Hybrid systems modeling of ecological population dynamics

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Abstract—Discrete-time models are the traditional approach for capturing population dynamics of insects living in the temperate regions of the world. These models are characterized by an update function that connects the population densities from one year to the next. We revisit classical discrete-time models used for modeling interactions between two insect species (a host and a parasitoid), and provide novel result on the stability of the population dynamics. In particular, for a class of models we show that the fixed point is stable, if and only if, the host equilibrium density is an increasing function of the host's reproduction rate. We also introduce a hybrid approach for obtaining the update functions by solving ordinary differential equations that mechanistically capture the ecological interactions between the host and the parasitoid. This hybrid approach is used to study the suppression of host density by a parasitoid. Our analysis shows that when the parasitoid attacks the host at a constant rate, then the host density cannot be suppressed beyond a certain point without making the population dynamics unstable. In contrast, when the parasitoid's attack rate increases with increasing host density, then the host population density can be suppressed to arbitrarily low levels. These results have important implications for biological control where a natural enemy, such as a parasitoid wasp, is introduced to eliminate a pest that is the host species for the parasitoid.

I. INTRODUCTION

Insect population dynamics has been extensively studied using two different approaches: continuous-time and discrete-time models. The continuous-time framework is generally used to model populations with overlapping generations and all year-round reproduction. In contrast, discrete-time models are more suited for populations in temperate regions of the world that have non-overlapping generations and reproduce in a discrete pulse determined by season [1].

Here we revisit discrete-time models capturing the antagonistic interaction between two insect species (a host and a parasitoid). A typical life cycle of the host and the parasitoid is shown in Fig. 1, and consists of adult

hosts emerging during spring, laying eggs that hatch into larvae. Host larvae then overwinter in the pupal stage, and metamorphose as adults the following year. As adult hosts die after laying eggs, there is no overlap between generations across years. The host becomes vulnerable to attacks by a parasitoid wasp at one stage of its life cycle. For the sake of convenience, we assume the host's vulnerable stage to be the larval stage. Adult female parasitoids emerge during spring, search and attack hosts by laying an egg into the body of the host. While adult parasitoids die after this time window, the parasitoid egg hatches into a juvenile parasitoid that grows at the host's expense by using it as a food source, and this ultimately results in the death of the host. The juvenile parasitoids pupate, overwinter, and emerge as adult parasitoids the following year. There are more than 65,000 different species of parasitoid wasps and we refer the reader to [2]–[4] for fascinating details on parasitoid classification, life history and behavior¹. Synchronized life cycles, with no overlap of generations in both the host and the parasitoid makes discrete-time models highly appropriate for these systems.

Fig. 1: Life cycle of the host and the parasitoid. Inset shows the picture of a parasitoid wasp laying an egg into the body of its host (spotted alfalfa aphid). Picture taken from <https://en.wikipedia.org/wiki/Parasitoid>.

We provide novel results on the stability of a general

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¹Host-parasitoid interactions motivated the 1979 Hollywood movie *Alien* where a human is infected by an alien life-form. The alien develops within the human and later emerges killing the human.

class of discrete-time models describing host-parasitoid interactions. Following a rich tradition of using hybrid or semi-discrete approaches to model ecological population dynamics [5]–[10], we discuss a hybrid formulation that solves a nonlinear differential equation to obtain discrete-time models for host-parasitoid systems. Importantly, this mechanistic derivation of models using the hybrid approach can provide qualitatively different results compared to earlier phenomenological approaches. Finally, in the context of biological control of pests, we investigate different forms of parasitoid attack rates that lead to efficient suppression of the host population.

II. MODEL FORMULATION

A model describing host-parasitoid dynamics in discrete-time is given by

$$H_{t+1} = RH_t f(H_t, P_t) \quad (1a)$$

$$P_{t+1} = kRH_t[1 - f(H_t, P_t)] \quad (1b)$$

where H_t and P_t are the adult host, and the adult parasitoid densities, respectively, at the start of year t [11]–[13]. If the host is vulnerable to the parasitoid at its larval stage, then RH_t is the host larval density exposed to parasitoid attacks at the start of the vulnerable stage, where $R > 1$ denotes the number of viable eggs produced by each adult host. Parasitoids attack host larvae during the vulnerable period leading to two populations of hosts: parasitized and un-parasitized larvae. The function $f(H_t, P_t) < 1$ is the fraction of host larvae escaping parasitism and can depend on both H_t and P_t . We assume f to be a continuously differentiable function in both arguments and refer to it as the *escape response*. In the absence of the parasitoid

$$f(H_t, 0) = 1, \quad (2)$$

and the host population grows unboundedly as

$$H_{t+1} = RH_t \quad (3)$$

where R can be interpreted as the host's growth rate. In (1), $RH_t f(H_t, P_t)$ is the total larval density escaping parasitism to become adult hosts for next year. Finally, $RH_t[1 - f(H_t, P_t)]$ is the net density of parasitized larvae, with each larva giving rise to k adult female parasitoids in the next generation.

The simplest formulation of (1) is the classical Nicholson-Bailey model

$$H_{t+1} = RH_t \exp(-cTP_t) \quad (4a)$$

$$P_{t+1} = kRH_t[1 - \exp(-cTP_t)] \quad (4b)$$

where $c > 0$ represents the rate at which parasitoids attack hosts, and T is the duration of the host vulnerable

Fig. 2: A typical host-parasitoid population time series for the Nicholson-Bailey model (top), model with weak host refuge ($\mu = 0.05$ in (5); middle) and moderate host refuge ($\mu = 0.40$ in (5); bottom). Host reproduction rate assumed to be $R = 2$, $T = 1$ and $k = 1$.

stage [14]. The model assumes that parasitoids search for hosts randomly, are never egg-limited, and have quick handling times. If the number of parasitoid attacks per host follows a Poisson distribution with mean cTP_t , then the escape response $f(H_t, P_t) = \exp(-cTP_t)$ is the probability of zero attacks in the Poisson distribution. In Section IV, we provide another mechanistic interpretation of the Nicholson-Bailey model. A typical time series of the Nicholson-Bailey model is shown in Fig. 2. Both populations grow at low densities, but at large host densities the parasitoid begins to overexploit the host. This leads to a crash in the host population, followed by a crash of the parasitoids. These cycles of overexploitation and crashes result in an unstable interaction with both populations exhibiting diverging oscillations. Interestingly, these diverging oscillations have been recapitulated in several laboratory studies of specific host-parasitoid species providing some model validation, at least in controlled lab settings.

Several mechanisms have been proposed in literature that can stabilize the host-parasitoid population dynam-

ics. One such mechanism is a host refuge where a constant fraction of hosts are protected from parasitism. A constant host fraction μ in the refuge leads to the following model

$$H_{t+1} = RH_t(\mu + (1-\mu)\exp(-cTP_t)) \quad (5a)$$

$$P_{t+1} = k(1-\mu)RH_t[1-\exp(-cTP_t)] \quad (5b)$$

[1]. While a weak-refuge results in bounded oscillations, a moderate-refuge stabilizes the population dynamics (Fig. 2). However, stability is again lost for a strong-refuge with both hosts and parasitoids growing unboundedly. Next, we provide some novel results on the stability of the discrete-time model (1).

III. GENERAL STABILITY ANALYSIS

The fixed point of the discrete-time model (1) are the population densities that remain constant across years. Substituting $P_{t+1} = P_t = P^*$ and $H_{t+1} = H_t = H^*$ in (1) shows that apart from the trivial fixed point $P^* = H^* = 0$, the non-trivial equilibrium is the solution to the following equations

$$1 = Rf(H^*, P^*), \quad P^* = k(R-1)H^*, \quad (6)$$

where H^* and P^* denote the host and parasitoid densities at equilibrium, respectively.

Solving these equations for the Nicholson-Bailey model yields a single non-trivial equilibrium point

$$H^* = \frac{\ln(R)}{(R-1)kcT}, \quad P^* = \frac{\ln(R)}{cT}. \quad (7)$$

Note that the host equilibrium levels decrease, while the parasitoid equilibrium levels increase, with increasing host growth rate R .

Considering small perturbations h_t and p_t

$$h_t = H_t - H^* + h_t, \quad p_t = P_t - P^*, \quad (8)$$

and linearizing model nonlinearities in (1) around the equilibrium, results in the following *linear* discrete-time system

$$\begin{bmatrix} h_{t+1} \\ p_{t+1} \end{bmatrix} = A \begin{bmatrix} h_t \\ p_t \end{bmatrix}, \quad A = \begin{bmatrix} a_{00} & a_{01} \\ a_{10} & a_{11} \end{bmatrix} \quad (9)$$

where the entries of the Jacobian matrix A are given by

$$\begin{aligned} a_{00} &= 1 + RH^* \frac{\partial f(H_t, P_t)}{\partial H_t} \Big|_{H_t=H^*, P_t=P^*} \\ a_{01} &= RH^* \frac{\partial f(H_t, P_t)}{\partial P_t} \Big|_{H_t=H^*, P_t=P^*} \\ a_{10} &= k(R-1) - kRH^* \frac{\partial f(H_t, P_t)}{\partial H_t} \Big|_{H_t=H^*, P_t=P^*} \\ a_{11} &= -kRH^* \frac{\partial f(H_t, P_t)}{\partial P_t} \Big|_{H_t=H^*, P_t=P^*}. \end{aligned}$$

Here $\frac{\partial f(H_t, P_t)}{\partial H_t} \Big|_{H_t=H^*, P_t=P^*}$ represents the partial derivative of the escape response with respect to the host density evaluated at the equilibrium point.

Standard stability analysis shows that the non-trivial equilibrium point is stable, if and only if, the following three conditions hold

$$1 - \text{tr}(A) + \det(A) > 0, \quad (10a)$$

$$1 + \text{tr}(A) + \det(A) > 0, \quad (10b)$$

$$1 - \det(A) > 0 \quad (10c)$$

where the trace and determinant of the A matrix are

$$\text{tr}(A) = a_{00} + a_{11}, \quad \det(A) = a_{00}a_{11} - a_{01}a_{10}, \quad (11)$$

respectively [15]. The Theorem below shows that in some cases these stability conditions can be remarkably simplified.

Theorem: Consider the discrete-time model

$$H_{t+1} = RH_t f(P_t) \quad (12a)$$

$$P_{t+1} = kRH_t[1 - f(P_t)] \quad (12b)$$

where the escape response $f(P_t)$ is a monotonically decreasing function of the parasitoid density only, with $f(0) = 1$. Then, the model has a unique non-trivial fixed point given by the solution to the equation

$$\frac{1}{R} = f(P^*), \quad P^* = k(R-1)H^*, \quad (13)$$

and this fixed point is stable, if and only if,

$$\frac{dH^*}{dR} > 0. \quad (14)$$

We refer the reader to the appendix for a proof of the theorem. Briefly, if the escape response $f(P_t)$ only depends on parasitoid density then the first two conditions in (10) always hold, and stability is completely determined by the third inequality $1 - \det(A) > 0$ which can be rewritten as (14). Recall that H^* in the Nicholson-Bailey model is decreasing with R , and its instability is reflective of this simplified stability criterion. Applying the theorem to the host refuge model (5) we obtain the following equilibrium host density

$$H^* = \frac{\ln\left(\frac{(1-\mu)R}{(1-\mu)R}\right)}{(R-1)kcT} \quad (15)$$

that is only defined for $\mu < 1/R$. Fig. 3 plots H^* as a function of R for different values of the refuge fraction μ . The plots shows that initially H^* decreases with increasing R (hence, an unstable equilibrium), but beyond a critical host growth rate, H^* increases with

increasing R leading to stability (as seen in Fig. 2). For example, when $\mu = 0.4$, the population dynamics is stabilized for $R > 1.375$.

Another mechanism known to stabilize host-parasitoid interactions is when the parasitoid's attack rate c in (4) decreases with increasing parasitoid density due to interference between parasitoids. Rewriting $c = c_1 P_t^{-m}$, where $c_1 > 0$ and $0 < m < 1$ results in the following discrete-time model

$$H_{t+1} = RH_t \exp(-c_1 T P_t^{1-m}) \quad (16a)$$

$$P_{t+1} = kRH_t[1 - \exp(-c_1 T P_t^{1-m})]. \quad (16b)$$

A straightforward application of the theorem shows that the model (16) is stable for sufficiently large value of m given by

$$\frac{R \ln(R) + 1 - R}{R \ln(R)} < m < 1, \quad (17)$$

which corresponds to $0.28 < m < 1$ for $R = 2$, and $0.5 < m < 1$ for $R = 5$.

Fig. 3: Host equilibrium density (15) for the refuge model (5) as a function of the growth rate R . For a given μ , H^* first decreases with increasing R (unstable equilibrium), but beyond a critical host growth rate, H^* increases with increasing R (stable equilibrium).

Finally, using the fact that $P^* = k(R-1)H^*$, the above condition on H^* can also be written in terms of the parasitoid equilibrium density

$$\frac{R}{P^*} \frac{dP^*}{dR} > \frac{R}{R-1}, \quad (18)$$

revealing that stability requires parasitoid densities to increase sufficiently fast with increasing R .

It is important to emphasize that condition (14) can only be used for a host-independent escape response. The above theorem begs the question: can this simple

Fig. 4: Stability regions for the host-parasitoid model (1) in terms of the sensitivity of the host density to the host growth rate dH^*/dR , and the sensitivity of the escape response to the host density df/dH^* . The Nicholson-Bailey model corresponds to $dH^*/dR < 0$ and $df/dH^* = 0$ and is unstable. Stability arises in two orthogonal ways: 1) an increase in dH^*/dR to make it positive, which happens with parasitoid interference/aggregation or host refuge; 2) a decrease in df/dH^* which happens with a Type III functional response in the parasitoid attack rate. For this figure, the host growth rate is assumed to $R = 2$, $k = 1$ and the stability region shrinks with increasing R .

stability criterion be generalized when $f(H_t, P_t)$ depends on both populations? It turns out that in this case, the stability conditions (10) can be graphically represented in terms of two biologically-relevant quantities:

$$\frac{dH^*}{dR} \quad \text{and} \quad \frac{df(H^*, P^*)}{dH^*}, \quad (19)$$

where the latter denotes the sensitivity of the escape response to the host density. Fig. 4 shows that stability arises in a narrow band, and is more likely to occur when the escape response is a decreasing function of the host density, rather than an increasing function. An interesting insight from this figure is that stability can arise in the Nicholson-Bailey model from two orthogonal mechanisms: a host refuge that moves the point upwards into the stability region; alternatively a Type-III functional response that moves the point to the left into the stability region. We discuss Type III functional response in more detail in the next section.

IV. HYBRID FORMULATION OF UPDATE FUNCTIONS

For a majority of host-parasitoid models the escape response f in (1) is phenomenologically chosen or designed to recapitulate field observations. Recent work has proposed a mechanistic hybrid framework for deriving the discrete-time model, where ordinary differential equations are used to track population densities within the host vulnerable period of a given year [16]–[18]. The solution of the differential equations at the end of the vulnerable period predicts the population densities for next year. We discuss this semi-discrete formulation in further detail below.

Let τ denote the time within the host vulnerable stage that varies from 0 to T corresponding to the start and end of the vulnerable stage. The densities of parasitoids, unparasitized and parasitized host larvae at time τ within the vulnerable stage of year t are represented by $P(\tau, t)$, $L(\tau, t)$, $I(\tau, t)$, respectively. These densities evolve as per the dynamical system

$$\frac{dP(\tau, t)}{d\tau} = -\gamma_P P(\tau, t) \quad (20a)$$

$$\frac{dL(\tau, t)}{d\tau} = -cP(\tau, t)L(\tau, t) - \gamma_L L(\tau, t) \quad (20b)$$

$$\frac{dI(\tau, t)}{d\tau} = cP(\tau, t)L(\tau, t) - \gamma_I I(\tau, t), \quad (20c)$$

where c represent the parasitoid's attack rate *per host*, and γ_P , γ_L , γ_I are the death rates of the respective species. Assuming P_t parasitoids, RH_t host larvae, and no parasitized larvae at the start of the vulnerable period ($\tau = 0$), solving the above differential equations with initial conditions

$$L(0, t) = RH_t, \quad P(0, t) = P_t, \quad I(0, t) = 0 \quad (21)$$

predicts the parasitized and unparasitized larval population at the end of the season ($\tau = T$). This leads to a more general discrete-time model

$$H_{t+1} = F(H_t, P_t) \quad (22a)$$

$$P_{t+1} = G(H_t, P_t) \quad (22b)$$

where update functions are obtained by setting

$$F(H_t, P_t) = L(T, t) \quad (23a)$$

$$G(H_t, P_t) = kI(T, t). \quad (23b)$$

Solving (20) for a constant attack rate c with no mortalities ($\gamma_P = \gamma_L = \gamma_I = 0$) yields

$$P(\tau, t) = P_t, \quad L(\tau, t) = RH_t \exp(-c\tau P_t) \quad (24a)$$

$$I(\tau, t) = RH_t [1 - \exp(-c\tau P_t)] \quad (24b)$$

which using (23) yields the Nicholson-Bailey model (4).

Interestingly, it turns out that discrete-time models formulated using the hybrid approach can give qualitatively different results than phenomenologically designed updated functions. This point was illustrated in [16] for the scenario when the attack rate c becomes dependent on the density of un-parasitized hosts

$$c = \frac{c_1 L(\tau, t)^q}{1 + c_1 T_h L(\tau, t)^{q+1}} \quad (25)$$

for positive constants c_1 , q and T_h . In ecological literature, the case of $q = 0$ has been referred to as a Type II functional response where

$$c = \frac{c_1}{1 + c_1 T_h L(\tau, t)}. \quad (26)$$

When $q = 0$, the parasitoid attack rate across all hosts takes the form

$$cL(\tau, t) = \frac{c_1 L(\tau, t)}{1 + c_1 T_h L(\tau, t)} \quad (27)$$

which saturate to

$$\lim_{L(\tau, t) \rightarrow \infty} cL(\tau, t) = \frac{1}{T_h} \quad (28)$$

at high host densities, where the handling time T_h can be interpreted as the average time taken by a parasitoid to finish parasitizing a host. The case of $q \geq 1$ is referred to as a Type III functional response where $cL(\tau, t)$ becomes a sigmoidal function of $L(\tau, t)$. Setting a host-dependent attack rate (25) in (20) results in a stable discrete-time model for $q > 1$ assuming that the handling time is significantly shorter than the vulnerable stage duration ($T_h \ll T$) [16]. Interestingly, the host equilibrium here is still a decreasing function of the host growth rate (as in the Nicholson-Bailey model), but a Type III response makes the fraction of hosts escaping parasitism a decreasing function of the host density. In the context of Fig. 4, this corresponds to shifting the Nicholson-Bailey point to the left into the stability region. In contrast, a Type II response ($q = 0$) moves the point to the right to further destabilize the population dynamics.

Several prior works incorporated functional responses phenomenologically by simply substituting

$$c = \frac{c_1 (RH_t)^q}{1 + c_1 T_h (RH_t)^{q+1}}, \quad q \geq 1 \quad (29)$$

in the Nicholson-Bailey model (4), and the resulting discrete-time model is unstable for all values of q [19]. In summary, a Type III functional response ($q > 1$) stabilizes the population interaction in the mechanistically formulated hybrid approach, but not in the phenomenological approach.

V. LIMITS OF HOST SUPPRESSION BY PARASITIDS

We next use the hybrid formulation to investigate the suppression of host population density by a parasitoid. As done in earlier models [20]–[22], we first consider a self-limitation in the hosts ability to grow (due to finite food resources or attacks by other nature enemies) by considering a host mortality rate $\gamma_L = c_h L(\tau, t)$ in (20) that is proportional to the host density. For a constant parasitoid attack rate c and $\gamma_P = \gamma_I = 0$, the above hybrid approach yields

$$H_{t+1} = \frac{RH_t \exp(-cTP_t)}{1 + c_h RH_t \frac{1 - \exp(-cTP_t)}{cP_t}} \quad (30a)$$

$$P_{t+1} = \frac{kcP_t}{c_h} \ln \left[1 + c_h RH_t \frac{1 - \exp(-cTP_t)}{cP_t} \right] \quad (30b)$$

[16]. As expected, in the limit $c_h \rightarrow 0$ this model converges back to the Nicholson-Bailey model. In the absence of parasitoids, this leads to

$$H_{t+1} = \frac{RH_t}{1 + c_h TRH_t}. \quad (31)$$

which has a stable fixed point

$$H^* = \frac{R-1}{c_h TR} \quad (32)$$

representing the host population before the introduction of the parasitoid. In addition to this no-parasitoid equilibrium, the other fixed point of (30) is given by

$$H^* = \left(\frac{\exp(\frac{c_h}{kc}) - 1}{1 - \exp(\frac{c_h}{kc})} \right) \frac{cP^*}{c_h R}, \quad P^* = \frac{\ln(R) - \frac{c_h}{kc}}{cT}, \quad (33)$$

and is stable for

$$z^* < \frac{c_h}{kc} < \ln(R), \quad (34)$$

where z^* is the solution to

$$z^* + 1 = \frac{R(\ln(R) - z^*)}{R - \exp(z^*)} \quad (35)$$

[16]. The quantity

$$\frac{R(\exp(\frac{c_h}{kc}) - 1)(\ln(R) - \frac{c_h}{kc})}{(R-1)(R - \exp(\frac{c_h}{kc}))} \quad (36)$$

represents the ratio of the host equilibrium with parasitoids and without parasitoids, as given by (33) and (32), respectively. As one varies c_h/c in the stability region (34), the maximum host suppression while ensuring the stability of the fixed point (33) is given by

$$\frac{(R \exp(z^*) - 1)(\ln(R) - z^*)}{(R-1)(R - \exp(z^*))}$$

and is computed to be 0.34 and 0.29 for $R = 2$ and 10, respectively. Thus, for a constant parasitoid attack rate, the host population density cannot be suppressed more than $\approx 30\%$ below its density in the absence of the parasitoid. Can host suppression be more efficient with a density-dependent parasitoid attack rate?

Fig. 5: Plots of host population density H_t as a function of time t for model (38). With increasing parasitoid attack rate parameter c_1 in (37), the host density can be suppressed to arbitrary low levels while ensuring population stability. Other parameters taken as $R = 2$, $c_h = 1$, $T = 1$ and $k = 1$.

To address this question, we consider a Type III functional response where the attack rate takes the form (25). For simplicity we consider the case of $q = 1$ and fast handling times ($T_h \rightarrow 0$) which reduce (25) to

$$c = c_1 L(\tau, t). \quad (37)$$

In essence, the ability of a parasitoid to locate, attack and parasitize a host, increases with increasing host density. Using (37), $\gamma_L = c_h L(\tau, t)$, $\gamma_P = \gamma_I = 0$ in (20) yields

$$H_{t+1} = \frac{RH_t}{1 + c_h TRH_t + c TRH_t P_t} \quad (38a)$$

$$P_{t+1} = \frac{kcTR^2 H_t^2 P_t}{1 + c_h TRH_t + c TRH_t P_t}. \quad (38b)$$

The model again has two non-trivial equilibria. The first is when the parasitoid is absent, and the host density converges to (32). The second fixed point where both species coexist is given by

$$H^* = \frac{1}{\sqrt{c_1 TRk}}, \quad P^* = \frac{(R-1)\sqrt{k}}{\sqrt{c_1 TR}} - \frac{c_h}{c_1}. \quad (39)$$

Stability analysis as outlined in Section III shows that (39) is stable as long as

$$c_1 > \frac{c_h^2 RT}{k(R-1)^2}. \quad (40)$$

This implies that the ratio of host density with and without parasitoids

$$\frac{c_h \sqrt{TR}}{(R-1)\sqrt{c_1 k}} \quad (41)$$

can be made arbitrarily small with increasing attack rate parameter c_1 but with a dependence that scales as $1/\sqrt{c_1 k}$. This point is illustrated in Fig. 5 where the time evolution of host densities are shown for increasing values of c_1 .

VI. CONCLUSION

In this contribution, we have focused on the ecological interaction between hosts and parasitoids that holds tremendous potential in biological control of pests [23]–[28]. We provide novel result on the stability of host-parasitoid interactions modeled as per (1), and characterized by an escape response $f(H_t, P_t)$. The result is graphically illustrated in Fig. 4 in terms of two quantities: the rate at which the host equilibrium changes with the hosts growth rate (dH^*/dR), and the sensitivity of the escape response to the host density at equilibrium (df/dH). For several models, such as (4), (5), (16) the escape response is invariant of the host density, in which case the stability reduces to the host density being an increasing function of the host growth rate. Another key insight that can be tested with field observations is that stability is more likely to emerge when the escape response is a decreasing function of the host density (i.e., a larger fraction of hosts do not get parasitized at higher host densities), than an increasing function.

We also introduced a hybrid approach for deriving the discrete-time model by solving a set of nonlinear differential equations describing the population dynamics during the host's vulnerable stage. The hybrid approach was used to study the limit of host suppression while still keeping the host-parasitoid interaction stable. Our prior work had shown that for a constant parasitoid attack rate, the host cannot be suppressed beyond a certain limit [16]. Interestingly, our analysis here shows that an attack rate proportional to the host density can lead to arbitrary low host suppression (Fig. 5). In future work, we will investigate host suppression with other stabilizing mechanisms, such as, host refuge, variation of risk across the host population [13], [29]–[31], and parasitoid aggregation [32]–[34].

Another aspect to explore using the hybrid formulation is spatial dynamics where host/parasitoid can move between patches [35]–[38]. Our preliminary work on this topic has been quite promising and shows that density-dependent movement between patches can have a stabilizing effect on the population dynamics [39].

APPENDIX

Consider the discrete-time model (12) whose unique non-trivial fixed point is given by

$$\frac{1}{R} = f(P^*), \quad P^* = k(R-1)H^*. \quad (42)$$

Denoting small fluctuation around the equilibrium H^* and P^* by $h_t := H_t - H^*$ and $p_t := P_t - P^*$, respectively, one obtains using linearization the following linear discrete system

$$\begin{bmatrix} h_{t+1} \\ p_{t+1} \end{bmatrix} = A \begin{bmatrix} h_t \\ p_t \end{bmatrix}, \quad (43)$$

with

$$A = \begin{bmatrix} 1 & RH^* f'(P^*) \\ k(R-1) & -kRH^* f'(P^*) \end{bmatrix} \quad (44)$$

where

$$f'(P^*) = \left. \frac{df(x)}{dx} \right|_{x=P^*} < 0. \quad (45)$$

The stability conditions (10) applied to (44) shows the model fixed point is stable, if and only if, the following inequalities hold

$$-kR(R-1)H^* f'(P^*) > 0 \quad (46)$$

$$2 - kRH^* f'(P^*) > 0 \quad (47)$$

$$1 + kR^2 H^* f'(P^*) > 0. \quad (48)$$

Given that $R > 1$ and the fact that $f'(P^*) < 0$ (f is a monotonically decreasing function), inequalities (46)–(47) always hold and the stability condition is given by inequality (48), which using $P^* = k(R-1)H^*$ becomes

$$-P^* f'(P^*) < \frac{1}{R} - \frac{1}{R^2}. \quad (49)$$

Differentiating the first equation in (42) with respect to R we have

$$\frac{1}{R^2} = -f'(P^*) \frac{dP^*}{dR}, \quad (50)$$

which using $P^* = k(R-1)H^*$ can be written as

$$\frac{1}{P^*} \frac{dP^*}{dR} = \left(\frac{1}{R-1} + \frac{1}{H^*} \frac{dH^*}{dR} \right). \quad (51)$$

Substituting (51) in (50) gives us

$$\frac{1}{R} - \frac{1}{R^2} = -P^* f'(P^*) \left(1 + (R-1) \frac{1}{H^*} \frac{dH^*}{dR} \right), \quad (52)$$

which using the stability condition (49) reduce to

$$\frac{dH^*}{dR} > 0. \quad (53)$$

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