The spatial dynamics of invasive species spread

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Abstract

The problem of invasive species spread requires timely analysis of the biological dynamics that lead to spatial dispersion. Here, a spatial dynamic model captures the invasive behavior of the recently introduced emerald ash borer (EAB) (*Agrilus planipennis*) and its impacts on host ash (*Fraxinus* spp.) trees. Parasite–host system dynamics are extended spatially using the Spatial Modeling Environment. The resulting model can serve as a repository for changing knowledge about EAB biology and behavior. Studies of the rapid EAB infestation in Michigan are used to inform simulations of its spread in DuPage County, Illinois, USA. We use a geographic information system to create heterogeneous host landscapes and to test alternative policy scenarios. We test the effectiveness of three suppression scenarios: the Michigan eradication strategy, firewood quarantines, and ash tree thinning. Simulations demonstrate that EAB spatial spread accelerates with degraded host capacity, with results pointing to firewood quarantines as the most effective solution. Copyright © 2006 John Wiley & Sons, Ltd.

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Introduction

While invasive species constitute a small fraction of non-indigenous species introduced to the United States (Williamson and Fitter 1996), they have become notorious for negative impacts on ecosystem and human health (Harty 1993). By the early 1960s, ecologists understood that accidental and premeditated introductions of species into areas outside their native range could wreak economic and environmental damage on a massive scale (Elton 1958; Hall 1963). As of 2000, environmental damage and losses inflicted by 50,000 non-indigenous species were estimated at $137 billion per year in the United States (Pimentel *et al.* 2000). These losses often occur as a result of widespread damage to native plant and animal communities, control costs, agricultural losses, and property damage.

This article addresses the spread of the invasive emerald ash borer (EAB) (*Agrilus planipennis*) in the upper Midwestern United States. We introduce a model of EAB biological dynamics and virulent parasitic behavior on host ash (*Fraxinus* spp.) trees. This dynamic model is then incorporated into a spatial

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framework to simulate the spatial dynamic spread of the EAB. This article extends previous work demonstrating that spatial dynamic models can act as flexible and powerful decision support systems for mitigating invasive species spread (BenDor *et al.* 2005a). We demonstrate that the integration of dynamic models into a spatial framework may prove essential in anticipating patterns of tree damage, as well as the associated economic and ecological impacts (see Nowak 2003 for more information on potential economic damage).

Background

A native of Asia, EAB populations were originally discovered in damaged ash trees during the summer of 2002. By this time, the EAB had already infested five southeastern Michigan counties (McCullough and Katovich 2004). Such infestations were targeted at common species of native ash trees (green ash (*Fraxinus pennsylvannica*), black ash (*F. nigra*), and white ash (*F. americana*)). EAB larvae consume inner bark and outer sapwood (cambium) of ash trees. Owing to the important role of the cambium in vital nutrient transport functions, EAB infestations are usually fatal (McCullough and Katovich 2004; Liu *et al.* 2003).

Immediately, concern focused on the role of humans as a long-distance spread vector.[1] Quarantines enacted to prevent the removal of ash firewood from southeastern Michigan and Ontario, Canada have thus far not proven effective in preventing the spread of the EAB into Ohio, Indiana, Maryland, or Virginia (McCullough and Katovich 2004).

Assessing and tracking the EAB's spread has been difficult for two reasons. First, the extremely small sizes of eggs and larvae coupled with limited early signs of infestation have hindered widespread detection and policy implementation. These barriers to infestation detection and policy implementation have introduced important delays into the system. Second, significant gaps remain in the biological knowledge of the EAB due to its recent introduction and adaptation to North American climates. Specifically, many aspects of the EAB's spread dynamics have not been fully explored, and many aspects of the EAB's life cycle are still unknown. In such cases, we used information of behaviorally similar insects such as the bronze birch borer (Barter 1957), or the best available professional knowledge of wood-boring beetles.[2]

Biological dynamics

The EAB life cycle consists of three significant stages: active larvae, inactive larvae, and adults. A pupae stage also exists between inactive larva and adult emergence, but for our purposes has been included in the inactive stage. Figure 1 illustrates the best approximation of the EAB life cycle over one year (Bauer *et al.* 2003a; Lyons *et al.* 2003), alongside our simplification of the life cycle into distinct, non-overlapping phases for the purpose of the model.

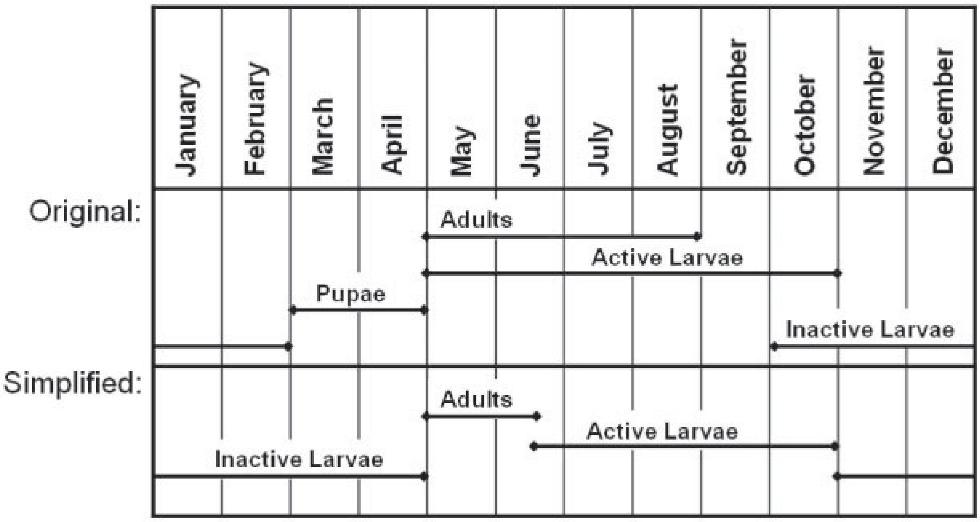


Fig. 1. EAB life cycle comparison

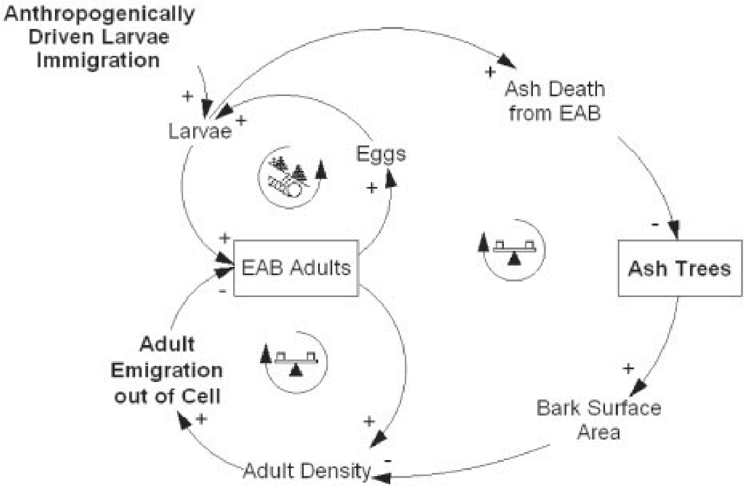
Both versions reduce temperature-dependent transitions into seasonal ones. Additional details of the EAB life-cycle are described in BenDor *et al.* (2005a).

The life cycle outlined in Figure 1 provides the basis for EAB population dynamics and predation on host ash trees. Namely, reproduction and flight occur in the adult stage, while feeding occurs in the larva stage. These population dynamics draw upon the classic Lotka–Volterra predator–prey model (Lotka 1925; Volterra 1926) to have finer resolution into the life stages of both the EAB and the ash trees that significantly impact their interaction. Moreover, EAB dispersion dynamics warrant explicit spatial representation.

Figure 2 outlines the dynamic hypothesis of causal relationships underlying EAB dispersion dynamics. The EAB larvae feed on cambium of the ash trees, cutting off circulation to cause a slow death. The resulting reduced carrying capacity of tree bark surface area necessitates EAB adult emigration to new host trees. This population density-dependent mechanism is central to the dynamic hypothesis. While the ash tree population dynamics are also considered, these dynamics occur on a much slower time scale than the EAB reproduction and dispersion dynamics. Therefore, we have omitted them from our central dynamic hypothesis.

Even the simple dynamic hypothesis in Figure 2 warrants explicit spatial representation of three elements: adult emigration, anthropogenic larvae spread (via firewood), and the landscape ash trees. In the next section, we introduce ways in which such spatial components may be adequately included in a system dynamics model.

Fig. 2. Simplified causal loop diagram illustrating dynamic hypothesis



Spatial modeling

Attempts to incorporate space into dynamic models have been warranted when landscape changes have major effects on the behavior of the system of interest. The history of system dynamics modeling includes a number of efforts to represent spatially non-uniform systems (e.g., Mass 1974; Sanders and Sanders 2004). These examples tend to view space in the form of distinct zones, with separate model structures representing the dynamics within and interrelationships between zones. Zone representation is intuitive and convenient for capturing spatial dynamics at a coarse level.

Another approach is to use grid-like “cells” to create a spatial template for system dynamics (e.g., Ahmad and Simonovic 2004; Deal *et al.* 2004). Ford (1999) illustrates a model in which nitrogen flows are simulated for 16 cells within a catchment. In this situation, a coarse spatial resolution and limited system complexity (basic diffusion of a single material) enable the model to capture the essential dynamics of the system in a compact form. A finer spatial resolution (e.g., 256 cells in a highly variable landscape) with a more dynamically complex system (e.g., the interaction of nitrogen and biomass in the environment) would quickly make the execution of a spatial system dynamics model intractable on conventional computer platforms.

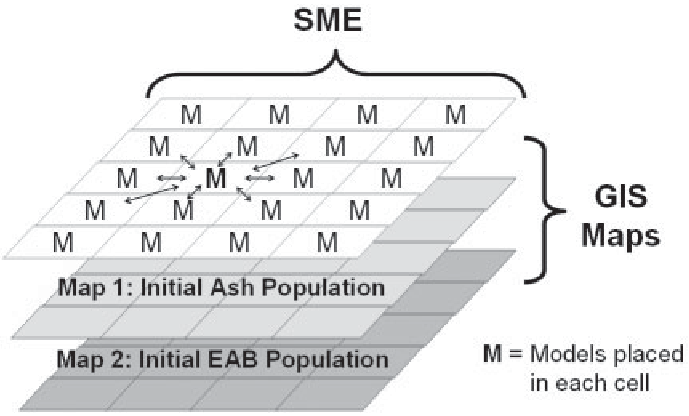
Fortunately, the increasing availability of high-quality remote sensing data, geographic information systems (GIS[3]), and parallel computer systems has removed many historical barriers to spatial dynamic modeling (Maxwell and Costanza 1997). Significant environmental heterogeneity often necessitates the use of detailed representations of the landscape. In such cases, explicit linkages between dynamic models through spatial relationships are warranted.

In our case, the EAB's intrinsic biological dynamics interact with an environmentally diverse host landscape to determine its spatial spread.

To adequately capture such dispersion, we utilize the Spatial Modeling Environment (SME) pioneered by Maxwell and Costanza (1997). This platform is an important tool for combining system dynamics models and common landscape abstractions. SME was designed to encourage collaboration among modelers via user accessibility while retaining functional usefulness. In particular, SME has attempted to overcome the tendency of the current generation of complex simulation models to be idiosyncratic and nearly incomprehensible (Acock and Reynolds 1990; Fall and Fall 2001). The SME framework enables experienced system dynamics practitioners to extend their models spatially with relative ease, such that highly resolute models are still explainable to a non-technical audience.

Analogous to most system dynamics software, SME highly abstracts technical details (mathematical details of equation solutions, cellular interactions, memory management, etc.) away from the user. This abstraction sets SME apart from standard distributed modeling packages (e.g., SWARM, RePast) that require significant technical expertise.[4] Concurrently, a focus on spatially explicit modeling sets it apart from standard, pure system dynamics models. Figure 3 provides a conceptual overview of SME in relation to the spatial distribution of ash trees and EAB adult population.

Fig. 3. Spatial modeling environment



The use of SME involves the incorporation of a generic system dynamics model into a spatial array whereby spatially heterogeneous parameters initialize the array of replicated system dynamics models. The spatial array may be parameterized using conventional GIS to process and represent spatial data in uniform grid cells (raster format). The spatially replicated dynamic models are updated through directional references to neighboring model variables.

The translation of a dynamic model into a spatial array evokes and extends the concept of a cellular automaton. A cellular automaton is a set of discrete spatial entities (cells) in which the state of each entity at a given time depends only upon its prior state and the state of its neighbors (Wolfram 2002). The same rules for updating apply to each entity in the automaton. While such rules may be simple or complex, they do not generally encompass continuous internal dynamics. Coupling spatially discrete cells with the continuous-time dynamics[5] of multiple state variables thus deviates from the commonly used meaning of cellular automata.

Model development

Our development of a spatial dynamic model using SME began with development of EAB and ash population sub-models in STELLA, along with the preparation of the initial host ash tree landscape with GIS software. Highlights of this model development are emphasized here, while additional model details are contained in BenDor *et al.* (2005a).

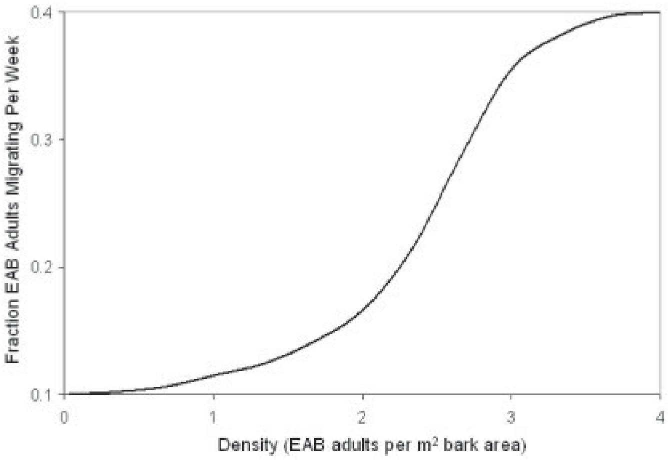
Population model

The EAB population dynamics are based upon the simplified life cycle introduced earlier (Figure 1). The larvae feed actively on ash trees for 20 weeks, where each week is a time step. Deaths at the larval stage are driven by density, where the maximum tolerable density is 300 larvae per square meter of bark surface area (McCullough *et al.* 2003). This bark surface area is computed by abstracting the tree trunk into a cylinder based on known dimensions of different tree age cohorts. We then represent larval death rate as a nonlinear, logistic function of larval density (BenDor *et al.* 2005a). Inactive larvae (including the pupae stage) cease feeding as they enter the winter diapause, serving simply to create a 22-week delay in the spread dynamics. A constant death rate for the inactive larvae stage captures the impacts of predation and harsh environmental conditions.

EAB adults generate the spatial dynamics of this model due to their flight dispersion. We consider the fraction of EAB adults leaving a given cell to be dependent upon population density, where the maximum density is four adults per square meter of bark surface area. The relationship between emigration fraction and EAB adult density ranges from 50 percent to 95 percent per year (McCullough *et al.* 2003). On a per-week basis, this translates to 10 percent at the minimum density to 40 percent at the maximum density (over the 6-week EAB adult life stage). Figure 4 illustrates the assumed relationship between emigration fraction and EAB adult density.

Emigrating EAB adults may travel up to 1.44 km away from their origin during their adulthood (within the range observed by Bauer *et al.* 2003b). Eq. 1

Fig. 4. EAB migration fraction as a function of adult density



describes the fraction of adults migrating from an origin cell (i) to a destination cell (j). This relationship creates an asymptotically declining migration fraction per cell as the destination cell becomes further away from the origin (BenDor *et al.* 2005a). This equation follows exponential decay functions relating the probability of adult dispersal stopping at a given distance discussed in Lewis (1997) and Shigesada and Kawasaki (1997).

$$B_{i\to j} = B_i\left(\frac{1}{r}\right)\frac{F\left(\rho_i\right)}{n\cdot y_{i\to j}} \tag{1}$$

where:

$B_{i\to j}$ = number of EAB adults flying from cell i to cell j
B_i = number of EAB adults originally in cell i
$F(\rho_i)$ = emigrating fraction from cell i as a function of EAB density ρ (Figure 4)
n = number of immediate neighbors surrounding cell i, up to 8 neighbors
$y_{i\to j}$ = shortest distance (cells traveled) to destination cell j from origin cell i
r = total number of migration rings defined by cell distance y from cell i, 4 rings in this model

We represented ash tree population dynamics by abstracting the three *Fraxinus* species (green, white, and black ash) commonly attacked by the EAB into a single species. The underlying assumption for this simplification is that the EAB attacks each of the three species at equal rates. This assumption could be relaxed in the presence of increased data and computational power. However, as mentioned earlier, the ash population dynamics occur on a much slower time scale than that relevant for EAB dispersion and mitigation. Ash trees are represented in distinct age cohorts, with germination, growth, and death rates contingent on land-use suitability (whether urban or not). Seed germination is not applicable for urban areas, but may be represented for non-urban areas using a seed bank (BenDor *et al.* 2005a). Urban trees are estimated to live for 75 years, while non-urban trees are estimated to live 180 years (within the range of Iverson *et al.* 1996). Urban trees are assumed to be at least 10 years old when planted. This age usually corresponds to the minimum trunk diameter (5 cm) for EAB infestation (Iverson *et al.* 1996).

Natural ash tree deaths (not influenced by the EAB) are caused by age as well as tree population density. The density considerations account for competition and shading. The maximum tree density is derived from our assumptions for the initial tree distribution. We base this conservative assumption on the rapid rate of urbanization in DuPage County since the Nowak (1994) study that provided the initial tree estimate. This natural tree death rate is assumed to be an S-shaped function of population density, and grows to a maximal rate of 33 percent per year (BenDor *et al.* 2005a).

Tree death rate due to EAB infestation is a function of the number of larvae in the cell, as well as the time it takes larval infestations to mortally wound a tree. This death delay is estimated to be approximately 2.5 years as indicated by heavy canopy dieback (McCullough and Katovich 2004). With these assumptions, ash death from the EAB is described in Eq. 2. We implemented this equation for death rate in the outflow of stock and flow dynamics which are illustrated conceptually in Figure 5.

$$DR_{ij} = T_{ij}\frac{T_{ij}L_j}{\alpha A_{ij}\tau\sum_i T_{ij}} \tag{2}$$

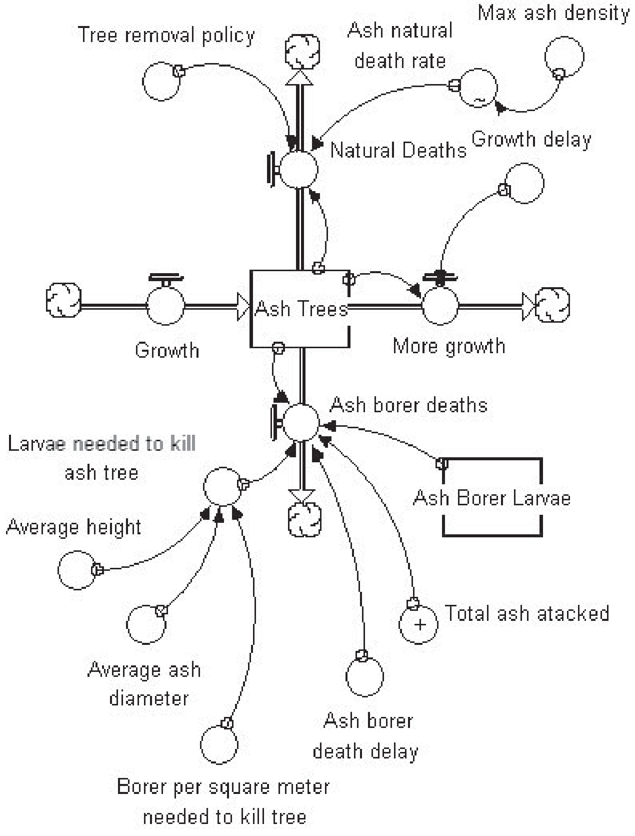
where:

DR_{ij} = Ash death rate due to EAB in cell j and tree age cohort i, trees/year
L_j = Active larvae in cell j
α = Lethal EAB larval density, 50 larvae/m2
τ = Death delay from EAB infestation, 2.5 years
A_{ij} = Tree bark surface area within cell j and age cohort i, m^2
i = One of four susceptible tree age cohorts (10–19, 20–39, 40–75, 76+ years)
T_{ij} = Trees of age cohort i located in cell j
j = Identity of the 60 m × 60 m grid cell defining location

Ash tree distribution

GIS maps that represented the population of host ash trees in each grid cell were derived from a mix of data sources. The population of ash trees was estimated from a survey of ash trees in the DuPage County of the Chicago region (Nowak 1994).[6] The relative location of DuPage County is illustrated in Figure 6.

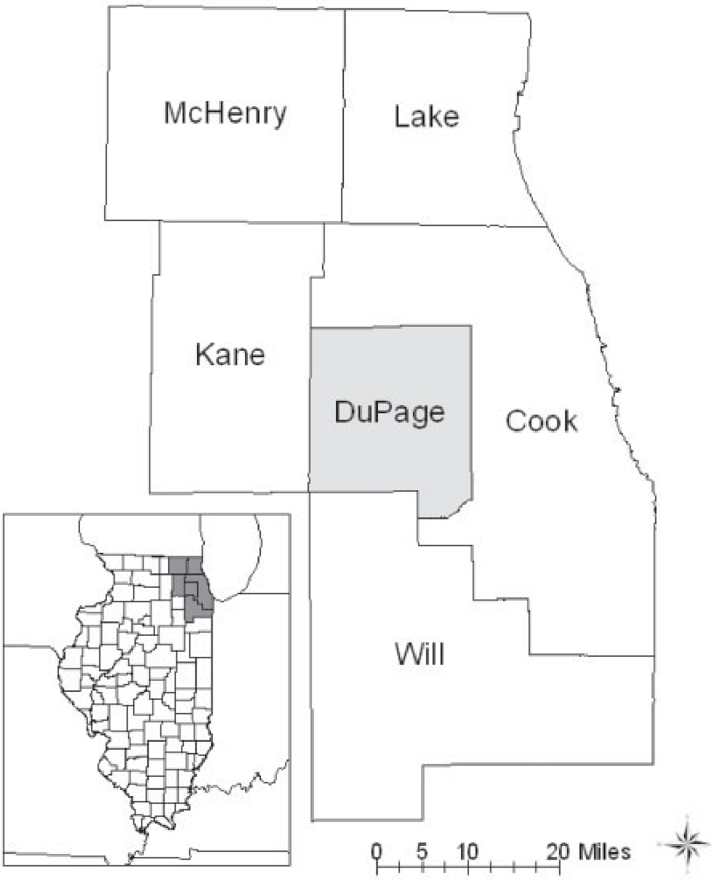
Fig. 5. Stock-flow diagram of EAB–ash interaction



The Nowak (1994) survey provided detailed estimates of tree species by broad land-use categories (e.g., institutional, residential, commercial, and vacant). These categories differ from those derived from remote sensing imagery characterizing surface permeability and vegetative differences. To achieve adequate spatial resolution, we used the land-use categories defined in the imagery-derived Land Cover of Illinois Database GIS (Luman *et al.* 2003). Luman *et al.* (2003) use remotely sensed electromagnetic signatures to define land cover classes such as high-density urban, low-density urban, upland forest, and savannah. Because the land cover classes of Luman *et al.* (2003) differ from the survey-derived Nowak (1994) estimates, we utilized Nowak (1994) data simply to estimate aggregate ash tree estimates in DuPage County and to derive heuristics for spatial allocation according to Luman *et al.* (2003) categories.

DuPage County contains an estimated 950,200 ash trees, 6.4 percent of the total tree cover in the county (Nowak 1994). We treated this as an upper

Fig. 6. Location of DuPage County in the Chicago Region



(conservative) bound for our estimate due to the recent urbanization of DuPage County. BenDor *et al.* (2005a) describe the allocation of trees using assumed densities for selected land cover classes. ESRI ArcGIS software (Ormsby *et al.* 2004) was used to transform the land cover map (Luman *et al.* 2003) of DuPage County into an ash tree population map. We decreased the raster resolution of the land cover map (from 30 m to 60 m square) to decrease computational complexity and increase compatibility with EAB flight behavior.[7]

Results

In this section we present a series of analyses using homogeneous and heterogeneous host tree landscapes. We begin with the simplest assumption of a uniform initial landscape to examine the dynamics of EAB dispersion.[8] Following from the dynamic hypothesis introduced in Figure 2, we anticipated that EAB dispersion would be accelerated by degraded carrying capacity (i.e., fewer host trees). Degraded carrying capacity (whether through anthropogenic thinning or through EAB attacks) effectively increases the EAB population density by reducing the denominator of bark surface area. The emigrating EAB fraction depends directly upon population density as specified in Figure 4. As population density increases, the fraction emigrating also increases.

Figure 7 illustrates the evolution of migration fraction over the 6-week adult life stage. The migration fractions have been averaged over 20 years of simulation time. Two cases are compared in Figure 7: sparse coverage (5 trees/cell) and dense coverage (10 trees/cell). The migration fraction is higher in the case of low carrying capacity (sparse coverage) because of the direct impact that fewer trees has on EAB population density.

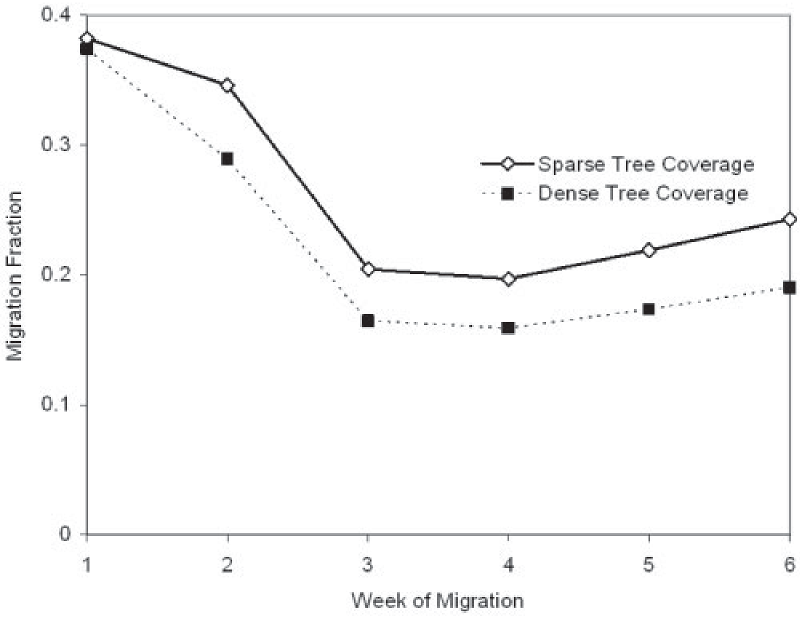


Fig. 7. Simulated migration fraction for differing carrying capacities

In the absence of migration, EAB population dynamics within individual cells exhibit overshoot and collapse behavior. These dynamics (illustrated in Figure 8) also confirm empirical observations of oscillatory seasonal cycles. The EAB population declines as it consumes the ash host. This simultaneous population decline serves to maintain EAB density in a dynamic equilibrium. Figure 8 shows the maintenance of population density alongside population decline.

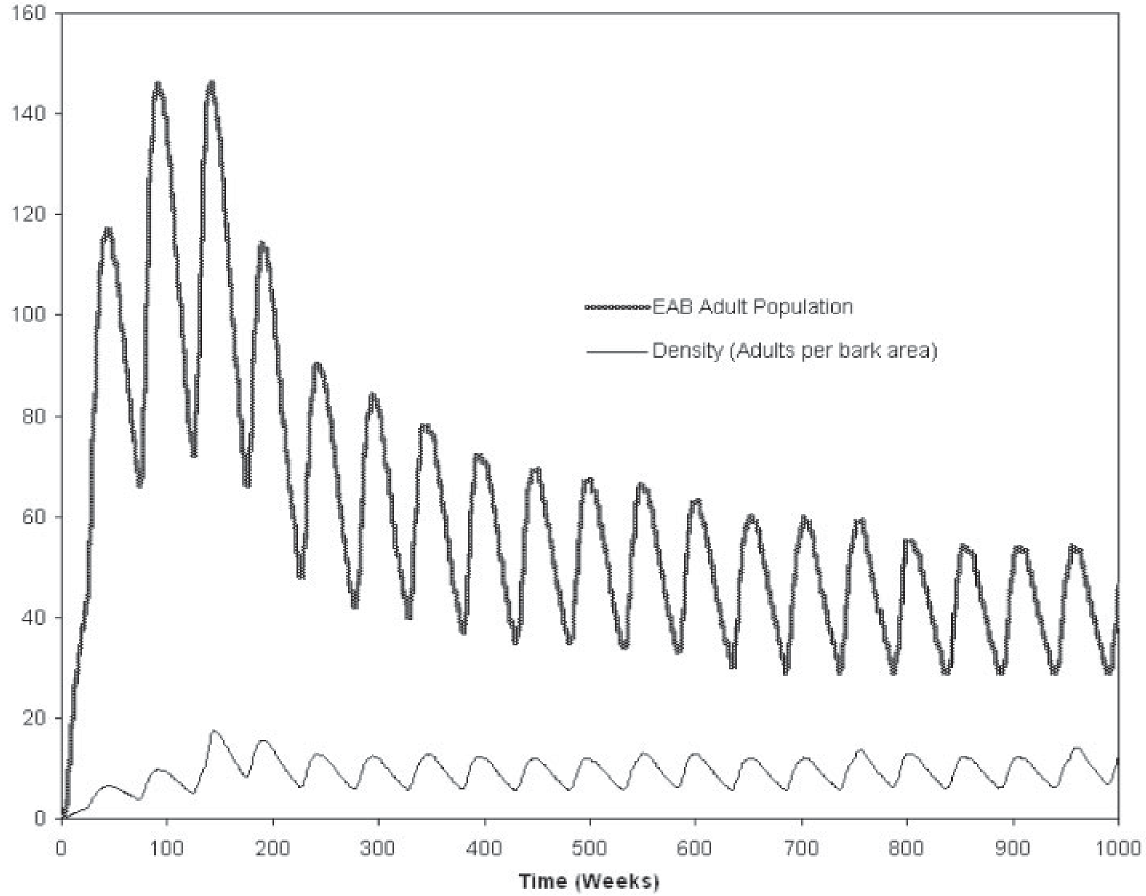
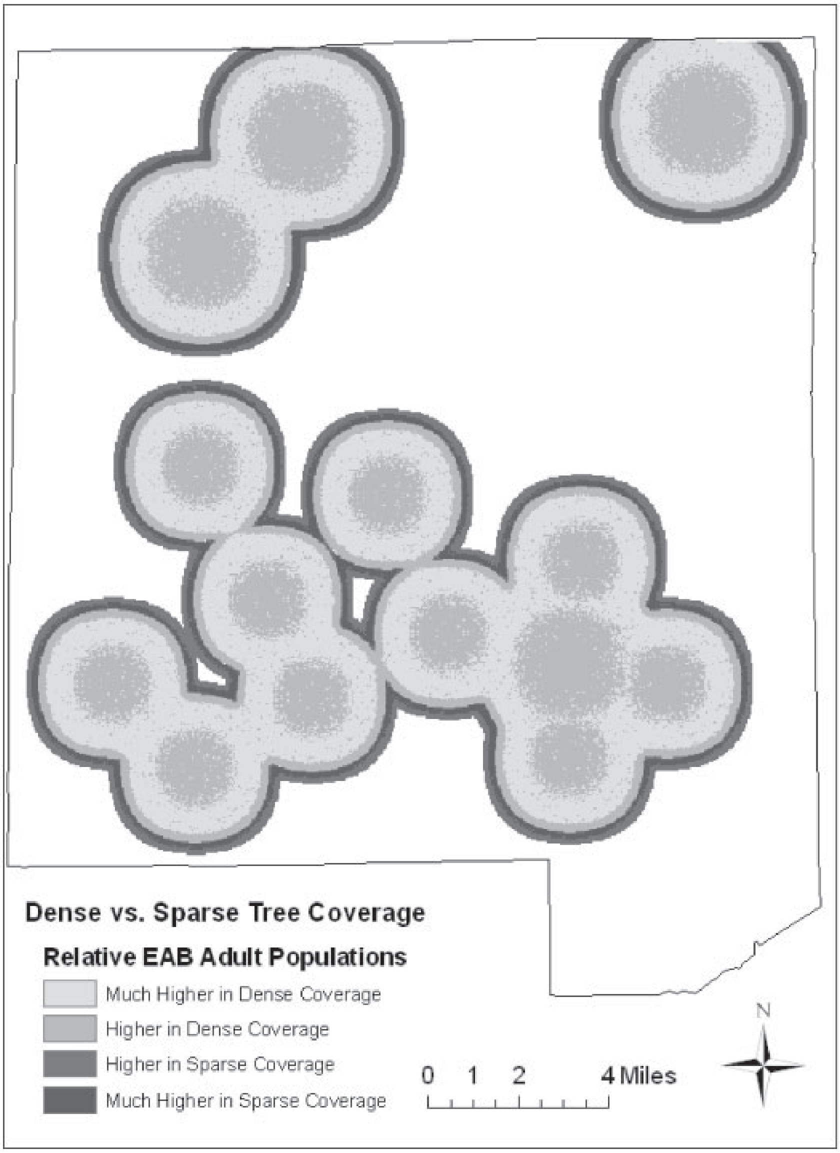


Fig. 8. Cellular dynamics of EAB adult population and density without migration

The dynamics of EAB emigration and immigration from cell to cell show that EAB movement is necessitated by loss of cellular carrying capacity due to its consumptive behavior. To demonstrate this behavior spatially, we compare EAB population on two homogeneous ash tree landscapes, representing dense (10 trees/cell) and sparse (5 trees/cell) coverage (the same conditions compared in Figure 7). Figure 9 provides a snapshot of EAB population differences 30 years after initial infestations. The circular rings expand from the locus of each infestation point. The dark outer rings in Figure 9 illustrate the greater EAB dispersion achieved in the sparse coverage (low carrying capacity) condition. The dense coverage condition results in greater EAB population near the locus, demonstrating that host trees remain available for consumption. This dense host coverage thus facilitates a higher population overshoot.

Fig. 9. Relative EAB dispersion in sparse and dense tree coverage



After examining the dynamics of degraded carrying capacity on homogeneous tree landscapes, we performed two scenario comparisons to test strategies for limiting EAB spread. Using the empirically derived heterogeneous tree landscape, these scenarios focus on two strategies to limit the spread of the EAB: a county-wide firewood quarantine, and an eradication program derived from the Michigan Eradication Strategy (Michigan Department of Agriculture 2003).

Modified Michigan Eradication Strategy

The Michigan Eradication Strategy (Michigan Department of Agriculture 2003) delineates the landscape into four major zones of consequence. The "core zone" is the area of known EAB infestation. Surrounding the core zone is a 3-mile wide band called the "suppression zone," which will soon host the natural spread of the EAB. The "firebreak zone" surrounding the suppression zone is a 3-mile wide band meant to be free of ash trees that prevents further EAB migration. The fourth and final area is the "uninfested zone" that is to remain EAB-free. The suppression zone acts as a buffer between the core zone and the firebreak zone since undetected areas may have already have been infected. Population reduction strategies in the suppression zone include selective tree removal as well as foliar and trunk chemical pesticide treatments. In addition to these strategies, the preventive removal of all ash trees in the firebreak zone is meant to ensure that no hosts remain for EAB dispersion.

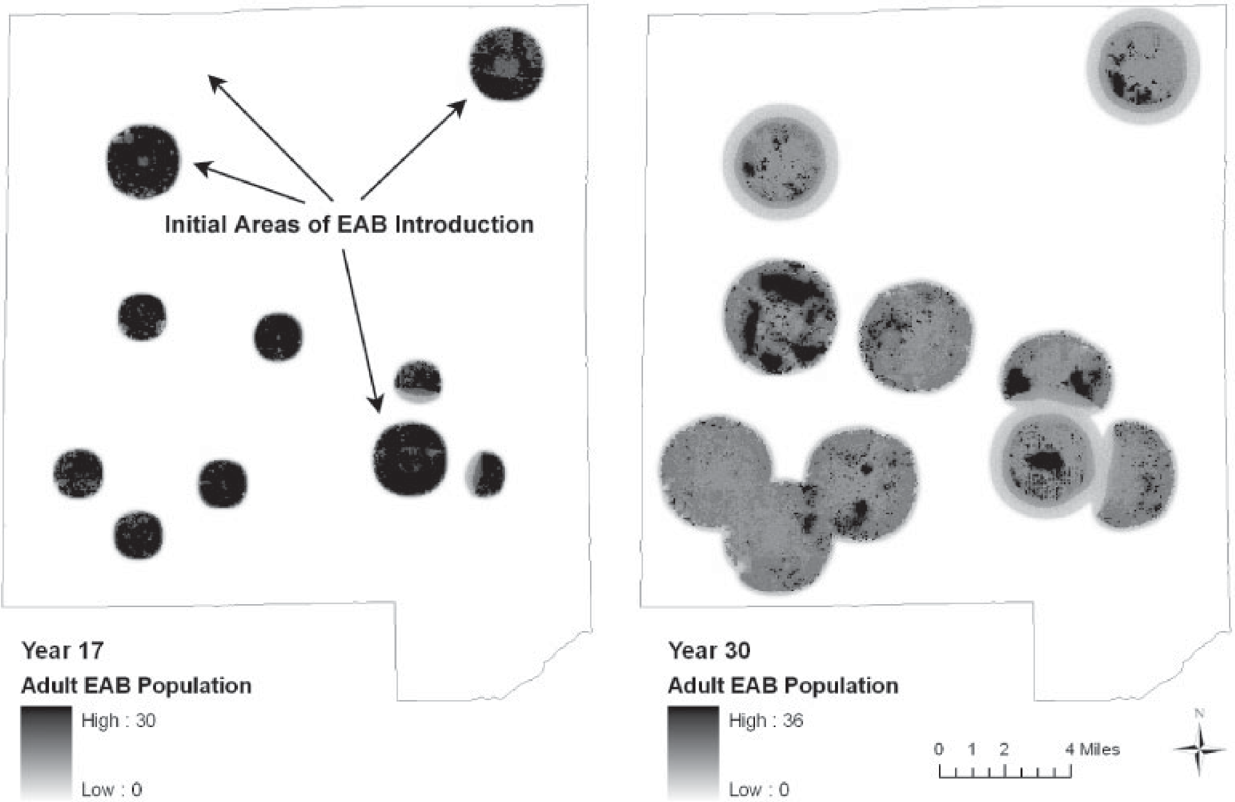


Fig. 10. EAB dispersion under modified eradication strategy

Our modified eradication strategy implements the suppression and firebreak zones as 1-mile wide bands around *detected* infestation sites.[9] These concentric bands are smaller than those proposed in the Michigan Eradication Strategy owing to the relatively small size of DuPage County relative to the size of southeastern Michigan. Figure 10 illustrates EAB dispersion for this eradication strategy using our heterogeneous tree landscape and allowing human-induced (anthropogenic) introductions of EAB via recreational firewood transport during the 30-year simulation. These anthropogenic introductions were simulated 3 years after the original infestations through the introduction of EAB larvae in 10 new locations within DuPage County. Seasonal timing of these introductions occurs in late April to correspond to firewood use during the camping season. Three of the original four infestations[10] in Figure 10 are treated with the eradication strategy.

Figure 10 compares EAB dispersion at two points in time: before and after the anthropogenic introductions have nullified the effectiveness of the eradication strategy. When in proximity, the EAB "front" of new introductions collides with the firebreak zone of treated infestations. This undermines the eradication strategy's attempt to keep the uninfested zone EAB free. If the new EAB introductions remain untreated, the new firebreak and suppression zones required at year 30 would involve massive decimation of ash trees. Figure 11 illustrates the spatial extent of these zones relative to the county size. The firebreak zone encompasses 55,630 acres (22,520 ha), and the suppression zone encompasses 62,180 acres (25,160 ha). In contrast, eradication of the three identified infestations in year three utilizes a firebreak zone of 21,950 acres (8,882 ha) and a suppression zone of 8,696 acres (3,519 ha). Delayed treatment thus dramatically compounds the EAB impact on the landscape.

Combined modified eradication strategy with firewood quarantine

Our final scenario combines the modified eradication strategy with a successful firewood quarantine, in which no new EAB introductions are made. Figure 12 reveals the success of the eradication strategy when combined with a comprehensive firewood quarantine. Here, the suppression zone successfully reduces both the EAB larvae and adult population, while the firebreak zone effectively halts EAB spread. EAB adults continue to spread from the fourth (untreated) introduction point, although spread within the firebreak zone is impossible since the zone has been rendered host-free. The spatial extent of the EAB infestation is 68,000 acres (27,520 ha) without the quarantine, in contrast to 22,300 acres (9,023 ha) with the quarantine in place.

The major insight emerging from this analysis is that firewood quarantines are most effective at reducing the extent of the EAB's spatial spread. While the modified eradication strategy effectively addresses identified infestations, its success is limited by EAB identification. If a firewood quarantine is effectively imposed, existing infestations may be treated without the threat of new EAB

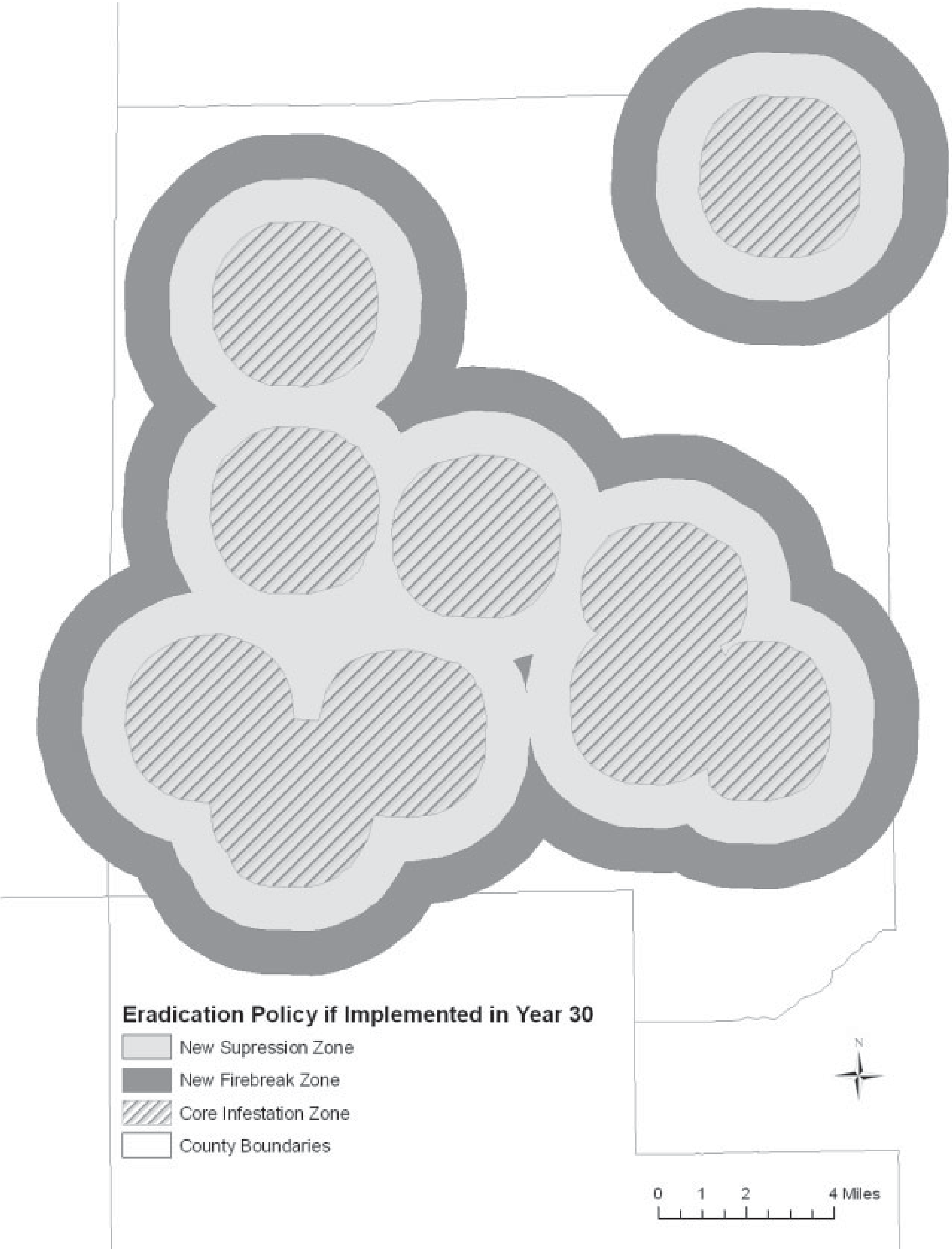


Fig. 11. Required size of eradication zones if implemented in year 30

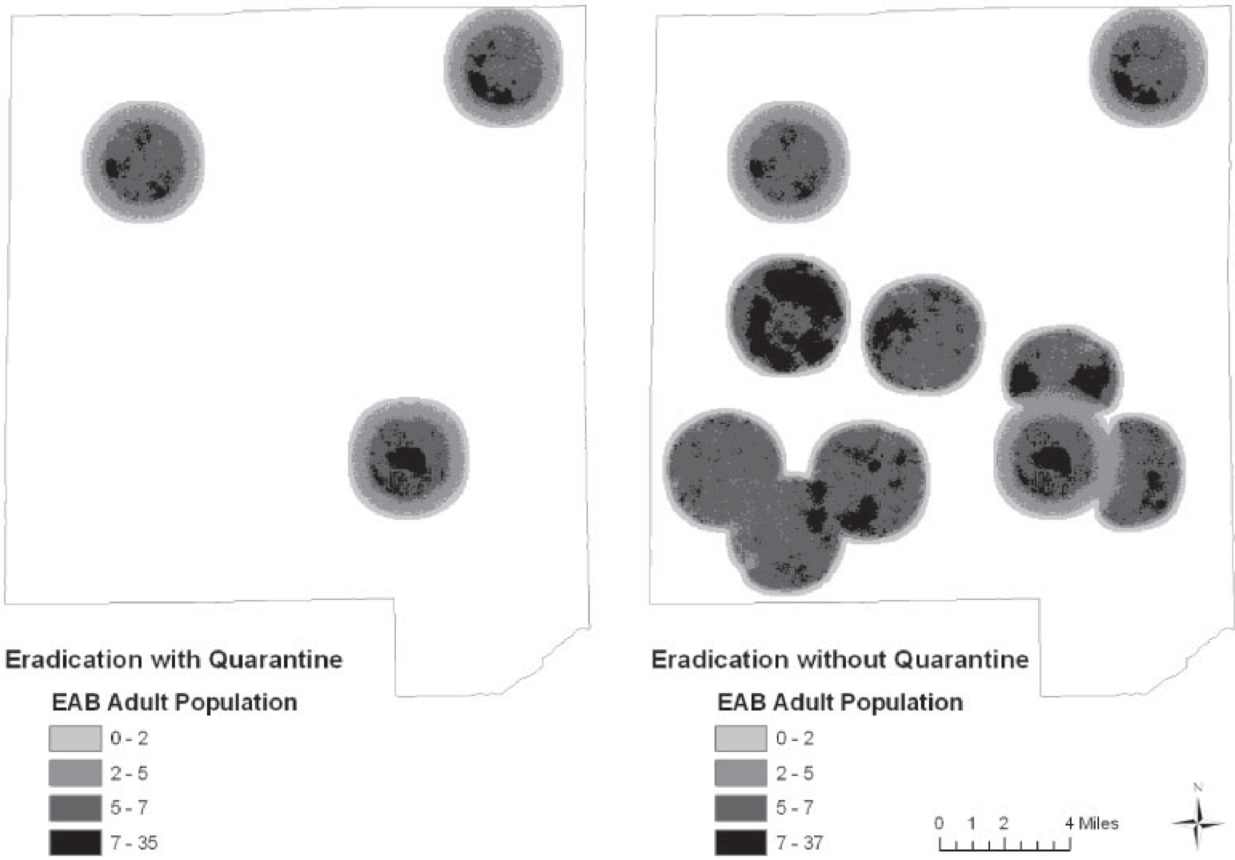


Fig. 12. Comparison of EAB dispersion with and without firewood quarantine

introductions. Moreover, the preventive measure of a firewood quarantine imposes less ecological and economic damage than the two-step eradication strategy of insecticide treatment (suppression zone) and tree removal (firebreak zone). By our estimates, firebreak zones remove approximately 30,980 ash trees per infestation, creating a major economic and aesthetic burden on state governments as well as local communities. Firewood quarantines offer a means of preventing such costs in the first place.

Discussion and conclusions

We employ spatial dynamic modeling as a means for understanding invasive EAB spread. The model structure serves as a knowledge repository for new information about the biology of the insect. Furthermore, simulated interactions between EAB and host ash populations demonstrate the role of degraded carrying capacity in EAB dispersion. Finally, the spatial dynamic modeling methodology facilitates timely analysis of policies for impeding EAB spread.

As a knowledge repository, the spatial dynamic modeling framework enables ready modifications of assumptions in response to rapidly changing information about EAB biology. Since its transplantation into North American climates, the Asian beetle has begun to adapt in ways that are not fully understood. Because adult emergence is temperature-dependent, some EAB populations have exhibited 2 and even 3-year life cycles with extended inactive larval periods. Predation on non-ash trees has also been observed, and biologists are working actively to update knowledge as the invasion continues (Wilson 2004).

The EAB is a particularly virulent invasive species whose spread is accelerated by high population densities (crowding). Our model utilizes this understanding to demonstrate that EAB spread is necessitated due to degradation of its own carrying capacity, the host ash trees. This model elucidates the extent to which the EAB depends upon space to survive. Each cellular model experiences an irruption of EAB activity (overshoot) due to population growth, after which carrying capacity plummets and the EAB is forced to emigrate (collapse and spread). The application of the system dynamics methodology in this parasitic interaction study is useful for understanding the persistent dynamics of sustained oscillations and overshoot and collapse (Sterman 2000). In this particular case, the spatial dynamics of this behavior are analogous to that of the Kaibab Plateau deer herd, whose early 20th-century population explosion was limited only by foliage (Ford 1999). These dynamics of degraded carrying capacity are exhibited spatially as EAB dispersion under sparse ash tree conditions exceeds that of dense coverage (Figure 9).

Using the spatial modeling environment, we tested both reactive and preventive policies to limit the spread of this invasive species. The reactive eradication strategy, while effective at addressing known infestation sites, is undermined by untreated dispersion from unidentified anthropogenic introductions. The natural spread rate of the insect is relatively slow in comparison to situations where humans assist in widening the reach of the EAB. Our analyses point to firewood quarantines as the most effective prevention measure. As evidenced by Michigan's experience, delays in policy response can be lethal for host ash populations. Anthropogenic introductions through firewood in Michigan may now number in the thousands, because firewood quarantines were not implemented until 5–10 years after the original infestation.

The policy insights of this model also underscore the importance of pesticide treatment of campfire and other transported wood vectors. Using the best available knowledge, these simulations demonstrate explicitly that the first step in limiting the damage inflicted by the EAB is the implementation and strict enforcement of comprehensive firewood quarantine programs. Figure 10 shows the damage that quarantine failures can inflict on the landscape, even in the face of otherwise effective eradication policies. This conclusion aligns with that of Moody and Mack (1988), who focus on controlling newly emerged anthropogenic "satellite" populations in limiting the spread of exotic-invasive plants. Furthermore, Taylor and Hastings (2004) also discuss prioritization of eradication efforts for isolated colonies of smooth cord grass (*Spartina alterniflora*), citing faster spread capabilities than dense populations seen in initial infestations.

This model also demonstrates the importance of monitoring to ensure the early identification of EAB infestations. As illustrated in Figure 11, eradication zones required in year 30 reveal the extent of damage that EAB infestations can inflict.[11] Early monitoring, combined with effectively implemented quarantines, appear to be most likely to inhibit the spread of EAB. However, social and economic barriers to quarantine implementation warrant further exploration of biologically based actions for EAB mitigation (e.g., introduction of EAB predators, innovation in chemical protection for ash trees).

Further extensions of this spatial dynamic model could incorporate human behavior relevant to EAB dispersion. For example, known campsites could be located through GIS analysis to gauge likelihood of specific introductions, and to guide quarantine enforcement. Specific tree management behaviors (e.g., planting and early removal) may also be represented as spatial parameter inputs. In addition, societal awareness of EAB damage and firewood quarantines may be represented through education and word of mouth dynamics.

Spatial dynamic modeling techniques are appropriate for a number of situations in which heterogeneous landscapes are persistent, pervasive, and relevant to the system of interest. This methodology has typically been applied to situations involving relatively continuous information or matter flows throughout a landscape. Such specific applications have included overland surface water flow (Voinov *et al.* 1998; Alexey *et al.* 1999), biomass and nutrient distribution (Costanza *et al.* 1988; Sklar *et al.* 1985), and large mammal movement (Deal *et al.* 2004; Shapiro *et al.* 2004). Applications can also extend to non-contiguous movement patterns such as urban sprawl (BenDor *et al.* 2005b; Deal and Schunk 2004). Moreover, the determination of neighborhood relationships remains flexible enough to incorporate abstract notions of space, such as social distance and competitive relationships between actors (Scheffran 2000).

The application of simulation modeling to the EAB invasion presents many avenues for further research. Methodologically, the integration of GIS with dynamic modeling has many applications in fields where spatial diffusion and movement are relevant. Substantive extensions of this research may involve the study of the effects of EAB chemical attractors (pheromones) on migration behavior. Furthermore, a detailed study of the effect of urban development (with the associated patterns of tree removal and disposal, often expressed as tree movement, along with associated infestations) on EAB dispersion may provide a more realistic picture of the EAB's ability to capitalize on human-driven vectors. BenDor *et al.* (2005b) began exploring the impact of different land use change patterns on the spread of the EAB. Another avenue is the application of this model to locations with small EAB infestations and high-quality tree data for fine-grained validation and calibration.

This research calls for the collection of high-quality tree distribution data. Knowledge of host locations will be imperative in the fight against the EAB in coming years as the insect spreads to an increasing number of metropolitan hubs. Many areas, including Chicago and Detroit, maintain susceptible ash trees as a high proportion of their municipal street trees. EAB infestations in these areas will be particularly damaging owing to the high density of affected trees as well as the soaring costs of tree removal and replanting.

Notes

1. Dispersal patterns have been studied as behaviors stratified by long- and short-term dispersal mechanisms by Moody and Mack (1988), Hengeveld (1989), Lewis (1997), and Shigesada and Kawasaki (1997).
2. The emerald ash borer is among several recently introduced wood-boring beetles that have invaded forested areas throughout North America (Haack and Poland 2002; Auclair *et al.* 2005; Smith and Hurley 2000).
3. For more information on GIS, see Ormsby *et al.* (2004).
4. The installation of SME still requires technical expertise. This is partially due to the open source nature of the software, as well as its origins in the Linux operating system, making its use more involved than standard Windows software. Non-standard use of SME for neighborhoods beyond the immediately adjacent cells also requires some insight into the inner workings of SME. See Acknowledgments for our credits.
5. In this model, continuous-time dynamics are approximated with numerical simulation of differential equations articulated in the STELLA software environment (http://www.hps-inc.com).
6. The Chicago Region was selected for study because of its role as a major port of entry near the already infested Detroit Region. DuPage County contains some of the wealthiest suburbs of Chicago—places in which aesthetic damage to ash trees could wreak havoc on real estate prices.
7. The processed cells were four times the size of the original cells (3,600 m^2). This conversion process utilized ArcGIS algorithms that assigned land-use type to the coarser cells based upon relative dominance of constituent 30 m × 30 m land-use types.
8. In all of the simulated scenarios, we initiate population dynamics with anthropogenic injections of 500 EAB larvae in a selected 60 m × 60 m cell.
9. For a visual depiction of the eradication zones, see BenDor *et al.* (2005a, p. 16).

10. Three of the original infestations are visible as loci of the concentric rings in Figure 10. The fourth infestation occurs in an area with very few trees and thus remains undetected.
11. This is instructive since the Michigan EAB introduction was not identified until 5–10 years after its introduction (McCullough and Katovich 2004).

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