

Positive and negative density-dependence and boom-bust dynamics in enemy-victim populations: a mountain pine beetle case study

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Abstract Negative density-dependent population regulation in exploitative species is well studied. Positive density-dependence can arise if exploiters must cooperate to obtain access to well-defended resources. Most studies, however, focus on the first type of density-dependence at the expense of the other. Using a parasitoid-host model, we explored how positive density-dependence driven by host defenses in combination with negative density-dependence due to competition for resources impact transient population dynamics. Inspired by interactions between the mountain pine beetle and its pine hosts, we formulated a model of enemy-victim

interactions in discrete-time in which the victim is capable of deadly self-defense against exploitation. We fitted the model to data and then analyzed its non-equilibrium dynamics to determine what conditions promote boom-bust dynamics. When present together, strong Allee effects and overcompensating competition for resources among exploiters can cause their populations to irrupt and then crash even though many exploitable resources remain. Accelerating population irruptions followed by precipitous collapse occur for realistic parameter values of our model of mountain pine beetle dynamics. Insect dynamics are often dominated by sudden irruptions and collapses on short time scales. Population crashes in exploitative species often happen enigmatically even when exploitable resources are not depleted. Herein, we argue that strong Allee effects in combination with overcompensation provide a plausible explanation for these boom-bust dynamics in some species.

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Keywords Allee effect · Bark beetle · Cooperative attack · Nicholson-Bailey · Mountain pine beetle · Plant defense

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Introduction

Classic models of trophic interactions (Thompson 1924; Volterra 1928; Nicholson and Bailey 1935) ignore the potential for exploited species to kill their exploiters in self-defense. Deadly resistance to exploitation can select for cooperative attack or exploiter aggregation to overcome the defenses of victims (Wallin and Raffa 2004). In some Hymenopteran parasitoids, for example, parasitoid egg mortality initially decreases with increasing numbers of eggs laid per host (Ikawa and Okabe 1985; Takagi 1985). Thus, some gregarious parasitoids, typically called superparasites, lay multiple eggs in a host to overwhelm its immune

defenses (Charnov and Skinner 1984; Takagi 1985). However, at high superparasite egg densities per host, intraspecific competition within parasitized hosts can increase the mortality of juvenile superparasites (Takagi 1985).

Original theoretical work on host-parasitoid systems by Godfray and Hassell (1991) explored how the host's ability to encapsulate and kill the eggs and larvae of parasitoids impacts the dynamics of host-parasitoid systems. Godfray and Hassell (1991) developed two models of encapsulation. In their first model, a fraction of hosts were impregnable and could not be parasitized because they encapsulated all eggs laid in them by superparasites. In their second model, the probability that a host was successfully parasitized increased with the number of times it encountered an ovipositing parasitoid. When a certain proportion of hosts were impregnable, the coexistence equilibrium of superparasites and hosts was stabilized. When the probability of survival of juvenile parasitoids in their host increased with the number of enemy-victim interactions, variability in the defensive capability of hosts contributed to stability of the coexistence equilibrium. Godfray and Hassell (1991) did not investigate Allee effects (Allee 1931) even though host defenses are known to generate them in some cases (Courchamp et al. 2008).

Tree killing bark beetles are in many ways analogous to Hymenopteran superparasites: the host tree typically dies as a result of parasitism; beetle superparasites lay many eggs per tree and numerous female beetles will attack a single host. Moreover, host defenses undoubtedly impact population dynamics as tree defense systems are capable of killing and excluding invading beetles (Raffa and Berryman 1983). As in Hymenopteran superparasites, there is evidence of within-host intraspecific competition in bark beetles that may lead to overcompensation (Berryman 1974; Raffa and Berryman 1983). However, unlike in gregarious Hymenopteran host-parasitoid systems, trees resisting attack by bark beetles are hypothesized to succumb to attack only after a critical number of attacks have been surpassed (Raffa and Berryman 1983; Berryman et al. 1989).

Prior work on the population dynamics of bark beetles has proposed separate models for the population outcomes of cooperative and competitive dynamics (Berryman (Berryman 1974), 1979, 1999). These models require expert opinion to decide at what population density the effects of cooperation cease and the effects of competition dominate. Moreover, the models of Berryman (1974), Berryman (1979), and Berryman (1999) are discontinuous at the beetle population density where the cooperation model and the competition model are joined. Later work on mountain pine beetles has fitted s-shaped curves to account for low mountain pine beetle attack success at low densities (Heavilin and Powell 2008), but these models do not relate the s-shape

to a specific host defense attribute or to a specific level of beetle aggregation. Because Heavilin and Powell (2008) assumed that trees successfully colonized by the mountain pine beetle produced a constant number of beetles, they did not explicitly account for intraspecific competition between beetle larvae. More recently, Duncan et al. (2015) modeled the mountain pine beetle infestation process using a Ricker-like model for scramble competition. Scramble competition occurs within species when resource exploitation by some individuals deprives other individuals, often resulting in starvation or reduced size or fecundity of resource-limited individuals (Price et al. 2011; Nicholson 1954). Bark beetle competition for resources under the bark has long been modeled using scramble competition models similar to the Ricker model (Berryman 1974; Raffa and Berryman 1983).

Inspired by aggressive bark beetle-host systems, we developed a mathematical model wherein the host is able to defend against parasitoid attack and requires a threshold number of attacks before its defense system fails. Once beetles overcome a host and oviposit under its bark, scramble competition occurs among beetle progeny within successfully colonized hosts. Unlike previous work, the model we propose does not require that separate cooperation and competition models be joined at a density selected by expert opinion. We analyzed our model to explore the short-term population dynamics of populations subject to strong positive and negative density-dependent feedback.

Methods

Model derivation

Starting from a host-parasitoid model similar to those of Nicholson and Bailey (1935) and Thompson (1924), we derive a host-parasitoid model suitable for a superparasite that must exceed a minimum number of attacks to colonize a host, but which experiences intraspecific scramble competition among hatchlings within hosts. We consider the number of attacks per host to be a random variable A_t , which describes the number of attacks per host given the mean number of attacks per host is a_t . The probability mass function for A_t is

$$\Pr\{A_t = i | a_t\} = f(i; a_t), \quad (1)$$

and the cumulative distribution function for A_t is

$$\Pr\{A_t \leq j | a_t\} = F(j; a_t) = \sum_{i=0}^j f(i; a_t). \quad (2)$$

If the minimum number of attacks needed to colonize a host is $\phi + 1$, then a general host-parasitoid model without intraspecific competition within hosts can be written as

$$P_{t+1} = cN_t(1 - F(\phi; a_t)), \quad (3a)$$

$$N_{t+1} = \lambda N_t F(\phi; a_t), \quad (3b)$$

where P_t and N_t denote parasitoid and host density in generation t . The c parameter represents the number of parasitoid progeny produced per host and is usually fixed to one for solitary parasitoids (Hassell 1978) while λ is the host geometric growth constant. In both the Thompson and Nicholson-Bailey systems, hosts become infested if they are attacked once or more ($\phi = 0$). Moreover, in the simplest version of both models, attacks or eggs are assumed to be randomly distributed among hosts such that $f(i; a_t)$ follows a Poisson distribution. The assumption of randomly distributed attacks, however, is not met in many systems as attacks tend to be clustered on some hosts while others are unaffected (May 1978). A common way to incorporate aggregation is to assume that $f(i; a_t)$ follows a negative binomial distribution (May 1978):

$$f(i; a_t) = \binom{k}{k+a_t}^k \frac{\Gamma(k+i)}{i! \Gamma(k)} \left(\frac{a_t}{k+a_t} \right)^i = \text{NB}(i; a_t, k), \quad (4)$$

where k is the aggregation parameter (smaller k corresponds to higher aggregation), and $\text{NB}(i; a_t, k)$ represents the corresponding negative binomial probability mass function. Therefore,

$$F(\phi; a_t) = \sum_{i=0}^{\phi} \text{NB}(i; a_t, k). \quad (5)$$

As shown in Appendix A, Eq. 5 can be written without the summation using the regularized incomplete beta function ($I(k, \phi + 1, q)$) (Pearson 1968). Not having to compute large sums greatly facilitates model simulation and fitting. A cumulative density function like Eq. 5 was first used in the context of mountain pine beetles to model aggregation thresholds (Burnell 1977) and then was subsequently adapted for attack thresholds (Krivan et al. 2016). Recently, a model of the form of Eqs. 3 and 5 that featured a cumulative density function was fitted to spatiotemporal mountain pine beetle outbreak data by Goodsman et al. (2016).

Because the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is a herbivorous superparasite that attacks pine tree hosts, Eq. 3 may be adapted to model mountain pine beetle dynamics. Several modifications of Eq. 3 are required, however, for it to be applicable to the mountain pine beetle system. In this system, attack dynamics occur

at much faster time scales (4–12 years) than the pine tree regrowth (20–100 years) and so it is reasonable to assume that $\lambda = 1$.

Female beetles initiate attack on potential host trees, but differ from many Hymenopteran parasitoids in that they typically only oviposit once tree's defenses have been overwhelmed and the tree is killed. Usually, around two thirds of the mountain pine beetle population in any given year is female (Amman and Walter 1983). We assume that each female beetle attacks only one tree. The aggregation modeled by assuming a negative binomial distribution of attacks, however, is an imperfect representation of the distribution of mountain pine beetle attacks because the negative binomial distribution with a high level of aggregation (a small k) implies that many trees in the stand will be attacked only a few times. In reality, because of the clustered nature of attacks in space, most trees in a stand are not attacked and attacks are focused on a small subset of trees (Logan et al. 1998) some of which may receive many more attacks than others. Thus, an appropriate mean attack density per host is

$$a_t = (1/\alpha)(2/3)P_t/N_t, \quad (6)$$

where α represents the proportion of trees that are attacked ($0 < \alpha \leq 1$).

Host trees are fortified against attacking beetles and resist by exuding resin or by encapsulating attackers within lesions. However, if beetles attack at sufficient densities, they exhaust the hosts resources and the host succumbs to attack (Lieutier et al. 2009). Thus, to be applicable to the mountain pine beetle, ϕ must be much greater than one. With these modifications, Eq. 3 becomes

$$P_{t+1} = c\alpha N_t(1 - F(\phi; a_t)), \quad (7a)$$

$$N_{t+1} = (1 - \alpha)N_t + \alpha N_t F(\phi; a_t). \quad (7b)$$

Even when ϕ is allowed to greatly exceed one, Eq. 7 still assumes that each successfully colonized host produces c beetle progeny. Bark beetle offspring are known to suffer from intraspecific competition while they develop under the bark of host trees (Raffa and Berryman 1983), so beetle productivity per tree depends on the density of colonizing beetles. Raffa and Berryman (1983) provided evidence for overcompensating negative density-dependence in mountain pine beetles. We model within-tree competition dynamics using a version of the Ricker equation that accounts for clustering and the higher attack density in successfully attacked trees. We follow an approach similar to that of Ives and May (1985) to derive an expression for beetle productivity in the presence of negative density dependence and aggregation. We assume that if a tree is attacked i times, then the probability of beetle survival decreases as $\exp(-\mu i) = z^i$. Thus, if attacks are clustered on trees according to the

negative binomial distribution and all attacked trees produce beetles, the average number of beetle offspring produced per tree is

$$P_{t+1}/(\alpha N_t) = c \sum_{i=0}^{\infty} i f(i; a_t) z^i, \tag{8}$$

where c is beetle fecundity per attack and the μ parameter in $z = \exp(-\mu)$ represents the negative density-dependence due to larval competition under the bark. Using the negative probability generating function approach outlined in Ives and May (1985), we can write Eq. 8 without the summation as

$$P_{t+1}/(\alpha N_t) = c \sum_{i=0}^{\infty} i f(i; a_t) z^i = c a_t z (1 + a_t/k(1-z))^{-(k+1)}. \tag{9}$$

However, Eq. 9 is the solution for beetle productivity if all attacked trees produce beetles regardless of how frequently they were attacked. In our prior models, we assumed that beetles only reproduce in trees in which the number of beetle attacks exceeds a threshold (ϕ). Therefore, beetle productivity in trees that they successfully attack is less than the productivity in Eq. 9:

$$\begin{aligned} P_{t+1}/(\alpha N_t) &= c \sum_{i=\phi+1}^{\infty} i f(i; a_t) z^i \\ &= c a_t z (1 + a_t/k(1-z))^{-(k+1)} \\ &\quad - c \sum_{i=0}^{\phi} i f(i; a_t) z^i. \end{aligned} \tag{10}$$

Using Eq. 10, system (7) can be rewritten as follows

$$P_{t+1} = c \alpha N_t \left(a_t z (1 + a_t/k(1-z))^{-(k+1)} - \sum_{i=0}^{\phi} i f(i; a_t) z^i \right), \tag{11a}$$

$$N_{t+1} = (1 - \alpha) N_t + \alpha N_t F(\phi; a_t). \tag{11b}$$

Note from Eq. 10 that when $iz^i = 1$, Eq. 11a reduces to Eq. 7a. This formulation accounts for the high level of competition that juvenile beetles experience in successfully attacked trees due to the high attack densities that are required to overcome host defenses. It, however, assumes that competition results from random encounters between juvenile beetles. In reality, beetle competition under the bark of host trees likely comprises multiple mechanisms including larvicide by other competing larvae, competition for food resources, and the transmission of disease and mites (Cole 1973).

Data and parameter estimation

Our model of mountain pine beetle dynamics (11) contains five parameters that need to be estimated (α , c , k , ϕ , and μ). The parameter c is the number of offspring that enters the life stage in which competition occurs (the larval life stage for mountain pine beetles). An estimate for the number of larvae per mated pair of mountain pine beetles was obtained from Goodsman et al. (2012). The estimate comes from counting the mean number of larval gallery starts per female ($c = 35$ offspring(female)⁻¹) in logs that were artificially infested at constant low densities (see Fig. 3a in Goodsman et al. (2012)). We estimated the remaining parameters (α , k , ϕ , and μ) by fitting Eq. 11 to data collected by Parker (1973) and Klein et al. (1978). These data record the initial number of host trees and the number killed by mountain pine beetle in each year of a 7-year mountain pine beetle outbreak that began in 1966 in Yellowstone National Park (USA). In addition, Klein et al. (1978) counted attack density as well as the number of beetle emergence holes in infested trees to estimate the number of adult flying beetles in each year in the same study plots.

To fit Eq. 11 to the data given in Klein et al. (1978) (reproduced in online Appendix B), we divided the parameters into two sets. To fit parameters related to host tree infestation (ϕ , α , and k), we fitted Eq. 11b to the density of hosts ($N_{t=1}$) in each year as a function of the number of hosts and emerged beetles in the previous years. We then estimated μ by fitting Eq. 11a to the density of emerged beetles in each year (P_{t+1}) given the density of emerged beetles and host trees in the previous year. In both cases, we fitted the square root of the right hand sides of Eq. 11a and b to the square root of the observed data as this normalized the residuals. All model fitting was done using the standard nonlinear least squared (nls) function in the free and open source R software package (Core Team 2015) (Code for model fitting is available upon request from the authors).

Analysis of dynamics

To analyze the mountain pine beetle host system (11), we defined as a new variable, the ratio (R_t) of emerged adult beetles to susceptible host trees:

$$R_t = \frac{P_t}{N_t}. \tag{12}$$

we then reformulated Eq. 11 into a single difference equation in terms of R_t :

$$R_{t+1} = \frac{c \alpha a_t z (1 + a_t/k(1-z))^{-(k+1)} - c \alpha \sum_{i=0}^{\phi} i f(i; a_t) z^i}{1 - \alpha + \alpha F(\phi; a_t)} = g(R_t), \tag{13}$$

in which $a_t = (1/\alpha)(2/3)R_t$. This difference equation is transcendental and, therefore, difficult or impossible to solve analytically for its steady states. Instead, we solved for the non-zero equilibria numerically using the `uniroot.all` function in the `rootSolve` (Soetaert 2009; Soetaert and Herman 2009) R package.

To compute the stability of equilibria in the ratio state space, we calculated the derivative of Eq. 13 with respect to R . By determining the magnitude and sign of this derivative with respect to R at the equilibria, we were able to compute their stability. We varied the beetle fecundity (c) and competition (μ) parameters with all other parameters fixed at the values estimated using the Klein et al. (1978) data.

The susceptibility of mountain pine beetle populations to collapse is of interest to managers who may want to push mountain pine beetle populations toward collapse. We call mountain pine beetle populations susceptible to collapse if there is a ratio of beetles to trees ($R_a < R_n < R_u$) that is above the Allee threshold (R_a) and below the upper equilibrium (R_u) but which, nevertheless, guarantees that R_{n+1} is below the Allee threshold. Note that in our mountain pine beetle model, the Allee threshold (R_a) is the stand-level manifestation of the tree-level attack threshold (ϕ), but the two are not equivalent. If the functional composition of the discrete-time map ($g(R_t)$) at its maximum value ($M = g(R_{max}) = \max g$) is less than the Allee threshold (R_a),

$$g^2(M) = g \circ g(M) < R_a, \tag{14}$$

then R_{max} satisfies the condition for susceptibility to collapse (the circle operator in 16 represents the functional composition). Therefore, initializing the population with R_{max} will result in the sudden collapse of the mountain pine beetle population (Fig. 1).

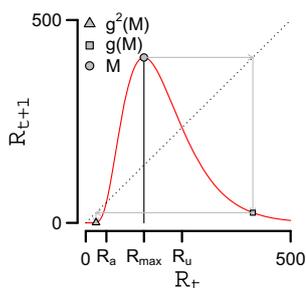


Fig. 1 Populations that experience strong Allee effects and overcompensating negative density-dependence may be susceptible to sudden collapse. If the functional composition of the discrete-time map with itself at M satisfies $g^2(M) < R_a$, then the population is susceptible to collapse as there is at least one value of R that is greater than the Allee threshold R_a and less than the upper equilibrium R_u that will lead to extinction

Error analysis

Prediction error due to uncertainty in model parameter estimates can be computed using error analysis. Our method of error analysis follows that of Mood (1950) and Pacala et al. (1996). To propagate error from parameter estimate uncertainty, we sampled from a multivariate normal distribution with means given by our vector of parameter estimates and variance and covariance given by the estimated covariance matrix. We drew 2000 random samples from this multivariate normal distribution and computed model predictions for each draw using Eq. 13. We were, thus, able to estimate quantile-based 95 % confidence intervals around model predictions of R_{t+1} as a function of R_t .

Demographic stochasticity

We constructed a version of Eq. 11 with demographic stochasticity for comparison to the deterministic model. To construct a stochastic version of Eq. 11, we assume that the number of beetles produced in the entire stand is a Poisson random variable (X_{t+1}) with a mean (x_{t+1}) that is derived from Eq. 11a and the number of surviving host trees is a binomial random variable (Y_{t+1}) with a probability of survival derived from Eq. 11b. Throughout this work, we have assumed that the number of beetle attacks per tree is a negative binomial random variable, but we now call this random variable Z_t and write it in terms of X_t and Y_t :

$$Z_t \sim NB((2/3)(1/\alpha)X_t/Y_t, k). \tag{15}$$

Thus, the equations that govern the Poisson number of beetles in the stand are

$$X_{t+1} \sim Poiss(x_{t+1}), \tag{16a}$$

$$x_{t+1} = c\alpha Y_t \left(Z_t z(1 + Z_t/k(1 - z))^{-(k+1)} - \sum_{i=0}^{\phi} if(i; Z_t) z^i \right), \tag{16b}$$

and the equations that govern the binomial number of remaining host trees are

$$Y_{t+1} \sim binom(Y_t, p_{surv}), \tag{17a}$$

$$p_{surv} = 1 - \alpha + \alpha F(\phi; Z_t), \tag{17b}$$

To iterate a stochastic version of Eq. 11, we initialized the stochastic model using a mean of R_0 and drew a negative binomial random variable, Z_0 according to Eq. 15. We then computed X_1 using Eq. 16 and Y_1 using Eq. 17 with an initial number of hosts set to Y_0 . Using X_1 and Y_1 , we drew a new random variable, Z_1 , from the negative binomial distribution. This procedure was iterated for 50 generations.

Results

Model fits

The population dynamics model (11 or equivalently 13) fitted the data well (Fig. 2). The ϕ parameter estimate (Table 1) is consistent with the attack threshold used by Powell and Bentz (2009) and the *per capita* beetle productivity predicted by our model (Fig. 2b) is similar to values estimated from data (Cerezke 1995). The validity of the other parameter estimates (α , k , and μ) is more difficult to establish as they have not previously been quantified.

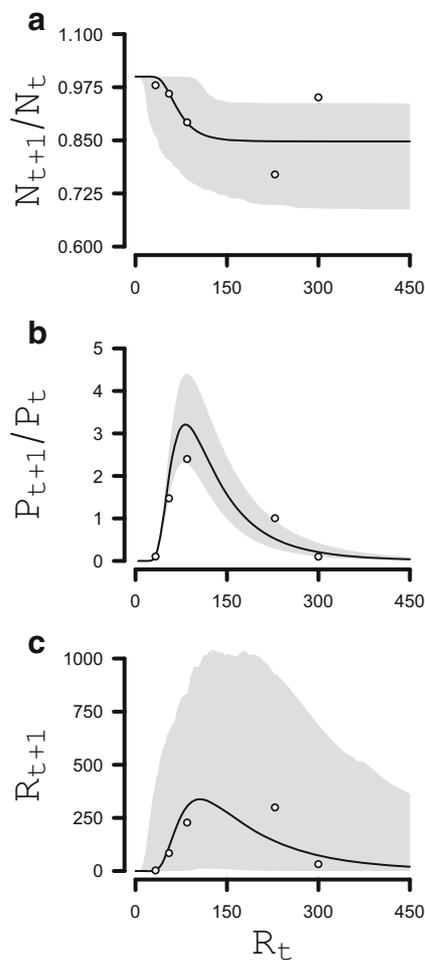


Fig. 2 Panel **a** shows the *per capita* host tree (N_t) mortality model derived from Eq. 11b fitted to data on mountain pine beetle caused tree mortality as a function of the ratio of emerged beetles to host trees (R_t); panel **b** shows the *per capita* beetle productivity model derived from Eq. 11a fitted to data on emerged beetles (P_t) as a function of R_t ; panel **c** shows the reduced discrete-time map (13) fitted to observed ratios of emerged beetles to host trees (R_t and R_{t+1}). All of the data shown are from Klein et al. (1978). Parameter estimates obtained by least squares fitting are in Table 1. Shaded regions represent 95% confidence intervals computed using error analysis as described in the text

Table 1 Estimates for the parameters in Eq. 11 obtained by nonlinear fitting to data from Klein et al. (1978) and from experimental results of Goodsman et al. (2012)

Parameter	Estimate (SE)	Units
α	1.52e-1 (6.73e-2) ^a	Unitless
ϕ	289.32 (142.93)	Attacks
k	8.47 (33.50)	Unitless
c	35.0 ^b (NA)	Offspring(female) ⁻¹
μ	4.18e-3 (4.22e-4)	(Attacks/host) ⁻¹

^aThis is the transformed standard error (parameter that was fitted was δ in $\alpha = \exp(-\delta)$)

^bThis parameter was estimated from Goodsman et al. (2012) for which estimates of the standard error are unavailable

Dynamical behavior

To understand the population dynamics predicted by Eq. 11 when its parameters are determined by fitting it to the data of Klein et al. (1978), we can iterate the discrete-time map of Eqs. 11 and 13 (Fig. 3). The model predicts an accelerating population explosion followed by a rapid collapse that is consistent with observations (Fig. 3).

When $\phi = 289$ attacks as estimated using the Klein et al. (1978) data set, and $k = 8.47$, but the degree of negative density-dependence within hosts (μ) and beetle fecundity (c) are varied over biologically realistic ranges, non-zero equilibria can disappear (marked as nonexistence in Fig. 4a). Conversely, the zero equilibrium of Eq. 13 always exists, is always stable, and corresponds to parasitoid collapse. In parameter ranges where non-zero equilibria existed, we always observed two (Fig. 4b). The lower non-zero equilibrium was always unstable when present (Fig. 4b) but the upper non-zero equilibrium was stable, stable and oscillatory or unstable and oscillating depending on the values of the c and μ parameters (Fig. 4). Note that the upper non-zero equilibrium of Eq. 13 is unstable and oscillating in the majority of the plausible parameter space of c and μ (Fig. 4a).

For the parameter values estimated using the Klein et al. (1978) data when $k = 8.47$, the dynamics of the system (11 or 13) can be classified as susceptible to collapse according to our criterion (14) (see point C in Fig. 4a). When parameter values satisfy this criterion, beetle populations are very likely to irrupt and then collapse suddenly even when they initially exceed the Allee threshold as oscillations about the upper equilibrium in ratio-state space quickly push the beetle population below its Allee threshold. Dynamics in the susceptible to collapse region of this parameter space (Fig. 4a) exhibit violent boom-bust dynamics characterized

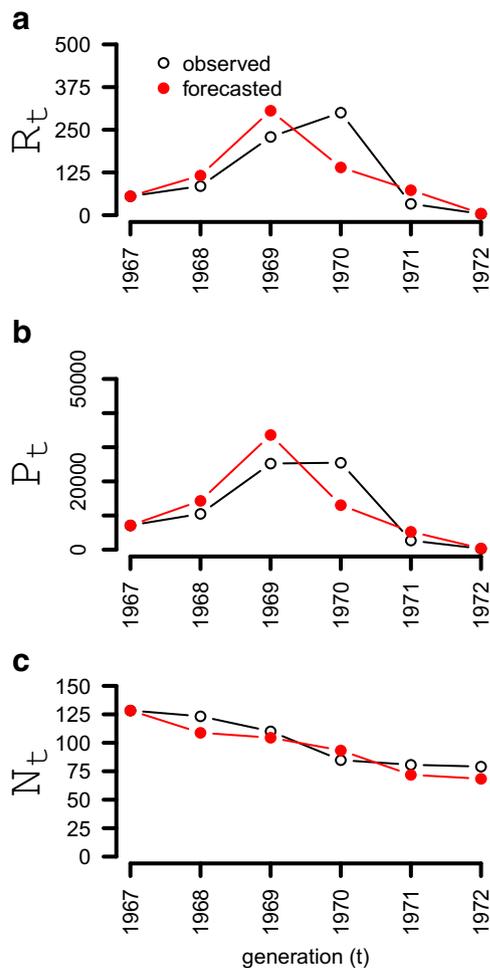


Fig. 3 A demonstration of the use of iteration to forecast the outbreak dynamics observed by Klein et al. (1978) using the fitted model (11) with $c = 35$ offspring(female)⁻¹, $\phi = 289$ attacks, $k = 8.4749$, and $\mu = 0.00418$ (attacks/host)⁻¹, and $\alpha = 0.152$. Panel a shows one step ahead forecasting using model (13) for the ratio of emerged beetles to host trees (R_t). Panel b shows one step ahead forecasting using the model (11a) for emerged beetles (P_t). Panel c shows one step ahead forecasting for the model (11b) for susceptible host trees (N_t). The outbreak collapses before all susceptible host trees are killed

by irruption followed by sudden collapse in the space of 5 or 6 years.

As mountain pine beetle fecundity increases, a bifurcation occurs and two non-zero equilibria appear in the ratio state space of Eq. 13 (Fig. 5a). The lower equilibrium is unstable, the upper equilibrium is initially stable (Fig. 5a), and the zero equilibrium is always stable. With further increases in fecundity, the upper equilibrium in ratio state space exhibits damped oscillations and then becomes unstable and oscillatory (Fig. 5a). However, the interpretation of the stability of the fixed points of Eq. 13 have a subtle meaning when translated back to the original system (11). Fixed points

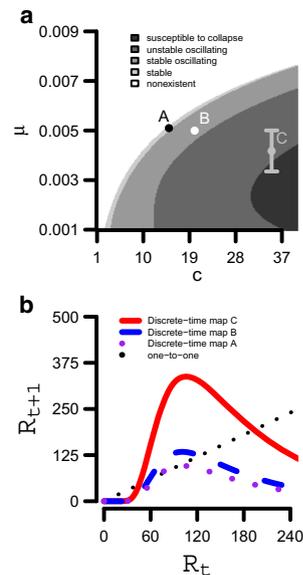


Fig. 4 Panel a shows analysis of the existence and dynamical behavior of the higher equilibrium in ratio state space of Eq. 13 with $k = 8.47$, $\phi = 289$ attacks, and $\alpha = 0.152$ when negative density-dependence (μ) and beetle fecundity (c) are varied. Note that equilibria in ratio state space do not imply equilibria in the original state space of the model (11). When beetle populations are susceptible to collapse, the upper equilibrium is oscillatory and unstable and condition (14) in the text is satisfied. The point C corresponds to the parameter estimates based on the data of Klein et al. (1978) in Table 1 with 95 % CI shown. In panel b, example discrete-time maps from the parameter space shown in the preceding figure are plotted. The upper equilibrium can be stable (map A), stable with dampening oscillations (map B), or unstable and oscillating (map C). For discrete-time map A, $c = 15$ offspring(female)⁻¹ and $\mu = 0.0051$ (attacks/host)⁻¹. For discrete-time map B, $c = 20$ offspring(female)⁻¹ and $\mu = 0.005$ (attacks/host)⁻¹

in the ratio state-space of Eq. 13 are lines and not points in the phase-plane of Eq. 11. Thus, the system exhibits a unique bistability, in which even when beetles are above the Allee threshold, they eventually go extinct as they deplete their supply of hosts (Fig. 5b). Note that the simultaneous extinction of hosts and beetles is a unique feature of our ratio-dependent formulation that differs from the original Nicholson-Bailey model in which parasitoids drive their host populations down and then go extinct, permitting a subsequent population explosion of hosts. As fecundity increases, the dynamics of the system transition from damped to unstable oscillations about the upper equilibrium in the phase-plane (Fig. 5c–d). These unstable oscillations generate transient population irruptions followed by rapid population collapses as beetle populations fall into the Allee trap. Note that the original system (Eq. 11) has no non-zero equilibria and that the non-zero equilibria in the ratio state space of (13) do not correspond to non-zero equilibria in the original state space of Eq. 11.

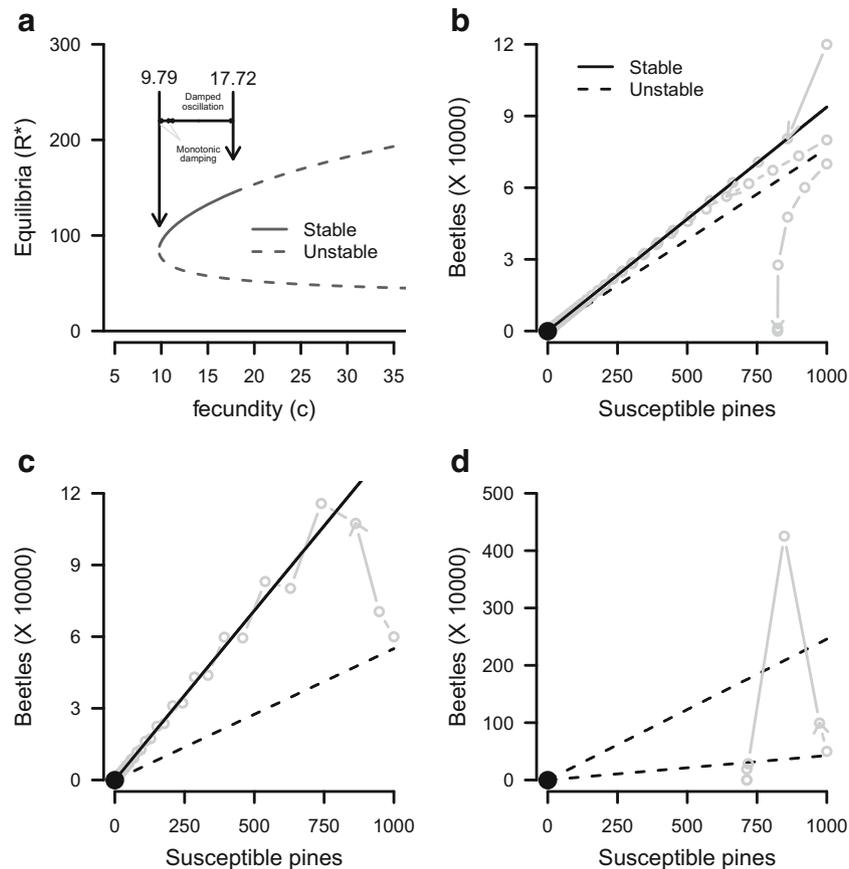


Fig. 5 The dynamics of Eq. 11 with $\phi = 289$ attacks, $\alpha = 0.152$, $k = 8.4749$, and $\mu = 0.00418$ (attacks/host) $^{-1}$ can be analyzed when fecundity (c) varies using a bifurcation diagram as shown in panel a. The unusual dynamics of Eq. 11 or equivalently Eq. 13 can be better understood using phase-plane diagrams in which gray lines with open circles represent model trajectories. In panel b, the phase-plane diagram for the parameter values listed above and $c = 10$ offspring(female) $^{-1}$ exhibits bistability with beetles going extinct if they are below the Allee threshold of Eq. 13 (dashed line).

When fecundity is higher ($c = 17$ offspring(female) $^{-1}$), the trajectory of systems initialized above the Allee threshold exhibit damped oscillations around the upper equilibrium (solid line) as shown in panel c. When $c = 35$ offspring(female) $^{-1}$ and $\mu = 0.0033$ (attacks/host) $^{-1}$, both non-zero equilibria are unstable (dashed lines) and trajectories that are initialized above the Allee threshold oscillate erratically around the upper equilibrium until pushed below the Allee threshold (lower dashed line) as shown in panel d

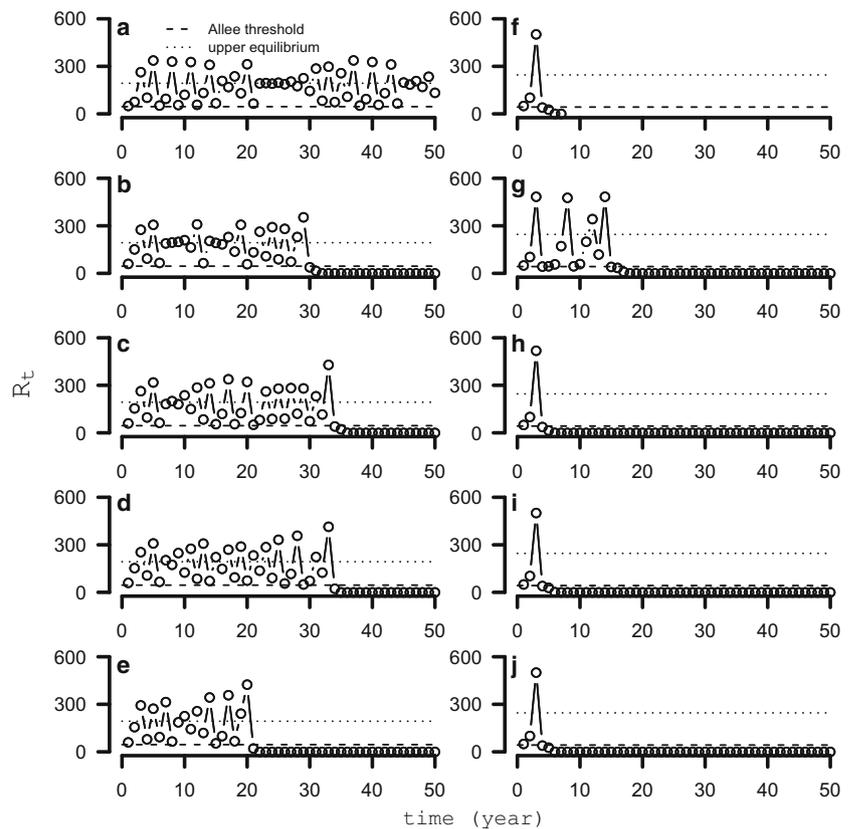
Demographic stochasticity

For simulations in which the upper equilibrium is unstable, as in point C in Fig. 4a–b, deterministic and stochastic simulations are generally quite similar. When $\mu = 0.00418$ (attacks/host) $^{-1}$ deterministic and stochastic dynamics in ratio space both appear chaotic (Fig. 6a–e). When we increased density dependence by decreasing μ to $\mu = 0.0033$ (attacks/host) $^{-1}$, which is the lower bounds of our 95 % confidence interval on the parameter estimate, boom-bust dynamics became apparent and stochastic dynamics were often indistinguishable from deterministic dynamics (Fig. 6f–j). Note that when $\mu = 0.0033$ (attacks/host) $^{-1}$ and $c = 35$ offspring (female) $^{-1}$, our criterion for susceptibility to collapse (14) is satisfied.

Discussion

Strong Allee effects in combination with overcompensating negative density-dependence can generate dramatic boom-bust dynamics in exploiter populations. That oscillating dynamics can drive populations below their Allee thresholds was anticipated by Schreiber (2003) for single species models with Allee effects and negative density dependence. In this paper, we provide empirical and theoretical support for the existence of such dynamics in the mountain pine beetle system. Unlike the models proposed and analyzed in Schreiber (2003), where the Allee effect and competition depend on the density of individuals in the population, our model has these features in the ratios of attackers (beetles) to hosts (trees). This leads to complex dynamics of the form

Fig. 6 A comparison of the dynamics of deterministic and stochastic versions of (11) or equivalently (13). Deterministic dynamics for two slightly different parameter sets are shown in the *top row* (panels **a** and **f**). Stochastic runs in panels **b–e** have the same parameters as the deterministic model run in panel **a** and stochastic runs in panels **g–j** share parameter values with the deterministic model run in panel **f**. In all model runs $k = 8.4749$, $\phi = 289$ attacks, $\alpha = 0.152$, and $c = 35$ offspring(female) $^{-1}$. In all simulations in the left column $\mu = 0.00418$ (attacks/host) $^{-1}$, whereas in all simulations in the right column $\mu = 0.0033$ (attacks/host) $^{-1}$. The value shown on the vertical axes in all cases is the ratio of beetles to host trees



shown in Fig. 5, where even a stable equilibrium in the ratio of attackers to hosts can lead to the eventual extinction of both. Although the asymptotic dynamics of the model may lead to some unrealistic predictions as host densities diminish, the transient dynamics of the model in the short term can generate booms and busts that are frequently observed in mountain pine beetle populations. The mountain pine beetle is subject to both positive and negative density-dependence of the type required for these irruptive dynamics.

Our argument for the importance of overcompensating negative density-dependence as a driver of boom-bust dynamics in this system does not negate the significance of winter beetle mortality in mountain pine beetle population crashes. Instead, we contend that in addition to the negative impacts of extreme cold, host depletion results in more beetles inhabiting fewer host trees—a scenario with potentially deleterious consequences for the mountain pine beetle. In fact, cold-weather events that increase mountain pine beetle mortality may interact with positive and negative density-dependent drivers of population dynamics. Specifically, stochastic cold-weather events could force populations below their Allee threshold, leading to a switch from an epidemic to an endemic regime where beetle populations are all but invisible. Such interactions between stochastic external drivers and endogenous unstable

thresholds can produce regime shifts due to alternate attractors (Heavilin and Powell 2008; Martinson et al. 2013). Alternatively, extreme warm events that lead to high beetle overwinter survival could destabilize populations leading to oscillations that quickly result in extinction when they force beetle populations below the Allee threshold.

Many herbivorous forest insect populations outbreak and then collapse before all susceptible hosts trees are infested or exploited (Cooke and Lorenzetti 2006; Kausrud et al. 2012). As we consider the mountain pine beetle to be a parasitoid, such a collapse could be considered an instance of the biological control paradox (Arditi and Berryman 1991). The paradox of biological control in the original Nicholson-Bailey model arises because efficient parasitoids deplete their hosts, precipitating their own extinction followed by an explosion of the unchecked host population. As parasitoid extinction is inevitable in the original Nicholson-Bailey model, ecologists have endeavored to stabilize the coexistence equilibrium in subsequent host-parasitoid models (Mills and Getz 1996).

For many forest insect systems, including the mountain pine beetle system, instability of the coexistence equilibrium may be more realistic than stable coexistence. Moreover, unlike in traditional host-parasitoid models, host tree populations in forest ecosystems do not appear to grow

geometrically when their exploiters go locally extinct because the time scale of insect attack is much shorter than the time scale of host reproduction. In this scenario, transient or non-equilibrium dynamics are more relevant than asymptotic dynamics (Hastings 2004). Dynamics that require hundreds of years to stabilize are overshadowed by the effects of regularly returning forest fires in pine systems. Therefore, dramatic transient changes to forests that occur over 5 or 6 years are more interesting and relevant to ecologists and forest managers than equilibrium predictions.

Our formulation of the mountain pine beetle host-parasitoid model is unique in that it allows us to analyze non-equilibrium dynamics using techniques conventionally used for the analysis of asymptotic dynamics. In fact, our original system (11) has no non-zero equilibria. However, by analyzing equilibria in ratio state space of Eq. 13 we are able to gain insight into the transient dynamics of Eq. 11. This was not planned during the derivation of our models. Instead, we drew inspiration from the host-parasitoid model of Thompson (1924). Models in which dynamics depend on the ratios of enemies to victims are relatively rare, but Crofton (1971) and May (1977) constructed models in which host mortality was a function of the ratio of parasites to hosts. The models of Crofton (1971) and May (1977), however, are fundamentally different from our own model because a host's death in their models results in the death of its internal parasites. In our models, and in those of Thompson (1924), Crofton (1971), and May (1977), enemy victim ratios increase without bounds as the density of victims becomes small. Thus, the use of ratios of enemies to victims in models can lead to unrealistic predictions. In our models, especially in their stochastic versions, this is of less concern because beetle populations generally collapse due to negative density dependence before they drive their hosts extinct. However, more complex and process-based representations of the beetle's interaction with its host do not rely on enemy victim ratios (White and Powell 1997; Logan et al. 1998).

Dynamical mountain pine beetle models fall on a complexity continuum. The most realistic of these are spatially explicit and account for beetle flight in an environment of diffusing host kairomones and attractive and repulsive beetle pheromones (White and Powell 1997; Logan et al. 1998; Strohm et al. 2013). We admit that more realistic models such as those of White and Powell (1997) and Logan et al. (1998) are likely to provide better predictions over a wider range of conditions than models such as our own. Another limitation of relatively simple difference equation-based models like ours is that incorporating more realistic representations of the phenology of attacking insects is difficult because most biological difference equation models implicitly assume that organisms reproduce and mature

in perfect synchrony. Imperfect synchrony, in the form of phenological variability, can have a profound impact on insect dynamics (Logan et al. 1998). However, the primary motivation behind our model of mountain pine beetle dynamics was to provoke and demonstrate that the interaction of positive and negative density-dependence may drive some of the boom-bust dynamics that we observe in populations of mountain pine beetles and other outbreak insects. Although it is relatively simple, the model we have proposed has much richer dynamics than other simple mountain pine beetle models featuring Allee thresholds. For example, the Allee threshold model of Heavilin and Powell (2008) is only capable of representing bistability in which beetle populations irrupt if they are above their Allee threshold and collapse if they are below it. Our model, although also simple, can exhibit transient oscillations in beetle populations that can either remain above the Allee threshold or can oscillate erratically until they fall below it.

The dynamics of laboratory populations of flour beetles (*Tribolium castaneum* Herbst) have been shown to coincide with the predictions of deterministic models similar to the one we use in this study (Dennis et al. 1995; Constantino et al. 1995; Dennis et al. 1997; Dennis et al. 2001). Subsequent studies, however, have highlighted some important differences between the dynamics of deterministic nonlinear population models and their stochastic analogs in which state variables are restricted to discrete values (Henson et al. 2001). Specifically, the addition of stochasticity and discrete-valued state variables can cause trajectories to alternate between different dynamical regimes expected in deterministic models (Henson et al. 2001). For example, a discrete valued stochastic model of the *Tribolium* system alternates between chaos and a six point cycle as do laboratory populations when their rates are appropriately manipulated (Henson et al. 2001). Based on these findings, it is natural to expect that the addition of demographic stochasticity might alter the dynamics that we predicted in our deterministic analysis. In our numerical study of stochastic versions of our host-parasitoid model, however, we found that when the upper equilibrium is unstable and oscillating, the deterministic and stochastic models exhibit very similar dynamics—especially when populations meet the criteria for susceptibility to collapse (14). The dynamics of deterministic and stochastic versions of our model do differ when the upper equilibrium of the deterministic model in ratio-space is stable and oscillating or unstable and oscillating: Whereas the deterministic model predicts persistence of beetles and their host trees, the stochastic model predicts a beetle outbreak that lasts 10–40 generations before eventually collapsing. Stochastic variability around the upper equilibrium drives this dynamic by eventually pushing the population below its Allee threshold, thereby leading to collapse. Thus, in stochastic systems, even when the population

gravitates toward a stable equilibrium, the presence of an Allee threshold can result in sudden crashes that are not predicted in deterministic systems.

In the system we have studied, parasitoids are not evenly or randomly distributed among potential hosts, however, and the aggregation parameter of the negative binomial distribution for the number of attacks allows some hosts to be attacked many times while the majority are attacked very few times or not at all. An implicit assumption in our models is that the level of aggregation remains constant over the outbreak period. Although this assumption facilitates model fitting, in reality, it is advantageous for organisms subject to positive and negative density-dependence to modulate aggregation to maximize positive density-dependent effects while minimizing negative density dependence as their density changes (Ives 1992; Rohani et al. 1994). In tree killing bark-beetles, for example, aggregation pheromones are produced by attacking beetles in order to attract a sufficient number of conspecifics to overcome host defenses (Conn et al. 1983). Once a tree succumbs to attack, anti-aggregation pheromones are released and conspecifics will move into surrounding host trees that are less crowded (Lindgren and Miller 2002). Because of this mechanism, small mountain pine beetle populations focus their attack on only one or two trees, whereas large populations may attack most of the susceptible host trees in a stand (Safranyik and Carroll 2006).

Capitalizing on strong Allee effects in forest insects to manage outbreaks is a popular idea in forest ecology (Liebhold and Tobin 2008; Tobin et al. 2011). The type of non-equilibrium dynamics we demonstrate in this work suggest that when strong Allee effects are present, negative density-dependence might also be exploited by forest managers to hasten outbreak collapse. For example, when exploiter populations are high, removing some of their potential host trees may force overcrowding in the remaining hosts which could lead to a sudden exploiter population crash.

Conclusion

That the dynamics of the mountain pine beetle host system depend on interactions that occur outside the host during the colonization process as well as on intraspecific competition inside the host will not be surprising to ecologists. What is surprising is how oscillating dynamics driven by overcompensating competition can generate boom-bust transient dynamics that are not predicted by mountain pine beetle models that ignore beetle competition. In this work, we have presented a model that illustrates how interactions between nonlinear positive and negative feedback that are hallmarks of insect populations may underlie the boom-bust dynamics they often exhibit.

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Appendix A: Negative binomial CDF

Here, we provide details that describe how the negative binomial cumulative distribution function can be written in terms of a regularized incomplete beta function ($I(k, \phi + 1, a_t)$). Pearson (1968) showed that Eq. 5 can be rewritten as

$$F(\phi; a_t) = I(k, \phi + 1, q), \tag{A.1a}$$

$$q = k/(k + a_t), \tag{A.1b}$$

where

$$I(k, \phi + 1, q) = \frac{B(k, \phi + 1, q)}{B(k, \phi + 1, 1)}. \tag{A.2}$$

The numerator in Eq. A.2 is the incomplete beta function

$$B(k, \phi + 1, q) = \int_0^q t^{k-1} (1 - t)^\phi dt, \tag{A.3}$$

and the denominator is the beta function

$$B(k, \phi + 1, 1) = \int_0^1 t^{k-1} (1 - t)^\phi dt. \tag{A.4}$$

Thus, the general host-parasitoid equation (3) can be rewritten as

$$P_{t+1} = cN_t(1 - I(k, \phi + 1, q)), \tag{A.5a}$$

$$N_{t+1} = \lambda N_t I(k, \phi + 1, q), \tag{A.5b}$$

$$q = k/(k + a_t), \tag{A.5c}$$

under the assumption that attacks are negative binomially distributed among hosts and an attack threshold of ϕ attacks must be exceeded for hosts to become exploitable.

Similarly, Eq 11 can be rewritten as

$$P_{t+1} = c\alpha N_t \left(a_t z (1 + a_t/k(1 - z))^{-(k+1)} - \sum_{i=0}^{\phi} i f(i; a_t) z^i \right), \tag{A.6a}$$

$$N_{t+1} = (1 - \alpha)N_t + \alpha N_t I(k, \phi + 1, q). \tag{A.6b}$$

$$q = k/(k + a_t), \tag{A.6c}$$

$$a_t = (1/\alpha)(2/3)P_t/N_t, \tag{A.6d}$$

and the corresponding discrete time map in ratio state space (13) can be written

$$R_{t+1} = \frac{c\alpha(a_t z(1 + a_t/k(1 - z))^{-(k+1)} - \sum_{i=0}^{\phi} i f(i; a_t) z^i)}{(1 - \alpha) + \alpha I(k, \phi + 1, q)}, \quad (\text{A.7a})$$

$$q = k/(k + a_t), \quad (\text{A.7b})$$

$$a_t = (1/\alpha)(2/3)R_t. \quad (\text{A.7c})$$

Although this notation makes the model slightly less readable, it makes it more amenable to fitting to data and simulation.

Appendix B: Data

Here we supply the data from (Klein et al. 1978) that we used to fit (11). We were unable to fit all five parameters (c , α , ϕ , k , and μ) in (11) at the same time with only five data-points and so we fixed the c parameter to 35 offspring(female)⁻¹, the estimate of the initial number of larvae produced per female with minimal competition (Goodsman et al. 2012). All other parameters were fitted to the (Klein et al. 1978) data.

The number of beetles present in study plots was estimated by (Klein et al. 1978) by counting emergence holes on successfully attacked trees and multiplying by the density of attacked trees. These data are expressed in terms of thousands of emergence holes(acre)⁻¹ in Fig. 4 of (Klein et al. 1978). Assuming that, on average, one beetle emerges from each emergence hole, we can estimate the number of beetles at large per acre in each year. These data were obtained from Fig. 4 (Klein et al. 1978) using WebPlot-Digitizer software (<http://arohatgi.info/WebPlotDigitizer/>). Because the density of trees that were susceptible to mountain pine beetle attack per acre was also recorded ((Klein et al. 1978) Table 1), it was simple to compute the ratio (ratio in table below) of beetles (emerged in table below) to

Table 2 Data from Klein et al. (1978) that were used to fit (11)

Emergence year	Emerged (1e3)(acre) ⁻¹	Hosts stems (acre) ⁻¹	Ratio
1967	7.11	128.40	55.37
1968	10.50	123.30	85.14
1969	25.22	110.10	229.11
1970	25.46	84.80	300.29
1971	2.69	80.70	33.29
1972	0.29	79.10	3.71

The year of emergence, an estimate of the number of emerging beetles in thousands per acre and an estimate of the density of host trees per acre are provided. The ratio variable is the density of emerged beetles divided by the density of host trees. Note that the original raw data have been rounded to two decimal places

susceptible trees (hosts in table below). Note that the density of hosts per acre is recorded but the smallest diameter class (six inch diameter at breast height) listed in Table 1 of (Klein et al. 1978) was not included as six inch diameter at breast height trees were too small to be susceptible to mountain pine beetle attack.

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