

Cyclic epidemics, population crashes, and irregular eruptions in simulated populations of the Mountain Pine Beetle, *Dendroctonus ponderosae*.

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Keywords

Mountain Pine Beetle; *Dendroctonus ponderosae*; agent-based model; cellular model

Abstract

The native Mountain Pine Beetle infests numerous native pine species in North America, and can cause extensive mortality when populations enter an epidemic state. We used an agent based cellular model of coupled beetle and host tree populations to investigate the effects on population dynamics of modifying three model components, representing factors that land managers have varying degrees of control over: number of host trees, health of host trees, and number of surviving beetle offspring. By varying model parameters corresponding to these three factors, we observed a range of population behaviors including regular spatially-spreading cycles of epidemics, sporadic epidemics, and beetle population crashes. The largest, recurring epidemics occurred in simulations with dense populations of mostly vigorous trees and moderately high beetle offspring production. The fewest epidemics occurred with low beetle reproduction, and low tree population density. With all other factors held constant, reducing the tree population below a threshold reduced the proportion of cells experiencing beetle population epidemics. These results are consistent with field observations of reduced tree losses to beetle epidemics in thinned forest stands.

1. Introduction

Native bark beetles with eruptive population dynamics, alternating between low-density endemic populations and large, high-density epidemic populations, are among the major disturbance types in temperate conifer forests (Bebi et al., 2003; Raffa et al., 2008; Veblen et al., 1994). Although population eruptions of these native insects may be viewed as part of the natural disturbance regime of forests, large scale epidemics generate intense public concern because of the potential for lost timber revenue (Dhar et al., 2016), impaired aesthetic and recreational value (Rosenberger et al., 2013), increased atmospheric carbon (Kurz et al., 2008; Logan and Powell, 2001), declining water quality (Mikkelsen et al., 2013), and a perceived risk of large forest fires (Hart et al., 2015). In addition, higher than average winter temperatures in recent decades have increased overwinter survival, leading to unprecedented outbreaks of several *Dendroctonus* species, exacerbating concerns regarding the impacts of native insect disturbances. For example, synchronized population eruptions of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins, hereafter MPB) in western North America have killed millions of hectares of several species of pine trees in the United States and Canada since the most

recent outbreaks began around in the mid-1990s (Raffa et al., 2008; Safranyik and Wilson, 2006).

Population eruptions that involve the transition from endemic to epidemic states often follow other disturbances, such as drought, fire, or storms, which can weaken trees and enhance the beetles' ability to attack host trees (Elkin and Reid, 2004; Marini et al., 2013; Raffa et al., 2008). In northern European forests, for example, after severe windstorms that cause large-scale tree death from windthrow, Norway Spruce bark beetle (*Ips typographicus*) populations take advantage of felled trees and transition into epidemics, resulting in the mortality standing healthy trees (Wermelinger, 2004). In North American forests, epidemic outbreaks of bark beetles with similar cyclical population dynamics in the genera *Ips* and *Dendroctonus* can be facilitated by previous disturbances such as drought and fire (Perrakis et al., 2011; Raffa et al., 2008). Recent large epidemics in western North America may also be related to climate trends such as warmer winters (Chapman et al., 2012).

The timing of MPB lifecycle events is heavily influenced by climatic factors, principally temperature (Bentz et al., 1991). In much of the MPB species range, low winter temperatures are the most prominent constraint on MPB survival. In some areas of the MPB range, minimum winter temperatures below -40°C and unseasonably cold temperatures during critical periods in the fall and spring cause widespread MPB mortality (Bentz et al., 1991; Safranyik and Carroll, 2006; Safranyik and others, 1978). Unusually mild winters can result in greater survival and larger populations of emerging beetles. Since the success of a MPB mass attack of a vigorous tree depends on the confluence of large numbers of beetles in a small area, beetle overwinter survival rates are critical to the transition of endemic populations to epidemics.

At low population levels, MPBs show preference for vigor-impaired trees that do not have the resources to fend off attacking beetles. When enough impaired trees are present, beetles can reproduce and increase their population sufficiently so that they are able to employ successful mass attacks on larger, more vigorous trees. These trees provide them with higher quality food and overwinter shelter, and hence help to further increase population numbers. Thinning forests at opportune times can halt the increase in beetle numbers by removing highly susceptible, vigor-impaired trees (Gillette et al., 2014). Studies also suggest that thinning interferes with the pheromone communication system used by MPBs. As beetles send chemical pheromones to one another in order to attract additional beetles to a tree already under attack, thinning may enhance wind flow through a stand, thereby disrupting the effectiveness of pheromones as a form of communication (Bartos and Amman, 1989; Logan et al., 1998).

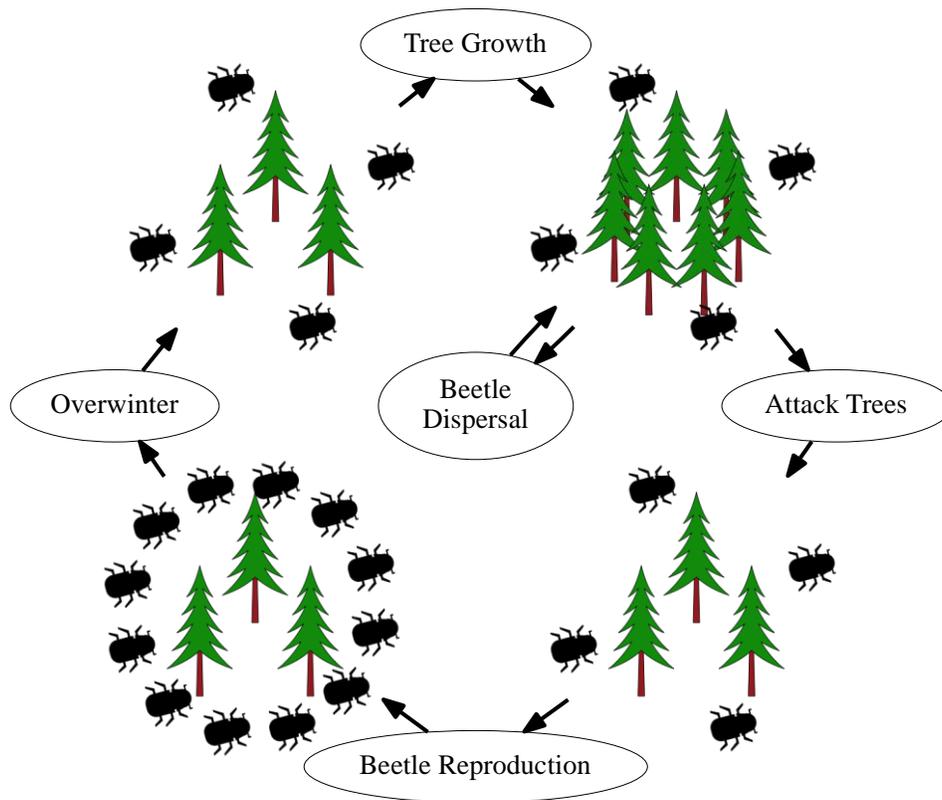


Figure 1 Conceptual diagram of major components of the beetle/host system.

Temperature mediated changes to MPB population are beyond the direct control of land managers. The primary tool available for the management of MPBs is thinning, i.e. reducing the number of trees per hectare. It is an indirect method that can increase the resistance of a tree, as well as a stand, to attack (Mitchell et al., 1983; Waring and Pitman, 1985).

Numerous disturbances affecting the transition between endemic and epidemic states in MPB populations, including temperature increase and drought resulting from climate change, attack from other beetles, and wildfire, have been studied via field observations, lab experiments, and modeling (e.g. Bentz and Jönsson, 2015; Bone and Altaweel, 2014; Perez and Dragicevic, 2012; Powell and Raffa, 2011; Trappe et al., 2009). While such studies provide insight into the drivers of MPB outbreaks, the majority of studies focus efforts on beetles in the epidemic state, and those that examine state transitions have only focused on the transition from endemic to epidemic populations. Although Louis et al (2016) emphasize that

understanding the dynamics of endemic populations that exist between outbreaks is equally important for understanding the entire system, few papers have examined the long-term cyclical nature of MPB.

The goal of this study is to characterize how stand-level tree and beetle population dynamics potentially respond to changes in forest conditions, some of which can be influenced by management practices, others of which are climatically controlled. Specifically, we investigate how the interactions among the number of surviving beetle offspring produced in vigor-impaired trees, the maximum number of host trees per hectare, and the ratio of vigorous to vigor-impaired trees, could affect the overall beetle and tree demographic patterns within a forest stand. We build upon previous MPB simulation work, which has mostly focused on single eruptions, by investigating temporal patterns of eruption dynamics over long time intervals. To accomplish this goal, we developed an agent-based model (ABM) of coupled MPB and host pine population to investigate regions of parameter space in which global model behaviors, such as regular or irregular beetle population eruption cycles, emerge from the interactions between MPBs and host trees.

2. Methods

2.1 The model

The following is a brief description of the components of the ABM developed for this study, which focuses the submodels that are most relevant to the objectives. For complete descriptions of all submodels and parameters, see the supplemental model description following the format of the Overview, Design concepts, and Details protocol (ODD) as specified in Grimm et al (2006, 2010), and the supplemental list of model parameters. The model was implemented in Java (version 1.8) using Repast Symphony libraries (North et al., 2013) that were used to stage individual simulation runs on a computing cluster. All analyses and graphics were created using R (R Core Team, 2016). The equations needed for all of the model algorithms and calculations are included in the supplemental ODD protocol.

The model consists of a grid of cells, each of which represents a 1-hectare square forest patch with coupled populations of pine trees and MPBs. The counts of beetles and host pines in each cell are state variables that change in response to model processes. Tree populations are immobile and do not interact directly with neighboring cells. Beetles, on the other hand, disperse to neighboring cells, thus mediating all among-cell interactions.

The beetle populations exist in two phases: (1) a mobile emerging/dispersing phase and (2) a stationary attacking/reproducing phase. In the first phase beetles that survived the winter emerge from their host trees and disperse in search of new hosts. In the second phase beetles attack potential hosts in the cells to which they dispersed and produce offspring that will emerge at the beginning of the following season (Figure 1).

Tree populations are subdivided into mature and immature trees, and a mature tree is then classified as vigorous (VT) or vigor-impaired (IT). Each year of the simulation, the cells' counts of VTs and ITs may be reduced by attacking beetles, reduced by age-related mortality, or increased by immature trees transitioning to a mature state. Beetles do not interact with the immature trees.

When mature trees are killed, they are replaced by a group of immature trees in a growth queue. Each group of immature trees spends 80 years in the queue after which they mature and are added to their cell's counts of VTs and ITs mature trees (ODD figure 1). The sum of all mature and immature tree on a cell is a constant set by a model parameter, which was varied between 200 and 2000 trees per hectare as described in the parameter sweep description below.

Emerging beetles may disperse to the 317 neighboring cells (the dispersal neighborhood) that fall within a 1km radius of the cell from which they emerge. Each cell has its own dispersal neighborhood, and the likelihood that beetles

emerging will travel to any cell in the neighborhood is determined by two factors: the distance from the emerging cell (i.e. the distance score) and an occupancy score calculated from the numbers of beetles and trees currently present in the cells. The distance scores decrease with increasing distance from the neighborhood center (ODD equation 5) representing the tendency for MPBs to preferentially disperse short distances (Safranyik et al., 1992).

Empty cells are only weakly attractive to beetles, but as beetles begin to arrive, the cells become more attractive to later-dispersing beetles. At first this creates a positive feedback until an optimum within-cell population is reached, after which point the arrival of additional beetles reduces the cell's attractiveness creating a negative feedback. These processes are a simplified representation of the density-dependent aggregating and anti-aggregating communication used by real MPBs (Safranyik and Carroll, 2006). Each cell's occupancy score is calculated from the counts of beetles and mature trees (ODD equations 4, 7, 8; ODD figure 2). The overall attractiveness of neighborhood cells to dispersing beetles is a weighted product of the distance and occupancy scores.

Mature trees are characterized by the minimum number of beetles required to successfully attack them and their maximum carrying capacity of beetles. MPBs begin the simulation attacking only the ITs (**B-IT**) but may transition to attacking VTs (**B-VT**) if both VTs and MPBs are present in sufficient numbers. ITs, which represent the weakened, resource-poor trees on which MPB populations subsist when they are in an endemic state require 10 beetles and have a carrying capacity of 300. Fewer beetles are required to successfully attack ITs, but VTs are a better food source, and therefore beetle reproduction is higher in VTs, which require 500 beetles to be attacked and have a carrying capacity of 1500 beetles. The beetles employ a mass attack strategy, whereby arriving beetles amass on a single tree, attempting to overcome its defenses. If too few beetles arrive to overcome the tree's attack threshold, the attack is unsuccessful, and the beetles die. If there are sufficient arriving beetles, the beetles continue to attack the tree until it reaches its carrying capacity, at which time the newly-arriving beetles select a new, empty tree to attack.

MPB populations have been observed to change their pattern of host selection when beetle population density is greater than approximately 300 – 500 beetles per hectare (Carroll et al., 2006). To mimic this transition, we defined a threshold of 500 beetles per hectare. Below the threshold beetles only attack ITs. If more than 500 attacking beetles arrive, and there are sufficient VTs, the cell will transition to an epidemic state in which beetles only attack the VTs. Although MPBs sometimes kill all host trees within stands during an epidemic, more commonly the mortality is not total (Safranyik and Carroll, 2006). To simulate this aspect of MPB epidemics, cells remained in an epidemic state until the density of VT hosts fell

below 10 per hectare, at which time the beetles transition back to only attacking ITs. Vigor-impaired trees require the arrival of 10 beetles to be successfully attacked, and have a carrying capacity of 300 beetles.

Dispersing beetles emerge from each cell in six daily batches, termed cohorts. In between cohorts, each cell updates its occupancy score and recalculates the relative attractiveness scores of all the cells in its dispersal neighborhood. The peak emergence of mountain pine beetles from trees in a stand typically lasts between 7 to 10 days (Safranyik et al., 1975). To represent emergence over a relatively short period, the daily dispersal of MPBs is for a dispersal period of 5 days, consisting of 30 total cohorts. Immigration of beetles from outside the area is mediated by a long-distance dispersal submodel, in which approximately 1000 randomly chosen cells receive packets of beetles, with an average size of 1000, each time step.

At the end of the active season, MPBs kill successfully attacked trees and reproduce. Beetles in VTs (B-VT) produce a mean of 35 offspring while the mean number of offspring in ITs was variable (Safranyik and Carroll, 2006; see parameter sweep description below). Lodgepole pine stands typically become susceptible to MPBs when the pines are between 80 to 100 years old (Safranyik and Carroll, 2006). To simulate the regrowth of trees, each killed tree is placed into a maturation queue and scheduled to become susceptible to MPBs between 78 and 80 years in the future. Trees staged for regrowth in the queue are not visible to beetles until they mature, at which time they are assigned a vigor status.

2.2 Parameter Sweeps

Three parameters were independently varied among simulations: the number of surviving offspring in ITs (**'fert'**), the proportion of newly maturing trees that are IT (**'vig'**), and the maximum number of trees per hectare (**'dens'**). Individual female beetles typically lay 60 – 80 eggs and mortality is typically within the range of 85 – 98 % (Safranyik and others, 2003). We, therefore, varied mean surviving offspring in ITs between 1.1 and 15 per beetle to bracket the observed range of surviving beetles. The classification of pines as VT or IT in real forest stands is difficult, however Carroll et al. (2006) estimated that approximately 30% – 70% of pines in lodgepole pine stands had at least one potential vigor-impairing injury. We varied the proportion of ITs of 0% – 100% assuming that not all of those putative vigor-impairing injuries affect the trees' suitability to MPB reproduction. Our range of potential mature trees per hectare (200 – 2000) brackets the range of stems per hectare observed in lodgepole pine stands by Carroll et al. (2006).

For each simulation, values of each of the three parameters were chosen uniformly and randomly from within the ranges described above. To gain a high-resolution picture of model behavior in the 3-dimensional parameter space, 5000

independent simulations were run for 1000 yearly time steps. All simulations were run on square grids of 200 x 200 cells (40,000 cells total). To avoid edge effects, grid edges wrapped to create an edgeless toroidal surface.

2.3 Initial conditions

Each simulation was initialized with a pulse of new trees set to begin regenerating in year 25 of the simulation (Figure ODD-2). This represented a forest in which a stand-replacing disturbance happened approximately 55 years before the beginning of the simulation. The cells in each patch were initialized with a randomly generated Poisson number of beetles ($\lambda = 50$) attacking ITs.

2.4 Simulation Long-Term Behavior: Behavior Schemata

To characterize the types of long-term behavior observed in the model simulations, we used three, non-mutually-exclusive, binary schemata to classify model runs focusing on different aspects of the results. **Schema 1** contrasted simulation runs in which the mean number of MPBs attacking IM trees was lower than the mean number of MPBs immigrating into the model from outside the area (80000 MPBs per year; '**crash**' runs) with simulations in which the mean number of MPBs was higher than 80000 but in which MPBs never transitioned to attacking VTs ('**endemic**' runs). **Schema 2** concerned those simulation runs with recurring cycles of transitions between beetles attacking ITs and VTs. Runs were classified by the standard deviation of the inter-cycle period over the last 500 simulation years with '**regular**' simulations having standard deviations of less than 12.0, while '**erratic**' simulations had standard deviations above 12.0 (Figure 2). **Schema 3** also classified runs having cyclic dynamics but focused on the mean length of the cycle length in the final 500 simulation years. In schema 3, '**short**' cycles were classified as having a mean period of 60 years, while '**long**' cycles were greater than 60 years, but shorter than 120 years (Figure 2).

[Insert Figure 2 here]

Figure 2. Histograms of the mean and standard deviation of the inter-epidemic cycle periods.

2.5 Summary Statistics: Population Indices

To summarize the patterns observed in the population dynamics in the individual model simulations, we developed the following three indices: 1) An epidemic index, **EP**, calculated as the number of cells with B-VT divided by the total number of simulation cells (Equation 1). 2) An index of B-VT (**BV**; Equation 2). 3)

An index of B-IT (**BI**; Equation 3). When calculating **BV** and **BI** for individual simulations, the values were normalized by the value of **Dens** for that simulation and the total number of cells in the simulation (40000) to create an index analogous to the number of beetles in each individual tree.

Equation 1

$$EP = (\# \text{ cells with B-VT}) / (40000)$$

Equation 2a

$$BV = (\text{sum of B-VT in all cells}) / (40000 * \text{Dens})$$

Equation 2b

$$BI = (\text{sum of B-IT trees in all cells}) / (40000 * \text{Dens})$$

Although model simulations were run for 1000 annual time steps, many individual simulations required several hundred burn-in steps before settling into a regular pattern. We thus treated the first 500 steps as a burn-in period and the three indices were calculated for each of the final 500 years in each simulation. The average values of the indices for each simulation over the final 500 simulation years were used for visualization in the parameter space.

2.6 Analyses: Classification and Regression

To analyze the system behavior of the model simulations in the parameter space, we used support vector machine (SVM) classification and regression models (Meyer et al., 2017). To analyze the system behavior of the model simulations in the parameter space, we used support vector machine (SVM) classification and regression models. Support Vector Machines (SVMs) are machine learning algorithms that were originally developed to classify samples into one of two possible categories based on their characteristics, i.e. their features. SVMs have since been extended for use with more than two categories as well as for regression modeling of continuous responses. SVMs are useful for data that exhibit complex and nonlinear patterns, which are not amenable to traditional regression techniques.

We created SVM regression models to visualize the three population indices in the 3-dimensional parameter space. To visualize the 3-dimensional decision boundaries for the simulation types in the three schemata, we created SVM classification models. In all SVMs, the predictors were the three variable model parameters (*fert*, *vig*, and *dens*). The SVMs were trained using 75% of the model simulation data and the remaining 25% was used to assess the models' performance. Based on preliminary, exploratory model building, models using Gaussian kernels and epsilon-regression or C-classification model types for the

population index regression and schemata classification, respectively, outperformed other configurations, and so these were used for further analysis.

3 Results

3.1 Simulation Behavior Types: Schemata

Relatively few simulations, ca. 15%, met the criteria for Schema 1. Of these, the majority were simulations resulting in population crashes (Table 1). In these crash simulations, the only beetles present were those arriving via long-distance immigration that did not establish breeding populations, and the tree populations reached stable equilibria (Figure 3a). In the endemic simulations, immigrating beetles had self-sustaining populations for some portions of the simulation, resulting in fluctuations of the tree populations (Figures 3b, c). Although these simulations did not have cyclic epidemic outbreaks, the population dynamics were linked to the tree time-to-maturity with population cycles having intervals of approximately 80 years (Figures 3b, c). Population crashes occurred, not surprisingly, when *fert* was below approximately 4.5, regardless of the values of the other parameters (Figure 4). A few crashes also occurred near the plane *vig* = 100% (Figure Schema 1 param. space). In the parameter space, the small number of endemic simulations clustered near the *vig* = 0 plane, evenly distributed with respect to the other two parameters.

[Insert Figure 3 here]

Figure 3. Tree and Beetle population dynamics for selected, representative individual simulations. (a) a typical ‘crash’ simulation. (b) an example of an ‘endemic’ simulation with cyclic population dynamics. (c) an ‘endemic’ simulation with self-sustaining and non self-sustaining periods. The dotted line in the beetles panel shows the mean number of beetles arriving via long-distance immigration submodel (the self-sustaining threshold). The dotted line in the trees panel is at 40000, the number of cells in the simulation, corresponding to an average of 1 tree per cell.

[Insert Figure 4 here]

Figure 4. 3D parameter space visualizations for Schema 1 simulations (top row) and the indices of beetles per vigorous (BV) and vigor-impaired trees (BI). 2D plots are slices of parameter space. Contour lines are either SVM decision boundaries (black lines) or SVM regression isosurfaces (rainbow color lines).

[Insert Figure 5 here]

Figure 5. Selected individual simulation population dynamics plots. (a) a simulation with regularly spaced (Schema 2), mid-length (Schema 3) epidemics. (b) a simulation with irregular epidemics. (c) a simulation with regularly-spaced short cycle epidemics.

[Insert Figure 6 here]

Figure 6. Spatiotemporal spread and collapse of an epidemic outbreak (black cells, in which beetles are attacking vigorous trees) through a simulated 100 by 100 toroidal grid.

Most of the simulations resulted in recurring cycles with periods of beetles attacking ITs alternating with epidemics. Simulations with regularly-spaced epidemic cycles tended to have epidemic outbreaks at approximately 80-year periods (Figure 5a). In the simulations with recurrent epidemic cycles, the typical outbreak was initiated by an increase in the numbers of ITs and/or VTs, followed closely by an increase in B-IT that allowed their populations to overcome the VT attack threshold some cells (Figures 5a, b). Following the initiation of an outbreak phase in a cell or cluster of cells, the outbreak spread radially outward, eventually exhausting the VTs in the center, forming an expanding donut shape that eventually swept across the whole landscape (Figure 6). A subset of simulations that had recurring epidemics were examined for the spatial characteristics of the spreading epidemics, and in most cases the epidemics swept across the entire grid as in Figure

6 (not shown). Regularly-spaced epidemics generally occurred immediately following the maturation of large numbers of trees.

In contrast, in the simulations with more erratically spaced epidemics the mature trees persisted in large equilibrium populations for longer periods between epidemics (Years 780 – 900 in Figure 5b). In these simulations, forest conditions were perched at a critical state, vulnerable to stochastic events pushing the MPB populations above the VT attack threshold in enough cells to start an epidemic. The same pattern of increasing IT/VT populations followed by beetle population booms and a transition from B-IT to B-VT were present in the Schema 3 simulations, the key difference being that the mid-cycle simulations developed approximately 80-year epidemic cycle (Figure 5a) while the short-cycle simulations usually had secondary, often smaller, epidemic episode in between the 80-year cycles (contrast Figures 5a, c).

The decision boundaries for the erratic/regular periods and mid/short return intervals of epidemics were both complex 3D surfaces that differed from each other (Figures 7, 8). Erratic return intervals tended to occur at mid to high values of *dens* while regularly spaced intervals tended to occur in the regions where *fert* was high and *dens* was low (Figure 7). High tree density was also associated with short return intervals, while simulations near the plane at *dens* = 100 tended to have periods closer to the tree regeneration time (Figure 8). Although high/low values of *dens* were very generally associated with different sides of the boundaries, the boundaries were not perfectly aligned with each other such that in different regions of the parameter space, different combinations of the classes in schemata 2 and 3 were predicted. For example, a simulation with *dens* = 2000, *fert* = 15, and *vig* = 0.5 is expected to have short but erratically-spaced epidemic return intervals. Keeping *fert* and *vig* the same, but changing *dens* to 200, the predicted outcome would be for longer, but still erratic return intervals. Although the two decision boundaries were different, they did share some general features, producing some regions in parameter space with consistent characteristics. Both surfaces very roughly divided the *dens* axis in two with short and erratic cycles occurring together at high densities and mid length regular cycles at lower densities (Figures 7, 8). This correspondence was strongest at mid to high values of *fert*.

[Insert Figure 7 here]

Figure 7. 3D parameter space views for simulations as classified under Schema 2. Interpretation and symbols are as described in figure 4.

[Insert Figure 8 here]

Figure 8. 3D parameter space views for simulations as classified under Schema 3. Interpretation and symbols are as described in figure 4.

[Insert Figure 9 here]

Figure 9. 3D parameter space views for the index of epidemic cells (Epi). Interpretation and symbols are as described in figure 4.

Schema	1		2		3	
SVM Model Prediction Accuracy	99%		72%		82%	
Class	crash	endemic	regular	erratic	short	long
Count	660	105	1832	2329	2078	2014

Table 1. Summary of Support Vector Machine decision models

3.2 Simulation Summary Stats: Population Indices

The indices for B-VT and B-IT (BV and BI, respectively) were relatively insensitive to changes in the density of host trees throughout much of the parameter space, as illustrated by the parallel orientation of the isosurfaces with respect to the tree density axis (Figure 4). BI was greatest at low values of *vig* and high values of *fert*. As with BI, the BV isosurfaces were mostly parallel to the tree density axis, indicating that the number of beetles attacking individual trees doesn't vary with the numbers of available trees, i.e. *dens*. (Figure 4). Intuitively, the main difference between the surfaces for BI and BV were that there were the most beetles per impaired tree when there was high beetle fertility and few vigorous trees, while the greatest beetles per vigorous tree occurred when most trees were vigorous. The shapes of the contours for the isosurfaces for BI and BV did not correspond to the decision boundary curves for any of the Schema indicating that the mean number of beetles per tree is not related to the long-term behavior of the system.

In contrast to the beetle indices, which were determined mostly by the interaction of offspring counts and proportion of VTs, the proportion of epidemic cells was determined by complex interactions of all three parameters as demonstrated by the complex shapes of the isosurfaces in Figure 9. The epidemic cell count was maximized at moderately high values of *vig* and high values of *dens*.

Not surprisingly, there were few epidemic cells when all three parameters were low; but, notably, epidemic cells could be lowered at high levels of *fert* and *vig* by reducing the density of trees per hectare. The lack of a maximum of EP when all parameters were maximized since while there are many VTs available for MPB to colonize, there were too few ITs in which an incipient MPB population could take hold, so epidemics were relatively rare.

Unlike the patterns for BI and BV, there was some correspondence between the Epi isosurfaces and the shapes of the decision boundaries for Schemata 2 and 3. The regions of high Epi roughly corresponded to areas in parameter space where short, erratically-spaced epidemic cycles were common. The region of greatest overlap was with moderate to high proportions of vigorous trees (approx. 40 – 100%), moderate to high *fert* (> approx. 4) and densities above 1000 trees/ha. Intuitively it is logical that these parameter combinations could result in shorter cycles, because there are many vigorous trees available, from the combination of high *dens* and *vig*, and beetles are quickly able to take advantage of spikes in populations of ITs because of their high *fert*. The cycles in this may be more irregular (and with shorter return intervals) because of the high number of constantly maturing VTs means that there are often sufficient numbers of VTs to support an epidemic, as opposed to simulations with a smaller number of VTs maturing outside of the main pulses.

4 Discussion

Our model captured numerous aspects of the population dynamics seen in the MPB/pine host system and was rich enough to generate very different long-term behaviors among simulation runs. Real populations undergo transitions between four phases (Carroll et al., 2006), resulting in cyclic epidemic outbreak populations that spread outward from an origin in space and time, eventually collapsing to pre-epidemic levels. The expanding epidemic fronts, with collapsing populations in the center generated by the model (Figure 6) are idealized representations of the spatial spread of MPB epidemics. The phases of the tree/MPB population dynamics with brief incipient epidemic phases with increasing B-IT populations coupled to tree maturation, followed by epidemic and population collapse phases are apparent in the temporal evolution of the model's coupled populations before, during, and after the cyclic outbreaks (Figure 5). Varying parameters allowed the model to exhibit different behavior regimes, with differences in regularity and length of epidemic cycles occurring in the simulations (Figure 5).

Several insights, which are not captured in models of a single epidemic, emerge from the long-term behavior of the model. In our formulation, the MPB and tree populations were tightly coupled, but the initiation of individual epidemics was

completely driven by the tree population dynamics. Whether the period of the epidemic outbreaks was highly regular or erratic, the initiation of the transition to B-VT always required the high populations of both VTs and ITs that were only present after many trees completed their maturation cycle. In the case of the irregular epidemics, tree populations reached large populations, temporarily at equilibrium. The system was then perched at a critical state, susceptible to stochastic fluctuations in the B-IT populations, waiting for sufficient MPB to accumulate in one or a few cells to transition to the B-VI state.

Another key insight was that in a model with only two tree classes, it was very difficult for endemic populations of B-IT to exist for long periods. Out of 5000 simulations, only 25 met our criteria to be classified as endemic. However, even within these few endemic simulations, the populations of MPB tended to spend much of the time below the self-sustaining threshold, with only fleeting periods in which the location population exceeded the number of immigrants (Figure 3). These brief self-sustaining periods generally coincided with the simultaneous maturation of large numbers of ITs (Figure 3). It is important to note that the simulations in which these endemic populations persisted at all were situated at an extreme of the parameter space (Figure 4). They could only exist when the proportion of VTs remained near zero, a scenario easy to create and maintain in a model, but probably an unrealistic long-term steady-state for real forests, managed or unmanaged. In most of the parameter space, the positive feedback generated by increasing MPB populations was too strong to avoid epidemics and allow beetle and tree populations to maintain long-term equilibrium populations.

In addition to the tree maturation process, long-term dispersal of MPB into the simulation area from outside the model was a critical driver of MPB population dynamics in the model. Even in those simulations with recurrent epidemics, outside immigration was required to supply sufficient MPBs when conditions became favorable for the incipient-epidemic phase to begin. Prior to the parameter sweep, during the model development phase, it was observed that without immigration, most resulted in complete population crashes, either immediately or after one or two epidemic cycles. This was the case even for parameter combinations that were extremely favorable to MPB such as high values of *fert* and *dens*. This phenomenon is apparent in the individual simulation population dynamic plots with recurrent epidemics, in which the number of B-IT was below the number of immigrants, and the numbers of trees per cell were very low, for much of the duration of simulations (Figure 5).

Interpreting the model outputs in the context of real forests generates several possible consequences for management. First, the three parameters varied in the sweep represent aspects of the forest over which managers have varying degrees of control. The density of trees per hectare, *dens*, is the easiest for managers

to manipulate, via thinning, while the proportion of vigorous trees may be indirectly managed but is subject to many external factors, and it is probably not possible for managers to influence the number of MPB offspring produced. Thinning, analogous to reducing *dens* in the model, is recommended as a tool to reduce tree loss to MPBs (Fettig et al., 2014; Gillette et al., 2014). These recommendations are supported by observations of reduced tree mortality in thinned forests (e.g. (McGregor et al., 1987; Mitchell et al., 1983; Whitehead and Russo, 2005).

The model results generally concur with these recommendations, and they suggest that thinning is most effective in very dense forests (Figure 9). In the simulated forests, decreasing *dens* generally reduced the epidemic index (Epi) when tree density was greater than approximately 1000 trees per hectare across much of the range of the *vig* and *fert* parameters. Below that density, however, further thinning produced much smaller reductions in Epi, suggesting that resources spent on thinning moderately dense forests may be better directed to dense forests. In the model, reducing *dens* was most effective for values of *fert* greater than approx. 3 (Figure EPI c), but estimating this parameter directly in real forests would be difficult for managers. Some factors, however, such as mild winters are understood to increase MPB overwinter survival, and that information may help managers make educated guesses about when and where thinning could be effective or not.

As with any model, care must be taken when not to overinterpret the results in the context of real forests. In these simulations, we considered relatively small, forested areas in isolation. The only interaction with areas outside the simulated region was via the immigrating packets of beetles (via the Long-Distance Dispersal submodel, see the supplemental ODD protocol). In addition, the simulated areas were toroidal to avoid edge effects. However, in real forests MPB epidemics spread via contagion and many managed forest patches of the sizes considered here exist in the context of larger contiguous forested areas, which may have abrupt and/or gradual boundaries. Expanding the maximum possible simulated area via further model code optimization and parallel computing would enable investigation of model behavior over greater spatial extents.

Incorporating spatial and temporal heterogeneity in the environmental parameters of the model would allow to explore, for example, whether small refugia in which MPB reproduction is always higher serve as sources for epidemics in surrounding managed regions. In this situation, beetles may be able to enter the managed patch in high enough numbers to surpass the requirement of an incubation period in ITs and attack the VTs directly. This could result in major losses, even though the results of the patch under consideration was in a state that in this model would not have been a candidate for a beetle epidemic.

Like all models, ours makes numerous implicit and explicit assumptions and simplifications, especially in the representation of trees. There is already a rich

tradition of mathematical and agent-based models of the MPB-pine system, each of which focuses on different aspects. For example, Safranyik et al. (1999) created a model of MPB population dynamics that explicitly considers host tree size classes, rather than a simple VT/IT representation. A more sophisticated submodel of tree growth taking into account tree sizes, such as a gap model (Pretzsch et al., 2015; Shugart and West, 1977) could be developed within our model.

A key advantage of a modeling approach, however, is to be able to examine how aspects of a real system are captured via simplified abstractions. Therefore, comparing the behavior of this model to future versions that incorporate more detailed submodels will provide a valuable opportunity to directly compare model behavior with differing levels of detail in the tree growth submodel. It is important to distinguish models that are designed to predict real phenomena from those that are created to gain insight into how systems may work, such as the model we present here (Epstein, 2008). From our simple model, a range of behaviors reminiscent of the variability of MPB dynamics in real forests emerged. It provides a stepping stone from which further model elaborations and refinements can help focus on different aspects of the MPB-pine system.

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6. References

- Adler, D., Murdoch, D., and others (2018). rgl: 3D Visualization Using OpenGL.
- Bartos, D.L., and Amman, G.D.; (1989). Microclimate: an alternative to tree vigor as a basis for mountain pine beetle infestations (Ogden, UT, United States: USDA Forest Service Intermountain Research Station).
- Bebi, P., Kulakowski, D., and Veblen, T.T. (2003). Interactions between fire and spruce beetles in a subalpine rocky mountain forest landscape. *Ecology* *84*, 362–371.
- Bentz, B.J., and Jönsson, A.M. (2015). Modeling bark beetle responses to climate change. *Bark Beetles Biol. Ecol. Native Invasive Species Acad. Press San Diego CA* 533–553.
- Bentz, B.J., Logan, J.A., and Amman, G.D. (1991). Temperature-dependent development of the mountain pine beetle (Coleoptera: Scolytidae) and simulation of its phenology. *Can. Entomol.* *123*, 1083–1094.

- Bone, C., and Altaweel, M. (2014). Modeling micro-scale ecological processes and emergent patterns of mountain pine beetle epidemics. *Ecol. Model.* 289, 45–58.
- Carroll, A.L., Aukema, B.H., Raffa, K.F., Linton, D.A., Smith, G.D., and Lindgren, B.S. (2006). Mountain pine beetle outbreak development: the endemic—incipient epidemic transition. *Pac. For. Cent. Vic. BC* 27.
- Chapman, T.B., Veblen, T.T., and Schoennagel, T. (2012). Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. *Ecology* 93, 2175–2185.
- Dhar, A., Parrott, L., and Heckbert, S. (2016). Consequences of mountain pine beetle outbreak on forest ecosystem services in western Canada. *Can. J. For. Res.* 46, 987–999.
- Elkin, C.M., and Reid, M.L. (2004). Attack and Reproductive Success of Mountain Pine Beetles (Coleoptera: Scolytidae) in Fire-Damaged Lodgepole Pines. *Environ. Entomol.* 33, 1070–1080.
- Epstein, J.M. (2008). Why Model? *J. Artif. Soc. Soc. Simul.* 11.
- Feng, D., and Tierney, L. (2008). Computing and Displaying Isosurfaces in R. *J. Stat. Softw.* 28.
- Fettig, C.J., Gibson, K.E., Munson, A.S., and Negrón, J.F. (2014). Cultural practices for prevention and mitigation of mountain pine beetle infestations. *For. Sci.* 60, 450–463.
- Gillette, N.E., Wood, D.L., Hines, S.J., Runyon, J.B., and Negrón, J.F. (2014). The once and future forest: Consequences of mountain pine beetle treatment decisions. *For. Sci.* 60, 527–538.
- Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., and Railsback, S.F. (2010). The ODD protocol: A review and first update. *Ecol. Model.* 221, 2760–2768.
- Hart, S.J., Schoennagel, T., Veblen, T.T., and Chapman, T.B. (2015). Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. *Proc. Natl. Acad. Sci.* 112, 4375–4380.
- Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T., and Safranyik, L. (2008). Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452, 987–990.
- Logan, J., and Powell, J. (2001). Ghost Forests, Global Warming, and the Mountain Pine Beetle (Coleoptera : Scolytidae). *Am. Entomol.* 47, 160–173.

- Logan, J.A., White, P., Bentz, B.J., and Powell, J.A. (1998). Model analysis of spatial patterns in mountain pine beetle outbreaks. *Theor. Popul. Biol.* *53*, 236–255.
- Louis, M., Toffin, E., Gregoire, J.-C., and Deneubourg, J.-L. (2016). Modelling collective foraging in endemic bark beetle populations. *Ecol. Model.* *337*, 188–199.
- Marini, L., Lindelöw, Å., Jönsson, A.M., Wulff, S., and Schroeder, L.M. (2013). Population dynamics of the spruce bark beetle: a long-term study. *Oikos* *122*, 1768–1776.
- McGregor, M.D., Amman, G.D., Schmitz, R.F., and Oakes, R.D. (1987). Partial cutting lodgepole pine stands to reduce losses to the mountain pine beetle. *Can. J. For. Res.* *17*, 1234–1239.
- Meyer, D., Dimitriadou, E., Hornik, K., Weingessel, A., and Leisch, F. (2017). e1071: Misc Functions of the Department of Statistics, Probability Theory Group (Formerly: E1071), TU Wien.
- Mikkelsen, K.M., Dickenson, E.R., Maxwell, R.M., McCray, J.E., and Sharp, J.O. (2013). Water-quality impacts from climate-induced forest die-off. *Nat. Clim. Change* *3*, 218–222.
- Mitchell, R.G., Waring, R.H., and Pitman, G.B. (1983). Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *For. Sci.* *29*, 204–211.
- North, M.J., Collier, N.T., Ozik, J., Tatara, E.R., Macal, C.M., Bragen, M., and Sydelko, P. (2013). Complex adaptive systems modeling with Repast Symphony. *Complex Adapt. Syst. Model.* *1*, 3.
- Perez, L., and Dragicevic, S. (2012). Landscape-level simulation of forest insect disturbance: Coupling swarm intelligent agents with GIS-based cellular automata model. *Ecol. Model.* *231*, 53–64.
- Perrakis, D.D., Agee, J.K., and Eglitis, A. (2011). Effects of prescribed burning on mortality and resin defenses in old growth ponderosa pine (Crater Lake, Oregon): Four years of post-fire monitoring. *Nat. Areas J.* *31*, 14–25.
- Powell, E.N., and Raffa, K.F. (2011). Fire Injury Reduces Inducible Defenses of Lodgepole Pine against Mountain Pine Beetle. *J. Chem. Ecol.* *37*, 1184–1192.
- Pretzsch, H., Forrester, D.I., and Rötzer, T. (2015). Representation of species mixing in forest growth models. A review and perspective. *Ecol. Model.* *313*, 276–292.
- R Core Team (2016). R: A Language and Environment for Statistical Computing (Vienna, Austria: R Foundation for Statistical Computing).

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., and Romme, W.H. (2008). Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions. *BioScience* 58, 501–517.

Rosenberger, R.S., Bell, L.A., Champ, P.A., and White, E.M. (2013). Estimating the economic value of recreation losses in Rocky Mountain National Park due to a mountain pine beetle outbreak. *West. Econ. Forum* 12, 31–39.

Safranyik, L., and Carroll, A.L. (2006). The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In *The Mountain Pine Beetle: A Synthesis of Its Biology, Management and Impacts on Lodgepole Pine.*, (Pacific Forestry Centre, Victoria, British Columbia, Canada: Canadian Forest Service), pp. 3–66.

Safranyik, L., and others (1978). Effects of climate and weather on mountain pine beetle populations.

Safranyik, L., and others (2003). Mountain pine beetle epidemiology in lodgepole pine. In *Mountain Pine Beetle Symposium: Challenges and Solutions*, pp. 33–40.

Safranyik, L., and Wilson, W.R. (2006). *The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine* (Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC).

Safranyik, L., Shrimpton, D.M., Whitney, H.S., and others (1975). An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Canada. *Manag. Lodg. Pine Ecosyst.* 1, 406–428.

Safranyik, L., Linton, D.A., Silversides, R., and McMullen, L.H. (1992). Dispersal of released mountain pine beetles under the canopy of a mature lodgepole pine stand. *J. Appl. Entomol.* 113, 441–450.

Safranyik, L., Barclay, H.J., Thomson, A., and Riel, W.G. (1999). *A Population Dynamics Model for the Mountain Pine Beetle, Dendroctonus Ponderosae Hopk.* (Coleoptera Scolytidae) (Pacific Forestry Centre Victoria, Canada).

Shugart, H.H., and West, D.C. (1977). Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. *J. Env. Manage* 5, 161–179.

Trappe, M.J., Cromack Jr, K., Trappe, J.M., Perrakis, D.D., Cazares-Gonzales, E., Castellano, M.A., Miller, S.L., and others (2009). Interactions among prescribed fire, soil attributes, and mycorrhizal community structure at Crater Lake National Park, Oregon, USA. *Fire Ecol.* 5, 30–50.

Veblen, T.T., Hadley, K.S., Nel, E.M., Kitzberger, T., Reid, M., and Villalba, R. (1994). Disturbance Regime and Disturbance Interactions in a Rocky Mountain Subalpine Forest. *J. Ecol.* *82*, 125–135.

Waring, R.H., and Pitman, G.B. (1985). Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* 889–897.

Wermelinger, B. (2004). Ecology and management of the spruce bark beetle *Ips typographus*—a review of recent research. *For. Ecol. Manag.* *202*, 67–82.

Whitehead, R.J., and Russo, G. (2005). “Beetle-proofed” lodgepole pine stands in interior British Columbia have less damage from mountain pine beetle.