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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