Dynamics of Mountain Pine Beetle Outbreaks

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INTRODUCTION

Native forest insects are the greatest forces of change in forest ecosystems of North America. In aggregate, insect disturbances affect an area that is almost 45 times as great as that affected by fire, resulting in an economic impact nearly five times as great (Dale *et al.*, 2001). Of these natural agents of ecosystem disturbance and change, the bark beetles are the most obvious in their impact, and of these, the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) has the greatest economic importance in the forests of western North America (Samman and Logan, 2000). The primary reason for this impact is that the mountain pine beetle is one of a handful of bark beetles that are true predators in that they must kill their host to successfully reproduce, and they often do so in truly spectacular numbers.

Although the mountain pine beetle is an aggressive tree killer, it is a native component of natural ecosystems; in this sense, the forests of the

American West have co-evolved (or at least co-adapted) in ways that incorporate mountain pine beetle disturbance in the natural cycle of forest growth and regeneration. Such a relationship in which insect disturbance is “part and parcel of the normal plant biology” has been termed a normative outbreak by Mattson (1996). This normative relationship between native bark beetles and their host forests is undergoing an apparent shift, exemplified by an unusual sequence of outbreak events. Massive outbreaks of spruce beetle have recently occurred in western North America ranging from Alaska to southern Utah (Ross *et al.*, 2001; Munson *et al.*, 2004). A complex of bark beetles are killing ponderosa pine in the southwestern United States at levels not previously experienced during the period of European settlement. Pinyon pines are being killed across the entire range of the pinyon/juniper ecotype, effectively removing a keystone species in many locations. Mountain pine beetle outbreaks are occurring at greater intensity, and in locations where they have not previously occurred (British Columbia Ministry of Forests, 2003). Any one of these events is interesting; that they are occurring almost simultaneously is nothing short of remarkable. In many of these instances the outbreaks are anything but normative; they are occurring in novel habitats with potentially devastating ecological consequences (Logan and Powell, 2001; Logan *et al.*, 2003).

What is going on here? The root of these unprecedented outbreaks appears to be directly related to unusual weather patterns. Although drought, particularly in the Southwest, is playing an important role in some of these outbreaks, the dominant and ubiquitous factor at the continental scale is the sequence of abnormally warm years that began somewhere in the mid-1980s (Berg, 2003; Logan and Powell, 2004). Regardless of the underlying causes, the impact of warming temperatures on bark beetle outbreaks has resulted in a renewed research interest focused on understanding and responding to the economic and ecological threat of native insects functioning as exotic pests. Because of its ecological importance and economic impact, the mountain pine beetle is receiving much of this interest. Development of predictive models is an important component of this research effort. This chapter develops a minimally complex model that, on a landscape scale, describes the spatial and temporal interaction between the mountain pine beetle and the lodgepole pine forest.

We first briefly review the biology of the mountain pine beetle and one of its primary hosts, lodgepole pine (*Pinus contorta* Douglas). Lodgepole pine is a shade-intolerant species that opportunistically colonizes areas following large-scale disturbances (Schmidt and Alexander, 1985). It is therefore an early successional species that typically initiates a sequence of

events that result in subsequent replacement by more shade-tolerant species. Over much of its distribution range, lodgepole pine would be replaced by spruce/fir forests without the intervening action of a major disturbance event. This disturbance is typically a stand-replacing crown-fire. Lodgepole pine reproduction is keyed to fire disturbance by producing a proportion of cones that release seeds only in the presence of high-heat (serotinous cones). The protected seeds inside the tightly closed cones remain viable for a prolonged time until the intense heat of a fire triggers their release. Seed establishment is also tied to conditions (exposed, mineral soil) created by stand-replacing fires (Muir and Lotan, 1985). Tree mortality caused by mountain pine beetles hypothetically plays a critical timing role in this reproductive cycle by creating the fuel conditions that predispose a stand to fire (Peterman, 1978).

The mountain pine beetle spends most of its lifecycle feeding in the protected environment of a host tree's phloem tissue (the nutrient rich inner bark). Adults emerge sometime in the summer (typically late July or early August) to attack new trees. If they are successful in overcoming the substantial host tree defensive chemistry and kill the host, the various life history events are subsequently carried out, resulting in continuation of the species' lifecycle. There are many subtle, and some not so subtle, nuances in the interplay between predator insect and prey tree. However, for a general synoptic model, the complex ecology of this beetle can be represented as a predator functional response curve. Simply stated, if enough beetles simultaneously attack a tree, tree defenses are overcome and the tree is killed; if not, the attack is unsuccessful and the tree lives. Beetle recruitment, in turn, is keyed to the number of trees that are killed during the previous attack cycle. Because beetle recruitment is keyed to the surrogate measure of trees killed (rather than actual beetle reproductive biology), this approach has been termed the "red-top" model because trees that are successfully attacked and killed begin to fade in color the summer following the attack, subsequently turning a characteristic bright orange or red.

Tree responses to beetle attack involve both constitutive and induced resin flow. When beetles attack a tree, the tree excretes pitch through the hole the beetle has chewed in the bark, creating "pitch tubes" (Amman and Cole, 1983). Resin flow contains toxic, defensive chemicals, and the resin flow induced by attack physically expels the attacking adult beetles. Not all trees have the same capacity to produce pitch for this defense because of varying size and fitness. Thus, not all trees are equally susceptible to attack. The lodgepole pine forest can be viewed as having three classes of trees from the perspective of susceptibility to beetle attack. Because the beetle

feeds on the phloem of the tree, attacking a tree of adequate size to create egg galleries and sufficient nutrient supply is important. The first class of trees are juveniles, which have a diameter breast height (DBH) of less than 20 cm. Although juvenile trees provide enough nutrients, they generally do not provide enough clearance in the phloem for larvae to develop. Larger trees, with a DBH between 20 and 38 cm, constitute the second class of vigorous trees. Vigorous trees are large enough to house egg galleries and offer a suitable nutrient source. However, they have the strongest defenses against beetle attack. As an adult tree ages, the crown remains relatively constant while the diameter of the tree trunk increases. The defenses employed against attack are then spread over a greater surface area, reducing their effectiveness (Amman and Cole, 1983). This suggests a third class of susceptible trees, older with weaker defenses than the vigorous trees. This class also accounts for trees suffering from drought, crowding, and other stresses. The defenses of this third class of trees are more easily overcome by the mountain pine beetle and still offer sufficient nutrients for beetle development, although, generally, brood production will be less because phloem is spread across a larger surface.

The objective of this model is to describe the evolution of spatial patterns of beetle attacks in both endemic and epidemic states, as well as to predict the spread of the beetle population. The analysis will analytically demonstrate the potential for this model to emulate observed patterns of forest disturbance. The final model incorporates the basic three-tier demography of susceptible pine populations. The juvenile cohort increases by contributions from the two mature classes of trees via propagation and decreases due to maturation into the vigorous cohort. The vigorous cohort, in turn, increases by contributions from the juvenile cohort and decreases through maturation into the adult cohort. This model assumes that there is no death rate in juvenile and vigorous cohorts, independent of the mountain pine beetle. Finally, the adult cohort increases through contributions by the vigorous cohort and decreases through death. This is the simple demography of a healthy lodgepole pine forest. Timber inventory data provide values for the birth, maturation, and death parameters for the healthy forest dynamics. Beetle-caused mortality is represented by the removal of vigorous and adult trees from the forest, making a direct contribution to an additional cohort of infected lodgepole pine trees, named infectives or red tops.

By using data collected from aerial surveys and satellite imagery, the method of estimating functions can return parameter values that fit the model parameters governing attack dynamics to the data. Then the predic-

tive capacity of the model can be tested against a decade of data collected in the Sawtooth National Recreation Area of central Idaho.

DERIVATION OF THE RED TOP MODEL

A disturbance model for lodgepole pine begins by constructing an age-structured model framework for the uninfected lodgepole pine forest. The age classes include a seed base (S_0), seedlings (S_1), and juvenile (J), vigorous (V), and adult (A) trees. Each of these classes subsists on contributions by their subordinate class, and contributes to the successive class in the hierarchy; the exception is the seed base, toward which both classes of reproducing trees (vigorous and adult) contribute. The following equations provide a starting point for this simplified model.

$$S_{0(t+1)} = (1 - s_0) S_{0t} + b_V V_t + b_A A_t \quad (1)$$

$$S_{1(t+1)} = s_0 S_{0t} + (1 - s_1) S_{1t} \quad (2)$$

$$J_{(t+1)} = s_1 S_{1t} + (1 - s_J) J_t \quad (3)$$

$$V_{(t+1)} = s_J J_t + (1 - s_V) V_t \quad (4)$$

$$A_{(t+1)} = s_V V_t + (1 - d) A_t \quad (5)$$

The discrete equations listed in Equations (1) to (5) describe the density of each class in the following time step, based on the current densities as well as fecundity, maturation, and death rates specific to each class. Equation (3), for example, represents the density of juvenile trees in the next time step based on the proportion of seedlings maturing to juveniles (s_1) and the proportion of juveniles that remain juveniles into the next time step ($1 - s_J$). Similarly, s_V is the proportion of vigorous trees that mature into adult trees. The contributions to the seed base are made by vigorous and adult trees, represented by b_V and b_A , respectively. Finally, the adult class is the only class that experiences mortality from aging. Because there is no age class to which the last class can transition, d represents the natural mortality in the adult class.

Availability of direct sunlight is important in the establishment of lodgepole pine stands. Shade intolerance makes it difficult for successive generations to mature beneath the canopy of adult lodgepole pines. In the absence of disturbance, the lodgepole pines are eventually replaced by more shade-tolerant species of conifers. The pressure caused by shading from larger trees can be modeled by a response function that retards the growth of one class of tree under the combined pressure of larger trees. Each understory class of

lodgepole pine tree experiences shading from larger trees; the smaller the tree, the greater the shading. To address shading in the model, we look for response functions that are functions of the densities of all larger trees. In the case of the seedling class, the function $g_s(J_t, V_t, A_t) = \gamma_s \left(\frac{(J_t + V_t + A_t)}{J_t + V_t + A_t + \beta_s} \right)$ has these properties, where β_s is a parameter that relates the percent of canopy closure in terms of tree density, and γ_s is tuned to the sensitivity of the seedling class to the effects of shading. Similarly, $g_j(V_t, A_t) = \gamma_j \left(\frac{(V_t + A_t)}{(V_t + A_t) + \beta_j} \right)$ and $g_v(A_t) = \gamma_v \left(\frac{(A_t)}{(A_t) + \beta_v} \right)$ are response functions modeling the shading experienced by the juvenile and vigorous classes, respectively.

Including these response functions yields the following system of equations:

$$S_{0(t+1)} = (1 - s_0) S_{0t} + b_v V_t + b_A A_t \quad (6)$$

$$S_{1(t+1)} = s_0 S_{0t} + (1 - s_1) S_{1t} - \gamma_s \left(\frac{J_t + V_t + A_t}{(J_t + V_t + A_t) + \beta_s} \right) S_{1t} \quad (7)$$

$$J_{(t+1)} = s_1 S_{1t} + (1 - s_j) J_t - \gamma_j \left(\frac{V_t + A_t}{(V_t + A_t) + \beta_j} \right) J_t \quad (8)$$

$$V_{(t+1)} = s_j J_t + (1 - s_v) V_t - \gamma_v \left(\frac{A_t}{A_t + \beta_v} \right) V_t \quad (9)$$

$$A_{(t+1)} = s_v V_t + (1 - d) A_t. \quad (10)$$

In the western North American lodgepole pine forests, the seedling class experiences shading by virtually any density of larger trees, which in the model implies that β_s is small. The remaining classes of larger trees are hardly affected by shading once they have passed the seedling class, $\gamma_v = \gamma_A \approx 0$. This allows us to approximate the effect of shading on the juvenile class by γ_s . Mountain pine beetle disturbance will not remove the juvenile class. Assuming β_s is small (i.e., seedlings are easily shaded out), the shading further is approximately a constant, γ_s . If we combine the three nonsusceptible classes, adding Equations (6) to (8) to yield a composite nonsusceptible class, $\hat{J}_t = S_{0t} + S_{1t} + J_t$, then we have a simplified equation,

$$\hat{J}_{(t+1)} = (1 - s_j) \hat{J}_t + b_v V_t + b_A A_t - \gamma_s S_{1t} + s_j (S_{0t} + S_{1t}). \quad (11)$$

In the absence of fire, the density of the juvenile class is significant in shading the seedling class. To further simplify, we will assume that the survivorship from the seedling class to the juvenile class, $s_j(S_{0t} + S_{1t})$, is roughly equal to the mortality caused by shading, $\gamma_s S_{1t}$, and therefore the last two terms in Equation (11) may be negated, given:

$$\hat{J}_{(t+1)} = (1 - s_J) \hat{J}_t + b_V V_t + b_A A_t, \quad (12)$$

$$V_{(t+1)} = s_J \hat{J}_t + (1 - s_V) V_t, \quad (13)$$

$$A_{(t+1)} = s_V V_t + (1 - d) A_t. \quad (14)$$

The simplified demographics may be written as the following Leslie matrix equation:

$$\begin{pmatrix} \hat{J}_{t+1} \\ V_{t+1} \\ A_{t+1} \end{pmatrix} = \begin{pmatrix} 1 - s_V & b_V & b_A \\ s_V & 1 - s_A & 0 \\ 0 & s_A & 1 - d \end{pmatrix} \begin{pmatrix} \hat{J}_t \\ V_t \\ A_t \end{pmatrix}.$$

Next we include the beetle's influence on the forest. Berryman *et al.* (1985) observed that the probability of a lodgepole pine tree being killed as a function of beetle attacks per square meter of tree surface fit a sigmoidally shaped curve such as that which results from the Holling III response function, $P(B) = \frac{B^2}{B^2 + a^2}$. This relationship can be read as the probability, P , as a function of the beetle density, B , with a parameter representing the effectiveness of the beetles, a , in attacking lodgepole pine trees. The units of a are beetles per hectare (the more effective the beetles are, the smaller the value of a). From this clue we can arrive at a model that describes the probability of successful attack by the mountain pine beetle as a function of red top density.

We let I_{t+1} represent a new class called infectives. These are the next year's density (in trees per hectare) of infected trees, resulting from beetle attacks, and let S_t be the density of susceptible trees in the current year, t ; then

$$I_{t+1} = P(B) \cdot S_t = \frac{B^2}{B^2 + a^2} S_t. \quad (15)$$

Considering that the beetles attack a tree for the purpose of building egg galleries and thus rearing young, each infected tree can be considered as having a beetle fecundity, f , in units of beetles per tree. Density of beetles is then related to density of infected trees, $B_t = fI_t$.

Substituting this relationship into the response function in Equation (15) gives:

$$I_{t+1} = P(B = f_t I_t) \cdot S_t = \frac{(f_t I_t)^2}{(f_t I_t)^2 + a^2} S_t. \quad (16)$$

This results in an equation relating one year's density of infected trees in terms of the prior year's density of infectives and the density of susceptible trees, effectively removing the density of beetles from the equation.

Then, factoring the fecundity from the response function, we introduce a new parameter, $\alpha = \frac{a}{f}$, with units of trees per hectare,

$$\frac{I_t^2}{I_t^2 + \left(\frac{a_t}{f_t}\right)^2} S_t = \frac{I^2}{I^2 + \alpha_t^2} S_t \quad (17)$$

This new parameter, α , can be interpreted as the beetle fecundity per tree that will result in a 50–50 chance of susceptible trees in an area becoming infected, as illustrated in Fig. 1. This parameter can also be viewed from the perspective of the beetle as a level of the beetles' effectiveness in their effort to attack healthy trees and reproduce.

Because the susceptibility and potential beetle fecundity differ between vigorous and adult lodgepole pine trees, it is useful to consider the source of infected trees coming from two cohorts, $S_t = V_t + A_t$. This necessitates the assignment of distinct α^2 parameters to each susceptible class. The contribution to the infectives class in the following year is the sum of the trees killed by the mountain pine beetle from the two susceptible classes.

FIG. 1 Low densities of beetles are not able to overcome the defenses of the tree. Once enough beetles have arrived at the tree, the beetle in turn releases a nonaggregating pheromone, which repels beetles from the tree and forces them to search out another victim. The a value equates to the point at which 50% of the susceptible trees can be successfully attacked.

Using this relationship between the population of infected trees and the next year's population of newly emergent beetles, substituting these values into the probability function for a successful attack as a function of beetle density, and multiplying by the population of the two cohorts that are susceptible to beetle attack (V_t and A_t), we arrive at an equation for the next year's infectives in terms of the current year's density of infectives and susceptible trees

$$I_{t+1} = \frac{I_t^2}{I_t^2 + \alpha_{V,t}^2} V_t + \frac{I_t^2}{I_t^2 + \alpha_{A,t}^2} A_t. \quad (18)$$

The simplified demographics may be written as the following Leslie matrix equation (Equation 19). We can now assemble a complete model for mountain pine beetle disturbance in lodgepole pine forest. The final step is including the mortality exerted on the forest by the beetles. In our model, this is accomplished by subtracting a portion of the trees from the overall forest demographic model and adding them to the infectives cohort.

$$\begin{pmatrix} \hat{J}_{t+1} \\ V_{t+1} \\ A_{t+1} \end{pmatrix} = \begin{pmatrix} 1 - s_V & b_V & b_A \\ s_V & 1 - s_A & 0 \\ 0 & s_A & 1 - d \end{pmatrix} \begin{pmatrix} \hat{J}_t \\ V_t \\ A_t \end{pmatrix} - \begin{pmatrix} 0 \\ \frac{I_t^2}{I_t^2 + \alpha_{V,t}^2} V_t \\ \frac{I_t^2}{I_t^2 + \alpha_{A,t}^2} A_t \end{pmatrix}, \quad (19)$$

$$I_{t+1} = \frac{I_t^2}{I_t^2 + \alpha_{V,t}^2} V_t + \frac{I_t^2}{I_t^2 + \alpha_{A,t}^2} A_t. \quad (20)$$

The model presented in Equations (19) and (20) describes the growth and mortality of the lodgepole pine forest under pressure from a local beetle population, neglecting the effects of dispersal to and from adjacent patches of forest, and assuming that shading mortality on seedlings roughly balances their rate of survivorship.

Dynamic Analysis Without Dispersal

If we consider the behavior of this model locally, say in a small stand of trees within the forest, and make some simplifying assumptions, we recognize compelling behavior even at this point in the model's development. We will show that the model without dispersal exhibits a lack of an endemic state of infected trees but, instead, describes an increase in susceptibility from encroaching infected trees that leads to periodic waves of beetle outbreak.

This suggests that there is no endemic state per se but that outbreaks elsewhere in the forest serve as a population reservoir.

For simplicity and to clarify model behavior, we will assume that the adult and vigorous classes may be combined into one susceptible class (i.e., $V_t + A_t = S_t$). This is often the case in western North America, where fire management has compromised the age structure of forests, leaving a homogeneous stand of lodgepole pine and completely removing one class of trees from the equation. With this in mind, the system of Equations (19) and (20) can be written as

$$\begin{pmatrix} \hat{J}_{t+1} \\ S_{t+1} \end{pmatrix} = \begin{pmatrix} 1-s & b \\ s & 1-d \end{pmatrix} \begin{pmatrix} \hat{J}_t \\ S_t \end{pmatrix} - \begin{pmatrix} 0 \\ \frac{I_t^2 S_t}{I_t^2 + \alpha_t^2} \end{pmatrix}, \quad (21)$$

$$I_{t+1} = \frac{I_t^2}{I_t^2 + \alpha_t^2} S_t. \quad (22)$$

Let us examine how the model behaves locally in a relatively healthy stand of trees. Considering the density of infectives to be very low in the area under consideration, $I_t \ll 1$, implies $\frac{I_t^2}{I_t^2 + \alpha_t^2} \ll I_t$. This means that, at low densities of infectives, the loss of susceptible trees to infectives is negligible and the model with three classes, Equations (21) and (22), decouples into a matrix model of healthy forest and an equation modeling the change in density of the infectives.

The eigenvalues of the Leslie matrix $\begin{pmatrix} 1-s & b \\ s & 1-d \end{pmatrix}$ are

$$\lambda_{1,2} = 1 - \frac{1}{2} \left(s + d \pm (s-d) \sqrt{1 + \frac{4sb}{s-d^2}} \right).$$

The long-term behavior of the healthy forest is governed by the dominant eigenvalue, $\lambda_{\max}$, which can be interpreted as the intrinsic growth rate of the population. At least one eigenvalue is greater than one for $b > d$, and we observe that the determinant of the matrix in Equation (21) is $\lambda_1 \lambda_2 = 1 - d - s + sd - bs > 0$ for sufficiently small s and d , implying that both λ_1 and λ_2 must be positive. We can therefore conclude $\lambda_{\max} > 1$, which means the densities of both forest classes are increasing. If we consider S_0 to be the density of susceptible trees at time zero, then $S_t \approx \lambda_{\max}^t S_0$ describes the increase in density of the susceptible trees over time. For small numbers of I_t , the decoupled infective class is described by

$$I_{t+1} = \frac{I_t^2}{I_t^2 + \alpha^2} \lambda_{\max}^t S_0. \quad (23)$$

We find a fixed point analysis of Equation (23) very helpful in explaining the local dynamics of forest disturbance and recovery. The fixed points for low densities in the decoupled equation are found by setting $I_{t+1} = I_t$ and the associated stability of these particular points indicates trends for densities of infectives (e.g., increasing or decreasing). Fig. 2 is a bifurcation plot of the fixed points of Equation (23) as the density of susceptible trees, $S_t = \lambda_{\max}^t S_0$, increases. We see that for very low densities of S_t , there is only one fixed point. This fixed point is at $I_t = 0$ and is termed the “trivial fixed point,” because an absence of beetles in the current time step implies that no beetles will be in the next time step. The trivial fixed point is attracting and is illustrated in Fig. 2 by the horizontal line of fixed points existing for infectives density of zero, $I_t = 0$. The local density of infectives appears to break away from the trivial fixed point through contributions from neighboring regions, but these small perturbations are quickly forced back to the extinction point.

FIG. 2 A bifurcation diagram of the emerging fixed points illustrates how, for low densities of infected trees, the trivial fixed point (at $I_t = 0$) pulls the densities of these infected trees down to extinction. But as the susceptible tree density increases, the repelling fixed point moves closer to the trivial attracting fixed point. When by chance the density of infected trees shoots above this lowered threshold (through contributions by neighboring areas), the density of infected trees is thrust away from the low-density levels, permitting an outbreak to occur.

While the density of infectives is at this benign level, the healthy forest grows in accordance with the decoupled Leslie matrix model. This unbridled growth of the susceptible class eventually reaches a density level where a nontrivial fixed point emerges. This nontrivial fixed point first comes into existence through a saddle-node bifurcation when $\lambda_{\max}^t S_0 = 4\alpha$. In Fig. 2, this appears at the point marked with an asterisk. The fixed point is found by setting $I_{t+1} = I_t$ and then through simple algebraic manipulation and use of the quadratic formula. When $S_0 > \frac{4\alpha}{\lambda_{\max}^t}$, this nontrivial fixed point at $I_t = \frac{\lambda_{\max}^t S_t}{2}$ bifurcates, or “splits” into two distinct fixed points, one attracting and the other repelling, represented by the solid and dotted curves, respectively. We ignore the nontrivial attracting fixed point because it violates the earlier assumption that I_t is small. It is the fixed point at the lower density that is of interest to us (the repelling point closer to the trivial fixed point). This fixed point near the extinction level of infectives is given by $I_t = \frac{\lambda_{\max}^t S_t - \sqrt{(\lambda_{\max}^t S_0)^2 - 4\alpha^2}}{2}$. This repelling fixed point pushes the density of infectives toward the extinction level. The model, therefore, predicts extinction for the infectives at this low level but, remembering that we are examining the behavior in a small stand of the forest, there are in fact contributions of infectives from the surrounding forest that continuously jump start the population. As time passes and the forest grows, the repelling fixed point moves closer and closer to the trivial fixed point. Eventually, the repelling fixed point moves so close to the trivial fixed point that even a small contribution to the infectives class from neighboring areas of the forest elevates the density of infectives above this repelling fixed point, at which time an epidemic occurs as the same repelling fixed point forces densities of infectives to increase. This leads to positive exponential growth and, consequently, the onset of an outbreak (Berryman *et al.*, 1984).

The picture that emerges is that of statistically periodic outbreaks. Starting with no red top trees, the forest grows increasingly vulnerable to ever-smaller invasions of mountain pine beetles. Eventually, some small external input of mountain pine beetles pushes the dynamics over the threshold and into an outbreak, which removes most of the susceptible class. A period of time must pass as juvenile trees grow to become susceptibles and eventually the cycle repeats. This explanation of the dynamics on a local scale depends on re-invasion from external sources of mountain pine beetles, as opposed to the existence of a stable, endemic population (which the model suggests does not exist). To complete this picture of periodic outbreak, we must explicitly include the effects of dispersal in space.

Including Dispersal in the Red Top Model

Thus far we have not addressed the spatial component of the beetle–forest interaction. But before we begin, let us consider two sensible options for investigating the spatial behavior of the beetle epidemic: one and two dimensions. Although it is obvious that the real world impact of the beetle outbreak can be protracted from a two-dimensional perspective, there are clear advantages to considering a lower dimensional interpretation of the phenomena (noting that a third dimension, height, is inconsequential compared to the landscape scale of the model).

When the region infected is large, as in the case of the Sawtooth National Recreation Area (SNRA), the spread of infected trees is essentially a one-dimensional event. Furthermore, in the particular case of the SNRA, the valley is relatively long and narrow, and patches of infected trees often span a significant breadth of the forest, leaving more or less only one dimension for an advancing infection. Protracting the forest in one dimension also allows for more simplified mathematical analysis, which can be directly applied to the higher order modeling. Stepping up from one dimension to two, we take with us the insights from the one-dimensional model and incorporate them into the two-dimensional model, thus allowing us to better interpret the results.

To this end, we now consider the beetles emerging from a host tree. To model the probability of a beetle at a point source (i.e., an infected tree) dispersing to a surrounding tree, we introduce a dispersal kernel. Neubert *et al.* (1995) propose a number of dispersal kernels that can describe dispersal behavior in one dimension. These kernels can be derived a priori from differential equations. If we assume that in a given year there is a density of flying beetles that are seeking a host tree and that these flying beetles find a host tree at some constant rate, we can model this by a system of equations that represent the density of dispersing beetles, $u(x, t)$, and the density of beetles that have settled on a tree, $v(x, t)$:

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} - \mu u. \quad (24)$$

$$\frac{\partial v}{\partial t} = \mu u. \quad (25)$$

where D is the diffusion parameter governing the rate at which beetles search out a host tree and μ is the constant rate at which beetles settle on a tree. If we assume that the dispersing beetles originate at a single point source (i.e., an infected tree) and consider a sufficiently long period over which all the dispersing beetles can find host trees, we can

define the dispersal kernel to be the final distribution of settled beetles, that is to say, the distribution of settled beetles as time goes to infinity (i.e., $\lim_{t \rightarrow \infty} v(x, t) = k(x)$).

Solving for the kernel under these assumptions results in the Laplacian distribution (or double exponential):

$$k(x) = \frac{1}{\sqrt{4\delta}} \exp^{-\sqrt{x^2/\delta}}. \quad (26)$$

Here we have made the substitution $\delta = D/\mu$, which has the virtue of representing the mean dispersal distance as the single parameter, δ .

This kernel has a “tent” shape, with a maximum at the origin, sloping down exponentially as the distance from the origin increases. The solution to the two-dimensional diffusion equation with a constant failure rate takes the form of ratios of modified Bessel functions, which have singularities at the origin. For the purposes of simplicity in our two-dimensional model, we employ a function that is analogous to the one-dimensional kernel:

$$k(\bar{x}) = \frac{1}{2\pi\delta^2} \exp\left(\frac{-\sqrt{(x_1^2 + x_2^2)}}{\delta}\right) \quad (27)$$

where a point in space is represented by the ordered pair $\bar{x} = (x_1, x_2)$. The behavior of this dispersal model is very similar to the correct, more complicated solution with Bessel functions. However, the advantage is that the simplified dispersal model is much easier to parameterize and understand in a biological context, not to mention removing the troublesome singularity. In the two-dimensional dispersal model, the mean dispersal distance is 2δ , and the units of the dispersal kernel are inverse hectares, $\frac{1}{ha}$.

Neubert *et al.* (1995) go on to describe how the convolution of the dispersal kernel with the initial population density function results in the population of organisms dispersed over space. One can think of the number of individuals located in a small interval dispersing according to the distribution kernel; thus, the probability that the individuals will be at $\bar{y} = (y_1, y_2)$ in the next time step, given that they were originally at $\bar{x} = (x_1, x_2)$ is $I(\bar{x}, 0) K(\bar{x} - \bar{y}) d\bar{y}$, where the dispersal kernel is shifted so that it is centered at the original locus of individuals, $\bar{x}$. The total population after a time step would then be the sum over all such infinitesimal intervals containing populations. This leads us to the convolution, I^* , of two functions I and K as defined by

$$I^* = (I * K)(\bar{x}) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} I(\bar{y}) K(\bar{x} - \bar{y}) d\bar{y}. \quad (28)$$

This is the concept behind the use of convolutions of dispersal kernels with spatial population density functions. In short, I^* can be interpreted as the population density of infected trees after dispersing in accordance with the probability density function K . So the final model is

$$\begin{pmatrix} \hat{J}_{t+1} \\ V_{t+1} \\ A_{t+1} \end{pmatrix} = \begin{pmatrix} 1 - s_V & b_V & b_A \\ s_V & 1 - s_A & 0 \\ 0 & s_A & 1 - d \end{pmatrix} \begin{pmatrix} \hat{J}_t \\ V_t \\ A_t \end{pmatrix} - \begin{pmatrix} 0 \\ \frac{I^{*2} V_t}{I^{*2} + \alpha_V^2} \\ \frac{I^{*2} A_t}{I^{*2} + \alpha_A^2} \end{pmatrix} \quad (29)$$

$$I_{t+1} = \frac{I^{*2}}{I^{*2} + \alpha_V^2} V_t + \frac{I^{*2}}{I^{*2} + \alpha_A^2} A_t, \quad (30)$$

where I^* is given by the convolution in Equation (28). Equations (29) and (30) form a stage-structured model of integrodifference equations, including a minimally complex description of forest recruitment, aging, and growth, with a realistic model for mountain pine beetle attack and dispersal on a stand scale (i.e., a scale larger than individual trees which allows for units of space to be comprised of similar vegetation). However, to compare the model to the real-world phenomenon of mountain pine beetle outbreaks, we need to find suitable values for the parameters in the model as they pertain to the epidemic in the SNRA. Only then can we begin to simulate and interpret the results of the model as compared to observations.

Parameter Estimation Based on Aerial Damage Survey Data

Nonlinear parameter estimation is recognized to be at best a challenging aspect of modeling real world phenomena. In the case of the Red Top Model, we are faced with the problem of fitting parameters to the nonlinear response functions used to model the growth of infected trees in the forest. The task is difficult because the response variable is defined on a stand scale, as opposed to individuals. This also involves the response of tree-stands to populations of dispersing mountain pine beetles [through I^* in Equation (28)], and these populations are impossible to measure directly either under the bark or in flight.

The data used to estimate parameters for the model are from the Aerial Damage Survey (ADS), collected from flights over the SNRA providing 30 m by 30 m resolution. Numbers of infected trees are detailed

on a map and then the data are converted to densities on a GIS cover map in ARCVIEW. Fig. 3 is a map of the SNRA generated from ADS data obtained in 1991.

The accuracy of this data collection is inherently limited. It is very difficult to pick out individual infected trees from a dense stand of forest while flying in an airplane. Similarly, clumps of infectives might not be properly articulated. The cover map, which describes the distribution of trees, both healthy and infectives, is mostly homogeneous, also a shortcoming. There are patches of sagebrush, grass, and nonhost conifers throughout the SNRA, interspersed with the lodgepole pine forest.

Because there are many years of spatial data for the spread of infected trees around the forest, one possible approach would be to find a least-squares or maximum-likelihood solution to the problem. But aside from the computational intensity of a multidimensional parameter search, there is also the risk of arriving at a suboptimal solution. Alternatively, we can employ the method of estimating functions. The method used here is an

FIG. 3 A map of the Sawtooth National Recreation Area generated from aerial damage survey data taken in 1991. Each cell in the map represents a 30 m by 30 m square of the SNRA. The cell is classified as lodgepole pine or nonlodgepole pine forest. Over this forest cover map is superimposed a map of infectives, where each pixel contains the density of red top trees. In this map, the infectives were scaled to simply reflect presence or absence in a cell. The white represents the location of susceptible lodgepole pine trees and the black is the presence of infectives.

adaptation of the method described by Lele *et al.* (1998), who also used estimating functions to arrive at dispersal parameter values based on gypsy moth trap data.

The following is a brief overview of the method of estimating functions used to approximate parameter values for spatially related data. We begin by assuming that the data are in a spatial array where each element contains a density of individuals in that cell, i.e., $I_{i,j,t}$, where i and j are spatial indices and t is the time index. We construct the estimating function from the response function in Equation (30) containing the parameters to fit, δ and α^2 . We assume that there is one cohort contributing to the infectives class and algebraically manipulate the equation

$$I_{i,j,t+1} = \frac{I_{i,j,t}^2}{I_{i,j,t}^2 + \alpha^2} S_{i,j,t} \quad (31)$$

to read

$$g(I_{i,j,t}, S_{i,j,t}, \alpha^2, \delta) = I_{i,j,t+1} (I_{i,j,t}^2 + \alpha^2) - S_{i,j,t} I_{i,j,t}^2 = 0. \quad (32)$$

The result in Equation (32) is an estimating function that relates the parameters to the data, with expected value zero. Since we have two parameters to estimate, we need two equations. We want to combine them in a useful way that allows us to solve for parameters α^2 and δ . According to Lele *et al.* (1998), a near optimal combination of these functions can be found by introducing weighting functions that minimize the sensitivity of Equation (32) to the data. These are formed by taking the derivative of the estimating functions with respect to the parameter of interest (i.e., $w_{\alpha^2} = \frac{dg}{d\alpha^2}$ and $w_{\delta} = \frac{dg}{d\delta}$). The resulting system of equations is

$$\sum_t \sum_{i,j}^{n,m} W_{\alpha^2} [g(I_{i,j,t}, S_{i,j,t}, \alpha^2, \delta)] = H(\delta, \alpha^2) = 0, \quad (33)$$

and

$$\sum_t \sum_{i,j}^{n,m} W_{\delta} [g(I_{i,j,t}, S_{i,j,t}, \alpha^2, \delta)] = G(\delta, \alpha^2) = 0. \quad (34)$$

Now by stepping through an interval that is assumed to contain the best parameter value for δ and choosing candidates, $\hat{\delta}$, we can solve Equations (33) and (34) for the respective α^2 in terms of $\hat{\delta}$. This results in candidates for a solution of the form $(\hat{\alpha}^2, \hat{\delta})$. The ordered pairs represent possible parameter solutions constituting a one-dimensional curve. Since the candidates in turn need to be the zeros of the estimating function, $\sum g(I_p, S_p, \alpha^2, \delta) = 0$, we simply search for the root of this curve to arrive at the estimate for the parameters. Computationally, this one-dimensional search for optima is far less intensive than a search through two-dimensional parameter space,

and all possible optima can be found and evaluated. Moreover, a one-dimensional root solving operation can be made arbitrarily accurate.

Because of heterogeneity in the SNRA in the form of water bodies, agricultural land, and a variety of vegetation classes, there are areas with zero host densities. To accommodate this patchiness, searches were carried out on a variety of subregions of varying sizes within the SNRA. There are also demographic differences between these subregions, such as stand age and density. The variability in demographics and composition results in differing parameter values throughout the SNRA. The parameter values listed in Table 1 are the averages of results of the estimating function procedure found on subregions of the forest using the two-dimensional Laplace kernel given in Equation (27).

Analysis with Dispersal in the One-Dimension Case

The spatial aspect of the model prompts the need to consider scale in the model. To begin with, let us consider a one-dimensional representation of the forest. It seems reasonable to assume that, for a sufficiently small forest, the spatial dynamics would not be evident, since it would emulate the non-spatial model. Consequently, we might think that there is a threshold area above which allows additional dynamics that result from dispersal. We therefore can postulate that although beetles cannot persist locally after killing all of the susceptible trees in a small area, a large enough forest might allow for beetles to find host trees in regenerated regions of the forest. In this manner, the beetles could persist in the forest despite decimating

TABLE 1 Average Values Resulting from the Estimating Function Procedure Applied to Patches of the Sawtooth National Recreation Area*

Year	δ_{ave}	α_{ave}^2
1990	5.9786	0.00008101
1991	4.6347	0.00581680
1993	4.6169	0.00581729
1995	4.8911	0.00537288
1997	4.9463	0.00537279
1998	5.2784	0.00469327
2000	5.2650	0.00469324
2001	5.3138	0.00452175

*Each year yields several solutions for δ and α^2 depending on the patch of forest over which the estimating function procedure is applied. For the years 1992, 1994, 1996, and 1999, the estimating function procedure did not converge to a set of solutions.

local populations. In light of this hypothesis, we consider the model's behavior in terms of the persistence of infectives throughout varying spatial scales. We run a sequence of 10 simulations at each forest size ranging in length from 1 km to 100 km at intervals of 5 km, fixing forest demographic parameters ($b = s = 0.06$) but selecting α^2 according to a uniform distribution from 0.004 to 0.005 for each year. A plot of the average number of years that the infectives class persists at each simulated forest size is shown in Fig. 4.

We see that for simulations with a forest length beyond this threshold near 40 km, there is qualitatively different behavior because of the spatial component of the model. For sufficiently large forests, we see the formation of waves of infectives that sweep back and forth across the simulation space as the forest regenerates. Fig. 5 illustrates a series of images taken at 10-year intervals as waves of infected trees swept across a simulation space of 50 km. Reading the frames from left to right and top to bottom, we can

FIG. 4 Graph of the average persistence of the infectives class in one-dimensional simulations, using the one-dimensional Laplace kernel from Equation (26). Parameter values are α^2 varying uniformly between 0.004 and 0.005, the mean dispersal distance $\delta = 200$ meters, and fixed forest demographic parameters, $b = s = 0.06$, and $d = 0$. Observe that for simulated forest lengths greater than 40 km the persistence of infectives increases markedly. It is at this point that the spatial aspect of the model allows for wave formation that does not dissipate, increasing the duration of persistence. We observe fluctuations in the duration of persistence for larger forest sizes. This is caused by constructive resonance-like behavior resulting from combinations of particular forest lengths and wave speeds.

FIG. 5 This sequence of frames illustrates the advance of infestation through a forest of healthy trees. Reading left to right and top to bottom are six frames taken at 10-year intervals. This one-dimensional simulation depicts the waves of infected trees (*solid lines*) moving into regenerated stands of vigorous trees (*dashed lines*). As the waves collide they annihilate each other, having exhausted the available supply of susceptible trees. The simulation space is 50 km long and the parameter values are $b = s = 0.06$, $d = 0$, $\delta = 200$ meters, α^2 varies uniformly between 0.004 and 0.005.

see colliding waves of infectives that annihilate one another after exhausting the supply of hosts in the area. Successive waves follow as the forest regenerates, in turn exhausting the population of healthy susceptibles. This observation is highly compatible with the conjecture made during the analysis of the model in the absence of dispersal, where locally the forest regenerates, becoming increasingly susceptible to invasion until an external perturbation catalyzes an outbreak.

Fig. 6 is a time series of the results illustrating the percentage of the forest that is occupied by infective trees compared to the percentage of the forest occupied by susceptible trees. The pulses of infectives follow pulses of sus-

ceptible trees, as predicted earlier. We also see that the model simulated long-term persistence of the infectives within the forest and, over the course of time, the density of infectives varies greatly, demonstrating both endemic and epidemic population levels.

RESULTS OF THE FULLY DEVELOPED MODEL

Using the ADS data that provided parameter estimates, we apply the model to each year of data to predict the subsequent year's distribution of infectives. The coarse nature of the ADS data precludes low densities of infectives from being recognized. To address this, we set a lower threshold to ignore densities of trees that result from the model's smooth dispersal mechanism (the convolution) that are too low to be observed aerially. In Fig. 7 the threshold was set to 10 trees per hectare, because ADS surveyors are expected to note patches at greater than 10 trees per hectare. Using the α_{ave}

FIG. 6 This graph illustrates the cycles of outbreaks, represented by spikes in forest density (*dashed line*) followed by a spike in the infected tree density (*solid line*). This time series reveals the waves of infected trees following regenerated forest densities. In this 50-km-long one-dimensional simulation space, the infectives class persisted over 2000 years before going extinct. The parameter values in the simulation are $b = s = 0.06$, $d = 0$, and $\delta = 200$ meters, and α^2 varies uniformly between 0.004 and 0.005.

FIG. 7 Maps of observed and predicted infected trees in the Sawtooth National Recreation Area. The white regions represent the location of healthy lodgepole pine trees. The black regions represent the presence of infected lodgepole pines at densities above 10 trees per hectare. The infected trees' distribution is predicted by the two-dimensional model based on the previous year's observed distribution. Each prediction employs the respective parameter values for α^2 and δ listed in Table 1.

and δ_{ave} parameter values resulting from the estimating function procedure and applying the model to the entire SNRA forest yields predictions for infectives.

To gain another perspective on the predictions of the model, we compare year-to-year predictions of the proportion of the SNRA infected with the aerial damage survey data, as illustrated in Fig. 3. The ratio of cells that contain infectives over the total number of cells in the cover map that contain susceptible trees gives the percentage of the forest area that is infected with red tops. Fig. 8 is a graph of observed and predicted percentage of forest infected. Years of data that did not yield parameter values for α^2 and δ are omitted. Although this graph does not allow for examining the spatial distribution of the epidemic, it does provide a way of assessing the severity of the outbreak, as well as illustrating how well the model follows the outbreak's history.

FIG. 8 Graph of the fraction of the total forested area of the Sawtooth National Recreation Area observed to contain densities of infectives (represented by o) and similarly the fraction of the forest predicted by the two-dimensional model using parameter values listed in Table 1 (represented by *). Predicted densities below 10 trees per hectare are ignored because it is believed that similar densities would not have been recorded by the aerial damage survey crew.

DISCUSSION AND CONCLUSION

In the preceding sections we used a variety of techniques and concepts to arrive at a model that, while relatively simple, still encapsulates the critical spatial and temporal mechanisms linking the mountain pine beetle distribution and forest recovery in space and time. Beginning with an understanding of bark beetle phenology and the attack dynamics observed in the forest, we proposed a relationship between the number of beetles and the number of infected trees in the forest. We also consider the probability of successful attack based on the density of infected trees in an area and use this to justify a Holling III response function that exhibited the desired Allee effect. Incorporating the notion of a dispersal kernel and a convolution to represent the spatial impact of current red tops on next year's fresh attacks, we arrived at a plausible heuristic for the spread of the mountain pine beetle through the lodgepole pine forest. These notions of density dependent attack dynamics and beetle dispersal in conjunction with a Leslie matrix describing the changing demographics of the forest form the integrodifference equations for the red top model.

Once we derived the red top model, we applied the theory of estimating functions to aerial damage survey data to find parameter values for beetle effectiveness and mean dispersal range. A range of parameter values resulted from this method, which is consistent with the understanding that beetle effectiveness is somehow temperature dependent, and in turn suggests that on a year-to-year basis the effectiveness of beetle attack on the lodgepole pine forest would fluctuate. There are clearly shortcomings of the data used to estimate parameter values. We were not able to ascertain densities of susceptible trees or infected trees and, as a consequence, we assumed a homogeneous standing timber and a homogeneous ratio of infected to susceptible trees in areas that contained infected trees. This is clearly a gross assumption and one that might be remedied by more accurate data. There are also years for which the estimating function procedure did not produce estimates for the parameters under investigation. This may be a consequence of too little beetle activity during those years or simply that the pattern of behavior did not lend itself to a solution.

Once we discovered what seemed to be reasonable parameter values to use in the model, we could investigate the behavior of the model and compare it to observed phenomena in the forest. We find that for small forest regions the model does not predict a nonzero stable equilibrium for the red top population, meaning that locally the forest cannot sustain an endemic population of mountain pine beetles. However, for a sufficiently large forested area, the reinvasion of beetles locally is facilitated by their presence

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in high densities elsewhere in the forest as waves of red tops move through susceptible stands of forest. We also observe that, just as in the real world situation, the size of the simulated forest plays a critical role in the persistence of the mountain pine beetle and forests that are too small to allow for regeneration after beetle attacks cannot sustain an endemic beetle population. Multiple simulations investigating persistence of the beetle population in a one-dimension forest found that, for an adequately sized simulation forest, the population of infected trees could persist for thousands of years. The effect of mountain pine beetle disturbance is to periodically reinfest forests with too many susceptible mature trees, removing this class and moving on. From the standpoint of our model, it seems quite reasonable that mountain pine beetle and lodgepole pine have co-adapted to maintain a dynamic self-regulation on large enough landscape scales.

In the case of the pine forests of western North America, in particular the SNRA, the mountain pine beetle has been presented with an undisturbed, contiguous, and mature forest structure that the model demonstrates is ripe for infestation. The advance of beetle attack is not mitigated by patches of previously disturbed forest regenerating from fire. Instead, crowding of susceptible trees has decreased the trees' defensive mechanisms and a sequence of unusually warm years has bolstered the beetle population above the unstable threshold described by the model. This eruptive outbreak observed in the SNRA is observed in the two-dimensional red top model.

Insect disturbance, as our model suggests, is important in maintaining a diverse age structure for lodgepole pine. Left to its own devices, lodgepole would develop into crowded and unhealthy forests of over-mature trees. With disturbances such as mountain pine beetles a certain homeostasis can be maintained, at least on sufficiently large spatial scales. As our model illustrates, insect disturbances can move at a self-limiting pace, balancing the rate of forest regeneration. Like fire (with which mountain pine beetle reforestation is associated), mountain pine beetle disturbance must be viewed as a normal and healthy part of ecosystem function on a sufficiently large scale. Our work helps establish on what scales, both in time and space, an insect disturbance such as that caused by mountain pine beetles can be expected to serve as a useful and normative disturbance.

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