Impacts of management on Mountain Pine Beetle spread and damage: A process-rich model

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ABSTRACT

The Mountain Pine Beetle (MPB, *Dendroctonus ponderosae*) is a major forest pest at epidemic densities, capable of killing entire stands of mature pine. There are a variety of tactics used by forest managers to control MPB epidemics, but the ecology of the insect and the large scale of MPB infestations make it difficult to evaluate the effectiveness of any management strategy. Using a partial differential equation framework, we develop a mathematical model describing the interactions between beetles, beetle pheromone, and susceptible trees across multiple years. We use our mathematical model to examine the effectiveness of various existing management approaches used to limit the spread of the MPB. In particular, our study focuses on management activities that were used in Banff National Park, in Alberta, Canada. Comparing the indirect controls of prescribed burning and clearcutting, we found the success of these methods is critically dependent on the level of MPB attraction to, and productivity in, partially burned trees. Our analysis also indicates that pheromone baiting in combination with tree removal is successful at reducing MPB impact at high beetle densities, but may lead to greater forest impact and greater MPB population growth at low beetle densities. Finally, we found that removal of beetle-attacked trees in the absence of baiting is the most successful strategy if managers are able to locate areas with significant MPB activity.

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1. Introduction

The Mountain Pine Beetle (MPB, *Dendroctonus ponderosae*) is an aggressive bark beetle that has had a major economic impact on the forestry industries in Canada and the United States. At endemic (low population) levels this beetle is a minor pest, killing trees weakened by drought, root rot, or lightning strikes (Powell et al., 2000; Safranyik and Wilson, 2006). In contrast, at epidemic levels, thousands of hectares of healthy, mature trees can be rapidly killed (Powell et al., 2000; Safranyik and Wilson, 2006). The widespread economic impact of the MPB has led to extensive management efforts, involving direct and indirect control (Fettig et al., 2014; Safranyik and Wilson, 2006). Indirect control aims to remove beetle habitat, while direct control aims to remove beetles (Fettig et al., 2014).

Indirect control methods often involve the creation of large gaps in the uninfested forest to act as dispersal barriers or obstructions (Barclay et al., 2005; Fettig et al., 2014). We consider two common methods of indirect control: prescribed burning and clearcutting (Safranyik and Wilson, 2006). Under prescribed burning, trees at the periphery of fires may be only damaged rather than killed, and these trees may be more attractive to the MPB than undamaged trees (Elkin and Reid, 2004; Fettig et al., 2008; Jenkins et al., 2014; Kulakowski and Jarvis, 2013; Powell et al., 2012). Other confounding factors are fire-induced changes in resin defenses (Reid, 2007), possibly higher reproductive MPB output (Powell et al., 2012) and the presence of other insects that inhabit weakened trees and compete with the MPB (Fettig et al., 2008; Tabacaru and Erbilgin, 2015).

Direct control can be implemented through the removal of individual trees containing beetles (Coggins et al., 2011; Fettig et al., 2014). These trees, termed "green attack" because the needles are still green, need to be visually detected from the ground. To increase the efficiency of finding such trees on the landscape, MPB pheromones may be used to bait trees and concentrate beetles into known locations. These locations are then searched and infested

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trees are felled and burned prior to the emergence of beetles (Fettig et al., 2014). Direct control methods are less destructive to the landscape than indirect control methods, but implementation is challenging because the insect spends most of its life cycle hidden beneath the bark making it difficult to locate infested trees at the landscape scale (Coggins et al., 2011).

For any control method, implementation must occur at the landscape scale, and so rigorous assessment of the effectiveness of the control method is very difficult. Equivalent forest and MPB environments are difficult to locate and, when comparisons are made, there are many confounding factors that make evaluation of any strategy problematic (Coggins et al., 2011; Trzcinski and Reid, 2008). Without reliable predictions for the effectiveness of any management intervention, it is impossible to determine whether or not the cost incurred is warranted. There is thus a very real need for models that can test and assess control methods *in silico*, cheaply and without irreversible damage to the landscape (Liebhold and Tobin, 2008). We develop such a model in this paper and use it to assess the effectiveness of current management approaches used to limit the spread of the MPB. In particular, we use the model to elucidate the effects of management activities applied in Banff National Park (Banff NP).

Parks Canada employed pheromone baiting and tree removal over multiple years, after the MPB were found at high densities in the park in 1997 (Dalman, 2003; Trzcinski and Reid, 2008). Prior to the initiation of control efforts, Banff NP was divided into two treatment zones, one in which MPB control efforts were applied and one in which MPB activity was simply monitored. Comparison of the two zones over the subsequent seven years revealed that the management activity limited the long-distance spread of the MPB, but did not reduce the area of lodgepole pine affected (Trzcinski and Reid, 2008). It is not certain, however, that the observed differences were due to the management activity as there were inevitable differences between the two zones, the most significant of which was a larger area of dense, susceptible lodgepole pine in the management area. In addition, it is not clear even how the control method could have led to the observed pattern. The Banff study highlights the need for a mathematical model to test the effects of management efforts.

Due to the importance of the MPB to the forestry industry, the interaction between MPB and lodgepole pine trees has been extensively studied. MPB models have investigated several processes including beetle phenology and temperature (Powell and Bentz, 2009), beetle–host tree interactions (Nelson et al., 2008; Raffa and Berryman, 1986), tree susceptibility (Shore and Safranyik, 1992), spatial spread of MPB (Berryman et al., 1984; Burnell, 1977; Geiszler et al., 1980; Heavilin and Powell, 2008; Polymenopoulos and Long, 1990; Strohm et al., 2013), and management impacts (Hughes et al., 2006; Powell et al., 1998; Riel et al., 2004; Safranyik et al., 1999; White and Powell, 1997). Few models however, have looked at beetle populations across multiple years. Of those that have, we are aware of no models that explicitly include both winter population dynamics and summer dispersal, including the interactions between beetles, beetle pheromones, tree kairomones (volatile chemical cues), and the forest landscape. These interactions however, are key determinants in the spread dynamics of the MPB.

Patterns of MPB spread will differ based on the whether the population is at endemic, incipient epidemic, or epidemic levels (Boone et al., 2011; Safranyik and Wilson, 2006; Strohm et al., 2013). Our results specify density of the source trees (from which MPB emerge) or the space between source trees as a measure of MPB density. Source tree density and source tree spacing is easier to measure for managers and practitioners than are beetle densities.

In this paper, we present a multi-year spatially explicit mathematical model (Section 2.2) for beetle spread and population growth. We test the effectiveness of the management strategies

of prescribed burning (Section 2.3.1) and baiting and tree-removal (Section 2.3.2). We find that (Section 4) among the indirect management strategies investigated, prescribed burning is more effective than monitoring and can be more effective than clearcutting if partially burned trees are not more attractive to MPB than unburned trees. Among the direct management strategies considered, tree removal alone, without baiting, is best, as long as the search region is large enough and at least 80% of infested trees in each search region are removed. Baiting with tree removal is almost as effective as tree removal alone at high MPB densities, but is worse than doing nothing when MPB densities are low.

2. Methods

2.1. Study system

The MPB preferentially uses lodgepole pine (*Pinus contorta* var. *latifolia*) as its host (Safranyik and Wilson, 2006). What distinguishes the MPB from most other tree pests is that it must kill the host in order to successfully reproduce. The beetles land on the host tree, then burrow through the bark to reach the nutrient-rich phloem, where they dig vertical galleries. The eggs laid in the galleries produce larvae that feed on the phloem, cutting off the tree's nutrient pathways. Consumption of the phloem tissue is almost always sufficiently extensive enough to cause tree death and the pine needles turn red by the following summer. Trees with reproducing beetles are termed "green-attack" trees, while trees that recently produced beetles are termed "red-attack" trees. Living lodgepole pines defend themselves against MPB attack by producing resin that exudes from attack holes, engulfing and killing attacking beetles and any eggs that are laid (Reid and Gates, 1970). MPB populations must therefore attack in sufficient numbers to overwhelm host defenses initially and subsequently kill the tree (Franceschi et al., 2005).

The life cycle of the MPB is generally univoltine (one generation per year) (Safranyik and Wilson, 2006), dependent upon ambient temperature. Eggs are generally laid from late July to mid-August, and these eggs hatch and typically develop through four larval instars prior to winter (Safranyik and Wilson, 2006). Development resumes in spring with maturation to adult completed by late June to mid-July. Adults emerge from the (now dead) tree in mid-July to mid-August and fly in search of a suitable (live) host tree. Search flight involves chemotactic movement toward semiochemicals produced by MPBs and potential host trees (Borden et al., 1987; White and Powell, 1997). In particular, once established (nesting) under the bark MPBs produce a suite of pheromones that are attractive to dispersing MPBs at low concentrations and repulsive at high concentrations (Borden et al., 1987; Miller et al., 2005). This switch in attractiveness enables mass attack but prevents too much competition with conspecifics. Host trees produce kairomones that are strictly attractive and may provide important cues for MPB selection of a susceptible tree (Miller and Borden, 2000).

2.2. Mathematical model

Our model consists of a summer model and a winter model. The summer model is a continuous set of reaction–diffusion–chemotaxis equations (1) for the beetle flight, emergence, and attack period (July–August). The winter model is a discrete set of difference equations (2) for the overwintering period (September-June). Existing theoretical and empirical work (Powell et al., 1998; Raffa and Berryman, 1983) informed the selection of functional forms and parameter values. We chose the partial differential equation framework as it allowed us to include