Bull Math Biol
DOI 10.1007/s11538-013-9886-6

ORIGINAL ARTICLE

Adaptive Release of Natural Enemies in a Pest-Natural Enemy System with Pesticide Resistance

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Received: 7 October 2012 / Accepted: 23 July 2013

Abstract Integrated pest management options such as combining chemical and biological control are optimal for combating pesticide resistance, but pose questions if a pest is to be controlled to extinction. These questions include (i) what is the relationship between the evolution of pesticide resistance and the number of natural enemies released? (ii) How does the cumulative number of natural enemies dying affect the number of natural enemies to be released? To address these questions, we developed two novel pest-natural enemy interaction models incorporating the evolution of pesticide resistance. We investigated the number of natural enemies to be released when threshold conditions for the extinction of the pest population in two different control tactics are reached. Our results show that the number of natural enemies to be released to ensure pest eradication in the presence of increasing pesticide resistance can be determined analytically and depends on the cumulative number of dead natural enemies before the next scheduled release time.

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Keywords IPM · Pest resistance · Frequency of pesticide applications · Biological control · Dynamic threshold · Cumulative number of deaths

1 Introduction

Pesticide spraying is the main method in pest control. However, after repeated applications and increasingly higher rates of pesticide usage for a protracted period more than 500 species of pests have now developed resistance to pesticides (Georghiou 1990; Kotchen 1999; Thomas 1999), leading to increasing crop losses. For example, in the USA, farmers lost 7 % of their crops to pests in the 1940s, while since the 1980s, the percentage lost has increased to 13 %, even though more pesticides are being used (Karaagac 2012).

After a pest population develops resistance to a particular pesticide, how can it be controlled? One method is to use chemical and non-chemical control techniques at the same time, adopting the integrated pest management (IPM) approach (Onstad 2008; Flint 1987; Van Lenteren and Woets 1988; Van Lenteren 1995, 2000), which usually helps with resistance management (Peck and Ellner 1997). IPM provides an alternative to the single weapon (pesticide) approach and it encompasses management of pests at economically reasonable levels rather than eradicating them completely. IPM seeks to minimize reliance on pesticides by emphasizing the contribution of other control methods, including biological control, host-plant resistance breeding, and cultural tactics.

Indeed, biological control, which is defined as the reduction of pest populations by natural enemies, has been an important tactic to control pests in an IPM strategy (Greathead 1992; Parker 1971). Typically, it involves an active human role, such as the supplemental release of natural enemies, known as augmentation. This control strategy is usually used by releasing natural enemies at a critical time to reduce a pest's population (Hoffmann and Frodsham 1993; Neuenschwander and Herren 1988). Relatively few natural enemies may be released at a critical time of the season (inoculative release) or millions may be released (inundative release) when insufficient reproduction of released natural enemies is likely to occur and pest control will be achieved exclusively by the released individuals themselves (Hoffmann and Frodsham 1993; Neuenschwander and Herren 1988).

Many pulse-like IPM strategies such as releases of natural enemies at critical times and killing pests instantly by spraying pesticides have been studied by mathematical models, including impulsive differential equations (Neuenschwander and Herren 1988; Tang et al. 2005, 2008, 2009, 2010, 2013; Tang and Cheke 2008) or periodic spraying of pesticides (Liang and Tang 2010; Parker 1971). Pulse-like culling of mosquitos has also been modeled in relation to the study of mosquito-borne diseases such as the West Nile virus (Gourley et al. 2007; Terry and Gourley 2010). The results of such studies indicate that there exist optimal releasing periods or optimal numbers of pesticide applications, which maximize the benefits of pest control.

However, none of the studies to date considered the relationship between the development of pesticide resistance and the number of natural enemies released when biological and chemical control are used in combination against the same pest. It is this subject, an example of which is the combined use of abamectin and Encarsia formosa Gahan (Hymenoptera: Aphelinidae) against the greenhouse whitefly, Trialeurodes vaporariorum Westwood (Homoptera: Aleyrodidae) (Zchori-Fein et al. 1994) that we address in this paper. Other cases when chemical and biological control have been used in combination include fipronil and a phorid fly, together with a fungal pathogen, against red imported fire ants Solenopsis invicta (Oi et al. 2008) and the ovicide clofentezine in conjunction with the predatory mite Phytoseiulus persimilis against the two-spotted spider mite Tetranychus urticae in Dwarf Hops (Lilley and Campbell 1999).

Mathematical models can be important for determining the optimal rates of natural enemy releases with development of pesticide resistance. In this paper, a model with an IPM strategy is investigated, i.e. the combination of chemical and biological control tactics with pesticide resistance is developed and studied. In particular, the relationship between the number of natural enemies to be released and the evolution of pest resistance is addressed, and an analytical formula for the calculation of the number of natural enemies to be released is also provided.

However, in many cases, there is an impact of the pesticide on the natural enemies. Indeed, a proportion of the natural enemies could be killed at the time the pesticide is sprayed to kill the pests, resulting in resurgence of the pest populations (Barclay 1982; Debach 1974; Ruberson et al. 1998). In order to reduce the adverse impact of pesticides on natural enemies, a model with different periods of pesticide spraying and natural enemy releases is also investigated. Again, the dynamic threshold condition which ensures the extinction of the pest population is given. Based on this, the relationship between the number of natural enemies to be released and the evolution of pest resistance in this new situation is addressed, with another analytical formula for the calculation of the number of natural enemies to be released provided.

Our results indicate that correct adjustments to the number of natural enemies to be released depend on the cumulative number of deaths amongst the natural enemies before the release time, and that the appropriate number for release can be calculated analytically.

2 Modelling the Evolution of Pest Resistance and the Threshold Condition for the Pest-Free Solution

In this section, we will develop a simple pest population growth model concerning the evolution of pest resistance. In particular, the effects of the frequency of pesticide applications are modelled and investigated. One of our main purposes is to investigate how to implement a chemical control strategy and manage pest resistance such that the pest population dies out eventually. In order to address this issue, we focus on the threshold condition which guarantees the extinction of the pest population.

Throughout this study, the pest population is assumed to grow logistically with an intrinsic growth rate of r and a carrying capacity parameter η. Then the pest population follows:

$$\frac{dP}{dt} = rP(1 - \eta P). \tag{1}$$

Because of the evolution of pesticide resistance, we assume that the pest population (P) is made up of two parts: susceptible pests (denoted by P_s) and resistant pests (denoted by P_r), and the proportion of susceptible pests in the population is denoted by a fraction ω (i.e. $\omega = P_s/P$), the remaining fraction $1-\omega$ is resistant. That is to say, $1-\omega$ can be thought of as the stock of the pesticide resistance (i.e. the evolution of pesticide resistance can be described by ω). So, we have the resistance evolution equation

$$\frac{d\omega(t)}{dt} = d_1\omega\big(\omega^{q_i} - 1\big), \quad \tau_{i-1} \le t \le \tau_i, i \in \mathcal{N}. \tag{2}$$

The deduction of Eq. (2) and its analytical solutions can be found in Appendix A. Where d_1 is the mortality rate of susceptible pests because of the application of pesticide, and q_i is a function of the number of pesticide applications, the dosage X_i of the ith pesticide application and the time interval $\Delta\tau_i = \tau_i - \tau_{i-1}$ between the ith and $(i-1)$-th pesticide applications (Milgroom 1990), and τ_{i-1} is the spraying time for $i \in \mathcal{N}$ with $\tau_0 = 0$, $\mathcal{N} = \{1, 2, 3, \ldots\}$.

One of the main purposes of this paper is to investigate how pesticide resistance affects the extinction of the pest population, in particular how it is affected by the number or frequency of pesticide applications. To address this question, we assume that a pest population with periodic application of pesticide (i.e. $\tau_i - \tau_{i-1} = T, i \in \mathcal{N}$) follows the general impulsive differential equation,

$$\begin{cases} \dfrac{dP(t)}{dt} = P(t)F\big(t, P(t)\big), & t \ne nT, \\ P\big(nT^+\big) = q(nT)P(nT), & t = nT, \end{cases} \tag{3}$$

where $q(nT)$ denotes the survival rate of the pest population after the nth pesticide application, which depends on $\omega(nT)$, and naturally we have $0 \le q(nT) < 1$ for all $n \in \mathcal{N}$. Function $F(t, P(t))$ is the growth rate of the pest population including logistic growth as a special case, and we assume that

(a) The function F is continuous at $t \ne nT$, $n \in \mathcal{N}$, and is continuous and differentiable with respect to P, and $\partial F/\partial P$ is continuous with respect to P;

(b) There exist two continuous functions φ and λ with $\varphi(P) > 0$ for $P > 0$ and $\lambda(t) \ge 0$ for $t \ge 0$, such that

$$\frac{\partial F}{\partial P}(t, P) \le -\varphi(P)\lambda(t), \quad \text{for } t \ge 0,\ P \ge 0,$$

and

$$\int_0^\infty \lambda(t)dt = \infty;$$

(c) There is a $\beta > 0$ such that
   (i) $F(t, 0) \le \beta$ for $t \ge 0$,
   (ii) $q(nT)\exp(\int_{l+(n-1)T}^{l+nT} F(s, 0)ds) \le 1$ for $0 \le l < T$ and $n \in \mathcal{N}$.

The general non-autonomous model (3) without impulsive effects has been investigated by Vance and Coddington (1989), and some sufficient conditions which ensure the permanence and the extinction of populations were provided. By using similar methods as those developed by Vance and Coddington (1989), we can obtain the following result on the extinction of the pest population in model (3).

Theorem 2.1 *Suppose that F in* (3) *satisfies* (a), (b), *and* (c), *then for any initial condition $P(0^+) = P_0 > 0$, the solution of* (3) *satisfies $P(t) \to 0$ as $t \to \infty$.*

The proof of this theorem is provided in Appendix B. Note that the main result in Theorem 2.1 will play a key role in determining the threshold conditions, which guarantee the extinction of the pest population under additional control strategies and in the presence of resistance.

3 Interaction Between Pest and Natural Enemy with IPM and Resistance to Pesticides

IPM involves choosing appropriate tactics from a range of pest control techniques including biological, cultural, and chemical methods to maintain the density of the pest population below the Economic Injury Level (EIL) (Flint 1987; Van Lenteren 1995, 2000; Van Lenteren and Woets 1988). It is well known that single chemical control tactics are usually inefficient, and chemical control may result in high rates of failure due to fast evolution of pest resistance. If so, a combination of biological control tactics is necessary for pest control. In fact, biological control is often a key component of an IPM strategy (Greathead 1992; Parker 1971). It is defined as the reduction of pest populations by natural enemies and typically requires impulsive perturbations such as augmentation, the supplemental release of natural enemies at a critical time of the season when insufficient reproduction of released natural enemies is likely to occur and pest control will be achieved exclusively by the released individuals themselves (Hoffmann and Frodsham 1993; Neuenschwander and Herren 1988).

Therefore, if the pest population follows the logistic growth rate, i.e. $F(t, P(t)) = r(1 - \eta P(t))$, then we can extend the model proposed in the above section by involving natural enemies and releasing them impulsively as follows:

$$\begin{cases} \left.\begin{aligned} \frac{dP(t)}{dt} &= rP(t)(1-\eta P(t)) - \beta P(t)N(t), \\ \frac{dN(t)}{dt} &= \gamma\beta P(t)N(t) - dN(t), \end{aligned}\right\} & t \neq nT, \\ \left.\begin{aligned} P(nT^+) &= (1-\omega(nT)d_1)P(nT), \\ N(nT^+) &= N(nT) + \delta_n, \end{aligned}\right\} & t = nT, \\ \frac{d\omega(t)}{dt} = d_1\omega(t)\big(\omega(t)^{q_n} - 1\big), \end{cases} \tag{4}$$

with initial value $P(0^+) = P_0,\ N(0^+) = N_0 + \delta_0,\ \omega(0) = \omega_0$, where $q_n = n/T$, and $N(t)$ is the population size of the natural enemy at time t, β denotes the attack rate of the predator, γ represents conversion efficiency, d is the mortality rate of the natural enemy and in each impulsive time nT there is an introduction δ_n for the natural enemy, $n \in \mathcal{N}$ and δ_0 is the number of natural enemies released at time zero.

What we want to address for model (4) is to investigate how to design the releasing constant δ_n as pesticide resistance develops. Of particular interest is to determine the value δ_n for the fixed period T such that the pest population dies out eventually without switching pesticides.

3.1 Threshold Condition for the Pest-Free Solution

The basic properties of the following subsystem:

$$\begin{cases} \dfrac{dN(t)}{dt} = -dN(t), & t \neq nT, \\ N\left(t^+\right) = N(t) + \delta_n, & t = nT, \\ N\left(0^+\right) = N_0 + \delta_0 \end{cases} \tag{5}$$

play key roles for the investigation of model (4), where $n \in \mathcal{N}$.

The analytical solution of this subsystem at any impulsive interval $((n-1)T, nT]$ gives

$$N^*(t) = N_0 e^{-dt} + \sum_{i=0}^{n-1} \delta_i e^{-d(t-iT)}, \quad (n-1)T < t \le nT. \tag{6}$$

Therefore, the expression for the pest-free solution of system (4) over the nth time interval $(n-1)T < t \le nT$ is given by

$$\left(0, N^*(t)\right) = \left(0, N_0 e^{-dt} + \sum_{i=0}^{n-1} \delta_i e^{-d(t-iT)}\right). \tag{7}$$

For $0 \le l < T$ and $n \in \mathcal{N}$, we denote

$$\begin{aligned} M(n,l) = {} & \left(\frac{\beta N_0}{d} e^{-d(l+(n-1)T)} + \sum_{i=0}^{n-1} \frac{\beta \delta_i}{d} e^{-d(l+(n-1-i)T)}\right)\left(e^{-dT} - 1\right) \\ & + \frac{\beta \delta_n}{d}\left(e^{-dl} - 1\right) \end{aligned}$$

and

$$R_0(n,T) = \left(1 - d_1 \omega(nT)\right) e^{rT}.$$

Then we have the following threshold theorem for the pest-free solution.

Theorem 3.1 *Let*

$$R_0^N(n,T,l) = R_0(n,T) \exp\left(M(n,l)\right), \tag{8}$$

for $0 \le l < T$, *and* $(P(t), N(t))$ *be any solution of system* (4). *Then the pest-free solution* (7) *is globally attractive if* $R_0^N(n,T,l) \le 1$ *for all* $n \in \mathcal{N}$.

Remark 3.2 Note that the formula $R_0^N(n,T,l)$ depends on the number of pesticide applications, i.e. n, which is dynamic. Although we will address how to determine the number of natural enemies to be released such that the $R_0^N(n,T,l)$ is less than one for all n in the coming section, it is very interesting to know, from the pest control point of view, how the threshold value $R_0^N(n,T,l)$ changes as the releasing number of n increases. Thus, we chose $R_0^N(n, T, l)$ as a sequence of threshold values in Theorem 3.1. From the mathematical point of view, this can be easily realized if we take the supremum over all n of $R_0^N(n, T, l)$, that is, if $\sup_{n\in\mathcal{N}} R_0^N(n, T, l) \le 1$, this will lead to a single threshold.

The proof of this theorem is provided in Appendix C. It is interesting to note that the expression of $R_0^N(n, T, l)$ given by (8) clearly shows the effects of IPM strategies on the pest control: if only the chemical control is applied, the threshold value $R_0^N(n, T, l)$ is reduced to $R_0(n, T)$ which is obviously no less than $R_0^N(n, T, l)$ due to

$$\begin{aligned} R_0^N(n, T, l) &= R_0(n, T)\exp\left(-\beta\int_{l+(n-1)T}^{l+nT} N^*(s)ds\right) \\ &= R_0(n, T)\exp\big(M(n, l)\big) \le R_0(n, T); \end{aligned}$$

if only the biological control is implemented, the threshold value $R_0^N(n, T, l)$ is reduced to $\exp(M(n, l))$. Therefore, the threshold condition $R_0^N(n, T, l)$ given in (8) confirms that an integrated control strategy is more effective than any single control strategy.

In particular, if $\delta_i = \delta$ for $i \in \mathcal{N}_0$, where $\mathcal{N}_0 = \{0, 1, 2, 3, \dots\}$, then for subsystem (5) there exists a unique periodic solution, denoted by $N^T(t)$ and

$$N^T(t) = \frac{\delta\exp(-d(t-(n-1)T))}{1-\exp(-dT)}, \quad t \in \big((n-1)T, nT\big], \ n \in \mathcal{N}$$

with initial value $N(0^+) = \delta/(1-\exp(-dT))$. It is easy to prove that for every solution $N(t)$ of (5) in the case of $\delta_i = \delta$ for $i \in \mathcal{N}_0$ we have $|N(t) - N^T(t)| \to 0$ as $t \to \infty$. For this special case, the threshold value given by (8) does not depend on $l \in [0, T)$, we therefore denote this by $R_0^{N_T}(n, T)$ and we have

$$\begin{aligned} R_0^{N_T}(n, T) &= R_0(n, T)\exp\left(-\beta\int_{l+(n-1)T}^{l+nT} N^T(s)ds\right) \\ &= R_0(n, T)\exp\left(-\frac{\beta\delta}{d}\right). \end{aligned} \tag{9}$$

Then the pest-free periodic solution $(0, N^T(t))$ is globally attractive provided that $R_0^{N_T}(n, T) \le 1$.

Note that if $\delta_i = \delta$ for $i \in \mathcal{N}_0$ in (4), then

$$\begin{aligned} R_0^N(n, T, l) &= R_0(n, T)\exp\left(\frac{\beta N_0}{d}e^{-d(l+(n-1)T)}\big(e^{-dT}-1\big) + \frac{\beta\delta}{d}e^{-d(l+nT)} - \frac{\beta\delta}{d}\right) \\ &\doteq \overline{R_0^N}(n, T, l), \end{aligned}$$

which indicates that $\overline{R_0^N}(n, T, l) \to R_0^{N_T}(n, T)$ as $n \to \infty$.

It follows from (24) that $\omega(nT)$ is a monotonically decreasing function with respect to the number of pesticide applications, i.e. the instant killing rate becomes smaller and smaller as the pesticide resistance develops, which results in an increasing of the threshold value $R_0(n, T)$. To prevent the threshold value $R_0^N(n, T, l)$ from falling below a given level as the pesticide resistance develops, possible options include switching to a different pesticide or releasing more natural enemies or both. The question is: if we do not switch the pesticides and rely on increasing the number of natural enemies released, how do we determine the new release number such that the threshold value $R_0^N(n,T,l)$ is less than a given level? This is the key question that we will focus on in the rest of this paper.

3.2 Determining the New Number of Natural Enemies to be Released

The threshold value $R_0^{N_T}(n,T)$ reveals how the chemical and biological control tactics contribute to the pest control, in which $R_0(n,T)$ shows the effects of the frequency of pesticide applications and development of pest resistance on the control output, and the second part $\exp(-\beta\delta/d)$ represents the contribution of natural enemies. We know that $R_0(n,T)$ is a monotonically increasing function with respect to n and T, which indicates that chemical control alone will quickly fail once strong pesticide resistance develops. So the question is how to release the natural enemies such that the threshold value $R_0^N(n,T,l)$ or $R_0^{N_T}(n,T)$ is relatively small, for example less than one forever? That is, how to determine δ_n or δ in $R_0^N(n,T,l)$ or $R_0^{N_T}(n,T)$ such that those threshold values equal a constant R_C? Due to the complexity of $R_0^N(n,T,l)$, we first consider the $R_0^{N_T}(n,T)$.

In fact, solving equation

$$R_0(n,T)\exp\left(-\frac{\beta\delta}{d}\right)=R_C \tag{10}$$

with respect to δ, yields

$$\delta=-\frac{d}{\beta}\ln\left(\frac{R_C}{R_0(n,T)}\right),\quad n\in\mathcal{N}. \tag{11}$$

If we aim to eradicate the pest population, then we can assume that the constant R_C is less than one. It is interesting to note from (11) that if $R_0(n,T)\le R_C$ for some $n\in\mathcal{N}$, then $\delta\le 0$, which means that the chemical alone can suppress the pest outbreak at the initial stage. But once the pest resistance develops such that $R_0(n,T)>R_C$, then pulsed releases of natural enemies are necessary to maintain $R_0^{N_T}(n,T)$ as a constant R_C. All these results confirm that the number to be released δ depends strictly on the number of pesticide applications n. Therefore, the number of natural enemies to be released δ for all $n\in\mathcal{N}$ can be defined as follows:

$$\delta=\delta_n=\begin{cases}\delta_c, & \text{if } R_0(n,T)\le R_C,\\ -\dfrac{d}{\beta}\ln\left(\dfrac{R_C}{R_0(n,T)}\right), & \text{if } R_0(n,T)>R_C,\end{cases} \tag{12}$$

where δ_c can be zero or a relatively small positive constant.

Note that in (12), δ is switched between δ_c and $-(d/\beta)\ln(R_C/R_0(n,T))$, which is similar to the idea of the well-known bang-bang control (Artstein 1980).

To show the effects of the releasing constant δ determined by formula (12) on the control of the pest with development of pesticide resistance, we carried out numerical

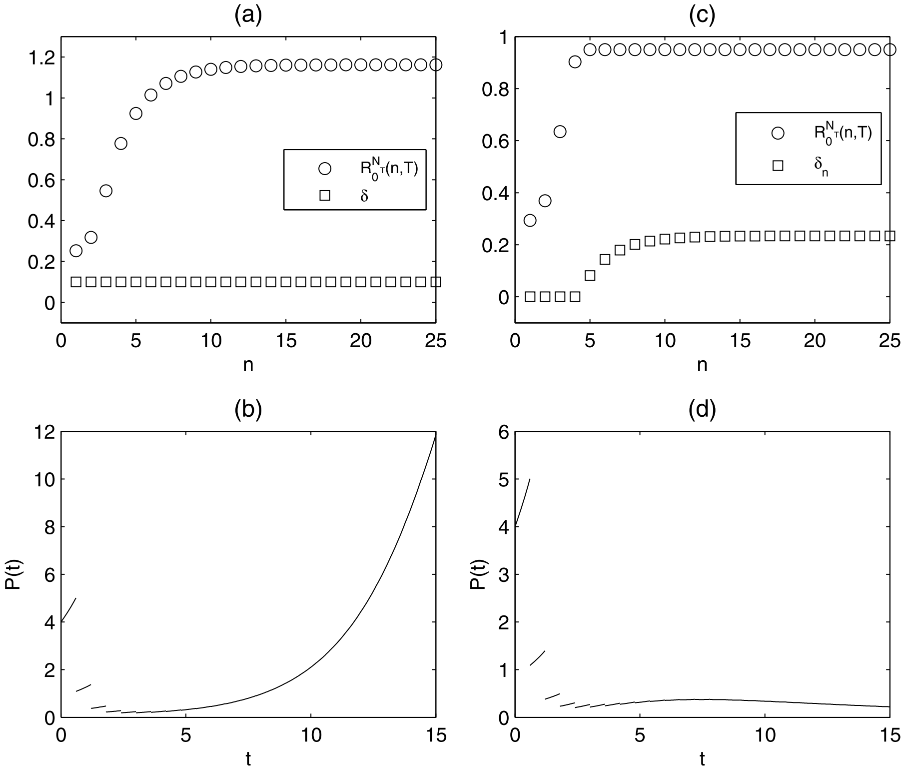

Fig. 1 Calculation of $R_0^{N_T}(n, T)$ and numerical simulations of model (4) with constant pulse releasing of natural enemies. The baseline parameter values are as follows: $d_1 = 0.8$, $r = 0.5$, $\omega_0 = 0.99$, $d = 0.2$, $\beta = 0.3$, $T = 0.6$, $R_C = 0.95$, $\delta_c = 0$ and $\delta = 0.1$. (**a**) The plot of $R_0^{N_T}(n, T)$ with respect to n; (**b**) The time series of the pest population associated with (**a**); (**c**) The plot of $R_0^{N_T}(n, T)$ with respect to n using the formula (12) to determine the δ; (**d**) The time series of the pest population associated with (**c**)

investigations of the model (4) in which δ_n is given by a constant or determined by formula (12). It follows from Fig. 1 that the threshold value $R_0^{N_T}(n, T)$ is increasing as the number of pesticide applications n increases if we fixed all parameters as those in Fig. 1(a), and then $R_0^{N_T}(n, T)$ will exceed one after six pesticide applications. If so, the density of the pest population will decrease firstly due to the high efficacy of the pesticide at the initial stage, and then the pest population will resurge exponentially (see Fig. 1(b)), which means that the constant releasing strategy cannot be successful for pest control. However, if we only release natural enemies once the pest resistance develops at a certain stage, for example $R_0(n, T)$ increases and exceeds a predefined level R_C (i.e. $R_0(n, T) > R_C$). That is we let $\delta_c = 0$ and assume that δ is determined by formula (12). Figure 1(c) provides an example of this strategy, and it is seen that the threshold value $R_0^{N_T}(n, T)$ is increasing firstly and then it maintains a constant R_C. The numerical solution for the pest population for this case is shown in Fig. 1(d), and it is interesting to note that the pest population decreases and will eventually go to extinction due to $R_C = 0.95$ for this example.

Now let us turn to the general case, i.e. the threshold value $R_0^N(n,T,l)$, which depends on the length of the interval $[0,T)$.

Let $R_{0_{\max}}^N(n,T,l)=\max_{0\le l<T}\{R_0^N(n,T,l)\}$, then

$$R_{0_{\max}}^N(n,T,l)<1 \quad \text{implies } R_0^N(n,T,l)<1$$

for all $l\in[0,T)$. In fact, we have

$$\frac{\partial R_0^N(n,T,l)}{\partial l}=R_0^N(n,T,l)\frac{\partial M(n,l)}{\partial l}$$

with

$$\begin{aligned}\frac{\partial M(n,l)}{\partial l}&=\left(\beta N_0e^{-d(l+(n-1)T)}+\sum_{i=0}^{n-1}\beta\delta_ie^{-d(l+(n-1-i)T)}\right)\big(1-e^{-dT}\big)-\beta\delta_ne^{-dl}\\&=\beta e^{-dl}\left(\left(N_0e^{-d(n-1)T}+\sum_{i=0}^{n-1}\delta_ie^{-d(n-1-i)T}\right)\big(1-e^{-dT}\big)-\delta_n\right)\\&\doteq\beta e^{-dl}(D_{n-1}-\delta_n),\end{aligned}$$

where $D_{n-1}=(N_0\exp(-d(n-1)T)+\sum_{i=0}^{n-1}\delta_i\exp(-d(n-1-i)T))\times(1-\exp(-dT))$, and note that

$$\left(N_0e^{-d(n-1)T}+\sum_{i=0}^{n-1}\delta_ie^{-d(n-1-i)T}\right)=N^*\big((n-1)T\big)$$

represents the total survival number of natural enemies at time $(n-1)T$. Therefore, D_{n-1} denotes the cumulative number of natural enemy deaths before time nT. Therefore, if $D_{n-1}\le\delta_n$, then $R_0^N(n,T,l)$ is a decreasing function with respect to l, thus $R_{0_{\max}}^N(n,T,l)=R_0^N(n,T,0)$; If $D_{n-1}>\delta_n$, then $R_0^N(n,T,l)$ is an increasing function with respect to l, thus $R_{0_{\max}}^N(n,T,l)=R_0^N(n,T,T)$.

By employing the same ideas as for the threshold value $R_0^{N_T}(n,T)$ and the same methods as above, we assume, without loss of generality, that there exists an integer $n'\in\mathcal{N}$ such that (i) $R_0(n,T)\le R_C$ for $n\le n'$ due to the high effectiveness of pesticide applications in the initial stage and (ii) $R_0(n,T)>R_C$ for $n>n'$. Thus, we let $\delta_n=\delta_c$ for $n\le n'$ and let $R_{0_{\max}}^N(n,T,l)=R_C$ for $n>n'$. In the light of the above, we consider the following two cases:

Case 3.1 $D_{n-1}\le\delta_n$ for all $n\in\mathcal{N}$, i.e. the new number to be released is not less than the cumulative death number.

In this case, $R_{0_{\max}}^N(n,T,l)=R_0^N(n,T,0)=R_C$. It follows from (8) that we have $M(n,0)=\ln(R_c/R_0(n,T))$, that is

$$\left(\frac{\beta N_0}{d}e^{-d(n-1)T}+\sum_{i=0}^{n-1}\frac{\beta\delta_i}{d}e^{-d(n-1-i)T}\right)\big(e^{-dT}-1\big)=\ln\left(\frac{R_C}{R_0(n,T)}\right).$$

This indicates that

$$\delta_n \geq D_{n-1} = -\frac{d}{\beta} \ln\left(\frac{R_C}{R_0(n,T)} \right).$$

Therefore, if $D_{n-1} \leq \delta_n$, then the minimum number of natural enemies released which maintains the threshold value $R_0^N(n,T,l) = R_C$ is D_{n-1}, denoted by $\min \delta_n$. That is, the new number to be released, δ_n, can be determined as follows:

$$\delta_n = \begin{cases} \delta_c, & \text{if } n \leq n', \\ \min \delta_n = -\frac{d}{\beta} \ln(\frac{R_C}{R_0(n,T)}), & \text{if } n > n'. \end{cases} \tag{13}$$

Comparing (13) with (12), we conclude that when the new number of natural enemies to be released, i.e. δ_n, is no less than the cumulative number of natural enemy deaths before time nT, the minimum number of natural enemies to be released can be determined by the same method as those in formula (12).

Case 3.2 $D_{n-1} > \delta_n$ for all $n \in \mathcal{N}$, i.e. the new number to be released is less than the cumulative death number.

In this case, we let $G_{n'} = N_0 + \sum_{i=0}^{n'} \delta_c \exp(diT)$, and

$$A_n = -\frac{de^{dnT}}{\beta(1-e^{-dT})} \ln\left(\frac{R_C}{R_0(n,T)} \right) - G_{n'}$$

for $n > n'$, the new number of natural enemies to be released δ_n can be determined as follows:

$$\delta_n = \begin{cases} \delta_c, & \text{if } n \leq n', \\ A_{n'+1} e^{-d(n'+1)T}, & n = n'+1, \\ (A_n - A_{n-1}) e^{-dnT}, & \text{if } n > n'+1. \end{cases} \tag{14}$$

The detailed deduction of formula (14) can be seen in Appendix D. Based on the methods proposed in Cases 3.1 and 3.2, the new number of natural enemies to be released for more complex cases can be determined by a combination of the formulae (13) and (14).

It is interesting to note that the number of newly released natural enemies in Case 3.2 is relatively small compared to those in Case 3.1. However, in formula (14) we always need $\delta_n < D_{n-1}$ for $n > n'$, which will result in some difficulty for implementation. Thus, in order to control the pest population successfully, careful monitoring of the densities of both pest and natural enemy populations should be carried out once the pests become highly resistant to the pesticide.

4 Different Patterns of Insecticide Applications and Natural Enemy Releases

In practice, there are some adverse impacts of many pesticides on natural enemies (Ruberson et al. 1998) and in order to reduce these we will consider in this section that there are different control periods between chemical control and biological control. Following the ideas proposed by Tang et al. (2010, 2013), we assume that the pesticide is sprayed at impulsive time τ_n, and a constant number of natural enemies is released at each impulsive time λ_m. Considering the evolution of pesticide resistance and different control periods between chemical control and biological control, we have the following model:

$$\begin{cases} \dfrac{dP(t)}{dt} = rP(t)\big(1 - \eta P(t)\big) - \beta P(t)N(t), \quad t \neq \tau_n, \\ \dfrac{dN(t)}{dt} = \gamma\beta P(t)N(t) - dN(t), \quad t \neq \lambda_m, \\ P\big(\tau_n^+\big) = \big(1 - \omega(\tau_n)d_1\big)P(\tau_n), \quad t = \tau_n, \\ N\big(\lambda_m^+\big) = N(\lambda_m) + \delta_n, \quad t = \lambda_m, \\ \dfrac{d\omega(t)}{dt} = d_1\omega(t)\big(\omega(t)^{q_n} - 1\big), \quad \tau_{n-1} \leq t < \tau_n \end{cases} \tag{15}$$

with initial value $P(0^+) = P_0$, $N(0^+) = N_0$, $\omega(0) = \omega_0$.

We consider in the following case that pesticides are sprayed more frequently than releases of natural enemies so that different patterns of insecticide applications and natural enemy releases are applied in the model (15) (Tang et al. 2010, 2013).

For simplicity, we assume that the natural enemies are released periodically with period T_N, i.e. $\lambda_{m+1} - \lambda_m \equiv T_N$ for all m, and pesticides are sprayed $k_p + 1$ times within the period T_N. In order to avoid applying pesticides and natural enemies simultaneously, we assume that for $n \in \mathcal{N}$,

$$(n-1)T_N < (n-1)T_N + \tau_1 < (n-1)T_N + \tau_2 < \cdots < (n-1)T_N + \tau_{k_p+1} < nT_N.$$

4.1 Threshold Condition for the Pest-Free Solution

The basic properties of the following subsystem

$$\begin{cases} \dfrac{dN(t)}{dt} = -dN(t), \quad t \neq hT_N, \\ N\big(t^+\big) = N(t) + \delta_h, \quad t = hT_N, \\ N\big(0^+\big) = N_0 \end{cases} \tag{16}$$

play key roles for the investigation of model (15), where $h \in \mathcal{N}$. Note that this is virtually Eq. (5) with different parameters.

By simple calculations, the analytical solution of system (16) at any impulsive interval $((h-1)T_N, hT_N]$ can be determined as follows:

$$N^*(t) = \left(N_0 + \sum_{i=1}^{h-1} \delta_i e^{idT_N}\right)e^{-dt}, \quad (h-1)T_N < t \leq hT_N. \tag{17}$$

Therefore, the expression for the pest-free solution of system (15) over the hth time interval $(h-1)T_N < t \leq hT_N$ is given by $(0, N^*(t))$.

In order to obtain the threshold conditions for the pest population fall to zero, we further assume that the pesticides are sprayed periodically with period τ, which satisfies $\tau_{j+1} - \tau_j = \tau$ for $j = 1, 2, \ldots, k_p$ and $T_N - \tau_{k_p+1} + \tau_1 = \tau$.

Denote

$$R_0(hT_N,\tau)=\big(1-d_1\omega(hT_N)\big)e^{r\tau},$$

and

$$D_{h-1}=e^{-d((h-1)T_N+\tau_{k_p})}\left(N_0+\sum_{i=1}^{h-1}\delta_i e^{idT_N}\right)\big(1-e^{-d\tau}\big).$$

Then for the pest-free solution we have following the threshold theorem.

Theorem 4.1 *Let*

$$R_0^{T_N}(h,T_N)=\begin{cases} R_0(hT_N,\tau)\exp\{\frac{\beta}{d}e^{-d((h-1)T_N+\tau_{k_p})}(N_0+\sum_{i=1}^{h-1}\delta_i e^{idT_N})(e^{-d\tau}-1)\}, \\ \quad D_{h-1}\le\delta_h, \\ R_0(hT_N,\tau)\exp\{\frac{\beta}{d}e^{-dhT_N}(N_0+\sum_{i=1}^{h}\delta_i e^{idT_N})(e^{-d\tau}-1)\}, \\ \quad D_{h-1}>\delta_h. \end{cases} \tag{18}$$

Then the pest-free solution $(0,N^*(t))$ *is globally attractive for solution of* (15) *if* $R_0^{T_N}(h,T_N)<1$.

The proof of this theorem is provided in Appendix E. The expression of $R_0^{T_N}(h,T_N)$ reflects the effects of pesticide resistance development, spraying period, the number of natural enemies released and their releasing period on the pest control. Obviously, it is not a constant and depends on the timings of the pesticide applications. In particular, the first term $R_0(hT_N,\tau)$ shows the effects of the pest's growth rate, pesticide resistance development, and active ingredient effectiveness on the threshold conditions, and the second term involves all factors related to natural enemies including their initial density (N_0), attack rate (β), releasing period (T_N) and the total number newly released ($\delta_i, i=1,2,\dots,h-1$). Therefore, it is quite difficult to maintain the threshold value $R_0^{T_N}(h,T_N)$ less than one or some given constant as the pesticide resistance evolves. So, in the following, we also choose the number of natural enemies newly released as parameters and fix all others with the aim of determining the new number of natural enemies to be released.

4.2 Determining the New Number of Natural Enemies to be Released

In this section, we will investigate how to release the natural enemies such that the threshold value $R_0^{T_N}(h,T_N)$ is relatively small, for example less than one forever. That is, how to determine δ_h in $R_0^{T_N}(h,T_N)$ such that those threshold values equal a constant R_C (<1)?

In fact, if $R_0(hT_N,\tau)<R_C$ for some h, then $R_0^{T_N}(h,T_N)<R_C$. As in Sect. 3.2, we assume that there exists an integer $h'\in\mathcal{N}$ such that (i) $R_0(hT_N,\tau)\le R_C$ for $h\le h'$ and (ii) $R_0(hT_N,\tau)>R_C$ for $h>h'$. Thus, we let $\delta_h=\delta_c$ for $h\le h'$ and let $R_0^{T_N}(h,T_N)=R_C$ for $h>h'$. Similarly, by using the same methods as those in Sect. 3 we can consider following two cases.

Case 4.1 $D_{h-1} \leq \delta_h$, i.e. the new number to be released is no less than the cumulative death number

In this case, let $R_0^{T_N}(h, T_N) = R_C$, we get

$$\begin{aligned}&\frac{\beta}{d} e^{-d((h-1)T_N+\tau_{k_p})}\left(N_0 + \sum_{i=1}^{h-1} \delta_i e^{idT_N}\right)\left(e^{-d\tau} - 1\right) \\ &\quad = \ln\left(\frac{R_C}{R_0(hT_N, \tau)}\right), \quad h \in \mathcal{N}. \end{aligned} \tag{19}$$

This indicates that

$$\delta_h \geq D_{h-1} = -\frac{d}{\beta} \ln\left(\frac{R_C}{R_0(hT_N, \tau)}\right).$$

Therefore, if $D_{h-1} \leq \delta_h$, then the minimum number of natural enemies released which maintains the threshold value $R_0^{T_N}(h, T_N) = R_C$ is D_{h-1}, denoted by $\min \delta_c$. That is, the new number to be released δ_h can be determined as follows:

$$\delta_h = \begin{cases} \delta_c, & \text{if } h \leq h', \\ \min \delta_h = -\frac{d}{\beta} \ln\left(\frac{R_C}{R_0(hT_N, \tau)}\right), & \text{if } h > h'. \end{cases} \tag{20}$$

Case 4.2 $D_h > \delta_{h+1}$, i.e. the new number to be released is less than the cumulative death number.

In this case, we let

$$A'_h = -\frac{de^{dhT_N}}{\beta(1 - e^{-d\tau})} \ln\left(\frac{R_C}{R_0(hT_N, \tau)}\right) - N_0 - \delta_c \sum_{i=1}^{h'} e^{idT_N}$$

for $h > h'$, the new number of natural enemies to be released δ_h can be determined as follows:

$$\delta_h = \begin{cases} \delta_c, & \text{if } h \leq h', \\ A'_{h'+1} e^{-d(h'+1)T_N}, & h = h' + 1, \\ (A'_h - A'_{h-1}) e^{-dhT_N}, & \text{if } h > h' + 1. \end{cases} \tag{21}$$

Comparing the formula (21) with the formula (14) obtained in Sect. 3.2, we conclude that the similar formula for the number of natural enemies newly released can be obtained under different patterns of pesticide applications and natural enemy releases. By the same methods as described in this section, we can study several other patterns such as natural enemy releases being more frequent than pesticide applications (Tang et al. 2010, 2013).

5 Discussion

In most cropping systems, application of pesticides is still the principal tactic for controlling pests once the density of pests reaches a certain threshold level such as the economic threshold. This is because pesticides can be relatively cheap and are easy to spray, fast-acting, and in most instances can be relied on to control the pests (Flint 1987; Van Lenteren 1995, 2000; Van Lenteren and Woets 1988). However, frequent use of one kind of pesticide may create selection pressure for evolution of pest resistance to that pesticide. If too large a proportion of a pest population develops resistance to the pesticide's active ingredient, the susceptibility of the entire pest population to it will be lost eventually, leading to pest resurgences and outbreaks.

How to manage or delay the development of pesticide resistance is a serious issue. The obvious principle for delaying the development of pesticide resistance is avoiding unnecessary pesticide applications. The main practical tactics for the management of pest resistance are switching pesticides periodically, leaving untreated refuges where susceptible pests can survive, using non-chemical control techniques, and adopting the integrated pest management (IPM) approach (Onstad 2008). Although the tactic of switching pesticides is useful for delaying the emergence of resistance against some pesticides, the frequency of pesticide spraying is still increasing and it could lead to multiple resistance. IPM approach often involves the release of natural enemies, in combination with application of pesticides. This approach has its own challenge. For instance, the effectiveness of pesticides may wear off (e.g. Zchori-Fein et al. reported 100 % mortality of natural enemies 2 hours after spraying abamectin, but 0 % 24 hours after (Zchori-Fein et al. 1994)). Also, repeated releases of the same number of natural enemies is either insufficient if they no longer suppress the pest population once resistance develops, or the number released is too large, which is not cost effective and may cause secondary outbreaks or pest resurgence. Therefore, in order to avoid multiple resistance, one possible way is to release different numbers of natural enemies according to the evolution of pesticide resistance. The key question is then how to determine the number of natural enemies to be released anew, with the aim of eradicating the pest population, i.e. how to determine the new number of natural enemies to be released at each control action?

To address this question, we first developed the single pest growth model with pulses of pesticide applications and evolution of pesticide resistance, and the threshold condition, which guarantees the extinction of the pest population was derived. Secondly, we extended the single pest growth model to include natural enemies with pulsed releases, and the threshold condition which guarantees the extinction of the pest population was obtained. Two interesting cases concerning the number of natural enemies released anew are discussed and analyzed. One case concerns when the number of natural enemies released at time nT is no larger than the cumulative number of their deaths before nT, and the other case concerns when the number of natural enemies released at time nT is larger than the cumulative number of their deaths before nT. For each case, the analytical formula for determining the new numbers of natural enemies to be released are provided, and the effects of key factors on newly released number of natural enemies have been discussed. This may help the design of the most cost-effective control strategy and help to manage pest resistance.

However, determining the number of natural enemies to be released is not the only issue involved in biological control tactics. Although we considered factors such as natural enemy attack rates, there are other characteristics of natural enemies such as their ability to exploit spatially heterogeneous populations of pests, variation in their generation times, pest refuges, and mutual interference that influence the dynamics (Beddington et al. 1978).

Finally, different patterns of releasing natural enemies and spraying pesticides are addressed, because most natural enemies are adversely affected by pesticides (Ruberson et al. 1998), which usually kill both the pest and their natural enemies (Debach 1974). In this study, we considered the reduction of such adverse impacts by examining a strategy involving pesticide spraying $k_p + 1$ times in one period of natural enemy releases T_N, while assuming that the releasing actions and spraying actions cannot occur simultaneously. The threshold condition which guarantees the extinction of the pest population and the new number of natural enemies to be released in this strategy were derived. We also mentioned that the strategy for releasing natural enemies more than once in each period of pesticide spraying can be studied similarly.

IPM strategies have been extensively used in practice, and mathematical modelling concerning IPM has significantly contributed to understanding of the interaction between pest and natural enemy populations and evaluating the effectiveness of pest control actions. Various mathematical models have been developed to describe the effects of multiple control methods including chemical and biological controls on successful pest management (Tang et al. 2005, 2008, 2010, 2013, 2012; Tang and Cheke 2008; Tang and Liang 2013), and some important questions concerning IPM strategies have been addressed. However, the most important factor, pesticide resistance, was not included in those models. In this study, we have tried to fill this gap by employing a pesticide resistance evolution equation, but there are still many key issues which need to be investigated in more detail, such as how to determine the switching frequency of unrelated pesticides once the pests have become highly resistant? Using real data sets to estimate the pesticide evolution rate is also problematic. We will address these questions in the near future.

In this work, the classical Lotka–Volterra predator-prey model (i.e. Holling type I functional response) has been employed to describe the interactions between the prey and predator populations. However, what we want to know is how the threshold dynamics change once other types of functional response functions including Holling type II have been chosen. Also, the impulsive releasing strategies were applied at fixed time moments, so another interesting question is how to determine the threshold value as shown in (12) if the continuous releasing method is used. We will focus on these problems in the near future.

Acknowledgements This work was supported by the Fundamental Research Funds for the Central Universities (GK201104009), and by the National Natural Science Foundation of China (NSFC, 11171199), and by the International Development Research Centre.

Appendix A: The Deduction of Eq. (2) and Its Solution

Because $P_s = \omega P$ and $P_r = (1-\omega)P$, and d_1 is the mortality rate of susceptible pests, d_2 is the mortality rate of resistant pests when the pesticide is sprayed, so we have

$$\begin{cases} \dfrac{dP_s}{dt} = \omega r P(1-\eta P) - d_1 P_s, \\ \dfrac{dP_r}{dt} = (1-\omega) r P(1-\eta P) - d_2 P_r. \end{cases}$$

However, for simplification we assume that the resistant pests display near-complete resistance to the pesticide, which means that $d_2 \approx 0$. Therefore,

$$\frac{dP}{dt} = \frac{dP_s}{dt} + \frac{dP_r}{dt} = rP(1-\eta P) - \omega d_1 P.$$

Then we get

$$\frac{d\omega}{dt} = \frac{d}{dt}\left(\frac{P_s}{P}\right) = d_1 \omega(\omega - 1).$$

This resistance evolution equation has been widely used recently in different fields (Hall et al. 2004; Bonhoeffer and Nowak 1997; Gubbins and Gilligan 1999; Laxminarayan and Simpson 2000; Milgroom et al. 1989).

In practice, the evolution of pesticide resistance is dependent on the dosage of the pesticide applications, the frequency of applications or the pesticide application period. Although linking the evolution of pesticide resistance to the pest growth model is a great challenge, it is well known that the less frequent are the pesticide applications (i.e. the longer the period between them), the slower the development of the pest resistance. One possible way is to consider the effect of each pulse spraying of pesticides on the evolution of pesticide resistance as a perturbation constant, i.e. we have

$$\frac{d\omega(t)}{dt} = d_1 \omega\big(\omega^{q_i} - 1\big), \quad \tau_{i-1} \le t \le \tau_i, \ i \in \mathcal{N},$$

with initial value $\omega(\tau_{i-1})$ at each time interval $t \in [\tau_{i-1}, \tau_i]$ and $\omega(\tau_0) = \omega(0) = \omega_0$ is given. Where q_i denotes the perturbation constant of the ith pulse spraying of pesticides, which depends the number of pesticide applications, dosage X_i of the ith pesticide application and time interval $\Delta\tau_i$. This equation resembles the classical Richards equation. As such, we anticipate the approach in resistant equation can be used to describe analytically the functional format of q_i.

The analytical solution of $\omega(t)$ can be determined as follows:

$$\omega(t) = \big(1 + e^{q_i d_1 (t-\tau_{i-1})}\big(\big(\omega(\tau_{i-1})\big)^{-q_i} - 1\big)\big)^{-\frac{1}{q_i}}, \quad \tau_{i-1} \le t \le \tau_i, \tag{22}$$

which indicates that

$$\omega(\tau_i) = \big(1 + e^{i d_1}\big(\omega(\tau_{i-1})^{-q_i} - 1\big)\big)^{-1/q_i}. \tag{23}$$

For simplification, we assume that the same dosage of pesticides is applied each time, and without loss of generality we let $X_i = 1$ for all $i \in \mathcal{N}$. It follows from the main text that one possible definition of q_i is as follows: $q_i = i/\Delta\tau_i$, and then $\Delta\tau_i = T$ for all $i \in \mathcal{N}$. For this special case, the evolution of ω at each time point nT can be expressed as

$$\omega(nT) = \bigl(1 + e^{nd_1}\bigl(\omega\bigl((n-1)T\bigr)^{-n/T} - 1\bigr)\bigr)^{-T/n}, \quad n \in \mathcal{N}. \tag{24}$$

Appendix B: The Proof of Theorem 2.1

For any given $\varepsilon > 0$ (ε small enough), we will first show that there exists a $\tau(\varepsilon) > 0$ such that

$$P(\tau) \le \varepsilon e^{-\beta T}. \tag{25}$$

Otherwise, $P(t) \ge \varepsilon \exp(-\beta T)$ for all $t \ge 0$. It follows from (b) that $\partial F/\partial P \le 0$ and then

$$F\bigl(s, P(s)\bigr) \le F\bigl(s, \varepsilon e^{-\beta T}\bigr), \quad \text{for } s \ge 0.$$

Since

$$F\bigl(s, \varepsilon e^{-\beta T}\bigr) - F\left(s, \frac{\varepsilon}{2}e^{-\beta T}\right) = \frac{\varepsilon}{2}e^{-\beta T}\frac{\partial F}{\partial P}\bigl(s, \eta(s)\bigr),$$

where $\frac{\varepsilon}{2}\exp(-\beta T) < \eta(s) < \varepsilon \exp(-\beta T)$. Again assumption (b) implies that

$$\frac{\partial F}{\partial P}\bigl(s, \eta(s)\bigr) \le -\varphi_0 \lambda(s),$$

where $\varphi_0 = \min\{\varphi(P) : \exp(-\beta T)\varepsilon/2 \le P \le \varepsilon \exp(-\beta T)\}$. Thus, we get

$$F\bigl(s, P(s)\bigr) \le F\left(s, \frac{\varepsilon}{2}e^{-\beta T}\right) - \frac{\varepsilon}{2}e^{-\beta T}\varphi_0\lambda(s) \le F(s,0) - \frac{\varepsilon}{2}e^{-\beta T}\varphi_0\lambda(s).$$

For any $t \ge 0$, there is a $h \in \mathcal{N}$, such that $(h-1)T < t \le hT$. Therefore,

$$\begin{aligned}
\varepsilon e^{-\beta T} &\le P(t) \\
&= \prod_{i=1}^{h-1} q(iT)P_0 \exp\left(\left(\int_0^T + \int_T^{2T} + \cdots + \int_{(h-2)T}^{(h-1)T} + \int_{(h-1)T}^{t}\right) F\bigl(s, P(s)\bigr)ds\right) \\
&\le \prod_{i=1}^{h-1} q(iT)P_0 \exp\left(\left(\int_0^T + \cdots + \int_{(h-2)T}^{(h-1)T} + \int_{(h-1)T}^{t}\right)\right. \\
&\quad \left. \times \left(F(s,0) - \frac{\varepsilon}{2}e^{-\beta T}\varphi_0\lambda(s)\right)ds\right) \\
&= \prod_{i=1}^{h-1} q(iT)P_0 \exp\left(\left(\int_0^T + \cdots + \int_{(h-1)T}^{t}\right) F(s,0)ds\right) \\
&\quad \times \exp\left(\int_0^t \left(-\frac{\varepsilon}{2}e^{-\beta T}\varphi_0\lambda(s)\right)ds\right).
\end{aligned}$$

For $\varepsilon > 0$ small enough and assumption (c) yields

$$q(iT)\exp\int_{(i-1)T}^{iT} F\left(s, \frac{\varepsilon}{2}e^{-\beta T}\right)ds \le 1, \quad i = 1, 2, \dots, h,$$

and $F(s, 0) \le \beta$. Hence,

$$\varepsilon e^{-\beta T} \le P(t) \le P_0 e^{\beta T}\exp\left(\int_0^t \left(-\frac{\varepsilon}{2}e^{-\beta T}\varphi_0\lambda(s)\right)ds\right) \to 0$$

as $t \to \infty$, in particular, $P(t) < \varepsilon\exp(-\beta T)$ for t large enough. This contradiction establishes that (25) is true for some τ.

Now we will prove that

$$P(t) \le \varepsilon \quad \text{for } t \ge \tau. \tag{26}$$

Suppose that $P(\tau_1) > \varepsilon \ge \varepsilon\exp(-\beta T)$ for some $\tau_1 > \tau$ and there is a $n \in \mathcal{N}$, such that $(n-1)T \le \tau_1 < nT$. Then there exists a $t_1 \in (\tau, \tau_1)$, such that

$$P(t_1) = \varepsilon e^{-\beta T},$$

and $P(t) > \varepsilon\exp(-\beta T)$, for t $\in$ (t$_1$, τ_1], which means that for any $k \in \mathcal{N}$, $t_1 \ne kT$, due to $0 \le q(kT) < 1$. Therefore, either $t_1 > (n-1)T$ or $t_1 < (n-1)T$. If $t_1 > (n-1)T$, (this indicates $\tau_1 > (n-1)T$), then $\tau_1 - t_1 < T$ and

$$\begin{aligned}\varepsilon < P(\tau_1) &= P(t_1)\exp\left(\int_{t_1}^{\tau_1} F\big(s, P(s)\big)ds\right)\\ &\le \varepsilon e^{-\beta T}\exp\left(\int_{t_1}^{\tau_1} F\big(s, \varepsilon e^{-\beta T}\big)ds\right)\\ &\le \varepsilon e^{-\beta T}e^{\beta T} = \varepsilon,\end{aligned}$$

this is a contradiction. So $t_1 < (n-1)T$, then there is a $m \in \mathcal{N}$, $m < n$ such that $(m-1)T < t_1 < mT$ (let $t_1 = (m-1)T + l,\ 0 < l < T$) and $\tau_1 - t_1 < T$, otherwise, $\tau_1 - t_1 \ge T$, i.e. $\tau_1 \ge T + t_1$, and $P(t) > \varepsilon\exp(-\beta T),\ t \in (t_1, t_1 + T]$. Therefore, $(m-1)T < t_1 < mT < t_1 + T < (m+1)T$, and solving (3) from t_1 to $t_1 + T$, we get

$$\begin{aligned}\varepsilon e^{-\beta T} &< P(t_1 + T)\\ &= q(mT)P(t_1)\exp\left(\int_{t_1}^{mT} F\big(s, P(s)\big)ds\right)\exp\left(\int_{mT}^{t_1+T} F\big(s, P(s)\big)ds\right)\\ &\le q(mT)\varepsilon e^{-\beta T}\exp\left(\int_{t_1}^{t_1+T} F\big(s, \varepsilon e^{-\beta T}\big)ds\right)\\ &= q(mT)\varepsilon e^{-\beta T}\exp\left(\int_{(m-1)T+l}^{mT+l} F\big(s, \varepsilon e^{-\beta T}\big)ds\right)\\ &\le \varepsilon e^{-\beta T},\end{aligned}$$

this is a contradiction, thus $\tau_1 - t_1 < T$. Therefore, if $\tau_1 > (n-1)T$, then

$$\begin{aligned}\varepsilon &< P(\tau_1)\\ &= q\big((n-1)T\big)P(t_1)\exp\left(\int_{t_1}^{(n-1)T} F\big(s, P(s)\big)ds\right)\exp\left(\int_{(n-1)T}^{\tau_1} F\big(s, P(s)\big)ds\right)\end{aligned}$$

$$
\begin{aligned}
&= q\big((n-1)T\big)P(t_1)\exp\left(\int_{t_1}^{\tau_1} F\big(s, P(s)\big)ds\right)\\
&\leq q\big((n-1)T\big)P(t_1)\exp\left(\int_{t_1}^{\tau_1} F\big(s, \varepsilon e^{-\beta T}\big)ds\right)\\
&\leq \varepsilon e^{-\beta T}e^{\beta T} = \varepsilon,
\end{aligned}
$$

it is a contradiction, if $\tau_1 = (n-1)T$, then

$$
\begin{aligned}
\varepsilon &< P(\tau_1)\\
&= P(t_1)\exp\left(\int_{t_1}^{(n-1)T} F\big(s, P(s)\big)ds\right)\\
&\leq P(t_1)\exp\left(\int_{t_1}^{(n-1)T} F\big(s, \varepsilon e^{-\beta T}\big)ds\right)\\
&\leq \varepsilon e^{-\beta T}e^{\beta T} = \varepsilon.
\end{aligned}
$$

This is a contradiction. Hence, such τ_1 does not exist. Therefore, $P(t) \leq \varepsilon$ for $t \geq \tau$, that is $\lim_{t\to\infty} P(t) = 0$. The proof is complete.

Appendix C: The Proof of Theorem 3.1

It is seen from the second equation of system (4) that $dN(t)/dt > -dN(t)$. Considering the following impulsive differential equation:

$$
\begin{cases}
\dfrac{dy(t)}{dt} = -dy(t), & t \neq nT,\\
y\big(t^+\big) = y(t) + \delta_n, & t = nT,\\
y\big(0^+\big) = N_0 + \delta_0.
\end{cases}
\tag{27}
$$

According to the comparison theorem on impulsive differential equations, B1 yields $N(t) \geq y(t) = N^*(t)$. It follows from the first equation of system (4) that

$$
\frac{dP(t)}{dt} \leq rP(t)\big(1 - \eta P(t)\big) - \beta P(t)N^*(t).
$$

Now we consider the following impulsive differential equation

$$
\begin{cases}
\dfrac{dx(t)}{dt} = rx(t)\big(1 - \eta x(t)\big) - \beta x(t)N^*(t), & t \neq nT,\\
x\big(nT^+\big) = \big(1 - \omega(nT)d_1\big)x(nT), & t = nT,\\
\dfrac{d\omega(t)}{dt} = d_1\omega(t)\big(\omega(t)^{q_n} - 1\big),\\
x\big(0^+\big) = P(0) \doteq P_0.
\end{cases}
\tag{28}
$$

Again according to the comparison theorem on impulsive differential equations we have $P(t) \leq x(t)$.

By using the formula of (24), we can easily have

$$\begin{aligned} q(nT) &\doteq 1-\omega(nT)d_1 \\ &= 1-\frac{d_1}{(1+e^{nd_1}((\omega((n-1)T))^{-\frac{n}{T}}-1))^{\frac{T}{n}}} \end{aligned}$$

and

$$F(s,x)\doteq r-r\eta x(s)-\beta N^*(s).$$

Now we test and verify the conditions of Theorem 2.1. It is easy to see that condition (a) holds true naturally, and

$$F(s,0)=r-\beta N^*(s)\le r$$

and

$$\frac{\partial F(s,x)}{\partial x}=-r\eta, \qquad \int_0^\infty \eta ds=\infty.$$

Therefore,

$$\begin{aligned} \exp\biggl(\int_{l+(n-1)T}^{l+nT}F(s,0)ds\biggr) &= \exp\biggl(\int_{l+(n-1)T}^{l+nT} r-\beta N^*(s)ds\biggr) \\ &= e^{rT}\exp\biggl(\int_{l+(n-1)T}^{l+nT}\bigl(-\beta N^*(s)\bigr)ds\biggr) \end{aligned}$$

with

$$\begin{aligned} &\exp\biggl(\int_{l+(n-1)T}^{l+nT}\bigl(-\beta N^*(s)\bigr)ds\biggr) \\ &= \exp\Biggl(\Biggl(\frac{\beta N_0}{d}e^{-d(l+(n-1)T)}+\sum_{i=0}^{n-1}\frac{\beta\delta_i}{d}e^{-d(l+(n-1-i)T)}\Biggr)\bigl(e^{-dT}-1\bigr) \\ &\quad +\frac{\beta\delta_n}{d}\bigl(e^{-dl}-1\bigr)\Biggr) \\ &= \exp\bigl(M(n,l)\bigr). \end{aligned}$$

Thus,

$$\begin{aligned} &q(nT)\exp\biggl(\int_{l+(n-1)T}^{l+nT}F(s,0)ds\biggr) \\ &= R_0(n,T)\exp\bigl(M(n,l)\bigr) \\ &\doteq R_0^N(n,T,l). \end{aligned}$$

According to Theorem 2.1, we can see that if $R_0^N(n,T,l)\le 1$, then $x(t)\to 0$ as $t\to\infty$. Consequently, we have $P(t)\to 0$ as $t\to\infty$ provided $R_0^N(n,T,l)\le 1$.

Next, we prove that $N(t)\to N^*(t)$ as $t\to\infty$. For any $0<\varepsilon<d/(\lambda\beta)$, there exists a $t_1>0$ such that $0<P(t)<\varepsilon$ for all $t\ge t_1$. Without loss of generality, we may assume that $0<P(t)<\varepsilon$ holds true for all $t>0$, then we have

$$-dN(t)\le\frac{dN(t)}{dt}\le(\lambda\beta\varepsilon-d)N(t).$$

For the left-hand inequality, it follows from impulsive differential equation (27) that $N(t) \geq y(t) = N^*(t)$. For the right-hand inequality, considering the following impulsive differential equation:

$$\begin{cases} \dfrac{dz(t)}{dt} = (\lambda\beta\varepsilon - d)z(t), \quad t \neq nT, \\ z\left(t^+\right) = z(t) + \delta_n, \quad t = nT, \\ z\left(0^+\right) = N_0 + \delta_0. \end{cases} \tag{29}$$

The analytical solution of the above system at any impulsive interval $((n-1)T, nT]$ gives

$$z^*(t) = N_0 e^{(\lambda\beta\varepsilon - d)t} + \sum_{i=0}^{n-1} \delta_i e^{(\lambda\beta\varepsilon - d)(t-iT)}, \quad (n-1)T < t \leq nT. \tag{30}$$

Therefore, for any $\varepsilon_1 > 0$, there exists a $t_2 > 0$ such that

$$N^*(t) - \varepsilon_1 < N(t) < z^*(t) + \varepsilon_1$$

for $t > t_2$. Let $\varepsilon \to 0$, then we have

$$N^*(t) - \varepsilon_1 < N(t) < N^*(t) + \varepsilon_1$$

for $t > t_2$, which indicates that $N(t) \to N^*(t)$ as $t \to \infty$. Therefore, the pest-free solution (7) is globally attractive if $R_0^N(n, T, l) \leq 1$. The proof is complete.

Appendix D: Determining the New Number of Natural Enemies to be Released for Case 3.2

In this case $R_{0_{\max}}^N(n, T, l) = R_0^N(n, T, T) = R_C$. It follows from (8) that we have $M(n, T) = \ln(R_c/R_0(n, T))$, that is

$$\left(\frac{\beta N_0}{d} e^{-dnT} + \sum_{i=0}^{n} \frac{\beta\delta_i}{d} e^{-d(n-i)T}\right)\left(e^{-dT} - 1\right) = \ln\left(\frac{R_C}{R_0(n, T)}\right),$$

this indicates that

$$G_{n'} + \sum_{i=n'+1}^{n} \delta_i e^{diT} = -\frac{de^{dnT}}{\beta(1 - e^{-dT})} \ln\left(\frac{R_C}{R_0(n, T)}\right). \tag{31}$$

That is

$$\sum_{i=n'+1}^{n} \delta_i e^{diT} = -\frac{de^{dnT}}{\beta(1 - e^{-dT})} \ln\left(\frac{R_C}{R_0(n, T)}\right) - G_{n'} \doteq A_n.$$

Therefore, when $n = n' + 1$ we get

$$\delta_{n'+1} = A_{n'+1} e^{-d(n'+1)T}.$$

When $n = n' + 2$, we have

$$\delta_{n'+1} e^{d(n'+1)T} + \delta_{n'+2} e^{d(n'+2)T} = A_{n'+2},$$

that is

$$\delta_{n'+2} = (A_{n'+2} - A_{n'+1})e^{-d(n'+2)T}.$$

Similarly, when $n = n' + 3$ we get

$$\delta_{n'+1}e^{d(n'+1)T} + \delta_{n'+2}e^{d(n'+2)T} + \delta_{n'+3}e^{d(n'+3)T} = A_{n'+3},$$

that is

$$\delta_{n'+3} = (A_{n'+3} - A_{n'+2})e^{d(n'+3)T}.$$

By induction, the new number of natural enemies to be released δ_n can be determined as follows:

$$\delta_n = \begin{cases} \delta_c, & \text{if } n \le n', \\ A_{n'+1}e^{-d(n'+1)T}, & n = n' + 1, \\ (A_n - A_{n-1})e^{-dnT}, & \text{if } n > n' + 1. \end{cases}$$

Appendix E: The Proof of Theorem 4.1

It is seen from the second equation of system (15) that $dN(t)/dt > -dN(t)$. Considering the following impulsive differential equation:

$$\begin{cases} \frac{dy(t)}{dt} = -dy(t), & t \ne hT_N, \\ y\big(t^+\big) = y(t) + \delta_h, & t = hT_N, \\ y\big(0^+\big) = N_0. \end{cases} \tag{32}$$

According to the comparison theorem on impulsive differential equations, (E1) yields $N(t) \ge y(t) = N^*(t)$. It follows from the first equation of system (15) that

$$\frac{dP(t)}{dt} \le rP(t)\big(1 - \eta P(t)\big) - \beta P(t)N^*(t).$$

Now we consider the following impulsive differential equation:

$$\begin{cases} \frac{dx(t)}{dt} = rx(t)\big(1 - \eta x(t)\big) - \beta x(t)N^*(t), & t \ne \tau_n, \\ x\big(hT_p^+\big) = \big(1 - \omega(hT_p)d_1\big)x(hT_p), & t = \tau_n, \\ \frac{d\omega(t)}{dt} = d_1\omega(t)\big(\omega(t)^{q_n} - 1\big), \\ x\big(0^+\big) = P(0) \doteq P_0. \end{cases} \tag{33}$$

Again according to the comparison theorem on impulsive differential equations, we have $P(t) \le x(t)$.

By using the formula of (24), we can easily have

$$\begin{aligned} q(nT) &\doteq 1 - \omega(nT)d_1 \\ &= 1 - \frac{d_1}{(1 + e^{nd_1}((\omega((n-1)T))^{-\frac{n}{T}} - 1))^{\frac{T}{n}}} \end{aligned}$$

and

$$F(s,x) \doteq r - r\eta x(s) - \beta N^*(s).$$

Now we test and verify the conditions of Theorem 2.1. It is easy to see that condition (a) holds true naturally, and

$$F(s,0) = r - \beta N^*(s) \le r$$

and

$$\frac{\partial F(s,x)}{\partial x} = -r\eta, \qquad \int_0^\infty \eta ds = \infty.$$

Therefore,

$$\begin{aligned}\exp\left(\int_{l+(h-1)T_N+\tau_{k-1}}^{l+(h-1)T_N+\tau_k} F(s,0)ds\right) &= \exp\left(\int_{l+(h-1)T_N+\tau_{k-1}}^{l+(h-1)T_N+\tau_k} r - \beta N^*(s)ds\right)\\ &= e^{r\tau}\exp\left(\int_{l+(h-1)T_N+\tau_{k-1}}^{l+(h-1)T_N+\tau_k} \big(-\beta N^*(s)\big)ds\right),\end{aligned}$$

where $k \ge 1$, $\tau_k = k\tau$, and

$$\begin{aligned}&\int_{l+(h-1)T_N+\tau_{k-1}}^{l+(h-1)T_N+\tau_k} \big(-\beta N^*(s)\big)ds\\ &\quad = -\beta \int_{l+(h-1)T_N+\tau_{k-1}}^{l+(h-1)T_N+\tau_k} \left(N_0 + \sum_{i=1}^{h-1}\delta_i e^{idT_N}\right)e^{-ds}ds\\ &\quad = \frac{\beta}{d}e^{-d(l+(h-1)T_N+\tau_{k-1})}\left(N_0 + \sum_{i=1}^{h-1}\delta_i e^{idT_N}\right)\big(e^{-d\tau}-1\big)\end{aligned}$$

for $l \in (0,\tau]$ and $1 \le k \le k_p$, thus

$$\begin{aligned}&\hat{R}_0^{T_N}(h,k-1,T_N,l)\\ &\quad \doteq q\big((h-1)T_N+\tau_k\big)\exp\left(\int_{l+(h-1)T_N+\tau_{k-1}}^{l+(h-1)T_N+\tau_k} F(s,0)ds\right)\\ &\quad = R_0\big((h-1)T_N+\tau_k\big)\\ &\qquad \times \exp\left(\frac{\beta}{d}e^{-d(l+(h-1)T_N+\tau_{k-1})}\left(N_0 + \sum_{i=1}^{h-1}\delta_i e^{idT_N}\right)\big(e^{-d\tau}-1\big)\right),\end{aligned}$$

where $R_0((h-1)T_N+\tau_k,\tau) = (1-d_1\omega((h-1)T_N+\tau_k))\exp(r\tau)$.

Moreover,

$$\begin{aligned}&\int_{l+(h-1)T_N+\tau_{k_p}}^{l+hT_N} \big(-\beta N^*(s)\big)ds\\ &\quad = \int_{l+(h-1)T_N+\tau_{k_p}}^{hT_N} \big(-\beta N^*(s)\big)ds + \int_{hT_N}^{l+hT_N} \big(-\beta N^*(s)\big)ds\end{aligned}$$

$$
\begin{aligned}
&= -\beta \int_{l+(h-1)T_N+\tau_{k_p}}^{hT_N} \left(N_0 + \sum_{i=1}^{h-1} \delta_i e^{idT_N} \right) e^{-ds} ds \\
&\quad - \beta \int_{hT_N}^{l+hT_N} \left(N_0 + \sum_{i=1}^{h} \delta_i e^{idT_N} \right) e^{-ds} ds \\
&= \frac{\beta}{d} e^{-d(l+(h-1)T_N+\tau_{k_p})} \left(N_0 + \sum_{i=1}^{h-1} \delta_i e^{idT_N} \right) \left(e^{-d\tau} - 1 \right) + \frac{\beta \delta_h}{d} \left(e^{-dl} - 1 \right) \\
&\doteq \Psi(l),
\end{aligned}
$$

therefore,

$$
\begin{aligned}
\hat{R}_0^{T_N}(h, k_p, T_N, l) &\doteq q(hT) \exp\left(r - \int_{l+(h-1)T_N+\tau_{k_p}}^{l+hT_N} \beta N^*(s) ds \right) \\
&= R_0(hT_N, \tau) e^{\Psi(l)},
\end{aligned}
$$

for $l \in (0, \tau]$.

According to Theorem 2.1, we can see that if $\hat{R}_0^{T_N}(h, k-1, T_N, l) \leq 1$, then $x(t) \to 0$ as $t \to \infty$. Consequently, we have $P(t) \to 0$ as $t \to \infty$ provided $\hat{R}_0^{T_N}(h, k-1, T_N, l) \leq 1$, for $k = 1, 2, \ldots, k_p + 1$.

Because $\hat{R}_0^{T_N}(h, k-1, T_N, l)$ increases with respect to k and l, for $k = 2, 3, \ldots, k_p$, we have

$$
\begin{aligned}
&\hat{R}_{0_{\max}}^{T_N}(h, k-1, T_N, l) \\
&\quad = \hat{R}_0^{T_N}(h, k_p - 1, T_N, \tau) \\
&\quad = R_0\big((h-1)T_N + \tau_{k_p}, \tau\big) \\
&\qquad \times \exp\left(\frac{\beta}{d} e^{-d((h-1)T_N+\tau_{k_p})} \left(N_0 + \sum_{i=1}^{h-1} \delta_i e^{idT_N} \right) \left(e^{-d\tau} - 1 \right) \right).
\end{aligned}
$$

From

$$
\begin{aligned}
\frac{\partial \hat{R}_0^{T_N}(h, k_p, T_N, l)}{\partial l} &= \hat{R}_0^{T_N}(h, k_p, T_N, l) \frac{\partial \Psi(l)}{\partial l} \\
&= \hat{R}_0^{T_N}(h, k_p, T_N, l) \beta e^{-dl} (D_{h-1} - \delta_h),
\end{aligned}
$$

we conclude that if $D_{h-1} > \delta_h$ then $\hat{R}_0^{T_N}(h, k_p, T_N, l)$ increases with respect to l, so

$$
\begin{aligned}
&\hat{R}_{0_{\max}}^{T_N}(h, k_p, T_N, l) \\
&\quad = \hat{R}_0^{T_N}(h, k_p, T_N, \tau) \\
&\quad = R_0(hT_N, \tau) \exp\left(\frac{\beta}{d} e^{-dhT_N} \left(N_0 + \sum_{i=1}^{h} \delta_i e^{idT_N} \right) \left(e^{-d\tau} - 1 \right) \right).
\end{aligned}
$$

We can easily see that $\hat{R}_{0_{\max}}^{T_N}(h, k-1, T_N, l) < \hat{R}_{0_{\max}}^{T_N}(h, k_p, T_N, l)$. Therefore,

$$\begin{aligned} R_0^{T_N}(h,T_N) &= \max\left\{\hat{R}_{0_{\max}}^{T_N}(h,k-1,T_N,l),\, \hat{R}_{0_{\max}}^{T_N}(h,k_p,T_N,l)\right\} \\ &= \max\left\{\hat{R}_0^{T_N}(h,k_p-1,T_N,\tau),\, \hat{R}_0^{T_N}(h,k_p,T_N,\tau)\right\} \\ &= R_0(hT_N,\tau)\exp\left(\frac{\beta}{d}e^{-dhT_N}\left(N_0+\sum_{i=1}^{h}\delta_i e^{idT_N}\right)\left(e^{-d\tau}-1\right)\right). \end{aligned}$$

If $D_{h-1} \le \delta_h$ then $\hat{R}_0^{T_N}(h,k_p,T_N,l)$ decreases with respect to l, so

$$\begin{aligned} &\hat{R}_{0_{\max}}^{T_N}(h,k_p,T_N,l) \\ &\quad= \hat{R}_0^{T_N}(h,k_p,T_N,0) \\ &\quad= R_0(hT_N,\tau)\exp\left(\frac{\beta}{d}e^{-d((h-1)T_N+\tau_{k_p})}\left(N_0+\sum_{i=1}^{h-1}\delta_i e^{idT_N}\right)\left(e^{-d\tau}-1\right)\right). \end{aligned}$$

Due to the development of pest resistance, we can see that $R_0(hT_N,\tau) > R_0((h-1)T_N+\tau_{k_p},\tau)$, thus $\hat{R}_0^{T_N}(h,k_p,T_N,0) > \hat{R}_0^{T_N}(h,k_p-1,T_N,\tau)$, that is $\hat{R}_{0_{\max}}^{T_N}(h,k-1,T_N,l) < \hat{R}_{0_{\max}}^{T_N}(h,k_p,T_N,l)$, therefore,

$$\begin{aligned} &R_0^{T_N}(h,T_N) \\ &\quad= \max\left\{\hat{R}_{0_{\max}}^{T_N}(h,k-1,T_N,l),\, \hat{R}_{0_{\max}}^{T_N}(h,k_p,T_N,l)\right\} \\ &\quad= \max\left\{\hat{R}_0^{T_N}(h,k_p-1,T_N,\tau),\, \hat{R}_0^{T_N}(h,k_p,T_N,0)\right\} \\ &\quad= R_0(hT_N,\tau)\exp\left(\frac{\beta}{d}e^{-d((h-1)T_N+\tau_{k_p})}\left(N_0+\sum_{i=1}^{h-1}\delta_i e^{idT_N}\right)\left(e^{-d\tau}-1\right)\right). \end{aligned}$$

thus, if $R_0^{T_N}(h,T_N) < 1$, then $P(t) \to 0$ as $t \to \infty$.

The following proof is the same as Theorem 3.1. The proof is complete.

Appendix F: Determining the New Number of Natural Enemies to Be Released for Case 4.2

In this case, solving equation

$$R_0^{T_N}(h,T_N) = R_C$$

with respect to δ_i, yields

$$\sum_{i=1}^{h}\delta_i e^{idT_N} = -\frac{de^{dhT_N}}{\beta(1-e^{-d\tau})}\ln\left(\frac{R_C}{R_0(hT_N,\tau)}\right) - N_0, \quad h \in \mathcal{N}. \tag{34}$$

Due to $\delta_i = \delta_c$, when $i \le h'$, we have

$$N_0 + \delta_c\sum_{i=1}^{h'} e^{idT_N} + \sum_{i=h'+1}^{h}\delta_i e^{idT_N} = -\frac{de^{dhT_N}}{\beta(1-e^{-d\tau})}\ln\left(\frac{R_C}{R_0(hT_N,\tau)}\right),$$

that is

$$\sum_{i=h'+1}^{h} \delta_i e^{idT_N} = -\frac{de^{dhT_N}}{\beta(1-e^{-d\tau})} \ln\left(\frac{R_C}{R_0(hT_N,\tau)}\right) - N_0 - \delta_c \sum_{i=1}^{h'} e^{idT_N} \doteq A'_h.$$

Therefore, when $h = h' + 1$, we have

$$\delta_{h'+1} = A'_{h'+1} e^{-d(h'+1)T_N}.$$

When $h = h' + 2$, we get

$$\delta_{h'+1} e^{d(h'+1)T_N} + \delta_{h'+2} e^{d(h'+2)T_N} = A'_{h'+2},$$

that is

$$\delta_{h'+2} = \left(A'_{h'+2} - A'_{h'+1}\right) e^{-d(h'+2)T_N}.$$

Similarly, when $h = h' + 3$, we get

$$\delta_{h'+3} = \left(A'_{h'+3} - A'_{h'+2}\right) e^{-d(h'+3)T_N}.$$

By induction, the new number of natural enemies to be released δ_h can be determined as follows:

$$\delta_h = \begin{cases} \delta_c, & \text{if } h \le h', \\ A'_{h'+1} e^{-d(h'+1)T_N}, & h = h' + 1, \\ (A'_h - A'_{h-1}) e^{-dhT_N}, & \text{if } h > h' + 1. \end{cases}$$

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