Simple Models of Natural Enemy Action and Economic Thresholds

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ABSTRACT Simple population models are linked to a widely used economic injury level model to produce equations for economic thresholds that include the effect of natural enemies. Two classes of models are recognized; those in which natural enemy dynamics are not coupled to that of the pest, such as gencralist predators, and those where coupling is integral to natural enemy dynamics such as pathogens, parasitoids, and specialist predators. Both of these models are extended to multiple species or complexes of natural enemies. Implications of these models are then discussed. The concept of biocontrol gain threshold is introduced as a method to balance the relative impact of a given natural enemy against the additional monitoring costs incurred as a result of adding the species to an integrated pest management program. The use of these models to reduce the risk of incorrect management decisions is also discussed.

One of the most basic concepts of decision making in integrated pest management (IPM) is the economic injury level (EIL), usually defined as the pest density at which damage caused by the pest equals the cost of using a given control (Pedigo et al. 1986). Although the original definition of the economic injury level is usually attributed to Stern et al. (1959), the mathematical definition was not solidified until Mumford and Norton (1984) and Pedigo et al. (1986) who first proposed the equation:

\[ EIL = \frac{C}{VIDK}, \]

where \( C \) is the cost of the chemical control action, \( V \) the value or price of a crop, \( I \) the injury inflicted by the pest, \( D \) the damage response (i.e., yield reduction) by the crop to that injury, and \( K \) the proportionate reduction in pest attack conferred by the control action. The units of an economic injury level are pest density, although some authors prefer to view pest density as an index of economic damage (Pedigo and Higley 1992, Funderburk et al. 1993).

Pedigo and Higley (1992) and Higley and Wintersteen (1992) have since extended the concept to include environmental quality and cost considerations. These extensions retain simple forms similar to equation 1 and, therefore, also retain the limitations of single-point decision making tools (Mumford 1992). Most limitations can be overcome by using more sophisticated models (Headley 1982, 1994), but the simplicity of the economic injury level approach has been key to its widespread adoption (Pedigo et al. 1989, Funderburk et al. 1993). Because of this practical value, several authors have called for a renewed commitment to developing economic injury levels that incorporate more holistic aspects of the crop production system such as environmental costs (Higley and Wintersteen 1992), risk strategies (Hutchins and Gehring 1993) and alternative (particularly biological) controls (Cate and Hinkle 1993).

Cate and Hinkle (1993) noted that the potential for using a biocontrol complex to moderate the damaging effects of pests long has been a recognized and intensively studied topic. Much of this work has been in the areas of population dynamics (either theoretical or applied) and is, thus, typically multigenerational. The remainder has been in assessment, such as sampling techniques and measuring pest population reduction caused by a current biocontrol population. However, surprisingly little work has been aimed at using information concerning the biocontrol complex in decisions about the management of the pest complex. A search of the Agricola database on 17 May 1996 found 19,370 citations under the subject “biological control,” but only 225 under subject “biological control and economic(s).” Of the latter, only 8 citations dealt with biocontrol complexes as opposed to a single biocontrol agent or species. None of these reported decision making tools as derived from models of the biocontrol complex.

The literature shows that there is a recent renewed interest in developing economic injury levels, but that this interest is primarily in expanding the general concept to include aspects other than chemical control decisions. This is particularly true for biological controls because “IPM relies first upon the maximum use of naturally occurring pest controls, including weather, disease agents, parasites, antagonists, and intolerant or resistant hosts so that pest populations are preventively managed to avoid outbreak status” (Cate and Hinkle 1993). A key phrase here is “preventively managed,” which implies a predictive capability.

The predictive aspect of the economic injury level is the economic threshold (ET), which is defined as the pest population density at which a control decision must be made to prevent a pest from exceeding its economic injury level (Pedigo et al. 1986). The economic threshold is the actual decision tool, based on the economic injury level, and anticipates pest population growth over time as well as time delays in implementing a control tactic. Like the economic injury level, the economic threshold is usually a measure of pest population density, although it can be viewed as a “measuring stick used to estimate the time at which to take action to suppress a pest” (Funderburk et al. 1993). Unlike the economic injury level, though, the economic threshold does not seem to have a generally accepted mathematical definition such as equation 1. Instead, it is often expressed simply as a percentage of the economic injury level, although the empirical bases for those percentages are often vague (Pedigo et al. 1989, Funderburk et al. 1993). Because the economic threshold is predictive (predicting injury by a pest population), unless we have a definitive mathematical model of how injury (=pest populations) increases, it is not possible to have a general mathematical description of the economic threshold. Consequently, objectivity in economic threshold development has been linked to various empirical methods for assessing pest population growth (Pedigo et al. 1989).

Because populations of biocontrol agents often fluctuate over time, an emphasis on predictive capability is necessary if they are to be used in economic decision making. Therefore, biocontrol agents need to be incorporated into economic thresholds as opposed to economic injury levels. In fact, the definition of economic injury levels account only for pest effects and cost considerations; therefore, incorporating biocontrols into economic injury levels would require redefinition of the concept. The alternative, incorporating biocon-
Into their webs. For this case, consider a single pest population \( P_c \) and a species. One example would be predation from web-spinning spiders that capture prey that randomly blunder into their webs. The work reported below represents an attempt to generalize economic thresholds so they will be treated separately.

### Two Economic Threshold Models

The environment in which economic injury level/economic threshold-based IPM decisions are made is a generalized one. A crop that is at risk from pest attack is monitored or scouted at assumed fixed time intervals (e.g., weekly). On each scouting date, the scout assesses both the crop maturity/growth stage and the density (and possibly age distribution) of one or more pest populations. For bio-control agents to be included in decisions as to whether or not the pest population requires preventative management (i.e., a management measure implemented when there is a likelihood that the pest population will achieve or exceed the economic injury level on or before the next scouting date), it is further assumed that the relevant bio-control agents also can be monitored. Furthermore, if scouting data are to be used to make management decisions, the scouting interval must comport with the reaction time of the crop manager.

The economic effect of bio-control agents is relative to this time frame and over such short time intervals, multigenerational population dynamics models might not be required. However, one aspect of general population dynamics is important and affects the specific form of economic threshold that is best suited to the particular pest-natural enemy interaction. Specifically, one can view all natural enemies of insect pest populations as being roughly divided into specialists and generalists. Here, specialists seek individual hosts or prey of a particular (in this case, pest) species, whereas generalists may attack a broad range of species. Specialists include parasitoids, pathogens, and some predators; most generalists are predators. This distinction is important from the perspective of the models used because the dynamics of a specialist population are closely coupled to that of their prey or hosts. Coupling involves a nonlinear relationship between pest and natural enemy populations in which the pest mortality inflicted by the natural enemy is dependent on the population density of the pest and the natural enemy. Populations of generalist predators, however, inflict a mortality rate that is dependent primarily on the number of predators because they are not coupled to any one prey population. In this case, number of prey killed can be estimated using a simple linear function of predator density. Each of these approaches yields somewhat different economic thresholds so they will be treated separately.

Case 1: Uncoupled Interactions. This case would be expected when the degree of biological control exerted by a complex of agents between scouting dates is dependent on the density of the bio-control agents themselves and independent of the density of the insect pest (host/prey) species. One example would be predation from web-spinning spiders that capture prey that randomly blunder into their webs. For this case, consider a single pest population \( P_c \) and a sin-
gle biological control agent \( (B_i) \) in time. A simple (linear, uncoupled) model of this system could be:

\[
P_{i,t} = P_{i,t-1} + r P_{i,t-1} - a B_{i,t}\tag{2a}
\]
\[
B_{i,t} = B_{i,t-1} + b B_{i,t-1} - m B_{i,t}\tag{2b}
\]

where \( r \) and \( b \) are fixed growth rates of the pest and biocontrol agent population, respectively, \( a \) the rate at which the biocontrol agent reduces the pest population, and \( m \) the biocontrol agent’s mortality rate. It is worth noting that, from equation 2a, the pest population will decrease if \( B_i > r P_{i,t} / a \). The populations are sampled or scouted at some fixed interval \( (\tau) \), which is sufficiently long so that management decisions can be made and acted upon between samples. The 4 parameters in this system \( (r, b, a, \text{and } m) \) are scaled necessarily to that scouting interval. As a simple example, if \( P_i \) is aphids, \( B_i \) is a population of a particular lady beetle, the lady beetles consume 10 aphids per day, and the crop to be protected from aphids is scouted once per week (7 \( \tau \)), then \( a = 70 \) aphids per lady beetle per week.

Assume there exists some known economic injury level that will be used to decide whether a naturally occurring biocontrol agent will suppress the pest to the extent that application of a given chemical control can be deferred or avoided. In equation 2, the economic injury level is a predefined pest population, \( P_{i,t} \). If the economic injury level is achieved at time \( t + \tau \), then the economic threshold is achieved at time \( t \) because the control decision must be made at that time. In the absence of the biocontrol agent \( (i.e., B_i = 0) \), the economic threshold can be solved for as

\[
EIL = (1 + r) P_i
\]
\[
P_i = ET_{\text{ac}} = EIL/(1 + r)\tag{3}
\]

The zero subscript in equation 3 is used to emphasize that this economic threshold does not incorporate the biocontrol agent. Economic thresholds that incorporate natural enemies in different ways will be subscripted differently \((\text{cf., below})\). The main point about equation 3 is that it provides a rather generalized definition for economic threshold, which may be stated “as the ratio of the EIL to the pest population growth rate per unit management (or scouting) time.” This definition does not appear to be recognized generally although DuToit (1986) proposed almost the same equation to relate the economic threshold, economic injury level, and pest rate of increase for the Russian wheat aphid, Diuraphis noxia (Mordvinko). For many pest populations, \( (1 + r) \) is often in the range of slightly over 1 \((i.e., \text{pest densities increasing slightly between scouting intervals})\) to 2 \((\text{pest densities double between scouting intervals})\) when population data are fit to equation 2; it is noteworthy that economic thresholds often are estimated to be nearly the same as the economic injury level to \( r = 0 \) of the economic injury level.

If we now consider the case of \( B_i > 0 \), then

\[
ET_{\text{abc}} = [(EIL + a B_{i,t})/(1 + r)]\tag{4}
\]

where the uBC subscript denotes that this economic threshold is for an uncoupled biocontrol interaction. Equation 4 shows that, in this simple case, the economic threshold is increased by the presence of the biocontrol agent. In other words, by including the biocontrol agent in the decision making, one can tolerate greater pest populations. Waiting until pest populations are larger means that one can delay using chemical control without incurring additional economic losses.

Assuming that a biocontrol agent does not affect any of the terms in equation 1, then the economic threshold becomes:

\[
ET_{\text{abc}} = [(C/VIDK) + a B_{i,t}]/(1 + r)\tag{5}
\]

Equation 5 shows that, with all terms constant except the economic threshold and \( B_i \), the economic threshold is linearly dependent on the biological control agent. Had a nonlinear model been used in equation 2, equation 5 would have likewise produced a nonlinear relationship \((\text{cf., below})\).

Consideration of equation 2 for the case of 2 biocontrol agents, \( B_{1,t} \) and \( B_{2,n} \), and following the above analyses yields

\[
ET_{\text{abc}} = [(C/VIDK) + (a_1 B_{1,t} + a_2 B_{2,n})]/(1 + r)\tag{6}
\]

where \( a_1 \) and \( a_2 \) are the parameters for each biocontrol agent, respectively. Extending equation 6 to the case of \( n \) biocontrol agents produces

\[
ET_{\text{abc}} = [(C/VIDK) + \sum_{i=1}^{n} a_i B_{i,t}]/(1 + r)\tag{7}
\]

Equation 7 has a number of limitations. Some of these limitations are associated with the original equation 2 such as no stage structure and ignoring externalities. Other limitations arise from the economic injury level model from equation 1 and include single period decision making. In addition to these problems, equation 7 does not allow for interactions between the biocontrol agents. Case 2: Coupled Systems. This case would arise in situations where biocontrol efficacy is codependent on the density of the biocontrol complex as well as the pest population. Examples of such situations include the specialized biological control agents that tend to have nonlinear, coupled relationships with their prey/host populations. Equation 2 can be rewritten to reflect this coupling as

\[
P_{i,t+1} = P_i (1 + r) - a B_{i,t} P_i\tag{8a}
\]
\[
B_{i,t+1} = B_{i,t} + \beta B_{i,t} P_i - m B_{i,t}\tag{8b}
\]

with \( m \) as before. The principal difference between equations 2 and 8 is the multiplicative interaction term that makes equation 8 a discrete Lotka-Volterra model. The \( B_i \), \( P_i \) product is a mass action principle that reflects the number of potential encounters between pest and natural enemy individuals \((\text{or, in the case of pathogens, infectious units})\). Because of this product, the predator parameters, \( a \) and \( \beta \), have slightly different meaning and units from the \( a \) and \( b \) parameters in equation 2. Where \( a \) was the rate at which the biocontrol agent reduces the pest population and \( b \) was the fixed growth rate of the natural enemy, \( a \) and \( \beta \) represent prey consumed \((a)\) or new births \((\beta)\) per potential encounters. When the coupled and uncoupled systems are compared \((\text{cf., below})\), the different units of these 2 sets of parameters need to be kept in mind and the use of different symbols in equations 2 and 8 will help maintain this distinction.

Proceeding as before and extending to \( k \) natural enemy species yields the coupled economic threshold, \( ET_{\text{abc}} \), for this case of

\[
ET_{\text{abc}} = EIL/[1 + r - \sum_{i=1}^{k} \alpha_i B_{i,t}]\tag{9}
\]

as the coupled analogue to equation 7. For this situation, the cumulative effects of the natural enemies are subtracted, but the subtraction occurs in the denominator thereby again increasing the economic threshold. This economic threshold is not linearly dependent on biocontrol agent density but, instead, is inversely proportional to that density.
Fig. 2. Probability of incorrect decisions as a function of the pest population at time $t$, $P_t$. The probability of an incorrect decision is highest when the pest population is actually at the economic threshold, $ET$. The probabilities on the left half ($P_t < ET$) represent the odds of failing to apply a needed control, and those in the right half ($P_t > ET$) are the odds of applying an unneeded control.

A pest under attack from multiple natural enemies that satisfied this condition would decline (i.e., $P_t > P_{\text{crit}}$). However, if only 1 natural enemy were considered, as in the case of equation 8, then the pest population would decline whenever $B_t > (1 + r)/a$. Because $r$ and $a$ are constant, comparing the density of a natural enemy to this ratio may be an acceptable alternative to using equation 9 in the case of a single natural enemy.

Coupled and uncoupled interactions can be mixed by modeling a pest population under attack by both a coupled biocontrol agent and an uncoupled agent as

$$P_{t,\text{crit}} = (1 + r) P_t - a B_t - a B_t P_t$$

where all terms are as before. Proceeding as above yields the combined economic threshold

$$ET_{\text{combined}} = \left(EIL + \sum_{i=1}^{n} a_i B_{t,i}\right)/(1 + r) - \sum_{i=1}^{k} a_i B_{t,i}$$

which has both linear and nonlinear biocontrol effects.

**Model Implications**

**Summation of Biological Control Samples.** The important aspect of equations 7, 9, and 11 is the summation of the impacts from various species in the biocontrol complex and the incorporation of this sum into an economic decision tool. This simple summation approach to using biocontrol agents as in equation 7 has been used successfully in a few pest management systems. A recent example is that of Sterling et al. (1993), working with flourhoppers (Miridae) in cotton, who reported that the “efficiency” of a complex of 10 species over time ($E_t$) could be predicted accurately by the relationship

$$E_t = \sum_{i=1}^{n} (E_i N_{i,\text{et}})$$

where $E_i$ was the efficiency of the $i$th species and $N_{i,\text{et}}$ was the population density of that species. These authors, along with Hartstack et al. (1990), cited 20 different validation studies of this model for various other predator complexes in the cotton system and all of them supported this model. Incidentally, Sterling et al. (1993) also were able to use equation 12 to calculate, through simulation studies, the economic value of the spider complex concluding that these spiders provided benefits of from $0.86 to $15.50/ha/year over a 5-yr period. Note that this implies an estimate of the 2nd term in equation 4, $\{aB_t/(1 + r)\}B_t$. They stated, however, that these figures applied only to the cotton flourhopper, *Pseudatomoscelis seriatus* (Reuter), and did not account for spider predation on other important herbivorous insects.

Sterling et al. (1993) used equation 12 as a component in a large and complex simulation model and did not attempt to distill their spider counts into a simple management decision tool. In fact, they pointed out that the economic value of spider populations depends on factors such as crop variety, target yield, and lint value. These factors already are incorporated in equation 1, which is inserted into equation 7.

An earlier example of equation 7 was derived by Tamaki et al. (1974), who were evaluating the impact of various predators of the green peach aphid, *Myzus persicae* (Sulzer), in sugarbeets. They modeled the total number of aphids killed ($K_i$) by the biocontrol complex at any time, $t$, as

$$K_i = \sum_{j=1}^{n} C_i N_{i,\text{et}}$$

where $N_{i,\text{et}}$ was the population density of the $i$th biocontrol agent and $C_i$ the per capita consumption rate of aphids by each biocontrol agent species. Tamaki et al. (1974) used equation 13 to predict the aphid population according to

$$A_{i,\text{et}} = q(A_i - EK_i)$$

where $q$ is the intrinsic rate of increase ($r$ in equation 2) and $E$ is an average predator efficiency (a constant) as determined by factors external to the predator–prey relationship (e.g., temperature, seasonality, host plant). Sterling et al. (1993) may not have been aware of Tamaki et al. (1974), but equation 13 is identical to 12 and the biocontrol component of 7 and 14 is a slightly different form of equation 2a. In fact, if $t$ is measured in units of scouting or management time and equation 14 is analyzed following equations 2 through 7, equation 14 yields a qualitatively similar result. Equation 14 is, therefore, an example of an uncoupled system. Tamaki et al. (1974) called this their “predator power and efficacy model.” Tamaki and Long (1978) extended this model so that $E$ became a function including the effect of temperature and the functional response of the predator complex. In numerous field tests, they found that this model had good predictive capability over short time frames and suggested that it be used in decisions concerning the need for inundative releases. However, as with Sterling et al. (1993), Tamaki and Long never developed their model as a tool for decision making with respect to chemical controls (G. E. Long, personal communication).

**Gain Threshold for Biological Control Agents and Scouting Costs.** Pedigo et al. (1986) described the relative economic advantage of using a control method as a “gain threshold,” which they defined as the difference in crop yield or price with and without a control. The same concept can be applied in the above equations by taking the difference in economic thresholds with and without biological control. This biocontrol gain threshold for the uncoupled case, $BG_{\text{U}}$, is

$$BG_{\text{U}} = ET_{\text{BIC}} - ET_{\text{B}} = [(EIL + \sum_{i=1}^{n} a_i B_{t,i})/(1 + r)] - [EIL/(1 + r)]$$

or

$$BG_{\text{U}} = \sum_{i=1}^{n} a_i B_{t,i}/(1 + r).$$

The biocontrol gain threshold for the coupled case is

$$BG_{\text{C}} = ET_{\text{BIC}} - ET_{\text{B}} = [EIL/((1 + r) - \sum_{i=1}^{k} a_i B_{t,i})] - [EIL/(1 + r)]$$
or

\[ k = \frac{\left( EIL \sum \alpha_i B_{i,t} \right) \left( (1 + r) \left( \sum_{i=1}^{k} \alpha_i B_{i,t} \right) \right)}{(1 + r) \left( \sum_{i=1}^{k} \alpha_i B_{i,t} \right)} \]

The significance of these biocontrol gain thresholds is that they can be used to determine whether or not biocontrol agents impact the economic threshold sufficiently to warrant the additional expense of sampling the natural enemies in an IPM scouting program. Equations 15 and 16 imply that the increased benefits (increase in the economic threshold due to the biocontrol agent) versus the increased scouting costs can be determined for each individual natural enemy species in a given crop production system or for the entire biocontrol complex, depending on the needs of the IPM coordinator or manager.

To illustrate this application, consider the situation in which an IPM coordinator is trying to decide whether or not to include a given natural enemy species in a scouting program. The coordinator does not want to invest scouting resources unless the presence of the natural enemy will increase the economic threshold by a minimum percentage (to be expressed as a proportion), \( \Phi \). For example, \( \Phi = 0.1 \) means that the natural enemy must increase the economic threshold by at least 10% in order for it to be considered worthwhile to sample. Then, for the uncoupled case, the criterion becomes

\[ \Phi < \frac{B_{GT}}{ET_o} \]

\[ \alpha B_i (1 + r) > \Phi ET_o \]

\[ B_i > \Phi (1 + r) \frac{ET_o}{\alpha} \]

\[ B_i > EIL (\Phi / \alpha) \] (17)

and, following the same approach, the criterion for the coupled case is

\[ B_i > \Phi (1 + r) / [\alpha(1 + \Phi)] \] (18)

Assuming that the terms in the original economic injury level equation 1 are constant, then the right hand side of the inequalities of equations 17 and 18 are constant.

The gain threshold for the uncoupled case, \( B_{GTuc} \), was independent of the economic injury level or economic threshold (equation 15) but the natural enemy threshold in equation 17 was linearly dependent on the economic injury level. The reverse was true for the coupled case in which \( B_{GTc} \), was dependent on \( ET_o \), but the inequality of equation 18 was independent of an economic level. This result is caused by the placement of the biocontrol effect in modifying equation 3. If the effect is in the numerator (uncoupled case), then the economic terms cancel in the derivation of the gain threshold. If the effect is in the denominator, then the terms do not cancel. The insertion of the economic threshold in the derivation of equations 17 and 18 reverses the cancellations.

In some cases, these equations may yield a biologically unrealistic result. For example, a spider population may have a calculated gain threshold of 1,000 spiders per square meter. This would mean that the spider population would have to be unrealistically large before it would economically impact the pest population. In other cases, and because the left hand side of these inequalities \( (B_i) \) is variable in time, it would be worthwhile to sample a biocontrol agent population during some scouting dates and not others. A natural enemy population might be too low to justify sampling early in the growing season but it would be hoped that it would increase until the appropriate (coupled or uncoupled) condition is met. At that point, an IPM program manager would be justified in commencing the sampling of the biocontrol agent. Presumably, before that point, scouts might use some less rigorous method of assessing the status of the biocontrol agent population such as qualitative ratings or simply recording their presence/absence. As a practical matter in such a situation, though, inequalities in equations 17 and 18 are insufficient because if it is not known that the appropriate inequality is satisfied until time \( t \), then the next opportunity to sample the biocontrol agent will be at \( t + \tau \) and this may be too late to use the biocontrol agent effectively.

One solution to this problem is to solve equations 2b and 8b for \( B_{GT} \), and substitute into the corresponding inequalities above to obtain...
\[ B_{t,r} > \text{EL}, \Phi / a (1 + b - m) \text{ } \text{uncoupled case} \]
\[ B_{t,r} > \Phi (1 + r) / [\alpha (1 + \beta P_{t,r} - m) (1 + \Phi)] \text{ } \text{coupled case}. \]

Given an economic injury level, the uncoupled case reduces to a single constant that can be determined whenever the economic injury level is calculated. The coupled case, as its name implies, is fundamentally linked to the pest population itself. For most situations, these inequalities require stretching the predictive reliability of the simple models in equations 2 and 8 quite a bit. However, the objective of these inequalities is simply to estimate when to begin formal sampling.

Finally, assume that before beginning formal sampling, an informal method is used, such as presence or absence, and that the natural enemy will be distributed randomly with respect to the informal sample units. A Poisson distribution then can be used such that the sample criterion, \( Z \), becomes

\[ Z > p(0) = \exp(-\text{RHS}), \]

where RHS is the right hand side of the inequalities above. In other words, the natural enemies can be rated as present or absent until the proportion of absence samples exceed this predetermined \( p(0) \). Other variations on this theme are possible, but most such variations will hinge on the use of the biocontrol gain threshold defined above.

The gain threshold described above is a specific application of the Pedigo et al. (1986) concept. As one reviewer of the current paper noted, it may be that "The basic principle here—recognizing the significance of different economic thresholds (or economic injury levels) under different conditions could have much broader application. For instance, economic injury levels determined for varieties with different responses to injury (e.g., tolerance) could allow the calculation of a 'tolerance gain threshold'. In this case, we might use the comparison to point to a specific economic benefit of tolerance." The point here is that the gain threshold concept has general utility for evaluating pest management tactics in an economic injury level and economic threshold context and that it could probably be more widely utilized.

Reducing Risk in Economic Threshold-Based Decisions. In practice, pest populations are constantly under attack by a variety of natural enemies that collectively reduce the growth rates of those populations. Because economic thresholds usually reflect experience with pest population rates of change, the impact of naturally-occurring biocontrol agents is implicitly included. However, in most cases, these economic thresholds are constant with respect to the pest population (though they may fluctuate with respect to external factors such as crop price and control costs). The abundance of biocontrol agents fluctuates within and between growing seasons so that the lack of direct incorporation of biocontrols subjects economic threshold-based decisions to additional uncertainty. Additional uncertainty results in an increased percentage of incorrect management decisions (i.e., deciding not to control when a control is warranted or deciding to control when such control actually is unnecessary).

If the pest population has a variable growth rate because of biocontrol agents or other factors, forecasts of the population between sampling intervals will have an associated error that will be manifested as a proportion of incorrect management decisions. Fig. 1 illustrates 4 possible decision outcomes using the model

\[ P_{t,r} = e P_{r} \]  

where \( e \) is a normally distributed random variable with mean \((1+r)\) and \( \sigma = \sqrt{(1+r)\theta} \), and \( \theta = 5 \). The values of both \( r \) and \( \theta \) are arbitrarily chosen here for the purposes of illustration although, in practice, the mean and standard deviation of a specific pest population growth rate would be estimated from either literature sources or experimentation. Given these parameters and assuming an economic injury level of 100, the economic threshold for this example is 50 from equation 3. Fig. 1 was created by selecting a random \( e \) from the above distribution and applying it in equation 19. Ten replications were performed for each integral \( P_r \) from 1 to 100.

Figure 1 shows the graph divided into 4 quadrants. In quadrant I, the pest population was found to exceed the economic threshold at time \( t \) and, assuming no control was applied, would have actually exceeded the economic injury level by time \( t + \tau \). Consequently, a correct decision to control the pest would have been made. Similarly, all points in quadrant III represent correct decisions to defer control because the pest population was below economic threshold at time \( t \) as well as below economic injury level at time \( t + \tau \). Quadrants II and IV, however, show points in which incorrect decisions would have been made. The points in quadrant II illustrate decisions to defer control resulted in the pest exceeding the economic injury level whereas points in quadrant IV represent unnecessary control. In total, 1,000 simulations were conducted for Fig. 1 of which 40.4% are in quadrant I, 3.9% are in quadrant II, 46.1% are in quadrant III, and 9.6% are in quadrant IV.

In Fig. 1, the proportion of incorrect decisions increases as \( P_t \), the economic threshold, the equation to calculate this density-dependent probability can be derived by example. If \( P_t < \text{the economic threshold} \), then, from equation 19 and its associated definitions for mean, \( \mu \), and standard deviation,

\[ \text{Prob}(P_{t,r} > \text{EL}) = \text{Prob} \left( \epsilon > \text{EL}/P_r \right) \]

\[ = \text{Prob}(e - \mu)/\sigma > (\text{EL}/P_r)/(1 + r)/[(1 + r)/\theta] \]

letting \( z = (e - \mu)/\sigma \), and simplifying yields

\[ \text{Prob}(z > \theta) \left( \text{EL} - [1 + r] P_r / (1 + r) P_r \right) \]  

(20)

A plot of these probabilities as a function of \( P_t \) is shown in Fig. 2. As inferred from Fig. 1, these probabilities do increase as \( P_t \) approaches the economic threshold so that when \( P_t = \text{ET} \), the probability of making an incorrect decision is 50%. Another noteworthy aspect of Fig. 2 is that the economic threshold bisects these probabilities so that, to the left of the economic threshold \( P_t < \text{ET} \), the plot represents the probability of a quadrant II occurrence from Fig. 1, whereas to the right of the economic threshold \( P_t > \text{ET} \), the plot represents the probability of a quadrant IV occurrence. These probability curves are not symmetrical to each other because of the nonlinear nature of equation 20 and because quadrant IV errors as shown in Fig. 1 are more probable than quadrant II errors.

The same analysis can be applied to the 2 biocontrol-based economic threshold models by writing

\[ \text{ET}_{\text{BAC}} = (\text{EL} - \omega)/\epsilon \]  

uncoupled case

\[ \text{ET}_{\text{BAC}} = \text{EL}/(\epsilon - \omega) \]  

coupled case,

where \( \omega \) is a normally distributed random proportionate kill of the pest population. The simulation shown in Fig. 1 can then be repeated for each of these cases over a range of values.

The results are shown in Fig. 3 A--C. The situation in which the economic threshold does not explicitly include biocontrol agents but does include a random rate of pest increase (\( \epsilon \)), is shown in Fig. 3A. If no biocontrols are present \( (\omega = 0) \), the percentages of decisions resulting in failure to control when control was necessary (quadrant II) and applying unnecessary controls (quadrant IV) are about the same as that described above for Fig. 1. However, as \( \omega \) is...
increased, the percentage of these errors also increases resulting in a total of 20–30% of the decisions being erroneous over most of the range in $r$. The percentage of quadrant II errors is decreased logically because the presence of biocontrols decreases the likelihood that a pest will increase at an unexpectedly high rate. However, this decrease is more than offset by the substantial increase in quadrant IV errors.

Repeating the analysis for the uncoupled and coupled cases where the economic threshold specifically incorporates the biocontrol agent shows that these errors do not increase with increasing natural enemy action (Fig. 3 B and C). In both cases, the total error rate remains constant at about 15% and the errors are roughly evenly distributed between the 2 error types. Although the quantitative aspects of these figures are dependent on the specific parameter values chosen for the equations, one would expect that the qualitative features of both constant and reduced risk of incorrect decisions would hold over a large portion of the parameter space.

This analysis weighted quadrant II and IV errors equally. In practice, producers who grow their crops for direct sale are generally more averse to quadrant IV errors, whereas farmers that grow a crop for on-farm use (primarily livestock operations) are more averse to quadrant II errors. There are probably few growers who would give equal treatment to these error types so the approach presented here should be construed as an illustration of general risk reduction using biocontrol. For this analysis to be applied to a real cropping system, one would need to assess the risk aversion priorities of the specific growers in that system relative to these error types.

**Discussion**

There has been a substantial effort to refine economic injury level concepts through generalized models, and this work has resulted in the widespread adoption of economic injury levels. General models of economic thresholds, however, have not been as intensively pursued and part of the work reported here (e.g., equation 3) addresses a general economic threshold model. This is necessary because the economic injury level includes the effects of pest attack but not the prior events that lead to those effects. Including factors that occur over time and influence pest attack requires a predictive capability that is found in the economic threshold.

One such factor is biocontrol, either through released or naturally occurring natural enemies, and this long has been recognized. However, biocontrol agents, particularly naturally occurring ones, generally have not been incorporated into IPM decision making, probably because such use would require a general predictive model whereas the emphasis has been on developing economic injury levels, which are the nonpredictive component of the EIL/ET pair. Fig. 3 suggests that this omission probably has resulted in many unnecessary chemical controls.

The biggest difficulty with the models presented in this article is that, for them to be used effectively, the natural enemy attack rates need to be estimated for each natural enemy species or complex. Although this would be a large undertaking, the models are not overly sensitive to these estimates. The standard deviations used in Fig. 3 for the attack rate parameters were the same as that for the pest in Figs. 1 and 2. However, they were much larger relative to their expected values (the abscissa in Fig. 3) with the coefficient of variation decreasing as $r$ increased. Because the error rates for low attack rates in Fig. 3B and C were still reduced relative to Fig. 3A, it appears that including even a relatively inefficient natural enemy whose parameters are poorly estimated still will improve the quality of decisions based on the models presented here.

The models presented here are based on the traditional model of the economic injury level. As such, they share all the limitations of that model. One of the chief limitations of equation 1 in particular is that it does not account for age structure. There are several ways in which age structure could be added here. The life table approach developed by Ostling and Pedigo (1986) is one method in which they emphasized the role of natural enemies. An alternative might be to express the pest and natural enemy populations, along with their associated parameters, in vector and matrix notation. Although this approach would have generalized the models, the models would have been rather cumbersome and the general concepts illustrated in this article would have been less clear.

Pedigo (1996) identified 2 general types of economic thresholds, fixed and descriptive. According to Pedigo, fixed economic thresholds are a fixed proportion of the economic injury level; thus, the economic threshold fluctuates with the economic injury level. Descriptive economic thresholds "take into account possible changes in pest population growth rate" and can therefore fluctuate even if the economic injury level remains constant. He noted that fixed economic thresholds are more widely used than descriptive economic thresholds because pest population growth rates are "seldom predictable." The models presented here, though, show that if we can predict these growth rates for very short time intervals (scouting intervals), even only roughly, we will be able to use biological controls in a much more objective fashion.

The source of economic injury level fluctuations is largely external to the cropping system. Of the economic injury level components, only $I$ and $D$ (see equation 1) are intrinsic to that system and they usually are assumed to be some average value set by the specific pest and crop variety. The dynamics of economic thresholds include that of the economic injury level but also add the population dynamics of the pests and its natural enemies. The models presented here suggest that incorporating even simple models of these dynamics into economic threshold equations increases substantially the quality of decisions based on economic thresholds without compromising the simplicity of EIL/ET methods that has been so important to their widespread use.

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