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Mathematical Elements of Attack Risk Analysis for Mountain Pine Beetles

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Three different mathematical approaches are combined to develop a spatial framework in which risk of mountain pine beetle (MPB) attack on individual hosts may be assessed. A density-based partial differential equation model describes the dispersal and focusing behavior of MPB. A local projection onto a system of ordinary differential equations predicts the consequences of the density equations at individual hosts. The bifurcation diagram of these equations provides a natural division into categories of risk for each host. A stem-competition model links host vigor to stand age and demographics. Coupled together, these models illuminate spatial risk structures which may also shed light on the role of climatic variables in population outbreaks. Preliminary results suggest that stand microclimate has much greater influence on risk of attack than host vigor and stand age.

1. Introduction

The interaction between mountain pine beetles (MPB, *Dendroctonus ponderosae* Hopkins) and pine tree hosts (in particular lodgepole, *Pinus contorta*, and ponderosa, *Pinus ponderosa*), is the backdrop for many interesting questions in mathematical biology, disturbance ecology, and resource management. MPB has long been considered a major pest in western forests; as an aggressive bark beetle it kills its host. Outbreaks can be both intensive (up to 80% or greater mortality) and extensive (covering thousands of contiguous hectares), resulting in serious economic consequences. Current research with mountain pine beetle indicates that spatial dynamics play a crucial role (Preisler & Haiganoush 1993; Mitchell & Preisler, 1991; Safranyik *et al*., 1992). At low population densities, MPB selectively attack trees weakened by disease or other stresses (Tkacz & Schmitz, 1986; Schmitz, 1988; Schowalter & Filip, 1993), but at high population densities infestations can kill many hectares of vigorous, healthy trees. The transition between these endemic and epidemic states, including mechanisms of host selection and roles of environmental and dynamic determinism in MPB dispersal, are only beginning to be understood, but it is clear that the transition is spatially mediated.

Over the past 3 years we have developed, parametrized, and begun to validate a spatial model for MPB dispersal and interaction with pine hosts (Powell *et al*., 1996; White & Powell, 1997a, b; Bentz *et al*., 1996, 1996; Logan *et al*., 1998; Powell & Rose, 1997; Powell *et al*., 1998a). Partial differential equations describe dispersing and nesting population densities, contingent on pheromone ecology and host vigor/immune

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response. A great deal of our past effort has focused on collecting data to parametrize this model and methodology to integrate this model rapidly enough to be of scientific value. While there is still room to improve the model's description of this complicated and challenging ecological interaction, we are now in a position to develop methodology to turn a dispersal model with realistic information into a risk assessment tool.

The mountain pine beetle is widespread, found throughout the range of its hosts, the genus *Pinus*. Forest managers would like to predict when and if a MPB epidemic will occur in a particular stand. Risk classification systems are tools developed for use by forest managers to help predict future insect activity relative to the location of a forest stand and conditions within the stand (Hicks *et al*., 1987). A plethora of risk classification systems have been developed to aid in managing lodgepole pine (LPP) forests when the mountain pine beetle is an influencing factor. These systems attempt to describe the relationship between MPB populations and forest stand conditions in a quantitative or qualitative manner. Because a MPB infestation usually results in death of the host trees, most of the developed systems have related risk to tree mortality in some manner. Some rating systems were based on regional descriptions such as an historic map depicting the frequency and intensity of MPB infestations (Crookston *et al*., 1977), and climate-related parameters (Safranyik *et al*., 1975). Other systems were based on stand and host tree characteristics including indices of stand competition (Schenk *et al*., 1980; Anhold & Jenkins, 1987), tree age, diameter, and climatic zone (Amman *et al*., 1977), host tree growth and vigor (Berryman *et al*., 1978; Mahoney, 1978; Waring & Pitman, 1980), physiological maturity (Shrimpton & Thomson, 1981), and a combination of several of these factors (Berryman, 1978; Stuart, 1984; Shore & Safranyik, 1992). Several of these systems were evaluated using stand data from northern Montana (Bentz *et al*., 1993), British Columbia (Shore *et al*., 1981), and southeastern Wyoming (Katovich & Lavigne, 1985). None of the systems evaluated provided adequate estimates of risk (measured as percent lodgepole pine mortality).

One important relationship that has not been adequately included in MPB risk-rating systems is the spatial nature of both host stands and beetle populations. The probability that a stand will experience a MPB outbreak is dependent upon MPB immigrating from surrounding stands, as well as tree characteristics and beetle population within the stand being evaluated. The importance placed on spatial arrangement of both the beetles and host trees is due to the chemical ecology of MPB populations. In order to reproduce, beetles must kill the host tree, and in order to kill the host, a mass attack of beetles must occur on the tree. MPB have evolved a complex pheromone system which enables them to do this. The spatial arrangement of live host trees ready to be attacked and source trees from which beetles emerge are both very important in this process. Consequently, spatial measures of beetle population and host spacing are necessary for MPB risk-rating systems to have predictive value better than the flip of a coin.

In this paper, we present and assemble theoretical elements to provide a spatial picture of risk. The spatial structure of dispersing MPB populations is described by our existing, parameterized spatial model (Powell *et al*., 1996, 1998a; Logan *et al*., 1998). Localization, attack on individual hosts, and a bifurcation-theoretic concept of risk comes from a local "projection" approach (Powell *et al*., 1996, 1998b; Powell & Rose, 1997). Host vigor and stand composition as a function of available water and stand age are provided by a stem model developed by Roberts *et al*. (1993). Together, these elements allow us to examine attack likelihood as a function of emergence density, host spacing, and stand demographics. To illustrate how these components work together, we will examine the risk presented to various stands by the existence of a "focus" tree, which may or may not initiate mass attack on nearby hosts depending on climatic variables such as mean wind speed and temperature.

2. Model Background

2.1. BIOLOGICAL BACKGROUND

Although a bark beetle spends most of its time 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. 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, 1966; 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 depends on a complicated series of competing rate reactions regulating 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 aggregation pheromones attracting both sexes (Pitman, 1971; Pitman *et al*., 1968; Hughes, 1973), resulting in mass attack on a single focus tree. However, the tree is a finite food resource that can be overexploited 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 and behaviors have evolved 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.

2.2. THE POPULATION/HOST MODEL

In previous papers (Powell *et al*., 1996; White & Powell, 1998a, b; Bentz *et al*., 1996a,b; Logan *et al*., 1998; Powell *et al*., 1998a; Powell & Rose, 1997), we have developed and validated a spatial model for MPB dispersal and mass attack in pine forests. The state variables are:

$P(x, y, t)$—population of flying MPB.

$Q(x, y, t)$—population of nesting/eating MPB.

$A(x, y, t)$—concentration of pheromone suite.

$R(x, y, t)$—resin capacity (related to xylem thickness and surface area of tree).

$H(x, y, t)$—number of entrance holes bored by attacking MPB.

The equations relating these state variables are presented here only briefly. An equation for density of nesting MPB,

$$\dot{Q} = r_1 \frac{R}{R_0} P - \beta r_3 RQ, \tag{1}$$

accounts for landings in proportion to unoccupied surface area ($r_1(R/R_0)P$) and "pitchout" by trees ($-\beta r_3 RQ$). The factor R/R_0 measures unoccupied surface area since the resin reservoir is distributed just under the bark and is depleted locally in the vicinity of MPB attack. Constitutive resin responses are described by

$$\dot{R} = [r_2(R_0 - R) - r_3 H]R, \tag{2}$$

with terms modeling induced resin response ($r_2 R(R_0 - R)$) and depletion due to attack ($-r_3 RH$). The number of attack holes satisfies

$$\dot{H} = r_1 \frac{R}{R_0} P - r_4 r_3 HR, \tag{3}$$

with terms ($-r_4 r_3 HR$) describing host recovery from attack through resin recrystallization. While eqns (1) and (3) appear very similar, the progress and success of attack depends sensitively on their competing rates; if H can be driven down more rapidly than Q overcomes tree defenses, then the tree will survive the attack. Thus, H measures a tree's current stress, while Q measures success of MPB attacks. The dispersing population itself satisfies a chemotactic

TABLE 1

The list of parameters appearing in the global PDE model for MPB redistribution. Density units are represented with respect to hectares (ha), *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* (f h), *of which there are approximately five per day*

Parameter definitions and units		
Parameter	Definition	Units
A_0	Critical concentration at which pheromones become repulsive	$\mu g\ ha^{-1}$
A_3	Saturation parameter for pheromones	—
a_1	Rate of pheromone production by nesting beetles	$\mu g\ f h^{-1}\ HMPB^{-1}$
b_1	Rate of pheromone diffusion	$ha\ f h^{-1}$
β	Mortality rate of beetles due to resin outflow	R_0^{-1}
δ_1	Loss rate of pheromone	$f h^{-1}$
μ	Diffusitivity of flying beetles due to random movement	$ha\ f h^{-1}$
v	Strength of directed MPB motion due to pheromone gradients	$ha^2\ \mu g^{-1}\ f h^{-12}$
R_0	Rest resin capacity of a healthy tree (resin volume/stem area)	R_0
r_1	Rate of landing and conversion from flying to nesting beetles	$f h^{-1}$
r_2	Rate of resin replenishment	$f h^{-1}$
r_3	Rate of resin outflow through holes bored by beetles	$f h^{-1}$
r_4	Rate of resin crystallization (tree recovery)	R_0^{-1}
$\gamma(x, y, t)$	Emergence rate in time and space	$HMPB\ ha^{-1}\ f h^{-1}$

reaction–diffusion PDE,

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

where A is the concentration of the pheromone suite and

$$f(A) = A_3 A_0\left\{(A_3 + 1)\ln\left[1 + \frac{A}{A_3 A_0}\right] - \frac{A}{A_0}\right\}.$$

This function accounts for MPB attraction to the pheromone plume in low concentrations, when most of the plume is composed of attractants. Later in the attack the suite is composed of a higher proportion of anti-aggregants, and this is modelled as bias away from larger pheromone levels. The source term for dispersing MPB, $\gamma(x, y, t)$, describes the emergence of young adults from the *previous* season's successful attacks. Thus eqns (1–4) are purely an in-season dispersal model; reproductive dynamics for MPB are *not* included or relevant to this particular discussion. Parameter descriptions are given in Table 1; sizes for these parameters and units are given in Table 2.

2.3. AN EDDY-DIFFUSION-BASED PLUME MODEL

An averaged, steady pheromone plume is modeled as

$$A(x, y) = \begin{cases} \dfrac{a_1 q}{2\sqrt{xb_1 u\pi}}\exp\left[-\left(x\dfrac{\delta_1}{u} + y^2\dfrac{u}{4xb_1}\right)\right], & x \geqslant 0 \\ 0, & x < 0 \end{cases} \qquad (5)$$

in the presence of variable winds of mean speed u, and will serve as the chemical footprint of infestation in a particular tree. This is a phenomenological model for the average concentrations dispersed by a wind with variable direction and speed, but *mean* speed of u and *mean* direction in the positive x direction. Equation (5) produces plumes which are significantly broader than expected from truly unidirectional winds. This choice is less artificial than it may sound; in most

TABLE 2

Parametric values for numerical simulation and units. The parameter $\hat{\gamma}$ is the spatially averaged emergence rate of dispersing adults. Units involving resin are measured relative to R_0. Other units are: μg (10^{-6} g), ha (10^4 *square meters* = ha), fh (*flight hours* ~5 fh/day). *Parameter values are based on observational and anecdotal data discussed in Biesinger* et al. (2000)

Parameter	Value	Parameter	Value
A_3	1	A_0	7.8 μg ha^{-1}
a_1	2 μg fh^{-1} HMPB^{-1}	b_1	0.324 ha fh^{-1}
β	0.43 R_0^{-1}	δ_1	360 fh^{-1}
μ	1 ha fh^{-1}	v	5.7 ha^2 μg^{-1} fh^{-1}
R_0	1 R_0	r_1	0.16 fh^{-1}
r_2	0.0045 fh^{-1} R_0^{-1}	r_3	0.0023 fh^{-1}
r_4	0.0045 R_0^{-1}	$\hat{\gamma}$	0.1 HMPB ha^{-1} fh^{-1}

mountainous environments in the western U.S. winds have a strong orographic component which keeps them directionally oriented, in the mean, for hours at a time, but instantaneous wind speeds/directions can be highly variable.

In what follows, we will scale the eddy diffusion (b_1) and loss rate (δ_1) with mean spacing between trees (ξ), canopy closure (σ), and mean velocity. In an open canopy pheromones are lost in proportion to the distance between trees, the characteristic loss scale of the plume model (5) relates to this spacing as

$$\xi^2 \simeq \frac{b_1}{\delta_1},$$

so that characteristic losses occur on a tree-to-tree scale in open-stand conditions. The rate of chemical mixing due to turbulence is related to the advection velocity using

$$u^2 \simeq 4 b_1 \delta_1,$$

where the "speed" on the right-hand side is the neutral speed of propagation generated by solution via the method of steepest descents. Solving these two expressions for b_1 and δ_1 gives

$$b_1 = \frac{u\xi}{2} \quad \text{and} \quad \delta_1 = \frac{u}{2\xi}. \tag{6}$$

As the stand canopy becomes more closed, the air below becomes isolated from the air above. For a particular choice of u this should not change the rate of horizontal diffusion, but will influence the rate of loss through the canopy. We therefore augment the description of δ_1 with a scaling factor, σ, reflecting the degree of closure of the canopy ($\sigma = 1$ means open stand conditions, $\sigma = 0$ means solid canopy). Choosing average wind speed of $u = 0.6$ m s^{-1} and average tree separation of loss of $\xi = 3$ m gives $b_1 = 0.324$ ha fh^{-1} and $\delta_1 = 360\sigma$ fh^{-1}.

3. Localization and Bifurcation Analysis

The chance that a tree will be successfully attacked depends on the spatial distribution of MPB at the location of the tree. In this paper, which is concerned primarily with introducing a new methodology for examining risk, we assume that a weak focus tree has been successfully colonized and assign risk to nearby secondary trees. This illustrates how our approach naturally includes the effect of breaking various symmetries in space. The dynamics of the "second" tree, to which we want to assign risk, are influenced by infestation of the "first", or focus, tree. The focus tree is assumed to be previously infested in the dispersal season with q_1 beetles. It is a source of pheromones, *but not attacking beetles.* MPB sources are only provided by successfully attacked trees in the previous year (that is, through $\gamma(x, y, t)$). The total pheromone plume is the superposition of plumes emitted by beetles in the

focus tree and in the second tree,

$$A(x, y; x_0, y_0, q) = \frac{a_1 q_1}{2\sqrt{x b_1 u \pi}} \exp\left[-\left(x\frac{\delta_1}{u} + y^2\frac{u}{4xb_1}\right)\right] + \frac{a_1 q}{2\sqrt{(x-x_0) b_1 u \pi}} \times \exp\left[-\left((x-x_0)\frac{\delta_1}{u} + (y-y_0)^2\frac{u}{4(x-x_0)b_1}\right)\right]. \quad (7)$$

Here q_1 is the number of beetles in the focus tree (located at the origin) and q is the number of beetles nesting in the second tree, located at (x_0, y_0). Note that the domain in this description must be restricted in obvious ways.

As is discussed in Powell *et al.* (1998a) and Powell & Rose (1997), the population in the vicinity of an attacked tree is attracted rapidly to a steady state given by

$$P = \frac{\hat{\gamma}}{r_1 + \omega_1} \mathrm{e}^{(v/\mu) f(A)}.$$

This solution is derived under the assumptions that (1) the locus of attack is far from discrete sources of emergence, which may be averaged into a mean background emergence ($\hat{\gamma}$), and (2) that in the vicinity of the attack are no other trees being attacked (which allows a linearization by means of assuming $R \sim R_0$ everywhere except at the site of attack). The adiabatic population response to the two-pheromone plumes is

$$P(x, y; x_0, y_0, q) = \frac{\hat{\gamma}}{r_1 + \omega_1} \exp\left[\frac{v}{\mu} A_3 A_0 \left((A_3 + 1) \times \log\left(1 + \frac{A(x_0, y_0; q)}{A_3 A_0}\right) - \frac{A(x_0, y_0; q)}{A_0}\right)\right]. \quad (8)$$

To understand the impact of this population density on individual hosts we must "localize" the PDE model, as discussed in Powell *et al.* (1996, 2000b) and Powell & Rose (1997). State variables in units of density are replaced with Gaussian counterparts,

$$Q = 2\frac{q(t)}{w}\mathrm{e}^{-l^2/w}, \quad R = 2\frac{r(t)}{w}\mathrm{e}^{-l^2/w},$$

$$H = 2\frac{h(t)}{w}\mathrm{e}^{-l^2/w},$$

where l is measured radially from the tree of interest, and the new independent variables are observables (number) at individual hosts (not densities). The governing equations become

$$\dot{q} = r\left(\frac{r_1}{R_0} I(q) - \frac{\beta r_3}{w} q\right),$$

$$\dot{h} = r\left(\frac{r_1}{R_0} I(q) - \frac{r_3 r_4}{w} h\right), \quad (9)$$

$$\dot{r} = r\left(\frac{r_2}{w}(R_0 - r) - \frac{r_3}{w} h\right).$$

The infestation function, $I(q)$, represents the number of attacks resulting from a pheromone plume produced by q MPB already nesting in that host.

The function $I(q)$ is determined by integrating 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 as

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

In general, we take $\rho = 2$ m. Equilibria to the nonlinear system (9) are parametrized by solutions to the single equation for q:

$$\frac{r_0 \beta r_3}{r_1 w} q - I(q) = 0. \quad (10)$$

The function $I(q)$ depends upon the behavior of $P(x_0, y_0; q)$ which in turn depends upon the behavior of $A(x_0, y_0; q)$. Bifurcation and stability diagrams depend on the spatial location of the second tree and the parameters r_0, β, r_3, r_1 and $\hat{\gamma}$ in the combination

$$\chi = \frac{r_0 r_3 q_1 \beta (r_1 + \omega_1)}{\hat{\gamma} r_1 w}.$$

Figures 1 and 2 describe the bifurcation diagrams for varying the location and r_0. In most cases (trees more than a few meters away) there are three branches to the bifurcation diagrams (see Powell *et al*., 1998b). Near the focus tree (or when r_0 is small) there is one high (attracting) branch, further away there are three branches (metastability), and for greater distances from the focus tree only a single, low-q branch exists. The location (relative to the first attacked tree) and the "vigor" of the second tree play important roles on the number of MPB that attack the second tree.

A host's risk is rated according to its status in these bifurcation diagrams, as described in Fig. 3. The highest risk region is defined by the existence of a single, attracting fixed point for large q. The medium risk category is the intermediate, metastable region in which a sufficiently intense attack is necessary to become infested. The final, low risk region is characterized by a single globally attracting fixed point for low-q. This three-tier risk categorization is suggested by the bifurcation diagram; its spatial consequences are examined in a later section. Now we must address the connection between host resistance, as it appears in our model, and true host observables (i.e. host diameter and stand demographics).

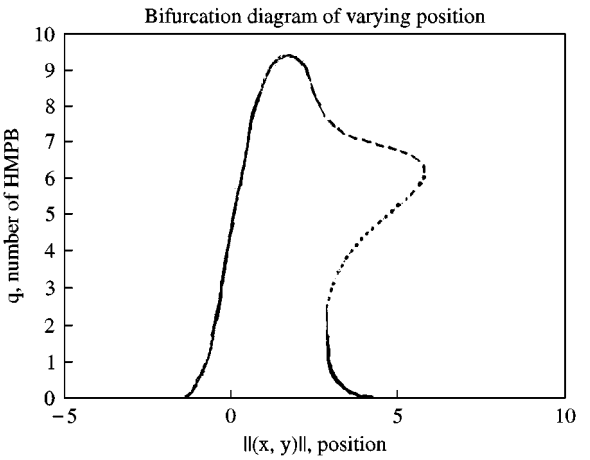

FIG. 1. Bifurcation diagram for varying the location of the second tree. (——) indicates the location of the fixed point of smallest magnitude, (– – –) the fixed point of largest magnitude, and the (· · · ·) any fixed point found between these two. Where it is distinct, the (…) indicates a threshold colonization level, below which a tree can beat off attackers and above which mass attack results in successful colonization of the host.

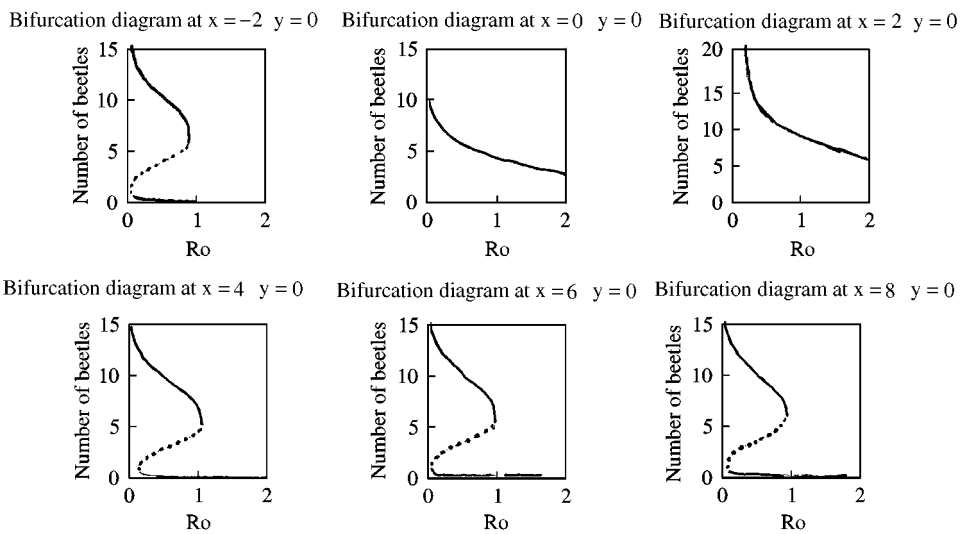

FIG. 2. Bifurcation diagrams for varying r_0 at different locations from the tree. Depending upon the location of the tree there are either three branches or one branch of the bifurcation diagram.

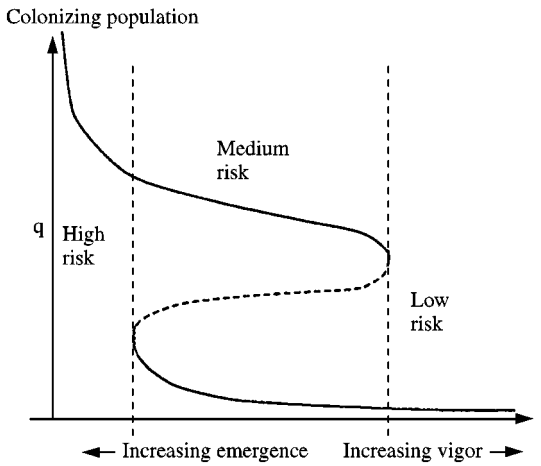

FIG. 3. Categories of risk as defined by the bifurcation diagram. The bifurcation parameter is $\chi = r_0\beta r_3 q_1(r_1 + \omega_1)/(r_1\hat{\gamma}w)$, which may be interpreted as the ratio between the vigor of the tree and infective pressure of emergence. Hosts to the left of the first turning point are at high risk because of the single large attracting fixed point. Individuals falling between the turning points are at lesser risk, conditioned on the need for a sufficiently strong attack. Hosts in the parameter region to the right are at low risk.

4. Relation between Forest Demographics and "Vigor"

The growth of a tree and its vigor depend on several factors: availability of resources, the size and species of the tree and the amount of competition for light with other trees. Lodgepole pine is a mesic, shade intolerant species, in competition with subalpine fir (*Abies lasiocarpa*), which need more water but are shade-tolerant, and Douglas-fir (*Pseudolsuga menziesii*), which is mesic and moderately shade-tolerant. These three species of conifer make up stands in much MPB habitat in the Intermountain West. Relative species densities are controlled by moisture, availability of light, stand management and the pattern of succession. We have used the Robert's model (Roberts *et al.*, 1993) described in the appendix, to produce stem-maps of lodgepole pine stands. These maps result from the competition among species for available water and light resources over long periods of time (50–200 yr). In this section, we will discuss how *DBH* (tree Diameter at Breast Height), a natural observable, can be related to "vigor" and resistance to MPB attack.

A stand of trees supports a fixed tree leaf area for given available resources. This leaf area depends on the tree species present and is distributed proportionally among all trees in the stand according to each tree's potential leaf area and size. The potential leaf area is a function of the size and species of the tree, and the ratio of actual tree leaf area to potential tree leaf area is one limiting factor in the tree's growth. Taller trees with larger *DBH* tend to shade smaller trees; this shade factor is the second limiting factor for growth. A third growth-limiting factor is availability of water in the stand. Year by year, the basal area of each tree can grow by a species-specific basal area increment (BAI), modified by the most restrictive of the limiting factors (W, which we take to be a dimensionless, fractional modifier on potential BAI; see the appendix). The potential amount of volumetric growth, $W * BAI * Height$, is a direct measure of a tree's excess energy, which may be used for growth or defense against pathogens.

The two parameters in our model which control host resistance to MPB attack are r_0 and r_2. As bark beetles attack and nest, the host tree uses resin to plug holes created by beetles and to mire or "pitch-out" attackers. The resin crystallizes, preventing further attacks through the same burrow. The tree's ability to successfully repel an attack depends on the initial reservoir of resin per surface area (r_0) and its ability to replenish resin once depleted (r_2). Relative vigor of trees is determined by how these two parameters relate to volumetric free energy.

Resin is carried in the xylem layer of the tree, which makes up part of the living wood area of the tree. The living wood has an approximate depth (living radius, or LR) of

$$LR = \min(10.35\text{ cm}, DBH/2)$$

from the surface of the tree. So the living wood volume is (*basal area – dead wood area*) times *Height*,

$$LV = \left[\pi\left(\frac{DBH}{2}\right)^2 - \pi\left(\frac{DBH}{2} - LR\right)^2\right] Height$$

$$= \pi(DBH - LR)\, LR\, Height.$$

The resin volume in the xylem is $W\,LV$, where W is the minimum of the dimensionless limiting factors for growth: relative leaf area, relative moisture and shade factor. Our rationale for this is that potential growth (of volume $W\,LV$) must be diverted into resin production in the advent of attack. The ratio of resin volume to surface area of the tree (r_0) is

$$r_0 \sim \frac{W\pi(DBH - LR)\,LR\,Height}{\pi DBH \cdot Height}$$
$$\sim W\left(1 - \frac{LR}{DBH}\right)LR.$$

All other parameters in our model scale with r_0 as a reference, so we normalize r_0 for a 10-in DBH tree under no stress (i.e. $r_0 = 1$ for such a tree).

The rate of resin replenishment also depends on the amount of "free energy" the tree has which can be directed towards resin production. In volumetric units this should be proportional to the ratio of new wood volume to the living wood volume. Thus, we define a unit-free "vigor", V, by

$$V \stackrel{\text{def}}{=} \frac{BAI\ Height}{\pi(DBH - LR)\,LR\ Height}$$
$$= \frac{BAI}{\pi(DBH - LR)LR'} \qquad (11)$$

and the resin replenishment rate, which has units $(r_0 - fh)^{-1}$, will be proportional to tree vigor,

$$r_2 \sim \frac{V}{r_0\,\mathrm{fh}}.$$

Again, r_2 is normalized so that a 10 in DBH lodgepole under no stress has values as designated in Table 2. With these definitions of r_2 and r_0, stem maps (like those presented in Fig. 4) become a set of spatially explicit parameter inputs for the risk assessment procedure.

5. A Spatial Understanding of Risk

At this point the elements are in place to begin a spatial assessment of risk in realistic stands. The approach is illustrated by placing a "focus" tree with 500 nesting MBP ($q_1 = 5$ HMPB) in each stand at the origin. Wind blowing from the left initializes a pheromone plume. Each nearby LPP of sufficient size (DBH > 20 cm) is examined for fixed points, determining its risk classification. For each tree, j, with r_{0j}, r_{2j} constitutive and induced resin parameters and location (x_j, y_j), eqn (10),

$$\frac{r_{0j}\beta r_3(r_1 + \omega_1)}{\hat{\gamma}\, r_1 \omega}\, q$$
$$= \int_{D_2(x_j, y_j)} \exp\left\{\frac{\nu}{\mu} f[A(x_j, y_j; q)]\right\} \mathrm{d}x\,\mathrm{d}y,$$

is examined numerically for fixed points in q. Here $D_2(x_j, y_j)$ represents the disk of radius two centered at (x_j, y_j) and the integrand is proportional to the steady-state population response to $q_1 = 5$ HMPB nesting at the origin and q HMPB nesting at (x_j, y_j). The spatial juxtaposition of high, medium and low risk hosts then provides an indication of stand risk.

To illustrate this procedure we examine how risk changes with four variables:

- *Stand age.* One contributing factor to an MPB outbreak may be declining vigor within a stand as it ages. This can arise from two sources; the general senescence of LPP within a stand as they grow older and competition with other, more shade-tolerant conifers in the stand. Accordingly, we will investigate risk in a single stand at various stages of secession.
- *Emergence density.* The density of beetle emergence, $\hat{\gamma}$, may increase depending on the number of sources (trees successfully attacked in the previous summer) and the temperature during the year and season of emergence. Understanding changes of risk structures as ad function of $\hat{\gamma}$ is therefore central to understanding how climate and population contribute to an outbreak.
- *Canopy closure.* MPB focus and mass attack individual hosts by virtue of pheromone plumes, whose dispersal depends on turbulent mixing among stems and losses through the canopy. By changing σ, the canopy permeability, we illustrate how spatial risk assessment may suggest or validate vegetation management strategies depending on crown thinning.

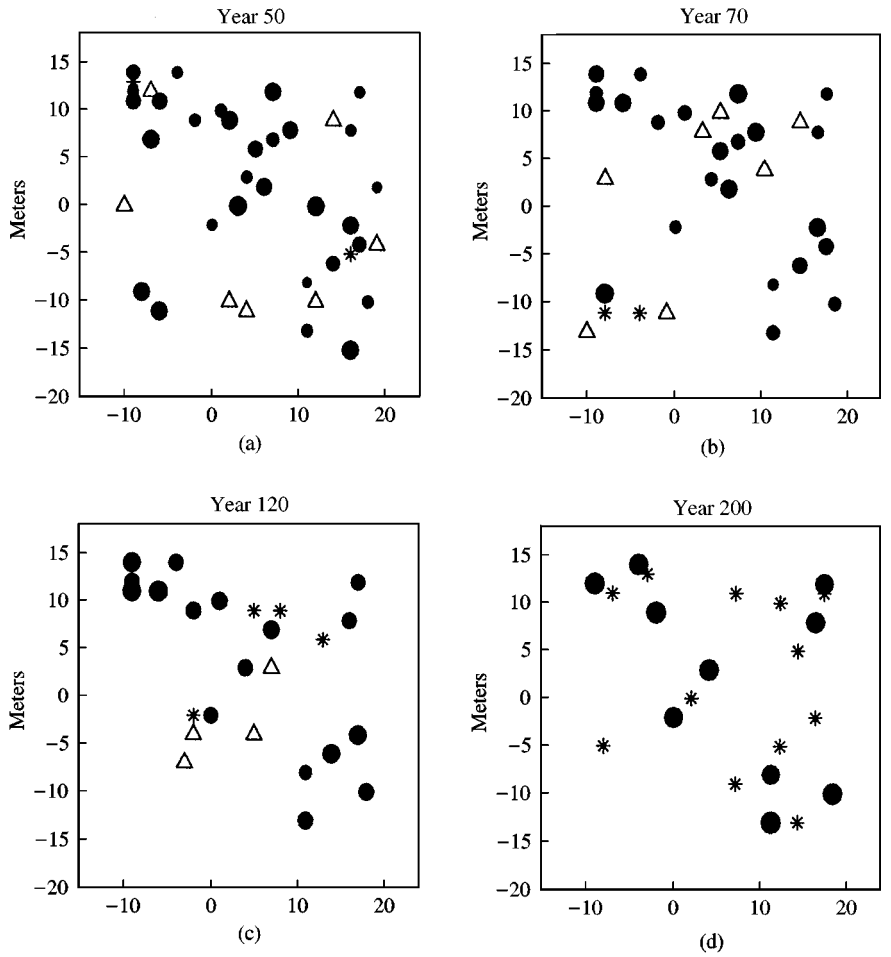

FIG. 4. Stand demographics and spacing as a function of time. The four plots are scaled in meters and represent different snapshots of the same stand in time. The stand after 50 yr of growth (from seedlings randomly distributed on bare ground) is depicted in (a), after 70 yr in (b), after 120 yr in (c) and after 200 yr in (d). Lodgepole pine appear as solid disks whose size is proportional to *DBH*. Triangles denote the location of subalpine fir, while Douglas-fir are marked with *. Only hosts with $DBH > 5.5$ cm are plotted.

- *Average wind speed*. Flow speed around the stem strongly influences dispersal of the pheromone plume. Changing the wind speed (not to mention direction) may therefore significantly alter risk patterns in areas experiencing more or less strong orographic flow. Moreover, average wind speed may be a micro-climate indicator of stand structure. We will illustrate how to examine the effect of wind speed on risk pattern.

The setup for these four cases is described below.

5.1. STAND AGE

To examine changes in the risk of MPB attack as a stand ages we generate virtual LPP stands using Robert's stem model (Roberts *et al.*, 1993, summarized in the appendix). Snapshots of a stand at 50, 70, 120 and 200 yr were used as input to the risk assessment procedure. Ages were chosen to represent the maximum number of > 20 cm DBH hosts (at 50 yr), a variety of hosts at maximum size (~ 50 cm at 200 yr), and two samples of spatial host structure in intervening years. These stands span the likely extremes of induced and constitutive resin responses which may be expected to arise due to intra-stand competition and secession.

Results are illustrated in Fig. 5, with all parameters held constant except stand age. The total number of hosts at high and medium risk declines with stand age, but so does the total number of

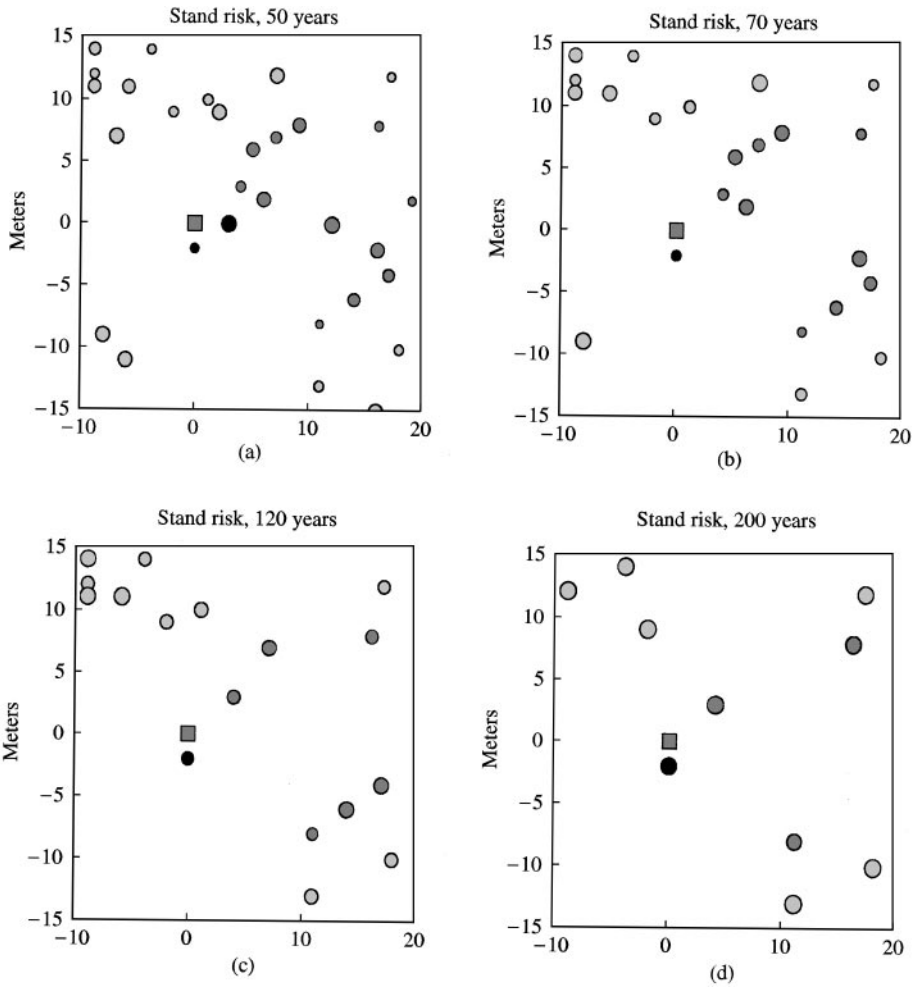

FIG. 5. Risk pattern as a function of stand aging. Hosts are denoted by disks sized in proportion to *DBH*. Trees at high risk have black disks, trees at medium risk are dark grey, and trees at low risk are light grey. The location of the focus tree is indicated by the shaded square at the origin.

hosts. No host which survives the full 200 yr changed its risk category, and the spatial limits of the risk profile are apparently the same. This is consistent with the idea that host vigor, *per se*, is less critical than micro-climate factors in controlling stand risk.

5.2. EMERGENCE DENSITY

Our second treatment was to vary emergence density ($\hat{\gamma}$) and examine changes in risk patterns in stands of a particular age (70 yr). The parameter, $\hat{\gamma}$, reflects both temperature and attack success in the previous year. As a point of reference, a single infested tree may contain 500 nesting MPB, which produce between 2 and 10 surviving offspring each. Taking 4 to be a likely value (although the temperature fluctuations throughout the year and quality of the food resource may influence this number strongly), each infested tree represents approximately 2000 emerging MPB. The rate of emergence is strongly dependent on temperature during the dispersal season as well as on temperature cues throughout the year (which help MPB synchronize their emergence for maximum effect). Assuming that dispersal occurs uniformly through the 3-week season ($\sim$100 fh), and that the forest has approximately one infested tree per hectare, we arrive at $\hat{\gamma} \approx 0.2$ MPB/(ha-fh).

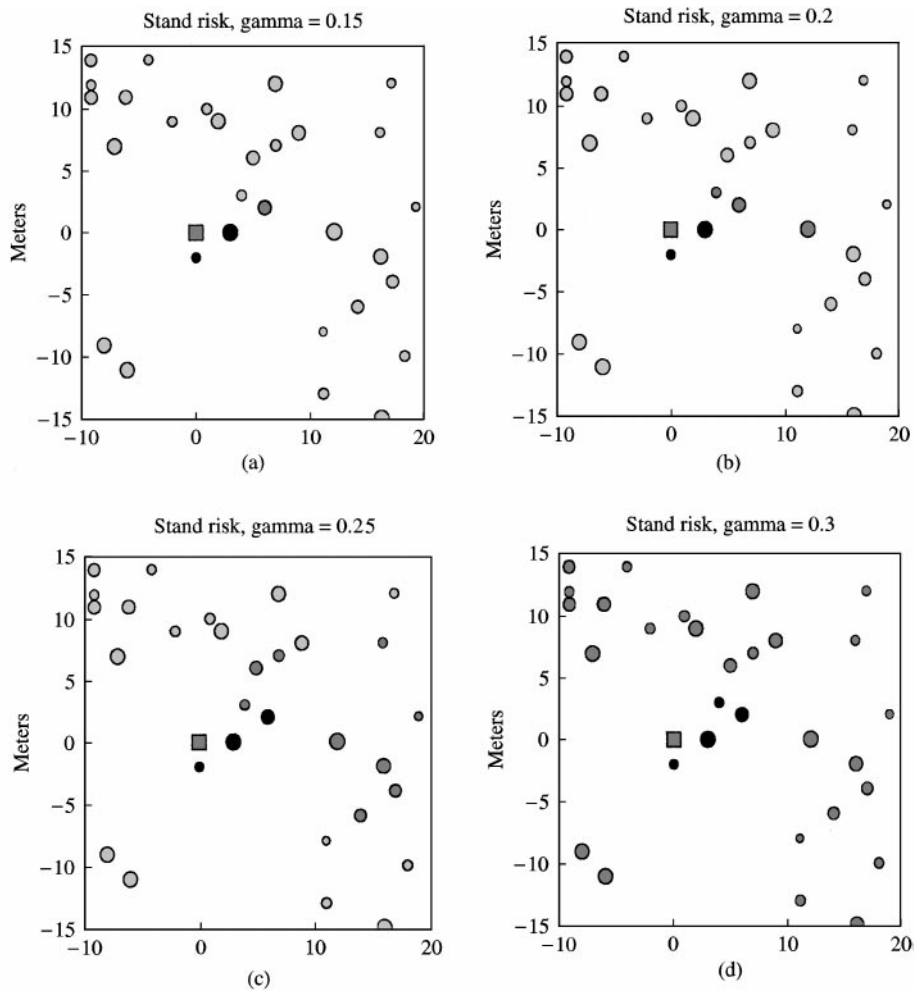

FIG. 6. Risk pattern as a function of emergence density. Emergence ranges from $\hat{\gamma} = 0.15$ (a) to $\hat{\gamma} = 0.2$ (b) to $\hat{\gamma} = 0.25$(c) to $\hat{\gamma} = 0.3$ (d). Hosts are denoted by disks sized in proportion to *DBH*. Trees at high risk have black disks, trees at medium risk and dark grey, and trees at low risk are light grey. The location of the focus tree is indicated by the shaded square at the origin.

We choose to vary $\hat{\gamma}$ from 0.15 to 0.3 and examine how risk shifts. Representative cases are presented in Fig. 6. As expected, for low levels of emergence only hosts proximal to the focus are at risk. As emergence increased so did the size of the risk footprint. At $\hat{\gamma} = 0.3$ the level of emergence was high enough that every host in the simulation was at some degree of vulnerability, even upwind from the focus tree. For lower levels of emergence (endemic population, $\hat{\gamma} < 0.2$) with only a few vulnerable trees, one might expect new patterns of attack to follow the risk pattern closely. At higher levels of emergence (epidemic, $\hat{\gamma} > 0.2$) the pattern is less spatially structured, and the results of dispersal would be less predictable by a risk analysis like the one under consideration.

5.3. CANOPY CLOSURE

One way to control MPB infestation is through stand thinning. Stems within a stand are selectively cut until a specified degree of crown separation is achieved. It has been hypothesized that this is effective because of the reduced within-stand competition and consequent higher average host vigor. It has also been hypothesized that thinning increases bole temperature through increased solar irradiance, thus making hosts in thinned stans less attractive to MPB. To evaluate

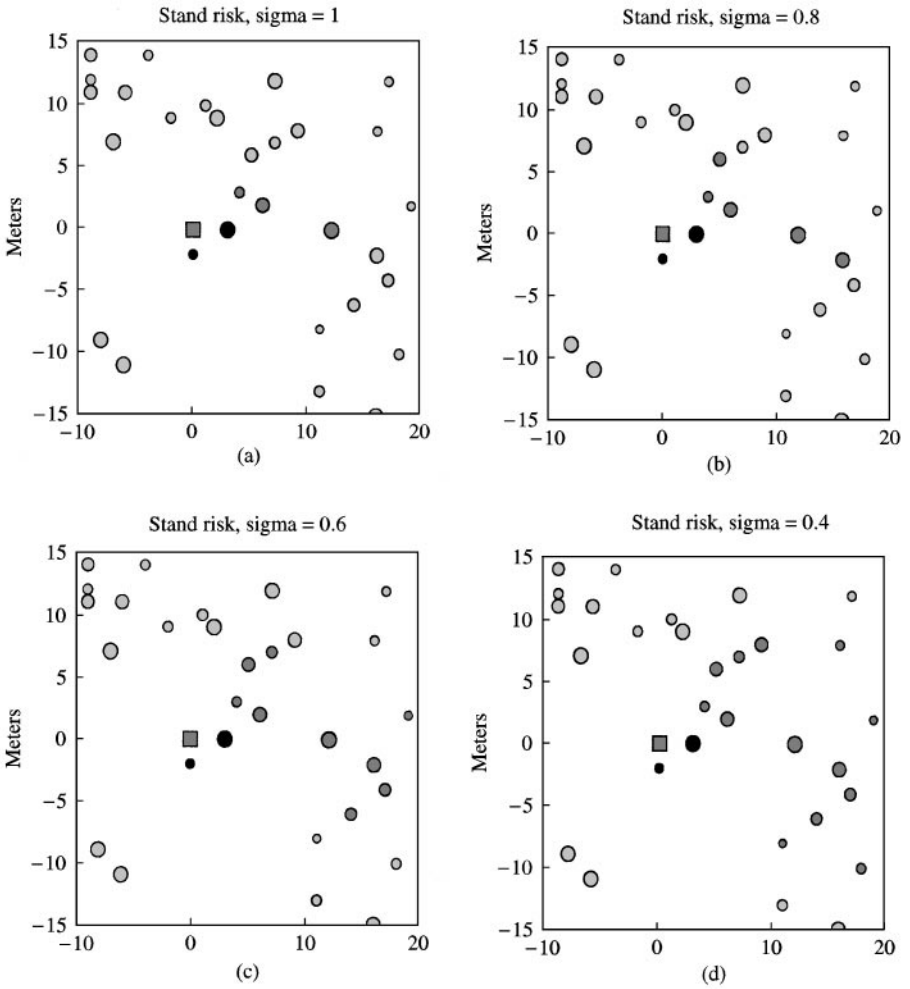

FIG. 7. Risk pattern as a function of canopy closure. Permeability ranges from $\sigma = 1$. (a) to $\sigma = 0.8$ (b) to $\sigma = 0.6$ (c) to $\sigma = 0.4$ (d). Hosts are denoted by disks sized in proportion to *DBH*. Trees at high risk have black disks, trees at medium risk and dark grey, and trees at low risk are light grey. The location of the focus tree is indicated by the shaded square at the origin.

whether interference with the pheromone plume might also be a factor, we examined the risk structure as a function of canopy permeability, σ.

Results are illustrated in Fig. 7 for permeability ranging from $\sigma = 1$ (open stand, as much open sky as canopy) to $\sigma = 0.4$ (crowns nearly touching). In an open-stand situation, only a few downwind hosts proximal to the focus tree are at risk. As canopy closure is increased (σ decreased) a larger contingent of downwind hosts experiences risk. While the region of highest risk does not change, the region of intermediate risk grows significantly. These results suggest that before host vigor can be altered by thinning (which should take a large fraction of the growth season for a tree), the microclimate changes induced by selective cutting could reduce the risk of an MPB attack. While it is beyond the scope of the present study to determine optimal cutting strategies to reduce stand risk, our techniques could clearly be applied in that way.

5.4. WIND SPEED

An additional effect of thinning would be to increase the average wind speed within a stand. This would occur because fewer stems and less canopy creates less flow friction and greater mixing between the free wind above and protected environment below the canopy. Moreover, western conifer stands occur at many different

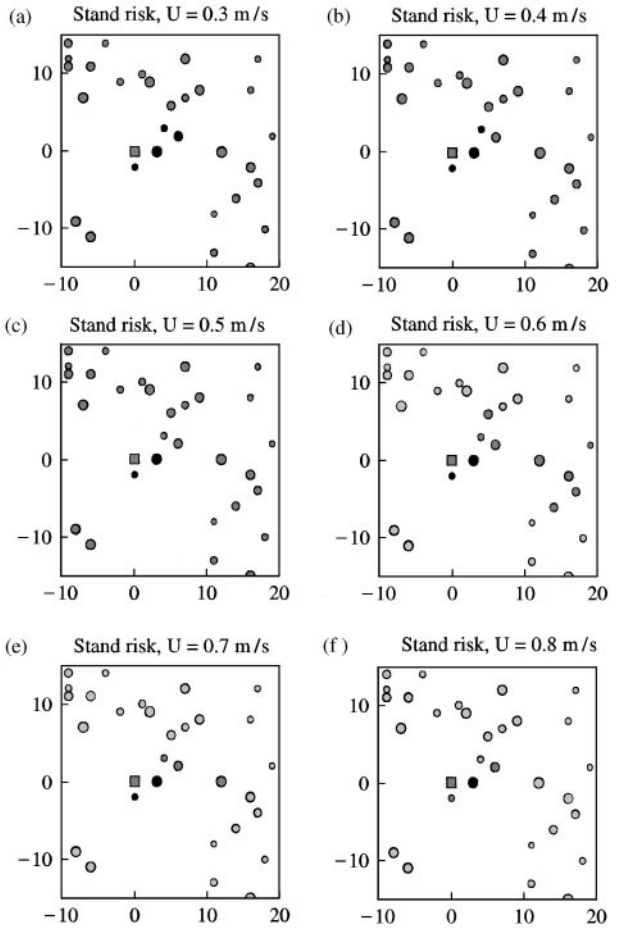

FIG. 8. Risk pattern as a function of average wind speed. Speeds range from $u = 0.3\,\mathrm{m\,s^{-1}}$ (a) to $u = 0.8\,\mathrm{m\,s^{-1}}$ (f). Hosts are denoted by disks sized in proportion to *DBH*. Trees at high risk have black disks, trees at medium risk are dark grey, and trees at low risk are light grey. The location of the focus tree is indicated by the shaded square at the origin.

elevations, slopes and latitudes, resulting in a range of average wind velocities. Since plume development depends so strongly on wind speed, an investigation of risk structure as a function of u is in order.

Illustrations of the current approach applied to varying mean wind are depicted in Fig. 8 for wind speeds between 0.3 and $0.8\,\mathrm{m\,s^{-1}}$. The trend indicated is a uniform increase in risk as wind speed is decreased. At high speeds only the closest downwind hosts are at risk from a focus tree, while the entire group of trees may be at risk for sufficiently small speeds. In particular, the region of high risk downstream of a focus tree continues to grow as speed is decreased, even when the entire group is experiencing conditional risk. These results are consistent with the idea that increasing canopy closure (thereby decreasing wind speed) increases stand risk, again, proving that this is the case is outside the boundaries of the current paper and will be the subject of future work.

6. Conclusion

In this paper, we have described an approach for using a deterministic PDE model as a risk assessment tool. The approach hinges on two prior results: separation of temporal scales and consequent existence of a quasi-steady population response and localization of density variables to scales appropriate for consequences at individual hosts. The localized equations admit at most two attracting steady states, one of which (the larger nesting population) corresponds to successful infestation of the host. When only the smaller state exists the host is classified at low risk; when only the larger exists the host is at high risk. In between is a region of medium risk in which successful infestation is contingent on sufficiently intense attack. To illustrate this procedure risk was examined in virtually generated conifer stands, using a turbulent-transport plume model for pheromone dispersal.

Our risk system reflects the spatially complex movement of MPB within a stand, as influenced by environmental and host factors, and the chemical ecology of the beetle. A mean wind direction was chosen to break symmetry and better illustrate the methodology. Infestation risk in each stand was evaluated relative to the existence of a "focus" tree embedded in the plot. Predicting *a priori* which tree in a stand will be attacked first is very difficult; focus trees in a plot are not necessarily the largest tree, but are often influenced by other stressing factors such as root disease or lighting strikes (Eckberg *et al.*, 1994; Tkacz & Schmitz, 1986; Schmitz, 1988; Schowatter & Filip, 1993). Attack risk to trees near a focus is evaluated based on host age, canopy closure, vigor of the host, wind speed and the surrounding beetle population density.

Our intent was not to perform an exhaustive study of risk, but to discuss the implementation of the risk procedure. Nonetheless, suggestive

results emerge, encouraging future research. When all parameters except host age were held constant, the spatial structure of the risk pattern in the stand remained the same as age increased. In other words, as all the trees became old, they did not all become high risk. This result indicates that something other than, or in addition to, age may be important in assessing risk to a tree. The background emergence of MPB is certainly important, as demonstrated in Fig. 6. Perhaps more important was the influence of canopy closure. As the canopy became more open, the number of trees in the stand with a moderate risk was reduced dramatically (Fig. 7). This indicates that microclimate changes in the stand, due to selective harvesting for example, may have more of a short-term influence on risk than host age or vigor. Affected would be both the dispersal of pheromone plumes through the canopy, which would indirectly affect the beetle, while increased solar radiation on the boles of trees would have a direct effect on the beetle population.

Developing a risk rating system for any bark beetle species is a daunting task. Past efforts have attempted to assign risk categories based on evaluation of beetle-caused mortality, after an outbreak. To truly understand what factors infuence a beetles choice of trees would require a long-term study, monitoring attacked trees beginning with an endemic population, following all trees through the epidemic phase. All aspects of tree and stand conditions would need to be monitored. We know that weather, individual host condition, stand characteristics, and beetle biology and movement are all important, just not how they all fit together. Our system is an attempt to bring these factors together. No attempt was made to correlate our risk predictions with data. Rather, since this is the first dynamically based conception of risk, our goal was to test the idea for feasibility, in realistic situations. Ideally, future work will expand the stand-based model to the landscape scale, comparing our risk predictions with actual attack data, following up on the suggestive results in this paper.

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APPENDIX

Details of the Stem Model

In this appendix we describe Robert's 1993 model (Roberts *et al.*, 1993) used to generate a simulated forest. A stand of trees will occupy a fixed area, and all characteristics are deformed at a stand level with randomly distributed trees. Every year limiting factors are calculated for every stem in a given area. Each tree's growth or chance of mortality is then assessed based on its size and the impact of limiting factors, including inter- and intra-specific competition for light. The details, parameters and rationale for this model are presented in Roberts *et al.* (1993).

The growth of a tree depends on a several factors: availability of resources, the size and species of the tree and the amount of competition for light with other trees. Trees are classified as either DRY, MESic, or WET depending on the amount of moisture they need, and are also classed by shade tolerance: INTolerant, MODerately shade tolerant and TOLerant species. Lodgepole pine is approximately MESINT, meaning it is moderately drought-tolerant and intolerant to shade. Sub-alpine fir (*Abies lasiocarpa*) is approximately WETTOL, while Douglas-fir (*Pseudotsuga menziesii*) is MESMOD.

A stand of trees can only support a fixed amount of tree leaf area given a fixed level of available resources. This leaf area is dependent on the species of tree present and is distributed proportionally among all trees in the stand according to their potential leaf area and size. The ratio of actual tree leaf area to potential tree leaf area is the first limiting factor in tree growth.

A second factor is shade. Trees with larger *DBH*, or diameter at breast height, tend to be taller and require more leaf area than smaller trees, so trees with more leaf area tend to shade trees with less leaf area. The amount of shade at a location in the canopy is measured by the sum of the leaf area above that location. Hence, the shade factor for each tree depends on the cumulative sum of of leaf area from canopy top down and the tree's shade tolerance.

The third limiting factor is the tree's ability to use available water, which depends on climatic and soil variables as well as tree type. This limiting factor we call the relative moisture of the species of trees considered. Year by year, the basal area of each tree can grow by a species-specific basal area increment (*BAI*), modified by the most restrictive of the limiting factors (W). Each tree's *DBH* and leaf area can then be calculated; trees which are unable to grow a prerequisite, species-specific amount are in danger of death.

Three species of trees are represented with the indexing convention given by Table A1. The index j will be used to refer to particular trees in the stand. On a yearly basis limiting growth factors are calculated for every tree, then each tree's state updated according to the impact of those factors. Maximum possible leaf area that can be produced in a stand given the available resources (mainly water) is calculated

$$Max\ SLA_i = \max\left[0, \alpha_{1,i}(1 - e^{\beta_{1,i}(Aw+\gamma_i)})\right],$$

where $\alpha_{1,i}$ is the species-specific maximum leaf area per square meter at optimum moisture, $\beta_{1,i} < 0$ is a species-specific coefficient of moisture sensitivity, $Aw = (Precipitation\ gains - Evaporation\ losses)$ is the available water (resources) and γ_i is the minimum level of resources required for each species (Table A1). The potential leaf area of each tree in the stand is directly related to *DBH* by

$$PTLA_j = \alpha_{2,spec_j} DBH_j^{\beta_{2,spec_j}},$$

where $PTLA_j$ is the potential leaf area for the j-th tree in the stand, $spec_j$ is an index of the species of the j-th tree ($spec_{10} = 3$, means that tree number ten is WETTOL), and $\alpha_{2,i}$ and $\beta_{2,i}$ are the leaf area/*DBH* conversion parameters which can

depend on the species of the tree, but we will assume are the same for the three species used, $\alpha_{2,i} = 0.1$ and $\beta_{2,i} = 2.4$. The potential stand leaf area for each species is then the sum of the individual tree leaf areas for that species,

$$SPLA_i = \sum_{spec_j = i} PTLA_j.$$

The total potential leaf area and total share are defined as

$$TotPLA = \sum_{i=1}^{NumSpec} SPLA_i \quad \text{and}$$

$$TotSHR = \sum_{j=1}^{NumTrees} PTLA_j^{0.925},$$

where *NumSpec* is the number of species of trees in the stand, and *NumTrees* is the number of trees in the stand. The 0.925 exponent in the *TotSHR* equation corresponds to larger trees getting a proportionally larger share of the total leaf area. Then the total stand leaf area is given as a weighted average of species potential leaf areas,

$$TotSLA = PltSize \sum_{i=1}^{NumSpec} \frac{SPLA_i\, MaxSLA_i}{TotPLA},$$

where *PltSize* is the size of the plot the stand occupies. The actual leaf area for each tree is determined by comparing its share of the stand leaf area with its maximum potential leaf area,

$$ActTLA_j = \min\left(PTLA_j, \frac{TotSLA \cdot PTLA_j^{0.925}}{TotSHR}\right).$$

We can now calculate the growth of each tree in the stand by finding the limiting resource: relative leaf area, shade factor or relative moisture. The relative leaf area is just the ratio of actual to potential leaf area,

$$RelLA_j = \max\left(0, \frac{ActTLA_j}{PTLA_j}\right).$$

The relative moisture available for each tree is species specific and is given by

$$RelMos_i = \max\left(0, \frac{MaxSLA_i}{\alpha_{1,i}}\right),$$

which is a measure of a tree's potential ability to use the resources available. The shade factor is determined by looking at the tree's position in the canopy, determined by calculating a cumulative leaf area distribution. An index is used to rank each tree based on its actual tree leaf area,

$$index_j = \min(10000, \lfloor Act\,TLA_j \rfloor + 1),$$

where $\lfloor \cdot \rfloor$ is the floor function (round down to next integer). Of $index_j = index_k$ then j-th and k-th trees are at approximately the same position in the canopy. The vertical leaf area distribution is given by

$$VLADist_k = \sum_{index_j = k} ActTLA_j,$$

where the sum is over all trees which are at the k-th position in the canopy. The cumulative leaf area distribution is a cumulative sum of all leaf area above a location in the canopy,

$$CLADist_l = \frac{\sum_{k=l}^{1000} VLADist_k}{PltSize},$$

and is scaled by the plot size. Next we calculate the canopy position based on the cumulative leaf area distribution,

$$index_j = \min(10000, \lfloor Act\,TLA_j \rfloor + 1),$$

where all trees with actual leaf area above 100 are considered to be in the top of the canopy and are self-shading only. The canopy position is given by

$$CanPos_j = \tfrac{1}{2}\,(CLADist_{index_j} + CLADist_{index_j + 1}).$$

Here the canopy position is not a vertical height, but a measure of the effective shading a tree experiences. A smaller tree would have

a lower *index* value and a larger *CanPos*, i.e. a smaller tree would be shaded more than a larger tree. The shade factor for each tree is then given by

$$ShdFac_j = \max\left(0, \frac{ShdTol_{spec_j} - CanPos_j}{ShdTol_{spec_j}}\right),$$

where the shade tolerance is given by Table A1.

The relative growth for each tree is based on a species-specific maximum growth potential, ω_i given in Table A1, and limited by the most restrictive leaf area, relative moisture, shade factor,

$$RG_j = \omega_{spec_j} \min(1, RelLA_j, RelMos_{spec_j}, ShdFac_j).$$

The potential basal area increment is given by

$$PBAI_j = \alpha_{3,spec_j} \exp\left(\frac{\beta_{3,spec_j} BA_j}{MaxBA_{spec_j}}\right),$$

where $BA_j = \pi DBH_j^2/4$ is the current basal area of the j-th tree, $\alpha_{3,i}$ and $\beta_{3,i}$ are relative basal area increment coefficients which depend on the species of the tree, and $MaxBA_i$ is the maximum basal area of a tree of species i (Table A1).

Finally, the actual basal area increment for each tree is given by

$$BAI_j = \max\left(0, RG_j PBAI_j BA_j + \frac{5}{BA_j}\right),$$

and the new DBH can be calculated from $BA_j + BAI_j$,

$$NDBH_j = 2\sqrt{\frac{BA_j + BAI_j}{\pi}}.$$

With BAI for each tree, we must finally determine which trees are over-stressed and insert mortality. Mortality is based on cumulative stress. If the basal area increment for a tree is less than a species-specific minimum growth then the tree is stressed and the cumulative stress for that tree is incremented by one. If the tree is not stressed during the current growth period then the cumulative stress is decremented by one (with a minimum cumulative stress of zero). Trees with a cumulative stress greater than five are inserted into a mortality queue. Mortality consists of removing one-fifth of the trees in the mortality queue for that growth period.

Along with mortality, this growth model includes reproduction. It is assumed that there is a seed source for each species in the stand. The number of new trees of each species entering the system is based on the species light/shade tolerance and the relative moisture. The species shade factor is given by

$$ShadFac_i = \max\left(0, \frac{ShdTol_i - CLADist_1}{ShdTol_i}\right),$$

where $ShdTol_i$ and $CLADist_1$ are the species shade tolerance and the first element in the cumulative leaf area distributions used above. $CLADist_1$ is used because a seedling is at the bottom of the canopy. The number of new trees entering the system of each species is then

$$NewTre_i = 20\, RelMos_i \min(1, ShdFac_i),$$

where each new tree starts with $DBH = 2.5$ cm.

This modeling approach was used to simulate the dynamics of a mixed conifer stand in the Intermountain Region of the United States. Available water was chosen yearly from a uniform distribution centered at the mean for the region, which virtual "seedlings" were spread at random in a 30×30 m plot. Invariably, LPP are the dominant trees for the first 200 yr due to their rapid growth and the initial lack of shading from other species (given no major disturbance, such as a MPB outbreak). After 200 yr the shade-tolerant species begin to out-compete seedling LPP for resources below the canopy, while the larger LPP are at the limits of their capacity for growth and begin to die off. By 300 yr, LPP are largely gone and the stand is dominated by the shade-tolerant species (assuming no fire), which is a realistic rendition of stand dynamics grown from the soil up. Snapshots of a representative stand, which we will use to illustrate the spatial risk analysis, are presented in Fig. 4 at 50, 70, 120, and 200 yr from simulation start. At 200 yr the

LPP reached a *DBH* of 50 cm, which is approximately the maximum sustainable size for LPP in the region, while at 50 yr the largest LPP are between 20 and 25 cm *DBH*. Thus, the virtual stand depicted in Fig. 4 is representative of the range of tree size and induced/constitutive resin responses which dispersing MPB may encounter in the Intermountain Region.