Mountain pine beetle spread in forests with varying host resistance

Micah Brush*[,1], Mark A. Lewis[2,3]

* Corresponding author. Email: mbrush@ualberta.ca. Present address: Department of Biology, University of Victoria, Cunningham 202, 3800 Finnerty Road, Victoria, BC V8P 5C2, Canada.

[1] Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton, AB, Canada

[2] Department of Mathematics and Statistics, University of Victoria, Victoria, BC, Canada

[3] Department of Biology, University of Victoria, Victoria, BC, Canada

Abstract

In the last few decades, mountain pine beetle (MPB) have spread into novel regions in Canada. An important aspect seldom captured in models of MPB spread is host resistance. Lodgepole pine, the predominant host of MPB, varies in resistance across the landscape. There is evidence for a genetic component of resistance, as well as evidence that hosts in areas where MPB has not been present historically are at risk of increased susceptibility. In addition to the spatially varying resistance of the primary host species, the eastward spread of MPB has brought them into jack pine forests. Host resistance in jack pine remains uncertain, but experiments indicate jack pine could be a suitable host. We develop a model of pine beetle spread that links pine beetle population dynamics and forest structure and resistance. We find that beetle outbreaks in the model are characterized by large transient outbreaks that move through the forest. We show how the speed of these outbreaks changes with host resistance and find that biologically plausible values for host resistance are able to stop the wave from advancing. We also find that near the threshold of resistance where the wave is able to advance, small changes in host resistance dramatically decrease the severity of the outbreak. These results indicate that planting trees selected for higher MPB resistance on the landscape may be able to slow or even stop the local spread of MPB. In terms of further eastward spread, our results indicate future outbreaks may move more quickly and be more severe if novel lodgepole pine hosts are indeed more susceptible to beetle attacks, although more research is needed into the susceptibility of jack pine.

Keywords: Mountain pine beetle; population spread; invasive species; forest management; host susceptibility; integrodifference equations;

1 Introduction

The mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins) is a bark boring insect native to Western North America (Safranyik and Wilson 2006). MPB have a one year life cycle, emerging in the summer and dispersing to infest hosts (predominately lodgepole pine (*Pinus contorta*). The female beetles bore egg galleries into the phloem of the tree, and the larvae overwinter in the tree before emerging in the following summer. Infested trees generally die the following year. MPB largely maintain small endemic populations, but occasionally erupt in large, landscape scale outbreaks. In western Canada, the most recent outbreak has had severe economic impacts (Corbett et al. 2016; Dhar et al. 2016) and has led to climate change facilitated spread into novel habitats, in particular over the Rocky Mountains and into Alberta (Carroll et al. 2003; Kurz et al. 2008; Sambaraju et al. 2012; Cooke and Carroll 2017; Bleiker 2019). While cold winters have slowed the spread of the beetle for now, there is still uncertainty about the risk of further eastward spread into the boreal forest of Canada (Safranyik et al. 2010; Cullingham et al. 2011; Bleiker 2019).

There are many models, both statistical and mechanistic, that aim to predict the spread of pine beetle (eg. Heavilin and Powell 2008; Powell and Bentz 2009; Strohm et al. 2013; Powell and Bentz 2014; Duncan et al. 2015; Goodsman et al. 2016; Cooke and Carroll 2017; Kunegel-Lion and Lewis 2020; Ramazi et al. 2021; Srivastava and Carroll 2023). One variable that is seldom accounted for explicitly in these models is host resistance (but see eg. Lewis et al. 2010), particularly variation over space. Lodgepole pine, the primary host of MPB, have developed defenses against MPB attack, including the production of a toxic resin to push MPB out of attack holes (Safranyik and Wilson 2006). Beetles can overcome these defenses by mass attacking in large numbers (Raffa and Berryman 1983). The ability of the tree to defend itself against beetle mass attack can vary substantially depending on factors including weather, host vigor, host size, and more (Waring and Pitman 1985; Safranyik and Wilson 2006; Lewis et al. 2010). There is also evidence for a genetic basis for resistance in lodgepole pine (Yanchuk et al. 2008; Erbilgin et al. 2017b; Six et al. 2018), and variation across the range, in particular in areas where MPB was not present historically (Cudmore et al. 2010; Peery et al. n.d.). Because of the genetic basis for resistance, breeding programs may selectively breed lodgepole pine for MPB resistance, which could lead to more resistant planted cut blocks in the future. In addition to variation in host resistance within lodgepole pine, MPB

have expanded their range into jack pine (*Pinus banksiana*) forests in eastern Alberta (Safranyik et al. 2010; Cullingham et al. 2011; Burns et al. 2019). Jack pine is a novel host for MPB, and its susceptibility to MPB attack is uncertain (Cerezke 1995; Safranyik et al. 2010; Rosenberger et al. 2017b; Erbilgin et al. 2017a; Bleiker et al. 2023). More modelling work is needed to understand how this variation in susceptibility across the range, and how future efforts at planting genetically resistant trees, could affect the spread of MPB.

A recent model that couples biologically grounded mountain pine beetle dynamics with forest growth includes explicit parameters for the threshold number of beetles needed to overcome tree defenses as well as the size of brood of MPB in successfully infested trees (Brush and Lewis 2023). The model finds that the population dynamics of the beetles are determined by the ratio of these parameters. The threshold parameter can be easily interpreted in terms of hosts ability to defend itself against mass attack and gives rise to an Allee effect (Goodsman et al. 2016). The brood size parameter can also depend on host quality, where, for example, larger trees produce more beetles (Safranyik and Wilson 2006). Overall then, we interpret the ratio of these terms as the resistance of the host against MPB attack.

We note that here, we refer to host resistance as the ability of an individual pine host to defend against MPB attack. We use the term host susceptibility to indicate both how likely the host is to succumb to infestation more broadly, which includes beetle host preference and host resistance. We make the distinction between host resistance and forest resilience, which we here use to refer to the ability of the forest to recover from MPB outbreaks. Host resistance is therefore one component of forest resilience, and the primary focus of this study.

The goal of the model we develop here is to address questions about MPB spread at the landscape scale with varying host resistance. For example, given evidence for the genetic basis for host resistance in lodgepole pine (Yanchuk et al. 2008; Cudmore et al. 2010; Erbilgin et al. 2017b; Six et al. 2018; Peery et al. n.d.), is it possible to plant high resistance stands from breeding programs in order to slow or even stop the local spread of a MPB outbreak and thereby give managers more time to respond? Or, given the uncertainty about the susceptibility of novel host species such as jack pine (Cerezke 1995; Safranyik et al. 2010; Rosenberger et al. 2017b; Erbilgin et al. 2017a; Bleiker et al. 2023), what are the risks of outbreak and how might outbreaks be different as MPB continues to move into novel habitat? These types of questions are challenging to answer with existing data or experiments given that they are about events

that have not yet occurred, and that MPB outbreaks are unpredictable and depend on environmental and climatic factors. The model we develop here can address some of these uncertainties by simulating MPB outbreaks across a wide range of biological plausible parameter ranges and investigating the qualitative differences in outbreaks across host resistance.

In this study, we extend the model of Brush and Lewis (2023) to include space explicitly in order to study the spread of MPB in hosts of varying resistance. We carefully relate the parameters in this model to MPB data in order to determine a biologically plausible range of host resistance, with realistic levels of spatial aggregation and beetle dispersal. We then investigate how the speed and severity of spread change with host resistance, and how these results may impact further spread at the local landscape scale.

2 Methods

2.1 Model summary

The model we use to investigate pine beetle spread over time in varying host resistance extends a recently developed model (Brush and Lewis 2023) to include space explicitly. The model is mechanistic and biologically grounded. It includes important aspects of mountain pine beetle biology, modelled after Goodsman et al. (2016), and couples their population dynamics with forest growth, modelled after Duncan et al. (2015). The model dynamics include a strong Allee effect, beetle aggregation over susceptible trees, and a threshold number of beetles for mass attack to overcome tree defenses. The forest structure assumes that new growth is light limited, that beetles do not attack juvenile trees, and that trees have no mortality from causes other than beetle attacks.

To summarize the model, in each year t we divide the juvenile trees into N age classes, where the number of adult shade equivalents of juvenile trees in each age class i is $j_{i,t}$. The juveniles grow each year with survival fraction s until they become susceptible trees S_t after N years. These trees are assumed to have negligible natural mortality and remain susceptible trees until they are killed by beetles. We define trees to be susceptible when they produce more beetles than it takes to overcome their defenses. The number of female beetles is given by B_t, with c as a parameter giving the number of female beetles emerging from each infested tree. The fraction of susceptible trees avoiding beetle infestation each year is then given by the function $F(m_t; k, \varphi)$, where $m_t = B_t/S_t$ is the mean

number of beetles per susceptible tree, k is a parameter indicating the strength of beetle aggregation, and φ is a parameter indicating the threshold number of beetles needed to overcome tree defenses. Finally, the number of infested trees is given by I_t. We assume these trees lose their needles over two years, where the number of red top trees is I_{t-1} and the number of gray snags is I_{t-2}. The total number of trees in the fall during census is given by

$$T = J_t + S_t + I_{t-1} + I_{t-2}, \tag{1}$$

where green infested trees are counted in the S_t class until the following year.

The full evolution of the model from year to year is given by

$$j_{1,t+1} = \underbrace{(1-s)J_t}_{\substack{\text{Recruitment from}\\ \text{juvenile mortality}}} + \underbrace{I_{t-2}}_{\substack{\text{Recruitment from}\\ \text{gray snags}}} \tag{2}$$

$$j_{i+1,t+1} = \underbrace{sj_{i,t}}_{\text{Juvenile survival}} \qquad \text{for } i = 1 \ldots N-1 \tag{3}$$

$$S_{t+1} = \underbrace{F(m_t;k,\varphi)S_t}_{\text{Survival of susceptible trees}} + \underbrace{sj_{N,t}}_{\text{Recruitment from juveniles}} \tag{4}$$

$$I_t = \underbrace{(1-F(m_t;k,\varphi))S_t}_{\text{Infested susceptible trees}} \tag{5}$$

$$B_{t+1} = \underbrace{cI_t}_{\text{Beetle productivity}} . \tag{6}$$

The beetles are assumed to be distributed among the susceptible trees according to a negative binomial distribution with aggregation parameter k, and the threshold number of beetles needed to overcome host defenses is φ. The function $F(m_t;k,\varphi)$ describes the fraction of susceptible trees that avoid infestation in year t and can be written explicitly as

$$F(m_t;k,\varphi) = \underbrace{\sum_{i=0}^{\varphi}}_{\substack{\text{Sum over trees attacked}\\ \text{below the threshold}}} \overbrace{\mathrm{NB}(i;m_t,k)}^{\substack{\text{Beetle distribution}\\ \text{over trees}}} = I_{\frac{k}{k+m_t}}(k,\varphi+1), \tag{7}$$

where $I_{\frac{k}{k+m_t}}(k,\varphi+1)$ is the cumulative distribution of the negative binomial distribution, which is the regularized incomplete Beta function. The model variables and parameters are summarized in Table 1. More details on the model

formulation and the analysis of its structure can be found in Brush and Lewis (2023).

Mathematically, host resistance in this model is defined by the threshold parameter φ. Given that the dynamics of this model depend primarily on the ratio of φ/c rather than on either value specifically (Brush and Lewis 2023), we additionally define the ratio φ/c as the resistance per tree brood. That this ratio affects the dynamics tells us that the host resistance with respect to the brood productivity parameter is more important for the dynamics than the absolute number of beetles.

Variables		Parameters	
$j_{i,t}$	Juvenile trees at age i	N	Number of age classes of juvenile trees
S_t	Susceptible trees	s	Survival fraction of juvenile trees
I_t	Infested trees	c	Number of beetles that emerge per infested tree
B_t	Beetles	φ	Threshold number of beetles needed to infest a tree
m_t	Mean number of beetles, B_t/S_t	k	Beetle aggregation

Table 1: Model variables and parameters.

2.2 Model extension to include space

We now extend the model to include space explicitly. We will use integrodifference equations, which are discrete in time but continuous in space (Goodsman et al. 2016; Lutscher 2019). We assume that the beetles disperse each year as they search for new trees to infest with a dispersal kernel K, which we discuss in more detail in the next section. We then make each variable dependent on a spatial location x. The spatially extended model is then

$$j_{1,t+1}(x) = (1-s)J_t(x) + I_{t-2}(x) \tag{8}$$

$$j_{i+1,t+1}(x) = sj_{i,t}(x) \text{ for } i = 1 \dots N-1 \tag{9}$$

$$S_{t+1}(x) = F(m_t(x); k, \varphi)S_t(x) + sj_{N,t}(x) \tag{10}$$

$$I_{t+1}(x) = (1 - F(m_{t+1}(x); k, \varphi))S_{t+1}(x) \tag{11}$$

$$B_{t+1}(x) = c\int_{-\infty}^{\infty} K(x-y)I_t(y)dy. \tag{12}$$

Note that at each spatial location, we still conserve the total number of trees, so $T = J_t(x) + S_t(x) + I_{t-1}(x) + I_{t-2}(x)$.

While this extension is theoretically continuous in space, we will consider

the case where space is discretized. In practice, this is necessary numerically, but we also interpret the discrete grid biologically. This means the continuous equations are really a continuous approximation of a discrete system. We interpret the discrete grid as individual forest stands with a total number of trees T. Within each grid cell the beetles aggregate and infest a fraction $1-F(m_t)$ of the susceptible trees within that stand. We assume that beetles disperse between grid cells, but do not aggregate. Thus, the grid spacing is representative of the scale of aggregation for the beetles.

2.3 Beetle dispersal

Mountain pine beetle dispersal is challenging to accurately model, and models quickly become complicated (Berryman et al. 1989; Safranyik et al. 1989; Aukema et al. 2008; Strohm et al. 2013; Powell and Bentz 2014). Beetles largely remain within a few hundred meters (Safranyik et al. 1992; Robertson et al. 2007; Kautz et al. 2011; Carroll et al. 2017), but can also ride convective currents en masse above the tree canopy, where they are taken long distances (tens to hundreds of kilometers) by wind (Furniss and Furniss 1972; Jackson et al. 2008). Both short distance and long distance dispersal can move significant numbers of beetles at the landscape scale (Robertson et al. 2009; Chen and Walton 2011), and there is evidence that beetle dispersal distance depends on stand density (Powell and Bentz 2014). Importantly, short distance dispersal is mediated through complex chemical signalling, where beetles are attracted by host tree semiochemicals, and release pheromones to aggregate for successful mass attack as well as to deaggregate to prevent overcrowding a single tree (Raffa and Berryman 1983; Safranyik et al. 2010; Progar et al. 2014).

Rather than a complex model incorporating wind, chemical signalling, and both short and long distance modes of transportation, we assume that beetle aggregation is accurately captured by the within-cell aggregation model (Eq. 7) and that beyond this scale the beetles follow a dispersal kernel K. This model can therefore accurately capture local dispersal, but does not reflect the rare long distance dispersal events.

In past simulations, 2D dispersal kernels are often fit to empirical infestation data (Heavilin and Powell 2008; Goodsman et al. 2016; Goodsman et al. 2017). For mathematical and computational simplicity, as well as to facilitate the interpretation of our model, we will simulate beetle spread in one dimension. This is as if we consider a planar wave in two dimensions, which is an approxima-

tion of the case where we have a radially expanding infestation as long as the radius is large enough that the curvature is small locally. To parameterize our simulations, we relate data from beetle dispersal in two dimensions to our one dimensional model using the methods found in Lewis et al. (2016).

We first determine the functional form of the dispersal kernel. In two dimensions, Goodsman et al. (2016), which has the same functional form for the beetle response function as in our model, find that a 2D diffusion and settling kernel outperformed a Gaussian kernel. This kernel can be derived by assuming that beetles disperse as a random walk but drop out onto trees at a constant rate (Broadbent and Kendall 1953; Van Kirk 1995), which is biologically plausible for beetle dispersal at the local scale provided the wind is relatively weak (Safranyik and Wilson 2006). This kernel can be written in two dimensions as

$$K(r) = \frac{\alpha^2}{2\pi} K_0(\alpha r), \tag{13}$$

where K_0 is the modified Bessel function of the second kind and zeroth order and α is a parameter. That same model of random walk dispersal with constant settling time in one dimension gives the Laplace distribution kernel,

$$K(x) = \frac{\alpha}{2} e^{-\alpha|x|}. \tag{14}$$

To relate the two dimensional planar case to the one dimensional case, we have to marginalize the 2D dispersal kernel in the direction of wave advance. It turns out that the marginalized probability distribution of Eq. 13 is in fact Eq. 14 (Lewis et al. 2016), and so the α parameter in the 1D kernel is the same parameter as that in the 2D kernel that we will use to relate to data.

There is an additional step to connect to data. In 2D, the available data is often the distribution of beetles over radii rather than the full density function. We denote this distribution as $\widetilde{K}(r)$, and integrate the full density distribution over all angles, $\widetilde{K}(r) = \int_0^{2\pi} K(r) r d\theta$. With the kernel in Eq. 13, we find

$$\widetilde{K}(r) = \int_0^{2\pi} \frac{\alpha^2}{2\pi} K_0(\alpha r) r d\theta = \alpha^2 r K_0(\alpha r). \tag{15}$$

We can now compare this function to data to obtain reasonable values of the parameter α that we can then use in our 1D kernel, Eq. 14. Assuming that in our data we find a fraction p_1 of beetles within a radius r_1, we obtain an estimate of α by integrating Eq. 15 out to r_1 and setting that equal to p_1. This

integral is equal to

$$\int_0^{r_1} \alpha^2 r K_0(\alpha r) = 1 - \alpha r_1 K_1(\alpha r_1) = p_1. \tag{16}$$

We can solve Eq. 16 numerically to obtain an estimate for α.

We consider three datasets to estimate α for our simulations. In a mark recapture experiment, Safranyik et al. (1992) recover 93% and 86% of beetles within 30 meters in two consecutive years (1982 and 1983). Note that these values are the percent of total captured beetles, and so there is likely a bias here where beetles that dispersed beyond the furthest trap at 250 m were not recaptured and are not included in this percentage. Goodsman et al. (2016) use the 93% figure to parameterize their dispersal kernel as they argue that in 1983 MPB had already depleted the tree stock and wanted to parameterize their model assuming a fully stocked stand. Setting $r_1 = 30$ m and $p_1 = 0.93$, we find $\alpha = 0.121$ m^{-1}. However, we note that this only takes into account very local dispersal and thus is likely to severely underestimate beetle dispersal. We can also estimate α using results from Robertson et al. (2007). In this study, field crews searched for green attacked trees within 100 m of previous infestations. They find that the the median distance between newly infested stands is 50 meters, assuming newly infested trees came from the nearest previously infested stand. Setting $r_1 = 50$ m and $p_1 = 0.5$ we find $\alpha = 0.025$ m^{-1}. Finally, Carroll et al. (2017) use detailed survey data from Alberta to look at infestation spread at a larger scale. They group all infested trees within 750m of each other together into a single parent polygon, which is buffered by 750 m, and then assign all infestations the following year to the closest parent polygon. They find that about 75% of all new infestations occur within 2 km of the nearest parent polygon when averaged across all years from 2007 to 2013. Setting $r_1 = 2750$ (including the buffer around the parent polygon) and $p_1 = 0.75$, we find $\alpha = 0.0008$ m^{-1}.

Across these three datasets, we find orders of magnitude of variation in α. While most beetles appear to travel only very short distances during an epidemic, the beetles that travel farther are able to infest trees. Given that the goal is to model pine beetle spread at the local landscape scale, we set $\alpha = 0.001$ m^{-1} in our simulations to accurately capture the spread observed in the highly detailed Alberta survey data.

Importantly, we note that the exact choice of α does not change our qualitative results as it corresponds effectively to a change of units. This is because

α has units of m^{-1} is always multiplied by a distance. As long as the scale of dispersal is significantly larger than the grid size of our simulation, our results for the speed of spread are scaled by $1/\alpha$. See Supporting Information A for more information and plots of the size and speed across the range of α values found here.

2.4 Beetle aggregation

In our model, beetles aggregate within a discrete grid cell when attacking host trees according to the survival function F. Given the construction of the survival function F, this means that the beetles distribute themselves amongst the trees in each cell according to a negative binomial distribution with parameter k. We will therefore choose grid spacing that corresponds to the scale of beetle aggregation. Thus while the parameter α determines the spatial spread of beetles, the parameter k measures how beetles aggregate within discrete grid cells.

We will assume that aggregation occurs at very small scales, within 10 to 30 meters. There are multiple lines of evidence for this scale of aggregation. First, visual evidence from small scale spatial maps, for example in Mitchell and Preisler (1991). Second, Thistle et al. (2004) find that surrogate pheromones disperse to within about 10% of their initial concentration within 10 meters and to only a few percent of their initial concentration within 30 meters. Third, Strohm et al. (2013) build a complex model for beetle dispersal that directly models aggregation pheromones. They use values for their diffusion and degradation parameters from Biesinger et al. (2000), which were derived from dimensional arguments to force the scale of loss of the pheromone to be about 3 m, which is approximately the distance between trees in an open stand. As derived in Chapter 5.2 in Lewis et al. (2016), the dispersal parameter α for a kernel with diffusion D and constant settling a is equal to $\sqrt{a/D}$, which with the values here is equal to 0.17 1/m. This corresponds to about 92% of aggregation pheromones remaining within 20 m. Finally, this scale of aggregation is consistent with the assumption in the more complicated mechanistic model of Powell and Bentz (2014), which is fit to aerial detection survey data. Here, we will use a grid spacing of $\Delta x = 16$ m.

The aggregation parameter k itself is more challenging to connect directly to data. It is likely that beetle aggregation changes over the course of an outbreak (Safranyik and Wilson 2006; Robertson et al. 2009; Boone et al. 2011; Chen and

Walton 2011) or with stand density (Powell and Bentz 2014). Fitting directly to data from Safranyik (1968), Peterman (1974), and Waring and Pitman (1985), we find best fit k values ranging from 1.6 to 100, with most values between $k = 4$ and 10. Qualitatively, we find that the negative binomial distribution describes the beetles distribution over trees fairly well, though we note that in some of these cases we fit a zero-inflated negative binomial to capture the many trees with negligible attack densities. We also note that the k values obtained here describe distributions where beetle populations are large enough to warrant measurement, and thus we would expect these beetles to be less aggregated than in very small populations. We note that part of the reason for the long tail for large k is that the distribution changes relatively slowly for large k and so the likelihood surface is relatively flat. More information on the data and plots of the fits can be found in Supporting Information B.

Given this variation in k, we instead assume that beetles are excellent aggregators at the small scale over which they can detect pheromones. We therefore allow the beetles to aggregate optimally for each value of beetle density. Specifically this means that for any given beetle density the aggregation parameter k is chosen so as to maximize the fraction of trees that succumb to infestation. This can also be interpreted as minimizing the fraction of trees that survive infestation. This is a reasonable assumption given the degree of chemical signalling that beetles use to coordinate mass attack (Raffa and Berryman 1983; Safranyik et al. 2010; Progar et al. 2014). Given that the survival function F depends on the mean number of beetles m, this also prevents unrealistic behaviour when the number of beetles stays constant but the number of susceptible trees in a stand increases. Without scaling the aggregation, this would mean that the same number of beetles would be less able to infest a more susceptible stand.

Mathematically, we minimize the survival function $F(m; k, \varphi)$ with respect to k for each value of m. At small values of m, this would lead to a divergence in k as $k \to 0$ and the beetles try to aggregate as strongly as possible. This would effectively remove the Allee effect except for very small numbers of beetles. Therefore, we set a minimum value of k, k_{min}. This makes sense biologically as the beetles can only aggregate up to a point and will not be perfect aggregators at very low densities. At the other end of the spectrum, when $m > \varphi$, $k \to \infty$ as the beetles would ideally spread completely uniformly across all trees. We again assume there is some maximum value of k, k_{max}, where the beetles will always aggregate to some extent even if their density is very high. This again makes sense biologically given that the aggregation pheromones are present before the

anti-aggregation pheromones (Progar et al. 2014).

We plot this optimized F, as well as the corresponding values of k that minimize the function for each value of m, in Fig. 1. We optimize F by minimizing the function for each integer value of m between a small value (chosen to be 11) and the threshold φ plus 100. For m below this value, we optimize for logarithmically spaced values between 0.01 and 10. For values of c greater than $\varphi + 100$, we also sample logarithmically up to $m = c$. We choose this range as for very small or large m, the function F is relatively insensitive to k and optimization becomes difficult numerically. Below and above this range of m, we set $F = 0$ and $F = 1$, respectively. Within this range we interpolate the function between the values of m where we optimized. In Fig. 1 and in our simulations we set $k_{min} = 10^{-2}$ and $k_{max} = 100$. We plot the Allee threshold for these values of the k cutoffs in terms of mean number of beetles per susceptible tree in Fig. 2.

Numerically, we find that changing k_{min} has a relatively large effect on the Allee threshold at very low beetle densities as it effectively increases the slope and reduces the curvature very near $m = 0$. This can make a large difference for when the beetles are able to infest new stands. We fix $k_{min} = 10^{-2}$ as the range of m where beetles can invade begins to stabilize around this value and does not increase drastically for smaller values. This small value biologically represents that beetles are excellent aggregators at small scales when their density is very small, less than one beetle per tree. We note that this minimum is intentionally smaller than the minimum value observed in the data as it is meant to represent beetle aggregation in populations well below the densities measured in any of the studies (Supporting Information B). Changing k_{max} has a relatively small effect on the Allee threshold, but when reduced below about $k_{max} = 100$ starts to round out the part of the curve above $m = \varphi$, reducing the percent of trees killed at moderately high densities and eventually decreasing the equilibrium number of beetles (as $1 - F(m)$ will intersect the 1:1 line at a smaller value). The exact value of the maximum should have less effect than the minimum given the relatively small changes in the distribution for very large k. More information about how these cutoffs affect the model can be found in Supporting Information C.

2.5 Parameters for population dynamics

The parameters for population dynamics in the model are the number of years before trees become susceptible N, the juvenile survival s, the brood size pa-

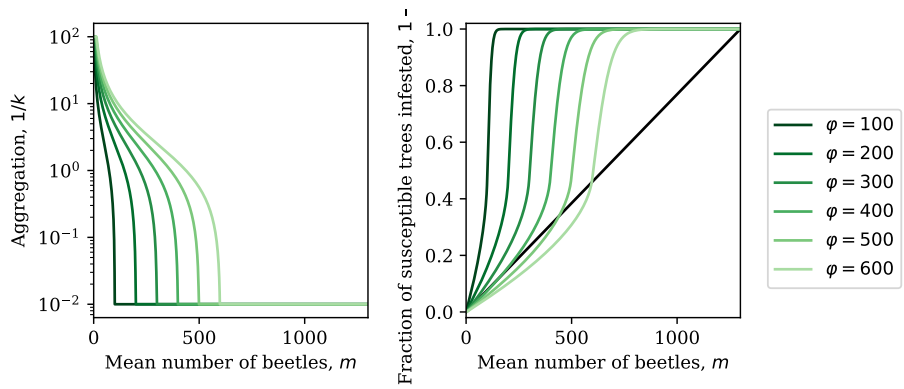

Figure 1: Optimized aggregation across mean beetle density and the corresponding function $1 - F(m)$ representing the fraction of susceptible trees infested for different values of the threshold φ and $c = 1300$. We set the bounds for k to be $k_{min} = 0.01$ and $k_{max} = 100$. These cutoffs are visible in the plot of $1/k$.

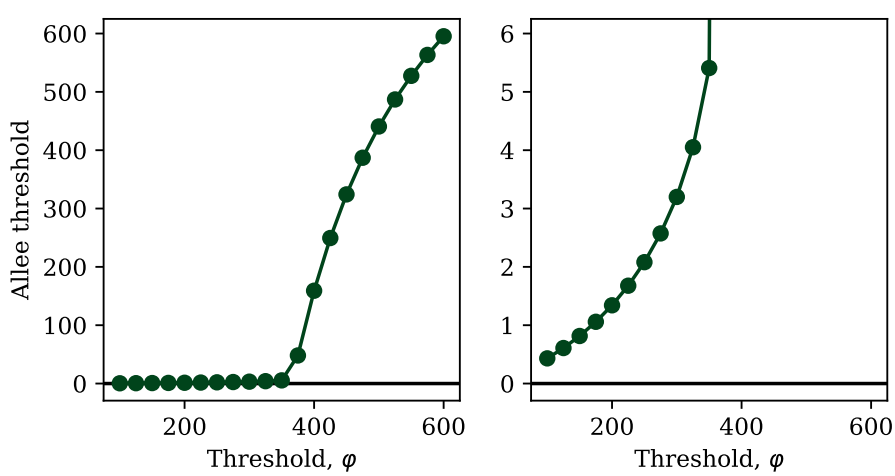

Figure 2: The Allee threshold at different values of the threshold parameter φ with $c = 1300$, given $k_{min} = 0.01$ and $k_{max} = 100$. The Allee threshold is given in terms of the mean number of beetles per susceptible tree. The second panel shows more closely how the Allee threshold changes at smaller values of the threshold φ.

rameter c, and the threshold parameter φ. We find plausible values for each of these parameters from available data in the literature for MPB in lodgepole pine. Table 2 summarizes the range we find for each parameter, and the single value used in simulations with fixed parameter values. We here summarize our parameter estimates and provide more details in Supporting Information D.

We estimate the number of age classes of juvenile trees N using two methods. In both cases, we note that because we assume brood size is the same across all susceptible trees, we define susceptible trees as those that produce more beetles than it takes to overcome their defenses. This means that the number of age classes of juvenile trees will be slightly larger than if we were to estimate only the number of years before trees could be attacked at all. First, in some outbreak data, tree age was recorded and we use that directly. In these data, we find that trees become susceptible around age 55 to 60 (Safranyik 1968; Safranyik and Wilson 2006; Shore and Safranyik 1992). Second, we estimate the diameter at breast height (dbh) cutoff for when trees become susceptible and combine that with estimates of growth. From data, we find the dbh cutoff varies between 18 cm and 35 cm (Klein et al. 1978; Mitchell and Preisler 1991; Safranyik and Wilson 2006; Safranyik et al. 1974; Cole and Amman 1969). We set the cutoff at 25 cm. For growth estimates, we use both radial growth rates and site index. We find radial growth rates vary between 1.2 mm/year and 2.4 mm/year Chhin et al. (2008), McLane et al. (2011), and Heath and Alfaro (1990). Rounding these to 1.5 mm/year to 2.0 mm/year with a dbh cutoff of 25 cm, this corresponds to $N = 63$ to 83. Given that growth rates are highly dependent on location, we also use site index combined with a height to dbh model (Huang 1999). Typical site indices in Alberta are 18 to 21 m (Monserud et al. 2008; Thrower et al. 1994), which corresponds to approximately 50 years to grow from a sapling at breast height to 25 cm dbh. We then add the 6 years it takes to reach breast height (Huang et al. 1994; Thrower et al. 1994; Nigh and Love 1999) to obtain $N \approx 56$. Combining all estimates, a plausible range is from $N = 50$ to 80 and we set $N = 60$ in simulations.

We estimate the survival fraction of juvenile trees s directly from juvenile survival data. We note that in reality juvenile mortality is higher for younger trees, though here we assume it is the same across all age classes. This means that this parameter will be larger than from data for 5 or 10 year survival rates. Estimates range from $s = 0.94$ to $s = 0.997$ (Brown and Navratil 1995; Bedford and Sutton 2000; Rweyongeza et al. 2007) for 10 year survival rates, and so we find a plausible range from $s = 0.98$ to 0.997 and set $s = 0.99$ in simulations.

Many sources of data for both the brood size per tree c and host resistance φ are measured in terms of beetles per m^2. To relate to these parameters, we have to estimate the surface area of a tree attacked by beetle. Previous estimates range between 4.4 and 8.1 m^2 per tree (Strohm et al. 2013; Powell and Bentz 2009; Klein et al. 1978). We average these estimates and round to 6 m^2 per tree, though note in cases with stand size distributions we make use of that information to obtain more accurate estimates.

We estimate the brood size parameter c from several different data sources, noting that this parameter is likely to be highly variable across years and host tree. Additionally, because we model only the population dynamics of the female beetles, we will assume that 2/3 of all beetle offspring are female (Amman and Cole 1983; Safranyik and Wilson 2006). We can estimate the brood size by multiplying the attack density per m^2, the attacked surface area, the number of offspring per attack, and the sex ratio of the offspring. Estimates using this method range from 400 to 3000 female beetles per tree (Klein et al. 1978; Raffa and Berryman 1983; Goodsman et al. 2016). We can also use direct estimates of emergence data per tree with known dbh, which range from a few hundred to 15 000 beetles, and then average over stand size distributions to obtain an estimate of around 1250 female beetles per tree (Safranyik 1968; Safranyik and Wilson 2006; Cole and Amman 1969). We find a plausible range from from $c = 400$ to 6000 female beetles per tree and set $c = 1300$ in simulations.

We estimate the threshold φ from experiments manipulating aggregation at 40 beetles per m^2 or $\varphi = 240$ beetles per tree (Raffa and Berryman 1983). We estimate a plausible range of host resistance to be $\varphi = 150$ to 720 beetles per tree using data from Waring and Pitman (1985) and the fit to that data in Lewis et al. (2010). Note however that the upper range here is only obtained by a few trees, and our parameter is at the stand level. We also obtain estimates between $\varphi = 250$ and 520 beetles per tree from our fits to data from Peterman (1974) (Supporting Information B). We find a plausible range from $\varphi = 150$ to 600 and set $\varphi = 250$ in simulations.

Finally, we note that the qualitative results of this model depend primarily on the ratio of φ/c, rather than on either value specifically (Brush and Lewis 2023). The range of c we find here varies by a factor of 15, and the range of the threshold φ varies by about a factor of 4; however both of these are likely to vary with similar factors (tree size, primarily (Safranyik and Wilson 2006)) and are not independent. Assuming they vary together linearly, the ratio φ/c varies between $600/6000 = 0.1$ and $150/400 = 0.375$. We can only estimate

this ratio directly using data from Raffa and Berryman (1983). They find a threshold of 40 beetles per m^2 and productivity between 200 and 500 beetles per m^2, corresponding to φ/c roughly between 0.08 and 0.2. If we were to vary φ across its plausible range from 150 to 600, this gives a similar range for φ/c of 0.12 to 0.46. In most plots we will round the plausible range to be from 100 to 600 beetles per tree, which corresponds to φ/c between 0.08 and 0.46. This also allows for the possibility that host defense thresholds are lower in jack pine or in novel stands.

Parameter	Value in simulations	Reasonable range	Units
N	60	50 - 80	-
s	0.99	0.98 - 0.997	survival/year
c	1300	400 - 6000	beetles/tree
φ	250	150 - 600	beetles/tree
α	0.001	0.001 - 0.1	1/m
Δx	16	10 - 30	m
k_{min}	0.01	-	-
k_{max}	100	-	-

Table 2: Values of model parameters used in numerical simulations, along with reasonable ranges from data.

2.6 Simulations

We simulate the mathematical model defined by Eqs. 8–12 in space with a discretized grid to investigate MPB spread. We set the initial conditions such that half of the forest is already infested by beetles and then simulate the model forward in time to observe the outbreak dynamics. We define metrics to characterize the speed and size of the outbreak and investigate how these change with host resistance.

On a technical level, we implement 1D spatial simulations on a discrete grid with spacing Δx in Python (code available at `https://github.com/micbru/MPBSpatialModel/`). We perform the convolution in Eq. 12 by taking the product of the infested tree density and the dispersal kernel in Fourier space by taking the discrete Fourier transform (DFT) using Fast Fourier Transforms (FFT), specifically using `scipy.fft` (Lutscher 2019, see for eg.).

We interpret the discrete grid as individual forest stands, as discussed above, where beetles aggregate and infest a fraction $1 - F(m_t)$ of the susceptible trees within that stand. Within each stand, the total tree density is fixed to 1 ($T = 1$

in Eq. 1) so that we interpret susceptible or infested tree density as a fraction of the total trees in the stand. We use a grid much larger than the range shown in plots or used to calculate wave speeds to avoid edge effects.

We initialize our simulations by first optimizing the beetle aggregation for our set of φ and c as described above, and then setting all variables on the left half of the spatial grid ($x < 0$) to their stable equilibrium values obtained by solving $1 - F(m) = m/c$. This makes the forest structure geometric. Given that the total number of trees depends on the number of infested trees in the two previous years (Eq. 1), we assume for $x < 0$ that the number of infested trees in the two previous years were also at equilibrium. For $x \geq 0$, we set all trees to be susceptible, $S_0(x \geq 0) = 1$. We assume that no trees were previously infested. This makes it easier to interpret the peak infestations as a fraction of the susceptible trees.

To determine the speed of the wave, we find the furthest point along the wave where the beetle population is greater than half of the equilibrium density at each time, x_t^{max}, and then take the difference to obtain the number of meters the population moves each year, $x_{t+1}^{max} - x_t^{max}$. We then average this distance over the second half of the simulation. Note that we also check to ensure the wave does not collide with the backwards travelling wave from edge effects, and if it does we only compute x_t^{max} up until the waves collide.

To determine the peak size of the wave, we take the maximum value of the wave at any point in space and average over a set time period. We start the time period at the first time the fraction of infested trees grows above its equilibrium value at $x = 0$ plus half of the period, and average over an entire period.

3 Results

We are interested in the characteristics of spread when beetles move between areas of different host resistance φ, or equivalently areas of different host resistance per tree brood φ/c. This could represent spread into a region of more genetically resistant lodgepole pine (Erbilgin et al. 2017b; Six et al. 2018), or into jack pine where host susceptibility is uncertain given host thresholds are likely to be lower but the beetles reproductive potential may also be lower (Safranyik and Linton 1982; Cerezke 1995; Safranyik et al. 2010; Rosenberger et al. 2017a; Rosenberger et al. 2017b; Bleiker et al. 2023).

In numerical simulations across a wide range of values of the threshold φ

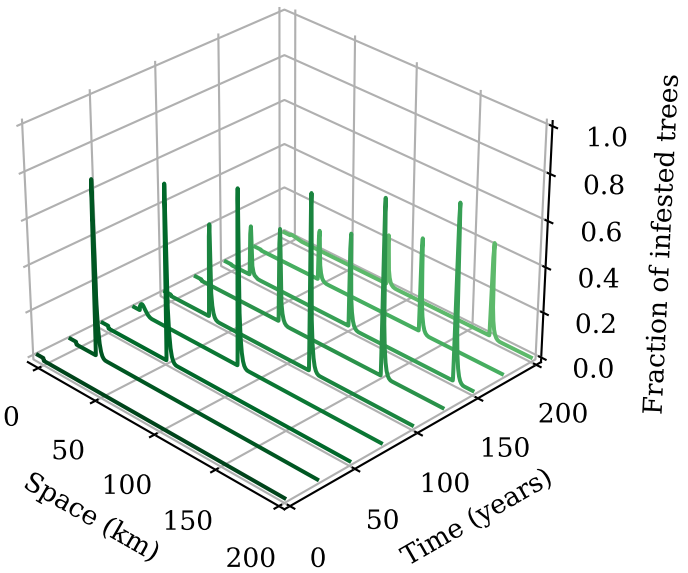

Figure 3: The fraction of infested trees over time and space. We initialize the forest structure and beetle population to their equilibrium values for $x < 0$. For $x \geq 0$, all trees are set to susceptible with no initial beetles. The parameter values are as in Table 2 ($c = 1300$) and we run the simulation for 200 years.

(and correspondingly φ/c), the infestation advances in space as a travelling transient pulse with beetle population densities much higher than at equilibrium. These travelling pulses are separated in time with period $N + 3$. This is as the transient waves in the non-spatial case in Brush and Lewis (2023), but here the waves are driven explicitly by beetles spreading over space into novel stands. Figure 3 shows a 3D representation of the beetle density over 200 years with the parameter values in Table 2, and Supporting Video A1 shows the same simulation as an animation.

Figure 4 shows the speed of spread for different values of φ with the other parameters fixed to their values in Table 2. Again, while we vary only φ, since the ratio φ/c determines the dynamics this is equivalent to holding φ fixed and varying c, or varying both parameters simultaneously with a specific ratio. The simulations were run for 200 years with increments of 25 for the threshold φ. The speed increases nearly linearly with decreasing $\varphi < 350$ ($\varphi/c < 0.27$), with a sharp change between $325 < \varphi < 375$ ($0.25 < \varphi/c < 0.29$) as soon as the wave

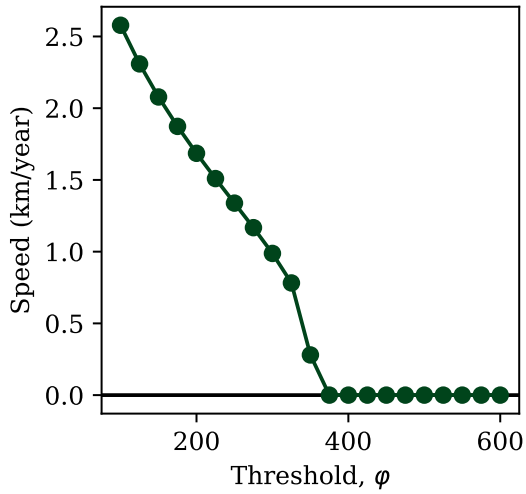

Figure 4: The speed of the transient wave pulse for different values of the host resistance. The other parameter values are as in Table 2 ($c = 1300$) and we run for 200 years. Points indicate values of the threshold where the speed was calculated and the line is the linear interpolation between the points.

is able to advance. For $\varphi > 350$ ($\varphi/c > 0.27$, the wave is unable to advance. Note that these speeds scale with $1/\alpha$, unless the scale of dispersal is similar to the scale of aggregation (Supporting Information A).

Figure 5 shows the averaged peak fraction of infested trees in the transient wave pulse for the same simulation as in Fig. 4. We again note the sharp jump in the size of the infestation when $\varphi \approx 350$ ($\varphi/c = 0.27$) as the wave is suddenly able to advance. Another potential metric for measuring the size of the outbreak would be total outbreak footprint, or the total number of infested trees over one period in time for one transient outbreak. In the asymptotic case considered here where all trees are susceptible, the total footprint of the outbreak is 1, or all trees are infested over the course of one transient wave. We note that in simulations where the right hand side started at equilibrium forest density rather than with all trees susceptible, we observe very similar dynamics, including speed, but the magnitude of the peak infestation was smaller.

In terms of the cutoffs k_{min} and k_{max}, we find that increasing k_{min} slightly decreases the speed of spread, and decreases the threshold when the wave is able to advance. In other words, when beetles aggregate less well at low densities they are less able to spread. As long as the wave is able to advance, the peak

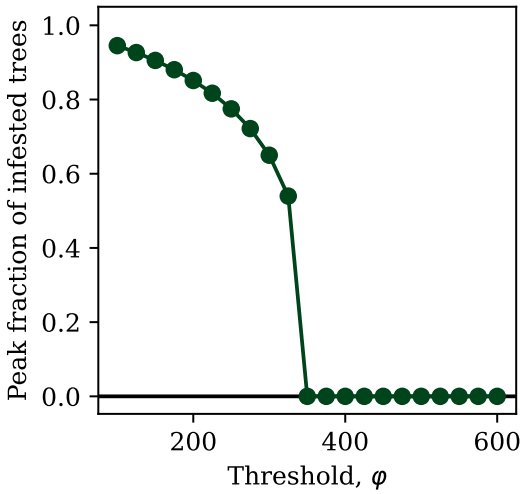

Figure 5: The averaged peak fraction of infested trees in the transient wave pulse for different values of the host resistance. The other parameter values are as in Table 2 ($c = 1300$) and we run the simulation for 200 years. Points indicate values of the threshold where the size was calculated and the line is the linear interpolation between the points.

size of the infestation is similar. Decreasing k_{min} below 10^{-2} and changing k_{max} have small effects on the speed. We find that the peak size of the infestation decreases slightly with decreasing k_{max}. See Supporting Information C for more information on the effects of the cutoffs.

We now focus on simulations with spatial variation in φ. Figure 6 shows how the wave advances from $\varphi = 200$ to 300 and then 400 ($\varphi/c = 0.15$, 0.23, 0.31), with Fig. 7 showing the dynamics at three fixed points in space in each of the different φ region. The results here reflect those in Fig. 4 in that the speed is slower when $\varphi = 300$ and the wave can no longer advance at $\varphi = 400$. The same simulation can be viewed as an animation in Supporting Video A2.

We also consider the case of a buffer zone where beetles pass through a section of higher resistance hosts. This could represent spread across a stand planted with trees from a breeding program that were selected for host resistance. The buffer section with higher resistance begins at $x = 0$ and extends for widths between 1 and 4 km in increments of 0.5 km. We set the threshold to overcome tree defenses for the buffer zone to be φ_b and vary it from 400 to 600 in increments of 25, with the lower bound chosen to be above the value where

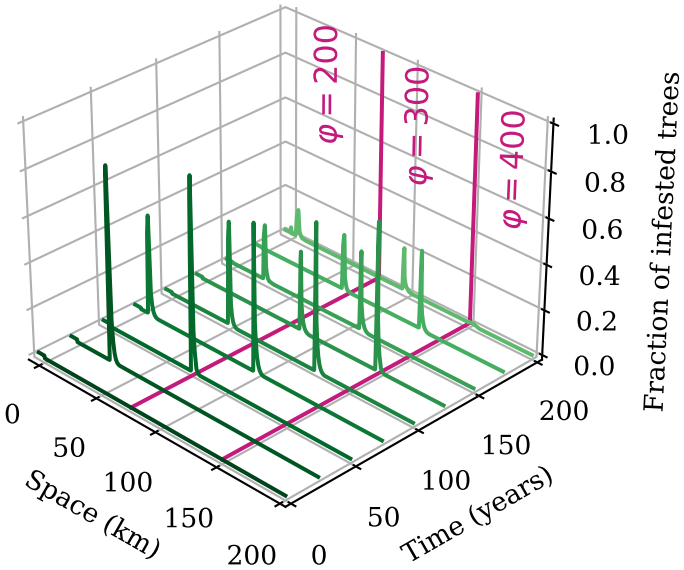

Figure 6: The fraction of infested trees over time and space with varying host threshold. We initialize the forest structure and beetle population to their equilibrium values for $x < 0$. For $x \geq 0$, all trees are set to susceptible with no initial beetles. We set the threshold φ to 200, 300, and 400 beetles per tree for $x < 75$ km, 75 km $\leq x <$ 150 km, and $x \geq 150$ km respectively. The other parameter values are as in Table 2 ($c = 1300$) and we run the simulation for 200 years.

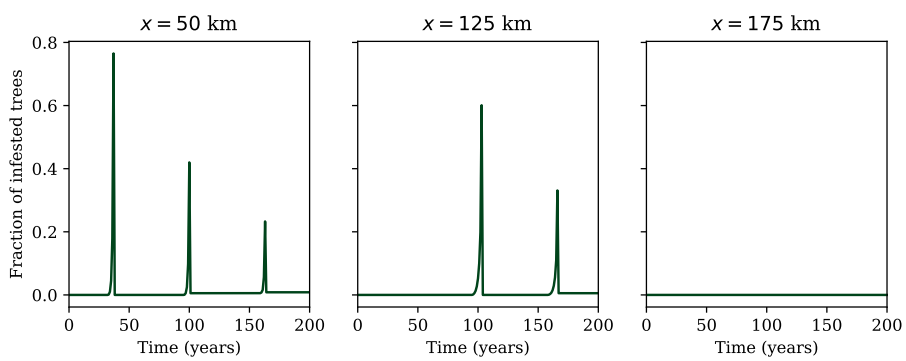

Figure 7: The fraction of infested trees over time with varying host threshold at three different fixed points in space. The simulation is as in Fig. 6. The three spatial locations are chosen to be within each of the different regions of the threshold φ.

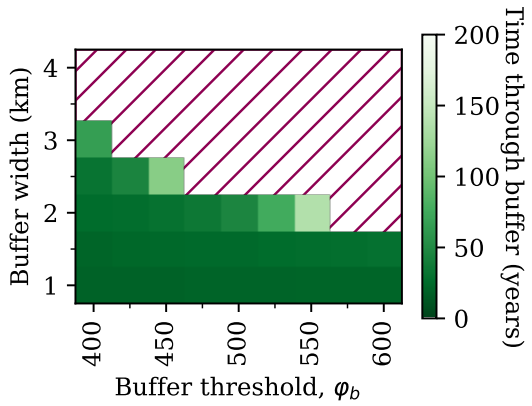

Figure 8: Beetle population spread through a buffer zone with higher host resistance for a variety of buffer widths and values of buffer host resistance. For each combination of parameters, we run the simulation for 200 years. If the beetles are able to pass through the buffer, we color the corresponding cell green with lighter colors indicating that the beetles took a longer time to pass through the buffer. Parameter regions where beetles are not able to pass through the buffer are indicated by dark red hashes. We initialize the forest structure and beetle population to their equilibrium values for $x < 0$. For $x \geq 0$, all trees are set to susceptible with no initial beetles. The buffer itself starts at $x = 0$ with threshold φ_b. All other parameters are as in Table 2 ($c = 1300$).

the wave would not spread from Fig. 4. In Fig. 8, we show the time it takes for the beetles to pass through the buffer for each combination of width and value of φ_b, where the dark hashed region in the upper right indicates the beetles were not able to pass through the buffer zone in the 200 years of the simulation. Supporting Videos A3 and A4 show animations of beetle density for scenarios where the beetle can and cannot spread beyond the buffer.

4 Discussion

Our model simulations show that spread of MPB at the landscape scale can be stopped at relatively intermediate values of host resistance (Fig. 4). Below that value when the spread does proceed, the speed of the outbreak depends approximately linearly on host resistance (Fig. 4), but the peak size of the outbreak is comparatively less affected by the host resistance (Fig. 5). Given that the value of host resistance where spread is stopped is within a plausible range of natural resistance, it is possible that planted trees selected for resistance

could slow or stop local spread, even if they are not planted everywhere on the landscape (Fig. 8). More research is needed to determine the relevant parameter values in jack pine, but recent research points towards lower brood sizes in jack pine (Bleiker et al. 2023), which could mean spread further east in Alberta will progress more slowly than in the past few decades.

Broadly, the outbreaks in our simulations of spatio-temporal dynamics of MPB dynamics are characterized by large transients that move through the susceptible trees, as in the non-spatial model (Brush and Lewis 2023). These transient waves of beetles are many times larger than the equilibrium beetle density and decay over time. When we view the outbreak from a fixed location in space, as in Fig. 7, the dynamics appear very similar to the non-spatial dynamics in Brush and Lewis (2023).

We find that the beetle population is no longer able to spread at the intermediate value of $\varphi = 350$ with $c = 1300$. This value of host resistance corresponds to approximately 60 beetle attacks per m^2 to overcome tree defenses, which is near the intermediate value of host resistance found in both Lewis et al. (2010) and Peterman (1974). This means that a relatively modest increase in host resistance may be able to slow or stop local spread for outbreaks of intermediate size, as this value of host resistance assumes $c = 1300$ beetles per tree. When we look instead at the value of host resistance per tree brood $\varphi/c \approx 0.27$, it is indeed greater than the maximum value of φ/c obtained from the data in Raffa and Berryman (1983), which is the only dataset for which we can calculate host resistance per brood tree. That this value is larger than the threshold value makes sense as the forest stands under study were undergoing an outbreak. It is unlikely that the host resistance per tree brood will be observed to be above about 0.25 as in that case the speed and size of the wave are very small or zero (Figs. 4 and 5), and such a small outbreak may be undetected or not studied in the level of detail necessary to obtain estimates for this ratio.

We note that the critical value of $\varphi/c \approx 0.27$ where the wave is no longer able to spread is much lower here than the appearance of the upper stable equilibrium at $\varphi/c \approx 0.6$ found in the non-spatial model (Brush and Lewis 2023). This means that φ/c must be substantially below the criteria for the existence of the upper equilibrium in order for the wave to spread. In the nonspatial model, this equilibrium corresponds to when φ/c is small enough that infested trees are able to replace themselves. In the spatial model, this value is smaller as beetles disperse out of infested cell and so either the brood size must be larger or the host resistance must be smaller in order for the beetles

to replace themselves. A mathematical approximation is that the outbreak is able to spread when the number of beetles in equilibrium divided by two is equal to the Allee threshold. The factor of one half comes from the fact that in our setup, half of the initial space is infested by beetles, and so the dispersing beetles contribute roughly half of the equilibrium number at $x = 0$. Numerically with parameter values from Table 2, we find the equilibrium number of beetles is about 15 beetles/cell. Assuming $k \approx k_{min}$ near the Allee threshold, we find that the approximate value of φ for which the wave advances is $\varphi = 366$ by solving $1 - F(m; k_{min}, \varphi + 1) = m/c$ with $m = 15/2$ and $c = 1300$.

From a theoretical perspective, we can obtain an upper bound for the value of φ/c where the speed is zero and the wave reverses direction by analyzing the model with no forest structure and where infested trees are immediately replaced by susceptible trees (or in other words, infested trees are not killed). The spread in this case is faster as there are always plenty of susceptible trees for the beetles, which is why this represents an upper bound. Mathematically, the model analysis in this case is simplified considerably and we can show that the wave is no longer able to advance when $\int_0^c dm(1 - F(m) - m/c) = 0$ (Wang et al. 2002; Li and Otto 2022). This is true for $\varphi \approx 750$ with $c = 1300$, or $\varphi/c \approx 0.58$ (see Supporting Information E). This is well beyond the realistic range for φ/c, and so while transient outbreaks may be slowed or stopped, they are unlikely to be reversed completely as that would require even larger φ/c.

We find that the spread speeds are consistent with data for intermediate length mountain pine beetle spread, or spot proliferation (Robertson et al. 2007; Robertson et al. 2009; Chen and Walton 2011). More specifically, our results for the speed of spread are consistent with the analysis of Robertson et al. (2009), who find that the median displacement from ground spread in three regions on the BC-Alberta border ranges from a few hundred meters to just over a kilometer (where spread over 2 km is classified as long distance dispersal). This is unsurprising given we parameterized our dispersal kernel using data from intermediate distance data from Carroll et al. (2017). We note here that setting α according to the results from Safranyik et al. (1992) or Robertson et al. (2007) would be more suitable for within stand dispersal, but that this scale is less relevant for determining the speed of spread as beetles do not move beyond the local stand. Since the speed of dispersal scales as $1/\alpha$, we find that when the dimensionless parameter $\Delta x \cdot \alpha$ is greater than about 2, the transient wave can fail to advance due to the discreteness of the grid. This is because the dispersal into the adjacent cell is not enough to overcome the Allee effect, and so the

wave is pinned (Keitt et al. 2001). With $\alpha = 0.001$ m^{-1}, we would only expect to see this pinning if beetles aggregated on the scale of roughly 2 km, which is far from realistic values. See Supporting Information F for more information.

Note that the spread speeds we find here are smaller by about an order of magnitude than the 80 km/year in Alberta found by Cooke and Carroll (2017); however that spread includes long distance spread events, which we do not model explicitly here. These long distance dispersal events happen when beetles are transported by the wind above the tree canopy (Furniss and Furniss 1972; Jackson et al. 2008) and are known to be important for infestations in new areas (Robertson et al. 2009; Chen and Walton 2011), even though a relatively small number of beetles (likely a few percent) disperse in this way (Safranyik et al. 1992). One possibility is to extend this model to include stratified diffusion (Shigesada et al. 1995) and to allow for a small number of beetles to travel above the canopy with a separate mode of dispersal.

In addition to the spread speed, we compare the peak fraction of infested trees to an outbreak in Yellowstone studied by Klein et al. (1978). Using our cutoff of 25 cm, or 10 inches to correspond with the units in their analysis, we find the peak fraction of infested trees to be $\approx 33\%$ in 1969. This peak fraction would correspond to an infestation that is just able to spread, around $\varphi/c = 0.25$, which makes sense given the relatively low density of lodgepole pine in the area. We are also able to estimate c from the peak emergence of ≈ 25 thousand beetles/acre with 27.4 infested stems/acre, or about 900 total beetles infested tree. This corresponds to $c \approx 600$ assuming a 2/3 sex ratio. Given the peak outbreak fraction, this would correspond to $\varphi \approx 150$. All of these parameter estimates are within a reasonable range.

The results from the spread into higher resistance trees and into the buffer zone indicate that more resistant trees could potentially slow or stop local spread and thus may give managers more chance to respond. The value of host resistance required to stop spread is well within the plausible range for forests, around $\varphi = 350$ or $\varphi/c = 0.27$, and small changes in host resistance can substantially reduce local spread speed given it is roughly linear below this threshold (Fig. 4). From a management perspective, these results suggest that lodgepole pine breeding programs selecting for host resistance may be effective in slowing local spread given the heritability of host resistance (Yanchuk et al. 2008; Six et al. 2018). Of course, this would require substantial investment in breeding programs as well as making it a priority to reforest with MPB resistant trees. Even if such a program were prioritized, it would likely take decades before its

effects were observed as these resistant trees would have to mature. We also note that because beetle brood size depends on factors other than host resistance, most importantly weather (Safranyik and Wilson 2006), a particularly good year for beetles may reduce the effect of planted resistant trees. This may be especially true with climate change, which may increase host susceptibility on a similar time scale to the implementation of such programs (Régnière and Bentz 2007; Safranyik and Wilson 2006; Matthews et al. 2018). Note that it is not yet clear how genetic host resistance affects MPB susceptibility mechanistically (Six et al. 2018; Cullingham et al. 2020), and so here genetically resistant trees could have an increased threshold φ, a decreased brood productivity c, or some combination of both.

In addition to pointing towards the potential success of breeding programs, our results have implications for MPB spread into the boreal forest and into jack pine. There is some evidence that lodgepole pine hosts in regions where MPB has not been found historically are less resistant (Cudmore et al. 2010; Peery et al. n.d.). If this is the case, we might expect that spread through the remaining lodgepole pine in Alberta will progress more quickly and be more severe. MPB range expansion into the jack pine and the boreal forest is uncertain. Jack pine may have lower thresholds for defense as it is less able to produce toxic resin, but MPB may also have reduced reproductive potential in jack pine (Safranyik and Linton 1982; Cerezke 1995; Safranyik et al. 2010; Rosenberger et al. 2017a; Rosenberger et al. 2017b; Bleiker et al. 2023). More research is needed to determine a biologically plausible range of the ratio φ/c in this novel host.

While this model is informative of pine beetle spread at the local landscape scale within a few kilometers, it ignores long distance dispersal. This is particularly important in interpreting our results from the resistant buffer in Fig. 8, where beetles may disperse beyond the higher resistance stand (potentially a newly planted stand bred for higher resistance) and begin a new infestation in the more susceptible hosts. This also may decrease the effectiveness of breeding programs as beetles may be able to bypass newly planted higher resistance stands. As mentioned above, model extensions to include the long distance mode of dispersal could improve the behaviour of the model on larger spatial scales.

In addition to simplifying assumptions around dispersal, our model does not include several important biological features. Here we have assumed that all susceptible trees produce the same number of beetles within a susceptible stand, and are equally susceptible. We interpret this as an average over the

successfully attacked trees in a stand assuming a reasonable distribution of stand diameters. A more realistic model might more explicitly include mean stand dbh to reflect that larger trees both have a higher threshold for defense and once infested can produce many more beetles (Safranyik and Wilson 2006). These parameters also vary with climate variables, as for example cold winters will kill larvae and reduce brood size, and drought will reduce tree thresholds (Régnière and Bentz 2007; Safranyik and Wilson 2006; Matthews et al. 2018). Connecting these parameters more directly to climate would also allow for a more detailed analysis of the effect of climate change on pine beetle spread.

Overall, our model predicts transient outbreaks in susceptible stands where beetles are able to infest large fractions of susceptible trees and spread at the speed of a few kilometers per year. We find that the ability for beetles to spread into new stands, and the size of the resulting outbreaks, changes quickly for realistic values of host resistance. More research is needed to determine the susceptibility of novel hosts, especially jack pine. Our simulation results point towards the potential of breeding programs that select for MPB resistant trees to be able to slow or stop local spread. However, for such a program to be successful it would require significant investment in selecting for and prioritizing planting these trees, and it would likely be decades before we would see the effects of such a program.

Acknowledgements

We would like to thank all Lewis Research Group members, in particular Evan Johnson, Xiaoqi Xie, and Kévan Rastello, for their feedback on this project. We would also like to thank the members of the TRIA-FoR project for their support. MAL gratefully acknowledges the Gilbert and Betty Kennedy Chair in Mathematical Biology. Funding for this research has been provided through grants to the TRIA-FoR Project to MAL from Genome Canada (Project No. 18202) and the Government of Alberta through Genome Alberta (Grant No. L20TF), with contributions from the University of Alberta and fRI Research (Project No. U22004). This work was supported by Mitacs through the Mitacs Accelerate Program, in partnership with fRI Research. MB acknowledges the support of the Natural Sciences and Engineering Research Council of Canada (NSERC), [PDF – 568176 - 2022].

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.

References

Amman, G. D. and W. Cole (1983). *Mountain Pine Beetle Dynamics in Lodgepole Pine Forests: Part II. Population Dynamics*. Intermountain Forest and Range Experiment Station, U.S. Department of Agriculture, Forest Service.

Aukema, B. H. et al. (2008). "Movement of outbreak populations of mountain pine beetle: influences of spatiotemporal patterns and climate". *Ecography* 31.3, pp. 348–358. DOI: 10.1111/j.0906-7590.2007.05453.x.

Bedford, L. and R. F. Sutton (2000). "Site preparation for establishing lodgepole pine in the sub-boreal spruce zone of interior British Columbia: the Bednesti trial, 10-year results". *Forest Ecology and Management* 126.2, pp. 227–238. DOI: 10.1016/S0378-1127(99)00090-0.

Berryman, A. A., K. F. Raffa, J. A. Millstein, and N. C. Stenseth (1989). "Interaction Dynamics of Bark Beetle Aggregation and Conifer Defense Rates". *Oikos* 56.2, p. 256. DOI: 10.2307/3565345.

Biesinger, Z., J. Powell, B. Bentz, and J. Logan (2000). "Direct and indirect parametrization of a localized model for the mountain pine beetle — lodgepole pine system". *Ecological Modelling* 129.2, pp. 273–296. DOI: 10.1016/S0304-3800(00)00240-4.

Bleiker, K. P., ed. (2019). *Risk assessment of the threat of mountain pine beetle to Canada's boreal and eastern pine forests : prepared for the Canadian Council of Forest Ministers, Forest Pest Working Group*. Canadian Council of Forest Ministers.

Bleiker, K. P., C. A. Ethier, and B. H. Van Hezewijk (2023). "Suitability of a Historical, Novel, and Occasional Host for Mountain Pine Beetle (Coleoptera: Curculionidae)". *Forests* 14.5, p. 989. DOI: 10.3390/f14050989.

Boone, C. K., B. H. Aukema, J. Bohlmann, A. L. Carroll, and K. F. Raffa (2011). "Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species". *Canadian Journal of Forest Research* 41.6, pp. 1174–1188. DOI: 10.1139/x11-041.

Broadbent, S. R. and D. G. Kendall (1953). "The Random Walk of Trichostrongylus retortaeformis". *Biometrics* 9.4, p. 460. DOI: 10.2307/3001437.

Brown, K. M. and S. Navratil (1995). *Analysis and interpretation of the research microsite projects in Alberta: effects of silvicultural and environmental factors on the post-planting performance of crop trees and competing vegetation*. [Report.] Canada-Alberta Partnership Agreement in Forestry 138. Edmonton, Alberta: Canada-Alberta Partnership Agreement in Forestry.

Brush, M. and M. A. Lewis (2023). "Coupling Mountain Pine Beetle and Forest Population Dynamics Predicts Transient Outbreaks that are Likely to Increase in Number with Climate Change". *Bulletin of Mathematical Biology* 85.11, p. 108. DOI: 10.1007/s11538-023-01215-7.

Burns, I., P. M. A. James, D. W. Coltman, and C. I. Cullingham (2019). "Spatial and genetic structure of the lodgepole × jack pine hybrid zone". *Canadian Journal of Forest Research* 49.7, pp. 844–853. DOI: 10.1139/cjfr-2018-0428.

Carroll, A. L., S. W. Taylor, J. Régnière, and L. Safranyik (2003). "Effects of climate change on range expansion by the mountain pine beetle in British Columbia". Vol. 399. Information Report BC-X-399. Kelowna, BC: Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, pp. 223–232.

Carroll, A., B. Seely, C. Welham, and H. Nelson (2017). *Assessing the effectiveness of Alberta's forest management program against the mountain pine beetle*. Tech. rep.

Cerezke, H. F. (1995). "Egg gallery, brood production, and adult characteristics of mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), in three pine hosts". *The Canadian Entomologist* 127.6, pp. 955–965. DOI: 10.4039/Ent127955-6.

Chen, H. and A. Walton (2011). "Mountain pine beetle dispersal: spatiotemporal patterns and role in the spread and expansion of the present outbreak". *Ecosphere* 2.6, art66. DOI: 10.1890/ES10-00172.1.

Chhin, S., E. (Hogg, V. J. Lieffers, and S. Huang (2008). "Influences of climate on the radial growth of lodgepole pine in Alberta". *Botany* 86.2, pp. 167–178. DOI: 10.1139/B07-120.

Cole, W. E. and G. D. Amman (1969). "Mountain pine beetle infestations in relation to lodgepole pine diameters". *Res. Note INT-RN-95. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 7 p.* 95.

Cooke, B. J. and A. L. Carroll (2017). "Predicting the risk of mountain pine beetle spread to eastern pine forests: Considering uncertainty in uncertain times". *Forest Ecology and Management* 396, pp. 11–25. DOI: 10.1016/j.foreco.2017.04.008.

Corbett, L. J., P. Withey, V. A. Lantz, and T. O. Ochuodho (2016). "The economic impact of the mountain pine beetle infestation in British Columbia:

provincial estimates from a CGE analysis". *Forestry: An International Journal of Forest Research* 89.1, pp. 100–105. DOI: 10.1093/forestry/cpv042.

Cudmore, T. J., N. Björklund, A. L. Carroll, and S. B. Lindgren (2010). "Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naïve host tree populations". *Journal of Applied Ecology* 47.5, pp. 1036–1043. DOI: 10.1111/j.1365-2664.2010.01848.x.

Cullingham, C. I., J. E. K. Cooke, S. Dang, C. S. Davis, B. J. Cooke, and D. W. Coltman (2011). "Mountain pine beetle host-range expansion threatens the boreal forest". *Molecular Ecology* 20.10, pp. 2157–2171. DOI: 10.1111/j.1365-294X.2011.05086.x.

Cullingham, C. I., R. M. Peery, C. E. Fortier, E. L. Mahon, J. E. K. Cooke, and D. W. Coltman (2020). "Linking genotype to phenotype to identify genetic variation relating to host susceptibility in the mountain pine beetle system". *Evolutionary Applications* 13.1, pp. 48–61. DOI: 10.1111/eva.12773.

Dhar, A., L. Parrott, and S. Heckbert (2016). "Consequences of mountain pine beetle outbreak on forest ecosystem services in western Canada". *Canadian Journal of Forest Research* 46.8, pp. 987–999. DOI: 10.1139/cjfr-2016-0137.

Duncan, J. P., J. A. Powell, L. F. Gordillo, and J. Eason (2015). "A Model for Mountain Pine Beetle Outbreaks in an Age-Structured Forest: Predicting Severity and Outbreak-Recovery Cycle Period". *Bulletin of Mathematical Biology* 77.7, pp. 1256–1284. DOI: 10.1007/s11538-015-0085-5.

Erbilgin, N. et al. (2017a). "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 Physiology* 37.3, pp. 338–350. DOI: 10.1093/treephys/tpw105.

Erbilgin, N. et al. (2017b). "Weathering the storm: how lodgepole pine trees survive mountain pine beetle outbreaks". *Oecologia* 184.2, pp. 469–478. DOI: 10.1007/s00442-017-3865-9.

Furniss, M. M. and R. L. Furniss (1972). "Scolytids (Coleoptera) On Snowfields Above Timberline In Oregon And Washington". *The Canadian Entomologist* 104.9, pp. 1471–1478. DOI: 10.4039/Ent1041471-9.

Goodsman, D. W., B. J. Cooke, and M. A. Lewis (2017). "Positive and negative density-dependence and boom-bust dynamics in enemy-victim populations: a mountain pine beetle case study". *Theoretical Ecology* 10.2, pp. 255–267. DOI: 10.1007/s12080-017-0327-2.

Goodsman, D. W., D. Koch, C. Whitehouse, M. L. Evenden, B. J. Cooke, and M. A. Lewis (2016). "Aggregation and a strong Allee effect in a cooperative outbreak insect". *Ecological Applications* 26.8, pp. 2623–2636. DOI: 10.1002/eap.1404.

Heath, R. and R. I. Alfaro (1990). "Growth response in a Douglas-fir/lodgepole pine stand after thinning of lodgepole pine by the mountain pine beetle: A case study". *Journal of the Entomological Society of British Columbia* 87, pp. 16–21.

Heavilin, J. and J. A. Powell (2008). "A novel method of fitting spatio-temporal models to data, with applications to the dynamics of mountain pine beetles". *Natural Resource Modeling* 21.4, pp. 489–524. DOI: 10.1111/j.1939-7445.2008.00021.x.

Huang, S. (1999). "Ecoregion-Based Individual Tree Height-Diameter Models for Lodgepole Pine in Alberta". *Western Journal of Applied Forestry* 14.4, pp. 186–193. DOI: 10.1093/wjaf/14.4.186.

Huang, S., S. J. Titus, and T. W. Lakusta (1994). *Ecologically based site index curves and tables for major alberta tree species*. Tech. rep. T/307. Forest Management Division, Land and Forest Services, Alberta Environmental Protection.

Jackson, P. L., D. Straussfogel, B. S. Lindgren, S. Mitchell, and B. Murphy (2008). "Radar observation and aerial capture of mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae) in flight above the forest canopy". *Canadian Journal of Forest Research* 38.8, pp. 2313–2327. DOI: 10.1139/X08-066.

Kautz, M., K. Dworschak, A. Gruppe, and R. Schopf (2011). "Quantifying spatio-temporal dispersion of bark beetle infestations in epidemic and non-epidemic conditions". *Forest Ecology and Management* 262.4, pp. 598–608. DOI: 10.1016/j.foreco.2011.04.023.

Keitt, T. H., M. A. Lewis, and R. D. Holt (2001). "Allee Effects, Invasion Pinning, and Species' Borders." *The American Naturalist* 157.2, pp. 203–216. DOI: 10.1086/318633.

Klein, W. H., D. L. Parker, and C. E. Jensen (1978). "Attack, Emergence, and Stand Depletion Trends of the Mountain Pine Beetle in a Lodgepole Pine Stand During an Outbreak". *Environmental Entomology* 7.5, pp. 732–737. DOI: 10.1093/ee/7.5.732.

Kunegel-Lion, M. and M. A. Lewis (2020). "Factors governing outbreak dynamics in a forest intensively managed for mountain pine beetle". *Scientific Reports* 10.1, p. 7601. DOI: 10.1038/s41598-020-63388-8.

Kurz, W. A. et al. (2008). "Mountain pine beetle and forest carbon feedback to climate change". *Nature* 452.7190, pp. 987–990. DOI: 10.1038/nature06777.

Lewis, M. A., W. Nelson, and C. Xu (2010). "A Structured Threshold Model for Mountain Pine Beetle Outbreak". *Bulletin of Mathematical Biology* 72.3, pp. 565–589. DOI: 10.1007/s11538-009-9461-3.

Lewis, M. A., S. Petrovskii, and J. Potts (2016). *The mathematics behind biological invasions*. New York, NY: Springer Berlin Heidelberg.

Li, B. and G. Otto (2022). "Wave speed and critical patch size for integro-difference equations with a strong Allee effect". *Journal of Mathematical Biology* 85.5, p. 59. DOI: 10.1007/s00285-022-01814-3.

Lutscher, F. (2019). *Integrodifference Equations in Spatial Ecology*. Vol. 49. Interdisciplinary Applied Mathematics. Cham: Springer International Publishing. DOI: 10.1007/978-3-030-29294-2.

Matthews, B. et al. (2018). "Transpiration deficits increase host susceptibility to bark beetle attack: Experimental observations and practical outcomes for Ips typographus hazard assessment". *Agricultural and Forest Meteorology* 263, pp. 69–89. DOI: 10.1016/j.agrformet.2018.08.004.

McLane, S. C., L. D. Daniels, and S. N. Aitken (2011). "Climate impacts on lodgepole pine (Pinus contorta) radial growth in a provenance experiment". *Forest Ecology and Management*. Environmental Stress and Forest Ecosystems: Case studies from Estonia 262.2, pp. 115–123. DOI: 10.1016/j.foreco.2011.03.007.

Mitchell, R. G. and H. K. Preisler (1991). "Analysis of Spatial Patterns of Lodgepole Pine Attacked by Outbreak Populations of the Mountain Pine Beetle". *Forest Science* 37.5, pp. 1390–1408. DOI: 10.1093/forestscience/37.5.1390.

Monserud, R. A., Y. Yang, S. Huang, and N. Tchebakova (2008). "Potential change in lodgepole pine site index and distribution under climatic change in Alberta". *Canadian Journal of Forest Research* 38.2, pp. 343–352. DOI: 10.1139/X07-166.

Nigh, G. D. and B. A. Love (1999). "A model for estimating juvenile height of lodgepole pine". *Forest Ecology and Management* 123.2, pp. 157–166. DOI: 10.1016/S0378-1127(99)00019-5.

Peery, R. et al. (n.d.). "The effect of lodgepole pine genotype on survivorship following a mountain pine beetle epidemic" ().

Peterman, M. (1974). "Some aspects of the population dynamics of the mountain pine beetle, *Dendroctonus ponderosae* in lodgepole pine forests of British Columbia". PhD thesis. University of British Columbia.

Powell, J. A. and B. J. Bentz (2009). "Connecting phenological predictions with population growth rates for mountain pine beetle, an outbreak insect". *Landscape Ecology* 24.5, pp. 657–672. DOI: 10.1007/s10980-009-9340-1.

— (2014). "Phenology and density-dependent dispersal predict patterns of mountain pine beetle (*Dendroctonus ponderosae*) impact". *Ecological Modelling* 273, pp. 173–185. DOI: 10.1016/j.ecolmodel.2013.10.034.

Progar, R. A., N. Gillette, C. J. Fettig, and K. Hrinkevich (2014). "Applied Chemical Ecology of the Mountain Pine Beetle". *Forest Science* 60.3, pp. 414–433. DOI: 10.5849/forsci.13-010.

Raffa, K. F. and A. A. Berryman (1983). "The Role of Host Plant Resistance in the Colonization Behavior and Ecology of Bark Beetles (Coleoptera: Scolytidae)". *Ecological Monographs* 53.1, pp. 27–49. DOI: 10.2307/1942586.

Ramazi, P., M. Kunegel-Lion, R. Greiner, and M. A. Lewis (2021). "Predicting insect outbreaks using machine learning: A mountain pine beetle case study". *Ecology and Evolution* 11.19, pp. 13014–13028. DOI: 10.1002/ece3.7921.

Régnière, J. and B. Bentz (2007). "Modeling cold tolerance in the mountain pine beetle, *Dendroctonus ponderosae*". *Journal of Insect Physiology* 53.6, pp. 559–572. DOI: 10.1016/j.jinsphys.2007.02.007.

Robertson, C., T. A. Nelson, and B. Boots (2007). "Mountain Pine Beetle Dispersal: The Spatial–Temporal Interaction of Infestations". *Forest Science* 53.3, pp. 395–405. DOI: 10.1093/forestscience/53.3.395.

Robertson, C., T. A. Nelson, D. E. Jelinski, M. A. Wulder, and B. Boots (2009). "Spatial–temporal analysis of species range expansion: the case of the mountain pine beetle, *Dendroctonus ponderosae*". *Journal of Biogeography* 36.8, pp. 1446–1458. DOI: 10.1111/j.1365-2699.2009.02100.x.

Rosenberger, D. W., B. H. Aukema, and R. C. Venette (2017a). "Cold tolerance of mountain pine beetle among novel eastern pines: A potential for trade-offs in an invaded range?" *Forest Ecology and Management* 400, pp. 28–37. DOI: 10.1016/j.foreco.2017.05.031.

Rosenberger, D. W., R. C. Venette, M. P. Maddox, and B. H. Aukema (2017b). "Colonization behaviors of mountain pine beetle on novel hosts: Implications

for range expansion into northeastern North America". *PLOS ONE* 12.5, e0176269. DOI: 10.1371/journal.pone.0176269.

Rweyongeza, D. M., N. K. Dhir, L. K. Barnhardt, C. Hansen, and R.-C. Yang (2007). "Population differentiation of the lodgepole pine (*Pinus contorta*) and jack pine (*Pinus banksiana*) complex in Alberta: growth, survival, and responses to climate". *Canadian Journal of Botany* 85.6, pp. 545–556. DOI: 10.1139/B07-053.

Safranyik, L. (1968). "Development of a technique for sampling mountain pine beetle populations in lodgepole pine". PhD thesis. University of British Columbia.

Safranyik, L. and D. A. Linton (1982). "Survival and development of mountain pine beetle broods in jack pine bolts from Ontario". *Canadian Forestry Service Research Notes* 2.3, pp. 17–18.

Safranyik, L., D. A. Linton, R. Silversides, and L. H. McMullen (1992). "Dispersal of released mountain pine beetles under the canopy of a mature lodgepole pine stand". *Journal of Applied Entomology* 113.1-5, pp. 441–450. DOI: 10.1111/j.1439-0418.1992.tb00687.x.

Safranyik, L., D. M. Shrimpton, and H. S. Whitney (1974). *Management of lodgepole pine to reduce losses from the mountain pine beetle*. Tech. rep. 4285. Pacific Forestry Centre.

Safranyik, L., R. Silversides, L. H. McMullen, and D. A. Linton (1989). "An empirical approach to modeling the local dispersal of the mountain pine beetle (*Dendroctonus ponderosae* Hopk.) (Col., Scolytidae) in relation to sources of attraction, wind direction and speed". *Journal of Applied Entomology* 108.1-5, pp. 498–511. DOI: 10.1111/j.1439-0418.1989.tb00484.x.

Safranyik, L. and B. Wilson, eds. (2006). *The mountain pine beetle a synthesis of biology, management, and impacts on Lodgepole Pine*. Victoria, British Columbia: Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre.

Safranyik, L. et al. (2010). "Potential for range expansion of mountain pine beetle into the boreal forest of North America". *The Canadian Entomologist* 142.5, pp. 415–442. DOI: 10.4039/n08-CPA01.

Sambaraju, K. R., A. L. Carroll, J. Zhu, K. Stahl, R. D. Moore, and B. H. Aukema (2012). "Climate change could alter the distribution of mountain pine beetle outbreaks in western Canada". *Ecography* 35.3, pp. 211–223. DOI: 10.1111/j.1600-0587.2011.06847.x.

Shigesada, N., K. Kawasaki, and Y. Takeda (1995). "Modeling Stratified Diffusion in Biological Invasions". *The American Naturalist* 146.2, pp. 229–251. DOI: 10.1086/285796.

Shore, T. L. and L. Safranyik (1992). *Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands*. Tech. rep. BC-X-336.

Six, D. L., C. Vergobbi, and M. Cutter (2018). "Are Survivors Different? Genetic-Based Selection of Trees by Mountain Pine Beetle During a Climate Change-Driven Outbreak in a High-Elevation Pine Forest". *Frontiers in Plant Science* 9.

Srivastava, V. and A. L. Carroll (2023). "Dynamic distribution modelling using a native invasive species, the mountain pine beetle". *Ecological Modelling* 482, p. 110409. DOI: 10.1016/j.ecolmodel.2023.110409.

Strohm, S., R. C. Tyson, and J. A. Powell (2013). "Pattern Formation in a Model for Mountain Pine Beetle Dispersal: Linking Model Predictions to Data". *Bulletin of Mathematical Biology* 75.10, pp. 1778–1797. DOI: 10.1007/s11538-013-9868-8.

Thistle, H. W. et al. (2004). "Surrogate Pheromone Plumes in Three Forest Trunk Spaces: Composite Statistics and Case Studies". *Forest Science* 50.5, pp. 610–625. DOI: 10.1093/forestscience/50.5.610.

Thrower, J., A. Nussbaum, and C. Di Lucca (1994). *Site index curves and tables for British Columbia: interior species. 2nd edition.* Land Management Handbook Field Guide Insert 6. B.C. Ministry of Forests, Research Branch.

Van Kirk, R. W. (1995). "Integrodifference models of biological growth and dispersal". Ph.D. United States – Utah: The University of Utah.

Wang, M.-H., M. Kot, and M. G. Neubert (2002). "Integrodifference equations, Allee effects, and invasions". *Journal of Mathematical Biology* 44.2, pp. 150–168. DOI: 10.1007/s002850100116.

Waring, R. H. and G. B. Pitman (1985). "Modifying Lodgepole Pine Stands to Change Susceptibility to Mountain Pine Beetle Attack". *Ecology* 66.3, pp. 889–897. DOI: 10.2307/1940551.

Yanchuk, A. D., J. C. Murphy, and K. F. Wallin (2008). "Evaluation of genetic variation of attack and resistance in lodgepole pine in the early stages of a mountain pine beetle outbreak". *Tree Genetics & Genomes* 4.2, pp. 171–180. DOI: 10.1007/s11295-007-0098-9.