

Local Consequences of a Global Model for Mountain Pine Beetle Mass Attack

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Abstract

A coupled partial differential equation model for interaction between mountain pine beetles (MPB) and lodgepole pine is reviewed. An asymptotic ‘one-tree’ solution is examined and time scale of the chemical response discussed. The equations are decoupled making an adiabatic assumption for MPB chemotaxis, and a ‘local’ projection is made using the leading eigenfunction for the MPB density equation. This projection yields a system of ordinary differential equations for the spatio-temporal response at a single tree. These equations are analyzed, and their behavior compared with observations.

1 Introduction

Mathematical reasoning has played a central role in ecological theory and application for at least the past seventy years (dating from the independent rediscovery of Verhulst’s (1845) [1] work by Pearl and Reed in 1920 [2]). From the very beginning of these applications, there has

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been an appreciation for the role that spatial dynamics play in ecological issues (see [3, 4] for a recent reviews). Irrespective of these attempts to include spatial considerations in ecological models, the preponderance of mathematical modeling applications have involved analysis of spatially independent, ordinary differential (difference) equation (ODE) models. This results not from the lack of perceived importance of spatial effects, but from the conceptual and procedural difficulty in dealing with partial differential (difference) equations (PDE), particularly in describing complex ecological interactions. The increased computational power offered by modern computers has resulted in a resurgence of interest and research on spatial dynamics in ecological phenomena. Indeed, the inclusion of spatial dynamics in meaningful ecological models has been termed the “last frontier” in ecological theory [5].

Spatial dynamics typically play a central role in the community dynamics of highly mobile insects [6]. For example, dispersal is one of the most important, yet least understood, factors of bark beetle population biology [7]. Current research with mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins), indicates that spatial dynamics play a crucial role [8, 9, 10]. MPB has long been considered a major pest in western forests. As an aggressive bark beetle (one that kills its host), eruptions of this species are impressive events. Outbreaks can be both intensive (up to 80% or greater mortality) and extensive (covering thousands of contiguous acres), resulting in serious economic consequences. It is also becoming recognized that disturbances, such as MPB outbreaks, may be central to maintaining the structure, function, and health of western forests.

Interpretation of MPB in this dual role as a serious economic competitor and as a co-evolved component of the ecosystem presents an interesting challenge. One important method to help address this challenge is development and analysis of quantitative models. Because of the ecological importance of MPB/host interactions, a wealth of spatially independent models have been developed [11, 12, 13, 14, 15, 13, 16, 17, 18, 6]. None of these models has been spatially explicit, although one [15] has been spatially extensive, in the sense of simulating many hosts without specific spatial locations. The qualitative dynamics

of almost all of these models has include the effects of a metastable point, corresponding to the need for critical MPB population levels to successfully attack hosts. At either the level of individual hosts or integrated biomass, these models have achieved some success. However, aggregation on and dispersal from a host are of such overriding importance to MPB ecology that including spatial dynamics in model representations is essential for ecological credibility. For many bark beetle species, including MPB, dispersal is only one part of the sequence of events necessary for successful population establishment and expansion. The self-focussing and self-dissipating aspects of the species chemical ecology are also integral components affecting population spatial dynamics. We are building on past models to develop a large-scale (e.g. forest-sized) reaction-diffusion PDE model of the spatial interaction between the MPB and its host trees, including critical components of this species' chemical ecology [19]. The mathematical construction for this model is reviewed below. We refer to the explicit, spatially dynamic model as the *global model* because it attempts to capture the full spatial extent of MPB pheromone ecology. From this modelling endeavor, we have observed that even starting with a completely homogenous environment, the positive and negative feedback generated by attacking beetles soon results in a rich, spatially dependent chemical landscape that tends to modify future events.

As discussed in [19], the global model has proved to be too complicated for easy ecological use. While progress has been made on integration of spatio-temporally stiff PDE [20], the PDE remains unsuited to experimentation and correlation with real data. A *local projection* was achieved, using a Gaussian *ansatz* for the dependent variables [19]. This model facilitated parametrization and experimentation, but the Gaussian assumption for the MPB density function was unable to sufficiently resolve the 'switching' behavior of MPB changing the locus of their attack from a primary focus tree to secondary trees. The switching may result from epidietic¹ pheromones produced by nesting MPB, causing nonlinear dispersal away from a colonized host. One possible consequence could be shielding of non-colonized trees

¹The term epidietic describes specific sorts of animal behavior which are used principally for population density regulation [21]

in the pheromone plume, which could potentially generate spatial complexity.

Our goal in this paper is to develop a local projection of the global model which captures both aggregation and dispersal in a single system of ODE. While some aspects of the global system are based on host-beetle models proposed by Berryman et. al. [12, 13], the advantage of the current approach is that the spatial structure of MPB aggregation is explicit. This gives a more realistic calculation of population thresholds for epidemic, since spatial focussing allows much lower densities of MPB to aggregate in a successful attack. It also allows the current approach to describe the ‘switching’ of MPB following a successful focus attack, which is an essentially spatial phenomenon. The explicit nature of pheromone/kairomone chemotaxis is included in the present model. A simple description of ‘shielding’ is a natural consequence of this projection approach. We will use eigenfunctions for MPB density, which implicitly encode both focussing and switching responses based on local pheromone concentration. The leading eigenfunction will then be used as the basis for a local projection, with Gaussian shapes for the other dependent variables. This projected model encodes all the redistribution behavior in the vicinity of a single tree. Moreover, its dynamics allow us to estimate critical parameters, including the radius of potential shielding and the number of successful attacks necessary to generate nonlinear focussing, or mass attack.

2 Derivation of the Global Model

2.1 Behavior of the Pine Beetle/Host Tree System

Because of its economic impact, MPB population dynamics has been the subject of sustained research efforts dating from the early 1900’s, focussed primarily on protection of valuable forest resources. Although this insect spends most of its life cycle under the bark feeding on phloem tissue, the relatively short phase of the life cycle in which emergence and attack of new hosts occurs is essential for continuing the population. It is during this time that complex spatial dynamics come into play.

The MPB is typically a univoltine species which attacks living pines. Unlike most phy-

tophagous insects, successful reproduction is contingent upon death of all or part of the host [22, 23]. Host trees, however, have evolved effective response mechanisms to defend themselves against bark beetle attacks [24, 25, 26, 27, 28, 29]. Almost all trees are capable of responding to bark beetle attacks, but only those with a rapid and sustained reaction are likely to survive [13, 29]. If many beetles attack the same tree over a short period of time (i.e. mass attack), they can exhaust the tree's defensive mechanisms. The final outcome of a bark beetle dispersal and colonization attempt is, therefore, dependent upon a series of competing rate reactions which regulate both beetle arrival and host response [13, 30, 17, 29].

The evolved relationship between the MPB and its host trees has resulted in an elaborate chemical communication system [29]. Through a chemically-mediated synergistic reaction with host chemical compounds, female beetles attacking a tree release trans-verbenol, which, when mixed with α -pinene, is an aggregation pheromone attracting both sexes [31, 32, 33]. At higher concentrations of trans-verbenol, higher proportions of males are attracted [34]. Attacking males produce exo-brevicomin which at low concentrations primarily attracts females [35]. This system of chemical communication results in mass attack on a single focus tree. However, the tree is a finite food resource that can be over-exploited by too many beetles [14]. Verbenone, an epidietic pheromone, is released by attacking males and inhibits the landing of additional beetles at high concentrations [36]. Once the concentration of verbenone sufficiently exceeds the concentration of aggregating pheromones, flying beetles in the area *switch* to nearby host trees [37, 38, 39]. When the incoming beetles switch, the new tree often has greater attack rates and is colonized more rapidly than the original focus tree [40]. The switching mechanism provides a means for efficiently utilizing the available population of attacking beetles.

Although density-dependent beetle pheromone responses play the dominant role, kairomones produced by the tree may also play a part [41]. At low population densities, attacking MPB selectively attack trees weakened by disease or other stresses [42, 43, 44]. It is hypothesized that stressed trees release a kairomone signal which attracts MPB flying in the vicinity, pro-

viding primary attraction to a particular tree [45, 46, 47]. An alternative hypothesis is that new hosts are found using a combination of random landings guided by visual cues [48, 22] followed by chemical and tactile cues once on the host tree [49, 30]. Most likely, both situations occur. Although the combination of factors that signals a weakened tree remains an open question, enough evidence exists for the effect of host compounds on beetle behavior [50, 51, 28] that models of MPB spatial dynamics should include some representation of host volatiles, as well as beetle-produced pheromones.

The complex chemical cues in the MPB/pine tree interaction act as self-focusing and self-dissipating forces. The interaction of these forces results in a non-linear density dependent response that results in complex spatial patterns of resource utilization. Although the explicit spatial feedback is critical to the ecological association of MPB with its hosts, there is no spatially explicit model of the interaction. In the next section we will review the construction of a spatio-temporal PDE model of the MPB/host spatial ecology.

2.2 The Global Model

We define the following variables, which depend on spatial location, x, y , and time, t :

- $P(x, y, t)$ – population of flying MPB.
- $Q(x, y, t)$ – population of (alive) nesting/eating MPB.
- $A(x, y, t)$ – concentration of pheromones.
- $C(x, y, t)$ – concentration of volatiles released by attacked trees.
- $S(x, y, t)$ – resin outflow.
- $R(x, y, t)$ – resin capacity (related to phloem thickness and size of tree).
- $H(x, y, t)$ – number of entrance holes bored by attacking MPB.

If we neglect spatial redistribution, the number of flying MPB decreases proportionally to the death rate, $\omega_1 P$ and the number of beetles who land and attempt to nest in a tree, $r_1 \frac{R}{R_0} P$. The term $r_1 P$ captures the rate at which MPB land to attack hosts. R_0 is the rest resin capacity of the tree, proportional to the surface area of the bole. Consequently the fraction $\frac{R}{R_0}$ measures the uninfested portion of the bole. This gives a dynamic equation for changes in flying MPB density:

$$\dot{P} = -\omega_1 P - r_1 \frac{R}{R_0} P + \gamma.$$

The term γ captures the emergence rate of flying MPB.

The nesting population, Q , grow proportionally to $r_1 P$. Nesting MPB die at some rate, $\omega_2 Q$. Finally, beetles may be killed by the natural defense mechanisms of the host, resin out-flow. The population of nesting MPB should decrease in proportion to the resin out-flow through occupied burrows, $\beta_1 S \frac{Q}{H}$. This gives an equation for Q ,

$$\dot{Q} = -\omega_2 Q + r_1 \frac{R}{R_0} P - \beta_1 S \frac{Q}{H}. \quad (1)$$

The rate of increase in the number of holes drilled is precisely equal to the number of MPB who have attempted to nest. On the other hand, resin crystallizes after flowing through burrows, slowly closing the hole. This means that the holes should be lost at a rate proportional to the amount of resin out-flow, S , which itself is proportional to the number of holes and the available resin capacity,

$$S = r_3 H R.$$

A rate equation for H is given by

$$\dot{H} = r_1 \frac{R}{R_0} P - r_4 H R. \quad (2)$$

It remains to be determined how the local resin capacity and the amount of resin outflow vary with time. Let R_0 be the reservoir capacity the tree would maintain naturally. When $R \rightarrow 0$ the tree has no capacity to replenish its reservoir, so that the rate of change of the resin capacity should be proportional to $R(R - R_0)$. Resin capacity is depleted proportionally to the number of entrance holes and the available amount of resin which can flow out through the holes. These two processes give

$$\dot{R} = [r_2(R_0 - R) - r_3 H] R. \quad (3)$$

This model for the tree defensive response is related to that proposed by Berryman et. al. [13]. In this earlier work the resin response was dependent on attack density, and the Berryman defensive variable is the resin available to flood a single nest gallery. The R used

here describes the total resin capacity of the attacked tree, and behaves like a bucket with as many punctures as current H . One advantage of this interpretation is that our resin capacity is proportional, in part, to the surface area of the host bole, which is convenient for analyzing rate of attack and the effect of resin exudation on nesting MPB. Otherwise, the host-MPB model above differs from Berryman et. al. by including host recovery (via the variable H) and an explicit mechanism for relating the number of attacks on a host to MPB population densities.

This set of equations reflects the temporal behavior without spatial redistribution. One mechanism for understanding spatial redistribution is to consider mass balances in some arbitrary spatial domain, Ω [52, 53, 3]. The total number of beetles in that domain is

$$N = \int_{\Omega} P dx dy,$$

and can change only due to movement of beetles across the boundary of Ω (flux) or loss/emergence of beetles within Ω (sinks/sources). This gives a simple law,

$$\frac{d}{dt}N = \text{Flux into } \Omega - \text{Flux out of } \Omega + \text{Source Terms} - \text{Sink Terms} .$$

The source and sink terms are described above. For brevity we will denote these terms as $f(P, A, x, y, t)$, so that

$$\text{Source Terms} - \text{Sink Terms} = \int_{\Omega} f dx dy.$$

The flux terms will quantify how the population of flying MPB disperse.

Denote the flux vector by $\vec{\phi}$. There are three basic components to the flux function, reflecting the beetles' recognition of potential hosts, their response to pheromones, and the degree of randomness in their behavior. This allows for an interplay between random and nonrandom movement, as in [54]. Thus,

$$\vec{\phi} = \vec{\phi}_C + \vec{\phi}_A + \vec{\phi}_P,$$

where

- $\vec{\phi}_C$ is flux along gradients of $C(x, t)$ due to chemotactic recognition of potential hosts,

$$\vec{\phi}_C = \kappa P \nabla C.$$

- $\vec{\phi}_A$ is flux due to the beetles' attraction to/repulsion from the suite of pheromones, A . The summed response of these pheromones is attractive in small concentrations, repulsive in larger concentrations, giving

$$\vec{\phi}_A = \nu P (A_0 - A) \nabla A.$$

- $\vec{\phi}_P$ is flux due to the beetles' random redistribution in the absence of other influences, dependent only on spatial changes in the density of flying beetles, which gives

$$\vec{\phi}_P = -\mu \nabla P.$$

Now we return to the balance law. The total flux into Ω will be the integral of the flux vectors around the boundary of the domain. This gives the expression

$$\frac{d}{dt} N = \int_{\partial\Omega} \vec{\phi} \cdot \vec{n} \, ds + \int_{\Omega} f \, dx dy = \int_{\Omega} [f - \nabla \cdot \vec{\phi}] \, dx dy.$$

Here \vec{n} is the unit normal vector to the boundary of Ω , $\partial\Omega$ and we have used the divergence theorem for the latter equality. Writing this expression in terms of only one integration,

$$\int_{\Omega} \left[\frac{\partial P}{\partial t} + \nabla \cdot \vec{\phi} - f \right] \, dx dy = 0.$$

Since Ω is completely arbitrary, the integrand must be zero, giving a spatio-temporal evolution equation for P ,

$$\frac{\partial}{\partial t} P = -\nabla \cdot \{[\kappa \nabla C + \nu(A_0 - A) \nabla A] P - \mu \nabla P\} - \omega_1 P - r_1 \frac{R}{R_0} P + \gamma. \quad (4)$$

This equation and its derivation are similar to equations for environmentally-induced movement in [55, 56, 57, 58].

We will assume that the chemical concentrations, A and C , obey standard diffusion laws, but with sources and sinks of their own. For the suite of pheromones released by nesting

beetles, sources are proportional to Q , while losses occur due to chemical decomposition. These effects give a linear diffusion equation for A ,

$$\frac{\partial}{\partial t}A = b_1\nabla^2A + a_1Q - \delta_1A. \quad (5)$$

For host kairomones, C , the source is resin outflow. Again, we expect some loss due to chemical decomposition, giving an equation similar to that for A ,

$$\frac{\partial}{\partial t}C = b_2\nabla^2C + a_2S - \delta_2C. \quad (6)$$

Equations (1 - 6) are a complete spatio-temporal description of the dependent variables controlling the behavior of MPB/pine relationship.

Parameter	Value	Units	Parameter	Value	Units
a_1	20	tmg hec ⁻¹ fh ⁻¹ mpb ⁻¹	γ_0	20	mpb hec ⁻¹ fh ⁻¹
b_1	50	hec fh ⁻¹	b_2	0	hec fh ⁻¹
δ_1	1000	fh ⁻¹	δ_2	.1	fh ⁻¹
A_0	3	tmg hec ⁻¹	ν	100	hec ³ tmg ⁻² fh ⁻¹
μ	.3	hec fh ⁻¹	κ	10	hec ² tmg ⁻¹ fh ⁻¹
ω_1	.0103	fh ⁻¹	ω_2	0	fh ⁻¹
r_1	.0513	fh ⁻¹	r_2	.1	R_0^{-1} fh ⁻¹
r_3	2.5×10^{-4}	fh ⁻¹	r_4	.1	R_0^{-1} fh ⁻¹
R_0	1	R_0	ρ	2	hec ^{1/2}
β	1.92×10^4	mpb R_0^{-1}			

Table 1: Parametric values for numerical simulation and units. Units involving resin are measured relative to R_0 . Other units are: tmg (10^{-5} grams), hec (10^4 square meters = hectares), fh (flight hours ~ 5 fh/day).

The model above was presented in [19], with a (rough) parametrization based, in part, on the work of Raffa and Berryman [14] and Geiszler et. al. [38, 39]. The numerical values of these parameters used in this paper are presented in table 1, and follow the table published in [19]. In what follows we will neglect C for brevity.

3 Pheromone Response and Asymptotic MPB Density

3.1 Asymptotic States in the Global Model

We begin by analyzing the response of flying MPB to a non-evolving chemical landscape. This information will be of use in later sections, where it will serve to represent the effects of spatial redistribution on a specific spatial location. Let

$$c \delta(\underline{x})$$

be the the chemical source due to nesting beetles at the location $\underline{x} = 0$. Integrating (5),

$$\frac{d}{dt} \int_{\Omega} A(\underline{x}, t) d\underline{x} = \int_{\partial\Omega} b_1 \nabla A \cdot \underline{n} d\sigma - \int_{\Omega} \delta_1 A(\underline{x}, t) d\underline{x} + \int_{\Omega} c \delta(\underline{x}) d\underline{x}.$$

If we consider the boundary of Ω to be at infinity, we expect the flux through $\partial\Omega$ to be zero.

This allows us to simplify to

$$\frac{d}{dt} \int_{\Omega} A(\underline{x}, t) d\underline{x} = - \int_{\Omega} \delta_1 A(\underline{x}, t) d\underline{x} + c.$$

This implies the change in the total amount of pheromone $\int_{\Omega} A(\underline{x}, t)$ over time will be zero when

$$\int_{\Omega} A(\underline{x}, t) = \frac{c}{\delta_1}$$

and the concentration will reach a steady state. This steady state is reached on time scales of δ_1^{-1} , which suggests that the chemical concentrations will be essentially in equilibrium on the time scales of MPB redistribution. Therefore, to examine the steady-state MPB response we take A to be known and stationary. Host kairomones, $C(\underline{x}, t)$, are neglected for the sake of brevity. We will also take $R = R_0$ —small, to denote the population response in an unattacked forest. These assumptions have the effect of decoupling the equation for $P(x, t)$:

$$\frac{\partial}{\partial t} P = -\nabla \cdot \{[\nu(A_0 - A)\nabla A] P - \mu \nabla P\} - (\omega_1 + r_1)P + \gamma, \quad (7)$$

from the rest of the system.

Let $\lambda = r_1 + \omega_1$. On any finite domain we may write the homogenous solution to (7) formally as

$$P = c_0 \rho(\underline{x}) e^{-\lambda t} + e^{-\lambda t} \sum_{i,j}^{\infty} c_{i,j} e^{-\lambda_{i,j} t} \rho_{i,j}(\underline{x}),$$

where $\lambda_{i,j} > 0$ and increasing to infinity and the $\rho_{i,j}$ are orthogonal functions. We may also take

$$\gamma = \gamma_0 \rho(\underline{x}) + \sum_{i,j}^{\infty} \gamma_{i,j} \rho_{i,j}(\underline{x}).$$

Then the formal asymptotic solution to (7) is

$$P = \frac{\gamma_0}{\lambda} \rho(\underline{x}) + \sum_{i,j}^{\infty} \frac{\gamma_{i,j}}{\lambda + \lambda_{i,j}}.$$

Since our aim is to use an explicit function as a surrogate for the spatial redistribution encoded in (7), an approximation is given by the first eigenfunction, or

$$P = \frac{\gamma_0}{\lambda} \rho(\underline{x}).$$

We can now set about determining the form of that first eigenfunction.

The change of variables

$$P = e^{-(\omega_1 + r_1)t} \rho(\underline{x})$$

gives

$$P_t = -(\omega_1 + r_1) \rho(\underline{x}) e^{-(\omega_1 + r_1)t}$$

upon differentiation with respect to t. The homogenous solution satisfies

$$0 = -\nabla \cdot \{ \nu [(A_0 - A) \nabla A] \rho - \mu \nabla \rho \},$$

and integrating once yields:

$$\nu (A_0 - A) \nabla A \rho - \mu \nabla \rho = \phi.$$

We take $\phi = \underline{0}$ for consistency with ∇A and $\nabla \rho \rightarrow \underline{0}$ at infinity. Then

$$\rho = c_1 e^{\frac{\nu}{\mu} (A_0 A - \frac{1}{2} A^2)}.$$

For consistency with the asymptotic form of the solution to (7) we will require

$$c_1 = \frac{\gamma_0}{r_1 + \omega_1}.$$

This gives a leading eigenfunction for the MPB population density which adapts according to the functional form of A . In particular, when $A < A_0$ at $r = 0$, flying MPB are focussed toward $r = 0$, whereas for $A > A_0$ MPB are repulsed in an epidietic wave. These two situations are depicted in figure 1. We will use the adaptive nature of the steady-state MPB response function to help construct a local model below.

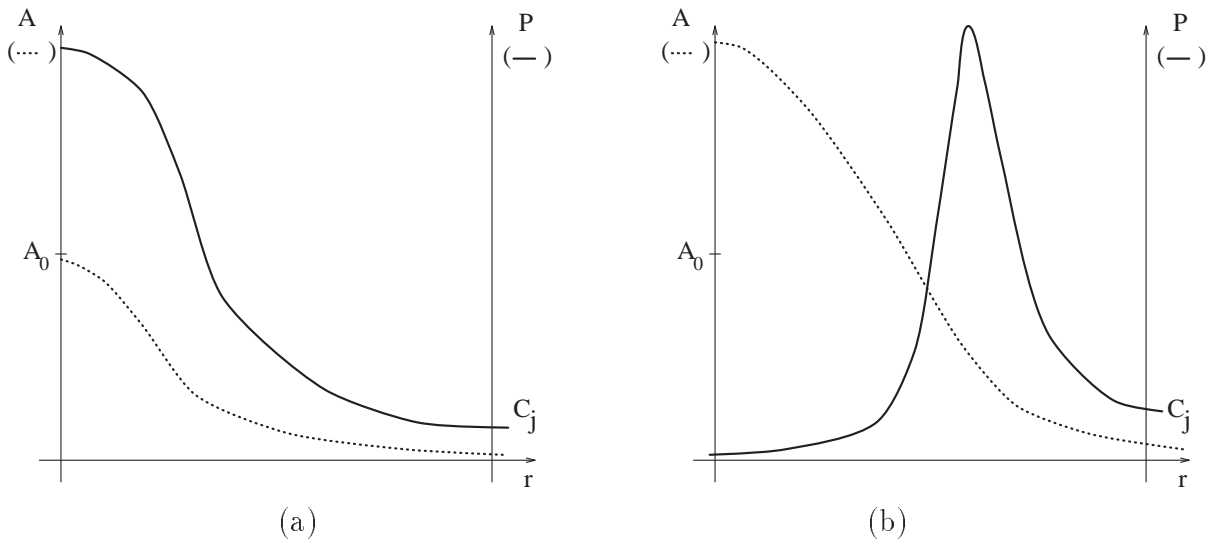


Figure 1: Steady-state response of MPB population in the case $A < A_0$ (a) and $A > A_0$ (b). The eigenfunction automatically encodes ‘switching’ in response to changing chemical concentrations. In each case the dashed line is the steady-state chemical signature generated by MPB nesting at $r = 0$, and the solid line is the (normalized) flying MPB response.

4 Constructing a Local Model

Integrating the global model is a difficult proposition, particularly considering that the parameters are unknown and existing data is temporally extended at a single spatial location. In this section we will investigate the consequences of the global model at a single spatial location using a local modelling technique initiated in [19]. The idea is to use the integrals

$$\int_0^\infty (\cdot) \ell d\ell \quad \text{and} \quad \int_0^\infty (\cdot) \ell^3 d\ell$$

to ‘project’ the equations (4 – 6) onto ODE for the evolution of Gaussian parameters. Equivalently, we may view this as an analytic calculation of the zeroth and second moments of the profile, which are then used to parametrize a Gaussian with the same moments. While this proved to be a very useful approach in [19], it was unsatisfying from the standpoint of resolving ‘switching’ and nonlinear dispersion in the wake of a successful attack. In what follows we will resolve this difficulty by using the leading eigenfunction to *replace* (4), thus achieving an adiabatic response for flying MPB density.

4.1 Projection onto Spatial Modes

To produce a local set of equations reflecting global redistribution we must *parametrize* spatial behavior in a local way, that is, to make requirements about the temporal evolution of parameters in a spatial description of variables. To do this, we must choose a parametrized spatial form for the variables, then allow the parameters to vary temporally in a way consistent with the governing PDE. We will assume that the the variables are Gaussian in space. Letting ℓ denote the distance from the focus tree,

$$\begin{aligned} A &= 2 \frac{a(t)}{w_a(t)} e^{-\ell^2/w_a(t)} \\ Q &= 2 \frac{q(t)}{w} e^{-\ell^2/w} \\ R &= 2 \frac{r(t)}{w} e^{-\ell^2/w} \\ H &= 2 \frac{h(t)}{w} e^{-\ell^2/w} \end{aligned}$$

This will not provide an exact solution of the PDE, but will reflect the character of the PDE behavior. The dependence of Gaussian parameters on time is explicit above. The number w is constant, representing the characteristic size of the tree of interest. The variables $Q, R, H,$ and S vary temporally only in size, reflecting the fact that their spatial scale is fixed. The variable P will be replaced with its leading eigenfunction,

$$P = \frac{\gamma_0}{r_1 + w_1} e^{\frac{\nu}{\mu}(A_0 A - \frac{1}{2} A^2)}.$$

For the diffusion of chemical concentrations, the Gaussian *ansatz* is exact: the radial diffusion equation maps Gaussians to Gaussians over time. On the other hand, if we had made a Gaussian *ansatz* for the the flying MPB, not only would it be extremely optimistic, it would fail to capture the repulsive wave following successful infestation, which has already been discussed.

To determine how the Gaussian parameters vary in time, we will integrate equation (5) over space. Noting that

$$\int_0^\infty 2\frac{M}{\lambda}e^{-\frac{\ell^2}{\lambda}}\ell d\ell = M,$$

and that

$$\int_0^\infty 2\frac{M}{\lambda}e^{-\frac{\ell^2}{\lambda}}\ell^3 d\ell = M\lambda,$$

integrating (5) over space gives

$$\begin{aligned}\dot{a} &= \frac{d}{dt} \int_0^\infty A\ell d\ell = \int_0^\infty \left[b_1 \frac{1}{\ell} \frac{\partial}{\partial \ell} (\ell A_\ell) + a_1 Q - \delta_1 A \right] \ell d\ell \\ &= a_1 q - \delta_1 a.\end{aligned}$$

Performing the same integration with an additional ℓ^2 in the integrand gives

$$\begin{aligned}\frac{d}{dt} aw_a &= \frac{d}{dt} \int_0^\infty A\ell^3 d\ell = \int_0^\infty \left[b_1 \frac{1}{\ell} \frac{\partial}{\partial \ell} (\ell A_\ell) + a_1 Q - \delta_1 A \right] \ell^3 d\ell \\ &= (4b_1 - \delta_1)aw_a + a_1 qw.\end{aligned}$$

These two equations may be simplified to give a system of two differential equations for the pheromone parameters $a(t)$ and $w_a(t)$,

$$\dot{a} = a_1 q - \delta_1 a, \tag{8}$$

and

$$\dot{w}_a = 4b_1 + a_1 q \frac{w - w_a}{a}. \tag{9}$$

4.2 A Local Model for Infestation

We replace the nonlinear redistribution equation with the quasi-steady response,

$$P \rightarrow P_0 = \frac{\gamma_0}{r_1 + \omega_1} e^{\frac{\nu}{\mu}(A_0 A - \frac{1}{2} A^2)}.$$

We need to determine how to convert this response function, which gives population density as a function of chemical forcing, into a number of flying MPB available locally to infest the focus tree, which we refer to as I .

Leaving I undetermined, the final system of ODEs is as follows:

$$\begin{aligned} \dot{a} &= a_1 q - \delta_1 a \\ \dot{w}_a &= 4b_1 + \frac{a_1 q}{a} (w - w_a) \\ \dot{q} &= r_1 \frac{r}{R_0} I - \beta r_3 q r \\ \dot{h} &= r_1 \frac{r}{R_0} I - r_4 h r \\ \dot{r} &= r[r_2(R_0 - r) - r_3 h] \end{aligned}$$

The number of infesting MPB, I , we take to be proportional to the number of flying MPB in the steady-state solution, evaluated at the location of the host tree,

$$I = 2\pi \int_0^{r_e} P r \, dr \approx \frac{\pi \gamma_0 r_e^2}{r_1 + \omega_1} \exp \left[\frac{\nu}{\mu} \left(A_0 A - \frac{1}{2} A^2 \right) \right].$$

The constant r_e is a ‘radius of engagement,’ or conversion factor for transforming the density of flying MPB into the number of MPB attacking the focus tree. It may be thought of as the distance at which an individual MPB can sight and orient on a particular tree. The approximation of the integral is based on a cylindrical approximation to the volume under P when $r_e \ll 1$.

5 Qualitative Analysis of the Local System

5.1 Non-Dimensionalization

Parameter	Definition	Description
ρ_1	$\frac{a_1 c_j r_1 r_e^2}{b_1 \delta_1 A_0}$	Relative amount of infestation
ρ_2	$\frac{R_0 r_2}{\delta_1}$	Relative speed of tree reinforcement
ρ_3	$\frac{b_1 r_3 r_4 A_0 R_0}{a_1 r_1^2}$	Relative tree damage
ρ_4	$\frac{r_4 R_0}{\delta_1}$	Relative host recovery rate
ϵ	$\frac{\delta_1 w}{b_1}$	Relative size of tree in diffusive units
Ω	$\frac{\beta r_3 R_0}{\delta_1}$	Relative effectiveness of tree defense
Δ	$\frac{r_1^2}{\delta_1 r_4 R_0}$	Ratio of infestation rate and tree recovery
χ	$\frac{\nu A_0^2}{\mu}$	Balance of directed and random movement

Table 2: The eight non-dimensional control parameters for the locally projected model.

Since the system of ODEs involves 20 variables and parameters, while employing only 6 different units, dimensional analysis should yield 14 dimensionless parameters. Nondimensionalization was accomplished using a time scale of δ_1^{-1} to resolve the most rapid time scale. When forced to choose how to define particular dimensionless parameters from among many possible combinations we tried to isolate control parameters of particular interest: the background level of infestation (resulting in ρ_1), the rate of resin reinforcement (resulting in ρ_2) and the defensive effectiveness of the tree (resulting in Ω). Below are non-dimensionalizing factors for dependent and independent variables; the subscript c denotes a reference level of the subscripted variable.

$$\begin{aligned}
a_c &= \frac{A_0 b_1}{\delta_1} & w_{ac} &= \frac{b_1}{\delta_1} \\
q_c &= \frac{A_0 b_1}{a_1} & h_c &= \frac{r_1^2}{r_4 r_3 R_0} \\
r_c &= R_0 & t_c &= \delta_1^{-1}
\end{aligned}$$

When the differential equations are rewritten in terms of these characteristic scales, they become

$$\dot{\bar{a}} = \bar{q} - \bar{a}, \quad (10)$$

$$\dot{w}_a = 4 + \frac{\bar{q}}{a}(\epsilon - \bar{w}_a), \quad (11)$$

$$\dot{q} = \rho_1 \bar{I} \bar{r} - \Omega \bar{q} \bar{r}, \quad (12)$$

$$\dot{h} = \rho_1 \rho_3 \bar{I} \bar{r} - \rho_4 \bar{h} \bar{r}, \quad (13)$$

$$\dot{r} = \bar{r}[\rho_2(1 - \bar{r}) - \Delta \bar{h}], \quad (14)$$

$$\bar{I} = e^{\frac{1}{2} \times (\frac{\bar{a}}{w_a} - \frac{\bar{a}}{4w_a^2})}. \quad (15)$$

The new, nondimensional parameters are given in table 2.

5.2 Fixed points and Their Interpretations

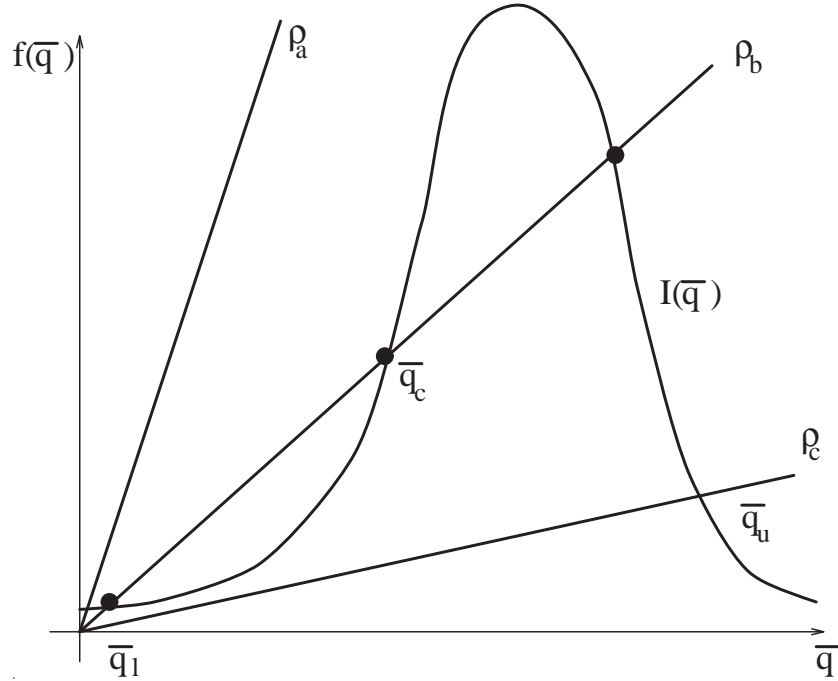


Figure 2: Graphical solutions of the local nondimensional equations for \bar{q} . There are at most three solutions for stationary attack densities. The bifurcation in number of solutions occurs as ρ_1 is varied from ρ_a to ρ_c , $\rho_a \ll \rho_b \ll \rho_c$.

Fixed points for the system of ODEs can be found by setting their right hand sides equal to zero and finding solutions. This generates the equations

$$\bar{q} - \bar{a} = 0,$$

$$4 + \frac{\bar{q}}{\bar{a}}(\epsilon - \bar{w}_a) = 0,$$

$$\rho_1 I \bar{r} - \Omega \bar{q} \bar{r} = 0,$$

$$\rho_1 \rho_3 I \bar{r} - \rho_4 \bar{h} \bar{r} = 0,$$

$$\bar{r}[\rho_2(1 - \bar{r}) - \Delta \bar{h}] = 0.$$

Solving yields:

$$\bar{a} = \bar{q},$$

$$\bar{w} = 4 + \epsilon,$$

$$\bar{r} = 0 \quad \text{or} \quad \bar{r} = 1 - \frac{\Delta \Omega \rho_3 \bar{q}_f}{\rho_2 \rho_4},$$

$$\bar{q} = \frac{\rho_1 I}{\Omega},$$

$$\bar{h} = \frac{\rho_3 \Omega \bar{q}}{\rho_4}.$$

In the case where $\bar{r} = 0$, (successful attack and death of the tree) \bar{q} and \bar{h} will be “free” and depend on the progression of the infestation. When $\bar{r} > 0$ there are at most three values of \bar{q} that can be fixed points, as depicted in figure 2. The smallest value is just that which can be maintained by random sampling of trees by a background level of beetles. MPB land on random pines of suitable size and attempt to build egg galleries, generating some small number of nesting MPB which does not seriously threaten tree health. The intermediate value, \bar{q}_c is shown to be unstable below, and corresponds to a cut-off at which the tree’s defenses are unable to forestall nonlinear chemical feedback and mass attack. The largest level, \bar{q}_u , is attracting and serves to ‘channel’ the course of infestation, as will be shown below.

5.3 Stability

The stability matrix is obtained by calculating the Jacobian matrix for the system of equations:

$$\mathbf{J} = \begin{pmatrix} -1 & 0 & 1 & 0 & 0 \\ -\frac{(\epsilon+w)}{a} & -1 & \frac{(\epsilon+w)}{a} & 0 & 0 \\ \rho_1 \bar{r} \frac{\partial I}{\partial \bar{a}} & \rho_1 \bar{r} \frac{\partial I}{\partial \bar{w}_a} & -\Omega \bar{r} & 0 & \rho_1 I - \Omega \bar{q} \\ \rho_1 \rho_3 \bar{r} \frac{\partial I}{\partial \bar{a}} & \rho_1 \rho_3 \bar{r} \frac{\partial I}{\partial \bar{w}_a} & 0 & -\rho_4 \bar{h} & \rho_1 \rho_3 I - \rho_4 \bar{h} \\ 0 & 0 & 0 & -\Delta \bar{r} & -2\rho_2 \bar{r} + \rho_2 - \Delta \bar{h} \end{pmatrix}.$$

Results of numerical evaluation of the eigenvalues of the Jacobian are summarized in figure 3, and indicate that the smallest, \bar{q}_l , and largest, \bar{q}_u , fixed points are stable, while the intermediate fixed point, \bar{q}_c , is unstable. This suggests that the intermediate level of infestation, \bar{q}_c , is critical for establishing the nonlinear self-focussing which results in mass attack. This contention will be made more rigorous below.

Holding that question in abeyance temporarily, figure 3 allows us to mathematically describe the potential course of infestation on an individual tree. In reality, the rate of emergence of MPB varies throughout the flight season, waxing as the season progresses and waning towards its end. This occasions a parametric variation in ρ_1 throughout the flight season, which we could interpret as motion along the lowest, stable branch of the bifurcation diagram, figure 3. If the rate of emergence in the vicinity of the focus tree exceeds the critical value for existence of the lowest fixed point, $\rho_{1_{\text{crit}}}$, then a catastrophic attack on this tree occurs. Otherwise, the tree can successfully withstand infestation through the flight season. We now turn our attention to demonstrating that \bar{q}_c is really critical for initiating a mass attack of MPB.

6 The Simplest Local System

The existence of only a few fixed points and their relative stability properties is very suggestive in terms of the qualitative dynamics of primary attraction and infestation in the

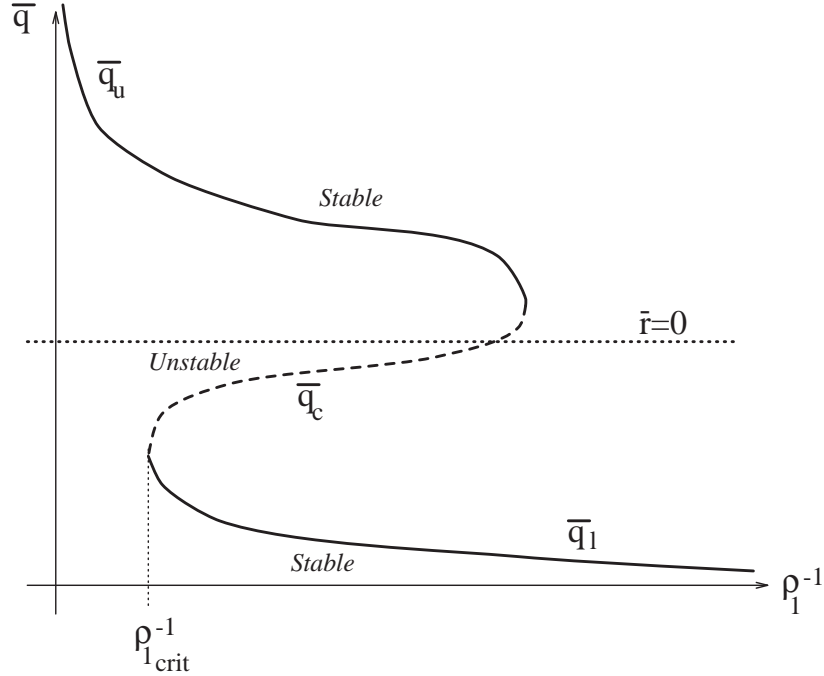


Figure 3: Stability diagram of fixed solutions as a function of ρ_1^{-1} . Infestations proceed along the \bar{q}_l branch as ρ_1 is varied, until $\rho_1 > \rho_{1 \text{ crit}}$, at which point mass attack occurs.

MPB model. However, the dimension of the phase space is too high for the analysis of fixed points to lend surety to the interpretation. Using center manifold methods it is possible to improve this situation. In this section we will establish the existence of a center-stable manifold which includes the fixed points described above. Analysis of the flow along this manifold indicates that the above description of the attack dynamics in this model is correct. That is, when the attack density exceeds a certain, quantifiable threshold MPB attack will be successful. Below this threshold an attacked tree can withstand colonization. This is not a new characterization of events (see, for example Berryman et. al. [13]). Rather, by developing mathematics that allows us to determine the single-host consequences of a global PDE model we can qualitatively validate that model by showing its consistency with prior descriptions of one-host events.

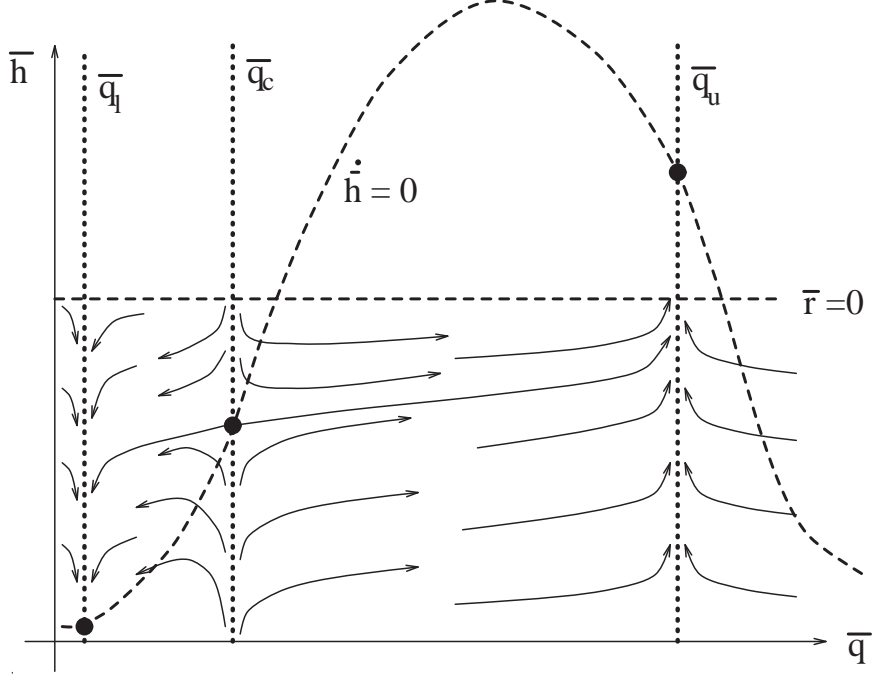


Figure 4: Phase space diagram of the simplest local system, a center manifold of the locally projected equations. There are potentially three fixed points, but the largest, \bar{q}_u , is above the ‘dead tree,’ or $\bar{r} = 0$ line. The attracting manifold $\bar{q} = \bar{q}_u$ organizes the dynamics of catastrophic infestations.

6.1 Existence of a Center Manifold

To begin with, we observe that the substitution

$$\bar{a} \rightarrow \bar{q} \quad \text{and} \quad \bar{r} \rightarrow 1 - \frac{\Delta}{\rho_2} \bar{h} \quad (16)$$

decouples equations (12), (11) and (13) from the system (10 – 15). As a consequence, if the manifold defined by the substitutions (16) is attracting, then the dynamics along this surface must mimic the dynamics nearby in phase space.

To demonstrate that this manifold is stable, make the substitution

$$\bar{a} \rightarrow \bar{q} + \xi \hat{a} \quad \text{and} \quad \bar{r} \rightarrow 1 - \frac{\Delta}{\rho_2} \bar{h} + \xi \hat{r}.$$

Assuming that $\xi \ll 1$ and linearizing equations (10) and (14) gives a linear system of equations at leading order in ξ ,

$$\dot{\hat{a}} = -\hat{a}, \quad (17)$$

$$\dot{\hat{r}} = [\rho_2(1 - 2\bar{r}) - \Delta\bar{h}] \hat{r}. \quad (18)$$

$$(19)$$

Equation (17) obviously leads to decaying \hat{a} . As to the size of perturbations \hat{r} , recall that \bar{r} is defined by

$$\rho_2(1 - \bar{r}) - \Delta\bar{h} = 0$$

and hence equation (18) reduces to

$$\dot{\hat{r}} = -\rho_2\bar{r}\hat{r}.$$

Since $\bar{r} \geq 0$, the size of perturbations in both \bar{a} and \bar{h} must decay, indicating that the manifold defined by the substitutions (16) is attracting.

On this manifold, equations (10 – 15) become

$$\dot{\bar{q}} = (\rho_1 I - \Omega\bar{q}) \left(1 - \frac{\Delta}{\rho_2}\bar{h}\right), \quad (20)$$

$$\dot{\bar{h}} = (\rho_1\rho_3 I - \rho_4\bar{h}) \left(1 - \frac{\Delta}{\rho_2}\bar{h}\right), \quad (21)$$

and

$$\dot{\bar{w}}_a = 4 + (\epsilon - \bar{w}_a), \quad (22)$$

where I is given by (15). Notice that equation (22) has only solutions which approach the steady state $4 + \epsilon$ exponentially rapidly. We therefore make the further substitution

$$\bar{w}_a \rightarrow 4 + \epsilon,$$

which gives

$$I = \exp\left[\frac{\chi\bar{q}}{4 + \epsilon} \left(1 - \frac{\bar{q}}{8 + 2\epsilon}\right)\right]. \quad (23)$$

The three equations (20), (21) and (23) define a second order nonlinear system which is equivalent to the local projection on a special, attracting manifold. We will refer to these equations as the *Simplest Local System* or *SLS*.

The dynamics of the SLS is reasonably simple. When

$$\bar{h} \geq \frac{\rho_2}{\Delta}$$

the tree has been rendered defenseless (since this corresponds to zero remaining resin capacity) and the MPB attack is successful. As in the more complicated system, there are three possible fixed points, given by

$$\Omega\bar{q} = \rho_1 I \quad \text{and} \quad \rho_4 \bar{h} = \rho_1 \rho_3 I.$$

The fixed point with the smallest \bar{q} is stable, while the next largest is unstable. The largest fixed point is stable, although frequently it corresponds to $\bar{r} < 0$, which is physically unrealistic. A phase space diagram indicating the behavior of the SLS is depicted in figure 4.

The most important feature of the SLS dynamics is the separating role played by the intermediate fixed value of \bar{q} which we will refer to as \bar{q}_c . Since equation (20) is homogenous in \bar{q} , the \bar{q} values at the fixed points globally separate solutions with growing and shrinking \bar{q} . Consequently, the behavior of solutions along the center-stable manifold bears out the description of global behavior in the previous section. Attacks which deliver more than \bar{q}_c nesting MPB are successful, while those which deliver less are unsuccessful. Since this description is exact in the SLS, it must hold in some open set of the global behavior possible in the locally projected system. Thus it seems that, regardless of initial conditions, successful attacks generally have the property that $\bar{q} \rightarrow \bar{q}_u$. This is consistent with the notion that the MPB/host system has co-evolved to deliver optimal numbers of MPB to specific hosts to maximize reproductive success [59].

6.2 Spatio-Temporal Scale of Shielding

The SLS allows us to make some simple predictions regarding the distances over which ‘shielding’ occurs in the chemotactic dispersal model. The analysis above indicates that on time scales of δ_1^{-1} solutions are attracted to the manifold of the SLS. Moreover successful-attack solutions to the SLS approach the largest fixed point, $\bar{q} = \bar{q}_u$ on a similar time scale. Thus, we may write

$$A(r, t) \approx \frac{2a}{w_a} e^{-\frac{r^2}{w_a}} \rightarrow \frac{2A_0\bar{q}_u}{4 + \epsilon} e^{-\frac{r^2\delta_1}{b_1(4+\epsilon)}}$$

on time scales of δ_1^{-1} . Flying MPB are repulsed from all areas in which $A > A_0$, and consequently a radius of shielding, r_s , about a focus tree can be calculated by inverting

$$A(r_s, \infty) \stackrel{\text{set}}{=} A_0$$

for r_s . This, in turn, gives

$$r_s^2 = \frac{b_1(4 + \epsilon)}{\delta_1} \log \left[\frac{2\bar{q}_u}{4 + \epsilon} \right].$$

Thus the local projection technique allows us to evaluate a qualitative prediction of the global model, namely the possibility of shielding, quantitatively. This prediction can then be used to either parameterize or falsify the model when compared with historical data sets, which we are in the process of procuring.

7 Conclusion

In this paper we have reviewed the construction of a global PDE model which describes the chemotactic interaction between MPB and lodgepole pine during the dispersal phase of the MPB life cycle. Simple properties of the PDE system suggest that in the epidietic phase of attack MPB are dispersed only a short distance from the focus tree. How this distance depends on parameters in the problem is discussed in the final section of the paper. One consequence of this finite dispersal is that the local modelling strategy described in [19] will not be accurate for the dispersal stage of an MPB attack.

Since local projection strategies are so useful for understanding qualitative dynamics, making predictions, and performing parametrizations, the rest of this paper concerned itself with improving on the previous local model. This was accomplished by using the exact MPB density steady-state response from the global PDE model, and then projecting the remaining equations. This yields a five-dimensional system with a constitutive equation for the MPB response. The ‘background’ population density away from the site of local projection becomes a parameter in the equations. Analysis of the fixed points of these equations suggests that there is a critical level of infestation, \bar{q}_c , which is necessary to generate a successful MPB

attack. Below this critical level, a tree's natural defenses kill attacking MPB rapidly enough to inhibit nonlinear focussing and mass attack of the MPB population.

A center manifold of the projected equations is examined, and on this manifold the criticality of attack behavior is exact. Attacks generating more than \bar{q}_c successfully nesting beetles succeed, while lesser attacks fail. There is a low level of sustainable attacks, corresponding to a level of non-organized attack commensurate with the background MPB population level. All of these various cut-offs are quantifiable, and may provide ways to discriminate between endemic and epidemic infestations. Qualitatively, this is in complete agreement with past descriptions of one-host/MPB interactions, in particular those of Berryman et. al. What the current analysis adds, in addition to the above, is the ability to validate a spatially extended PDE model by examining its local, or single-host consequences.

Perhaps more importantly, we have developed a framework in which many different kinds of global behaviors can be prototyped easily. For example, as more information is collected about MPB pheromone ecology, we may find that a different form of directed movement or chemotaxis is appropriate. With the projection methodology described above we can investigate the consequences of different PDE models without being forced to integrate a spatio-temporally stiff equation. Moreover, parametrizations can be effected at a local level, which will allow for statistical hypothesis testing. Currently we are working with the USDA Forest Service Intermountain Research Station Mountain Pine Beetle Project to develop experiments and data-collection techniques for use with the local modelling procedures described in this paper.

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