Eruptive insect outbreaks from endemic populations under climate change

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Abstract

Insects, especially forest pests, are frequently characterized by eruptive dynamics. These types of species can stay at low, endemic population densities for extended periods of time before erupting in large-scale outbreaks. We here present a mechanistic model of these dynamics for mountain pine beetle. This extends a recent model that describes key aspects of mountain pine beetle biology coupled with a forest growth model by additionally including a fraction of low vigor trees. These low vigor trees, which may represent hosts with weakened defenses from drought, disease, other bark beetles, or other stressors, give rise to an endemic equilibrium in biologically plausible parameter ranges. The mechanistic nature of the model allows us to study how each model parameter affects the existence and size of the endemic equilibrium. We then show that under certain parameter shifts that are more likely under climate change, the endemic equilibrium can disappear entirely, leading to an outbreak.

Keywords: Mountain pine beetle; forest pests; outbreak dynamics; endemic populations; climate change.

1 Introduction

Insect outbreaks are often characterized by dramatic year to year changes in population abundances (Barbosa and Schultz 1987). Many species are characterized by eruptive dynamics, where they maintain low densities over a long time before outbreaking at the landscape scale. This includes species such as spruce budworm (Ludwig et al. 1978; Pureswaran et al. 2016), spongy moth (Elkinton and Liebhold 1990), and bark beetles such as spruce beetle (Werner et al. 2006) and mountain pine beetle (Safranyik and Wilson 2006). Outbreaks are therefore particularly hard to predict due to their irregular intervals and dependence on stand conditions and low population densities that are challenging to measure (Berryman and Stark 1985). The impact of insect outbreaks are expected to worsen with climate change (Bale et al. 2002; Logan et al. 2003; Liebhold 2012), creating additional challenges for managers (Day and Pérez 2013; Ayres and Lombardero 2018) and leading to large economic losses (Ayres and Lombardero 2000).

We here focus on mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins) as an example species of these types of endemic to outbreak dynamics. MPB is one of the most destructive forest pests in North America, with outbreaks in the past few decades affecting more than 18 million hectares of forest in Western Canada (Dhar et al. 2016; Corbett et al. 2016). In the historical range in British Columbia, outbreaks were found to occur every 30 to 40 years (Alfaro et al. 2010; Axelson et al. 2009), with evidence that these outbreaks are driven by climatic conditions in combination with forest management (Sambaraju et al. 2019; Safranyik and Wilson 2006).

For MPB, outbreaks often begin from a low level endemic population (Safranyik and Wilson 2006). Beetles in the endemic state preferentially attack trees with compromised defenses from disease, age, or other bark beetles (Safranyik and Wilson 2006; Boone et al. 2011; Bleiker et al. 2014). When conditions are right, beetle populations grow large enough that they are able to mass attack and overcome the defenses of larger, more vigorous trees (Safranyik and Wilson 2006; Raffa and Berryman 1983), increasing their brood size in the higher quality host and thus leading to a transition into an outbreak state.

There are several phenomenological models of this endemic to epidemic transition (Nelson et al. 2008; Cooke and Carroll 2017). These models rely on the idea that weakened trees can give rise to an endemic equilibrium, with another, larger threshold for healthy trees that gives and epidemic equilibrium state. This then gives rise to bistable dynamics, where shifts in the recruitment curve can push endemic beetle populations above the threshold for the epidemic state. Cooke and Carroll (2017) consider their conceptual model in the context of climate change and find that several different impacts of climate change could lead to the disappearance of the endemic equilibrium, allowing MPB populations to suddenly grow to their epidemic state.

We here develop a mechanistic model built from first principals. We extend a recent model of MPB (Brush and Lewis 2023) to include low vigor host trees. This model includes key biological features such as beetle aggregation

and a threshold for beetles to overcome host defenses, as well as a forest growth model. We show that this model extension allows for a stable, endemic beetle population, as expected biologically and from the phenomenological models. We then consider realistic ranges for each of the model parameters to investigate under which conditions an endemic beetle population can exist, and how that may be altered under climate change.

2 Methods

2.1 Model description

We begin with the model described in Brush and Lewis (2023). This model includes key aspects of pine beetle biology (Goodsman et al. 2016) and couples the beetle population dynamics to a forest growth model (Duncan et al. 2015). Beetles in this model aggregate to overcome a host defense threshold, an abstraction of the complex chemical signalling beetles use for mass attack (Raffa and Berryman 1983; Berryman et al. 1985; Safranyik and Wilson 2006). The forest grows with age classes tracking juvenile trees before trees becomes susceptible when large enough to support beetle populations. New saplings grow wherever there is space on the forest floor.

Mathematically, we use discrete time to represent the annual life cycle of the beetles, with each variable indexed by the year t. The variables are the number of beetles B_t, the number of susceptible trees S_t, the number of infested trees I_t, and the number of juvenile trees in each age class i, $j_{i,t}$. The model parameters are the juvenile survival rate s, the number of age classes of juvenile trees before they become susceptible N, the host defense threshold φ, the beetle brood size c, and the beetle aggregation parameter k. The beetles are distributed among the susceptible trees according to a negative binomial distribution with the aggregation parameter k, with the mean number of beetles per tree given by $m_t = B_t/S_t$. The fraction of surviving trees is given by the function

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

where $I_{\frac{k}{k+B_t/S_t}}(k, \varphi+1)$ is the cumulative distribution of the negative binomial distribution, which is the regularized incomplete Beta function. For notational simplicity, we drop the explicit dependence on the parameters and write

$$F\left(\frac{B_t}{S_t}; k, \varphi\right) = F\left(\frac{B_t}{S_t}\right) \tag{2}$$

In terms of forest growth, we assume that infested trees block light for two years, first as red tops and then as grey snags, before new saplings grow in their

place. New saplings also replace juvenile trees that do not survive to the next age class. This means the total number of trees T is conserved as

$$T = J_t + S_t + I_{t-1} + I_{t-2}, \tag{3}$$

where J_t is the total number of juvenile trees, $J_t = \sum_{i=1}^{N} j_{i,t}$. The model can then be written as

$$j_{1,t+1} = \underbrace{(1-s)J_t}_{\substack{\text{Recruitment from}\\ \text{juvenile mortality}}} + \underbrace{I_{t-2}}_{\substack{\text{Recruitment from}\\ \text{grey snags}}} \tag{4}$$

$$j_{i+1,t+1} = \underbrace{sj_{i,t}}_{\text{Juvenile survival}} \qquad \text{for } i = 1 \ldots N-1 \tag{5}$$

$$S_{t+1} = \underbrace{F\left(\frac{B_t}{S_t}\right) S_t}_{\text{Survival of susceptible trees}} + \underbrace{sj_{N,t}}_{\text{Recruitment from juveniles}} \tag{6}$$

$$I_t = \underbrace{\left(1 - F\left(\frac{B_t}{S_t}\right)\right) S_t}_{\text{Infested susceptible trees}} \tag{7}$$

$$B_{t+1} = \underbrace{cI_t}_{\text{Beetle productivity}} . \tag{8}$$

We now extend the model to include low vigor trees, which represent trees that could be weakened by disease or other pests, older trees with compromised defenses, or trees under more severe drought stress, among other things. These trees will have less resistance to pine beetle attacks, but due to thinner or less nutrient dense phloem will produce fewer beetles once infested (Safranyik and Wilson 2006).

We assume that a small fraction f of susceptible trees each year are low vigor trees. We refer to the remaining fraction $1-f$ of trees as high vigor trees. We use the subscript L to denote parameters relating to the lower vigor trees and the subscript H to denote parameters relating to the high vigor trees. We denote the threshold to overcome the defenses of these trees as φ_L, which should be less than the threshold φ_H. Similarly, we denote the brood size in these trees as c_L, where again c_L should be lower than c_H. Additionally, we assume that the beetles aggregate differently on both low and high vigor trees, with parameters k_L and k_H. Finally, we assume that the beetles attack low vigor trees with proportion β. The mean number of beetles attacking the low vigor trees is then given by $\beta B/fS$, or $\beta m/f$ using $m = B/S$ as before. The mean number of beetles attacking the high vigor trees is then given by $(1-\beta)m/(1-f)$. Note then that when $\beta = f$ and the beetles attack the trees in the same fraction they are present, the mean number of beetles attacking each type of tree simplifies to m.

In the analysis, we will allow the fraction β to itself be a function of the mean number of beetles present, given evidence that beetles preferentially attack

lower vigor trees at low densities and switch to preferentially attack large, higher vigor trees at higher densities (Boone et al. 2011; Bleiker et al. 2014; Safranyik and Wilson 2006). For notational simplicity, we omit this dependence in the following equations.

We turn to the full set of equations including the low vigor trees. The structure of the juvenile trees is unchanged. We use the same function F to describe how beetles overcome tree defenses, but we now have functions with two different mean numbers of beetles, aggregation parameters, and thresholds. We define the function representing the survival of high vigor trees as

$$F\left(\frac{1-\beta}{1-f}\frac{B_t}{S_t}; k_H, \varphi_H\right) = F_H\left(\frac{B_t}{S_t}\right), \tag{9}$$

and the corresponding function representing the survival of the low vigor trees as

$$F\left(\frac{\beta}{f}\frac{B_t}{S_t}; k_L, \varphi_L\right) = F_L\left(\frac{B_t}{S_t}\right). \tag{10}$$

The total number of infested trees is then given by

$$\begin{aligned} I_t &= \left(1 - F_H\left(\frac{B_t}{S_t}\right)\right)(1-f)S_t + \left(1 - F_L\left(\frac{B_t}{S_t}\right)\right) f S_t \\ &= \left(1 - (1-f)F_H\left(\frac{B_t}{S_t}\right) - f F_L\left(\frac{B_t}{S_t}\right)\right) S_t. \end{aligned}$$

The number of surviving susceptible trees is modified similarly. Note that if $\varphi_H = \varphi_L$, $k_H = k_L$, and $\beta = f$, this simplifies to the case without low vigor trees. The number of emerging beetles is further modified as the infested low vigor trees produce a different number of beetles, and is given by

$$\begin{aligned} B_{t+1} &= c_H\left(1 - F_H\left(\frac{B_t}{S_t}\right)\right)(1-f)S_t + c_L\left(1 - F_L\left(\frac{B_t}{S_t}\right)\right) f S_t \\ &= \left(c_H(1-f)\left(1 - F_H\left(\frac{B_t}{S_t}\right)\right) + c_L f\left(1 - F_L\left(\frac{B_t}{S_t}\right)\right)\right) S_t. \end{aligned}$$

Note that for this equation to simplify to the case without low vigor trees (ie. $B_{t+1} = cI_t$), we additionally require $c_H = c_L$.

The full set of equations is then given by

$$j_{1,t+1} = \underbrace{(1-s)J_t}_{\substack{\text{Recruitment from}\\ \text{juvenile mortality}}} + \underbrace{I_{t-2}}_{\substack{\text{Recruitment from}\\ \text{grey snags}}} \tag{11}$$

$$j_{i+1,t+1} = \underbrace{sj_{i,t}}_{\text{Juvenile survival}} \qquad \text{for } i = 1 \dots N-1 \tag{12}$$

$$S_{t+1} = \Bigg(\underbrace{(1-f)F_H\left(\frac{B_t}{S_t}\right)}_{\substack{\text{Survival of}\\ \text{high vigor trees}}} + \underbrace{fF_L\left(\frac{B_t}{S_t}\right)}_{\substack{\text{Survival of}\\ \text{low vigor trees}}}\Bigg)S_t + \underbrace{sj_{N,t}}_{\substack{\text{Recruitment from}\\ \text{juveniles}}} \tag{13}$$

$$I_t = \underbrace{\left(1-(1-f)F_H\left(\frac{B_t}{S_t}\right) - fF_L\left(\frac{B_t}{S_t}\right)\right)}_{\text{Total fraction of infested susceptible trees}}S_t \tag{14}$$

$$B_{t+1} = \Bigg(\underbrace{c_H(1-f)\left(1-F_H\left(\frac{B_t}{S_t}\right)\right)}_{\text{Beetles from high vigor trees}} + \underbrace{c_L f\left(1-F_L\left(\frac{B_t}{S_t}\right)\right)}_{\text{Beetles from low vigor trees}}\Bigg)S_t. \tag{15}$$

2.2 Parameter values

For the high vigor hosts, parameter values are determined from existing literature as in Brush and Lewis (2024) and Brush and Lewis (*in prep*). Parameter values for the low vigor hosts are more difficult to determine due to the challenge of collecting data on endemic beetle populations. We therefore allow these to have a wider range of values. The parameter values we consider are summarized in Table 1.

Brood size, c_H. This parameter is likely highly variable given the environment in a given year, as well as non-climate factors such as the size of the host tree (Safranyik and Wilson 2006). We estimate this parameter from historical data (Klein et al. 1978; Raffa and Berryman 1983; Safranyik 1968; Cole and Amman 1969; Safranyik and Wilson 2006), and consider that climate change is likely to increase the average brood size by decreasing overwinter mortality (Régnière and Bentz 2007; Cooke and Carroll 2017). This is likely to be realized from fewer very cold winters (Hayhoe and Stoner 2019; Eum et al. 2023). In the model extension considered here, we find that the results are not that sensitive to the value of c_H, and so we fix $c_H = 1500$. This is within the expected historical range and that projected under climate change (Brush and Lewis 2024) (Brush and Lewis (*in prep*)).

Tree threshold, φ_H. This parameter is very important for determining the Allee threshold for the beetles to outbreak, and so we consider a range meant to capture extreme values that correspond to tree defenses being weakened by increased drought stress under climate change (Safranyik and Wilson 2006; Cooke and Carroll 2017; Eum et al. 2023). Previous work finds a reasonable central value for this threshold in a beetle outbreak to be $\varphi_H = 250$ beetles per tree (Raffa and Berryman 1983; Waring and Pitman 1985; Lewis et al. 2010; Peter-

Parameter		Values considered
c_H	High vigor brood size	1500
φ_H	High vigor tree threshold	50, 150, 250
k_H	High vigor aggregation	6
c_L	Low vigor brood size	50, [1, 250]
φ_L	Low vigor tree threshold	5, [1, 25]
k_L	Low vigor aggregation	100
N	Generation time	55, [40,80]
s	Juvenile survival	0.994, [0.98,0.998]
f	Fraction of low vigor trees	0.01, 0.1, 0.25
$\beta(m)$	Beetle preference	$\exp\left((2\log(f)m)/(\varphi_H+\varphi_L)\right)$

Table 1: Parameter values for high and low vigor trees estimated from the literature. The brood size and tree threshold are in units of beetles per tree. Parameters with a single number are fixed, those with multiple values are varied in discrete increments, and those with a single value followed by values in parentheses are fixed at the single value in some plots and elsewhere varied continuously within the range.

man 1974; Brush and Lewis 2024). A reasonable lower estimate under current climate conditions is around $\varphi_H = 150$ (Brush and Lewis 2024). We additionally allow for the very low value of $\varphi_H = 50$, which could reflect a significant decrease in host defenses under frequent or more severe drought.

Low vigor parameters, φ_L and c_L. These parameters are very challenging to estimate from data, given the challenge of collecting data on endemic beetles, so we consider a range for both. The threshold φ_L may be only a few beetles per tree for low vigor hosts (Safranyik and Wilson 2006), as these low threshold trees may be predominately trees already infested by other bark beetles or otherwise have very weakened defenses. We consider a relatively generous range of $\varphi_L = 1 - 25$ beetles per tree, though the lower range of this estimate is likely more consistent with available data. We expect that successfully reproducing beetles in low vigor hosts are likely only able to achieve 1.5 – 2 new beetles per female (Safranyik and Wilson 2006; Klein et al. 1978), with a reasonable maximum of 10 new beetles per female (Raffa and Berryman 1983). Given this, c_L should be at maximum a few times φ_L. Again, we consider a generous range from $c_L = 1 - 250$ beetles per tree, with the most likely values towards the lower end of this range.

Beetle aggregation, k_H and k_L. We set k_H according to fits to data from Peterman (1974) which indicate that somewhere between 6 and 10 is reasonable (see Brush and Lewis 2024). We note that our results are not particular sensitive to any value in this range and set $k_H = 6$ here. We set k_L to be very large, $k_L = 100$, effectively assuming that the beetles are randomly distributed among the low-vigor trees. Biologically, we do this because at very low densities, we do not expect the beetles aggregation pheromones to be very effective, and brood sizes are small, so the beetles should not be very clustered. Note that effectively

this means we are replacing the negative binomial distribution with a Poisson distribution for the low vigor hosts.

Tree growth parameters, N and s. The number of years to become susceptible N and the juvenile survival s affect the value of the endemic equilibrium, and are needed for forward in time simulations. We explore a reasonable range of these parameters for a well-adapted lodgepole pine stand in Alberta, following Brush and Lewis (*in prep*). We allow N to vary between 40 and 80 years, with a central value of 55 years, which comes from site index projections (Monserud et al. 2008) together with a height to dbh model (Huang 1999). We allow s to vary between 0.98 and 0.998 1/years, with a central value of 0.994 1/years, based on data from Brown and Navratil (1995), Bedford and Sutton (2000), and Rweyongeza et al. (2007).

Fraction of low vigor trees, f. This parameter is likely to vary significantly from stand to stand, as hosts may be compromised from many different causes, such as pathogens, self-thinning, or other bark beetles. Previous work has found that in lodgepole pine, the number of damaged trees suitable for endemic beetles is between 6 – 13 trees per ha (Pokorny 2021). Given a stand density of 1000 to 2000 stems per ha in thinned stands (Baah-Acheamfour et al. 2023), this corresponds to around 1% of total trees. Other bark beetles have been found in direct association with endemic MPB at similar densities of between 5-10 attacked trees per ha (Safranyik and Wilson 2006). In the case of some pathogens, such as western gall rust, diseased stands may have a very high percent of infested trees (Van Der Kamp and Spence 1987), and in many stands, the majority of pine are affected by at least one pest (Maclauchlan and Brooks 2022). In stands that are not thinned for forestry, there is also likely to be a supply of low-vigor trees with suppressed growth (Safranyik and Wilson 2006). We here investigate a range between $f = 0.01$ and $f = 0.25$ to represent stands that are likely to be able to support an endemic beetle population.

Beetle preference, β. We model $\beta(m)$, where m is the mean number of beetles per tree $m = B/S$, as a decaying exponential. Thus at low densities the beetles attack only the low vigor trees, and at high densities nearly all beetles attack the high vigor trees. This is to correspond with observations of beetle behavior (Boone et al. 2011; Bleiker et al. 2014; Safranyik and Wilson 2006). To parameterize the exponential, we assume that at moderate beetle densities the beetles attack the trees in roughly the fraction they are present, so $\beta(m) = f$ for moderate beetle densities. We choose the moderate beetle densities to be when the mean number of beetles is equal to the average of the two thresholds, $m = (\varphi_H + \varphi_L)/2$. Setting $\beta(m) = f$ for this value of m with the functional form of $\beta(m)$ given by a decaying exponential gives

$$\beta(m) = \exp\left(\frac{2\log(f)}{\varphi_H + \varphi_L} m\right) = f^{2m/(\varphi_H+\varphi_L)}. \tag{16}$$

Note that because $f < 1$, $\log(f)$ is negative, and so this is indeed a decaying exponential. This assumption is equivalent to assuming that the beetle preference can be modeled as a power law in f.

Parameter		Initial value	Final value
c_H	High vigor brood size	1500	1500
φ_H	High vigor tree threshold	150	50
c_L	Low vigor brood size	50	100
φ_L	Low vigor tree threshold	15	5
f	Fraction of low vigor trees	0.1	0.25

Table 2: Parameter values for high and low vigor trees varied in our numerical simulation, with their initial historical values and their final projected values. The brood size and tree threshold are in units of beetles per tree. Parameters not included in this table were held fixed at their values in Table 1.

2.3 Numerical simulation

In addition to our numerical analysis of the equations, we conduct a numerical simulation of a beetle outbreak from an endemic population. This is meant to simulate how changes in parameters can lead to the disappearance of the endemic equilibrium, and push the system towards outbreak. We do this by changing the parameter values from a condition similar to a forest now to one that could be considered drought stressed, which may be the result of fluctuations in environmental conditions.

Numerically, we begin with the stand at its endemic equilibrium, which we calculate numerically. We then change each parameter by linearly increasing or decreasing its value from $t = 10$ to $t = 60$, from the initial to final parameter values in Table 2.

3 Results

3.1 Model fixed points

The mathematical analysis of this model is similar to that in Brush and Lewis (2023). In particular, if $c_H = c_L$ and β is fixed rather than a function of m, then we can substitute

$$F\left(\frac{B_t}{S_t}; k, \varphi\right) \to (1-f)F_H\left(\frac{B_t}{S_t}\right) + fF_L\left(\frac{B_t}{S_t}\right), \tag{17}$$

everywhere in the original equations and the analysis follows from Brush and Lewis (2023), but with a more complicated form of the function F. If $c_H \neq c_L$, the model analysis is more complicated as the number of red tops I_{t-1} cannot be written in terms of the number of beetles in the current year B_t, and so we cannot rewrite the right hand side Eq. 11 in terms variables at time t and must analyze the lagged system.

We now consider the fixed points of this model. The trivial fixed point with no beetles and only susceptible trees ($B = 0$, $S = T$) is as in the previous model, and we similarly expect this point to be stable given the stability of the previous

analysis did not depend on the function F. We can solve for the non-trivial fixed points of this model from Eq. 15 by dividing both sides by S, with $m = B/S$. The fixed points are given by

$$m = c_H(1-f)\left(1 - F_H\left(m\right)\right) + c_L f\left(1 - F_L\left(m\right)\right). \tag{18}$$

We can then solve for the remaining fixed points by combining Eqs. 11 to 14 together with the conservation of the total number of trees in Eq. 3. We set $T = 1$ so we can interpret the number of trees in terms of fraction of the total stems in the stand. Solving in terms of the number of infested trees, assuming this is non-zero, yields

$$I = \left(2 + \frac{1-s^N}{1-s}\frac{1}{s^N} + \frac{1}{1-(1-f)F_H(m) - fF_L(m))}\right)^{-1} \tag{19}$$

$$B = \frac{m}{1-(1-f)F_H(m) - fF_L(m)} I \tag{20}$$

$$S = \frac{B}{m} = \frac{I}{1-(1-f)F_H(m) - fF_L(m)} \tag{21}$$

$$J = \frac{1-s^N}{1-s}\frac{I}{s^N} \tag{22}$$

$$j_i = \frac{I}{s^{N+1-i}} \text{ for } i = 1 \ldots N. \tag{23}$$

where m is calculated numerically from Eq. 18.

Under certain parameter conditions, we find four non-trivial fixed points. This is two additional fixed points compared to the previous model. Figure 1 demonstrates graphically how these fixed points arise. The fixed points from Eq. 18 are effectively a weighted superposition of those from the model without low vigor trees, and a model with only low vigor trees. Without any low vigor trees present ($f = 0$), we have an Allee effect as before and the upper fixed point is stable. With only low vigor trees present ($f = 1$), we still have the same model as before with an Allee effect and a stable upper fixed points, but the threshold number of beetles to overcome the Allee effect is much lower, as is the upper fixed point. With only a small fraction of these low vigor trees then, the associated Allee effect and the fixed point are very small, leading to a small endemic beetle equilibrium, with another higher threshold and fixed point coming from the other susceptible trees.

Intuitively, given how these fixed points arise, we expect that the trivial fixed point is stable, and the following fixed points alternate between unstable and stable with increasing mean number of beetles (ie. stable, unstable, stable, unstable, stable, from the trivial fixed point). In other words, introducing a small fraction of low vigor trees is unlikely to change the stability of the fixed points of the model without these trees. However, there may be small range of parameter space that result in unexpected stability behavior, as in Brush and Lewis (2023). We find that numerical simulations with biologically plausible parameters are consistent with the intuitive stability structure outlined here. In

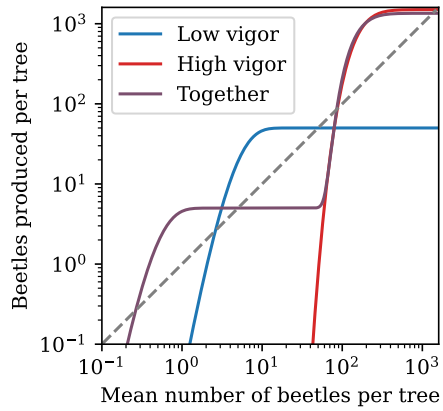

Figure 1: Comparison of the fixed points with the model with no low vigor trees ($f = 0$), with only low vigor trees ($f = 1$), and with a small number of low vigor trees ($f = 0.1$). We fix $\varphi_H = 150$, $\varphi_L = 5$, and $c_L = 50$, with other parameters set to their estimated values given in Table 1. With this set of parameters, two additional fixed points appear in the model corresponding to an endemic equilibrium.

the case $c_H = c_L$ and $\beta = f$, we can calculate the spectral radius numerically by modifying the survival function as in Eq. 17. With $c_H = c_L = 500$, $\varphi_H = 150$, $\varphi_L = 5$, $f = 0.1$, and other parameters fixed as in Table 1, we find fixed points at $m = 0, 2.6, 50.2, 97.3$, and 494.7 with corresponding spectral radii $\rho = 0.961, 3.837, 0.989, 2.710, 0.995$, which matches our expectations for stability.

Biologically, the additional stable fixed point at low number of beetles can be interpreted as an endemic beetle population that persists on low vigor trees, consistent with known behavior (Safranyik and Wilson 2006; Boone et al. 2011; Bleiker et al. 2014). We note that this arises from assuming only that low vigor trees exist in a small fraction and are easier to infest with a lower brood productivity, and we did not assume the existence of endemic beetle populations.

3.2 Existence of endemic equilibrium

We now wish to find the conditions and parameter ranges where these additional endemic fixed points exist. We plot the value of the endemic fixed point in Fig. 2 with the parameter values in Table 1. In regions where the endemic equilibrium exists, the value in terms of number of beetles per tree is given by the color. Dark areas in black and grey are regions of parameter space where the endemic equilibrium does not exist, where we have separated the underlying reason that this point does not exist into two cases represented by the two colors. In black regions, no endemic equilibrium exists as the low vigor hosts are not able to produce enough beetles to achieve a stable equilibrium. This corresponds to the case where the curve in Fig. 1 would be below the 1:1 line until passing the

threshold from the high vigor trees. In grey regions, no endemic equilibrium exists because the low vigor hosts produce enough beetles to overcome the higher threshold of the high vigor trees. This corresponds to the case where the curve in Fig. 1 would always be above the 1:1 line after crossing the initial smaller threshold from the low vigor trees. The grey regions are interesting as they allow for possible outbreaks from the endemic state and are considered further in the following section.

The regions where the endemic equilibrium does not exist can be roughly approximated analytically in order to gain some intuition for where endemic beetles can persist. As a rule of thumb, an endemic equilibrium is possible if $c_L \cdot f >$ Allee threshold of the low vigor trees. This can be understood as when the beetles are present at low densities, they mostly attack the low vigor trees ($\beta(m) \approx 1$, so $F_H(B_t/S_t) \approx 0$), and so depending on parameters can saturate the survival function corresponding to the low vigor hosts ($F_L(B_t/S_t) \approx 1$) and infest most of these hosts at each time step. Therefore, the number of beetles produced per susceptible tree is approximately $c_L \cdot f$ (since $F_L(B_t/S_t) \approx 1$ and $F_H(B_t/S_t) \approx 0$). If this is greater than the number of beetles needed to saturate the survival function (ie. the Allee threshold), then an endemic equilibrium exists. Mathematically, we can see this by first assuming m is small such that $\beta(m) \approx 1$ (Eq. 16). Then Eq. 18 is approximately

$$m = c_L f \left(1 - F\left(\frac{1}{f} m; k_L, \varphi_L\right)\right). \tag{24}$$

If the right hand side of this expression is greater than the left hand side for some small m, then the function passes above the 1:1 line and there will be an endemic equilibrium. Therefore, if there is a (small) value of m such that $c_L \cdot f > m/\left(1 - F\left(\frac{1}{f} m; k_L, \varphi_L\right)\right)$, then an endemic equilibrium exists.

We can also look at how each model parameter affects the existence of the endemic equilibrium. The low vigor parameters determine if the endemic equilibrium exists. The low vigor tree threshold φ_L controls the rise of the first part of the curve in Fig. 1, and thus if this curve rises fast enough to be above the 1:1 line. The low vigor brood size c_L controls the height that the first part of the curve in Fig. 1 rises to, together with the fraction of low vigor trees f. Note that increasing this fraction also decreases the value of the upper equilibrium as there are fewer high vigor trees with larger brood size. Finally, the high vigor tree threshold φ_H controls the outbreak Allee threshold.

To connect with data, we need to know the number of infested trees rather than the number of beetles per tree at the endemic equilibrium, as the number of infested trees is much easier to measure in the field. In this case, we use Eq. 19 to calculate the number of infested trees at the endemic fixed point and plot the results in Fig. 3. Equation 19 depends explicitly on the tree growth parameters s, the juvenile survival, and N, the generation time, and so we consider how the number of infested trees at equilibrium depends on these parameters. We find that the equilibrium number of infested trees does not appear to vary strongly with the beetles parameters of brood size or threshold, and so hold them fixed

in this plot.

3.3 Outbreak from endemic equilibrium

We now discuss the conditions necessary for an outbreak to occur from the lower endemic beetle equilibrium. From Fig. 1, we expect this to occur when the endemic fixed point disappears as the curve moves above the 1:1 line. Figure 4 shows how this could occur as the parameters change values under climate change. The parameter values used in the simulation are given in Table 2. Another way to think about when these conditions are met is in terms of the grey regions in Fig. 2, where if the system were previously in a region with an endemic equilibrium and transitions to a grey region where the low vigor hosts produce enough beetles to overcome the high vigor host defenses, the stand outbreaks. This is shown for the parameter values in Table 2 in Fig. 5. Note that this could occur given changes in any combination of the parameters likely to be effected by climate change.

We plot the resulting outbreak in Fig. 6. As with other simulations with similar versions of this model (Brush and Lewis 2023; Brush and Lewis 2024), the outbreaks are transient with large fluctuations in the beetle populations and with period given by the time of recovery of the forest. Here, the outbreak begins as a result of the loss of the endemic equilibrium, rather than from the migration of beetles from adjacent stands.

4 Discussion

We have here extended a mechanistic model of mountain pine beetle population dynamics by adding a small fraction of low vigor trees. This small fraction gives rise to a small, stable endemic equilibrium. This is as expected biologically (Safranyik and Wilson 2006) and as has been found in previous phenomenological models (Nelson et al. 2008; Cooke and Carroll 2017). In our model, the endemic equilibrium is not assumed but instead arises naturally from the fraction of low vigor trees, allowing the beetles to reproduce at low densities in weakened trees. The endemic population exists for most realistic values of model parameters (Fig. 2). However, for some regions of parameter space with particularly low high vigor host resistance, the endemic equilibrium disappears as endemic beetles are able to overcome the threshold for the high vigor hosts themselves, leading to an outbreak. These parameter regimes are potentially more common with climate change, which would make it more likely for beetles to outbreak from endemic to epidemic conditions.

The endemic equilibrium predicted from the model are realistic compared to data. Note that while the model parameters were estimated from data, the number of infested trees at the endemic equilibrium is a model prediction, implying that our model is correctly capturing aspects of mountain pine beetle dynamics. From Fig. 3, we find that endemic infestations in terms of the fraction of total trees are between 0.5 and 2% of total trees. Given stand densities of

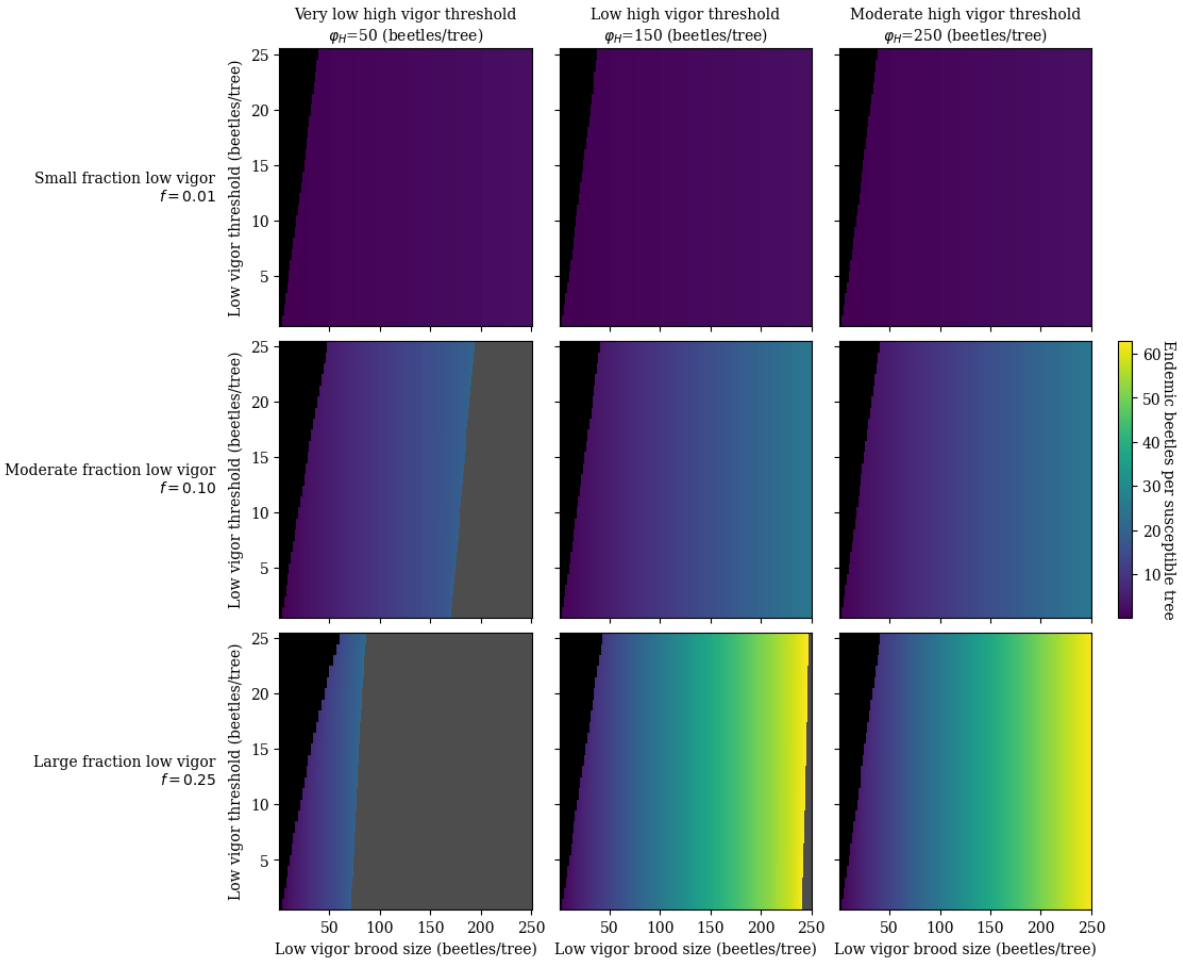

Figure 2: The endemic equilibrium as a function of model parameters. The parameter values are as in Table 1, with rows corresponding to varying the fraction of low vigor trees f, and columns corresponding to varying the threshold number of beetles needed to overcome high vigor host defenses φ_H. Within each plot, we vary the threshold and brood size in the low vigor trees. The color represents the number of beetles per susceptible tree at the endemic equilibrium. Black regions correspond to where no endemic equilibrium exists and the low vigor hosts do not provide enough beetles to replace themselves (ie. the beetles produced per tree is below the 1:1 line), and grey regions correspond to where no endemic equilibrium exists but the low vigor hosts produce enough beetles to overcome the Allee threshold for the high vigor hosts (ie. the beetles produced per tree is above the 1:1 line, and stays above the 1:1 line with increasing number of beetles). For most realistic values of model parameters, an endemic equilibrium exists. The grey region, which represents areas where outbreaks could occur from the endemic equilibrium, is largely only present at a very low threshold for the high vigor hosts.

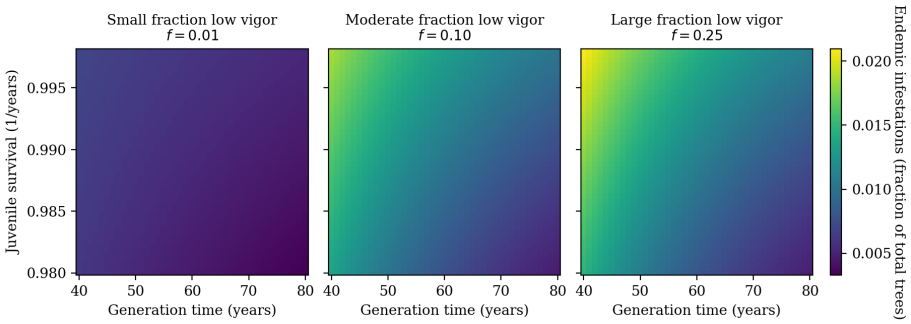

Figure 3: The endemic equilibrium number of infested trees. The color here represents the number of infested trees, in contrast to the equilibrium number of beetles per tree plotted in Fig. 2. Here we vary the parameters s and N, which enter through the equilibrium number of trees (Eq. 19). We consider three different fractions of low vigor trees f and hold other parameters fixed at $\varphi_H = 150$, $\varphi_L = 5$, and $c_L = 50$, which is in a parameter space where the endemic equilibrium exists (Fig. 2). The fraction of total trees infested in the endemic equilibrium is in a reasonable biological range, especially in forests with a small fraction of low vigor hosts.

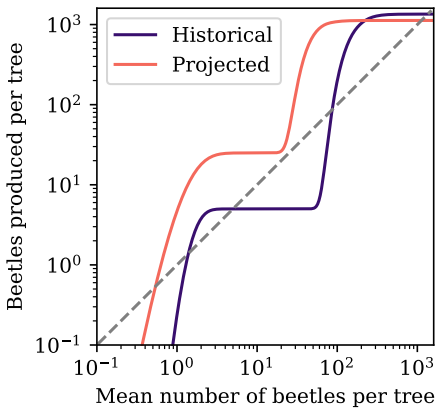

Figure 4: Comparison of the fixed points with parameters set to their estimated historical values and their estimated projected values given in Table 2. The endemic equilibrium disappears under the more favourable conditions for beetles, resulting in an outbreak.

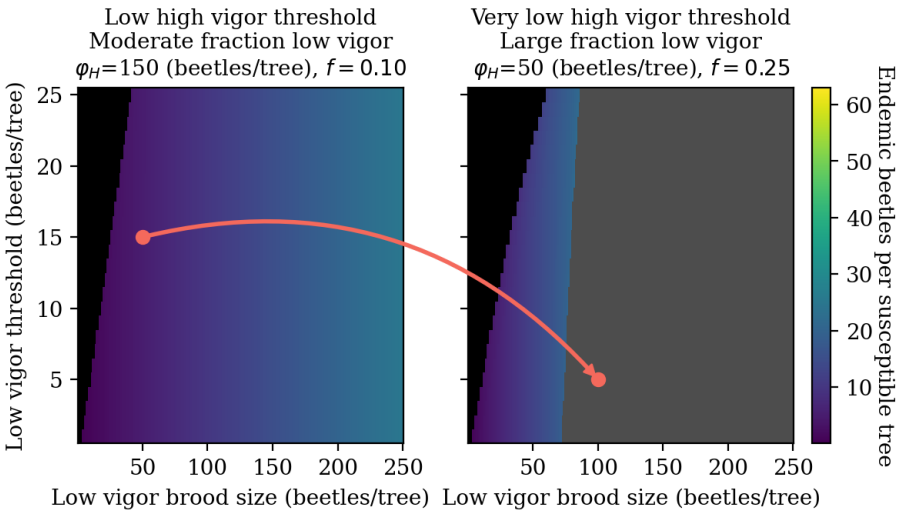

Figure 5: Points show the locations in parameter space for the historical and projected values given in Table 2 and shown on plots similar to Fig. 2, with black and grey regions representing areas of parameter space without an endemic equilibrium as in that figure. The orange dots show the location in parameter space before and after, connected with an arrow. This demonstrates how a change in parameters can lead to the disappearance of the endemic equilibrium in the grey region, leading to an outbreak.

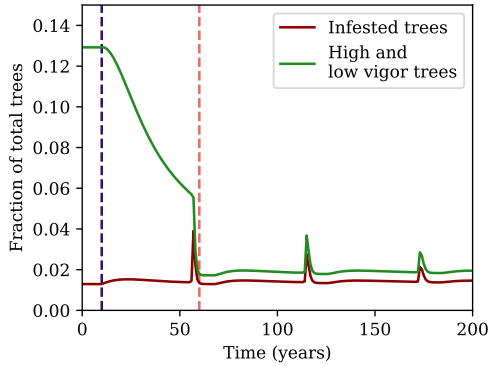

Figure 6: Outbreak from endemic beetles. Infested trees are shown in dark red, and the high and low vigor trees are combined in green, with both plotted as a fraction of the total number of trees. Note that many trees are juvenile, which are not plotted here. The initial condition is equal to the endemic equilibrium with parameters set to their estimated historical values, and the parameters are then reduced linearly over 50 years to estimated projected values. The first, darker vertical line shows where the parameters begin to change, and the second, lighter vertical line shows where the parameters have attained their final values. The outbreaks are transient pulses of infested trees.

1000 to 2000 stems per ha for thinned commercial stands (Baah-Acheamfour et al. 2023), this corresponds to 5 to 40 endemic infested trees per ha. Endemic populations are frequently considered to be stands with less than 5 attacked trees per ha (Boone et al. 2011), with studies finding between $3-6$ infested trees per ha in mature lodgepole pine stands (Safranyik and Wilson 2006) and $1-2$ attacked trees per ha in the lodgepole x jack hybrid zone in Alberta (Bleiker et al. 2014). Another study fitting a model in British Columbia found $7-14$ attacking beetles per ha (Koch et al. 2021), which for $\varphi_L = 5$ roughly corresponds to $1-2$ infested trees per ha. These estimates from available data correspond to the low end of our model predictions for the endemic equilibria, and specifically are attained for a small fraction of low vigor trees of around 1%. This value is also perhaps the most realistic for endemic populations given available data (Pokorny 2021; Safranyik and Wilson 2006), but we note that this fraction may increase during the transition from endemic to outbreak.

This model provides a mechanistic underpinning for the phenomenological models of Nelson et al. (2008) and Cooke and Carroll (2017). These models also assume low vigor trees give rise to an additional fixed point. In Nelson et al. (2008), the introduction of the low vigor hosts is nearly identical to here, where a second peak in the recruitment curve corresponds exactly to the low vigor hosts. In Cooke and Carroll (2017), these curves come from arguments about increasing growth rate at low density (Boone et al. 2011) followed by decreasing growth rates at high densities (MacQuarrie and Cooke 2011), together with an

endemic niche. Here, mechanistically, the rising growth rates comes from more beetles able to overcome host defenses, and this eventually decreases as beetles are able to saturate the available susceptible trees.

Cooke and Carroll (2017) also consider the effects of climate change on the endemic niche and the potential for outbreaks. They consider three perturbations which may lead to a saddle-node bifurcation whereby the endemic niche disappears and the endemic beetles outbreak. The three scenarios they consider are climate warming leading to increased brood size from increased overwinter survival, which here corresponds to an increase in c_L and c_H, host defense weakening through increased drought stress, which here corresponds to a reduction in φ_H, and forest degradation, which here corresponds to an increase in f. In all cases, we find that these changes in parameters in our model can also lead to an outbreak from the endemic equilibrium (Fig. 2). In particular, our simulation shown in Fig. 6 corresponds to a scenario where all three of these changes occur, and leads to the exact scenario discussed in Cooke and Carroll (2017).

Compared to the original model without low vigor trees (Brush and Lewis 2023), this model extension allows for more realistic outbreaks from endemic beetles rather than from immigrating beetles. Originally, beetles immigrating from an adjacent stand were required to overcome the Allee threshold and drive the system to transient outbreaks, but here outbreaks can occur directly from changing parameter values leading to the disappearance of the endemic equilibrium, as in Fig. 6. Biologically, this is often how outbreaks of mountain pine beetle begin (Safranyik and Wilson 2006). Another difference from that original model is the dynamics depend on the parameter φ_H directly rather than the ratio φ_H/c_H. This is because there are two brood size parameters, c_H and c_L, and so we can no longer non-dimensionalize by the brood size in the high vigor trees (ie. we can no longer divide through by c_H in Eq. 15).

Our model has several limitations. Most importantly, parameter uncertainty is quite high. We have tried to mitigate this by considering a wide range of parameters, and we find that not all parameter values lead to realistic levels of endemic infestation. Parameter values are particularly uncertain under our projected climate change scenarios, and many impacts from climate change that may affect beetle dynamics that are not included here (Cooke and Carroll 2017; Bentz et al. 2022). Other than parameter uncertainty, our model produces an unrealistic behavior at the endemic equilibrium. For the endemic equilibrium to be in balance, beetles consume all of the available low vigor hosts in each year before they are replaced in the following year. This is unrealistic as very small numbers of beetles are unlikely to be able to find every possible low vigor host, which is also hinted at by the difference in estimated available hosts, $6 - 13$ trees per ha (Pokorny 2021), and endemic population sizes, around 5 trees per ha (Boone et al. 2011; Safranyik and Wilson 2006; Bleiker et al. 2014). However, the values obtained here are still within a biologically plausible range, and we can instead interpret the fraction f as the effective fraction of low vigor trees available to the beetles.

Future work could include more simulations, for example where parameters are drawn from distributions rather than held fixed in order to address some

degree of parameter uncertainty, or where we incorporate immigrating beetles in addition to the endemic beetles. We could also make this model spatially explicit, as in Brush and Lewis (2024). Finally, we note that rather than a fixed function for $\beta(m)$, we could allow $\beta(m)$ to optimize the number of infested trees for each value of m, or try a different functional form such as a sigmoidal function to model the switch from attacking low vigor to high vigor hosts. We found that optimizing $\beta(m)$ was more difficult numerically and realistically low-level beetle populations are unlikely to have that much information about their own density, but we do not feel that the exact form of $\beta(m)$ used here is unique.

In summary, we find that realistic values of our model parameters lead to biologically plausible levels of endemic infestations. We find that a low fraction of low vigor trees, together with a small low vigor brood size and low vigor threshold yields observed levels of endemic infestations. Given that a wide range of parameter values allow for an endemic equilibrium, our model suggests lodgepole pine forests in Alberta are likely to enter endemic states following the most recent outbreaks. Under climate change, model parameter values may shift towards values that lead to a higher risk of undergoing an endemic to outbreak transition. More generally, given the difficulty of monitoring low-level endemic populations of forest pests, mechanistic models such as this one can be useful for understanding these endemic populations and how they may change in the future.

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