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Theoretical Analysis of "Switching" in a Localized Model for Mountain Pine Beetle Mass Attack

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The dynamic interaction between mountain pine beetles (MPB) and hosts (generally lodgepole pine) is reviewed briefly. In particular, successful "switching" from initial foci of attack to nearby hosts which may be higher-quality resources is a potentially critical element initiating the transition from endemic to epidemic population levels. A coupled partial differential equation model for MPB dispersal and host response is reviewed. 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 responses at individual trees. These equations are analysed to determine what factors control successful "switching" in a two-tree model. The results suggest that stand thinning ameliorates outbreaks mainly through interference with the chemical ecology via a change in micro-climate, rather than by altering host vigor.

1. Introduction

Mathematical reasoning has played a central role in ecological theory and application for at least the past 70 years [dating from the independent rediscovery of Verhulst's (1845) work by Pearl & Reed in 1920]. From the very beginning of these applications, there has been an appreciation for the role that spatial dynamics play in ecological issues [see Holmes *et al.* (1994); Turchin (1989)]. 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 (Kareiva, 1994).

Spatial dynamics typically play a central role in the community dynamics of highly mobile

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insects (Turchin & Thoeny, 1993). For example, dispersal is one of the most important, yet least understood, factors of bark beetle population biology (Anon., 1989). Current research with mountain pine beetle (MPB, *Dendroctonus ponderosae*, Hopkins), indicates that spatial dynamics play a crucial role (Preisler & Haiganoush, 1993; Mitchell & Preisler, 1991; Safranyik *et al.*, 1992). 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 insect outbreaks, may be central to maintaining the structure, function, and health of western forests (Schowalter *et al.*, 1981; Romme *et al.*, 1986; Mattson & Addy, 1975; Roe & Amman, 1970).

Interpretation of MPB in this dual role as a serious economic competitor and as a coevolved 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 (Berryman, 1976, 1982; Berryman *et al.*, 1984, 1989; Raffa & Berryman, 1983, 1986; Burnell, 1977; Safranyik *et al.*, 1989; Polymenopoulos & Long, 1990). None of these models have been spatially explicit, although one (Raffa & Berryman, 1986) has been spatially extensive, in the sense of simulating many hosts without specific spatial locations. The qualitative dynamics of almost all of these models have included 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, for many bark beetle species, including MPB, dispersal is only one part of the sequence of events necessary for successful population establishment and expansion. 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. MPB aggregation on a new host is accomplished through a series of synergistic semio-chemical reactions between insect and host. These reactions result in a rapid mass attack of individuals on a host. It has been hypothesized that attacks which have been focused on a single tree may switch to nearby trees as the original focus tree becomes fully colonized (Geiszler *et al.*, 1980), thereby causing nonlinear dispersal away from a colonized host, with a greater attack rate on those trees which are switched to. This behavior may enable successful attack of more vigorous hosts which the beetles would be unable to overcome otherwise.

We have built 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 (Powell *et al.*, 1996; Powell & Rose, 1997; White & Powell, 1997). The mathematical construction of 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 Powell *et al.* (1996), the global model has proven to be too complicated for easy ecological use. While progress has been made on integration of spatio-temporally stiff PDE (White & Powell, 1997), the PDE remains unsuited to experimentation and correlation with real data. A *local projection* was achieved, using a Gaussian *ansatz* for the dependent variables (Powell *et al.*, 1996; Powell & Rose, 1997). 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. Our goal in this paper is to analyse a local projection of the global model which captures both aggregation and dispersal in

a single system of ODE, particularly with reference to the switching behavior of attacking beetles.

2. Derivation of the Model Equations

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 1900s, focused 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 phytophagous insects, successful reproduction is contingent upon death of all or part of the host (Wood, 1972). Host trees, however, have evolved effective response mechanisms to defend themselves against bark beetle attacks (Smith, 1963; Reid *et al.*, 1967; Nebeker *et al.*, 1993; Raffa *et al.*, 1993). Almost all trees are capable of responding to bark beetle attacks, but only those with a rapid and sustained reaction are likely to survive (Berryman *et al.*, 1989; Raffa *et al.*, 1993). 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, binary, but dependent upon a complicated series of competing rate reactions which regulate both beetle arrival and host response (Raffa & Berryman, 1979).

The evolved relationship between the MPB and its host trees has resulted in an elaborate chemical communication system. Through a chemically-mediated synergistic reaction with host defensive compounds, female beetles attacking a tree release trans-verbenol, which, when mixed with α-pinene, is an aggregation pheromone attracting both sexes (Pitman, 1971; Pitman *et al.*, 1968; Hughes, 1973). At higher concentrations of trans-verbenol, higher proportions of males are attracted (Renwick & Vite, 1970). Attacking males produce exo-brevicomin which at low concentrations primarily attracts females (Conn *et al.*, 1983). 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, and it is therefore to the advantage of individuals to redirect their attacks after the target host has exhausted its defensive response. A complex suite of derived compounds have evolved (e.g. verbenone, frontalin, *exo*-brevicomin) resulting in a close-range redirection of responding beetles to nearby trees (Borden *et al.*, 1987; McCambridge, 1967; Geiszler *et al.*, 1980; Bentz *et al.*, 1996). This switching behavior therefore gives each beetle an improved chance to successfully attack hosts and simultaneously avoid placing its offspring in direct competition for resources. It may also serve to allow MPB to attack more vigorous hosts which represent higher quality food resources.

At low population densities, attacking MPB selectively attack trees weakened by disease or other stresses (Tkacz & Schmitz, 1986; Schmitz, 1988; Schowalter & Filip, 1993). It is hypothesized that stressed trees release a kairomone signal which attracts MPB flying in the vicinity, providing primary attraction to a particular tree (Gara *et al.*, 1984; Moeck & Simmons, 1991). An alternative hypothesis is that new hosts are found using a combination of random landings guided by visual cues (Schonherr, 1976; Sheppard, 1966) followed by chemical and tactile cues once on the host tree (Hynum & Berryman, 1980; Raffa & Berryman, 1979). Most likely, both situations occur. Although the combination of factors that signal a weakened tree remains an open question, enough evidence exists for the effect of host compounds on beetle behavior (Norris & Baker, 1967; Raffa & Berryman, 1982; Raffa, 1988) that models of MPB spatial dynamics should include some representation of host volatiles, as well as beetle-produced pheromones.

Over the past few years our team has developed a partial differential equation (PDE) model for seasonal MPB dispersal, including a representation of the pheromone/kairomone ecology and explicit locations for hosts (Powell

et al., 1996; White & Powell, 1997a, b; Powell & Rose, 1997; Logan *et al.*, 1997; Biesinger, 1998; Powell *et al.*, 1997). The model is intended to be applicable during the 3–4 weeks in late summer during which MPB emerge from dead hosts and disperse to attack healthy, uninfested hosts. The complex chemical cues in the MPB/pine tree interaction act as self-focusing and self-dissipating forces. These forces create a nonlinear, density dependent response that results in complex spatial patterns of resource utilization. In the next section we will review the construction of the (global) PDE model (see Table 1 for parameters).

2.2. THE GLOBAL MODEL

We define the following dependent variables, which vary with spatial location, x, y, and time, t:

$P(x, y, t)$—population of MPB dispersing from previous year's infested trees

$Q(x, y, t)$—population of MPB attacking susceptible trees

$A(x, y, t)$—concentration of pheromones

$S(x, y, t)$—resin outflow

$R(x, y, t)$—resin capacity of initially uninfested trees

$H(x, y, t)$—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 colonize a tree, $r_1(R/R_0)P$. 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 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. To avoid confusion at this point, we stress that this model is to be an "in-season" model of dispersal. Thus, *next year's* rate of emergence (γ will depend on the success of this year's attacking population, Q). During the time period for which the model is valid, γ is spatio-temporal data representing brood-production in previously infested trees, while R accounts for the defensive capacity of susceptible trees during the dispersal season.

The nesting population, Q, grows 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

TABLE 1

The list of parameters appearing in the global PDE model for MPB redistribution. Density units are represented with respect to hectares (hec), amounts of pheromone with respect to micrograms ($\mu g = 10^{-6} g$), and numbers of MPB are counted in hundreds (HMPB). The basic time unit is the flight hour *(fhr), of which there are approximately five per day*

Parameter	Definition	Units
A_0	Critical concentration at which pheromones become repulsive	$\mu g\ hec^{-1}$
α	Saturation parameter for pheromones	—
a_1	Rate of pheromone production by nesting beetles	$\mu g\ fhr^{-1}\ HMPB^{-1}$
b_1	Rate of pheromone diffusion	$hec\ fhr^{-1}$
β	Mortality rate of beetles due to resin outflow	R_0^{-1}
δ_1	Loss rate of pheromone	fhr^{-1}
μ	Diffusivity of flying beetles due to random movement	$hec\ fhr^{-1}$
ν	Strength of directed MPB motion due to pheromone gradients	$hec^2\ \mu g^{-1}\ fhr^{-1}$
R_0	Rest resin capacity of healthy (susceptible) trees	R_0
r_1	Rate of landing and conversion from flying to nesting beetles	fhr^{-1}
r_2	Rate of resin replenishment	$hec\text{-}fhr^{-1}$
r_3	Rate of resin outflow through holes bored by beetles	$hec\text{-}fhr^{-1}$
r_4	Rate of resin crystallization (tree recovery)	$hec\text{-}R_0^{-1}$
γ	Density of MPB emergence from previously infested trees	$HMPB\text{-}hec^{-1}\text{-}fhr^{-1}$

in proportion to the resin out-flow through occupied burrows, $\beta_1 S\frac{Q}{H}$. This gives an equation for Q,

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

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,

$$S = r_3 HR.$$

A rate equation for H is given by

$$\dot{H} = r_1\frac{R}{R_0}P - r_4 r_3 HR. \qquad (2)$$

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 an uninfested tree maintains naturally. When $R \to 0$ 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

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

This model for an uninfested tree's defensive response is essentially that proposed by Berryman *et al.* (1989), with the difference in interpretation that the R used here describes the total resin capacity, whereas the Berryman defensive variable is the resin available to flood a single nest gallery. 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 analysing 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.

The above equations reflect the temporal behavior without spatial redistribution. One mechanism for understanding spatial redistribution is to consider mass balances in some arbitrary spatial domain, Ω (Keller & Segel, 1971; Murray, 1989; Holmes *et al.*, 1994). The total number of beetles in that domain is

$$N = \iint_\Omega P\,dx\,dy,$$

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

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

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

Denote the flux vector by ϕ. There are two 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 non-random movement, as in Morris & Kareiva (1991). Thus,

$$\boldsymbol{\phi} = \phi_A + \phi_P,$$

where

- $\boldsymbol{\phi}_A$ 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

$$\boldsymbol{\phi}_A = vP\frac{A_0 - A}{A_0 + \alpha A}\nabla A.$$

TABLE 2

Parametric values for numerical simulation and units. Units involving resin are measured relative to R_0. *Other units are:* μg (10^{-6} *grams*), *hec* (10^4 *square meters = hectares*), *fhr* (*flight hours* $\sim$ 5 *fhr day*$^{-1}$). *Parameter values are based on observational and anecdotal data discussed in Biesinger* (1998)

Parameter	Value	Parameter	Value
α	1	A_0	7.8 μg hec^{-1}
a_1	2 μg fhr^{-1} HMPB^{-1}	b_1	0.324 hec fhr^{-1}
β	0.43 R_0^{-1}	δ_1	360 fhr^{-1}
μ	1 hec fhr^{-1}	ν	5.7 hec$^2\mu$g^{-1} fhr^{-1}
R_0	1 R_0	r_1	0.16 fhr^{-1}
r_2	0.0045 hec-fhr^{-1}	r_3	0.0023 hec-fhr^{-1}
r_4	0.0045 hec-R_0^{-1}	γ	0.1 HMPB hec^{-1} fhr^{-1}

In fact, since one may interpret this term multiplying P as a peak velocity of MPB movement in response to the presence of a pheromone gradient, we choose $\alpha = 1$. This makes the peak velocity of MPB movement chemically independent, which is clearly sensible.

- $\boldsymbol{\phi}_P$ 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

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

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

$$\frac{\mathrm{d}}{\mathrm{d}t} N = \iint_{\partial\Omega} \boldsymbol{\phi}\cdot\mathbf{n}\, \mathrm{d}s + \iint_{\Omega} f\, \mathrm{d}x\, \mathrm{d}y$$

$$= \iint_{\Omega} [F - \nabla\cdot\boldsymbol{\phi}]\, \mathrm{d}x\, \mathrm{d}y.$$

Here $\mathbf{n}$ is the unit 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,

$$\iint_{\Omega} \left[\frac{\partial P}{\partial t} + \nabla\cdot\boldsymbol{\phi} - F \right] \mathrm{d}x\, \mathrm{d}y = 0.$$

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

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

where

$$f(A) = \alpha A_0 \left\{ (\alpha + 1) \ln\left[1 + \frac{A}{\alpha A_0} \right] - \frac{A}{A_0} \right\}.$$

This equation and its derivation are similar to equations for environmentally-induced movement in Shigesada *et al.* (1979), Shigesada (1980), Okubo (1987) and Brew (1987).

We assume that the chemical concentration, A, obeys standard diffusion laws, but with sources and sinks of its own. For the suite of pheromones released by nesting beetles, sources are proportional to Q, while losses occur mainly due to advection through the canopy. These effects give a linear diffusion equation for A,

$$\frac{\partial}{\partial t} A = b_1 \nabla^2 A + a_1 Q - \delta_1 A. \quad (5)$$

Equations (1)–(5) are a complete spatio-temporal description of the dependent variables controlling the behavior of MPB/pine relationship during the 3–4 weeks during which MPB leave infested trees and attack uninfested trees. Approximate parameter values, based on observational and anecdotal evidence and discussed in Biesinger (1998) and Powell *et al.* (1997), are presented in Table 2.

3. Construction and Meaning of the Local Model

While the above-described "global" or spatially-extended PDE model for MPB dispersal and attack is descriptive in broad terms, it presents many problems from a scientific perspective. First and foremost among these is that it does not represent an easily falsifiable hypothesis—that is, it is extremely difficult to compare the PDE model with observations or measurements and determine whether or not it is a reasonable description of natural events. Density of dispersing MPB are very hard to observe directly. For the MPB/pine system, the most natural observable is number and timing of MPB attacks at an individual host. Even the units of these observations (numbers of MPB, or numbers of MPB per flight hour) are not consistent with the PDE description, which deals strictly in densities (that is, MPB/hectare or something similar). In this sense the global model is probabilistic, like the Schrödinger equation of quantum physics. What is needed is a way to "collapse" the probability functions whose evolution is described by eqns (1)–(5) into actual observables at the individual tree level. This is the goal of our "local" model—to develop a system of ordinary differential equations (ODE) which represents the consequences of the PDE description at a single host pine.

3.1. LOCALIZATION OF THE PDE

Some of the state variables in eqns (1)–(5) are not hard to localize—the density of nesting MPB (Q), resin capacity (R), and number of open attack holes (H) all have direct interpretation on an individual-host level. For these quantities we define local state variables:

q—number of nesting MPB in this tree
r—resin capacity of this tree
h—number of open attack holes in this tree.

We will use the convention that upper case state variables represent densities, while lower case state variables represent numbers at a particular host. The variables which evolve dynamically in space, A and P present more of a challenge. We make the *ansatz* that each nesting beetle makes a specific chemical signature based on its rate of pheromone production and the steady-state response of the chemical field. Thus, an individual tree creates a plume in proportion to the number of nesting MPB,

$$A \simeq 2\frac{a_1 q}{4b_1 + \delta_1 w}\exp\left[-\frac{\delta_1 l^2}{4b_1 + \delta_1 w}\right].$$

As discussed in Powell *et al.* (1996) and Powell & Rose (1997) this can be viewed as a "fitted" version of the actual chemical profile to a Gaussian, with l representing the distance from the tree of interest and w the characteristic size (area) of the tree. In general, w is small enough that $\delta_1 w$ may be neglected, which we will do below.

The remaining details for localizing the global PDE model are to represent the population of dispersing MPB, and to connect this population density with the actual number of attacks at the tree of interest. The closest thing to a steady-state solution for P is an approximate solution assuming that A is temporally constant and the background emergence, γ is located far enough away from the tree of interest to make an impact only in a diffuse sense, as though it were a spatial constant. The details of finding this solution are presented in Powell & Rose (1997). Under these circumstances, an approximate solution is

$$P \simeq \frac{\gamma}{r_1 + \omega_1}\exp\left[\frac{\nu}{\mu}f(A)\right].$$

Since we are viewing A as the chemical footprint of an individual host, P becomes a function of only q, l and γ,

$$P(q, l) \simeq \frac{\gamma}{r_1 + \omega_1}\exp\left[\frac{\nu}{\mu}\alpha A_0\left\{(\alpha+1)\ln\left[1 + \frac{\frac{a_1 q}{2b_1}\exp\left[-\frac{l^2\delta_1}{4b_1}\right]}{\alpha A_0}\right] - \frac{\frac{a_1 q}{2b_1}\exp\left[-\frac{l^2\delta_1}{4b_1}\right]}{A_0}\right\}\right].$$

This equation now represents the local population density of dispersing MPB only in terms of conditions at an individual host and distance.

In the global model, flying beetles are drawn to a tree via their complex pheromone communication system (as described earlier). In the local model we assume this process has occurred and beetles are now influenced only by conditions at an individual host. At this point visual cues play an increasingly important role. To represent the number of attacks at an individual tree in terms of the reduced population density, we integrate P over an area surrounding the tree, corresponding to the distance at which MPB are able to visually identify an individual host. If ρ is this visual distance, or the "radius of engagement," then the number of attacks at an individual host could be written

$$I \propto r_1 \int_0^{2\pi} \int_0^{\rho} P(q, l) l \, \mathrm{d}l \, \mathrm{d}\theta.$$

Unfortunately, the actual integration indicated above is difficult, and numerical evaluation would render analysis difficult. Instead we choose to approximate the integral with its value at the tree multiplied by the area of integration,

$$I(q) \approx r_1 \pi \rho^2 P(q, l = 0).$$

3.2. THE TWO-TREE MODEL

The pheromone plume controls the behavior of beetles attacking a host. As this plume becomes large, it will overlap with other trees, altering the attack characteristics at a neighboring tree. This overlap of pheromone levels can be modeled by linearly superposing the pheromone levels of the trees, resulting in a summed pheromone level for all of the trees in the domain of interest. Because the equations are local, each tree inherits its own set of local equations, coupled via pheromones. The spatial and temporal pheromone levels of two trees, labelled x and y, are represented by A_x, A_y, while the coupled pheromone level is denoted by A_{total}:

$$A_{total} = A_x + A_y. \tag{6}$$

In order to transform the global PDE model to a simpler local model, tree-centered state variables are assumed to have the form of a Gaussian. This will not give a completely accurate spatial representation, but will allow for the general behavior to be deduced. The global variables in Gaussian space are represented by:

$$A_i = \frac{2a_i(t)}{w_{ai}(t)} \mathrm{e}^{-l_i^2/w_{ai}(t)}$$

$$Q_i = \frac{2q_i(t)}{w} \mathrm{e}^{-l_i^2/w}$$

$$R_i = \frac{2r_i(t)}{w} \mathrm{e}^{-l_i^2/w}$$

$$R_{0i} = \frac{2r_{0i}(t)}{w} \mathrm{e}^{-l_i^2/w}$$

$$H_i = \frac{2h_i(t)}{w} \mathrm{e}^{-l_i^2/w}$$

The lower case variables represent the total quantity associated with a particular host. The variable l_i is the distance between the point in question and the i-th tree, w_{ai} represents the (time-dependent) area of the chemical plume for host i, and w is a surrogate for the size (area) of the tree.

The actual "projection" involves integration. We illustrate the technique on the pheromone concentrations. To derive an equation of motion for a_i, the amount of pheromone being released at the i-th tree, we integrate centered on that tree, and assume that the super-exponential decrease of the Gaussians from other trees provides only negligible contribution:

$$\iint_{\mathbf{R}^2} A_{total} l_i \, \mathrm{d}l_i \, \mathrm{d}\theta$$

$$= 2\pi \sum_{j=1}^{N} \int_0^{\infty} \frac{2a_j(t)}{w_{a_j}(t)} \mathrm{e}^{-l_j^2/w_{a_j}(t)} l_i \, \mathrm{d}l_i \approx 2\pi a_i(t).$$

Inserting the Gaussian *ansatz* into the PDE for A from the global system:

$$\frac{\mathrm{d}}{\mathrm{d}t} a_i = 2\pi \frac{\mathrm{d}}{\mathrm{d}t} \int_0^{\infty} A_{total} l_i \, \mathrm{d}l_i$$

$$= 2\pi \int_0^{\infty} (b_1 \frac{1}{l} \frac{\mathrm{d}}{\mathrm{d}l_i} l_j A_{l_i} + a_1 Q + \delta_1 A) l_i \, \mathrm{d}l_j$$

which gives

$$\dot{a}_i = a_1 q_i - \delta_1 a_i.$$

Repeating for both trees, $i = x, y$, and the other dependent variables results in two sets of local equations:

$$\dot{a}_i = a_1 q_i - \delta_1 a_i, \tag{7}$$

$$\dot{w}_{ai} = 4b_1 + a_1 q_i \frac{w - w_{ai}}{a_i}, \tag{8}$$

$$\dot{q}_i = \frac{r_i}{r_{0i}} I_i(A_{total,i}) - \frac{\beta_i r_3}{w} q_i r_i, \tag{9}$$

$$\dot{h}_i = \frac{r_i}{r_{0i}} I_i(A_{total,i}) - \frac{r_4}{w} h_i r_i, \tag{10}$$

$$\dot{r}_i = r_i \left[\frac{r_2}{w}(r_{0i} - r_i) - \frac{r_3}{w} h_i \right]. \tag{11}$$

Note that eqn (8) is generated using the second-moment integral, $\int(\cdot) l_i^3 \, dl_i$, as discussed in Powell *et al.* (1996) and Powell & Rose (1997). At this point each tree is now coupled by the total pheromone level evaluated at location i, $A_{total,i}$, and through the infestation function, I_i, which is evaluated at the tree in question:

$$I_i(A_{total}) = r_1 \pi \frac{\rho^2 \gamma}{r_1 + \omega_1} \times \exp\left[\frac{v}{\mu} \alpha A_0 \left\{ (1 + \alpha) \ln\left(\frac{A_0 \alpha + A_{total,i}}{A_0 \alpha} \right) - \frac{A_{total,i}}{A_0} \right\} \right].$$

4. Bifurcation Analysis of Switching

Our goal is to use the localized model to analyse the behavior and success of "switching", to understand the circumstances under which the successful attack of a focus tree will lead to successful attack on a second, nearby tree. Our approach will be to assume that the focus tree, x, has reached an equilibrium solution to (7)–(11), corresponding to $r_x = 0$. The nesting MPB in the focus tree (q_x) will then create a pheromone plume which influences events at the second tree, y. We will then pursue a bifurcation and stability analysis of the equations at the second tree to determine its likelihood of attack as a function of parameters and separation from the focus tree.

After simplification of the equilibrium solutions and use of the Gaussian form of A, the determining equations for fixed points at the focus, $i = x$, tree become:

$$q_x - k_x I_x(A_x) = 0,$$

$$A_x = 2 \frac{a_1 q_x}{4b_1 + \delta_1 w},$$

$$k_x = \frac{w \rho^2 r_1 \gamma}{r_{0x} \beta r_3 (r_1 + w_1)}.$$

These equations have one, two, or three solutions depending on the value of k_x, as depicted in Fig. 1. In biological terms, k represents the competing ratio of rates of beetle success and tree defensive success. The solutions correspond to separate fixed points. The solution for the smallest and largest fixed point of beetles are stable and attracting, while the middle is unstable and repelling. As a result of the middle fixed point being unstable, once the population exceeds a critical number of nesting MPB a nonlinear feedback loop is initiated, resulting in the successful infestation of the focus tree. Note that on this reduced, single-tree level the metastable behavior is equivalent to that described by Berryman *et al.* (1984, 1989).

To investigate the behavior of attacks at a secondary tree, we begin by assuming that the focus tree has been successfully infested with a population of nesting MPB, q_x. Now we can examine the behavior at a secondary tree, y to which the incoming beetles may switch their attack. The total pheromone response now receives contribution from both trees, because the secondary tree will now also have a group of beetles producing pheromones as it undergoes attack. The equilibrium equations for the secondary tree are:

$$q_y - k_y I_y(A_{total,y}) = 0,$$

$$A_{total,y} = 2 \frac{a_1 q_y}{4b_1 + \delta_1 w} + 2 \frac{a_1 q_x}{4b_1} + \delta_1 w \exp\left[\frac{-l^2 \delta_1}{4b_1 + \delta_1 w} \right],$$

$$k_y = \frac{w \rho^2 r_1 \gamma}{r_{0y} \beta r_3 (r_1 + \omega_1)}.$$

These equations have one to three solutions, and will give the values to which q_y will converge. However, because of the presence of a focus tree, the location and behavior for the fixed point diagram for the second tree is altered significantly, as shown in Fig. 2. Plotting q_y vs. k_y gives the bifurcation diagram of the system as seen in Fig. 3. In those regions with one (large) fixed point the secondary tree will be successfully attacked once an attack starts, since the only fixed point is attracting and large. When the single fixed point is small the risk to the secondary tree is low, since the single attracting fixed point corresponds to a very small nesting population. Between these regions, where there are three fixed points, attacks will only be successful after passing a threshold described by the unstable intermediate fixed point.

The parameter values which separate regions A (one large fixed point) from B (three fixed points) therefore describe the boundary between successful and unsuccessful switching. Let

$$F(q_y, k_y) \overset{\text{def}}{=} q_y - k_y I_y(A_{total}) = 0 \qquad (12)$$

describe the bifurcation curve. The turning-point bifurcation separating A from B occurs when:

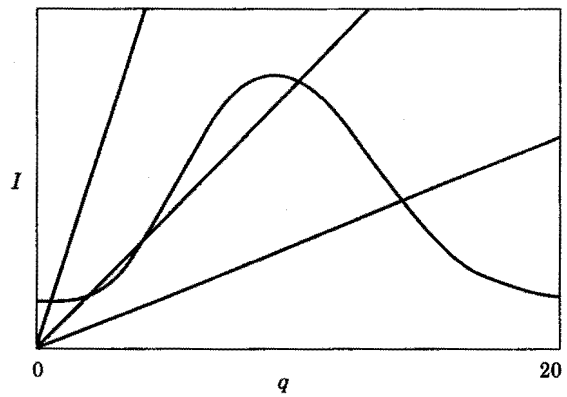

FIG. 1. Graphical solutions yielding equilibrium solutions at the focus tree, $I(q) = kq$. The horizontal axis measures the number of MPB nesting in a tree, while the function I is the integrated response of the dispersing population to q nesting MPB. Solutions are generated between the lines (with slope k) and the infestation curve. The constant k measures the relative efficacy of MPB attack and tree defensive response; as k increases the tree's response is overwhelming and only one (small) fixed point for the nesting population exists. At the other extreme, when k is small the tree's response is weak and the fixed point corresponds to a large nesting population.

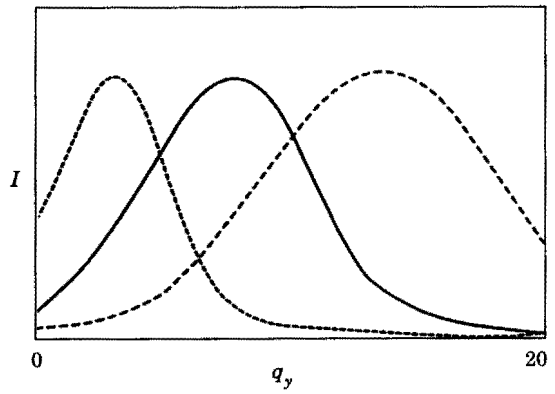

FIG. 2. The infestation function at a secondary tree for differing densities of attack on the focus tree (—). As the density of attack (q_x) increases the peak response of the infestation curve moves to left (- - -), or occurs for smaller q_y (the number of attacking MPB in the secondary tree), making successful switching easier to realize. As the trees are separated (– – –) the peak response requires much higher nesting densities, making switching less likely to be successful.

$$\frac{F(q_y, k_y)}{dq_y} = 0 \qquad (13)$$

Generally, two such points exist in the bifurcation diagram, Fig. 3. The first, corresponding to the smaller beetle population, will give the location of the desired boundary. By solving eqns (12) and (13) simultaneously, we can

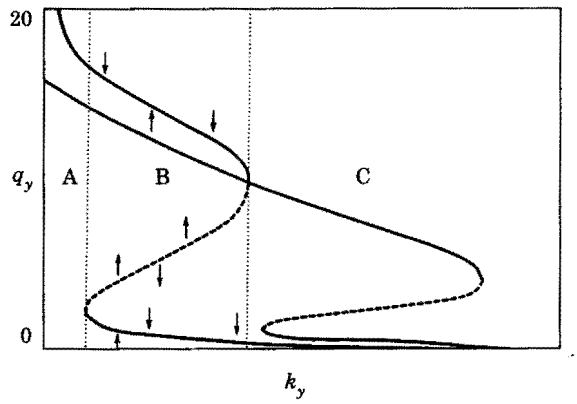

FIG. 3. Two bifurcation plots of $I_y(A_{total}) = k_y q_y$. The bifurcation diagram is shifted to the right by decreasing the separation between focus and secondary hosts. The risk-regions A, B and C, associated with the turning points of the first bifurcation curve, divide the parameter space into areas of high, medium and low risk, respectively. If this were the diagram for a tree which may be switched to, A would represent the parameter space in which the switching is successful once initiated, while B represents the area in which switching is only conditionally successful.

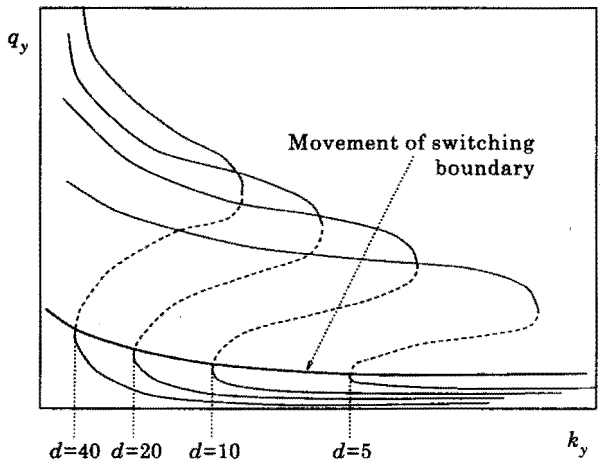

FIG. 4. Location of critical points as a function of distance (in meters). Each bifurcation diagram corresponds to a different choice of distance between focus and secondary trees. As distance is increased, the lower turning point moves to the left, indicating that the likelihood of successful switching to the second tree decreases with distance. The bifurcation points are connected in this plot.

determine the location of the switching boundary in a two-dimensional parameter space, as described in Fig. 4.

5. Results and Discussion

We can now begin to predict the likelihood of successful switching as a function of critical parameters. While there are many degrees of freedom, the following parameters will receive most of our interest:

- r_0—vigor of secondary tree. In general we expect the success of switching attacks to decrease proportionally to host resistance. We have normalized our model so that $r_0 = 1$ reflects the vigor of a 10" DBH lodgepole pine tree in open-stand conditions.
- l—separation between focus and second tree. As a general rule, success of switching should decrease with increased distance between the two trees; exactly how rapidly the success should decrease is what we intend to examine.
- δ_1—rate of pheromone loss through the canopy. This parameter, we believe, is a strong indicator of stand density in the model. As the canopy becomes closed, $\delta_1 \to 0$, while δ_1 may be as large as several hundred in windy conditions in an open-grown stand. As a general rule, when the stand becomes more open (δ_1 increases) we expect the success of switching to be diminished.
- γ—rate of emergence. This constant varies with the number of trees attacked in the previous year, depending on brood mortality through winter and temperature, among other factors. Speaking loosely, a single attacked tree may produce on the order of 2000 young adults; consequently $\gamma = 0.2$ corresponds to approximately one infested tree per hectare, with beetles emerging over a 20 day ($\sim$100 flight hour) season.

Our approach will be to determine the location of the successful switching boundary as a function of two parameters, holding other parameters constant at values in Table 2.

5.1. VIGOR AND DISTANCE

Figure 5 illustrates the relationship between vigor of the second tree and its separation from the focus tree. Also illustrated is the effect of canopy closure (as reflected by the loss rate, δ_1) on the switching boundary. As the degree of closure changes from completely open ($\delta_1 = 360$) to 70% open ($\delta_1 = 240$) the spatial location of the switching boundary can move as much as 4 m, corresponding to a 100% increase in the area affected by a focus tree. By comparison, a 50% change in vigor of the secondary host (from $r_0 = 1$ to $r_0 = 1.5$) occasions only a 1 m change in boundary location, which indicates a greater sensitivity of the system to micro-environment than to host vigor. In any event, switching is very likely to be successful for any host within 10 m of a successfully attacked focus tree. Field observations of successful switching events range from 3.2 to 7.3 m (Preisler & Haiganoush, 1993; Bentz *et al.*, 1996; Raffa & Berryman, 1983).

5.2. CANOPY CLOSURE, VIGOR AND DISTANCE

Stand thinning is one of the only successful ways known to interfere with successful MPB attack (Amman & Logan, 1998). Traditionally this is believed to be due to the fact that thinned stands become more vigorous, and thus more resistant to MPB attack. However, reduced infestation can occur immediately after thinning and before residual trees could express changes in vigor (Amman *et al.*, 1988; Amman & Logan,

1998). This suggests that factors such as temperature (Bartos & Amman, 1989) and the effects of microclimate on pheromones could also be important. Generally speaking, in a closed canopy stand pheromone losses may be quite small, while in reasonably open, thinned stands the loss rate may be large enough to cause a significant decrease on a host-to-host scale (corresponding to a loss rate in the 100s/flight hour). This effect would be immediate, whereas one might expect that it might take at least a growth season before stand thinning would significantly affect host vigor directly (Amman & Logan, 1998).

The boundary between successful and unsuccessful switching as a function of loss rate, δ_1, and host separation is depicted in Fig. 6. This figure suggests that stand thinning will tend to inhibit successful switching by interfering with the chemical profile of focus trees. At higher loss rates (open canopy), successful switching can only occur for separations on the order of meters, or less. In a closed canopy (lower loss rate), by contrast, switching may successfully occur on larger scales. (This should not be interpreted to mean that stands with average stem separation of 10 m are capable of closed canopy, but rather as meaning that in closed canopy stands, a tree 10 m away from a focus tree may be successfully switched to). Changes in vigor are less significant, generally altering boundary location by less than 10%. Based on these modelling results, one may infer that the utility of stand thinning as a control measure depends much more on interfering with the chemical communication system of MPB than by changing host vigor by removing competition.

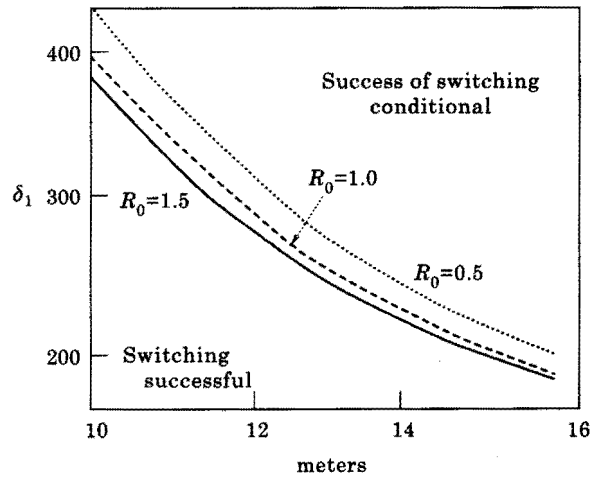

FIG. 6. Switching success as a function of pheromone loss rate and distance (l). The parameter δ_1 represents pheromone loss rate through the canopy, and consequently increases with thinning and shrinks with canopy closure, with 360 being an approximate value for losses in an open stand with randomly directed, calm winds. Also depicted is the influence of host vigor, varying from $r_0 = 0.5$ to $r_0 = 1.5$. This figure suggests that stand thinning will tend to inhibit successful switching by interfering with the chemical signature of focus trees.

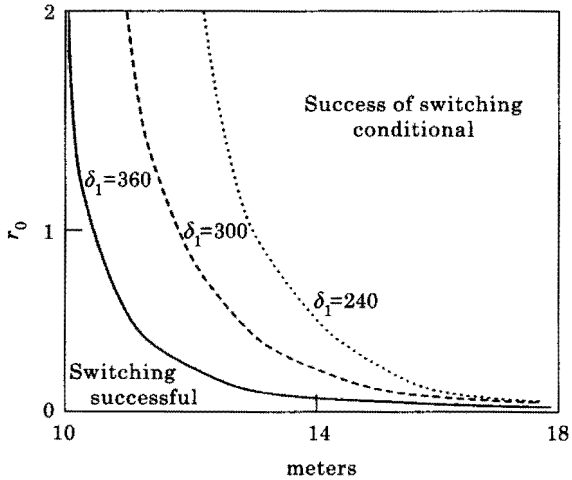

FIG. 5. Two parameter plot of r_0 vs. separation between host and secondary tree (measured in meters), with variation in these boundaries for varying pheromone loss rates (δ_1) indicated. The parameter r_0 measures the vigor or resistance of the second tree. Changing canopy openness by 30% (changing δ_1 from 360 to 240) can move the switching boundary by several meters, while changing host vigor has only a small effect.

5.3. EMERGENCE AND HOST SEPARATION

Figure 7 illustrates the sensitivity of the boundary to intensity of emergence (γ) and separation between focus and secondary host. The location of the boundary appears to move with the root of the emergence, which indicates a linear growth in the area affected by a focus tree as a function of emergence. In this figure, the effect of changing host vigor is also indicated. For high levels of background emergence ($\gamma > 0.2$) the resistance of the second host does

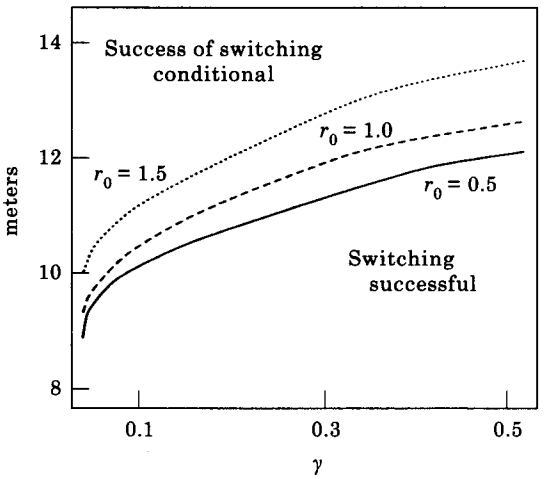

FIG. 7. Switching success as a function of distance (l) and emergence density, γ. The strength of emergence varies from weak endemic ($\gamma \simeq 0.05$ HMPB/fhr-hec) to epidemic ($\gamma \simeq 0.5$ HMPB/fhr/hec). Over this range of emergence the location of the switching boundary can move several meters, corresponding to a 100% change in affected area. By contrast, varying host vigor (r_0) at a particular level of emergence only moves the boundary a meter or two.

not have much impact, moving the boundary a meter or two at most. For more endemic levels of emergence $\gamma \sim 0.05$ the effect of vigor can be much larger, suggesting that host vigor plays a much more important role in the behavior of endemic infestations than epidemic infestations (as suggested by Raffa & Berryman, 1983).

It is important to mention that γ is not a constant in time, and may vary wildly from day to day depending on temperature and weather conditions. No doubt this significantly alters the sorts of patterns formed by MPB attack. From the standpoint of the circumstances described in Fig. 7, when the temperatures wax and wane (a 15°C noontime temperature change from day to day is not uncommon on our observation plots) γ may vary from 0 to 0.2, which may change the area affected by an infestation focus from zero to 100 square meters. This, in turn, suggests an extreme sensitivity of endemic infestation pattern to stochastic variables like host spacing, stand demographics, wind direction, and temperature fluctuation.

6. Conclusion

Spatially explicit representations of ecological phenomena are important to a full understanding of complex systems. We have described the localization of a mathematically complex PDE model to an ODE model which can be parametrized using field-collected data. The switching behavior of MPB populations from a focus tree to other nearby trees is one of many important factors contributing to their success as a periodic outbreak species. We have evaluated our model of switching with respect to changes in the value of several parameters: vigor of the secondary tree, distance between the focus and secondary trees, strength of background emergence and the rate of pheromone loss through the canopy. All four factors play an important role in the successful colonization of hosts in an area.

One clear indication which emerges is that control measures based on stand thinning are probably successful, at least in part, because of interference with the MPB chemical communication. In most of the cases we examined the boundary within which switching is likely to be successful was relatively insensitive to host vigor. The boundary's spatial location was very sensitive to chemical loss rate through the canopy, which is probably the parameter most strongly reflecting stand density in this model. Consequently, our work suggests that interference with chemical communication is a critical component of stand thinning as a control strategy; increasing host vigor by minimizing intra-specific competition seems to have a much smaller effect. The exception to this observation is the behavior of the system at very low emergence densities, at which host vigor plays a critical role.

Switching itself may play a critical role in the transition from endemic and epidemic infestations. In general, one may suppose that more vigorous trees represent higher-quality food resources for attacking MPB. At very low population levels, however, vigorous trees are difficult for MPB to attack. Consequently, future populations based on current infestations will continue to be low. When circumstances conspire to make successful switching to vigorous hosts more likely population levels can begin to build. This is a process which may require several years, as successful switching attacks increase a discrete amount each year

based on population gains made in the previous years. However, in each growth year the conspiracy of factors contributing to successful switching to vigorous hosts must continue. If it does not, population levels will crash back to endemic levels. The picture which emerges, then, is not that of a stable endemic population level separated from a stable epidemic population by an unstable population level. Instead, the behavior is much more likely to be that of a stable endemic population which, in some circumstances, can destabilize and produce epidemic excursions. If this is so, the predictions made in this paper may become critical in determining which real-world populations are capable of making such excursions.

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