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Ecological Insights Gained From Model Analysis of Mountain Pine Beetle Outbreaks

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Abstract.

Implementation of ecosystem management requires an expanded view of the role that natural disturbance agents play in maintaining forest health. As a part of this expanded conceptual framework, it is necessary to view natural disturbances within the overall context of a functioning ecosystem. The mountain pine beetle (MPB) is economically the most destructive native insect pest of western forests, and, as a result, significant resources have been expended on MPB research. Even though a great deal of knowledge exists regarding individual aspects of MPB ecology, some of the most basic questions regarding outbreaks remain unanswered. In our opinion, one reason for the lack of ecological synthesis is the inadequate treatment of spatial dynamics in outbreak theories. In this paper we first provide the rationale for our modeling effort. We then describe the explicit spatial model we have developed. We conclude with a discussion of model application used to explore three important ecological questions that involve explicit spatial dynamics: (1) the switch from environmental to dynamic determinism that accompanies the progression of an outbreak; (2) the effect of synchronous adult emergence on precipitation of an outbreak; and (3) the effect of spatial arrangement of nurse trees in outbreak induction.

Introduction.

The ecological adaptation of MPB as an aggressive bark beetle that must kill its host to successfully reproduce has resulted in an organism that is both economically important and ecologically significant. Outbreaks of MPB can be truly spectacular events, with resulting tree mortality that is both intensive (often in excess of 80% mortality) and extensive (sometimes thousands of acres). As a consequence of this economic and ecological significance, a great deal of monetary and intellectual resources have been expended trying to understand the underlying ecological basis of these spectacular outbreak events. This attention has resulted in an impressive knowledge base that is well documented in the scientific literature (e.g. Lessard et al. 1986). In spite of this significant effort, some of the most basic questions regarding MPB outbreaks remain unanswered. Among these are: What actually triggers an outbreak? What determines its intensity and spatial extent? Although several hypotheses have been put forward (Berryman 1976, Berryman et al. 1984, Cole and Amman 1980, Amman 1978, Raffa and Berryman 1986), a generally accepted synthesis remains an illusive goal. In our opinion, one important reason for the lack of synthesis and ability to predict outbreaks is the inadequate treatment of spatial dynamics in outbreak theories.

Our basic thesis is that outbreak dynamics are inherently dependent on dispersal behavior as well as local population dynamics, and that to understand

outbreaks in a large-scale spatial domain, one must consider dispersal behavior as well as local conditions. Integrating ecological processes across spatial and temporal scales is a daunting task. First, the very nature of outbreaks leads to a great deal of interest when a raging epidemic is in progress, but interest quickly wanes during periods of remission. As a result, empirical information is skewed towards measurements made after an outbreak is already in progress and much less data exist during the critical times leading up to outbreak initiation. Secondly, it is physically and logistically difficult to conduct experiments in mountainous terrain on the spatial scale that is required. As a result, most empirical experiments have been conducted at the individual tree, or at most, stand level. In response to the difficulties in on-the-ground empirical analysis of outbreak events, we have formulated a mathematical model of MPB chemical ecology and the spatial interaction between MPB and host forests. Analysis of this model is itself fraught with difficulties due to spatial complexity of turbulence resulting from inherent nonlinearity (Taubes 1995). Due to these mathematical and computational difficulties, our work to date (Powell et al. 1996, White and Powell in press, Powell and Rose in press) has dealt largely with the analytical and numerical aspects of the model. In this paper, we begin to apply this model in the analysis of ecological questions regarding the nature of MPB outbreaks.

Methods.

Our objective is to explore some critical aspects of MPB ecology through simulations with a model of chemical ecology, spatial redistribution, attack, and tree mortality. In a sense, we are using the model as a tool for testing hypotheses regarding the sufficiency of certain critical attributes of MPB ecology, especially those pertaining to the self-focusing and self-dissipating effects of pheromone chemistry, as the cause of observed mortality patterns. The mountain pine beetle is typically a univoltine species that spends most of its life cycle protected under the bark feeding on phloem tissue. However, for a few weeks each year, the critical processes of spatial redistribution, attack, and colonization take place. It is this spatially dynamic phase of the life cycle that we are concerned with in this paper. Model description of spatial redistribution and attack requires a system of six coupled partial differential equations (MPBpde, Table 1). Three of these, while spatially distributed, are not spatially dynamic (space enters into these equations only parametrically). These equations (Eqs. 1-3) describe: the dynamics of live nesting beetles (Q); host tree resin capacity (R) which is a surrogate for individual tree health; and boring holes (H) the dynamics of which are used to model tree recovery from beetle attack. The remaining three equations result from spatial fluxes. These spatially dynamic equations are used to model: the concentration of host volatiles (C) that are attractive to beetles (kairomones); the diffusive characteristics of beetle produced pheromones (A); and, most importantly, the chemically mediated population dynamics of emerged, flying beetles (P).

Table 1. Model of Mountain pine beetle redistribution and attack (MPBPDE)

Dynamic Equations Describing the Pine / Mountain Pine Beetle Interaction

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

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

$$\dot{H} = r_1 \frac{R}{R_0} P (1 + \sigma A) - r_4 S. \quad (3)$$

$$\frac{\partial P}{\partial t} = -\nabla \cdot \{[\kappa \nabla C + v \nabla f(A)] P - \mu \nabla P\} - \omega_1 P - r_1 \frac{R}{R_0} P (1 + \sigma A) + \gamma. \quad (4)$$

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

$$\frac{\partial C}{\partial t} = b_2 \nabla^2 C + a_2 S - \delta_2 C. \quad (6)$$

This system of six state variables (Table 2) requires 21 parameters to describe the critical processes that define the interaction between pine trees and the mountain pine beetle (Table 3). The level of description of the model is intermediate between a complex simulation model (Raffa & Berryman 1986) and the typically abstract level of a

purely theoretical model. In this model we have attempted to include the minimum level of descriptive detail required to maintain ecological credibility. The result is a mathematically tractable (though complex) model that includes both self-focusing (pheromone attraction) and self-dissipating (anti-attraction or pheromone inhibition) terms in addition to random movement. It is this ecologically coevolved chemical communication system represented by nonlinear flux terms of Eq. 3 that is largely responsible for both the persistence of the system in ecological time, and the resulting complex spatial pattern of killed trees.

Table 2. List and description of state variables used in MPBpde.

STATE VARIABLE	DESCRIPTION
$P(x,y,t)$	Population of flying beetles
$Q(x,y,t)$	Population of alive, nesting beetles
$A(x,y,t)$	Concentration of composite pheromone
$C(x,y,t)$	Concentration of volatiles released by host trees (kairomones)
$S(x,y,t)$	Resin outflow (the rate at which tree defenses are depleted)
$R(x,y,t)$	Resin capacity (relative resistance)
$H(x,y,t)$	Number of boring holes made by attacking beetles

Results and Discussion.

Environmental vs. dynamic determinism.

In response to the need for objective ways to compare outbreak patterns as they evolve in space, White and Powell (1997) suggested using the temporal evolution of spatial correlation between Q and R_0 (the point-by-point correlation between the values of Q and R_0). The first beetles to emerge (pioneering beetles) encounter a chemical landscape that is devoid of the strong pheromone signals. Dispersal is driven at this time by random events, visual cues, and the relatively weak kairomones that signal weakened trees (C) (Gara et al. 1984, Moeck and Simmons 1991, Hayes and Strom 1995, Hobson 1995). At the beginning of emergence, these relatively weak signals are the only non-random forces influencing MPB dispersion, and they are solely a product of the environment. As pioneer beetles begin to successfully attack trees, they begin producing the strong forces of attracting pheromones. If there are enough attacking beetles to overcome tree defenses, the resulting self-generated chemical landscape dominates all other factors. These chemically mediated processes result in temporal evolution of a spatial signature that characterizes the progression of an infestation from endemic to an epidemic. In the endemic phase, beetle distribution is primarily determined by the distribution of weakened trees in the forest. White and Powell (1997) have used the spatial correlation between Q and R_0 as a measure of the

Table 3. List of parameter definitions appearing in MPBpde.

PARAMETER	DESCRIPTION
κ	A measure of the beetles' perception of and attraction to weakened trees.
ν	Attractiveness of the composite pheromone.
μ	Diffusivity of flying beetles due to randomness.
A_0	Critical concentration at which composite pheromone become repulsive.
A_3	Saturation parameter for composite pheromone.
a_1	Rate of pheromone production by nesting beetles
b_1	Rate of pheromone diffusion.
δ_1	Loss rate of pheromone.
a_2	Rate of resin exudation by host tree.
b_2	Rate of kairomone diffusion.
δ_2	Loss rate of kairomone.
R_0	Local peak resin capacity, a measure of tree health.
σ	Rate of pheromone enhanced attack.
r_1	Rate of landing and conversion from flying to nesting beetles.
r_2	Rate of resin replenishment.
r_3	Rate of resin outflow through holes bored by beetles.
r_4	Rate of resin crystalization (tree recovery).
ω_1	Background mortality rate of flying beetles.
ω_2	Background mortality of nesting beetles
β	Mortality rate of nesting beetles due to tree defenses.
$\gamma(x,y,t)$	Emergence rate of flying beetles, spatially and temporally dependent.

influence of weakened trees on successful attacks. The correlation coefficient is zero if there is no match in the spatial patterns of \underline{Q} and \underline{R}_0 . When the spatial correlation is close to -1, the dispersal pattern is environmentally determined, meaning that the pattern of successful attacks (\underline{Q}) is almost completely determined by the pattern of weak (\underline{R}_0 small) trees in the forest. Conversely, as attacking beetles switch to healthy trees adjacent to weak "focus" trees, this correlation is lost. A large negative correlation is, therefore, termed "environmental determinism" and the subsequent loss of correlation is termed "dynamic determinism."

Model Initialization. As an example, consider a series of simulations with parameters as defined in Table 4, with the exception of varying γ to result in increasingly severe beetle pressure. In these simulations, γ was introduced as a uniform background distribution, i.e. no initial spatial complexity to emergence. The rate of emergence ranged from 0.075 (for an integrated total number of beetles equal to 786) to 0.15 (for an integrated total number of beetles equal to 1536). The background forest was randomly generated from a uniform sampling distribution with a mean \underline{R}_0 of unity and a range of ± 0.5 . All simulations were allowed to run for 40 beetle flight hours.

Table 4. Parameter values used in simulation runs. We have used fh for flight hour, hec for hectare, tmg for tens of micrograms, R_0 is initial resin capacity scaled to 1 for a healthy tree of average resistance.

Paramete r	Value	Units	Paramete r	Value	Units
κ	8	hec ² tmg ⁻¹ fh ⁻¹	σ	15	hec tmg ⁻¹
ν	10	hec ³ tmg ⁻² fh ⁻¹	r_1	0.15513	fh ⁻¹
μ	1	hec fh ⁻¹	r_2	0.05	R_0^{-1} fh ⁻¹
A_0	2	tmg hec ⁻¹	r_3	0.025	fh ⁻¹
A_3	0.2	-	r_4	0.1	R_0^{-1} fh ⁻¹
a_1	400	tmg hec ⁻¹ fh ⁻¹ MPB ⁻¹	ω_1	0.1	fh ⁻¹
b_1	50	hec fh ⁻¹	ω_2	0.001	fh ⁻¹
δ_1	200	fh ⁻¹	β	100	MPB R_0^{-1}
b_2	50	hec fh ⁻¹	$\gamma(t)$	varies	MPB hec ⁻¹ fh ⁻¹
δ_2	0.1	fh ⁻¹			
R_0	1 \pm 0.5	R_0			

Simulation Results. Loss of environmental determinism occurred at the two

highest emergence rates. Simulation results demonstrated a clear distinction in spatial pattern between the endemic phase where only weakened or stressed trees are overcome (the two lowest emergence rates) and the outbreak phase where healthy trees are overcome by mass attacking beetles. It is also evident that although γ was increased in a smooth, continuous fashion, the increase resulted in a dramatically different spatial pattern for the two higher emergence rates. This threshold effect is an important hallmark of an outbreak, and the spatial correlation coefficient results in standard statistical criteria that can be used to separate an outbreak population from an endemic population. A time plot of the spatial correlation of the four simulations. The dramatic loss of spatial correlation at the higher beetle densities is evident, as is the outbreak nature of the shift from environmental to dynamic determinism. Graphical results of the simulations and the plot of spatial correlation as a function of time are given in Figures 2 and 3, respectively, in Logan et al. (1998).

Discussion. The concept of environmental determinism provides a useful criteria for comparing spatial patterns that result from differing initial conditions, parameter values, or model structure. It therefore provides one tool that can be used to compare different model runs, or in fact, to test hypotheses through comparison of model runs with field observations. The concept also has important implications apart from a useful way to compare spatial patterns. In particular, a great deal of effort and resources have been expended over the years in attempts to characterize susceptibility (expected loss should an outbreak occur) of a stand to MPB infestation (Bentz, et al. 1993, Shore and Safranyik 1992) and risk (the probability of an outbreak occurring). In fact, several risk rating schemes have been devised (Amman et al. 1977, Mahoney 1978, Berryman 1978, Schenk et al. 1980). Bentz et al. (1993) found little predictive value when these were applied in a prospective manner. They concluded that major problems existed in interpreting existing susceptibility and risk rating systems because no distinction was made between stand attributes measured during endemic and epidemic population phases. We note that most of the interest in outbreak insects occurs during times of epidemics, and therefore much of the data is collected during outbreaks. Figures 2 and 3 in Logan et al. (1998) clearly illustrate that during outbreaks the significant correlation (an inverse measure of susceptibility) relationship between Q and R_0 is lost.

The loss of environmental determinism that accompanies an outbreak would mask the critical effects of tree or stand attributes related to susceptibility. During the endemic population phase, trees that are successfully attacked may well be those that express measurable attributes that could be used to predict susceptibility. This suggests two experimental strategies for susceptibility/risk analysis. The first is to restrict data to endemic phase populations when correlation exists. A second strategy is to sample in an outbreak setting, but to sample with sufficient temporal and spatial resolution to detect the loss of environmental determinism (Eckberg et al. 1994, McCambridge 1967, Geiszler and Gara 1978, Geiszler et al. 1980a).

Temperature effects on synchrony of emergence.

Weather, and in particular the seasonal patterns of temperature, has a profound effect on poikilothermic organisms living in temperate environments. Temperature is

recognized as the single most important factor of the physical environment impacting MPB populations (Cole 1974, 1981, Safranyik 1978). One important aspect of temperature is its effect on synchronization of adult emergence. Synchronous adult emergence is critical to a successful mass attack strategy necessary for overcoming tree defenses. The ecological implication of seasonality as manifested by synchronous adult emergence has been recognized for some time (Amman and Cole 1983, Salom et al. 1987). Weather and temperature effect the synchronization and duration of adult emergence through the annual cycle of phenological events (Bentz et al. 1991, Bentz 1995), and by the more proximate effect of cool temperatures prolonging and depressing emergence. As a first step toward developing a tool for assessing the impact of seasonal weather on synchronous adult emergence and, subsequently, outbreak potential, we have analyzed results from simulated temporal emergence patterns. The objectives of this analysis were to (1) evaluate the sensitivity of outbreak to synchrony in adult emergence, and (2) begin to develop quantitative criteria for field applications in risk assessment.

Model Initialization. Variation in the degree of synchronous adult emergence could result from either an unseasonable period of cool temperatures during emergence, or as an emergent property of temperature events that occurred earlier during times of phenological sensitivity (Bentz et al. 1991). In order to test the ecological effects of synchronous emergence, we initialized the model with parameters as listed in Table 4, with the exception of γ . As in the previous example, γ was spatially independent, i.e. we provided a constant "beetle pressure" throughout the simulated forest. However, in contrast to the previous example, we varied the temporal magnitude and the duration of γ in such a way that the integrated total number of beetles equaled 1280 in all cases, but the emergence duration varied from 30 flight hours to 60 flight hours. The net result was a uniform pulse of beetles that varied in duration but not in integrated magnitude. As before, the initial forest was generated randomly from a uniform distribution with mean $R_0=1$ and a range of ± 0.5 .

Simulation Results. Results of these simulation experiments indicate that as synchrony increases, healthy trees near initially weak trees are overcome by the focused attacking beetles. The threshold effect is even more apparent in the switch from environmental determinism to dynamic determinism that accompanies the increasingly synchronous emergence. Even though the time pulse is varied continuously (increasing the emergence period by a constant 10 flight hours), the effect is expressed as a discontinuous threshold - an outbreak. Graphical results of the simulation and the plot of spatial correlation as a function of time are given in Figures 3 and 4, respectively, in Logan et al. (1998).

Discussion. Results are a striking demonstration of the potential impact of weather mediated synchronous emergence on outbreak potential. These results also considerably expand the interpretation of the importance of temperature on MPB ecology. Bentz, et al. (1991) demonstrated that differences in low temperature thresholds between instars was primarily responsible for compression of the prolonged ovipositional curve to the synchronous emergence curve. Unusually mild winter temperatures, or a shift in climate, could be disruptive to maintaining an appropriate seasonality. As a consequence, both the average annual temperature cycle (climate)

and particular events (weather during the emergence period) are critical determinants of population success (Safranyik 1978, Rasmussen 1980). Such insights may help to more fully understand climatic limitations to the geographic distribution of MPB, and the potential for shifts in geographic distribution due to factors such as global climate change.

Our simulation results indicate that including the effect of weather influence on synchrony in γ could substantially improve risk assessment. One key variable that has been ignored in most susceptibility/risk assessments is the inclusion of estimated MPB population performance (but see Shore and Safranyik 1992). Synchrony in adult emergence is one such indicator of population performance.

Spatial arrangement of nurse trees.

The role that stress plays in precipitating bark beetle outbreaks has been a point of debate for many years. There is general agreement that different sources of stress (e.g. drought, pathogens) can reduce the defensive capabilities of host trees (see Schowalter and Filip 1993 for a review). There is less consensus, however, in the role that tree stress may play in precipitation of outbreaks. Some hypothesize that a general stress induced reduction in tree vigor is the primary trigger for an outbreak. According to this hypothesis, an overall reduction in tree resistance due to some stressing factor releases the beetle population from regulation and an outbreak occurs (e.g. Berryman 1978). Drought is one widespread stressing factor which could cause a rapid decline in stand vigor, and drought is often considered the triggering event for an outbreak (Berryman 1976).

Although the hypothesis of drought induced stress operating as a triggering event to MPB outbreaks is widely accepted, observations and theoretical arguments (Lorio 1993) indicate that other events may be more important. MPB outbreaks in the interior west appear to be more related to periods of moisture abundance than drought (Barbouletos et al. 1994). Even though drought stress reduces tree resistance, the resulting stressed tree is typically not a high quality food resource (e.g. Thompson et al. 1985). Amman (1978) proposed an alternative hypothesis for the switch between endemic and epidemic beetle population phases that is based on a combination of conditions rather than a specific triggering mechanism. These necessary conditions include: (1) a sufficient population of beetles, (2) an abundant high-quality food resource, and (3) weather conducive to population success. Once these conditions exist, chance events (e.g. proximity of trees weakened by root disease to act as nurse trees) result in enough beetles in an area to overcome healthy trees with thick phloem. High brood production from these healthy trees then induces the outbreak. The major difference between the drought and a "random proximity" hypothesis is the spatial pattern of stressed and healthy trees. A widespread climatic anomaly such as prolonged drought will produce a more homogeneous forest of weakened trees, whereas stresses such as pathogens often result in a patchy forest of intermixed weak and healthy trees. In the latter scenario, endemic populations are supported in the refugia of weaker trees (Tkacz and Schmitz 1986), while the healthy trees provide the food source necessary for population buildup.

Although we do not view these two hypotheses as being mutually exclusive, an

interesting and important question is: what is the nature of effects that result from proximity of nurse trees during the endemic population phase? As a step towards answering this question, we have performed simulations where we keep both the density of emerging beetles and the number of sources constant, but we vary the proximity of emerging beetle sources.

Model Initialization. The model was initialized in the same manner as the previous example, with the following exceptions. Instead of a spatially homogeneous background of emerging beetles, they were concentrated at two point sources. Integrated beetle densities in all runs were held constant at 80 per spot. The two epicenters were then moved progressively further apart in successive simulations. In all instances, the temporal emergence curve (γ) was a square wave of 80 time steps (flight hours) duration. Simulations were allowed to proceed for a total of 100 flight hours.

Results of Simulation. Simulations were run long enough beyond the end of emergence to allow tree recovery unless it was successfully attacked and killed. Recall, the state variable R is a surrogate for tree health, and when R approaches zero, the tree is dead. The effects of proximity were apparent in the pattern of killed trees in the simulations. Even more striking is the obvious outbreak effect. In the simulations with beetle sources the furthest removed from one another, no trees were killed (as measured by at least 90% resin depletion). By contrast, when the trees were in close proximity, significant mortality occurred. It is easy to see how the process could be self-propagating. Weakened trees in close proximity produce enough beetles to overcome even healthy trees. These trees in turn are the producers of large quantities of brood the following year which are again in close proximity (Cole et al. 1985). Such positive feedback potential is symptomatic of instabilities such as outbreaks. Graphical results of the simulation and a plot of accumulated depletion (an indication of tree mortality) as a function of time are given in Figures 8 and 9, respectively, in Logan et al. (1998).

Discussion. The importance of including a measure of the spatial distribution of red-tops in risk assessment during endemic phases is well illustrated in this simulation experiment. Our results indicate the potential for spatial feedback generating an outbreak in the absence of either a wide-spread external modification of the environment (e.g. drought) or in the genetic composition of the population.

The effects of spatial feedback in self-focusing systems indicates the importance of research designed to more clearly elucidate the spatial nature and arrangement of host stress factors. Water-stressed trees are a good example. Drought produces large expanses of water stressed trees, but other sources of water stress can result in spatially complex patterns of water stress without the widespread reduction in host quality that most likely accompanies a general drought. Coniferous/deciduous ecotones between pine and aspen, or edaphic characteristics are good examples of factors that can result in spatially heterogeneous patterns of water stress.

Among other spatially distributed causative agents of stress, root disease or other host pathogens, are probably the most studied (Schmitz 1988, Schowalter and Filip 1993). The driving forces behind the spatial distribution of host pathogens may have important implications for MPB outbreaks such as providing epicenters for

outbreaks. Indeed, the spatial distribution of host pathogens may well be the driving force behind the periodicity of MPB outbreaks. Geiszler et al. (1980b) have hypothesized such a mechanistic link between MPB, fungi, and fire in lodgepole pine ecosystems.

Finally, an interesting question is raised regarding the geometry of killed trees in an endemic setting. Are there particular spatial arrangements that are more conducive to precipitating an outbreak than others? What is the effective distance between killed trees for production of epicenters? MPBpde is a powerful tool that can be effectively used in conjunction with field empirical studies to address such issues.

Conclusions.

In this paper we have described a spatially explicit model of MPB redistribution and attack of host trees, and the response of the host to attack. We have further applied simulations with this model for analysis of three ecological issues central to MPB outbreak ecology. These simulation experiments have demonstrated that nonlinear spatial effects, namely self-focussing and self-dissipation, can by themselves be responsible for observed attack and outbreak phenomena. In the analysis of simulation results, we have introduced the concept of environmental vs. dynamic determinism that captures the difference between spatial complexity due to environmental heterogeneity (exogenous factors) and spatial complexity driven by inherent, nonlinear spatial dynamics. A statistical measure, spatial correlation coefficients, was introduced to discriminate between environmentally and dynamically mediated spatial complexity. Simulation results from these experiments imply that many of the rate-competition issues between tree host and tree attack can only be meaningfully studied by taking spatial issues into account. As a result, these simulation experiments demonstrate that management activities should include spatial considerations, probably at the landscape scale.

The simulations we have discussed are our first attempts to use the model in a hypothesis testing mode. As such, they are representative of the types of ecological issues we will address in future applications of the model. Such exercises force serious scrutiny of the current literature and available knowledge for parameter estimation. The model is also helping us design field experiments that are of a spatial nature, i.e. determining effective radius of pheromone traps. An interesting question is, how useful would such a model be as a management tool? As we move from the existing paradigm of forest pest management to a more balanced view of incorporating natural disturbance within the ecosystem management of sustainable systems, we will not only need to include meaningful landscapes, but we will also need to address issues of large spatial scale and long time frames. The modeling effort we have described will continue to be a central organizational and conceptual paradigm for our MPB research, and also holds the potential to result in a valuable management tool capable of addressing the critical issues of expanded spatial and temporal scales.

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interaction, and stimulated us to further scrutinize our model representation of that interaction. The authors wish to acknowledge support received from a National Science Foundation grant to Utah State University (DMS-9505327).

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