The Red Top Model: A Landscape-Scale Integrodifference Equation Model of the Mountain Pine Beetle-Lodgepole Pine Forest Interaction

Justin Heavilin
Utah State University

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THE RED TOP MODEL
A LANDSCAPE SCALE INTEGRODIFFERENCE EQUATION MODEL
OF THE MOUNTAIN PINE BEETLE- LODGEPOLE PINE
FOREST INTERACTION

by

Justin Heavilin

A dissertation submitted in partial fulfillment
of the requirements for the degree
of
DOCTOR OF PHILOSOPHY
in
Mathematical Sciences

UTAH STATE UNIVERSITY
Logan, Utah
2007
ABSTRACT

The Red Top Model:
A Landscape-Scale Integrodifference Equation Model of the Mountain Pine Beetle-Lodgepole Pine Forest Interaction

by

Justin Heavilin, Doctor of Philosophy
Utah State University, 2007

Major Professor: Dr. James Powell
Department: Mathematics and Statistics

Under normative conditions the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) has played a regulating role in healthy lodgepole pine (*Pinus contorta*) forests. However, recently eruptive outbreaks that result from large pine beetle populations have destroyed vast tracts of valuable forest. The outbreaks in North America have received a great deal of attention from both the timber industry and government agencies as well as biologists and ecologists.

In this dissertation we develop a landscape-scaled integrodifference equation model describing the mountain pine beetle and its effect on a lodgepole pine forest. The model is built upon a stage-structured model of a healthy lodgepole pine forest with the addition of beetle pressure in the form of an infected tree class. These infected trees are produced by successful beetle attack, modelled by response functions. Different response functions reflect different probabilities for various densities. This feature of the model allows us to test hypotheses regarding density-dependent beetle attacks.

To capture the spatial aspect of beetle dispersal from infected trees we employ dispersal kernels. These provide a probabilistic model for finding given beetle densities at some distance from infected trees. Just as varied response functions model different attack dynamics, the choice of kernel can model different dispersal behavior. The modular nature of the Red Top Model yields multiple model
candidates. These models allow discrimination between broad possibilities at the landscape scale: whether or not beetles are subject to a threshold effect at the landscape scale and whether or not host selection is random or directed. We fit the model using estimating functions to two distinct types of data: aerial damage survey data and remote sensing imagery. Having constructed multiple models, we introduce a novel model selection methodology for spatial models based on facial recognition technology.

Because the regions and years of aerial damage survey and remote sensing data in the Sawtooth National Recreation Area overlap, we can compare the results from data sets to address the question of whether remote sensing data actually provides insight to the system that coarser scale but less expensive and more readily available aerial damage survey data does not.
ACKNOWLEDGMENTS

I would like to acknowledge Linda Skabelund, Nancy Smart and the cast of professionals who keep the mathematics department running smoothly. Also to my advisor, Dr. James Powell, for spirited discussions on matters ranging from the tangential to the orthogonal, for advice on teaching and research, for keeping me between the ditches and kicking open some doors. I would also like to acknowledge Dr. Joe Koebbe, who has always demonstrated concern and regard for graduate students and acted as a reliable mediator, as well as providing advice on bird hunting. Dr. Jesse Logan needs to be thanked for his general enthusiasm coupled with the experience of a career field scientist, his inspiration as a lifelong outdoorsman and advocate of environmental issues. I thank Dr. James Haefner for his dedication to excellence as a researcher as well as a mentor, and Dr. Brynja Kohler for her assistance in the final stages of this project. Finally, a special thanks to Leslie Brown for her willingness to help me long after her formal commitment to the project had expired.

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Justin Heavilin
PREFACE

My work with the mountain pine beetle in lodgepole pine forests began with fieldwork in the Sawtooth National Recreation Area (SNRA) of central Idaho. It is a beautiful valley framed by rugged peaks and scattered with mountain lakes. It was here that I saw firsthand the impact of the mountain pine beetle. Over the course of three summers I saw the epidemic spread with the appearance of rust colored trees throughout the valley in ever increasing numbers. It is during this time that I had the chance to cut my teeth as a field technician, hanging cages on infected lodgepole pine to monitor emergence of beetles later in the fall, counting beetles in funnel traps, and logging the daily attacks on selected trees.

I believe that the opportunity to perform this sort of work in association with the development of an ecological model is very valuable and allows for insight into the system that can not be gained by simply reading the published literature. Work in interdisciplinary mathematics requires grounding in more than just the associated applied mathematical and statistical techniques. It requires an investment in the context to which the mathematics are applied. I am very grateful to have had the opportunity to address both of these during my PhD program.
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CHAPTER 1
INTRODUCTION

Conservative estimates claim there are over 350,000 species of beetles; over twenty percent of the species on Earth are beetles. There are hundreds of species of bark beetles in America and among the most environmentally destructive is the mountain pine beetle (MPB, *Dendroctonus ponderosae Hopkins*) (Amman, 1978; Berryman et al., 1989). This beetle has carved out an impressive niche in the lodgepole pine forest, evolving a complicated method of coordinated attack on pine trees. Attack coordination necessitates forest-wide synchronized beetle development in egg galleries within host trees (Amman and Cole, 1983), pheromone communication during simultaneous dispersal from host trees and attack on vigorous pines (Raffa and Berryman, 1983; Berryman et al., 1989; Biesinger et al., 2000; Powell et al., 2000).

These adaptations have allowed the mountain pine beetle to endure for centuries as a regulating influence in the forest. Beetles seek out trees suffering from lightning strikes, fire, drought or other stressors, and establishes egg galleries, killing the host tree. Under normal forest conditions this has a stabilizing effect, culling the forest of weakened or damaged trees (Samman and Logan, 2000). However, in recent years the mountain pine beetle has changed from playing the role of regulator to the role of predator, attacking healthy trees en masse as epidemic beetle population densities expand throughout the forest (Berryman et al., 1985; Powell et al., 1998). Aiding this outbreak are increasing temperatures which allow beetles to expand into regions that were previously too cold (Caroll et al., 2004).

Adult mountain pine beetles emerge from egg galleries, disperse, attack new host trees and establish new egg galleries and then die within a small window of time. Most of this activity occurs within a week or two during the summer (Amman and Cole, 1983). This period of synchronized emergence allows for high densities of beetles to attack pine trees, collectively over-coming the trees defenses. This density dependent attack behavior was characterized by Holling, who popularized the Type II and Type III response functions that commonly used to describe density dependent predation (Holling, 1959). For the rest of the year the subsequent generation of MPB feed on phloem that carries nutrients down the trunk of lodgepole pine host trees. The mountain pine beetle typically completes its life cycle in one year (Logan and Powell, 2001). Systems such as this with distinct
generations lend themselves to discrete time modelling techniques where a prediction for a future time-step is based on information from a the previous time-step.

Additionally the MPB-pine forest system has important spatial structure (Mitchell and Preisler, 1991; Haiganough and Preisler, 1993). Dispersal kernels have been used in other modelling efforts for the spread of invading organisms, and this modelling approach is also well suited to describe mountain pine beetle dispersal.

A spatially continuous dispersal phenomenon coupled with a discrete time event essentially describes the integro-difference equation modeling approach, effectively combining both discrete time and continuous space in one model (Kot, 1992; Kot et al., 1996). Integro-difference equation models have been applied to modeling efforts of disease spread (Medlock and Kot, 2003), dispersal patterns in predator-prey systems (Neubert et al., 1995) and invasion speeds of structured populations (Neubert and Caswell, 2000). Such an integro-difference equation approach is well suited to model the annual dispersal and attack dynamics of the MPB. The Red Top Model presented in this dissertation is built upon a discrete-time, stage-structured model of healthy lodgepole pine forest under pressure from beetle attacks. The stage structuring accounts for various classes of lodgepole pine tree densities. One class of trees being unsuitable hosts for the beetle and therefore not susceptible to beetle attack as well as classes of trees with varying susceptibility to beetle attack. We add another class of trees to include those that have become hosts for beetles, termed infected trees. After a tree is attacked and overcome by beetles the tree dies, the needles of the dying tree change color over the course of a year, leaving the crown a bright rust red color. The Red Top Model is named after these infected trees. The growth of the infected tree class is modelled by response functions describing probabilities of successful attack based on densities of infected trees (and in turn density of beetles). By changing the shape of the response curve we can effectively change the measure of success that beetles have in attacking vigorous lodgepole pine. The Red Top Model also allows for a versatile array of dispersal kernels to be used in modelling the spread of infected trees throughout a forest. Each kernel implies a pattern of dispersal, and by allowing different kernels to be tested against one another we can draw conclusions about the manner of mountain pine beetle dispersal from host trees.

The mountain pine beetle has been under investigation in the Sawtooth National Recreation Area (SNRA) in central Idaho for several decades. There researchers have been observing and recording the spread of an outbreak which has resulted in tree stand mortality exceeding fifty percent in some
areas. Planes piloted over regions of outbreak have regularly recorded locations and densities of trees that had been attacked the previous year, recognizable by their rust red crowns. These are aerial damage survey (ADS) data, and it is these aerial damage surveys that provide input for the Red Top Model in the SNRA.

More recently (e.g. 2001 through 2003) satellite data were acquired which allows for a comparison of model results between two different types of data covering the same region.

The second chapter of this dissertation includes a detailed discussion on the MPB and its attack and dispersal behavior. We also present a complete derivation of the Red Top Model as well as a discussion of the local and landscape scaled dynamics it exhibits. We apply the model to the ADS data by way of an interesting but uncommon parameter fitting method, estimating functions, and discuss these results.

In the third chapter we take advantage of the modular design of the Red Top Model and arrive at four models, each employing subtly different assumptions about the beetle's attack dynamics and dispersal. We then introduce a novel approach to model-selection using facial recognition technology and apply this to the results of four Red Top Models fit to the ADS data in the SNRA. This way we attempt to tease more information from aerial survey data about the beetle-forest interaction such as threshold attack dynamics.

The fourth chapter applies the ideas developed in the previous chapters to remote sensing data from satellites and aerial photography. We discuss the difficulties in processing this data for our purposes. Much of the necessary information for accurate modelling, such as tree stand density and size distributions, can not be easily interpreted from remote sensing data. The results of this effort are then compared to results from ADS data to determine if more data mean clearly better results.
CHAPTER 2
DYNAMICS OF MOUNTAIN PINE BEETLE OUTBREAKS

2.1. Introduction

Native forest insects are the greatest forces of change in forest ecosystems of North America. In aggregate, insect disturbances impact an area that is almost 45 times as great as fire, resulting in an economic impact that is 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 currently undergoing an apparent shift that is 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). A complex of bark beetles are killing ponderosa pine in the southwestern U.S.A. 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,
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, 2003). 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.

The goal of this chapter is to develop a minimally complex model that, on a landscape scale, describes the spatial and temporal interaction between mountain pine beetle and lodgepole pine forest.

We will 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. 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 only release seeds 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. 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 life cycle 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' life cycle. 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 there are enough beetles that 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. Since 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 (Black et al., 2001) since trees that are successfully attacked and killed begin to fade in color the summer following attack, subsequently turning a characteristic bright orange or red.

Tree responses to beetle attack involve both constitutive and induced resin flow. Constitutive resin flow persists within lodgepole, functioning independently of damage by beetles. Induced resin response resulting from beetle attacks reduce beetle survival and reproductive output (Karban and Baldwin, 1997). The induced resin response in lodgepole pine contains toxic, defensive chemicals as well as results in the creation of “pitch tubes” arising at the entrance hole chewed by the attacking beetle. The resin flow induced by attack physically expels the attacking (Amman and Cole, 1983). Not all trees have the same capacity to produce pitch for this defense due to varying size and fitness. In light of this, 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 8 inches (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 8 and 15 inches (20-38 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 demonstrate analytically 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.

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

2.2. 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, with the exception of 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.

\[
\begin{align*}
S_{0(t+1)} &= (1 - s_0) S_{0t} + b_V V_t + b_A A_t \\
S_{1(t+1)} &= s_0 S_{0t} + (1 - s_1) S_{1t} \\
J_{(t+1)} &= s_1 S_{1t} + (1 - s_J) J_t \\
V_{(t+1)} &= s_J J_t + (1 - s_V) V_t \\
A_{(t+1)} &= s_V V_t + (1 - d) A_t 
\end{align*}
\]  

(2.1a) (2.1b) (2.1c) (2.1d) (2.1e)

The discrete equations listed in Eqs. (2.1a) - (2.1e) 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 (2.1c), 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. Since 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 due to shading from larger trees can be modelled by a response function which 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 \(\gamma_S\) is a parameter that relates the percent of canopy closure in terms of tree density, and \(\beta_S\) 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 modelling the shading experienced by the juvenile and vigorous classes, respectively.
Including these response functions yields the following system of equations:

\[ S_{0(t+1)} = (1 - s_0) S_{0t} + b_V V_t + b_A A_t \]  
\[ S_{1(t+1)} = s_0 S_{0t} + (1 - s_1) S_{1t} - \gamma_S \left( \frac{J_t + V_t + A_t}{(J_t + V_t + A_t) + \beta_S} \right) S_{1t} \]  
\[ J_{(t+1)} = s_1 S_{1t} + (1 - s_J) J_t - \gamma_J \left( \frac{V_t + A_t}{(V_t + A_t) + \beta_J} \right) J_t \]  
\[ V_{(t+1)} = s_J J_t + (1 - s_V) V_{1t} - \gamma_V \left( \frac{A_t}{A_t + \beta_V} \right) V_t \]  
\[ A_{(t+1)} = s_V V_t + (1 - d) A_t. \]

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 \( \beta_S \) 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 \( \gamma_S \). Mountain pine beetle disturbance will not remove the juvenile class. Assuming \( \beta_S \) is small (that is, seedlings are easily shaded out), the shading further is approximately a constant, \( \gamma_S \). If we combine the three non-susceptible classes, adding Eqs. (2.2a) - (2.2c) to yield a composite nonsusceptible class, \( \tilde{J}_t = S_{0t} + S_{1t} + J_t \), then we have a simplified equation,

\[ \tilde{J}_{(t+1)} = (1 - s_J) \tilde{J}_t + b_V V_t + b_A A_t - \gamma_S S_{1t} + s_J (S_{0t} + S_{1t}) \].

We note that, in the absence of manual thinning or 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 Eq. (2.3) may be negated, given:

\[ \tilde{J}_{(t+1)} = (1 - s_J) \tilde{J}_t + b_V V_t + b_A A_t, \]  
\[ V_{(t+1)} = s_J \tilde{J}_t + (1 - s_V) V_t, \]  
\[ A_{(t+1)} = s_V V_t + (1 - d) A_t. \]
The simplified demographics may be written as the following Leslie matrix equation:

\[
\begin{pmatrix}
J_{t+1} \\
V_{t+1} \\
A_{t+1}
\end{pmatrix} =
\begin{pmatrix}
1 - s_V & b_V & b_A \\
s_V & 1 - s_A & 0 \\
0 & s_A & 1 - d
\end{pmatrix}
\begin{pmatrix}
J_t \\
V_t \\
A_t
\end{pmatrix}.
\]

(2.5)

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 Type III response function popularized by Holling (1959), \( P(B) = \frac{B^2}{B^2 + a^2} \). 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

\[
I_{t+1} = P(B) \cdot S_t = \frac{B^2}{B^2 + a^2} S_t.
\]

(2.6)

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, \( B_t = f I_t \).

Substituting this relationship into the response function in Eq. (2.6) gives:

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

(2.7)
Figure 2.1. 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 non-aggregating pheromone, which repels beetles from the tree forcing them to search out another victim. The $a$ value equates to the point at which 50% of the susceptible trees can be successfully attacked.
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, $\alpha = \frac{9}{7}$, with units of trees per hectare,

$$\frac{I_t^2}{I_t^2 + \left(\frac{9}{7}\right)^2}S_t = \frac{I_t^2}{I_t^2 + \alpha_t^2}S_t$$

This new parameter, $\alpha$, 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 Figure 2.1. 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.

Since there is a difference in the susceptibility and potential beetle fecundity 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 $\alpha^2$ 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.

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 which 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

$$I_{t+1} = \frac{I_t^2}{I_t^2 + \alpha_t^2}V_t + \frac{I_t^2}{I_t^2 + \alpha_t^2}A_t.$$  

The simplified demographics may be written as the following Leslie matrix equation (Eq. 2.10). 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.

\[
\begin{pmatrix}
J_{t+1} \\
V_{t+1} \\
A_{t+1}
\end{pmatrix} =
\begin{pmatrix}
1 - s_V & b_V & b_A \\
s_V & 1 - s_A & 0 \\
0 & s_A & 1 - d
\end{pmatrix}
\begin{pmatrix}
J_t \\
V_t \\
A_t
\end{pmatrix} -
\begin{pmatrix}
0 \\
\frac{I_t^2}{I_t^2 + \alpha_V} V_t \\
\frac{I_t^2}{I_t^2 + \alpha_A} A_t
\end{pmatrix}
\]

(2.10)

\[
I_{t+1} = \frac{I_t^2}{I_t^2 + \alpha_V} V_t + \frac{I_t^2}{I_t^2 + \alpha_A} A_t.
\]

(2.11)

The model presented in Eqs. (2.10) and (2.11) 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.

2.2.1. Dynamical 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 the lodgepole pine forests that we are concerned with are mature stands and are more or less homogeneous, obviating the need for two distinct classes of susceptible tree. With
this in mind, the system of Eqs. (2.10) and (2.11) can be written as

\[
\begin{pmatrix}
    I_{t+1} \\
    S_{t+1}
\end{pmatrix}
= \begin{pmatrix}
    1 - s & b \\
    s & 1 - d
\end{pmatrix}
\begin{pmatrix}
    I_t \\
    S_t
\end{pmatrix}
- \begin{pmatrix}
    0 \\
    \frac{t^2 S_t}{t^2 + \alpha_t^2}
\end{pmatrix},
\]

(2.12)

\[I_{t+1} = \frac{I_t^2}{I_t^2 + \alpha_t^2} S_t.
\]

(2.13)

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 \(I_t^2 \ll I_t\). This means, at low densities of infectives, the loss of susceptible trees to infectives is negligible and the model with three classes, Eqs. (2.12) and (2.13), 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, \(\lambda_{\text{max}}\), 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 Eq. (2.12) is \(\lambda_1 \lambda_2 = 1 - d - s + sd - bs > 0\) for sufficiently small \(s\) and \(d\), implying that both \(\lambda_1\) and \(\lambda_2\) must be positive. We can therefore conclude \(\lambda_{\text{max}} > 1\), 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 \(S_t = \lambda_t^{\text{max}} S_0\) describes the increase in density of the susceptible trees over time. For small numbers of \(I_t\), the decoupled infective class is described by

\[I_{t+1} = \frac{I_t^2}{I_t^2 + \alpha_t^2} \lambda_t^{\text{max}} S_0.
\]

(2.14)

We find a fixed point analysis of Eq. (2.14) 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. Figure 2.2 is a bifurcation plot of the fixed points of Eq.
FIGURE 2.2. 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.

(2.14) 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, since an absence of beetles in the current time step implies that there will be no beetles in the next time step. The trivial fixed point is attracting and is illustrated in Figure 2.2 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. While the density of infectives is at this benign level, the healthy forest grows in accordance with the de-coupled Leslie matrix model. This unbridled growth of the susceptible class eventually reaches a density level where a nontrivial fixed point emerges. This non-trivial fixed point first comes into existence through a saddle-node bifurcation when $\lambda_{\max}^t S_0 = 4\alpha$. In Figure 2.2, 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 $S_0 > \frac{4a}{\lambda_{max}}$, this nontrivial fixed point at $I_t = \frac{\lambda_{max} S_t}{2}$ 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 non-trivial attracting fixed point because it violates the earlier assumption that $I_t$ is small. It is the fixed point at the lower density which 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 $I_t = \frac{\lambda_{max} S_t}{2} - \sqrt{\left(\frac{\lambda_{max} S_t}{2}\right)^2 - 4a^2}$. 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 which 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.

2.2.2. 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 in which 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 modelling. 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 \textit{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, $v(x,t)$.

\begin{align}
\frac{\partial u}{\partial t} &= D \frac{\partial^2 u}{\partial x^2} - \mu u. \quad (2.15a) \\
\frac{\partial v}{\partial t} &= \mu u. \quad (2.15b)
\end{align}

where $D$ is the diffusion parameter governing the rate at which beetles search out a host tree, and $\mu$ 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 of 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., $\lim_{t \to \infty} v(x,t) = k(x)$.)
Solving for the kernel under these assumptions results in the Laplacian distribution (also called the double exponential (Neubert et al., 1995))

\[ k(x) = \frac{1}{\sqrt{4\delta}} \exp^{-\sqrt{x^2/\delta}}. \quad (2.16) \]

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

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:

\[ k(\vec{x}) = \frac{1}{2\pi\delta^2} \exp\left(-\frac{\sqrt{(x_1^2 + x_2^2)}}{\delta}\right) \quad (2.17) \]

where a point in space is represented by the ordered pair \( \vec{x} = (x_1, x_2) \). 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 removes the troublesome singularity. In the two-dimensional dispersal model, the mean dispersal distance is \( 2\delta \), 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 \( \vec{y} = (y_1, y_2) \) in the next time step, given that they were originally at \( \vec{x} = (x_1, x_2) \) is \( I(\vec{x}, 0)K(\vec{x} - \vec{y})dy \), where the dispersal kernel is shifted so that it is centered at the original locus of individuals, \( \vec{x} \). 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

\[
I^* = (I * K)(x) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} I(\bar{y}) K(x - \bar{y}) \, d\bar{y}.
\]  

(2.18)

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

\[
\begin{pmatrix}
\dot{J}_{t+1} \\
\dot{V}_{t+1} \\
\dot{A}_{t+1}
\end{pmatrix} =
\begin{pmatrix}
1 - s_V & b_V & b_A \\
s_V & 1 - s_A & 0 \\
0 & s_A & 1 - d
\end{pmatrix}
\begin{pmatrix}
\dot{J}_t \\
\dot{V}_t \\
\dot{A}_t
\end{pmatrix} -
\begin{pmatrix}
0 \\
\frac{I^* V_t}{I^* + \alpha_V} \\
\frac{I^* A_t}{I^* + \alpha_A}
\end{pmatrix}
\]  

(2.19)

\[
J_{t+1} = \frac{I^* V_t}{I^* + \alpha_V} + \frac{I^* A_t}{I^* + \alpha_A},
\]  

(2.20)

where \( I^* \) is given by the convolution in Eq. (2.18). Equations (2.19) and (2.20) 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.

2.3. 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 Eq. (2.18)), and these populations are impossible to measure directly either under the bark or in flight.

The data used to estimate parameters for the model is Aerial Damage Survey (ADS) data collected from flights over the SNRA providing 30 by 30 meter resolution. Numbers of infected trees are detailed on a map and then these data are converted to densities on a GIS cover map in ARCVIEW®. Figure 2.3 is a map of the SNRA generated from ADS data taken in 1991.

The nature of this data collection has inherent limitations on accuracy. 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 non-host conifers throughout the SNRA, interspersed with the lodgepole pine forest.

Since 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 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 Eq. (2.20) containing the parameters to fit, \( \delta \) and \( \alpha^2 \). We assume that there is one cohort contributing to the infectives class and algebraically manipulate the equation

\[
I_{i,j,t+1} = \frac{I_{i,j,t}^*}{I_{i,j,t}^* + \alpha^2} S_{i,j,t}
\]

(2.21)

to read

\[
g (I_{i,j,t}, S_{i,j,t}, \alpha^2, \delta) = I_{i,j,t+1} (I_{i,j,t}^* + \alpha^2) - S_{i,j,t} I_{i,j,t}^* = 0.
\]

(2.22)
Map of 1991 Infectives in the SNRA from ADS Data

Figure 2.3. Above is 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 by 30 meter square of the SNRA. The cell is classified as lodgepole pine or non-lodgepole 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.
The result in Eq. (2.22) 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 $\alpha^2$ and $\delta$. 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 Eq. (2.22) to the data. These are formed by taking the derivative of the estimating functions with respect to the parameter of interest (i.e., $W_{\alpha^2} = \frac{\partial g}{\partial \alpha^2}$ and $W_{\delta} = \frac{\partial g}{\partial \delta}$). The resulting system of equations is

$$
\sum_{i,j} \sum_{t=1}^{T-1} W_{\alpha^2} \left[ g \left( I_{i,j,t}, S_{i,j,t}, \alpha^2, \delta \right) \right] = H (\delta, \alpha^2) = 0,
$$

(2.23)

and

$$
\sum_{i,j} \sum_{t=1}^{T-1} W_{\delta} \left[ g \left( I_{i,j,t}, S_{i,j,t}, \alpha^2, \delta \right) \right] = G (\delta, \alpha^2) = 0.
$$

(2.24)

By stepping through an interval that is assumed to contain the best parameter value for $\delta$ and choosing candidates, $\hat{\delta}$, we can solve Eqs. (2.23) and (2.24) for the respective $\alpha^2$ in terms of $\hat{\delta}$. This results in candidates for a solution of the form $\left( \hat{\alpha}^2, \hat{\delta} \right)$. 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, $\sum g \left( I_t, S_t, \alpha^2, \delta \right) = 0$, 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.

Due to heterogeneity in the Sawtooth National Recreation Area 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 sub-regions of varying sizes within the SNRA. There are also demographic differences between these sub-regions, 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 2.1. are the averages of results of the estimating function procedure found on sub-regions of the forest using the two-dimensional Laplace kernel given in Eq. (2.17).
TABLE 2.1. Average values resulting from the estimating function procedure applied to patches of the Sawtooth National Recreation Area. Each year yields several solutions for $\delta$ and $\alpha^2$ 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.

<table>
<thead>
<tr>
<th>Year</th>
<th>$\delta_{ave}$</th>
<th>$\alpha^2_{ave}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1990</td>
<td>5.9786</td>
<td>0.00008101</td>
</tr>
<tr>
<td>1991</td>
<td>4.6347</td>
<td>0.00581680</td>
</tr>
<tr>
<td>1993</td>
<td>4.6169</td>
<td>0.00581729</td>
</tr>
<tr>
<td>1995</td>
<td>4.8911</td>
<td>0.00537288</td>
</tr>
<tr>
<td>1997</td>
<td>4.9463</td>
<td>0.00537279</td>
</tr>
<tr>
<td>1998</td>
<td>5.2784</td>
<td>0.00469327</td>
</tr>
<tr>
<td>2000</td>
<td>5.2650</td>
<td>0.00469324</td>
</tr>
<tr>
<td>2001</td>
<td>5.3138</td>
<td>0.00452175</td>
</tr>
</tbody>
</table>

2.4. 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 for additional dynamics to emerge 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 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 $\alpha^2$ 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 Figure 2.4. We see that, for simulations with a forest length beyond this threshold near 40 km, there is qualitatively different behavior due to 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. Figure 2.5 is 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 see colliding waves of infectives that annihilate one
Persistence of Infectives as a Function of Space

Figure 2.4. Graph of the average persistence of the infectives class in one-dimensional simulations, using the one-dimensional Laplace kernel from equation 2.16. Parameter values are $\alpha^2$ 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 there is a marked increase in the persistence of infectives. 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 due to constructive resonance-like behavior resulting from combinations of particular forest lengths and wave speeds.
FIGURE 2.5. The above 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, and $\alpha^2$ varies uniformly between 0.004 and 0.005.

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. Figure 2.6 is a time series of the results illustrating the percent of the forest that is occupied by infective trees compared to the percent of the forest occupied by susceptible trees. The pulses of infectives follow pulses of susceptible trees as earlier predicted. 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.
FIGURE 2.6. The above 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 $b = s = 0.06$, $d = 0$, $\delta = 200$ meters and $\alpha^2$ varies uniformly between 0.004 and 0.005.
2.5. 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 Figure 2.7 the threshold was set to 10 trees per hectare, since ADS surveyors are expected to note patches at greater than 10 trees per hectare. Using the $\alpha_{ave}$ and $\delta_{ave}$ 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 Figure 2.3. The ratio of cells that contain infectives over the total number of cells in the cover map that contain susceptible trees gives the percent of the forest area that is infected with red tops. Figure 2.8 is a graph of observed and predicted percent of forest infected. Years of data that did not yield parameter values for $\alpha^2$ and $\delta$ 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.

2.6. 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 Type III response function that exhibited the desired Allee affect. Incorporating
FIGURE 2.7. Above are four maps of the Sawtooth National Recreation area. The white regions represent the location of healthy lodgepole pine trees. The black region represents the presence of infected lodgepole pines at densities above 10 trees per hectare. The right hand column is the observed distribution of infectives and the left hand column is the distribution predicted by the two dimensional model based on the previous year's observed distribution. Each year's simulations employed the predicted parameter values for $\alpha^2$ and $\delta$ listed in Table 2.1.
FIGURE 2.8. Above is a 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 2.1 (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.
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 which 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 non-zero 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 re-invasion of beetles locally is facilitated by their presence 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 re-infest 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 Sawtooth National Recreation Area, 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 like 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 like that caused by mountain pine beetles can be expected to serve as a useful and normative disturbance.
CHAPTER 3
SELECTION OF A LANDSCAPE MODEL OF MOUNTAIN PINE BEETLES IN THE SAWTOOTH NATIONAL RECREATION AREA

3.1. Introduction

The mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins) co-evolved in lodgepole pine forest (*Pinus contorta* Douglas) ecosystems to use trees as hosts for brood production and under normal conditions this interaction can lead to stability of the ecosystem through a natural cycle of forest growth and regeneration. As a univoltine species, each year of attacking beetles subdues pine trees to create hosts for the subsequent generation. The beetles accomplish this by chewing through the bark and burrowing galleries into the phloem, just below the bark. There the phloem provides nutrients for the next generation of beetles during their development. The tree is far from passive in this process; a healthy lodgepole pine under attack will excrete pitch through the hole created by an attacking beetle. As a result the trunk of an attacked tree is speckled with small pillars of pitch. These "pitch tubes" expel some of the attacking beetles, and can ward off a moderate attack. However if sufficiently many beetles aggregate at the tree, then these defenses can be overwhelmed allowing the beetles to colonize the tree. The following summer a new generation of adult beetles emerge from the host tree to repeat the cycle. This process of colonization results in the death of the host tree, and over the course of the subsequent year needles on host trees yellow and then turn red. From the air the otherwise green forest appears spotted with rust red colored trees.

In recent times we observe a break from the normative beetle forest interaction (Mattson, 1996). A general change in weather patterns favoring beetle growth has opened the door to outbreak conditions in many parts of western North America. In addition to mature homogeneous tree stands suffering from crowding and other resource limitations, the mountain pine beetle has benefited from several years of favorable temperature regimes, upon which the developmental rate of the beetle is dependent (Logan and Powell, 2001; Powell and Logan, 2005). Warmer years produce larger populations of beetles which dramatically increase beetle pressure on the pine forest. These factors have led mountain pine beetles to become the most damaging of all forest insects, devastating large areas of forest every year (Berryman et al., 1984, 1989).
Because of the obvious economic as well as the ecological impacts, interest in this system of beetle-tree interaction has long attracted the attention of biologists, foresters and policy makers. There is over a decade of remote sensing data available on mountain pine beetle impact in the Sawtooth National Recreation Area (SNRA) of central Idaho alone. Although satellite imagery promises greater resolution, aerial damage survey (ADS) data provides a more complete set, recording the advance of mountain pine beetles through the SNRA from 1990 to 2002. Such a contiguous library of data allows us to observe the advance of the beetle outbreak over a time scale on order with outbreak durations recorded elsewhere.

These observations are crucial because, in spite of a long history of study, understanding of mountain pine beetle population dynamics and dispersal at the landscape scale is limited. For example, it has been accepted for years (Berryman et al., 1989; Powell et al., 1996) that at an individual tree level there is a strong Allee effect, produced by the need to overwhelm host defenses. But at the landscape scale, where it can be argued that there are always weakened trees available due to root disease, drought stress, or lightning strikes, it is possible that populations grow linearly. The situation is analogous to disease dynamics; at an individual level, host resistance, immunity, intensity of exposure all condition the probability of successful infection, creating, in essence, an Allee effect and nonlinear response. However, at the much larger scale of populations, which invariably include weakened and aged individuals, linear growth of infected populations is the order of the day. In this paper we will create models which allow us to distinguish between linear growth and nonlinear (Allee effect) growth for MPB populations at the landscape scale.

Since successful reproduction of MPB results in death of the host, dispersal to new hosts is another critical component of the landscape process. Here again the long history of tree-scale observations sheds little light on the landscape process. Often beetles disperse past obvious hosts to attack seemingly equivalent hosts some distance away, prompting Safranyik to suggest that some distance of flight is required for MPB to become fully sexually mature. It is absolutely clear that once a tree is attacked, nonlinear dynamic attack rates and pheromone plumes condition attacks (Biesinger et al., 2000; Powell et al., 2000). However, the initial selection of a host tree could be spatially random and independent of population density as proposed by Burnell (1977) and Berryman and Ashraf (1970), with patterns generated by selections from a spatial random-walk process. Alternatively, MPB may select larger trees, as posited by Cole (1983) and Safranyik et al. (1974), or beetles may be sensitive to subtle cues that are just not apparent to human observers.
As discussed by Powell and Zimmermann (2003), the spatial result at a landscape scale of directed movement and choice of small scale stopping areas (in this case tree) is dispersal via exponential kernels. These kernel generally have much longer tails than probability kernels consistent with random walk motion. Below we will create models which accommodate both dispersal possibilities and allow us to select between them based on the ADS data.

Our objective in this paper is to derive a modelling framework for this system based on observable behavior of the beetle population in the forest, and to fit the result to available data on the SNRA outbreak. We will investigate a set of models resulting from a modular approach to representing beetle dispersal and attack dynamics. Beetle movement will be modelled by two dispersal kernels and attack dynamics modelled by two response functions. After fitting these models to the data by using estimating functions, we address the task of model selection. To this end we introduce a new approach to assess the fit of spatial models to data. More familiar methods, like summing squared residuals, fail to account for spatial structure. A trivial example of this failure is that of a model that perfectly replicates the observed population distribution and densities, but is shifted slightly in space. Despite such accurate results being desirable, the sum of squared errors measure could easily label the model as a very bad fit. Employing facial recognition technology in determining the best fit among model results offers a new method that is consistent with more familiar methods traditionally employed, but potentially more appropriate to the task. From this set of four models we will select the model that best represents the observed phenomena and discuss what this best model can tell us about the system.

3.2. The Red Top Model

3.2.1. A Structured Lodgepole Pine Forest Model

Our first task is to develop a minimally complex model that rests firmly upon a theoretical foundation, as well as offers an apt description of the forest-beetle interaction in the Sawtooth National Recreation Area. There are many factors that contribute to the success of mountain pine
beetle attacking lodgepole pine trees. Principal among them are two factors: the age and health of the tree stand and the yearly temperature patterns influencing beetle attack dynamics. Healthy stands of trees are more effective in resisting beetle attack than stressed, overly mature trees, but also produce larger beetles due to greater nutrient availability (Amman and Cole, 1983; Berryman et al., 1989). Second, beetle development is linked strongly to temperature, which plays a role not only in the survival of beetles but also the synchrony of emergence in the summer, and subsequently the effectiveness of beetle attacks (Amman and Cole, 1983; Bentz et al., 1991; Logan and Powell, 2001). A model that describes the beetle-forest interaction must therefore include these two principal factors. Furthermore, an appropriate spatial model also must include the dispersal dynamics of the mountain pine beetle.

Most of the dispersal activity of the beetle happens in a small window of time during the summer, resulting in relatively discrete time steps in the advance of beetle outbreaks (Amman and Cole, 1983). Each year a new generation of red topped trees is created through the successful colonization of a host tree for beetle brood production. Therefore this system lends itself to a discrete time modelling approach based on annual time steps.

As large trees age, their crowns remain relatively constant in size while the diameter of the trunk increases. This increase in diameter means that the same quantity of phloem passing beneath the bark is spread over a larger area, in turn reducing the concentration of nutrients available for a brood of developing beetles (Amman and Cole, 1983). Therefore susceptible lodgepole pine stands are composed of classes of trees based on diameter breast height (DBH) of the trunk. Unfortunately there is no way to resolve these classes from the ADS data. As a result the model considers only one class of susceptible trees, and assumes a non-susceptible class consisting of juvenile trees, which are too small to provide adequate space and nutrients to rear galleries of beetles. These juveniles are trees with DBH less than 0.2 meters. We define \( J_t \) as the density of juvenile, non-susceptible trees and \( V_t \) as the density of susceptible vigorous trees.

A transition matrix models the growth of the healthy forest in the absence of beetle disturbance. The parameters \( s, b \) and \( d \) are lodgepole pine maturation, birth and death rates, respectively,

\[
\begin{pmatrix}
J_{t+1} \\
V_{t+1}
\end{pmatrix} =
\begin{pmatrix}
1-s & b \\
    s    & d
\end{pmatrix}
\begin{pmatrix}
J_t \\
V_t
\end{pmatrix}.
\] (3.1)
The parameters appearing in the matrix are easily fit from available forest inventory data and are not the focus of this paper. Instead we present the transition matrix model in Eq. (3.2.1) as a foundation upon which we build the Red Top Model.

3.2.2. Beetle Attack Dynamics

Raffa and Berryman established that mountain pine beetle attacks on pine trees require a threshold density for success (Raffa and Berryman, 1983). Below a minimum level of attacking beetles, the tree’s defensive mechanisms are able to repel beetles via pitch tubes. But beetle attacks are pheromone coordinated, and if sufficient numbers of beetles aggregate at the tree under attack, the tree’s defenses can be overcome. After sufficient beetles have established themselves in the tree, a de-aggregation pheromone is released, repelling flying beetles from the newly created host tree, and the attack process continues on another tree. This strongly nonlinear response at a tree level results in very homogenous attack densities, so that each attacked tree has approximately the same number of colonizing MPB. At the landscape scale, a simple way to represent this dynamic is through response functions which represent the probability of successful beetle attack as a function of beetle density. If an attack is successful, the tree becomes a red top host in the next generation of beetles.

We view this varying probability of attack success in terms of the effectiveness of beetles present as well as their density. Beetle effectiveness varies year to year because of the general health of the forest, temperature dependent beetle development, and the relative abundance of simultaneously emerging beetles. Next we will discuss how these factors can be incorporated into the response function modelling beetle attack.

We assume the probability of successful attack to be a function of beetle density, \( \phi(B_t) \), where \( \phi \) is any monotonically increasing function from zero to one. The chance of a vigorous tree becoming an infected tree is \( \phi(B)V \). Although a variety of response functions may be deemed appropriate, given the threshold dynamics of the pheromone coordinated beetle attack, we might expect promising candidates to display a sigmoidal shape. We will consider two response functions, one exhibiting threshold dynamics, the Type 3 response function: \( \phi \left( B_t, a^2 \right) = \frac{B_t^2}{B_t^2 + a^2} \), and one that does not, the Type II: \( \phi \left( B_t, a \right) = \frac{B_t}{B_t + a} \). In this way we can test the importance of including threshold dynamics.
in a landscape model for this system.

In both response functions the parameter \( a \) reflects the effectiveness of the beetles in overcoming susceptible tree defenses; the smaller \( a \), the greater the effectiveness. As well, \( B_t = a \) can be viewed as the density of beetles required to reach a 50\% successful attack probability. It is therefore reasonable to expect \( a \) to vary from year to year, reflecting the temperature dependent survival and synchrony of the beetle population mentioned in Section 3.2.1.

We assume that every infected tree results in a subpopulation of emerging beetles the following year. Infected trees are viewed as having a beetle fecundity, \( \rho \), implying beetle density in the subsequent year is proportional to the density of infected trees, \( B_{t+1} = \rho I_t \). By solving for infected tree density in terms of beetle density, we can remove the response function's dependency upon beetles and write the model expressly in terms of trees, thus creating a model of red top trees producing new red top trees. In the case of the Type III function we have

\[
\phi(I_t) = \frac{\rho^2 I_t^2}{\rho^2 I_t^2 + a^2} = \frac{I_t^2}{I_t^2 + (a/\rho)^2} = \frac{I_t^2}{I_t^2 + a^2}.
\] (3.2)

Equation 3.2 introduces the parameter \( \alpha \) which is the ratio of beetle effectiveness to infected tree's beetle fecundity. Together this ratio is a measure of the overall effectiveness that beetles have in a given year.

Based on field observations and data collected through laboratory studies, we can establish an anticipated range of values for \( \alpha \) with the following back-of-the-envelope calculation. To begin with, we observe that \( P(\alpha) = 0.5 \) in both response functions. Susceptible trees have a DBH greater than 0.2 meters and lodgepole pine grow to about 0.5 meters in diameter. There are roughly ten meters of exposed tree trunk below the canopy which yields 12 to 31 square meters of exposed tree trunk which beetles may attack. Data presented in Cole and McGregor (Cole and McGregor, 1983) suggest densities of 0.2 to 0.5 meter DBH trees in the Bechler River Drainage of the Yellowstone National Park Forest to be between 192 and 322 trees per hectare. Assuming this forest structure is similar to that of the Sawtooth National Recreation Area, we arrive at 2300 to 9900 square meters per hectare accessible to beetles for attack. Berryman observed that attack densities of 60 attacks per square meter of exposed tree trunk surface results in fifty percent mortality of the lodgepole pine (Berryman et al., 1985), suggesting that the number of beetle attacks per hectare yielding a 50\% mortality of susceptible trees (what we have termed \( a \) in the original response functions) lies...
between 138,000 and 594,000 beetles per hectare. Studies that involve caging infected lodgepole pine and counting the number of emerging beetles provide a measure of the fecundity of an infected tree (unpublished data). These studies place $\rho$ at around 5000 beetles per tree. From this we can conclude that $\alpha$ should fall around 27 to 119 infected trees per hectare, where smaller numbers reflect greater effectiveness of beetles in establishing galleries in lodgepole pines. We will see in Section 4.2.1 that the parameter values arrived at through fitting the model to the ADS data fall within this interval.

Incorporating the response function’s dependence on infected tree density into the model results in a stage structured model of the forest under pressure from beetle attack,

\[
\begin{pmatrix}
J_{t+1} \\
V_{t+1} \\
I_{t+1}
\end{pmatrix} =
\begin{pmatrix}
1 - s & b & 0 \\
s & d - \phi(I_t) & 0 \\
0 & \phi(I_t) & 0
\end{pmatrix}
\begin{pmatrix}
J_t \\
V_t \\
I_t
\end{pmatrix}
\]

The model in Eq. (3.2.2) satisfies the principal factors mentioned in Section 4.2: forest structure and beetle attack dynamics. Even prior to including the spatial aspect, the model demonstrates desirable properties, like meta-stable states for low beetle densities and periodic beetle outbreaks when a sufficient density of susceptible trees is reached (Chapter 2). Our next step is to include the spatial aspect of beetle dispersal.

3.2.3. Beetle Dispersal

When the temperature becomes warm enough in the summer, a generation of beetles emerges from red-topped host trees to seek out hosts for the next generation of pine beetles. Dispersal from a host tree may take beetles to nearby trees or many kilometers away. Then beetles may attack an old tree or a tree damaged by lightning strike or they may opt for attacking a seemingly vigorous tree standing right next to either. Although the exact mechanism by which the beetles select a prospective host tree to initiate attack is not completely understood, we do have measurements of beetle densities from source trees as a function of distance and these suggest that dispersal
probabilities decrease rapidly with distance (Safranyik et al., 1992; Elkin and Reid, 2005).

We use a probability density function (pdf) to model the dispersal of beetles at the time of emergence. The pdf is termed a dispersal kernel and is a measure of the probability of dispersing to and attacking a tree some distance from a currently infected host tree. As with the choice of response functions, there are many kernel candidates to choose from. Here we wish to distinguish between two different broad possibilities: host selection at random in space (i.e. due to a random walk process), which would follow a Gaussian dispersal kernel (Kot et al., 1996), and host selection due to directed motion, which would follow an exponential or Laplace distribution (Powell and Zimmermann, 2003).

\[
\text{Gaussian: } K(x, y, \delta) = \frac{1}{2\pi\delta^2} e^{-(x^2+y^2)/2\delta^2} \tag{3.4a}
\]
\[
\text{Exponential: } K(x, y, \delta) = \frac{1}{2\pi\delta^2} e^{-\sqrt{x^2+y^2}/\delta} \tag{3.4b}
\]

The kernels themselves can suggest a manner of beetle dispersal. The Gaussian is derived from a random walk assumption and follows from the law of large numbers. This kernel therefore may suggest that the beetles follow a random search pattern when seeking a prospective host tree. On the other hand, the Exponential has “fatter tails” which allow for greater probabilities for dispersing farther than the Gaussian, suggesting that beetles are more “directed” in searching out a susceptible tree to attack. When we convolve the density of infected trees with either dispersal kernel, we arrive at the post dispersal influence of infected trees resulting from the summer emergence of beetles. We employ the notation \(I^*\) to represent the density of infected trees resulting from dispersed beetles where

\[
I^* = I \ast K = \iint_{-\infty}^{\infty} K(\bar{x}) I(\bar{x} - \bar{y}) d\bar{x}
\]

and \(\bar{x}\) is the position vector.

Just as in the case of the parameter \(\alpha\) we can anticipate values for the dispersal parameter, \(\delta\). Capture and release studies show emergence distributions were exponentially decreasing and 90% of beetles recaptured fell within 30 meters of the release point (Safranyik et al., 1992; Elkin and Reid, 2005). If we consider the Gaussian kernel, a quick calculation yields \(\delta \approx 14.0\) meters and 7.8 meters for the Exponential kernel. We will also see, as with our estimates for anticipated \(\alpha\) values, that this approximation matches quite closely with the fitting results given in Section 4.2.1.
3.2.4. Complete Red Top Model Including Dispersal

We now have a model that incorporates the fundamentals of forest susceptibility to beetle attack and the dispersal of beetles through the forest,

\[
\begin{pmatrix}
J_{t+1} \\
V_{t+1} \\
I_{t+1}
\end{pmatrix} =
\begin{pmatrix}
1-s & b & 0 \\
s & d-\phi(I_t^*) & 0 \\
0 & \phi(I_t^*) & 0
\end{pmatrix}
\begin{pmatrix}
J_t \\
V_t \\
I_t
\end{pmatrix}
\]

(3.6)

where \( I_t^* = I_t \times K \) is the density of dispersed infected trees shown in Eq. (3.5) and \( \phi(I^*) \) is the response function modelling beetle attack.

The modularity of the model allows us to test the appropriateness of assumptions made regarding beetle attack dynamics (threshold versus mass action) and dispersal (random versus directed searching) by changing the response function, \( \phi \), and the dispersal kernel, \( K \). We will compare the results of various combinations of response functions and dispersal kernels against the available data to determine the most appropriate model and most suitable assumptions.

3.3. The Data

The ADS data in the SNRA is gathered annually by observers in low flying aircraft who sweep the valley while taking note of the presence and approximate numbers of infected trees in patches throughout the valley. These data are converted to maps of infected tree densities. There are many difficulties that undermine the accuracy of ADS data. Some of the most important limitations are a lack of corresponding healthy tree stand densities, the error of approximating numbers of trees in a patch, and attributing one year’s red tops to another year of attack. Despite these shortcomings, these data are useful because they are a consistent, spatially vast and temporally contiguous data set corresponding reasonably well with the advance of the outbreak observed in the SNRA. The data is a grid of cells covering an area roughly 25 kilometers east to west by 40 kilometers north to south. Each cell represents a 30 by 30 meter area. Figure 3.1 is the map created by the ADS data for
2001. The forest of lodgepole pine is given in gray, and infected trees are in black. The terrain in the SNRA is varied; patches of lodgepole pine trees litter the valley, separated by fields, bodies of water and geological relief from mountain ridges running into the valley. This fragmentation may inhibit beetle dispersal during periods of low beetle density, but with outbreak populations the progress of infestation seems unhindered.

The cover map of healthy lodgepole pine only records their presence, not density. We arrive at a uniform density for the SNRA cover map by considering measurements from a similar forest structure. Cole and McGregor (1983) provide density measurements on the Bechler River Drainage of Yellowstone National Park Forest. Here density of healthy pine trees in excess of 20 cm diameter breast height ranges from 192 to 322 trees per hectare. We take the average of these densities for our forest cover map, 257 vigorous lodgepole pine trees per hectare. Although this value is seemingly arbitrary, it is a reasonable approximation of the forest structure, and as we will see shortly, results in acceptable parameter values.

3.4. The Estimating Function Procedure

Once we have developed a model for the interaction between the mountain pine beetle and the lodgepole pine trees, we can use the ADS data to fit parameters. An elegant method that is particularly well-suited to this task is the method of estimating functions as described in a paper by Lele (Lele et al., 1998). By definition an estimating function is any function of the parameters and data that has mean error zero (Godambe and Kale, 1991). As pointed out by Lele, the method of estimating functions uses the model to construct a function of the data and parameters which can reduce a multidimensional search for minima to a much simpler one dimensional root search. In addition to this computational time saving advantage, the one dimensional search ensures that optimal solutions are not overlooked, since a complete search of all possibilities is possible along a line. Here we will discuss the method of estimating functions as it applies to the specific case of the Red Top Model using the Type III response function and the Gaussian dispersal kernel, Model GIII.

To begin with, we construct a function of the data and parameters derived from the response
FIGURE 3.1. Map of the Sawtooth National Recreation Area reveals a highly fragmented pattern of lodgepole pine forest, here seen in gray, with patches of infected trees seen in black. The center of the valley is mostly agricultural fields and sagebrush. Mountain ridge lines run into the valley from the East and West creating pockets of lodgepole stands.
function used,

\[ I_{t+1} = V_t \frac{I_t^2}{I_t^2 + \alpha^2} \rightarrow G \left( I_{t+1}, I_t, \alpha^2, \delta \right) = V_t I_t^2 - I_{t+1} I_t^2 - \alpha^2 I_{t+1} \tag{3.7} \]

where \( I_t^* \) are the infected trees convolved with the Gaussian dispersal kernel,

\[ \* = I \ast K = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \frac{1}{2\pi \delta^2} e^{-\left(x_1^2 + x_2^2\right)/2\delta^2} I(x_1 - y_1, x_2 - y_2) \, dx_1 \, dx_2. \tag{3.8} \]

Numerically this convolution is facilitated using fast Fourier transforms. Although Eq. (3.7) is not a unique formulation of the data and parameters, it does have the virtue that \( \alpha^2 \) appears linearly in the function. This enables us to easily solve for \( \alpha \) after selecting \( \delta \) with which to disperse the beetles.

If we made the gross assumption that the model was a perfect fit to the data, then the correct parameters would yield \( G \left( I_{t+1}, I_t, \alpha^2, \delta \right) = 0 \). However, if we assume that the model is simply a reasonable description of the observed phenomena, an application of the model with the correct parameters to cell \((i,j)\) is

\[ G_{i,j} \left( I_{t+1,i,j}, I_{t,i,j}, \alpha^2, \delta \right) = V_{t,i,j} I_{t,i,j}^2 - I_{t+1,i,j} I_{t,i,j}^2 - \alpha^2 I_{t+1,i,j} = \epsilon_{i,j}. \tag{3.9} \]

For the correct parameters, the mean value of the errors, \( \epsilon_{i,j} \), will be zero, meaning we are not generally over estimating or underestimating a parameter. If we aggregate to the entire space, the function \( G \) tends to zero for the correct parameters.

\[ \sum_{i,j} G_{i,j} \left( I_{t+1,i,j}, I_{t,i,j}, \alpha^2, \delta \right) = \sum_{i,j} \epsilon_{i,j} \rightarrow 0. \tag{3.10} \]

The convergence is accelerated by weighting functions which effectively push poor parameter sets further from zero. The use of weighting functions also provides a convenient way to construct a system of linear equations which enable us to solve for any number of linear parameters in the model. It can be shown that an optimal set of weighting functions is provided by the expected values of the partial derivatives of Eq. (3.10) with respect to the parameters of interest (Lele et al., 1998).

In the Red Top Model GIII there are two parameters that need fitting, \( \delta \) and \( \alpha^2 \). In this case
the associated weighting functions are

\[
\frac{\partial G_{i,j}}{\partial \alpha^2} = -I_{i+1}
\]

(3.11a)

\[
\frac{\partial G_{i,j}}{\partial \delta} = 2I_t^* (I_{t+1} - V_t) \frac{x^2_j + y^2_j - 2\delta^2}{2\pi \delta^5} e^{-(x^2_j + y^2_j)/2\delta^2}.
\]

(3.11b)

We now have a homogeneous system of linear equations in terms of the parameters, with expectation zero,

\[
\sum_{i,j} \frac{\partial G_{i,j}}{\partial \alpha^2} G_{i,j} (I_{t+1,i,j}, I_{t,i,j}, \alpha^2, \delta) = 0,
\]

(3.12a)

\[
\sum_{i,j} \frac{\partial G_{i,j}}{\partial \delta} G_{i,j} (I_{t+1,i,j}, I_{t,i,j}, \alpha^2, \delta) = 0.
\]

(3.12b)

The parameter \(\delta\) is nested nonlinearly in the dispersal kernel, but \(\alpha^2\) appears linearly in the response function. This allows us to simply solve for a corresponding \(\alpha^2\) in Eq. (3.12a) for each \(\delta\) candidate in the one-dimensional parameter space. This approach results in a one-dimensional parameter search for \(\delta\) over some reasonable range (in our case 1 to 100 meters), and for each \(\delta\) candidate, there is an associated \(\alpha^2\). The \(\delta\) associated with the root of Eq. (3.12b) provides the set of parameter solutions that best fit the model to the data. The parameters resulting from this procedure applied to the four red top models under consideration are given in Table 3.1.

In the case of the Gaussian kernel with the Type III response function we select \(\delta \in (1, 100)\) allowing us to disperse the beetles in accordance with Eq. (3.8), then solving Eq. (3.12a) for \(\hat{\alpha}\)

\[
\hat{\alpha}^2 = \frac{\sum_{i,j} I_{t+1,i,j}^2 I_{t,i,j}^2 - \sum_{i,j} I_{t+1,i,j} I_{t,i,j}^* V_t}{-\sum_{i,j} I_{t+1,i,j}^2},
\]

(3.13)

yielding a candidate pair, \((\hat{\alpha}, \hat{\delta})\), which we then use to evaluate Eq. (3.12b),

\[
G_{i,j} (I_{t+1,i,j}, I_{t,i,j}, \hat{\alpha}^2, \hat{\delta}) = \sum_{i,j} 2I_t^* (I_{t+1} - V_t) \frac{x^2_j + y^2_j - 2\hat{\delta}^2}{2\pi \hat{\delta}^5} e^{-(x^2_j + y^2_j)/2\hat{\delta}^2} \left( V_t I_{t}^* - I_{t+1} I_{t+1}^* - \hat{\alpha}^2 I_{t+1} \right).
\]

(3.14)

The final step is to solve for the root of Eq. (3.14). In doing so we have the best pair of parameter
3.5. Selection Techniques for Red Top Model

At this point we have constructed four models, representing the four crossed landscape-level model possibilities, and presented a method to determine parameters from data. Now we address the question: which one provides the best fit to the data? To answer this question we may consider traditional methods like minimizing residual sums of squared errors. However these methods are not well suited to deal with spatial representations of data if there are pronounced differences in the structure between models. For example in Figure 3.2 we see maps of hypothetical randomly generated observed and predicted infected trees. Model 2 appears to be most similar in spatial structure to the hypothetical observed data and has the smallest sum of squared error, but Model 3 has the smallest sum of log error and smallest sum of absolute value of error. To address this concern, we propose viewing each model map as a photo of the forest and applying a facial recognition algorithm to determine which result is closest to the observed data.

The method of projecting an image from its original high dimensional space onto a lower dimensional space via Principal Component Analysis (PCA) has been under development in the arena of facial recognition for many years (Turk and Pentland, 1991; Belhumeur et al., 1997; Zhao et al., 2003). PCA is an unsupervised method that results in a linear subspace of the original feature space. In the case of our maps of infected trees, each map can be viewed as an $m \times n$ matrix. This matrix is converted into a vector of length $mn$, interpreted as a point in a high dimensional space. A collection of maps amounts to a data set in this high dimensional space. Applying PCA to this data set yields a projection that best represents the variability of the data (Duda et al., 2001). Employing a simple Euclidean measure of distance we ascertain the closest model to the observation in the lower dimensional projection of the original data. An advantage of this method over non-spatial measures of fitness is that the dominant eigenvectors resulting from PCA illuminate the areas of greatest variability between the candidate maps. Loosely speaking, when these eigenvectors are used to project the observation onto the face space created by the models, the location of the error becomes as important as the errors themselves. In this way a balance is created between the
FIGURE 3.2. For the purpose of illustration, the figure above displays three results of the Eigenface recognition algorithm applied to hypothetical images of infected trees in the Sawtooth National Recreation Area. The maps represent patches of infected trees with varying densities. Listed below each map is a traditional non-spatial methods of selection, sum of squared residuals. Prediction 1 would be selected based on the measures of sum of residual error but Prediction 2 is closest to the observed map judging by the Euclidean distance between the observed and modelled data when projected onto a three dimensional Eigenspace. Despite a greater discrepancy in the densities of infected trees, the spatial structure of the image provided by Prediction 2 has a stronger resemblance to the Observed image.
accuracy of prediction in each cell and the spatial structure of the prediction.

The example illustrated in Figure 3.3 shows five maps, each containing a ring and a dot. The dot is located in the same place in each map while the ring is shift to a different location. Applying PCA to these maps, then projecting the maps onto a two-dimensional space illustrates how maps D and E are closest to one another. In Figure 3.4 we see that the first two eigenvectors resulting from PCA highlight the variability between the maps, and in doing so, completely ignore the dot in the upper left corner since it is the same in each map. See Appendix A for a more detailed explanation of this method.

![Figure 3.3](image)

**Figure 3.3.** Above are five maps each containing an identically placed dot in the upper left corner, but with a ring that is shifted slightly from map to map. The maps D and E appear most similar to one another. When we see their relative location in the subspace we observe that they are in fact closest to one another, and also that B is the most different.
3.6. Results

Prior to fitting the parameters we anticipate a range of values independently for $\alpha^2$ and $\delta$ based on field data and forest demographics. From these we conclude $\alpha$ should fall in the range of 27 to 119 infected trees per hectare. The parameter values we arrive at when applying the estimating function procedure to the ADS data yield results compatible with our expectations. For the Type III response function the resulting parameter values are $\alpha = 21.3 \pm 10.3$ (mean value plus or minus one standard deviation). We note here that the corresponding values for the Type II response function do not overlap with the anticipated values ($\alpha = 4.9 \pm 1.8$), suggesting that it is not a suitable model for the beetle's attack dynamics. Moreover since the Type III response function parameters are on the low end of the range for anticipated values, the beetles are slightly more effective in the SNRA than where previously studied. This might be expected given the outbreak conditions in the area. The anticipated value for the dispersal parameter associated with the Gaussian kernel is $\delta \approx 14.0$ meters and for the Exponential kernel $\delta \approx 7.8$ meters. The parameter values yielded by the estimating function procedure for the Gaussian kernel are $\delta = 11.19 \pm 0.38$ and for the Exponential $\delta = 9.38 \pm 1.42$. Neither of these parameter estimates seem unreasonable and we find that both kernels are often equivalent in the selection process.

We also notice that the dispersal parameter associated with either kernel is more or less constant,
unlike the more varied values for $\alpha$. This is to be expected since beetle effectiveness, and hence the $\alpha$ value, is highly influenced by annual temperatures, while we expect the average distance a beetle flies is more or less the same over the years, provided that the habitat remains relatively unchanged.

The detailed results of PCA as applied to the ADS data using the parameters resulting from the estimating function procedure are listed in Tables 3.2 and 3.3. Here we considered all years but 1994, when we assumed that no beetles emerged and instead considered 1995 to be the result of beetle galleries created in 1993. Columns P3 lists the Euclidian distance from the observation to the corresponding model in the projection of the eigenvectors associated with the three largest eigenvalues resulting from PCA. The next columns are the error measurements by sums of squared error, $\sum \epsilon^2$, sum of logarithm of one plus squared error, $\sum \log(1 + \epsilon^2)$, and finally the sum of absolute error, $\sum |\epsilon|$. We see that in the seven instances where one model was unanimously selected, six of these models employ the Gaussian dispersal kernel. As mentioned in Section 3.2.3, the kernels themselves suggest a manner of dispersal. The Exponential kernel implies a directed search for host trees, while the Gaussian reflects a random search. Given that our selection methodology clearly prefers the Gaussian kernel, one can argue that a random walk is a better description of beetle dispersal that a directed search. This lends support to the argument by Burnell (1977) and Berryman and Ashraf (1970) that emerging beetles attack trees at random, as opposed to the hypothesis set forth by Cole (1983) and Safranyik et al. (1974), suggesting that beetles actively seek out larger diameter trees. Moreover all 44 model choices favored models with the Type III response function. This tells us that even at a landscape scale, the threshold attack dynamics are still important.

In Figure 3.5 we see that there is a strong shift to the north around 1994. Additionally, field observations suggest that the mountain pine beetle outbreak accelerated after this same year. Both a Wilcoxon Rank Sum test and Welch 2 sample t-test reveal that the $\alpha$ values of both the Type III and Type II response functions prior to 1994 are significantly larger than those of later years. This means that the beetles increased their effectiveness in the later of these two time periods, and are in fact more successful now than at the beginning of the data. This, in fact, reflects results presented by Powell and Logan (2005), based on phenological analysis of temperatures in the Sawtooth Valley. These authors noticed that in the years 1995 and on, temperatures were such that populations would be synchronous and univoltine (that is, have sufficient thermal energy to complete one generation in a year) for years after 1994, whereas in years previous to 1995 temperatures created asynchronous
fractional voltinism. Since univoltinism is associated with population success for MPB, results presented here for beetle effectiveness tend to confirm the observations of Powell and Logan.

The versatility of the estimating function procedure allows us to calculate parameter values spanning multiple years simply by summing Eqs. (3.12a) and (3.12b) over the time period of interest, in this case summing over years 1990-1995 and 1995-2002. Combining data in this manner we arrive at parameter values for each set of data. These are listed in Table 3.4. The results of the fitting algorithms applied to the models using these parameters are given in Tables 3.5 and 3.6. What is interesting here is that for all but one year under consideration, a model is unanimously selected and this model is the Gaussian kernel with the Type III response function to model the infestation in the SNRA. Based on this result, combined with the success of Model GIII in the year by year analysis, we propose Model GIII as the best model for the data. Implicit in this recommendation is the suggestion that beetle dispersal in the SNRA tends to be more random as opposed to a more directed approach modeled by exponential dispersal, suggested by Amman and Cole (1983).

Having proposed Model GIII for this system, a possible next step is to consider the spread of infection. Considering the center of mass of the density of infected trees in each year, we can chart the northward movement of the infected trees from 1990 to 2002. Figure 3.5 illustrates this general northward trend. Between the years 1990 and 1998 the center of mass of infected tree densities moved over 13 kilometers northward. This is clearly a greater spread of infestation than can be described by the dispersal parameters we have found. The Red Top model includes the dispersal from infected trees, but does not model long distance dispersal caused by thermal plumes that can carry large numbers of beetles over great distances or the explosion of an endemic subpopulation located ahead of a wave front of infected trees. Therefore, the dispersal parameter results of this model should not be confused with long range dispersal phenomena. Considering the mechanisms included in the Red Top Model, an appropriate context for this model is for regions experiencing epidemic levels of mountain pine beetles as described by Safranyik and Carroll (Safranyik and Carroll, 2006).
3.7. Conclusion

In this paper we have developed a model framework suitable for discriminating among various model possibilities at the landscape scale for the MPB-lodgepole system. Our modelling approach to beetle attack and dispersal dynamics results in a versatile model fit not only with parameters, but with underlying mechanisms of these dynamics. We are thus able to use the model to test hypotheses about the system under study. The strongest indication is that the Allee effect for MPB populations at the individual tree scale persists at the landscape scale, as opposed to a Type II response, which would indicate that there are always enough weakened hosts in a landscape-level population to sustain an initial linear response to infestation. There is less strong discrimination between the hypotheses for dispersal (random walk vs. directed motion), but overall the models with random walk dispersal seem to do a better job than those with directed motion. The strong agreement between anticipated parameter values and the values resulting from the estimating function procedure applied to the Red Top model are encouraging, suggesting that the assumptions we have made are appropriate for this system in the Sawtooth National Recreation Area.

We have introduced an additional model selection tool designed to select the overall best "looking" model as opposed to purely non-spatial measures of fitness. Application of facial recognition technology for spatial models demonstrates results very much in keeping with traditional methods, but offering another metric for selection when it is not entirely clear which model is the better choice. By having more certainty about model selection, we are able to draw more confident conclusions about assumptions made in the four models.

Having developed a model for the beetle-lodgepole pine forest interaction complete with parameters for the Sawtooth National Recreation Area we now have a platform upon which we can draw inference and test other hypothesis regarding beetle phenology and adaptation as well as infestation spread in other forest systems.
TABLE 3.1. This table contains the parameter values resulting from the estimating function procedure applied to the ADS data for each of the four models under consideration. The year 1993 was unseasonably cold and as a result there was little measurable beetle attack. As a consequence, the parameter value returned for that year’s attacks reflects an artificially high level of beetle attack effectiveness. Because the data suggests that beetles did not emerge in significant numbers during 1994, the rest of the analysis considers 1993 beetles to emerge in 1995. Powell and Logan predict semi-voltinism in this years, offering further justification of this assumption (Powell and Logan, 2005)

<table>
<thead>
<tr>
<th>Year</th>
<th>Model GIII</th>
<th>Model GII</th>
<th>Model EIII</th>
<th>Model EII</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\delta$ (m)</td>
<td>$\alpha$ (tree/ha)</td>
<td>$\delta$ (m)</td>
<td>$\alpha$ (tree/ha)</td>
</tr>
<tr>
<td>1991</td>
<td>10.774</td>
<td>42.02</td>
<td>11.052</td>
<td>7.9691</td>
</tr>
<tr>
<td>1994</td>
<td>11.009</td>
<td>0</td>
<td>11.116</td>
<td>0</td>
</tr>
</tbody>
</table>
FIGURE 3.5. The latitudinal position of the center of mass for each years map of infected trees is graphed relative to the center of mass for 1990. There is a northward trend in beetle infestation for most of the data. During the final years of the data, field observations indicate the beetle infection is moving westward out the north end of the SNRA valley.
Table 3.2. The results of various selection methods applied to the four models using the parameter values listed in Table 3.1, excluding the year 1994. The column labelled $P_3$ is the Euclidean distance between observed and predicted maps of infected trees for the three dimensional projection. The remaining three columns are the sum of squared error, $\sum e^2$, sum of the logarithm of one plus squared error, $\sum \log (1 + e^2)$, and sum of absolute value of error, $\sum |e|$, between the observed and predicted maps of infected trees. When one model for a given year was unanimously selected, an asterisk is printed next to the year.

| Year  | Model | $P_3 \times 10^4$ | $e^2 \times 10^2$ | $\ln (1 + e^2) \times 10^4$ | $|e| \times 10^5$ |
|-------|-------|------------------|------------------|------------------------|-----------------|
| 1990* | GIII  | 1.138            | 0.717            | 4.674                  | 1.643           |
|       | GII   | 7.630            | 6.409            | 5.977                  | 4.959           |
|       | EIII  | 0.995            | 0.687            | 4.656                  | 1.617           |
|       | EII   | 7.552            | 6.291            | 6.393                  | 5.101           |
| 1991  | GIII  | 2.340            | 2.107            | 5.377                  | 2.663           |
|       | GII   | 13.133           | 18.808           | 8.991                  | 12.063          |
|       | EIII  | 2.328            | 2.101            | 5.387                  | 2.664           |
| 1992* | GIII  | 3.345            | 2.191            | 4.621                  | 2.722           |
|       | GII   | 8.427            | 8.174            | 5.309                  | 5.277           |
|       | EIII  | 3.397            | 2.226            | 4.645                  | 2.753           |
|       | EII   | 8.432            | 8.183            | 5.650                  | 5.445           |
| 1993* | GIII  | 2.933            | 1.919            | 4.394                  | 2.589           |
|       | GII   | 12.147           | 15.814           | 6.711                  | 9.645           |
|       | EIII  | 2.934            | 1.920            | 4.440                  | 2.614           |
|       | EII   | 12.179           | 15.893           | 7.402                  | 9.985           |
| 1995* | GIII  | 4.903            | 3.028            | 2.536                  | 2.746           |
|       | GII   | 9.161            | 9.017            | 3.031                  | 4.935           |
|       | EIII  | 4.911            | 3.036            | 2.567                  | 2.755           |
|       | EII   | 9.169            | 9.031            | 3.348                  | 5.095           |
TABLE 3.3. The results of various selection methods applied to the four models using the parameter values listed in Table 3.1, excluding the year 1994. The column labelled \( P3 \) is the Euclidean distance between observed and predicted maps of infected trees for the three dimensional projection. The remaining three columns are the sum of squared error, \( \sum e^2 \), sum of the logarithm of one plus squared error, \( \sum \log(1 + e^2) \), and sum of absolute value of error, \( \sum |e| \), between the observed and predicted maps of infected trees. When one model for a given year was unanimously selected, an asterisk is printed next to the year.

| Year | Model | \( P3 \times 10^3 \) | \( e^2 \times 10^4 \) | \( \ln(1 + e^2) \times 10^2 \) | \( |e| \times 10^5 \) |
|------|-------|-------------------|-----------------|-----------------|------------------|
| 1996*| GIII  | 1.161             | 0.451           | 0.842           | 0.458            |
|      | GII   | 3.538             | 1.568           | 1.025           | 0.937            |
|      | EIII  | 1.258             | 0.475           | 0.872           | 0.476            |
|      | EII   | 3.661             | 1.657           | 1.230           | 1.074            |
| 1997 | GIII  | 1.706             | 0.481           | 1.327           | 0.742            |
|      | GII   | 5.413             | 3.121           | 1.721           | 2.041            |
|      | EIII  | 1.704             | 0.480           | 1.337           | 0.746            |
|      | EII   | 5.397             | 3.103           | 1.874           | 2.104            |
| 1998 | GIII  | 2.540             | 0.970           | 2.167           | 1.333            |
|      | GII   | 6.281             | 4.269           | 2.615           | 2.816            |
|      | EIII  | 2.492             | 0.946           | 2.179           | 1.323            |
|      | EII   | 6.267             | 4.253           | 2.858           | 2.918            |
| 1999 | GIII  | 1.771             | 0.689           | 4.041           | 1.592            |
|      | GII   | 7.280             | 5.675           | 4.913           | 4.227            |
|      | EIII  | 1.728             | 0.674           | 4.055           | 1.581            |
|      | EII   | 7.199             | 5.558           | 5.181           | 4.315            |
|      | GII   | 13.314            | 25.000          | 20.417          | 16.851           |
|      | EII   | 13.360            | 25.122          | 21.238          | 17.373           |
|      | GII   | 24.738            | 162.171         | 59.082          | 69.404           |
|      | EIII  | 9.437             | 109.877         | 54.100          | 48.779           |
|      | EII   | 24.774            | 162.345         | 59.872          | 69.827           |

Table 3.4. The parameter values resulting from the estimating function procedure reflecting beetle effectiveness and dispersal for aggregate years 1990 through 1993 and then 1995 through 2002. We can see that although the \( \delta \) values are similar between these two sets, there is a difference in the \( \alpha \) values, specifically all \( \alpha \) values are smaller in the set of later years indicating that the beetle effectiveness is greater than in prior years.

<table>
<thead>
<tr>
<th>Year</th>
<th>Model GIII</th>
<th>Model GII</th>
<th>Model EIII</th>
<th>Model EII</th>
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<td>28.5</td>
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<td>11.7</td>
<td>8.7</td>
<td>9.4</td>
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</table>
Using the parameter values listed in Table 3.4 that average over the two sets of years, excluding the year 1994, we arrive at the above fits for the models to the data. As in Tables 3.2 and 3.3, when one model for a given year was unanimously selected, an asterisk is printed next to the year. Here we see that for all years Model GIII is selected except for 1996, where there is an even split between Model GIII and Model EIII. Columns labelled $P_3$ are the Euclidean distance between observed and predicted maps of infected trees for the three dimensional projection. The remaining three columns are the residual sum of squared error, $\sum e^2$, sum of the logarithm of one plus the error, $\sum \log (1 + e^2)$, and sum of absolute value of error, $\sum |e|$, between the observed and predicted maps of infected trees. (Results continue in Table 3.6)

| Year  | Model | $P_3 \times 10^3$ | $e^2 \times 10^4$ | $\ln (1 + e^2) \times 10^4$ | $|e| \times 10^5$ |
|-------|-------|------------------|-------------------|-----------------------------|------------------|
| 1990* | GIII  | 1.521            | 0.921             | 4.769                       | 1.825            |
|       | GII   | 1.869            | 1.039             | 5.184                       | 2.224            |
|       | EIII  | 1.682            | 0.973             | 4.810                       | 1.875            |
|       | EII   | 1.890            | 1.047             | 5.326                       | 2.258            |
| 1991* | GIII  | 3.635            | 3.442             | 6.098                       | 3.711            |
|       | GII   | 4.005            | 3.725             | 7.212                       | 5.031            |
|       | EIII  | 3.952            | 3.683             | 6.222                       | 3.899            |
|       | EII   | 4.131            | 3.828             | 7.689                       | 5.191            |
| 1992* | GIII  | 1.074            | 0.518             | 3.995                       | 1.422            |
|       | GII   | 2.167            | 0.873             | 4.439                       | 1.962            |
|       | EIII  | 1.207            | 0.549             | 4.035                       | 1.466            |
|       | EII   | 2.202            | 0.888             | 4.587                       | 2.001            |
| 1993* | GIII  | 2.564            | 1.743             | 4.311                       | 2.439            |
|       | GII   | 3.667            | 2.430             | 5.218                       | 3.574            |
|       | EIII  | 2.843            | 1.893             | 4.426                       | 2.591            |
|       | EII   | 3.761            | 2.500             | 5.579                       | 3.711            |
| 1995* | GIII  | 5.155            | 3.395             | 2.570                       | 2.912            |
|       | GII   | 8.825            | 8.525             | 3.017                       | 4.798            |
|       | EIII  | 5.396            | 3.648             | 2.635                       | 3.030            |
|       | EII   | 8.898            | 8.654             | 3.305                       | 4.971            |
TABLE 3.6. (Continuation of Table 3.5) Using the parameter values listed in Table 3.4 that average over the two sets of years, excluding the year 1994, we arrive at the above fits for the models to the data. As in Tables 3.2 and 3.3, when one model for a given year was unanimously selected, an asterisk is printed next to the year. Here we see that for all years Model GIII is selected except for 1996, where there is an even split between Model GIII and Model EIII. Columns labelled \( P_3 \) are the Euclidean distance between observed and predicted maps of infected trees for the three dimensional projection. The remaining three columns are the residual sum of squared error, \( \sum e^2 \), sum of the logarithm of one plus the error, \( \sum \log (1 + e^2) \), and sum of absolute value of error, \( \sum |e| \), between the observed and predicted maps of infected trees.

| Year | Model | \( P_3 \times 10^3 \) | \( e^2 \times 10^7 \) | \( \ln (1 + e^2) \times 10^4 \) | \( |e| \times 10^5 \) |
|------|-------|---------------------|---------------------|---------------------|---------------------|
| 1996 | GIII  | 1.474               | 0.719               | 0.880               | 0.589               |
|      | GII   | 2.879               | 1.331               | 1.000               | 0.860               |
|      | EIII  | 1.454               | 0.713               | 0.907               | 0.593               |
|      | EII   | 2.951               | 1.372               | 1.164               | 0.953               |
| 1997*| GIII  | 3.123               | 1.447               | 1.508               | 1.337               |
|      | GII   | 5.686               | 3.705               | 1.767               | 2.232               |
|      | EIII  | 3.228               | 1.514               | 1.545               | 1.376               |
|      | EII   | 5.735               | 3.761               | 1.966               | 2.347               |
| 1998*| GIII  | 3.364               | 1.767               | 2.289               | 1.774               |
|      | GII   | 6.345               | 4.662               | 2.674               | 2.965               |
|      | EIII  | 3.460               | 1.833               | 2.345               | 1.815               |
|      | GII   | 7.403               | 7.548               | 4.987               | 4.810               |
|      | EIII  | 4.545               | 4.133               | 4.726               | 3.514               |
|      | EII   | 7.475               | 7.654               | 5.219               | 4.964               |
| 2000*| GIII  | 6.859               | 11.967              | 19.274              | 11.910              |
|      | EIII  | 7.237               | 12.499              | 19.377              | 12.150              |
|      | EII   | 12.226              | 22.211              | 20.765              | 16.275              |
| 2001*| GIII  | 9.173               | 110.053             | 53.807              | 48.774              |
|      | GII   | 19.131              | 138.238             | 57.749              | 61.566              |
|      | EIII  | 10.204              | 122.061             | 54.483              | 49.850              |
|      | EII   | 19.296              | 138.870             | 58.410              | 62.025              |
CHAPTER 4
FITTING AND MODEL SELECTION OF THE RED TOP MODEL
USING REMOTE SENSING DATA

4.1. Introduction

The Red Top Model has been applied to the Sawtooth National Recreation Area (SNRA) in an attempt to better understand the interaction between the mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins) and the lodgepole pine forest (*Pinus contorta* Douglas). The lodgepole pine is used as a host by mountain pine beetles. Beneath the bark the beetle burrows galleries in which they mate and lay eggs. The eggs hatch and the next generation of beetles remains in the galleries carved between the bark and the xylem. There developing beetles feed from the phloem which conducts nutrients down the trunk of the tree. The beetle's development is highly dependent upon temperature and the quality and availability of phloem in the host tree. The following summer adult beetles emerge and continue the cycle. This process of colonization results in the death of the host tree, and over the course of the subsequent year needles on host trees yellow and then turn red. From an aerial perspective the otherwise green forest appears spotted with rust red colored trees.

The SNRA is a particularly well suited case study in this beetle-forest interaction since there are abundant data recording the spread of what has become a full scale epidemic. In addition to mature homogeneous tree stands suffering from crowding and other resource limitations, the mountain pine beetle has benefitted from several years of favorable temperature regimes (Logan and Powell, 2001; Powell and Logan, 2005). Warmer years produce larger populations of beetles which dramatically increase beetle pressure on the pine forest. These factors have led mountain pine beetles to become the most damaging of all forest insects, devastating large areas of forest every year (Berryman et al., 1989, 1984). During the recent epidemic in the SNRA mortality among trees forest wide is over 50%. Although there is more than a decade of data on this infestation, applying these data to a mechanistic model to arrive at some understanding of the rate of spread and then to make any prediction of the course of the infestation is a formidable task.
To this end there are two types of data available: aerial damage survey (ADS) and remote sensing data. The ADS data is prone to accuracy errors, mis-representing the density of infected trees and is dependent upon a cover map of susceptible trees which represents the location of trees, but has no measure of their density. Furthermore, the nature of data collection (low altitude flights over the area, marking the location of infected trees manually on a clipboard) makes it difficult to determine not only the number of infected trees but in which year the infected tree was attacked by beetles. The presence of errors is made obvious by the cumulative recording of more infected trees in some locations than the cover map can support.

High resolution remote sensing data gathered by satellite or aerial photography has its own set of problems. These include first and foremost classification of the data. There are a variety of classification techniques available for remote sensing data. The accuracy of these techniques is determined by and measured against training data. Training data is used to calibrate the classification scheme. Therefore, the more training data available, the better able are the algorithms to discern, for example, a tree from a rock. Naturally the quality of the training data is important, since errors in the training data are propagated throughout the entire data set. Consistent data is also important and in the case of the SNRA we do not have a consistent source of remote sensing data, but rather three very distinct sources; distinct in the type of remotely gathered data, the resolution of the images, and the time of year when the data were gathered. As a consequence, employing the same measure over multiple years is not reliable and instead we need to adjust the data on a year by year basis.

In this paper we will apply the Red Top Model to these remote sensing data. Doing so requires some post-processing of the data and a discussion of the errors in the data. We propose adjustments to the data that are minimally offensive to correct or compensate for the errors in classification and the training data. We will also use various aggregations of the data in an effort to find a characteristic scale for this landscape model. Aggregating data is performed by simply combining data from smaller cell sizes into a new cell with larger dimensions, and in doing so, averaging the densities of several cells into one cell. As we will see, this is an important tool in assessing the distribution and structure of the data, as well as mitigating small positional errors. We will investigate the trade-offs between fine and coarse resolution, minimizing loss of information while still protracting the landscape phenomena of beetle-forest interaction. Finally we will compare the results from these remote sensing data with those of the ADS data.
4.2. The Red Top Model

The Red Top Model is a minimally complex model based on the dispersal and attack behavior of the mountain pine beetle and the structure of the lodgepole pine forest. In Eq. (4.1) juvenile trees, $J_t$, are assumed to be immune to attack since they do not provide a suitable host environment for the beetles. Vigorous trees, $V_t$, are susceptible to attack and this susceptibility is a function of infected trees in the vicinity, $I_t$. The pressure on the vigorous tree stand by beetles is density dependent, and is modelled by a response function based on the density of infected trees. We will consider two response functions, one exhibiting threshold dynamics, the Type III response function: 

$$ \phi(I_t, \alpha^2) = \frac{I_t}{I_t + \alpha}, $$

and one that does not, the Type II: 

$$ \phi(I_t, \alpha) = \frac{I_t}{I_t + \alpha}. $$

In this way we can test the importance of including threshold dynamics in a landscape model for this system. If an attack is successful, the tree becomes a red top host in the next generation of beetles. The parameter $\alpha$ is the ratio of beetle effectiveness to infected tree's beetle fecundity. Together this ratio is a measure of the overall effectiveness that beetles have in a given year. We use a probability density function (pdf) to model the dispersal of beetles at the time of emergence. For this investigation we have restricted ourselves to kernels that include one dispersal parameter, $\delta$, that impacts the shape of the pdf. As with the choice of response functions, there are many kernel candidates to choose from. Here we wish to distinguish between two different broad possibilities: host selection at random in space (i.e. due to a random walk process), which would follow a Gaussian dispersal kernel 

$$ K(x, y, \delta) = \frac{1}{2\pi \delta^2} e^{-(x^2 + y^2)/2\delta^2} $$

(Kot et al., 1996), and host selection due to directed motion, which would follow an exponential distribution 

$$ K(x, y, \delta) = \frac{1}{2\pi \delta} e^{-\sqrt{x^2 + y^2}/\delta} $$

(Powell and Zimmermann, 2003). When we convolve the density of infected trees with either dispersal kernel, we arrive at the post-dispersal influence of infected trees resulting from the summer emergence of beetles. We employ the notation $I^*$ to represent the density of infected trees resulting from dispersed beetles where

$$ \begin{pmatrix} J_{t+1} \\ V_{t+1} \\ I_{t+1} \end{pmatrix} = \begin{pmatrix} 1 - s & b & 0 \\ s & d - \phi(I^*_t) & 0 \\ 0 & \phi(I^*_t) & 0 \end{pmatrix} \begin{pmatrix} J_t \\ V_t \\ I_t \end{pmatrix}. $$

In Eq. 4.1 parameters $b$, $s$, and $d$ refer to the birth, maturation and death rates, respectively, of the healthy lodgepole pine forest. The modularity of the model allows us to test the appropriateness...
of assumptions made regarding beetle attack dynamics (threshold versus mass action) and dispersal (random verses directed searching) by changing the response function, $\phi$, and the dispersal kernel, $K$. Combinations of response functions and dispersal kernels yield four Red Top Models. We will compare the results of models against the available data to determine the most appropriate model and most suitable assumptions. For a more detailed derivation of the Red Top Model including an explanation of related assumptions, please see (Chapter 2).

4.2.1. Parameter Values from Estimating Functions

The method of estimating functions was employed in Heavilin (Chapter 2, Chapter 3) to fit the Red Top Model's parameters to the ADS data. This method takes a function of the parameters and the data and reformulates it into a zero valued function for when the model perfectly fits the observations. The estimating functions are applied to the entire space and yield a set of parameter values that on average are not over or underestimated. See Chapter 2 for a more detailed explanation.

This procedure applied to the ADS data by Heavilin and Powell (Chapter 3) yielded results that were consistent with anticipated values and allowed for meaningful interpretation of the model in the SNRA. But as we will discuss shortly, there is a lack of confidence in the exact locations of infected trees. Moreover, as discussed in the previous section, remote sensing data were acquired in three different scales (4 meter, 0.6 meter and 1 meter cell sizes) and were aggregated to 1 meter cell sizes to be used by the Red Top Model. We address this concern in Section 4.3.

4.2.2. Model Selection Using Facial Recognition Algorithm

The Red Top model provides a way for us to compare different response functions and dispersal kernels within the modeling framework to determine if one mechanism better approximates the phenomena. We therefore wish to compare the Red Top Models under consideration to see if threshold densities are important in beetle attack dynamics, or if the nature of dispersal from an infected tree is important at a local or landscape scale. To this end we use the method applied by
Heavilin (Chapter 3) to select the best model. We view each model map as a photo of the forest and apply a facial recognition algorithm to determine which result is closest to the observed data. This technique of projecting a high dimensional space onto a lower dimensional space via Principal Component Analysis (PCA) has been used successfully for facial recognition (Turk and Pentland, 1991; Belhumeur et al., 1997; Zhao et al., 2003), and given that the remote sensing images are photos, the technique is particularly well suited to this application. PCA provides an unsupervised method that results in a linear subspace of the original space. In our case the original space is the set of maps and model predictions. A collection of maps amounts to a data set in this high dimensional space. Applying PCA to this data set yields a set of eigenvectors emphasizing the locations of variability between the maps (Duda et al., 2001). Employing a simple Euclidean measure of distance we determine the closest model to the observation in the lower dimensional projection of the original data. For a more detailed description of this technique applied to spatial data see (Chapter 3).

4.3. Data

Previous applications of the Red Top Model to the SANRA have used ADS data. This data is presented at 30 meter square cell sizes. Unlike the ADS data for which there are many years of systematically collected data, the remote sensing data available is far less consistent. Here we will discuss the uncertainty in the data, the steps taken to arrive at appropriate data for use with the Red Top Model, and corrections taken during post-processing.

4.3.1. Remote Sensing Data

There are three years of remote sensing data available for analysis and application to the Red Top Model ranging from 2001 to 2003. This allows for two sets of parameters to be calculated for the pairs of sequential years. However, the source of the imagery is not consistent. For classification purposes training data were collected for classifying the remote sensing data; GPS coordinates of
vigorous and infected trees were recorded for this purpose. However, instead of using the training data directly, it was necessary to use a supervised method of looking for vigorous or infected trees in the neighborhood of the GPS points to produce the final training data for classification. This is because locations of infected trees observed in the field sites did not reconcile well with corresponding locations in the satellite maps. This was due in part to a lack of accuracy from the GPS service. In addition to this error, the disconnect between the satellite image and GPS-identified locations is a result of the satellite’s position at the time the photo was taken. Since the satellite was not directly overhead of the SNRA, the position of the tops of the trees are displaced relative to the trunks. In some cases the slope of the terrain aggravated this displacement. Coupling this with the technical limitations of the GPS service, we found that errors in location in the image were several meters. In Section 4.2.1 we will discuss in more detail the impact that this error at fine resolution has on parameter values.

The data from 2001 are provided by a 4-band multispectral IKONOS satellite image of the entire SNRA valley at a resolution of four meters. Quadratic discriminant analysis (QDA) provided classification of ten classes including vigorous and infected trees, sagebrush, grass and shadow. One notable error in the classification of this year’s data is the high rate of misclassification between lodgepole pine and Douglas fir. To correct for this, all Douglas fir below 7100 feet elevation are reclassified as lodgepole pine. The resulting map is a pixel by pixel identification of the two classes of interest: vigorous and infected lodgepole pine trees. From this classified map two sample areas are selected to produce the maps for 2001 of infected and vigorous lodgepole pine trees. From here on we refer to these areas as the northern and southern areas.

In 2002 low level aerial photography provided hundreds of photos that were stitched together to form maps of the same areas selected from the IKONOS satellite data. Because the IKONOS image provided a cover map of lodgepole pine, the 2002 data were classified purely for rendering a map of infected trees. The classification method differed from the 2001 data, involving a supervised and iterative comparison between the original image and the classified map in the two areas of interest. Moreover, this year’s image was delivered at one meter resolution, finer than the IKONOS.

In the final year, 2003, again we have satellite data, collected this time by QUICKBIRD. This data is provided in two distinct images of the same areas. However the resolution of these images is 0.6 meters. A similar classification process was used for this year as was used for the 2002 aerial photography.
Although the three years of data were gathered at a variety of scales, the scales were standardized to one meter squares in order to be compatible with the Red Top Model. Choosing a one meter resolution, each data cell in the IKONOS image was simply divided into 16 identical one meter cells. The QUICKBIRD image was interpolated from 0.6 meters to match the IKONOS data using ARCVIEW®.

We now have four data files for both the northern and southern areas: one map of vigorous trees termed the cover map of the forest, and a map for each year 2001 through 2003 of infected trees. All maps contain boolean values reflecting presence or absence of trees. The locations of the northern and southern areas within the SNRA are illustrated in Figure 4.1. For a complete description of the classification procedure see Cutler et al. (2003).

To convert the data from presence and absence to densities, ground data were collected at plot locations in both the northern and southern areas. These surveys recorded the number and size of vigorous trees and the estimated year of attack of infected trees within the plots. These survey numbers within a site are then compared to the number of pixels the classification method identified as vigorous or red top tree in the matching location. These data allow us to regress a pixel to tree conversion for each of the eight files mentioned. Table 4.1 lists the names of the sites throughout the SNRA, their associated pixel count of red top trees and the number of infected trees observed in the field.

We regressed these data to arrive at a pixel to tree conversion factor specific to each map and area. Since the satellite image from 2001 covered the entire valley and provided the cover map of vigorous trees and the 2001 infected trees, the plot data were combined yielding a pixel to tree conversion applied to both areas for that year. Figure 4.2 shows the regression lines correlating pixel number to observed trees for each of the years.

To see if the results of our regression are credible we consider the following cursory investigation. Table 4.2 lists the mean density of cells that contain trees. These values for the infected maps are reasonably close to the highest density one would expect to find in a densely packed stand of timber. However, the value for the cover map of healthy lodgepole pine far exceeds any reasonable stand density of mature trees. At 12,987 trees per hectare, the forest would need to have trees standing less than one meter apart. In the best of circumstances, stand densities are near one thousand trees per hectare. A more reasonable maximum for tree density in the SNRA of a mature stand is less than this (Smith et al., 2002). There are two places where this error could have been introduced.
Table 4.1. A list of the plots where ground data was collected for the pixel to tree conversion. Each column lists pixel counts in the plot and the number of trees observed.

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<td>Pixels Trees</td>
<td>Pixels Trees</td>
<td>Pixels Trees</td>
<td>Pixels Trees</td>
<td>Pixels Trees</td>
</tr>
<tr>
<td>Cheddar</td>
<td>109</td>
<td>93</td>
<td>45</td>
<td>16</td>
<td>555</td>
</tr>
<tr>
<td>Destruction</td>
<td></td>
<td></td>
<td>41</td>
<td>10</td>
<td>720</td>
</tr>
</tbody>
</table>

Either the classification applied to these maps over classified the pixels as green trees and/or the regressions for pixel to tree conversion underestimated pixel to tree conversion. Unfortunately it is not possible to reprocess the maps with new training data. Therefore the only fix is to adjust the pixel to tree conversion so that the densities more closely reflect what one expects to find in a lodgepole pine forest in the Intermountain Northwest. Since the density is roughly 20 times the average vigorous lodgepole pine density one would expect to see in the SNRA, we remedy this error by multiplying the pixel to tree conversion for these data by a factor of 20. We scale the map of infected trees for 2001 along with the cover map because both of these maps were generated from the same remote sensing data and classified by the same scheme.

Another adjustment to the data involves correcting locally for over-classification of infected trees in particular cells of the 2002 and 2003 maps. In any given cell on the map, the density of infected trees can not exceed the density of the vigorous trees in the previous year. We therefore filter the
TABLE 4.2. Densities of trees in the northern and southern areas. As the maps are aggregated, high densities of trees are spread throughout the neighboring space, resulting in the presence of infected trees in more cells, but at lower densities. After scaling the map of healthy lodgepole pine trees by 20, the resulting maps reflect densities of trees more compatible with densities we expect to see in a forest such as the SNRA. We scale the map of infected trees for 2001 along with the cover map because both of these maps were generated from the same remote sensing data and classified by the same scheme.

<table>
<thead>
<tr>
<th>Map</th>
<th>Trees/Hectare</th>
<th>Trees/Hectare After Scaling</th>
</tr>
</thead>
<tbody>
<tr>
<td>North 2001</td>
<td>2,703</td>
<td>135</td>
</tr>
<tr>
<td></td>
<td>1,715</td>
<td>1,715</td>
</tr>
<tr>
<td></td>
<td>3,390</td>
<td>3,390</td>
</tr>
<tr>
<td>South 2001</td>
<td>2,703</td>
<td>135</td>
</tr>
<tr>
<td></td>
<td>664</td>
<td>664</td>
</tr>
<tr>
<td></td>
<td>6,849</td>
<td>6,849</td>
</tr>
<tr>
<td>Cover Map 2001</td>
<td>12,987</td>
<td>649</td>
</tr>
</tbody>
</table>

2002 and 2003 maps according to this rule. Although this occurs in a relatively small number of cells, it can introduce numerical anomalies at fine resolutions.

Thus far we have discussed some of the sources of uncertainty in the data as well as measures taken to correct for errors. We have also pointed out that the fine resolution images yielded maps that may contain positional errors of several meters. In the next section we will discuss how parameter values are impacted by these errors and suggest that there is a scale above which the errors are mitigated, while still retaining the spatial integrity of the data.

4.3.2. Estimating Parameters with Simulated Data

It seems reasonable that the $\delta$ and $\alpha$ values would change as the map cells are aggregated. But we might ask, "Is there an aggregation scale up to which the spatial structure of the data is still relatively unaffected while still being fine enough to take advantage of the information provided by high resolution data?" We begin our investigation by considering simulated data, modelled in accordance with the Red Top Model. We start with the 2001 map of infected trees and the associated cover map, apply the Red Top Model to generate the subsequent year's infected trees, then solve for the parameter values used in the simulation. This way we start with a known set of parameter...
values and observe the effects of aggregation on resulting parameters.

An intuitive argument can be made regarding how aggregation might affect values of $\delta$. Since aggregation implies ever-increasing distances between adjacent information in the data sets, the mean dispersal distance (and therefore the values arrived at for $\delta$) will increase. For example, if the true value for $\delta$ on a five by five meter map is 15 meters, then by aggregating, the information that resulted in the true value is partially contained in cells spanning ever greater distances, forcing an increase in the parameter value purely as an artifact of the aggregation. It can be shown in a simple case that for a fixed $\delta$ the value of $\alpha$ is averaged as we aggregate from finer to coarser resolutions, and that dividing into finer resolution does not change the value of $\alpha$ (see Appendix C).

Now we consider what happens in a controlled experiment by aggregating a portion of the vigorous and infected tree data taken from the 2001 remote sensing data sets and simulating the next year’s density of infected trees using the Red Top Model. Aggregating these data by summing the contents of adjacent cells and re-applying the estimating function procedure to the maps of ever-increasing cell sizes we see that the parameter values for $\alpha$ increase, as do the values resolved for $\delta$. This is consistent with our predictions. Figure 4.3 illustrates the parameter values resulting from the same data aggregated up to 100 meter cells. We see that the values for $\delta$ and $\alpha$ are relatively stable, at least until an aggregation of 20 meter squares. Thereafter we see a heteroscedastic trend emerge in the data with increasing variance in the values for both parameters. Beyond 60 meter cells there is a general increasing trend in addition to increasing variance.

In the case of the remote sensing data, we are aware of errors in the location of infected trees. To assess how these errors may affect parameter values we simulate this positional error in the simulated data used for Figure 4.3. We move over the map of infected trees in blocks of five meters; within each block we reposition a random number of cells. This results in slightly “misplaced” infected trees, never more than a few meters from their actual location. When we execute the same parameter fitting algorithm to the modified data over the same set of cell aggregations we find that for small cell sizes (low aggregations) the fitting algorithm has difficulty resolving a solution, sporadically finding approximations for $\delta = 25$ meters and $\alpha = 200$ trees per hectare. Not until the aggregation scale manages to average-over the relative misplacement of infected trees do we begin to see a pattern of reasonable approximations for the parameters. Again after 60 meters we see an increasing trend in the values for $\delta$.

We suggest that from Figure 4.3 and 4.4 we can find an interval wherein errors in the data can be
mitigated while still retaining meaningful spatial structure. It is within this interval of aggregations that we look for a scale to apply the Red Top Model to the actual remote sensing data. We apply the parameter fitting technique mentioned in Section 4.2.1 to each of the four models under consideration for each pair of data (i.e. 2001-2002 and 2002-2003 northern and southern areas) at an aggregation scale satisfying our constraints. We arrive at a collection of models requiring a selection criteria to choose the best model and in doing so are able to infer characteristics of the beetle-forest interaction. We accomplish this task by using the facial recognition algorithm discussed in Section 4.2.2.

4.4. Results

In this section we now apply the techniques mentioned in preceding sections to the remote sensing data. To do so we need to address the question of a characteristic scale for the landscape model; is there a cell size which will reflect the beetle-forest interaction at a landscape scale? We propose aggregating to 30 meters to observe landscape behavior for reasons we will explain shortly. To justify a landscape scale for the Red Top Model, we look to retain as much spatial information by choosing a low level of aggregation, while still using densities that reflect landscape scaled behavior and average over the positional errors in the data. The simulation in Section 4.3.2 illustrates that aggregations below 20 meters does not average over the errors of misplaced trees. Since we are free to choose a scale above this while staying below larger aggregations that compromise spatial structure (> 60 m) we decide upon a convenient scale of 30 meters which matches the ADS data. This allows for a comparison between the ADS data and the remote sensing data in the following section. We also note here that at 30 meters, the cover map's mean density is 259 trees per hectare. This is very close to the 257 trees per hectare density employed in previous applications of the Red Top Model to the SNRA using ADS data (Chapter 3).

With the parameter values listed in Table 4.3 we are able to arrive at predictions from each model (GII, GIII, EII and EIII). Then by applying the model selection algorithm described in Section 4.2.2 we generate the graphs in Figure 4.5. In these figures we see that model GIII is the best fitting model for all cases.
TABLE 4.3. The parameter values resulting from the estimating function procedure applied to the 30 meter aggregated remote sensing data.

<table>
<thead>
<tr>
<th>Data Set</th>
<th>Model GIII</th>
<th>Model GII</th>
<th>Model EIII</th>
<th>Model EII</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>δ m</td>
<td>α tree/ha</td>
<td>δ m</td>
<td>α tree/ha</td>
</tr>
<tr>
<td>North 2001-2002</td>
<td>18.1</td>
<td>55.8</td>
<td>18.5</td>
<td>8.8</td>
</tr>
<tr>
<td>North 2002-2003</td>
<td>16.8</td>
<td>49.3</td>
<td>17.0</td>
<td>6.7</td>
</tr>
<tr>
<td>South 2001-2002</td>
<td>11.8</td>
<td>32.9</td>
<td>11.9</td>
<td>7.4</td>
</tr>
<tr>
<td>South 2002-2003</td>
<td>11.8</td>
<td>25.0</td>
<td>11.9</td>
<td>4.5</td>
</tr>
</tbody>
</table>

4.5. Discussion

In the preceding section we fit the Red Top Model to the high resolution data at 30 meter aggregations and selected GIII (Gaussian kernel with the Type III response function) as the best fitting model for the particular forest system under investigation. We have results for two pairs of years (2001-2002 and 2002-2003) for which the 2001-2002 overlaps with ADS data of the SNRA. This allows us to compare the results from the high resolution data to the results from the ADS data. We now invite the question, is there a benefit to remote sensing data when modeling at the landscape scale? What, if anything, do we gain by acquiring satellite images? Can parameters reflecting the beetle's behavior and the spread of the infestation be derived from less expensive and more readily available survey data?

TABLE 4.4. Results of the ADS and high resolution 2001-2002 data aggregated to 30 meter squares.

<table>
<thead>
<tr>
<th>Data Set</th>
<th>Model GIII</th>
<th>Model GII</th>
<th>Model EIII</th>
<th>Model EII</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>δ m</td>
<td>α tree/ha</td>
<td>δ m</td>
<td>α tree/ha</td>
</tr>
<tr>
<td>North 2001-2002</td>
<td>17.5</td>
<td>15.6</td>
<td>17.8</td>
<td>3.8</td>
</tr>
<tr>
<td>ADS</td>
<td>18.1</td>
<td>55.8</td>
<td>18.5</td>
<td>8.8</td>
</tr>
<tr>
<td>High Resolution</td>
<td>11.9</td>
<td>8.0</td>
<td>12.0</td>
<td>2.5</td>
</tr>
<tr>
<td>South 2001-2002</td>
<td>32.9</td>
<td>11.9</td>
<td>7.4</td>
<td>11.7</td>
</tr>
<tr>
<td>ADS</td>
<td>11.8</td>
<td>8.0</td>
<td>12.0</td>
<td>2.5</td>
</tr>
<tr>
<td>High Resolution</td>
<td>11.8</td>
<td>32.9</td>
<td>11.9</td>
<td>7.4</td>
</tr>
</tbody>
</table>

Parameters found using the ADS data and the remote sensing data at the 30 meter square aggregation scale are listed in Table 4.4. Considering the very different sources and processing of the two types of data, the parameters describing dispersal and attack dynamics of the mountain pine beetle are quite similar for this system. It is interesting to note that when we choose the best from
eight predictions to fit to the ADS data, including both the remote sensing as well as the ADS data, the best model is still the Gaussian kernel with the Type III response function using high resolution data in the SNRA. However, due to the problems encountered in processing the remote sensing data, it is difficult to infer very much about beetle attack and dispersal behavior based on the selection results. Despite the shortcomings in the data, the model predictions are consistent with Chapter 3.

We have focused on two parameters, each representing two very different aspects of the model. The first is $\alpha$ which reflects the effectiveness of beetles in attacking trees. This parameter is very sensitive to the density of both the vigorous and infected trees. Because there were significantly different maps resulting from the different classification methods used, we see very different values for $\alpha$ between sets of years. It is hard to say whether 2001 was over classified without asking if 2002 and 2003 were somehow also under-classified. Furthermore, since the cover map came from the 2001 classification but in effect was used for all years, including 2002 and 2003, we have essentially combined apples and oranges to model the third year.

The second parameter, $\delta$, reflects the dispersal distance of emerging beetles. This parameter is related to the mean dispersal distance of the associated kernel, Gaussian or Exponential. We do see that the mean dispersal distance for each kernel is more or less the same.

We have seen how this parameter increases with aggregation, and also pointed out that aggregation is useful when considering a landscape scale. This stresses again the importance of a credible cover map, since the misclassification of vigorous lodgepole pine in locations where none actually exist alter the result for $\delta$ just as the cover map’s incorrect densities alter the values for $\alpha$. We can say that an obvious way to improve the results of the Red Top Model is to start with a better cover map.

Since the dispersal parameter values found at the 30 meter scale for the remote sensing data and the ADS data are relatively close, it is not clear that the remote sensing data gained us much at the landscape scale. In addition, knowing the distribution of tree sizes would be useful in improving model results. From the perspective of a satellite or airplane there is no way to determine the sizes of trees in the forest, since the crowns remain relatively constant for mature trees. Only by surveying the forest can we obtain the forest composition. With this information we could model the forest with more stages of susceptible trees, giving each tree class specific parameters relating susceptibility to attack. Currently we assume that every tree on the cover map is a susceptible tree. Particularly at endemic beetle densities, this is a suspect assumption.
Figure 4.1. Above is a map of the Sawtooth National Recreation Area. The dark squares illustrate the locations of the northern and southern areas for which there are classified remote sensing data.
FIGURE 4.2. Observed numbers of trees and pixel counts from the three sets of data. The regression line is calculated through zero and the slope of this line is used to calculate the pixel to tree conversion in each respective classified image.
FIGURE 4.3. The above graphs are the parameter values, $\alpha$ and $\delta$ resulting from the estimating function procedure when applied to simulated data using $\delta = 25$ meters and $\alpha = 200$ trees per hectare. The simulated data is then aggregated from one meter cells up to 100 meter square cells. We see that the values for $\delta$ and $\alpha$ are relatively stable at least until an aggregation of 20 meter squares. Thereafter we see a heteroscedastic trend emerge in the data with increasing variance in the values for both parameters. Beyond 60 meter cells there is a general increasing trend in $\delta$ as well as increasing variance. The values obtained for $\alpha$ display an increasing trend consistent with our predictions.
FIGURE 4.4. By taking the data used in Figure 4.3 and displacing randomly selected infected trees from their original location by one to five meters we arrive at the above graphs. At low aggregation levels we see very few solutions for δ that match the actual parameter value used in the simulation and accordingly there are few associated α values. Not until the aggregation level is above 20 meters does aggregating cells compensate for the random displacement of infected trees. At this point we see values for both δ and α that reasonably approximate the true values (δ = 25 meters and α = 200 trees per hectare). Once again, beyond 60 meter cells there is a general increasing trend in δ as well as increasing variance.
FIGURE 4.5. Projections of model predictions onto the two-dimensional subspace reveal the model "closest" to the observations (here centered at the origin). This model selection method applied to 30 meter square data selects the Gaussian kernel with the Type III response function in all cases. This is consistent with the results of the Red Top Model applied to the ADS data in Chapter 3.
CHAPTER 5
SUMMARY AND FUTURE WORK

The goal of this project was to develop a landscape spatial model to describe and predict densities of trees infected by mountain pine beetles in lodgepole pine forests. Landscape scaled models encounter many difficulties, ranging from scaling issues and data quality to validation.

In chapter two we began with the Red Top Model. Here we succeeded in presenting a model that is based upon fundamental mechanisms of beetle attack and dispersal dynamics as they are currently understood. The use of estimating functions for parameter fitting facilitated speedy results with large data sets.

The third chapter contained four versions of the Red Top Model. Again we used estimating functions to fit the models. We also introduced a method of model selection for dealing with spatial models, since current methods leave much to be desired. The facial recognition algorithm provided a way to arrive at a subset of models that were clearly superior and eventually select a model that best represents the system over the course of available ADS data.

The third chapter centered around analysis and application of high resolution remote sensing data gathered by both satellite and aerial photography. We found that with the higher resolving power of remote sensing data comes the question of scale. We discussed possible scales of aggregation which are appropriate for the data to provide a landscape perspective. We chose thirty meter aggregations of the data to balance errors in the data with loss of spatial structure. It is in this chapter that we find the parameter fitting method of choice almost indispensable. Estimating functions allowed for a thorough testing of ideas at a variety of scales. The computational burden of other popular fitting techniques, like minimizing residual sums of squares, would have been very limiting. We were able to match the regions of remote sensing data to the ADS data and compare the parameters resulting from these areas in the forest. We concluded that the remote sensing data, and their associated parameters, provided even a better prediction of the ADS than the ADS data itself. However, the parameter values returned from both data types (ADS and remote sensing) are very similar, precluding stating confidently that the ADS data is inferior.
5.1. Difficulties with Landscape Models

It is worth recognizing several prominent difficulties we encountered during our research. To begin with, we would be remiss in not emphasizing that there is a clear relationship between the parameter values that describe dispersal distance, $\delta$, and the scale at which the data is aggregated. Once the data has been aggregated beyond a size comparable to the value for $\delta$, there is a bias accumulated with each meter of aggregation. This suggests that the similarity between the 30 meter ADS data and the same scaled remote sensing data could be an artifact of the bias at that scale, rather than a reflection of the true dispersal distance of the beetles. This points to a weakness in the method of aggregation used to scale the data. In Section 5.2 we propose this topic as one avenue of further work that can be done to improve the model.

Other published work on landscape spatial models have offered confidence intervals for the parameter values used in the model (Lele et al., 1998). Although this is a reflection of the robustness of the fitting technique employed, there is some doubt as to the meaningfulness of offering 95% confidence bands for parameters resulting from data that does not provide comparable accuracy. It begs the question, "how can we be certain of parameter values associated with spatial structure when we are not certain that the tree actually exists within five or ten meters of its position on the map?" The same can be said regarding the parameter $\alpha$, which is closely linked to the density of both the healthy and infected lodgepole pine trees. Determining a confidence interval for beetle effectiveness is hardly meaningful if there is no clear value set on the tree stand density. By adjusting the cover map density one can affect the $\alpha$ yielded by the estimating function procedure.

Finally, in an attempt to provide some confidence in the parameter values once we assume an appropriate scale and assume tree densities, we considered a number of approaches. Among them, sub-sampling from the larger map to construct confidence bands about our parameter values, and various "bootstrapping-like" procedures aimed at exploiting the linearity of the integral transform used to model dispersal (the convolution). Since altering the spatial structure should alter the resulting parameter values, we can expect that these techniques would result in predictably different parameter values. We found that the bias was toward larger values for $\delta$ and smaller values for $\alpha$. None of our efforts to establish confidence in our parameter values resulted in meaningful confidence intervals containing the original parameter values. In the end, providing confidence intervals for
the parameters applied to the SNRA proved illusive. To honestly address this question, we need to apply the Red Top Model to a number of forest systems that have similar stochastic properties as the SNRA, and from this pool of forest systems we could ascertain the quality of the parameter results.

5.2. Future Work

This is only a first step in the development of a more comprehensive model for this system. There are primarily three areas of interest where the Red Top Model could be improved.

First, tree stand composition and health strongly determine the resistance and resilience of a forest stand. The data we have been working with does not provide adequate information about the forest structure to take full advantage of the Red Top Model. We needed to combine all susceptible classes into one because we were not able to determine distributions of various diameter breast height based on the crown of the tree. We were also forced to assume a constant tree stand density throughout the forest where lodgepole pine were present. We know this not to be the case in the SNRA and heterogeneity of tree stand density can play an important role in beetle dispersal and attack (Haiganough and Preisler, 1993; Preisler and Haiganough, 1993; Mitchell and Preisler, 1991). Coupling the Red Top Model with better forest data would greatly enhance the strength of the Red Top Model.

Second, there is a clear need to aggregate high resolution data to overcome the local positional errors we discovered. However simple arithmetic averaging of the densities was not truly adequate. Exploring alternative averaging methods would be helpful in describing a characteristic scale, and result in more accurate parameter values. Finally, we know that temperature plays an important role in beetle development and incorporating a beetle phenology model into the Red Top Model may explain the yearly variability in beetle attack effectiveness and in turn proliferation of infected trees.

These areas for improvement would enhance the predictive capacity and thereby the usefulness of the Red Top Model. As it stands the Red Top Model had yielded ecologically meaningful parameter values that are based upon data available for the SNRA. It affords the chance to relate our results to findings from other studies regarding beetle dispersal and their attack on lodgepole pine with those
of the model, either adding credibility to an assumption (i.e. the importance of threshold attack dynamics) or weakening the assumption as they pertain to this system.
REFERENCES


APPENDICES
APPENDIX A
FACIAL RECOGNITION ALGORITHM

Using the technique described by Turk and Pentland (Turk and Pentland, 1991) we treat each model prediction map as a matrix of \( n \times m \) observations. We convert the \((n, m)\) map into a vector, \( \Gamma_{(1,m\times n)} \), or equivalently a point in a \( m \times n \) dimensional space which in the parlance of facial recognition technology is termed “face space”. We concatenate these vectors into a \((m \times n, p)\) matrix, where \( p \) is the number of model candidates, in our case four. A library of maps is then assembled, which is a set of points in this high dimensional space.

\[
\begin{array}{c|c|c|c|c|c|c}
\hline
x_{1,1} & \cdots & x_{1,n} & y_{1,1} & \cdots & y_{1,n} \\
\hline
x_{2,1} & \cdots & x_{2,n} & y_{2,1} & \cdots & y_{2,n} \\
\hline
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
\hline
x_{m,1} & \cdots & x_{m,n} & y_{m,1} & \cdots & y_{m,n} \\
\hline
\end{array}
\Rightarrow
\begin{array}{c|c|c|c|c|c|c}
\hline
x_{1,1} & y_{1,1} & \cdots & x_{1,2} & y_{1,2} & \cdots & x_{1,n} & y_{1,n} \\
\hline
x_{2,1} & y_{2,1} & \cdots & x_{2,2} & y_{2,2} & \cdots & x_{2,n} & y_{2,n} \\
\hline
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
\hline
x_{m,1} & y_{m,1} & \cdots & x_{m,2} & y_{m,2} & \cdots & x_{m,n} & y_{m,n} \\
\hline
\end{array}
\]

Next we calculate the average point in face space by constructing a mean vector of the observations, \( \Psi = \frac{1}{p} \sum_{i=1}^{p} \Gamma_i \) and with it calculate the covariance matrix. Each map differs from the mean by \( \Phi_i = \bar{x}_i - \Psi \). This yields the covariance matrix \( C = \frac{1}{m} \sum_{n=1}^{m} \Phi_n \Phi_n^T \). Using Principle Component Analysis we find the set of Principle Components (PC’s) which are just an orthonormal basis composed of the eigenvalues and eigenvectors of the described covariance matrix,

\[
\lambda_i = \max \left( \frac{1}{p} \sum_{n=1}^{p} (u_i^T \Phi_n)^2 \right) : u_i^T u_k = \delta_{lk} = \begin{cases} 
1 & : l = k \\
0 & : \text{otherwise.}
\end{cases}
\]

To avoid calculating the eigenvectors of an \((n \times m)\) by \((n \times m)\) matrix, which in the case of our forest maps is a 1,974,829 by 1,974,829 matrix, it can be shown that the maximum eigenvalues of \( B = \frac{1}{m} \sum_{n=1}^{m} \Phi_n^T \Phi_n \) are equal to \( \lambda_i \) resulting from PCA applied to \( C \) (Turk and Pentland, 1991). The advantage is that \( B \) is only a \( p \times p \) matrix (in our case 4), yielding \( p - 1 \) meaningful vectors.

Eigenvalues and eigenvectors of the matrix \( B \) satisfy \( \Phi \Phi^T \Phi u = \lambda u \). Pre multiplying the equation by \( \Phi \):

\[
\Phi \Phi^T \Phi u = \Phi \lambda u = \lambda \Phi u \quad \rightarrow \quad \Phi \Phi^T (\Phi u) = \lambda (\Phi u) \quad \rightarrow \quad \Phi \Phi^T \mu = \lambda \mu
\]
and we see that $\lambda$ is an eigenvalue of $\Phi \Phi^T$ as well. Finally, we need only multiply $v$ by $\Phi$ to arrive at the eigenvector of the full covariance matrix, $\mu$, associated with $\lambda$. We use these eigenvectors to find the projection of the predicted maps onto lower dimensional spaces and determine to which one the projection of the observation lies most closely.
APPENDIX B

ESTIMATING FUNCTIONS FOR THE RED TOP MODEL

In the case of the Red Top Model using the Type II response function in the equation for the density of infected trees, we algebraically rearrange the response function to become an estimating function.

\[ I_{t+1} = \frac{I_t}{I_t + \alpha} \rightarrow G(I_{t+1}, I_t, \alpha, \delta) = V_t I_t^* - I_{t+1} I_t^* - \alpha I_{t+1} = 0 \]  
\[(B.1)\]

Here \( G(I_{t+1}, I_t, \alpha, \delta) \) is the estimating function, which by definition is simply any function of the data and parameters which also has a distribution of errors with mean zero. Since we realize that the model will not perfectly fit the data, but instead produce an error on a cell by cell basis,

\[ G_{i,j} (I_{t+1,i,j}, I_{t,i,j}, \alpha, \delta) = V_{t,i,j} I_{t,i,j}^* - I_{t+1,i,j} I_{t,i,j}^* - \alpha I_{t+1,i,j} = \epsilon_{i,j} \]  
\[(B.2)\]

For the correct parameter values, the sum over all space and time of all \( G_{i,j} (I_{t+1,i,j}, I_{t,i,j}, \alpha, \delta) \) will converge to zero. For our purposes we calculate parameters on a year by year basis, and therefore only sum over the space.

\[ \sum_{i,j} G_{i,j} (I_{t+1,i,j}, I_{t,i,j}, \alpha, \delta) = \sum_{i,j} \epsilon_{i,j} \rightarrow 0. \]  
\[(B.3)\]

The convergence is accelerated by weighting functions which effectively push poor parameter sets further from zero. The use of weighting functions also provides a convenient way to construct a system of linear equations which enable us to solve for any number of linear parameters in the model. It can be shown that an optimal set of weighting functions is provided by the expected values of the partial derivatives of Eq. (B.1) with respect to the parameters of interest (Lele et al., 1998).

We now have a homogeneous system of linear equations in terms of the parameters, with expec-
The parameter $\delta$ is nested nonlinearly in the dispersal kernel, but $\alpha$ appears linearly in the response function. This allows us to simply solve for a corresponding $\alpha$ in Eq. (B.4a) for each $\delta$ candidate in the one dimensional parameter space. This approach results in a one dimensional parameter search for $\delta$ over some reasonable range, and for each $\delta$ candidate, there is an associated $\alpha$. The $\delta$ associated with the root of Eq. (B.4b) provides the set of parameter solutions that best fit the model to the data.
APPENDIX C
ESTIMATING PARAMETERS WITH AGGREGATED DATA

We will consider a special case upon which to base our prediction about the effects of aggregation on $\alpha$. The complete unmolested form for the solution of $\alpha$ for the Type II response function over an $m$ by $n$ map is given by

\[
\alpha = \frac{\sum_{i,j=1}^{m,n} V_{i,j} I_{t_{i,j}}^* - \sum_{i,j=1}^{m,n} I_{t+1,i,j} I_{t_{i,j}}^*}{\sum_{i,j=1}^{m,n} I_{t+1,i,j}}.
\]  

(C.1)

Considering the very simple case of $m = n = 2$, we collect four cells into one cell, we add the number of trees in each of the four cells to arrive at an aggregated cell tree count, then divide by the larger area to arrive at the tree density. If the entire map were just these four cells, the solution for the original parameter value, $\alpha_0$ by processing two of these maps would be given by

\[
\alpha_0 = \frac{V_a I_{t+1,a}^* + V_b I_{t+1,b}^* + V_c I_{t+1,c}^* + V_d I_{t+1,d}^* - I_{t+1,a} I_{t_{a}}^* - I_{t+1,b} I_{t_{b}}^* - I_{t+1,c} I_{t_{c}}^* - I_{t+1,d} I_{t_{d}}^*}{I_{t+1,a} + I_{t+1,b} + I_{t+1,c} + I_{t+1,d}}.
\]  

(C.2a)

\[
= \frac{(V_a - I_{t+1,a}) I_{t_{a}}^* + (V_b - I_{t+1,b}) I_{t_{b}}^* + (V_c - I_{t+1,c}) I_{t_{c}}^* + (V_d - I_{t+1,d}) I_{t_{d}}^*}{I_{t+1,a} + I_{t+1,b} + I_{t+1,c} + I_{t+1,d}}.
\]  

(C.2b)

where $V_t$, $I_{t+1}$ and $I_t^*$ are given in densities of trees. However, aggregating the maps in the following manner

\[
\begin{array}{ccc}
\text{Year } t & \otimes & \text{Year } t + 1 \\
\begin{array}{cc}
a & b \\
c & d \\
\end{array} & \Rightarrow & \begin{array}{cc}
a & b \\
c & d \\
\end{array} \\
\end{array}
\]  

\[
\begin{array}{ccc}
\text{Year } t & \otimes & \text{Year } t + 1 \\
\begin{array}{cc}
a & b \\
c & d \\
\end{array} & \Rightarrow & \begin{array}{cc}
a & \text{A} \\
c & \text{B} \\
\end{array}
\]  

would yield

\[
\alpha_1 = \frac{(V_a - I_{t+1,a}) \hat{I}^* + (V_b - I_{t+1,b}) \hat{I}^* + (V_c - I_{t+1,c}) \hat{I}^* + (V_d - I_{t+1,d}) \hat{I}^*}{I_{t+1,a} + I_{t+1,b} + I_{t+1,c} + I_{t+1,d}}.
\]  

(C.3)

\[
\text{where } \hat{I}^* = \frac{I_{t+1,a} + I_{t+1,b} + I_{t+1,c} + I_{t+1,d}}{4}.
\]

This form of $\alpha$ is very similar to that given in Eq. (C.2) except that the dispersed infected trees are now averaged over the space. Since dispersal itself tends to spread the density of infected trees into surrounding cells, averaging dispersed infected tree density has a
minor effect on the value for $\alpha$ under modest aggregation.

If we are going to be able to compare remote sensing data at a one by one meter scale to ADS data at 30 by 30 meters another worthy question is, “Can we break down the cell into a finer resolution without introducing a bias?” In this case

\[
\begin{array}{ccc}
\text{Year } t & \text{Year } t + 1 & \text{Year } t & \text{Year } t + 1 \\
A & \otimes & B & \rightarrow & a_A & b_A & a_B & b_B \\
& & & & c_A & d_A & c_B & d_B
\end{array}
\]

The associated equation for $\alpha$ is

\[
\alpha_0 = \frac{V_A I_{I_{t_{\Delta}}}^* + V_B I_{I_{t_{\Delta}}}^* + V_C I_{I_{t_{\Delta}}}^* + V_D I_{I_{t_{\Delta}}}^* - I_{t+1_{I_{t_{\Delta}}}}^* - I_{t+1_{I_{t_{\Delta}}}}^* - I_{t+1_{I_{t_{\Delta}}}}^* - I_{t+1_{I_{t_{\Delta}}}}^* - I_{t+1_{I_{t_{\Delta}}}}^* - I_{t+1_{I_{t_{\Delta}}}}^*}{I_{t+1_{I_{t_{\Delta}}}} + I_{t+1_{I_{t_{\Delta}}}} + I_{t+1_{I_{t_{\Delta}}}} + I_{t+1_{I_{t_{\Delta}}}}}. \tag{C.6}
\]

Since the densities for each sub-cell are identical, Eq. (C.6) reduces to

\[
\alpha_0 = \frac{V I_{I_{t_{\Delta}}}^* - I_{t+1_{I_{t_{\Delta}}}}^*}{I_{t+1_{I_{t_{\Delta}}}}} \tag{C.7}
\]

which is $\alpha$ resulting from the original larger scaled maps, and so the solution for $\alpha$ is unchanged.

These simplified special cases suggest that, at least to some degree of aggregation and division of cells, the parameter values will stay within a neighborhood of the original $\alpha_0$. 
APPENDIX D

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APPENDIX E
CURRICULA VITAE
Education
Utah State University  Ph.D. Applied Mathematics: graduating Spring, 2007
Adviser: James Powell
Humboldt State University  M.S. Mathematical Modelling: Spring, 1996
Thesis Topic: "A Model of Intraspecific Competition for a Dynamically Modelled Resource"
Adviser: Kathline Crowe
Humboldt State University  B.A. Mathematics: Spring, 1994
Universität Bielefeldt  Two years studying abroad in Bielefeldt, German

Awards
Second place: Presentation at the Utah State University Graduate Research Symposium. April 2006.
Graduate Teacher of the Year. Mathematics and Statistics Department, Utah State University. 2003 & 2004.

Research Interests

Work Experience
Field technician in the Sawtooth National Recreation Area collecting data on mountain pine beetle emergence, tree phloem temperature time series, and recording GPS data. Summers 2002-2005.

Publications


Presentations

