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Modeling mountain pine beetle infestation with an agent-based approach at two spatial scales

Liliana Perez*, Suzana Dragicevic

Spatial Analysis and Modeling Laboratory, Department of Geography, Simon Fraser University, 8888 University Drive, Burnaby, BC, Canada V5A1S6

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ABSTRACT

Extensive outbreaks of tree-killing insects have been occurring in many parts of North America, including the province of British Columbia, raising concerns about the health of pine forest ecosystems. The dynamic phenomenon of mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins, infestation outbreaks is an inherent spatial and temporal complex process. Agent-based modeling (ABM) facilitates simulating spatial interactions that describe the ecological context in which insect populations spread. The main objective of this study was to develop a model of the MPB forest infestation dynamics. This spatially explicit model integrates geographic information systems (GISs) and ABM to simulate MPB outbreaks at the *tree* and *landscape* scales, providing spatiotemporal information of annual distribution and patterns of MPB outbreaks. This prototype was implemented with geographic data generated from aerial overview surveys carried out by the B.C. Ministry of Forests and Range, for the study site in Kamloops, Canada. Results show the direct influence that vigorous forest stands and trees have on higher breeding rates, and therefore in the MPB population increment at a *tree* scale, in a period of 5 years. The simulation results at the *landscape* level help to determine the most probable locations of future MPB infestations in a time frame of 10 years.

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Software availability

Name of the Model: Mountain Pine Beetle Simulation Developer: Liliana Perez, Spatial Analysis and Modeling Laboratory, Department of Geography, Simon Fraser University.

Software Required: ArcGIS 9.3, Repast Simphony (a free and open source agent-based modeling toolkit).

Program Language: JAVA

Availability: free download from http://repast.sourceforge.net/download.html

Code Availability: The source code for this prototype is still under further development for another study and would potentially be available in near future.

1. Introduction

Assessment and monitoring of forest health represents a key point for environmental policy and for the management of environmental resources (Ferretti, 1997; Allen, 2003). Likewise, as with any other environmental resource, proper management of forests should be based on the knowledge of their status as well as on the

recognition of changes and disturbances in their condition. As the importance of spatial structures and processes in forest ecosystem dynamics is well recognized (Malanson and Armstrong, 1996), and for this reason it is essential to study how and why geographic space affects and is affected by disturbance agents in forest environments.

Disturbances, both human-induced and natural, shape forest systems by influencing their composition, structure, and functional processes. Among the natural disturbances, insect outbreaks are considered to have one of the greatest effects on Canadian forests (Taylor and Carroll, 2003). In order to learn about the spatial dynamics product of insect colonies or swarms interaction with their environment, it is important to acknowledge that their behaviour is robust, flexible, adaptive, self-organized, intuitive, and scalable. Therefore, it is necessary to use an approach that allows exploring the underlying interactions between insects and host trees, as well as the emergent phenomenon resulting from the ongoing relationships. Complex systems theory offers an advantageous framework for spatiotemporal modeling of forest epidemics phenomena.

Complex forest ecosystems and the dynamics taking place between host trees and insects within them at both the tree level and landscape levels, form part of a complex geographic process that requires extensive theoretical and practical approaches to provide insights for understanding and controlling the impacts of

^{*} Corresponding author. Tel.: +1 778 7825628; fax: +1 778 7825841. E-mail addresses: lperezca@sfu.ca (L. Perez), suzanad@sfu.ca (S. Dragicevic).

insect outbreaks. In order to comprehend and represent the internal organization of such forest ecosystems and interactions caused by insect outbreaks, bottom-up simulation models such as agent-based models (ABMs) can be used. Likewise, geographic information systems (GISs) provide a computational platform to handle the storage, manipulation and visualization of large volumes of geographic information regarding the phenomena under study. Although GISs are particularly useful for representing model input and output of a geospatial nature, GISs are not well suited to model dynamic phenomena due to their inability to adequately represent spatial changes over time. For that reason, it is important to explore the opportunity of linking (through coupling or integration) a GIS with ABMs.

Agent-based approach has emerged from complex systems theory as a valuable tool in the exploration of space–time dynamics within environmental systems since it allows studying the relationships between micro-level individual actions and the emergent macro-level phenomena (Gimblett, 2002; Bousquet and Le Page, 2004). This type of spatiotemporal modeling approach is based on individual agents that behave or make decisions in a certain way that affects their environment. This ability makes it possible to simulate how the agents' behaviour and interaction between each other and their environment produce emerging global patterns over time (Parker et al., 2003).

The emerging characteristics from often indirect interactions of individuals that constitute forest ecosystems are simple compared to the complexity of the entire system. Self-organization and emergence properties of forest ecosystems can be explored in forestry studies through an ABM approach to model the interaction between groups of agents and resource dynamics, emphasizing how agents affect resources and the exchanges of information and agreements among these agents (Ekbia and Reynolds, 2006). Abundant research exists regarding the development and use of ABMs have been built for experimenting and exploring geographical phenomena such as land use and land cover change, and specifically linking them to GIS has become one important trend for the study of spatial development of these phenomena (Gimblett, 2002; Benenson and Torrens, 2004; Parker, 2005). Other models deal with the assessment of the influence of demographic changes in deforestation and its impact on forest ecology, stream hydrology and changes in water availability (Bithell and Brasington, 2009; Smajgl et al., 2009). Likewise, ABMs have been created to deal with the design of regulations related to the purchase of environmental services from agriculture as well as policies for water access rights (Smajgl et al., 2009; Viaggi et al., 2009). Another example of a geographic ABM application is the development of a multi-agent model to facilitate the sustainable management of boat traffic in the Saguenay-St. Lawrence Marine Park and Marine Protected Area in Quebec (Anwar et al., 2007).

The objective of this study was to develop an integrated agentbased GIS capable of capturing, representing and examining mountain pine beetle populations' at two spatial scales. MPB interactions were modeled at the tree scale and landscape scale to represent how MPB outbreaks start at micro-level and create patterns of infestation that affects forest health at macro scales. Specifically, this study analyzed how insect behaviour and environmental conditions influence the distribution of attacking insect populations, their preferences of trees to attack. The approach proposed in this study depicts MPB behaviour in order to attain a better understanding of the insect's adaptability to new landscapes and the nature of severe attacks of MPB on lodgepole pine, Pinus contorta, forests. MPB outbreaks represent a catastrophic natural disaster that triggers widespread mortality of lodgepole pine, one of the most abundant commercial tree species in British Columbia, Canada. This study contributed to determine the emergence of spatial patterns as product of this phenomenon, in order to predict forest disturbances of MPB infestation.

2. Existing modeling approaches of MPB infestations

Various methods have been proposed to model spatial distribution of mountain pine beetle populations and attack patterns. To monitor forest health conditions over space and time, remote sensing methods provide information for identifying forest landscapes at risk to medium- and long-term changes. Detection and mapping of attacked trees makes it possible to plan mitigation activities, and can also aid in parameterizing models of epidemic outbreaks designed to reduce future hazards and impacts on forests. Refining image processing and classification procedures have permitted reliable early detection of a spreading mountain pine beetle infestation using digitally converted multispectral and normal colour aerial photography (Roberts et al., 2003). For example, QuickBird satellite imagery were used to characterize stands' attributes to determine the likelihood of sustaining redattack damage resulting from an infestation of MPB in an area of British Columbia that has traditionally been outside the beetle's biological range (Coops et al., 2006). In addition, Landsat imagery was used to predict red-attack damage with 86% accuracy reported (Wulder et al., 2006). The outcomes of these studies indicate that for particular sites with mixed forest stands and variable terrain, remotely sensed and ancillary spatial data can be combined to create a mountain pine beetle red-attack likelihood surface that accurately identifies damaged forest stands at a landscape scale. Point data generated from global positioning system (GPS) helicopter surveys have been used to determine the location and magnitude of mountain pine beetle outbreaks in forest landscapes of British Columbia (Nelson et al., 2006). Fuzzy sets, GISs and high resolution multispectral aerial photographs were used to derive susceptibility maps of pine beetle infestations (Bone et al., 2005).

Parallel to remote sensing methods, various equation-based models (EBM) have been created to model MPB population distributions. EBM consist of a set of equations, and its implementation involves evaluating them; such models of differential equations have been proved to be a useful and practical form of mathematical models since the days before computers due to their extremely rapidly execution using numerical integration.

Different equation-based simulations range from models based on pheromone ecology at the stand level (Logan et al., 1998) to the atmospheric models of long-range dispersal across landscapes (Carroll et al., 2003). To simulate mountain pine beetle population dynamics, a population dynamic model was designed to operate in a 1 ha area of pure lodgepole pine (Safranyik et al., 1999). This MPB model was enhanced by adding a spatial component through the use of SELES software (Riel et al., 2003). The model SELES-MPB simulates beetle impacts on landscapes making use of climate and topography data corresponding to the zone of study, keeping the 1 ha spatial resolution. Although different approaches have been used to depict, predict, assess and manage MPB outbreaks, equation-based models are generally used to model these phenomena. These models provided important conceptual and mechanistic insights into the formation and distribution of the MPB outbreaks. However, most of them have been implemented using mathematic equations without taking into account some of the spatial dynamics that influence the phenomenon.

In terms of describing spatiotemporal dynamics of MPB outbreaks, Markov Chain approach was used to describe the dispersal patterns of the beetle and the effect of dispersal on infestation, and to identify the time series hotspots and coldspots of outbreaks and the conditions that contribute to the occurrence of these spots (Lewis and He, 2006). Spatial distribution of MPB has

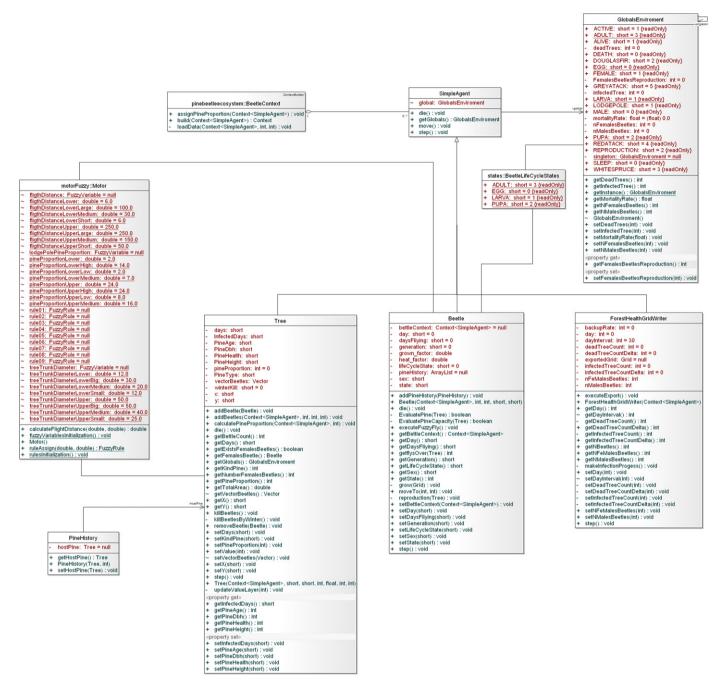


Fig. 1. UML class diagram of the agent-based model simulation of MPB infestation.

also been studied through the application of a range of spatial statistic methods (e.g. *K*-means cluster analysis) (Campbell et al., 2007). A GIS-based cellular automata (CA) model was proposed to simulate spatiotemporal dynamics of MPB attacks to determine the distribution of tree mortality (Bone et al., 2006). In addition, the potential of GIS-CA modeling approach was used for evaluating the complexities of forest management practices (Bone et al., 2007). However, complex spatiotemporal interactions happening between MPB attacks at tree scale and their impact at larger scales have not been yet well captured.

It is necessary to conceptualize the insects as autonomous agents that interact and make decisions based on the condition of the environment at the local – *tree* – scale and also to determine how forest dynamics are driven by these infestations at a larger –

landscape – scale. The spatial dynamics of mountain pine beetle exhibit a behaviour that is suitable for simulating with ABMs. These models offer significant benefits over equation-based models in respect to the underlying structure of a model and the ability to provide a realistic and comprehensible representation of a system (Parunak et al., 1998). Likewise, ABMs appear to be especially suitable for processes that involve individuals such as MPB that exhibit certain intelligence that is manifested through making spatial decisions. Agent-based geocomputational model can be used to simulate spatial interactions in environmental processes in order to understand changes in disturbed landscapes. These simulation models provide norms for comparison with real behaviour, and the differences between model and reality provide the basis for improvement of our understanding of the general

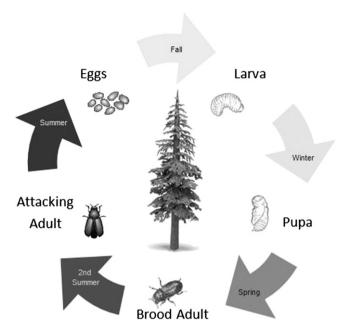


Fig. 2. Mountain pine beetle life cycle.

principles encoded into the ABMs. Therefore the main goal of this study was to propose a MPB infestation model based on complexity theory using an agent-based approach and geographic information system (GIS) to evaluate the emerging behaviours from the interaction between MPB populations at two spatial scales.

3. Methods

The GIS-AB model and the prototype tool was developed in this study to implement the simulation of MPB infestation over forest landscapes, consisting mainly of lodgepole pine. This model permitted to acquire understanding on how local behaviours at the local – *tree* scale influence global dynamics over time, and to incorporate the elements of complex systems theory into a forest infestation model. The *tree* scale as well as the *landscape* scale model consisted of two types of agents, *Beetle agent* and *Tree agent* that permit the representation of the mountain pine beetle behaviour and the tree health evolution respectively, as well as their interaction and mutual influence within the dynamic process of the forest infestation phenomenon. The conceptual model representation is synthesized in an UML class diagram that shows all the classes of the model with their attributes, functions and their relationships (Fig. 1). Subsequent sub-sections explain the emerging, dispersal and attacking behaviour of beetles, as well as the survival rate of MPB populations growing under different climatic circumstances, and their influences in the health of the lodgepole pine forest ecosystem.

3.1. Agents – tree scale

3.1.1. Agent beetle

The behaviour of an agent type beetle was portrayed by a series of rules or steps that it had to follow in order to decide where to fly within the forest ecosystem and also to select the tree to attack and brood. Mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is a small (0.5 cm) black beetle, which typically kills host trees in order to successfully reproduce (Logan et al., 1998). The beetle is a naturally occurring part of the lodgepole pine forest ecology as it exists at low population levels in all lodgepole pine forests (Safranyik and Carroll, 2006). Their beetle larvae feed on the inner bark of mature pine trees, girdling the trees and killing them (Cole, 1973). The host trees must be sufficiently large and have thick inner bark for the beetles to

Table 1Parameters of order of emergence within the beetle population.

Emergence order (initial attack)	Size	Attribute that determines the size (DBH)
First	Big	43-50 cm
Second	Medium	23-42 cm
Third	Small	12–22 cm

Table 2Fuzzy membership functions for flying distance of mountain pine beetles in a forest landscape. The membership function describes the membership of the different variable in the fuzzy set.

Fuzzy membership functions to determine flying distance of MPB			
Variable	Fuzzy set description	membership function	Range
Flying distance Flying distance Flying distance	Short Medium Long	Triangle Triangle Triangle	6–50 m 30–150 m 100–250 m

Fuzzy membership functions to determine flying distance of MPB based on DBH

Variable	Fuzzy set description	membership function	Range
DBH	Small	Linear	12-25 cm
DBH	Medium	Linear	20-40 cm
DBH	Big	Linear	30-50 cm
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Note: this is a Euclidian Distance, measured from the centre of the cell that represents one tree where the mountain pine beetle is located.

Fuzzy membership functions to determine flying distance of MPB based on lodgepole pine proportion in the forest landscape

Variable	Fuzzy set description	membership function	Range
Lodgepole pine proportion	Low	Linear	2–8 trees (cells)
Lodgepole pine proportion	Medium	Linear	7-16 trees (cells)
Lodgepole pine proportion	High	Linear	14-24 trees (cells)

successfully reproduce and reach epidemic populations (Amman and Cole, 1983). When food supplies over a sufficient area and climatic conditions over a sufficient period of time are favourable, the small endemic populations undergo explosive growth resulting in a beetle epidemic (Amman, 1982a,b). Epidemics end when the desirable food supply of large lodgepole pine trees is no longer continuous enough to support the population or when climatic conditions become unfavourable for the beetle. Climatically ended epidemics will reoccur after a period of favourable weather allows populations to rebuild (Heavilin et al., 2005).

In order to present the forest infestation phenomenon, multiple raster based GIS data sets were used to represent continuous forest landscape in several GIS layers. The beetles characterized as autonomous agents were displayed in the model simulation as a GIS layer with discrete data points dispersed over the forest landscape. Each cell within the GIS raster data layer of the forest represented one tree. Many beetles that form a colony of beetles coexisted within the same cell, and were able to stay and initiate the feeding and reproduction process based on a set of rules that permitted them to stay in a tree or fly to another tree within the simulation environment. Agents representing mountain pine beetle had a unique attribute that allowed discriminating the beetle population by gender; therefore the simulation involved identification of female and male beetles, with a male:female sex ratio 1:2 (Safranyik and Carroll, 2006).

3.1.1.1. Agent beetle attack behaviour - emergence and movement. MPB leave their currently infested trees in late July to early August in search of a new tree to attack (Fig. 2). Females first emerge and fly varying distances in search of a new host tree. The initial flight by newly emerged mountain pine beetles tends to disperse them widely throughout the forest. Even in the presence of aggregation pheromones, the majority of beetles may disperse out of a stand (Safranyik et al., 1999). In the simulation, the initial attack behaviour was modeled using ABM where the rule for the first beetles to emerge from the dead trees was based on the query of the agent gender attribute. Although female agent beetles should emerge first, not all emerge at the same time. In this prototype, each beetle agent had to query the Diameter at Breast Height (DBH) of the tree that it inhabits at the moment right before the emergence. Therefore, the first females to emerge were living or located in large trees, followed by female beetles that are located in medium trees, and finally the female beetles placed in small trees. Table 1 presents the parameters of emergence order within the mountain pine beetle population. Large female beetles tend to emerge earlier than small females, and the development of the beetles depends on the size (DBH) of the trees (Safranvik and Carroll, 2006). The emergence of the male beetles is initiated only when at least one of the female beetles has located and selected a new host.

After the emergence has been initiated, the dispersal or movement of the new adults away from natal hibernation sites starts (Raffa et al., 1997). Newly emerged beetle adults tend to be positive phototactic – i.e., moving themselves towards a source of light when leaving a breeding site (Raffa et al., 1997). The movement during the initial flight of newly emerged mountain pine beetles is fundamentally driven by host stimuli (Shepherd, 1966). This prototype models the MPB movement behaviour through random displacements in one of eight directions (northwest, north, northeast, west, east, southwest, south, and southeast) towards mature host

Table 3Parameters evaluated as a first step to select the host tree and then establish the amount of eggs to be laid per tree.

Health state of the tree	Type of tree	Tree age [years old]	DBH [cm]	Number of MPB flights ^a	MPB decision	Number of MPB eggs	State of the agent "Beetle" after laying the eggs
Dead	_	_	_	_	Leave the tree	_	_
Alive	Douglas-fir or white spruce	-	-	-	Leave the tree	-	_
Alive	Lodgepole pine	80-140	40-49	-	Stay in the tree	60-80	Dead
Alive	Lodgepole pine	61-79	23-39	>1	Stay in the tree	30-60	Dead
Alive	Lodgepole pine	20-60	14-22	>2	Stay in the tree	≤30	Alive

^a The number of MPB flights represent the number of additional times that an agent beetle is allow to fly to attack and/or laid more eggs in a different tree, before it dies.

trees with high values of DBH. The distances that the agents beetle fly are non-deterministically specified by a number of fuzzy set rules.

3.1.1.2. Agent beetle attack behaviour - determining the flying distances for dispersal. During dispersal most beetles fly several meters below tree crowns but above the undergrowth (Schmitz et al., 1980; Safranyik et al., 1989). The direction of this flight is normally downwind until beetles encounter an attractive host tree (Safranyik and Carroll, 2006). Beetles that do not disperse from the stand in which they develop usually locate suitable host trees within two days of emergence, but are capable of searching for several days (Safranyik et al., 1992). Studies have established that the minimum distance for a beetle to travel in order to find a suitable tree is 6 m (Safranyik and Carroll, 2006). When beetles fly through a lodgepole pine stand the maximum distances that a MPB have to fly can reach up to 50 m (Safranyik et al., 1999). However, some unpredictable flight patterns arise due to wind and terrain influences. MPB often disperses within a small radius into nearby forests but can travel several kilometres with the appropriate wind conditions (Berryman et al., 1989). Although shorter dispersal flights allow greater investment of energy in reproduction, longer flights enable beetles to locate habitats with higher quality host trees (Elkin and Reid, 2005). In order to define the flying distance of each agent beetle without any bias or deterministic decision, the agent beetle decides how many meters to fly based on a set of rules that make use of fuzzy logic to establish some ranges of distances for the agent to make a decision. Likewise, the model captures the influence of wind in the flying distances by allowing the agent beetle to fly ranges from 6 m up to 250 m.

The decision rules for determining the flying distance were created based on the fuzzification – process of transforming crisp values into grades of membership for linguistic terms of fuzzy sets (Tso and Mather, 2001) of three variables that made possible to come to a decision: 1) flying distance, 2) DBH, and 3) lodgepole proportion, as presented in Table 2. The first variable represents the decision that has to be made in relation to the last two variables. The last two variables were chosen because they represent the ideal source of food that can be identified by the beetle agents. Numerous authors have reported tree diameter as a landing stimulus (Hopping and Beall, 1948; Cole and Amman, 1969), and that large, dark silhouettes (Shepherd, 1966) and vertically oriented cylinders, like the lodgepole pine, are attractive to beetles (Billings et al., 1976). Likewise, other studies suggest that beetles land at random, during the first flight, on larger trees due to their larger surface area (Burnell, 1977; Hynum and Berryman, 1980).

Making use of the fuzzy variables the agents' type beetle reached a decision regarding the distance to fly in order to look for a suitable host. The decision rules were:

Rule 1:

If LodgepolePineProportion is High and DBH is Big

Then FlyingDistance is Short

Rule 2:

If LodgepolePineProportion is High and DBH is Medium

Then FlyingDistance is Short

Rule 3:

If LodgepolePineProportion is High and DBH is Small

Then FlyingDistance is Short

Rule 4:

If LodgepolePineProportion is Medium and DBH is Big

Then FlyingDistance is Short

Rule 5

If LodgepolePineProportion is Medium and DBH is Medium

 \pmb{Then} FlyingDistance is Medium

Rule 6:

If LodgepolePineProportion is Medium and DBH is Small

Then FlyingDistance is Medium

Rule 7:

If LodgepolePineProportion is Low and DBH is Big

Then FlyingDistance is Medium

Rule 8:

If LodgepolePineProportion is Low and DBH is Medium Then FlyingDistance is Long

Rule 9:

If LodgepolePineProportion is Low and DBH is Small Then FlyingDistance is Long

3.1.1.3. Agent beetle attack behaviour – selecting the host. After pioneer beetles land on a potential host tree, the agents initiate the process of evaluation to determine if the actual tree fulfill their requirements of food and allows them to breed. This selection process was based on four parameters: 1) health state of the tree, 2) type of tree, 3) tree age and 4) DBH. The first rule to select the host is evaluated consulting the characteristics of each tree, after which point a specific decision is reached. Table 3 shows the detailed rules based on these four parameters.

Once the agent beetle makes the decision to stay in the tree, the second rule was applied to find out if the agent is allowed to stay in the tree to feed and breed, or if it had to leave the tree due to overcrowding. To minimize the effects of intraspecific competition, the mountain pine beetle has evolved a mechanism to terminate host colonization on individual trees at or near optimum attack densities, approximately 60 attacks per m² of bark, using chemical cues (Raffa and Berryman, 1983). The second rule that finally permit the agent to determine if it is allowed to stay in the tree was based on a calculation performed by the agent type tree, which provides the agent beetle with information about how many other beetles are per 1 m². The decision is taken based on the next condition (second rule):

If the population density of beetle agents <60 per 1 m²

Then the agent beetle is able to stay in the tree and initiate its feeding and reproduction cycle

If the population density of beetle agents >60 per 1 m²

Then the agent beetle has to fly again to find a suitable tree to initiate its feeding and reproduction cycle

The *Attack Behaviour* is completed once all the ABM rules are performed for a single iteration, which is equivalent to the time span of one day. This time length was used with the purpose of capturing and understanding in detail the behaviour during the three weeks of emergence and attack of the insect. In the same way, the use of this temporal scale permit to follow-up the life cycle of the agents' type beetle and know approximately when each beetle emerges from a tree (Fig. 2).

3.1.1.4. Agent beetle – life cycle simulation. Once a new host is selected, female beetles begin to construct a gallery and in the process instigate a mass attack. A mass attack involves a complex synergism of host-produced (kairomones) and beetle-produced (pheromones) volatile chemicals (Amman, 1982a,b) as the female bores through the bark and releases a chemical compound that attracts male beetles to the same tree. The tree's defensive mechanisms are overcome once a sufficient number of MPB have attacked the tree (Powell et al., 1998). The aggregation pheromones result in a mass attack and the process is normally completed in one to two days on an individual tree. In trees where attack densities are low, females may abandon their egg galleries, even after laying a complement of their eggs, and search for another tree to lay more eggs (Amman, 1982a,b). This behaviour was captured by the AB model by allowing the beetles to fly more than one time when attacking young

Table 4Different stages of the MPB life cycle within 365 days, from the egg to the attacking adult

Days	Life cycle stage
1	Eggs
+7	Hatch
+1	Larva
+260	Pupa
+(83-96)	Brood adult – attacking adult

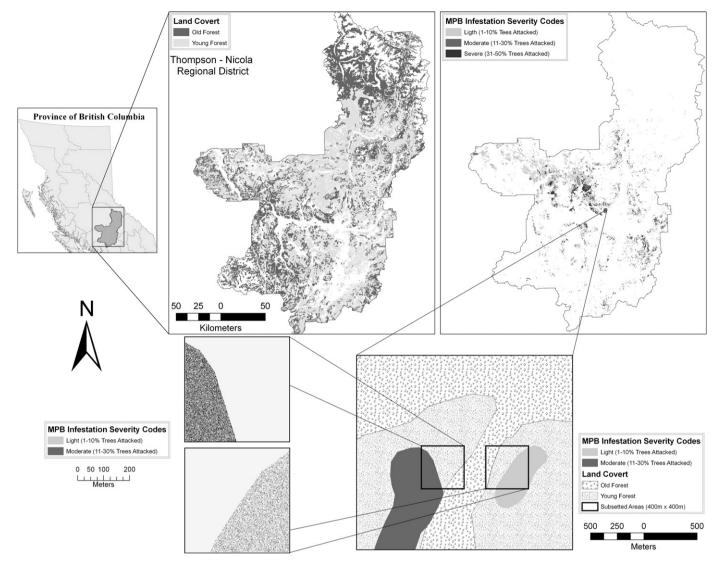


Fig. 3. Location of study area – Thompson-Nicola Regional District, British Columbia, Canada. The subset areas (three lower windows) were used to test the model at two different spatial scales.

trees, which usually have small DBH. Table 3 also presents the parameters to select a host tree and establish the amount of eggs to be laid per tree. However, an agent beetle could not wander more than thirty days looking for a tree to lay and/or mate. If after this period of time the agent was not able to find a suitable tree to feed and brood, the agent die.

Inside the galleries of newly attacked trees, eggs are laid and normally hatch within a week or so following deposition and young larvae commence feeding immediately. Larvae often reach third or early fourth instars before temperatures become too low for continued development. Larvae resume feeding in the spring once temperatures are sufficiently high at which point they complete their development and transform to pupae by June. New adults occur during late June to mid July (Fig. 2). Within the host tree, low temperature is often the largest single source of mortality in mountain pine beetle populations (Safranyik et al., 1999).

In order to simulate the life cycle of mountain pine beetles the AB model made use of additional rules to ensure the evolution of beetle agents' population, which are explained as follows:

- a) Once the beetle agents were within a tree, they had to query the age of the tree in order to establish the number of eggs to be laid. The number of eggs was randomly generated once the age of the tree was stated. This random number of eggs was allocated within a range given in Table 3.
- b) After laying the eggs (which constituted the next generation of agents' type beetle), the parent agents die, with the exception of those agents that were attacking younger trees (20–60 years old). These agents were allowed to fly again and look for another tree to lay more eggs. This rule was created with the purpose to simulate newly discovered behaviours on MPB such as

- attacking younger pines instead of only attacking mature pines (Maclauchlan, 2006).
- c) Once the new agents were created, the gender attribute was assigned maintaining the nature balanced observed in forest ecosystems, male:female sex ratio (1:2).
- d) To follow the natural process of MPB life cycle, the evolution of the eggs to become an adult beetle was captured in a time period between 352 and 365 days. This range of time was randomly selected within the simulation, and it allowed accounting for those beetles that emerge early from the tree as well as for those that emerge exactly one year after being born. Different stages well as accessible as an attribute of each agent beetle from the moment it is an egg to the moment it becomes a brood adult. Table 4 presents the mountain pine beetle life cycle stages, through 365 days.
- e) Before reaching adulthood the agents beetle may be threatened by cold weather. MPB experience high levels of mortality each winter when low temperatures have detrimental effects on the developing stages of the beetles. During moderate winters, it is common to have a mortality level of 80% due to low temperatures. However, under a severe winter the mortality rate may increase up to 90% of MPB (Carroll et al., 2003; Safranyik and Carroll, 2006).
- f) The process of emergence, flying, host selection and brood is reinitiated once the agent reached its adulthood.

3.1.2. Agent tree

The agent type representing a tree was depicted by the continuous surface of cells in a raster GIS database layer where each cell represents a single tree. This type of agent has its own thread of control, allowing it to identify its state and attributes

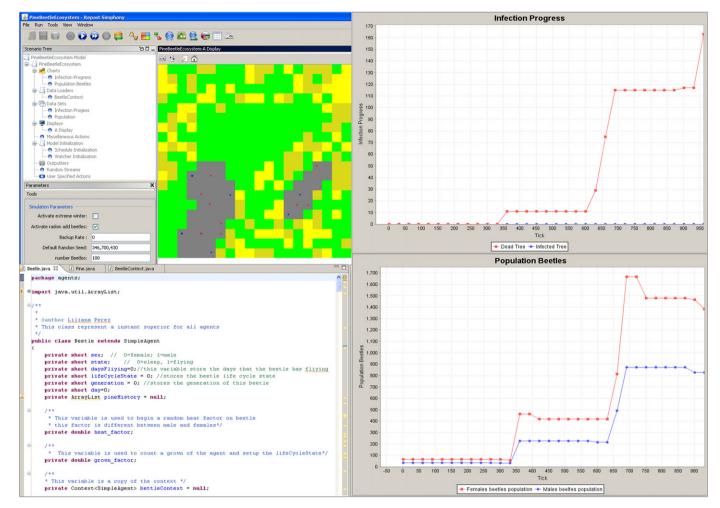


Fig. 4. Graphic User Interface developed using RepastS and Eclipse IDE software, with 2D display (dots represent Beetle Agents, different shades in the landscape represent different types of Tree Agents) and charts of mountain pine beetle simulations.

and modify its behaviour. Agents tree have also individual rules and goals, making them appear like active objects with initiative. These autonomous entities observe their own set of internal responsibilities and are capable of sending messages to the agents' type beetle. These messages inform the agents of a particular event like the tree carrying capacity. The attributes of the tree (type, age, height, health state, and DBH) provide important input information to the agent-based model. The first calculation performed by the tree agents is the total bole surface area (S_t) in order to estimate the beetle population density per tree:

$$S_t = 0.3455 + 1.9708 \times D \times H \tag{1}$$

where the constants are regression coefficients calculated by Safranyik (1988); H is total tree height (m) and D is the tree diameter (m) at 1.37 m (Safranyik et al., 1999). After computing the total bole surface area the agent tree inquires how many agents beetle are located within it and proceed to evaluate the agent beetle population density per 1 m². The agent tree also updates its health state after the initial attack of the mountain pine beetle, consecutively trough each year going from a green attack stage (once the tree is killed, but still with green foliage), to red-attack stage (approximately twelve months after the green attacked) and finally to gray-attack stage (approximately three years after being attacked) (Wulder et al., 2006).

3.2. Agents - landscape scale

At a *landscape* scale the *Agent Beetle* maintain its behaviour; however at this scale this agent does not represent an individual beetle but a group of insects that occupy a tree. Each group of insects has the same goal, which is to look for the most suitable forest stand. The *Agent Tree* does not represent a unique tree, but a forest stand with attributes of type (tree species), average age, average height, average DBH and tree health status information.

While most of the *tree* scale methods are kept, modifications and simplifications were necessary to portray the MPB infestation at a different spatial resolution. First, each group of agents lack the gender attribute, so they emerge only

based on the DBH information obtain from each forest stand. The movement and flying distances of insect groups are determined using only the fuzzy rule for flying long distances (Table 2) in order to account for the influence of the winds in the spatial spread of MPB swarms. Host selection behaviour considers the evaluation of the same four variables: 1) health state of the stand, 2) type of stand, 3) average age and 4) average DBH. At the landscape scale there is no rule to avoid intraspecific competition based on the number of beetle agents per m², but all the beetle groups cannot attack the same stand at a time. The MPB life cycle behaviour at this scale is not simulated; it is assumed that the number of MPB swarms grows exponentially every year. However, based on the winter temperatures (high or low) these populations decrease due to the mortality rates as a result of the changes in temperature.

4. Model implementation and simulation results

4.1. Model input data

For implementation purposes of the proposed forest MPB infestation model, simulations of the insect outbreak in a forest ecosystem were generated to apply the methodological framework. These simulations correspond to two different scenarios: 1) *Scenario 1 – Landscape Scale Scenario*: represents a study area of 4 km², with a course spatial resolution of 100 m \times 100 m cell size, and 2) *Scenario 2 – Tree Scale Scenario*: represents two subset study areas, each of 400 m \times 400 m, with fine resolution of 1 m \times 1 m, where each raster cell represents a single tree. These two scenarios depict two different spatial scales at which the MPB phenomenon occurs. The study area used for this study represents

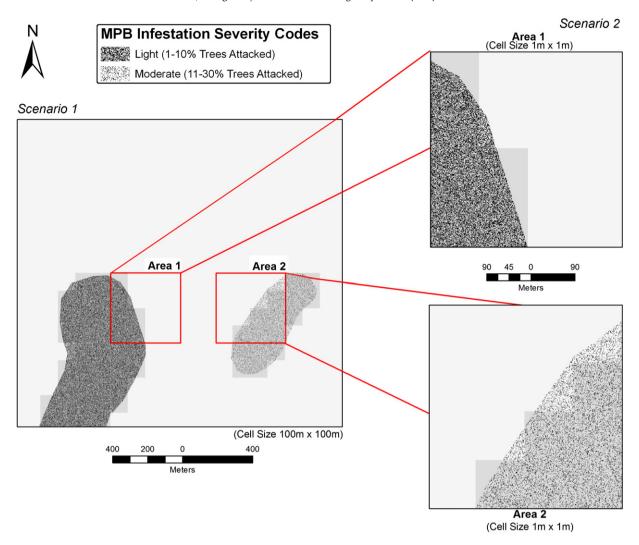


Fig. 5. Localization of *Scenario 2* two subset areas; each area had previous MPB attack. For the selected Area (1) the pest severity code reported by BC Ministry of Forest and Range is Moderate (11–30% attack) and for the selected Area (2) the pest severity code is Light (1–10% attack). Spatial resolution of *Landscape Scale Scenario* (1) is 100 m \times 100 m, and 1 m \times 1 m for *Tree Scale Scenario* (2). Blocky light shade shows the representation of the same areas at a coarser resolution (100 m \times 100 m).

a forest landscape of the Kamloops Forest District in the central interior of British Columbia (Fig. 3), which contains a high concentration of dead trees due to a number of previous MPB infestations. The forest consists of three different species of trees: 1) Lodgepole Pine, *Pinus contorta*, which dominates the landscape; 2) Douglas-fir, *Pseudotsuga menziesii*, with relatively smaller proportions and 3) White Spruce, *Picea glauca*, distributed throughout the landscape.

For the simulations, five different raster GIS data sets were used in order to feed the model with information regarding tree species, health state, diameter at breast height (DBH), tree age, and tree height. Forest cover attributes – i.e. tree species, age and height and georefenced data sets were obtained from GeoBC (GeoBC, 2008). The vector format file from GeoBC was converted into a raster format creating two different sets of raster files each one with different cell sizes (1 m \times 1 m and 100 m \times 100 m). In the absence of DBH values, these were randomly assigned based on tree age (Reid et al., 2004). Trees between twenty and sixty years old were assigned DBH between 14 and 22 cm; trees between sixty-one and seventy-nine years old were assigned DBH between 23 and 39 cm; trees between eighty and hundred and forty years old were assigned DBH between 40 and 49 cm (Roberts et al., 2003). The handling of the GIS data sets was carried out using ArcGIS 9.3.

The chosen study areas were extracted from the B.C. Ministry of Forests and Range data sets created by means of aerial overview surveys (Fig. 3). These surveys record only red trees representing recent damage that is visible from the air and tend to over-estimate the numbers of trees killed particularly as the scale decreases. The dataset used in this study was mapped at 1:250,000 (B.C. Ministry of Forests and Range, 2004). The aerial overview severity codes due to the widespread mountain pine beetle outbreak include five classes that describe the severity of the MPB attack over forest stands: Trace (T) (<1% attack), Light (L) (1–10% attack), Moderate (M) (11–30% attack), Severe (S) (31–50% attack) and Very Severe (V) (>50% attack) (Koot, 1997). Two patches of dead lodgepole pine that can be observed in Fig. 5, acted as the seed trees area from which MPB disperse and search for new host trees to attack.

4.2. Simulation toolkits and user interface developed

To implement the designed agent-based modeling approach, RepastS (Argonne National Laboratory, 2008) and its Java libraries were used. ArcGIS software (ESRI, 2008) and GIS libraries of Geo-Tools (Codehaus Foundation, 2006) were employed to make possible the integration of the GIS with ABM. In addition, the NRC FuzzyJ toolbox (National Research Council of Canada's Institute for

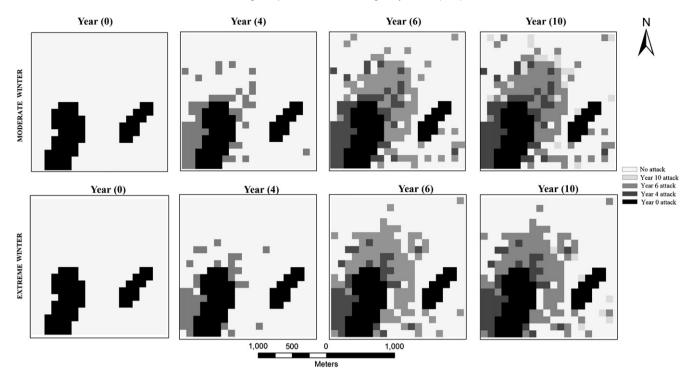


Fig. 6. Ten-year simulation output of the integrated GIS-ABM used to understand and predict spatial and temporal evolution of MPB infestation at a spatial resolution of $100 \text{ m} \times 100 \text{ m}$.

Information Technology, 2006) for the implementation of the fuzzy rules in Java was sourced for RepastS integration.

Repast Simphony (RepastS) serves as simulation toolkit to develop and execute AB models for applications such as forest infestations simulation within an integrated two-dimensional raster GIS environment. The implementation of the proposed model was accomplished using Java language. The programming code was written to execute the model by introducing a population of MPB agents located in a geographic space with defined spatial interactions among them, as well as with the forest environment. Thus, each agent beetle had a spatial location and was able to identify and move towards the spatial location of trees in the forest.

The graphic user interface (GUI) was created to facilitate model execution through choice of parameters as well as visual display of generated simulations (Fig. 4). GUI permits visualization from beetle agents interacting in space, display of histograms and charts, as well as various simulated scenarios all depicting the progress of the infestation.

4.3. Implementation

The implementation of the AB model integrated with GIS was made using two scenarios: Landscape Scale Scenario (1) and Tree Scale Scenario (2). Fig. 5 depicts the study area used in the first scenario and the localization within it of the subset areas with a finer spatial resolution. The use of two different spatial resolutions for model implementation was considered in order to provide a global and local understanding of the phenomena behaviour at two different spatial resolutions. Modeling at a more detailed scale was intended to provide specific knowledge about changes in density of attacks in small size areas such as forested areas with light attacks transforming into areas with moderate to severe attacks of MPB. In contrast, when observed and modeled at a courser resolution, the MPB infestation process started to exhibit an epidemic behaviour by spreading into larger areas of forest land-cover.

Long Term MPB Infestation of Lodegepole Pine Stands

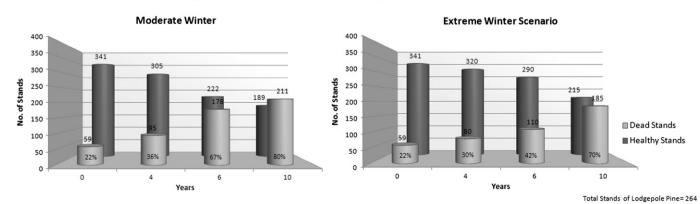


Fig. 7. Percentage of lodgepole pine attacked by MPB in a time lapse of ten years.

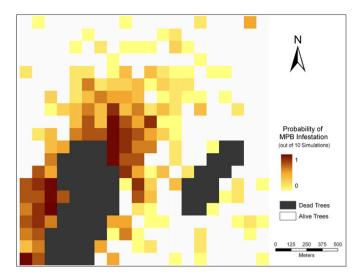


Fig. 8. Probability of MPB outbreaks location after two years of infestation. Overlay of outcomes of ten simulations.

Initially, the simulation of a mountain pine beetle outbreak performs over the study area used in *Landscape Scale Scenario* (1), where forest stands are composed of pure lodgepole pine, Douglasfir, and white spruce. A series of ten simulations were initialized with 100 agents each, representing groups of MPB spreading

through the forested landscape. This first part of the simulation examined the emergence of spatial patterns product of the MPB outbreak spatial patterns using different MPB mortality rates observed under moderate and extreme winters. MPB experience different levels of mortality each winter when low temperatures have detrimental effects on the developing stages of the beetles. During outbreaks occurring under moderate or normal winters (e.g. –18 °C), it is common to have a mortality level of 80%; however, when the temperatures are extremely low (e.g. –32 °C or lower) the environmental conditions change and mortality levels increase to 90% (Safranyik and Carroll, 2006). This coarser scale provided insight about where to expect beetle infestations. One of the affected areas was used to perform the second part of the simulation at finer scale.

The simulation for *Tree Scale Scenario* (2). This generated for two selected areas (Fig. 5) that had different MPB infestation levels. For the two subsets of forest landscape, the *moderate* and *extreme winter* mortality rates were also taken into account. A total time period of 5 years was used for the simulation of MPB infestation in the study areas that make part of the *Tree Scale Scenario* (2). This time frame was used in order to analyze the spread of the outbreak trough time. A total of ten simulations were generated for each of the two areas that make part of the *Tree Scale Scenario*.

There are a number of factors that drive the MPB outbreaks, including tree age, stem density, basal area, year-round temperatures and drought. However, this first prototype only takes into account variables such as tree size (DBH and height), tree age and

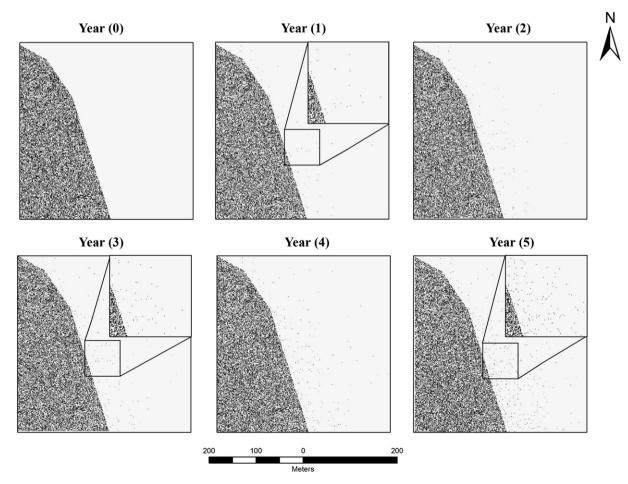


Fig. 9. Five-year simulation output of the integrated GIS-ABM used to understand and predict spatial and temporal evolution of MPB infestation for *moderate winter*, Area $1400 \text{ m} \times 400 \text{ m}$, spatial resolution $1 \text{ m} \times 1 \text{ m}$.

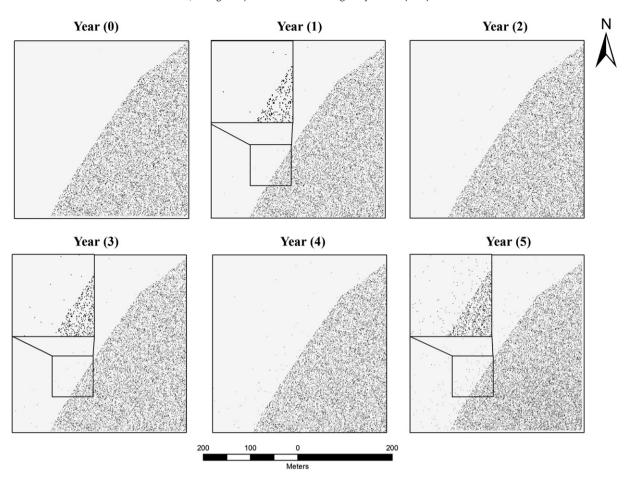


Fig. 10. Five-year simulation output of the integrated GIS-ABM used to understand and predict spatial and temporal evolution of MPB infestation for *moderate winter*, Area $2400 \text{ m} \times 400 \text{ m}$, spatial resolution $1 \text{ m} \times 1 \text{ m}$.

winter temperature as drivers of MPB outbreaks in order to keep the model simple. These variables are generally considered as key elements to determine forest susceptibility to MPB attacks (Shore et al., 2000; Hicke and Jenkins, 2008).

4.4. Results

The findings from the simulation for Landscape Scale Scenario (1) are presented in Fig. 6, which depicts the simulated locations of the mountain pine beetle infestation over a long-term period (10 years), using both moderate and extreme winter mortality rates. These results portray that MPB during the first four years is mainly located close to the areas where previous attacks were observed: however, some spotted attacks occurred away from initial dead trees. After the fourth year, the spread consistently remains near areas with previous mass attacks; however, in year six some new infested cells are noticeable far away (upper right and left corners) from the initial infestation. These new spotted attacks are consistent with the growth of the beetle populations due to the fact that the model allows the MPB population to grow but they have to interact within the same boundaries. This produces greater populations of beetles that rapidly consume all the food resources that are available in the area.

Fig. 7 presents simulation outcomes generated for *Landscape Scale Scenario* (1), these charts depict the number and percentage of MPB-killed tree stands in a time period of ten years. Between years four and six in the moderate winter, the percentage of dead stands increases by 31%. In meanwhile in the extreme winter, the

percentage of dead stands increases only by 12% showing how weather acts as a natural control mechanism trying to establish equilibrium within the ecosystem. Nonetheless, the lodgepole forest ecosystem continue being disturbed by the MPB infestation since the MPB populations keep growing, and almost 80% of the trees are dead after a period of ten years from the initial attack. The reason for the increase and variation in MPB populations is that the average lodgepole pine tree diameter in the study area was 31 cm, allowing a larger rate of survival. Biologist consider that beetle survival rates are more closely related to tree diameter and phloem thickness than any other factor (Safranyik et al., 1999). Therefore when the lodgepole pine trees have a good size, beetles living in them are able to survive low temperatures better than those beetles living in thinner trees. The quantitative summary of the simulation outcomes (Fig. 7) also indicates a range of difference between the number and location of lodgepole pine stands attacked during the infestation progress under the moderate and extreme winter scenario despite the fact that patterns were not visually identifiable.

Due to the stochasticity of the model, a series of ten simulations were generated for each geographic area that constitute part of the *Scenario* (1) and *Scenario* (2). The replication of the simulations showed that the random components lead to different results each time. Fig. 8 presents the overlay of the outcomes of ten simulations. This figure shows the probability of location of MPB spread after the second year of infestation for *Scenario* (1). Areas with the higher probability have a value of one (1), and areas with the lower probability have values close to zero (0).



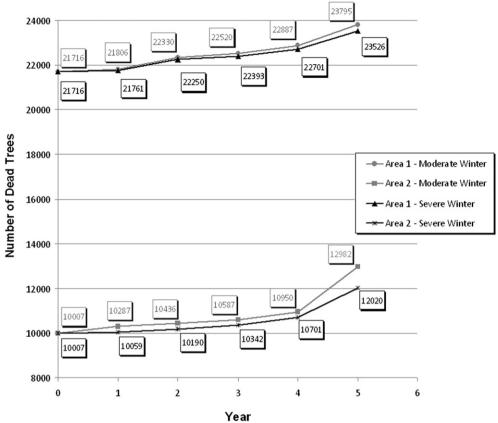


Fig. 11. Charts of the trees killed by MPB attack during a period of time of five years. Diagrams depict the results for the two different subset areas, considering a moderate winter scenario.

Once simulations for the *Landscape Scale Scenario* (1) were generated, the model was executed using *Tree Scale Scenario* (2) for the Kamloops area. British Columbia Ministry of Forest and Range reported that the spatial location of the latest scenario was undergoing attack by MPB (B.C. Ministry of Forests and Range, 2004). Simulations were performed using both *moderate* and *severe winter mortality rate* scenarios. The results of these simulation outcomes for *moderate winter mortality rate scenario* and normal climatic conditions (mean temperature of $-17.9\,^{\circ}$ C) are presented in Figs. 9 and 10 respectively for area 1 and area 2.

The outcomes of the model simulations demonstrate the evolution of the infestation and its dependence on the structure of the landscape. In forested areas where previous attacks were registered, the MPB prefer to fly short distances. For this reason, spread was not very prominent outside the previous infested zone during the first two years of the infestation but the number of killed trees increased in areas close to previous spotted attacks. However, after the second year of outbreak, the MPB populations started to spread outside the previous attacked zones. This is more evident in the area 1 where the density of previous attacks is higher than in area 2, for both moderate and severe winter mortality rate scenarios (Fig. 11). The reason for this difference in spatial behaviour is the number of initially attacked trees in each subset. In the area 1, the percentage of MPB-dead trees is 14%, therefore the area is considered to hold a moderate attack (11-30% of trees are dead). In area 2, there is a 6% of MPB-dead trees, thus the area is considered to hold a light attack (1–10% of trees are dead). The density of the initial attack produces a different pattern of MPB infestation in the simulation. As a result, the areas with less MPB-killed trees will have an increase in mortality of the closest trees and beetles start looking for food outside the areas previously attacked after certain point is reached, resulting in longer flying distances. At the same time, MPB populations located in areas where the number of MPB-killed trees is higher tend to fly outside the zone boundaries with a high percentage of previously attacked trees. In previously attacked zones, reported to have a moderate pest code by the BC Ministry of Forest and Range, the increment in trees killed by MBP is not visually notorious. However, the counts made from generated simulation maps indicate that the number of trees attacked from one year to another expand, increasing the percentage of dead trees and modifying the previously established pest codes.

5. Conclusions

In this study, the integrated GIS-AB model was developed and implemented using data sets from the BC Ministry of Forest and Range for a study site in Kamloops, BC, Canada area known as much affected with pine beetle infestations. The obtained results revealed that MPB-induced mortality patterns can be spatially modeled using an agent-based approach due to its ability to capture the exhibiting behaviour of the mountain pine beetle phenomenon process. The integration of GIS and an agent-based approach provides a valuable tool for exploring the space-time dynamics within the forest landscape, taking into consideration the effect of the interaction between the forest and the mountain pine beetle and also permits to simulate the robust behaviour and

adaptability of MPB populations to different landscape structures. This study emphasizes the utility of ABM for modeling ecological processes where individual agents interact and self-organize at a micro-level generating specific and structured patterns at a macro-level.

One of the most important features of using AB modeling approach for forest infestation process is the capability of incorporating in the model natural behaviours observed in disturbance agents like mountain pine beetle swarms. This potential makes possible to simulate MPB populations growth and life cycle, feeding and breeding habits, as well as flying and attack patterns. This study demonstrated the potential of using an integrated GIS–agent-based modeling approach that permits representation of spatial dynamics of the spread of MPB outbreaks through forest landscapes. The temporal and spatial behaviour of the model outcomes are explored by analyzing the spatial allocation of new outbreaks and quantifying the new infected trees through time.

The simulation results in this study revealed the influence that higher diameter trees had on higher breeding rates, therefore in forest stands with big and mature pines new MPB population levels increased. However, as the outbreak proceeded through time, the attack of larger trees was not possible due to scarce food resources, forcing MPB to attack younger stands of lodgepole pine tree. These findings were better depicted using Landscape Scale Scenario (1), which indicates that MPB outbreaks at a landscape scale depend on the food availability and favourable weather conditions that allow higher beetle survival rates. The outcomes of the proposed model and implemented prototype using the *Tree* Scale Scenario (2) also depict the spatial patters in pine mortality produced by MPB infestation. Simulation maps indicated that the areas undergoing a light MPB attack (1-10% trees attacked) turned into moderate MPB attack, due to the behaviour of the insect tent to aggregate instead of flying very long distances. Conversely, the simulations for the areas undergoing a moderate MPB attack (11-33% trees attacked) depicted that the infestation spread out

Agent-based modeling offers a useful approach for analyzing and understanding the complexities of forest insect infestation; however, future research in this field requires a focus on the issue of model testing and validation. This involves comparing the modeled outcomes to reality, the latter being typically represented in a dataset of the same geographic area as the model input, but from an afterwards moment in time. Agent-based modeling evaluation and validation is a challenging research endeavour and research work in testing validation of ABM is not yet fully elaborated in the scientific literature. In respect to the MPB modeling one of the main challenges is that the information required is often unavailable. Geoferenced data sets, used in models like the one presented in this study, contain considerable data such that are extremely expensive and time consuming to collect at such detailed scale and for sustained number of years. Another issue regarding real data of MPB infestation is that given the spread, often governmental decisions of clear-cut were made in areas that are bigger than the infested site and all the data about the outbreaks are therefore unavailable for number of consecutive years. In addition, even if data could be collected over different periods of time, complex geographic processes are subject to feedbacks and random events that can lead to different results. In this way, a validation dataset may represent only one of a set of possible outcomes. For these reasons, AB models validation requires special research efforts that are important but make part of another ongoing research study. The prototype model tool presented in this study represents the first step of a work in progress that looks forward to assuring that the model generates emergent patterns that can be used in real forest management applications. The findings from this study can help to improve comprehension of the spatially explicit spread dynamics and take better steps towards the reduction of their impact on forest landscapes. The implemented prototype of the model proposed in this study is generic and can be replicated in different study sites as long as the input information required by the model is available.

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References

- Allen, E., 2003. Forest health assessment in Canada. Ecosystem Health 7, 28–34.Amman, G.D., 1982a. Characteristics of mountain pine beetles reared in four pine hosts. Environmental Entomology 11 (3), 590–593.
- Amman, G.D., 1982b. The mountain pine beetle identification, biology, causes of outbreaks, and entomological research needs. In: Proceedings of the Joint Canada/USA Workshop on Mountain Pine Beetle Related Problems in Western North America, Fairmont Hot Springs, British Columbia. Environment Canada, Canadian Forestry Service.
- Amman, G.D., Cole, W.E., 1983. Mountain Pine Beetle Dynamics in Lodgepole Pine Forests. Part II: Population Dynamics. Intermountain Forest & Range Experiment Station, USDA Forest Service, Ogden.
- Anwar, S.M., Jeanneret, C.A., Parrott, L., Marceau, D.J., 2007. Conceptualization and implementation of a multi-agent model to simulate whale-watching tours in the St. Lawrence Estuary in Quebec, Canada. Environmental Modelling & Software 22 (12), 1775–1787.
- Argonne National Laboratory, 2008. Repast: Recursive Porous Agent Simulation Toolkit. http://repast.sourceforge.net (Last accessed November 2008).
- B.C. Ministry of Forests and Range, 2004. Aerial Detection for Bark Beetle Management Activity. Forest Practices Branch and Canadian Forest Service, Victoria, BC, Canada. http://www.for.gov.bc.ca/hcp/fia/landbase/aerial_ detection.htm (Last accessed November 2008).
- Benenson, I., Torrens, P., 2004. Geosimulation: Automata-Based Modeling of Urban Phenomena. John Wiley & Sons, London.
- Berryman, A.A., Raffa, K.F., Millstein, J.A., Stenseth, N.C., 1989. Interaction dynamics of bark beetle aggregation and conifer defense rates. Oikos 56 (2), 256–263.
- Billings, R.F., Gara, R.I., Hrutfiord, B.F., 1976. Influence of ponderosa pine resin on response of *Dendroctonus ponderosae* to synthetic trans-verbenol. Environmental Entomology 5 (1), 171–179.
- Bithell, M., Brasington, J., 2009. Coupling agent-based models of subsistence farming with individual-based forest models and dynamic models of water distribution. Environmental Modelling & Software 24 (2), 173–190.
- Bone, C., Dragicevic, S., Roberts, A., 2005. Integrating high resolution remote sensing, GIS and fuzzy set theory for identifying susceptibility areas of forest insect infestations. International Journal of Remote Sensing 26 (21), 4809–4828.
- Bone, C., Dragicevic, S., Roberts, A., 2006. A fuzzy-constrained cellular automata model of forest insect infestations. Ecological Modelling 192, 107–125.
- Bone, C., Dragicevic, S., Roberts, A., 2007. Evaluating forest management practices using a GIS-based cellular automata modeling approach with multispectral imagery. Environmental Modeling and Assessment 12 (2), 105–118.
- Bousquet, F., Le Page, C., 2004. Multi-agent simulations and ecosystem management: a review. Ecological Modelling 76 (3–4), 313–332.
- Burnell, D.G., 1977. A dispersal-aggregation model for mountain pine beetle in lodgepole pine stands. Researches on Population Ecology 19 (1), 99–106.
- Campbell, E.M., Alfaro, R.I., Hawkes, B., 2007. Spatial distribution of mountain pine beetle outbreaks in relation to climate and stand characteristics: a dendroecological analysis. Journal of Integrative Plant Biology 49 (2), 168–178.
- Carroll, A.L., Taylor, S.W., Régnière, J., Safranyik, L., 2003. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. In: Mountain Pine Beetle Symposium: Challenges and Solutions, Kelowna, British Columbia. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre.
- Codehaus Foundation, 2006. GeoTools: the Open Source Java GIS Toolkit. http://geotools.codehaus.org (Last accessed November 2008).
- Cole, W., 1973. Crowding effects among single-age larvae of the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). Environmental Entomology 2 (2), 285–293.
- Cole, W., Amman, G.D., 1969. Mountain Pine Beetle Infestations in Relation to Lodgepole Pine Diameters. USDA Forest Service, Intermountain Forest and Range Experiment Station, Research Note INT-95. 8 pp.
- Coops, N.C., Johnson, M., Wulder, M.A., White, J.C., 2006. Assessment of QuickBird high spatial resolution imagery to detect red attack damage due to mountain pine beetle infestation. Remote Sensing of Environment 103 (1), 67–80.

- Ekbia, H., Reynolds, K., 2006. Decision support for sustainable forestry: enhancing the basic rational model. In: Thompson, A., Reynolds, K.M. (Eds.), Forestry Management: the Past and the Future. Springer Verlag, pp. 497–514.
- Elkin, C.M., Reid, M.L., 2005. Low energy reserves and energy allocation decisions affect reproduction by mountain pine beetles, *Dendroctonus ponderosae*. Functional Ecology 19, 102–109.
- ESRI, 2008. ArcGIS 9.3: the Complete Enterprise GIS. http://www.esri.com (Last accessed November 2008).
- Ferretti, M., 1997. Forest health assessment and monitoring issues for consideration. Environmental Monitoring and Assessment 48, 45–72.
- GeoBC, 2008. BC's Geographic Gateway. http://www.geobc.gov.bc.ca (Last accessed June 2009).
- Gimblett, H.R. (Ed.), 2002. Integrating Geographic Information Systems and Agent-Based Modeling Techniques for Simulating Social and Ecological Processes. Oxford University Press, Oxford, U.K.
- Heavilin, J., Powell, J., Logan, J., 2005. Dynamics of mountain pine beetle outbreaks. In: Johnson, A.J., Miyanishi, K. (Eds.), Plant Disturbance Ecology: the Process and the Response. AP/Elsevier, Oxford, UK.
- Hicke, J.A., Jenkins, J.C., 2008. Mapping lodgepole pine stand structure susceptibility to mountain pine beetle attack across the western United States. Forest Ecology and Management 255 (5–6), 1536–1547.
- Hopping, G.R., Beall, G., 1948. The relation of diameter of lodgepole pine to incidence of attack by the bark beetle *Dendroctonus monticolae* Hopkins. Forestry Chronicle 24 (2), 141–145.
- Hynum, B.G., Berryman, A.A., 1980. *Dendroctonus ponderosae* (Coleoptera: Scolytidae): preaggregation landing and gallery initiation on lodgepole pine. The Canadian Entomologist 112, 185–191.
- Koot, P., 1997. Overview Aerial Survey Standards for British Columbia and the Yukon. Forest Health Network Report 97-1. Victoria, British Columbia, Canada, Natural Resources Canada, Canadian Forest Service, p. 1–14.
- Lewis, M.A., He, F., 2006. Modeling Spatio-temporal Patterns of MPB Infestation. University of Alberta, Edmonton.
- Logan, J.A., White, P., Bentz, B.J., Powell, J.A., 1998. Model analysis of spatial patterns in mountain pine beetle outbreaks. Theoretical Population Biology 53 (3), 236–255.
- Maclauchlan, L., 2006. Determining Susceptibility of Young Pine Plantations to the Mountain Pine Beetle, *Dendroctonus Ponderosae*, and Manipulating Future Stands to Mitigate Losses. Ministry of Forests Southern Interior Region, Victoria, B.C.
- Malanson, G.P., Armstrong, M.P., 1996. Dispersal probability and forest diversity in a fragmented landscape. Ecological Modelling 87 (1–3), 91–102.
- National Research Council of Canada's Institute for Information Technology, 2006. NRC FuzzyJ Toolkit. http://www.iit.nrc.ca/IR_public/fuzzy/fuzzyJToolkit2.html (Last accessed November 2008).
- Nelson, T., Boots, B., Wulder, M.A., 2006. Representing large area mountain pine beetle infestations. Forestry Chronicle 82 (2), 243–252.
- Parker, D.C., 2005. Integration of geographic information systems and agent-based models of land use: prospects and challenges. In: Maguire, D.J., Batty, M., Goodchild, M.F. (Eds.), GIS, Spatial Analysis, and Modeling. ESRI Press, Redlands, CA, pp. 403–422.
- Parker, D.C., Manson, S.M., Janssen, M.A., Hoffmann, M.J., Deadman, P., 2003. Multiagent systems for the simulation of land-use and land-cover change: a review. Annals of the Association of American Geographers 93 (2), 314–337.
- Parunak, H.V.D., Savit, R., Riolo, R.L., 1998. Agent-based modeling vs. equation-based modeling: a case study and users' guide. In: Multi-Agent Systems and Agent-Based Simulation (MABS'98). Springer, Paris, France.
- Powell, J., Tams, J., Bentz, B., Logan, J., 1998. Theoretical analysis of "switching" in a localized model for mountain pine beetle mass attack. Journal of Theoretical Biology 194, 49–63.

- Raffa, K., Phillips, T., Salom, S., 1997. Strategies and mechanisms of host colonization by bark beetles. In: Schowalter, T., Filip, M. (Eds.), Beetle–Pathogen Interactions in Conifer Forests. Academic Press, Corvallis.
- Raffa, K.F., Berryman, A.A., 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera Scolytidae). Ecological Monographs 53 (1), 27–49.
- Reid, D.E.B., Lieffers, V.J., Silins, U., 2004. Growth and crown efficiency of height repressed lodgepole pine; are suppressed trees more efficient? Trees Structure and Function 18 (4), 390–398.
- Riel, W.G., Fall, A., Shore, T.L., Safranyik, L., 2003. A spatio-temporal simulation of mountain pine beetle impacts on the landscape. In: Mountain Pine Beetle Symposium: Challenges and Solutions, Kelowna, British Columbia. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre.
- Roberts, A., Dragicevic, S., Northrup, J., Wolf, S., Li, Y., Coburn, C., 2003. Mountain Pine Beetle Detection and Monitoring: Remote Sensing Evaluations. Simon Fraser University, Vancouver.
- Safranyik, L., 1988. Estimating attack and brood totals and densities of the mountain pine beetle in individual lodgepole pine trees. The Canadian Entomologist 120 (4), 323–331.
- Safranyik, L., Carroll, A.L., 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In: Safranyik, L., Wilson, B. (Eds.), The Mountain Pine Beetle: a Synthesis of Biology, Management, and Impacts on Lodgepole Pine. Pacific Forestry Centre, Victoria, BC, pp. 3–66.
 Safranyik, L., Barclay, H., Thomson, A., Riel, W.G., 1999. A Population Dynamics
- Safranyik, L., Barclay, H., Thomson, A., Riel, W.G., 1999. A Population Dynamics Model for the Mountain Pine Beetle, *Dendroctonus Ponderosae* Hopk. (Coleoptera: Scolytidae). Pacific Forestry Centre, Victoria, British Columbia, 41 pp.
- Safranyik, L., Linton, D.A., Silversides, R., McMullen, L.H., 1992. Dispersal of released mountain pine beetles under the canopy of a mature lodgepole pine stand. Journal of Applied Entomology 113 (5), 441–450.
- Safranyik, L., Silversides, R., McMullen, L.H., Linton, D.A., 1989. An empirical approach to modelling the dispersal of the mountain pine beetle (*Dendroctonus ponderosae* Hopk.) (Col., Scolytidae) in relation to sources of attraction, wind direction and speed. Journal of Applied Entomology 108 (5), 498–511.
- Schmitz, R.F., McGregor, M.D., Amman, C.D., 1980. Mountain pine beetle response to lodgepole pine stands of different characteristics. In: Proceedings of the Second IUFRO Conference on Dispersal of Forest Insects: Evaluation, Theory and Management Implications, Pullman, WA.
- Shepherd, R.F., 1966. Factors influencing the orientation and rates of activity of *Dendroctonus ponderosae* (Coleoptera: Scolytidae). The Canadian Entomologist 98, 507–518.
- Shore, T.L., Safranyik, L., Lemieux, J.P., 2000. Susceptibility of lodgepole pine stands to the mountain pine beetle: testing of a rating system. Canadian Journal of Forest Research 30, 44–49.
- Smajgl, A., Heckbert, S., Ward, J., Straton, A., 2009. Simulating impacts of water trading in an institutional perspective. Environmental Modelling & Software 24 (2), 191–201.
- Taylor, S.W., Carroll, A.L., 2003. Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: a historical perspective. In: Mountain Pine Beetle Symposium: Challenges and Solutions, Kelowna, British Columbia. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre.
- Tso, B., Mather, P., 2001. Methods Based on Fuzzy Set Theory. Classification Methods for Remotely Sensed Data. CRC Press, Boca Raton, FL, pp. 149–185.
- Viaggi, D., Bartolini, F., Raggi, M., 2009. Combining linear programming and principal-agent models: an example from environmental regulation in agriculture. Environmental Modelling & Software 24 (6), 703–710.
- Wulder, M.A., White, J.C., Bentz, B., Alvarez, M.F., Coops, N.C., 2006. Estimating the probability of mountain pine beetle red-attack damage. Remote Sensing of Environment 101, 150–166.