Deconstructing Geospatial Agent-Based Model: Sensitivity Analysis of Forest Insect Infestation Model

Taylor Anderson and Suzana Dragićević

Abstract Agent-based models (ABM) can be used to represent the spatio-temporal dynamics of real world geospatial phenomena, however because of their complexity, they can be difficult to implement and validate. This study uses the invariant-variant validation approach to further model testing of a developed ABM of forest insect infestation representing spatio-temporal dynamics of the emerald ash borer (EAB). The invariant-variant method deconstructs model results to facilitate an improved understanding of the model's sensitivity to changes in input parameters and focuses on EAB agents' access to information. Obtained results indicate that the developed EAB agent-based model represents and maintains both process accuracy and spatial similarity.

Keywords Complex systems • Agent-based models • Model testing • Invariantvariant method • Emerald ash borer

1 Introduction

Ecological phenomena such as insect infestations can be modelled using a complex systems approach such as cellular automata and agent-based models to better understand how interactions between individuals and their local environment generate spatial patterns at much larger scales [1]. This approach acknowledges that local variation has a significant impact on emergent system behavior. Traditional equation-based ecological models tend to ignore local heterogeneity and model ecological processes from the top-down, limiting their ability to capture system complexity [2]. As an alternative, geospatial agent-based models (ABM) represent the system from the bottom-up, overcoming these limitations. ABMs implement discrete, heterogeneous "agents" to represent real world entities (i.e. an insect) and capture system processes at the local scale. As agents interact with one another

T. Anderson (🖂) • S. Dragićević

Spatial Analysis and Modeling Research Laboratory, Department of Geography, Simon Fraser University, 8888 University Drive, Burnaby, BC, Canada V5A 1S6, e-mail: taylora@sfu.ca; suzanad@sfu.ca

[©] Springer International Publishing AG 2018

L. Perez et al. (eds.), *Agent-Based Models and Complexity Science in the Age of Geospatial Big Data*, Advances in Geographic Information Science, DOI 10.1007/978-3-319-65993-0_3

and their virtual environment over time, complex system level behavior and spatial patterns emerge. Furthermore, ABMs can be integrated with geographic information systems (GIS), facilitating the representation of the environment in which the agents interact using real geospatial data.

It has been demonstrated that geospatial ABMs can capture the complexity of the real-world systems and have been used to accurately represent ecological phenomena such as fish [3], birds [4], and forest insect infestations such as the mountain pine beetle [5, 6] and the emerald ash borer [7, 8]. ABMs provide a useful methodology for the evaluation of future policy decisions and actions, sometimes referred to as scenario planning [9]. For example, using an ABM as a virtual laboratory, Anderson & Dragicevic [8] develop scenarios to explore and optimize the biological control of the EAB forest insect infestation i.e. determine how many biological control agents need to be released and where they need to be released to be effective.

To use an ABM in the decision-making process, the level of confidence of the model to represent the phenomena realistically must be demonstrated. However, building and implementing an ABM capable of capturing the complexity of real world geospatial phenomena presents unique challenges in both understanding and communicating their validity. Particularly, as ABMs represent behavior of various agents, they rely on stochasticity, and thus may produce a variety of results, even when using the same input parameters [10]. This can make testing using traditional map comparison techniques and accuracy assessments that measure spatial similarity between model outputs and reference data difficult, as these measures may hide or ignore these important variations [11].

For example, the variation in results may be a function of path dependence, where positive and negative feedback processes have driven the model produce two or more distinct spatial patterns across model runs. The patterns that emerge from these processes may fluctuate between matching the patterns found in reference data and vice versa. However, as a bottom-up modelling methodology, ABMs seek to represent the underlying dynamics and processes in producing complex system level behavior and thus their usefulness may not be fully measured through aggregate pattern matching. Thus, it may be valuable to also explore the model's process accuracy and increase confidence that the model can represent the *processes* driving the spatial patterns of the phenomena. Additionally, small changes in ABM input parameters may generate disproportionally large variations in output spatial patterns. Understanding how model input parameters affect model outputs is an important step in developing functional and useful ABMs [12].

The invariant-variant method developed by Brown et al. [13] makes the distinction between model results that remain consistent across model runs (invariant) and model results that change across model runs (variant). The deconstruction of model results into these two classes is useful in the identification of the underlying model processes that give rise to emergent spatial patterns. Furthermore, the invariantvariant method and can aid in sensitivity analysis to clearly understand how changes in input parameters change model results. These methods have been advanced to account for not only spatial variation, but also temporal variation across model runs [14], where Bone et al. develop a temporal invariant-variant approach to account for transition between land use classes over time. The purpose of this study is to further the model testing of a forest insect infestation geospatial ABM developed by Anderson & Dragicevic [7, 8] using the invariant-variant method. The developed ABM simulates emerald ash borer (EAB) forest insect infestation dynamics and spread in Oakville, Ontario, Canada for 2 years (2008–2009). Geospatial data delineating real EAB extent in 2009 obtained from Oakville facilitates model testing using this approach. The main objective of this study is to deconstruct and better understand model results using the invariant-variant method and to test the sensitivity of the model parameters. The following sections will provide a brief outline of the developed EAB ABM and present the model testing method and results, finishing with a discussion and conclusions.

2 Background

2.1 Emerald Ash Borer (EAB)

The emerald ash borer (EAB) is an invasive bark beetle, native to countries in Asia [15]. The beetle was thought to be introduced into North America in the late 1990s and was discovered in 2002 in Detroit, Michigan, USA. Since its introduction into the region, the pest has been responsible for the decline of the North American ash tree population, creating devastating ecological and economic impacts. Eradication has been unsuccessful due to challenges in infestation detection, a lack of native predators, and long-distance dispersal patterns that are difficult to predict [16].

EAB complete their lifecycle in one (sometimes two) years and consists of the stages: active larvae, inactive larvae, pupae, and adulthood [17]. The EAB eggs mature into larvae and then into adulthood while under the bark of ash trees, a process that takes almost 1 year, before emerging in early June through August, with peak emergence in mid-July [18]. The beetle uses olfactory and visual cues to determine the most suitable hosts and prefer to lay their eggs in ash trees that are stressed [19], have a lower natural resistance to insect infestations such as green, black, and white ash [20], and are larger in size and capable of supporting the larval galleries [21]. EAB find their hosts through local dispersal, travelling on average 2.8 km/day [22]. The beetles spread can be exacerbated by long-distance dispersal, facilitated by the movement of infested saplings or firewood. These two dispersal mechanisms generate a pattern called stratified dispersal, where eventually the natural front of infestation and satellite populations coalesce [23].

2.2 EAB ABM

It is important to understand the spatial patterns and processes of insects' dispersal, interactions, and dynamics, but this information can be difficult to obtain from field measurements. Existing EAB models use differential equations [24] and diffusion

State variables and parameters of EAB						
Variable	Description					
ID	The agent's unique identifier					
Age	The agent's age					
Geography	The location (decimal degrees) of the agent					
EAB adult agent parameters						
Parameter	Description	EAB value				
Maximum flight distance/day	Flight mill tethering distance that females can travel/day	2.8 km/day [22]				
Chance of fertility	Average fertility rate of females	82% [27]				
Maximum number of offspring	Average threshold for maximum offspring	Randomly selected value between 60 and 90 offspring/individual [28]				
Survival rate of eggs	Survival rate as a function of chance	Randomly selected between and 53–65% survive [28]				
EAB larvae agent parameters						
Sex ratio	Female: Male	1:1, 50% [18]				
Survival rate of larvae	Survival rate as a function of tree resistance, disease, and predation via other species i.e. woodpecker	Host tree defense: max 21.5% Disease: 3% Woodpecker: max 17% [29]				

Table 1 State variables and parameters of EAB adult and EAB larvae

models [25], however are limited in their representation of complexity inherent to insect infestation processes and behavior of the beetles [26]. Alternatively, ABMs can be used to simulate these processes and better understand complexity of the infestation dynamics and use scenarios to aid in management and decision making.

Anderson and Dragicevic [7] have proposed an EAB ABM to simulate spatiotemporal dynamics of EAB in Oakville, Ontario, Canada for 2 years (2008–2009), and was further enhanced [8] to explicitly represent EAB population dynamics. The model is composed of agents that represent individual EAB in larvae and adult stages. Agents are programmed with state variables and parameters that are unique to each individual (Table 1). State variables track the state of an agent at each iteration such as age and location. Parameters characterize an individual agent's biological properties such as the chance of fertility and the maximum number of offspring an individual may produce. These parameters are determined using biological information documented in EAB literature. Agent behavior is driven using several subroutines that execute stages in the life cycle including local dispersal, long-distance dispersal, mating and fertility, maturity, infestation of ash trees, and death (Table 2).

The model simulates EAB spatio-temporal dynamics over a period of two seasons of EAB infestation from June 1st, 2008 (T_1) when the EAB was first introduced to the region, to the end of August 2009 (T_{460}) [8]. Each iteration in the model (T_i) represents 1 day i = (1, 460) in the real world. Due to random processes in the model, no two simulation outputs are the same. Therefore, the model is executed 50 times to generate a statistically significant distribution of results, where each run generates a variation of the emergent patterns of EAB infestation in 2009.

Agent processes					
EAB adult agent					
Process	Description				
Aging	The age of each agent is increased by 1 day at each new iteration. The age (in days) of an agent triggers the execution of life cycle processes				
Short-distance dispersal	Short distance dispersal is the process whereby agents change their location. Short distance dispersal begins after EAB adults emerge at the age of 1 day and continues throughout the rest of the agent's lifetime. The distance in which an individual EAB agent will move at each model iteration is a function of: (1) the average distance EAB travel per day (2.8 km) [22] and (2) host suitability [30] The flight distance of 2.8 km per day bounds the EAB agents' access to information about their environment (i.e. what trees are available). Each EAB may search within a radius of their average daily flight distance for host trees and compare them with one another based on their suitability. The comparison between trees by EAB is controlled by a host selection algorithm, developed by Anderson & Dragicevic [7] that allows EAB agents to optimize their decision of which tree to infest based on their preferences. EAB host selection preferences have been studied extensively and are a function of (1) tree distance, (2) tree type, (3) tree stress, and (4) tree size. Specifically, EAB prefer trees which are closer in distance, tree types of lower resistance to infestation such as the green ash, trees which are under stress perhaps due to existing infestation or age, and trees larger in size				
Mate	EAB agents may become fertile based on their chance of fertility. Those that become fertile, mate at the age of 7 days. EAB are randomly assigned a maximum number of offspring between 60 and 90 individuals [31]				
Oviposit	EAB agents become fully mature and begin seeking suitable ash trees using the host selection algorithm to host their larval galleries at age 10 days. At each iteration, EAB oviposit a random number of eggs onto their choice of tree. This process continues until the maximum number of offspring have been produced. The number of eggs may be reduced based on their chance of survival				
Death	EAB agents die once they have produced their maximum number of offspring				
Long-distance dispersal	Long distance dispersal is a random process in the model where satellite populations (sometimes 1% of the original population) becomes established in regions of high susceptibility to this process i.e. along major transportation networks or near campgrounds. The environment in which the EAB interact is representative of Oakville's urban forest and is based on Oakville's tree inventory geospatial data sets				
EAB larvae agent					
Death	Larvae may die as a result of tree resistance, disease, and native predators [29]. This process uses a random number generator to determine how susceptible the larvae is to these factors				
Emergence	EAB larvae emerge when they reach the age of 340 days and if it is female. A random number generator is used to determine the sex of the larvae				

 Table 2
 Subroutines that generate agent behavior

3 Methods

Initial model testing of the EAB ABM has been performed. The model has been calibrated to simulate the real-world rate of spread, determined by using real world data delineating the extent of EAB infestation from 2002–2010 [7, 8]. Specifically, the model has a simulated rate of spread from the epicenter of infestation in 2008 to the delineation of EAB infestation in 2009 of 2.119 km/year in comparison to the observed rate of spread in reality of 2.098 km/year. Additionally, the model simulates spread with an average distance of 4238.77 m and a maximum distance of 11049.50 m in comparison to the observed average distance of 4196.17 m with a maximum distance of 11186.3 m [7].

Although research has shown tree type, tree size, tree stress, and tree distance are the driving factors in host selection and are included in the host selection algorithm, the order in which EAB prioritize these factors is unknown. Therefore, Anderson & Dragicevic [8] performed the sensitivity analysis to determine the sensitivity to the order in which these factors are preferred i.e. whether EAB prefer trees that are closer or are more stressed. Initial model validation used traditional methods of map comparison between model outputs and real-world data and included the following metrics: (1) the spatial agreement between the model output and the realworld data in location of infestation in 2009 and (2) the spatial agreement between the model output and the real-world data in severity of infestation. The level of agreement of the state of the trees between model outputs and real-world data was determined. The overall accuracy of the model calculated by using these methods was found to be 72% in simulating the location of EAB infestation [7, 8] and 64% overall accuracy in forecasting location of severity of infestation [7]. Although a useful starting point for evaluating the overall performance of the model, simple accuracy assessments using map comparison techniques may not allow for in depth exploration of the model processes that may be contributing to the distribution of model results. Therefore, the invariant-variant method is used to further the EAB ABM model testing and sensitivity analysis.

3.1 Invariant-Variant Method for Analysis of EAB ABM

In the case of the EAB ABM, the *invariant region* can be defined as the trees that are always or almost always infested or always or almost always not infested and the *variant region* can be defined as the trees that are sometimes infested and sometimes not infested. To determine which trees are invariant or variant across model runs, the EAB ABM was run 50 times, producing a statistically significant distribution of results. Each run of the EAB ABM outputs a geospatial dataset containing all trees and their corresponding attributes (i.e. tree height, tree DBH) and infestation status (i.e. whether the tree has been simulated as infested or not). The infestation status of a tree across all model runs is used to calculate the proportion of runs in which

the tree is infested, denoted as t_{xy} at location x, y. For example, if tree t is infested in 46 of a possible 50 runs, $t_{xy} = 0.92$, meaning that the tree is infested in 92% of the model runs.

The invariant and variant trees are partitioned using a threshold θ . For example, trees that are invariant and infested *ID* are defined by a threshold $\theta = 0.9$, as used by Brown et al. (2005), and as such must be infested in at least 90% of model runs. Therefore, *ID* is the number of trees $t_{xy} > \theta$. The *ID* region is compared with the real-world data delineating EAB infestation in 2009 and sub-classified into invariant correct *IC* and invariant incorrect *II*. *IC* are trees that are infested in 90% of model runs and infested in reality. Conversely, *II* are trees that are infested in 90% of model runs and are not infested in reality. Because these trees are invariant, every model run will have nearly the same value for *IC* and *II*. In contrast to *ID*, trees that are rarely infested, $t_{xy} < 1-\theta$, are denoted as *IU*, meaning they are infested in less than 10% of model runs.

Trees that are *variant* are sometimes simulated as being infested (11–89% of model runs). In addition to trees that are correctly simulated as infested in the *invariant* region *IC*, trees may be correctly simulated as infested in the *variant* region. The number of variant correct *VC* is a function of a particular run *k*. If C_k is used to denote the number of infested locations that are predicted by a single run *k*, then $C_k = IC + VC_k$. *VC* can be plotted using a histogram to show model behavior across all of the runs. A histogram that has a set of runs with extremely high *VC* and a set of runs with low *VC* may indicate multiple *paths*.

Decomposing model results into its invariant and variant regions allows for the identification of patterns that may not be obvious when looking at the overall generated spatial patterns of infestation. A small *IC* and a large *VC* may indicate that the model is path dependent, where complex dynamics of the phenomena represented by the ABM causes the generation of multiple spatial patterns. For example, in some runs infestation spreads to unexpected locations and in others, infestation coincides with the reference data. This is important, because when calculating a simple accuracy assessment, a model that produces this variation in results may not be within acceptable limits of accuracy, however the model may be path dependent, evidence of the model's ability to capture system processes accurately. In contrast, if *IC* is large and *VC* is small on average, it can be concluded that the accuracy of the developed EAB ABM model primarily originates from getting the large invariant region correct.

3.2 Bounded Rationality Sensitivity Tests

The sensitivity of the model to the EAB agent's access to information was tested. To test the impact that an increase in EAB access to information would have on the model simulation outcomes, the model was run 50 times with an increased flight distance of 5.6 km per day, double that of the original distance. Furthermore, the

impact that a decrease in the EAB agents' access to information on the model simulation outcomes was tested using a flight distance of 1.4 km/day, half of the original distance, and was run 50 times.

4 Results

4.1 Invariant-Variant Method for Analysis of EAB ABM

The simulation results obtained by the invariant-variant analysis for the EAB ABM are presented in Table 3A and Fig. 1a. The EAB ABM model generates a high IC (invariant infested correct) at 1419 trees and a high IUC (invariant uninfested correct) at 2089 trees versus a low VC (variant correct) at 926 trees, meaning that the models map comparison accuracy primarily comes from getting the invariant region correct.

The invariant region, where infestation occurs in over 90% of model runs, is located near the center of the study area, the core zone, where EAB first were identified in this region in the real-world (Fig. 1a). The simulated invariant region

Distance	Description	(A) 2.8 km/day	(B) 1.4 km/day	(C) 5.6 km/day
Invariant infested (ID)	Simulated as infested in 90% or more of model runs	1619	727	1912
Invariant correct (IC)	Simulated as infested in 90% or more of model runs and is in agreement with the reference data	1464	724	1643
Invariant incorrect (II)	Simulated as infested in 90% or more of model runs and is not in agreement with the reference data	155	3	269
Invariant uninfested (IU)	Simulated as uninfested in 90% or more of model runs	3355	4829	1904
Invariant ucorrect (IUC)	Simulated as uninfested in 90% or more of model runs and is in agreement with the reference data	2089	2445	1242
Invariant uincorrect (IUI)	Simulated as uninfested in 90% or more of model runs and is not in agreement with the reference data	1266	2384	662
Variant (V)	Sometimes simulated as infested	1208	626	2336
Variant correct (VC)	Sometimes simulated as infested and is infested in reality	926	548	1351
Variant incorrect (VI)	Sometimes simulated as infested and is not infested in reality	282	78	1015

 Table 3
 Invariant-variant analysis results for sensitivity of EAB agents' (A) access to information using a flight distance of 2.8 km/day, (B) reduced access to information using a distance of 1.4 km/day, and (C) increased access to information using a distance of 5.6 km/day



Variant
 Invariant Infested

Fig. 1 Locations of variant and invariant trees based on simulations incorporating EAB agents' with (a) access to information using a flight distance of 2.8 km/day, (b) reduced access to information using a distance of 1.4 km/day, and (c) increased access to information using a distance of 5.6 km/day

mostly falls within the delineation of EAB infestation obtained from real-world data. The variant region, where infestation occurs in some runs and not in others, is located on the perimeter of this core invariant zone and in satellite population zones. In addition, there are a few variant infested trees that fall between the core zone and the satellite population zones.

As presented in Fig. 1a, the model underestimates the number of infested trees, meaning that 1266 invariant uninfested trees are infested in the real world. The model does well at predicting the number of invariant infested trees and rarely does the model predict a tree is infested when it is not infested in reality. The distribution of model runs k and the number of trees accurately simulated as infested is presented in Fig. 2. The histogram depicts the variance across model runs.

4.2 Bounded Rationality Sensitivity Tests

The results indicate that the EAB ABM is sensitive to the EAB agents' access to information. Specifically, as presented in Fig. 1b, reducing the EAB agents' access to information affects the simulated outcomes in the following ways: (1) the invariant infested region is smaller, but more accurate; (2) the invariant uninfested region becomes much larger, but becomes much less accurate; and (3) the variant region becomes smaller, but more accurate. In general, reducing the EAB agents' access to information underestimates the number of trees that are infested in the real-world by almost double of that of the original model at 2384 trees (Table 3B).



Fig. 2 Variability of number of trees correctly simulated as infested across 50 model runs including invariant correct and variant correct

Reducing the EAB agents' access to information maintains the emergence of the invariant region located in the core zone. Variant regions emerge around the perimeter of this core zone and in satellite population zones. All trees infested in the simulation in this scenario fall within the real-world delineation of the EAB infestation (Fig. 1b). Reducing the EAB agents' access to information eliminates the variant region between the two zones.

In contrast, as presented in Fig. 1c, increasing the EAB agents' access to information affects the simulated outcomes as such: (1) the invariant infested region is slightly larger, with similar accuracy to the original model; (2) the invariant uninfested region is much smaller, but does not overestimate uninfested trees; (3) the variant region becomes much larger, larger than the invariant infested region, but overestimates infestation in trees that are not infested in reality at 1015 trees (Table 3C).

Increasing the EAB agents' access to information maintains the generation of the invariant region located in the core zone and the invariant region around the perimeter of the core zone and in satellite zones and increases the variant region that falls between these two zones (Fig. 1c).

5 Discussion and Conclusions

The variable distribution of the frequency of trees correctly predicted as infested across model runs (Fig. 2) may indicate that EAB ABM generates multiple paths. A primary assumption would be that the stochastic long-distance dispersal processes

are generating the variation in accuracy from model run to model run. In the simulation outputs, small satellite populations sometimes appear in the south-west part of the study site due to the location's proximity to the highway and the Bronte Creek Provincial Park and because long distance dispersal is a random process in the model, simulated satellite populations are always variant. There is a slight positive relationship ($R^2 = 0.38$) between the model's overall accuracy and the accuracy in forecasting satellite populations, meaning that model runs that predict satellite populations are sometimes more accurate and thus may explain some of the variability in model runs. Long distance dispersal is not often spatially similar to the locations of reference data, which would reduce the accuracy of the model when using traditional map comparison and accuracy assessments. However, long distance dispersal may be variant correct, indicating process accuracy.

The invariant-variant analysis demonstrates that the model is sensitive to reducing the EAB agents' access to information. Reducing the flight distance to 1.4 km/day results in a severe underestimation of the number of trees infested in reality. This is evident by the decrease in the invariant infested region and the increase in the invariant uninfested region (Table 2; Fig. 1b). In contrast, the results suggest that the model is less sensitive to an increase in the EAB agents' access to information with a flight distance of 5.6 km/day. Specifically, the invariant infested region and the original model parameter of 2.8 km/day (Table 2). This can be attributed to the host selection algorithm which acts as a negative feedback mechanism by prioritizing the infestation of trees that are closer in distance and thus accurately simulates infestation processes. However, with an increase in access to information, the variant region increases substantially (Fig. 1c) which means that in some model runs, EAB infestation is overestimated.

Real-world EAB infestation at regional scales undergo the process of stratified dispersal, where the core zone and satellite population zones merge, advancing the front of EAB spread at increased rates. Evidence of the stratified dispersal process can be identified in the simulations, where the core zone and satellite zones begin to merge in some simulation runs, thus developing a variant infested region between the two. Specifically, the early stages of a merge between infestation in the core zone and satellite population zones occurs in some runs of the original model and is even more pronounced when the EAB agents' access to information is increased. In the reference data, however, the two zones including the core zone and the satellite population zones are entirely separate. Thus, traditional accuracy assessments and map comparisons would deem model runs that simulate stratified dispersal as inaccurate and ignore the value in the model's ability to simulate this important process.

In summary, ABM testing can be a challenging process. Common spatial model evaluation measures such as map comparison or other simple accuracy assessments are difficult to apply since ABMs produce a variable distribution of outputs across model runs in response to agents' individual behavior and interactions in combination with stochasticity, local heterogeneity, feedbacks, and evolution in the model [6]. Using these conventional measures may provide an understanding of the spatial

similarity between aggregate spatial patterns in the reference data and aggregate spatial patterns generated as model outputs. This can provide initial confidence in model performance. The invariant-variant analysis breaks down the aggregate measure of spatial similarly and provides insight as to what may be influencing these measures, thus improving the understanding of the model processes that generate model results and help the modeler gain confidence that the real-world phenomena is represented realistically.

EAB infestation poses significant threats to forest ecosystems across Canada and in the US. The developed EAB ABM can be used to aid in meeting management goals by evaluating how various management actions impact infestation dynamics. However, naturally, before the results can be used to make decisions, sufficient data demonstrating that the model's results are valid must be attained. The invariantvariant analysis demonstrates the proposed agent-based model possesses the ability to represent underlying processes driving emergent patterns of EAB spread to assist and give confidence to decision makers such as stakeholders or policy makers in model outputs and reduce the possibility of making unsuitable decisions and risk time and money. In particular, the variant and more unpredictable nature of satellite populations may require a focus of resources by decision makers in order to slow the infestation front and reduce large scale negative impacts of EAB infestations.

Acknowledgments This study was fully funded by a Natural Sciences and Engineering Research Council (NSERC) Canadian Graduate Scholarship-Doctoral (CGS D) awarded to the first author and Discovery Grant awarded to the second author. The datasets were provided by the Town of Oakville, Canada. The authors are thankful to Compute Canada WestGrid high-performance computing facility for enabling model simulations.

References

- DeAngelis DL, Mooij WM (2005) Individual-based modeling of ecological and evolutionary processes. Annu Rev. Ecol Evol Syst 36:147–168
- 2. Grimm V, Railsback SF (2005) Individual-based modeling and ecology. Princeton University Press, New Jersey
- Letcher BH, Rice JA, Crowder LB, Rose KA (1996) Variability in survival of larval fish: disentangling components with a generalized individual-based model. Can J Fish Aquat Sci 53(4):787–801
- 4. Travis JM, Dytham C (1998) The evolution of dispersal in a metapopulation: a spatially explicit, individual-based model. Proc R Soc Lond B Biol Sci 265(1390):17–23
- Pérez L, Dragićević S, White R (2013) Model testing and assessment: perspectives from a swarm intelligence, agent-based model of forest insect infestations. Comput Environ Urban Syst 39:121–135
- Bone C, Altaweel M (2014) Modeling micro-scale ecological processes and emergent patterns of mountain pine beetle epidemics. Ecol Model 289:45–58
- Anderson T, Dragićević S (2015) An agent-based modeling approach to represent infestation dynamics of the emerald ash borer beetle. Ecol Inform 30:97–109
- Anderson T, Dragicevic S (2016) Geospatial pest-parasitoid agent based model for optimizing biological control of forest insect infestation. Ecol Model 337:310–329

- McLane AJ, Semeniuk C, McDermid GJ, Marceau DJ (2011) The role of agent-based models in wildlife ecology and management. Ecol Model 222(8):1544–1556
- Wilensky U, Rand W (2015) An introduction to agent-based modeling: modeling natural, social, and engineered complex systems with NetLogo. MIT Press, Massachusetts
- Pontius RG (2000) Quantification error versus location error in comparison of categorical maps. Photogramm Eng Remote Sens 66:1011–1016
- Ligmann-Zielinska A, Sun L (2010) Applying time-dependent variance-based global sensitivity analysis to represent the dynamics of an agent-based model of land use change. Int J Geogr Inf Sci 24(12):1829–1850
- 13. Brown DG, Page S, Riolo R, Zellner M, Rand W (2005) Path dependence and the validation of agent-based spatial models of land use. Int J Geogr Inf Sci 19(2):153–174
- Bone C, Johnson B, Nielsen-Pincus M, Sproles E, Bolte J (2014) A temporal variant-invariant validation approach for agent-based models of landscape dynamics. Trans GIS 18(2):161–182
- Straw NA, Williams DT, Kulinich O, Gninenko YI (2013) Distribution, impact and rate of spread of emerald ash borer Agrilus Planipennis (Coleoptera: Buprestidae) in the Moscow region of Russia. Forestry 86(5):515–522
- 16. Fahrner SJ, Lelito JP, Blaedow K, Heimpel GE, Aukema BH (2014) Factors affecting the flight capacity of tetrastichus planipennisi (hymenoptera: Eulophidae), a classical biological control agent of Agrilus Planipennis (Coleoptera: Buprestidae). Environ Entomol 43(6):1603–1612
- Cappaert D, McCullough DG, Poland TM, Siegert NW (2005) Emerald ash borer in North America: a research and regulatory challenge. Am Entomol 51(3):152–165
- 18. Lyons DB, Jones GC (2005) The biology and phenology of the emerald ash borer. In: Proceedings, 16th US Department of Agriculture interagency research forum on gypsy moth and other invasive species, pp 62–63
- McCullough DG, Poland TM, Anulewicz AC, Cullough DGMC (2009) Emerald ash borer (Coleoptera: Buprestidae) attraction to stressed or baited ash trees. Environ Entomol 38(6):1668–1679
- Rebek EJ, Herms DA, Smitley DR (2008) Interspecific variation in resistance to emerald ash borer (Coleoptera: Buprestidae) among north American and Asian ash (Fraxinus spp.) Environ Entomol 37(1):242–246
- Mercader RJ, Siegert NW, Liebhold AM, McCullough DG (2011) Influence of foraging behavior and host spatial distribution on the localized spread of the emerald ash borer, Agrilus Planipennis. Popul Ecol 53(2):271–285
- 22. Taylor RA, Poland TM, Bauer LS, Windell KN, Kautz JL (2007) Emerald ash borer flight estimates revised. In: Proceedings of the emerald ash borer/Asian longhorned beetle research and technology. FHTET-2007-04, US Department of Agriculture Forest Service, Forest Health Technology Enterprise Team, Morgantown, West Virginia
- 23. Siegert NW, McCullough DG, Liebhold AM, Telewski FW (2008) Dendrochronological reconstruction of the establishment and spread of emerald ash borer. In: Mastro V, Lance D, Reardon R, Parra G (eds). In: Proceedings, the emerald ash borer and asian longhorned beetle research and technology development meeting. Morgantown, West Virginia
- 24. Barlow LA, Cecile J, Bauch CT, Anand M (2014) Modelling interactions between forest pest invasions and human decisions regarding firewood transport restrictions. PLoS One 9(4):e90511
- 25. Muirhead JR, Leung B, Overdijk C, Kelly DW, Nandakumar K, Marchant KR, MacIsaac HJ (2006) Modelling local and long-distance dispersal of invasive emerald ash borer Agrilus Planipennis (Coleoptera) in North America. Divers Distrib 12(1):71–79
- 26. With KA (2002) The landscape ecology of invasive spread. Conserv Biol 16(5):1192-1203
- 27. Rutledge CE, Keena MA (2012) Mating frequency and fecundity in the emerald ash borer Agrilus Planipennis (Coleoptera: Buprestidae). Ann Entomol Soc Am 105(1):66–72
- 28. Jennings DE, Taylor PB, Duan JJ (2014) The mating and oviposition behavior of the invasive emerald ash borer (Agrilus Planipennis), with reference to the influence of host tree condition. J Pest Sci 87(1):71–78

- Duan JJ, Ulyshen MD, Bauer LS, Gould J, Van Driesche R (2010) Measuring the impact of biotic factors on populations of immature emerald ash borers (Coleoptera: Buprestidae). Environ Entomol 39(5):1513–1522
- 30. MacFarlane DW, Meyer SP (2005) Characteristics and distribution of potential ash tree hosts for emerald ash borer. For Ecol Manag 213(1):15–24
- 31. BenDor TK, Metcalf SS, Fontenot LE, Sangunett B, Hannon B (2006) Modeling the spread of the emerald ash borer. Ecol Model 197(1–2):221–236