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Balancing ecological complexity in predictive models: a reassessment of risk models in the mountain pine beetle system

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Summary

1. The nature of ecological risk assessment is to predict the probability of an event, such as extinction or invasion, in a location where the event has rarely occurred. This typically requires developing risk models from data on events in different locations. One perplexing challenge in developing these models is to find the optimal balance of model complexity that reflects the tactical details of a system, but is sufficiently strategic to be applicable under a wide range of situations.
2. Here we address the balance of complexity in risk models for the mountain pine beetle system. Mountain pine beetles (*Dendroctonus ponderosae* Hopkins) are destructive pests of pine forests in western North America. Much effort has gone into collecting empirical evidence and developing mechanistic models of infestation dynamics, which has resulted in a wealth of process-based information. Current risk models, however, are based solely on indices of stand susceptibility that do not incorporate much of this ecological understanding. In practice, current risk models have proven ineffective at predicting the risk or extent of an infestation.
3. We assemble an ecological framework of the beetle–host interaction that allows us to compare across phenomenological and mechanistic models. We demonstrate that current risk models predict only ranked risk among forest stands, as opposed to absolute risk, and thereby provide an explanation for their limited ability to predict risk in practice. By comparing existing models with the ecological framework, we identify the primary factors determining risk, and propose which dynamical processes should be modelled explicitly, and which might be strategically abstracted.
4. *Synthesis and applications*. Balancing model complexity in predictive risk models is challenging for systems with complex ecology and imperfect information. Here we draw together a wide range of empirical and modelling work in the mountain pine beetle system to develop a strategic framework of the ecological interactions. Through this framework, we demonstrate why current risk models have been ineffective in predicting risk, and suggest a starting point for future risk models that explicitly describe the dynamical processes necessary to predict absolute risk.

Key-words: absolute risk, hazards, host–pathogen models, model complexity, pattern-oriented modelling, ranked risk, risk management, strategic models, tactical models

Introduction

Risk assessment is a common focus of applied ecology. Whether the goal is to prevent population extinction (Bradbury *et al.* 2001; Kotiaho *et al.* 2005), manage a biological invasion (Carlton 1996; Kolar & Lodge 2001), or control an epidemic (Keeling *et al.* 2003; Ferguson *et al.* 2005), there is a need for quantitative models that can predict the risk of such events. The intrinsic nature of ecological risk assessment, however, is to predict the probability of an event, such as extinction or invasion, in a location where the event has rarely occurred. Consequently, we are challenged to develop risk models based on past experience in other areas, even though the factors that cause risk (referred to as 'hazards') may be different, or have changed in magnitude. The implication is that risk models need to be based on sufficient ecological mechanisms to quantify hazards in new locations, as well as relating them to the probability of the event occurring.

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One challenge in 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 (Nisbet & Gurney 1982; Godfray & Rees 2002; Grimm *et al.* 2005). Tactical models are developed to study specific systems, either involving a large number of parameters and detailed mechanisms, or based on purely statistical relationships. The complexity and specificity of tactical models can make them difficult to understand, and limits their ability to predict in new areas. Strategic models, in contrast, are developed to study the consequences of general ecological interactions. However, the sparse nature of strategic models means they can omit details that limit their utility for practical applications. In the context of models for risk prediction, the distinction between tactical vs. strategic types of model relates to which hazards are included in a model, and how these hazards are related to the risk of an event (Suter 1992). The optimal balance between tactical and strategic approaches is achieved by evaluating the ability of a model to predict the risk of an event in areas that were not used for model development. The process of finding the optimal balance of model complexity should include elements of systematic model development and empirical validation because of the potential for model structure to influence predicted management strategies (Wood & Thomas 1999; Harwood 2000).

Here we address the problem of balancing ecological complexity in predictive risk models for the mountain pine beetle system. Mountain pine beetles (*Dendroctonus ponderosae* Hopkins) are a destructive pest of pine forests in western North America (Logan & Powell 2001; Safranyik & Carroll 2006). The current outbreak in the interior of British Columbia, Canada has killed nearly 10 million ha of lodgepole pine, resulting in massive economic loss and imposing serious ecological problems (Natural Resources Canada 2005). To minimize the economic and ecological cost of beetle infestations, forest managers use preventive measures such as forest thinning (Oester *et al.* 2005). However, such measures are expensive and often can be applied only to small areas of forest. To aid managers in the design of intervention and harvest strategies, risk models are developed to predict the probability that a forest stand will experience a given level of tree mortality from beetles over a given time frame (Shore *et al.* 2000).

The mountain pine beetle system is well suited to address the question of how to balance ecological complexity because, while the abundance of modelling work in this system spans the full range from tactical to strategic, current risk models are heavily weighted to tactical approaches. Current risk models are based on forest susceptibility, which is quantified using indices such as average tree age, density and vigour in the stand (Bentz *et al.* 1993; Shore *et al.* 2000). While these models are successful in describing the damage caused by beetles when fitted to data on old infestations, they systematically fail to predict the risk of tree mortality from mountain pine beetle infestations in new areas (Stuart 1984; Katovich & Lavigne 1986; Bentz *et al.* 1993). As a result, current risk models provide little effective guidance for forest management.

The singular emphasis on stand susceptibility in current risk models is in stark contrast to the diversity of ecological interactions that have been the focus of much empirical and theoretical work in the mountain pine beetle system. Some studies are more strategic, such as looking at interactions across different species of bark beetles (e.g. Berryman 1974), while others are more tactical and focused on specific geographical locations (e.g. Cole 1974). The result is a large gap between what is considered relevant among ecologists, and what is included in current risk models – with no consensus about which interactions are strategic components essential to predicting risk and which interactions are tactical details. While much of this research was not developed for the purpose of predicting risk (see reviews by Coulson 1979; Christiansen *et al.* 1987; Raffa 2001; Safranyik & Carroll 2006), it provides an invaluable body of knowledge from which to develop risk models.

Here we demonstrate the minimal ecological hazards necessary to predict risk in the mountain pine beetle system, and lay the foundation for a new generation of risk models. We begin by reviewing an ecological framework based on empirical research that allows us to synthesize existing theoretical work. Through this process, we reveal why current models fail to predict risk in new areas, and demonstrate the minimal set of ecological components required to predict the risk of damage. We argue that the next generation of risk models need to move away from the current paradigm of static models to dynamic models that can properly incorporate ecological mechanisms. Our use of a single conceptual framework to synthesize both the empirical and theoretical work, as well as our demonstration of the minimal ecological components for risk, provide the first steps towards finding the balance of ecological complexity that will most successfully predict the risk of forest damage from mountain pine beetle infestations.

Ecological framework

There are several excellent reviews of mountain pine beetle ecology (Coulson 1979; Christiansen *et al.* 1987; Raffa 2001; Raffa *et al.* 2005; Safranyik & Carroll 2006), which collectively describe a large number of ecological interactions that could influence beetle dynamics. In this section, we use this body of empirical work to describe a structured life-cycle graph that summarizes the main ecological interactions. Rather than attempting to review all the empirical research in the mountain pine beetle system, we focus on the processes that have been studied repeatedly across different forest stands. As empirical studies are often limited by what processes it is possible to investigate, and we consider only a subset of these, this approach does not guarantee that we have incorporated all the relevant ecology. However, by focusing on the processes across regions, the framework necessarily contains a strategic foundation to assess current risk models and discuss the necessary components of future risk models. The ecological framework discussed below has an organization similar to other frameworks in the literature (e.g. Berryman 1974). However, as our focus is on the ecological processes observed across different regions, it differs in the specific processes considered.

ECOLOGICAL PROCESSES

Mountain pine beetle populations are typically univoltine, completing a single generation each year (Fig. S1 in Supplementary material; Safranyik & Carroll 2006). Much of the life cycle is spent within the host trees. Recently developed adults emerge from their host trees in late summer to search for, and attack, new hosts. 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 egg galleries. If insufficient beetles attack and the host survives, then most egg galleries are unsuccessful. In response, attacking beetles emit aggregation pheromones to recruit additional beetles into mass attacks. If sufficient beetles are available, then host defences can be overwhelmed and beetles successfully construct egg galleries in the phloem tissue. The eggs develop into larvae through the autumn, and usually overwinter as late-instar larvae. Pupation occurs in early spring and new adults emerge in late summer.

The structure of a life-cycle graph can be defined in various ways. There are two common approaches in the mountain pine beetle literature: the first groups beetles according to the physiological stages of the life cycle, such as eggs, larvae, pupae and adults (e.g. Fig. S1, Supplementary material; Bentz *et al.* 1991); the second groups beetles based on similar activities, such as flying beetles and nesting beetles (e.g. Fig. 1; Berryman *et al.* 1989; Powell *et al.* 1996). Both approaches are equally valid because they constitute complete life cycles that can incorporate all ecological processes – the choice between them reflects the ease with which different processes can be described. Here we take the second approach, and structure the life-cycle graph into stages of similar activity (Fig. 1). Specifically, we consider three stages: emerging beetles, attacking beetles and nesting beetles, because they separate the main ecological processes of attack, reproduction and dispersal (Raffa & Berryman 1987). A brief review of these processes can be found in Appendix S2, Supplementary material.

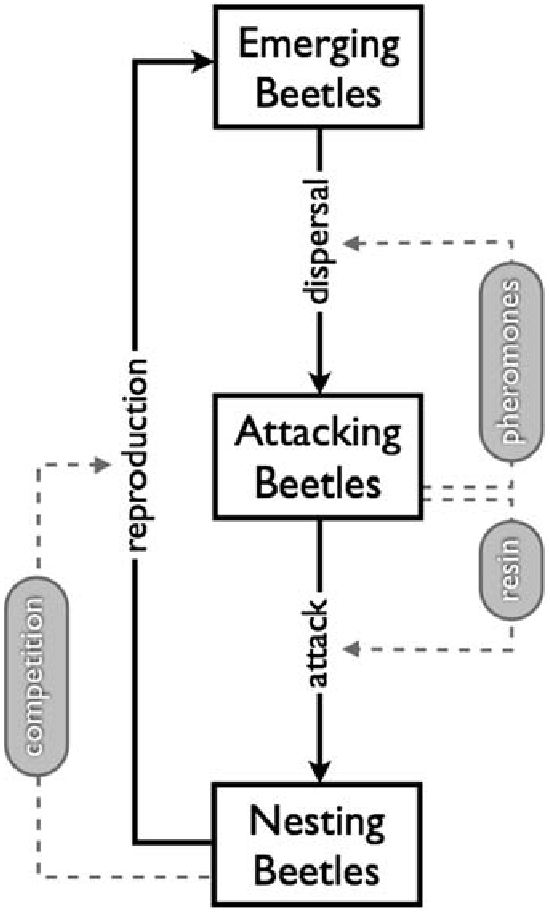

Fig. 1. Ecologically structured life-cycle graph of the mountain pine beetle. Solid lines, beetle transitions between stages; dashed lines, main ecological interactions. The stages are the number of beetles emerging from each host, number of beetles attacking new hosts, and number of beetles that have successfully attacked new hosts. The transitions between stages are by the processes of attack, reproduction and dispersal. The attack process is influenced by host defences, dispersal by pheromone communication, and reproduction by intraspecific competition.

THEORETICAL WORK

The rich collection of ecological interactions revealed by empirical work has led to an equally diverse collection of mechanistic models. For the purpose of review, we divide the models into two groups: either within-generation dynamics in the form of process models, or between-generation dynamics in the form of population models (see Table S1 in Supplementary material). Process models are used to study subsets of the mountain pine beetle life history in detail, such as the process of attacking host trees (e.g. Berryman *et al.* 1989), or the process of pheromone-mediated dispersal (e.g. Geiszler *et al.* 1980). Population models (e.g. Berryman 1979) combine these ecological processes into a complete life cycle that can be used to predict beetle dynamics through time. Population models – either explicitly or phenomenalistically – embody the emergent properties of process models. We begin by reviewing process models developed for the main ecological processes of attack, reproduction and dispersal.

Berryman & Stenseth (1989) developed the first process 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 defences. Host resin increased based on the ability of the host to produce resin (vigour), and decreased as a result of defence against attacking beetles. There are two possible outcomes from this 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 flying beetles, and that the density of beetles required to overwhelm a host depended on host vigour. The beetle–host interaction described by the model is arguably minimal, but it captures the observation that the risk of individual host mortality depends on whether the density of attacking beetles is above or below a vigour-dependent threshold (Fig. 2a).

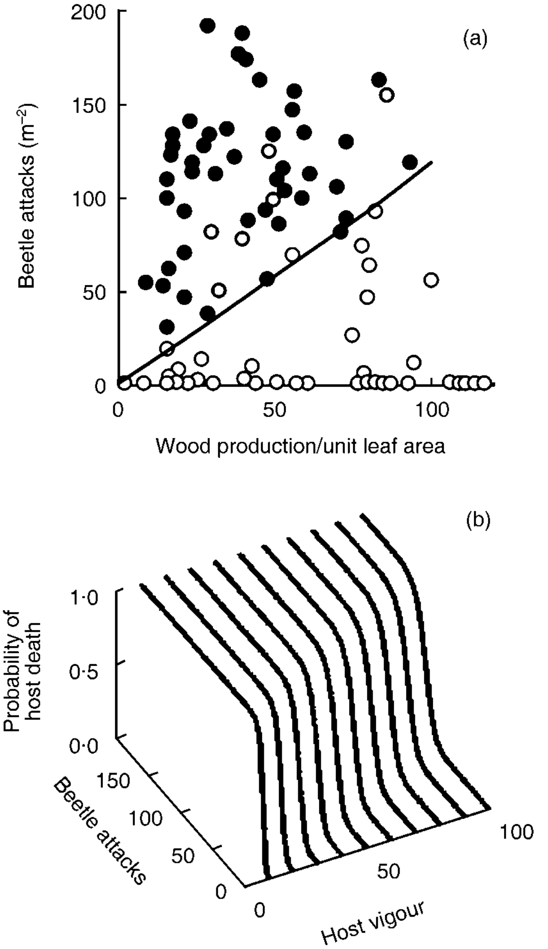

Fig. 2. Host mortality as a function of beetle density and host vigour. (a) Data redrawn from Waring & Pitman (1983). Vertical axis, density of beetle attacks per m^2 of bark; horizontal axis, host vigour. Black circles, dead hosts; grey circles, strip-attacks (only part of the host is killed); open circles, are live hosts. The line was hand-drawn by the original authors. (b) Conceptual relationship between beetle pressure, host vigour and probability of host mortality.

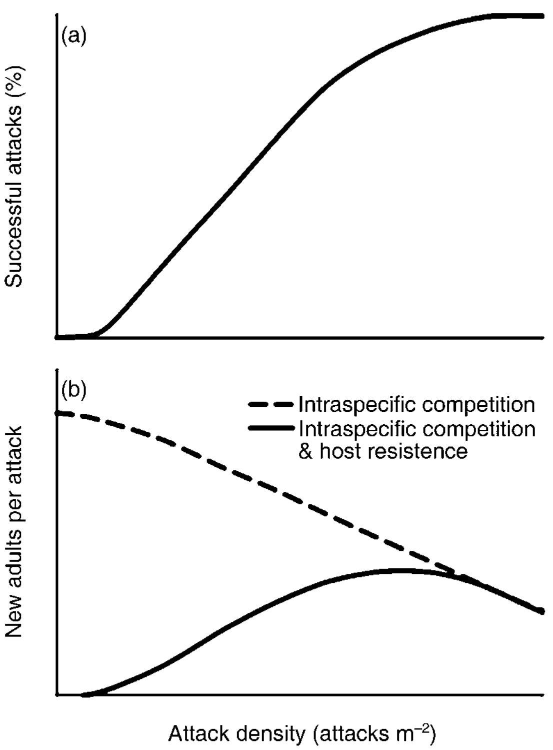

Fig. 3. Average effect of attack density on intraspecific competition and host defences for a stand (from Raffa & Berryman 1983). (a) Proportion of successful attacks increases with attack density, reflecting the ability of higher beetle densities to overwhelm host defences. (b) Decline in *per capita*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

The empirical evidence for a threshold of individual host mortality is encouraging because it suggests that the risk of mortality for an individual tree is reasonably deterministic. The disadvantage is that it requires a knowledge of vigour for each host tree. When host vigour is unavailable, researchers often report the success of beetle attacks using what we refer to here as attack–success curves, which describe the average proportion of attacks that successfully produce galleries as a function of the density of attacking beetles on an average host tree (Fig. 3a; Raffa & Berryman 1983; Elkin & Reid 2004). Attack–success curves have the advantage that the attack process is summarized into a single function for the whole stand. However, as the proportion of successful attacks is determined by host mortality, and as host mortality depends on both attack density and host vigour, each host of a different vigour level has a separate attack–success curve (Fig. 2b). Thus an attack–success curve reported for a whole stand averages over hosts of different vigour. The implication is that predicting the attack–success curve for a particular stand requires some knowledge of the vigour distribution within the stand.

Reproduction

Intraspecific competition among the attacking beetles can significantly reduce the number of new adults that emerge from each gallery as the density of galleries increases (Raffa & Berryman 1983). Some of the reduction comes from lower egg-laying rates at high densities, and some from reduced larval survivorship. While intraspecific competition occurs at the scale of an individual host tree, researchers often average across trees and report the average number of new adults produced from each successful gallery as a function of attack density (Fig. 3b; Raffa & Berryman 1983). The advantage is that the total reproductive output for a stand can be described by the product of the attack–success curve and the per-successful-gallery adult production rate (Fig. 3b; Berryman 1974; Raffa & Berryman 1983; Raffa 2001). The resulting density-dependent relationship is referred to as a productivity curve (Berryman 1974).

For a single host, optimal beetle productivity occurs at intermediate attack densities (Fig. 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. Despite the variation in host vigour 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 & Berryman 1983). While largely phenomenalistic at the stand level, this feature is key to generating the outbreak dynamics in the first generation of bark beetle population models.

Dispersal

The first mathematical model of host selection was developed by Geiszler *et al.* (1980). They considered a situation where a focal tree was undergoing attack, and modelled the pheromone dynamics and behaviour of the flying beetle population. They found that 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, resulting in a spatial clump of attacked trees. The authors concluded that switching success depends on the density of attacking beetles and their proximity to the focal tree.

The first model to incorporate host selection as well as explicit attack dynamics was developed by Powell *et al.* (1996). The model is spatially explicit and includes 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. Simplification of the above model allowed researchers to study the qualitative effects of host selection (Powell *et al.* 1996; White & Powell 1997; 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.

Risk models in theory

We contend, as others have (e.g. Bentz *et al.* 1993), that risk analysis in the mountain pine beetle system should be based on the predictions of population-scale models. For the risk of a population outbreak, this is apparent because the risk objective is a measure of population growth between generations. The risk of damage to host trees, however, also emerges from population models because of the dependence on beetle density. While it is possible to estimate the densities of attacking beetles in a stand using baited traps, such data are generally inadequate for management because the fate of the attacked hosts is determined before intervention can be implemented (but see the less common approach of pheromone disruption, e.g. as described by Borden *et al.* 2006). As a result, it is often necessary to predict the density of attacking beetles from attacks in previous years. A practical way to predict beetle densities is to use the location and density of dead host trees, which requires either an explicit or implicit formulation of reproduction and dispersal. Thus the risk of damage to a stand also requires a population model of the life cycle.

The theoretical origins of risk models in the mountain pine beetle system can be traced to the early population models based on stand-level productivity curves (Berryman 1979). Consider an abstract forest where all hosts have the same vigour, where the quantity of the host material stays constant over time (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 (no pheromone-mediated dispersal). As the productivity curve phenomenalizes the processes of attack and reproduction, it will determine the dynamics of a beetle population in our abstract forest. The population model can be written as:

$$\begin{aligned} N_{t+1} &= r(N_t)N_t \\ r(N_t) &= p(N_t)s(N_t) \end{aligned} \qquad \text{eqn 1}$$

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 survival is constant, [$s(N_t) = s_0 =$ constant], the replacement curve is proportional to the productivity curve (Berryman 1979). The population is at 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 (Fig. 4a). The first equilibrium is unstable and results from the interaction with host defences; the second equilibrium is stable and results from intraspecific competition. Thus the population dynamics will settle on a beetle equilibrium maintained by competition.

Consider the same abstract forest as above, but with two classes of host vigour – call them 'weak' and 'normal' trees. In such a forest, the replacement curve comprises the productivity curves from both classes of vigour. If the normal trees provide more phloem habitat, then the two classes of vigour may produce a bimodal replacement curve for the beetle population (Fig. 4b; Berryman 1979). The bimodal replacement curve has four equilibrium points: two unstable points that reflect the host resistance of each vigour class, and two stable points that reflect competition in each vigour 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. Beetle densities above the critical threshold point will grow into epidemics; beetle densities below the threshold point will remain at endemic levels.

Naturally, the assumption that host materials remain constant over time is unrealistic. The quantity of host material in a forest, and the distribution of host vigour, changes as a result of tree growth, competition and beetle attacks. The result is that the replacement curve changes over time as the stand condition cycles through different phases of beetle attack (Berryman *et al.* 1984; Raffa & Berryman 1986). For example, after a strong epidemic the forest comprises mostly

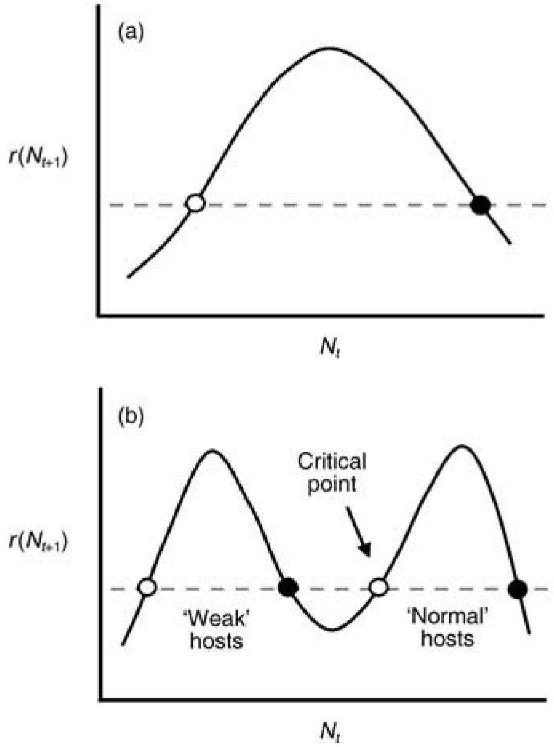

Fig. 4. Productivity-curve population models for the mountain pine beetle following Berryman (1979). (a) The replacement curve that maps beetle density (N) in year t to $t + 1$ is shown as the solid line. The 1 : 1 line is shown in grey. Open circle, unstable equilibrium point; solid circle, stable equilibrium 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 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.

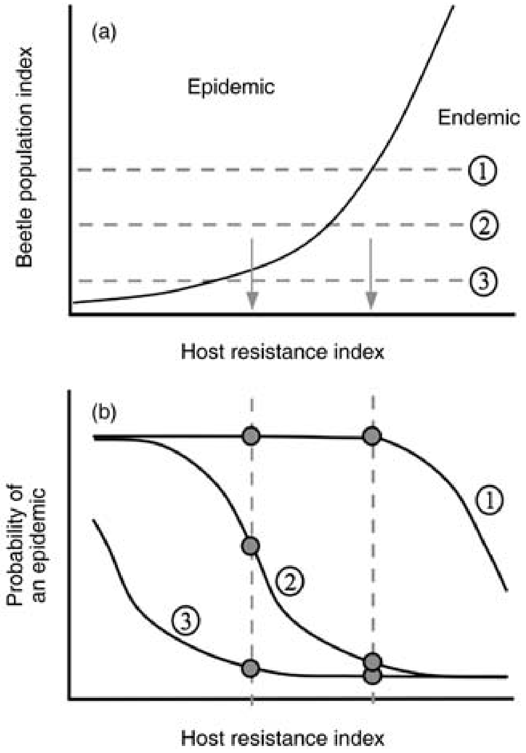

Fig. 5. Absolute and ranked risk of beetle outbreaks. (a) The threshold curve (solid line) predicted from the critical threshold point of the replacement curve as a function of beetle pressure and host resistance (after Berryman 1978). Forest stands with combinations of beetle density and host resistance above the threshold are considered to be in an epidemic state; those below are considered to be in an endemic state. Grey arrows, two stands with different indices of resistance. Dashed grey lines, three example beetle densities. (b) 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 predicts only ranked risk.

unsuitable and low-vigour 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 kill much of the forest and return it to a state with little suitable habitat. The changing replacement curve reflects the changing distribution of vigour within the stand through time.

The observation that the replacement curve changes dynamically through time has important implications for the application of threshold risk models. The long-standing paradigm in mountain pine beetle risk assessment is that risk at the scale of a stand is determined by a threshold model as a function of beetle density and stand resistance (Fig. 5; Safranyik & Carroll 2006). However, the dynamic replacement curve suggested by the theoretical models means that the critical threshold also changes through time, and will disappear entirely during times when the replacement curve is unimodal (Berryman *et al.* 1984). As a result, it is not possible to state whether a given beetle density will lead to an epidemic, or how much damage will result, without considering how both beetle density and stand resistance change through time. For example, a beetle population could increase in the first year, but if the threshold increases, the infestation may die-out in the second year without causing much damage. If the threshold doesn't increase, then the infestation may continue, killing most of the host trees. Thus there is no way to predict the fate of the infestation, or the extent of the damage, without modelling the dynamics of the replacement curve that is generating the critical threshold.

Relatively few mathematical models have been developed that consider beetle population dynamics with a dynamic replacement curve (Berryman *et al.* 1984; Berryman & Stenseth 1989). These models describe the replacement curve as a function of stand biomass, and assume that stand resistance can be characterized by a single average vigour level that is inversely related to stand biomass. However, empirical observations suggest that replacement-curve dynamics may be more complex, and depend on both the structure of vigour within a stand, and how the attacking beetles distribute themselves among the vigour classes (Fig. 2). As the vigour structure within a forest changes through time as an infestation progresses, beetle dynamics may need to be described by the coupled interaction between a changing beetle population and the changing vigour structure of a forest. While this type of coupled interaction has been considered in a computer-based simulation of beetle dynamics (Raffa & Berryman 1986), it has not been described mathematically. In our discussion of future directions below, we consider one approach to explicitly modelling the dynamics of vigour structure within a stand that is amenable to mathematical modelling.

Risk models in practice

The use of risk models, which are often referred to as risk or hazard systems, have a long history in the mountain pine beetle system (Amman *et al.* 1977; Berryman 1978; Bentz *et al.* 1993; Shore *et al.* 2000). The primary objective of these models is to predict the amount of damage caused by an infestation, usually measured as the proportion of basal area killed (%BAK). The terms 'risk' and 'hazard' are used in the mountain pine beetle literature to distinguish between different time scales – risk is defined as the short-term probability of host damage; hazard is defined as the stand characteristics that affect the 'likelihood of attack and damage' (Shore *et al.* 2000) or the ability of a stand to 'support an epidemic' (Bentz *et al.* 1993). In this context, hazard is considered a measure of eventual damage to a stand, the argument being that it is an index of the 'maximum mortality (in terms of percentage of stand basal area) a stand would receive in the event of a mountain pine beetle infestation' (Shore *et al.* 2000). The rationale for distinguishing the time scales is based on the assumption that risk at the longer time scale does not depend on beetle density (Shore *et al.* 2000).

The definition of hazard used in the mountain pine beetle literature is inaccurate. In the larger field of risk assessment, hazard is defined as the factor that gives rise to risk, and risk as the probability of an event occurring from the hazard(s) (Suter 1992). In terms of mountain pine beetle infestations, the characteristics of a stand are certainly a hazard, as is the density of beetles, but the use of a hazard index to predict the likelihood of attack or damage is a model of risk. The value of clarifying these definitions here is to recognize that what have been distinguished in the literature as models of risk and hazard are, in fact, both models of risk – the only difference being whether they use a single hazard index, or use both stand susceptibility and beetle density as hazard indices.

Numerous hazard indices have been developed for mountain pine beetles, based on climate in the region where the stand is located; the density, species composition, age and diameter of trees in the stand; the levels of host vigour within the stand; or a combination of factors. These hazard indices are developed using regression models and professional judgement, which are calibrated (through a risk model) to empirical observations in stands that have already been infested. Such retrospective analyses do a good job of describing the damage caused by mountain pine beetles as a function of stand-level attributes (Schenk *et al.* 1980; Stuart 1984; Perkins & Roberts 2003; Negron & Popp 2004; Fig. 6a). However, these models systematically fail to predict risk in stands that were not used in the model development (Stuart 1984; Katovich & Lavigne 1986; Bentz *et al.* 1993; Fig. 6b). The implication is that while current risk models can describe risk retrospectively, they cannot predict risk.

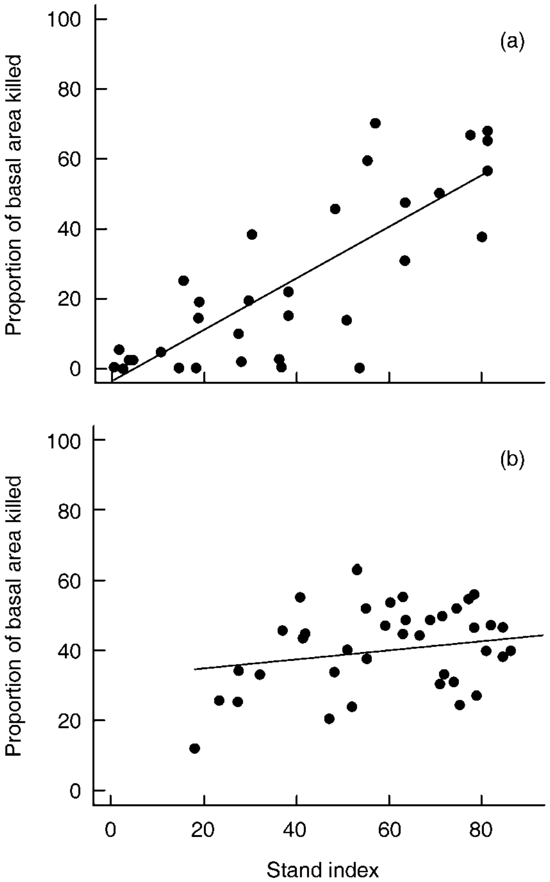

Fig. 6. Fitted and predicted host damage based on a hazard index of stand characteristics. Data redrawn from Shore *et al.* (2000). Each symbol represents a stand; the proportion basal area killed by mountain pine beetle is plotted against the stand index developed by Shore & Safranyik 1992. Line shows results of a linear regression. (a) Description of host damage in stands that were used to develop the index. (b) Prediction of host damage in independent stands showing no predictive relationship ($P > 0{\cdot}05$; see Appendix S1 in Supplementary material for details).

Why do current risk models fail? We contend that the primary reason is because beetle density – which has been identified as an important component in both empirical work (Waring & Pitman 1983; Raffa & Berryman 1983) and theoretical models (Berryman 1979, 1982; Powell *et al.* 1996) – has been removed as a hazard index in current risk models. While many researchers recognize that beetle density plays an important role in predicting the amount of host damage, some have argued that it can be ignored by considering risk on a longer time scale that predicts the eventual, or maximum, damage from an infestation (Shore *et al.* 2000). The flaw in this approach is that there is no stand-independent beetle density above which a beetle population is expected to break out. An infestation may be over in 1 year, or may expand over several years, which makes it difficult to predict the extent of damage.

It is useful to distinguish three types of risk: absolute, relative and ranked risk. Absolute risk is the probability of an event occurring over a given time frame (Suter 1992). Relative risk is the ratio of absolute risk between groups. For example, if the probability of losing half the trees in a stand over the next 50 years is m_A for stand A and m_B for stand B, then the relative risk between stands is given by m_A/m_B. Ranked risk indicates the qualitative rank order of risk among groups (e.g. $m_A > m_B$). Relative risk provides a conditional probability, but ranked risk does not contain information about the probability of the event occurring.

What do stand susceptibility indices tell us? Under certain conditions, they tell us about ranked risk. Consider a forest where risk is given by a simple threshold (Fig. 5a). If one stand has a larger resistance index than the other, and we can assume that the density of attacking beetles is the same for both stands, then we can say that the more resistant stand is at a lower risk of being attacked. However, the quantitative difference in risk among stands may be small, or very large, depending on beetle density (Fig. 5b). If beetle density is low, the 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 – at best – only predict the inequality of risk among stands.

The problem is that ranked risk does not provide sufficient guidance to managers. Forest managers typically need to balance the cost of intervention with the benefits of reduced damage, to both determine the optimum level of management and identify the stands that are at high risk. For example, if two stands within a management area have an absolute risk of losing half their trees over a 50-year time span that in both cases is <10%, then the best management strategy may be to do nothing. However, if both stands have an absolute risk >90%, then the best strategy may be to intervene in both areas. Absolute risk provides the necessary information to determine both the optimal extent and optimal allocation (amount of effort at each location) of intervention, and has been the long-standing objective for risk models in the mountain pine beetle system (Bentz *et al.* 1993; Shore *et al.* 2000). Relative risk provides less information because the overall scale of risk is unknown. For example, if stand A has twice the probability of being infested as stand B, but the absolute risk for stand B is very small, then the optimal strategy may be different from the case where the absolute risk for stand B was larger, even though the relative risk is unchanged. As a result, relative risk provides only the necessary information to determine the optimal allocation of intervention. Ranked risk indicates which stands are at greater risk, but does not provide any information to determine either the optimal extent or the optimal allocation of resources.

Discussion

There is a need to develop models in the mountain pine beetle system that can predict the absolute risk of host damage or population outbreak for a given stand (Bentz *et al.* 1993; Shore *et al.* 2000). Our ecological understanding suggests that the interactions responsible for host mortality can be complex – involving processes such as spatial aggregation, tree defences and intraspecific competition among attacking beetles. While such complexity has probably contributed to the difficulties in developing simple predictors of forest damage, we feel that the effort spent studying the mountain pine beetle system has resulted in a wealth of process-based information and stand-level observations that are sufficient for developing models capable of predicting the absolute risk of stand-level damage.

The challenge is to distil the ecological complexity into a model that can predict the probability that a specific forest will experience a given level of tree mortality. Such risk models involve two components: the first is identifying which hazards are most important for predicting risk; the second is determining how to relate the risk of host damage to the hazard. These issues are at the heart of balancing ecological complexity for predictive models (Godfray & Rees 2002). Strategic models that ignore too many ecological processes may be unable to predict risk because they miss key hazard indices, or are too imprecise to relate the hazards to the risk of damage in a natural system. On the other hand, tactical models with too many details, or with region-specific empirical relationships, may be unable to predict risk outside the region where they were developed. With the goals of forest management in mind for the mountain pine beetle system, the model that best achieves this balance between strategic and tactical is the one most able to predict the risk of damage in new regions. Data sets with observations at multiple hierarchies are particularly valuable for model development because they contain information on ‘lower-level’ patterns that more closely reflect the ecological processes, as well as the overall pattern of stand-level damage (referred to as ‘pattern-oriented modeling’, Grimm *et al.* 2005).

As the first step towards achieving this balance in the mountain pine beetle system, we assembled an ecological framework (described above) based on processes that have been observed across different regions, and often across different species. Without a doubt, these represent only a subset of the processes that occur in natural stands. For example, we have ignored competition with other species of bark beetles (Safranyik & Carroll 2006); ignored the evidence that host selection can change with beetle density (Wallin & Raffa 2004); ignored the fact that winter temperatures can influence larval survivorship (Safranyik & Carroll 2006); and ignored the work on temperature-dependent beetle phenology (Bentz *et al.* 1991; Jenkins *et al.* 2001) – to name just a few. However, while incomplete, the ecological framework contains a minimal set of interactions that must either explicitly or phenomenalistically be a component of beetle–host population models. As host damage is an emergent property of population models, the framework provides a starting point to develop, evaluate, and then redevelop risk models.

Using this framework, we demonstrated that current risk models predict only ranked risk among stands, and only when it can be assumed that beetle pressure is the same among stands. Current risk models are based on indices that reflect stand susceptibility, which is only one of the two hazards identified by empirical work. While the ranked risk predicted by these models may indicate which stand among those compared is more likely to suffer a given level of damage, it does not reflect the actual risk of damage. As a result, our results provide a clear explanation for why current risk models have systematically failed to predict risk in new areas, and demonstrate that the minimal set of hazards that must be included in an absolute risk model for the mountain pine beetle system are both beetle density and stand susceptibility.

How should the next generation of models be developed to predict absolute risk in new areas? Clearly they need to include both hazard indices of beetle density and stand susceptibility, but the manner in which they are incorporated, as well as the scales considered, could take on a number of different forms. Here we propose an alternative direction for future risk models based on the ecological framework discussed above, and motivated by the work of Powell *et al.* (2000). Empirical observations of the attack process suggest that the risk of mortality for an individual tree is reasonably deterministic (Fig. 2). As damage results from the number of trees killed, the risk of damage to a stand is related to the risk of individual tree mortality. Thus we propose that an alternative approach to predicting stand-level risk is through the cumulative risk of individual tree mortality. By developing a stand-level risk model from tree-level mortality, many of the ecological complexities observed in natural systems (e.g. changing vigour structure, pheromone-based dispersal, host preference) are considered more explicitly. This approach focuses on a 'bottom-up' rather than a 'top-down' perspective to risk modelling (Grimm & Railsback 2005). To describe population-level dynamics, the mathematical model could be cast as a structured population model where individual trees are divided into categories based on vigour. Such a model would account for the combined influence of tree vigour and attack density as shown in Fig. 2, and explicitly describe the time dynamics of the population-level replacement curve discussed in equation 1. Appendix S3 (Supplementary material) proposes solutions to some of the potential challenges faced by the style of risk model described here.

The challenges and questions for future risk models reflect, in part, the more general problem of how much ecological complexity is necessary to predict risk. Some of the details discussed above, such as host selection, may not be necessary to model explicitly – while others not considered here may end up being essential. We have suggested a minimal set of hazards, as well as an initial framework for the ecological interactions that relate the hazards to the absolute risk of damage. However, the optimal balance of ecological complexity required to predict risk will be achieved through an iterative process of model development and model evaluation against independent data. In particular, the main challenges of estimating vigour distribution and predicting host selection 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 behavioural responses to pheromone signals in natural stands. 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. Risk models in this system have gone through one full iteration of empirical observation, model development, and independent evaluation – we hope that our work here can provide some insight and guidance for the next iteration.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Reanalysis of the data presented in Shore *et al.* (2000).

Appendix S2. Brief review of the three main ecological processes for bark beetles.

Appendix S3. Solutions to some of the challenges faced by a tree-level risk models.

Table S1. Summary of theoretical models reviewed.

Fig. S1. Physiologically structured life-cycle graph.

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