



Research article

Mountain pine beetle outbreak duration and pine mortality depend on direct control effort

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ABSTRACT

The efficacy of direct control methods in bark beetle outbreaks is a disputed topic. While some studies report that control reduces tree mortality, others see little effect. Existing models, linking control rate to beetle population dynamics and tree infestations, give insights, but there is a need to take into account the environment spatial variability and its impact on beetle life cycle. Here, we use natural variability found in a carefully monitored and controlled infestation to simulate outbreak dynamics under different control effort and to explore the impact of control on outbreaks suppression and tree mortality. Our semi-empirical predictive model of the number of infested trees as a function of ecological and environmental variables is coupled to a simulation model for infestation dynamics. We show that even a little control can have a major impact on the number of infested trees after several years of sustained effort. However, a moderate control of 60% is required to reduce the beetle population on the long term. Furthermore, a control rate of 69%–83% is needed to achieve outbreak suppression in under 13 years depending on the abundance of incoming flights from outside sources.

1. Introduction

Bark beetle outbreaks are a major threat for western North American pine forests, impacting tens of thousands of square kilometres (Fettig and Hilszczański, 2015). Beetle epidemic populations cause a decline of pine forests and changes in forest structure and composition, resulting in significant economic losses (Diskin et al., 2011; Walton, 2013). Detection of infested trees is typically via aerial surveys, ground-based surveys, or a combination of the two (Fettig and Hilszczański, 2015). Managers employ various approaches to reduce levels of tree mortality and these can be divided into indirect – or preventive – and direct control. In this paper, we focus on direct control. The potential of direct control methods to be effective depends on the ability to detect bark beetle infestations. In turn, the level of direct control impacts outbreak duration and the extent of tree mortality.

The mountain pine beetle, *Dendroctonus ponderosae* is a bark beetle causing significant pine losses in western North America (Fettig and Hilszczański, 2015). Although beetle outbreaks have been co-occurring with pine forests and shaping coniferous ecosystems, they have recently increased in size and severity (Six et al., 2014). They cause in some places more damage than fires and intense climatic events such as storms (Dale et al., 2001). Due to climate change, temperature suitability for mountain pine beetle increased in western Canada, leading to an increase in outbreak severity and a range expansion toward

higher latitudes and elevations (Bentz et al., 2010; de la Giroday et al., 2012). In the United States, mountain pine beetle outbreaks affected over five millions hectares between 1999 and 2003 (Wulder et al., 2006). The mountain pine beetle outbreak occurring in western Canada pine forests since the early 2000's has killed more than half of the merchantable timber volume (Walton, 2013). In the Cypress Hills area, located at the boundary between the provinces of Alberta and Saskatchewan, the first recorded outbreak occurred in the 1980's (Taylor et al., 2006). In 2006, a new outbreak started in this area. This outbreak continues today and is declining.

Mountain pine beetles typically have a one-year life cycle (Safranyik and Carroll, 2006) although completing the life-cycle can take two years in colder regions (Logan and Powell, 2001) and some warmer areas show evidence of a second generation in the summer (Mitton and Ferrenberg, 2012; Bentz and Powell, 2014). During the summer, adults emerge and attack new pines by drilling galleries under the bark. There, they mate and females lay eggs. The new generation overwinters as larvae before resuming their development to adult stage in the summer. Beetle development is controlled by temperatures (Bentz et al., 1991). Parent adults usually do not survive the winter. During outbreaks, mountain pine beetles utilize pheromones to mass attack large, healthy pines in sufficient number to overwhelm tree defences (Safranyik and Carroll, 2006). Therefore, weather factors, such as temperatures, and

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stand characteristics, such as tree size, can impact considerably beetle attack and development, thereby explaining differences in outbreak dynamics (Campbell et al., 2007). The mountain pine beetle is a threat for almost every pine species (Safranyik and Carroll, 2006). In western North America, its main host is the lodgepole pine (*Pinus contorta*, Dougl. ex Loud. var. *contorta* Engelm).

Managers typically carry out aerial and ground-based surveys to obtain the necessary information on mountain pine beetle infestations location and implement control methods. Aerial surveys using helicopters and/or fixed-wing aircraft are efficient for detecting previously infested trees in a relatively limited area (Fettig and Hilszczański, 2015). For larger areas, remote sensing methods help detect infested trees from aerial imagery, such as Landsat and Lidar, using image recognition (Meddens et al., 2011, 2013; Bright et al., 2014). Aerial detection is made possible by the fact that pine trees infested by mountain pine beetle in the previous year display a bright red crown which starts to appear within a year of the beetle attack (Safranyik and Carroll, 2006). These red-top trees typically do not contain live brood anymore. On the other hand, ground-based surveys are the primary methods used to identify currently infested trees. Ground crews detect currently infested trees by the presence of pitch tubes around beetle entry holes and larvae galleries under the bark. Using aerial surveys of previously infested trees to inform ground-based surveys allows managers to direct detection resources to susceptible locations by using the propensity of beetles to engage in short-distance dispersal from the previously infested trees to attack new trees (Safranyik and Carroll, 2006). Since a successful mountain pine beetle attack typically leads to the tree's death, pines trees cannot be reinfested.

Once an outbreak is detected, control can be implemented. Direct control aims to actively reduce beetle population and slow beetle spread, for example by felling and burning infested trees, in order to protect tree resources. Several studies have compared different direct control methods (e.g. Nelson et al., 2006; Seidl et al., 2008; Strom and Clarke, 2011). The methods differ in control efficiency due either to a different detection rate or to a different beetle removal success. Since, the number of infested trees is a good proxy for beetle population size (Safranyik, 1988; Carroll et al., 2006), using the number of infested trees treated for mountain pine beetle allows for a fair comparison of methods.

The efficacy of direct control of mountain pine beetle outbreaks is disputed: while some studies report significant reduction in the levels of tree mortality due to direct control, others notice little to no effect compared to uncontrolled areas. For example, Wulder et al. (2009) reported that control activities in the Rocky Mountains slowed the rate of increase of infested trees compared to no control. However, Trzcinski and Reid (2008) reported that beetle populations in Banff National Park continued to increase at the same rate in treated and untreated areas and that between 45% and 79% of infested trees were left undetected in the treated area due to difficulty of the terrain and remoteness of the area. Note that attempts at implementing biological control for mountain pine beetle were unsuccessful (Safranyik et al., 2002). Indeed, mountain pine beetle natural enemies cannot reach densities high enough to affect beetle mortality during epidemic population phases. It is generally accepted that extremely high detection and control rates are required to reduce mountain pine beetle populations below epidemic levels, thereby decreasing the overall number of trees killed (Six et al., 2014).

In order to obtain quantitative information on the relationship between control rates and mountain pine beetle outbreaks, Carroll et al. (2006) built a simple and non-spatial theoretical framework describing the proportion of infested trees that must be treated to maintain a constant beetle population size P as a function of the yearly rate of increase of infested trees R :

$$P = 1 - 1/R. \quad (1)$$

Combined with the following geometric growth population model of beetle population N at time t

$$N_t = N_0 (R(1 - P_a))^t, \quad (2)$$

where P_a is the actual proportion of infested trees treated, they were able to show, theoretically, how many years of sustained control effort is necessary to achieve outbreak suppression depending on the rate of increase and the control effort. Indeed, when the actual proportion of infested trees treated P_a reaches the proportion of infested trees that must be treated P , Eq. (2) becomes $N_t = N_0$, meaning that the population size stays the same over time. For example, for $R = 2$, $P = 0.80$, and $N_0 = 10\,000$, about 10 years of sustained control are necessary to achieve suppression. It becomes 20 years for $R = 3$. While this gives useful insights, it does not fully account for spatial and temporal heterogeneities found in natural environments. For example, variations in temperatures, host densities, or host vigour impact beetle development rate and survival (Safranyik and Carroll, 2006) and thus, the rate of increase of infested trees. In addition, outbreaks are typically not isolated in space. Given the possibility of incoming flights from adjacent uncontrolled areas into the focus area, outbreaks are susceptible to rebound even under control. Thus, there is the need for evaluation of the efficacy of control measures in spatially and temporally variable environments by coupling theoretical models to detailed data regarding environmental conditions and infestation levels.

In this study, we analyse quantitatively the impact of control effort on bark beetle and pine populations under the influence of a spatially and temporally changing environment with beetle immigration from outside sources. The objectives are: (1) to build a semi-empirical model of infestation using mountain pine beetle and environmental data from the Cypress Hills area, (2) to simulate outbreaks in space and time under different control rates, and (3) to explore the impact of control effort on beetle and pine population sizes.

2. Materials and methods

In this section, we first describe the data used to parametrize the different components of the model (Section 2.1). Second, we define a model that simulates how the number of beetle infested trees varies over time and space depending on the proportion of infested trees treated by managers (Section 2.2). Within this simulation model, the baseline pine population growth rate in the absence of beetle attacks is estimated from a simple submodel described in Section 2.2.1. The number of infested trees is predicted for a specific location and year by a semi-empirical submodel described in Section 2.2.2 that uses observed values of environmental covariates from the Cypress Hills area. These components are put together to create the simulation model in Section 2.2.3.

2.1. Study area and data

The data used to calculate the pine population growth rate, parametrize the predictive model, and initiate the simulation model comes from the mountain pine beetle infestation in the Saskatchewan portion of Cypress Hills interprovincial park. This park is located at the border between the provinces of Saskatchewan and Alberta. The main mountain pine beetle host tree in this area is the lodgepole pine. The Saskatchewan portion of the park is divided in two sections that are 20-km apart. Their combined extent covers 184 km².

The Saskatchewan Forest Service is responsible for managing mountain pine beetles in this portion of the park. Every year, a complete aerial survey of the park extent is performed in order to detect red-top trees (Saskatchewan Ministry of Environment, 2016). These are later ground-truthed for beetle attacks and trees fading from other causes than mountain pine beetle are removed from the survey. The ground survey technical details are available in supplementary material. Finally, the currently infested trees are treated, primarily using a fall and

Table 1
Description and range of the variables used in the model predicting the number of infested pines.

Description	Range	Unit
Highest maximum daily temperature in July and August	26.3–38.1	°C
Cold tolerance index from Régnière and Bentz (2007) estimates the probability of larva survival over the winter given daily temperatures	24.3–86.0	%
Average relative humidity from March to May	56.9–73.8	%
Average wind speed in July and August	9.7–15.4	km/h
Height of the dominant tree species in the cell when the pine cover is greater than 50%	0.0–38.7	m
Number of pine trees greater than 10 cm at breast height	0–35 825	pines
Elevation	1117–1377	m
Slope	0.0–17.5	%
Northernness (spatial property of a slope to face North)	–1–1	–
Easternness (spatial property of a slope to face East)	–1–1	–

burn tactic to ensure that the broods are killed. All detected infested trees are controlled. The Forest Service has been following this procedure since the mountain pine beetle infestation was detected in 2006 up to the current collapse in 2018. From these surveys, we obtained the locations of all infested trees (technical details in supplementary material). In addition to the infested trees within the park limits, there were infestations just outside the park in the south. These infestations were not recorded nor managed.

The ecological and environmental covariates and the infestation response value were discretely distributed in space and time. We superimposed a grid of 722 cells of size 500 × 500 m over the park extent, counted how many infested trees fell in each cell, and obtained ecological and environmental variable values described in Table 1 for each cell over the study period from 2005 to 2018.

To reflect the impact of high temperatures on mountain pine beetle emergence and dispersal (Safranyik and Carroll, 2006), we included the maximum temperature over the spring and summer. Because mountain pine beetle larvae are very sensitive to sudden changes in minimum temperatures in the fall, winter, and spring (Safranyik, 2004), we included the cold tolerance metric from Régnière and Bentz (2007). A small fraction of mountain pine beetles engage in long-distance dispersal events and disperse further than a few hundred metres by getting caught in the wind (Safranyik and Carroll, 2006). Therefore, we included the wind speed during spring and summer which corresponds to the dispersal season. Water stress reduces the pines' ability to resist mountain pine beetle attacks (Safranyik, 1978; Erbilgin et al., 2017). Therefore, we included the relative humidity during the spring. Weather variables were estimated for each grid cell and each year using the BioSIM software (Régnière et al., 2014).

In addition to weather variables, we included elevation, slope, northernness and easternness to address bias in mountain pine beetle dispersal due to spatial configuration and wind direction. Topography variables were calculated from the Canadian Digital Elevation Map downloaded from the Geogratis website (geogratis.cgdi.gc.ca). We also included in our list of covariates pine height and number of pines per cell. Vegetation variables were estimated from Beaudoin et al. (2014) (see supplementary material for the technical details).

2.2. Model

The simulation model used a baseline pine population growth rate γ and predictions of the number of infested trees I_x^{t+1} depending on ecological and environmental variables X_x^t and number of pines H_x^t at year t for the same location.

Table 2
Description of the symbols used in the model.

Symbol	Description
R_x^t	Geometric rate of increase of infested trees from year t to $t + 1$
X_x^t	Vector of environmental variable measurements at year t
H_x^t	Number of pine trees in a cell x at year t
β	Vector of parameters associated with variables X_x^t and H_x^t
M_x^t	Number of uncontrolled infested trees at year t and location x
$N(x)$	Von Neumann neighbourhood of location x
w	Weight associated with the number of uncontrolled infested trees in each cell of the neighbourhood $N(x)$
r_0	Number of infested trees from other sources
I_x^{t+1}	Number of infested trees at year $t + 1$ and location x
B_x^t	Number of uncontrolled infested trees added to M_x^t to describe boundary conditions at year t and location x

2.2.1. Pine population growth rate

The pine population growth rate in the absence of mountain pine beetles provides a baseline to which we can compare the observed pine mortality.

Using the number of pines H_x^t in 2001 and in 2011 only for cells where no beetles were present between 2001 and 2011, we calculated the pine yearly growth rate using the equation:

$$\gamma = \left(\frac{\sum_x H_x^{2011}}{\sum_x H_x^{2001}} \right)^{1/(2011-2001)} \tag{3}$$

In addition, we estimated variability in the pine population growth rate by calculating the standard deviation of the yearly pine population growth rate per cell.

2.2.2. Predicting the number of infested pines

In this section, we describe the semi-empirical infestation sub-model used to predict the number of infested trees from ecological and environmental variables. The submodel symbols are defined in Table 2.

An infested tree at year t produces new infested trees at year $t + 1$ according to Poisson(R_x^t) where R_x^t is the geometric rate of increase of infested trees at year t and location x . We assume that the rate of increase of infested trees in a cell depends on the number of pines available H_x^t as well as other ecological and environmental variables X_x^t described in the previous section. We express the rate of increase of infested trees R_x^t as

$$R_x^t = e^{\beta_0 + \beta_1 H_x^t + \sum_{i \geq 2} \beta_i X_{x,i}^t} \tag{4}$$

At a location x , the sources of new infestations at $t + 1$ are:

1. M_x^t : number of uncontrolled infested trees at t in the same location x ,
2. $\sum_{\xi \in N(x)} M_\xi^t$: number of uncontrolled infested trees at t in the Von Neumann neighbourhood of x ,
3. B_x^t : number of uncontrolled infested trees at t in the cells outside the park limits and adjacent to x , this variable allows us to include boundary conditions in the model,
4. r_0 : number of infested trees arising from other sources, such as long-distance dispersal events originating from inside or outside the park limits and transitions from endemic to epidemic population level, and representing a background infestation level.

The number of infested trees I_x^{t+1} at year $t + 1$ and location x is a sum of R_x^t for each source of infestation, and thus, a Poisson-distributed random variable itself. Therefore, we can write

$$I_x^{t+1} \sim \text{Poisson} \left(\left(\frac{M_x^t + w(B_x^t + \sum_{\xi \in N(x)} M_\xi^t)}{1 + 4w} + r_0 \right) R_x^t \right) \tag{5}$$

where w is the weight associated with each location adjacent to x . The term $1 + 4w$ arises due to the weight of 1 attributed to the number of uncontrolled infested trees at the same location and the weight of w

attributed to the number of uncontrolled infested trees in each of the 4 cells of the Von Neumann neighbourhood.

Eq. (5) can be rewritten as

$$I_x^{t+1} \sim \text{Poisson}\left(\left(M_x^t + w(B_x^t + \sum_{\xi \in N(x)} M_\xi^t) + \tilde{r}_0\right) \tilde{R}_x^t\right). \tag{6}$$

where

$$\tilde{r}_0 = r_0(1 + 4w) \tag{7}$$

and

$$\tilde{R}_x^t = \frac{R_x^t}{1 + 4w}. \tag{8}$$

Therefore, the expected value of I_x^{t+1} is

$$\begin{aligned} E(I_x^{t+1}) &= (M_x^t + w(B_x^t + \sum_{\xi \in N(x)} M_\xi^t) + \tilde{r}_0) \tilde{R}_x^t \\ &= e^{\ln(M_x^t + w(B_x^t + \sum_{\xi \in N(x)} M_\xi^t) + \tilde{r}_0)} e^{\beta'_0 + \beta_1 H_x^t + \sum_{i \geq 2} \beta_i X_{x,i}^t} \\ &= e^{\ln(M_x^t + w(B_x^t + \sum_{\xi \in N(x)} M_\xi^t) + \tilde{r}_0) + \beta'_0 + \beta_1 H_x^t + \sum_{i \geq 2} \beta_i X_{x,i}^t}, \end{aligned} \tag{9}$$

where $\beta'_0 = \beta_0 - \ln(1 + 4w)$.

The boundary conditions were such that cells outside the park limits had a number of infested trees equal to 0 except for cells just outside the park southern border which had a number of infested trees greater or equal to 0. This allowed us to take into account the fact that there were no significant mountain pine beetle flights from outside the park limits except outside the park southern border (Rory McIntosh, *pers. comm.*). We made the reasonable assumption that the infestations outside the park limits lasted from 2006 to 2014 (estimated from Brian Poniatowski, *pers. comm.*). However, the precise boundary values are unknown. To find acceptable boundary conditions and, in turn, be able to estimate the parameters of interest in Eq. (9), our approach was to choose the boundary values that produce the best match between the observed and predicted number of infested trees in the domain. For each cell x adjacent to the infested border, we added to $\sum_{\xi \in N(x)} M_\xi^t$ a value b'_x chosen with an optimization algorithm described in Supplementary Information. Thus,

$$B_x^t = \begin{cases} b'_x & \text{if } x \text{ is adjacent to the infested border,} \\ 0 & \text{otherwise.} \end{cases} \tag{10}$$

To fit Eq. (9) to data, we divided the dataset in folds by holding out a different year for each fold. We only kept the folds where the year holdout was between 2009 and 2018 as the years 2006 to 2008 had a very small number of cells with $I_x^t > 0$. Therefore, we had 10 folds. With the function `gnm` of the R package `gnm`, we fit, on the training set of each fold, a Poisson nonlinear model using Eq. (9). We evaluated each of the 10 fits on the test set of the corresponding fold using the coefficient of determination r^2 between observed and predicted number of infestation. Then, we fit the model on the entire dataset.

2.2.3. Simulations

We simulated, between 2006 and 2018, outbreaks subject to different control efforts e ranging from 0.01 to 0.99 to explore the effect of small, moderate, and high direct control. We used a time unit of 1 year and a spatial unit of a 500×500 m cell. Table 3 shows the state variables used in the simulations.

At each time step and for each location, the number of infested trees is the sum of the number of controlled and uncontrolled trees:

$$I_x^t = M_x^t + C_x^t. \tag{11}$$

For each control effort e , we ran 1000 simulations. The initial values corresponded to the park observations in 2006. The total number of infested trees in 2006 was $\sum_x I_x^{2006} = 3$. Starting with $t = 2006$, we repeated the following process over the years for each location:

Table 3

State variables used in the simulation model.

Variable	Description
S_x^t	Number of pines susceptible to beetle attacks at year t and location x
H_x^t	Number of pines surviving after beetle attacks at year t and location x
I_x^t	Number of infested pines at year t and location x
M_x^t	Number of uncontrolled infested pines at year t and location x
C_x^t	Number of controlled infested pines at year t and location x

1. We drew a baseline pine population growth rate g_x^t in a normal distribution with mean γ and the standard deviation calculated in the previous section.
2. We calculated the number of pines susceptible to beetle attacks using $S_x^{t+1} = g_x^t H_x^t$.
3. We predicted the number of infested trees I_x^{t+1} using the model described in Eq. (9) and parameters fitted in the previous section.
4. We drew the number of controlled infested trees C_x^{t+1} in Binomial (e, I_x^{t+1}).
5. We calculated the number of uncontrolled infested trees using $M_x^{t+1} = I_x^{t+1} - C_x^{t+1}$.
6. We calculated the number of pines surviving the year using $S_x^{t+1} = H_x^{t+1} - I_x^{t+1}$.

To compare the simulations to the observations in Cypress Hills, we performed the simulations with the observed control effort e'_{obs} each year. The observed control effort e'_{obs} was calculated using the observed values of C_x^t and I_x^t following the equation:

$$e'_{\text{obs}} = \frac{\sum_x C_x^t}{\sum_x I_x^t}. \tag{12}$$

We ran these simulations for two scenarios: (1) the park southern border is a source of beetles ($b'_x \geq 0$) using the estimates calculated in the previous section to represent the presence of uncontrolled infestations outside the study area and (2) the park southern border is not a source of beetles ($b'_x = 0$) meaning that our study area would have been isolated from the influence of adjacent uncontrolled infestations.

3. Results

In this section, we first present the results for the components of the simulation model: estimating the pine population growth rate (Section 3.1) and fitting the predictive submodel to data (Section 3.2). Then, we show the results obtained from the simulation model when we use the control effort observed in the park as a way to validate the simulation model (Section 3.3.1) and when we vary the control effort (Section 3.3.2).

3.1. Pine population growth rate

In the absence of mountain pine beetle, the pine geometric growth rate estimated using Eq. (3) was 0.95, indicating a diminishing pine population. The standard deviation of the pine population growth rate per cell was 0.17.

3.2. Predicting the number of infested trees

To estimate the values of b'_x , we matched the observed and predicted number of infested trees in the domain over the entire time period. We obtained the maximum coefficient of determination $r^2 = 0.72$ for the b'_x values described in Table 4.

To evaluate the predictive submodel of the number of infested trees, we compared the observed and predicted values on the 10 folds of the dataset using the coefficient of determination r^2 . The average r^2 was 0.63 with a minimum of 0.21 and a maximum of 0.86. Visually, the predicted infested areas correspond to the observations (see Fig. 1 for a



Fig. 1. Predicted (top) vs observed (bottom) number of infested trees I_x^{2013} per 500×500 -m cell in 2013 on a log scale.

Table 4
Parameter values estimated for b'_x .

Year	Cell									
	1	2	3	4	5	6	7	8	9	10
2006	1	4	2	0	0	0	0	2	8	0
2007	3	0	25	37	41	14	0	0	0	0
2008	45	10	128	65	63	167	72	18	0	11
2009	67	13	80	78	72	135	95	19	7	0
2010	22	26	37	59	80	84	37	0	0	34
2011	11	0	108	34	525	261	128	1	58	0
2012	53	0	88	42	202	191	2	16	0	3
2013	0	0	58	30	164	210	107	11	0	0
2014	32	7	0	0	123	105	25	0	0	0

typical example). We obtained the parameter values $\tilde{r}_0 = 0.045 (\pm 0.002 \text{ SE})$ and $w = 0.089 (\pm 0.004 \text{ SE})$.

Therefore, using, Eq. (7), r_0 is equal to 0.033. Using Eq. (8), we obtain the values of R'_x from \tilde{R}'_x . Forested areas have a mean R'_x equal to 2.1 (see Fig. S.1 in Supplementary Information for a typical example). The areas with no pine cover as estimated from aerial imagery indicate R'_x values greater than 0 to be able to handle the possibility of isolated pines in the simulation model. The sum of the predicted infested trees over the domain each year matches the sum of the observed infested trees (Fig. 2).

3.3. Simulations

3.3.1. Simulation model validation

Using Eq. (12), we calculated the observed control effort in Cypress Hills and obtained a median of 62% of controlled infested trees over the years (Fig. S.2 in Supplementary Information). Using these control proportions each year in our simulations, we obtained the total number of infested trees, the number of uncontrolled infested trees and the number of pines that match the observed or estimated values in the park (Fig. 3). The model described with good precision the outbreak dynamics although the simulated number of infested trees is lower at the peak than the observations.

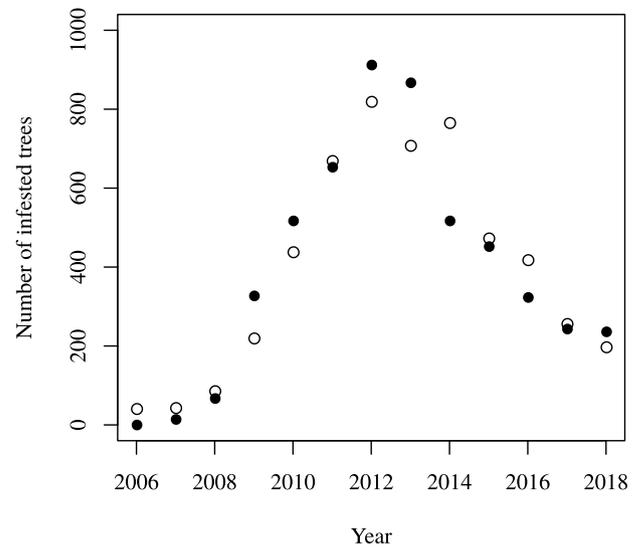


Fig. 2. Predicted (white) vs observed (black) number of infested trees per year in the entire domain $\sum_x I'_x$.

3.3.2. Varying control effort

As control effort decreases, outbreaks were less likely to be suppressed and the number of infested trees increased exponentially over time (Fig. 4).

Even a small control effort allowed a substantial decrease in the number of infested trees compared to no control whether there was an outside source of beetles or not. For example, implementing 30% control reduces the number of infested trees after 10 years to 8.35% (no outside source) and 10.42% (outside source) of the number of infested trees under a 1% control (Fig. 4 and Table 5).

Likewise, respectively 50% and 65% control are necessary to reduce the number of infested trees after 10 years to close to 1% and 0.1%. Control effort above 55%–65% actively reduced the total beetle population over time whether there was an outside source of beetles or

Table 5
Sustained control effort necessary to obtain, after 10 years, close to 10, 5, 1, or 0.1% of the infested trees obtained under 1% control.

Control effort	No outside source		Outside source	
	Number of infested trees	Percentage of infested trees	Number of infested trees	Percentage of infested trees
1%	152795	100.00%	183944	100.00%
30%	12765	8.35%	19152	10.42%
40%	3768	2.47%	6504	3.54%
50%	894	0.58%	2015	1.10%
65%	44	0.03%	283	0.15%

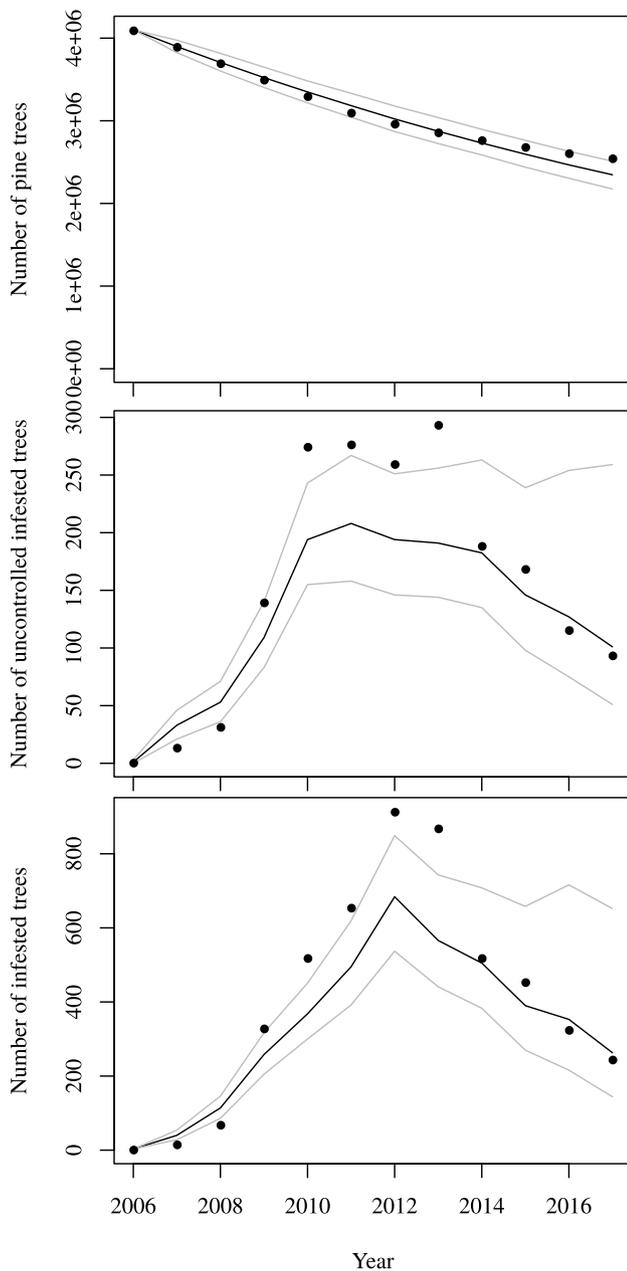


Fig. 3. Simulated number of pine trees $\sum_x H_x^t$ (top), number of uncontrolled infested trees, $\sum_x M_x^t$ (middle), and number of infested trees $\sum_x I_x^t$ (bottom) over the years for a control effort matching the observed control. The black and grey lines are, respectively, the median and 95% confidence interval over 1000 simulations. The points represent the observations.

not (Fig. 4). When under 99% control, the tree population decreased by 45% over 13 years whereas it decreased by 61% when under 1% control whether there was an outside source of beetles or not (Fig. 5).

Outbreak suppression refers to the act of driving epidemic populations below the eruptive threshold. Therefore, when one or less mass-attacked tree remains, managers achieve outbreak suppression although a small number of beetles might persist in the domain. For the scenario without outside source of beetles, the number of years of sustained control effort necessary to achieve suppression of half of the outbreak simulations went from over 13 years for a proportion of controlled infested trees up to 68% to 12 years at 69% control and three years as managers approach complete control of the infestations (99%) (Fig. 6 left panel). Achieving suppression of mountain pine beetle in 95% of the outbreak simulations in less than 13 years required a proportion of controlled infested trees to be at least 83%. For the scenario with outside source of beetles, the number of years of sustained control effort necessary to achieve suppression of half of the outbreak simulations went from over 13 years for a proportion of controlled infested trees up to 82% to 12 years at 83% control and 10 years as managers approach complete control of the infestations (99%) (Fig. 6 right panel). Achieving suppression of mountain pine beetle in 95% of the outbreak simulations in less than 13 years required a proportion of controlled infested trees to be at least 92%.

4. Discussion

In this study, the model demonstrated that treating a small number of mountain pine beetle infested trees significantly decreased beetle populations and tree loss compared to a no-control scenario after controlling for environmental factors. However, moderate control (55%–65%) is required to reduce the beetle population over time despite the outbreak being initially supported by outside flights. In addition, high control (above 69%) can lead to true outbreak suppression under 13 years. The presence of flights from adjacent uncontrolled areas increase outbreak duration but does not change the overall effect of beetle control.

In our study, even a small control effort reduces tree loss. This is consistent with the analysis of *Wulder et al. (2009)*, showing that a greater proportion of trees were attacked in an area with no control compared to a managed area over three years. However, it contrasts with another study reporting no significant change in area colonized by mountain pine beetle between controlled and uncontrolled sites (*Trzcinski and Reid, 2008*). In this study, the lack of ability to detect difference between controlled and uncontrolled sites in terms of tree loss could be partially explained by the short four year period of time during which control was implemented. This study also showed a trend toward less beetle colonization in the managed site (*Trzcinski and Reid, 2008*). Therefore, depending on outbreak and control history, the reduction in tree loss might not be directly evident. This result emphasizes the need to sustain control throughout the outbreak duration as mentioned in previous studies (*Carroll et al., 2006*).

Levels of control and outbreak duration are rarely reported together in the literature, mostly because control is typically not sustained over the entire outbreak period (*Carroll et al., 2006*). However, we know

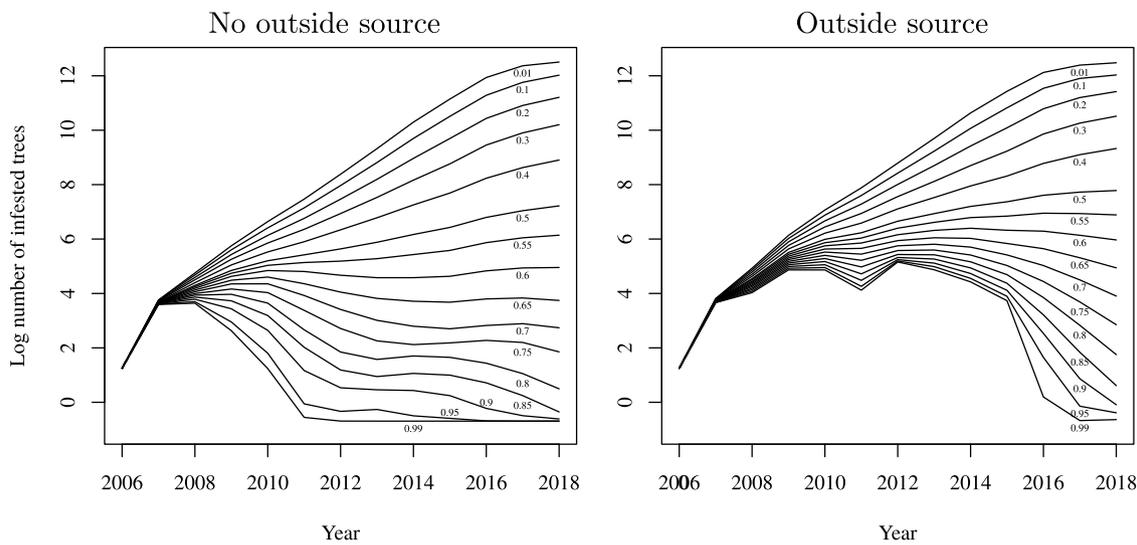


Fig. 4. Total number of infested trees in the domain $\sum_x I_x^t$ without (left) or with (right) outside source of beetles for control rates between 0.01 and 0.99 on a log scale. Each line represents the average over 1000 simulations for a control rate.

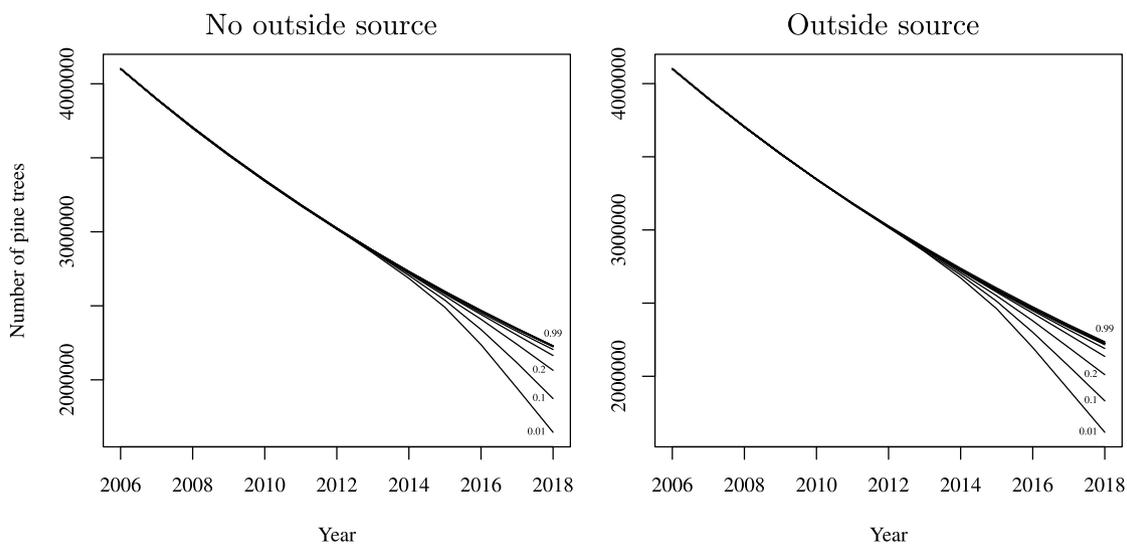


Fig. 5. Total number of pine trees in the domain $\sum_x H_x^t$ without (left) or with (right) outside source of beetles for control rates between 0.01 and 0.99. Each line represents the average over 1000 simulations for a control rate.

that a mountain pine beetle outbreak in the early 1940’s was subjected to very intensive control since the apparition of the first infested trees and was suppressed after 2 years near Banff, Alberta. Two mountain pine beetle outbreaks happened in the 1950’s and 1980’s and lasted 11 and seven years, respectively (Wood et al., 1996). In Cypress Hills, in the 1980’s, an outbreak subjected to intermittent control lasted 11 years (Cerezke, 1989). In Wyoming, in the 1960’s, a mountain pine beetle outbreak lasted 7 years (Klein et al., 1978). In comparison, other eruptive bark beetles have similar outbreak durations. *Ips typographus* outbreaks in Sweden in the 1970’s and 2000’s lasted 11 and four years, respectively (Kärvelo and Schroeder, 2010). The outbreaks of *Dendroctonus rufipennis* in Colorado since 1850 lasted between four and 13 years (Hart et al., 2014). Outbreak dynamics of eruptive bark beetles typically depends on abiotic factors in opposition to species presenting cyclical dynamics driven by negative and positive density dependence feedback (Berryman et al., 1987). However, interspecific competition and predation play a major role on mountain pine beetle population dynamics at small beetle population size. Therefore bark beetle outbreak eruption and collapse are not easily predicted.

Outbreak duration depends on a large variety of factors, including the availability of susceptible pines. Indeed, when an infested area is not controlled and the weather is favourable, a beetle population can rapidly reach high population levels and deplete susceptible hosts which leads to outbreak collapse (Safarynik, 2004; Fettig et al., 2014). However, we do not observe this behaviour in our study as the number of susceptible pines is not limiting. Moreover, during an outbreak, mountain pine beetle populations display a positive density-dependence, meaning that the annual rate of increase of beetle populations is the highest at intermediate population size (MacQuarrie and Cooke, 2011; Cooke and Carroll, 2017). Therefore, decreasing the size of an epidemic population by a small amount would likely boost their potential for increase, thereby increasing outbreak duration. This is why suppression effort can lead to extended and more frequent outbreaks by preserving a high number of susceptible hosts in the habitat (Clarke et al., 2016). However, in some cases such as national and provincial parks, preserving those susceptible trees is essential to the forest management policy. Cost-benefit analyses can help managers decide whether tree protection is worth the control effort.

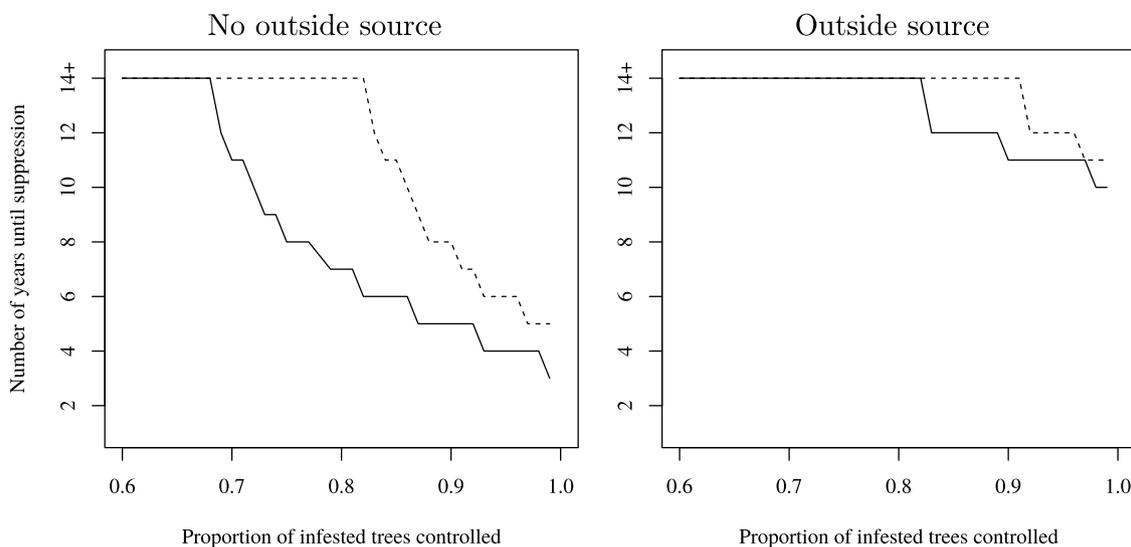


Fig. 6. Number of years of sustained control effort until outbreak suppression without (left) or with (right) outside source of beetles depending on the control rate. The solid line represent the number of years necessary to achieve outbreak suppression in half of the 1000 simulations and the dashed line in 95% of the simulations.

As expected, outside flights from adjacent uncontrolled areas help sustain beetle populations which increases outbreak duration. There is typically a connectivity at the landscape scale among infested areas due to beetle dispersal ability, providing a source for new infestations (e.g. Aukema et al., 2006; Chen and Walton, 2011). For example, intensive control or no control of *I. typographus* lead to similar tree mortality, mostly because of outside beetle flights coming into the intensively managed area (Grodzki et al., 2006). For *I. typographus*, some results suggest that outbreaks on the decline rebound because of long-distance dispersal events (Hlásny and Turčáni, 2013). We included this connectivity in our model by considering the beetle pressure from outside the park southern border and a background infestation level. Because of it, after the initial increase, the outbreak only started to decline once the infestations just outside the park limits had died out.

Due to the lack of post-hoc assessment of direct control on beetle populations as well as the difficulty to make comparisons among areas subjected to different control levels, direct control efficacy and its relationship with outbreak duration is not well-known (Six et al., 2014). When looking at the beetle population recruitment or rate of increase, which is the ratio population size at year $t+1$ over population size at year t , the impact of control activities on beetle populations is not always clear. Indeed, our study shows that even an isolated outbreak subjected to extremely intensive control can still first peak (rate of increase above 1) before collapsing (rate of increase below 1). Therefore, one needs to study the entire outbreak instead of a limited selection of years to have a good idea of the impact of direct control.

Under climate change, the beetle population rate of change would likely increase making outbreak larger and longer (Cooke and Carroll, 2017). The warming trend observed in the past few decades in western Canada is likely responsible for the spatial extent and duration of the recent mountain pine beetle outbreak in British Columbia and the breach over the Rocky Mountains into Alberta (Bentz et al., 2016; Cooke and Carroll, 2017). Indeed, the outbreak in British Columbia that started in 1999 is projected to last about 20 years (Walton, 2013) and in Cypress Hills, the current outbreak started in 2006 and is still ongoing despite intermediate sustained control effort. Therefore, to be able to reduce population size over time, a larger control effort would be necessary compared to historic climatic conditions.

In Cypress Hills over the study period, the average rate of increase of infested trees was 2.1 with three trees initially infested. With these values, an outbreak is suppressed in average before 13 years for a

control rate of at least 81%. This result is of the same order of magnitude as the results of Carroll et al. (2006) although they are assuming a fixed rate of control and 10 000 initially infested trees. Using the model described by Carroll et al. (2006) and parametrized for a study area at the border of the provinces of British Columbia and Alberta, Canada, Coggins et al. (2011) estimated that 11 years of continuous control effort was necessary to achieve outbreak suppression with a control rate of 70%. The difference we observe among those results is likely partly due to the difference in infestations spatial connectivity as we show that the presence of incoming flights changes noticeably the outbreak duration. In addition, the spatial heterogeneity of environmental conditions plays a considerable role in outbreak dynamics. For example, cold snaps in fall or early winter can have a devastating effect on beetle populations leading to outbreak collapse (Safranyik and Carroll, 2006) whereas warm and dry weather helps increase beetle population size (Creeden et al., 2014). Therefore, taking into account the context of each outbreak is essential to determine the efficacy of direct control.

Using a semi-empirical predictive model is useful to get estimates of relevant parameters. For example, using our predictive model parameters, we could back-calculate the yearly rate of increase in Cypress Hills and found that it has an average of 2.1 in forested areas, meaning that an infested trees produces 2.1 new infested trees the following year in average. Likewise, we found that the background infestation level is 0.03. This indicates that for each 500×500 m cell, we expect an average of 0.03 pine (i.e. 0.0012 pines/ha) to get infested from long-distance dispersal events or transitions from endemic to epidemic population. This extremely low number suggests that most new infestation in the study area came from a neighbouring cell, meaning that long-distance dispersal events are quite rare. Measuring the importance of short- and long-distance dispersal on the field would be long and costly. However, modelling studies can get an estimate of their respective influence on new infestations (e.g. Chen and Walton, 2011). With our model, we easily get an estimation by separating the sources of new infestations.

Moreover, models predicting infestation locations from ecological and environmental variables such as this one can be very useful in developing management plans and determining when and where to control for mountain pine beetle. In Cypress Hills, using similar data for the current outbreak in a boosted classification tree, we were able to predict infested locations a year ahead with a predictive accuracy of 0.92 (AUC) and we show that increasing the ground survey plot size

would increase control efficiency in a cost effective manner. Predicting infested locations can be done at different spatial scales and locations depending on the scale of the management unit. Successful predictions use a combination of weather factors and stand characteristics in addition to beetle pressure (e.g. Aukema et al., 2008; Preisler et al., 2012; Seidl et al., 2016).

Forest managers need to take into account more than just the relationship between outbreak dynamics and control effort into their forest management plans. Indeed, different levels of tree mortality implies different impacts on forest ecosystems. The death of pines from bark beetles usually results in dead trees standing, or snags, which are not immediately replaced as snags shade the forest floor for a couple of years after the tree death (Duncan et al., 2015). This has several effects on water, carbon and nitrogen cycles. Under a no-direct-control scenario, pine death decreases transpiration from the canopy which increases soil moisture (Edburg et al., 2012). In turn, increase in soil moisture changes the energy budget, increasing energy storage in the soils and decreasing energy storage in the vegetation (Reed et al., 2018). Widespread tree mortality decrease carbon uptake and increase future emissions due to tree decay (Kurz et al., 2008). Those changes differ from the effect of wildfire and clearcuts due to incomplete mortality and the fact that recruitment is delayed in beetle killed stands (Pfeifer et al., 2011). Therefore tree protection is essential to preserve the forest ecosystem function.

One limitation of this study is that we were constrained to the time period and location of the current Cypress Hills outbreak in order to use ecological and environmental factors as input for our model. Because of that, we were not able to have a precise estimate of the number of years of sustained control effort required to achieve outbreak suppression for control rate lower than 69%. However, we were able to determine that control levels above 55%–65% are effectively decreasing beetle population sizes over time and so should eventually lead to suppression.

The predictive model accuracy when comparing number of infested trees per cell is average. However, when taking into account the overall spatial distribution of the number of infested trees in the domain, the predictions of the highly or little infested areas correspond to the observations to a large extent. This correspondence between observed and predicted infested areas is reflected by the fact that the sum of the predicted number of infested trees in the domain over the years overlap well with the observed number of infested trees.

In conclusion, this study allowed to bridge the gap between theory and field observations. Direct control impacts beetle outbreak duration and pine mortality even at a low level. Moderate control can suppress mountain pine beetle infestations in the long term. However, a significant control rate is needed to achieve a quick suppression. Future work could examine the spatial patterns of infested and non-infested trees for outbreaks under different control effort or climatic conditions in order to get further insights.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Mélodie Kunegel-Lion: Conceptualization, Methodology, Software, Formal analysis, Writing original draft, Visualization. **Mark A. Lewis:** Conceptualization, Methodology, Writing - review & editing, Supervision, Funding acquisition.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.jenvman.2020.110167>.

References

- Aukema, B.H., Carroll, A.L., Zheng, Y., Zhu, J., Raffa, K.F., Dan Moore, R., Stahl, K., Taylor, S.W., 2008. Movement of outbreak populations of mountain pine beetle: influences of spatiotemporal patterns and climate. *Ecography* (ISSN: 1600-0587) 31 (3), 348–358, URL <http://onlinelibrary.wiley.com/doi/10.1111/j.0906-7590.2007.05453.x/abstract>.
- Aukema, B.H., Carroll, A.L., Zhu, J., Raffa, K.F., Sickley, T.A., Taylor, S.W., 2006. Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. *Ecography* (ISSN: 1600-0587) 29 (3), 427–441, URL <http://onlinelibrary.wiley.com/doi/10.1111/j.2006.0906-7590.04445.x/abstract>.
- Beaudoin, A., Bernier, P., Guindon, L., Villemaire, P., Guo, X., Stinson, G., Bergeron, T., Magnussen, S., Hall, R., 2014. Mapping attributes of Canada's forests at moderate resolution through kNN and MODIS imagery. *Can. J. Forest Res.* (ISSN: 0045-5067) 44 (5), 521–532, URL <http://www.nrcresearchpress.com/doi/full/10.1139/cjfr-2013-0401>.
- Bentz, B.J., Duncan, J.P., Powell, J.A., 2016. Elevational shifts in thermal suitability for mountain pine beetle population growth in a changing climate. *Forestry* 89 (3), 271–283, (ISSN: 0015-752X, 1464-3626), URL <http://forestry.oxfordjournals.org/content/89/3/271>.
- Bentz, B.J., Logan, J.A., Amman, G.D., 1991. Temperature-dependent development of the mountain pine beetle (Coleoptera:Scolytidae) and simulation of its phenology. *Can. Entomol.* 123 (5), 1083–1094, (ISSN: 0008-347X, 1918-3240), URL https://www.cambridge.org/core/product/identifier/S0008347X00024457/type/journal_article.
- Bentz, B.J., Powell, J.A., 2014. Mountain pine beetle seasonal timing and constraints to bivoltinism: A comment on Mitton and Ferrenberg, “mountain pine beetle develops an unprecedented summer generation in response to climate warming”. *Amer. Nat.* (ISSN: 0003-0147) 184 (6), 787–796, URL <http://www.journals.uchicago.edu/doi/abs/10.1086/678405>.
- Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., Seybold, S.J., 2010. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. *BioScience* 60 (8), 602–613, (ISSN: 0006-3568, 1525-3244), URL <http://bioscience.oxfordjournals.org/content/60/8/602>.
- Berryman, A.A., Stenseth, N.C., Isaev, A.S., 1987. Natural regulation of herbivorous forest insect populations. *Oecologia* 71, 174–184. <http://dx.doi.org/10.1007/BF00377282>.
- Bright, B.C., Hudak, A.T., Kennedy, R.E., Meddens, A.J.H., 2014. Landsat time series and lidar as predictors of live and dead basal area across five bark beetle-affected forests. *IEEE J. Sel. Top. Appl. Earth Obs. Remote Sens.* 7 (8), 3440–3452, (ISSN: 1939-1404, 2151-1535).
- Campbell, E.M., Alfaro, R.I., Hawkes, B., 2007. Spatial distribution of mountain pine beetle outbreaks in relation to climate and stand characteristics: A dendroecological analysis. *J. Integr. Plant Biol.* (ISSN: 1744-7909) 49 (2), 168–178. <http://dx.doi.org/10.1111/j.1744-7909.2007.00423.x>.
- Carroll, A.L., Shore, T.L., Safranyik, L., 2006. Direct control: theory and practice. In: Safranyik, L., Wilson, B. (Eds.), *The Mountain Pine Beetle: A Synthesis of Biology, Management, and Impacts on Lodgepole Pine*. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, ISBN: 0-662-42623-1, pp. 155–172, UR <https://cfs.nrcan.gc.ca/publications?id=26044>.

- Cerezke, H., 1989. Mountain pine beetle aggregation semiochemical use in Alberta and Saskatchewan, 1983–1987. In: *Proceedings from the Symposium on the Management of Lodgepole Pine To Minimize Losses To the Mountain Pine Beetle*, Kalispell, Montana July 12–14, 1988. In: *General Technical Report INT, USDA Forest Service, Intermountain Research Station, Ogden, UT*, pp. 108–113.
- Chen, H., Walton, A., 2011. Mountain pine beetle dispersal: spatiotemporal patterns and role in the spread and expansion of the present outbreak. *Ecosphere* (ISSN: 2150-8925) 2 (6), 1–17. <http://dx.doi.org/10.1890/ES10-00172.1>.
- Clarke, S.R., Riggins, J.J., Stephen, F.M., 2016. Forest management and southern pine beetle outbreaks: A historical perspective. *Forest Sci.* (ISSN: 0015-749X) 62 (2), 166–180. <http://dx.doi.org/10.5849/forsci.15-071>.
- Coggins, S.B., Coops, N.C., Wulder, M.A., Bater, C.W., Ortlepp, S.M., 2011. Comparing the impacts of mitigation and non-mitigation on mountain pine beetle populations. *J. Environ. Manag.* (ISSN: 03014797) 92 (1), 112–120, URL <https://linkinghub.elsevier.com/retrieve/pii/S0301479710002641>.
- Cooke, B.J., Carroll, A.L., 2017. Predicting the risk of mountain pine beetle spread to eastern pine forests: Considering uncertainty in uncertain times. *Forest Ecol. Manag.* (ISSN: 03781127) 396, 11–25, URL <http://linkinghub.elsevier.com/retrieve/pii/S0378112716312543>.
- Creeden, E.P., Hicke, J.A., Buotte, P.C., 2014. Climate, weather, and recent mountain pine beetle outbreaks in the western United States. *Forest Ecol. Manag.* 312, 239–251, WOS:000328802700026.
- Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., Wotton, B.M., 2001. Climate change and forest disturbances. *BioScience* (ISSN: 0006-3568) 51 (9), 723–734, URL <https://academic.oup.com/bioscience/article/51/9/723/288247>.
- de la Giroday, H.-M.C., Carroll, A.L., Aukema, B.H., 2012. Breach of the northern rocky mountain geoclimatic barrier: initiation of range expansion by the mountain pine beetle. *J. Biogeogr.* (ISSN: 1365-2699) 39 (6), 1112–1123, URL <http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2699.2011.02673.x/abstract>.
- Diskin, M., Rocca, M.E., Nelson, K.N., Aoki, C.F., Romme, W., 2011. Forest developmental trajectories in mountain pine beetle disturbed forests of Rocky Mountain National Park, Colorado. *Can. J. Forest Res.* (ISSN: 0045-5067) 41 (4), 782–792, URL <https://www.nrcresearchpress.com/doi/full/10.1139/x10-247>.
- Duncan, J.P., Powell, J.A., Gordillo, L.F., Eason, J., 2015. A model for mountain pine beetle outbreaks in an age-structured forest: Predicting severity and outbreak-recovery cycle period. *Bull. Math. Biol.* 77 (7), 1256–1284, (ISSN: 0092-8240, 1522-9602), URL <http://link.springer.com/article/10.1007/s11538-015-0085-5>.
- Edburg, S.L., Hicke, J.A., Brooks, P.D., Pendall, E.G., Ewers, B.E., Norton, U., Gochis, D., Gutmann, E.D., Meddens, A.J., 2012. Cascading impacts of bark beetle-caused tree mortality on coupled biogeophysical and biogeochemical processes. *Front. Ecol. Environ.* (ISSN: 1540-9295) 10 (8), 416–424, URL <http://www.esajournals.org/doi/abs/10.1890/110173>.
- Erbilgin, N., Cale, J.A., Lusebrink, I., Najjar, A., Klutsch, J.G., Sherwood, P., (Enrico) Bonello, P., Evenden, M.L., 2017. Water-deficit and fungal infection can differentially affect the production of different classes of defense compounds in two host pines of mountain pine beetle. *Tree Physiol.* (ISSN: 0829-318X) 37 (3), 338–350, URL <http://academic.oup.com/treephys/article/37/3/338/2549088>.
- Fettig, C.J., Gibson, K.E., Munson, A.S., Negrón, J.F., 2014. Cultural practices for prevention and mitigation of mountain pine beetle infestations. *Forest Sci.* 60 (3), 450–463.
- Fettig, C.J., Hilszczański, J., 2015. Chapter 14 - management strategies for bark beetles in conifer forests. In: Vega, F.E., Hofstetter, R.W. (Eds.), *Bark Beetles*. Academic Press, San Diego, ISBN: 978-0-12-417156-5, pp. 555–584, URL <http://www.sciencedirect.com/science/article/pii/B9780124171565000149>.
- Grodzki, W., Jakuš, R., Lajzová, E., Sitková, Z., Maczka, T., Škvarenina, J., 2006. Effects of intensive versus no management strategies during an outbreak of the bark beetle *Ips typographus* (L.) (Col.: Curculionidae, Scolytinae) in the Tatra Mts. in Poland and Slovakia. *Ann. Forest Sci.* 63 (1), 55–61, (ISSN: 1286-4560, 1297-966X), URL <http://www.edpsciences.org/10.1051/forest:2005097>.
- Hart, S.J., Veblen, T.T., Eisenhart, K.S., Jarvis, D., Kulakowski, D., 2014. Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology* (ISSN: 1939-9170) 95 (4), 930–939, URL <http://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/13-0230.1>.
- Hlásný, T., Turčáni, M., 2013. Persisting bark beetle outbreak indicates the unsustainability of secondary Norway spruce forests: case study from Central Europe. *Ann. Forest Sci.* (ISSN: 1297-966X) 70 (5), 481–491. <http://dx.doi.org/10.1007/s13595-013-0279-7>.
- Kärvmö, S., Schroeder, L.M., 2010. A comparison of outbreak dynamics of the spruce bark beetle in Sweden and the mountain pine beetle in Canada (Curculionidae: Scolytinae). p. 10.
- Klein, W.H., Parker, D.L., Jensen, C.E., 1978. Attack, emergence, and stand depletion trends of the mountain pine beetle in a lodgepole pine stand during an outbreak. *Environ. Entomol.* 7 (5), 732–737, (ISSN: 1938-2936, 0046-225X), URL <https://academic.oup.com/ee/article-lookup/doi/10.1093/ee/7.5.732>.
- Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T., Safranyik, L., 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* (ISSN: 1476-4687) 452 (7190), 987–990, URL <http://www.nature.com/articles/nature06777>.
- Logan, J., Powell, J., 2001. Ghost forests, global warming, and the mountain pine beetle (coleoptera : Scolytidae). *Am. Entomol.* 47 (3), 160–173, URL <http://digitalcommons.usu.edu/barkbeetles/187>.
- MacQuarrie, C.J., Cooke, B.J., 2011. Density-dependent population dynamics of mountain pine beetle in thinned and unthinned stands. *Can. J. Forest Res.* (ISSN: 0045-5067, 1208-6037) 41 (5), 1031–1046, URL <http://www.nrcresearchpress.com/doi/10.1139/x11-007>.
- Meddens, A.J.H., Hicke, J.A., Vierling, L.A., 2011. Evaluating the potential of multispectral imagery to map multiple stages of tree mortality. *Remote Sens. Environ.* (ISSN: 0034-4257) 115 (7), 1632–1642, URL <http://www.sciencedirect.com/science/article/pii/S003442571100068X>.
- Meddens, A.J.H., Hicke, J.A., Vierling, L.A., Hudak, A.T., 2013. Evaluating methods to detect bark beetle-caused tree mortality using single-date and multi-date Landsat imagery. *Remote Sens. Environ.* (ISSN: 0034-4257) 132, 49–58, URL <http://www.sciencedirect.com/science/article/pii/S0034425713000060>.
- Mitton, J.B., Ferrenberg, S.M., 2012. Mountain pine beetle develops an unprecedented summer generation in response to climate warming. *Amer. Nat.* (ISSN: 0003-0147) 179 (5), E163–E171, URL <http://www.journals.uchicago.edu/doi/abs/10.1086/665007>.
- Nelson, T., Boots, B., White, K.J., Smith, A.C., 2006. The impact of treatment on mountain pine beetle infestation rates. *J. Ecosyst. Manag.* 7 (2), URL <http://jem.forrex.org/index.php/jem/article/view/539>.
- Pfeifer, E.M., Hicke, J.A., Meddens, A.J.H., 2011. Observations and modeling of aboveground tree carbon stocks and fluxes following a bark beetle outbreak in the western United States. *Global Change Biol.* (ISSN: 1365-2486) 17 (1), 339–350, URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2486.2010.02226.x>.
- Preisler, H.K., Hicke, J.A., Ager, A.A., Hayes, J.L., 2012. Climate and weather influences on spatial temporal patterns of mountain pine beetle populations in Washington and Oregon. *Ecology* (ISSN: 1939-9170) 93 (11), 2421–2434, URL <http://onlinelibrary.wiley.com/doi/10.1890/11-1412.1/abstract>.
- Reed, D.E., Ewers, B.E., Pendall, E., Frank, J., Kelly, R., 2018. Bark beetle-induced tree mortality alters stand energy budgets due to water budget changes. *Theor. Appl. Climatol.* (ISSN: 1434-4483) 131 (1), 153–165. <http://dx.doi.org/10.1007/s00704-016-1965-9>.
- Régnière, J., Bentz, B., 2007. Modeling cold tolerance in the mountain pine beetle, *Dendroctonus ponderosae*. *J. Insect Physiol.* (ISSN: 0022-1910) 53 (6), 559–572, URL <http://www.sciencedirect.com/science/article/pii/S0022191007000534>.
- Régnière, J., Saint-Amant, R., Béchard, A., 2014. BioSIM 10 - User's manual. Tech. Rep., Natural Resources Canada, Canadian Forest Service, Laurentian Forest Centre, Québec (QC), URL <http://cfs.nrcan.gc.ca/pubwarehouse/pdfs/34818.pdf>.
- Safranyik, L., 1978. Effects of climate and weather on mountain pine beetle populations. In: Berryman, A.A., Amman, G., Stark, R. (Eds.), *Proceedings of Symposium on Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*, April 25–27, 1978, Washington State University, Pullman, Washington. College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow, Idaho, pp. 77–84, URL <http://www.cfs.nrcan.gc.ca/publications/?id=1819>.
- Safranyik, L., 1988. Estimating attack and brood totals and densities of the mountain pine beetle in individual lodgepole pine trees. *Can. Entomol.* 120 (4), 323–331, (ISSN: 1918-3240, 0008-347X), URL <https://www.cambridge.org/core/journals/canadian-entomologist/article/estimating-attack-and-brood-totals-and-densities-of-the-mountain-pine-beetle-in-individual-lodgepole-pine-trees/929783A8F3D771C4AC97EDE3F5345522>.
- Safranyik, L., 2004. Mountain pine beetle epidemiology in lodgepole pine. In: Shore, T., Brooks, J., Stones, J. (Eds.), *Mountain Pine Beetle Symposium: Challenge and Solutions*. October 30–31, 2003, Kelowna, British Columbia. In: *Information Report BC-X-399*, Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, B.C., pp. 33–40.
- Safranyik, L., Carroll, A.L., 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In: Safranyik, L., Wilson, B. (Eds.), *The Mountain Pine Beetle: A Synthesis of Biology, Management and Impacts on Lodgepole Pine*. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, Canada, pp. 3–66, URL <http://www.cabdirect.org/abstracts/20073248170.html>.
- Safranyik, L., Shore, T., Moeck, H., Whitney, H.S., 2002. *Dendroctonus ponderosae* hopkins, mountain pine beetle (coleoptera: Scolytidae). In: Mason, P., Huber, J. (Eds.), *Biological Control Programmes in Canada, 1981–2000*. CABI Publishing, New York, pp. 104–109.
- Saskatchewan Ministry of Environment, 2016. Mountain pine beetle operational procedures document.
- Seidl, R., Müller, J., Hothorn, T., Bässler, C., Heurich, M., Kautz, M., 2016. Small beetle, large-scale drivers: how regional and landscape factors affect outbreaks of the European spruce bark beetle. *J. Appl. Ecol.* (ISSN: 1365-2664) 53 (2), 530–540, URL <https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2664.12540>.
- Seidl, R., Rammer, W., Jäger, D., Lexer, M.J., 2008. Impact of bark beetle (*Ips typographus* L.) disturbance on timber production and carbon sequestration in different management strategies under climate change. Impacts of forest ecosystem management on greenhouse gas budgets, *Forest Ecol. Manag.* (ISSN: 0378-1127) Impacts of forest ecosystem management on greenhouse gas budgets, 256 (3), 209–220. URL <http://www.sciencedirect.com/science/article/pii/S0378112708003198>,

- Six, D.L., Biber, E., Long, E., 2014. Management for mountain pine beetle outbreak suppression: Does relevant science support current policy? *Forests* (ISSN: 19994907) 5 (1), 103–133, URL <https://doi.org/10.3390/f5010103>.
- Strom, B., Clarke, S., 2011. Use of semiochemicals for southern pine beetle infestation management and resource protection. In: *Southern Pine Beetle II. In: General Technical Report (GTR), (SRS-140), U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC*, pp. 381–397.
- Taylor, S.W., Carroll, A.L., Alfaro, R.I., Safranyik, L., 2006. Forest, climate and mountain pine beetle outbreak dynamics in western Canada. In: Safranyik, L., Wilson, B. (Eds.), *The Mountain Pine Beetle: A Synthesis of Biology, Management and Impacts on Lodgepole Pine*. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, Canada, pp. 67–94, URL <http://www.cabdirect.org/abstracts/20073248170.html>.
- Trzcinski, M.K., Reid, M.L., 2008. Effect of management on the spatial spread of mountain pine beetle (*Dendroctonus ponderosae*) in Banff National Park. *Forest Ecol. Manag.* (ISSN: 03781127) 256 (6), 1418–1426, URL <https://linkinghub.elsevier.com/retrieve/pii/S0378112708005604>.
- Walton, A., 2013. Provincial-Level Projection of the Current Mountain Pine Beetle Outbreak: Update of the Infestation Projection Based On the Provincial Aerial Overview Surveys of Forest Health conducted from 1999 through 2012 and the BCMPB model (year 10). Tech. Rep., BC Ministry of Forests, Lands and Natural Resources Operations, Victoria, BC, URL <https://www.for.gov.bc.ca/ftp/hre/external/publish/web/bcmpb/year10/BCMPB.v10.BeetleProjection.Update.pdf>.
- Wood, C.S., Unger, L.S., et al., 1996. Mountain pine beetle. A history of outbreaks in pine forests in British Columbia, 1910 to 1995.
- Wulder, M.A., Dymond, C.C., White, J.C., Leckie, D.G., Carroll, A.L., 2006. Surveying mountain pine beetle damage of forests: A review of remote sensing opportunities. *Forest Ecol. Manag.* (ISSN: 0378-1127) 221 (1–3), 27–41, URL <http://www.sciencedirect.com/science/article/pii/S0378112705005736>.
- Wulder, M.A., Ortlepp, S.M., White, J.C., Coops, N.C., Coggins, S.B., 2009. Monitoring the impacts of mountain pine beetle mitigation. *Forest Ecol. Manag.* (ISSN: 03781127) 258 (7), 1181–1187, URL <http://linkinghub.elsevier.com/retrieve/pii/S0378112709004022>.