 and 0.24, respectively). Incorporating the effects of sink trees slightly increased the fit of the simulation model to the expected detections in 2011 (Fig. 3). This was supported by simple linear regressions of the observed expected detections and the simulation results by distance class in 2011, which yielded equivalent r^2 values (base model: $r^2 = 0.9368$, treatments included: $r^2 = 0.9373$). The absence of a substantial effect of the insecticide or sink treatments is not surprising, given that considerably less than 1% of the ash trees or ash phloem available to *A. planipennis* across the SLAM project area were treated with insecticide or girdled across this extensive project area.

3.2.2. Descriptive model approach

The model incorporating the effects of the girdled sink trees generated the lowest AICc value and indicated a substantially better fit than the base model for the combined Moran and St. Ignace project areas ($\Delta_i = 5.22$; Table 1). In contrast, including the insecticide treatment alone provided a lower fit than the base model ($\Delta_i = 2.01$), the model including the sink treatment alone ($\Delta_i = 7.23$), and the model including both treatments ($\Delta_i = 4.66$). Furthermore, including the insecticide treatment along with the sink treatment provided a lower fit ($\Delta_i = 2.57$) than including only the sink trees alone.

These results corroborate those from the mechanistic model. Both indicated that insecticide treatments did not substantially reduce the observed spread, while the girdled sink trees had a small, but significant effect on EAB spread.

4. Discussion

Stratified dispersal, which has been observed for many invasive taxa, results in formation of discontinuous satellite colonies ahead of the main invasion front, which expand and ultimately coalesce with the main invasion, accelerating the overall rate of spread of the organism (Shigesada and Kawasaki, 1997; NRC, 2002; Liebhold and Tobin, 2008). Stratified artificial dispersal resulting from anthropogenic transport of infested ash material contributed substantially to the initial spread of EAB across southeast Michigan (Siegert et al., 2014, 2015). Dendrochronology data from southeast Michigan indicated EAB-caused ash mortality spread at a rate of 3.84–12.9 km yr^{-1} from 1998 to 2003 (Siegert et al., 2014, 2015). Because EAB was not identified until 2002, numerous instances of anthropogenic transport of EAB-infested ash nursery trees, along with infested logs and firewood occurred during this period, clearly contributing to the overall expansion of EAB. Quarantines and associated regulations implemented since 2002 have drastically reduced artificial dispersal of EAB.

The rates of EAB spread in the SLAM project areas, which ranged from 0.4 to 0.7 km yr^{-1} in the St. Ignace infestation and from 1.2 to 1.7 km yr^{-1} in the larger and presumably older Moran infestation, were considerably slower than the expansion of ash mortality in southeast Michigan (Siegert et al., 2014). Spread rates observed in the St. Ignace area were, however, notably similar to those reported from previous field studies where ash were felled and sampled within 800 m of the origin, either one or three years after EAB establishment (Mercader et al., 2009; Siegert et al., 2010). The similarity in spread rates, combined with the generally healthy appearance of ash trees in the St Ignace area even in 2011, suggest this infestation was detected shortly after establishment.

In contrast to the St. Ignace infestation, the Moran infestation spread more rapidly, as a result of numerous satellite infestations that became established beyond the main infestation, as well as higher EAB densities in the epicenter (McCullough et al., 2015; Mercader et al., 2015). Formation of the satellite populations around Moran could be due to natural dispersal of adult EAB or human-aided dispersal, ostensibly through movement of infested firewood. However, substantial local outreach and education efforts were undertaken to inform residents and visitors about EAB, the SLAM project and quarantine regulations restricting transport of ash firewood, logs and related materials. The satellites around Moran were not associated with campgrounds, sawmills or similar destinations for potentially infested wood. While we cannot exclude the possibility of human transport, it is much more likely that the majority of the satellite populations reflect long-range dispersal of mature adult EAB females. Female EAB feed on ash leaves for at least two weeks to complete maturation, then lay a few eggs at a time over a period of days, between bouts of leaf-feeding and resting. Little is known about host selection and dispersal behavior of female EAB and whether long-range flights are triggered by disturbance, population density, wind or host

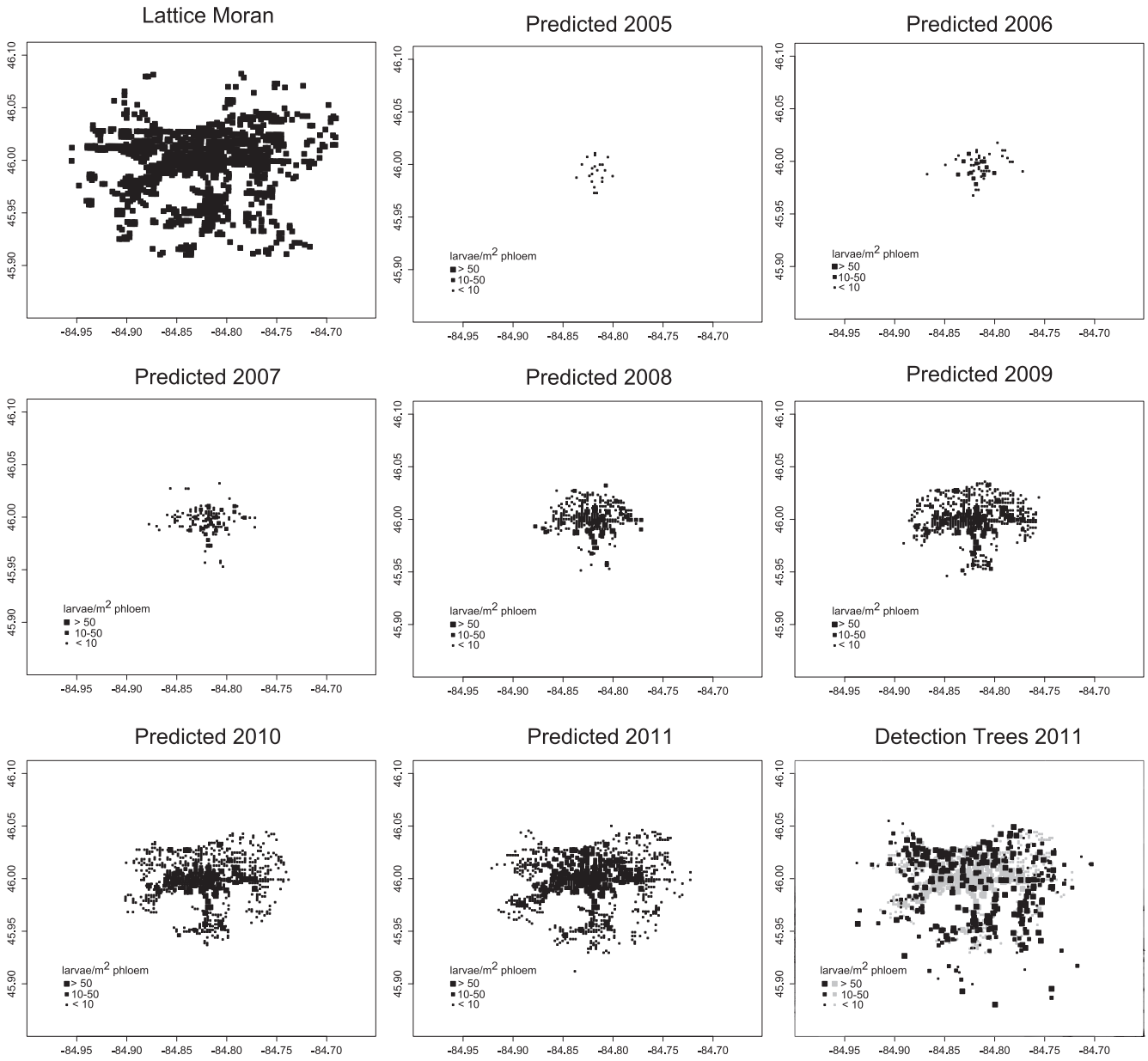

Fig. 4. Spread in larvae per m^2 of phloem predicted by mechanistic model from 2004 to 2011 in the Moran area. The first panel, "Lattice" represents the 200 × 200 m cells within the lattice containing ash trees. The final panel, "Detection trees 2011", represents the density of larvae per m^2 of phloem observed in detection trees in 2011 in black overlaid unto the predicted spread for 2011 in gray. Note that there are more ash containing cells in the lattice than detection trees.

condition, or if a proportion of females are simply predisposed to undertake long flights (Mercader et al., 2012; Siegert et al., 2015). Previous field studies, which involved systematically felling and debarking ash trees within 800 m of a known EAB introduction point, showed females laid over 90% of the eggs on trees within 450 m of the origin and less than 0.5% of the eggs on trees 700–800 m from the origin (Mercader et al., 2009; Siegert et al., 2010, 2015). In these studies, however, the labor-intensive, destructive sampling was limited to a relatively small portion of the available ash and trees were not sampled beyond the area defined by an 800 m radius. The SLAM data provide a more extensive perspective on EAB dispersal over a much larger area and a period of four years. Not surprisingly, larval counts were highest in girdled detection trees near the epicenters of the Moran and St. Ignace infestations, but each year, some female beetles appear to have laid at least a portion of their eggs on trees 2000 m or more from the epicenter. This effectively created natural satellite infestations, each of which grew and contributed to the overall spread of EAB across the entire project area over time.

Results of the mechanistic model highlight the difficulty caused by the presence of satellite infestations in attempts to delineate and predict spread rates of EAB populations. We used the observed spread of EAB to adjust dispersal in the model presented in Mercader et al. (2011a) for larger and more heterogeneous areas. Simulations in Mercader et al. (2011a) indicated that dispersal in heterogeneous environments would be considerably different than dispersal in more homogeneous environments and that assumptions regarding the dispersal and ovipositional behavior of female EAB have significant implications for the spread of a given population. The rate of spread observed in Moran was considerably greater than would be expected based on data from mark-recapture studies (Fraser et al., 2006) and the distribution of infested trees recorded from the small, intensive field studies where one to three generations of EAB dispersed from a known

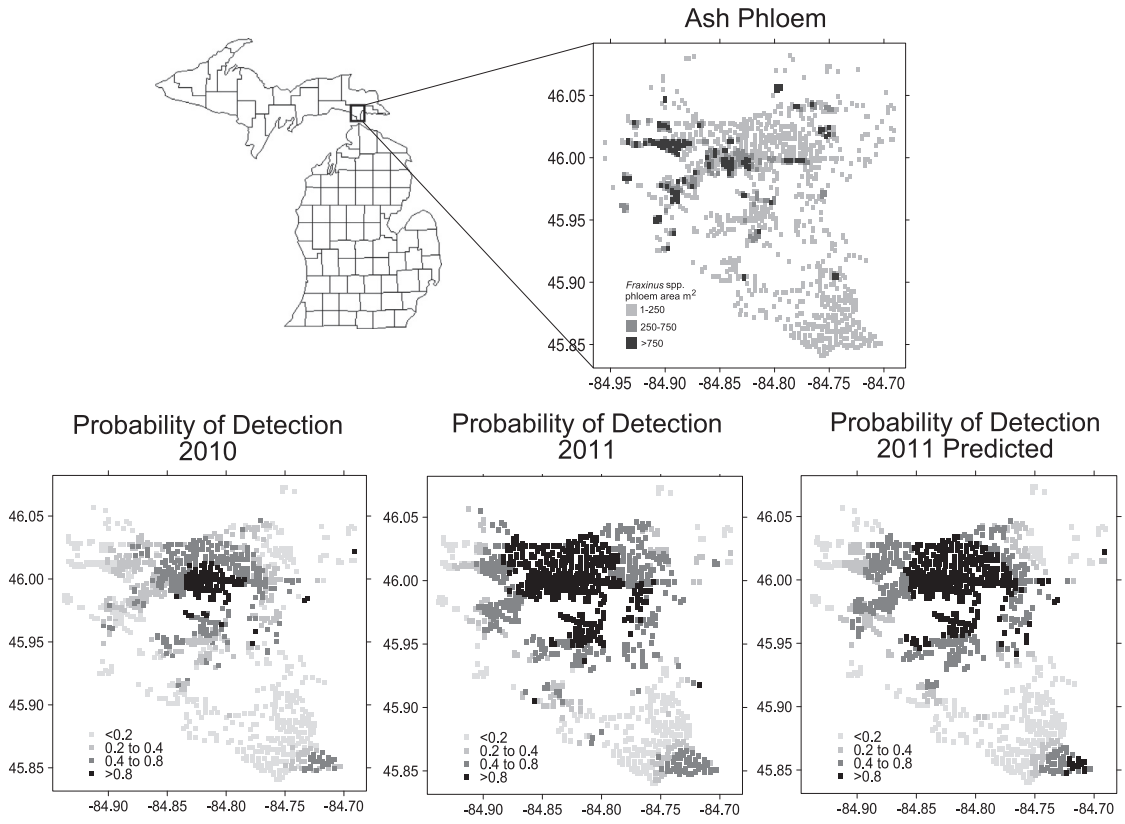

Fig. 5. Expected probability a single detection tree will be detected as positive per 200 × 200 m cell in the Moran and St. Ignace areas in 2010, 2011, and predicted for 2011 by the descriptive model.

Table 1
Parameter estimates for the descriptive spread model run over the Moran and St. Ignace areas. Corrected Akaike Information Criterion (AICc) values were estimated using the parameter estimates fit for the base model and models including the effects EAB population density (Population Density), total area of insecticide-treated ash phloem in cells (Insecticides), total area of phloem in girdled ash trees in cells (Sink), or both treatments (Insecticide and Sink).

Models	$a \pm SE$	$b \pm SE$	AICc
Base	1.849 ± 0.027	$2.652 \times 10^{-9} \pm 1.62 \times 10^{-5}$	2738.33
Base + Population density	2.244 ± 0.04	$1.378 \times 10^{-9} \pm 1.61 \times 10^{-5}$	2726.36
Treatment effects			
Base + Insecticide	1.849 ± 0.027	$1.184 \times 10^{-9} \pm 1.621 \times 10^{-5}$	2740.34
Base + Sink	2.134 ± 0.086	$1.012 \times 10^{-9} \pm 1.403 \times 10^{-5}$	2733.11
Base + Insecticide and Sink	2.094 ± 0.0814	$8.274 \times 10^{-10} \pm 1.337 \times 10^{-5}$	2735.68
	$u \pm SE$	$v \pm SE$	
Population density	$34.93 \pm 1.568 \times 10^{-4}$	NA	
Insecticide	$62.224 \times 10^{-07} \pm 2.616 \times 10^{-4}$	NA	
Sink	NA	$5.573 \times 10^{-2} \pm 2.486 \times 10^{-2}$	
Insecticide and sink	$1.740 \times 10^{-8} \pm 1.152 \times 10^{-4}$	$5.89 \times 10^{-2} \pm 2.211 \times 10^{-2}$	

origin (Mercader et al., 2009; Siegert et al., 2010). Our model, therefore, requires an estimate of the propensity for long distance dispersal by EAB females. Simulations including a fairly high rate of long distance dispersers, such as 20% of the population (Mercader et al., 2012), more closely resemble the spread rates observed in the Moran area, suggesting that long distance dispersal by mature EAB females may be relatively common. Contrasting the mechanistic model to the observed data also appears to indicate a high prevalence of long distance dispersers. Specifically, the model overestimated the detectable spread early but did not account for the large number of satellite populations that ultimately formed, suggesting small satellites established far from the edge of the main population are likely to remain undetected. These results, which are similar to those generated by simulation models (Mercader et al., 2011a,b), indicate that the preemptive removal of ash trees in newly infested sites may affect local population growth but is not likely to reduce EAB spread of the infestation overall (Sargent et al., 2010; Mercader et al., 2011a, 2011b).

The importance of the formation of satellite populations is evident in the differences observed in the estimated spread rate in the Moran infestation when satellite populations were included or excluded. In particular, the higher estimated spread rate when satellite populations were excluded from the analysis illustrates how the stratified dispersal process leads to coalescence, even during the initial phases of population expansion. The St. Ignace infestation, although detected in the same year, was considerably smaller either due to being initiated more recently or by a smaller initial number of EAB. The eventual coalescence of the two infestations in 2011 likely resulted from dispersal of beetles out of the older and larger Moran infestation. Therefore, the spread rate of

the St. Ignace population was less than half that observed in the Moran infestation. The differences in the spread dynamics between the two sites highlight the need to better understand factors affecting the propensity for female EAB to undertake long distance dispersal.

Despite the inability to realistically predict the formation of satellite populations, the simulation model results are promising. As exemplified by the St. Ignace and Moran infestations, however, it is exceedingly difficult to gauge the true size and extent of an initial infestation. Therefore, the simulation model applied here is likely to prove useful as a base model to simulate potential treatments or management strategies, but not to make precise predictions of the spread of any given infestation. Moreover, managers are unlikely to use a mechanistic model to predict EAB spread in specific locations because of the expense and logistical difficulties of acquiring the detailed ash inventory and EAB population and distribution data. Alternatively, the descriptive model simply requires presence–absence data on EAB and ash to inform the model. Furthermore, inclusion of population density estimates did not greatly increase the relationship between observed and predicted spread (base $r^2 = 0.799$, base with population density $r^2 = 0.801$). Although the fit of the model was not as good as the simulation model ($r^2 = 0.9368$), it did provide a reasonable fit, suggesting this approach may provide a functional tool for managers.

The primary goal of the SLAM Pilot Project was to evaluate whether tactics such as girdled trees and treating trees with the emamectin benzoate insecticide could slow EAB population growth, thereby slowing the onset and progression of ash decline and mortality (Poland and McCullough, 2010; McCullough et al., 2015; Mercader et al., 2015). Restrictions associated with federal lands in the project areas, however, limited the number of ash trees that could be treated with the systemic insecticide. Distribution of injected trees was also less than optimal; nearly all treated trees were either growing along roads or in a few areas of private land (McCullough et al., 2015; Mercader et al., 2015). Although only a very small proportion of the ash trees in the Moran and St Ignace project areas were injected with the insecticide in 2009–2011 (total of 587 trees), the treatment significantly slowed EAB population growth and the rate of ash decline (McCullough et al., 2015; Mercader et al., 2015). However, the insecticide-treated trees had no detectable effect on the rate of spread of the EAB populations when the treatment was included in either the mechanistic or the descriptive model. This apparently contradictory result partly stems from the placement of insecticide treatments in this study. In particular, the majority of insecticide treated trees were located at the center of the infestations, thereby not affecting the leading edge of the spread. Simulations have shown it is feasible to use insecticide-treated trees to substantially reduce the spread of a local EAB population (Mercader et al., 2011b), but the density of treated trees must be considerably greater than that of the SLAM pilot project areas.

Girdled ash trees exerted a small, but significant effect on the spread of EAB in both the mechanistic and descriptive models. Between 2008 and 2011, a total of 2650 ash trees (603–855 per year) were girdled and debarked in the systematic grids set up across the project areas. In the mechanistic model, the effect of girdled trees was modeled as an attraction to girdled trees by egg-laying females and the removal of EAB larvae present within girdled trees. The removal of EAB individuals in these simulations had virtually no effect on spread, but altering attraction of adult females to girdled trees led to an increased retention of beetles in cells containing girdled trees, an effect responsible for the small but increased model fit. This effect was more evident in the descriptive model, where the effect was modeled simply as a reduction in the probability of a cell containing girdled trees to lead to an infestation in an uninfested cell. Therefore, the substantially greater fit observed in the model resulted from the retention of beetles within areas containing girdled trees.

One of the challenges for local managers is that the rapid rate of spread of an EAB infestation makes it difficult to effectively target treatments unless the population is detected very soon after establishment, which rarely happens (McCullough and Mercader, 2012; Herms and McCullough, 2014). Girdled trees provide a potential means to retain or pull beetles to a specific area, providing managers with an opportunity to focus treatments such as application of systemic insecticides, which are an economically viable option in urban and residential areas (McCullough and Mercader, 2012; Kovacs et al., 2014). Creating lethal trap trees by girdling ash previously injected with a systemic insecticide or intermixing insecticide-treated trees with girdled trees could perhaps increase the number of EAB exposed to the insecticide, enhancing the overall effectiveness of the treatments (McCullough et al., 2015a, in press). Given the economic and ecological impacts of EAB observed in North America to date, effective management of this invader will require further studies to increase our understanding of factors affecting EAB behavior, spread and population dynamics.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.02.005.

References

Anulewicz, A.C., McCullough, D.G., Cappaert, D.L., 2007. Emerald ash borer (*Agrilus planipennis*) density and canopy dieback in three North American ash species. Arboric. Urban For. 33, 338–349.

Aukema, J.E., Leung, B., Kovacs, K., Chivers, C., Britton, K.O., Englin, J., Frankel, S.J., Haight, R.G., Holmes, T.P., Liebhold, A.M., McCullough, D.G., Von Holle, B., 2011. Economic impacts of non-native forest insects in the continental United States. PLoS ONE 6 (9), e24587. http://dx.doi.org/10.1371/journal.pone.0024587.

Aukema, J.E., McCullough, D.G., Von Holle, B., Liebhold, A.M., Britton, K., Frankel, S.J., 2010. Historical accumulation of nonindigenous forest pests in the continental United States. Bioscience 60, 886–897. http://dx.doi.org/10.1525/bio.2010.60.11.5.

Bolker, B.M., 2008. bbmle: Tools for General Maximum Likelihood Estimation (R package, Version 0.8.2 <www.cran.r-project.org/>.

Cappaert, D.L., McCullough, D.G., Poland, T.M., Siegert, N.W., 2005. Emerald ash borer in North America: a research and regulatory challenge. Am. Entomol. 51, 152–165.

Crook, D.J., Mastro, V.C., 2010. Chemical ecology of the emerald ash borer *Agrilus planipennis*. J. Chem. Ecol. 36, 101–112. http://dx.doi.org/10.1007/s10886-009-9738-x.

Donovan, G.H., Butry, D.T., Michael, Y.L., Prestemon, J.P., Liebhold, A.M., Gatziolis, D., Mao, M.Y., 2013. The relationship between trees and human health: evidence from the spread of the Emerald ash borer. Am. J. Preventative Med. 44, 139–145. http://dx.doi.org/10.1016/j.amepre.2012.09.066.

Donovan, G.H., Michael, Y.L., Gatziolis, D., Prestemon, J.P., Whitsel, E.A., 2015. Is tree loss associated with cardiovascular-disease risk in the Women's Health Initiative? A natural experiment. Health Place 36, 1–7. http://dx.doi.org/10.1016/j.healthplace.2015.08.007.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N. L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., Webster, J.R., 2005. Loss of foundation species: consequences for the

structure and dynamics of forested ecosystems. Front. Ecol. Environ. 3, 479–486. http://dx.doi.org/10.1890/1540-9295(2005) 003[0479:LOFSCF]2.0.CO;2.
Etkind, P.H., ODell, T.M., Shama, S.K., Finn, A.M., Tuthill, R., 1982. The gypsy moth caterpillar: a significant new occupational and public health problem. J. Occup. Environ. Med. 24, 659–662.
Fei, S., Phillips, J., Shouse, M., 2014. Biogeomorphic impacts of invasive species. Annu. Rev. Ecol., Evol. Syst. 45, 69–87. http://dx.doi.org/10.1146/annurev-ecolsys-120213-091928.
Fraser, I., Mastro, V.C., Lance, D.R., 2006. Emerald ash borer dispersal – a release and recapture study. In: Mastro, V., Reardon, R., Parra, G. (Eds.), Proceedings of the Emerald Ash Borer Research and Technology Development Meeting, Pittsburgh, Pennsylvania, 26–27 September 2005. FHTET-2005-16. United States Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, Morgantown, West Virginia, United States of America, P. 9.
Haack, R.A., 2006. Exotic bark-and wood-boring Coleoptera in the United States: recent establishments and interceptions. Can. J. For. Res. 36, 269–288. http://dx.doi.org/10.1139/x05-249.
Herms, D.A., McCullough, D.G., 2014. Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Ann. Rev. Entomol. 59, 13–30. http://dx.doi.org/10.1146/annurev-ento-011613-162051.
Kovacs, K.F., Haight, R.G., McCullough, D.G., Mercader, R.J., Siegert, N.W., Liebhold, A. M., 2010. Cost of potential emerald ash borer damage in U.S. communities, 2009–2019. Ecol. Econ. 69, 569–578. http://dx.doi.org/10.1016/j.ecolecon.2009.09.004.
Kovacs, K.F., Haight, R.G., Mercader, R.J., McCullough, D.G., 2014. A bioeconomic analysis of an emerald ash borer invasion of an urban forest with multiple jurisdictions. Res. Energy Econ. 36, 270–289. http://dx.doi.org/10.1016/j.reseneeco.2013.04.008.
Leung, B., Springborn, M.R., Turner, J.A., Brockerhoff, E.G., 2014. Pathway-level risk analysis: the net present value of an invasive species policy in the US. Front. Ecol. Environ. 12, 273–279. http://dx.doi.org/10.1890/130311.
Liebhold, A.M., Tobin, P.C., 2008. Population ecology of insect invasions and their management. Annu. Rev. Entomol. 53, 387–408. http://dx.doi.org/10.1146/annurev.ento.52.110405.091401.
Loo, J.A., 2009. Ecological impacts of non-indigenous invasive fungi as forest pathogens. Biol. Invasions 11, 81–96. http://dx.doi.org/10.1007/s10530-008-9321-3.
McCullough, D.G., Siegert, N.W., 2007. Estimating potential emerald ash borer (Coleoptera: Buprestidae) populations using ash inventory data. J. Econ. Entomol. 100, 1577–1586. http://dx.doi.org/10.1603/0022-0493(2007) 100[1577:EPEABC]2.0.CO;2.
McCullough, D.G., Poland, T.M., Cappaert, D., 2009a. Attraction of the emerald ash borer to ash trees stressed by girdling, herbicide, or wounding. Can. J. For. Res. 39, 1331–1345. http://dx.doi.org/10.1139/X09-057.
McCullough, D.G., Poland, T.M., Anulewicz, A.C., Cappaert, D., 2009b. Emerald ash borer (Coleoptera: Buprestidae) attraction to stressed or baited ash trees. Environ. Entomol. 38, 1668–1679. http://dx.doi.org/10.1603/022.038.0620.
McCullough, D.G., Mercader, R.J., 2012. Evaluation of potential strategies to SLow Ash Mortality (SLAM) caused by emerald ash borer (*Agrilus planipennis*): SLAM in an urban forest. Int. J. Pest Manage. 58, 9–23. http://dx.doi.org/10.1080/09670874.2011.637138.
McCullough, D.G., Mercader, R.J., Siegert, N.W., 2015. Developing and integrating tactics to slow ash mortality caused by emerald ash borer. Can. Entomol. 147, 349–358. http://dx.doi.org/10.4039/tce.2015.3.
McCullough, D.G., Poland, T.M., Lewis, P., 2015. Lethal trap trees: a potential option for emerald ash borer management. Pest Manage. Sci. http://dx.doi.org/10.1002/ps.4083 (in press).
McCullough, D.G., Poland, T.M., Anulewicz, A.C., Lewis, P., Cappaert, D., 2011. Evaluation of *Agrilus planipennis* (Coleoptera: Buprestidae) control provided by emamectin benzoate and two neonicotinoid insecticides, one and two seasons after treatment. J. Econ. Entomol. 104, 1599–1612. http://dx.doi.org/10.1603/EC11101.
Mercader, R.J., Siegert, N.W., Liebhold, A.M., McCullough, D.G., 2009. Dispersal of the emerald ash borer, *Agrilus planipennis*, in newly-colonized sites. Agric. Forest Entomol. 11, 421–424. http://dx.doi.org/10.1111/j.1461-9563.2009.00451.x.
Mercader, R.J., Siegert, N.W., Liebhold, A.M., McCullough, D.G., 2011a. Simulating the effectiveness of three potential management options to slow the spread of emerald ash borer, (*Agrilus planipennis*) populations in localized outlier sites. Can. J. For. Res. 41, 254–264. http://dx.doi.org/10.1139/X10-201.
Mercader, R.J., Siegert, N.W., Liebhold, A.M., McCullough, D.G., 2011b. Influence of foraging behavior and host spatial distribution on the localized spread of the emerald ash borer, *Agrilus planipennis*. Pop. Ecol. 53, 271–285. http://dx.doi.org/10.1007/s10144-010-0233-6.
Mercader, R.J., Siegert, N.W., McCullough, D.G., 2012. Estimating the influence of population density and dispersal behavior on the ability to detect and monitor *Agrilus planipennis* (Coleoptera: Buprestidae) populations. J. Econ. Entomol. 105, 272–281. http://dx.doi.org/10.1007/s10144-010-0233-6.
Mercader, R.J., McCullough, D.G., Bedford, J.M., 2013. A comparison of girdled ash detection trees and baited artificial traps for *Agrilus planipennis* (Coleoptera: Buprestidae) detection. Environ. Entomol. 42, 1027–1039. http://dx.doi.org/10.1603/EN12334.
Mercader, R.J., McCullough, D.G., Storer, A.J., Bedford, J.M., Heyd, R., Poland, T.M., Katovich, S., 2015. Evaluation of the potential use of a systemic insecticide and girdled trees in area wide management of the emerald ash borer. For. Ecol. Manage. 350, 70–80. http://dx.doi.org/10.1016/j.foreco.2015.04.020.
Mota-Sanchez, D., Cregg, B.M., McCullough, D.G., Poland, T.M., Hollingworth, R.M., 2009. Distribution of trunk-injected ^{14}C imidacloprid in ash trees and effects on emerald ash borer (Coleoptera: Buprestidae) adults. Crop Protect. 28, 655–661. http://dx.doi.org/10.1016/j.cropro.2009.03.012.
National Research Council, Board of Agriculture, Natural Resources, National Academy of Science, 2002. Predicting Invasions of Nonindigenous Plants and Plant Pests. National Academy Press, Washington, DC, 198p.
Petrice, T.R., Haack, R.A., 2006. Effects of cutting date, outdoor storage conditions, and splitting on survival of *Agrilus planipennis* (Coleoptera: Buprestidae) in firewood logs. J. Econ. Entomol. 99, 790–796. http://dx.doi.org/10.1603/0022-0493-99.3.790.
Poland, T.M., McCullough, D.G., 2010. SLAM: a multiagency pilot project to SL.ow A. sh M.ortality caused by emerald ash borer in outlier sites. Newslett. Mich. Entomol. Soc. 55, 4–8.
Poland, T.M., McCullough, D.G., 2014. Comparison of trap types and colors for capturing emerald ash borer adults at different population densities. Environ. Entomol. 43, 157–170. http://dx.doi.org/10.1603/EN13137.
Poland, T.M., McCullough, D.G., Anulewicz, A.C., 2011. Evaluation of double-decker traps for emerald ash borer (Coleoptera: Buprestidae). J. Econ. Entomol. 104, 517–531. http://dx.doi.org/10.1603/EC10254.
R Development Core Team, 2015. R: A Language and Environment for Statistical Computing. Royal Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0 <http://www.R-project.org>.
Rebek, E.J., Herms, D.A., Smitley, D.R., 2008. Interspecific variation in resistance to emerald ash borer (Coleoptera: Buprestidae) among North American and Asian ash (*Fraxinus* spp.). Environ. Entomol. 37, 242–246. http://dx.doi.org/10.1603/0046-225X(2008) 37[242:IVIRTE]2.0.CO;2.
Sargent, C., Raupp, M., Bean, D., Sawyer, A.J., 2010. Dispersal of emerald ash borer within an intensively managed quarantine zone. Arboric. Urban For. 36, 160–163.
Shigesada, N., Kawasaki, K., 1997. Biological Invasions: Theory and Practice. Oxford University Press, New York.
Siegert, N.W., McCullough, D.G., Williams, D.W., Fraser, I., Poland, T.M., Pierce, S.J., 2010. Dispersal of *Agrilus planipennis* (Coleoptera: Buprestidae) from discrete epicenters in two outlier sites. Environ. Entomol. 39, 253–265. http://dx.doi.org/10.1603/EN09029.
Siegert, N.W., McCullough, D.G., Liebhold, A.M., Telewski, F.W., 2014. Dendrochronological reconstruction of the epicentre and early spread of emerald ash borer in North America. Divers. Distrib. 20, 847–858. http://dx.doi.org/10.1111/ddi.12212.
Siegert, N.W., Mercader, R.J., McCullough, D.G., 2015. Spread and dispersal of emerald ash borer (Coleoptera: Buprestidae): estimating the spatial dynamics of a difficult-to-detect invasive forest pest. Can. Entomol. 147, 338–348. http://dx.doi.org/10.4039/tce.2015.11.
Smitley, D.R., Doccola, J.J., Cox, D.L., 2010. Multiple-year protection of ash trees from emerald ash borer with a single trunk injection of emamectin benzoate, and single-year protection with an imidacloprid basal drench. Arboric. Urban For. 36, 206–211.
Tanis, S.R., Cregg, B.M., Mota-Sanchez, D., McCullough, D.G., Poland, T.M., 2012. Spatial and temporal distribution of trunk-injected ^{14}C-imidacloprid in *Fraxinus* trees. Pest Manage. Sci. 68, 529–536. http://dx.doi.org/10.1002/ps.2281.
Tanis, S.R., McCullough, D.G., 2012. Differential persistence of blue ash and white ash following emerald ash borer invasion. Can. J. For. Res. 42, 1542–1550. http://dx.doi.org/10.1139/x2012-103.
Tanis, S.R., McCullough, D.G., 2015. Host resistance of five Fraxinus species to *Agrilus planipennis* (Coleoptera: Buprestidae) and effects of paclobutrazol and fertilization. Environ. Entomol. 44, 287–299. http://dx.doi.org/10.1093/ee/nvu005.
Taylor, R.A.J., Bauer, L.S., Poland, T.M., Windell, K.N., 2010. Flight performance of *Agrilus planipennis* (Coleoptera: Buprestidae) on a flight mill and in free flight. J. Insect Behav. 23, 128–148. http://dx.doi.org/10.1007/s10905-010-9202-3.
Tluczek, A.R., McCullough, D.G., Poland, T.M., 2011. Influence of host stress on emerald ash borer (Coleoptera: Buprestidae) adult density, development, and distribution in *Fraxinus pennsylvanica* trees. Environ. Entomol. 40, 357–366. http://dx.doi.org/10.1603/EN10219.
Whitehill, J.G.A., Popova-Butler, A., Green-Church, K.B., Koch, J.L., Herms, D.A., Bonello, P., 2011. Interspecific proteomic comparisons reveal ash phloem genes potentially involved in constitutive resistance to the emerald ash borer. PLoS ONE 6 (9), e24863. http://dx.doi.org/10.1371/journal.pone.0024863.