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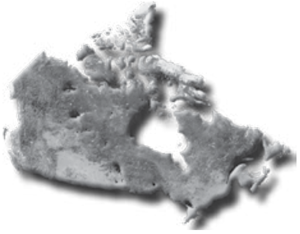

The balance of complexity in mechanistic modeling: Risk analysis in the mountain pine beetle

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Mountain Pine Beetle Initiative
Working Paper 2006-03

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The balance of complexity in mechanistic modeling: Risk analysis in the mountain pine beetle

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Mountain Pine Beetle Initiative PO # 8.19

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2006

Printed in Canada

ABSTRACT

In most fields of applied ecology, there is a need to predict and manage the risk of pest outbreaks. One challenge to the development of mechanistic risk models is striking a balance between the tactical details of a system, and the strategic simplifications necessary to maintain generality and mathematical tractability. In this review we analyze the balance of complexity for risk models in the mountain pine beetle system. Mountain pine beetles are the single most destructive pine-forest pest in western North America. Much effort has gone into collecting empirical evidence and developing mechanistic outbreak models. Yet, current risk models only utilize tree-susceptibility indices that have proven ineffective at predicting the risk or extent of an infestation. We develop a conceptual framework of the beetle-host interaction that allows us to compare across both phenomenological and mechanistic models. From this framework, we demonstrate how current risk models emerged and why they predict ranked-risk as opposed to absolute-risk. Existing mechanistic models include a wide variety of possible interactions which has lead to disagreement about the ingredients essential for beetle outbreaks. By contrasting these models against the ecological framework, we extract systematic insight into the factors that determine risk, and suggest what dynamical processes must be modeled explicitly and what can be strategically abstracted.

RÉSUMÉ

Dans la plupart des domaines d’écologie appliquée, il est indispensable de prévoir et de gérer les risques d’invasions de parasites. Un des défis que pose le développement de modèles mécanistes de risque est d’équilibrer les détails tactiques d’un système et les simplifications stratégiques nécessaires au maintien d’un caractère général et d’une résolubilité mathématique. Dans cette revue, nous analysons l’équilibre de la complexité pour les modèles de risque des systèmes du dendroctone du pin ponderosa. Cet insecte est le parasite le plus destructeur des pinèdes de l’ouest de l’Amérique du Nord. Beaucoup d’efforts ont été déployés afin de collecter des preuves empiriques et de constituer des modèles mécanistes d’invasions. Pourtant, les modèles de risque actuels n’utilisent que des indices de sensibilité des arbres qui ont été incapables, par le passé, de prédire le risque ou l’étendue d’une infestation. Nous élaborons un cadre conceptuel sur l’interaction entre le dendroctone et son hôte qui nous permet de comparer les deux modèles, phénoménologiques et mécanistes. À partir de ce cadre, nous montrons comment les modèles de risque actuels sont apparus et pourquoi ils prédisent un risque classé par opposition à un risque absolu. Les modèles mécanistes existants comprennent une grande variété d’interactions possibles, ce qui a mené à des désaccords à propos des composantes essentielles des invasions de dendroctones. En opposant ces modèles au cadre écologique, nous extrayons des connaissances systématiques pour les appliquer aux facteurs qui déterminent le risque, et nous suggérons quels processus dynamiques doivent être modélisés explicitement et ce qui pourrait être soustrait de façon stratégique.

INTRODUCTION

Risk assessment is a common focus of applied ecology. Whether the goal is to conserve a population (e.g., Bradbury *et al*. 2001; Kotiaho et al. 2005), manage a biological invasion (e.g., Carlton 1996; Kolar and Lodge 2001), or prevent an epidemic (e.g., Keeling et al. 2003; Ferguson et al. 2005), there is a need for quantitative models that can predict the risk of such events. In reality, however, the need goes even further—quantitative models should not only predict risk, but also have sufficient ecological mechanisms to reliably manage risk (Caughley 1994).

The challenge to developing mechanistic risk models is to strike a balance between the tactical details of a particular system, and the strategic simplifications necessary to maintain generality and mathematical tractability (Nisbet and Gurney 1982; Godfray and Rees 2002; Grimm et al. 2005). Tactical models are developed to study specific systems, and often involve a large number of parameters and detailed mechanisms. The complexity and specificity of tactical models makes them difficult to understand and limits their generality. Strategic models, in contrast, are developed to study the consequences of general ecological interactions. However, the sparse nature of strategic models means that they often omit details that limit their utility for practical applications. There is no set way to achieve the correct balance between tactical and strategic in models designed for risk assessment, but the process should include elements of systematic model development and empirical validation because the resulting model structure can have a large influence on predicted management strategies (e.g., Wood and Thomas 1999; Harwood 2000).

In this review, we tackle the problem of balancing ecological complexity in mechanistic risk models for the mountain pine beetle system. Mountain pine beetles (*Dendroctonus ponderosae* Hopkins) occur naturally throughout much of western North America and are the single most destructive pathogen of pine forests (Logan and Powell 2001; Logan et al. 2003). As a result of much effort and funding, a wealth of observational and experimental data has been collected for many parts of the beetle life-cycle (Safranyik and Carroll 2006). This research has led to the development of mechanistic models that range from strategic population models of beetle outbreaks (e.g., Berryman et al. 1989) to tactical behavioral models describing how beetles select host trees (e.g., Powell et al. 1996)—all of which identify the importance of beetle dynamics and host susceptibility as determinates of outbreak dynamics. Yet, and in spite of this theoretical work, current risk models rely entirely on host susceptibility indices that have proven ineffective at predicting the risk or extent of beetle outbreaks (Bentz et al. 1993). Here we synthesize both the theoretical work and empirical evidence to demonstrate the minimal ecological components necessary for reliable risk models. We discuss absolute risk objectives, which quantify the likelihood and extent of an epidemic for a particular stand, and ranked risk objectives, which quantify the order of risk among a set of stands. We argue that future risk models need to move away from the current paradigm of static models to dynamic models that can incorporate the ecological mechanisms from all phases of the beetle life-cycle.

There are several excellent and thorough reviews on the ecology of the mountain pine beetle (e.g., Coulson 1979; Christiansen et al. 1987; Raffa 2001; Safranyik and Carroll 2006). Since our purpose here is to review the empirical evidence in the context of theoretical work, we focus on the subset of the ecological literature that is necessary to develop a conceptual framework of the ecological interactions.

ECOLOGICAL UNDERSTANDING

Mountain pine beetle populations are typically univoltine, completing a single generation each year (Safranyik and Carroll 2006; Figure 1). Recently developed adults emerge from their host trees in late summer and search for new hosts to attack. Attacking beetles bore through the outer bark of live trees into the phloem tissue. Healthy trees can resist attacks by producing resin to slow down or stop beetles from constructing tunnels (galleries). In response, attacking beetles emit aggregation pheromones that recruit additional beetles into mass attacks. If sufficient beetles are available, then host resin defenses can be overwhelmed and beetles successfully construct egg galleries in the phloem tissue. The eggs develop into larvae which create feeding galleries that girdle and kill the host tree. Beetle populations often over-winter as late instar larvae, and resume development in the spring. Pupation occurs in early spring and adults emerge in late summer. While able to breed in many species of pine, mountain pine beetles are most often found in stands of lodgepole pine (*Pinus contorta*) and ponderosa pine (*Pinus ponderosae*).

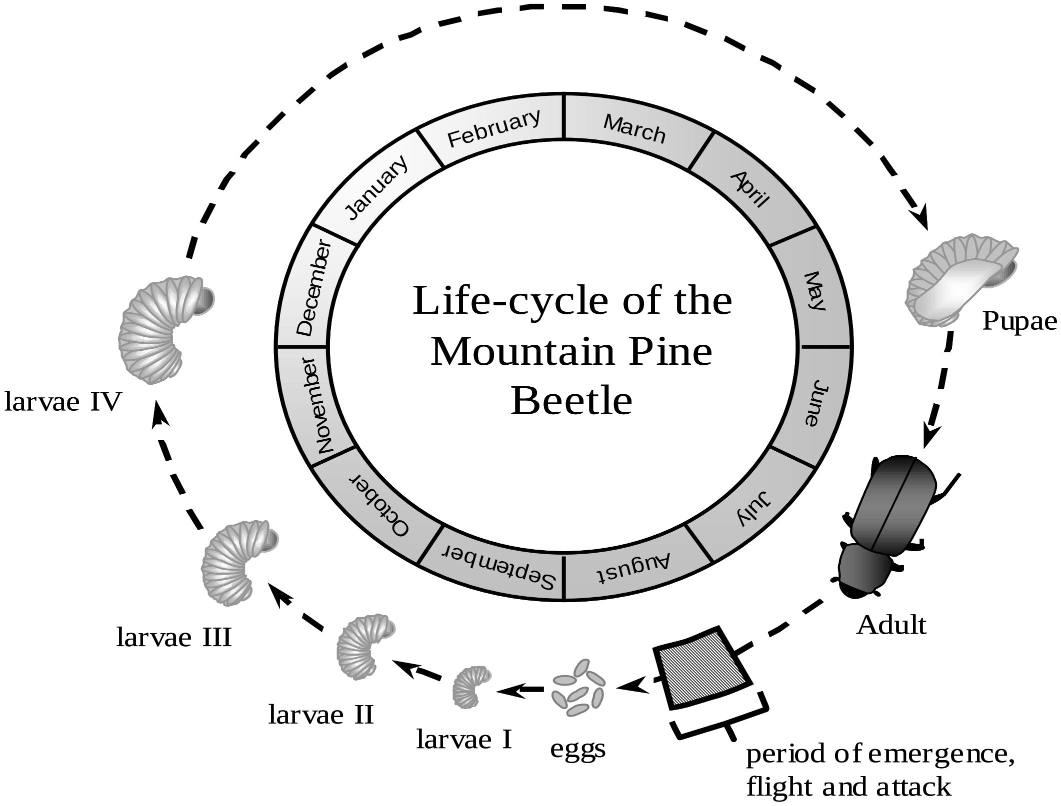

Figure 1. Mountain pine beetle life-cycle. Much of the life-cycle is spent in the phloem habitat, except when adults emerge and disperse to attack new host trees (hatched area). Eggs are laid in freshly excavated galleries and develop through four larval stages that feed on the phloem tissue. Beetles often over-winter in the larger larval stages, and pupate in late spring. Adults develop further in the phloem tissue and emerge during the brief flight period.

As a result of gallery construction, much of the mountain pine beetle life-cycle is engraved in the host trees. This has allowed ecologists to collect a wealth of information on beetle fecundity and mortality. The processes governing dispersal and aggregation, however, are not as well understood because they are more difficult to observe. To facilitate the modeling synthesis, we briefly review what is known about the ecological interactions between the beetles and their host trees. The life-cycle can be broken into three phases: attack, reproduction, and dispersal (Figure 2).

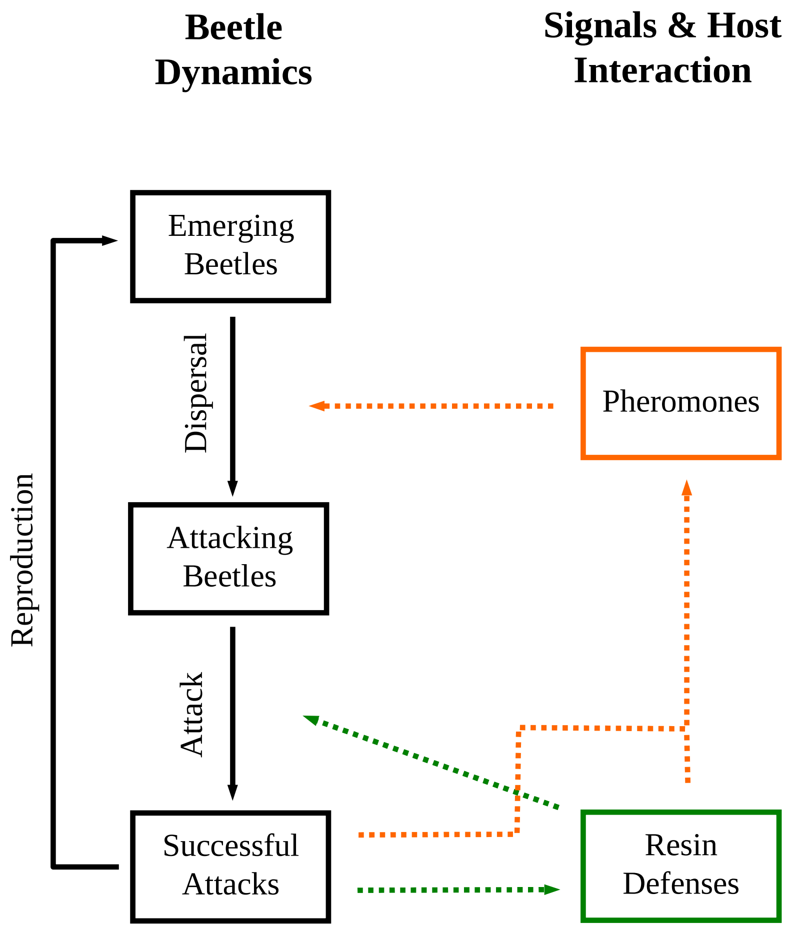

Figure 2. Idealized ecological framework of the host-pathogen interaction. Mountain pine beetle population dynamics are governed by the processes of attack, reproduction, and dispersal (black). Attack processes are influenced by the interaction with host defenses (green), and dispersal is influenced by the pheromone communication (orange). The dispersal phase includes the processes of host selection. Solid lines represent the beetle life-cycle, and dashed lines represent the feedback loops whereby the pheromones and host defenses influence the transition rates.

Attack

The greatest challenge for aggressive bark beetles is to overcome host defenses and access the phloem habitat. While pine trees produce a range of chemical and physical products, the primary defense mechanism against bark beetles is resin (Reid et al. 1967; Berryman 1969, 1972; Dunn and Lorio 1992). The attacking beetles cut into special ducts, causing resin to flow out of the wound. Sufficient flow can flush an attacker out of its entrance hole. If the attacking beetle is not flushed out, resin may plug the entrance hole and prevent the emission of the beetle's aggregation pheromones (Raffa and Berryman 1983). Hosts also initiate a secondary resin response by producing oleoresin in the egg galleries that the beetles are constructing. If the host tree has not been killed by the attacking beetles, this secondary response can kill the freshly laid eggs (Reid and Gates 1970; Christiansen et al. 1987).

At low attack densities, a healthy tree can repel all attacks (Mulock and Christiansen 1986). As the attack density (attacks per area of bark) increases, the proportion of attacks that successfully produce offspring also increases (Raffa and Berryman 1983; Elkin and Reid 2004), which we refer to here as an *attack-success* curve (Figure 3a). This relationship simply reflects the effect that attack density has on host condition (Raffa and Berryman 1983). If enough beetles attack to kill the host, then most galleries are successful. If insufficient beetles attack and the host survives, then most galleries are unsuccessful. Thus, the key determinant of attack success is whether or not the host defenses have been overwhelmed.

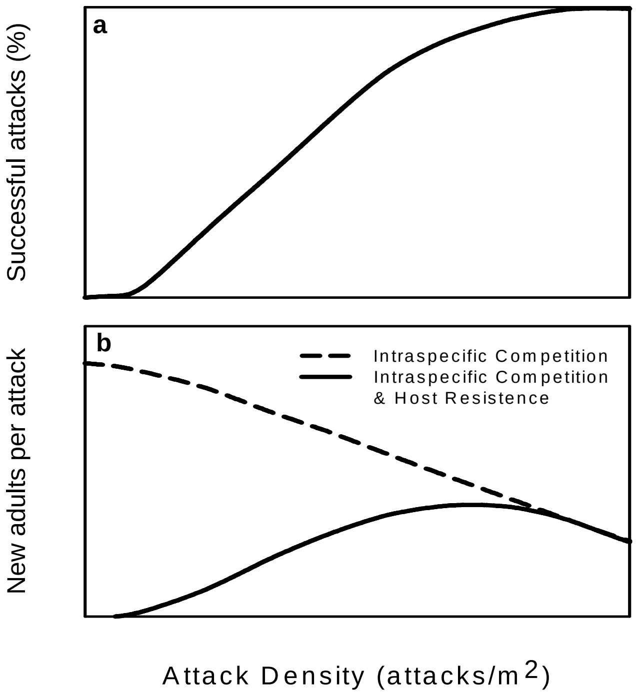

Figure 3. The average effect of attack density on intraspecific competition and host defenses for a stand (from Raffa and Berryman 1983). a) The proportion of successful attacks increases with attack density, reflecting the ability of higher beetle densities to overwhelm host defenses. b) The decline in per capita reproduction begins at very low attack densities (dashed line). The productivity-curve reflects the combined effects of intraspecific competition and host resistance (solid line).

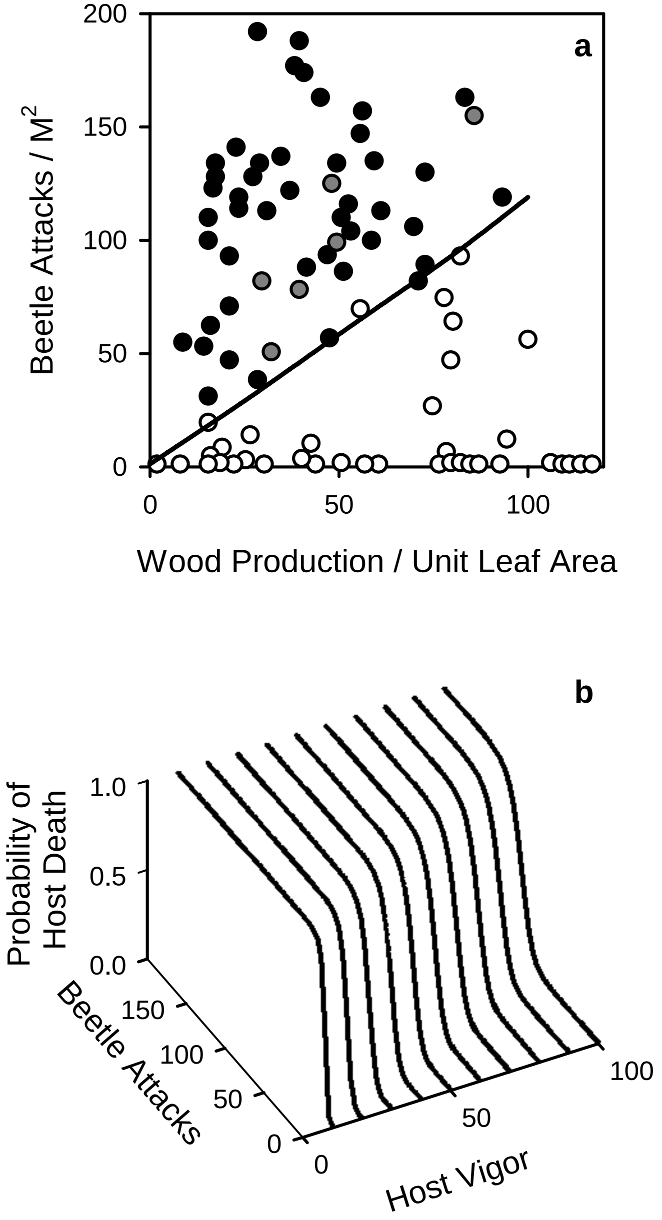

Figure 4. Host mortality as a function of beetle density and host vigor. a) Data are redrawn from Mullock and Christiansen (1986). The vertical axis is the density of beetle attacks per square meter of bark, and the horizontal axis is an index of host vigor. The solid black circles are dead hosts, the solid gray circles are strip-attacks (only part of the host is killed), and the open circles are live hosts. b) Conceptual relationship between beetle pressure, host vigor and the probability of host mortality.

The capacity of a host to defend against beetle attacks is related to host vigor, which is usually thought of as a measure of efficiency, such as the amount of stem growth per leaf area (Shrimpton and Thomson 1983; Larsson *et al*. 1983). Trees with greater vigor have potentially greater reserves of carbohydrates, and can produce greater amounts of resin per unit of bark area (Christiansen et al. 1987). More vigorous hosts can repel greater densities of attacking beetles (Waring and Pitman 1983; Mulock and Christiansen 1986; Figure 4a).

Reproduction

The density of attacking beetles has both a positive and negative influence on the density of new adults that emerge the following year. The positive influence results from the need to overwhelm host defenses, as discussed above. The negative influence results from increased intraspecific competition.

Each successful beetle attack produces a single gallery. The size of the gallery and the number of eggs laid decreases as the density of galleries increases (Cole 1962). The result is a decline in the number of new adults produced per gallery as attack density increases (Cole 1962; Raffa and Berryman 1983; Figure 3b). This negative density-dependence begins at even the lowest possible attack densities (Raffa 2001), indicating that, in the absence of tree defenses, the maximum per capita growth rate is attained by a single attack. At high attack densities, the density-dependence can be sufficient to reduce per-capita fecundity to below one (Raffa and Berryman 1983). This likely results from a combination of reduced egg laying rates and increased mortality from larval competition (Cole 1962).

The combined effects of both positive and negative density-dependence on reproductive success creates a unique tension for aggressive bark beetles. The increase in beetle density required to overcome host defenses translates into a direct reduction in the per-capita reproductive success. There is good evidence to suggest that the positive and negative density-dependent mechanisms operate independently of one another, such that the number of new adults emerging from each attack can be described by the simple product of per-capita reproductive success and proportion of successful attacks (Berryman 1974; Raffa and Berryman 1983; Raffa 2001; Figure 3b). The influence of other factors, such as temperature and host vigor, can be understood by their independent effects on each of the two density-dependent processes.

Dispersal

The dispersal phase of the mountain pine beetle is probably the most famous part of the life-cycle—yet it is also the least understood. This phase is characterized by beetle dispersal from last season's hosts, followed by aggregation and attack on new hosts. Aggregation is coordinated by the chemotactic response of flying beetles to pheromone signals generated by the beetles that are in the process of attacking new hosts (Raffa and Berryman 1983). Individual beetles rarely take longer than a few days to emerge, disperse and attack new hosts (Safranyik and Carroll 2006). The flight period for the entire population usually lasts about two weeks. The first beetles to emerge in the flight season are referred to as pioneer beetles because they produce the initial pheromone signals.

Pioneer beetles disperse into an environment without any guidance from pheromone cues. Such movement appears to be a random search for suitable hosts (Burnell 1977; Safranyik et al. 1992), perhaps influenced by a preference for larger trees (e.g., Shepherd 1966). Unfortunately, there is little data to determine how beetles are assessing potential hosts during this dispersal phase, or how they respond to other physical factors such as wind. Once beetles have landed on a tree, they must decide whether or not to initiate gallery construction. Beetles assess host quality by chewing into the bark (Raffa and Berryman 1982). If the host is not perceived to be suitable based on the chemicals present in the bark, then beetles continue flight. The behavior of pioneer beetles may have an impact on the spatial dynamics of an infestation because these beetles establish the first pheromone plumes that focus subsequent aggregation.

As with all aggressive bark beetles, mountain pine beetles show a strong chemotactic response to pheromones. Two broad classes of pheromones have been identified: those that aggregate and those that repel (Purswaran et al. 2000; Raffa 2001). While a number of the chemicals responsible for the aggregate and repellent behavior have been identified (Purswaran et al. 2000), it is difficult to quantify the spatial or temporal pattern of these chemicals in a natural stand of trees. As a result, the proposed mechanisms of pheromone communication are based on indirect inference from the observed relationships between beetle attacks and host condition.

Pheromones are produced by attacking beetles using host materials (Raffa 2001). The attractiveness of a particular host appears to be correlated with resin flow, which suggests that pheromones may be derived directly from resin (Raffa and Berryman 1983; Borden et al. 1987). Such a mechanism has appealing properties: as long as the host can produce resin defenses, beetles will have a substrate from which to produce pheromones that in turn will attract more beetles. When a host is overwhelmed and resin flow stops, the aggregation pheromones will no longer be produced and intraspecific competition will be reduced (Raffa 2001).

While some researchers believe that the end of the host attack is initiated by a decline in aggregation pheromones (Raffa and Berryman 1983; Raffa 2001), others believe that it is initiated by anti-aggregation pheromones (Pureswaran et al. 2000; Borden et al. 2003). Anti-aggregation pheromones are produced by both male and female beetles, but it has been hypothesized that some are produced by males in response to crowded conditions (Pureswaran et al. 2000). The debate between the two alternative mechanisms that terminate the attack process, however, is not of great importance for model development because they have a similar effect.

THEORETICAL INSIGHT

While not complete, much is known about the ecology of the mountain pine beetle. For the purpose of creating a dynamic population model, the beetle life-cycle can be broken into three stages: the density of beetles emerging from each host, the density of attacking beetles on new hosts, and the density of beetles that have successfully attacked (Figure 2). Here, as is standard in the literature, density refers to the number of beetles (in a particular stage) per unit area of bark. The three stages are linked by the processes of dispersal, attack and reproduction.

We begin by discussing models of attack and reproduction because they form the foundation for all mountain pine beetle population models. From this framework, we demonstrate where and why current risk assessment models have made a departure from the ecological interactions, and how this has inadvertently led to models of relative risk as opposed to absolute risk. We then discuss how recent developments in understanding pheromone-driven dispersal could contribute to risk models, and conclude with a discussion of how future risk models should be developed and validated for the mountain pine beetle system.

Models of attack and reproduction

Berryman *et al*. (1989) developed the first mechanistic model of beetle attack and host resistance. They considered a dynamic model for a single host tree where the density of attacking beetles could increase by recruiting flying beetles and decrease as a result of host resin defenses. Host resin increased based on the ability of the host to produce resin (vigor), and decreased as a result of defense against attacking beetles. There are only two possible outcomes of this host-pathogen interaction—either the host successfully repels the attacks or the host is overwhelmed. The authors found that the likelihood of host mortality increased with the density of available flying beetles, and that the density of beetles required to overwhelm a host depended on host vigor. The host-pathogen interaction described by the model is arguably minimal, however, empirical observations suggest that it captures the key ecological interaction—host mortality within a stand is well described by host vigor and the density of attacking beetles (Waring and Pitman 1983; Mulock and Christiansen 1986; Figure 4a). While attack models have not developed to a point where they can predict *a priori* the threshold beetle density that will kill a host tree, such determinism in natural systems is rare.

The conclusion that host mortality depends on both attack density and host vigor leads to a slightly different interpretation of the attack-success curves discussed above (Figure 3a). Attack-success curves, which describe the proportion of attacks that produce successful galleries, are often reported as the average of all trees in a stand (e.g., Raffa and Berryman 1983; Figure 3a). However, since the proportion of successful attacks is largely determined by host mortality, and since host mortality depends on both attack density and host vigor, each host of a different vigor level has a separate attack-success curve (Figure 4b). The attack-success curve reported for a stand of trees averages over hosts of different vigor, which poses a challenge for comparing among stands with different, or potentially unknown, distributions of host vigor.

Reproduction maps the density of attacking beetles in one season to the density of emerging beetles in the following season (Figure 2). The number of new adults produced by each successful attack is strongly influenced by intraspecific competition (Berryman 1974, 1976; Raffa and Berryman 1983; Figure 3b). The per-capita fecundity of attacking beetles can be obtained from the product of the proportion of attacks that are successful, and the number of offspring produced per successful attack. The resulting density-dependent relationship is referred to as the *productivity-curve* (Berryman 1974). For a single host, optimal beetle productivity occurs at intermediate attack densities (Figure 3b). If there are too few attacking beetles, then fecundity is low because most attacks will be unsuccessful; if there are too many attacking beetles, then fecundity is lowered from intraspecific competition. Hosts with different vigor levels have different productivity-curves. In spite of the variation in host vigor within a stand, empirical evidence reveals that the optimal level of the stand-average productivity-curve still occurs at intermediate densities of beetle attacks (Berryman 1974; Raffa and Berryman 1983). This feature, while largely phenomenalistic at the stand level, is key to generating the outbreak dynamics discovered in the first generation of bark beetle population models.

Productivity-curve population models

Early beetle population models were based on the phenomenalistic stand-level productivity-curve that describes the density of emerging beetles from the density of attacking beetles in the previous generation (Figure 3b). If we assume an abstract forest where all hosts have the same vigor, where the quantity of the host material stays constant over time (i.e., every host killed is immediately replaced with a live host), and where the density of emerging beetles is a good predictor of resulting attack densities (i.e., no pheromone mediated dispersal), then the productivity-curve determines the dynamics of the beetle population (Berryman 1979; Figure 2). The population model is written as

$$N_{t+1} = r(N_t)N_t$$

$$r(N_t) = p(N_t)s(N_t)$$

where N_t is the density of beetles in year t, and $r(N_t)$ is the replacement curve that includes the productivity-curve $p(N_t)$ and flight survival $s(N_t)$. If we assume the simplest situation where mortality is constant ($s(N_t) = s_o = constant$), the replacement curve is proportional to the productivity-curve (Berryman 1979). The population is at an equilibrium when the replacement curve is equal to one, which is the point where each beetle exactly replaces itself. For the mountain pine beetle, two equilibria emerge because the unimodal replacement curve is equal to one at both low and high beetle densities (Figure 5a). The first equilibrium is unstable and results from the interaction with host defenses; the second equilibrium is stable and results from intraspecific competition. Thus, the population dynamics will settle on a beetle equilibrium that is maintained by competition.

Consider the same abstract forest as above, but with two classes of host vigor—call them ‘weak’ and ‘normal’ trees. In such a forest, the replacement curve comprises the productivity-curves from both classes of vigor. If the normal trees provide substantially more phloem habitat, then the two classes of vigor may produce a bimodal replacement curve for the beetle population (Figure 5b). The bimodal replacement curve has four possible equilibrium points: two unstable points that reflect the host resistance of each vigor class, and two stable points that reflect competition in each vigor class. Berryman (1979) defined the stable equilibrium in the weak hosts as the *endemic* state, and the stable equilibrium in the normal hosts as the *epidemic* state. The unstable equilibrium of the normal hosts that sits between the two stable equilibria is defined as the *critical threshold point* (Berryman 1979; Figure 5b). Beetle densities above the critical threshold point will grow into epidemics, beetle densities below the threshold point will remain at endemic levels. These arguments are the genesis for the conceptual outbreak model of aggressive bark beetles that permeates the literature today (e.g., Safranyik and Carrol 2006).

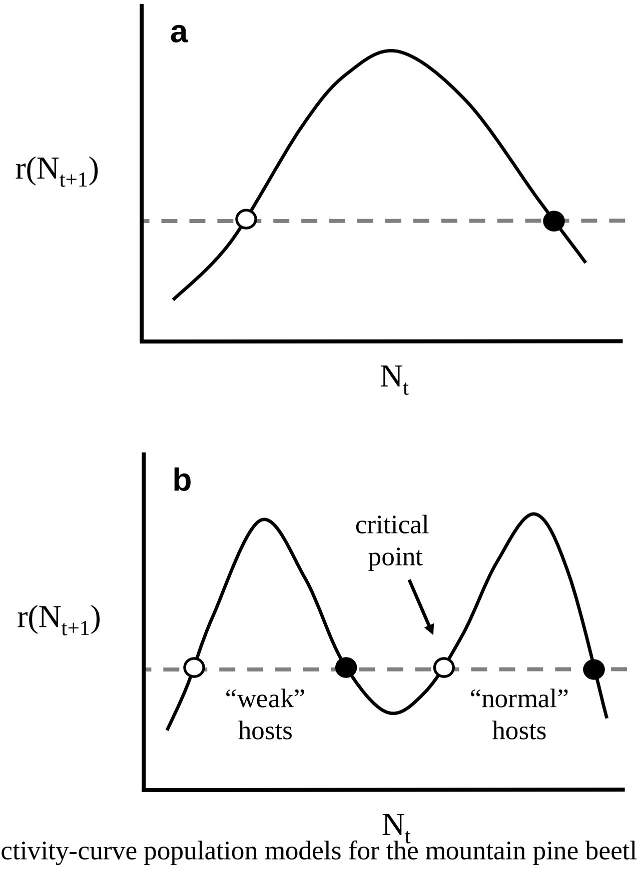

Figure 5. Productivity-curve population models for the mountain pine beetle following Berryman (1979). a) The replacement curve that maps beetle density (N) in year t to $t+1$ is shown as the solid line. The 1:1 line is shown in gray. The open circle is an unstable equilibrium point, and the solid circle is a stable equilibrium point. b) The replacement curve shown assumes that a certain fraction of the hosts are ‘weak’ and the remainder are ‘normal’ hosts. The lower stable equilibrium is defined as the endemic state, and the upper stable equilibrium is defined as the epidemic state. The unstable equilibrium between the endemic and epidemic state is referred to as the critical threshold point.

Naturally, the assumption that host materials remain constant over time is unrealistic. The quantity of host material and the distribution of host vigor in a forest changes as a result of tree growth, competition, and beetle attacks. The implication is that the replacement curve changes over time as the stand condition cycles through different phases of beetle attack (Raffa and Berryman 1986). For example, after a strong epidemic the forest comprises mostly unsuitable and low vigor hosts, which results in a unimodal beetle replacement curve. As host availability increases through growth, the replacement curve may become bimodal. Once the beetle population is large enough to jump to the epidemic state, the beetles decimate the forest and return it to a state with little suitable habitat. Thus, the replacement curve has its own dynamics through time—a point that we return to when discussing risk models below. In contrast to early productivity-curve models with fixed forests, models with dynamic forests do not predict a persistent epidemic state simply because beetle attacks during the epidemic state deplete host material much faster than the forest can regenerate.

Productivity-curve models, regardless of whether the forest dynamics are fixed or explicitly modeled, reach the same general conclusion about what controls beetle outbreaks. Given stand characteristics such that the replacement curve is bimodal, outbreaks are triggered by increases in beetle density or decreases in host vigor (Berryman et al. 1984; Raffa and Berryman 1986). If beetle populations increase from immigration, an increase in the number of weakened trees, or a particularly favorable winter, then an outbreak is triggered as densities are pushed over the critical threshold. If environmental stresses, such as drought, cause host vigor to decrease, then endemic beetle densities may likewise be sufficient to trigger an outbreak.

Productivity-curve models generate many of the qualitative features observed in natural infestations. Beetle populations persist at low endemic states for many years, punctuated by episodes of severe outbreaks. Yet, these models ignore many of the detailed mechanisms and ecological interactions that have been the focus of significant theoretical and empirical research over the years. For example, productivity-curve models assume that the density of emerging beetles directly translates into the density of attacking beetles, even though much evidence suggests that the behavioral processes of host selection has a large impact on determining attack densities within a stand. Are productivity-curve models sufficient? Do we need to include more mechanisms, or can we get away with fewer? The answers depend on the goals of the model development. In the sections that follow, we clarify the goals of risk analysis for the mountain pine beetle system. By synthesizing the development of risk models, we discover the rationale behind current approaches, and where they have deviated from dynamic productivity-curve models.

Risk models

The development of risk assessment models for the mountain pine beetle system have followed a parallel—but distinct—path from the development of dynamic productivity-curve models (see Shore *et al*. 2000 and Bentz et al. 1993 for excellent reviews). Two types of risk objectives have emerged in the mountain pine beetle literature. The first type is the risk of an epidemic, where a manager seeks to understand the likelihood that a particular stand will undergo a beetle epidemic in the near future (e.g., Berryman 1978, 1982). The second type is the risk of host mortality, where the goal is to predict how much damage will be caused by a beetle infestation (e.g., Stuart 1984; Katovich and Lavigne 1986; Anhold and Jenkins 1987). It is often considered that the two types of risk reflect different time horizons—the risk of an epidemic is a short-term risk because it depends on beetle density, and the risk of host mortality is a long-term risk that is independent of beetle density (e.g., Shore *et al*. 2000). However, such distinctions are arbitrary because the two types of risk are both outcomes of the same host-pathogen interaction and, as we discuss below, both depend on beetle density.

Early epidemic risk models in the mountain pine beetle system can be traced to the early productivity-curve models that assume the quantity of host material stays constant over time. Recall that the critical threshold point is given by the unstable equilibrium point between the so-called endemic and epidemic states in a bimodal replacement curve (Figure 5b). If beetle densities are elevated above this threshold, or the threshold is reduced, then the beetle population is predicted to increase the following year. Plotting beetle density at the critical threshold point as a function of stand vigor describes a critical threshold curve (Figure 6a). The original idea was that if the density of beetles and stand vigor were known, then the future level of infestation, either endemic or epidemic, could be predicted (e.g., Berryman 1982). However, this perspective ignores the fact that the replacement curve, and therefore the critical threshold curve, are not fixed in time. The replacement curve depends on the characteristics of the live hosts, and changes from year to year as trees in the stand are killed by attacking beetles. One consequence of having a dynamic critical threshold is that simply having beetle densities above the critical threshold curve does not guarantee that a stand of trees will undergo an epidemic. Thus, the risk of an epidemic, and the extent of host mortality, depend on the initial beetle density and the stand vigor, as well as how the replacement curve changes throughout the infestation.

Managers recognize that the risk of an epidemic depends on both beetle density and host characteristics (e.g., Bentz et al. 1993; Shore et al. 2000). However, it is more effort to estimate the density of attacking beetles because, in contrast to stand characteristics that change slowly, beetle densities change from year to year and require a continuous monitoring program. In response, the first epidemic risk models assumed that the density of attacking beetles could be estimated by the amount of phloem in a stand of trees (Berryman 1978, 1982). The assumption was based on the observation that greater densities of beetles emerge from hosts with thicker phloem. However, this rationale is flawed because the density of emerging beetles depends on both the phloem habitat and the density of beetle attacks in the previous year. In essence, it is not possible to estimate attacking beetle density from attributes of the hosts without explicitly predicting the temporal beetle dynamics, which—at a minimum—still requires the initial beetle density. While based on mechanistic host-pathogen interactions, the resulting epidemic risk models depend only on host characteristics.

The second, and more common, type of risk objective is concerned with predicting host mortality. Risk models of host mortality use indices of stand susceptibility based on climatic and stand characteristics such as temperature, host age, diameter, vigor, and stand density (e.g., Krajicek et al. 1961; Waring and Pitman 1983).

However, as discussed above, it is not possible to predict the risk or extent of an epidemic using only indices of stand susceptibility. This conclusion is well supported by results from independent tests of risk models based on susceptibility indices (e.g., Bentz et al. 1993; Shore et al. 2000). When beetle pressure is controlled among stands, which is often done by locating stands within a region that experienced uniform beetle densities, then stand characteristics such as average host diameter, growth, and density correlated with the probability that a specific stand was attacked, as well as the level of host mortality (Schenk *et al*. 1980; Stuart 1984; Perkins and Roberts 2003; Negron and Popp 2004). Essentially, this is equivalent to looking across a transect of stand vigor at a fixed level of beetle pressure (Figure 6a). Retrospective studies such as these suggest the exciting possibility that beetle dynamics at the stand level are as deterministic as they are at the host level (Figure 4a). However, the success of susceptibility indices is contingent on having similar beetle pressure among stands. Tests of risk models that do not control for beetle density by sampling design, systematically fail to provide any information about the likelihood of an epidemic, or the extent of host mortality (e.g., Bentz et al. 1993).

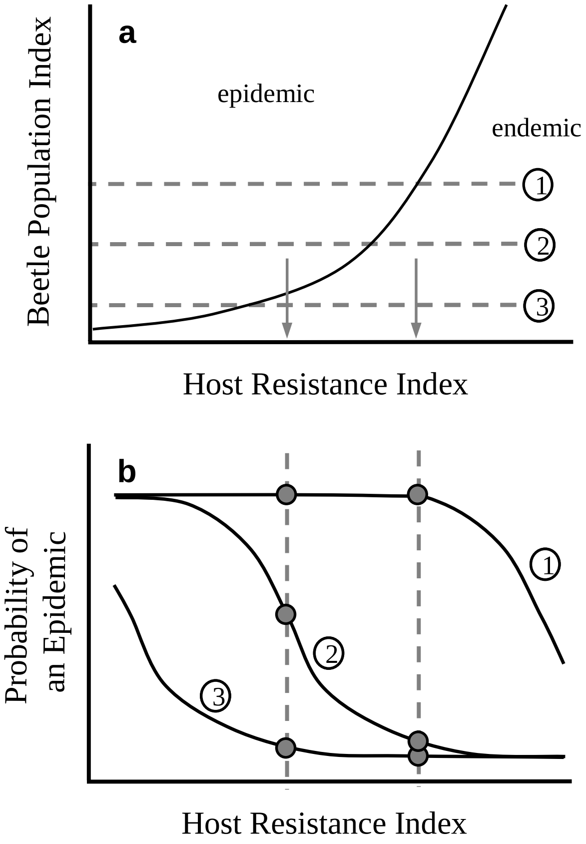

Figure 6. Absolute and ranked risk of beetle outbreaks. a) The threshold curve (solid line) that is predicted from the critical threshold point of the replacement curve as a function of beetle pressure and host resistance (after Berryman 1978). Forest stands with combinations of beetle density and host resistance above the threshold are predicted to undergo a beetle epidemic; those below are predicted to be in an endemic state. The gray arrows represent two stands with different indices of resistance. The dashed gray lines are three example beetle densities discussed in the lower panel. b) This shows the ranked risk between the two example stands in the upper panel, at each of the three beetle densities. This figure highlights that beetle density and host resistance together give estimates of absolute risk, whereas host resistance alone only predicts ranked risk.

Absolute and ranked risk

What do stand susceptibility indices tell us? Under certain conditions, they tell us about *ranked* risk. Consider an ideal forest where risk is given by a simple threshold model (e.g., Figure 6a). If one stand has a larger susceptibility index than another, then the more susceptible stand is at a greater risk of being attacked. However, the quantitative difference in risk among stands may be small, or very large, depending on beetle density (Figure 6b). If beetle density is low, then neither stand is likely to be infested and the difference in risk between the stands is small. If beetle density is intermediate, then the more susceptible stand can have a much greater risk than the more resistant stand. If beetle density is high, then both stands are likely to be infested and again the difference in risk will be small. Thus, risk models that do not consider the densities of attacking beetles can only predict the inequality of risk among stands.

The likelihood of an epidemic, or of host mortality, for a given stand without reference to any others, is *absolute* risk. Models of absolute risk are more challenging to develop because they require estimates of the attacking beetle density. Are absolute risk models necessary, or do ranked risk models provide sufficient guidance to managing mountain pine beetle infestations? The answer depends on the goals of risk analysis. To understand the needs of forest managers, we revisit the objectives that are stated in the risk literature. The overarching goals of risk analysis stated by entomologists and forest ecologists are either to predict “...the likelihood of an outbreak population occurring in a stand…” (Bentz et al. 1993) or “...the potential damage to lodgepole pine stands by the mountain pine beetle...” (Shore *et al*. 2000). These are goals of absolute risk.

Productivity-curve models, in their current state, could be used to predict absolute risk (e.g., Raffa and Berryman 1986). However, when compared against the ecological framework of the host-pathogen interaction (Figure 2), it becomes apparent that they lack the more tactical details of host selection. Productivity-curve models assume that the map from emerging beetle density to attacking beetle density is direct, which may be unrealistic considering the aggregating behavior of mountain pine beetles. While the process of host selection during dispersal is the least understood part of the beetle life-cycle (Safranyik and Carroll 2006), recent modeling efforts have started to tackle the implication of behavioral aggregation for the development of risk models (Powell et al. 1996, 2000).

Models of host selection

Host selection is the process that determines how the emerging population of beetles will redistribute among new hosts and give rise to new densities of attacking beetles (Figure 2). In contrast to productivity-curve models that are developed at the resolution of a stand, the mechanisms germane to host selection are modeled at the finer resolution of an individual host tree. This poses an additional challenge to developing absolute risk models because it is necessary not only to develop and validate the tree-level process of host selection, but also to abstract the cumulative effect of host selection into stand-level productivity-curve models. While the theoretical study of host selection is still in its infancy, some general properties are emerging.

Geiszler et al. (1980) developed the first mechanistic model of host selection. They considered a situation where a focal tree was undergoing attack, and modeled the pheromone dynamics and behavior of the flying beetle population. Once a focal tree was well under attack, high pheromone concentrations caused flying beetles that were attracted to the local area to be repelled from the focal host. If the repelled beetles successfully switched to adjacent hosts, then the attack and aggregation feedback could be maintained. The authors concluded that switching success depends on the density of attacking beetles and their proximity to the focal tree. Interestingly, they found that host vigor had little influence on the success of secondary attacks.

The first model to incorporate mechanistic host selection as well as attack dynamics was developed by Powell et al. (1996). Since the focus of the work was to study host selection, the models consider only the dynamics from emerging to attacking beetle density in a single generation. These models are spatially explicit and include the density of flying beetles, attacking beetles, pheromone production, host volatiles, host resin and attack holes—resulting in a model comprising six coupled partial differential equations. While this detailed model captures the temporal dynamics of attack for a focal tree (Powell et al. 1996), it is too mathematically complex to study in detail.

Strategic simplification of the above model has allowed researchers to study the qualitative effects of host selection (Powell et al. 1996; Powell and Rose 1997; White and Powell 1997; Logan et al. 1998; Powell et al. 2000). The authors conclude that weak trees form the focus of infestations, and that the spot-like patterns that emerge at the stand level are the result of secondary pheromone oriented attacks. They found that the likelihood of a beetle epidemic depended on the success of secondary attacks, which was largely governed by the density of emerging beetles. In terms of risk to a particular tree, the most important factor was the proximity to other attacked hosts. As with the model of Geisler et al. (1980), host vigor had little influence on the success of secondary attacks.

Powell et al. (2000) proposed a risk model for a single host tree based on the likelihood of a secondary attack. Given a focus host under attack, the risk of a secondary attack on adjacent hosts could be quantified using models of host selection and attack dynamics. The risk to a stand could then be given by the cumulative risk of secondary attacks over all the hosts. However, this approach assesses risk relative to the focus trees that are under attack. In the model of Powell et al. (2000), focal trees are the first, or primary, hosts attacked in a stand. It seems unlikely that focal trees could be predicted in practice. Thus, future risk models that incorporate host selection need to predict absolute risk without reference to focal trees.

Host selection models are in the early stages of development. Nonetheless, they all agree on two points: host risk is determined mostly by the density of emerging beetles and by the proximity to other hosts that are under attack. Contrary to the predictions from mechanistic attack models, host vigor is not predicted to play a significant role in determining the risk of attack. The contrasting predictions from host selection models and attack models can be assessed qualitatively using spatial patterns of observed beetle attacks within a stand. Such statistical analyses often use autologistic regression to model the probability of host attack as a function of host size, age, vigor, and proximity to other attacked trees (Mitchell and Preisler 1991; Preisler 1993; Preisler and Mitchell 1993). In agreement with host selection models, they find that the probability of attack is influenced by the proximity to attacked trees. For example, small trees were attacked more often if they were near other attacked trees than on their own. However, in agreement with attack models, they also find that host vigor has an influence on the probability of attack. This suggests that host selection models have revealed the importance of proximity for attack risk, but that they need further development to refine the attack process.

CONCLUSIONS

Finding the appropriate balance of ecological complexity in predictive models is difficult for any applied problem. Nevertheless, the minimum ingredients should include both systematic model development and independent evaluation to help ensure that the models provide reliable management tools. Through our synthesis of empirical evidence and theoretical developments in the mountain pine beetle system, we have demonstrated that the minimum components for models of absolute risk must consider both beetle pressure and stand susceptibility. Models that include only one of these indices provide only estimates of ranked risk. This perspective sheds new light on the mixed performance of current risk models. Since current risk models only consider host characteristics, they predict the ranked risk of infestation and host mortality among stands. Many independent evaluations of these risk models have controlled for beetle density by their sampling design, and thus have tested—often successfully—for ranked risk (e.g., Shore et al. 2000). When beetle density is not controlled by sampling design (e.g., Bentz et al. 1993), the evaluation is a test of absolute risk, and models of ranked risk have failed to provide any information.

Forest managers seek models that can predict the absolute risk of a mountain pine beetle epidemic, as well as the extent of host mortality. The current paradigm for risk analysis is based on static threshold models (e.g., Figure 6a). The threshold is derived from replacement curves, which describe the per-capita change in the beetle population from year to year. Specifically, threshold models are based on the unstable equilibrium between the two peaks in a bimodal replacement curve. Yet, theoretically there are situations where the replacement curve for a particular stand is unimodal (e.g., Raffa and Berryman 1986), which questions the generality of defining thresholds in such a manner. Moreover, even with a knowledge of the initial beetle densities and stand susceptibility, static threshold models are of limited value because the threshold changes through time as attacking beetles remove hosts from a stand. Essentially, static threshold models indicate how a beetle population may change in one year, which may or may not indicate the risk that an infestation will develop into an epidemic. Thus, we believe that the next generation of risk models should be based on dynamic models that encompass the key processes of dispersal, attack and reproduction (Figure 2). We feel that dynamic models of absolute risk can be based on existing productivity-curve models that consider the processes of attack and reproduction, but expanded to include the effects of host selection on the process of dispersal.

There are two areas where further research would aid in the development of absolute risk models. The first area is understanding how to predict the density of attacking beetles from the density of emerging beetles, and the second area is understanding how to predict the replacement curve of the beetle population from host and stand characteristics.

The map from emerging beetle density to attacking beetle density provides an important link to monitoring strategies. The density of attacking beetles can only be observed after an infestation, but the density of emerging beetles can be estimated using the number of recently attacked hosts from aerial or ground surveys (Bentz et al. 1993). The challenge is to predict the density of attacking beetles from estimates of emerging beetles. Models of host selection suggest that this may be a complex process requiring explicit spatial models of pheromone dynamics. Undoubtedly, the mechanisms of behavioral aggregation are important for predicting attack risk for a particular tree, but how important are they at larger spatial scales such as a forest stand? Unlike the development of productivity-curve models, host selection models are less grounded by empirical data. There is a strong need to continue the development of these models. In particular, the development process must become more closely tied to empirical validation so that researchers can begin to understand, and scale up, the influence of host selection on the dynamics of stand-level outbreaks.

The second challenge is to predict the replacement curve that describes beetle population dynamics and host mortality. Much research has been done on the ecological mechanisms of attack and reproduction, which has lead to the development of productivity-curve models. However, the study of productivity-curve models with dynamics forests has been restricted to simulation models that are difficult to understand and generalize (e.g., Raffa and Berryman 1986). We feel that this is where strategic simplification can contribute to the success of absolute risk models. For example, since the success of an attack changes with host vigor, it is necessary to track reproduction and host mortality for each class of host vigor. If, however, the vigor classes can be approximated by a continuous distribution of vigor, then approaches such as integral projection models could provide valuable mathematical frameworks (e.g., Godfray and Rees 2002). The abundance of empirical evidence on the mechanisms of attack and intraspecific competition can be utilized to guide and validate the process of strategic simplification.

We have highlighted the need for a new direction in the development of risk models for the mountain pine beetle system. However, the framework and guidelines that we have proposed here will only prove useful if the process of model development is tightly coupled to empirical validation—preferably at multiple spatial and temporal scales. Both of the main challenges will benefit from renewed empirical efforts. Due to the difficulty of observing the dispersal process, there is a large void in the direct empirical evidence for the host selection phase of the life-cycle. Some of this could be filled with mark-recapture experiments specifically designed to elicit the mechanisms behind behavioral responses to pheromones signals. There is a continuing need for detailed observations of natural epidemics. Data on the density of beetle attacks and emergence from each host in a stand provide an invaluable validation tool for the processes of attack and reproduction. Empirical validation is key to developing reliable risk models, and reliable risk models are vital to successful management.

There are numerous other factors that affect the host-pathogen interaction that have not been considered here. For example, factors such as temperature (Bentz et al. 1991), competition with secondary bark beetles (Safranyik and Carroll 2006), and long distance dispersal (Safranyik 1978) are considered to influence beetle dynamics. Since the risk analysis framework that we propose is based on a well established framework of ecological interactions, it can be easily expanded to consider these factors. Risk models in this system have gone through one full iteration of empirical observation, model development, and independent evaluation—we hope that our synthesis can provide some insight and guidance for the next iteration.

Acknowledgements

We would like to thank Marjorie Wonham, Chris Jerde and Che Elkin for insightful comments on an earlier draft of the manuscript. This study was funded by Natural Resources Canada, Canadian Forest Service under the Mountain Pine Beetle Initiative. Publication does not necessarily signify that the contents of this report reflect the views or policies of Natural Resources Canada, Canadian Forest Service. MAL gratefully acknowledges support under a Canada Research Chair.

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This publication is funded by the Government of Canada through the Mountain Pine Beetle Initiative, a program administered by Natural Resources Canada, Canadian Forest Service (web site: mpb.cfs.nrcan.gc.ca).

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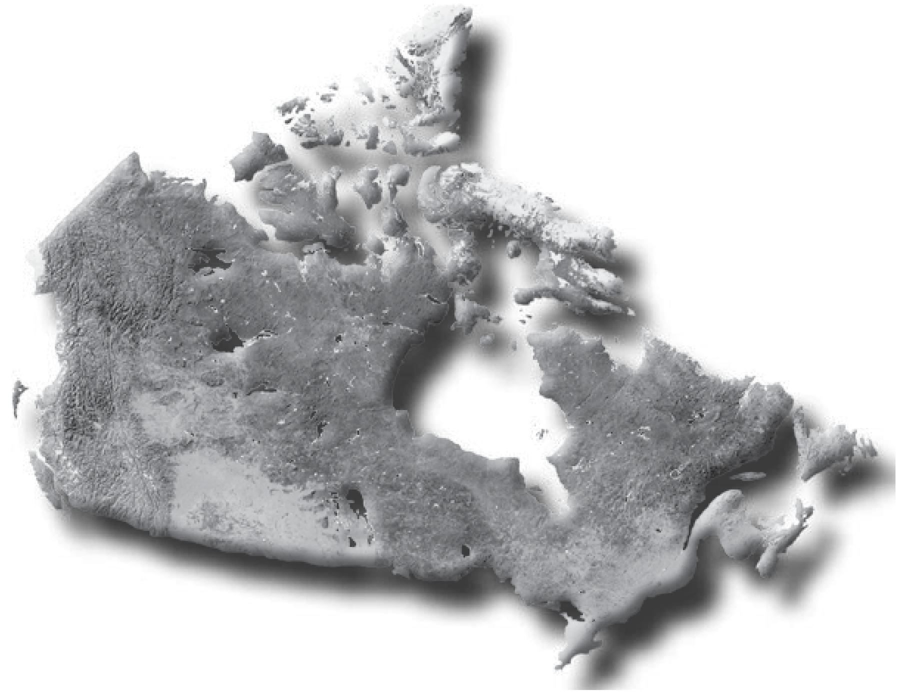

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