ORIGINAL ARTICLE

# Influence of foraging behavior and host spatial distribution on the localized spread of the emerald ash borer, *Agrilus planipennis*

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**Abstract** Management programs for invasive species are often developed at a regional or national level, but physical intervention generally takes place over relatively small areas occupied by newly founded, isolated populations. The ability to predict how local habitat variation affects the expansion of such newly founded populations is essential for efficiently targeting resources to slow the spread of an invasive species. We assembled a coupled map lattice model that simulates the local spread of newly founded colonies of the emerald ash borer (Agrilus planipennis Fairmaire), a devastating forest insect pest of ash (Fraxinus spp.) trees. Using this model, we investigated the spread of A. planipennis in environments with different Fraxinus spp. distributions, and explored the consequences of ovipositional foraging behavior on the local spread of A. planipennis. Simulations indicate that increased larval density, resulting from lower host tree density or higher initial population sizes, can increase the spread rate during the first few years after colonization by increasing a density-dependent developmental rate and via host resource

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Northern Research Station, USDA Forest Service, 180 Canfield Street, Morgantown, WV 26505, USA depletion. Both the radial spread rate and population size were greatly influenced by ovipositional foraging behavior. Two known behaviors of ovipositing *A. planipennis* females, attraction towards areas with high ash tree density and attraction to stressed trees, had opposing effects on spread. Results from this model illustrate the significant influence of resource distribution and foraging behavior on localized spread, and the importance of these factors when formulating strategies to monitor and manage invasive pests.

**Keywords** Biological invasions · Buprestidae · Dispersal · Forest insect pests · Invasive species · Ovipositional behavior

## Introduction

Biological invasions are strongly dependent on interactions between the invading organisms and the biotic and abiotic properties of the community being invaded (Hastings et al. 2005; Liebhold and Tobin 2008). A key component of these interactions is resource availability, which has long been recognized as an important component of the invasibility of communities and the spread of invasive species (Davis et al. 2000). In particular, resource availability has been proposed as a primary determinant of invasibility (Davis et al. 2000), while the spatial heterogeneity of resources has been proposed to directly influence the rate at which invasive species spread (e.g., Shigesada and Kawasaki 1997; With 2002, 2004).

Habitat invasibility can determine where populations become established and thereby influence spread, particularly for alien species that exhibit stratified dispersal. Stratified dispersal, a common mechanism of spread observed across many taxa, is defined by the simultaneous occurrence of both short- and long-distance dispersal mechanisms (Shigesada and Kawasaki 1997). When coupled with population growth, stratified dispersal can result in discontinuous satellite colonies ahead of the main invasion front. These satellite populations will themselves expand and ultimately coalesce with the main invasion front (Shigesada and Kawasaki 1997). Understanding population dynamics in these satellite colonies is of great practical value. Various management models have shown that control of these smaller populations can slow invasion spread (e.g., Moody and Mack 1988; Sharov and Liebhold 1998; Taylor and Hastings 2004).

An important component to understanding how habitats influence the invasion process is resource heterogeneity. The influence of resource heterogeneity on the spread rate of organisms depends on the scale at which dispersal is observed. Heterogeneity at a scale greater than that of the organisms' dispersal capabilities is predicted to significantly decrease the rate of spread (With 2002, 2004; Simpson et al. 2008). In contrast, heterogeneity at a scale lower than the dispersal capability of an organism is expected to increase its spread if the organisms use low resource patches as intermediaries to access high resource patches (With 2002, 2004; Simpson et al. 2008). If an organism does not act as an optimal forager, however, the prediction that heterogeneity will increase the rate of spread would no longer be valid.

Immature stages of many insects are relatively immobile and consequently, the larval environment is determined entirely by the ovipositing female. Colonization, therefore, is dependent on adult female behavior. Host availability and quality generally influence population growth for most plant feeding insects (e.g., Ylioja et al. 1999; Larsson et al. 2000; Underwood 2004, 2007), but the correlation between adult host choice and larval performance for many phytophagous insects is often weak (e.g., Mayhew 1997, 2001; Lazarus 2003), and ovipositing insects do not always act as ideal foragers. Likewise, the assumption that ovipositing females select available hosts at random is equally unwarranted, as most insects have significant interspecific and intraspecific host preferences. For example, Agrilus planipennis (Fairmaire) females exhibit significant ovipositional preferences among Fraxinus spp. (Anulewicz et al. 2008) and preferentially oviposit on stressed trees over healthy trees (McCullough et al. 2009a, b).

However, the likelihood of deriving spatially explicit empirical data to assess the influence of host driven population dynamics on the rate of spread of a recently discovered invasive species is daunting at best. Simulation models provide a flexible and cost effective tool to incorporate our best (albeit often limited) understanding of an organism to investigate the potential impacts of unknown factors. One such recently discovered invasive species is the aforementioned *A. planipennis*, a phloem-feeding buprestid beetle specializing on ash trees (*Fraxinus* spp.). *Agrilus planipennis* was first discovered in North America in southeast Michigan, USA, and Windsor, Ontario, Canada, in June 2002 (Cappaert et al. 2005), but is believed to have been present in North America since at least the early 1990s (Siegert et al. 2007a). As of 2008, more than 50 million ash trees had been killed by *A. planipennis* (EAB Info 2010).

Larvae of A. planipennis feed under the bark and leave their host tree only after completing development to the adult stage, limiting the natural dispersal of A. planipennis to the ovipositional foraging behavior of adult females. Unfortunately, human-mediated transport of infested wood has led to the development of numerous satellite colonies at significantly greater distances than possible through natural dispersal (Cappaert et al. 2005; EAB Info 2010). There is no evidence that adult A. planipennis produce long-range attraction pheromones (Lelito et al. 2007), and trees exhibit no external symptoms of infestation until larval densities build (Cappaert et al. 2005). Due to these limitations, identifying newly established populations is exceedingly difficult. However, dozens of satellite populations have been identified since 2002, typically after populations build and trees begin to decline (Cappaert et al. 2005; Siegert et al. 2007a). This situation, and the likelihood that additional satellite populations will be discovered, means that a better understanding of the spread of A. planipennis from recently colonized locations is crucial.

Towards this end, we developed a spatially explicit simulation model of the localized dispersal of *A. planipennis*. The simulation model is implemented as a coupled map lattice with values in each cell representing the amount of ash phloem available for *A. planipennis* larval development. Using this model, we investigate the influence of host spatial distribution and adult female ovipositional foraging behavior on the local spread of isolated *A. planipennis* populations. Specifically, we use the model to contrast four types of adult foraging behaviors on population size and radial spread: (1) simple diffusion; (2) avoidance of areas devoid of resources; (3) two forms of bias towards high resource areas; and (4) bias towards areas with stressed trees.

## Materials and methods

# Model description

A coupled map lattice model was constructed to represent the spatially explicit growth and dispersal of an isolated *A. planipennis* population following initial colonization. The lattice consists of a grid of *n* square cells of equal size, each containing ash phloem with quantities initialized at specific levels. Spatial realism can be incorporated into the model by performing simulations over environments initialized using actual ash phloem data collected from specific outlier sites. Across the map lattice, the model simulated three population processes relevant to the spread of the *A. planipennis*: (1) larval development to adults; (2) dispersal of fertilized females among cells; and (3) population growth (encompassing oviposition by females and survival) and phloem consumption by larvae. The code (R Development Core Team 2010) for the couple map lattice model is included in Appendix A in the Electronic supplementary material (ESM). Below, we describe each successive step of the model and the derivation of parameter estimates in detail.

# Larval development to adults

Agrilus planipennis development from larvae to adult is phenotypically plastic, requiring either 1 or 2 years. The number of adults emerging in any year thus represents the sum of the adults that developed from eggs laid the previous year and the adults that developed from eggs laid 2 years earlier. Larval development rate appears to be strongly affected by host vigor (Siegert et al. 2007b; Tluczek 2009). Larvae developing in stressed trees are more likely to develop in a single year, while larvae developing in healthy trees are more likely to require 2 years for development. As *A. planipennis* population densities increase, the proportion of trees that are stressed increases (due to larval feeding), leading to a greater proportion of univoltine (1-year) larvae.

Here, the proportion of larvae developing in 1 or 2 years for each cohort is determined by the relationship between larval density and the proportion of larvae with 2-year development recorded at known isolated populations. During 2006 and 2007, a total of 206 infested trees in 16 outlier sites in eight counties in Michigan, USA, were felled and debarked in late autumn. The number and stage of larvae were recorded and standardized per  $m^2$  of exposed phloem for each tree. Mean larval density observed in these sites ranged from 1 to 101 larvae per  $m^2$ and the proportion of larvae undergoing 2-year development ranged from 0 to 100%. Using this information, the proportion of larvae with 2- versus 1-year development was regressed on larval density (larvae per  $m^2$  phloem).

The proportion of larvae with 2-year development was significantly and negatively correlated with larval density  $(F_{1,17} = 60.83, P < 0.001, \text{ adj. } R^2 = 0.78)$ . This relationship is described by  $y = -0.194\ln(x) + 0.986$ , where y is the proportion of 2-year larvae and x is the number of larvae per m<sup>2</sup> (see Appendix B in ESM).

#### Dispersal of fertilized adult females

Mercader et al. (2009) quantified the short-range dispersal of fertilized *A. planipennis* females based on the distribution of larvae following initial colonization at known locations in two intensively sampled sites. In that study, dispersal closely followed a negative exponential function. Most larvae produced by dispersing females were found within 100 m of the adult emergence point. The function determined by Mercader et al. (2009) was used to determine the proportion of beetles remaining or entering each cell, as described for cell *i* at time t + 1 in Eq. 1 below,

$$N_{t+1}^{i} = \sum_{j=1}^{n} N_{t}^{j} \frac{\mathrm{e}^{-bD_{ji}}}{\sum_{j=1}^{n+1} \mathrm{e}^{-bD_{ji}}}$$
(1)

where  $N_t^i$  is the number of individuals present in cell *j* at time *t*, *j* denotes all cells in the site including cell *i* (i.e., the number of beetles remaining in cell *i*), *b* represents the parameter previously estimated for the negative exponential function, 0.037 (Mercader et al. 2009), and  $D_{ji}$  is the distance between cell *j* and cell *i*.

The negative exponential function of Mercader et al. (2009) was fit using larval counts in F. pennsylvanica trees that were continuously distributed and relatively homogeneous along a corridor. Host resource quality and quantity did not vary substantially in these habitats. In contrast, ash distribution in many environments (e.g., most forests, residential areas) can be exceedingly patchy and include large areas where no ash phloem is available. While most ovipositing A. planipennis adult females select hosts close to their point of emergence when ash trees are available (Mercader et al. 2009), mated A. planipennis females are capable of flying up to 1.8 km/ day (Taylor et al. 2006). Adult females that fail to encounter ash trees therefore are highly unlike to remain in ash-free locations and will likely seek areas where ash trees occur. In addition, Siegert et al. (2010) reported a significant bias in A. planipennis adult dispersal towards areas with abundant ash phloem.

In the simulation model, the influence of foraging behavior of adult female *A. planipennis* was investigated by increasing or decreasing the likelihood of beetles entering cells. To accomplish this, the movement into or out of specific cells was altered in accordance with the behavior we seek to simulate. To accomplish this Eq. 1 was adjusted by adding two modifiers, *y* and *a* (see Eq. 2 below). These modifiers act to increase or decrease movement of adults from the donor cell into the receiving cell. Although functionally analogous, these modifiers can be used to alter the movement in two different ways. Modifier *y* acts by altering the "functional distance" of two cells, thereby increasing or decreasing adult movement between two cells along the exponential function determined by Mercader et al. (2009). Here, y was used to simulate beetle avoidance and/or failure to remain in empty or low resource cells and increase beetle movement into high resource areas. Modifier a alters the movement into or out of a cell by a specific proportion. In effect, a is used to alter the relative attractiveness of a recipient cell relative to another cell equally distant from the donor cell. Here, a was used to simulate the effect of the presence of stressed trees (see "Influence of oviposition site foraging behavior and host spatial distribution on population spread" below).

$$N_{t+1}^{i} = \sum_{j=1}^{n} N_{t}^{j} \frac{a_{i} \mathrm{e}^{-b(D_{ji}+y^{i})}}{\sum_{j=1}^{n+1} a_{i} \mathrm{e}^{-b(D_{ji}+y^{i})}}$$
(2)

A positive value for  $y^i$  would be used if cell *i* is avoided (e.g., it is devoid of ash) and a negative value for  $y^i$  would be used if a cell is more attractive (e.g., contains a high quantity of ash). The values of  $y^i$  reflect the strength of the effect being simulated. A value for  $a_i > 1$  represents an increase in attractiveness for a cell (e.g., a cell containing stressed trees) and a value between 0 and 1 represents avoidance.

It is important to note that dispersal in Eq. 2 is calculated as a proportion and adjusting the dispersal between two cells affects the number of adults entering or exiting a cell in relation to all the other cells in the environment. For example, to simulate the avoidance and/or failure to remain in areas without any available ash phloem, the distance of any cell devoid of phloem is increased by placing a positive value for y in Eq. 2. A positive value for y in cells without ash phloem decreases the proportion of beetles that disperse into that cell, which will cause those beetles to move into neighboring cells containing ash phloem. Likewise, a positive value for y for cells without phloem will increase the movement of beetles out of these cells and into cells containing ash phloem.

For computational purposes, dispersal in the model was computed using a "moving window" consisting of the cell of interest and all neighboring cells up to 50 cells away. This process effectively reduces the maximum distance at which dispersal occurs to 50 cell units. This resulted in a very slight truncation of the dispersal function over long distances, but it did not substantially affect simulation results. This study focuses on localized spread and longdistance dispersal has little effect here. Since the location of beetles within a cell is unknown, the distribution of beetles within cells was considered to be uniform. Therefore, the distance between a cell and itself (used to determine the proportion of beetles remaining within a cell) was calculated as the distance between the center of a cell and the absolute value for the midpoint between the center and the edge of the cell. Calculating the distance between a cell and itself is important for A. planipennis because over 50% of realized dispersal can occur within 50 m of the adult emergence point (Mercader et al. 2009), and resource estimates are unlikely to be conducted at resolutions below  $50 \times 50$  m cell sizes. In addition, using a finer grid becomes computationally demanding and limits the practical size at which simulations are run or the maximum distance beetles can disperse.

# Dispersal in a heterogeneous site

Investigative traces by regulatory agencies of ash trees shipped from nurseries in infested counties in southeast Michigan led to the discovery of an isolated A. planipennis infestation in Saginaw Co., MI, USA. This infestation originated from a single founding population transported in infested nursery trees planted in a single location in 2003. The site was highly heterogeneous and included wooded, residential, and urban areas. In February 2004, regulatory officials established a grid of  $100 \times 100$  m cells centered on the point source of the infestation, and tallied all ash trees (>2.5 cm in diameter) by size class within 800 m of the point source  $(2 \text{ km}^2 \text{ area})$ . Siegert et al. (2010) felled and debarked 1-2 ash trees per grid cell to locate the larval progeny of the adults that dispersed from the original nursery trees. Eight infested trees were detected and their locations indicated dispersal was strongly biased towards areas where ash phloem was relatively abundant within 200 m of the origin (Siegert et al. 2010). Because sampling was limited to 1–2 trees per  $100 \times 100$  m cell, the probability of detecting larvae was relatively low and varied with ash density. Although data collected in this site are limited, they provide an approximate spatial characterization of larval distribution in this isolated population.

The quantity of ash phloem (in  $m^2$ ) was estimated for each  $100 \times 100$  m cell at the Saginaw Co. site following the methods described by McCullough and Siegert (2007). Using this environment and an initial population size of 250 (125 females), a single dispersal event from the infestation point source and 1 year of population growth (see below) was simulated using four forms of dispersal. The four forms of dispersal simulated were unbiased dispersal (Eq. 1), avoidance of areas devoid of ash phloem, and two forms of bias towards high resource areas. Avoidance of areas devoid of ash phloem was simulated by increasing the functional distance (y in Eq. 2) of cells lacking phloem by the median value for flight potential recorded from flight mill studies over 1 day (1.8 km) (Taylor et al. 2006). We assume that A. planipennis adults can only fly for a single day prior to encountering an ash tree because adult A. planipennis must feed on ash leaves to survive (Cappaert et al. 2005). This treatment effectively prevents beetles from remaining or entering empty cells under most circumstances.

The first form of bias towards high resource areas represented an attraction towards the direction with the highest quantity of ash phloem within 200 m, as reported by Siegert et al. (2010). To simulate this bias, all cells within 200 m of the infested cell were separated into quadrants ranked on the quantity of available ash phloem. Subsequently, the functional distance for the cells in the direction of the quadrant with the highest quantity of ash within 200 m was reduced by 33% (or 66%) and the functional distance of cells located in the off diagonals adjacent to these cells were reduced by 16.5% (or 33%). The second form of bias towards high resource areas assumed beetles preferentially fly towards high resource areas within the environment, irrespective of their immediate environment. To simulate this form of bias towards resource-rich areas in the model, the functional distance of cells containing resources in the upper 25th percentile was decreased by 33% (or 66%) and the distance of cells containing resources in the lower 25th percentile of the area was increased by 33% (or 66%). For both forms of bias towards high resource areas, we also assumed that areas devoid of ash would be avoided as above.

#### Population growth and phloem consumption by larvae

Females were assumed to produce a constant number,  $r^0$ , of adult female offspring and that this growth is limited only by the resources present in each cell (i.e., the quantity of remaining ash phloem, *A*). Specifically, we determined the number of individuals that would successfully develop to the next generation as,

$$N_{t+1}^{i} = \begin{cases} r^{0}N_{t}^{i}, \ r^{0}N_{t}^{i} \le \frac{A_{t}^{i}}{C} \\ \frac{A_{t}^{i}}{C}, \ r^{0}N_{t}^{i} > \frac{A_{t}^{i}}{C} \end{cases}$$
(3)

where *C* is the consumption of phloem in m<sup>2</sup> per individual insect,  $r^0$  is the population growth rate, and  $A_t^i$  is the quantity of phloem present in cell *i* at time *t*. The value for  $A_t^i$  is determined as  $A_t^i = \max(0, A_{t-1}^i - N_{t-1}^i C)$ .

*Parameter estimates* The per capita growth rate,  $r^0$ , was estimated using sequential *A. planipennis* larval densities collected in 2006 and 2007 from *F. pennsylvanica* trees in an isolated, low-density satellite location in Clinton Co., MI, USA (Tluczek 2009). Each year, 30 trees (31.5 ± 1 cm diameter at breast height) were randomly selected felled and the trunk and branches (>5 cm in diameter) were completely debarked. Larval density was determined and standardized by the area of phloem exposed on each tree. The ratio of the mean larval density in 2007 to the mean larval density in 2006 was used to estimate the population growth rate. Bootstrap estimates of the ratio performed using the R statistical package (R Development Core Team 2010) indicated the growth rate to be  $10.35 \pm 3.02$ .

Phloem consumption per individual larva, *C*, was determined from the average number of *A. planipennis* adults that can develop per m<sup>2</sup> of phloem as reported by McCullough and Siegert (2007). Using data from 71 *F. pennsylvanica* and *F. americana* trees killed by *A. planipennis*, they found that on average,  $88.9 \pm 4.6$  beetles developed and emerged per m<sup>2</sup> of phloem. Based on these results, we estimated an individual larva would consume approximately  $0.0113 \pm 0.0006$  m<sup>2</sup> of phloem before completing development.

## Simulations

#### Environments used in simulations

Three environments varying in the spatial distribution of phloem but with equal total quantities of phloem were developed. All three environments consisted of  $205 \times 205$  matrices, each with  $50 \times 50$  m cells, and containing a total of 8,405,000 m<sup>2</sup> of phloem. The first environment ("homogenous") consisted of a homogeneous distribution of phloem, such that each cell contained 200 m<sup>2</sup> of phloem. The second environment ("clumped") consisted of a combination of cells with and without phloem. Cells containing phloem were arranged in equally spaced clusters of 25 cells and each cell contained 784.4 m<sup>2</sup> of phloem (see Appendix C in ESM). The final environment ("random") consisted of a heterogeneous environment with a random distribution of phloem, consisting of cells containing 0–400 m<sup>2</sup> (in 25-m<sup>2</sup> increments) of phloem.

Three additional "low resource" environments were developed by reducing the phloem quantity in each cell above by 50%. These environments were otherwise identical to the three described above with the exception of containing lower quantities of ash phloem.

# Influence of oviposition site foraging behavior and host spatial distribution on population spread

In each of the environments described above, simulations were performed using five alternative forms of foraging behavior. The first four forms of foraging behavior were those described earlier: (1) unbiased; (2) avoidance of areas devoid of ash phloem; (3) bias towards the direction with the highest quantity of ash phloem within 200 m; and (4) bias towards areas with high quantities of ash in the environment irrespective of their immediate environment. For both forms of bias towards high phloem areas, the functional distance of biased cells was reduced or increased by 33%.

The fifth form of foraging behavior simulated was an increased attraction to locations containing stressed ash trees. Agrilus planipennis females preferentially oviposit on stressed trees (McCullough et al. 2009a, b), and appear to be attracted to the general vicinity of stressed trees (N.W. Siegert, unpublished data). Larval densities, for example, were 4.6–7 times greater higher on trees in 4-ha plots containing 12 girdled ash trees than in plots that had no stressed trees (N.W. Siegert, unpublished data). To simulate an attraction to areas containing stressed trees, cells with over a third of the initial phloem consumed and >0.0016 m<sup>2</sup> of ash phloem per m<sup>2</sup> (the approximate density of phloem in girdled trees in the 4-ha plots) were assumed to contain sufficiently stressed trees to generate a level of attraction similar to that provided by the 12 girdled ash trees in a 4-ha plot. Based on this assumption, we increased the attraction of cells containing stressed trees by increasing the value of a in Eq. 2 for cell i by the product of the maximum attraction increase  $(7\times)$  and the ratio of damaged phloem in the cell over a third of the initial available phloem. The value of a was bounded between 1 and 7; limiting the maximum attraction level to a sevenfold increase when a third or more of the initial ash phloem was consumed. The quantity of damaged phloem in a cell was calculated as the amount of phloem consumed since the start of the simulation. Cells containing  $< 0.0016 \text{ m}^2$  of ash phloem per m<sup>2</sup> were considered to have no damaged phloem. Here, beetles were again assume to avoid areas devoid of ash phloem.

All five types of foraging behaviors were simulated in each of the three environments described above for a 15-year period. Each simulation began with initial populations of 100 or 1,000 adult beetles at the center of the environment.

To further evaluate the overall effect of resource variation on local spread, two additional sets of simulations were performed. The first set were intended to mimic environments with clumped distribution of ash trees with decreasing levels of distance and size of ash clusters. This was accomplished by running simulations in four additional environments with a similar organization as the "clumped" environment. These four environments were composed of clusters of 1, 4, 9, or 16 cell(s) and separated by 1, 2, 3, or 4 cell(s), respectively. As with the previous environments, the value of phloem contained per cell was adjusted so that all environments contained an equal amount of phloem. Simulations in these environments were performed for a 15-year period with the founding population size set at 100 individuals and foraging beetles were again assumed to avoid areas devoid of ash.

A final set of simulations were evaluated to further assess A. planipennis movement across environments with increasing levels of heterogeneity. For computational purposes, simulations were carried-out over smaller environments consisting of  $35 \times 35$  cells each of  $50 \times 50$  m cells for a 10-year period (605 total simulations). Initial distributions of ash phloem in these environments were determined by randomly drawing the phloem quantity per cell from a normal distribution with mean of 200 and standard deviations ranging from 0 (homogeneous) to 200 in increments of 5 standard deviations. In these environments, all negative values for ash phloem derived from the random number generator were rounded to zero. Simulations were run for each of the foraging behaviors described above on three environments developed for each standard deviation value with founding population sizes set at 100 individuals.

#### Habitat quality

The extent to which host quality or temperature affects *A. planipennis* population growth and spread is unknown. *Fraxinus* spp. composition is markedly variable among North American regions and the suitability of *F.* spp. for *A. planipennis* development may vary considerably among species. In addition, tree condition can affect the suitability of trees for larval development (Siegert et al. 2007b; Tluczek 2009). Likewise, temperature is well known to directly affect the development of insects (Scriber and Slansky 1981).

Variation in habitat quality is likely to have an effect on the local spread of *A. planipennis* primarily by affecting the survival and development of *A. planipennis* larvae. Here, we simulated the potential impact of variation in available habitat quality on the local spread of *A. planipennis*. Specifically, we varied three parameters within the model that are likely to be affected by host quality and temperature  $\pm 25$  and 50% of their standard values: (1) the proportion of individuals expected to complete development in a single year; (2) the quantity of phloem consumed per larvae; and (3) the per capita growth rate.

Simulations varying the above parameters were run in the homogeneous, clumped, and random environments over 15-year time periods with founding population sizes set at 100 individuals and assuming beetles would avoid areas devoid of ash (see above). In addition, effects of varying the above parameters were explored in smaller environments by varying the degree of host heterogeneity simulations. As before, simulations varying the above parameters were run for a 10-year period in  $35 \times 35$  cell lattices (each of  $50 \times 50$  m) with initial ash phloem per cell determined by random draws from a normal distribution with mean of 200 and standard deviations varying from 0 (homogeneous) to 200 by increments of 5 standard deviations.

#### Results

## Dispersal in a heterogeneous site

The expected results from the 1-year dispersal and growth simulations in the environment mimicking the site described in Siegert et al. (2010) are summarized in Fig. 1. The only simulation that yielded results similar to the spatial distribution of A. planipennis observed in the field site was the one which incorporated 66% bias in dispersal in the direction of the highest ash tree density within 200 m of the emergence point. Siegert et al. (2010) detected larvae considerably further from the point of origin than all models except those with the strongest bias (i.e., 66%) (Fig. 1). The standard model not only failed to predict larval presence at sufficient distances, it also yielded unrealistically low numbers of larvae (217), due to adults entering and remaining in cells without any available hosts. Incorporating adult avoidance of cells devoid of phloem corrected the issue of low larval numbers, yielding 2588 larvae in the environment (i.e., the expected number of larvae given the growth rate an initial population size). However, the predicted dispersal distance was also too low, even when resource biases of 33% were included. The 66% bias towards areas with abundant ash phloem, irrespective of the immediate environment encountered by adult females, predicted larvae at distances equivalent to those observed in the field. However, this form of bias failed to predict presence of beetles in several cells (containing low ash quantities) where larvae were found by Siegert et al. (2010).

Influence of oviposition site foraging behavior and host spatial distribution on population spread

Not surprisingly, an increase in the size of the founding population hastened spread, both in terms of the growth of the total population size over time and the increase in the radius of the colonized area calculated as the maximum distance between an individual larva and the origin of the infestation (Fig. 2). Increasing the founding population size had a considerable affect on the median distance of the populations, calculated as the distance from the origin of the infestation containing 50% of the population. Of particular note is the greater lag time observed in the rate of increase for the median distance when the founding population was small (Figs. 2 and 3). The relative importance of the founding population size was strongly dependent upon the environment in which the simulation was run. After 15 years, the difference between the radius of the infestation or the median distance at which individuals were present in simulations with initial population sizes of 100 and 1,000 was far greater in the clumped environment than the homogeneous or random environments (Fig. 2). Variation in the final population size among the environments indicated a similar situation, with differences of 67.5, 21.8, and 10.3%, respectively.

Resource distribution also had a significant impact on the overall influence of ovipositional foraging behavior on spread of *A. planipennis* (Figs. 4 and 5). The relative impact of including a bias in the direction of high resource areas, irrespective of the immediate environment, was highly dependent upon the environment (Figs. 4, 5 and 6).



**Fig. 1** Observed and predicted results for *A. planipennis* distribution for a site in Saginaw Co. in eastern mid-Michigan, USA. For this site, *black cells* identify locations where an infested tree was observed, and *grayscale* for the predicted number of larvae for simulations with (1) unbiased foraging (Standard), (2) avoidance of phloem free areas

(Avoidance), (3) a 33 or 66% bias towards cells containing high ash quantities (Resource Bias All), and (4) a 33 or 66% bias towards the direction containing high ash quantities within 200 m (Resource Bias Within 200 m)



Fig. 2 Radius of infestation, median distance of beetles and total number of beetles present during 15-year period for simulations of the model in the **a** homogeneous, **b** clumped, and **c** random environments when initial propagule size is set at 100 or 1,000 individuals

Likewise, the effect of including a bias towards cells containing stressed trees was dependent upon the environment simulated. Radial spread and population size decreased below what was observed when adult avoidance of areas devoid of phloem were included in both the homogeneous and random environments, but not in the clumped environment (Fig. 4). In contrast, including a bias in the direction of ash phloem within 200 m increased the



Fig. 3 Delay observed between the start of the simulation and the presence of a constant increase in the location of the median distance of the population present when initial propagule size is either 100 or 1,000 individuals. Simulations were run for a 15-year period in the homogeneous, clumped, and random environments

radial spread in all environments (Figs. 4, 5 and 6). Likewise, simply including adult avoidance of cells devoid of ash greatly increased the radial spread and the number of beetles present in all environments (Fig. 4). This effect was particularly apparent in the loss of the weakly negative relationship present between heterogeneity and the radial spread for random (standard) oviposition behavior when avoidance of cells devoid of phloem was included in the simulation (Fig. 6). This difference was also evident when simulations were run in environments with clumped resource distributions varying the size and distance between clusters (Appendix D, Fig. D1 in ESM). In the environments with clumped resource distributions, radial spread and population sizes were significantly lower than those in a homogeneous environment when adult avoidance of areas devoid of phloem was not included. When avoidance of areas devoid of phloem was included, the values for the radial spread and population size in environments with clumped resources oscillated fairly closely to the values observed in homogeneous environments (Appendix D, Fig. D1 in ESM).

In the simulations assessing *A. planipennis* movement across environments with increasing levels of heterogeneity, a very weak, positive relationship between resource heterogeneity and the radius of the colonized area was observed when avoidance of areas devoid of ash phloem was included (Fig. 6). In contrast, a negative relationship between radial spread and environmental heterogeneity was observed when avoidance of areas devoid of phloem was not included (Fig. 6). In the clumped environment,



Fig. 4 Radius of infestation and total number of *A. planipennis* beetles over time for simulations conducted in the homogeneous, clumped, and random environments for (1) unbiased foraging (Standard); (2) avoidance of phloem free areas (Avoidance); (3) bias

towards cells containing stressed trees (Stress); (4) bias towards cells containing high ash quantities (Resource Bias All); and (5) bias towards the direction containing high ash quantities within 200 m (Resource Bias Within 200 m)

which included large areas devoid of phloem, the population size and radial spread was greatly reduced when avoidance of areas devoid of phloem was not included (Figs. 4 and 5). Including an avoidance of areas devoid of phloem caused the radial spread and population size to greatly increase and were actually greater than those observed in the homogeneous environment (Figs. 4 and 5; Appendix D, Fig. D1 in ESM).

# Habitat quality

Not surprisingly, modifying the per capita growth rate by  $\pm 25$  or 50% had a strong impact on both the number of beetles in the area and the radius of the colonized area (Figs. 7 and 8; Appendix D, Fig. D4 in ESM). The proportional effect of altering the per capita growth rate rapidly increased and decreased (Fig. 7; Appendix D,

Fig. D4 in ESM), indicating a stronger effect during the initial stages of the spread. As with population growth rate, altering the relationship between larval density and the proportion of larvae with 1-year development had a noticeable impact on the number of beetles and the radius of the infested area during the initial stages of the simulations (Figs. 7 and 8; Appendix D, Fig. D4 in ESM).

Altering the rate of larval phloem consumption also had a strong impact on the number of beetles present (Figs. 7 and 8; Appendix D, Fig. D4 in ESM), but a negligible effect on the radial spread (Fig. 7). The result of altering phloem consumption was unlike the effect of reducing ash phloem in the homogeneous environment. Reducing ash phloem led to a small increase in the radial rate of spread in addition to the proportionally similar reduction in the number of beetles (Fig. 9).



Fig. 5 The maximum distance from the point of initial infestation that individuals were present in simulations after a 15-year time period. Simulations were conducted in the **a** homogeneous, **b** clumped, and **c** random environments for unbiased foraging (Standard); avoidance of phloem free areas (Avoidance); bias towards cells containing stressed trees (Stress); bias towards cells containing high ash quantities (Resource Bias All); and bias towards the direction containing high ash quantities within 200 m (Resource Bias Within 200 m)

# Discussion

Analytical models, including simple diffusion models (e.g., Skellam 1951), often provide surprisingly accurate estimates of spread rate (Shigesada and Kawasaki 1997; Bullock et al. 2008; Liebhold and Tobin 2008). These analytical models offer significant advantages over



**Fig. 6** Radius of infestation (**a**) and total number of *A. planipennis* beetles present, (**b**) from simulations in environments containing  $35 \times 35$  cells, each with a mean of 200 m<sup>2</sup> phloem and 0–200 SDs. Simulations were performed for 10-year for (1) unbiased foraging (Standard), (2) avoidance of phloem free areas (Avoidance), (3) bias towards cells containing stressed trees (Stress), (4) bias towards cells containing high ash quantities (Resource Bias All), and (5) bias towards the direction containing high ash quantities within 200 m (Resource Bias Within 200 m)

simulation models, in the form of ease of parameter estimation and providing analytical solutions. However, it is sometimes difficult to adapt analytical models to represent certain types of relationships. In contrast to spatially implicit analytical models, coupled map lattice models can incorporate spatial variation and, although analytical solutions are not simple (see Campos et al. 2008 for an example of analytical solutions for coupled map lattice models), simulating the role of resource patch dynamics and unknown behaviors on dispersal are straightforward. The results presented here illustrate how environmental heterogeneity and behavior can have complex effects on the spread of an invasive species such as *A. planipennis*.

The importance of environmental heterogeneity on dispersal is evident in the lack of fit between the dispersal of *A. planipennis* observed in a homogeneous environment and in a heterogeneous environment (Fig. 1). Although the



Fig. 7 Radius of infestation and total number of beetles over time for simulations conducted in the homogeneous environment including avoidance of areas devoid of phloem and varying the population growth rate, developmental rate, and consumption rate by  $\pm 25$  or 50%

data observed by Siegert et al. (2010) in the heterogeneous environment illustrated in Fig. 1 are limited, larvae were detected well beyond the range predicted by the dispersal observed in two separate homogenous sites (Mercader et al. 2009). This indicates that there are likely to be important differences in adult dispersal behavior in sites with homogenous versus heterogeneous host distributions. It is worth noting that, in Mercader et al. (2009), the vast majority of larvae were found within 100 m of the infestation source. In contrast, in the site studied by Siegert et al. (2010), no ash phloem was present in the  $100 \times 100$  m cell where the infestation originated. However, including an avoidance of areas devoid of phloem, which caused all beetles to exit the cell of origin, also greatly underpredicted the distance at which larvae were detected (Fig. 1). The lack of fit when adult avoidance of cells without phloem is accounted for indicates that, in the absence of readily available hosts, dispersal behavior differs beyond simply moving towards the nearest host patch.

Incorporating a significant dispersal bias towards the direction with the highest quantity of ash phloem within 200 m yielded a pattern of *A. planipennis* abundance which most closely matched the observed pattern of infested trees

(Fig. 1). However, including an overall dispersal bias towards cells containing high ash quantities (irrespective of the immediate surroundings) failed to predict the presence of larvae in some cells where larvae were observed. It is important to note that the selection of a dispersal bias based on the quantity of ash phloem within 200 m was initially incorporated in the model because it was identified by Siegert et al. (2010) and therefore the observed simulation results do not validate this form of dispersal. In addition, in these simulations, the bias towards high resource areas was accomplished by altering the functional distance by a percentage, which caused the dispersal bias to disproportionately increase the attractiveness of more distant cells. Including this dispersal bias, in essence, selectively increased the dispersal range. This suggests that the discrepancy observed between the results observed in Mercader et al. (2009) and Siegert et al. (2010) is likely due to both an increased dispersal rate and a bias towards areas with high resources. The absence of ash phloem in the immediate surroundings in the site studied by Siegert et al. (2010) may have affected the behavior of dispersing females, potentially increasing the potential for longdistance dispersal.



Fig. 8 Average radius of infestation and total number of beetles present from environments containing  $35 \times 35$  cells with a mean of 200 m<sup>2</sup> phloem and 0–200 SDs (5 environments for each SD).

Simulations were performed for 10-year including avoidance of areas devoid of phloem and varying the population growth rate, developmental rate, and consumption rate by  $\pm 25$  or 50%



Fig. 9 Radius of infestation and total number of beetles present after 15-year of the model in the standard and reduced phloem (50% reduction) homogeneous environments

An important issue not addressed by the local spread model presented here is the role of long-distance dispersal events. It is currently unknown whether some proportion of *A. planipennis* mated females engage in long-distance dispersal flights despite the presence of available local ash resources. Individual variation in dispersal limits the explanatory power of phenomenological distributions, such as the negative exponential function used in this study (Yamamura 2002; Hapca et al. 2009; Hawkes 2009). Variation in the likelihood of individual dispersal is better explained by "fat-tailed" dispersal kernels (e.g., Kot et al. 1996; Yamamura 2002, 2004; Yamamura et al. 2007). The importance of variation in the common fit of "fat-tail" dispersal kernels was studied by Lindström et al. (2008), who found that effects of variance on the fit of dispersal kernels were more important than kurtosis on population processes. These studies highlight the potential of individual variation to affect the dispersal kernel used in this study. Unfortunately, dispersal data for A. planipennis are exceedingly limited. This insect does not produce a longrange attraction pheromone and identifying newly infested trees typically requires felling and debarking trees, a destructive and highly labor-intensive survey method (McCullough et al. 2009b). As trapping techniques for A. planipennis improve, researchers will be able to evaluate the extent of variation in the propensity for long-distance flights by A. planipennis and effects of long-distance dispersal on population processes.

The importance of the foraging behavior of fertilized females to the localized spread of invasive insects is further supported by the effects observed on the overall local spread depicted in our simulations. Laboratory flight mill studies indicate that mated *A. planipennis* females are physiologically capable of flying considerable distances (Taylor et al. 2006). Avoidance of ash-free areas by

A. *planipennis* females is presumably common. Simply including this component in the model greatly increased the spread relative to what would be predicted from random foraging in homogeneous sites (Figs. 4 and 5). Travelling wave models based on random diffusive dispersal predict that resource heterogeneity should decrease spread rates (Shigesada and Kawasaki 1997). Including the ability to avoid unprofitable patches (e.g., areas devoid of phloem) in our simulation model effectively removed the deleterious effect of landscape heterogeneity on local spread.

In addition to simply reacting to the availability of ash phloem, A. planipennis beetles are significantly attracted to stressed trees (McCullough et al. 2009a, b). This behavior is not surprising, as in its native range A. planipennis primarily infests weakened trees (Gould et al. 2006). Including an attraction to stressed trees in the simulation model increases the local population density which, in turn, increases the proportion of larvae developing in 1 year rather than 2 years (i.e., faster development). Conversely, it also reduces the likelihood that beetles will exit cells containing stressed trees, leading to a reduction in population growth by maintaining beetles in areas with proportionally lower quantities of available phloem (Fig. 4). The inclusion of a bias in dispersal towards areas containing higher quantities of ash leads to the opposite effect, increasing the proportion of beetles exiting cells and leading to lower population densities per cell. In cells with lower population densities, fewer ash trees are stressed, thereby increasing the proportion of larvae developing in 2 years (i.e., slower population growth). However, a dispersal bias towards high ash areas also prevents beetles from remaining in areas with decreasing ash availability, leading to an overall increase in the spread and population size in environments without a homogeneous phloem distribution (Figs. 4 and 6). The relative strength of these two dispersal biases may be influenced by site conditions, disturbance or other factors, but additional work on adult A. planipennis behavior is needed.

Simple reaction-diffusion models predict constant rates of radial spread that are unaffected by initial population size (Shigesada and Kawasaki 1997). Simulations confirmed that founding population size did not affect asymptotic radial rates of spread in both the homogeneous and random environments (Fig. 2a, c). However, a significant delay in the onset of the stable rate was observed in all the environments when initial population size was lower. This delay observed in the rate of spread is particularly evident when contrasting the center (median) of the populations (Figs. 2 and 3). The median distance of the populations represents the distance from the origin of the infestation containing 50% of the population, while the radial spread represents the edge of the population. The greater differences observed in the population median distance than in the radial spread between these simulations indicates that a smaller initial population size may lead to a proportionally more diffuse invasion wave during the initial stages of establishment. Little is known about how an Allee effect (Liebhold and Tobin 2008) may influence *A. planipennis* dynamics and Allee effects were not included in our simulation model. If Allee effects influence *A. planipennis* population growth or spread, the proportionally more diffuse invasion wave predicted when population sizes are low should exacerbate these effects. From a management perspective, this would increase the importance of reducing population sizes for reducing the potential spread of *A. planipennis*.

The cause of the initially slower movement of populations observed when founding populations were smaller reflect the time required by local populations to achieve densities sufficient to cause most larvae to complete development in 1 year (Appendix B in ESM). The increase in larvae developing in 1 year when densities are high is due to an increased developmental rate on stressed trees (Siegert et al. 2007b; Tluczek 2009), which increases proportionally as larvae feed on trees. When initial population sizes are high, generation time decreases, which in turn leads to an earlier onset of the maximum radial spread rate (Fig. 2). Decreasing the available ash phloem can also decrease the time required for trees to become stressed, which may also increase the spread (Fig. 9; Appendix D, Fig. D3 in ESM). Furthermore, in the presence of avoidance behavior, increased population sizes or lower resource levels accelerate depletion of resources and thereby promote longer-range dispersal, which also facilitates spread (Appendix D, Figs. D1 and D2 in ESM).

From a management perspective, increasing the temporal lag before the spread rate of a population increases could be potentially valuable. Therefore, it may be preferable to implement practices that decrease population sizes and/or maximize resource levels. Reduction of *A. planipennis* population levels via cutting large numbers of infested or potentially infested trees may simultaneously reduce resource levels and inadvertently increase the local spread rate. In contrast, management practices that reduce the population size without affecting the ash resource (e.g., insecticide applications) may provide a greater and more predictable reduction in local spread rate.

Variation in local habitat quality is also likely to affect the spread of *A. planipennis*, via effects on population growth rates, developmental time, and phloem consumption. For example, temperature affects the larval developmental rates of many insects, which could significantly influence the relationship between larval density (host stress level) and development time observed for *A. planipennis* (see Appendix B in ESM). Variation in diapause (or dormancy) has been proposed to be a factor increasing invasion success in stochastic environments as a bet hedging strategy (e.g., Menu et al. 2000; Chen et al. 2006; Mahdjoub and Menu 2008). However, using integro-difference deterministic and low variability stochastic models, Mahdjoub and Menu (2008) indicated a significant decrease in spread rate with increasing duration of diapause. In the deterministic model presented here, a significant increase in the local spread of A. planipennis when the proportion of larvae developing in 1 year was increased was also found (Fig. 7), but reducing the proportion of 1-year larvae had a far smaller effect (Fig. 7). This asymmetrical response is caused by the relative effect of altering this relationship being primarily present during the first few years when population sizes are small, below 20 larvae per  $m^2$  (Fig. 8; Appendices B and D in ESM). As the range of A. planipennis spreads into warmer regions, increased local spread induced by increasing the proportion of 1-year larvae could become significant. However, interactions between an increase in larval development rate and the requirement to experience a "chill period" to break diapause will presumably lead to a complex invasion process in warmer regions.

Variation in habitat quality may directly affect adult fecundity and larval survival rates, potentially increasing the population growth rate. As would be expected, altering the population growth rate lead to a proportional increase or decrease in the radial spread and population size (Fig. 7; Appendix D, Fig. D4 in ESM). Furthermore, the magnitude of the proportional increase or decrease in growth rate on the radial spread and population size was virtually identical for environments with no or high levels of resource heterogeneity (Fig. 8). Similarly, altering the phloem consumption per larva had a significant impact on population size, but only a minimal impact on the radial spread (Fig. 7; Appendix D, Fig. D4 in ESM). Increases in consumption rate essentially translated into lower resource availability, but decreases in consumption rate did not lead to similar effects as increased resource availability. The primary reason for this difference is that altering only the consumption rate did not affect the larval density used to determine the proportion of larvae developing in 1 year. In reality, consumption rate will likely have a significant impact on the injury and stress sustained by trees in relation to larval density. Therefore, the impact of variation in larval consumption will likely reflect a combination of altered resource availability and the proportion of larvae developing in 1 year.

Given the critical need to identify strategies to reduce the local spread of this invasive species, a better understanding of the foraging behavior of ovipositing females, larval growth, and survival in varying habitats is badly needed. Efforts over the last 50+ years since Skellam's introduction of reaction-diffusion models to model invasion (Skellam 1951) have enhanced our ability to understand and predict invasion spread, including fairly sophisticated spatially explicit models with great predictive power (Dunning et al. 1995; Hastings et al. 2005). These models, however, are often highly specialized and require a significant amount of detailed information, which can hinder their use (Turner et al. 1995), particularly when applied to recently discovered invaders. Identifying relevant components of the biology of organisms remains a challenge in our efforts to provide a balance between the predictive power of highly specialized models and the functionality of less parameterized general models. The tight linkage between A. planipennis and Fraxinus spp. allowed us to identify the importance of considering foraging behavior and to build a simple flexible model of the local spread of this invasive species. Although components of the biology of this recently discovered invasive species remain unknown, this model provides a framework to aid the development of strategies to mitigate the spread of A. planipennis.

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