MODELING THE EFFECT OF LANDSCAPE PATTERN ON MOUNTAIN PINE BEETLES

by

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Abstract

Mountain pine beetles (*Dendroctonus ponderosae* Hopkins) are the second most important disturbance agents (after fire) in the lodgepole pine (*Pinus contorta* subsp. *latifolia* (Engelmann) Crichtfield) forests of western North America. Despite ecological and management importance, little is known about the effect of forest landscape structure on the spread of mountain pine beetle infestations. The general prediction from other work is that forest fragmentation at some scale might slow the spread of infestations. However, mountain pine beetle dispersal ecology is complicated by requirement for attack *en masse* and a pheromone based communication system that facilitates this congregation process. One interesting possibility is that infestations might spread more slowly over habitat gaps across which beetles cannot communicate. To investigate this possibility, I develop an individually-based model of mountain pine beetle dispersal, aggregation and attack, and conduct a series of simulation experiments to explore the effects of habitat patch size, patch compaction (habitat density), communication distance, and flight behaviour on the spread rate and final extent of infestations.

In the base experiment I find that decreasing patch compaction does slow infestation spread irrespective of patch size, though not as much as expected. When I remove the tendency of beetles to fly for some period before becoming receptive to pheromones (free flight), patch size becomes important and spread rate only varies with habitat density when patch size is small. At face value, the prediction arising from this is that beetles will be somewhat sensitive to forest fragmentation at small scales, but insensitive to variation in patch size because of their free flight behaviour. However, parameter values and the adequacy of model form are uncertain so these ideas require further evaluation. Two more robust conclusions are that apparently minor changes to dispersal behaviour can significantly alter beetle response to landscape pattern, and that despite 100 years of research on this system many aspects of mountain pine beetle dispersal ecology remain unknown.

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1 INTRODUCTION

1.1 MANAGEMENT CONTEXT AND MOTIVATION

A current mountain pine beetle outbreak in the central interior region of British Columbia has spread over approximately 1.2 million hectares of forest since it began 8 to 10 years ago (R & S Rogers Consulting Inc. 2001). In one in a series of actions aimed at slowing this outbreak, the Government of British Columbia has increased the rate of logging by 25% (5.4 million cubic metres) in the 9.1 million hectare region of the province (R & S Rogers Consulting Inc. 2001). Despite logging the beetle infestation continues to spread, raising questions about mountain pine beetles.

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is an aggressive bark beetle native to much of the lodgepole pine (*Pinus contorta* subsp. *latifolia* (Engelmann) Crichtfield) forest of western North America (below 56^o North latitude). In most places throughout this range mountain pine beetles have a 1-year life cycle (for overviews of mountain pine beetle biology see Amman 1978; Amman et al. 1984; Safranyik 1989; Samman and Logan 2000). They attack live or recently dead pine trees in late summer, boring under the bark to construct egg galleries in the phloem. Emergent larvae feed on the inner bark through the fall and spring, before emerging as adults in July or August to find new host trees. Fungi, bacteria and yeast carried by the beetles attack the living tissue of trees, and, if infection is successful, eventually kill them. Pines resist attack by secreting resin into the path of the beetle, which physically impedes progress, interferes with pheromone signals, seals the living cells from infection by fungus, and drowns eggs and larvae. Thus, beetles must attack in groups large enough to exhaust the resin pool and kill all or part of the tree in order to ensure brood survival and attack success. When beetle populations are low, they persist by attacking old and damaged trees with low resin reserves. However, if beetle populations increase beyond some critical threshold they can overwhelm the defenses of more vigorous trees. Since vigorous trees provide more food that allows better reproductive success, beetle populations that have risen enough to kill these trees may continue to increase rapidly, or outbreak. Once populations have risen to outbreak levels, they typically remain high until the supply of suitable hosts is exhausted, or cold winter reduces populations to below critical outbreak numbers (Amman 1978; Samman and Logan 2000). For the purposes of this discussion an outbreak of beetles within a small area or single forest stand is referred to as an infestation, while the term outbreak is generally reserved for larger landscape scale phenomena.

Models of the population dynamics of mountain pine beetles and other insects (Berryman 1978; Clark et al. 1979; Thompson et al. 1981; Raffa and Berryman 1986; Mawby 1989; Safranyik et al. 1999) and more general understanding of system dynamics (Ludwig et al. 1997) predict that outbreaks should be much easier to prevent than to control. A long history of failed or dubiously successful control efforts (Wood et al. 1985; Amman and Logan 1998) is consistent with the theory, prompting calls for more “proactive” management (Amman and Safranyik 1984; Amman and Logan1998; Samman and Logan 2000). However, proactive management is more easily preached than successfully achieved. Social, political and institutional inertia can prevent even universally beneficial actions from being taken. In this case, there are also real ecological concerns with some approaches to proactive management.

Strategies for reducing the risk of outbreaks before they occur include: beetle trapping; cutting, burning, or chemical treatment of brood trees in small infestation centres; thinning or “beetle proofing” forest stands to reduce their susceptibility to beetle infestation; and logging of forest stands at susceptibility to or high risk of infestation (Amman et al. 1984; Amman and Safranyik 1984; Maclauchlan and Brooks 1994; Natural

Resources Canada 2001). This last strategy is common because removed timber can be valuable.

The susceptibility of forest stands to mountain pine beetle infestation depends on local climate, species composition, stand density, and tree age (Shore and Safranyik 1992), as well as various aspects of tree condition. Lodgepole pine trees become susceptible to attack when the phloem becomes thick enough to support large beetle broods, typically at about 15 centimetres diameter or 60 to 80 years of age. As trees get older resin production declines and they become less resistant to attack, so old forest stands are most susceptible. Old forests also tend to have high biodiversity, wildlife, recreation and other non-timber values, and herein lies the conflict. A bid to reduce beetle risk by logging susceptible stands amounts to a systematic elimination of old forest from the landscape. To many, a landscape without old forest is unacceptable. A landscape-scale mountain pine beetle epidemic like the current one in central British Columbia is also undesirable from a number of perspectives, so some strategy to reduce overall landscape susceptibility to large outbreaks while retaining old forest would be ideal.

Some promise for such a strategy lies in the consideration of landscape pattern and spatial heterogeneity. Research in the fields of landscape and disturbance ecology, epidemiology, and population ecology has shown that population dynamics can depend not only on the amount of available habitat, but also on the spatial arrangement of that habitat. For instance, increasing the complexity or heterogeneity of landscapes at some scales may decrease the rate of spread and extent of diseases and disturbances (Turner et al. 1989; Rodriguez and Torres-Sorando 2001), decrease the survival and reproductive rates of some organisms (Simberloff 1988; Cantrell and Cosner 1991; Saunders et al. 1991; Andren 1994; Bender et al. 1998; Heibeler 2000), and globally stabilize locally unstable population dynamics (Hastings 1977; May 1978; Reeve 1988; Taylor 1990). In forests, the juxtaposition of stands of different age classes can reduce overall landscape flammability (Franklin and Forman 1987; Turner and Romme 1994; Turner et al. 1999), and isolated forest patches are less likely to be infested by the western spruce budworm (*Choristoneura occidentalis*) (Bergeron et al. 1995).

These general results give some reason to believe that landscape pattern could affect beetle population dynamics, and in particular that increased heterogeneity at some scale might slow the spread of infestations, decrease the magnitude of outbreaks, and stabilize overall population dynamics. Despite this promise, the effect of the spatial arrangement of habitat on the spread of mountain pine beetle infestations is unknown (Bentz et al. 1993). There is also reason for skepticism. The effect of landscape pattern depends on complex interactions between landscape and the habitat preferences and dispersal ecology of individual species (Saunders et al. 1991; Andren 1994; Coulson et al. 1999), and increasing heterogeneity can even promote insect outbreaks in some cases (Franklin and Forman 1987; Kareiva 1987). Given such variability, results from other systems can only guide the development of hypotheses. The only way to find out how pattern affects mountain pine beetles is to study mountain pine beetles.

Before launching wholeheartedly into a quest for beetle management by forest landscape manipulation, it is worth pausing here for a cautionary moment. Just as targeted harvesting may result in a reduction of old forest, unfettered beetle landscape management might result in systematic fragmentation of forest landscapes. From an ecological perspective, this is troubling. First, fragmentation could harm species that humans want to conserve (Saunders et al. 1991; Andren 1994; Bender et al. 1998; Poiani et al. 2000). Second, because species response to pattern is unique, patterns that slow beetles might disrupt or destabilize other forest processes in ways we cannot predict (Franklin and Forman 1987; Kaufmann and Regan 1995; Irwin 1999). Even if fragmentation will slow beetles, and even if we do not care about negative impacts on rare or threatened species, changing landscape pattern might destabilize other forest species and processes unexpectedly, causing more severe outbreaks of other insects or other unexpected and undesirable effects. Thus, it seems prudent to be wary of actions that increase forest fragmentation even if these actions seem likely to slow mountain pine beetles.

What role then for landscape level beetle management? Restoration is one interesting possibility. Forest structures and disturbance regimes in many parts of North America have been altered since European settlement by a variety of causes, including disruption of burning by aboriginal peoples, extensive fires during early European settlement, more recent fire suppression, logging, and climate change (Whelan 1995). Opinions differ about whether beetle outbreaks historically spread over areas as large as recent outbreaks, but one possibility is that recent changes to forest structure have altered mountain pine beetle population dynamics, and are in part responsible for recent outbreaks (Gara et al. 1984; Geiszler et al. 1980a; Rogers et al. 1996; Goyer 1998; McCullough et al. 1998). Restoration of historic forest conditions has been promoted to maintain ecological and aesthetic values, and reduce fire risk (Landres et al. 1999; Whelan 1995). If it turns out that historic forest structures also confer greater resistance to mountain pine beetle outbreaks, then some possibility for a happy resolution of timber and other values exists.

Unfortunately, there is also the possibility that landscapes most resistant to mountain pine beetle may be neither “natural” nor good for all other species. In this case, conflict between beetle and other management objectives will remain. It might be that better understanding of the effect of pattern on beetles would increase the pressure to further fragment forest landscapes. However, potential costs of landscape level beetle management must be weighed against the realized costs of current management. In British Columbia targeted harvesting of old forest is common in non-outbreak periods. During outbreaks, the rate of clearcutting is increased and requirements for planning, consideration of public input, and environmental protection are relaxed (Hughes and Drever 2000). Compared to this status quo, an opportunity for a more carefully considered and balanced approach seems attractive. So, with caveats in place, I proceed.

1.2 OBJECTIVES

Understanding how landscape structure may or may not affect the spread of mountain pine beetle infestations will require experimentation on real landscapes, or minimally, examination of the relationships between past spread patterns and underlying forest structure. However, in this study I do neither. Instead, I look at the effect of landscape pattern on the behaviour of a spatially explicit model of mountain pine beetle dispersal, aggregation, and attack.

Modeling studies range in purpose from conceptually provocative to predictive, and this study lies towards the speculative end of the scale. There are not enough available data or understanding to predict how beetles might spread on a particular landscape in a particular year. Rather, my purposes are more general: to motivate interest in the subject, clarify hypotheses, identify knowledge gaps, and gain insight into the mechanisms of infestation spread and the conditions under which pattern effects may or may not occur. More particularly, I am interested in how unique features of mountain pine beetle dispersal ecology might alter their response to landscape pattern. From a management point of view, this should clarify whether the general promise of heterogeneity might apply to beetles, and at what scale. Ecologically, the hope is for some insight into the robustness of generic expectations.

1.3 EXPECTATIONS

1.3.1 Effect of Pattern in General

Before considering how landscape pattern might affect beetles in particular, it is worth a brief review of the effects of pattern in general. First, note that my concern is with a very narrow range of effects arising from variation in the spatial arrangement of habitat. Changing forest pattern can significantly affect radiation fluxes, wind patterns, water fluxes, predator abundance, and other aspects of the ecosystem that might in turn affect mountain pine beetles (Saunders 1991). While these effects are no doubt important, here I consider only the direct effects of patch size and remoteness on the ability of mountain pine beetles to successfully spread from one habitat patch to another.

The effect of habitat connectivity on the spread of agents has been of particular concern in the fields of epidemiology (May and Anderson 1984; Rodriguez and

Torres-Sorando 2001; Bolker 1999), metapopulation biology (Taylor 1990) and disturbance ecology (Turner et al. 1989). Classical epidemiology has focussed on understanding models of simple epidemics with removal (SIR – Susceptible/Infective/Removed) (see Capasso 1993 for overview). In these models, disease is transmitted from infective to susceptible population members, which then become infective. After some period, infective individuals either die, or recover and become resistant to the disease. These models have been used to describe the progress of diseases such as measles for which permanent immunity is developed after infection, or plant diseases that kill their host. Like these diseases, mountain pine beetles also kill their hosts as they spread, so results from this class of models may give some insight into mountain pine beetle epidemiology.

A recent study by Bolker (1999) examined the effect of host spatial heterogeneity, or patchiness, on the spread of an SIR type disease through plant populations. He used analytic and stochastic simulation models to demonstrate that increasing spatial autocorrelation in host distributions can increase both the rate of spread and the final size of epidemics, while even spacing of host plants may decrease rate of disease spread. This result is consistent with previous theoretical work in epidemiology, and the effect has also been observed in several experimental studies (Bolker 1999).

A central result in metapopulation theory is that dissecting populations can allow regional stability of locally unstable predator-prey interactions by limiting the extent of local oscillations or outbreaks (Taylor 1990). Upon first consideration, this may seem in conflict with the epidemiological work, which suggests that increasing patchiness should most often increase the spread rate of outbreaks. This apparent conflict may be resolved by recognizing that the two groups use different reference conditions. The epidemiologists assume that average initial transmission rate, or the initial ratio of hosts to non-hosts, is constant, so their finding is that epidemics spread faster when hosts are aggregated than when hosts are dispersed randomly *over the same geographical area*. In contrast, metapopulation biologists are concerned with increasing the isolation of or distance between host patches, so they hold patch size constant and increase the distance between hosts or effectively, the geographic area across which hosts are dispersed. Thus, the disagreement appears to be due to different interpretations of what increasing “patchiness” might mean. Metapopulation biologists find that increasing the distance between patches will tend to slow the spread of organisms, given constant patch size. If area is constant, then increasing patch size or the clumpiness of habitat also increases the distance between patches, but epidemiologists seem to find that the benefit of increasing the distance between patches is outweighed by the cost of larger patch size, so more clumping increases the spread of outbreaks.

Both the epidemiological models and the metapopulation models discussed so far assume that all patches are close enough together that dispersal may occur between them.

However, this is not always the case. In the other extreme, classic percolation models assume that spread or infection can only happen between nearest neighbors, so the total extent of an outbreak or disturbance is absolutely constrained by the size of habitat patches (Turner et al. 1989). An interesting result from these latter models is that the effect of increasing habitat abundance on total patch size or infestation extent is not linear, but varies with the amount of habitat already present. At intermediate habitat abundance, landscapes reach a critical threshold, where small increases in habitat can dramatically increase disturbance extent by linking large patches. Percolation models also emphasize that the effect of increased patchiness should depend on the relative abundance of habitat - if habitat is so common that it tends to form large contiguous patches when distributed randomly, then increased clumping may decrease average patch size and outbreak extent, even though this aggregation may increase spread rate within patches. In contrast, if habitat is sparse then increased clumping may increase the overall extent of outbreaks. Empirical studies of birds and mammals support the general conclusion that pattern effects depend on the relative abundance of habitat (Andren 1994).

In most situations, the dispersal reality is probably somewhere between two extremes. No organisms can traverse infinite distances, but most can travel some distance through inhospitable habitat. Thus, the “functional connectivity” of habitat is usually something less than infinite, and something more than the physical connectivity of habitat patches (Tischendorf and Fahrig 2000). Keitt et al. (1997) have highlighted that clusters of habitat patches separated by less than dispersal distance may be linked into effective super-patches or percolation clusters by dispersal. Results from percolation theory should apply to these clusters, suggesting that changes to pattern which decrease average cluster size should decrease the average size of outbreaks. Within clusters, increasing clumpiness might increase the spread rate of outbreaks as predicted by epidemiological models.

1.3.2 Consequences of Pheromone Mediated Congregation

As noted earlier, trees resist attack, and mountain pine beetles must attack in groups to be successful. To facilitate mass attack, beetles generally disperse together over a short period of two or three weeks in early summer, and use a system of at least five different pheromones (beetle produced volatile chemicals) and kairomones (host produced volatile chemicals) to attract others to areas where attack is insufficient, and later repel them from areas that are full (see Borden 1987 for review). Pheromone mediated congregation is an inherently spatial process, and it seems reasonable that this phenomenon might alter the effect of pattern on mountain pine beetles.

Discussions of functional connectivity often focus on dispersal ability as the limiting factor (Keitt et al. 1997; Tischendorf and Fahrig 2000). For organisms that can successfully colonize new habitat alone or in small numbers, this may be appropriate. However, mountain pine beetles must group together (or congregate) if they are to successfully overcome host defences. If congregation is required for success then it seems that landscapes across which organisms cannot effectively congregate should be functionally fragmented, whether or not individuals can successfully disperse from patch to patch. Thus, my proposition is that, if congregation is important for success, functional connectivity should depend on the scale of pheromone communication, and fragmentation at the scale of pheromone communication should alter the rate and extent of infestation spread.

That the ability of species to detect habitat over some distance might alter the interaction between species and landscapes is not a new idea. In another modeling study, Fahrig and Paloheimo (1988a) found that the ability of organisms to detect new patches was a more important determinant of overall population size than the rate of dispersal or the overall distance across which these organisms could disperse. Essentially, if organisms can detect new patches then they are less likely to get lost and die during dispersal. Fahrig and Paloheimo (1988b) further point out that the effect of changing pattern varies with detection distance. If the average distance between patches is either much larger or much smaller than the detection distance, then changes in the spatial arrangement of patches do not matter much. However, changes in spatial arrangement that increase the distance between patches beyond the scale of detection distance can significantly affect dispersal success and overall population size. In essence, this is the same sort of critical threshold that percolation theory predicts for simple spread models. However, in this case detection ability, rather than dispersal ability, limits spread.

Fahrig and Paloheimo’s results are interesting, but perhaps not entirely applicable to mountain pine beetles. These beetles not only orient toward likely hosts over distance, but towards each other. For clarity, I follow Turchin (1998), and refer to the first behaviour as *aggregative* dispersal, and the second as *congregative*. Both behaviours are similar in that they can result in high density of organisms in quality habitat. However, my concern is whether more subtle differences between the two processes might lead to substantially different landscape pattern effects.

Other authors have also suggested that attraction between conspecifics might affect population and metapopulation dynamics, but these effects have not been well enough studied to yield any further insight (Smith and Peacock 1990). Turchin (1989) used an advection-diffusion model to explore the interaction between patch size and congregative movement, and found that congregation can alter the relationship between population and patch size, increasing population density in large patches. However, Turchin assumes that insects that leave a patch are immediately lost to the system, so insect density at patch boundaries is always zero. Since insects that are attracted to areas of high insect density will by definition avoid these lethal boundaries more often, it should be no surprise that these populations will reach higher densities than populations of insects that fail to avoid patch boundaries. However, this same avoidance effect might be expected from insects that are attracted to good habitat, so this work does not help clarify how the effects of congregation might differ from the effects of directed movement in general.

1.3.3 Consequences of Free Flight

The spatial aspect of mountain pine beetle population ecology has intrigued other authors, and a number of other spatially explicit beetle models have been built. Thus far, most of these authors have taken a continuum reaction-diffusion approach, where movement is approximated by a simple diffusion or advection-diffusion process, written as a partial differential equation (Polymenopoulos and Long 1990; Turchin and Theony 1993; Logan et al. 1998). The most complete and comprehensive of these efforts, and the one most directly applicable to my present pursuit is an effort by Powell, Logan, Bentz and others (referred to as the MPBpde) (Powell et al. 1996, White and Powell 1997, Logan et al. 1998, Powell et al. 1998, White and Powell 1998, Biesinger et al. 2000). While I have not chosen the same approach, it is on this model that much of my thought and conceptual framework is based. I pause here to acknowledge this overall intellectual debt, which arises in particulars throughout much of the remainder of this document, and on which the following discussion is largely based.

The diffusion approach to movement modeling arises from the result that simple diffusion equations can approximate the aggregate dynamics of randomly moving particles, or, in biological terms, random-walkers (Turchin 1998). While the classic application is to an uncorrelated random walk, diffusion and advection-diffusion equations can also be derived to approximate more complicated movement behaviours, including correlated random walks and various forms of taxis, or directed movement (Patlak 1953; Turchin 1998; Grunbaum 1999).

The diffusion approach has several significant advantages, including generality, flexibility, and analytical tractability (Okubo 1980; Turchin 1991, 1998). Thanks to a long history of use and analysis in several fields, the mathematics of these models is well understood. The relationship between individual movement behaviour and the average population flux described by generalized diffusion models is also well understood, so behavioural assumptions are clear and explicit. There are, however, also some problems. First, the range of movement behaviours that can be represented is limited. For example, many bark beetle species require some period of exercise, or “free flight”, before they become responsive to pheromones (Borden et al. 1986). Field studies of *Ips typographus* suggest that free flight periods may significantly alter dispersal patterns (Helland 1984; Helland 1989), and indirect evidence for the effect on mountain pine beetle dispersal is given by the fact that some beetles fly past nearby attractive sources (Safranyik et al. 1989), and that infestations tend to spread before all the hosts within an infested area are depleted (Mitchell and Preisler 1991; Borden 1993; Shore, T., personal communication). In diffusion approximations, individuals are considered in aggregate, without respect to the time since they emerged. Since mountain pine beetles do not emerge all at once, but continuously over the flight period, a diffusion approximation cannot capture the free flight behaviour.

That diffusion approximations are not biologically “correct” does not automatically render them useless. For example, another oddity of all diffusion approximations is that signals propagate infinitely quickly, or, in biological terms, some proportion of organisms can move infinitely fast. Despite the obvious biological absurdity of this assumption, the consequences for many diffusion applications are often not severe. Equilibrium solutions are largely not affected, and in simple diffusion only such a small proportion of the population travels far that whether their linear speed is limited may be irrelevant. Thus, the relevant question is not whether diffusion approximations are right, but whether they are “good enough”. In other words, does adding more complexity fundamentally alter the results of interest?

The question of which approach is most appropriate for modeling mountain pine beetle dynamics is complicated by technical challenges. A major virtue of some simple diffusion models is that they are analytically tractable, and thus allow general understanding. However, nonlinearities in either the aspatial (reaction) or spatial (advection-diffusion) terms render these equations intractable (Turchin 1998). Chemotactic beetle models belong to this class of non-linear models, and thus must be approximated numerically. Unfortunately, this task is not trivial as approximation is confounded by the stiffness of the model (White and Powell 1998; Powell et al. 1998).

In general, stiffness occurs when rates of change vary by orders of magnitude over time, space, or between state variables. To understand stiffness in practical terms, consider the following description of beetle movement (Logan et al. 1998):

$$\frac{\partial P}{\partial t} = m\nabla^2 P - \nabla[uP\frac{A_o - A}{A_o + A/A_3}\nabla A]$$

P is beetle density, A is pheromone concentration, A_0 and A_3 determine the relationship between pheromone concentration and attractiveness for beetles, and μ and ν are coefficients that affect beetle speed. The rate of beetle population (P) redistribution is given by the flux due to random motion (the diffusion term $m\nabla^2 P$) and movement up pheromone gradients (the advection term $-\nabla[uP\nabla A(A_o - A)/(A_o + A/A_3)]$). Beetles move fastest when the coefficients μ or ν are large, when attractiveness at the place of origin (A) is low, and when pheromone gradients (∇A) are steep. μ and ν are constant throughout the simulation, but attractiveness is a dynamic quantity that varies with nesting beetle density over time and space. As beetles move faster, the time-step over which beetle movement must be simulated decreases (given a constant grid spacing or spatial discretization). Thus, very small time-steps are needed to solve this system accurately in places where beetles have congregated and pheromone gradients are steep. Unfortunately, smaller time-steps increase the amount of computation required to complete a simulation. Finding a numerical scheme that remains accurate and stable when attractiveness gradients are steep, and is also computationally efficient enough to be useful, is a formidable challenge. Researchers have tried several approaches to solving this problem with the MPBpde, with varying success (White and Powell 1998; Powell et al. 1998). In another attempt, Tatiana Marquez-Lago implemented a slightly modified MPBpde model using a first order Imex method (Ascher et al. 1995), but we found the result too cumbersome to be useful (unpublished).

In all the figuring about how best to address the problem of spatial stiffness in this model, an essential biological detail has perhaps received too little attention. That is, spatial stiffness arises from the fact that the net rate of beetle displacement becomes faster as pheromone gradients become steeper, and, as noted earlier, there is no limit to the speed beetles move. I wonder whether at least some of the stiffness displayed by this model is an artifact of the diffusion approximation, not a biological reality. Perhaps some of the numerical and technical challenges might be avoided with a more biologically accurate model.

The problem of infinite velocity in the diffusion approximation has been pointed out before, and alternatives have been proposed (see Holmes 1993 for summary). In particular, the telegraph equation (Goldstein 1951; Okubo 1980) may be a useful alternative with some of the same theoretical advantages as the diffusion equation (Holmes 1993). Niwa (1998) has successfully adapted the basic approach to describe the movement of fish schools in response to temperature gradients, suggesting that the telegraph approach may be flexible enough to model a variety of directed movement behaviours in addition to random walks. However, without the aid of previous work, deriving and implementing a speed limited model to describe mountain pine beetle movement is a task beyond the scope of this project.

Continuum reaction-diffusion models are just one among a range of options for modeling movement (Turchin 1998). At the other extreme, individual based models treat the movement of each organism independently. The individual based approach allows more flexible movement rules, and the implementation of these rules is largely intuitive. The drawbacks are that individual based models are more difficult to analyze and more difficult to communicate (Grimm et al. 1999). Even greater flexibility is not always a virtue because individual based models are often species specific, difficult to compare, and less conducive to general insight than diffusion models (Turchin 1998; Grimm 1999; Grimm et al. 1999). However, this complaint goes both ways. Results from diffusion models are general and elegant, but they may be missing crucial biological detail. Neither approach is perfect, and better understanding of the effect of complex behaviour on general results would be useful. Having been frustrated in my attempts at continuous modeling, I have taken an individual based approach for largely practical reasons. However, this choice also offers opportunity to explore the limits of simple assumptions. How do the complications of mountain pine beetle dispersal behaviour alter their response to landscape pattern? Do general predictions from simpler models hold?

Mountain pine beetle dispersal is complicated by a number of behaviours in addition to free flight. For example, in order to search out suitable hosts more efficiently, beetles tend to fly down or perpendicular to the prevailing wind until they detect a pheromone plume, which they then follow upwind to the source (Choudhury and Kennedy 1980; Byers 1988; Safranyik et al. 1989). Observations of beetles flying up above canopy and new infestation spots arising far from old ones suggest that mountain pine beetles have a long-distance, above-canopy dispersal mode that is qualitatively different from local, pheromone directed dispersal (Safranyik et al. 1989; Safranyik, L., personal communication). Mountain pine beetles are not strong fliers, and rising above the canopy might allow beetles to hitchhike on air currents to avoid local competition for resources. While these behaviours are interesting and potentially important, I ignore them here for practical reasons, and restrict myself to the more manageable task of investigating free flight as one example of the larger phenomena of complex dispersal behaviour.

2 METHODS

2.1 THE MODEL

Loosely, the annual cycle of the mountain pine beetle can be divided into two distinct parts: the flight period, which consists of several weeks in late summer when beetles emerge, disperse, and attack new hosts, and the rest of the year, when beetles feed, mate, and reproduce under the bark of host trees. I have extended the model over multiple years in order to integrate the effects of pattern over whole landscapes, and reduce the effects of local variability. However, since this study is concerned with dispersal and spatial dynamics, I focus largely on the flight phase. Here, I describe the model of mountain pine beetle dispersal within a single flight period, and later conclude with a brief description of how the model is extended over multiple years.

2.1.1 Conceptual Overview of the Flight Model

The MPBpde model developed by Logan, Powell, Bentz and others follows flying beetles, nesting beetles, number of beetle holes, tree resin capacity (a measure of tree vigour), pheromones and kairomones over a single dispersal period (Powell et al. 1996, White and Powell 1997, Logan et al. 1998, Powell et al. 1998, White and Powell 1998, Biesinger et al. 2000 – for simplicity, this group of citations will be referred to collectively as Powell et al. through the remainder of this document). To capitalize on the considerable effort that has gone into developing the MPBpde, I have used their conceptual approach, model formulations and parameter values where possible. However, I have altered several aspects to create a model better suited to my purpose. Throughout this description I note where I have deviated from the MPBpde, and explain my reasoning.

Since my interest is in the effect of spatial pattern on the spread of beetle infestations, and the influence of pheromone mediated communication on this interaction, at minimum the flight model must track the dynamics of flying beetles, nesting beetles, and pheromones over time and space. In this I follow the sprit of the MPBpde, but to accommodate free flight I treat flying beetles and nesting beetles individually, rather than collectively. Individual beetles can be either *waiting* to emerge, *flying* and unreceptive to chemical attractants (*uflying*), flying and receptive to chemical attractants (*rflying*), *nesting*, or *dead*.

The probability that a beetle will be flying at location (*i*,*j)* and time *t* is a function of the basic processes of emergence, death, landing, and movement, which in turn depend on the previous state of that beetle. Note that throughout this document probabilities will be denoted by the symbol Π to distinguish them from flying beetle populations, which are denoted by P:

$$\Pi\{flying_{i,j,t}\} = \text{if } waiting_{\mathrm{i,\,j,\,t\text{-}1}} \text{ then } ?\ (emergence)$$

$$\text{else if } flying_{i,j,t\text{-}1} \text{ then } (1\text{-}\Pi(landing,\ death, or\ movement\ to\ another\ location))$$

$$\text{else if } flying_{i+n,\,j+m,\,t-1} \text{ then } \Pi(movement to\ location(i,\,j)) \tag{1}$$

When flying beetles land they become nesting beetles, which then either die or survive to produce pheromones to attract or deter other flying beetles. Thus, the dynamics of nesting is simply a function of landing and death.

$$\Pi\{nesting_{i,j,t}\} = \text{if } flying_{i,j,t\text{-}1} \text{ then } ?\ (landing)$$

$$\text{else if } nesting_{i,j,t\text{-}1} \text{ then } (1 \text{ - } ?\ (death)) \tag{2}$$

The overall population of flying beetles (P) and nesting beetles (Q) at each location *(i,j)* and time *t* is

$$P_{i,j,t} = \sum flying_{i,j,t} \tag{3}$$

$$Q_{i,j,t} = \sum nesting_{i,j,t} \tag{4}$$

State variables in this model vary across space as well as time, so the value of variable P at location *(i,j)* and time *t* is $P_{i,j,t}$. For convenience, I have dropped the subscript notation on state variables, which are denoted by capital letters. All other parameters are aspatial constants unless otherwise noted.

Following Powell et al., the change in pheromone concentration (A) over space and time is the sum of production, diffusion, and decay (or loss through the canopy):

$$\frac{\partial A}{\partial t} = production - decay + diffusionin - diffusionout \tag{3}$$

I am concerned about whether and under what conditions congregative dispersal is functionally different from aggregative dispersal. To address this concern, I include some mechanism of aggregative dispersal for comparison. Conveniently, there is evidence for such a mechanism in mountain pine beetle ecology. Early emerging mountain pine beetles do not seem to attack randomly, but orient towards suitable hosts using chemical and visual cues (see Powell et al. 1996 for summary). Primary attraction has also been established for other scolytids, and a modeling study of *Ips typographus* suggests that this strategy may improve attack success and survival significantly (Gries et al. 1989). See “Kairomone production, diffusion, and decay” for more details. For now, it suffices that unattacked host trees emit kairomones (C) that diffuse like pheromones, and are also attractive to beetles. Kairomone concentration is given by:

$$\frac{\partial C}{\partial t} = production - decay + diffusionin - diffusionout \tag{4}$$

Mountain pine beetles communicate via several semiochemicals with different functionality, production, and decay rates (see Borden et al. 1987 for summary). Powell et al. have chosen to model the functionality of this chemical complex with a single pheromone, and I have done the same. In principle one could include as many volatiles as necessary, following the same conceptual approach as in Equation 4, with different production and decay functions for each chemical.

Apart from representing mountain pine beetles individually, my most fundamental divergence from the MPBpde approach is to model aspatial dynamics more implicitly, ignoring the dynamic response of trees to attack, and assuming success or kill rate depends only on the cumulative number of attacks over a flight period, the total capacity for beetles, and resistance of trees. Like Powell et al., I represent forest resistance with a static variable, R, that varies between 1 and 0, and determines the shape of the relationship between cumulative attacks and kill. A second forest variable is also included to represent carrying capacity (K) for beetles at each location (Beetle Capacity – K). This allows me to tie both landing rate and pheromone production to an easily interpretable quantity, and to ensure that areas do not continue to be attractive after they are “full”, or vice versa. Representing forest state with both a capacity for and a resistance to beetles also allows that some trees may be less resistant than others of the same size, and that those areas may act as refugia for beetles and foci for attack.

2.1.2 Mountain Pine Beetle Dispersal

Each individual beetle can be in one of five possible modes: *waiting* to emerge, flying and unreceptive to pheromones or kairomones (*uflying*), flying and receptive to pheromones and kairomones (*rflying*), *nesting* once they have landed, or *dead*. Each beetle also has a location, and if they do not land, flying beetles may remain in place or move from their current location to one of four neighboring locations. Thus, the state of a beetle is given by its mode and location, and one state transition per beetle may occur at each time-step (*t* to *t+1*). I write the probability of these transitions as:

$$\Pi\{k_{\mathrm{i,\,j}} : l_{\mathrm{i+n,\,j+m}}\} \tag{5}$$

where *k* and *l* can be any of the five dispersal modes, *i* and *j* are the row and column location of the beetle at time *t*, and *n* and *m* are integers between –1 and 1. All but eleven of these transition probabilities are zero. The remainder are defined as follows.

Beetle emergence rate varies with temperature and weather patterns that are beyond the scope of this modeling exercise (Safranyik et al. 1989). For simplicity, I follow Powell et al., and assume that beetles emerge at a uniform rate over the flight period. Thus, the probability of a waiting beetle emerging in any particular hour is given by the inverse of the total flight period, *T*.

$$\Pi\{waiting_{\mathrm{i,\,j}} : flying_{\mathrm{i,\,j}}\} = 1/T \tag{6}$$

The number of waiting beetles depends on the number of successful beetles at a location in the previous season. This dependence is explained more fully in the section on extending the model over multiple years. For simplicity, I ignore the possibility of beetles dying before emergence. Thus, the probability of waiting beetles remaining in the same state is:

$$? \{waiting_{i,j} : waiting_{i,j}\} = 1\text{-}1/T \tag{7}$$

For further simplicity, I assume that once a beetle has landed it does not return to flying. However, assessing nesting death is more problematic. In practice, the death rate of nesting beetles will depend on host resin response. However, since the dynamic response of trees to beetle attack is not considered explicitly, I cannot include mortality explicitly. Instead, I include all nesting death in my assessment of over-winter survival and success. Thus, the probability of nesting beetles becoming something else within a flight period is zero, and:

$$\Pi\{nesting_{i,j} : nesting_{i,j}\} = 1 \tag{8}$$

Since I do not explicitly consider nesting death, the number of nesting beetles (Q) is more accurately interpreted as the cumulative number of attempted attacks at each location.

To include the free flight mechanism, I follow Helland et al. (1984) and assume that mountain pine beetles are unreceptive to pheromones and kairomones upon emergence, and unreceptive beetles (*uflying*) become receptive (*rflying*) at some constant rate, r_f.

$$\Pi\{uflying_{i,j} : rflying_{i,j}\} = r_f \tag{9}$$

I assume that unreceptive beetles neither land nor respond to chemical cues.

Defining transition probabilities for flying beetles is more problematic since these beetles can undergo any of six transitions, and these transitions are mutually exclusive. To ensure that beetles do not both die and move, flying beetle transitions are assessed hierarchically. Thus, the transition probabilities that follow are conditional upon one another.

First, beetles either live or die. Following Powell et al., I assume a constant flying death rate, w_1, that does not vary with receptive status. Thus, the probability of death is simply:

$$\Pi\{\, flying_{\mathrm{i,j}} : dead_{\mathrm{i,j}} \} = w_1 \tag{10}$$

Provided that a beetle didn’t die, it then may land. Assessing this landing probability is one of the most conceptually difficult aspects of this modeling exercise, and I discuss the details and reasons for my approach in the following section. For now, it suffices that:

$$\Pi\{ rflying_{\mathrm{i,j}} : nesting_{\mathrm{i,j}} \} = landing\ rate_{\mathrm{i,j}} \tag{11}$$

If beetles neither die nor land they may move. As noted earlier, scolytids tend to fly down or across wind until they encounter a pheromone plume, and then follow the plumes upwind to their source (Choudhury and Kennedy 1980; Byers 1988; Safranyik et al. 1989). For simplicity I have not included wind in this model, so I cannot model this behaviour directly. However, Zollner and Lima (1999) have shown that straight or nearly straight search strategies are more efficient than purely random ones. To ensure that I do not underestimate the search efficiency of beetles too badly, I assume that unreceptive beetles follow a correlated random walk search pattern derived from the exponential distribution:

$$\Pi\{ uflying_{\mathrm{i,j}} : uflying_{\mathrm{i+m,j+n}} \} = \frac{e^{\frac{-(1-\cos(a_{i+m,j+n}))}{(1-\cos(a_m))}}}{\sum_{g=-1}^{1}\sum_{h=-1}^{1} e^{\frac{-(1-\cos(a_{i+g,j+h}))}{(1-\cos(a_m))}}} \tag{12}$$

$a_{i+m,j+n}$ is the angle between the last move and the potential move (proposed turning angle), and a_m is approximately the average turning angle when average turning angle is small (~<60 degrees) (see Figure 1 for sample curves). When average turning angle is large, a_m overestimates because the range of possible turning angles is finite.

If beetles are receptive and some gradient of attractive chemical is present then the probability of movement to each location depends on the relative attractiveness of that location:

$$\Pi\{rflying_{i,j}:rflying_{i+m,j+n}\}|\nabla A \; or \; \nabla C = \frac{Attractiveness_{i+m,j+n}}{\sum_{g=-1}^{1}\sum_{h=-1}^{1} Attractiveness_{i+g,j+h}} \tag{13}$$

Since it is in the interest of beetles not only to find good hosts but to find good hosts already attacked by other beetles, I assume that beetles only follow kairomone gradients until they encounter pheromone gradients. This assumption is supported by evidence that aggregative pheromone signals effectively overpower any tendency of mountain pine beetles to land preferentially on suitable host trees (Pureswaran and Borden 2002). First, each beetle checks for a local pheromone gradient. If a gradient is detected, then attractiveness of each location depends only on the local pheromone concentration:

$$Attractiveness_{i+m,j+n}|\nabla A = (A_{i+m,j+n} + \frac{a_r}{a_s - 1})^{a_l} \tag{14}$$

$A_{i+m,j+n}$ is the concentration of pheromones at location $i+m,j+n$, a_r is the minimum concentration of pheromones detectable by beetles, and a_s determines the relative preference of beetles for low pheromone over no pheromone areas. The attractiveness parameter, a_l, controls the sensitivity of mountain pine beetles to pheromone gradients. The attractiveness function is designed to make beetles more sensitive to differences in pheromone concentration when pheromone concentrations are low. Figures 2 and 3 show the effect of a_l and a_s on attractiveness and relative attractiveness, respectively.

If a pheromone gradient is not present, then I assume mountain pine beetle follow kairomone gradients in a similar manner. The attractiveness function in this case is:

$$Attractiveness_{i+m,\,j+n} | \nabla C,\, !\nabla A = (C_{i+m,j+n} + \frac{c_r}{c_s - 1})^{c_l} \tag{15}$$

Finally, if neither pheromones nor kairomones are available to give guidance, then receptive beetles behave like unreceptive beetles. In this case, the transition probabilities are:

$$\Pi\{rflying_{i,j} : rflying_{i+m,j+n}\} | !\nabla C,\, !\nabla A = \frac{e^{\frac{-(1-\cos(a_{i+m,j+n}))}{(1-\cos(a_m))}}}{\sum_{g=-1}^{1} \sum_{h=-1}^{1} e^{\frac{-(1-\cos(a_{i+g,j+h}))}{(1-\cos(a_m))}}} \tag{16}$$

2.1.3 Landing and Pheromone Production

Conceptually, the biggest challenge in this modeling exercise is to formulate an appropriate pheromone production and response model. As noted earlier, mountain pine beetles facilitate mass attack using a system of at least five semiochemicals that differ in the message they carry, the rates at which they are produced and decay, and the time at which they are produced. Modeling the mechanics of this system would require representation of pheromone production by individual beetles and pheromone diffusion at the scale of individual galleries and trees. Not only do we not have the detailed data to support such representation, we also could not investigate large-scale landscape dynamics with such a fine scale model. Thus, some abstraction of the pheromone communication system is required that adequately reproduces the large-scale behaviour of beetle populations without explicitly representing the small scale processes that give rise to that behaviour.

Before developing this abstraction, it is worthwhile to review what is known about mountain pine beetle pheromone ecology and its landscape scale consequences. To begin, Borden et al. (1987) have developed a conceptual model of the role of pheromones in attack dynamics based on a summary of the literature. In brief: Early in attack, females produce trans-verbenol, an attractive pheromone. Males attracted by this initial pheromone release *exo*-brevicomin and frontalin over a period of several days after landing on the host. Both of these latter pheromones are multi-functional, meaning they are attractive at low concentrations and repulsive at high concentrations. This multi-functionality may induce incoming beetles to space themselves at some distance, helping to avoid overcrowding while still promoting enough aggregation to overcome host resistance.

Later in the attack, females stop producing trans-verbenol while males stop producing exo-brevicomin but continue releasing frontalin. Verbenol, an antiaggregant, is produced by autoxidation of trans-verbenol and by microorganisms in association with female beetles. In this last phase, high levels of verbenone and frontalin deter beetles from approaching or landing at the attacked site. The clumped attack patterns and switching behaviour characteristic of mountain pine beetle could be explained by the differential decay rates of these two later pheromones. Since verbenone photoisomerizes rapidly on exposure to sunlight (Kostyk et al. 1993) and frontalin is more stable, frontalin is likely to diffuse further from the source tree. Beetles would continue to be attracted to those adjacent areas where verbenone was absent and frontalin was present in low (attractive) concentrations.

The net effect of this sequence is that areas become attractive early in attack, and unattractive at some point later. However, we do not know precisely how the transition from attractive to unattractive states relates to the state of the trees or beetle population at a location. Thus, a model of this system must remain in part speculative.

Powell et al. have chosen to model a single pheromone that is attractive at low concentrations and repulsive at high concentrations. One consequence of this approach is that the transition from attraction to repulsion occurs independent of both the resistance and the capacity for beetles at any location. Thus, areas with low capacity (or few trees) may never accumulate enough beetle attacks to become repulsive, while areas with high capacity may become repulsive before enough beetles aggregate to overcome host defences. I do not know for certain that the transition from attraction to repulsion is dependent on local forest conditions, but, upon consideration, it seems likely.

A more troubling consequence of Powell et al.'s formulation is that unattractive areas can create highly effective barriers to beetle spread. Since beetles will prefer to stay in areas where there are no trees than travel through a highly infested area in search of new hosts, they may become trapped in poor areas. Experimental evidence suggests that this may be a problem with the conceptual model rather than a problem faced by real beetles. Mountain pine beetles attack trees baited with verbenone (a repellent) and *exo*-brevicomin (at attractive concentrations) significantly less than trees baited with only *exo*-brevicomin, but do not attack verbenone-baited trees less than unbaited trees (Shore et al. 1992). Thus, it seems that while verbenone does act effectively to mask or neutralize attractive signals, it does not seem to actively deter beetles.

To guide the development of an alternative pheromone model, I assume that the aggregation system is optimally designed to facilitate mass attack while minimizing overcrowding, and that flying and nesting beetles each behave selfishly to maximize their own fitness. It is interesting to note that the interests of flying beetles and nesting beetles need not always align. Once host resistance has been overcome, it is in the interest of beetles already nesting to discourage further attack, and so minimize competition. Thus, nesting beetles should stop producing attractants at this point. However, flying beetles may gain by landing in places where host defences have been depleted, as long as competition with other beetles is not so intense that it offsets the advantage of avoiding host defences. Thus, flying beetles should keep aggregating and landing until the space (or capacity) for beetles is full, even though nesting beetles should stop actively producing an aggregation signal before this.

To avoid erecting pheromone barriers and deterring flying beetles from areas that are not yet full, I assume that the antiaggregative effects of verbenone and the multi-functional pheromones remain local within each cell. Thus, for flying beetles areas may cease to be attractive, but never become actively unattractive to dispersal. However, once a beetle has arrived in an area, antiaggregants may deter it from landing if beetle capacity is full. Thus, I treat the antiaggregative effects of pheromone implicitly by considering the relationship between space left and landing rate directly. In the absence of other nesting beetles, flying beetles prefer to land in areas with low resistance to attack, so base landing rate is given by:

$$r_{base} = r_b (1-R)^{r_2} \tag{17}$$

where R is a value between 0 and 1 that determines the relative resistance of trees to attack, and r_2 controls the selectivity or preference for low resistance over high resistance areas. In general, areas become more attractive as the number of nesting beetles increases, so landing rate also increases. Finally, landing rate peaks at some intermediate number of beetles, and declines to zero as the number of nesting beetles reaches capacity. In sum:

$$landing\,rate_{i,j} = [1-(\frac{Q}{K})^{r5}]*[r_{base} + (r_m - r_{base})(1-e^{-r_1 \frac{Q}{K}(1-R)^{r3}})] \tag{18}$$

r_m is the maximum possible landing rate. r_1 determines how fast landing rate increases with the number of nesting beetles, r_3 determines how the relative preference of flying beetles for low resistance areas persists as the number of nesting beetles increases, and r_5

determines the sensitivity of flying beetles to crowding (see Figures 4 and 5 for sample curves).

The long-range attractive effects of trans-verbenol and the two multi-functional pheromones are modeled with a single attractive pheromone, A. This pheromone diffuses across the landscape exactly like the multi-functional pheromone modeled by Powell et al., but its production and effect differ. Per beetle production rate is maximum (a_m) when nesting beetles are sparse, and decreases to zero as host capacity is reached:

$$pheromone\,production\,rate_{i,j} = \mathrm{Q} * a_m * (1 - \frac{1+e^{a_1 R^{a_6}(R^{a_3}-1)}}{1+e^{a_1 R^{a_6}(R^{a_3}-Q/K)}}) \tag{19}$$

The point at which pheromone production reaches one half of maximum increases with resistance, R, with the rate of increase determined by a_3. The parameter a_1 determines the steepness of production decline, and a_6 ensures that initial pheromone production is maximum unless host resistance is very nearly zero (see Figures 6 and 7 for sample curves).

I have supposed that there is a conflict between the interests of flying and nesting beetles, and that flying beetles should keep aggregating and landing until areas are full, while nesting beetles should stop actively producing aggregating pheromones as soon as host resistance is overcome. While the suppositions remain speculative, it is interesting to note that a conflict between the interests of flying and nesting beetles could account for the multi-functionality of frontalin and exo-brevicomin. In the interest of reducing competition, it makes sense that nesting beetles should put some resources toward producing an “antiaggregation” signal, rather than simply falling silent. However, following the argument above, flying beetles should interpret this signal as an indicator of a secure resource, and aggregate towards it until they are so near to the signaling beetle that the cost of competition equals the advantage of security. Finally, the rapid decay rate of verbenone (Kostyk et al. 1993) could explain why this pheromone functions only as an antiaggregant.

While it is encouraging that some aspects of pheromone ecology are consistent with my assumptions, in reality it may not be that the mountain pine beetle aggregation system is optimal. In particular, asserting that flying beetles aggregate and land until all the susceptible trees in an area have been fully attacked assumes that flying beetles can tell precisely when an area is full, and that beetles tend to kill all of the infested trees at a location before moving on. The reality is that spots do not spread evenly, but often skip, leaving susceptible trees unattacked (Mitchell and Preisler 1991; Borden 1993). It is not clear how to model this skipping behaviour while still avoiding pheromone traps using a simple biased random walk dispersal rule, suggesting once more that beetle dispersal is more complex than this model. One interesting possibility is that an alternate above canopy dispersal mode might give trapped beetles a way out. However, not enough is known about when or how often beetles rise above the canopy, how they travel once they have risen, or how they decide to come down (but see Safranyik et al. 1992). Since we have neither the data nor the understanding to support a more complex dispersal model at this time, I leave the challenge for future research, and continue.

2.1.4 Pheromone Diffusion and Decay

Following Powell et al. I represent pheromone dynamics using a simple diffusion model with a constant decay rate, δ_a.

$$\frac{\partial A}{\partial t} = b_a \nabla^2 A + pheromone\, production\, rate_{i,j} - d_a A \qquad (20)$$

2.1.5 Kairomone Production, Diffusion and Decay

There is some evidence of primary attraction in mountain pine beetle attack dynamics (Moeck and Simmons 1991; Pureswaran and Borden 2002). However, my interest is not in modeling primary attraction as it occurs, but in comparing the effect of movement towards suitable hosts and movement towards conspecifics, controlling for as many other factors as possible (see Section 1.3.2 for more thorough discussion). Thus, it is more important that primary and secondary attraction occur at the same intensity over the same spatial scales in this model than that they are biologically accurate. I refer to my primary attractant as a “kairomone”, but true kairomones (host volatiles) may not have the properties or dynamics I attribute to them here. I assume that beetles are most attracted by the volatiles of trees with low resistance, so that kairomone production declines with increasing resistance:

$$kairomone\,production\,rate_{i,j} = c_m(1-R) \tag{21}$$

Note that this formulation differs from the MPBpde, where kairomone production is proportional to the number of mountain pine beetle attack holes and the resistance of host trees (White and Powell 1998; Logan et al. 1998). Trees that have been killed by beetles cease to produce kairomones that make them attractive to other beetles. Finally, kairomone spread and decay is a simple dissipative diffusion process, so the rate of change in kairomone over time is given by:

$$\frac{\partial C}{\partial t} = b_c \nabla^2 C + c_m(1-R) - d_c C \tag{22}$$

2.1.6 Complete Model of Dispersal, Aggregation and Attack

In sum, at any point in time, *t*, throughout the flight period, mountain pine beetles may be in one of five modes. Possible mode transitions and their associated probabilities are summarized in Table 1. The population of flying beetles at each location is given by P, and the population of nesting beetles is given by Q.

$$P = \sum uflying_{i,j} + \sum rflying_{i,j} \tag{23}$$

$$Q = \sum nesting_{i,j} \tag{24}$$

At each time-step, *t* to *t+1*, flying beetles can also change locations, and transition probabilities between adjacent locations are given by:

$$\Pi\{uflying_{\mathrm{i,j}} : uflying_{\mathrm{i+m,j+n}}\} = \frac{e^{\frac{-(1-\cos(a_{i+m,j+n}))}{(1-\cos(a_m))}}}{\sum_{g=-1}^{1}\sum_{h=-1}^{1} e^{\frac{-(1-\cos(a_{i+g,j+h}))}{(1-\cos(a_m))}}} \tag{25}$$

$$\Pi\{rflying_{i,j} : rflying_{i+m,j+n}\} = if\ \nabla A\ then\ \frac{(A_{i+m,j+n} + \frac{a_r}{a_s - 1})^{a_l}}{\sum_{g=-1}^{1}\sum_{h=-1}^{1}(A_{i+g,j+h} + \frac{a_r}{a_s - 1})^{a_l}} \Pi\{rflying : rflying\}$$

$$else\ if\ \ \nabla C\ then\ \frac{(C_{i+m,j+n} + \frac{c_r}{c_s - 1})^{c_l}}{\sum_{g=-1}^{1}\sum_{h=-1}^{1}(C_{i+g,j+h} + \frac{c_r}{c_s - 1})^{c_l}} \Pi\{rflying : rflying\}$$

$$else\ \frac{e^{\frac{-(1-\cos(a_{i+m,j+n}))}{(1-\cos(a_m))}}}{\sum_{g=-1}^{1}\sum_{h=-1}^{1} e^{\frac{-(1-\cos(a_{i+g,j+h}))}{(1-\cos(a_m))}}} \Pi\{\mathrm{rflying} : \mathrm{rflying}\} \tag{26}$$

Finally, pheromones and kairomones arise, spread, and decay according to:

$$\frac{\partial A}{\partial t} = b_a \nabla^2 A + \mathrm{Q} * a_m * (1 - \frac{1 + e^{a_1 R^{a6} (R^{a3} - 1)}}{1 + e^{a_1 R^{a6} (R^{a3} - Q/K)}}) - d_a A \qquad (27)$$

$$\frac{\partial C}{\partial t} = b_c \nabla^2 C + c_m (1 - R) - d_c C \qquad (28)$$

See Table 2 for a summary of model processes and interactions between variables. See Figure 8 for a graphical summary of same.

2.1.7 Extending the Model Over Multiple Years

My primary interest is in the effect of landscape pattern on the spread of beetle infestations over several years. To extend the model, I consider the attack efficiency of beetles within cells. Provided trees that are at least somewhat resistant, beetle success, measured as per capita reproductive rate, should be low when the density of nesting beetles is low, and increase as the number of nesting beetles increases enough to overcome host defences. As the number of nesting beetles increases even further towards carrying capacity, I expect that per capita reproductive rate will eventually decrease as competition for host resources becomes limiting (Safranyik et al. 1999). Furthermore, the point at which host defences are overcome and survival reaches maximum should be the point at which pheromone production by nesting beetles declines. An equation with these properties is:

$$reproduction\ rate_{i,j} = r_w * \left(1 - \frac{(Q/K)^{s_5}}{s_4}\right) * \left(\frac{1 + e^{s_1 R^{s6} (R^{s3} - 1)}}{1 + e^{s_1 R^{s6} (R^{s3} - Q/K)}}\right) \tag{29}$$

where the parameters s_1, s_3, and s_6, control the relationship between reproductive rate and resistance in the same way that a_1, a_3, and a_6 control the relationship between pheromone production and resistance. Generally, the value of these parameters should be equal so that pheromone production decreases as success increases, and vice versa. r_w determines the maximum per capita reproductive rate in the absence of resistance or competition, s_4 determines the minimum reproductive rate that flying beetles will tolerate (or the reproductive rate at carrying capacity) and s_5 determines the rate at which reproductive success decreases due to crowding. If beetles do not tend to crowd each other so much that total reproduction declines then $s_4 = s_5 + 1$. It also seems reasonable that landing rate might decrease with reproductive rate due to crowding, in which case s_5 should be equal to r_5, the crowding parameter in Equation 18.

In passing, it is worth noting that there are a number of complications to mountain pine beetle survival and reproduction I have not addressed. First, the quality of host trees, the duration and severity of winter cold, competition and any other factor that stresses the population seems to disproportionately affect males and thus alter sex ratios (Amman and Cole 1983). Upon reflection, it seems that a higher proportion of females might compensate for higher mortality rates, so reducing the effect of density dependent competition on net reproduction, but it is not clear to me how exactly this might alter infestation spread over all.

Of potentially more direct concern is that average beetle size decreases with egg gallery density (competition), increases with phloem thickness, and increases also when winter temperature is low (Amman and Cole 1983; Safranyik 1976). Large females have higher reproductive potential, and, more importantly, large beetles of either sex may have a longer flight period and a longer free flight period (Borden et al. 1986; Safranyik 1976). At face value, the prediction might be that crowded beetles spread less far because they are in poor physical condition. This seems logical, but also unfortunate for beetles. I wonder if some behavioural mechanism like rising above the canopy might help beetles get away from crowded situations even with limited physiological resources. At any rate, it seems that density dependence in dispersal distance and free flight behaviour could alter infestation spread. This possibility deserves further attention.

Nesting beetles in year *n* give rise to Q*reproduction rate offspring in year $n+1$, which emerge at a constant rate over the flight period in the following year. Thus, $\gamma_{i,j,n+1}$, the emergence rate at each location in year *n*, is given by:

$$g_{i,j,n+1} = Q_n * reproduction\ rate_{i,j,n} \big/ p_f \qquad (30)$$

where p_f is the duration of the annual flight period in flight hours.

If trees have no resistance, then the proportion of trees killed at a location is equal to the proportion of trees attacked. Given the simplifying assumption that beetles fill trees to capacity before moving on, kill rate is given by Q/K. If trees have resistance, then kill rate will be less than Q/K, and I assume the decrease is equal to the ratio of realized reproduction rate to maximum reproduction rate. Realized reproduction rate is given by Equation 29, and maximum reproduction rate is the realized rate when R = 0. Dividing through, we get:

$$kill\ rate_{i,j} = \frac{Q}{K} * \frac{(1+e^{s_1 R^{s6}(R^{s3}-1)})}{(1+e^{s_1 R^{s6}(R^{a3}-Q/K)})} \tag{31}$$

As trees are killed, capacity declines by kill rate:

$$K_{n+1} = K_n\left(1-\frac{Q_n}{K_n} * \frac{(1+e^{s_1 R_n^{s6}(R_n^{s3}-1)})}{(1+e^{s_1 R_n^{s6}(R_n^{s3}-Q_n/K_n)})}\right) \tag{32}$$

However, assuming that surviving trees fully recover before the next flight period, and all trees within a stand have the same relative resistance, then resistance within the stand remains constant over the course of the outbreak:

$$R_{n+1} = R_n \tag{33}$$

See Figures 9, 10 and 11 for sample success and kill rate curves.

2.2 PARAMETERS AND IMPLEMENTATION

2.2.1 Base Model Parameterization

I have used the parameter values from the MPBpde work where possible. However, many of the parameters in my model do not have analogues in the MPBpde. Where available I have used estimates from other literature, and where not I have taken a calibration approach, relying on literature, common sense and arbitrary decree to guide my expectations about the appropriate behaviour of model subcomponents.

For the purposes of calibration and testing, I approached the model in 5 stages: forest composition, beetle flight behaviour in the absence of pheromones or kairomones, pheromone and kairomone production and diffusion, beetle response to volatiles, and beetle survival and reproduction. First, the forest at each location is characterized by a capacity for beetles, K, which is the number of beetles that can land before that location becomes unattractive to other beetles. The MPBpde contains no analogous parameter, and the capacity for beetles is an emergent property of that model, rather than an input. However, in a field study designed to parameterize the MPBpde, Biesinger et al. (2000) found that the average number of nesting beetles in colonized trees ranged from 567 to 1496 MPB tree^{-1}. Stands susceptible to mountain pine beetle attack typically range from between 750 to 1500 stems ha^{-1} (Shore and Safranyik 1992; Whitehead et al. 2001). Assuming average stand density of 1000 susceptible stems per hectare suggests an average beetle capacity, K_0, on the order of 1,000,000 MPB ha^{-1}.

Due to computational constraints I cannot model all beetles individually. Instead, I model “individual” groups of 1000 beetles that emerge and move together. Note that this may increase the efficiency of spread at the margins of the infestation, but as long as congregation of several groups of beetles is still required for success I do not expect the increase in spread rate to be excessive. To avoid confusion or misrepresentation I present all results and parameter values in thousands of MPB, or TMPB. Thus, the average carrying capacity is 1000 TMPB ha^{-1}.

Following Powell et al., I assume some variability in forest composition over space so that weak, low capacity areas can provide foci for attack. Thus, beetle capacity is uniformly distributed with a mean of 1000 TMPB ha^{-1}, a minimum of 500 TMPB ha^{-1}, and a maximum of 1500 TMPB ha^{-1}. I also assume that resistance varies normally across the landscape, with a mean of 0.5, and a standard deviation of 0.3.

Before adding the complications of chemotaxis, it is worthwhile to consider how beetles move in the absence of pheromone or kairomone cues. Together, the parameters K_o, R_o, w_1, r_f, a_m, r_b, r_2, and the beetle step rate Dt determine the distance traveled by beetles across a contiguously forested landscape in the absence of pheromones or kairomones. Following Biesinger et al. (2000), I use a constant death rate (w_1) of 0.01 fh^{-1} (beetles fly for only a few hours each day so following Powell et al. the base unit of time in this analysis is the flight-hour, fh - there are approximately 5 fh per day). The free flight duration of mountain pine beetles is not known, but related bark beetle species require an average of between 30 and 90 minutes flight exercise before becoming receptive to olfactory stimuli (Borden et al. 1986). Lacking better estimates, I assume that beetles become receptive to pheromones at a rate (r_f) of 0.65 fh^{-1}. Finally, I assume that beetles turn an average of angle, a_m, of 35^{o} at each step. This leaves the base landing and step rate parameters to be determined. Biesinger et al. (2000) assume that flying beetles follow a simple random walk movement pattern with a diffusivity of 1 ha fh^{-1}. However, since I have not taken a diffusion approach I cannot use this diffusivity estimate directly. Instead, I return to the study from which Biesinger et al. (2000) derived their movement parameter estimates, where Turchin and Theony (1993) found that 50 % of southern pine beetles disperse less than 0.69 km, and 99% disperse less than 3.29 km. A step rate (Dt) of

0.25 fh cell^{-1} (where each raster cell is 50 by 50 metres or 0.25 ha) and a maximum base landing rate (r_b) of 0.2 fh^{-1} gives an average travel distance of 0.64 km on contiguous habitat, and 1.3 km on a landscape without habitat (but note that the latter may be an underestimate due to edge effects – see Figure 12 for details). 90% of beetles travel less than 1.5 km on contiguous habitat (Figure 12).

Biesinger et al. (2000) estimate that pheromones are produced at a rate of 20 μg fh^{-1} TMPB^{-1}, diffuse at an average of b_a = 0.648 ha fh^{-1}, and decay at a an average rate of δ_a = 180 fh^{-1} in a stand of average openness with a wind speed of 0.6 m s^{-1}. I accept the base diffusivity and decay rate estimates as they are, and assume a maximum pheromone production rate, a_m, of 20 μg fh^{-1} TMPB^{-1}. Following Geiszler et al. (1980b), I assume that beetles are sensitive to concentration of pheromone greater than 3*10^{-3} ng m^{3}, or assuming that chemicals diffusing higher than 3 metres above the ground are lost to the system, a_r = 0.1 μg ha^{-1}. On a grid cell resolution of 0.25 ha, these spread parameters yield a radially symmetric pheromone plume with cross section shown in Figure 13. Note that true communication distance will always be one cell greater than measured communication distance or plume width, as beetles in cells adjacent to the plume can respond to pheromones in adjacent cells, even if there is no pheromones in the cell they currently occupy. The prediction that beetles can only communicate effectively over distances less than 50-100 metres is supported by experience with pheromone baited trapping, where baits should be set no more than ~75 metres apart to be most effective (Borden, J. personal communication). This implies that the scale at which pheromones interact with forest pattern is probably small (on the order of tens to hundreds of metres, rather than kilometres). I exclude kairomones from the base case, and examine their effects in a later sensitivity analysis.

Finally, I am left with the reproduction, pheromone production, and landing parameters to choose. First, I assume that pheromone production declines to zero as reproductive rate increases to maximum. Thus, the parameters that control the reproduction and pheromone production curves are equal ($a_1 = s_1$, $a_3 = s_3$, *and* $a_6 = s_6$). Similarly, I assume that landing rate declines with reproduction rate, so $r_5 = s_5$. Somewhat more arbitrarily, I assume that per area beetle production rate is maximum when beetles are at capacity (Q = K), which implies that $s_4 = s_5+1$. The ratio of emerging to attacking beetles must be at least greater than 1 for the population to increase, and in this case I select $r_w = 3$ for the base case. This leaves the production parameters s_1, s_3, s_5, s_6, and the landing parameters r_1 and r_3 to choose by some combination of presumption, calibration and sensitivity analysis.

The parameter s_1 determines the steepness with which success increases as Q increases. This will depend on the aggregation efficiency of beetles within stands. I have no clear *a priori* expectation for how this parameter might affect the success of beetles or the importance of aggregation, and no data to inform the decision. Thus, I arbitrarily assume a baseline value of 20, and explore the effect of alternative values with sensitivity analysis. Figure 10 shows the effect of this parameter on pheromone production and success rates.

Similarly, the parameter r_1 determines the steepness of the landing curve, or eagerness of flying beetles to land next to other beetles. Higher values will make beetles eager to land where other beetles have landed, regardless of the resistance of the trees there. If beetles are present in sufficient number to overcome the defences of resistant hosts, then this should increase overall success rate by increasing the efficiency of aggregation. However, if beetles are scarce then this may decrease average success rate by making beetles eager to land in high resistance areas where they may not succeed. In reality, the willingness of beetles to land will probably vary with the abundance of suitable hosts. In practice, I have chosen an arbitrary value of 20, and explore the consequences of this choice later. Figure 5 shows the effect of this parameter on landing rate.

The parameter s_6 determines the base reproductive rate when Q is very low. If resistance is zero, then reproductive rate should be maximum even when Q is very low. However, since my purpose is to investigate the situation where congregation is essential for survival, I assume that if resistance is greater than zero, then success or reproductive rate is essentially zero until enough beetles have aggregated to overcome host resistance ($s_6 = 0.001$). While this assumption ensures that congregation is important for success, the true biological situation is probably less absolute.

The parameter s_3 determines the relationship between R and the point where reproductive rate reaches half of maximum, and thus also affects the degree which congregation is important for success. Again, I choose this parameter to ensure that congregation is essential for success, and explore the consequence of this assumption through sensitivity analysis (Figure 10). Finally, I choose a value of 0.3 for the parameter that controls the persistence of mountain pine beetle preference for low resistance areas, r_3. Figure 5 shows the sensitivity of landing rate to this parameter.

In sum, the parameters s_1, s_3, s_6, r_1, r_2, r_3 and r_b determine relationship between Q, resistance, and success and the landing behaviour of beetles respectively. Since I have no data to inform my decisions about the value of these parameters, one of the main results of this study is an investigation of how assumptions about these parameters affect the influence of pattern on infestation spread. For baseline simulations, I have chosen values that seem likely to lead to the behaviour I wish to observe. That is, I have chosen values that make congregation essential for success. For a complete description of all parameters and their associated baseline values, see Table 3.

2.2.2 Numerical Methods and Model Implementation

The mixed reaction-diffusion and individual based modeling approach taken narrows the range of options for implementation available. Software well equipped to numerically solving partial differential equations is not well designed to represent individuals, and tools helpful for individual based modeling do not include more advanced mathematical capacities. To resolve this dilemma without excessive programming difficulty, I used an explicit first order forward-Euler method for solving the diffusion equations. This method is less accurate and has more restrictive stability conditions than other available options, but the advantage is that it can be implemented without the use of sparse-matrix solvers or other mathematical tools.

I implemented the model using SELES, a domain-specific declarative modeling language for spatio-temporal modeling (Fall and Fall 1999 a, b; Fall and Fall 2001 -- note that the language has been expanded to allow individuals since the original release. Contact A. Fall for most recent documentation). Reflective boundary conditions are assumed throughout.

2.2.3 Spatial Extent and Resolution

The problems of spatial and temporal stiffness in this model can be addressed by using a very fine spatial grid or a multi-grid approach, where areas of focus and attack are resolved at a finer grid spacing than the rest of the landscape (White and Powell 1996). Both of these methods are computationally demanding, and ultimately the problem of spatial stiffness is not so much resolved as endured in a compromise between computational demand, edge effects and aggregation error.

In order to assess the spatial grain required to resolve pheromone diffusion, I simulated the diffusion of pheromones from a single continuous source and measured the radius of their detectable pheromone plume given base parameter estimates. Given these values, pheromone plume extent ranges between 50 and 100 metres depending on the number of nesting beetles present at the source and the carrying capacity of source habitat. At the other end of the scale, Turchin and Theony’s (1993) finding that 50% of southern pine beetles disperse 0.69 km or less, and 90% disperse less than 3 km suggests that a landscape extent of at least several kilometers is required.

In a compromise between minimizing edge effects and minimizing computational demand, I chose a spatial extent of 5 km by 5 km, or 2500 ha, and grid cell resolution of 50 by 50 metres, or 0.25 ha cell^{-1}. Given that pheromones in the base case only spread from 50 to 100 metres a grid cell resolution of 50 metres is barely sufficient to resolve this spread at all. However, to increase to a finer landscape resolution I must either decrease spatial extent or accept an increase in the computational time required to run the model. My main purpose here is to investigate pattern effects at the scale of communication ability rather than dispersal ability, but decreasing the spatial extent of my model below the characteristic dispersal distance of beetles causes edge effect problems that are difficult to resolve. The second option – to increase spatial resolution while maintaining spatial extent – increases the computational demand of the model so much as to make the experimental simulation approach impractical. Thus, I compromise with a landscape that is just barely large enough resolved at a scale that is just barely fine enough. Running all simulations on a square landscape 5 by 5 km large, resolved at 0.25 ha cell^{-1}, gives a total of 10,000 cells per landscape.

2.2.4 Temporal Extent and Resolution

The problem of temporal stiffness arises largely because pheromones decay on much faster time-scales than beetles diffuse, land, or die. That pheromones decay at a rate of 180 fh^{-1} and spread at a rate of 0.648 ha fh^{-1} (Biesinger et al. 2000) suggests that pheromone dynamics must be resolved at time step of less than 1/180 fh. In contrast, beetles diffuse at a rate of 1 ha fh^{-1}, and land or die at a rate of less than 1 fh^{-1}, suggesting that a time-step of 1/4 fh is adequate to resolve beetle dynamics. To avoid the computational cost of resolving all model dynamics on the faster pheromone time-scale, White and Powell (1996) developed a time-scale splitting approach by recognizing that beetles dynamics evolve so slowly with respect to pheromones that they are essentially constant over the time-scale at which pheromones evolve. After splitting the beetle and pheromone time-scales, White and Powell (1996) solve the pheromone and kairomone equations analytically over the beetle time-step. I follow the spirit of this approach, but lacking the tools required for transformation to Fourier space, I solve the pheromone and kairomone equations using an explicit numerical method. After each beetle time-step I simulate pheromone dynamics until the chemical landscape is near enough to equilibrium that further simulation causes changes of less than 10^{-3} μg ha^{-1} in chemical concentration and then proceed directly to the next beetle time-step.

Following Logan et al. (1998) I assume a baseline flight period of eight days with five flight hours per day, giving a total annual flight period, p_f, of 40 flight hours. I ran each simulation for 25 years, or 1000 fh, which was long enough for beetles on contiguous habitat to successfully kill all susceptible trees. Beetle dynamics are resolved with a time-step of Dt = 0.25 fh. Pheromones and kairomones I solve on a time-step of Dt_a

= 1/500 fh, which is small enough that further decreases to the size of the time-step do not significantly alter the shape or extent of the pheromone plume.

2.2.5 Initial conditions

Since I am interested in the effect of pattern on the spread of a single infestation, I begin each run with 1,250,000 successful beetles in the centre of each landscape, giving an initial emergence rate of $1250 * r_w / p_f = 93.75$ TMPB fh^{-1} from the centre pixel.

2.3 EXPERIMENTAL DESIGN AND ANALYSIS

2.3.1 Pattern generation and experimental design

Binary landscapes were simulated using a spreading algorithm modified from a simple fire model (Fall 1998). Habitat patches are placed at random, subject to the constraint that new patches cannot start within old ones. Patch sizes are Weibull distributed, and the complexity of patch shape depends on the number of neighbours to which each cell spreads in each step. New patches do not spread over old ones, but spreading may continue until patches adjoin one another. Patches are initiated and spread sequentially until the proportion of habitat within the landscape reaches a predetermined level. The distributions of patch size and shape are each controlled by 2 parameters.

I further constrained the patterns by insisting that the first patch initiate in the centre of each landscape. Since initial beetles are always released from this central location, this is equivalent to requiring that infestations always arise within a habitat patch. This is a biologically reasonable constraint that controls for the initial distance to habitat, which might otherwise overwhelm the effect of pattern on beetle success.

Landscape fragmentation, or, for the purposes of this discussion, the average minimum distance between patches, is affected both by the size and shape of habitat patches, and the average density (or total amount) of habitat across the landscape. Increasing aggregation within patches (patch size) also increases the distance between patches, and the tradeoff between these two factors depends on overall habitat density (Andren 1994). To explore these interactions, I used a multi-factorial experimental design, with 4 levels of average patch size from small (0.39 ha) to large (14.2 ha), 4 levels of habitat density from 10 to 40 percent of the landscape at intervals of 10 percent, and 5 replicates of each resulting pattern type. Since I am interested in the effects of the spatial arrangement of habitat, rather than the quantity, I held total habitat supply constant, and varied the amount of area over which this habitat was distributed (see Figure 14 for a schematic diagram of the experimental design and examples of each pattern type). Pattern parameter values were chosen so that the range of fragmentation scales (measured here as average minimum distance between patches) spans the range of pheromone communication scales (<50 to >200 metres).

I ran the initial pattern and communication distance experiments on this full 4 by 4 factorial pattern array. However, all other sensitivity analyses were run on a reduced 2 by 4 pattern array, omitting the two intermediate patch sizes to reduce computation time and thus allow more comprehensive experimentation.

2.3.2 General Analysis Procedure

The output from each model run is a time series of area (which can also be interpreted as volume of timber) killed per year. Area killed ranges from 0 to 250 ha or 0 to 100%, since initial habitat supply is constant across all landscapes. Output curves are characteristically sinusoidal, as beetle outbreaks spread exponentially until populations are limited by accessible habitat supply. See Figure 15 for sample curves.

My basic analytical approach is to fit a non-linear regression to each output curve (kill vs. time), and then treat the estimated coefficients of each regression as multiple response variables that can be analyzed using standard regression techniques (Cook and Ware 1983). In the analysis of growth curves, it is somewhat more common to fit polynomials to non-linear data, as this ensures that the maximum amount of residual variation will be accounted for. The main drawback of this latter approach is that polynomial terms are difficult to interpret biologically. Since my main intent here is to understand biological effects, I have opted to fit less complicated models with fewer, more easily interpretable parameters.

To select a regression model, I fit 4 alternative 3 parameter sinusoidal curves (from Ratkowsky 1990) to each of the base experiment runs and examined the distribution of residuals and fit (Figure 16). Of the 4 models, the Weibull-type curve had the lowest maximum residuals, lowest average variance, and the best looking fit. Note that the rigorousness of selection of the “best” regression model is also not of great concern, as the models are used to describe curves, rather than to predict. If the fit is adequate then comparison of the curves should be consistent regardless of the model used (Potvin et al. 1990). Note also that residuals in all of the models are correlated because points in the time series are not independent. This violates regression assumptions, rendering significance tests meaningless and raising the possibility of bias in parameter estimates. However, in this case the violations are not of great concern because the significance of the regressions is not important, and any bias should be consistent across all curves.

The Weibull-type model has three parameters – a_w, g_w, and d_w. a_w can be easily interpreted as the asymptote or maximum value of the s-curve (Figure 17). g_w and d_w together determine the rate at which values increase to the maximum, but their meanings cannot be so easily teased apart. In general, increases in either g_w or d_w lead to increased slope (Figure 18). Finally, note that I do not analyze the estimated asymptote data (a_w), but instead consider the maximum area killed after 25 years (kill_f). Maximum kill is a better measure because curves that are low but slowly increasing at the end of the simulation do not provide enough information for a meaningful estimate of asymptote.

The distributions of the slope parameters g_w and d_w allow a continuous statistical modeling approach. The maximum area killed, in contrast, is bimodally distributed, with beetles killing either all or very little of the available habitat within the 25 year period (Figure 19). In all runs, final infestation extent was either less than 15% (37.5 ha) or greater than 95% (237.5 ha) of initial habitat. To avoid violating regression assumptions I converted this area killed response to a binomial variable by classifying all cases as either "outbreak" (>= 95% of the available habitat is killed after 25 years) or "non-outbreak" (< 95% killed). No technique is available to treat both the binomial and the continuous response variables in the same experiment, so I tested the experimental effects on kill rate (g_w, d_w) and area killed separately.

I varied communication distance and other model parameters within each incidence of pattern, so the experiments have a repeated measure or split-block design. The two kill rate responses were analyzed using mixed models to avoid violating the restrictive circularity assumption of randomized block or split-plot ANOVA (von Ende 2001). Patch size and shape are between-subject factors, and all other experimental factors are repeated within pattern. Unstructured covariance matrices were assumed, and all response values were log transformed to equalize variance between groups.

Analyzing the binary outbreak data was somewhat more challenging. In general, levels of communication distance are not independent, since if beetles can outbreak when communication distance is short they are nearly certain to outbreak also at longer communication distances. However, lack of variation in response at some levels of communication distance prevented the estimation of more appropriate covariance matrices, leaving me in the ironic position of being unable to analyze the data properly because the experimental effects are too strong. Being unable to fit an appropriate repeated measures model, I pooled the three repeated measures into one response variable by counting the number of outbreaks that occurred on that pattern across all levels of the within subject factor. I then tested for effects of patch size and patch compaction on this overall chance of an outbreak by fitting a mixed model with a Poisson distribution and a log link function. Sampling zeros and lack of variation at some levels were corrected for by adding a small amount (0.001) to each outbreak count.

Post-hoc comparisons were challenging due to the large number of possible pair-wise comparisons (4560 in the base experiment with four levels of patch size, four levels of patch compaction, three levels of communication distance, and two response variables). To navigate through this bewildering abundance, I tried two approaches. First, I examined marginal variation in each factor by looking at pairs that differed only in a single factor. I also looked at comparisons between each group mean and the maximum and minimum group means in the experiment to see which kill rates were significantly greater than “low” or significantly less than “high”. These two approaches did not yield greatly different insights, and since the latter is easier to summarize and present graphically, I present only these results. Note that although I only examined a subset, all pair-wise comparisons are adjusted for the full set of comparisons using the Tukey-Kramer method. In retrospect, comparisons could have been adjusted for the reduced set of comparisons that I actually considered. Given that a more conservative correction was used, some significant results may have been missed, but significant differences that have been reported are very likely to be true.

Data manipulations and non-linear regressions were done with S+ using the NLREGB function (Insightful Corp. 2001). Continuous mixed models were fit using the

MIXED procedure in SAS, and multinomial mixed models were fit using the GENMOD procedure (SAS Institute Inc. 2000).

3 EXPERIMENTS AND RESULTS

Following from the introduction there are three main areas of interest:

1) What is the effect of patch size and patch aggregation on infestation spread rate and extent, and how does pheromone communication distance alter these effects? Is beetle success directly constrained by pheromone connectivity, and can beetles aggregate efficiently only over gaps across which they can communicate?

2) Under what conditions are pheromones a) important for success, and b) functionally different from kairomones?

3) How does the tendency of beetles to fly for some period before becoming responsive to pheromones alter the results from part 1?

Each of these questions is addressed with a separate experiment, and it is least confusing to communicate the design, analysis and results of each together, rather than dividing methods and results into separate sections that leave each experiment disjointed.

3.1.1 Clarifying hypotheses

My underlying hypothesis about the effect of pattern is that beetles are constrained by pheromone connectivity, which is in turn influenced by the pattern of the forest mosaic. That is, infestations should spread efficiently between patches connected by pheromone communication distance, and slowly or not at all across gaps larger than communication distance.

To measure how landscapes are connected by pheromones, the approach of Keitt et al. (1997) would be to join patches less than pheromone distance from one another into connected clusters. I follow this general approach, but since beetles spread from the centre in all landscapes, the measure of connectivity I use is size of the centre cluster (Figure 20). The reasoning is that if beetle spread is strictly limited by whether or not beetles can communicate across gaps then the final extent of the infestation should be equal to the centre cluster size in each landscape.

The simple way to test whether centre cluster size determines the extent of beetle infestations is to examine the relationship between these two variables. However, regressions between kill extent and centre cluster size can only indicate whether centre cluster size predicts kill, not how the effect of pattern on kill differs from the effect of pattern on centre cluster size. Since the latter is my greater concern, it is most informative to use centre cluster size indirectly to guide expectations about the effect of pattern, rather than to test relationships with kill extent directly. To do this, I calculated centre cluster size for each pattern, and analyzed the results using mixed models similar to the analysis of growth rate (g_w and d_w) data. This analysis also gives some indication of whether the sample sizes and pattern ranges are sufficiently large; if the effect of patch size, patch compaction, and communication distance on centre cluster size is significant, there is some comfort that the experiment is sufficient to detect the response we expect if that response occurs.

In general, the effect of increasing any of patch compaction (p), patch size (w), and communication distance or buffer width (d) while holding the others constant is to either increase centre cluster size or leave it unchanged. Interactions between variables significantly alter the amount of increase ($ccs \sim d*w*p$, n=320, $p<0.0001$ – Note: throughout the remainder of this document, the notation “response ~ factor1*factor2” followed by a sample size (n) and a p-value indicates that these two factors significantly interact in their effect on the response variable. Sample sizes are for both within and between-subject factors, but remember that all factors except p and w are within-subject so the number of independent samples is less than n. The three possible response variables are abbreviated as: *ccs* = centre cluster size, *kr* = kill rate, and *op* = outbreak probability, and a significant effect of *rpt* indicates that the two kill rate parameters (g_w,d_w) differ in their response to the experimental factors. Parameter and factor abbreviations are defined elsewhere). When patch size is small (w0) and communication distance is large (*d* = 200 m), the distance between patches is less than 200 metres, so the landscape is connected (centre cluster size ~100%) regardless of patch compaction level (Figure 21, w0, *d* = 200 m). Increasing patch compaction decreases the distance between patches enough to move the landscape from almost completely unconnected to completely connected when communication distance is intermediate (Figure 21, w0, *d* = 50 m/100 m). When communication distance is zero, the effect of patch compaction is insufficient to connect the landscape (Figure 21, w0, *d* = 0 m).

When patch size is small the transition from connected to unconnected occurs over a relatively small range of patch compaction (10-20%), demonstrating the threshold-type behaviour characteristic of percolation networks (Figure 21, w0). As patch size becomes larger (w10-w50), the distance between patches becomes both larger and more variable. As this happens, differences between communication distance levels tend to diminish (Figure 21). The effect of patch compaction also becomes more continuous, and threshold effect disappears.

3.2 EXPERIMENT I – BASE CASE

3.2.1 Question

What is the effect of patch size and patch aggregation on infestation spread rate and extent, and how does pheromone communication distance alter these effects? Is beetle success directly constrained by pheromone connectivity, and can beetles aggregate efficiently only over gaps across which they can communicate?

3.2.2 Approach

Pheromone communication distance can be altered by adjusting one of two parameters in the model. All else being equal, decreasing pheromone diffusivity (b_a), and increasing decay rate (d_a) both decrease the extent of a pheromone plume. Diffusivity has a relatively small effect on plume extent, so I consider only the effect of changing decay rate. To see how the effect of pattern varies with communication distance I vary pheromone decay rate across three levels. d50 is 0-50 metres, d100 is 50-100 metres, and d200 is 100-200 metres (Figure 22).

3.2.3 Expectations

Both outbreak frequency and kill rate (g_w, d_w) should increase with increasing patch compaction, communication distance, or patch size. Since the overall prediction is that centre cluster size should determine kill rate and infestation extent, interactions between variables should occur as in Figure 21.

3.2.4 Results

The effect of patch compaction is significant (*kr* ~ *p*, n = 240, p=0.003), and kill rate generally increases with patch compaction as expected (Figure 23). The interaction between communication distance and the two response variables (g_w, d_w) is also significant (*kr* ~ *d*rpt*, n = 240, p<0.0001). Increasing communication distance from 50 to 100 metres consistently increases kill rate as expected. However, increasing communication distance from 100 to 200 metres only appears to increase kill rate when patch compaction is low (Figure 23). When patch compaction is high kill rate tends to decrease as communication distance increases from 100 to 200 metres. This apparent interaction between patch compaction and communication distance is not quite significant (*kr* ~ *d*p*rpt*, n = 240, p=0.0701), but that the trend is consistent over all patch sizes suggests that it may be real. Kill rate appears to increase slightly with patch size, especially when communication distance is small (d50), but this effect is also not quite significant (*kr* ~ *w*, n = 240, p=0.077).

As noted earlier, in all runs final infestation extent was either less than 15% of habitat, or more than 95%. Since 92% of patterns have centre cluster sizes somewhere between these two extremes, it is clear that infestation extent is not directly constrained by centre cluster size. In general, trends in outbreak probability mirror trends in kill rate, except that kill rate may vary between cases where outbreak probability is uniformly 100% (Figure 23). However, relationships between outbreak frequency and the experimental factors are not significant (Figure 24).

For reference, information from each experiment, including experimental design, sample size, significant test results, noteworthy trends and comments are summarized in Table 4.

3.3 EXPERIMENT II – THE UNIQUENESS OF PHEROMONES

3.3.1 Question

Under what conditions are a) pheromones important for success, and b) functionally different from kairomones?

3.3.2 Approach

To test whether and under what conditions pheromones are important for success and functionally different from kairomones I compare the effect of patch compaction and patch size (w0,w50 only) on beetles with pheromones (*pher*), kairomones (*kai*) or no volatiles (*nv*) in the case where a) mass attack is important for success and b) mass attack is not important for success. To facilitate comparison, I chose kairomone production, spread, decay, and attractiveness parameters so that the kairomone and pheromone plumes are similar shapes and sizes, and produce a similar response from beetles (Figure 25). Communication distance was high (d200) to ensure that beetles with pheromones would be successful. Success is measured as kill rate and/or outbreak probability.

3.3.3 Expectations

If aggregation is required for success then success with pheromones (*pher*) should be higher than success with no pheromones (*nv or kai*). If aggregation is not required for success, then there are three possibilities:

If success with pheromones is equal to success with no volatiles then:

1) volatiles are only important when aggregation is required for success.

Otherwise, if success with pheromones is equal to success with kairomones, but not success with no volatiles then:

2) volatiles are important for success always, but if aggregation is not required for success then pheromones and kairomones are functionally equivalent.

Finally, if success with pheromones is not equal to success with either kairomones or no volatiles, then:

3) pheromones and kairomones are not functionally equivalent even when aggregation is not required for success.

3.3.4 Results

As predicted, beetles using pheromones have higher kill rates (d_w) and higher outbreak probabilities when mass attack is required for success (Figure 26). When mass attack is not required for success kill rate and outbreak probability are uniformly high, though beetles using pheromones appear to spread slightly slower than beetles using kairomones or no volatiles at all (Figure 26). Note that the effects of attack requirement (*atr*) and communication system (*vty*) also vary significantly with response variable, patch compaction, and patch size (*kr ~ atr*vty*p*w*rpt*, n=240, p=0.014). However the effects of patch size and patch compaction, while statistically significant, are difficult to interpret and uncompelling graphically (Figure 26).

3.4 EXPERIMENT III – THE EFFECT OF FREE FLIGHT

3.4.1 Question

How does the tendency of beetles to fly for some time before becoming responsive to pheromones alter the results from Experiment I?

3.4.2 Approach

Repeat the Experiment I with no free flight period (r_f=4) and a reduced pattern set (w0 and w50 only).

3.4.3 Expectations

Without free flight, centre cluster size might be more likely to constrain infestation size because beetles are less likely to fly towards areas without attractants as they do in free flight. Overall, I expect that free flight should be advantageous to beetles.

3.4.4 Results

Removing free flight alters both the qualitative and quantitative behaviour of this model. The effect of free flight on kill rate varies with response variable (g_w or d_w) and communication distance ($kr \sim r_f * d * rpt$, n=240, p<0.0001), with response variable (g_w or d_w) and patch compaction ($kr \sim r_f * p * rpt$, n=240, p=0.0486), and with communication distance and patch size ($kr \sim r_f * d * w$, n=240, p=0.0053) (Figure 27). Removing free flight also increases the frequency of outbreaks overall ($op \sim r_f * rpt$, n=20, p<0.0001) (Figure

28). Essentially, removing free flight eliminates all experimental effects by increasing spread rate and outbreak frequency when communication distance is small , and decreasing spread when communication distance is intermediate and patch compaction is high (Figure 27).

3.5 EXPERIMENT III EXTENSION – SENSITIVITY WITHOUT FREE FLIGHT

3.5.1 Question

Overall, kill rate in the absence of free flight is very high (Experiment III). I am curious whether the patch compaction, communication distance or patch size might have an effect if overall success rate was not so high.

3.5.2 Approach

Decreasing winter reproductive rate (r_w) should decrease the chance of an outbreak and the overall success of beetles. Varying other model parameters no doubt also decreases overall success, but for this abbreviated analysis I chose only $\mathrm{r_w}$. To test the effect of decreased overall success on the relationship between success and patch compaction in the case with no free flight I repeated Experiment III with a lower reproductive rate (r_w=3).

3.5.3 Expectations

When overall success rate is decreased so that kill rate is not uniformly high, kill rate and outbreak frequency should depend on patch compaction, communication distance, and patch size.

3.5.4 Results

Decreasing winter reproductive rate (r_w) significantly alters the relationship between kill rate and patch compaction, and this effect varies significantly with patch size ($kr \sim r_w * w * p$, n=240, p<0.0124). Decreasing r_w also alters the relationship between kill rate, communication distance, patch size and response variable (g_w and d_w) ($kr \sim r_w * d * w * rpt$, n=240, p<0.0002). Decreasing reproductive rate also decreased the frequency of outbreaks overall ($op \sim r_w * rpt$, n=20, p<0.0001). Essentially, when both reproductive rate and patch size are small, kill rate and outbreak probability increase with both patch size and patch compaction as expected (Figure 29 and 30). Increasing patch size largely eliminates these effects.

4 DISCUSSION

4.1 SUMMARY OF RESULTS

In the base case (with free flight) kill rate increased with communication distance and patch compaction. Patch size had no significant effect in the base case. Curiously, it appears that beetles with intermediate communication distance (d100) spread slower than beetles with high communication distance (d200) when patch compaction is low as expected, but when patch compaction was high the reverse became true. However, this interaction, though consistent across patch size, is not statistically significant. Experimentation with volatile types showed that pheromones are essential for success and functionally different from kairomones when mass attack was required for success (Expt. II). When mass attack was not required success was high regardless of whether volatiles were present, and beetles using pheromones seemed to spread slightly slower.

Removing free flight caused effects that were both strong and somewhat surprising. First, removing free flight caused beetles to do substantially better when communication distance was low, contrary to expectations (Expt. III). Beetles without free flight were sensitive to patch compaction and communication distance as expected (Expt. III extension). Though beetles with free flight were also sensitive to patch compaction and communication distance, the trends in that case were less clear and consistent (Expt. I). In the absence of free flight increasing patch size increased kill rate and eliminated the effect of patch compaction and communication distance, while in the base case (with free flight) patch size had no significant effect.

See Table 4 for more complete summary of experimental results.

4.2 MODEL VERIFICATION AND VALIDATION

Before considering what the results of this study might indicate about mountain pine beetles it is worth first pausing to consider whether model behaviour is reasonable. Do the observed outcomes reflect some real aspect of mountain pine beetle ecology, or are they simply artifacts of a poor model? I have not undertaken any formal model validation in this study, but I do have some clear expectations about model behaviour. Conformation of results to these expectations should give some comfort that model behaviour is not unreasonable. Conversely, clearly unreasonable behaviours should cast doubt on the model and the meaningfulness of other results.

First, the striking result from Experiment III is that, at low levels of communication distance, beetles with a free flight period have lower kill rates and less probability of outbreak than beetles without a free flight period. Note first that kill rate is not a perfect measure of beetle success, since at high mountain pine beetle densities individual success (measured as per capita reproductive rate) may decrease while kill rate continues to increase (Figure 9). However, that beetles with free flight die tend to die out completely (final infestation extent < 40 ha) while beetles with free flight spread over the whole landscape suggests that the disadvantage of free flight is real. Mechanistically, this effect probably occurs because free flying beetles disperse beyond the range of pheromone cues and get lost, making aggregation less efficient. In general, there is no guarantee that biology is optimum, and biologists are well advised to be wary of claims that behaviour should be advantageous just because it is done (Gould and Lewontin 1979). However, while it is possible that free flight is an evolutionary accident or constraint rather than an adaptive trait, in this case it seems unlikely. First, many different beetle taxa exhibit delayed sensitivity to olfactory stimulus (free flight), but within each of these taxa there tends to be wide variation between individual beetles (Borden et al. 1986). If free flight were as maladaptive in reality as it is in this model, it seems that strong selective pressure should work quickly to favour the beetles with shorter free flight periods, given that these beetles already exist. Thus, it seems prudent to assume that in reality free flight is advantageous under at least some circumstances, and to doubt a model that predicts otherwise.

Noting that free flight is neutral or slightly advantageous (not significant) when communication distance is large or when communication distance is intermediate and patch compaction is high (Figure 27), I suspect the modeled flight period is too long, and that a shorter flight period might allow beetles to avoid over-dispersal while still avoiding over-crowding. Another possibility is that free flight may be advantageous under forest landscape or population conditions not studied here, and that the advantages of free flight under those circumstances balance the observed cost. For example, free flight could be useful for escaping predators or discovering scarce resources during periods of scarce resource availability. Finally, it may be that beetles' flight behaviour is more complex, including some other mechanisms to avoid over-dispersion not included in this study. It would be interesting to investigate these possibilities to better understand whether the tradeoff between over-dispersion and over-aggregation in free flight is real, and if so, how beetles might resolve this tradeoff. In the meantime, the unexpected free-flight consequence casts some doubt on other results.

There are several other aspects of model behaviour that are not realistic. First, infestation spread rates are too slow; real infestations can spread over a 250 ha area within four or five years, in contrast to the nine or ten years predicted by this model (Figure 15) (Safranyik, L., personal communication). I suspect this is because the conditions for successful attack are more stringent in my model than in the real world. Real beetles probably also fly further more often than beetles in this model, especially under crowded conditions or when suitable habitat is scarce (Figure 12) (Safranyik, L., personal communication). Whether or not longer distance dispersal would substantially alter the effect of small scale pattern probably depends on whether beetles that travel long distances concentrate at some locations (as could be the case in some locations if persistent downdrafts prompt beetles to land), or whether they diffuse more broadly across the landscape. It is not known how effectively long distance travelers congregate, or how much this phenomenon alters small-scale landscape dynamics, but in any case lack of long distance dispersal remains a significant difference between the real world and this model.

Another notable difference between the behaviour of this model and that of real beetles is that beetles in the model frequently kill 100% of available habitat. Realistically, it is rare that 90% of susceptible hosts in a stand are killed, and mortality rates of 30 to 70% are more common (Safranyik, L., personal communication). Unrealistically high kill rates are a direct and unsurprising consequence of the oversimplified stand model I have used. A more realistic stand model might better predict the intensity of kill, but I do not expect that it should greatly alter the effect of landscape pattern.

Finally, lest we get too critical, the results of the kairomone experiment give some comfort that, while the model might not be entirely adequate, it has some reasonable attributes. When mass attack is required for success, mountain pine beetles dispersing at random by kairomone cues are not successful, while mountain pine beetles using pheromones fare much better (Figure 26). In contrast, when mass attack is not required for success, mountain pine beetles are successful regardless of their navigation system. It is a bit surprising that there is no difference at all between pheromone, kairomone, and undirected flight when mass attack is not required for success, as it seems that mountain pine beetles following pheromones or kairomones should still find scarce habitat more effectively. However, noting that infestation spread rates are very high, I wonder whether differences between the three dispersal systems become more significant if habitat is more scarce or reproductive rates are lower.

4.3 ON MOUNTAIN PINE BEETLE ECOLOGY

In the base case, with best guess parameters, I found that increasing patch compaction increased kill rate, but changing patch size had no significant effect. In contrast, when free flight was removed changing both patch size and the distance between patches could alter spread rates dramatically. Thus, at face value the prediction from the model is that landscape pattern at the scale and in the manner represented does not affect the spread of mountain pine beetle infestations as much as expected, in part because free flight reduces pattern sensitivity. There are several reasons, however, why this result might be suspect. First, as noted earlier, free flight has other apparently unreasonable consequences that give some reason to doubt the model, and it is probably wise not to put too much faith in pattern predictions until these doubts are resolved.

Apart from the adequacy of the free flight model, there are at least three other reasons why the small effect of pattern in the base case might not be entirely compelling. First, parameter values or initial conditions might be wrong, or rather, landscape pattern might have the expected effect given some other combination of parameter values and initial conditions. I have not formally addressed this concern here, and systematic sensitivity analysis could certainly make results more compelling.

Second, significant pattern effects in the base case might not be observed because sample size and statistical power are too low (Peterman 1990). Most notably, in the profile plots for the base case there appears to be an interaction between communication distance and patch compaction (Figure 23). When patch compaction is low beetles with intermediate communication distance spread slower than beetles with high communication distance. However, when patch compaction is high the situation reverses. This interaction is not statistically significant ($p = 0.0701$), but that the trend is consistent over all patch sizes suggests that it may be real. Kill rate also appears to increase slightly with patch (p=0.077), and increasing sample size might well make these more subtle effects significant. However, sample size was adequate to detect the effect of both patch size and patch compaction on centre cluster size, so while the failure to detect significant effects and interactions does not mean there are none, at least we can trust that the effect of landscape pattern is not as strong as expected.

Finally, pattern effects could be small because something essential has been left out of the model. At points throughout this text I have noted various omissions, and I will not repeat the list here. However, upon reflection one omission deserves further notice.

There is a great deal of evidence that thinning reduces forest susceptibility to attack (Cahill 1978; Cole et al. 1983; Mitchell et al. 1983; Waring and Pitman 1985; McGregor et al. 1987; Amman et al. 1988; Mitchell 1994). Tree mortality rate decreases immediately after thinning, suggesting that changing microclimate rather than changing host vigour is responsible for this effect (Amman and Logan 1998). High bark temperatures on the south sides of exposed trees can impede brood development, increased light intensity and wind speed can alter or disrupt beetle flight patterns, and increased temperature differentials and wind speeds in open forest stands can also disrupt pheromone plumes and pheromone communication (Amman and Logan 1998). In other words, reproductive rate, flight behaviour and pheromone decay and diffusion rates probably all vary with forest structure, and from this it seems a small step to suppose that the spatial arrangement of habitat might be important not because of some inherent effect of pattern *per se*, but due to the indirect effects of pattern on these other factors. In fact, thinning studies already provide some compelling evidence that this is probably so. However, studies so far have only focused on the effects of thinning, rather than a more broad range of cutting patterns and practices. The mechanisms by which thinning affects mortality also remain speculative, so more work remains to be done.

Others have pointed out that variable decay rates of pheromones may be essential in determining the risk of beetle mortality (Amman and Logan 1998; Powell et al. 2000), and it is not because I presumed these factors to be unimportant that I omitted them from the model. Rather, it seemed worthwhile to understand the workings of a simple model before adding complexity, even if indirect effects are most important. However, while this analysis may not have been without reason, it remains incomplete. Even if pattern does not affect beetles directly, it remains quite likely that indirect effects might occur.

In sum, pattern effects could be small in the base case because beetles are insensitive to pattern, because essential aspects of beetle ecology are missing from the model, because model form is wrong, because the wrong parameters were used, or because sample size is inadequate. The two latter possibilities cannot be ruled out, but seem unlikely to account for the unexpected result. More importantly, counterintuitive model behaviour does suggest problems with model form, and knowledge of pine beetle ecology suggests some key processes might be missing. Given this doubt, the robust result is not that beetles are insensitive to pattern, but that predictions about the spatial dynamics of infestation spread at small scales can depend strongly on relatively minor details of dispersal behaviour. In particular, it seems that free flight, which has thus far been omitted from beetle dispersal models, might be important. Thus, one lesson from this work is that free flight behaviour deserves more attention. The other is that small-scale pattern effects cannot be reliably predicted from current understanding.

Beetle free flight behaviour is one important area of uncertainty highlighted by this work. Throughout the process of model building and testing a number of other significant uncertainties also became clear. Having decided to force the aspatial model to behave “reasonably”, I was stuck specifying what reasonable behaviour might be. A good deal is known about the rate and sequence in which pheromones are produced by individual nesting beetles at the scale of single trees. However, the area-wide consequences of pheromone dynamics, and overall consequences of pheromone-mediated communication for mountain pine beetle success remain speculative.

Although based upon it, my modeling approach diverged from the MPBpde on several counts, in part because I doubt some of the assumptions on which the MPBpde is based. While the concerns seem reasonable, and I have constructed the most reasonable alternative model within my grasp, both the criticisms and the solutions remain speculative. Our differences in opinion highlight more areas of significant uncertainty regarding mountain pine beetle ecology.

First, since there is no link between the pheromone concentration at which an area becomes unattractive (A=Ao) and the point at which landing rate declines to zero (R=0), it seems that areas with very low resistance (and therefore low beetle capacity) might never become unattractive, while areas with high resistance might become unattractive before host resistance is overcome. I can imagine that some highly resistant trees might become unattractive before they are overcome, but it seems unlikely that weak trees ever become eternal sinks for real beetles. In contrast, my model assumes that beetles continue to attack trees in an area until all susceptible hosts are killed. This is also not realistic, so the link between resistance, capacity, and landing rate remains poorly understood.

My second concern was that a flying beetle in an area with no trees, ringed on all sides by areas full of nesting beetles (and high, unattractive pheromone concentrations), will tend to remain in place, even though there is nowhere for it to land. That verbenone seems to act more as a neutralizer than an antiaggregant lends support to the idea that whole areas do not become actively repellent to mountain pine beetles (Shore et al. 1992). It is also an interesting possibility that beetles might rise above the canopy to avoid overcrowding (Safranyik et al. 1989; Safranyik, L., personal communication).

Finally, the situation is complicated by observations that beetle size and condition (and hence dispersal ability) vary with beetle population density and host condition (Amman and Cole 1983; Safranyik 1976). It is not known how all these factors might interact, and it remains that the behaviour of beetles in crowded situations is not well understood.

In sum, on the basis of this work I cannot answer whether or how small scale pattern might affect the spread of mountain pine beetle infestations. Mainly, the work has helped clarify some outstanding questions and identify missing information that might be particularly important. The hope is that this may be useful in guiding future thinking and research about mountain pine beetle spatial ecology.

4.4 ON PREDICTIONS REGARDING THE EFFECT OF PATTERN

Apart from the general expectation that pattern should affect infestation spread, I began this work with two predictions based on a review of past theoretical work. First, percolation theory points out that if agents spread only between “connected” habitat patches, then the extent of spread will the limited by habitat connectivity. Proposing that only patches nearer to each other than communication distance will be “connected” if aggregation is important for success, I reasoned that infestation extent should be limited by pheromone connectivity. This was not the case in any of my experiments, which in retrospect is no great surprise. If the density of dispersing beetles is high then enough may reach the same susceptible habitat by chance, even if they are not drawn there by pheromones. Thus, it makes sense that infestations could spread across gaps larger than communication distance if mountain pine beetle density is high, and that infestation extent is not strictly limited by pheromone connectivity.

The second prediction from previous theory was that within habitat clusters, increasing habitat clumpiness or patch size should increase spread rate. The other effect of increasing patch size is to increase the distance between patches, which in turn will decrease the size of habitat clusters when patch compaction and communication distance are high (Figure 21). Thus, if infestation extent was limited by centre cluster size, the net effect of increasing patch size should be to increase infestation spread rate, decrease infestation extent when patch compaction and communication distance are high, and increase infestation extent otherwise. Since infestation extent is not limited by centre cluster size, the subtleties of this prediction are lost in practice. If anything, kill rate tends to increase with patch size, suggesting that any slowing of spread rate due to increased distance between patches is more than compensated for by larger patch sizes. In as far as it goes, this seems consistent with predictions from epidemiology that increasing the clumpiness of hosts should increase infection spread rates (Bolker 1999).

4.5 ON MOVEMENT MODELING

Whether or not actual beetles are pattern sensitive, it is interesting that a simple change in free flight behaviour changes organism response to pattern so significantly. Others have recognized that organisms often deviate from random walk or correlated random walk movement patterns (Okubo 1980; Levin 1992; Turchin 1998), but the consequences of deviation have not been systematically studied. Real-world successes with correlated random walks and related diffusion approximations indicate that these models are robust to some behavioural complexity, and more general than their simplicity suggests (Levin 1992; Turchin 1998). However, the strong effect of free flight here suggests that not all behavioural complexity is without consequence. It would be interesting to better understand the limits of diffusion and correlated random walk models, and the types of behaviour that render these models inadequate.

It is easy to state that more understanding would be nice, and much harder to get it. The array of possible dispersal behaviours is bewildering enough that I doubt whether testing arbitrary possibilities is a good use of time or effort. It is probably more productive to focus on understanding the behaviour of particular organisms in particular situations. However, studies of the dispersal of particular organisms do not automatically contribute to more general understanding. Thus far, general insight from individually based models has been hampered by lack of systematic reference to theory and lack of a common framework that would make it possible to meaningfully compare models (Turchin 1998; Grimm 1999; Grimm et al. 1999). In response, some authors have advocated a hierarchical approach, where understanding is sought by comparing the behaviour of simple models to those incrementally more complex (Turchin 1998; Grimm et al. 1999). This is the approach I have attempted, and I agree in general that it is useful. My only comment in passing is that many of the criticisms of individual based modeling (and spatio-temporal simulation in general), while valid, are also not easily addressed. It is true that many simulation efforts would benefit from more comprehensive experimentation and more systematic reference to the framework of classical theoretical ecology (Grimm 1999). However, those setting out with ambition to right the wrongs of spatial modeling should probably do so with a realistic view of the technical and computational challenges involved. For instance, in one memorable encounter, a friendly statistician suggested that if I just ran 1000 replicates of each simulation instead of five, I could circumvent many of my statistical challenges. He is correct, of course, but on a PC with 1 GHz of processing speed it would take approximately 1200 months of continuous computing to run these simulations. While I am sure that with effort and expertise this model could be further optimized to reduce processing time, the essential problem remains: spatial simulation is computationally demanding.

Apart from theoretical concerns and concerns over inadequate data, complex individual based models have been criticized because they are hard to develop, hard to communicate, and hard to understand (Grimm et al. 1999). Individual based models implemented with general purpose programming languages have been plagued by software bugs, awkward software design, and general incomprehensibility (Grimm et al. 1999). In response to these challenges, a number of software tools have been developed to help separate the details of model form from model implementation, and thus make implementation, verification and communication easier (Lorek and Sonnenschein 1998, 1999; Fall and Fall 2001). I did not try alternative methods for implementing this model, so I cannot systematically compare their relative merits in this case. However, the process of incremental component testing and experimentation was greatly aided by the modeling tool that I used, and some aspects of this experience are worth note.

In the gap between general purpose programming languages and system specific models are domain specific modeling languages that provide support for a particular class of model. SELES (spatially explicit landscape event simulator) is one of several such tools available to support landscape ecology models (Fall and Fall 1999 a, b; Fall and Fall 2001). Although initially designed to represent continuous spatial attributes and the processes or events that alter them, the SELES framework has recently been expanded to accommodate individuals (contact A. Fall for updated documentation).

There is a necessary tradeoff between the simplicity and flexibility of modeling tools, and SELES is no exception. However, while it is certainly not suitable for all applications, my experience is that the SELES framework can be remarkably flexible. Most notably, SELES allows discrete entities (mountain pine beetles) and continuous quantities (pheromones) to spread and change at different time-scales, while still interacting with one another, and more complex mixed-type models could also be accommodated. Solving partial differential equations with SELES is challenging, as the conceptual framework is not geared towards such applications. The capability for implicit and spectral methods is lacking entirely, but with a little creativity explicit finite difference schemes can be solved. Undoubtedly this is not the best tool for all modeling purposes, but I found the transparency, modularity, computational efficiency, and capacity for mixing model types without immense programming effort and expertise immensely useful in this case, and would encourage others to consider this option.

One of the strengths of the diffusion approach is that diffusion approximations can be derived directly from individual based movement models, making underlying assumptions about movement clear and explicit (Turchin 1991, 1998). Several types of tactic search behaviour have been modeled in this way, including area-restricted search strategies, in which animals turn more frequently or move more slowly in response to high levels of environmental attractant, and directionally tactic strategies, in which animals turn less frequently or move more rapidly in response to positive environmental gradients (see Grunbaum 1996 for summary). The former has been used to describe the response of foragers to changing prey density (Kareiva and Odell 1987; Dukas and Real 1993; Veit et al. 1993), while the latter were developed largely with bacterial and cellular chemotaxis in mind (Keller and Segel 1971; Segel 1978, 1982). Presumably mountain pine beetles respond to pheromone gradients, rather than concentration, but beyond this it is not known what search strategy these beetles use. Do they turn less abruptly when faced with attractive gradients, or less often, or do they speed up? Different search strategies have different consequences for success, and better mountain pine beetle models will require more information about beetle search behaviour. In individual based or random walk models assumptions about movement behaviour are explicit and difficult to ignore, but the assumptions underlying diffusion approximations are easier to miss. Thus, it seems worth emphasizing that diffusion approximations also embody particular assumptions about the behaviour of organisms, and that no matter which modeling approach is used some care should be given to understanding the suitability and consequences of these assumptions.

4.6 ON FUTURE RESEARCH – DIRECTIONS AND TRADEOFFS

Clearly, more research is necessary to understand the effect of pattern variation on infestation spread. So what research would be most useful? Loosely, there are two alternative approaches to the issue at hand. First, research can focus on better understanding the mechanisms of infestation spread, either by more detailed field studies of beetle dispersal behaviour and pheromone dynamics, or by more modeling work. The second alternative, which has received less attention through this discussion so far, is to study infestation spread directly through either experimental manipulation of landscapes or retrospective analysis of past infestations.

Regarding more basic mechanistic understanding, throughout this discussion I have noted a number of questions regarding mountain pine beetle ecology that must be answered before we can hope to predict the effect of pattern. Broadly, these questions can be subsumed under a declaration that in order to predict the spread of infestations we must better understand how flying beetles move, and what prompts them to attack. More particularly, free flight behaviour, movement decision hierarchies, and area-wide relationships between host carrying capacity, host resistance, nesting beetle abundance, pheromone production, and the movement and landing of flying beetles all require further study.

There is also more work that could be done with modeling. My exploration of the behaviour of this model is not complete, and it would be interesting to do more sensitivity analysis, to better understand the effect of free flight, and to explore the effect of landscape pattern on beetles with free flight behaviour that is not detrimental to overall beetle success. It would also be interesting to add wind and variable pheromone decay rates to explore the possibility that landscape pattern might affect infestation spread indirectly through these mechanisms.

Finally, the effect of pattern on infestation spread could be studied directly, either experimentally or through retrospective pattern analysis. Experimental analysis could be feasible for pattern effects on a small scale within forest stands, but might be prohibitively difficult and expensive at larger spatial scales. Historical sketch map data is generally too coarsely resolved and inaccurate to be useful for small scale pattern analysis. More promisingly, red mountain pine beetle attacked trees can be identified from Landsat satellite imagery at 30 m resolution with a relatively high degree of accuracy. Forest pattern can also be characterized from Landsat imagery so it should be possible to measure infestation spread and landscape pattern over time and space, and test for relationships between these variables. Recent and current outbreaks across British Columbia could provide ample opportunities for study (Hughes and Drever 2001). Discontinuous infestation spread, multiple infestation centres, spatially autocorrelated data, variation in climate, microclimate and topography, and uncertainty about which aspects of pattern to measure would make this a challenging endeavor. However, it seems at least promising.

All of these areas of research are interesting, and all of them could use further study and effort. However, rather than glibly conclude with a recommendation to study everything more, I would like to encourage some attention to the costs, benefits and tradeoffs between these different approaches. In particular, I suggest that enthusiasm for more comprehensive modeling should be tempered by a realistic assessment of the time and effort required. Just because modeling involves no field time does not mean it is effortlessly quick and easy, and in this case attempts to thoroughly explore the potential effects of uncertain factors and their interactions could easily be bogged down in an overwhelming morass of possibility. There may be benefits and insights to be gained from more modeling that are worth the effort, and we may not know what is worthwhile until we try. However, future research would benefit from careful consideration of the costs and benefits of alternative approaches.

4.7 ON MANAGEMENT

There is nothing in the results of my study to alter the initial management premise that small scale fragmentation might alter infestation spread. There is still reason to believe that forest pattern might affect the spread of beetle infestations, and it remains that management could benefit from further consideration of this possibility (Bentz et al. 1993; Hughes and Drever 2001). This point deserves emphasis, but is neither new nor surprising. So what more, if anything, can be learned that applies to management from my particular results?

Essentially, I began with predictions from simple spatial models, tried to replicate these results in a slightly more complicated model system, and was surprised by unexpected results. One lesson from this might be that simple models are not necessarily robust or generally correct. Certainly, this is true, and for those inclined to overstate the certainty or generality of theoretical results it might be worth emphasizing. However, in the case of mountain pine beetle management, I do not think the problem is that managers put too much stock in theoretical predictions about the effect of pattern. Rather, I would emphasize that failure to observe strong pattern effects in this case does not mean that pattern effects do not occur, nor that important lessons cannot be learned from simple models.

The main surprise in this exercise was that free flight changed model behaviour so significantly. I retreated to an individually based modeling approach for technical reasons, and included free flight as an afterthought. I did not set out thinking that free flight would be particularly important. In retrospect it is quite reasonable that free flight should significantly alter the effect of pattern. However, it still seems noteworthy that an apparently minor detail of mountain pine beetle behaviour has such dramatic consequences for overall model behaviour.

That one uncertain and apparently minor aspect of mountain pine beetle biology can substantially change the effect of pattern would not be so concerning if there were only a few such uncertainties to investigate. However, a second important point about this system is that much remains unknown. Since its first scientific description in 1902 (Hopkin 1902), mountain pine beetle has been one of the most studied insects in North America (Furniss 1997; Amman and Logan 1998). Many fascinating details of beetle pheromone ecology, dispersal behaviour and population ecology are known, but despite 100 years of research not enough is known to adequately parameterize or even dictate the form of this model. It might be that mountain pine beetle dispersal ecology is inherently complex, and understanding the spatial dynamics of other organisms would be easier. Certainly, this system is interesting in part because of its complexity. However, a more likely possibility is that we would find other organisms equally complex if we knew enough about them.

That life is complex and difficult to understand is certainly nothing new in ecology. Indeed, one could argue this is among the most robust, important and central results of a discipline sometimes overwhelmed by variety. Management theorists are also not strangers to complexity, and finding ways to accommodate both diversity and uncertainty has been a central focus of much recent thinking about resource management in general and forest management in particular (Walters and Holling 1990; Franklin 1994; Grumbine 1994; Holling and Meffe 1995; Christensen et al. 1996; Ludwig et al. 2001). While some effort has been made to broaden the scope of forest management (Forest Ecosystem Management Team 1993; Clayoquot Sound Scientific Panel 1994; British

Columbia Ministry of Forests 1995, 1999), more could certainly be done (Cashore et al. 2001; Page et al. 2002).

In this management context, mountain pine beetles are an interesting and important case. First, they are not merely an ecological curiousity but a direct and conspicuous agent of enormous ecological and economic impact, historically second only to fire, and arguably more important now (Rogers 1996; McCullough et al. 1998). Second, while the wisdom and long term consequences of fire suppression may be questioned, there is no doubt that we have been quite good, on average, at putting out fires (Whelan 1995). In contrast, the record for mountain pine beetle suppression is thus far poor (Klein 1978; Wood et al. 1985; Amman and Logan 1998). It may be that this failure is in part technical, and that if we were as aggressive with small beetle infestations as we are with small fires we could have the same measure of success with beetles (Borden, J., personal communication). It may also be that the effects of forest landscape pattern on infestation spread, if they exist, are too subtle and variable to be useful for management. However, whether or not understanding landscape pattern is the key to mountain pine beetle management, it seems noteworthy that, after 100 years and a huge amount of effort, there are still so many important things we don’t understand about the most economically important and abundantly studied insect in forestry. That ecological systems are complex and difficult to understand is nothing new, but until management actions adequately address this complexity it is a point worth emphasizing.

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6 APPENDICES

Table 1: Probabilities for transitions between five beetle modes. Each individual beetle can be either *waiting* to emerge, flying and unreceptive to pheromones or kairomones (*uflying*), flying and receptive to pheromones and kairomones (*rflying*), *nesting* once they have landed, or *dead*, and each beetle may undergo one mode transition per beetle time-step (Δt). *T* is the length of the annual flight period, ω_1 is the death rate of flying beetles and r_f is the rate at which unreceptive free flying beetles become receptive to pheromones. The landing rate of flying beetles at each location (*landing rate*$_{i,j}$) depends on the number of nesting beetles (Q), host capacity (K) and host resistance (R) at that location. See the model description in the Methods section for more detailed explanation.

		Beetle Mode at Time t+1				
		waiting	**uflying**	**rflying**	**nesting**	**dead**
Beetle Mode at Time t	**waiting**	1-1/T	1/T	0	0	0
	uflying	0	$1-r_f-(1-r_f)\omega_1$	r_f	0	$(1-r_f)\omega_1$
	rflying	0	0	$1-\omega_1 -(1-\omega_1)*$ landing rate$_{i,j}$	$(1-\omega_1)*$ landing rate$_{i,j}$	ω_1
	nesting	0	0	0	1	0
	dead	0	0	0	0	1

Table 2: Summary of model processes and relationships between state variables within the flight period. A process is anything that alters the value of a state variable. Arrows indicate material flow between states, where the same process affects the value of more than one variable.

State Variable Description	State Variable Name	Process	State variables on which the process depends
Beetles			
waiting to emerge	waiting	• emergence	• none
flying, unreceptive to pheromones	uflying	• emergence • death • spread • transition to receptive	• none • uflying • uflying • uflying
flying, receptive to pheromones	rflying	• transition to receptive • death • spread • landing	• uflying • rflying • rflying, A, C • rflying, Q, K, R
nesting	Q	• landing	• rflying, Q, K, R
Pheromones	A	• production • diffusion • decay	• Q, K, R • A • A
Kairomones	C	• production • diffusion • decay	• R • C • C
Forest			
capacity for beetles	K	• static within flight period	
resistance to beetles	R	• static within flight period	

Table 3: Model parameters and their associated base values. Where available, sources of parameter estimates are cited. Parameters for which no estimates are available were chosen either by calibration, reasoning, or (reasonable) arbitration. Values marked by (*) are subject to sensitivity analysis because they are uncertain, values marked by (**) are subject to sensitivity analysis because they are variable and important, and values marked by (***) are also uncertain or arbitrary, but are not subject to sensitivity analysis. See model description and parameterization sections for more complete explanation. Units are: $\mu g = 10^{-6}$ grams; ha = hectare; fh = flight-hour (~5fh/day); TMPB = thousands of mountain pine beetles.

Parameters	**Description**	**Base Value**	**Units**	**Source**
Flight (Figures 1-3)				
α_m	approximately average turning angle in the absence of pheromone or kairomone cues	35^o	degrees	arbitrary *
a_l	pheromone sensitivity parameter	1.3	..	arbitrary *
a_r	minimum detectable pheromone concentration	0.1	$\mu g\ ha^{-1}$	Geiszler et al. 1980
a_s	pheromone sensitivity parameter	4	..	arbitrary *
c_l	kairomone sensitivity parameter	l_a	..	reasoning
c_r	minimum detectable kairomone concentration	a_r	$\mu g\ ha^{-1}$	reasoning
c_s	kairomone sensitivity parameter	a_s	..	reasoning
r_f	free flight parameter	0.65	fh^{-1}	Borden et al. 1986**
Landing (Figures 4,5)				
r_m	maximum possible landing rate	0.8	fh^{-1}	arbitrary *
r_b	maximum pioneer landing rate (landing = r_b when R = 0 and Q = 0)	0.2	fh^{-1}	arbitrary *
r_1	controls the rate at which landing increases with Q	20	..	arbitrary *
r_2	controls the effect of R on pioneer landing rate	2	..	arbitrary *
r_3	determines the persistence of preference for low R areas as Q increases	0.3	..	arbitrary *
r_5	controls the rate at which landing decrease with crowding	4	..	arbitrary *

Table 3 continued:

Pheromone (Figures 6, 7, 13 and 22)				
a_m	maximum possible pheromone production rate	20	μg ha^{-1}	Biesinger et al. 2000
a_1	controls the rate at which pheromone production declines with Q	20	..	arbitrary *
a_3	determines the effect of R on the Q value at which pheromone production reaches half of maximum	0.3	..	arbitrary *
a_6	ensures that beetles that land in areas with no resistance (R = 0) do not produce pheromones, but beetles that land anywhere else produce pheromones at maximum rate until resistance is overcome.	0.001 (very small)	..	reasoning *
b_a	pheromone diffusivity	0.685	ha fh^{-1}	Biesinger et al. 2000
δ_a	pheromone decay rate	180	μg ha^{-1}	Biesinger et al. 2000
Kairomone (Figure 25)				
c_m	maximum kairomone production rate	a_m*1000	μg fh^{-1}	reasoning
b_c	kairomone diffusivity	b_a	ha fh^{-1}	reasoning
δ_c	kairomone decay rate	δ_a	μg ha^{-1}	reasoning
Survival (Figures 9,19 and 11)				
ω_1	flying beetle death rate	0.01	fh^{-1}	Biesinger et al. 2000
r_w	maximum per capita beetle reproduction rate ($Q_{waiting, n} / Q_{nesting, n-1}$)	3.5	year^{-1}	arbitrary*
s_1	controls the rate at which beetle success increases with Q	a_1	..	reasoning
s_3	determines the effect of R on the Q value at which beetle success reaches half of maximum	a_3	..	reasoning
s_4	determines the average reproductive rate at carrying capacity (Q = K)	$r_5 + 1$	..	reasoning
s_5	determines the rate at which reproductive success decreases to minimum as Q approaches K.	r_5	..	reasoning
s_6	ensures beetles landing in areas with no resistance reproduce at maximum, but beetles landing elsewhere are not successful unless resistance is overcome.	a_6	..	reasoning

Table 3 continued:

Landscape				
P_I	initial beetle population	1250	TMPB	arbitrary *
R_0	average initial resistance	0.5	..	arbitrary
R_{dev}	standard deviation of initial resistance	0.3	..	arbitrary *
K_0	average initial carrying capacity	1000	TMPB	Biesinger et al. 2000**
K_{dev}	maximum deviation of initial carrying capacity from average initial carrying capacity	500	TMPB	arbitrary
M	spatial extent	100	cells	reasoning ***
h	spatial resolution	0.25	ha $cell^{-1}$	reasoning ***
Time				
T	length of annual flight period	40	fh $year^{-1}$	Logan et al. 1998
Δt	beetle time step	¼	fh	calibration
Δt_a	pheromone time step	1/500	fh	reasoning

Table 4: Summary of experimental results. **Abbreviations**: Experimental factors are denoted by *w* (patch size), *p* (patch compaction), and *d* (communication distance). *kr* indicates overall kill rate response, *rpt* refers to response variable (g_w or d_w – if *rpt* is significant then g_w and d_w differ in their response to the experimental factors), and *op* is overall outbreak probability. In Experiment II, *atr* refers to requirement for mass attack – cooperation can either be required (*rq*), or not (*nrq*). Similarly, *vty* is volatile type, which can be either pheromones (*pher*), kairomones (*kai)*, or no volatiles (*nv*). Other parameters are as in Table 3. **n:** Two sample sizes given for each experiment are the number of model runs (between*within subject factors) and, in brackets, the number of landscape instances (between subject factors only). **Design:** All experiments have fully crossed factorial designs. For example, "*kr ~ d|w|p*" indicates that all independent effects (*d*, *w*, *p*) and all possible interactions (*d*w*, *d*p*, *w*p*, *d*w*p*) were tested for. **Test Results:** Only significant interactions are shown. Statistical ***p*** values are distinguished from patch compaction references by bolding and context. **Summary of Effects:** Only interesting trends are notes – for more complete picture of trends and interactions see appropriate figures. Up (↑), down (↓) or sideways (↔) arrows indicate positive, negative or neutral relationships, respectively, between the response variable (right side) and the experimental factor (left side). Notably strong and consistent effects are shown in bold (Ý). Effects that are conditional upon the value of other factors are qualified with the key word *given*, followed by a list of conditions. For qualitative variables, the keyword *when* followed by one or more conditions indicates that response in these conditions is higher (↑) or lower (↓) than in other possible conditions. See sections, figures and tables as indicated for more details.

Experiment	n	Design	Test Results	Summary of Effects	Notable Results
I base case Section 3.2, Figures 23 and 24	240 (80)	kr ~ d | w | p | rpt op ~ w | p	kr ~ d* rpt, ***p*** < 0.0001 kr~p, ***p*** = 0.0003 no op effects significant	kr Ý d kr ↑ p	• no effect of patch size (w) • effect of patch compaction (p) not as strong as expected.
II The uniqueness of pheromones Section 3.3, Figure 26	240 (40)	kr ~ atr| vty| w | p | rpt	kr ~ atr* vty* w*p*rpt, ***p*** = 0.014 no op tests because no variation in response.	g_w ↓ *when* nrq g_w ↑ p *given* pher (??) g_w ↓ p *given* rq, w0, kai (??) g_w ↓ p *given* nrq, kai or nv (??) d_w ↑ *when* nrq d_w ↑ *when* rq, pher op Ý *when* nrq op Ý *when* rq, pher	• pheromones are functionally unique when mass attack is required for success. • effects of patch size (w) and patch compaction (p) statistically significant but difficult to interpret.

Table 4 continued:

III the effect of free flight Section 3.4, Figures 27 and 28	240 (40)	kr ~ r_f | d | w | p | rpt op ~ r_f | w | p	kr ~ r_f* d* rpt, $\boldsymbol{p} < 0.0001$ kr ~ r_f * p* rpt, $\boldsymbol{p} = 0.0486$ kr ~ r_f * d* w, $\boldsymbol{p} = 0.0053$ op ~ r_f, $\boldsymbol{p} < 0.0001$	when r_f = base, effects are as in the experiment I extension. kr Ý *when* r_f = 4 *given* d=0-50 kr ↑ *when* r_f = 4 *given* d=50-100 and p<30 kr ↓ *when* r_f = 4 *given* d=50-100 and p>20 kr ↓ *when* r_f = 4 *given* d=100-200 op Ý *when* r_f = 4	• free flight (r_f=base) disadvantageous to beetles unless communication distance (d) is high, or communication distance is low and patch compaction (p) is also low. • effect of communication distance (d) and patch compaction (p) not robust to absence of free flight (r_f=4).
III extension sensitivity without free flight Section 3.5, Figures 29 and 30	240 (40)	kr ~ r_w| d | w | p | rpt op ~ r_w | w | p	kr ~ r_w* d*w* rpt, $\boldsymbol{p} = 0.0002$ kr ~ p* rpt, $\boldsymbol{p} < 0.0001$ kr ~ r_w* w*p, $\boldsymbol{p} = 0.0124$ op ~ r_w, $\boldsymbol{p} < 0.0001$	kr Ý p *given* r_w=3, w0, d=0-50 kr ↑ p *given* r_w=3, w0, d=50-100	• patch compaction (p), patch size (w) and communication distance (d) effects significant in the absence of free flight (r_f=4) when overall success rate is reduced.

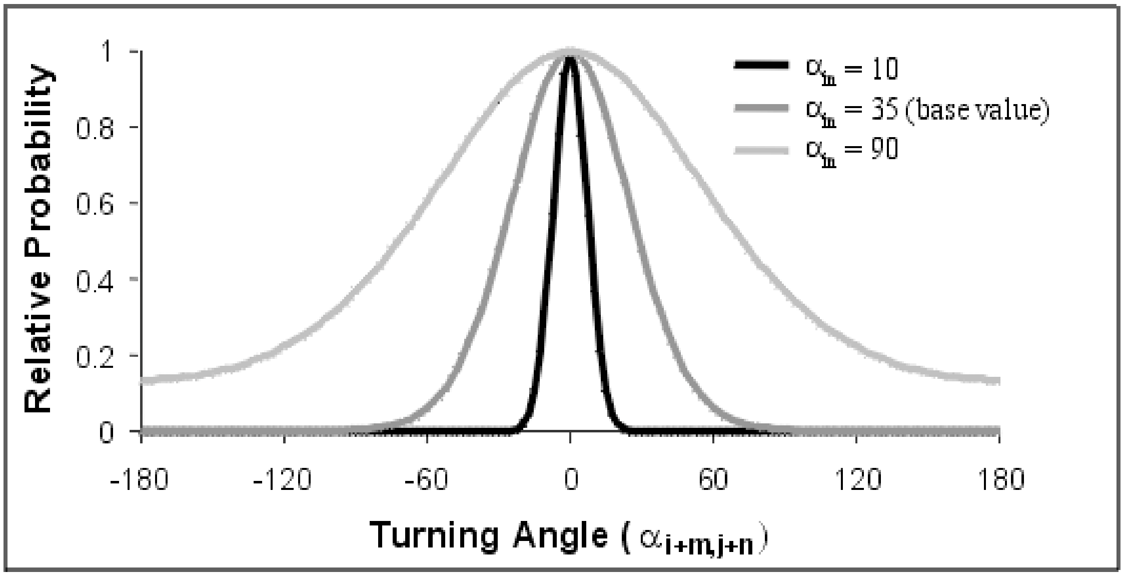

Figure 1: Effect of a_m on the distribution of mountain pine beetle turning angles in free flight or the absence of chemical attractants. The quantity (1-cos($a_{i+m,j+n}$)) is exponentially distributed with parameter a_m, which is approximately equal to the average turning angle when a_m is small (~<60^o). Average turning angle does not continue to increase indefinitely with a_m because the finite range of possible turning angles truncates the exponential distribution.

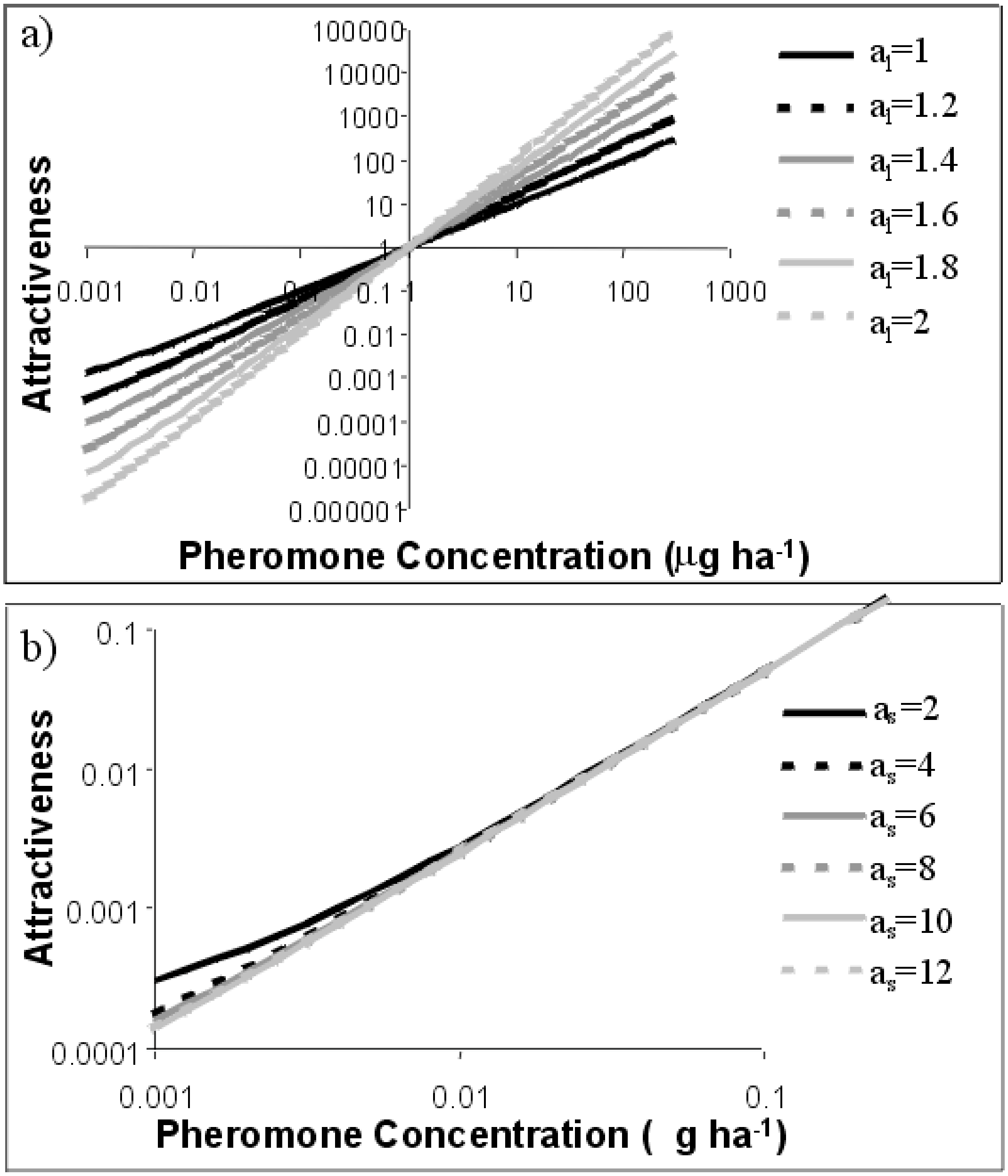

Figure 2: The sensitivity of attractiveness to the gradient sensitivity parameters, a_l (a), and a_s (b). The attractiveness parameter, a_l, controls the sensitivity of mountain pine beetles to pheromone gradients, and a_s determines the relative preference of beetles for low pheromone over no pheromone areas. Curves derived from Equation 14.

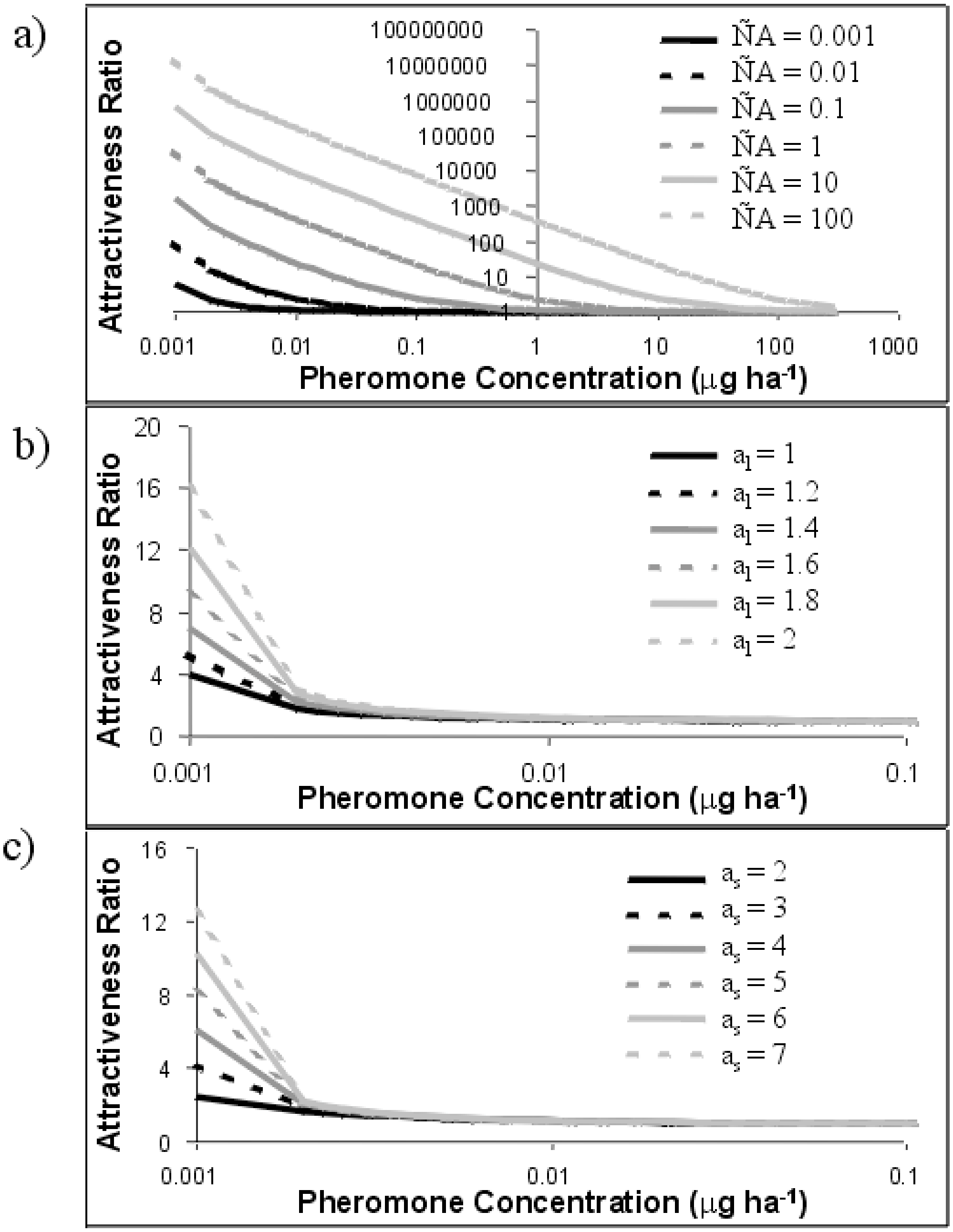

Figure 3: Sensitivity of the relative attractiveness of pheromones to gradient size (∇A) and gradient sensitivity parameters a_l and a_s. The probability a beetle will choose high pheromone location over a lower pheromone location is given by the attractiveness ratio, (Att_{high}/Att_{low}). The attractiveness ratio depends on (a) the difference in pheromone concentration between the two locations (∇A), (b,c) the attractiveness parameters a_l and a_s, and the base pheromone concentration (x-axis). The attractiveness function is designed so that beetles are more sensitive to differences in pheromone concentration when pheromone concentrations are low. Curves derived from Equation 14.

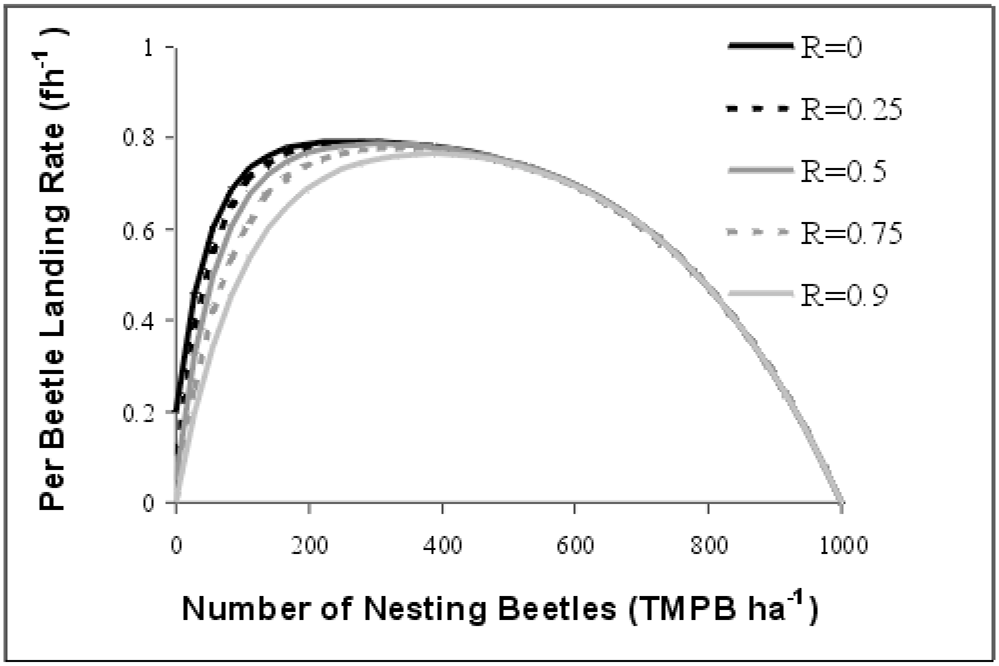

Figure 4: Sensitivity of the relationship between per beetle landing rate and number of nesting beetles (Q) to host resistance (R). Note that the measure is of permanent landings or attacks, and does not include beetles that land and then take off again. Curves derived from Equation 18.

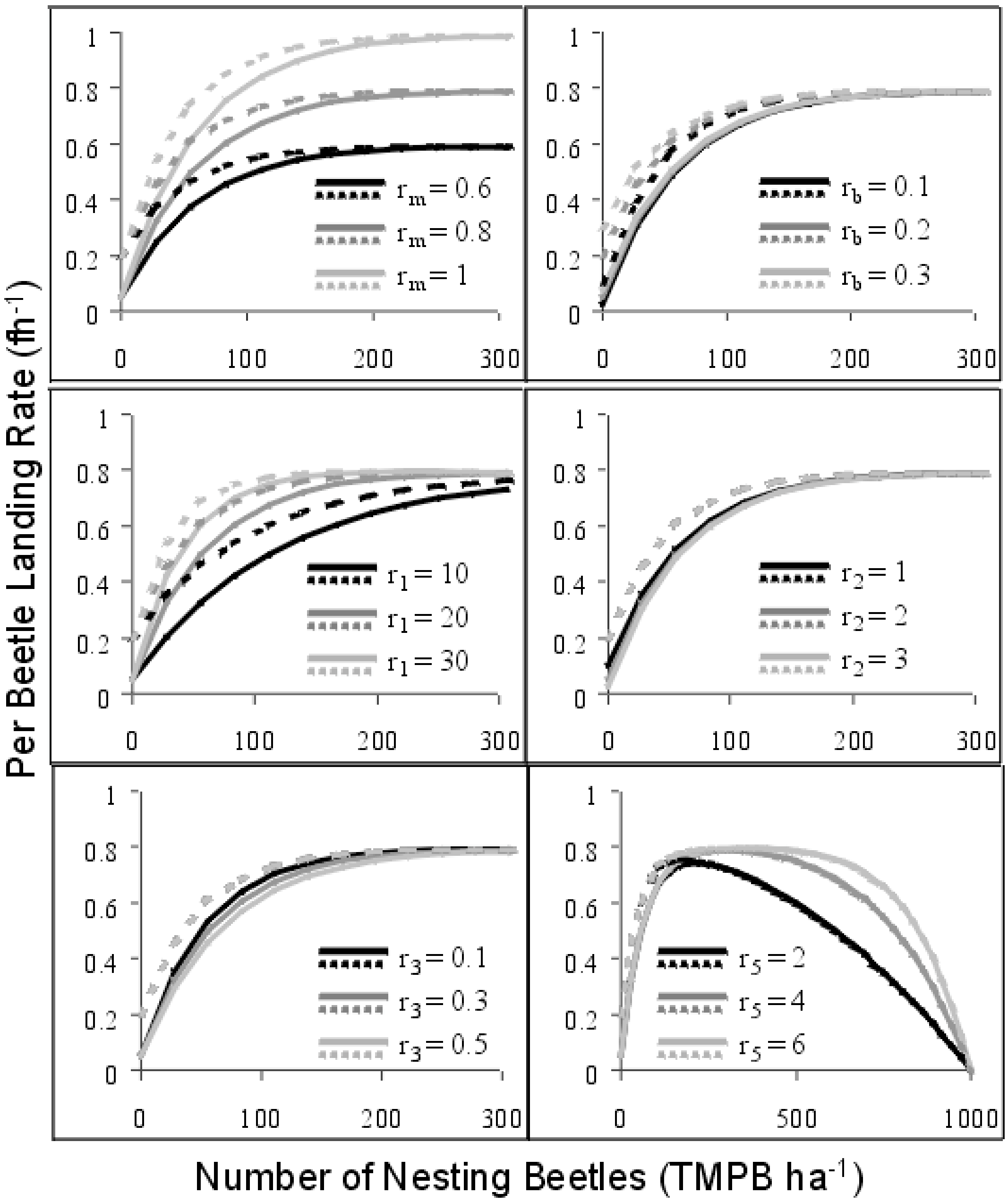

Figure 5: Sensitivity of landing rate to 6 model parameters. Solid lines indicate the case where resistance (R) is 0.5. Dotted lines indicate R = 0. Curves derived from Equation 18.

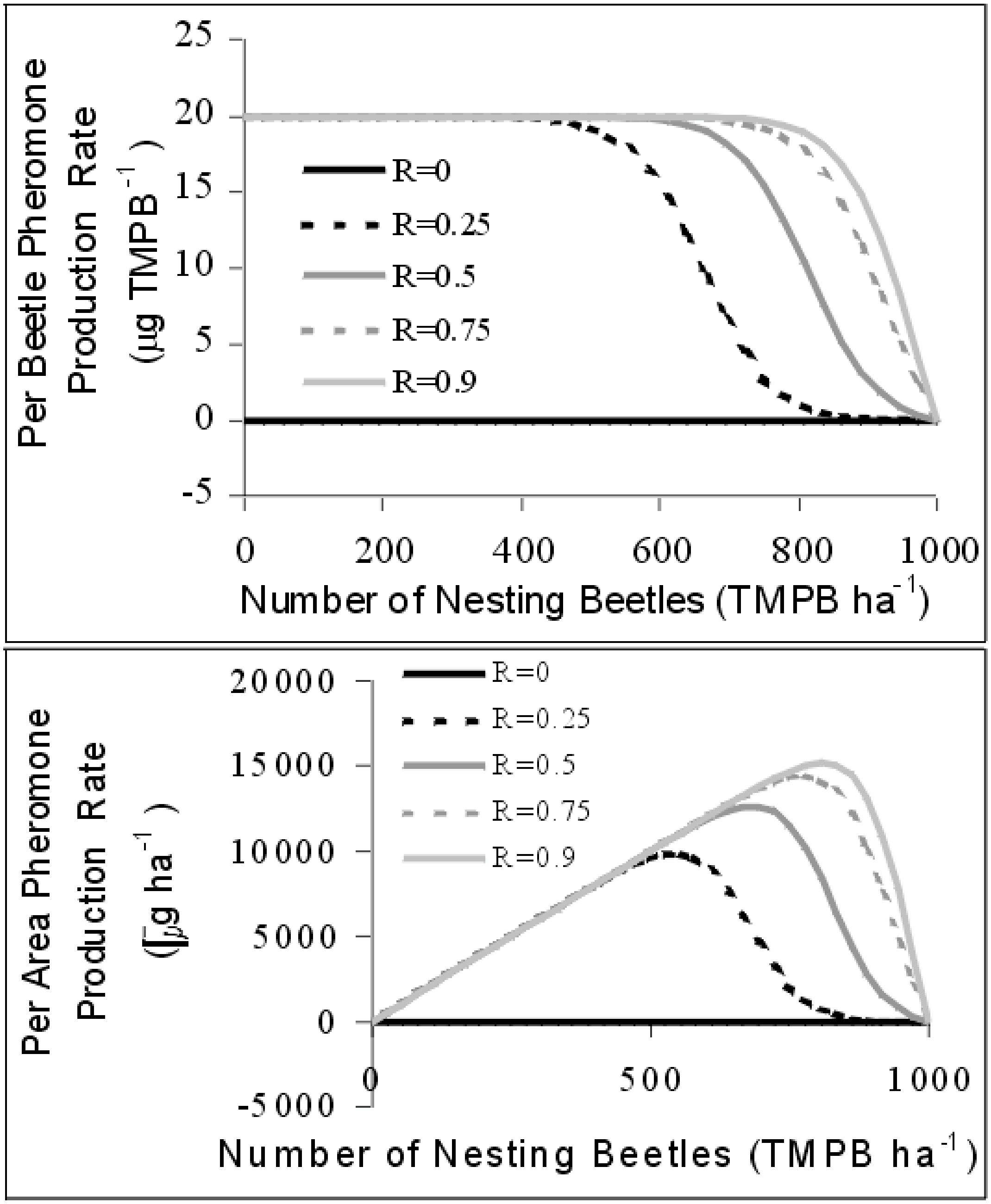

Figure 6: Sensitivity of per beetle and per area pheromone production rates to host resistance (R). Curves derived from Equation 19.

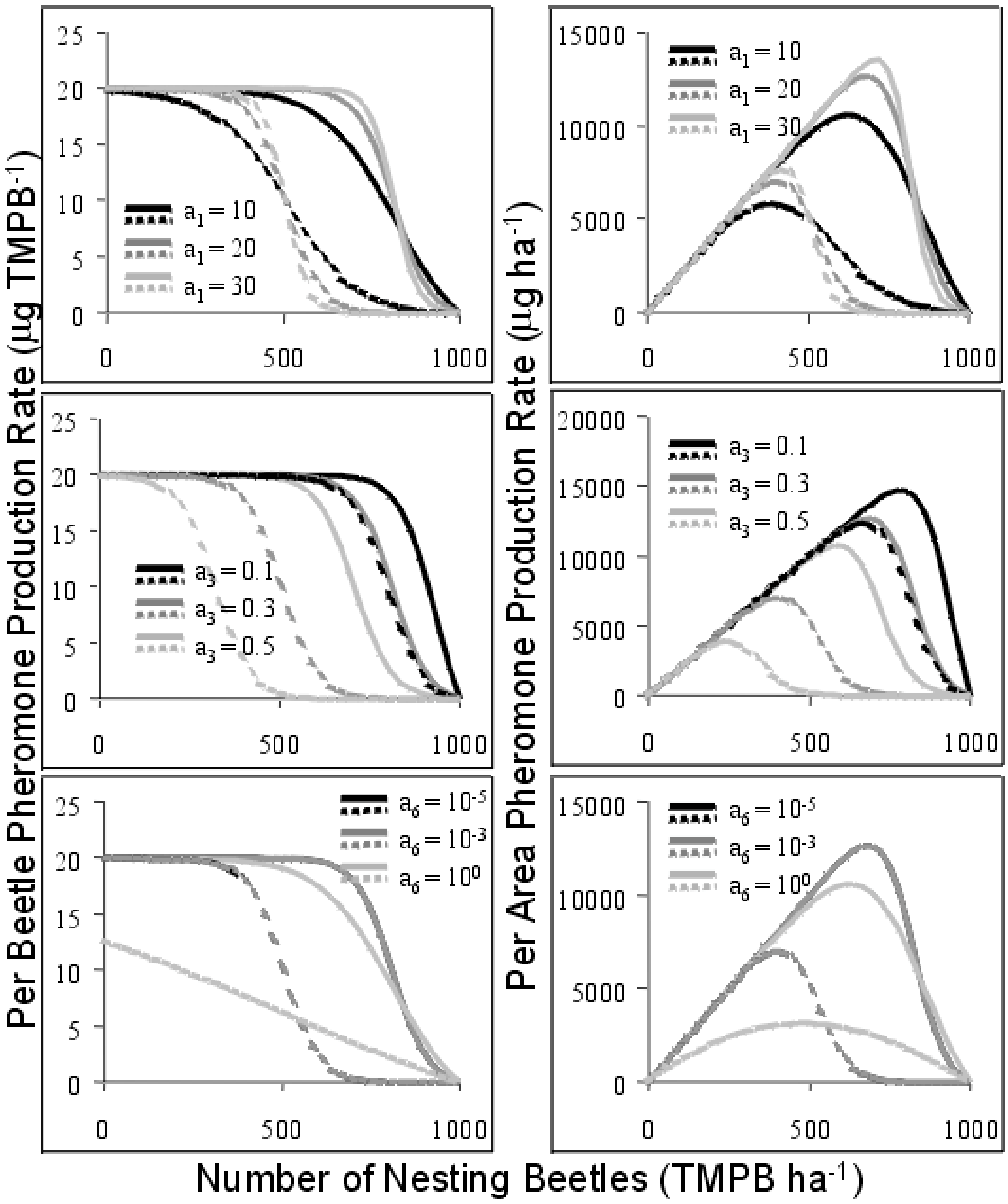

Figure 7: Sensitivity of per capita and per area pheromone production to 3 model parameters. Solid lines indicate the case where resistance (R) is 0.5. Dotted lines indicate R = 0. Curved derived from Equation 19.

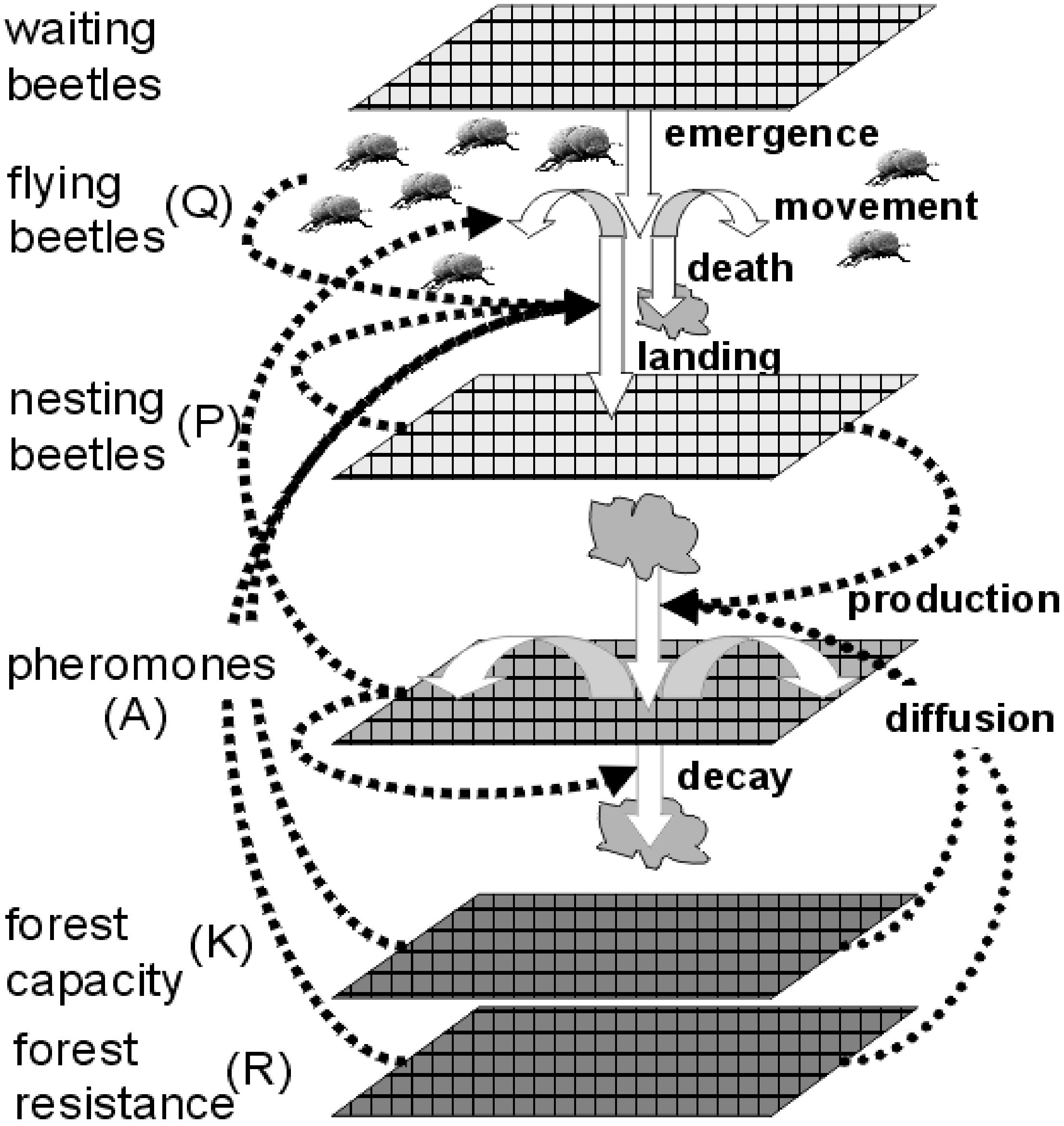

Figure 8: Summary of model within the flight period. Continuous state variables are represented by grids, while individually modeled flying beetles are drawn in separately. Descriptions of each state variable are given on the left hand side, with variable names following in brackets. Material flows of pheromones and beetles are indicated by white block arrows. Flows can either be between states (beetles only, vertical arrows), between locations within the same state (horizontal arrows), or between the modeling system and the external world (vertical arrows beginning or ending in clouds). Flow processes are labeled on the right hand side. Black dotted arrows indicate the effects of state variables on flow rates.

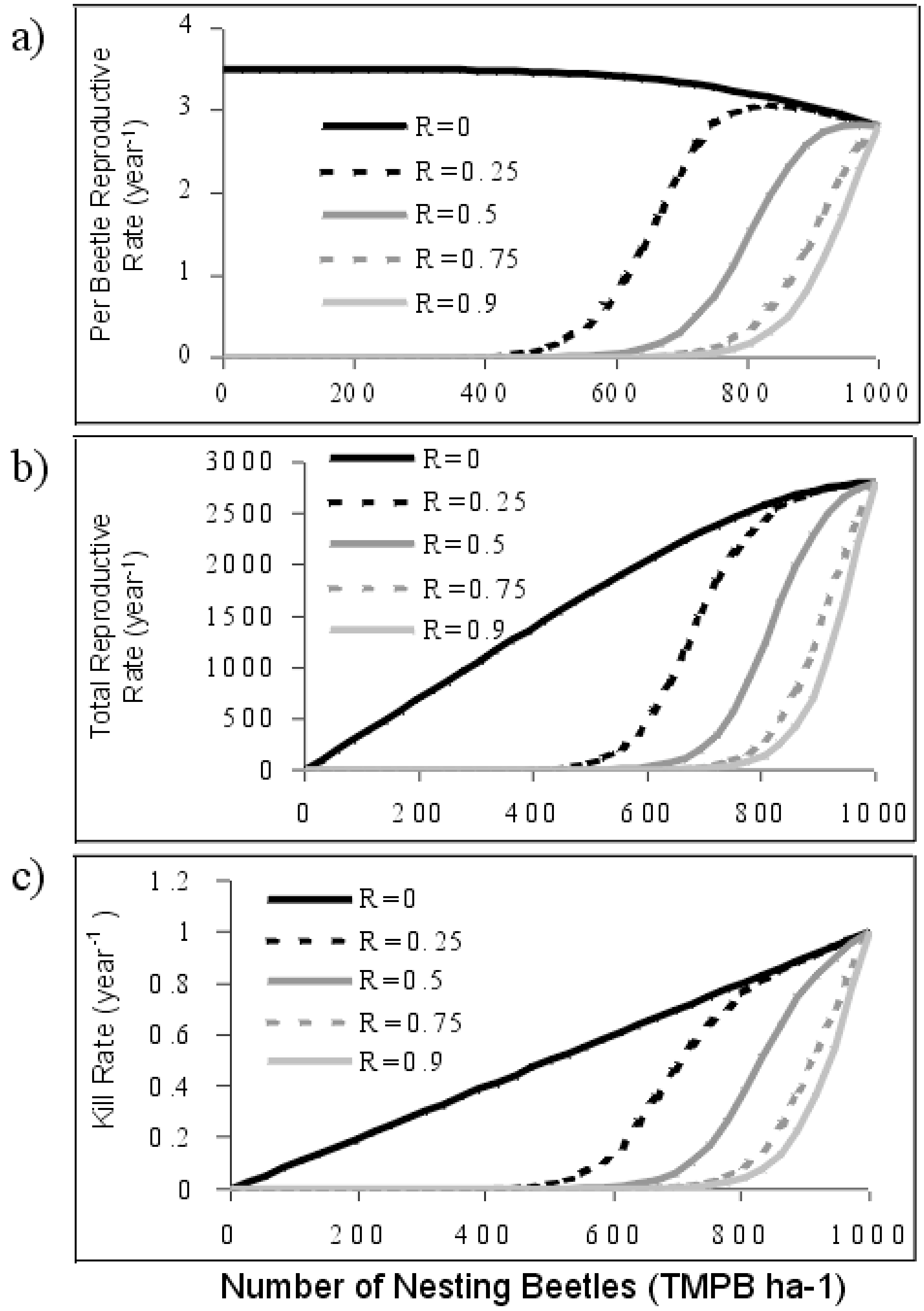

Figure 9: Sensitivity of (a) per capita reproductive rate, (b) total reproductive rate, and (c) forest kill rate to host resistance. Curves derived from Equations 29 and 31.

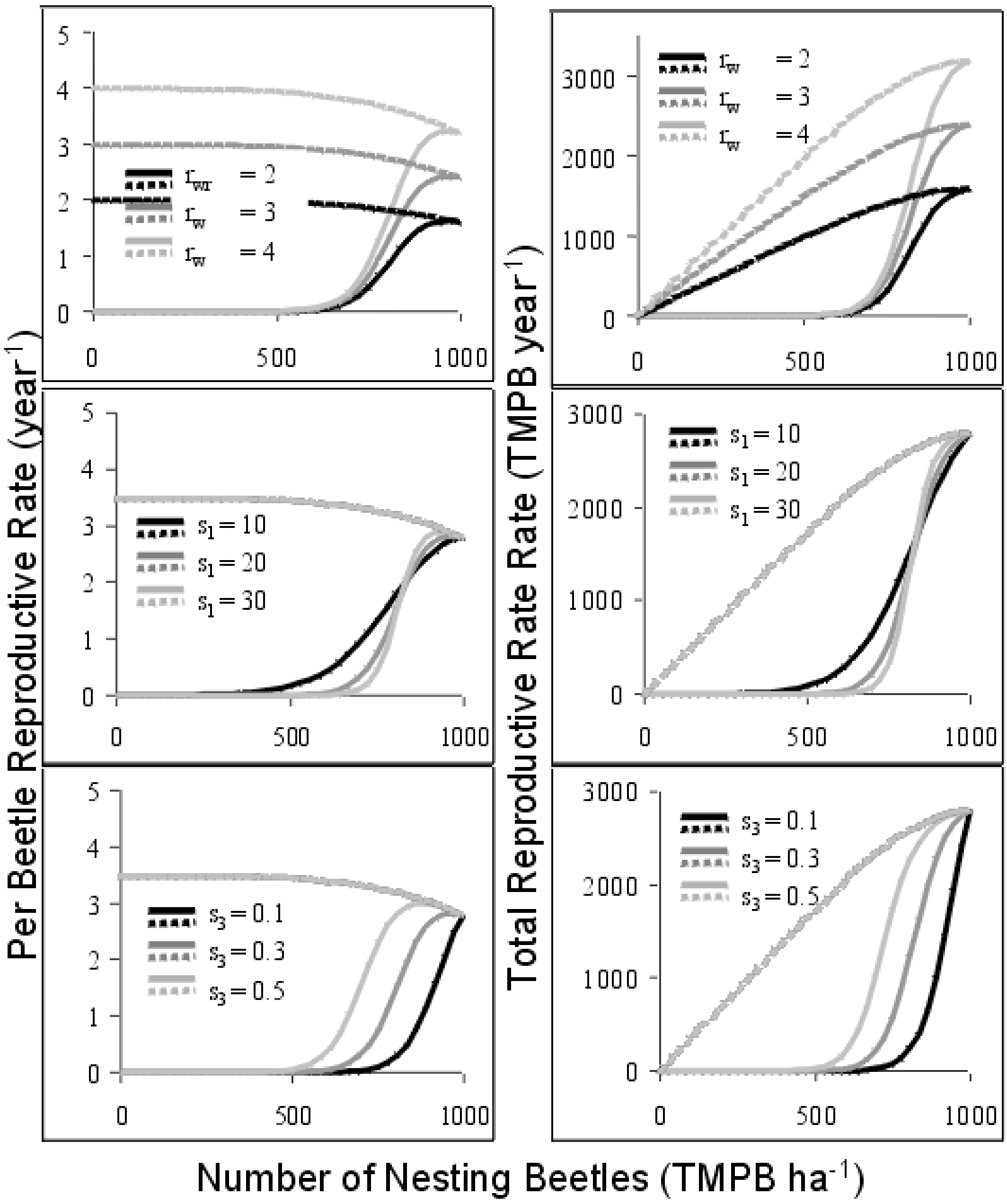

Figure 10: Sensitivity of per capita and per area reproductive rate to 3 model parameters. Solid lines indicate the case where resistance (R) is 0.5. Dotted lines indicate R = 0. Curves derived from Equation 29.

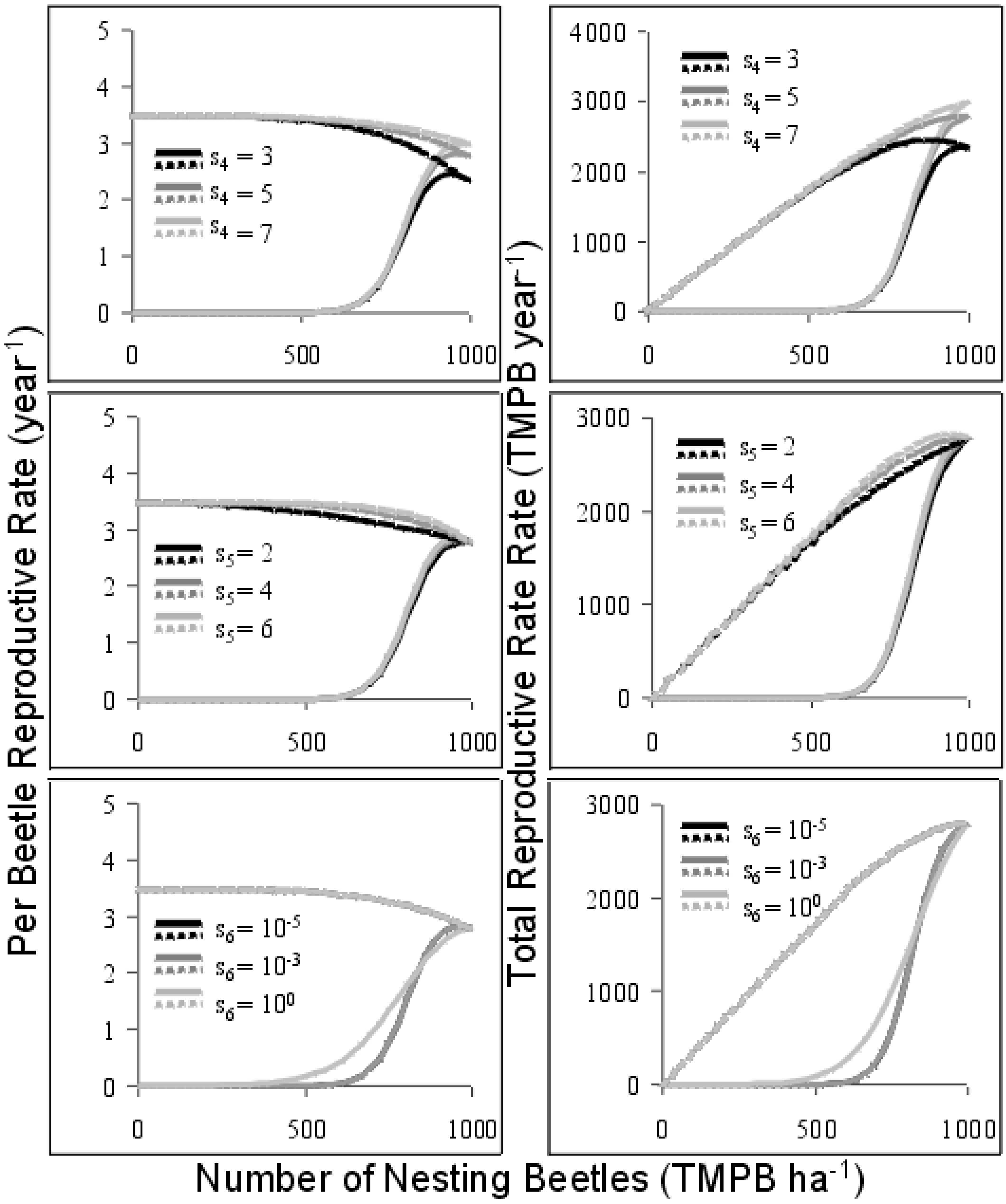

Figure 11: Sensitivity of per capita and per area reproductive rate to 3 model parameters. Solid lines indicate the case where resistance (R) is 0.5. Dotted lines indicate R = 0. Curves derived from Equation 29.

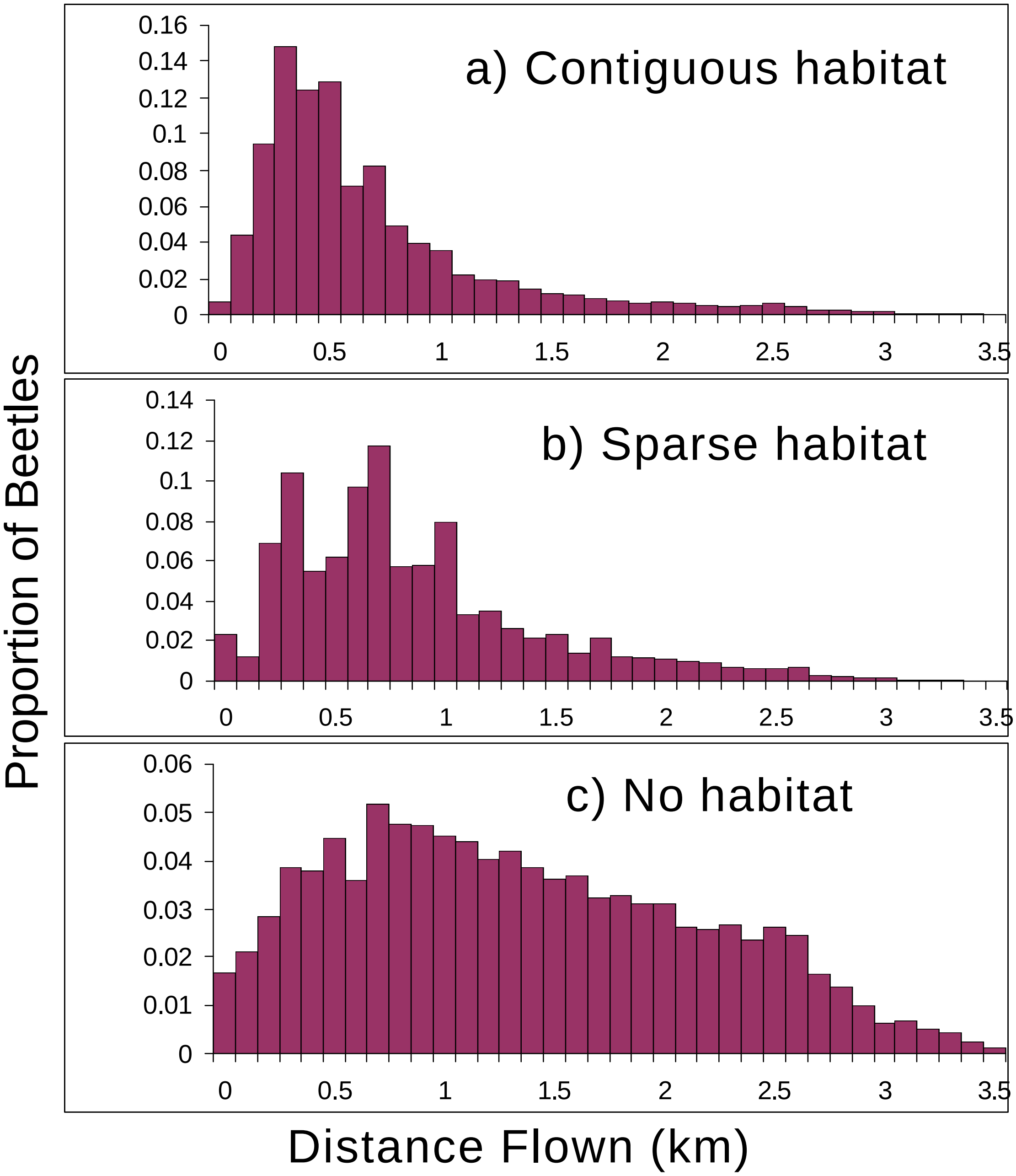

Figure 12: Distances flown by mountain pine beetles in the absence of pheromones or kairomones on a) contiguous habitat (100% of the landscape suitable for landing b) sparse habitat (10% of the landscape suitable) and c) no habitat (0% of the landscape suitable). In the first two cases beetles can either die or land, but in the absence of habitat flight distance is limited by death alone. The average flight distance on contiguous habitat is 0.64 km, and the median is 0.48 km. With no habitat the average flight distance is 1.3 km, and the median is 1.2 km. Note that beetles cannot fly more than 3.5 km from their source at the centre pixel because the square landscapes are only 5 km across. The flight distance distributions suggest that when habitat is available edge effects are not severe, but in the absence of habitat they are more so.

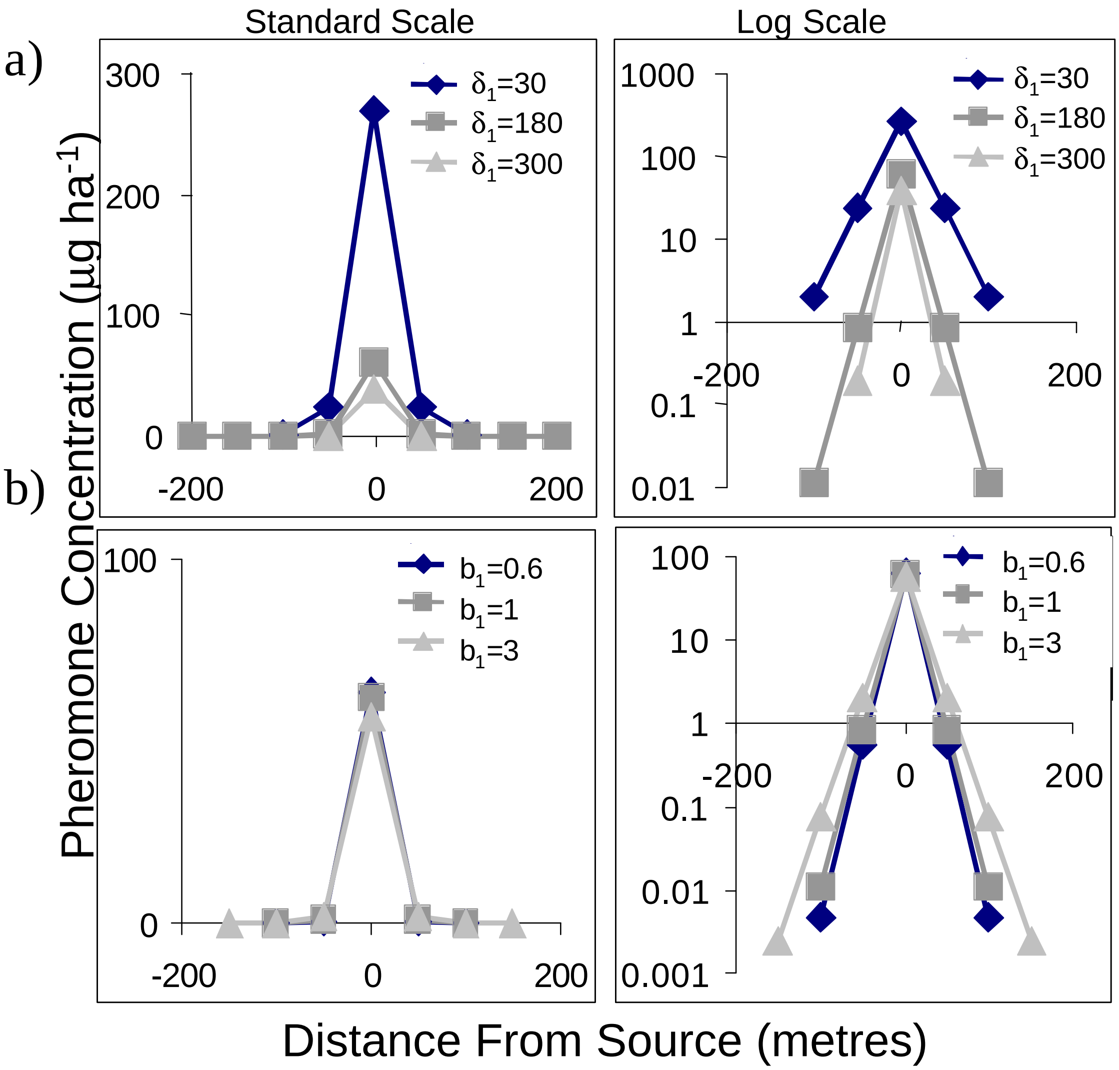

Figure 13: Sensitivity of pheromone plume size and shape to (a) pheromone decay rate (d_1) and (b) pheromone diffusivity (b_1). The number of nesting beetles, Q, is 3/5 of carrying capacity (K).

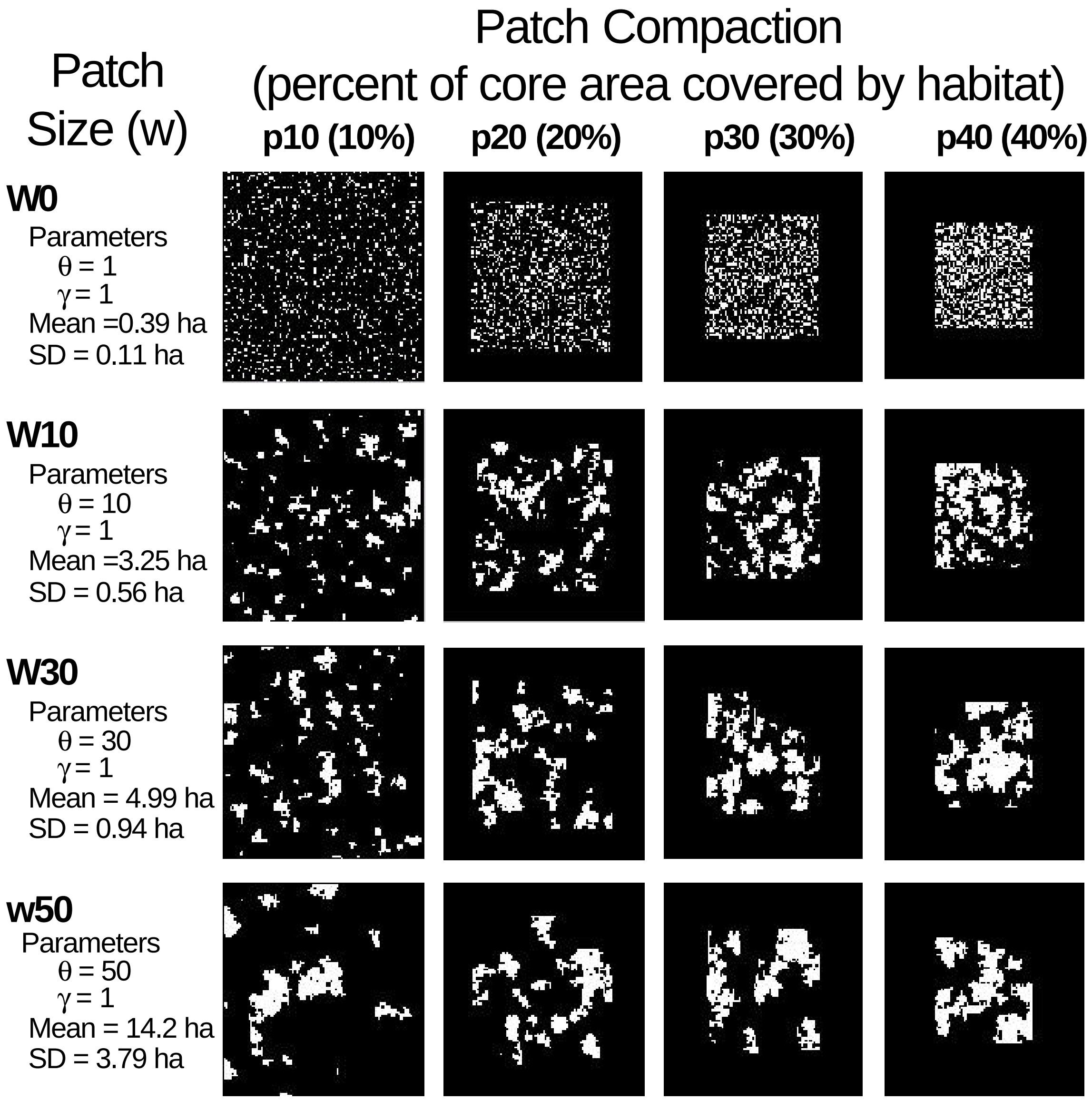

Figure 14. Experimental design scheme showing variation in patch size and patch aggregation. Variation in the Weibull scale parameter (θ), but the shape (γ) of the distribution remains constant. The mean and standard deviation (SD) are given for the case where patch compaction is low (p10). Realized patch size will increase with patch compaction as close patches merge. Each group contains 5 replicate patterns, one of which is shown here. Communication distance and other experimental factors are repeated within pattern in a split plot experimental design.

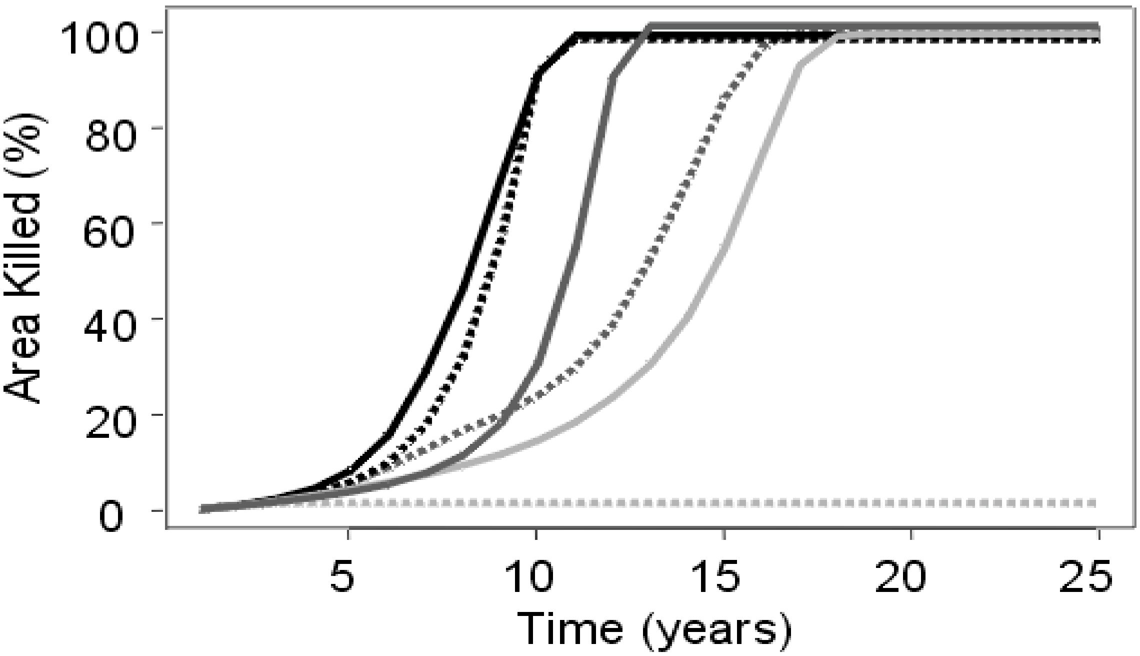

Figure 15: Characteristic model output. If conditions allow mountain pine beetles to overcome host defenses then outbreak extent increases exponentially until beetle populations are limited by habitat supply. Total available habitat is held constant across all landscapes at 250 ha.

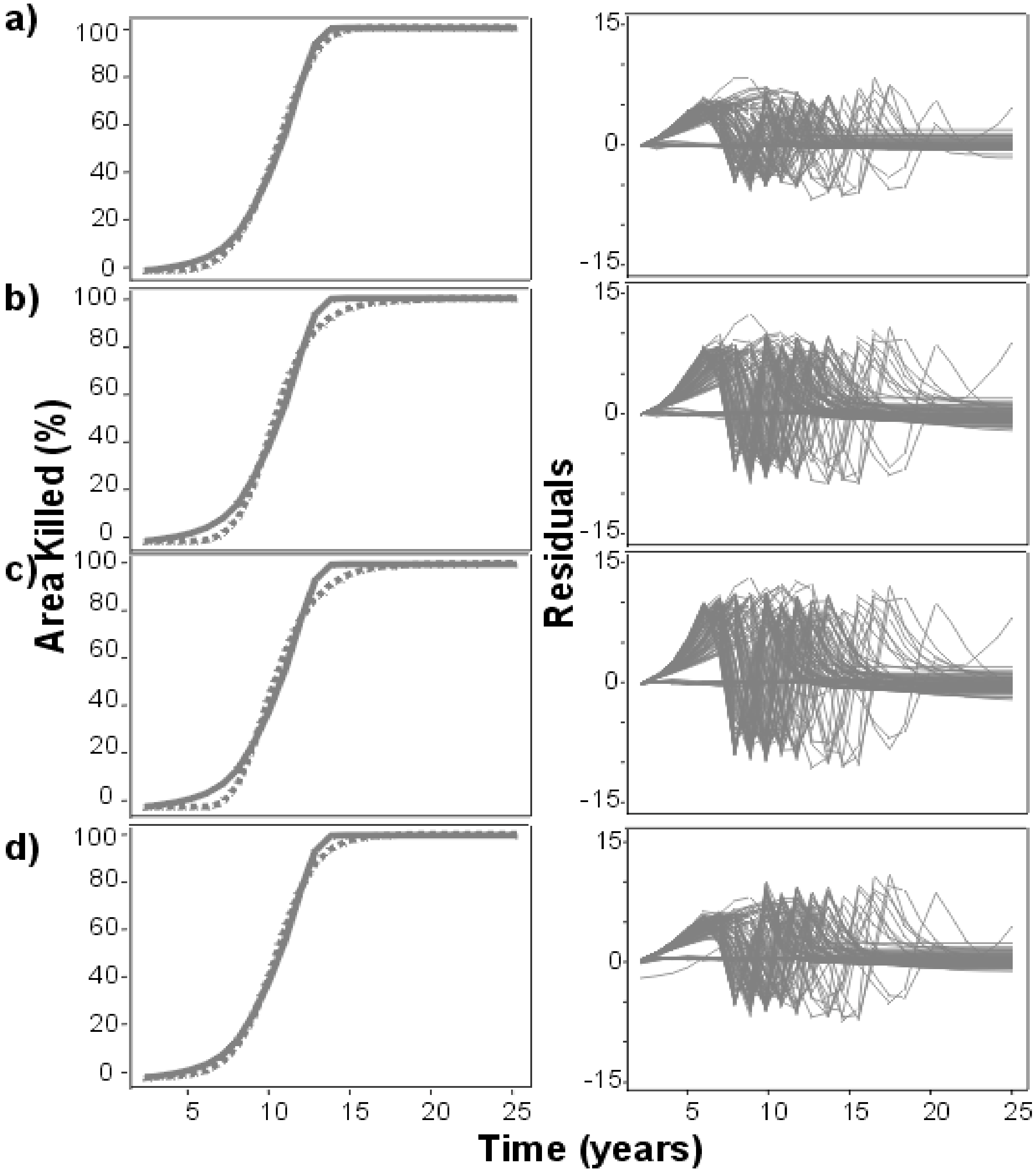

Figure 16: Sample fits and residuals for four alternative sinusoidal curves. The Weibull-type curve (a) has lower maximum and average residuals than the Mercer-Morgan-Flodin (b), the Gompertz (c) and the logistic (d) curves. Pattern in the residuals shows that residual variation is left unexplained by all four curves, but models with more parameters are more difficult to interpret biologically.

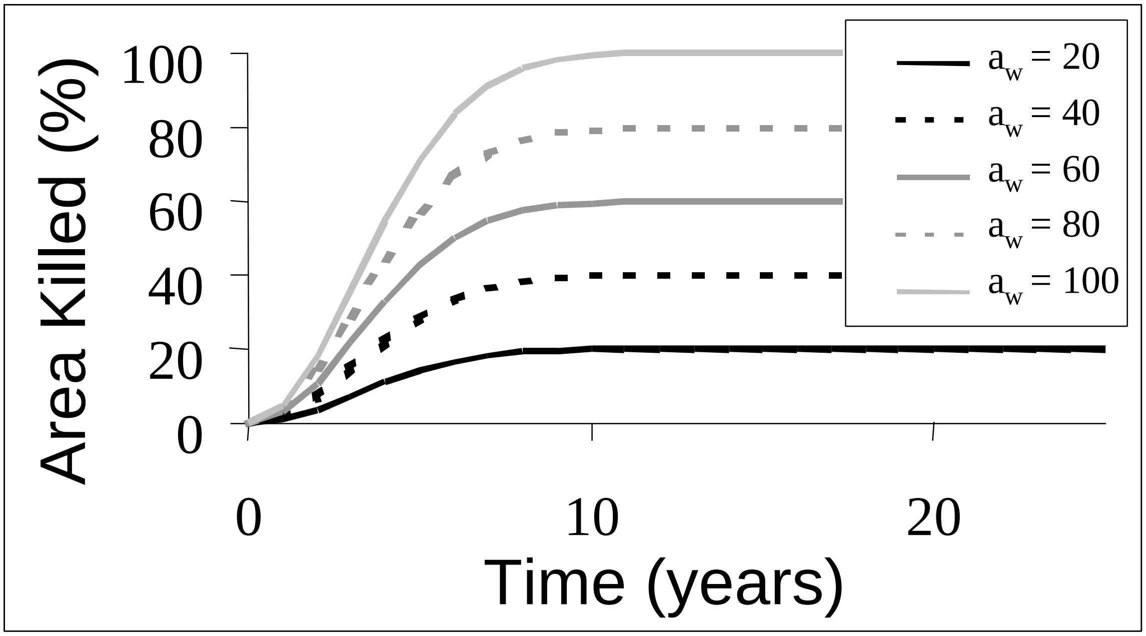

Figure 17: Sensitivity of Weibull-type curve to a_w parameter.

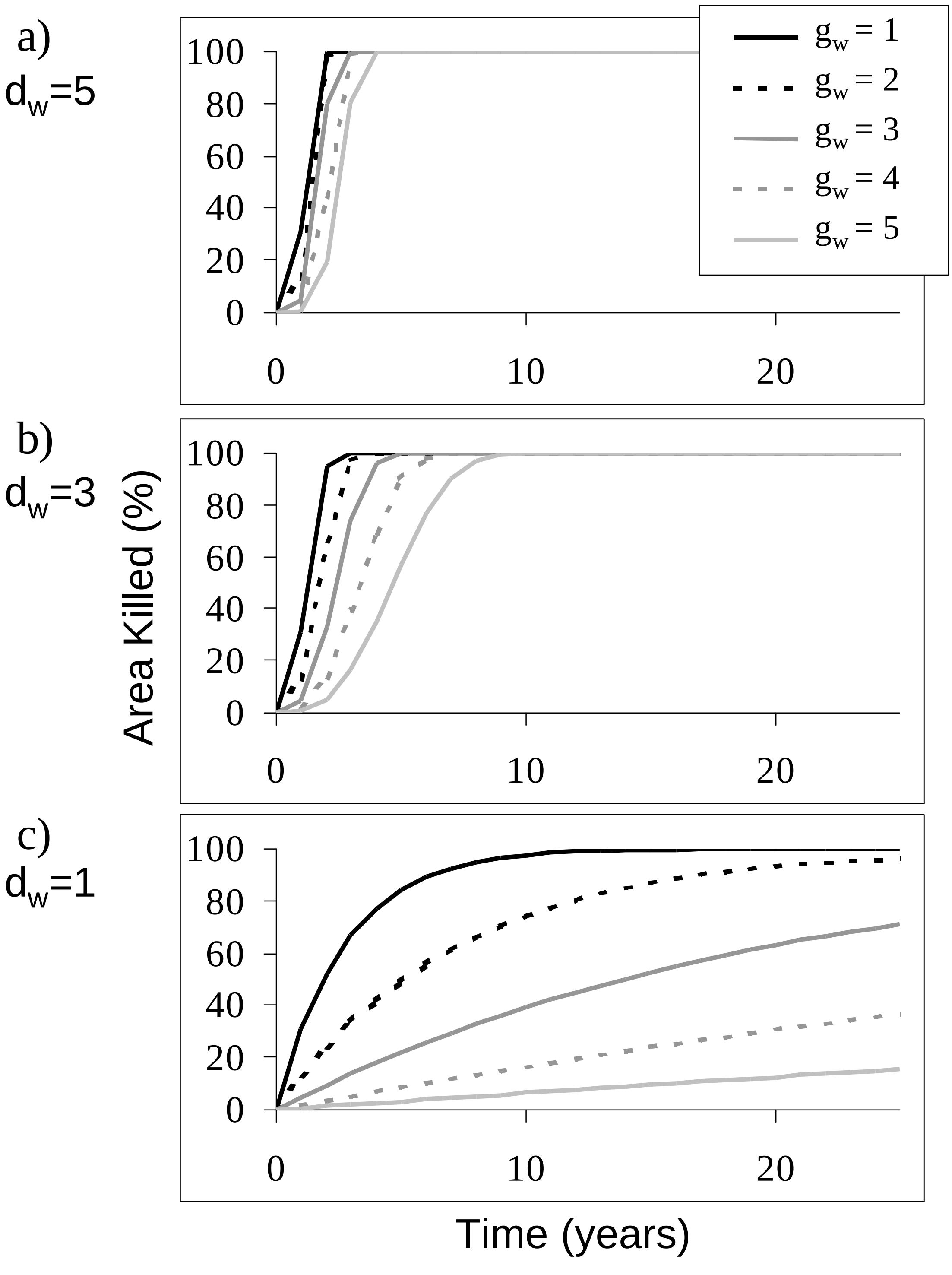

Figure 18: Sensitivity of Weibull-type curve to g_w and d_w parameters.

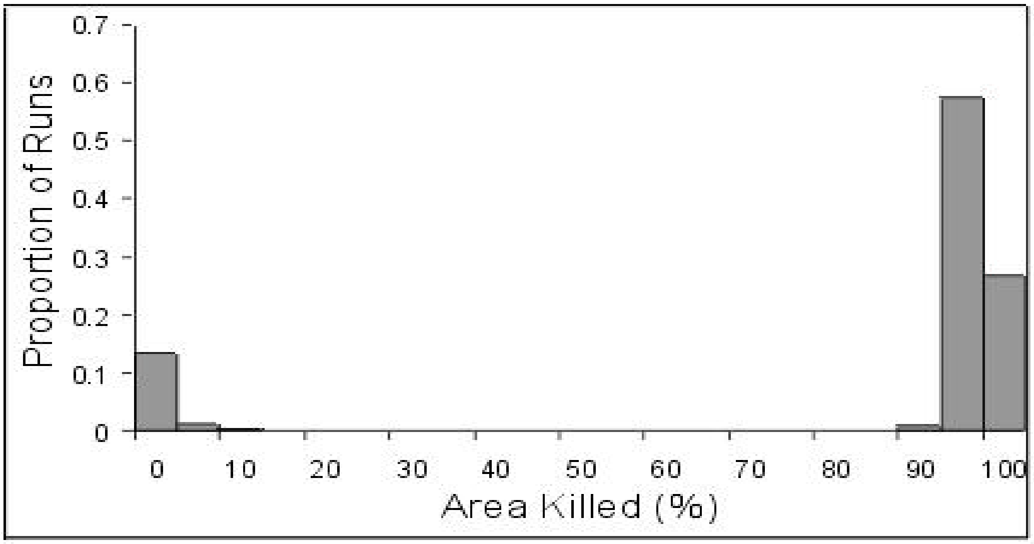

Figure 19: Bimodal distribution of kill data. In most cases, mountain pine beetles kill either nearly all or almost none of available hosts by the end of the simulation. Thus, the distribution of maximum area killed ($kill_f$) is bimodally distributed, with all of simulation runs having less than 15% or more than 95% of available habitat killed after 25 years. For analysis, data classified into outbreak (>95% kill) or non-outbreak (<95% kill) cases.

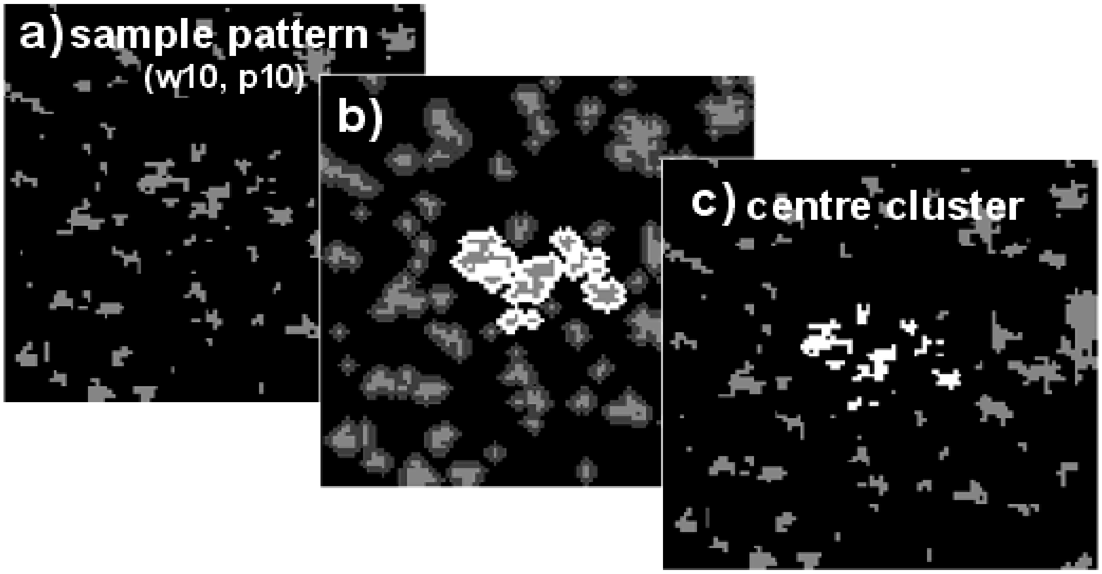

Figure 20: Definition and calculation of centre cluster size. Patches nearer together than communication distance (200 m, in this case) are joined to delineate connected "clusters" of habitat (b). The centre cluster consists of the habitat patch at the centre of the landscape, and all habitat patches to which it is connected (c). Centre cluster size is the sum of habitat area within this cluster.

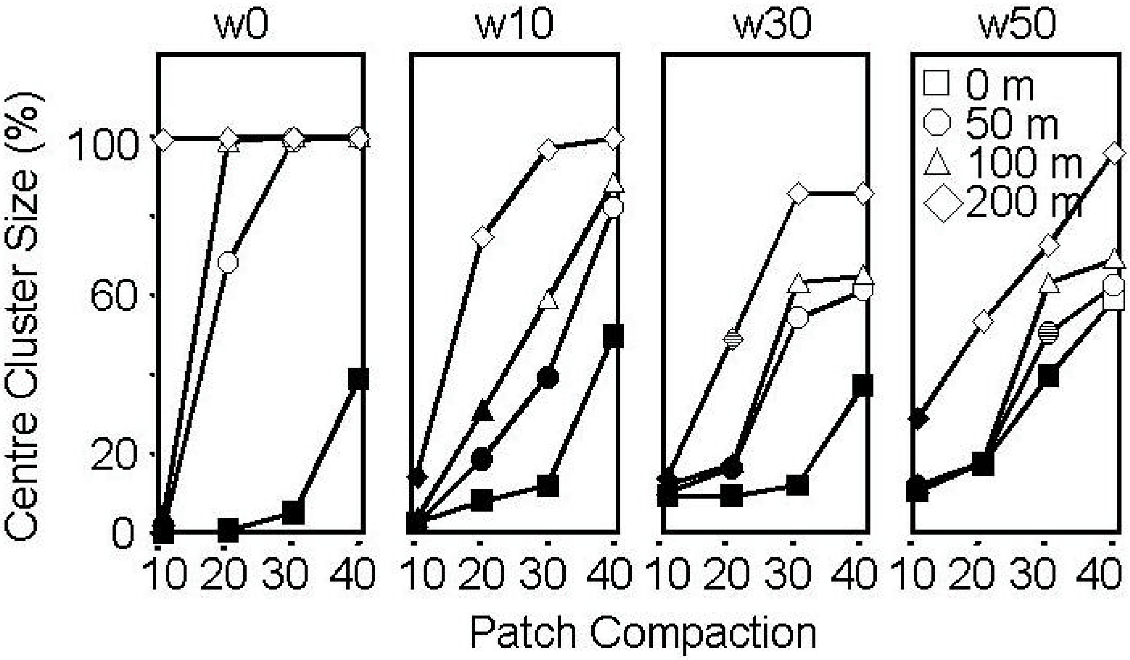

Figure 21: The effect of patch compaction (*p*), patch size (*w*), and communication distance (buffer width, *d*) on centre cluster size (see text and Figure 19 for detailed explanation of centre clusters). If infestations can only spread efficiently over habitat gaps across which beetles can communicate then centre cluster size should predict final infestation extent. Thus, panels 1-4 show the experimental effects expected if this hypothesis is correct. Overall, the interaction between all three variables is significant (p=0.0001). Open symbols show group means that are not significantly different from the maximum (250 ha), while closed symbols indicate no significant difference from the minimum. Group means marked with stripes are significantly different from both the maximum and the minimum. Each point marks the mean value for five replicate patterns.

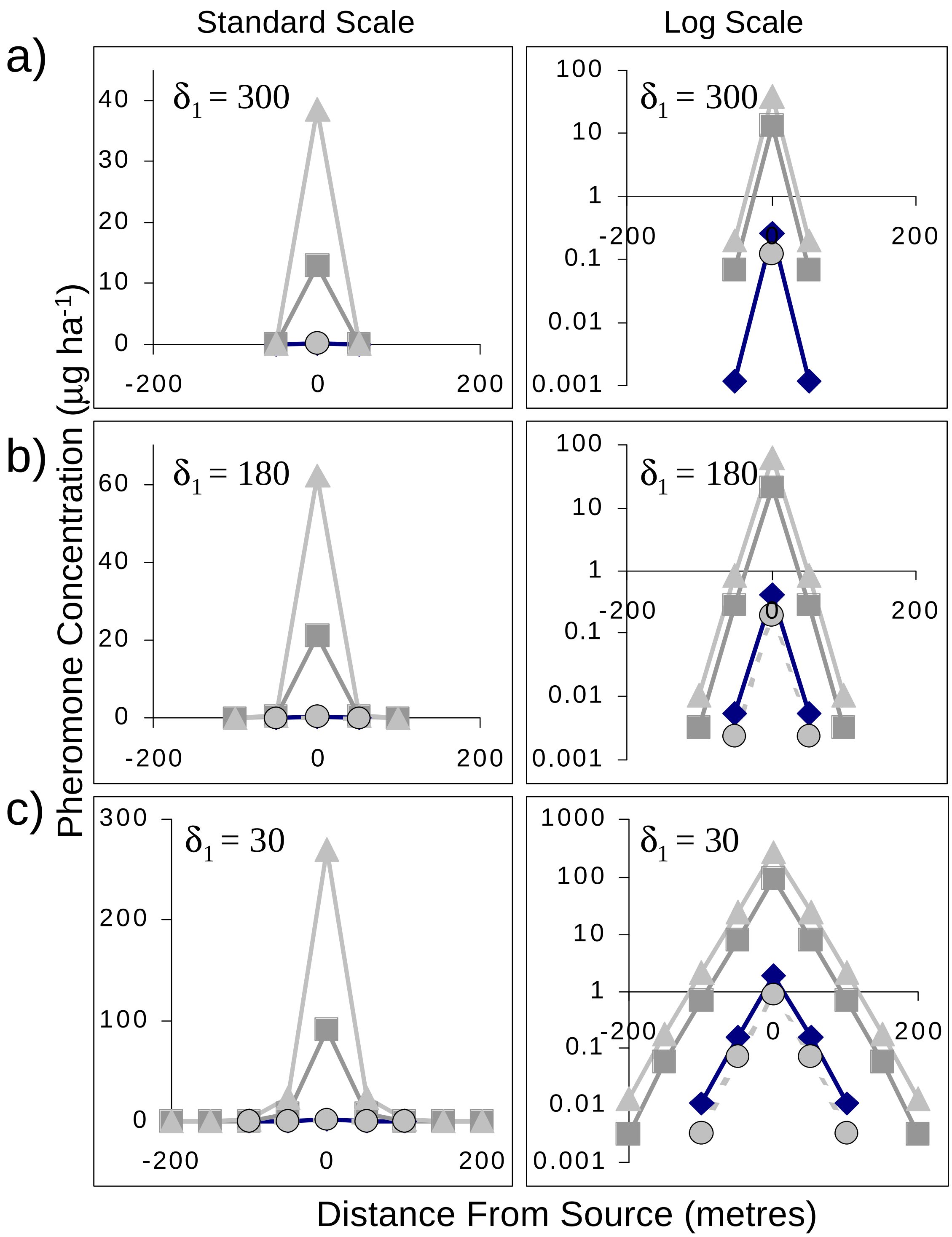

Figure 22: Pheromone plumes used in base experiment. Graphs a) through c) show how changing pheromone decay rate (d_1) alters the relationship between pheromone plume size and shape and the number of nesting beetles, Q. ◆ : Q = 0.001*K, ■: Q = 0.2*K, ▲: Q = 0.6*K, ○: Q = 0.996*K. A decay rate of d_1 = 300 (a), given a communication distance of 0-50 metres (d50), d_1 = 180 (b) gives a distance if 50-100 metres (d100), and d_1 = 300 (c) gives a distance of 100-200 metres (d200).

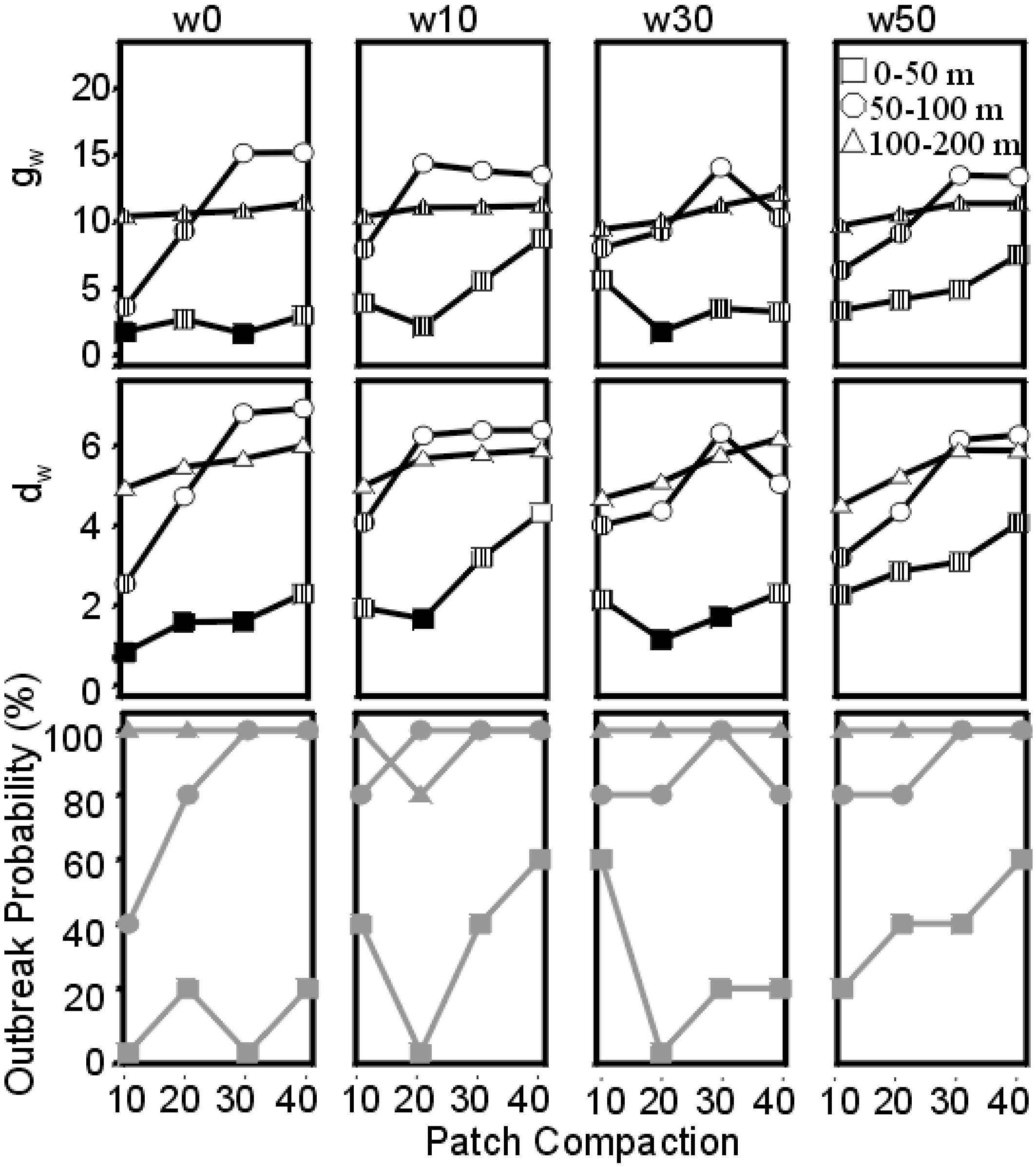

Figure 23: The effect of patch compaction (*p*), patch size (*w*) and communication distance (*d*) on kill rate (g_w, d_w) in the base case. Note that the interaction between communication distance and response variable is significant ($p<0.0001$), as is the effect of patch compaction ($p=0.0003$), but the effect of patch size is not. Open symbols show group means that are not significantly different from the maximum, while closed symbols indicate no significant difference from the minimum. Groups marked with stripes are not significantly different from either the maximum or the minimum. Outbreak probabilities are shown for interest, but the data could not be analyzed in this form due to lack of variation when communication is maximum (100-200 m).

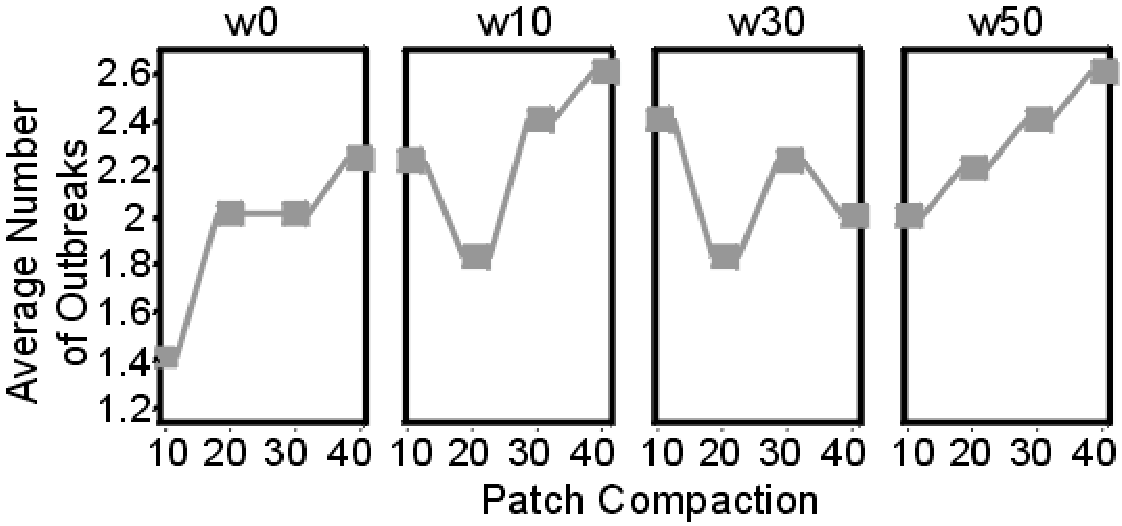

Figure 24: The effect of patch compaction (*p*) and patch size (*w*) on the average number of outbreaks (*op*) in the base case. Outbreaks are tallied across three levels of communication distance for each pattern, so the maximum number of outbreaks possible is 3, and the minimum is 0. However, no landscape had less than 1 outbreak in this case because outbreaks always occurred when communication distance was large (Figure 22). Unlike in the case of kill rate, patch size (*w*) and patch compaction (*p)* do not have a significant effect in this analysis.

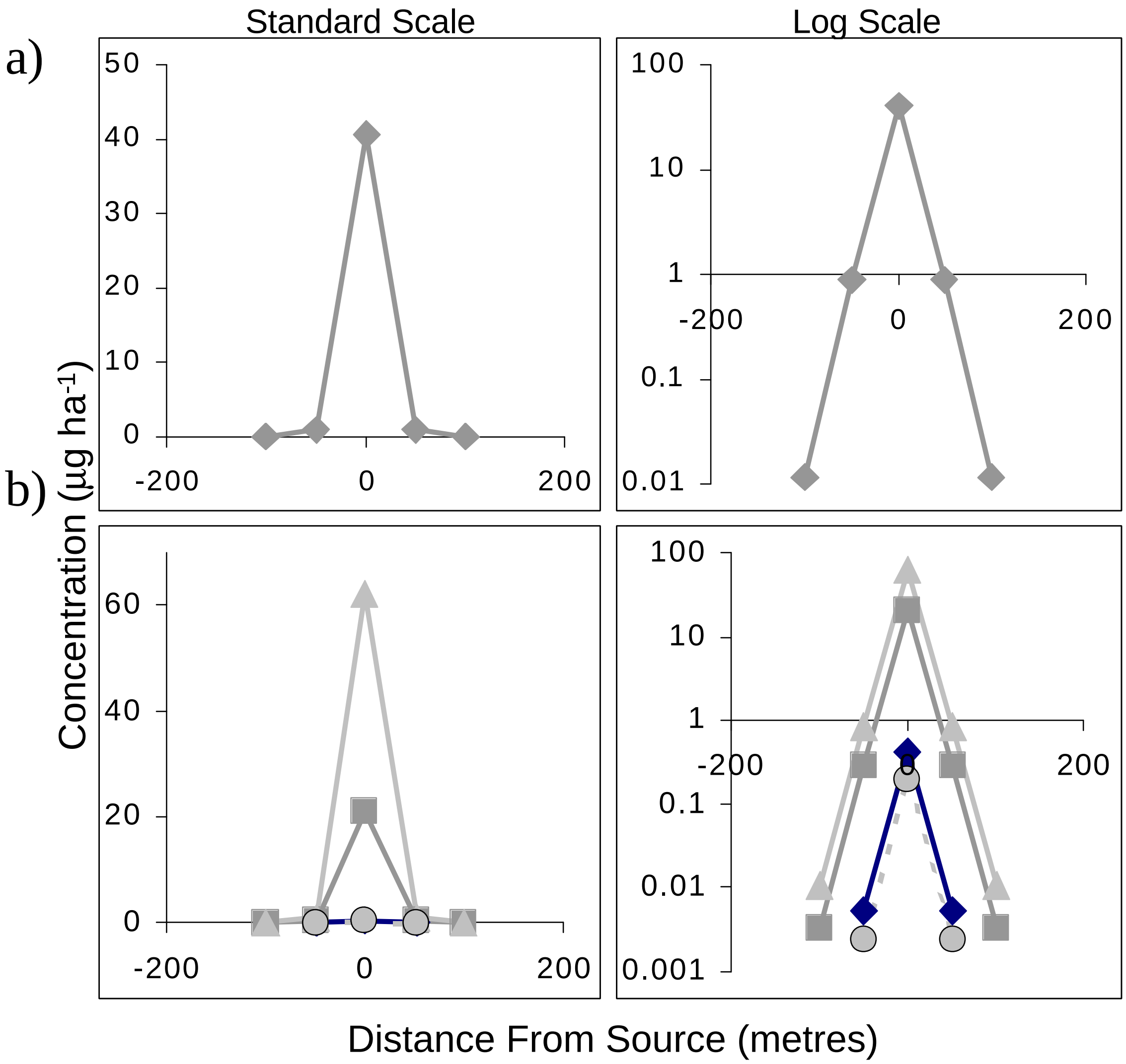

Figure 25: Kairomone plume used in Experiment II (a), with pheromone plume for comparison (b). ◆ : Q = 0.001*K, ■ Q = 0.2*K, ▲ Q = 0.6*K, ○ Q = 0.996*K.

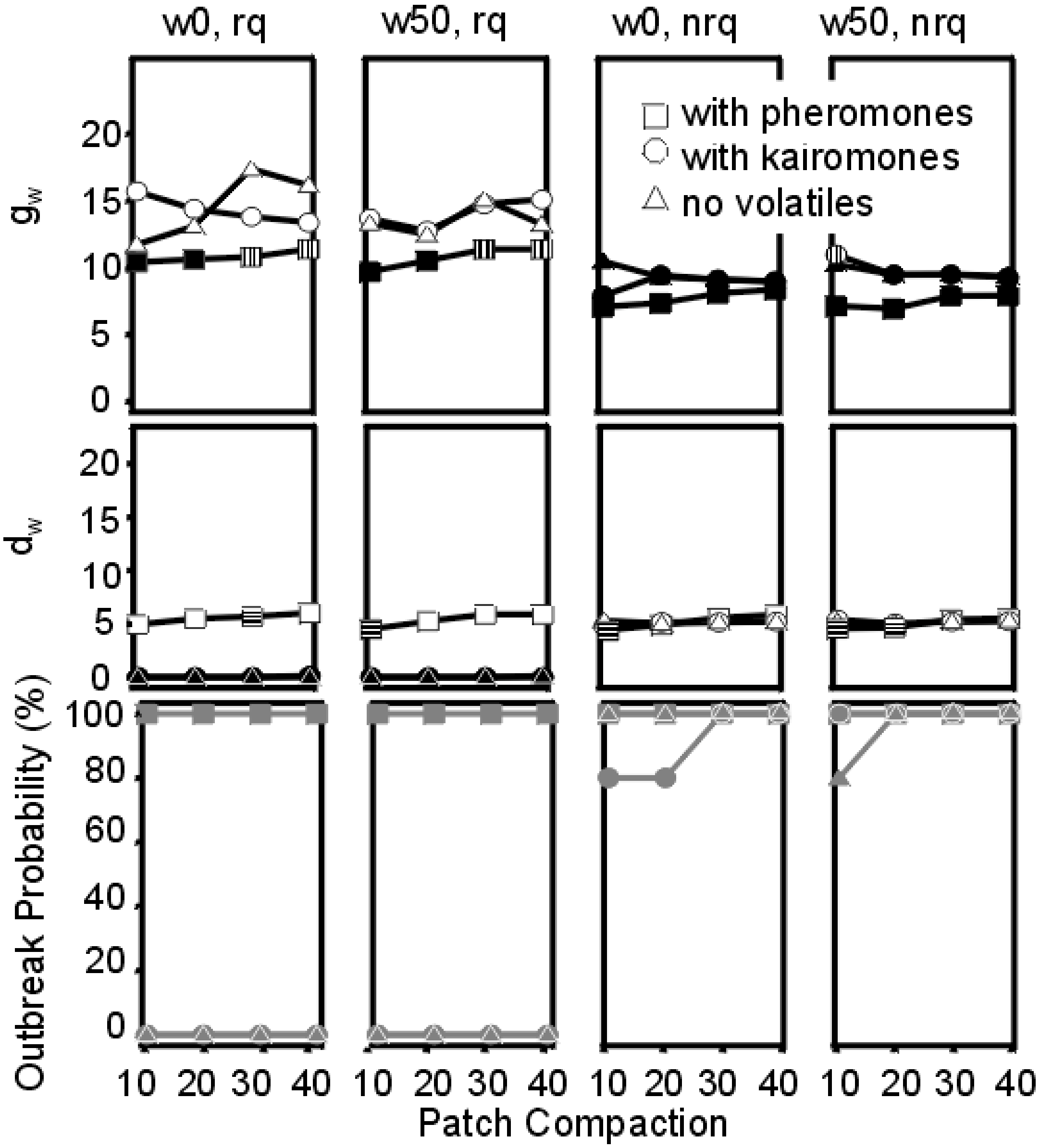

Figure 26: The effect of patch compaction (*p*), patch size (*w*), communication system (*vty*), and requirement for mass attack (*atr*) on kill rate (g_w, d_w). Mass attack can either be required (*rq*) or not required (*nrq*) for success. Note that the interaction between all factors (*vty*atr*w*p*rpt*) is significant (p=0.014). See Figure 22 for more explanation.

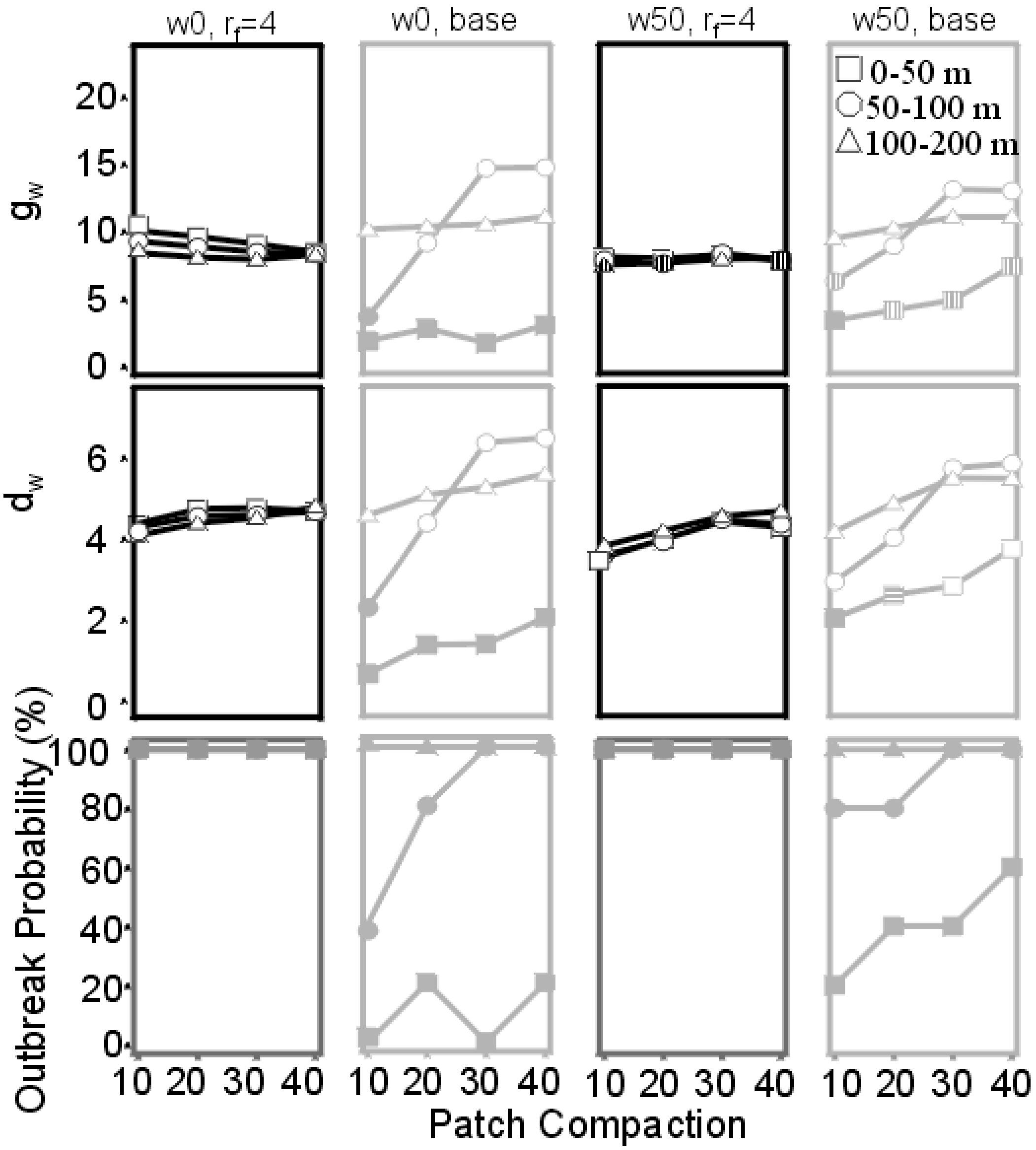

Figure 27: The effect of patch compaction (*p*), communication distance (*d*) and free flight (r_f) on kill rate (g_w, d_w) in Experiment III. Note that the interaction between patch size, communication distance, and free flight is significant ($p = 0.0053$), as is the interaction between free flight, response variable and patch compaction ($p = 0.0486$) and the interaction between free flight, response variable and communication distance ($p < 0.0001$). Grey panels are repeated from Figure 24, shown here for comparison. See Figure 22 for more explanation.

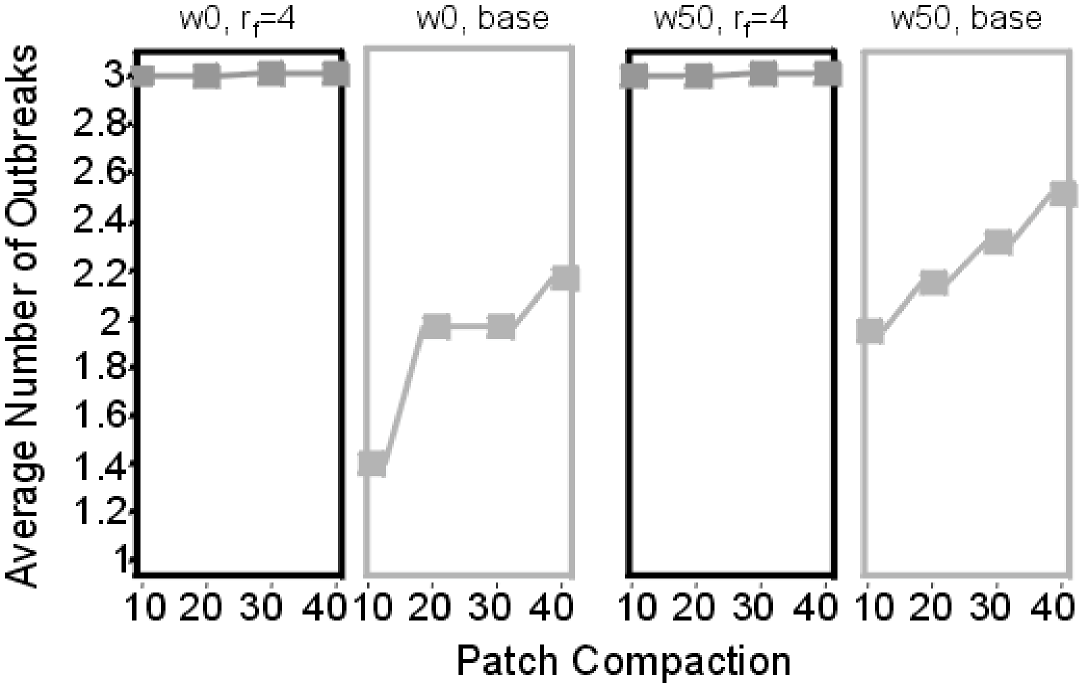

Figure 28: The effect of patch compaction (*p*), patch size (*w*) and free flight (r_f) on the average number of outbreaks (*op*) in Experiment III. Note that outbreak frequency increases significantly with free flight (r_f) status ($p<0.0001$), but no other experimental effect are significant.

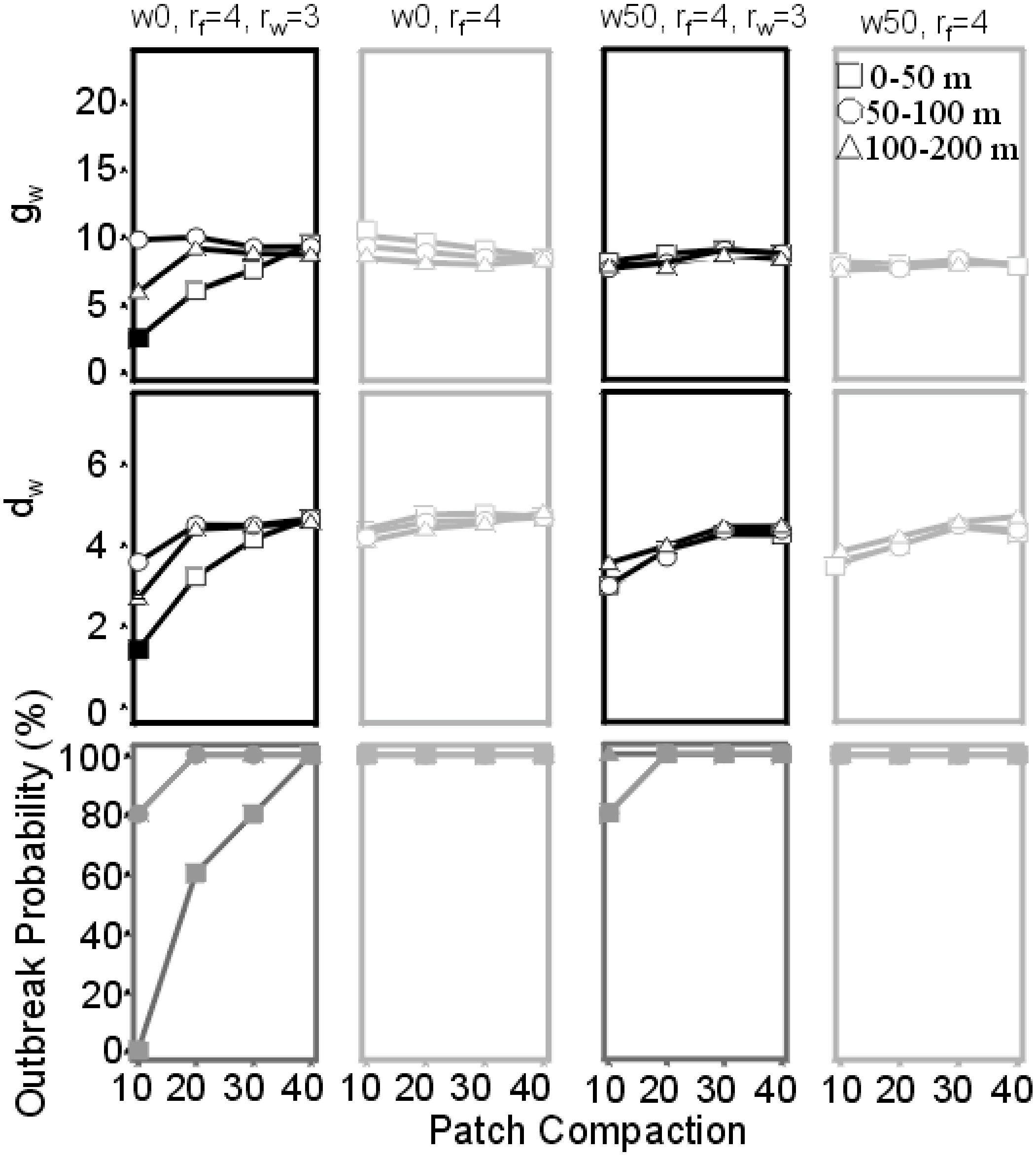

Figure 29: The effect of winter reproductive rate (r_w) on the results from Experiment III. The interaction between reproductive rate, communication distance, patch size, and response variable is significant (p=0.0002), as is the interaction between patch compaction and response variable (p<0.0001) and the interaction between reproductive rate, patch size and patch compaction (p=0.0124). Symbols are filled as in Figure 22.

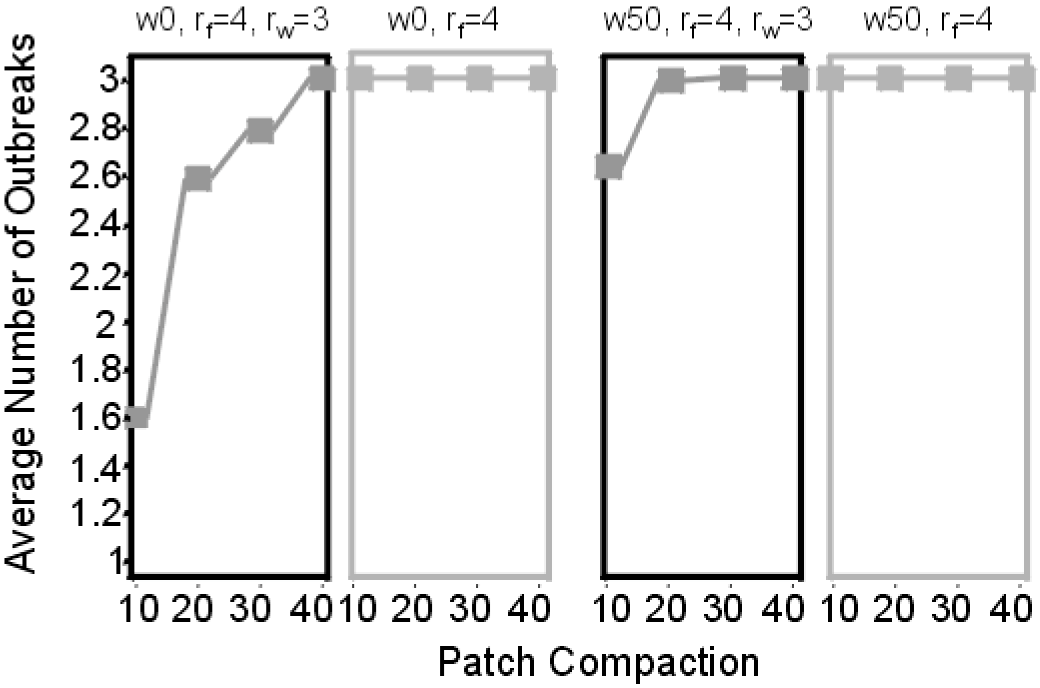

Figure 30: The effect of winter reproductive rate (r_w) on the results from Experiment III. Note that outbreak frequency increases significantly with free flight (r_f) status ($p<0.0001$), but no other experimental effect are significant.