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An agent-based modeling approach to represent infestation dynamics of the emerald ash borer beetle

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ABSTRACT

Agent-based modeling (ABM) is a bottom-up approach capable of operationalizing complex systems. The approach can be used to reproduce the spatio-temporal patterns in ecological processes such as insect infestation by representing individual dynamics and interactions between "agents" and their environment from which complex behavior emerges. The emerald ash borer (*Agrilus planipennis*; EAB) is an invasive species native to southeast Asia which has infested and killed millions of ash trees (*Fraxinus* sp.) across the eastern United States as well as Ontario and Quebec in Canada. Efforts to model the insect's behavior are ongoing, but current models are limited to approaches that do not address the complexity that emerges from the dynamics between individual beetles and their varying spatial environments. The objective of this study is to develop an ABM to represent the interactions of the EAB and the emerging spatio-temporal pattern of the insect spread. The model is implemented on real datasets from the Town of Oakville, Ontario, Canada from 2008 to 2010. Tree inventory and land use data acquired from the Town of Oakville were used to represent the spatial environment of the EAB agents. The EAB interactions are implemented in the model as subroutines, each representing a stage in the EAB life cycle using a temporal resolution of one day. Model verification was performed based on the literature documenting the life cycle processes of the EAB to represent EAB behavior. The model is calibrated using the rate of spread observed in the Town of Oakville from 2008 to 2009 and is validated using datasets delimiting the spatial extent and severity of EAB infestation in 2009. When comparing simulated and observed data, there is a 72% agreement for the locations of the infestation. This indicates that the developed ABM approach offers a model able to capture the complex behavior of EAB where both the spatial extent and severity of infestation are simulated realistically. The model generates insights about the underlying processes governing EAB behavior, highlights areas of uncertainty in modeling the complex spatio-temporal patterns of EAB infestation, and is a useful tool for forest and pest management.

1. Introduction

Invasive insect infestations, once established, can have widespread social, ecological, and economic impacts (Liebhold et al., 1995). Eradication of large scale infestations requires meeting a number of objectives including the delimitation to determine the extent of infestation, evaluation of eradication options, examination of the influence of geographical characteristics, communication with stakeholders and the public, and monitoring of insect population size and spread (Brockerhoff et al., 2010). Field surveys used to track and monitor infestations to meet these objectives can be time consuming and expensive, and can further damage host ecosystems (Ferretti, 1997), motivating the development of new techniques and tools to supplement eradication efforts. Models can be used as a tool to help forecast infestation, population size, and patterns of tree mortality.

Ecological processes such as insect infestation are complex. Not only are these processes composed of a large number of interacting individuals or components, but also the properties, behavior, and interactions of these individuals which determine the behavior of the system as a whole, vary from individual to individual, change over space and time, and adapt to changes in their environment or to maintain their individual needs (Grimm and Railsback, 2013; Levin, 2005). These factors result in non-linear behavior, meaning that the system properties are not simply the sum of the properties of the individuals that the system is composed of, making its overall behavior difficult to represent and model (Batty and Torrens, 2005). Early insect infestation models use linear, top-down, mathematical representations of infestations such as the gypsy moth (Campbell, 1967), the winter moth (Varley and Gradwell, 1968), the spruce budworm (Morris, 1963), and the western pine beetle (Stark and Dahlsten, 1970). The development of these models faced many challenges, particularly in capturing the complexity of species interactions that generate spatial patterns of spread and ultimately resulted in the failure to generate accurate predictions of pest population and trajectories (Liebhold, 1994).

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Individual-based ecology (IBE) is motivated by the idea that classical ecological models, still very important in studying ecological systems, usually ignore the concept that individuals are heterogeneous and adaptive (Grimm and Railsback, 2013; Parunak et al., 1998). For example, in contrast to the linear perspective that insect infestation population size is a result of birth and death rate, IBE considers that adaptation to maximize fitness and ensure survival and reproduction at an individual level may influence growth, reproduction, and death and thus population size (Grimm and Railsback, 2013). IBE employs bottom-up modeling approaches such as agent-based models (ABM) to represent spatio-temporal phenomena. ABMs are composed of a number of heterogeneous interacting agents within a virtual environment that are programmed using methods of artificial intelligence to make decisions, meet objectives, learn, and adapt their state and behavior in response to other agents and their environment (Castle and Crooks, 2006; McLane et al., 2011). The representation of individuals and their unique characteristics and interactions within their local environment allows for the generation of emergent, complex spatio-temporal behavior at the large scale. Moreover, the integration of geospatial data and geographic information systems (GIS) can further enrich the ability of the ABM to represent the dynamic phenomena within realistic landscapes (Sengupta and Sieber, 2007).

In the ecological modeling literature, ABM approaches have been used to represent complex ecological processes to offer a new perspective in contrast to top-down traditional modeling approaches and meet research objectives that cannot be addressed using classical methodologies (Parunak et al., 1998; Wilson, 1998). The earliest ABMs provided significant contribution to the establishment of IBE and ABM development. These models include: (1) the JABOWA model, developed to understand how forest succession dynamics is driven by local interactions (Botkin et al, 1972); (2) a fish cohort growth model which determines how the state of the initial distribution of the population determines the distribution of the population at the end of the growth period (DeAngelis et al., 1980); and (3) a model demonstrating the non-linearity in dragonfly clusters (Kaiser, 1975) where Kaiser (1975) indicates that it is not possible to determine the behavior of a system by only looking at the behavior of the system's components. The ABM approach has been used more recently in modeling insect infestation propagation to better understand harmful insect populations as climate change and increased global transportation threatens to open pathways and new environments for insect population establishment (Brockerhoff et al., 2010). The ABM approach has been applied to model mosquito populations (de Almeida, 2010), the potato moth (Rebaudo et al., 2010), the forest tent caterpillar (Babin-Fenske and Anand, 2011), and the mountain pine beetle (Bone and Altaweel, 2014; Perez and Dragićević, 2010, 2011).

Of recent concern to the sustainability of eastern North American forests is the emerald ash borer (EAB), *Agrilus planipennis*, an invasive wood-boring beetle species native to Asia (Muirhead et al, 2006). The EAB infestation was first identified in Michigan, US in 2002, although a new study reveals that the infestation could have been established as early as 1997 (Siegert et al., 2014). Shortly after its discovery in the US, EAB populations were identified in south-eastern Ontario, Canada and the infestation has since spread to over 30 counties (Tanis and McCullough, 2012). EAB targets and kills ash tree species, specifically green ash (*F. pennsylvannica*), black ash (*F. nigra*), white ash (*F. americana*) and blue ash (*F. quadrangulata*), which collectively make up a large portion of North American forests (Muirhead et al., 2006). The infestation's extensive ecological and economic impacts (Muirhead et al., 2006; Town of Oakville, 2008) have motivated a research agenda to better understand EAB biology (Lyons and Jones, 2009; Wang et al., 2010), life cycle (Bauer et al., 2003; Cappaert et al., 2005), behavior (de Groot et al., 2008; Lelito et al., 2009), future economic impact (Kovacs et al., 2010), climatic impacts (DeSantis et al., 2013), and patterns of infestation and dispersal via field surveying and model development (Mercader et al., 2009).

Current modeling approaches to EAB infestation include both mathematical models and spatially-explicit methodologies. Equation-based models of EAB infestation have been developed in order to represent the diffusion rates of EAB spread using ordinary differential equations (ODE) (Barlow et al., 2014), logistic regression (Siegert et al., 2010), and probabilistic modeling (Marshall et al., 2011; Muirhead et al., 2006). In response to the demand for models that consider how dispersal and behavior are influenced by spatial patterns within the landscape, geographic information systems (GIS) have been used in representing EAB spread in response to different landscape types (Bendor and Metcalf, 2006; Bendor et al, 2006; Mercader et al., 2011). Additionally, Prasad et al. (2009) developed a hybrid model using GIS and mathematical equations to generate EAB infestation in Ohio, Illinois. These models represent patterns of infestation on a large scale based on EAB preferences, but do not represent the individual. The existing models do not address concepts of complexity, heterogeneity, non-linearity, and the representation of small scale dynamics and interactions between pest and ash tree host, important considerations in representing complex insect infestation processes and spread.

The objective of this study is to develop an ABM of EAB infestation capable of representing individual pest-host dynamics at the micro-scale and generate EAB patterns of infestation over space and time at the macro-scale. This study determines how individual EAB host preference and decision making in their local spatial environment determines patterns of infestation in an urban setting and provides the levels of infestation severity. The proposed ABM of EAB infestation uses real-world geospatial datasets from the Town of Oakville, Ontario, Canada for 2008–2010.

2. EAB characteristics

2.1. EAB biology and life cycle

In order to represent the behavior of the EAB using an ABM, it is important to understand the biological characteristics of EAB with respect to its life cycle. The EAB life cycle takes place over the span of one year, although the life cycle may take up to two years to complete in healthy ash trees (Cappaert et al., 2005) and consists of four stages: (1) active larvae, (2) inactive larvae, (3) pupae, and (4) adulthood. Following emergence from their ash tree hosts in the months of late May through to early August, with peak emergence in June, EAB feed on ash tree leaves for about seven days to build up strength before mating. During feeding, female EAB beetles communicate with male EAB beetles through conspecific attraction, where female EAB release the compound macrocyclic lactone that attracts male EAB as mates (Bartelt et al., 2007). Once mated, female EAB will search for a suitable host and at maturation will begin to oviposit eggs. Female EAB will deposit their eggs on the surface of the ash tree, either in its crevices or cracks or just under the outer bark of the tree and will deposit on average 60–90 eggs within their lifetime, either individually or in groups (Jennings et al., 2014). Male EAB live on average for 13 days and female EAB life on average for 22–25 (Buck, 2015). Eggs hatch in approximately one week into active larvae, the longest stage of the EAB life cycle. Active larvae bore into the ash and feed on the ash phloem for twenty weeks from mid-June to October, causing a slow death to the tree (Wang et al., 2010). In late October, active larvae cease feeding and bore into the outer sapwood of the tree in preparation for overwintering. The larvae become inactive for roughly twenty weeks during the winter months. During this time, inactive larvae are highly susceptible to predation and environmental factors. The inactive larvae pupate in spring and begin to take the form of an adult beetle.

2.2. EAB host selection

EAB spread is governed by resource availability. EAB are not perfect foragers in that they do not choose the most suitable host every time,