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Quantifying the Effects of Integrated Pest Management in Terms of Pest Equilibrium Resilience

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1. Introduction

Bistability is increasingly recognized as a mechanism underlying patterns in a wide variety of ecological time series (reviewed in Scheffer & Carpenter, 2003). One consequence of bistability is that a system can be in either of two stable states for a given set of conditions, each stable state being surrounded by a basin of attraction. Such bistability provides one explanation for pest outbreaks because pest populations can cross a threshold from a low-density, biologically-controlled equilibrium and enter into the basin of attraction of a high-density outbreak equilibrium (see e.g., Ludwig et al., 1978). In such systems, integrated pest management has the dual goal of simultaneously decreasing the magnitude of the outbreak basin of attraction and perturbing the pest population back across the threshold to the biologically controlled state. Decreases in the magnitude of the outbreak basin of attraction arise when management strategies alter basic biological parameters, such as the realized rate of population growth. For example, releasing sterile males decreases fecundity, and hence, birth rates diminish in relation to death rates (Knipling, 1970). Similarly, introduction of predators with larger half-saturation constants changes the landscape of equilibria in favor of biological control (Drury & Lodge, 2008). In the presence of such factors, the required magnitude of direct pest reductions decreases, because the state of the outbreak system moves closer to the threshold between equilibria (e.g., moving leftwards on the top line in Fig. 1). Relatively smaller pest reductions can therefore move the state of the system across the threshold and into the biologically controlled basin of attraction. Here we quantify the effects of such species manipulations in terms of equilibrium resilience to demonstrate how targets can be computed so that pest control schedules can be devised (e.g., Drury, 2007). Our definition of resilience is the distance between an equilibrium and a threshold, which is one component of classical definitions describing the characteristic return time to equilibrium following perturbations (Pimm, 1984).

2. The spruce budworm model

The Spruce budworm model has a long history in ecological pest management (Ludwig et al., 1978) and has the advantage of being a relatively simply model that nevertheless contains components of integrated pest management while generating bistable dynamics (Strogatz,

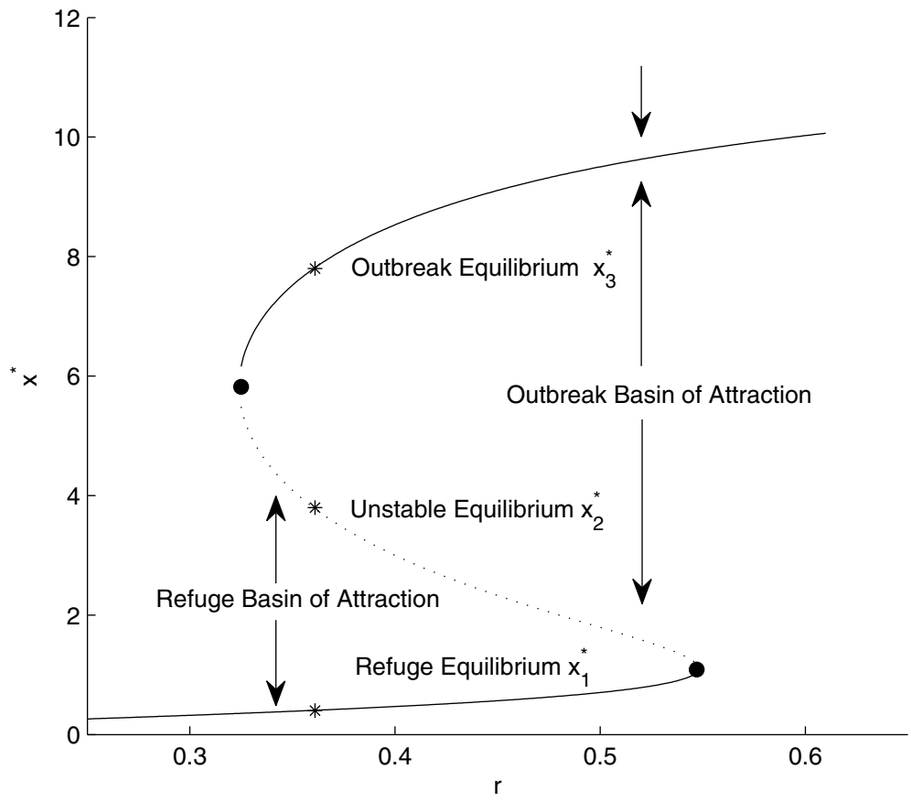

Fig. 1. As the parameter r (from Eq. (2)) is increased above 0.3, two new equilibria emerge and the potential for outbreaks is introduced. At large values of r, only the outbreak equilibrium exists.

Parameter	Meaning	Value in this study
R	population growth rate	0.25
K	carrying capacity	15
B	maximal predator attack rate	0.75
A^2	predator half-saturation constant	1

Table 1. Parameters of Eq. (1), their meanings, and representative values used in this study.

1994). Letting X represent pest population density, and using the parameters in Table 1, the model is,

$$\frac{dX}{dt} = RX\left(1 - \frac{X}{K}\right) - \frac{BX^2}{A^2 + X^2}, \tag{1}$$

where the first term represents logistic growth and the second term represents a Holling type III functional response, which means that predators switch to the pest at some intermediate density, but nevertheless become sated at higher densities thus allowing the pest to escape control.

The dynamics of Eq. (1) are often studied at equilibrium by first nondimensionalizing (see e.g., Murray, 2002). For example, with $x = \frac{X}{A}$, $r = \frac{AR}{B}$, $k = \frac{K}{A}$, and $\tau = \frac{Bt}{A}$ as nondimensional parameter groups this yields

$$r\left(1 - \frac{x}{k}\right) = \frac{x}{1 + x^2}. \tag{2}$$

This strategy has the advantage of specifying the left-hand side as a linear function of x that when equal to the right-hand side, specifies equilibria. It is thus a simple matter to plot the two sides of the equation on the same axes to see where they intersect (see the solid lines in Fig. 2). Furthermore, the effects of changes to r and k can be seen by fixing one and varying the other and evaluating the effects on equilibria values. This qualitative approach has obvious intuitive appeal and provides heuristic guidance for pest management. Nevertheless, as composite parameter groupings, r and k can be difficult to interpret in practice. Additionally, direct pest control measures often require specific objectives, e.g., assessment of pest populations in relation to some economic threshold (Pedgrigo & Zeiss, 1996), which can be difficult to extract from such qualitative exercises. Thus, we revisit Eq. (1) with the goal of developing quantitative methods for assessing the effects of integrated pest management in terms of relative equilibria positions, which in turn allows quantitative predictions of necessary direct pest control measures (such as spraying insecticides).

3. Model analysis

To analyze Eq. (1), we first recognize that at equilibrium it is a cubic in X,

$$RX\left(1 - \frac{X}{K}\right) - \frac{BX^2}{A^2 + X^2} = 0 \tag{3}$$

$$-X^3 + KX^2 - X\left(A^2 + \frac{KB}{R}\right) + KA^2 = 0 \tag{4}$$

Following standard methods for solving cubic equations (Uspensky, 1948), Eq. (4) can be solved yielding three roots, X_1, X_2, and X_3, corresponding to the three possible equilibrium states of the system. As management actions change parameter values, the values of these equilibria change and at bifurcation points even emerge or vanish (see, e.g., Fig. 1-2). Our approach allows assessment of the effects of integrated pest management on pest equilibrium values. Here, we use a simplified version of Cardano's method of solving cubics to evaluate the effects of management activities that alter the intensities of R and B and the magnitudes of A and K. We then apply this strategy to the spruce budworm model to solve for the three equilibria. The method is quite general, however, and could be used to solve any cubic model, which are common in pest control, because of the ubiquity of the type III functional response.

3.1 Solving for equilibrium pest values: The general case

Consider the general monic cubic equation (i.e., with leading coefficient of 1),

$$f(x) = x^3 + ax^2 + bx + c = 0. \tag{5}$$

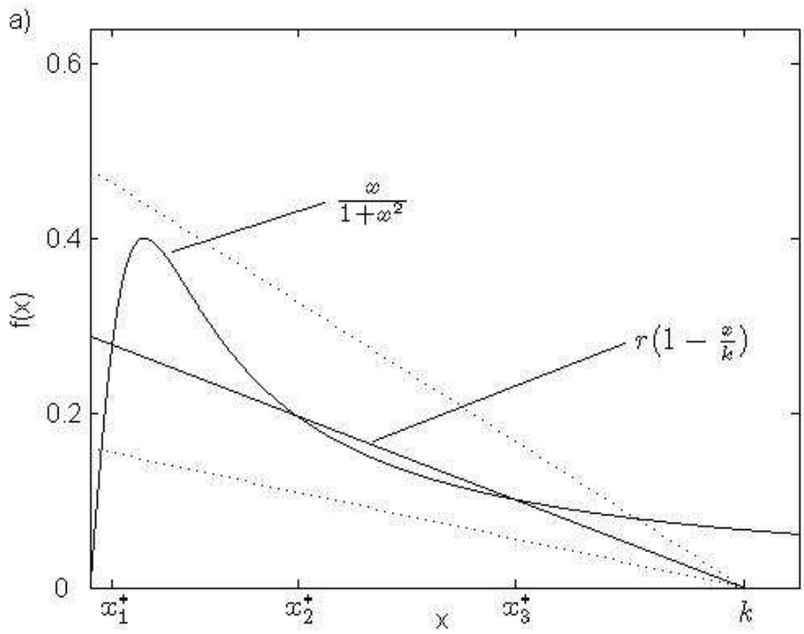

Fig. 2. The left-hand side of Eq. (2) (solid, straight line) crossing the curve described by the right-hand side in three places, correspondig to the three equilibria in Fig. (1), x_1, x_2, x_3. The two dotted straight lines signify the effects of changing r on the existence and value of equilibria. The lower dotted line, representing small values of pest intrinsic growth rate, only crosses the curve at a relatively low pest population size; pest outbreaks are not possible. In contrast, the upper dotted line only crosses the curve at a relatively high pest population size; biological control is not possible.

Cardano's technique, dating to the first half of the sixteenth century, involves simplifying Eq, (5) so that it no longer contains the second power of x. This is achieved by introducing a new variable y and setting,

$$x = y + k, \tag{6}$$

where k is as yet an arbitrary constant.

To specify k, we begin by using Taylor's formula to approximate $f(y+k)$ by

$$f(y+k) = f(k) + f'(k)y + \frac{f''(k)}{2}y^2 + \frac{f'''(k)}{6}y^3. \tag{7}$$

The terms on the right-hand side of Eq. (7) can be related to the terms of our monic cubic, Eq. (5) yielding,

$$f(k) = k^3 + ak^2 + bk + c, \tag{8}$$

$$f'(k) = 3k^2 + 2ak + b, \tag{9}$$

$$\frac{1}{2}f''(k) = 3k + a, \tag{10}$$

$$\frac{1}{6}f'''(k) = 1. \tag{11}$$

Simplification is now possible because we can choose k in Eq. (10) so that,

$$3k + a = 0, \qquad \text{or} \qquad k = -\frac{a}{3}. \tag{12}$$

With k so defined (i.e., the so-called "Tschirnhaus transformation") our solution is translated to the origin and we can substitute it into the remaining equations to arrive at,

$$f'\left(-\frac{a}{3}\right) = b - \frac{a^2}{3}, \tag{13}$$

$$f\left(-\frac{a}{3}\right) = c - \frac{ba}{3} + \frac{2a^3}{27} \tag{14}$$

After substituting $x = y - \frac{a}{3}$ and equating coefficients of like powers of y and k in Eqs. (7) and (8–11) respectively, Eq. (5) is transformed into,

$$y^3 + \alpha y + \beta = 0, \tag{15}$$

where

$$\alpha = b - \frac{a^2}{3}, \qquad \beta = c - \frac{ab}{3} + \frac{2a^3}{27}. \tag{16}$$

By a simple reverse transformation, any formula for the roots of Eq. (15) can be transformed into a formula for the roots of Eq. (5), i.e., by substituting Eq. (16) into Eq. (15) and using $x = y - \frac{a}{3}$. Thus, in the sequel, we consider only Eq. (15).

Cubic equations of the form, Eq. (15), referred to as "depressed cubics", can be solved by introducing two new variables u, v such that,

$$y = u + v. \tag{17}$$

Upon substituting this expression into Eq. (15) we see that u and v must satisfy the equation,

$$u^3 + v^3 + (\alpha + 3uv)(u + v) + \beta = 0, \tag{18}$$

which has two unknowns. Thus, the problem is indeterminant without another known relation between u and v, Eq. (17) being one. Another relation that is consistant with Eq. (18) is to take

$$\alpha + 3uv = 0, \tag{19}$$

or,

$$uv = -\frac{\alpha}{3}. \tag{20}$$

It then follows from Eq. (18) that,

$$u^3 + v^3 = -\beta, \tag{21}$$

Solving the cubic Eq. (15) can now be achieved by solving the system of two equations,

$$u^3 + v^3 = -\beta, \tag{22}$$

$$uv = -\frac{\alpha}{3}. \tag{23}$$

Because it is convenient to know the sum and product of two unknown quantities, in this case u^3 and v^3, we take the cube of the latter equation yielding,

$$u^3 v^3 = -\frac{\alpha^3}{27}. \tag{24}$$

The reason these quantities are convenient is that upon solving one in terms of the other and substituting, a single quadratic equation results. To see this rearrange Eq. (22) as follows,

$$u^3 = -(v^3 + \beta), \tag{25}$$

and substitute this expression for u^3 into Eq. (24) giving,

$$-(v^3 + \beta)v^3 = \frac{-\alpha^3}{27}. \tag{26}$$

We next expand the left-hand side of Eq. (26) giving,

$$-v^6 - \beta v^3 = \frac{-\alpha^3}{27}, \tag{27}$$

or, substituting $t = v^3$ and dividing through by (-1),

$$t^2 + \beta t - \frac{\alpha^3}{27} = 0. \tag{28}$$

Thus, apparently, u^3 and v^3 can be computed from the roots of Eq. (28). Equating v^3 to the positive root that results from applying the quadratic formula, we have,

$$v^3 = -\frac{\beta}{2} + \sqrt{\frac{\beta^2}{4} + \frac{\alpha^3}{27}}, \tag{29}$$

or

$$v = \sqrt[3]{-\frac{\beta}{2} + \sqrt{\frac{\beta^2}{4} + \frac{\alpha^3}{27}}}. \tag{30}$$

Now we take advantage of the relationship in Eq. (25) to solve for u yielding,

$$u^3 = -(v^3 + \beta), \tag{31}$$

$$= -\left(-\frac{\beta}{2} + \sqrt{\frac{\beta^2}{4} + \frac{\alpha^3}{27}} + \beta\right), \tag{32}$$

$$= \frac{\beta}{2} - \sqrt{\frac{\beta^2}{4} + \frac{\alpha^3}{27}}, \quad \text{or,} \tag{33}$$

$$u = \sqrt[3]{\frac{\beta}{2} - \sqrt{\frac{\beta^2}{4} + \frac{\alpha^3}{27}}}. \tag{34}$$

We can now write an expression for y, which was set equal to $u + v$ in Eq. (17) yielding,

$$y = u + v, \tag{35}$$

$$= \sqrt[3]{\frac{\beta}{2} - \sqrt{\frac{\beta^2}{4} + \frac{\alpha^3}{27}}} + \sqrt[3]{-\frac{\beta}{2} + \sqrt{\frac{\beta^2}{4} + \frac{\alpha^3}{27}}}. \tag{36}$$

The final step is to use the relation $x_i = y_i - \frac{a}{3}$ where $i \in \{1,2,3\}$ to return the three equilibrium solutions to our original model. Note that at certain values of α and β a bifurcation occurs and two of the real solutions disappear to be replaced by imaginary solutions. In this study, we have used parameter values that yield three real solutions. In the case of a single real equilibrium the basin of attraction of the outbreak equilibrium either does not exist (i.e., outbreaks are not possible) or consists of the entire space (i.e., biological control is not possible).

3.2 Solving for equilibrium pest values: The spruce budworm model

As we have seen, the spruce budworm model, Eq. (1), can be expanded to its cubic form yielding,

$$x^3 - Kx^2 + (A^2 + \frac{KB}{R})x - KA^2 = 0, \tag{37}$$

(after multiplying through by -1) or, more simply,

$$x^3 + px^2 + qx + r = 0, \tag{38}$$

where,

$$p = -K, \tag{39}$$

$$q = A^2 + \frac{KB}{R}, \tag{40}$$

$$r = -KA^2. \tag{41}$$

Forming the depressed cubic requires removing the quadratic term from Eq. (38). To do so, let

$$x = y - \frac{p}{3}, \tag{42}$$

and to simplify the resulting equation, let,

$$\alpha = \frac{1}{3}(3q - p^2), \tag{43}$$

$$\beta = \frac{1}{27}(2p^3 - 9pq + 27r), \tag{44}$$

yielding,

$$y^3 + \alpha y + \beta = 0. \tag{45}$$

We can now simply substitute our particular model parameters, embodied in α and β, through p, q, and r into Eqs. (35–36) yielding,

$$y = u + v, \tag{46}$$

$$= \sqrt[3]{\frac{\beta}{2} - \sqrt{\frac{\beta^2}{4} + \frac{\alpha^3}{27}}} + \sqrt[3]{-\frac{\beta}{2} + \sqrt{\frac{\beta^2}{4} + \frac{\alpha^3}{27}}}. \tag{47}$$

Finally, back transforming the solution into terms of x we use the relation,

$$x_i = y_i - \frac{p}{3}, \qquad i \in \{1,2,3\}. \tag{48}$$

4. Results

Having explicitely solved the cubic equation, we can now evaluate the effects of parameter manipulation on equilibrium resilience. For example, Fig. 3 shows that the magnitude of the outbreak basin of attraction changes relatively rapidly with increasing K and R. It is not possible to evaluate the relative effects of changes to each using this graph because of the different scales and units. Nevertheless, it is apparent that these two familiar parameters both influence the magnitude of the outbreak basin of attraction.

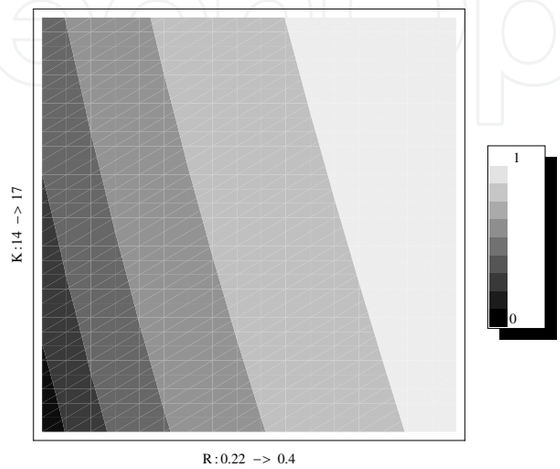

Fig. 3. Shaded contours of the magnitude of the basin of attraction of the outbreak equilibrium as intrinsic growth rate R and carrying capacity K are changed. Scale is normalized from 0 to 1 such that darker colors represent smaller, and lighter colors larger, basins of attraction. Thus, as expected, large values of R and K both yield large potential for outbreaks.

When the square root of the predator's half-saturation constant A is varied, its effects can be compared to the large changes caused by changes in K because they both have units of individuals (Fig. 4). The roughly vertical contours indicate that changes to carrying capacity have a much greater effect than changes to A, at least over ranges of each that yield bistability. Note that the slight concave down character of these contours indicates that changes in resilience following changes in A are slightly more likely at high values of K. The reason for such changes to equilibium resilience can be seen in Fig. (5). Specifically, as the predator half-saturation constant A^2 increases, the $\frac{dx}{dt}$ curve is shifted downwards, increasing the magnitude of the biologically controlled basin of attraction at the expense of the outbreak basin.

Finally, changes to the maximal predator attack rate have a large effect on the resilience of the both the biologically controlled equilibrium and the outbreak equilibrium. Specifically, increasing B, the maximal predator attack rate *increases* the magnitude of the biologically controlled equilibrium. This matches our intuition, because higher attack rates presumably favor the predator, not the pest. To analyze the effects of changing B, we used both a higher value of B and a lower value and inspect the effects on the magnitudes of each basin of attraction.

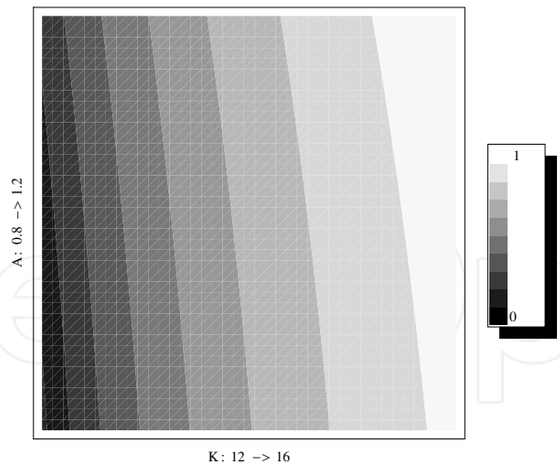

Fig. 4. Shaded contours of the magnitude of the basin of attraction of the outbreak equilibrium as carrying capacity K and the square root of half-saturation constant A are changed. Scale is normalized from 0 to 1 such that darker colors represent smaller, and lighter colors larger, basins of attraction.

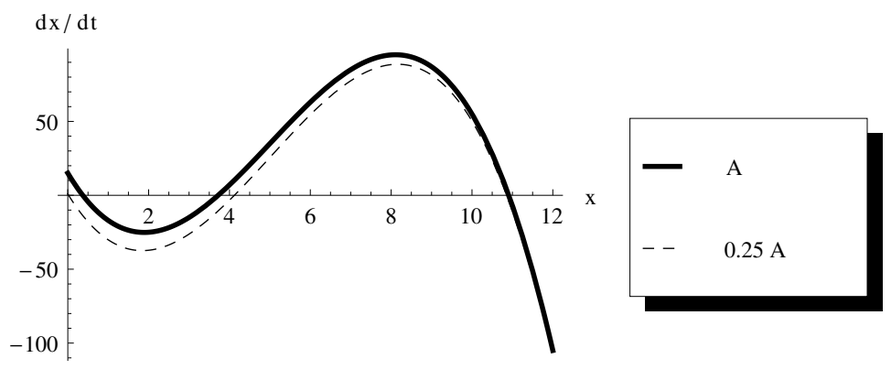

Fig. 5. Effect of changing A in the spruce budworm model. Increases in A generate increases in the magnitude of the biologically controlled basin of attraction by decreasing the value of the lower equilibrium and increasing the value of the unstable, middle equilibrium.

Figure 6 shows that increasing B lowers the entire dx/dt curve. In contrast, increasing R raises the curve, which also has an intuitive effect, because increased growth rate is expected to favor outbreaks. As Fig. 7 shows, increasing R increases the magnitude of the outbreak basin of attraction at the expense of the biologically controlled basin of attraction.

The net sum effects of changes in R and B are depicted in Fig. 8, which shows that lower attack rates and higher pest growth rates both increase the magnitude of the outbreak basin of attraction. In contrast, high attack rates and low growth rates decrease that basin and increase the biologically controlled basin of attraction.

5. Discussion

We have undertaken an analysis of a simple model of pest population dynamics with the goal of understanding the role of specific, commonly encountered model parameters on the

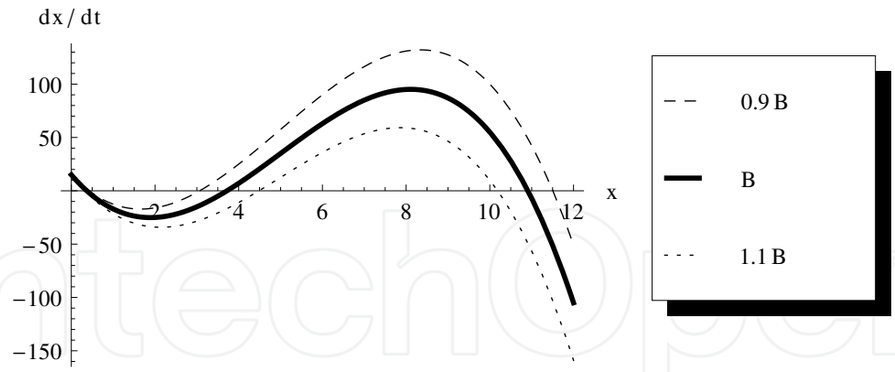

Fig. 6. The rate of change in pest population growth rate versus pest population size according to the spruce budworm model. As the maximal predator attack rate B increases, the magnitude of the biologically controlled basin of attraction increases, as evidenced by the reduced distance between the two right-most points where $dn/dt = 0$. In contrast, when B is dereased, the magnitude of the outbreak equilibrium is increased.

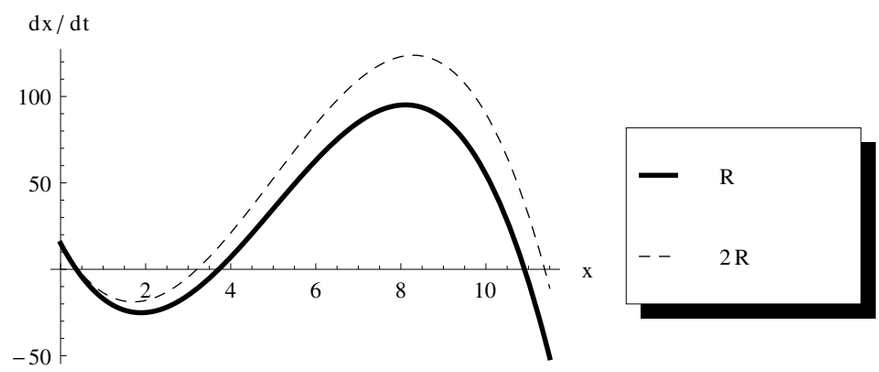

Fig. 7. The rate of change in pest population growth rate versus pest population size according to the spruce budworm model. As R is increased, the curve, dx/dt shifts upward bringing the two left-most equilibrium points where $dx/dt = 0$ closer together. Thus, the basin of attraction of the biologically controlled equilibrium decreases.

resilience of equilibria. Furthermore, the parameters we have studied are those typically affected by integrated pest management. We defined equilibrium reslience as the distance between the stable equilibria and the unstable equilibrium, which marks the threshold betweem the basins of attraction for the biologically-controlled, and outbreak equilibria.

Our results show that the pest carrying capacity has a large effect on the resilience of the outbreak equilibrium. Specifically, changes in K generate large changes in the magnitude of the outbreak basin of attraction. In terms of integrated pest management, this means that pest control strategies that decrease the pest's carrying capacity, such as intercropping to break up monocultures, move the outbreak equilibrium closer to the threshold of the biologically controlled equilibrium. Thus, smaller culling events, or smaller releases of enemies, achieve the desired shift to the biologically controlled equilibrium than otherwise.

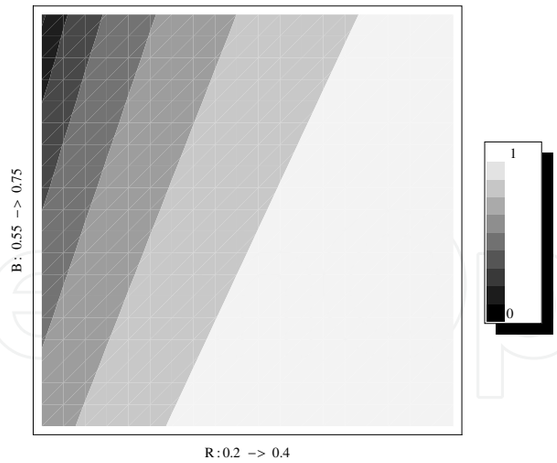

Fig. 8. Shaded contours of the magnitude of the basin of attraction of the biologically controlled equilibrium as intrinsic growth rate R and maximal attack rate B are changed. Scale is normalized from 0 to 1 such that darker colors represent smaller, and lighter colors larger, basins of attraction. At large values of R and small values of B the outbreak basin dominates, while at high values of B and low values of R, it goes to zero.

The effects of pest population growth rate are two-fold. First, increasing pest growth rate increases the outbreak basin of attraction, an intuitive result, because higher pest population growth rates are expected to favor outbreaks. At the same time, increasing r decreases the magnitude of the biologically controlled basin of attraction, making escape from predator control more feasible.

The magnitude of the outbreak basin of attraction decreases with increasing half-saturation constant. This constant is comprised of (attack rate $\times$ handling time)$^{-1}$ (Gotelli, 1995). Thus, the effects of A^2 depend on the relationship between these two biological parameters. In our analysis, for simplicity we used $A = 1$. Increases in the half-saturation constant mean that the predators require higher densities of prey in order to begin being sated. Thus, they can consume more prey before the saturating effects of the functional response take effect.

The maximum feeding rate B also has a large and intuitive effect on equilibrium resilience. Because this feeding rate is the inverse of handling time (Gotelli, 1995) introducing natural predators with shorter handling times generates meaningful decreases in the magnitude of the outbreak basin of attraction. Additionally, Kidd & Amarasekare (2011) demonstrated that predators with shorter handling times induce weak transient dynamics of short duration relative to predators with longer handling times. Thus, according to their analysis, when predators with short handling times are introduced (i.e., those with larger maximum feeding rates), large oscillations in the prey population are less likely. According to our analysis, when predators with short handling times and correspondingly higher maximal attack rates are released, outbreaks become less likely.

Using the approach we outline here, schedules for integrated pest management can be developed based on knowledge of specific equilibrium values. For example, solving the model for x_1, x_2, and x_3 allows one to compute the needed change in density to change a system from the outbreak state to the biologically controlled state. Furthermore, our approach permits evaluation of the effects of individual components of integrated pest management on

distance to the threshold between equilibria. Thus, the effects of strategies such as release of sterile males and enhancement of natural predators can be understood in terms of decreased culling requirements.

Acknowledgements: Professor Adam Hammett kindly read the manuscript and made useful comments that improved clarity, especially in the final steps of the solution of the cubic.

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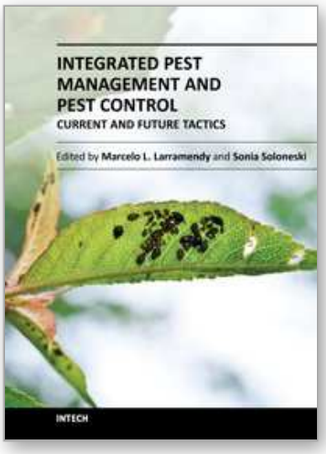

Integrated Pest Management and Pest Control - Current and Future Tactics

Edited by Dr. Sonia Soloneski

ISBN 978-953-51-0050-8
Hard cover, 668 pages
Publisher InTech
Published online 24, February, 2012
Published in print edition February, 2012

Integrated Pest Management is an effective and environmentally sensitive approach that relies on a combination of common-sense practices. Its programs use current and comprehensive information on the life cycles of pests and their interactions with the environment. This information, in combination with available pest control methods, is used to manage pest damage by the most economical means and with the least possible hazard to people, property, and the environment.

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