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Modeling micro-scale ecological processes and emergent patterns of mountain pine beetle epidemics

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ABSTRACT

Forest insect outbreaks can impose significant tree mortality across vast forested landscapes. The current epidemic of mountain pine beetle, *Dendroctonus ponderosae* Hopkins, for example, has led to the mortality of pine trees in western Canada and the U.S. spanning tens of millions of hectares. The ecological processes driving mountain pine beetle outbreaks are governed by multiple feedback mechanisms, thresholds, and external constraints that exist along a spatial continuum from individual insect–tree interactions to landscape level change. These components of mountain pine beetle epidemics need to be explicitly parameterized in modeling efforts that aim to predict where insect disturbance will occur in a forest each year and the amount of tree mortality that will ensue as a result. However, do date, minimal efforts exist that examine how local level interactions between beetles and trees translate into broader patterns of tree mortality, and those that do are limited to relatively local scales. In this study, we present an agent-based model that simulates how tree mortality results from the combination of beetle–tree interactions, beetle-to-beetle communication, tree defense to beetle attack, beetle density dynamics, host tree availability, dispersal behavior, and landscape heterogeneity. Our model is tested using data from an area in central British Columbia, Canada, that is near the center of the current outbreak in that region. The model simulates both overall tree mortality and spatial patterns of tree mortality, producing results that are similar to those observed in aerial surveys of tree health. Moving forward, the computational efficiency of our model demonstrates the capability to be applied to large, regional landscapes when implemented with sufficient computing resources.

1. Introduction

The current epidemic of mountain pine beetle (MPB), *Dendroctonus ponderosae* (Hopkins), across the pine forests of western North America is a complex system involving local insect–host interactions leading to large-scale patterns of landscape change. The MPB is native to the forests of lodgepole pine, *Pinus contorta*, and ponderosa pine, *Pinus ponderosae*, in several western U.S. states and the Canadian provinces of British Columbia and Alberta. At times, the insect resides in an endemic state in which small populations colonize trees with compromised health. However, under favorable bioclimatic conditions with abundant susceptible hosts, MPB populations escalate to incipient levels that lead to mass numbers of beetles attacking and killing individual trees (Preisler et al., 2012). As bioclimatic and host conditions become even more favorable for beetle survival, MPB populations reach epidemic levels that induce regional scale tree mortality that can persist until available hosts are exhausted, or until significantly cold winter temperatures lead to widespread beetle mortality (Carroll et al., 2006).

The current MPB epidemic has witnessed pine mortality across millions of hectares in British Columbia (Westfall and Ebata, 2012) and in the western U.S. (Jenkins et al., in press), and is currently impacting new areas in the boreal forests in northern Alberta. The epidemic is a result of the recent regional warming trend that has resulted in the decline of beetle mortality during the winter months, and increased the susceptibility of host trees to attack during the summer months due to prolonged drought conditions that compromise tree vigor (Creeden et al., 2014). Furthermore, decades of increased fire suppression in the pine forests of western North America have ensured a vast available source of host trees for MPB populations to thrive (Taylor and Carroll, 2003). The combination

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of these factors has led to the most significant outbreak of MPB on record and pushed the insect beyond its historic range (Cudmore et al., 2010; Cullingham et al., 2011; Coops et al., 2012; Erbilgin et al., 2014).

The extent of damage caused by the MPB has motivated a research agenda in recent decades aimed at understanding the insect's attack behavior in order to provide knowledge that could help mitigate or prevent future outbreaks. While this body of literature is extensive (a Web of Science search for articles from 1964 to 2014 with the topic of "mountain pine beetle" resulted in 1121 scholarly publications), minimal research has examined how insect–host relationships lead to broader scale patterns of tree mortality. This gap in the literature (one that is defined by a methodological disconnect between spatial scales of inquiry) needs to be addressed in order to better manage forests in the presence of insect disturbances that are driven by forest management decision (e.g., fire suppression policies) and climate change.

Epidemics of MPB and other bark beetles are governed by feedback mechanisms and thresholds that define MPB population states (i.e., endemic, incipient, or epidemic). Raffa et al. (2008) describe a list of thresholds existing along a spatial continuum, from the finest of scales where beetles penetrate into trees to the broadest of scales where anthropogenic activities create regime shifts in host availability. The potential of beetle populations to reach and surpass these thresholds is dictated by a set of internal and external controls, many of which have been previously studied with regards to their relationship with MPB survival. For example, the threshold of host entry (i.e., beetles attacking a tree) is impacted by beetle behavior and physiology (Wood, 1982; Raffa and Berryman, 1983), and the defensive chemistry of the tree (Raffa and Smalley, 1995; Paine et al., 1997). Beetle reproduction is governed by MPB density and attack rate (Safranyik et al., 2007), the dynamics of several microbes (Shrimpton, 1973; Rankin and Borden, 1991), the thickness of the outer portion of the tree (Amman, 1972; Berryman, 1976), MPB competitors (Rankin and Borden, 1991), predators (Raffa and Berryman, 1982), and ambient temperature (Bentz et al., 1991; Bentz and Mullins, 1999; Hicke et al., 2006). At larger scales, outbreaks within a stand or at the landscape level are constrained by host availability (Taylor and Carroll, 2003), density and age of hosts (Mitchell et al., 1983), dispersal behavior (Nelson et al., 2007; Safranyik et al., 2007; Powell and Bentz, 2014), and landscape heterogeneity of hosts (Safranyik et al., 2010).

Research focusing on how these thresholds and controls impact MPB populations is crucial for improving our understanding of beetle behavior and why we are currently witnessing an unprecedented epidemic. However, methodological challenges exit when trying to connect the distinct scales at which these thresholds and controls operate, which hinders our ability to predict when and where populations are likely to spread each year. Several types of predictive models have been developed that are advantageous in specific contexts. For example, forest health survey data have been used in conjunction with forest inventory data for estimating MPB species range expansion (Robertson et al., 2009), relating infestation severity to forest patch characteristics (Bone et al., 2013a), and, most commonly, predicting areas likely to be attacked by MPB in the near future (Zhu et al., 2008; Robertson et al., 2008; Bone et al., 2013b). At even broader scales, climate data has been utilized with forest model outputs for estimating the potential of MPB expansion into the boreal forest of western Canada (Coops et al., 2012). While these models are useful for defining MPB risk, there is insufficient focus on the dynamics, interactions, feedbacks, emergent properties, and thresholds that occur at the multiple spatial scales that produce risk estimates. Models that can identify larger patterns and display relevant small-scale interaction are, therefore, needed to better assess and understand MPB interactions.

The objective of this study is to develop a computational model for simulating how local MPB processes lead to emergent patterns of tree mortality. We present an agent-based model (ABM) that simulates how tree mortality results from the combination of beetle–tree interactions, beetle-to-beetle communication, tree defense to beetle attack, beetle density dynamics, host tree availability, dispersal behavior, and landscape heterogeneity. We build on the seminal work of Perez and Dragićević that developed an agent-based modeling approach to simulate MPB within stands and at varying, yet relatively small, spatial scales (2010, 2011). The research presented here is the next step in utilizing an ABM for simulating MPB, as our model simulates individual insects and trees as computational agents across larger areas than previous studies, and in a manner that is scalable because larger areas can be simulated with greater computational resources. We demonstrate the utility of this model through its implementation on a forested dataset representing 10,000 ha in an area of British Columbia that experienced significant MPB-induced tree mortality during the initial years of the current epidemic.

2. Background

This section of this paper provides a background to MPB infestation behavior, focusing on the concepts of MPB dispersal, beetle communication, host selection, and MPB mortality. These three concepts, selected from the list of controls provided by Raffa et al. (2008), are used for calibrating the model in this study.

2.1. Dispersal

Each summer, adult beetles emerge from a their host tree where they have spent the winter and disperse varying distances in search of a new host to attack. While dispersal is arguably one of the least understood characteristics of the MPB (Chen, 2014), findings demonstrate that the majority of beetles disperse to a tree within the stand, while fewer beetles engage in long-distance dispersal (Shore and Safranyik, 1992). Local dispersal occurs under the stand canopy, and is controlled by a number of factors, including beetle densities, host availability, and host size (Mitchell and Preisler, 1991). Given an ideal mixture of these characteristics, beetles will disperse to nearby trees and begin their attack. However, the likelihood of long distance dispersal increases when localized MPB densities are elevated beyond what local host resources support (Powell and Bentz, 2014). At this point a proportion of the population rises above the canopy and is transported some distance by prevailing winds. While estimates vary, some observations note beetle dispersal as far as 110 km/day (Jackson et al., 2008). Given the dispersal behavior of MPB, it is necessary to include density dependent population effects in conjunction with host resource availability in order to adequately simulate the movement of beetles across a landscape.

2.2. Communication

Beetles disperse and select a susceptible host tree to attack. As beetles begin boring through the bark of a tree, a chemical pheromone is processed and spreads though the air acting as a communication cue. Pheromones attract more beetles to the tree to ensue a mass attack in effort to overcome a tree's defensive mechanism (Logan et al., 1998). Trees under attack produce pitch tubes, which are masses of resin that push boring beetles out of the tree. However, a critical mass of beetles can overcome the ability of a tree to thwart off an attack. Once a tree has been successively attacked, the production of chemical cues transition from pheromones to verbanone, an anti-aggregation chemical that signals to beetles that a tree under attack has reached a certain beetle capacity and no longer requires additional beetles to assist in overcoming the tree's defenses (Lindgren et al., 1989). This density dependent communication strategy ensures that somewhat optimal numbers of attackers are attracted to trees, leaving residual beetles to find other trees to attack. This behavior results in clusters of tree mortality as MPB search for hosts in close proximity to ones that have reached population capacity (Birch, 1984).

2.3. *Host selection*

MPB select hosts based on a tree's resistance and its potential for providing suitable resources. Resistance declines when trees are physiologically compromised due to disease or senescence because they are less able to produce quantities of resin necessary for thwarting an attack (Shrimpton, 1973; Shore and Safranyik, 1992). However, vigorous trees are typically more plentiful, and more nutritionally suitable for MPB reproduction and overwinter survival needs due to having thicker phloem (Raffa et al., 2008). Thus, a tradeoff persists between selecting hosts that are easier to attack versus hosts that provide more advantageous resources for MPB survival. MPB navigate this tradeoff by selecting hosts with compromised health when beetle populations are below the threshold necessary for overcoming the defensive capabilities of more vigorous trees, and selecting more vigorous hosts that increase likelihood of survival once beetle populations increase beyond a necessary threshold (Wallin and Raffa, 2000). The selective strategy employed by MPB challenges several models used for estimating risk to attack because the relationship between beetle population and host selection is ignored.

2.4. *MPB mortality*

When attacking a tree, MPB create vertical galleries in the phloem, mate and lay between approximately 60–80 eggs, with two-thirds of those eggs hatching female larvae (Safranyik, 2003). Once eggs hatch, the larvae consume phloem by boring horizontally under the bark of the tree. The larvae are able to overwinter under the bark by metabolizing an alcohol called glycerol that serves as an antifreeze agent to protect beetles against cold temperatures. However, sustained temperatures below −40 °C during the middle of winter can lead to 100% mortality, as can temperatures in the range of −20 °C to −30 °C in late fall or early spring when glycerol levels are not sufficient (Carroll and Safranyik, 2003; Regniere and Bentz, 2007). Once temperatures cease to reach these cold levels at specific times of the winter, the likelihood of MPB survival, and hence tree mortality, increases. Given the approximate number of eggs produced by each beetle, a population can experience 97.5% mortality and still maintain its viability. Meanwhile, a mortality level as high as 80% can witness an eight-fold increase in population size (Carroll et al., 2006). The fact that small changes in mortality levels can lead to large changes in population growth needs to be consider in models of MPB infestations because mortality is directly linked to how micro-level processes influence broader scale patterns of change.

3. Methods

The model is described here using the ODD (Overview, Design concepts, Details) protocol developed by Grimm et al. (2006, 2010). The model is written in Java using Repast Simphony (2014) 2.0, and is compatible with 2.1, with code and model data downloadable from here: http://discovery.ucl.ac.uk/1430284/.

3.1. *Purpose*

The purpose of the ABM is to simulate the interaction amongst a significantly high number of insects and trees and to evaluate if such interactions are able to reproduce tree mortality patterns consistent with measured observations. An ABM approach provides a suitable method for achieving this objective because individual representation provides a bottom-up approach whereby small-scale interactions lead to emergent patterns of change. While others have employed ABMs in the past to simulate insect infestations (Babin-Fenske and Anand, 2011; Sturtevant et al., 2013), our model provides a strategic means for representing insects and forests through space and time that permits simulations on large datasets.

3.2. *Entities, state variables and scales*

There are three main entities in the model: beetles agents (referred hereafter as beetles), tree agents (trees), and grid cells. Each beetle represents a single MPB that, at the start of each time step, vacates its current host in search for a new host to attack. The state variables defining each beetle are sex (s) and location (l). The beetle population consists of approximately 66.6% females and 33.3% males, with the exact ratio in a given run instantiated using a random number generator that reflects the ratio of eggs resulting from reproduction. Variable l indicates the geographic coordinates of the grid cell center point where a beetle resides at any moment in time during the model simulation. As described above, MPB can disperse varying distances, and in doing so they influence the flight behavior of other beetles through chemical communication strategies. Thus, tracking location during all components of the simulation is important.

A tree is defined by the following variables: tree diameter at breast height (DBH), tree resistance (r), and number of beetles (n) in the tree. DBH is used to calculate tree resistance to attack, as previous research has demonstrated that likelihood of attack is correlated with tree diameter (Shore and Safranyik, 1992). Resistance is represented as a real number between 0 and 1, where higher values indicate greater resistance. The variable n is a count of the total number of beetles that are attacking the tree at a single moment. Trees do not require a *location* variable; location is only required by beetles in order to drive the dispersal process. As described below in section 3.6, each cell contains a variable number of trees whose characteristics are drawn from a random distribution of values pertaining to each variable.

Grid cells are the spatial units in which insect–host interactions play out. The initial number of beetles and trees in each cell is determined during the initialization phase of the model. The size of the forested area that grid cells represent is flexible, allowing for both fine and coarse resolution input data to be used in the model. Each time step in the model represents a single year.

3.3. *Process overview and scheduling*

The ABM consists of processes depicted in Fig. 1. The first process to commence at each time step is local dispersal that simulates beetles leaving their hosts in search of a new tree within their current or nearby stands. This process occurs asynchronously across the landscape in order to represent that an entire MPB population does not emerge at a single moment in time from their different hosts. If location beetle populations are too high and available tree resources to low, beetles will not be able to locate a cell with available trees and as such engage in long distance dispersal. Both types of dispersal involve beetle communication via simulated pheromone production. Once a cell is located through either local or long distance dispersal, the model simulates beetle attack on susceptible trees, followed by tree mortality. However, if no cell is located in which

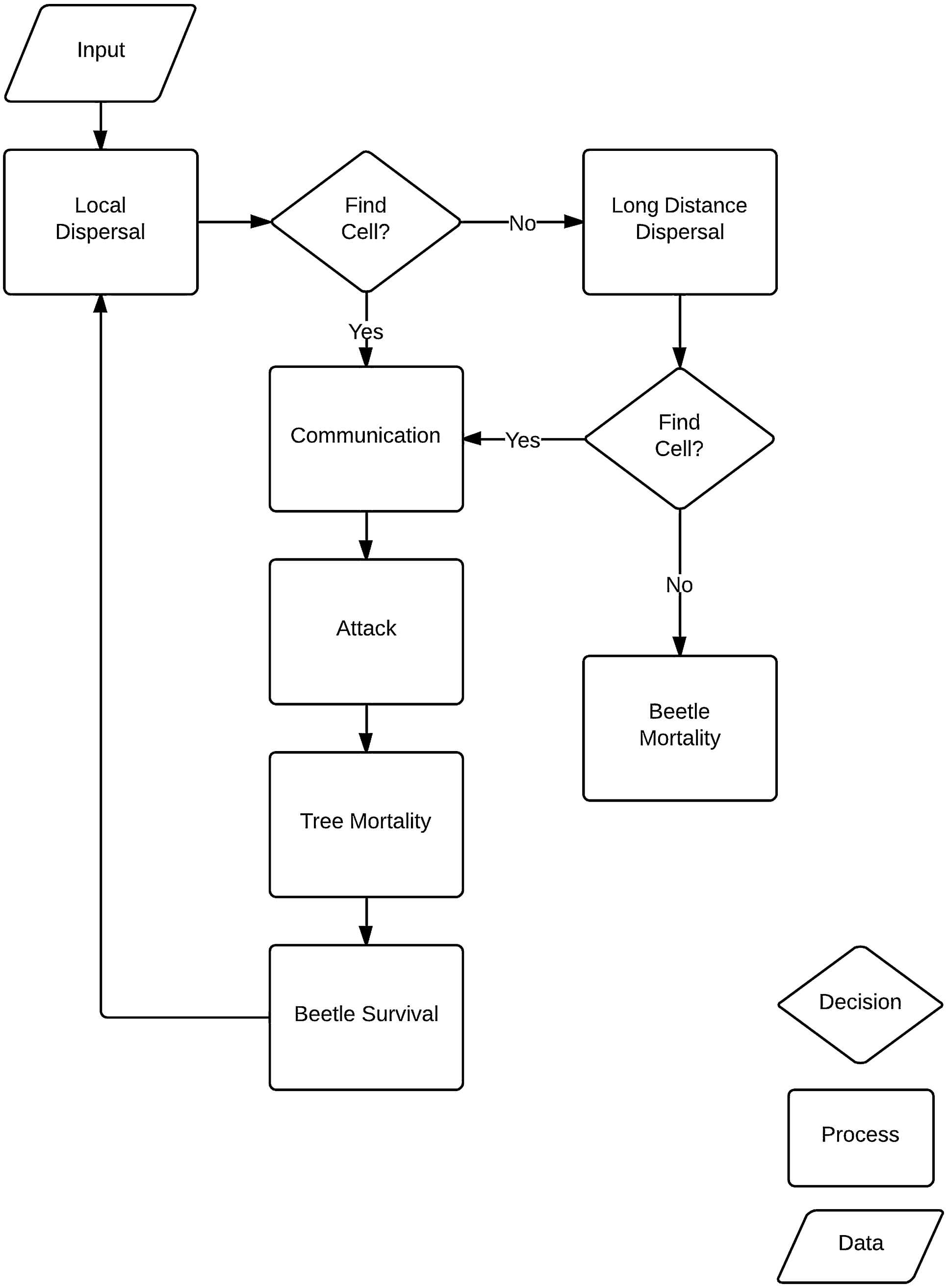

Fig. 1. Flowchart of the multiple sub-models of the ABM.

available susceptible hosts exist, the searching beetles die. Those beetles that do locate and attack susceptible trees are next subject to a survival step where a proportion of beetles die based on calibrated parameters. Beetles that survive become the adult beetles in the dispersal portion of the model at the beginning of the following time step. This process continues for a number of time steps representing a specified number of years.

3.4. Design concepts

3.4.1. Basic principles

The basic principles of the ABM are derived from a stand-level mathematical model of MPB dispersal described by Shore and Safranyik (1992). Several MPB risk models have since been developed that use principles defined in the Shore and Safranyik model (e.g., Robertson et al., 2008); however, only few have taken a spatially explicit approach incorporating bottom-up methodology, but these have typically been applied at local scales. The intention with our model is to utilize the mathematical components by the Shore and Safranyik risk rating system for parameterizing how MPB interact with host trees in order to simulate tree mortality patterns at local and broader scales.

3.4.2. Emergence

The key emergent patterns from the model are (1) the spatial patterns of tree mortality, (2) the total tree mortality across the landscape at each time step, and (3) the total number of beetles at each time step. The spatial patterns of tree mortality represent the emergent phenomenon resulting from insect–host interactions, as these patterns will depend on the feedbacks between the availability of susceptible hosts and the location and population size of beetles. These emergent spatial patterns are evaluated against observed patterns of tree mortality that can be identified, for example, through aerial overview surveys that estimate the severity of beetle-induced tree mortality. Emergent patterns 2 and 3 are more tightly imposed by the model rules and less dependent on the behaviors of individual agents; therefore, they will serve as a means for model calibration.

3.4.3. *Adaptation*

Beetles adapt their search behavior based on localized beetle densities and the availability of susceptible hosts. The likelihood that beetles search within either the current or nearby stands is higher when beetle densities are low and available hosts are high. However, as beetle densities increase and available hosts become depleted, the likelihood that beetles engage in long distance dispersal increases.

3.4.4. *Objectives*

The objective of each beetle in the model is to locate a susceptible host and ensue a successful attack. A successful attack allows beetles to produce young that, pending their survival over the winter, can disperse and find a new host the following year.

3.4.5. *Sensing*

During the insect dispersal stage, beetles sense whether a selected grid cell is suitable for locating a susceptible host by estimating the number of other beetles in that grid cell. This is akin to the use of a chemical communication system, whereby individual insects emit a pheromone plume when attacking a tree in order to attract other insects to assist in overcoming a tree's defensive mechanisms. However, once population levels become saturated (i.e., there is no more room for additional beetles in a tree), the insects begin to emit an anti-attractant chemical that signals to searching beetles that they need to look elsewhere.

3.4.6. *Interactions*

The main interactions in the model take place between (1) beetles and trees, where the former acts to attract additional beetles in order to overwhelm the tree so that they can reproduce, and (2) individual beetles whereby chemical communication assists in the host searching process.

3.4.7. *Stochasticity*

Stochasticity is present in defining agent state variables (e.g., beetle sex, tree DBH), dictating beetle dispersal behavior, and determining which beetles succumb to overwinter mortality. These are further indicated in the notation below. The sex of each beetle is determined by assigning a sex of either female or male with a likelihood of 66.6% or 33.3%, respectively. The diameter of a tree is determined by randomly sampling a normal distribution of tree diameters as defined by the input data. Diameter is then used to define resistance using a deterministic equation as defined by information in Shore and Safranyik (1992). Beetle dispersal includes stochasticity as grid cells are randomly selected to begin the dispersal phase of the model, and beetles randomly select grid cells within a defined neighborhood when selecting a new host. Finally, the model utilizes a normal distribution to determine the likelihood of eggs and mature beetles surviving until the next year.

3.4.8. *Observation*

At each time step of the model, data is collected on tree mortality and the number of beetles in each grid cell. This permits evaluation of emergent patterns of tree mortality and global values for tree mortality and insect survival.

3.5. *Initialization*

The initial state of the ABM at time $t = 0$ corresponds to a specific time period during a MPB infestation. The stage of the infestation can be endemic, incipient, or epidemic, but must include some MPB population in order to have beetle agents that can disperse to new hosts. Three model parameters require calibration for the initial state of the model: (1) survival – the percentage of MPB that survive the winter. This variable acts as a proxy for the impacts of cold temperatures on MPB mortality. (2) Resistance – a value assigned to each tree representing the number of beetles required to overcome its defensive mechanisms. The value for resistance for each tree is the result of an equation that describes the relationship between tree DBH and its resistance to attack. The calibration procedure evaluates different slopes of a curve defining this relationship. The resulting value is a proxy of how external climatic factors impact the ability of a tree to withstand attack. (3) Pheromones – a value representing the strength of chemical communication between beetles. A low pheromone value indicates that a relatively high number of beetles emit weak communication signals to other beetles for attracting them to a tree under attack, while a high pheromone value indicates that a low number of beetles can produce a strong chemical signal for assisting attack.

3.6. *Input data*

Input data for the model is required to be in the format of a gridded dataset containing the following information for each cell: number of trees, percent of trees that are either lodgepole pine or ponderosa pine, average DBH, and the number or percent of trees that were infested with MPB in a specific year. This information is used to create for each cell a specific number of tree agents, some of which are alive and others that are infested by MPB. All trees are given a value for DBH that is randomly drawn from a normal distribution surrounding the average DBH of the cell. Beetle agents are then created for each tree infested with MPB. The process of creating tree and beetle agents is repeated at the beginning of each time step because, as discussed in the following section, details pertaining to tree and beetle agents are aggregated at the conclusion of each time step as a means for improving computational efficiency and allowing for the implementation of the ABM on large datasets.

3.7. *Sub-models*

Each sub-model is represented in the flowchart in Fig. 1, and is described below.

3.7.1. *Dispersal*

The Dispersal sub-model consists of three functions, localDispersal(), communication(), and longDistanceDispersal(). The localDispersal() method is an operation utilized by beetles to locate a new grid cell in which they will seek trees to attack. For each cell (c_i) where at least one beetle i exists, all cells in neighborhood N_{ci} are evaluated to determine their likelihood for beetle attack. The search for a new cell is expressed as

localDispersal():

$$\begin{aligned}
&at_{cj} > 0 \rightarrow c_j \in N_{ci}\\
&ad_{cj} = 1 - (x \sim P(l_{ci} - l_{cj}))\\
&ak_{cj} = \frac{at_{cj}}{t_{cj}}\\
&ac_{cj} = ad_{cj} \times aw_{cj} \times ak_{cj}
\end{aligned} \tag{1}$$

where a new cell (c_j) with alive trees (at) greater than 0 is found within N_{ci}. Once a cell is found, a value is calculated from three cell characteristics to determine an attack threshold. The first characteristic is distance (ad), which is based on a random number (x) chosen from the empirical distribution P based on possible location l of cell c with beetle i, and the new location of the a new cell at location l_{cj}. Lower values for ad signify closer cells to the beetle's current location. The second characteristic is ak, which represents the proportion of the total number of trees t in the cell that are under attack at. Higher values of ak represent a cell with existing beetle infestations and hence a higher likelihood of attack. The third characteristic is aw, which uses the average DBH of a cell divided by the maximum average DBH of all cells in the study area. Larger values of aw equate to a larger threat to MPB attack because it represents a cell with larger diameter trees, and hence that stand a higher likelihood of attack. The susceptibility of the cell ac is the product of these three characteristics (ad, ak, and aw). Once cells in N_{i} are searched, the cell chosen is determined by:

$$c_{\mathrm{j}} \leftarrow ac_{\mathrm{cj}} \geq th \tag{2}$$

A cell where ac is greater or equal to the attack threshold (th) will enable beetles to travel to c_{j} for attacking new host trees. Adjustments to ac are then performed in the communication() method described as

communication():

$$ac'_{\mathrm{cj}} = ac_{\mathrm{cj}} + ph \tag{3}$$

where ph is a real number between 0 and 1 representing the increase in pheromone production. This variable is updated after each beetle is added to a cell in order to represent how the addition of individual beetles impacts communication strategies. The moment at which ac becomes larger than th represents the timing of when beetles reach capacity and switch from pheromone production to verbenone production in order to signal that additional beetles should search elsewhere for new host to attack. If no cells have capacity for additional beetles, longDistanceDispersal() is called to simulate beetles searching for new hosts beyond their immediate surroundings.

longDistanceDispersal():

$$\begin{aligned}
&at_{\mathrm{cj}} > 0 \rightarrow c_{\mathrm{i}} \subseteq N_{\mathrm{ci}}(|l_{\mathrm{ci}} - d_{\mathrm{cj}}|)\\
&ad_{\mathrm{cj}} = 1 - (x \sim P(l_{\mathrm{ci}} - l_{\mathrm{cj}}))\\
&ak_{\mathrm{cj}} = \frac{at_{\mathrm{cj}}}{t_{\mathrm{cj}}}\\
&ac_{\mathrm{cj}} = ad_{\mathrm{cj}} \times aw_{\mathrm{cj}} \times ak_{\mathrm{cj}} \leftarrow n_{\mathrm{cj}} > 0\\
&ac_{\mathrm{cj}} = ad_{\mathrm{cj}} \times aw_{\mathrm{cj}} \times ak_{\mathrm{cj}} \times 0.5 \leftarrow n_{\mathrm{cj}} = 0
\end{aligned} \tag{4}$$

where N_{ci} is a neighborhood determined by Euclidian distance between cell c_{i} and a cell at some distance (d). As before, ad is determined by the cell i's location (l_{ci}) and the new potential beetle location (l_{cj}) using an empirical distribution. All cells where $at > 0$ are returned. While this method has the same variables and is similar to localDispersal(), one key difference is ac is modified differently depending on if there are beetles (n) in c. The choice of cells is determined by:(5)$c_{\mathrm{j}} = \max(\{ac \ldots ac_{\mathrm{cj}+n}\})$where the cell with the maximum ac value is traveled to and trees attacked by beetles from c_{i}.

3.7.2. Insect–host interaction

Once all beetles have been assigned to a cell, the attack() method is called:

attack():

$$\begin{aligned}
&T_{\mathrm{cj}} \sim P(0, t_{\mathrm{cj}} \leftarrow ts_{t\mathrm{j}} = 1)\\
&s_{\mathrm{i}} = 1 :\\
&n_t = 1 \leftarrow n_t = 0\\
&n_t = attackTree() \leftarrow (n_t > 0\hat{s}_{\mathrm{i}} = 2)\\
&s_{\mathrm{i}} = 2 :\\
&n_t \leftarrow attackTree() \leftarrow (n_t > 0)
\end{aligned} \tag{6}$$

where a tree t is chosen from a random uniform distribution of all trees (T) that are alive ($ts = 1$) in a cell. If the sex (s) of an attacking beetle i is a female (i.e., $s = 1$), then a given number of attacking beetles (n) is determined for a tree based on the fact there are other beetles attacking the tree and other attacking beetles include at least one male (i.e., $s = 2$). For male beetles, other beetles must already be attacking the tree before the male commences attack. The treeMortality() sub-method is called:

treeMortality():

$$\begin{aligned}
&x_t = 0.4 + \frac{(0.4 \times n_t - 10)}{10}\\
&as_t = \frac{1}{(1 + e^{-12(x_t - r_{\mathrm{cj}})})}\\
&rn \sim P(0, 1)\\
&ts_t = 0 \leftarrow as_t > rn
\end{aligned} \tag{7}$$

which determines if a given tree survives ($ts = 0$; dead tree) based on cell resistance (r) and the effect of beetles attacking a tree (x). This is based on a given threshold (as) for tree survival to be greater than a random number (rn) chosen from a uniform distribution (P) between 0 and 1.0.Beetle survival

Beetle survival is determined by calculating the number of beetles that survive to the next time step. The survival() method is expressed as:

survival():

$$\begin{aligned}
&eg_t = nf_t \times (rn \sim P(\mu = 70, \sigma = 4))\\
&nl_t = eg_t \times m\\
&np_t = nl_t \times m\\
&na_t = np_t \times m\\
&n_t = 0.065 \times (na_t \times m)\\
&\forall s_i \in B_t : 2/3 \approx P(s_i = 1)
\end{aligned} \tag{8}$$

where a random number (rn) is determined from a normal distribution (P) that has a mean of 70 and standard deviation of 4 that determines the number of eggs for a tree (e.g.) based on the number of females in the tree (nf). These numbers are approximate representations of reproduction values presented by (Safranyik, 2003). Then final number of mature beetles (n) found in the tree in the next cycle is determined by the mortality parameter (m) calculated for a series of beetle lifecycle stages (nl, np, and na), with 0.065 representing a fixed mortality factor that determines which beetles survive. The final line in the above notation states that each new beetle from the total beetles (B) in t will have a 2/3 probability (P) of being female (i.e., $s = 1$). At the completion of each time step all beetles and trees are aggregated into summary values in each grid cell for computation efficiency. Aggregate values are then disaggregated onto individual beetles and trees at the commencement of the following time step. This process avoids the need to explicitly represent each agent throughout the duration of a model run, which releases a significant amount of computational memory, especially when using large datasets.

Fig. 2. Map of the location of the 10,000 ha study site in British Columbia.

The ABM of MPB infestation behavior was implemented on a gridded dataset representing a 10,000 ha forested area in central British Columbia (Fig. 2) that was significantly impacted during the early years of the current epidemic. The study site was selected by placing a 10,000 ha square over an area that demonstrated both early infestations during the temporal extent of the model as well as areas that experienced increasing infestations as time progressed. The study site is largely composed of lodgepole pine that ranges in age from 5 years to 140 years.

Each cell in the grid represents a 1 ha forest stand. Simulation runs were executed using Repast Simphony (2.0; code and data provide above) and applied to a high-performance cluster. The input data for the model is derived from two sources. Information on MPB-induced tree mortality was collected from the British Columbia aerial overview survey (AOS; British Columbia Ministry of Forests, 2000). The second data source is the Vegetation Resources Inventory (VRI) that provides data on multiple forest stand characteristics, including the number of trees and average diameter at breast height (DBH) over a given area (British Columbia Ministry of Sustainable Resource Management, 2002). The VRI data was converted from polygons to a cellular grid in order to match the AOS-derived data. Both datasets were analyzed in order to provide the number of trees per cell, the average DBH per cell, and the number of trees infested with MPB. The input data represents a start date of 2000, a year close to the beginning of the current epidemic. The model was run for six time steps, spanning years 2001–2006. The AOS-derived data on MPB-induced tree mortality was used for model calibration and validation.

Calibration was accomplished by performing a sweep of three parameters that govern beetle–tree interactions and survival. The parameters and their ranges were: beetle mortailty (m) = 0.0–0.5, pheromones (ph) = 0.0–1.0, and tree resistance (as) = 0.0–1.0. Annual tree mortality was then used as a measure to compare model runs against observation data. For each combination of parameter settings, a correlation coefficient was calculated to measure the similarity in tree mortality between each time step of the model and each year in the observation data. The selected parameter settings were then used for performing 100 runs of the model from which the mean and median tree mortality in each grid cell is compared against observation data.

4. Results

The calibration results involving the parameter sweep of mortality (m), pheromones (ph), and tree survival (as) are displayed in Fig. 3. The highest correlation value was 0.94565 for $m = 0.5$ (which translates into a 50% mortality rate), $ph = 0.7$ (depicting a relatively strong influence of chemical communication between beetles), and $as = 0.1$ (which corresponds to very low resistance to attack). Several other variable settings display correlation greater than 0.9, as seen in Fig. 3.

A comparison between annual tree mortality for observed data and the average tree mortality from the 100 calibrated modeled simulations is presented in Fig. 4. The model results display a similar trajectory of increasing tree mortality each year as compared to the observed data. While first-year estimates are higher and estimates for the remaining years are below observations, differences between model results and observations are relatively minimal given the total number for tree mortality occurring each year. This finding reveals that the calibration routine was effective at ensuring that the simulated outcomes are similar to those observed in the landscape.

Observed MPB-induced tree mortality for 2001–2006 is presented in Fig. 5. MPB activity is at its strongest in early years in the north and northwest part of the study site, and quickly spreads south and east to other cells. A notable observation is that not all cells exhibit tree mortality, likely because some areas do not contain susceptible hosts given localized beetle population numbers, or

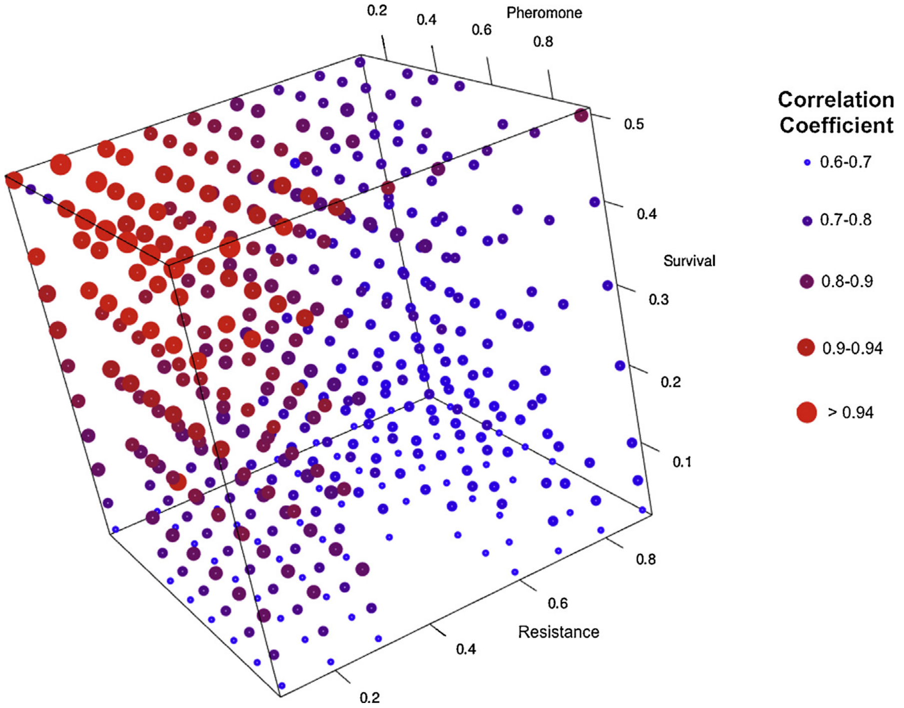

Fig. 3. Correlation results for parameter sweep of mortality (*m*), pheromones (*ph*), and beetle survival (*as*).

beetle behavior resulted in concentrations of tree mortality to specific cells. Average tree mortality from the 100 model runs using the calibrated parameters is displayed in Fig. 6. Similar to the observed data, tree mortality is highest in the northern part of the study site in early years and then exhibits a southward and eastward spread. Unlike the observed data, at least some tree mortality occurs in the majority of cells in the study site. A plausible explanation for this difference is that pheromone attraction as parameterized in the model is weaker than what exists in reality, causing tree mortality patterns to be slightly more spread out than in the observed data.

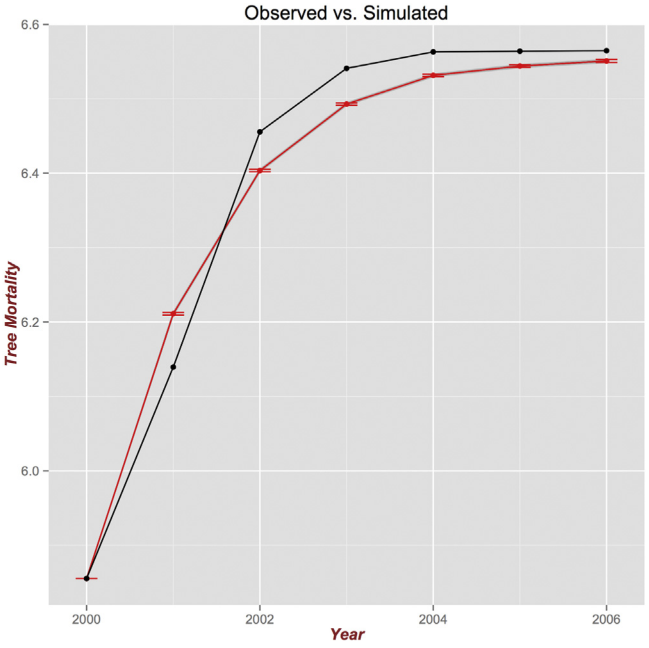

Fig. 4. Observed (black) and modeled (red) annual MPB-induced tree mortality. Modeled results are the average tree mortality over 100 runs. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

We evaluate the utility of the model by comparing the pattern of tree mortality for each time step of the model against the observed data. Fig. 7 displays the results from subtracting simulated tree mortality from observed tree mortality; higher values thus represent cells where the model simulated less mortality than was observed, while low values represent cells where the model simulated more mortality than was observed. Values closer to 0.0 indicate cells where the model simulates a relatively similar mortality to the observed data. The results exhibit a relatively low discrepancy between observed data and model results, with the model underestimating tree mortality in those cells where tree mortality observations are highest, and overestimating tree mortality in those cells that received little to no tree mortality.

The coefficient of variation of the 100 model runs is shown in Fig. 8. Model runs exhibit minimal variation in early time steps of the simulation, but increases throughout the study site over time. The spatial distribution of variation across the study site exhibits an increasingly clustered pattern each time step; these clusters emerge in areas where tree mortality is relatively low, demonstrating the greater variation in model simulation exists in areas receiving minimal infestation over time.

5. Discussion

The objective of this study is to enhance existing efforts to connect local scale processes with macro scale patterns of MPB infestations. Agent-based modeling presents a suitable means for attaining this objective because the modeling structure permits representation of individual objects such as insects and trees, and rules can be explicitly defined describing how such objects interact with each other over time to produce change. Given the behavior of MPB and insect–host interactions, it is not enough to estimate the number and spatial pattern of tree mortality based on susceptible areas or tree mortality in previous years. Insect disturbances are complex processes in which the positive feedbacks governing

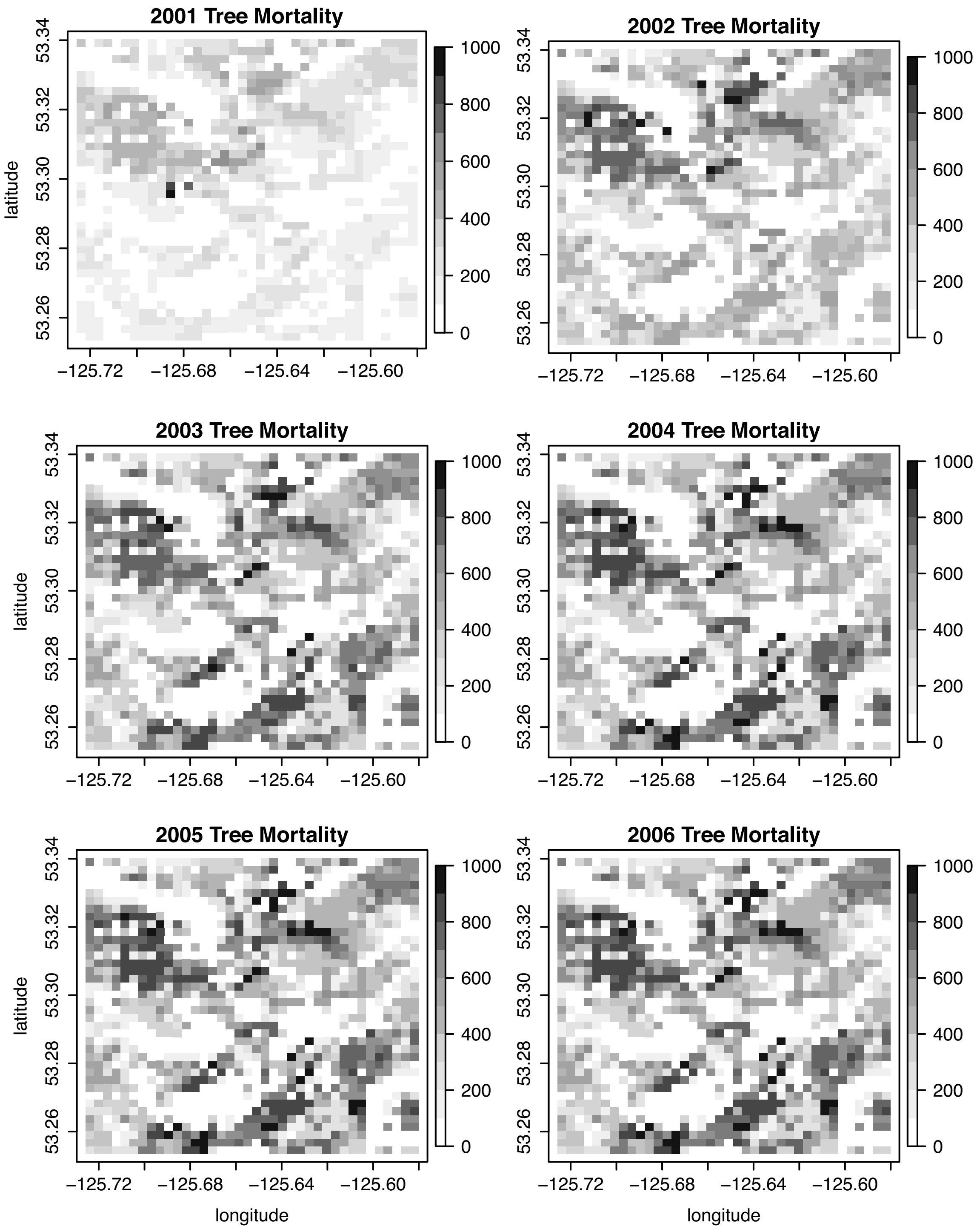

Fig. 5. Observed patterns of tree mortality in the study site from 2001 to 2006. Tree mortality represented in the color ramp represents number of trees killed in each 1 ha cell.

insect population growth and the negative feedbacks of host resistance and availability present tensions at multiple spatial and temporal scales. The explicit representation of individuals and their behaviors in a computational model provides a means to simulate how such feedbacks are imposed, and how they impact the overall pattern that emerges from system dynamics.

Our study advances existing research on complex systems modeling approaches for simulating MPB infestations (Bone et al., 2006; Perez and Dragicevic, 2010, 2011) by providing more efficient computation and a suitable method for calibrating parameters that govern simulation outcomes. Efficient computation comes by way of releasing the memory used to explicitly represent individual beetle and tree agents at the completion of each time step. Information pertaining to beetles and trees are aggregated to the level of the cell, and disaggregated in an appropriate fashion at the beginning of the next time step. This method of “memory dumping” takes place without loosing important information necessary for simulating the interactions among individual beetles and trees, as well as the communication between beetles, across the landscape. The results from the model implementation demonstrate that releasing

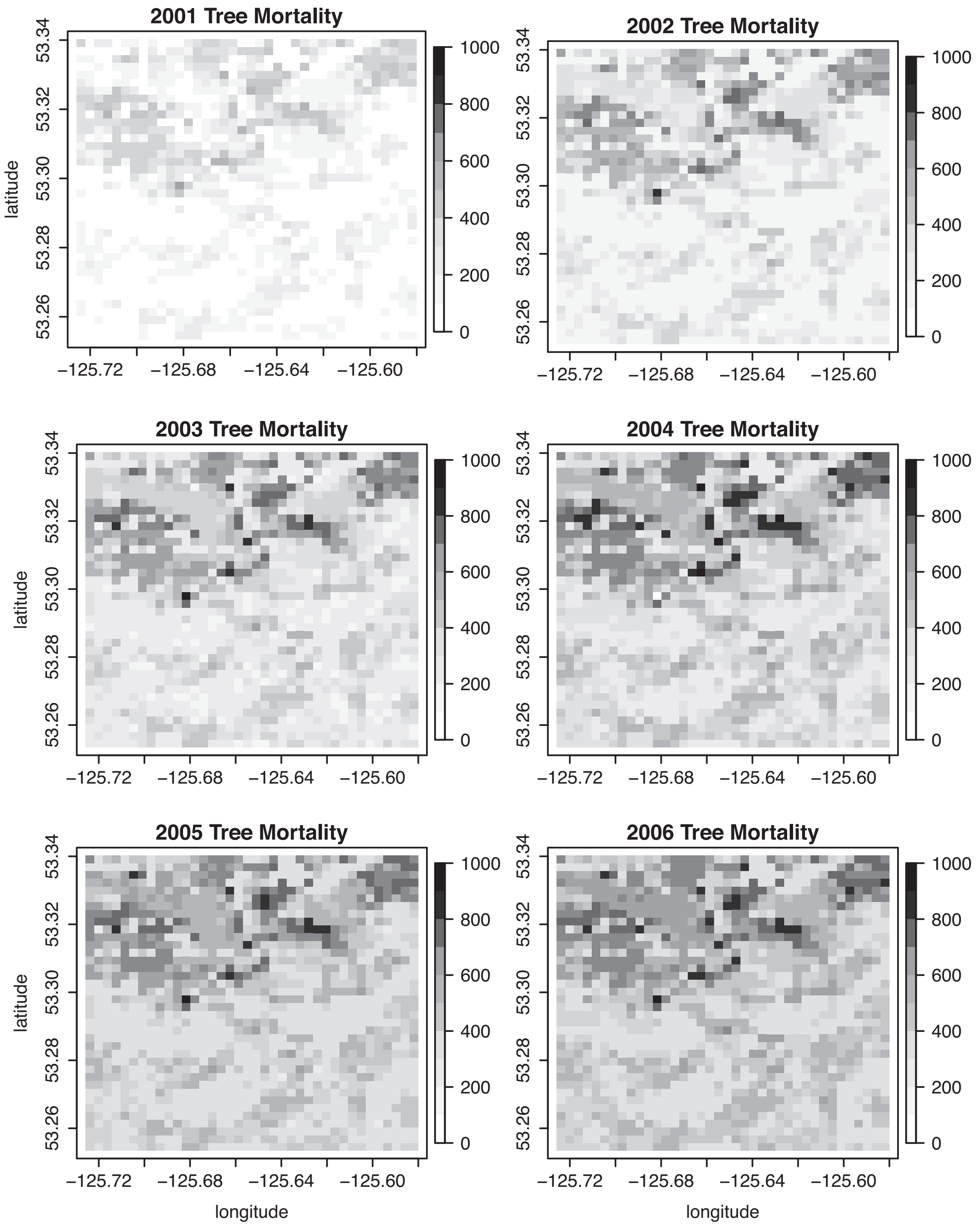

Fig. 6. Simulated patters of tree mortality for years represented 2001–2006. Values represent tree morality average over 100 model runs. Tree mortality represented in the color ramp represents number of trees killed in each 1 ha cell.

memory can occur without comprising the ability of the model to produce results that emulate the spread and attack behavior of MPB. Furthermore, distributing model parameter variations in a high-performance cluster enhances the speed of investigating the model's parameter space.

The results reveal that the ABM is able to simulate tree mortality numbers relatively similar to those observed from data collected through aerial surveys of MPB infestations. The calibration procedure assisted in determining parameter settings that provided a significantly high correlation between modeled results and observed data. The model was able to simulate relatively similar numbers of tree mortality, and a similar tree mortality trajectory over time. However, calibrating the model based on total tree mortality values leads to error in where tree mortality occurred in the landscape. The evaluation of tree mortality patterns revealed that the pheromone parameter did not simulate an optimal strength of attraction caused by pheromone communication as the model produced a less concentrated tree mortality pattern. To address this, future efforts for calibrating the model should focus on refining the process of simulated beetle dispersal that is governed by

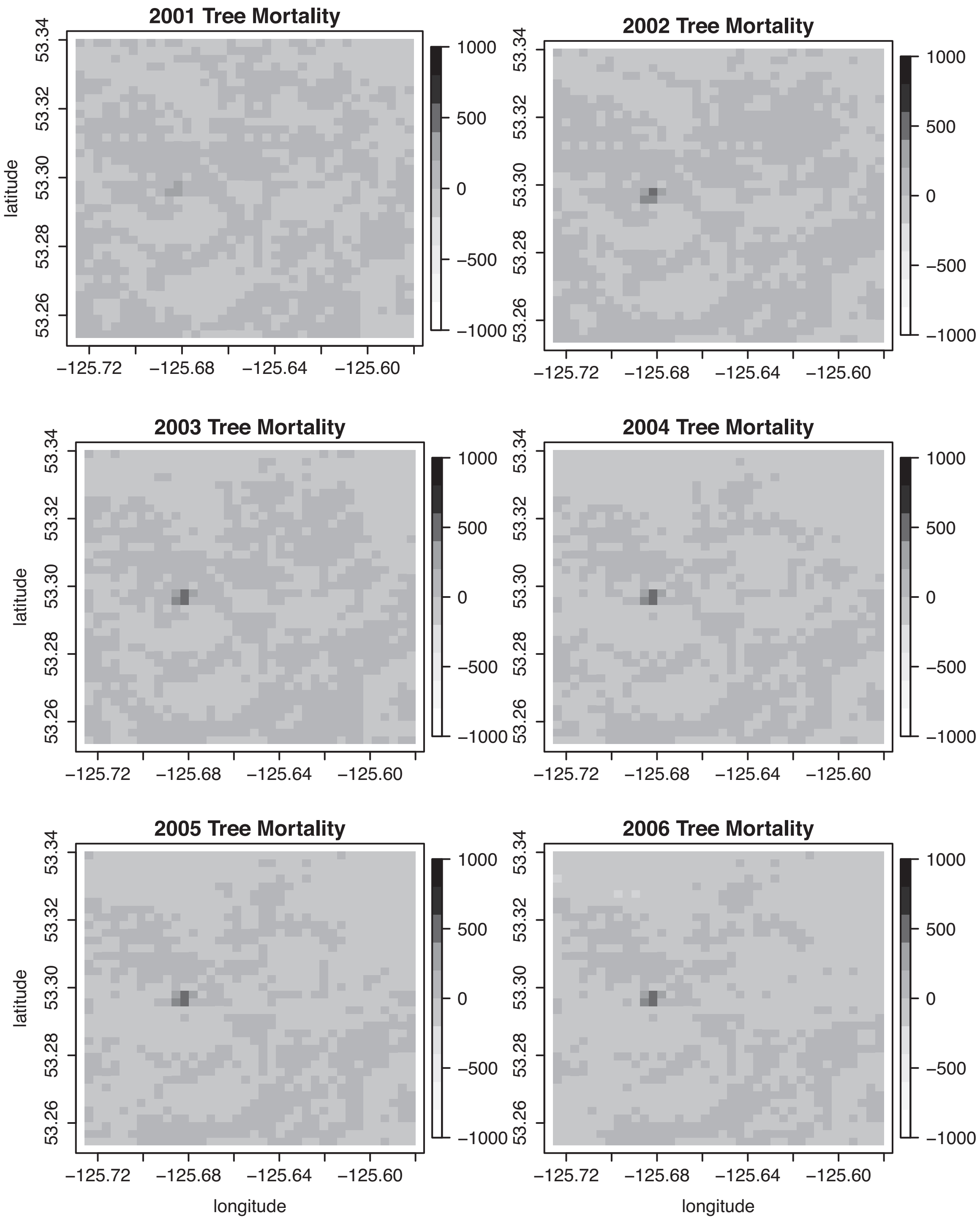

Fig. 7. Difference between observed and simulated tree mortality in each 1 ha cell. Lighter colors indicate cells where tree mortality was underestimated, while darker colors represent cells where tree mortality was overestimated.

pheromone communication. This can be accomplished by testing how varied findings from the literature on beetle dispersal impact overall outbreak patterns, and by testing the sensitivity of model outcomes to individual model parameters that influence beetle dispersal.

Moving forward, one of the challenges facing ABMs of insect disturbances is the ability to represent individual trees and insects at regional scales. This challenge is important to address as distant insect populations, especially in the case of MPB, have demonstrated spatial synchronization in their dispersal and attack behaviors over very large areas (Aukema et al., 2006). When synchronization between spatially segregated populations occur, the number of insects that can disperse into new areas can increase significantly. Thus, models need to be applied onto increasingly larger landscapes in order to address questions surrounding synchronization of insect behavior and its impacts on tree mortality. Models are also needed for simulating outbreaks over larger temporal extents in order to demonstrate transitions between endemic, incipient and epidemic states, which would require detailed representation of both insect population and forest vegetation dynamics. Currently

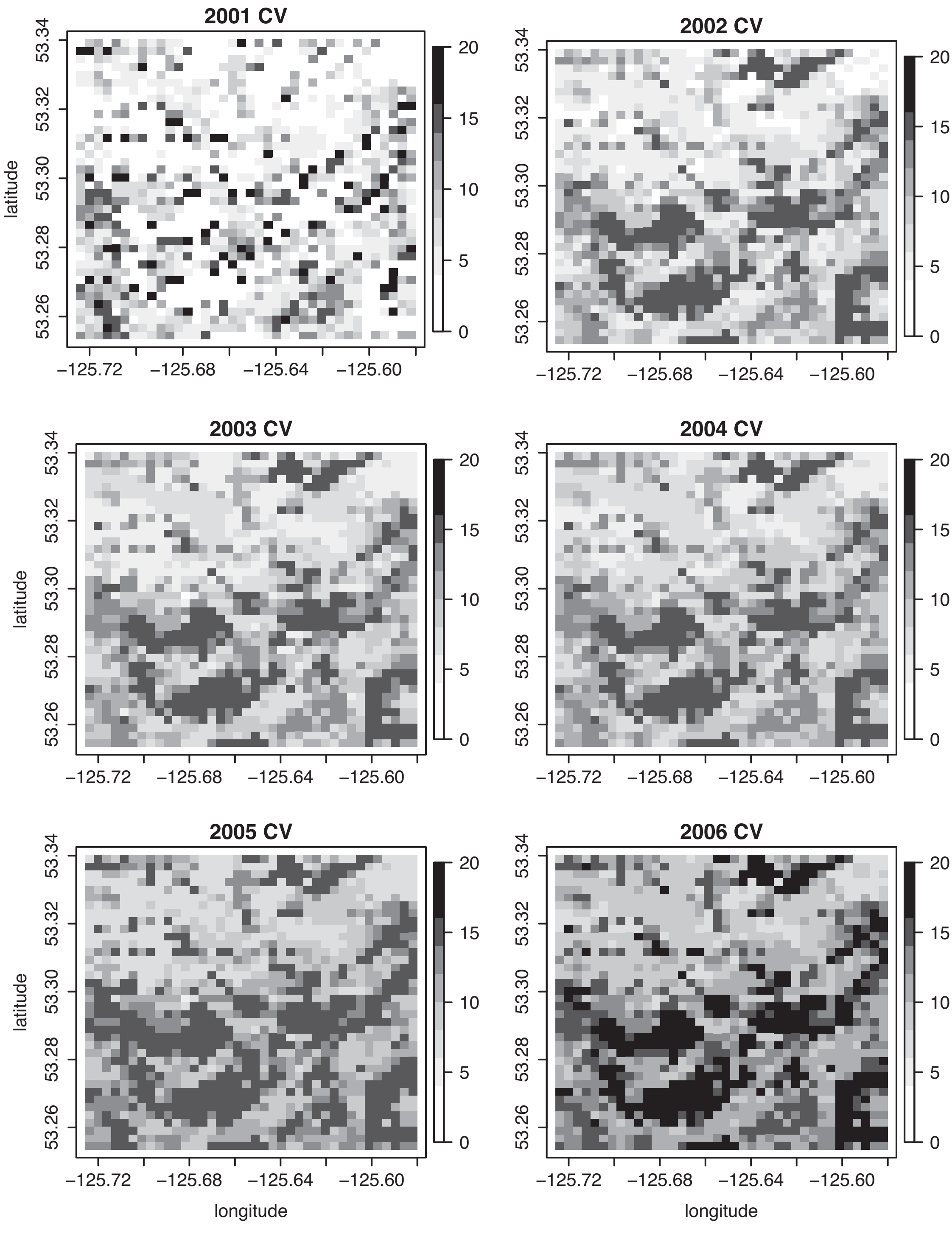

Fig. 8. Coefficient of variation of tree mortality from the 100 model runs for each 1 ha cell.

our model does not simulate changes to forest characteristics or structure as we assumed that the relatively short temporal extent of the simulations did not require explicit representation of how the forest changes over time and consequentially influences individual tree susceptibility. However, over longer time periods, representation of these dynamics cannot be ignored if measuring changes in beetle population levels is of interest.

Developing ABMs that can be applied on significantly large datasets requires advanced computational resources that permit simulating thousands of model runs and analyzing outcomes for providing meaningful findings. High-performance, distributed computing is becoming a necessity with large-scale modeling because various tasks can be partitioned amongst processors to allow for efficient simulation. However, minimal research exists that examines how distributing ecological processes across multiple processors can effectively represent the system being modeled. For example, one can distribute the several processes of the MPB lifecycle amongst multiple processors, but the degree to which the timing and sequencing of computation matches that of the ecological processes being simulated has yet to receive noteworthy attention in the literature. Several other methodological issues need to be addressed before ABMs become commonplace in modeling ecological processes across large landscapes, which include combining several bioclimatic variables that are represented at varying spatial and temporal resolutions; simulating beetle dispersal over ranges observed by field studies, such as the 30–110 km/day range recorded by Jackson et al. (2008); combining disparate data of the same variable (e.g., MPB-induced tree mortality) collected by different agencies or organizations; and representing the variety of processes, both human and ecological, that impact the large scale patterns of change. Keeping these issues at the forefront of future research on the use of ABM for large-scale MPB processes will help leverage the use of simulation models to address this significant ecological problem.

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