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Assessing the effectiveness of Alberta's forest management program against the mountain pine beetle

Final report for fRI Research project 246.18 parts 1 and 2

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Executive Summary

Between 2006 and 2016, nearly $500 million was spent on direct control efforts in Alberta to slow the eastward spread of the mountain pine beetle (MPB), and yet the efficacy of these efforts was unknown. This report details the results of a two-phase project initiated to evaluate the efficacy of MPB management in Alberta. Three distinct, but interrelated research activities were conducted. We employed empirical data provided by Alberta Agriculture and Forestry and Industrial Partners (Alberta Newsprint Company, Alberta Pacific Forest Industries, Canfor, Millar Western Forest Products, West Fraser, Weyerhaeuser) to (i) develop a model to predict the productivity of MPB (*r*; the number of offspring per female beetle) in relation to forest, climate and topographical conditions (*r*-model), and (ii) directly assess the efficacy of direct control efforts to reduce local MPB populations. We combined the *r*-model, control efficacy assessment, forest inventory and climatic data to (iii) develop a spread model (MPBSpread) to evaluate the relative impact of the current versus alternative control strategies at slowing the spread of MPB across north-central Alberta.

The *r*-model was developed using a long-term, extensive data set comprising MPB productivity assessments (*r*-values) conducted by Alberta Agriculture and Forestry forest health staff. The data were derived over 9 years from >1,600 plots spread across most of western Alberta. Tree diameter (DBH) was determined to be the most important variable for predicting MPB productivity. Other significant variables included minimum winter temperatures, and elevation and latitude. Minimum winter temperatures were positively correlated with MPB productivity through their impact on over-winter mortality of larvae; however, the influence of winter minimum temperatures was dependent upon the diameter of infested trees. Small-diameter trees afforded thermal protection to MPB during mild winters (minimum temperatures ≥ -35°C), but not during cold winters (minimum temperatures < -35°C). Due to the extensive spatial and temporal nature of the *r*-value data, the complete *r*-model is highly robust and accurate, explaining approximately 86% of the annual variation in MPB productivity. The potential value of the *r*-model to forest managers for targeting and prioritizing stands for direct control has led to early adoption and implementation by Alberta Agriculture and Forestry.

The efficacy of direct control at limiting the growth of local MPB infestations was assessed using data on the annual location and intensity of Level 1 (i.e. detection and destruction of individual infested trees) treatments applied from 2007-2013 by Alberta Agriculture and Forestry. To ensure appropriate comparison of treated to untreated populations, we isolated individual infestations from the larger pool of survey data taken across north-central Alberta. Individual 'parent' infestations were identified within each survey year based upon proximity to one another using a data-derived grouping distance of 750m. The efficacy of Level 1 treatments were evaluated by examining subsequent MPB attack intensity in 1km and 2km zones of influence (ZOI) surrounding treated and untreated parent polygons. The extent to which green-attack (i.e. newly infested) trees were detected

and removed in treated stands (detection efficiency) was also examined using sequential years of survey data. Our analysis revealed three key findings. First, detection efficiencies (for green-attack trees in treated parent polygons) were surprisingly low ranging from 54-68% in non-immigration years and 38-44% in immigration years. With a green-attack detection/treatment rate of ≤68%, suppression of a MPB outbreak is impossible if its rate of increase exceeds 3-fold annually. Moreover, if detection/treatment rates do not exceed rates of MPB increase by a large margin, successful suppression will take many years. Second, felling and burning infested trees (Level 1 control) was effective in reducing subsequent MPB attack intensities in both 1km and 2km ZOI areas, but treatment efficacy declined with increasing intensity of MPB attack in parent polygons. Third, direct control efforts led to an average reduction in subsequent attack intensity of 41% within the 1km ZOI area and 33% within the 2km ZOI area; however, there was significant variability in treatment effects within and between years. The rate of treatment (% of parent MPB polygons treated) had a substantial impact upon the success of the treatments, suggesting that during years with relatively low rates of direct control, beetles from nearby untreated areas move into ZOI areas around treated polygons. We conclude that felling and burning of infested trees can be an effective means of limiting the local growth and spread of MPB populations provided (i) efforts are devoted to increase detection efficacy, (ii) inasmuch as possible, treatment is applied early, before infestations begin to grow, and (iii) treatments are aggressive and consistent from year to year.

The results of our MPB productivity model and direct control efficacy assessments were incorporated together with vegetation inventory and climatic data to create a model of MPB spread through Alberta pine forests and thereby evaluate the relative impact of the current versus alternative control strategies at slowing the spread of the beetle. MPBSpread is a spatially explicit cellular automata model that simulates MPB spread through application of a series of rules describing beetle behavior in relation to infestation and host characteristics. These rules are used to calculate, from one year to the next, the probability of colonization from an occupied cell to suitable but unoccupied 'recipient' cells. The model was validated against data from central British Columbia (using MPB productivity associated evolutionary experienced pine), and modeled spread and impact projections were in close agreement with documented outcomes. In Alberta, empirical data on area colonized agreed well with MPBSpread predictions (using MPB productivity associated evolutionary naïve pine) under the ongoing slow-the-spread (StS) scenario. Area colonized by MPB was almost always lower under StS than a "do nothing" scenario (DN), and separation between the two scenarios increased over time such that by 2018, StS had reduced area colonized to roughly 70% of that predicted under DN. Area colonized was particularly sensitive to the efficacy of early detection and eradication, and the amount of level 1 control (single tree treatments), but not level 2 control (clear cut harvesting). Furthermore, under StS, the size of the infestation in year 1 (pine infested ha^{-1}) had a significant impact on the total area of infested pine after 10 years, but there was no such relationship under DN, further indicating the benefits of direct control.

Our analyses indicate that efforts to date to slow the eastward spread of MPB across Alberta have achieved some success. We have also shown that improvements could be achieved through better efficacy at the detection and treatment of small infestations. We recommend that future research efforts be devoted to improved survey methods for on the ground green-attack detection

Table of Contents

Executive Summary 2

1.0 Introduction 7

2.0 The *r* model: predicting MPB productivity from stand, site and climate characteristics 9

- 2.1 Introduction 9
- 2.2 Methods: Predicting *r* from stand and site conditions 9
  - 2.2.1 Dataset development 9
    - 2.2.1.1 Data screening 11
  - 2.2.2 Analysis of climate relationships to *r*-values 11
  - 2.2.3 Statistical analyses 11
- 2.3 Results & Discussion 12
  - 2.3.1 Relationship between infestation size and *r* 12
  - 2.3.2 Relationship between stand and site factors and *r* 13
  - 2.3.3 Relationship between DBH, *r*-value and over-winter survival 14
  - 2.3.4 Relationship between location temperature effect (LTE) and *r* 15
  - 2.3.5 Relationship between climate and *r* 15
- 2.4 Development of the predictive *r* model 17
- 2.5 Conclusions 18

3.0 Assessment of the efficacy of Level 1 treatment using spatial survey and treatment data 20

- 3.1 Introduction 20
- 3.2 Methods 21
  - 3.2.1 Identifying isolated infestations for spatial analysis 22
  - 3.2.2 Determining the zone of influence around parent infestations 24
  - 3.2.3 Calculating treatment efficacy 24
  - 3.2.4 Determining detection efficiency 25
- 3.3 Results & Discussion 26
  - 3.3.1 Detection efficiency 26
  - 3.3.2 Treatment effects on attack intensity 27
- 3.4 Conclusions 28

4.0 Evaluating the efficacy of current and alternative management actions to control mountain pine beetle, using the MPBSpread model 30

- 4.1 Introduction 30
  - 4.1.1 Current control efforts 30
- 4.2 Methods 31
  - 4.2.1 Model structure 31
  - 4.2.2 Core elements 31
  - 4.2.3 Calculating P*i,t* and annual colonization 35

4.2.4 Model validation 37
4.2.5 Simulating MPB control tactics 38
4.2.6 Assessing treatment efficacy 39
4.3 Results 41
4.3.1 Model validation 41
4.3.2 Evaluating control efforts 41
4.3.2.1 “Slow-the-spread” versus “do nothing” 41
4.3.2.2 “Slow-the-spread” versus alternative control scenarios 41
4.3.2.3 Assessing the importance of early detection 41
4.4 Discussion 44
4.4.1 Model validation 44
4.4.2 Assessing control measures 45
4.4.2.1 ‘Slow-the-spread” versus ‘Do nothing’ 45
4.4.2.2 Enhancing control efficacy 46
5.0 General Discussion & Conclusions 48
6.0 Acknowledgments 50
7.0 Literature Cited 50

1. Introduction

The most frequently documented examples of the impacts of a warming environment are distributional changes by highly mobile organisms (Parmesan et al. 2006, Parmesan 2006, Musolin 2007, Deutsch et al. 2008). These changes comprise both range expansions (Parmesan et al. 1999, Hickling et al. 2005, 2006), and range contractions (Wilson et al. 2005). Range shifts by herbivorous insects capable of eruptive dynamics leading to widespread growth loss and/or mortality of host plants is of particular concern, especially in forest ecosystems where impacts to evolutionarily naïve host-tree populations or species may threaten the resilience of these systems and fundamentally alter their structure and function (Raffa et al. 2008).

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins, hereafter MPB) is an eruptive forest insect native to the pine forests of western North America. It is an aggressive bark beetle that feeds and reproduces within the phloem tissue of its host trees. Successful colonization by MPB is conditional upon the death of the tree (Safranyik and Carroll 2006). Although it breeds successfully in most species of pine, lodgepole pine (*Pinus contorta* var. *latifolia*) is the beetle's main host through most of its range (Safranyik and Carroll 2006). Several outbreaks have been recorded during the past century in western North America (Taylor et al. 2006); however, the most recent outbreak has exceeded previous episodes in size and severity by approximately an order of magnitude. Since its beginning during the mid-1990s MPB has caused the mortality of trees over approximately 20 million ha [ca. 16 million ha in Canada (Westfall and Ebata 2014), 4 million ha in the US (USDA Forest Service 2014)].

The ongoing, unprecedented outbreak by MPB is in part due to a significant climate change-induced range expansion (Carroll et al. 2004; Safranyik et al. 2010; Sambaraju et al. 2012). Despite its extensive distribution, the beetle has historically been restricted to areas west of the Rocky Mountains and south of 56° N (Safranyik and Carroll 2006). Consequently, it has occupied only a fraction of its potential range. Lodgepole pine extends north into the Yukon and Northwest Territories and east across much of Alberta where it hybridizes with jack pine (*Pinus banksiana*); another viable host for MPB [Fig. 1 (Cullingham et al. 2012)]. In the past, the potential for MPB to expand north and east was limited by climate (Logan and Powell 2001, Carroll et al. 2004; Safranyik et al. 2010). In recent decades, climatic restrictions to MPB distribution have relaxed (Carroll et al. 2004; Safranyik et al. 2010), and since 2002, MPB populations have breached the northern Rocky Mountains and have begun to spread toward the boreal forest (Nealis and Cooke 2014).

Between 2006 and 2016, nearly $500 million was spent on direct control efforts in Alberta to slow the spread of MPB, and yet the efficacy of these efforts was unknown. It may be, for example, that control efforts are largely ineffectual and that resources may be better spent in mitigating the long-term impacts on the industry and the resource. Decision-makers need to understand the effectiveness of the management strategies and tactics implemented to date and their potential efficacy in the future.

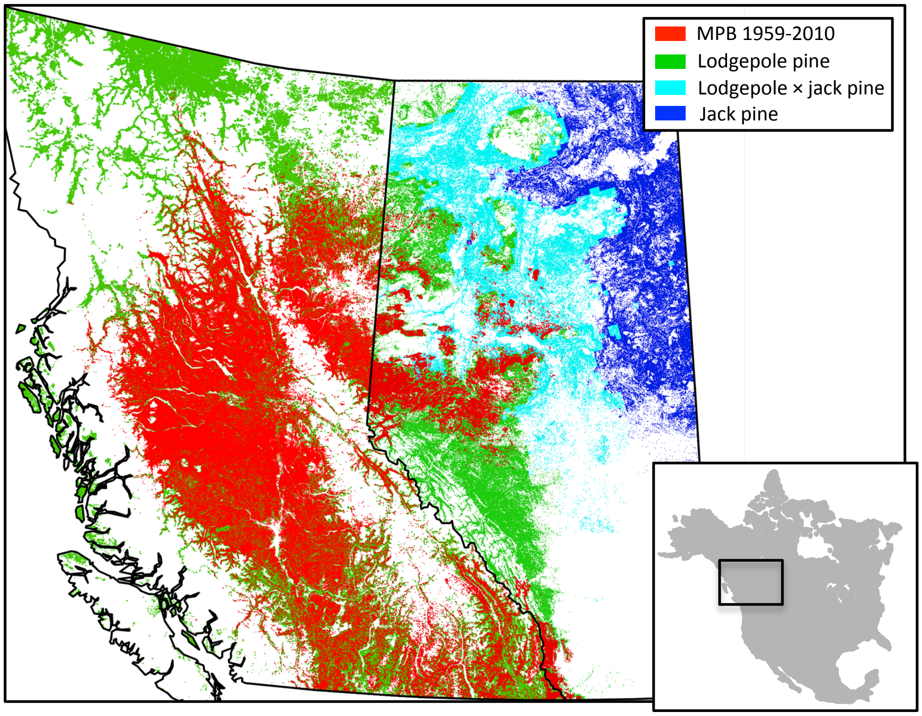


Figure 1.1. Pine species distributions in western Canada according to genetic markers (Cullingham et al., 2012), as well as the cumulative distribution of mountain pine beetle (MPB) infestations.

In 2013, we initiated a project to evaluate the efficacy of MPB management in Alberta. Our primary objective was to determine the effectiveness of current direct control efforts at slowing the spread of MPB in Alberta's pine forests in comparison to alternative strategies, one of which includes 'do nothing'. The work was conducted in two phases comprising three distinct activities. In Phase 1 we (i) developed a model to predict the productivity of MPB in relation to forest, climate and topographical conditions (*r*-model), and (ii) directly assessed the efficacy of single tree removals (level 1 treatments) to reduce local MPB populations. In Phase 2 we combined the *r*-model, control efficacy assessment, data regarding clear cutting to remove MPB (level 2 treatments), and forest inventory data to (iii) develop a spread model (MPBSpread) to evaluate the relative impact of the current versus alternative control strategies at slowing the spread of MPB across north-central Alberta. The following report details the results of each aspect of the project.

2. The *r* model: predicting MPB productivity from stand, site and climate characteristics

2.1 Introduction

In 2006, Alberta Agriculture and Forestry [(AAF) formerly Alberta Environment and Sustainable Resources Development] initiated a detailed survey program to evaluate the state of invading MPB populations across the province, with a focus on vulnerable pine forests in central and northern Alberta. The program comprised two principal components. The first component was designed to document the spread of MPB through Alberta pine forests using aerial and ground surveys to locate recently killed, and currently infested, trees. The second component was focused on measurements of MPB productivity to better predict rates of beetle spread and to prioritize stands for direct control efforts. Potential sites for measurements of beetle productivity were identified based on the results of annual tree mortality surveys. Plots were subsequently established in newly attacked areas in the spring prior to beetle emergence.

The assessment of MPB productivity at a given site begins with selection of a currently infested tree to serve as the plot center. All trees within a radius of 50 meters are then examined for attack and measured in the case of infestation. If additional attacked trees are identified new radii are established and assessed until no new trees are found. The rationale behind this approach is that each plot would be representative of an individual infestation. An index of beetle productivity (henceforth referred to as the *r*-value) is calculated for each plot as the ratio of surviving offspring to parent attacks. The parameter, *r*, is determined by removing a standard area of bark from two sides of an infested tree and counting the number of attack initiations (i.e. number of females) and the number of surviving offspring in the spring prior to beetle emergence. Raw data are collected for all attacked trees within the identified plot area. However, to accurately reflect the status of a given infestation, *r* must be calculated as the aggregation of the number of attack starts and the number of surviving offspring for all infested trees within a specific plot (BC MFLNRO 1995). A plot-level *r*-value is calculated as the ratio of the sum of all surviving offspring to the sum of all attacks determined for each plot in each year. Since calculation of *r* for a MPB infestation requires an accurate quantification of the number of surviving offspring, assessments are conducted as close as possible to the completion of offspring development (i.e. just before beetle emergence and dispersal) to ensure that all mortality associated with overwintering has accrued. However, due to the large number of sample sites and the vast area sampled, *r*-value measurements are generally conducted by AAF throughout the month of May in each year.

2.2 Methods: Predicting *r* from stand and site conditions

2.2.1 Dataset development

Plot data collected during the period of 2007 through 2015 were utilized for the analysis. A total of 1,617 unique plots were measured during the 9-year period with a total of 11,207 attacked trees sampled. Plot locations, by sampling year, are shown in Figure 2.1.

To develop a model to predict *r* based upon readily available data, a suite of variables known or suspected to influence MPB populations was assembled from a variety of sources. The diameter of trees at breast height [(DBH) 1.3m above the ground] is known to be a key trait influencing both host selection and subsequent offspring production by MPB (Safranyik and Carroll 2006). DBH was recorded for each attacked tree in a given plot during *r*-value assessments and used to calculate a mean plot-level DBH of attacked trees. Additional plot-level data recorded included: total number of attacked trees, coordinates of plot centers, sampling date, and site elevation.

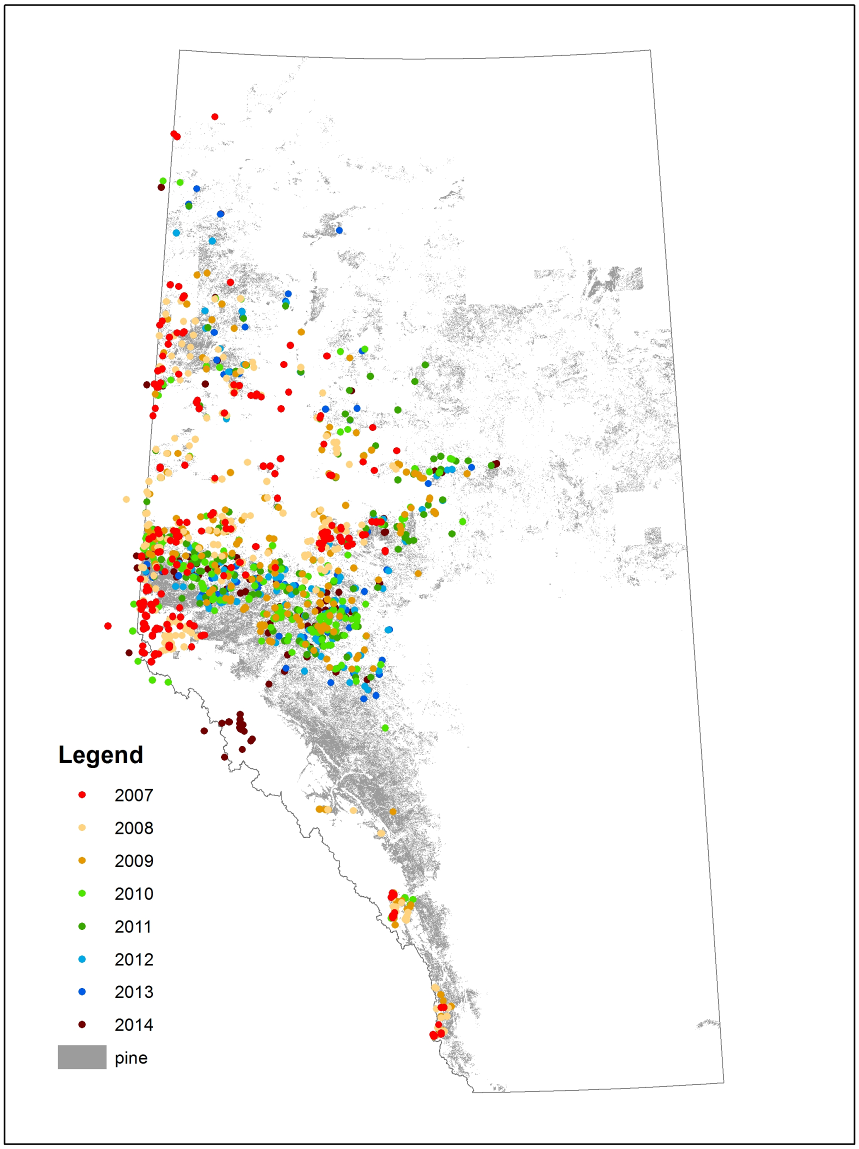


Fig 2.1. Locations of sample plots for *r*-value data collection from 2007-2014.

Alberta vegetation inventory (AVI) data (Alberta Environmental Protection, 1991) were obtained for the study region through data sharing agreements with industrial forestry partners (Alberta Newsprint Company, Alberta Pacific Forest Industries, Canfor, Millar Western Forest Products, West Fraser, Weyerhaeuser). Forest attribute data were extracted from the AVI for each plot location using standard overlay techniques. Stand attributes, such as the percentage of susceptible pine basal area, stand age and density, are known to affect MPB populations and have been used develop a stand susceptibility index (SSI) (Shore and Safranyik 1992; Shore et al. 2000). Moreover, SSI has been applied to support management decisions throughout western North America. The original susceptibility index also included a "location factor" to account for variation in MPB dynamics within its historic range (primarily west of the Rocky Mountain range). A modified Shore and Safranyik index (SSI) without the location factor was computed by AESRD and overlaid with the plot-level *r*-value data.

A daily climate data time series from Jan. 1, 2006 through Aug. 31, 2016 was assembled using data from the Edson climate station (Lat: 53°34'49.007" N; Long: 116°27'12.007" W; Elevation: 927m). The Edson station was selected among several potential stations as it contained a complete daily climate record, it is centrally located within the study area, and its elevation is near the mean for the field plots included in the study.

2.2.1.1 Data Screening

Prior to completing the statistical analyses, the plot-level *r*-value data were screened to identify factors that could potentially inhibit the detection of predictive relationships. An initial analysis of the data showed that plots in which fewer than 3 trees were attacked had considerably lower *r*-values relative to those with 3 or more attacked trees. Considering that measured *r*-values in these plots were largely driven by beetle numbers rather than site and stand features, plots with < 3 attacked trees were excluded from the statistical analysis. However, the relationship between the number of attacked trees in a given plot and the resulting *r*-values was explored in detail. Finally, plots with *r*-values exceeding 20 were excluded from the statistical analysis as they were determined to be outliers and biologically unlikely (Safranyik and Carroll 2006).

2.2.2 Analysis of climate relationships to *r*-values

The daily climate data were evaluated fo*r* relationships to *r*-value data using a wide range of derived climate indices including but not limited to: degree-day sums, number of cold days below different temperature thresholds, minimum temperatures during different months and time periods associated with the beetle development cycle, and drought indices.

2.2.3 Statistical analyses

An array of site and stand-level variables from each plot were evaluated with respect to plot-level, measured *r*-values using linear regression methods. The variables evaluated included: mean DBH of attacked trees, site elevation, effective latitude [plot latitude adjusted for elevation based upon Hopkins Bioclimatic Law (Hopkins 1920)], inventory-derived SSI, and inventory-derived %pine (percent pine component in the inventory polygon linked to the plot). In addition, a regional location temperature effect factor (LTE) was developed to account for the effect of elevation and latitude on temperature within the study area (Eq. 2.1). The Rocky Mountain range runs through the southeastern part of the study area leading to substantial elevation effects on temperature regimes that are not well captured in the effective latitude calculation.

$$LTE = T_{Base} - T_{Elev} - T_{Lat} \tag{2.1}$$

where:
LTE = Location temperature effect (°C)
T_{Base} = 0 (°C)
T_{Elev} = if Elevation < 1000m then 0, else (Elevation - 1000)/100 (°C)
T_{Lat} = (Latitude - Lat_{Base}) * 0.7 (°C)
Elevation = plot elevation (m)
Latitude = plot latitude (°N)
Lat_{Base} = 49.6 (°N) (represents southern most plot)

The *r*-value data were highly variable. In an effort to clarify the relationships in the plot-level *r*-value data, each of the variables were binned into continuous classes for which mean *r*-values with standard errors were calculated. Bin sizes were set to maximize the number of continuous classes while maintaining a minimum of 5 plots in each class. The mean *r*-value results for each of the continuous classes were subsequently evaluated using regression analyses comparing the mid-point class value against the mean *r*-value calculated for the class. The effect of bin size on the nature of the correlation was also examined to ensure it wasn't leading to substantial differences in the inferred relationship. Finally, a predictive model was developed using a stepwise regression analysis including stand, site and climate variables that showed potential based on correlation with *r*-values. The model was evaluated with respect to its fit using both plot-level data and binned model output for *r*.

2.3 Results & Discussion

2.3.1 Relationship between infestation size and *r*

Mean *r* increased markedly when the number of attacked trees exceeded 2, reached a peak around 10 trees and then gradually declined (Fig. 2.2). The variability in the data was high and resulted from a number of factors including differences in habitat quality and year-to-year climate variation.

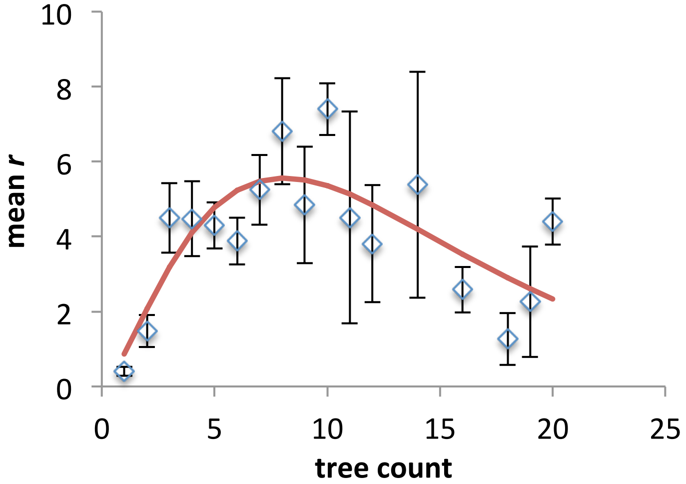


Figure 2.2. Mean *r* in plots grouped by the number of beetle-attacked trees in the survey plot. Data from years 2007-2015 were included and standard errors are shown. A curve was fit to the data with the equation $y = ab^x x^c$, where: a = 1.0467, b = 0.8271, c =1.5341.

2.3.2 Relationship between stand and site factors and r

A summary of the plot-level and binned regression analyses conducted for each of the stand and site characteristic variables is shown in Table 2.1. As expected, the coefficients of determination were consistently higher for the binned variables. Among the variables measured or estimated at the plot level, mean DBH of attacked trees showed the strongest relation with measured *r*-values, followed by location temperature effect factor (LTE) and elevation. Effective latitude (Hopkins 1920) was no better than simple elevation in terms of its potential as a predictor of *r*-values. Interestingly, SSI and %Pine were poorly correlated with *r*-value for both plot-level and binned variables.

Table 2.1. Results of the regression analysis for the plot-level and binned version of each variable including the coefficient of determination (R^2), slope, and intercept.

			Plot-level			Binned		
Variable	range	bin size	R^2	slope	Intercept	R^2	slope	Intercept
DBH (cm)[1]	13.3 to 54.1	2cm	0.26	0.18	-2.2	0.86	0.20	-1.5
Elevation (m)	381 to 2055	100m	0.05	-0.001	4.4	0.58	-0.003	6.1
Effective Latitude	60 to 67	0.5	0.06	0.21	-9.8	0.17	0.05	0.8
SSI	0 to 81	2	0.09	0.02	2.1	0.28	0.02	3
%Pine (%)	1 to 100	10%	0.06	0.007	2.2	0.59	-0.15	5
LTE (°C)[2]	-5.7 to 0	-0.5	0.10	0.36	5.1	0.78	0.77	8.1

[1] Mean DBH of all attacked trees in a plot.

[2] Location temperature effect; see text for details.

2.3.3 Relationship between DBH, *r*-value and over-winter survival

In general, beetle productivity, as measured by *r*-value, increased linearly with host tree diameter (Fig. 2.3a). This is not surprising as larger trees provide relatively greater phloem material as a food source compared to smaller trees (Safranyik and Carroll 2006). There was also a clear interaction between winter temperatures and DBH with respect to survival rates (Fig. 2.3b). To illustrate this interaction, the *r*-value data were divided into years with cold winters (coldest day < -35 °C) and years with mild winters (coldest day ≥ -35 °C). In general, the probability of survival ($r > 0$) for overwintering MPB larvae increased with diameter of the host tree, especially during cold winters. This suggests that larger trees with thicker bark provide increased insulation against extreme cold, whereas small-diameter host trees will not protect beetle larvae during cold winters (Safranyik and Carroll 2006).

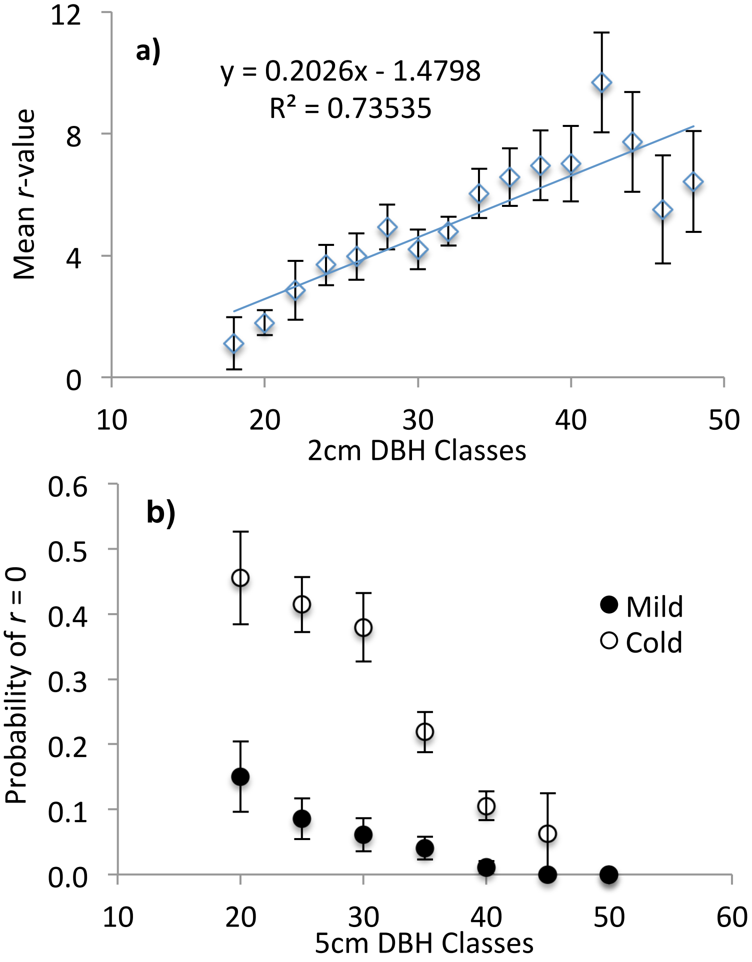


Figure 2.3. a) Mean *r*-value in plots grouped into continuous 2cm DBH bins. Standard errors and a regression line are shown. b) Probability of mortality ($r = 0$) by 5 cm DBH class for years with mild winters (coldest day > -35 °C) and cold winters (coldest day < -35 °C). Means and standard errors are shown for each 5cm DBH size class.

2.3.4 Relationship between location temperature effect (LTE) and *r*

Conventional application of the bioclimatic law (Hopkins 1920) to account for variation in MPB productivity due to elevation and latitude, or combined as effective latitude, produced unsatisfactory results (see Table 2.1). Two issues within the study area were the likely source of this outcome. First, mean *r* did not show a linear relationship with elevation as would be expected from the standard relationship between elevation and air temperature (Hopkins 1920). Instead, mean *r* only exhibited a steady pattern of decline at elevations greater than 1000m (Fig. 2.4a). At lower elevations, mean *r*-values were highly variable and tended to increase with elevation. Moreover, most of the lower elevation sites were located at higher latitudes (Fig. 2.4b), further contributing to the 1000m threshold. Second, cold air drainage (e.g. Bergen 1969) likely dampened the elevation effect at mid elevations adjacent to mountainous regions.

To account for the effects of regional variation in climate on mean *r*, a regional location factor called the Location Temperature Effect (LTE) was derived using a temperature lapse rate of -1°C for every 100m of elevation gain in areas where elevation is ≥ 1000m, and a latitude temperature lapse rate of -0.7 °C for every degree of latitude above 49.6° N (the southern limit of the study area). The relationship between calculated LTE and mean r-values was best described using a logistic regression curve as illustrated in Figure 2.4c, leading to an acceptable fit to the data.

2.3.5 Relationship between climate and *r*

The potential influence of climate on MPB productivity was examined using a wide range of metrics, but only the coldest daily temperature during the over-wintering period was a good predictor of mean *r*-values for a given generation of beetles. The relationship between coldest day and mean *r* (for all plots measured within that year) is shown in Figure 2.5. Both linear and logistic regression curves were fit to the data shown, but the logistic regression curve was selected for use in the predictive *r* model (see Section 2.3) as it was better suited to capture the threshold effect evident when temperatures drop below -37 °C. Several studies have found that -37°C represents a key threshold below which significant beetle mortality is likely to occur (e.g. Régnière and Bentz, 2007). A linear equation will tend to overestimate *r* at temperatures just below -37 °C. Data comprising more years with temps below -37 °C would be required to adequately verify this conclusion.

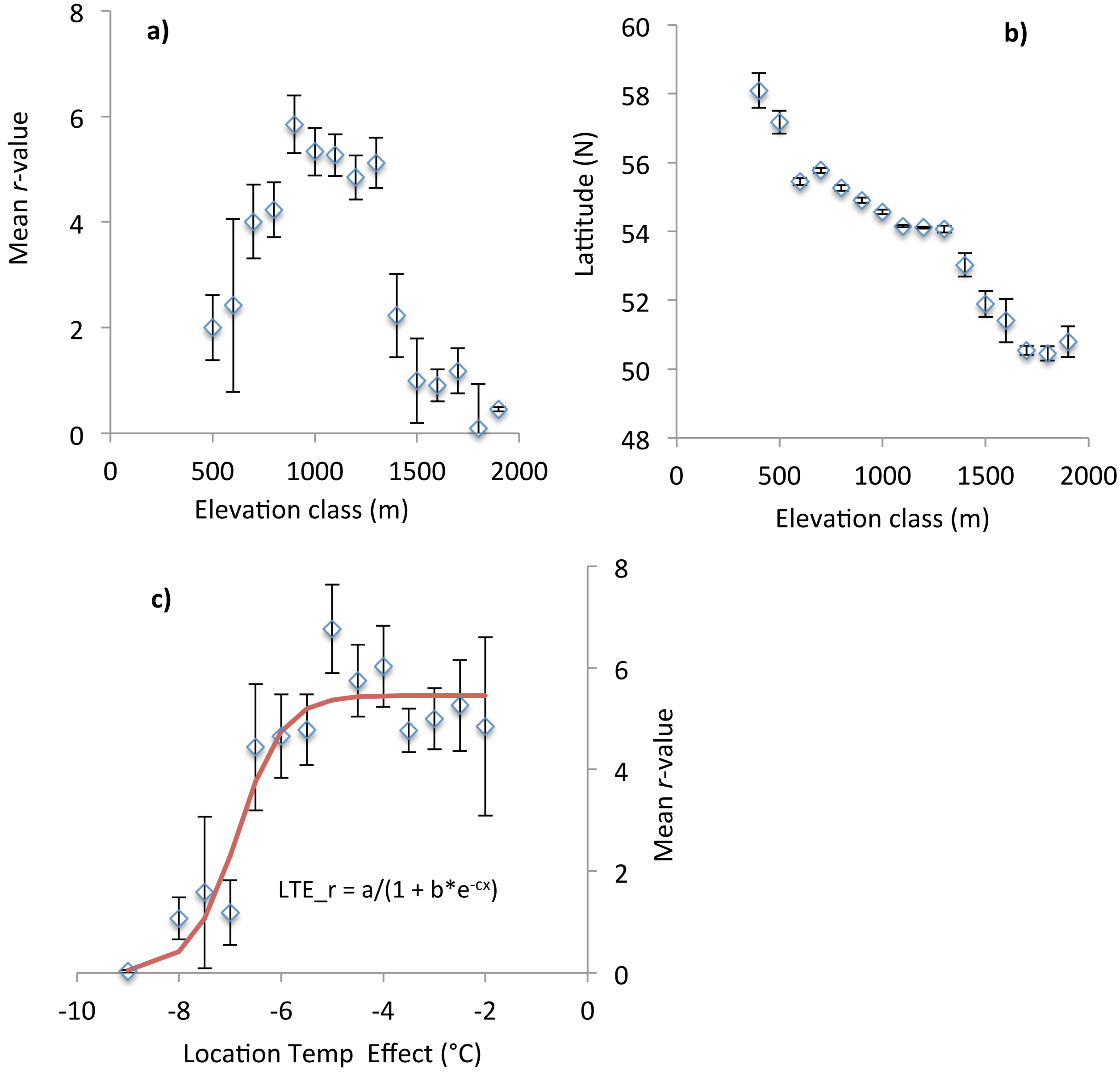


Figure 2.4. a) Mean *r* and b) mean latitude in plots grouped into continuous 100m elevation classes. c) Mean *r* in plots grouped in continuous location temperature effect (LTE) classes. LTE was calculated for each plot based upon the following rule set: where elevation > 1000m, temperature declines 1 °C for each 100m in elevation gain; temperature declines 0.7 °C for every degree of latitude north of 49.6° N. Regression coefficients: $a = 5.46$, $b = 2.87*10^{-7}$, $c= 2.20$.

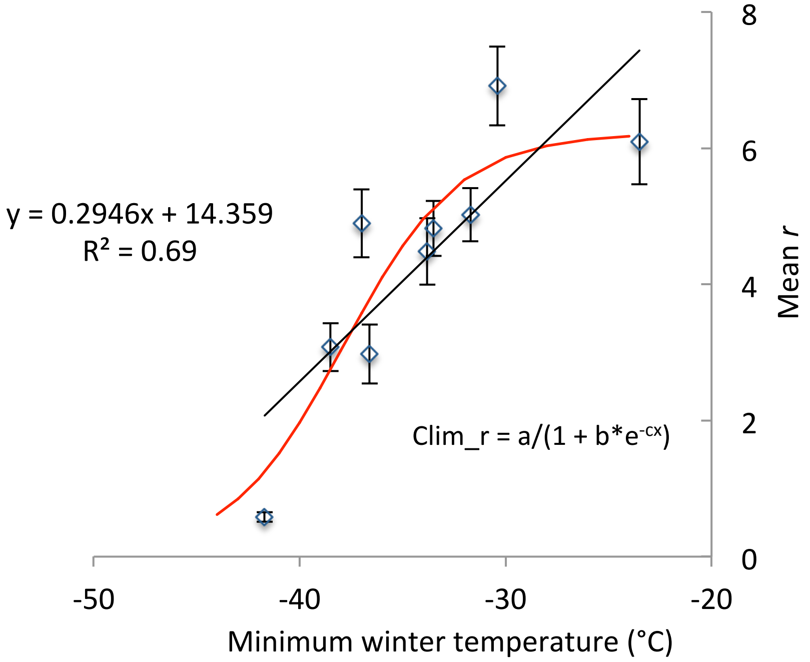


Figure 2.5. Relationship between annual mean *r* and the coldest day during the overwintering period. The following parameters describe the logistic regression curve shown: a = 6.21, b = $1.29*10^{-6}$, c= $3.58*10^{-1}$.

2.4 Development of the predictive *r* model

A predictive *r* model was developed using multiple linear regression including plot data from 2007-2015. Variables represented in the model included DBH and two calculated variables LTE_r and Clim_r derived from the curve fitting exercises described in Sections 2.2.4 and 2.5.5, respectively. Potential interactions between variables were also tested in the analysis. Results from the stepwise regression are shown in Table 2.2

Table 2.2 Results of the stepwise multiple linear regression used to construct the predictive model. The final model fit had 1302 degrees of freedom and an adjusted R^2 of 0.17.

Parameter	Estimate	nDF	Prob>F	AICc[1]
Intercept	-6.821	1	1	
DBH	0.147	2	<0.0001	7451.7
Clim_r	0.831	2	<0.0001	7307.8
LTE_r	0.183	1	0.033	7305.2
(DBH-31.3)*(Clim_r-3.9)	0.022	1	0.032	7302.6

[1] Akaike information criterion (AICc) indicates the relative “goodness of fit” of each model iteration

A comparison of modeled *r* in plots (binned into 2-cm DBH classes) against mean measured *r*-values suggests that the model is able to predict beetle productivity with good accuracy (Fig 2.6). The point that falls below the trend line in Fig. 2.6 (at approximately *r*=6) represents the second largest DBH class (46cm) and has a relatively small sample size (n=15) compared to the other DBH classes shown. It is not clear why this particular class had relatively low measured *r*-values; however, it is evident that variation in measured *r*-values appears to increase in the largest DBH classes, which occur on the far right of the figure. These classes tend to have fewer samples, which would also account for larger standard error terms. Moreover, depending on site conditions, phloem thickness may decline in large, old lodgepole pine trees as these trees exceed maturity and begin to senesce (Safranyik and Carroll 2006).

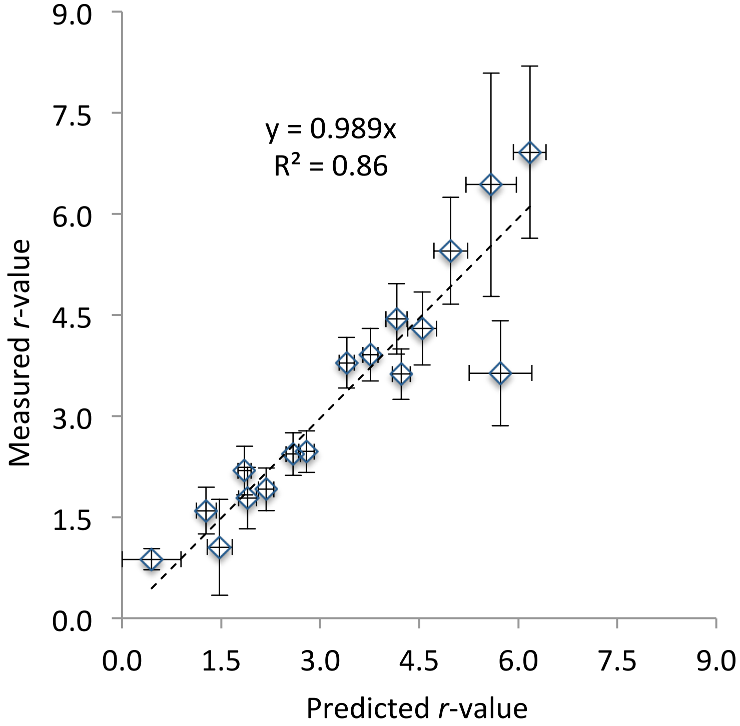


Figure 2.6. Predicted *r*-value relative to measured r-value for plot data from 2007-2015 where measured $r < 20$. Mean values and standard errors are shown for plots binned into 2cm DBH classes. A linear regression was fit to the points.

2.5 Conclusions

The potential productivity of MPB within the pine forests of western Alberta can be accurately estimated from several basic parameters representing stand (DBH), region-specific topographical features (LTE) and climate (minimum winter temperatures). Given that the *r* model was developed from a very large data set including over 1,600 plots with measurements spanning 9 years, it comprises a robust evaluation of variables influencing beetle productivity. Since DBH is not a parameter that is not always included in forest available in was determined to be the most important variable for predicting beetle productivity as is it a good indicator of host quality in terms of food resources and shelter. Other significant variables included elevation and latitude, which were incorporated into a location temperature effect variable (LTE) and minimum winter temperatures. Minimum winter temperatures were positively correlated with mean *r*-value through their impact on over-winter mortality of larvae. Further, the analysis showed that small diameter trees were able to sustain beetles during mild winters (minimum air temperatures ≥ -35°C) but showed high mortality during cold winters (minimum air temperatures < -35°C). A predictive r model was developed and evaluated using field data spanning nine years of consecutive measurements. The model, which incorporates DBH, the Location Temperature Effect (LTE), and an annual climate effect (Clim-r) was able to predict *r*-values with good accuracy. In fact, it is already being used by AAF to help target stands for Level 1 treatment.

3. Assessment of the efficacy of Level 1 treatment using spatial survey and treatment data

3.1 Introduction

Following the breach of the Rocky Mountain geo-climatic barrier, AAF Forest Health personnel have collected detailed survey data on the annual status of the invading MPB population (Fig. 3.1). Since 2006, nearly $500 million has been spent on activities designed to control the spread and impact of the MPB and yet its utility is largely unknown.

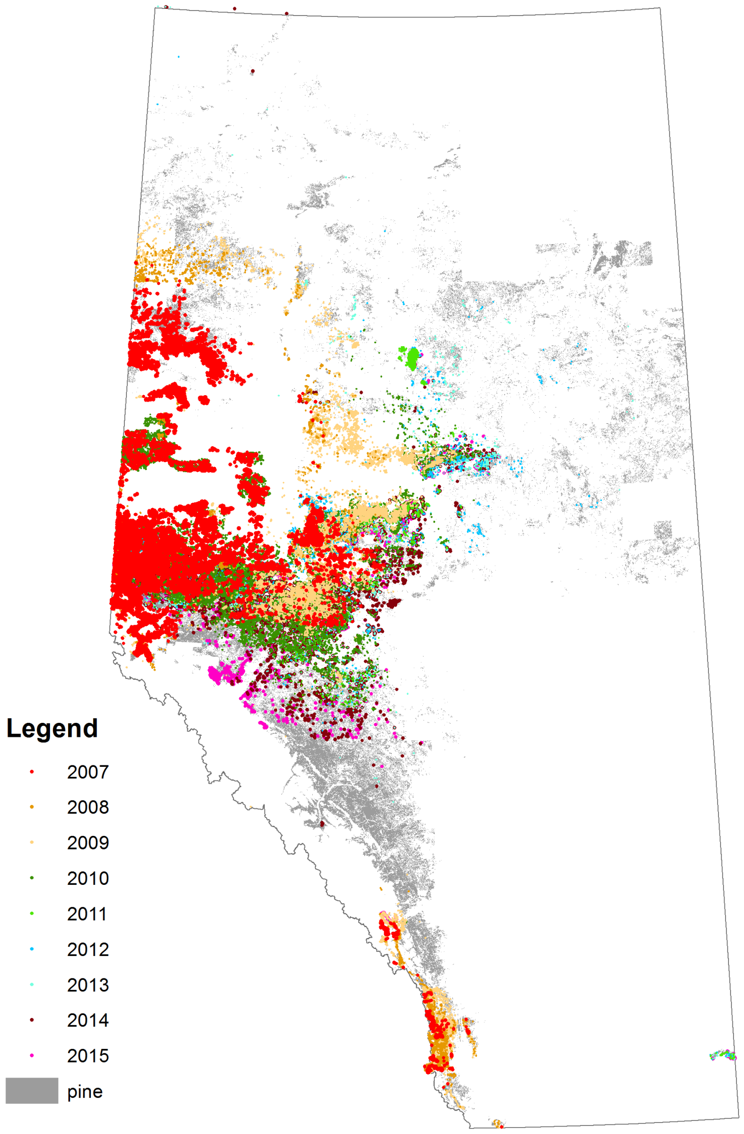


Figure 3.1. Annual areas of MPB infestation (2007 – 2015) in Alberta as indicated by newly killed trees detected during aerial surveys.

Two tactics have been employed in Alberta to reduce the impacts of invading MPB populations. The most widely used tactic (Level 1) involves the location of infested stands using annual, intensive aerial surveys to identify newly killed (i.e. red-attack) target areas. Currently infested (i.e. green-attack) trees in the vicinity of red attacks are subsequently located using ground crews searching the area within a 50m radius of the initial red-attack target. When an infested tree is located, a new radius is established and explored. All green-attack trees are spatially referenced, cut down and destroyed. The challenges associated with this approach are twofold. First, due to resource limitations it is not possible to send crews to all the potential green-attack locations based on the identification of red-attack trees. As such, certain areas must be prioritized for treatment and others left untreated. Second, it is often difficult to detect and treat all of the green-attack trees within an identified target area. The rate at which these trees are detected (detection efficiency) is an important metric that may be used to help evaluate the overall efficacy of treatments (Carroll et al. 2006). The only other tactic currently available for the direct control of MPB involves the clear-cut harvesting of infested stands. This method is referred to as Level 2 treatment and tends to be used in areas behind the leading edge of the MPB infestation, and is generally limited to stands with large MPB populations within close proximity to existing hauling roads.

The objective of this portion of the study was to employ spatial analysis techniques to determine the degree to which Level 1 treatments have been effective in reducing the growth of MPB infestations.

3.2 Methods

An analysis of the efficacy of Level 1 treatments was completed using a method designed to isolate subpopulations from the larger pool of AAF survey data. The underlying premise is that these isolated survey points (MPB populations) constitute relatively new beetle infestations spreading into otherwise uninfested pine forests. Further, to be included in the analysis, survey points were only considered if they were sampled consistently across consecutive years. Individual survey points were grouped into infestations based upon proximity to other points (See Section 3.2.1). The distance between a parent infestation (in year *t*) and its resultant offspring infestation survey points (year *t+1*) was calculated for all points and survey years. These data were examined to estimate a 'zone of influence' around a parent infestation that constitutes the distance within which a majority of offspring would be expected to disperse (See Section 3.2.2). Treatment efficacy was then calculated by comparing attack intensity in the zone of influence around parents with and without Level 1 treatment (Fig. 3.2). This process is described in detail in Section 3.2.3.

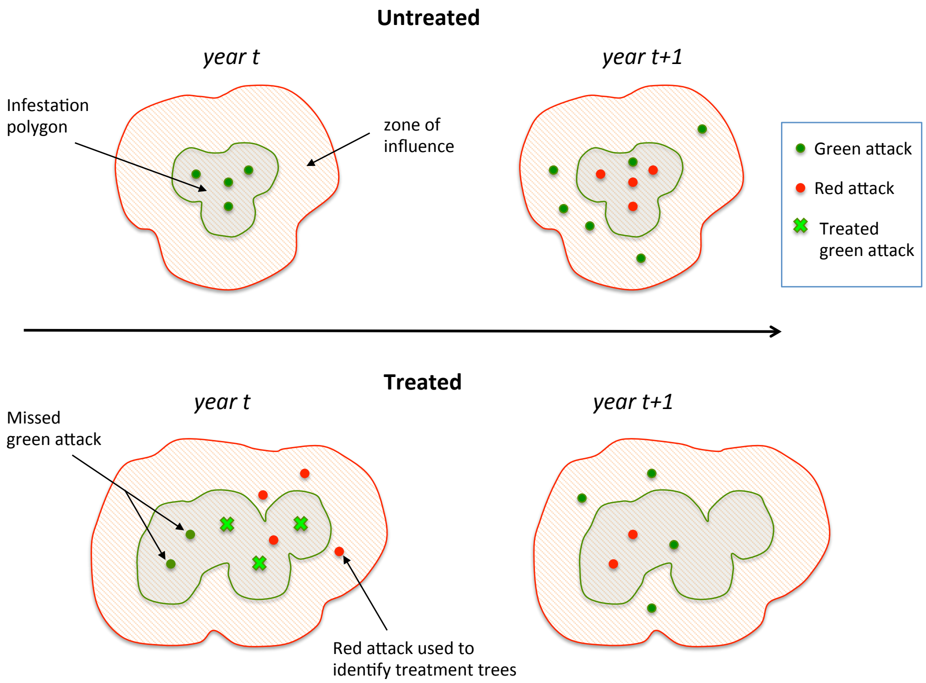


Figure 3.2. A graphical representation of the method used to determine detection and treatment efficacy within infestation polygons, and attack intensity in the zone of influence area around identified infestation polygons in the subsequent year. The upper panel shows the case of an untreated infestation and lower panel shows a treated infestation.

3.2.1 Identifying isolated infestations for spatial analysis

Given the complexity of MPB population dynamics, we developed an approach to identify isolated subpopulations that constitute relatively new beetle infestations expanding into previously unaffected pine stands. By focusing the analysis on this 'local' scale, it was easier to elucidate the basic principles of spread, infestation, and subsequent treatment effects. Alternatively, if we were to include heavily infested areas in the analysis, it would be extremely difficult to determine the source of new infestations and, therefor, the efficacy of Level 1 treatments. The method used to identify suitable survey points included two steps:

1. Overlay survey points onto a 2km × 2km raster grid and mask cells that include point densities greater than 200 points/cell.
2. Cross-reference surveyed areas from consecutive years to ensure that areas were surveyed in both years. Some areas had to be excluded, as they were not surveyed in subsequent years.

An example of the selection method including the masking process is shown for the 2011 survey data in Figure 3.3. This process resulted in a set of eligible survey points from each survey year.

The next step was to identify individual 'parent' infestations within each survey year based upon proximity to one another. We evaluated multiple grouping distances in 50m increments ranging from 100m to 2000m by comparing the resulting number of groups against the expected number of groups for a randomly distributed population. A distance of 750m was determined to be the natural grouping distance based on this analysis. Thus, all survey points within 750m of each other in a given survey year (*t*) were grouped into a single parent polygon with a buffer of 750m around each point used to form the outer boundary of each parent polygon. Points in the following survey year (*t+1*) were considered to be offspring derived from the identified parents. Each offspring point was assigned to the closest parent and the distance from that parent was recorded for use in determining the zone of influence around a given parent infestation (see Section 3.2.2).

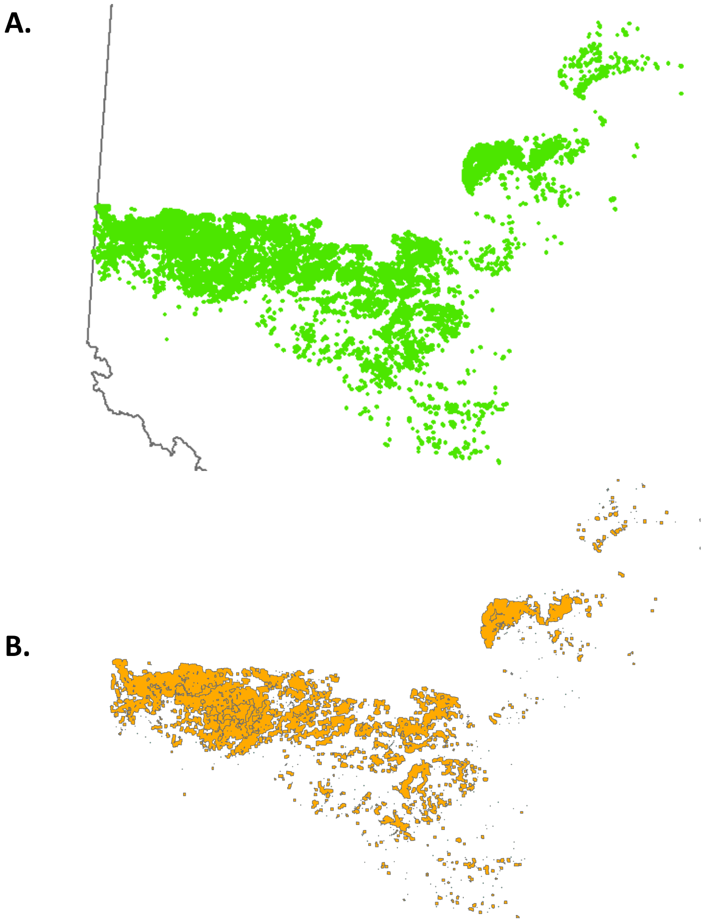


Figure 3.3. An example of the masking process used to identify isolated populations for use in the spatial analysis. Panel A) shows all of the MPB survey points for the 2011 year. Panel B) shows the areas that were excluded by masking due the high density of MPB survey points within 2km × 2km grid cells. (> 100 points per cell).

3.2.2 Determining the zone of influence around parent infestations

The concept of 'zone of influence' (ZOI) was developed to determine the extent of the area surrounding parent polygons that should be examined in the year following the initial infestation. We found that >80% of offspring survey points occurred within 4km from the border of the closest identified parent polygon from the previous time step. Cumulative frequency histograms were constructed for each survey year to evaluate the zone of influence (Fig. 3.4). It was determined that buffers of 1km and 2km should be used to represent meaningful zones of influence as > 50% of survey points occurred within 1km of parents and > 75% occurred within 2km of parents when averaged across all years.

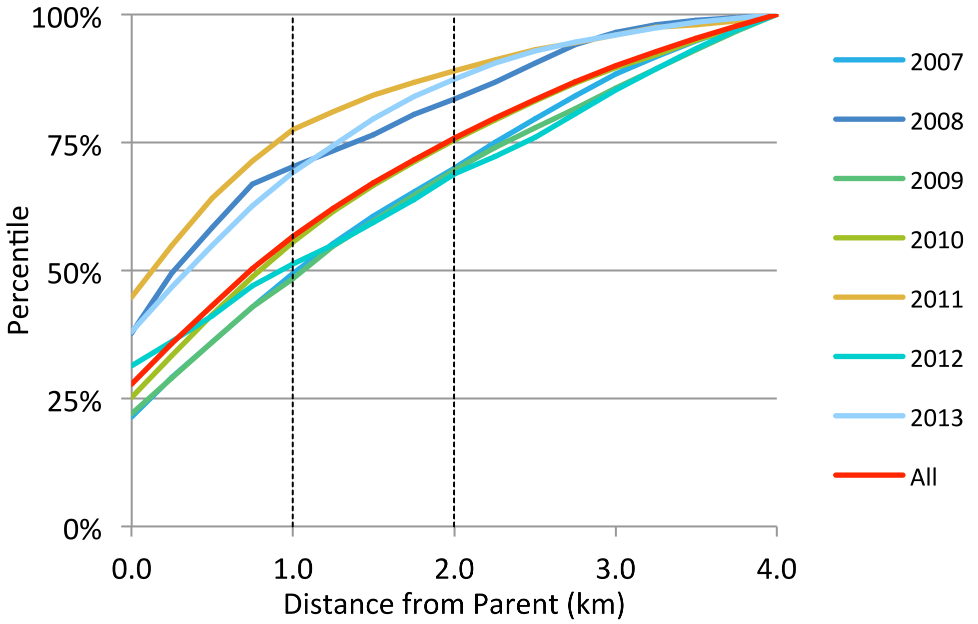


Figure 3.4 Results from the spatial analysis showing the cumulative percentile distribution of the distance from offspring to the nearest parent polygon for each survey year. The 1km and 2km thresholds have been highlighted with dashed lines.

3.2.3 Calculating treatment efficacy

The efficacy of Level 1 treatments was evaluated by calculating attack intensity (dead trees/km^2) in the ZOI areas (1km and 2km) around each parent polygon in the following year (*t+1*). This was done for both treated and untreated parents. The attack intensities of treated polygons were subsequently compared against those for untreated polygons to determine if there was a reduction in attack intensity around treated polygons. An example of the spatial representation of this approach with actual data is shown for the 2011 survey year in Figure 3.5.

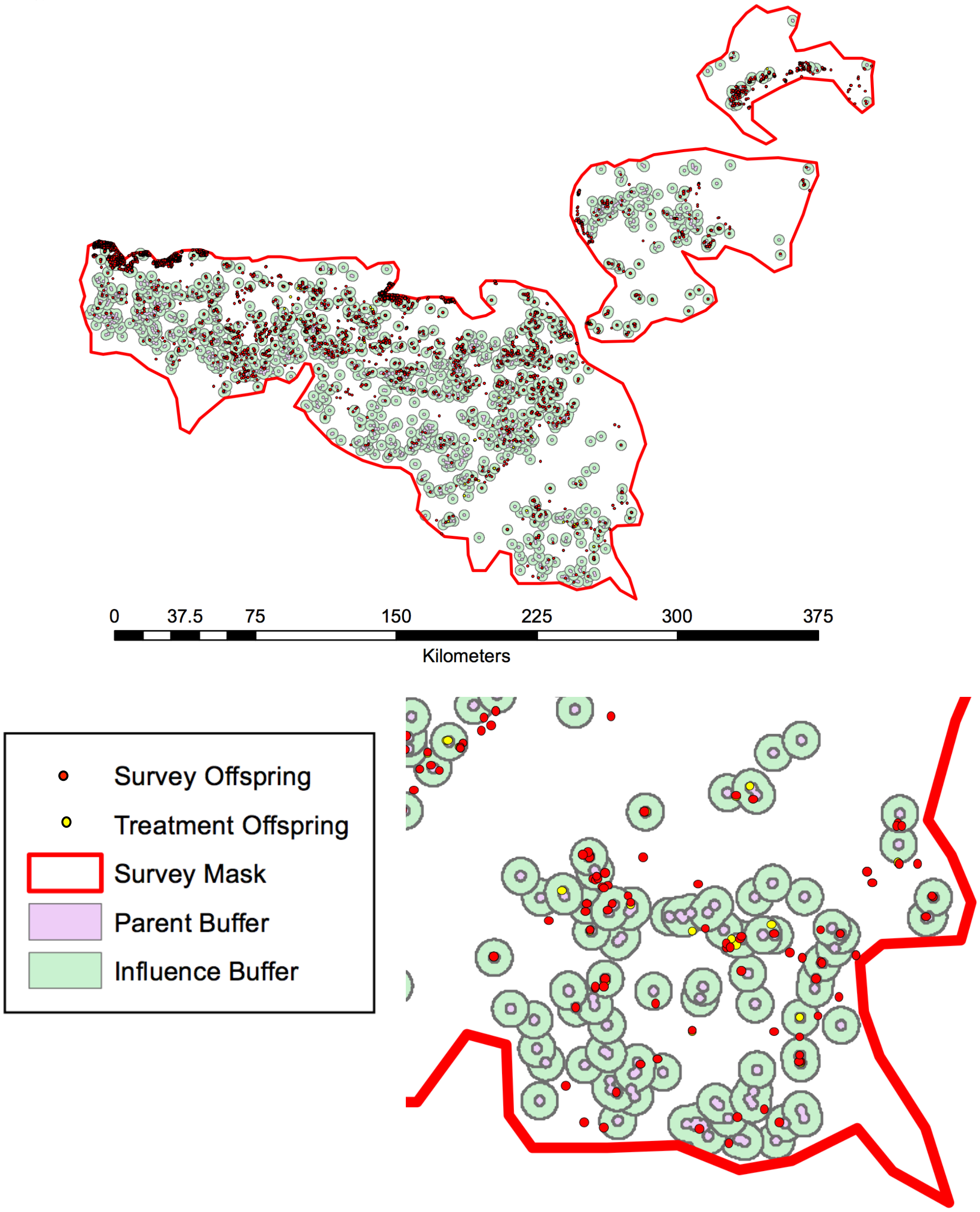


Figure 3.5. Graphical representation of the spatial analysis used to calculate the effect of Level 1 MPB treatments on attack intensity in the following time step. The upper panel shows the entire area examined for the 2011 survey year and the lower panel shows a zoomed in portion of the same data. The offspring points (treated and untreated) from the following year (2012) are also shown. The survey mask area represents the area that was surveyed in both years.

3.2.4 Determining detection efficiency

In addition to attack intensity, the other key metric evaluated in the analysis was detection efficiency. As described in Section 3.1, detection efficiency was assessed by comparing detected and treated trees in a given parent polygon in year *t* with undetected trees (new red/dead trees in year *t+1*) in the same polygon in the next year (see Fig. 3.2). Specifically, detection efficiency was calculated as follows:

$$\text{Detection efficiency}_t = \text{initial}_t/(\text{initial}_t + \text{new dead}_{t+1}) \quad (3.1)$$

where:

initial_t = green attack trees identified within parent polygons and removed in year *t*
new dead_{t+1} = new dead trees (red attack) within the original parent polygon that were missed by the field crew but identified as dead in the year *t+1* survey

3.3 Results & Discussion

3.3.1 Detection efficiency

Two years (2006 and 2008) showed reduced levels of detection efficiency (38-44%) relative to other years (Fig. 3.6). Both 2006 and 2008 are known to be 'immigration' years during which significant numbers of beetles arrived from outside local areas. The fact that immigration years showed lower detection efficiencies than non-immigration years is likely the result of more diffuse distributions of beetles arriving from further distances making green-attack trees more difficult to locate. In non-immigration years, detection efficiency for green-attack trees in treatment areas was surprisingly low, ranging from 54-68%. The implication of missing a large proportion (32 to 46%) of green-attack trees in treatment areas will most certainly limit the impact of treatment intended to slow the spread of beetles into adjacent pine forests. Indeed, Carroll et al. (2006) showed that detection/ treatment rates must exceed 67% to suppress a MPB population increasing by threefold annually – a modest rate of increase during an outbreak (Safranyik an Carroll 2006). These results suggest improvements could and should be made in techniques used to locate green-attack trees within treatment areas.

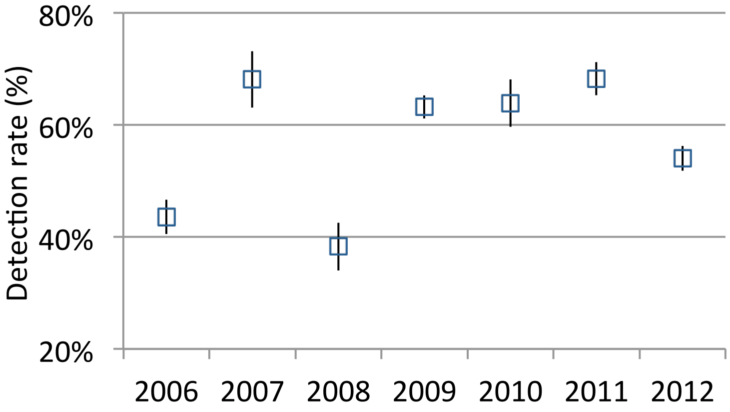


Figure 3.6. Mean detection efficiency of MPB infested trees in Level 1-treated parent infestation polygons by year [(detection efficiency = initial treated/(initial + new dead)]. The years 2006 and 2008 were considered to be immigration years (i.e. beetles arrived from outside the study area).

3.3.2 Treatment effects on attack intensity

An analysis of MPB attack intensity within the ZOI areas surrounding parent polygons showed that treated areas had consistently lower attack intensities relative to untreated areas for both 1km (Fig. 3.7a) and 2km ZOI areas (Fig. 3.7b). However, treatments appeared to have little or no effect in ZOI areas when the attack intensity of the treated parent polygons was at the high end of the observed range (i.e. >8-10 infested trees/km²). In general, attack intensities in ZOI areas were correlated with those in the associated parent polygon (Fig 3.7). Interestingly, the correlations were more pronounced in treated relative to untreated areas, further suggesting that the treatments were less effective in areas with elevated pre-treatment MPB attack intensities.

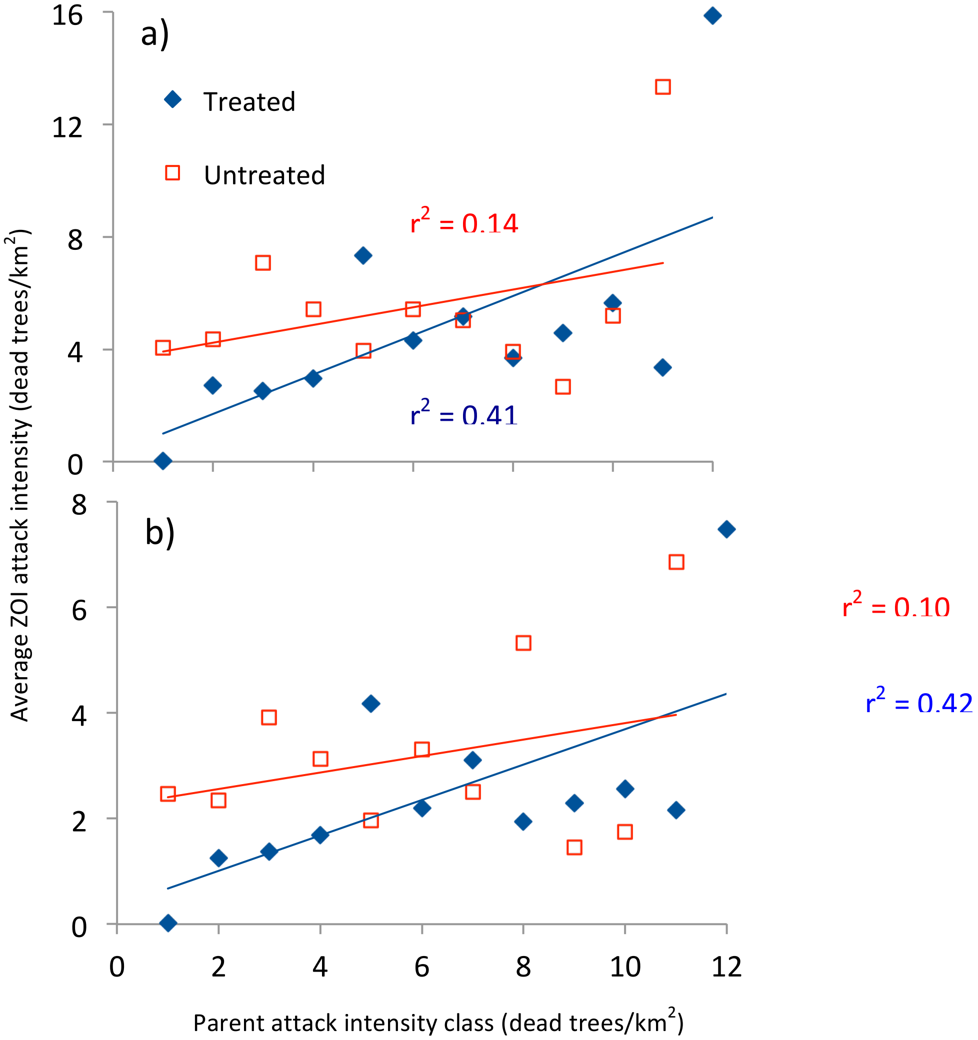
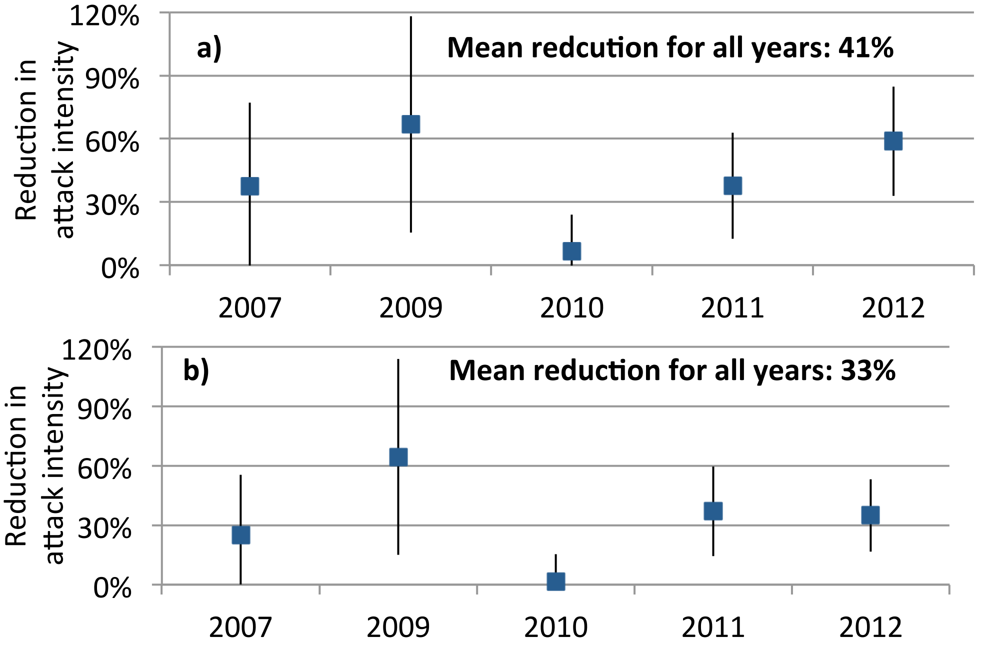


Figure 3.7 A comparison of attack intensity in parent polygons against a) 1km, and b) 2km zone of influence (ZOI) areas for treated and untreated parent infestations across all survey years. Lines represent linear regressions.

An examination of the effect of treatment on mean attack intensity in ZOI areas stratified by year shows that treatments reduced attack intensity by an average of 41% within the 1km

ZOI area (Fig. 3.8a) and by 33% within the 2km ZOI area (Fig. 3.8b). The response to treatment was variable both within years (as evidenced by large error bars) and between years for both ZOI buffer sizes. The 2010 survey year showed the lowest level of treatment response (7% reduction in 1km ZOI areas, and 1% reduction in 2km ZOI areas). The lack of a treatment response in 2010 relative to other years is likely related to the fact that only 6% of identified parent MPB polygons were treated in this year (the lowest level for all years) (Fig 3.8c). The converse was also true in the case of the 2009 survey year when greatest treatment rate occurred (31% of the parent polygons were treated), and which showed the greatest reduction in attack intensity following treatment (67% in 1km ZOI areas and 64% in 2km ZOI areas). This suggests that during years with low treatment rates, beetles from nearby untreated areas moved into ZOI areas around treated polygons and thereby limited the impact of the treatment.



c)

Proportion of infestations treated in each year				
2007	2009	2010	2011	2012
17%	31%	6%	14%	29%

Figure 3.8. Mean annual reduction in attack intensity due to Level 1 treatments in a) 1km zone of influence areas, and b) 2km zone of influence areas. Data from 2008 were excluded as it was a year with significant immigration from outside the study area. The proportion of identified infestations treated in each calendar year is shown in c).

3.4 Conclusions

Several key findings are evident from our analysis of the efficacy of detection and treatment of small MPB infestations in north-central Alberta since its whole-scale invasion in 2006.

First, detection efficiency of currently infested (i.e. green attack) trees was surprisingly low – less than 64% on average during years without widespread inputs of beetles from western populations. This could have serious implications to the slow-the-spread strategy in Alberta. During outbreaks, MPB populations may exhibit rates of increase as high as 8-fold annually (Safranyik and Carroll 2006). Carroll et al. (2006) showed that to achieve suppression of a MPB population where the annual rate of increase is 8, then detection and treatment rates must exceed 87.5%. For an average detection/treatment rate of 64%, suppression of a MPB outbreak is possible only if its annual rate of increase remains less than 2.8. Moreover, if detection/treatment rates do not exceed rates of MPB increase by a large margin, successful suppression can take many years, and in some cases decades, to achieve (Carroll et al. 2006). The fact that MPB populations have not spread at a rapid rate across the pine forests of Alberta in recent years suggests that, for now, climatic conditions have limited MPB population growth, and control efforts applied so far have minimized spread rates (see section 4); however, even minor climatic perturbations may significantly alter the rate of spread and severity of impacts in the near future (Cooke and Carroll 2017).

Second, felling and burning (i.e. Level 1) treatments are effective in reducing subsequent MPB attack intensities, but the effectiveness of treatments declines with increasing intensity of MPB attack. MPB dynamics are characterized by positive feedbacks that manifest once threshold population densities are exceeded (Safranyik and Carroll 2006; Raffa et al. 2008). This means that as small populations grow, their rates of increase will abruptly increase, thereby negating the effects of Level 1 treatments. Once infestations exceed approximately 8 – 10 infested trees/km^2, the efficacy of Level 1 interventions disappears. This suggests that, in terms of the slow-the-spread strategy in Alberta, treatments will be most effective in frontline areas with relatively low beetle levels.

Finally, across the area considered in our study, Level 1 treatments led to an average reduction in subsequent attack intensity of 33 - 41%; however, there was substantial variability in treatment effects within years and between years. The rate of treatment (% of parent MPB polygons treated) had a substantial impact upon the success of the treatments suggesting that during years with low treatment rates, beetles from nearby untreated areas immigrate into areas around treated polygons and thereby limit the apparent impact of the treatment.

We conclude that felling and burning of infested trees can be an effective means of limiting the local growth and spread of MPB populations provided (i) efforts are devoted to increase detection efficacy, (ii) inasmuch as possible, treatment is applied early, before infestations begin to grow, and (iii) treatments are aggressive and consistent from year to year.

4. Evaluating the efficacy of current and alternative management actions to control mountain pine beetle, using the MPBSpread model

4.1 Introduction

Past forestry practices and fire suppression have given rise to homogeneous, even-age forests of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) which, combined with climate change, has led to an unprecedented MPB outbreak throughout western North America (Samman and Logan 2000; Taylor and Carroll 2004; Safranyik et al. 2010). In BC, the current MPB epidemic is estimated to have killed at least 700 million m^3 of pine across an area exceeding 16 million ha (Westfall and Ebata 2014). By 2006, large numbers of beetles had moved across the Rocky Mountain divide and become established in the lodgepole pine forests of western Alberta – an area that had historically been climatically unsuitable for MPB (Safranyik et al. 2010). Over subsequent years, populations grew dramatically, both in size and distribution, and beetles are now established further east in the zone of hybridization between lodgepole and jack pine (*Pinus banksiana*). Recent surveys also identified isolated infestations in 'pure' jack pine (Cullingham et al. 2011). Aside from its economic impact in Alberta, the growing epidemic poses risks across Canada. The pan-Canadian distribution of jack pine represents a potential corridor for MPB to spread across the country, and into areas where it intermixes with several other susceptible pine species such as eastern white pine and red pine (Safranyik et al. 2010).

4.1.1 Current control efforts

Control efforts can be grouped into three broad categories based upon their mode of action: cultural and mechanical treatments that entail killing beetles by destroying the bark of infested trees; semiochemicals involving signal-bearing volatile compounds to manipulate beetle aggregation behavior, used in concert with direct control; and (rarely) the application of insecticides either directly or as systemics (Carroll et al. 2006). Controls may be applied to individual infested trees, or more broadly to whole stands or groups of stands.

In Alberta, management decisions are oriented around a 'slow-the-spread' strategy (Samis and Eegion 2013) based on a 3-zone system; leading edge, holding and salvage zones. The main objective in the leading-edge zone is to halt the further spread of MPB by eliminating new infestations. Aerial surveys are conducted annually to identify isolated sites with new red-attack trees (infested by beetles from the previous year), followed by intensive ground surveys in the vicinity to locate the currently infested green-attack trees (see Carroll and Safranyik 2004, for details on the MPB life cycle). Control tactics entail the felling and destruction of infested trees, thereby killing the beetles, either by burning the logs when the infestation is small (i.e. level 1 treatment), or by clear cutting and milling trees from an entire stand when the infestation is larger and accessible by conventional harvesting equipment (i.e. level 2 treatment). In the holding zone, infestations have typically grown larger than is feasible to manage by level 1 treatments. Pine stands have already experienced substantial beetle-caused mortality, and the objective is to ensure that MPB populations remain static. Generally, the goal is to treat 50 to 80 per cent of infestations using level 2 treatments. Finally, areas with extensive pine mortality constitute the salvage zone. Activities in this zone are focused on harvesting all merchantable timber (dead and alive), rather than beetle control.

Zonal control is a strategy intended specifically to slow the beetle's eastward movement by suppressing MPB populations predicted to have the highest likelihood of promoting additional spread[1]. A key question is how well does this approach actually work? The ongoing spread of the beetle and its implications for the forestry sector suggest a need to develop better management tools. Preliminary analyses based on field surveys indicates that control can be somewhat effective, at least in the early stages of an infestation (see Section 3). Using MPBSpread, we evaluated the efficacy of current direct control efforts at slowing the immediate spread of MPB in comparison to the tactic, 'do nothing'. Additional alternative tactics are also evaluated with respect to potential modifications in detection and eradication. This information will have utility in operational planning by helping prioritize objectives and refine management strategies.

4.2 Methods

4.2.1 Model structure

MPBSpread uses a spatially explicit cellular automata approach (*sensu* Wolfram 1986) to simulate MPB spread. This involves the application of a series of rules describing MPB behavior in relation to infestation and host characteristics. These rules are used to calculate, from one year to the next, the probability of colonization from an occupied cell to suitable but unoccupied 'recipient' cells (see Molofsky and Bever 2004). Actual colonization events are then triggered as binary events (colonized, or not) by a randomization process.

4.2.2 Core elements

The model is used to calculate $P_{i,t}$, the probability of successful MPB colonization of a given unoccupied cell, i, in year, t, as:

$$P_{i,t} = HQ_i \sum_{j=1}^{n} (BEF_{j,t} \cdot G_{j,t} \cdot W_{i,j}) \tag{4.1}$$

where HQ_i is the habitat quality of an unoccupied cell. Collectively, the terms inside the summation represent the probability of beetles from an occupied cell, j, infesting an unoccupied cell within a given year. $BEF_{j,t}$ is a MPB export factor, an index of annual dispersal from an occupied cell; $G_{j,t}$ a directional scalar accounting for wind direction; and $W_{i,j}$ a distance weighting factor between an occupied cell and a given unoccupied cell. All terms are scaled between 0 and 1. The architecture of the model is similar to that developed by Prasad et al. (2010), to predict risk of spread in emerald ash borer (*Agrilus planipennis*).

HQ_i has similarities to the stand susceptibility index (SSI) derived by Shore and Safranyik (1992; see also Shore et al. 2000). The SSI is calculated using four variables: percentage of

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[1] https://www.agric.gov.ab.ca/app21/forestrypage?cat1=Mountain%20Pine%20Beetle%20in%20Alberta&cat2=Alberta's%20Strategy

susceptible pine, stand age, diameter at breast height (DBH), and a location factor. There does not appear to be a strong relationship between SSI and brood production, however (Bjorklund et al. 2009), and so we modified HQ_i to more directly link host availability to MPB reproductive potential. HQ_i is calculated as (percent pine in an unoccupied cell * r_{DBH}), where r_{DBH} indexes MPB reproductive output to pine DBH (as per equation 4.5; see also Bjorklund and Lindgren 2009).

With the exception of DBH, all variables were obtained directly from the Alberta vegetation inventory data (see section 2.2.1). DBH (cm) was estimated for cells > 10 m average height, as follows; shorter trees were assumed to have a DBH = 0 (and thus were excluded):

$$\text{DBH} = a + b \bullet \text{Height} + c \bullet \text{Age} \qquad (4.2)$$

where a, b, and c are parameters (Table 4.1).

The beetle export factor, $\text{BEF}_{j,t}$, is calculated annually for every infested cell:

$$\text{BEF}_{j,t} = r_t \bullet M_{at} \bullet E_t \bullet \text{Pine}_{adj,t} \qquad (4.3)$$

where, r_t is MPB reproductive output (the number of offspring per female) in year *t*, M_{at} is annual beetle-induced pine mortality (%), E_t (%) an annual beetle emigration factor, and $\text{Pine}_{adj,t}$, the amount (%) of susceptible pine within a cell in a given year after accounting for any previous MPB-induced mortality.

Reproductive output in the initial infestation year, r_1, is first calculated (see below), after which r_t is simply decremented annually by 20% of the preceding year's value. The latter represents the impact of accumulating mortality on the quality of remaining pine in terms of host suitability (see, for example, Bjorklund and Lindgren 2009).

$$r_1 = r_{DBH} \bullet r_{brood} \bullet r_{temp} \qquad (4.4)$$

where r_{DBH} indexes MPB reproductive output to the initial pine DBH (equation 4.5; Bjorklund and Lindgren 2009), r_{brood} is the maximum temperature during incubation for the first MPB brood (equation 4.6), and r_{temp} is a location-based temperature index (see below; see also Shore and Safranyik 1992).

$$r_{DBH} = a \bullet \text{Cell mean DBH} - b \qquad (4.5)$$

where a and b are parameters (Table 4.1). Note that if $r_{DBH} \leq 0$ cm, then $r_{DBH} = 0$.

$$r_{brood} = a \bullet T_{max} + b \qquad (4.6)$$

where a and b are parameters (Table 4.1), and T_{max} is the maximum daily temperature during the MPB brood incubation period (March – June).

r_{temp} is calculated as the product of two terms, an elevation temperature (T_{Elev}) and a location temperature (T_{locale}; see also section 2.3.2), and the result scaled between 0 and 1.

$$T_{Elev} = (\text{Elevation} - 1000)/100 \tag{4.7}$$

At elevations ≤ 1000 m, $T_{Elev} = 0$.

$$T_{locale} = (\text{Latitude} - 49.6) \bullet 0.7 \tag{4.8}$$

At latitudes ≤ 49.6 ° N, $T_{locale} = 0$.

Annual pine mortality in a colonized cell, M_a, is first calculated for the initial infestation year, M_{a1}, using the following modified logistic equation:

$$M_{\mathrm{a}1} = \frac{a}{(1+b\, e^{c\, P_{i,t}})} \tag{4.9}$$

where a, b, and c are parameters (see Table 4.1), and $P_{i,t}$ the probability of an unoccupied cell being colonized, as per equation (4.1)

In subsequent years, M_a is calculated as:

$$M_{ai} = \frac{a}{(1+b\, e^{c\, r_t})M_{max1}} \tag{4.10}$$

where a, b, and c are parameters (see Table 4.1), and r_t is defined in equation (4.4). M_{max1} is defined in equation (4.12) and used as a scaling factor to account for the pine content of an infested stand.

Cumulative mortality occurs until stand maximum mortality (M_{max}) is reached:

$$M_{max} = M_{max1} \,.\, M_{Max2} \tag{4.11}$$

$$M_{max1} = \frac{a}{(1+b\, e^{c\, Pine_{adj}})} \tag{4.12}$$

where, a, b, and c are parameters (Table 4.1) and $Pine_{adj}$ is as defined above (equation 4.3).

$$M_{max2} = \frac{a}{(1+b\, e^{c\, r_{DBH1}})} \tag{4.13}$$

where, a, b, and c are parameters (Table 4.1) and r_{DBH1} refers to MPB reproductive output in the first year of an infestation (see equation 4.4).

Emigration (E_t; %), the proportion of beetles leaving the infested cell in a given year, and is represented as a simple linear function:

$$E_t = a \bullet Y_{infest} - b \tag{4.14}$$

where a and b are parameters (Table 4.1), and Y_{infest} the year of infestation.

Gt is derived by summarizing daily wind data from climate stations located within the area of interest during the main MPB dispersal period (August 1 to September 15), and time of day (1200 – 1800 h) (Carroll and Safranyik 2004). For each day, hourly wind direction is classified into one of 8 cardinal directions. These data are then summarized into frequency distributions for each cardinal direction and converted to probabilities. The latter are used in equation (4.1) as the probability of MPB dispersal in the direction from an occupied cell to any given unoccupied cell.

In the final term of equation (4.1), $W_{i,j}$ weights the distance between an occupied and an unoccupied cell, beginning with the following equation:

$$W_{i,j} = e^{-D_{i,j}/a} \tag{4.15}$$

where a is a shape parameter (Table 4.1), and D the distance between an occupied and an unoccupied cell (i, and j, respectively; km). Given the structure of equation (4.15), unoccupied cells located in close proximity to occupied cells will always receive a higher weighting than distant cells. The potential for long-distance dispersal is therefore introduced in the form of a fat-tailed distribution (FTD). The FTD generates a higher probability of extreme values than would be derived simply from the application of equation (4.15). Hence, short-distance dispersal is described by the negative exponential function until it reaches a threshold probability after which the probability remains constant and thus is distance invariant (see Clark 1998; Schwartz et al. 2001). This combination of simple diffusion and the FTD is referred to as 'stratified dispersal' (Shigesada et al. 1995). $W_{i,j}$ was converted to a fat-tailed distribution by constraining its threshold value at 0.00005. This latter value was derived qualitatively from a series of simulations conducted using MPBSpread and comparing the predicted distance distribution against that observed in a British Columbia epidemic (see below).

Table 4.1. Parameters employed in equations 4.1 – 4.15, and their values.

	Parameter values		
Parameter	**a**	**b**	**c**
DBH	14.8	0.7	0.02
r_{DBH}	0.25	2.71	
r_{brood}	0.042	2.13	
M_{a1}, M_{ai}	0.550	2.694	-1.600
M_{max1}	1.154	7.350	-4.268
M_{max2}	0.992	123.2	-1.815
E_t	0.19	0.08	
$W_{i,j}$	1.7		

4.2.3 Calculating P*i,t* and annual colonization

We assumed a univoltine life cycle for MPB throughout the area of simulation (Safranyik and Carroll 2006). Hence, $P_{i,t}$ values were calculated annually. A cell-based representation of the landscape was used, with cell size set at a 400 x 400 m (16-ha) resolution. Cell attributes were derived using inventory data assigned to polygons within a given cell, and included information on the dominant tree species, stand age, height, density, and infestation status. A cell could contain more than one inventory polygon. In this case, the polygon with the largest area was used to assign the cell's attributes.

Simulations were initiated by 'seeding' the study area with cells occupied by MPB. These are the only 'immigration' events represented within the model. This is consistent with other model results, which suggest that immigration is a dominant feature of population growth only in the early stages of an outbreak. Once established, weather factors and management-related activities predominate (Fall et al. 2004).

$P_{i,t}$ values were calculated each and every year (Figure 4.1, panel a). For every uninfested cell, the product of BEF, G, and W was calculated for all infested cells and summed (see equation 4.1). This value was then multiplied by the HQ index of the uninfested cell to generate its $P_{i,t}$ value. An uninfested cell very close to numerous infested cells could, in principle, receive an infestation probability $\geq$ 1.0. In this case, the cell was given a 100% probability of being infested in that year. For cells with summed probability of infestation < 1, a random number < 1.0 was chosen from a cumulative normal distribution (CND). All cells with $P_{i,t}$ values that exceeded the random number were infested in that model step (Figure 4.1, panel b). This element of stochasticity is designed to account for interannual variability in climate conditions and other factors not accounted for within the model. Evidence suggests the relative susceptibility of pine to MPB attack depends on their evolutionary history. The lodgepole pine stands in BC, for example, have a long history of coexistence with MPB whereas the lodgepole and jack pine stands in Alberta are novel hosts. BC pine therefore have well-developed mechanisms for resisting attack with the result that it requires more beetles to kill an individual tree than in Alberta (Burke et al. 2017; Goodsman and Lewis 2017). We used two CND functions, experienced and naïve, to represent the relative susceptibility of the two populations of pine to MPB (Figure 4.2).

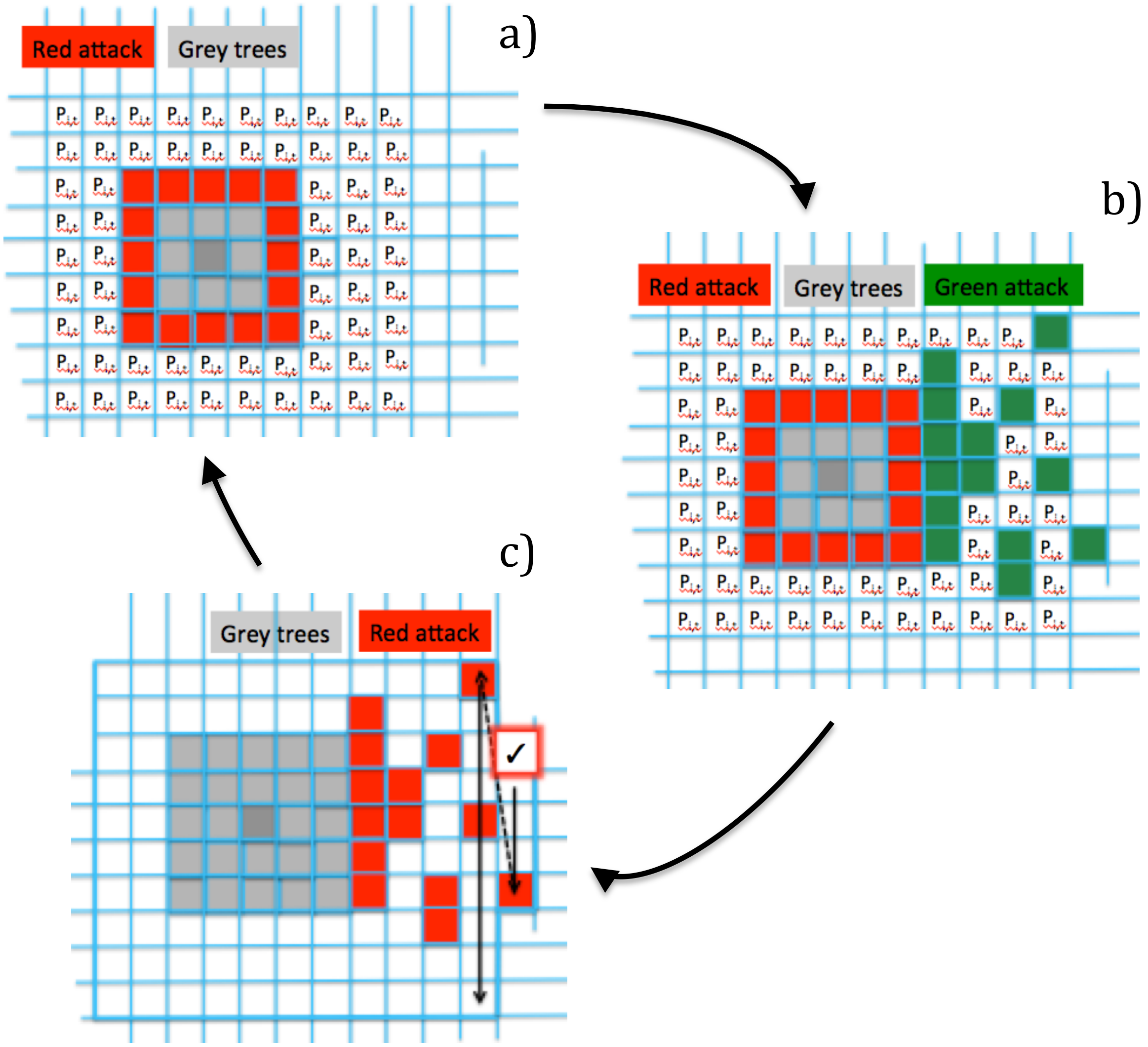


Figure 4.1. Application of the MPBSpread model. The probability of infestation in a given year for all cells not currently occupied by MPB, $P_{i,t}$, is calculated (a). The probabilities ($P_{i,t}$ values) are then assessed for actual colonization events (b). Following colonization, control activities are initiated beginning with the cell at the easternmost longitude and corresponding highest latitude within the study area (c). Cell sampling to initiate control activities proceeds sequentially by longitude to the southernmost cell within the area and then onto the northernmost cell to the immediate west. This process is continued until all cells within the study area have been sampled or the total area allocated for control in a given year is reached. Trees labelled 'grey' were attacked by MPB in previous years and are already dead. 'Red' trees were killed in the previous year, while 'green' trees are being attacked in the current year. See text for further details.

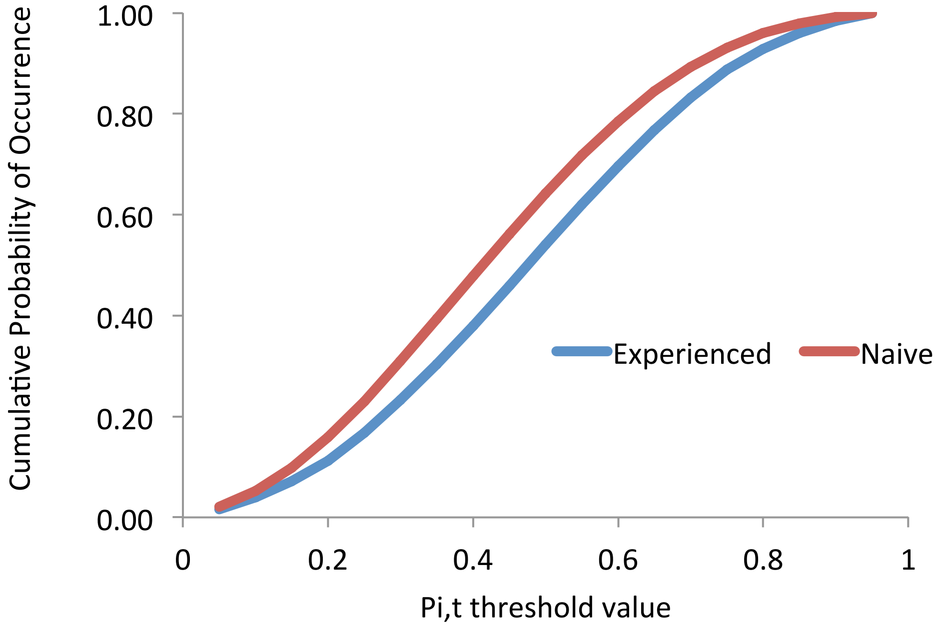


Figure 4.2. Cumulative probability of occurrence for a given threshold value for $P_{i,t}$. Experienced pine are those in British Columbia that have a higher relative threshold than the naïve pine located in Alberta. See text for further details.

4.2.4 Model validation

Model performance was assessed using MPB colonization data from central British Columbia, within 5 forest management units (Vanderhoof, Lakes, Prince George, Quesnel, and 100 Mile House) located within the Chilcotin Plateau (Figure 4.3). The area was subject to a large MPB epidemic from 1999 through 2008. Detailed spatial survey data of the spread and impact of the outbreak were supplied by the British Columbia Ministry of Forests, Lands and Natural Resource Operations. We used survey data from the beginning of the epidemic (1999) to seed the model and projected the spread of MPB throughout the landscape for 10 years. Ten simulations were conducted and the mean and 95% confidence intervals calculated of the area colonized by MPB and cumulative pine mortality. These projections were compared to the survey data.

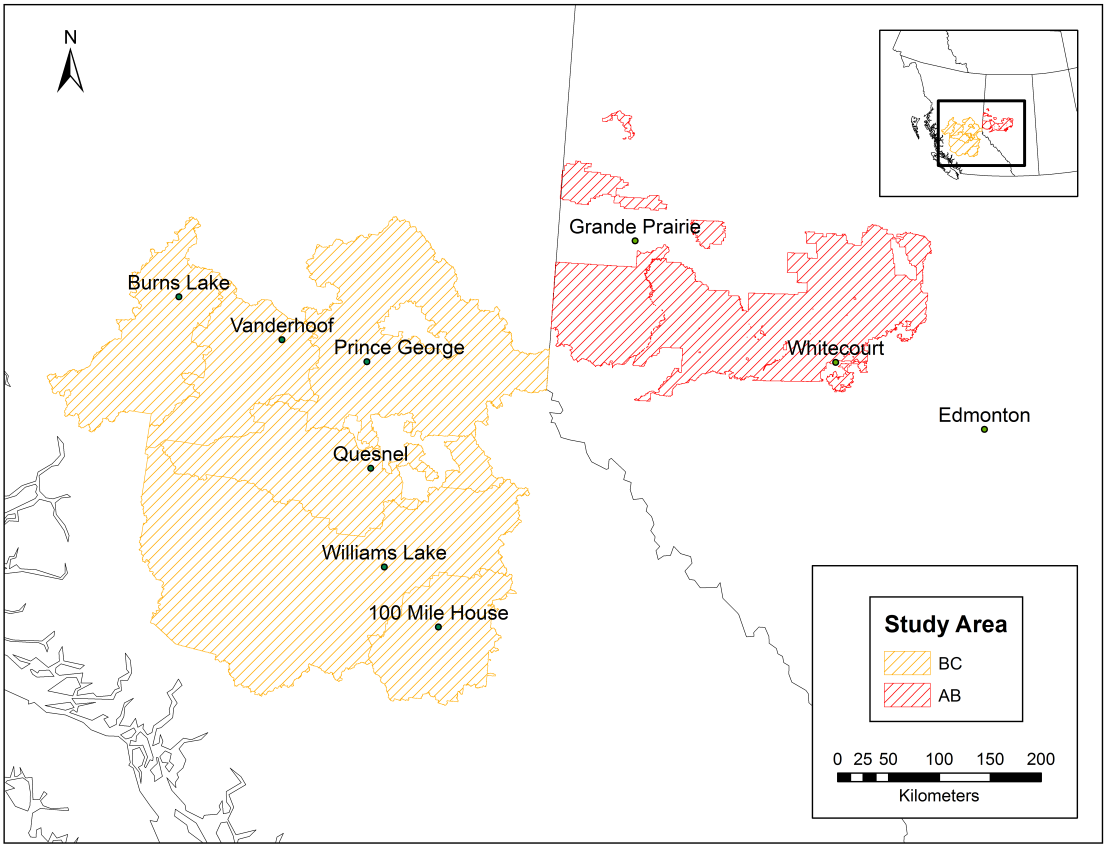


Figure 4.3. Study areas in British Columbia and Alberta.

4.2.5 Simulating MPB control tactics

Computer-coded cell-based rules were designed to emulate the 'leading edge' approach to MPB control employed in Alberta, Canada (Samis and Eegion 2013). Under this approach, control efforts are focused primarily on eradicating new, isolated outbreaks to prevent the beetle population from becoming established and slow further spread. The study area was located in central Alberta, within the vicinity of Fox Creek (54.4022° N, 116.8089° W; see Figure 4.3). This region was selected due to an emerging MPB infestation problem (beginning in 2008), and because we were able to obtain high quality, geo-referenced inventory and management data.

As described above, available MPB control tactics in the leading edge zone comprise either level 1 or level 2 treatments. Within MPBSpread, level 1 was applicable to any cell where an infestation was detected within 2 years of establishment. Cells with infestations of ≥3 years duration and ≤7 km from a road would potentially be treated with level 2 measures. Controls were implemented annually, subject to a detection probability (see below). In all other cases, no treatment occurred and the infestation continued until host availability was sufficiently depleted that further beetle reproduction within the cell was not possible.

Sampling for potential treatment began with the cell at the easternmost longitude and corresponding highest latitude within the study area, and proceeded sequentially by longitude to the southernmost cell (Figure 4.1, panel c). It was then continued with the northernmost cell to the immediate west, and so on. Each infested cell had a probability of being detected (P_{detect}), and a subsequent probability of successful eradication ($P_{eradicate}$). P_{detect} and $P_{eradicate}$ were derived from Alberta survey data, from which minimum values of 0.9 and 0.65, respectively, were derived (Table 4.2). The latter are similar to values reported in Coggins et al. (2008). With level 1 control, either all or a proportion of green attack was removed. This is determined from a random number (RN) drawn between 0 and 1. Eradication occurred within a cell with $RN \leq P_{eradicate}$. If eradication was unsuccessful ($RN > P_{eradicate}$), pine mortality for that year was calculated as (M_a [as per equation 4.10] * ($RN - P_{eradicate}$)). The latter term was designed to account for the decrease in pine mortality within a cell associated with the control effort. Under level 2 control, all trees were removed within a cell (and hence, $P_{eradicate} = 1$).

The sampling process was continued until all cells within the study area had been sampled or the total area allocated for control in a given year was reached. The latter reflects that fact that sampling is expensive and thus is limited by budgetary constraints.

4.2.6 Assessing treatment efficacy

A combination of aerial and point survey data are collected annually in Alberta to document the current status of the MPB infestation, and for use in management planning and control. This information was used to calibrate the MPBSpread model by inputting the locations of red-attack trees within a cell and the amount of associated currently infested green-attack trees, for the year 2008, the starting year of the simulations.

Annual spread of the population to uninfested cells was then modelled by the application of equation (4.1), with a total run length for each scenario of 10 years. A series of control scenarios were simulated (Table 4.2); each scenario was replicated 40 times. The same annual colonization patterns derived from the randomization process (see above) were used in each of the control scenarios to facilitate direct comparison.

Table 4.2. Control scenarios employed in MPBSpread to evaluate alternative strategies to managing mountain pine beetle impacts in Alberta.

No.	**Description**	**Level 1**	**Level 2 (2008)**	**Level 2 (2017)**	**P_{Detect}[1]**	**$P_{eradicate}$[2]**	**Host status**
0	Do nothing[3]	-	-	-	-	-	Naïve
1	StS[4]	10000	1500	3000	0.9	0.65	Naïve
5	L1×0.5[8]	5000	1500	3000	0.9	0.65	Naïve
2	L1×2[7]	20000	1500	3000	0.9	0.65	Naïve
3	L2×2[6]	10000	3000	6000	0.9	0.65	Naïve
4	L1×2[7]	20000	1500	3000	0.9	0.65	Naïve
6	⇧Det, ⇧Erad[9]	10000	1500	3000	0.95	0.8	Naïve
12	L1×2; L2×4; ⇧Det; ⇧Erad[11]	20000	6000	12000	0.95	0.8	Naïve

[1] Probability of detecting cells with red attack.
[2] Probability of eradicating an MPB infestation. Note, this applies to Level 1 treatments only.
[3] No controls exercised.
[4] Current slow-the-spread strategy (see text)
[5] Level 1, area doubled; Level 2, area progressively enhanced by 166.7 ha each year.
[6] Level 2, area doubled initially and then progressively enhanced by 333.3 ha each year.
[7] Level 1, area doubled.
[8] Level 1, area halved; Level 2, area doubled.
[9] Enhanced detection.
[10] Pine has genotypes displaying enhanced resistance to MPB attack.
[11] Level 1 doubled; Level increased by 4 fold initially and then progressively enhanced by 666.7 ha each year; Increased detection and eradication.

4.3 Results

4.3.1 Model validation

A comparison of projections from MPBSpread and empirical data from the epidemic in British Columbia is shown in Figure 4.4. Overall, there is close agreement between the two. However, regressing the predicted against empirical values with the line through the origin indicated that area colonized was slightly over-predicted ($y = 1.08x$, $r^2 = 0.88$), particularly in the first three years of the simulation, and pine mortality under-predicted ($y = 0.84x$, $r^2 = 0.99$) in the later years.

In Alberta, empirical data on area colonized agreed well with MPBSpread predictions under the ongoing slow-the-spread (StS; see Table 4.1) scenario ($y = 0.96x$, $r^2 = 0.73$) but deviated from 'do nothing' (DN) in later years (2012 onwards; $y = 0.75x$, $r^2 = 0.53$) (Figure 4.5).

4.3.2 Evaluating control efforts

4.3.2.1 "Slow-the-spread" versus "do nothing"

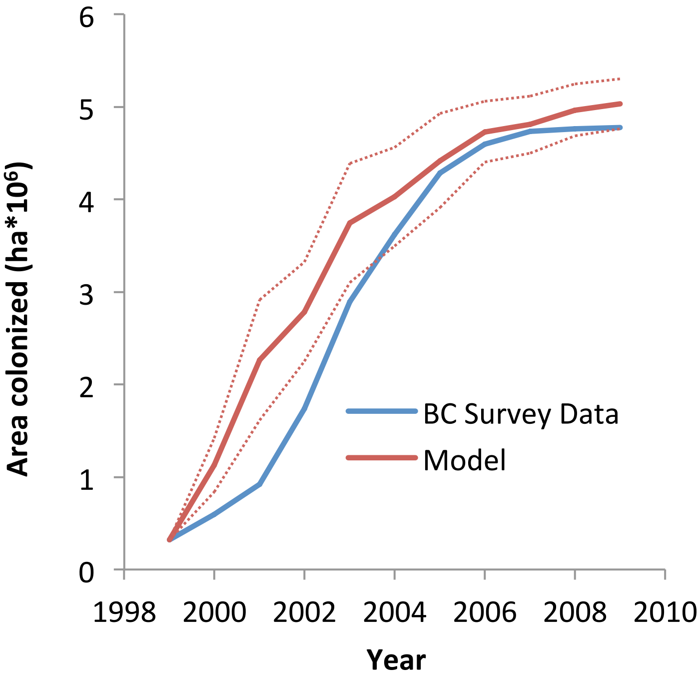
Area colonized by MPB was almost always lower under StS than DN, and separation between the two scenarios increased across years (Figure 4.5). By the year 2018, the StS scenario had reduced area colonized to roughly 70% of that predicted under DN, though there was still overlap in the confidence intervals.

4.3.2.2 "Slow-the-spread" versus alternative control scenarios

Most alternative scenarios reduced the mean area colonized by MPB relative to DN (Figure 4.6). With respect to specific measures, area colonized was particularly sensitive to early detection and eradication, and the amount of level 1 control, but not level 2 control (Figure 4.6). Reducing level 1 control treatments by half increased the area colonized relative to StS, whereas the area was reduced significantly when level 1 was doubled. Increasing detection and eradication had a similar effect to doubling level 1 treatments. Doubling level 2, in contrast, had no impact on area colonized relative to StS. The greatest impact of enhanced control was realized when levels 1 and 2 were increased, along with improved detection and eradication efficacies.

4.3.2.3 Assessing the importance of early detection

Under StS, the size of the infestation in year 1 (pine infested ha^{-1}) had a significant impact on the total area of infested pine after 10 years (Figure 4.7). There was no such relationship under DN, however. At a given level of year-1 infestation, 10-year outcomes were always more favorable (on average) under StS than DN, except when early infestation was in excess of about 175,000 ha (Figure 4.7).



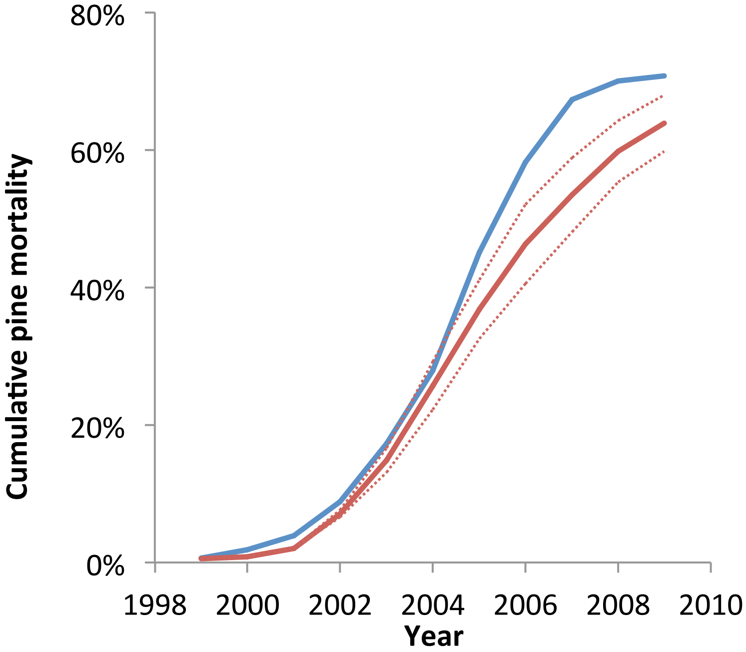


Figure 4.4. Predictions of MPB impacts in central British Columbia in relation to empirical estimates.

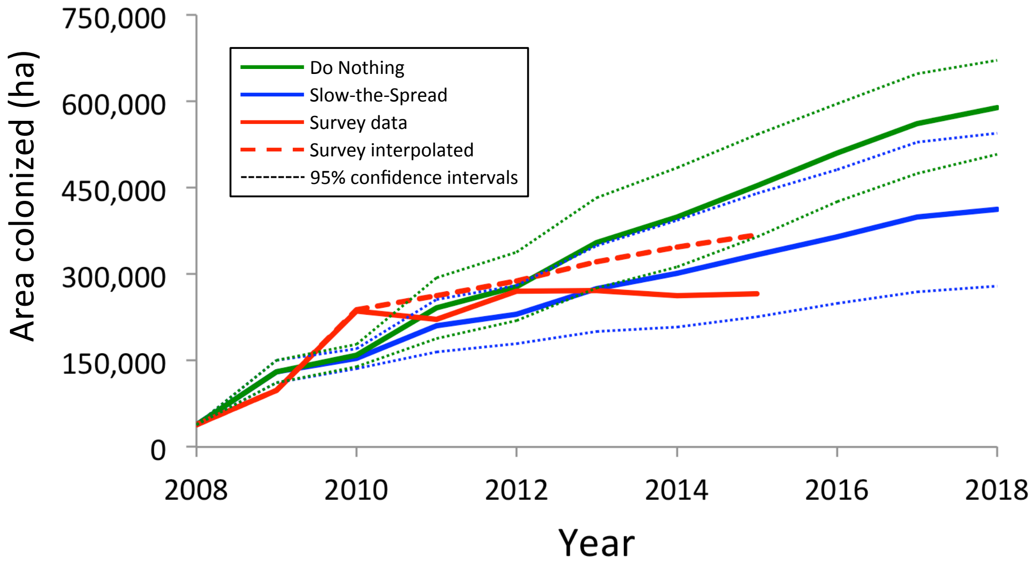


Figure 4.5. Area colonized by year in the Alberta study area. Survey data are shown as reported (solid red line) and interpolated (dashed red line) values to account for areas that were surveyed up to 2011, but then omitted thereafter. "Do nothing" and "slow-the-spread" projections were derived from 40 MPBSpread simulations.

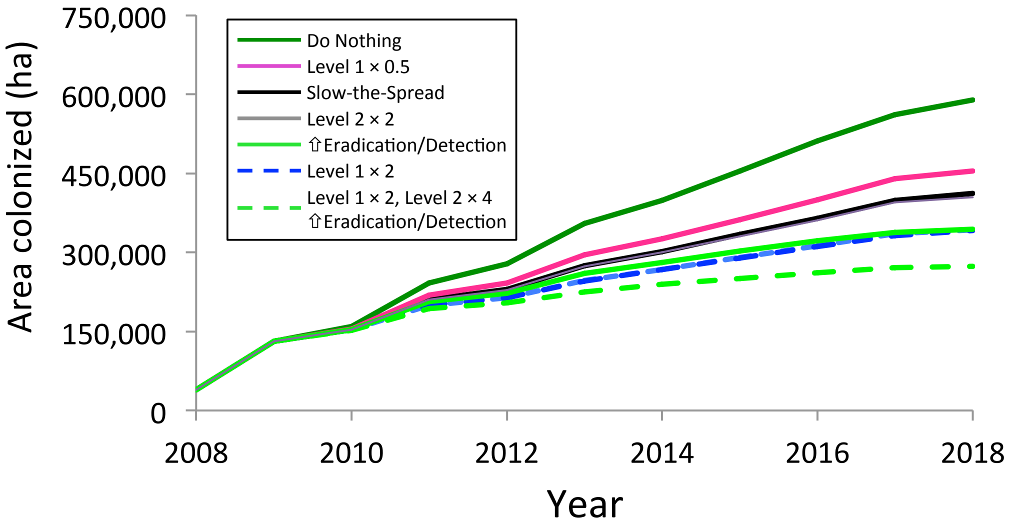


Figure 4.6. Mean area colonized by year in relation to different MPB management scenarios. The "do nothing " and current "slow-the-spread" scenarios are added for reference. Multipliers refer to scenarios where level 1 or level 2 treatments were halved (×0.5), doubled (×2), or quadrupled (×4); ⇧ refers to increased detection and eradication efficacies relative to the slow-the-spread scenario. See text for further details.

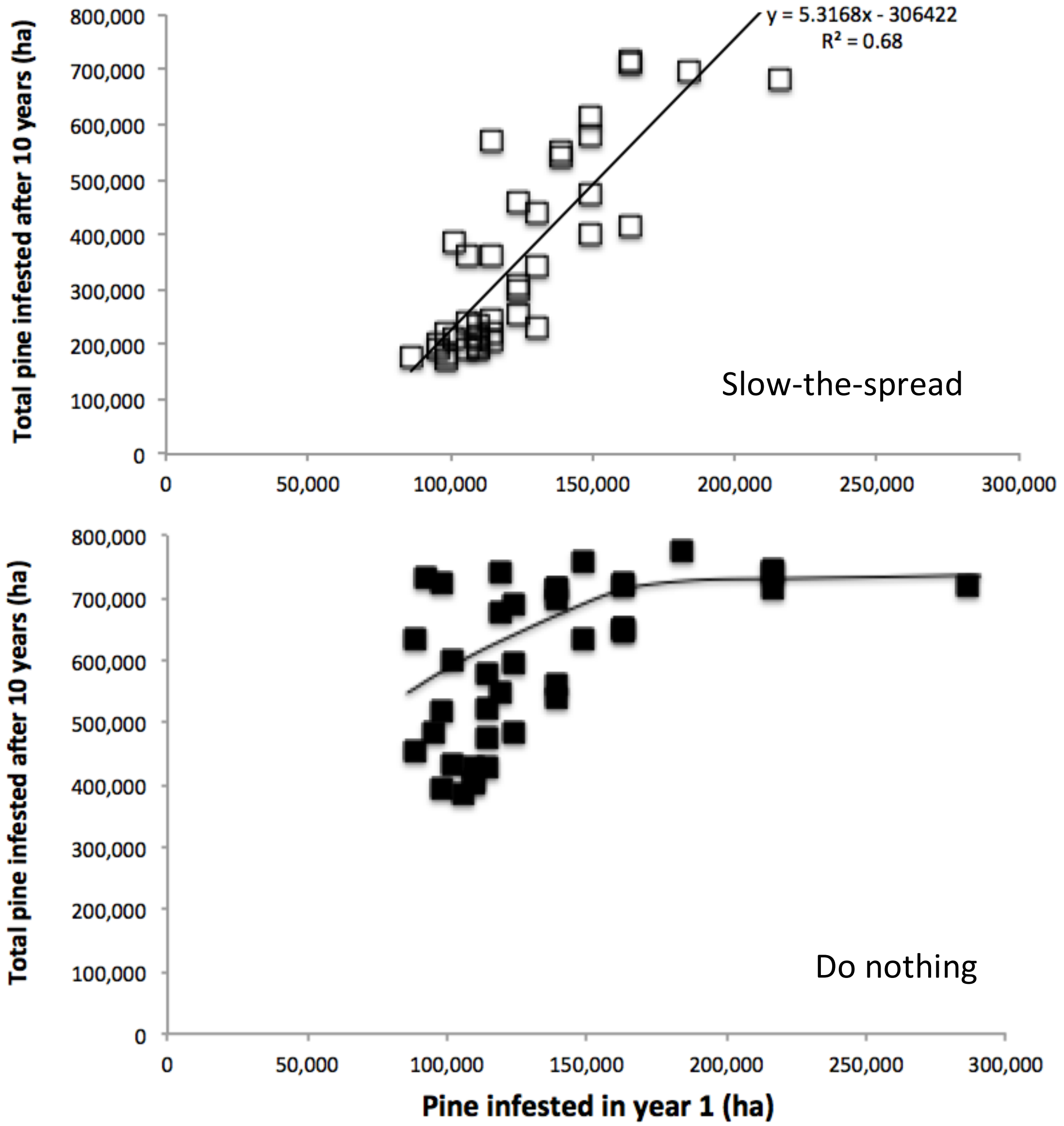


Figure 4.7. The relationship of pine area infested in year 1 to the total infested area after a 10-year simulation period under the existing "slow-the-spread" strategy (top panel) and a do nothing scenario (bottom panel). A total of 40 MPBSpread simulations were run for each scenario.

4.4 Discussion

4.4.1 Model validation

MPBSpread projections compare very favorably against other models designed to predict the spread of MPB, in both BC (Fall et al. 2004; Strohm et al. 2013; Bone and Altaweel 2014) and Alberta (Riel et al. 2010). Although its projections were a good fit to the empirical data, there were relatively small deviations in prediction accuracy. In British Columbia, area colonized tended to be over-predicted in the first 4 years of the simulation (Figure 4.4).

During this interval, active MPB control was implemented within the study area before being abandoned in 2004, and thereafter. Treatment can suppress MPB populations, even if temporarily (Carroll et al. 2006, Fettig et al. 2014), which could have reduced the area colonized.

MPBSpread accurately predicted pine mortality in British Columbia over the first 5 years of the simulation but under-predicted mortality for the later years, even though area colonized was very similar during this period (Figure 4.4). Under-predicting pine mortality during the later stages of an outbreak may be a consequence of the basic structure of MPBSpread. For simplicity, model components were designed to represent the spread dynamics and life history attributes of “typical” epidemic populations (Safranyik 2004). During the waning years of the outbreak in central British Columbia, epidemic MPB populations were far from typical. The dynamics of epidemic MPB populations are characterized by positive feedbacks where increasing beetle densities lead to increasing growth rates given the density-dependent requirement for mass attacks of the highest quality, yet most defensive host trees (Safranyik and Carroll 2006; Raffa et al. 2008). The increased availability of high quality trees for MPB (mature lodgepole pine) due to fire suppression and selective harvesting in central British Columbia (Taylor and Carroll 2004), facilitated a rapid and enormous increase in beetle populations leading to “spillover attacks” onto trees not normally attacked by epidemic beetles [small and/or young pines (e.g. Westfall and Ebata 2014)]. Thus, levels of tree mortality in British Columbia were higher than anticipated within the areas colonized by the beetle.

In Alberta, despite the extensive distribution of MPB as suggested in Figure 1.1, beetle densities are not yet near the levels reached in British Columbia (Cooke and Carroll 2017). Relatively lower population densities may be why the “slow-the-spread” strategy (StS) projections and actual colonized area were even better matched than for the BC dataset (see Figs. 4.4 and 4.5). Interestingly, in 2010 the area colonized was higher than predicted by MPBSpread. This was likely due to a significant immigration event (Nealis and Cooke 2014) beyond the initial ‘seeding’ event implemented to initiate the MPBSpread model runs. Even though current MPB densities may be relatively lower in Alberta versus British Columbia, it is worth emphasizing that evidence suggests that extremely high pine mortality rates may occur in the future as a consequence of very minor changes in climate and/or forest conditions (Cooke and Carroll 2017).

4.4.2 Assessing control measures

4.4.2.1 ‘Slow-the-spread” versus ‘Do nothing’

MPBSpread projections of area colonized by MPB in Alberta indicate that current control measures (StS; see Table 4.2) are indeed reducing area colonized by MPB in Alberta, relative to no control (do nothing; DN). At the conclusion of the 10-year simulation, area colonized under StS was reduced by about 30% (Figure 4.5). Model results by Fall et al. (2004), also showed a positive impact of control on the spread of MPB in British Columbia. Few empirical studies of treatment efficacy on the spread of MPB have been conducted and it therefore difficult to draw firm conclusions or appropriate guidance (Six et al. 2014). As Fettig et al (2014) point out, however, there is evidence that control strategies are effective at reducing MPB-caused mortality within treated sites, if not to suppress outbreaks. From the perspective of limiting spread, our results indicate that population levels must be low along with a high degree of detection accuracy and intensity of mitigation (further details below).

Under StS, the area of infestation after 10 years was linearly related to the initial area attacked when the latter was less than about 175,000 ha (Figure 4.7). This relationship no longer held when early infestation exceeded this value. The suitability of direct control thus depends on the spatial scale of the infestation (Nelson et al. 2006, and reference therein). Once a population becomes established at a high enough level, control is largely ineffective (see also, Fall et al. 2004) because any reduction in beetle reproduction is simply outstripped by the scale of new infestations.

A number of studies have argued for the importance of early detection and suppression as critical to slowing beetle spread (Carroll et al. 2006, Coggins et al. 2008, 2011, as examples). MPB control measures require considerable resources and planning and are expensive to implement. While there must be cases where beetles do not successfully establish in newly colonized stands (without control efforts), our results highlight the substantial risk of adopting a ‘wait-and-see’ approach. Under DN, initial colonization size was a poor predictor of long-term impacts but not when MPB controls were implemented (Figure 4.7). Furthermore, another benefit of control is that it can minimize the extent of the infestation area. This improves economic returns since a greater proportion of harvesting will occur in live trees rather than as salvage logging. Wood quality deteriorates fastest during the first two years after successful beetle attack (Magnussen and Harrison 2008). Trees are also discolored by ‘blue-stain’, caused by a fungus introduced by the beetle, and which can reduce their economic value (Byrne and Uzunovic 2005).

Alberta is committed to reducing high-susceptible pine forests with proactive harvesting via approved forest management plans and through supplementary logging. The latter, termed the ‘healthy pine strategy’ (HPS), has a goal of reducing the area of highly susceptible (80 to 120 year-old) stands by 75% over 20 years; prescribed burning may be utilized in inaccessible areas. Minimizing pine mortality via Level 1 and 2 controls thus serves to enhance the planning window for the subsequent harvesting of vulnerable stands.

4.4.2.2 Enhancing control efficacy

For successful direct control of MPB, infestations must be reliably detected and aggressively treated; however these requirements are seldom achieved under operational MPB management programs (Carroll et al. 2006). Indeed, Six et al (2014) reviewed previous efforts at MPB control and found that rates of detection in treated stands ranged from as little as 45%, to a maximum of 79% - almost certainly below levels needed to stabilize, let alone reduce MPB populations (Carroll et al. 2006). The results derived from MPBSpread showed that under StS, the combined detection and subsequent eradication probabilities for Level 1 and 2 treatments equaled 0.585 and 0.9, respectively (see Table 4.2). Typically, in the early stages of an infestation all cells within the study area were ‘sampled’ by the model for the presence of MPB (data not shown). This means that on a per-ha basis, the overall average detection and eradication probability under StS was only about 63%, well within the range reported above (see section 3.3.1) and in keeping with data from other jurisdictions (Six et al. 2014). It should be noted that cells where MPB was detected but not eradicated by Level 1 control still incurred a reduction in the beetle population (see Methods). Nevertheless, area colonized increased steadily under StS.

Increasing the level of detection and eradication reduced the area colonized by 14% below StS, after 10 years (Figure 4.6), corresponding to a total area of about 56,500 ha. Enhancements in detection and eradication were relatively modest (Table 4.2), but they emphasize their importance in limiting MPB spread. This is evident in the early stages of an infestation, particularly when initial population sizes are low (see Figure 4.7). Though we did not consider each factor in isolation, control efficacy relies on detection - the greater its accuracy the more successful mitigation can be. Future research should be devoted to determining more effective means of green-attack detection during ground surveys.

Detection and eradication are important as a local response to infestation. How much effort is allocated to Level 1 and 2 measures, however, is an indication of the pervasiveness of control across the landscape. In that regard, enhancing Level 1 control (doubling the total annual area) had a negative impact on colonization but that was not the case with Level 2 control (Figure 4.6). This is likely due, in part, to the fact that the upper limit on the areas subject to Level 1 control was much greater than Level 2. In addition, Level 1 controls were applied within a given cell during the early stages of an infestation when populations still had the potential for substantial growth and beetle export. Level 2 controls, in contrast, were applied to cells with older infestations when beetle populations were already in decline.

A final consideration in the spread of MPB, which we did not consider, is the fact a significant proportion of the landbase does not receive any beetle control because areas are inaccessible, too visually sensitive (parks, for example), or otherwise restricted (riparian, special conservation or wildlife areas, military sites). MPB populations are thus largely free to grow unchecked in these areas, which adds to the overall infestation burden. To our knowledge, the impact of this factor on MPB dynamics has not been given explicit consideration.

5. General Discussion & Conclusions

A successful direct control program for MPB requires (i) prompt and thorough application of the most appropriate treatments (ii) at a magnitude dictated by the population size and rate of increase. The first two elements of our research project considered both of these criteria in terms of the effort to slow the eastward spread of MPB. Regarding the size and rate of increase of populations, this aspect has traditionally received insufficient attention during past management efforts over most jurisdictions and therefore has been at the root of their failures (Carroll et al. 2006). Our development of the *r* model from the extensive data set comprising MPB productivity assessments (*r*-values) conducted by Alberta Agriculture and Forestry, combined with detailed annual aerial overview surveys, can be used to determine both infestation size and rates of increase for individual populations over the landscape. This information can be used to facilitate targeting and prioritization of stands for direct control, thereby enhancing the efficacy of the control effort. Furthermore, given that the *r* model is based on readily available vegetation inventory, weather and topographical data, potential MPB productivity can be projected in the absence of direct sampling allowing forest companies to adjust harvest schedules in a way that targets stands with the highest likelihood of generating large numbers of beetles in the event they are colonized – an activity in direct keeping with Alberta's Healthy Pine Strategy.

To date, the most appropriate treatment of high-priority infestations in the leading edge of the MPB invasion in Alberta has been primarily felling and burning infested trees (termed Level 1 control by Alberta Agriculture and Forestry). Our analysis of this approach in terms of the promptness and thoroughness of its application revealed three key findings. First, the rate of detection of newly infested (green-attack) trees was lower than expected (maximum 68% in 2011). As detailed in Carroll et al. (2006), suppression of a MPB outbreak that is increasing at just 3-fold each year will be impossible if detection/treatment rates are ≤68%. A rate of increase of approximately 3 is common within MPB outbreaks (Safranyik and Carroll 2006), and although it appears that populations within Alberta have not yet uniformly reached this level of growth, the threshold nature of MPB population dynamics ensures that rapid changes in rates of increase can occur with very minor changes in climatic and/or forest conditions (Cooke and Carroll 2017). Second, Level 1 treatments reduced subsequent attack intensities, but the effectiveness of treatments declined with increasing infestation size. The dynamics of epidemic MPB infestations are characterized by positive feedbacks that cause the rate of increase to rise as populations grow (Safranyik and Carroll 2006; Raffa et al. 2008). This means that as small populations grow, so too will their growth rates, and the efficacy of Level 1 treatments will decline. We found that once infestations exceeded approximately 8 – 10 infested trees/km^2, the efficacy of Level 1 interventions disappeared. Therefore, treatments intended to low the spread of MPB in Alberta will likely be most effective in frontline areas with relatively low beetle densities. Finally, across the area considered in our study, Level 1 treatments led to significant declines in subsequent attack intensity (33 - 41%); however, there was substantial variability in treatment effects within and among years. Furthermore, the rate of treatment had a substantial impact upon the success of the treatments suggesting that during years with low treatment rates, beetles from nearby untreated areas immigrated into areas around treated infestations and thereby limited the apparent impact of the treatment. From the results of the first two objectives of our research we conclude that felling and burning of infested trees can be an effective means of limiting the local growth and spread of MPB populations provided (i) efforts are devoted to increase detection efficacy, (ii) inasmuch as possible, treatment is applied early, before infestations begin to grow, and (iii) treatments are aggressive and consistent from year to year.

Our spatially explicit cellular automata model, MPBSpread, was derived from the results of the first two elements of our project. It allowed us to evaluate the relative impact of the current versus alternative control strategies at slowing the spread of the beetle. Projections by MPBSpread corresponded very well with empirical data of area colonized within Alberta under the ongoing slow-the-spread (StS) scenario. More importantly, the area colonized by MPB was lower under StS than a simulated "do nothing" scenario (DN), and the efficacy of StS improved over time such that the area colonized was ca. 70% of that predicted under DN by the end of the simulation (2018). Interestingly, the area colonized was particularly sensitive to the efficacy of early detection and eradication, and the amount of Level 1 control, but not Level 2 control (clear cut harvesting). This was likely due to the reasons described above where, due to positive feedbacks in MPB populations (Safranyik and Carroll 2006; Raffa et al. 2008), the potential efficacy of treatments will decline as infestations grow.

Using a simple demographics model, Carroll et al. (2006) estimated that 97.5% of beetles in an area must be killed to stabilize a mountain pine beetle population. MPBSpread is not a population model so we cannot address this prediction explicitly. Model results, however, indicate that neither the StS controls nor any single control enhancement is sufficient to achieve population stability, at least in the 10-year time horizon we considered. It appears, however, that an approach that combines direct control with a greater and persistent effort at detection/treatment can be successful (see Figure 4.6). A critical issue that may limit the application of an enhanced strategy is its added cost. This will need to be balanced against the ecological, economic, and social impacts of the MPB infestation, which have been severe and are ongoing. In Alberta, the forest industry is worth $9 billion annually and employing 38,000 workers; 14 of 25 major forest companies relying on it as a major harvestable species. More than 1.54 million hectares of Alberta forest have sustained at least some level of MPB damage. Should MPB continue its eastward movement, the economic impact will be much more widespread.

At present, MPB densities are relatively lower in Alberta versus the levels that were reached during the outbreak in British Columbia (Cooke and Carroll 2017). Our results emphasize the critical need to act aggressively when populations are low – a conclusion consistent with earlier assessments of MPB control efforts (Carroll et al. 2006; Six et al. 2014). Recent evidence of altered dynamics by MPB in newly invaded pine forests further strengthens this point. Lodgepole, hybrid and jack pine populations growing outside the historic range of MPB (i.e. Alberta) are evolutionarily 'naïve' to MPB attacks due to a lack of long-term interactions with the beetle (Burke et al. 2017). Defensive resin production in novel pine hosts is quantitatively and qualitatively different when compared to trees in the native range (Clark et al. 2010, 2014; Burke et al. 2017), and reduced defensive capacity has been suggested as the proximate cause of higher MPB attack densities (Clark et al. 2010) and productivity (Cudmore et al. 2010), and higher rates of spread and impact in novel habitats (Robinson 2015). Furthermore, Burke and Carroll (2016) found that naïve host trees may be more attractive to foraging MPB, potentially further exacerbating MPB impacts. These facts, combined with the unpredictable nature of MPB population eruptions and its proximity to the transcontinental boreal forest (Cooke and Carroll 2017), render an aggressive direct control program more imperative than at any other time in history.

In conclusion, our analyses indicate that efforts to date to slow the eastward spread of MPB across Alberta have achieved some success. We have also shown that improvements could be achieved through better efficacy at the detection and treatment of small infestations. We recommend that future research efforts be devoted to improved survey methods for on the ground green-attack detection.

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