Linking parasitoid-driven host density suppression with density-dependence in host growth

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Abstract

Leveraging the discrete-time formalism of the Nicholson-Bailey model, we investigate the ecological population dynamics of host-parasitoid interactions with an arbitrary form of density-dependence in the host growth rate, and map out regimes allowing stable coexistence of the consumer (parasitoid) and the resource (host). If the parasitoid-free host population dynamics is stable, we provide sufficient conditions that ensure stability is maintained with the inclusion of the parasitoid irrespective of the level of parasitism. When parasitoids parasitize hosts at a constant rate, high parasitism levels are shown to always destabilize the population dynamics. This results in a limit of host suppression that we quantify using the ratio of host density (just before stability is lost for high parasitism levels) and the host's parasitoid-free carrying capacity. We systematically examine this limit for different types of intrinsic self-limitations in host growth. Our analysis shows that for both Ricker and Beverton-Holt-type host population dynamics, this parasitoid-driven host suppression limit is 33% for slow-growing hosts and $10-20\%$ for fast-growing hosts. Moreover, our results reveal that these limits can be much higher for Hill-type density-dependence in host growth rate. In summary, this contribution characterizes the impact of coupling different forms of intrinsic host population dynamics with and without additional stabilizing factors (such as a fraction of hosts protected from parasitism). These results have important implications for using parasitoids as natural enemies against arthropod pest populations, and the success of such biological control is inherently tied to the form of self-limitation in host growth.

I. Introduction

The classical framework for modeling host-parasitoid population dynamics is the discrete-time formalism of the Nicholson-Bailey model [1]–[4] that takes the form

$$H_{t+1} = RH_t e^{-cTP_t}, \tag{1a}$$

$$P_{t+1} = kRH_t\left(1-e^{-cTP_t}\right). \tag{1b}$$

In this model, H_t and P_t are the population densities of the adult host and parasitoid, respectively, in year $t \in \{1,2,3,\ldots\}$. $R>1$ quantifies the host reproduction and the absence of any host growth self-limitation in (1) results in geometric growth in host density

$$H_{t+1} = RH_t \implies H_t \propto R^t, \tag{2}$$

when the parasitoid is not present ($P_t = 0$). Key assumptions of the Nicholson-Bailey model are that parasitoids are not egg-limited and search for hosts randomly parasitizing them at a constant rate c with fast handling times corresponding to a Type I functional response. We refer to c as the *parasitoid attack rate*, and $1/c$ can be interpreted as the average time taken by a parasitoid to search, locate, and successfully parasitize a host. In (1), T denotes the overall period of host vulnerability to parasitoid attacks, and without loss of any generality, we will set it as $T=1$. Finally, $k \geq 1$, is the number of adult hosts emerging from a single parasitized host.

Apart from the trivial fixed point $(H_t, P_t) = (0,0)$ which is unstable for $R>1$, the model (1) has a unique non-trivial fixed point

$$H^* = \frac{\log(R)}{(R-1)kc}, \quad P^* = \frac{\log(R)}{c} \tag{3}$$

where both species are present and log represents the natural logarithm. It is well known that this fixed point is unstable resulting in population density oscillations that increase in amplitude over time, eventually leading to parasitoid extinction [5]. A myriad of ecological mechanisms have been characterized that stabilize the host-parasitoid population dynamics including, some hosts protected from parasitism [6], host-to-host differences in susceptibility to parasitism [7]–[13], and host feeding [14]. While Type III functional responses have a stabilizing effect under specific parameter regimes [15]–[17], Type II responses are destabilizing [18], [19].

In this contribution, we investigate the role of density-dependent host growth that sets the host density at a carrying capacity in the absence of the parasitoid. Such self-limitation in host growth has been known to stabilize the host-parasitoid interaction [20]–[24]. Interestingly, the relative timing of parasitism with respect to when the self-limitation acts on the host population critically influences the population dynamic [25]. Moreover, recent results show that parasitism acting after host-growth limitation provides the most efficient stable suppression of host population density below the carrying capacity [26]. Such a scenario can arise when, for example, self-limitation in host growth arises from resource competition at the larval stage, and parasitoids attack the host pupal stage (Fig. 1).

Considering an arbitrary form of self-limitation in host growth, we mathematically characterize the region allowing stable coexistence of both the host and the parasitoid. When parasitoids attack hosts at a constant rate, sufficiently large parasitism levels always destabilize the population dynamics and we explore the limit to which host density can be suppressed while still ensuring a stable consumer-resource coexistence. Intriguingly, our analysis shows that for a general class of models describing the host's population dynamics, this limit is always one-third of the host's parasitoid-free population density when $R \approx 1$, and the limit further decreases with increasing values of R. Our results also characterize stability regions when density-dependent host growth is combined with density-dependent parasitoid search efficiency ensuring a stable population interaction even for high levels of parasitism that suppress host density to arbitrarily low levels.

II. Host population dynamics

In the parasitoid's absence, the population dynamics of the host species follow the discrete-time model

$$H_{t+1} = RH_t f_H(H_t), \quad R > 1 \tag{4}$$

where the self-limitation in host growth is captured via the function $f_H(x) \in [0,1]$ that is defined for $x \geq 0$. This self-limitation could arise as a result of either intraspecific competition for resources or density-dependent predation by consumers other than the specific parasitoid in consideration. f_H is assumed to be a *continuously differentiable* and a *monotonically decreasing* function with $f_H(0) = 1$.

An ecologically-relevant form for this function is

$$f_H(H_t) = \frac{1}{\left(1 + \frac{\left(R^{\frac{1}{q}} - 1\right) H_t}{K}\right)^q} \tag{5}$$

where $K, q > 0$, and specific values of the quotient q correspond to different classical models of single-species population dynamics [27]–[29]. For example, $q = 1$ results in the Berveton-Holt model

$$H_{t+1} = \frac{RH_t}{1 + \frac{(R-1)H_t}{K}}. \tag{6}$$

Using the fact that

$$\lim_{q \to \infty} \left(1 + \frac{\left(R^{\frac{1}{q}} - 1\right) H_t}{K}\right)^q = R^{\frac{H_t}{K}}, \tag{7}$$

in the limit $q \to \infty$, (4)-(5) converge to the Ricker model [30]

$$H_{t+1} = H_t R^{1 - H_t/K}. \tag{8}$$

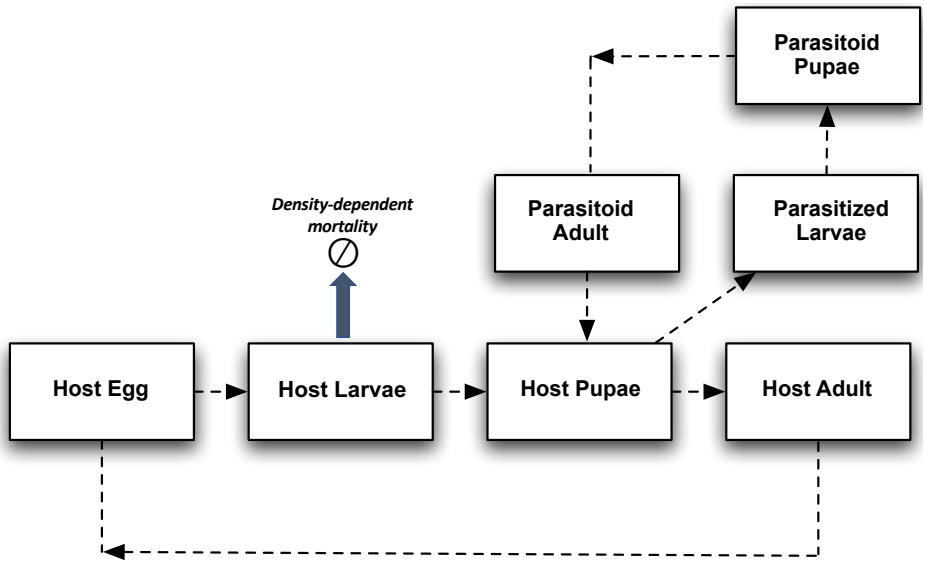

Fig. 1: Host-parasitoid life cycles, with self-limitation in host growth occurring at the larval stage due to density-dependent mortality as a result of either predation or resource competition. Parasitoids attack hosts at the pupal stage after host self-limitation has acted on the population.

The model (4) is assumed to have a unique non-trivial fixed point $H_t = K$ that represents the host's parasitoid-free population density satisfying

$$f_H(K) = \frac{1}{R}. \tag{9}$$

It is convenient to characterize the stability of this fixed point in terms of the dimensionless quantity

$$S_H(x) := \frac{x}{f_H(x)} \frac{df_H(x)}{dx}, \tag{10}$$

that is the log sensitivity of the function f_H with respect to the host population density and can be interpreted as the strength of density-dependent host growth. The fixed point $H_t = K$ is asymptotically stable, if and only if,

$$-2 < S_H(K) < 0 \tag{11}$$

[31]. For f_H as given by (5), the log sensitivity takes the form

$$S_H(H_t) = -q \left(1 - \frac{1}{1 + \frac{\left(R^{\frac{1}{q}} - 1\right) H_t}{K}} \right) \implies S_H(K) = -q \left(1 - \frac{1}{R^{\frac{1}{q}}} \right). \tag{12}$$

Given that $R > 1$, one can see that the stability condition (11) is always satisfied for $0 < q \leq 2$. Thus, the fixed point $H_t = K$ is stable for any level of host reproduction when $0 < q \leq 2$. When $q > 2$, (11) is satisfied for

$$1 < R < \left(\frac{q}{q-2} \right)^q \tag{13}$$

with the range of R allowing stability shrinking with increasing q. For example, when $q = 3$, (13) corresponds to $1 < R < 27$, and when $q \to \infty$ (the Ricker model), it shrinks to $1 < R < e^2 \approx 7.39$.

Another model formulation of host self-limitation that we will use later in the manuscript is

$$H_{t+1} = \frac{RH_t}{1+(R-1)\left(\frac{H_t}{K}\right)^q}, \tag{14}$$

which considers a Hill-type density dependence for which

$$S_H(H_t) = -q\left(1 - \frac{1}{1+(R-1)\left(\frac{H_t}{K}\right)^q}\right) \implies S_H(K) = -q\left(1-\frac{1}{R}\right). \tag{15}$$

In this case, the fixed point $H_t = K$ is always stable for $0 < q \leq 2$, and stable for

$$1 < R < \frac{q}{q-2} \tag{16}$$

when $q > 2$. While both (5) and (14) are identical for $q = 1$, difference arises when $q \gg 1$, in which case while (5) converges to the Ricker model, model (14) corresponds to a sharp sigmoidal reduction in host growth when $H_t > K$.

III. Host-parasitoid population dynamics

Having defined the host population dynamics, we now introduce the parasitoid resulting in the two-dimensional consumer-resource model

$$H_{t+1} = RH_t f_H(H_t) f_P(P_t) \tag{17a}$$

$$P_{t+1} = kRH_t f_H(H_t)\left(1 - f_P(P_t)\right), \tag{17b}$$

where the function $f_P(P_t)$ is the *escapre respose* quantifying the fraction of hosts escaping parasitism to become adult hosts for the following year. The model makes several key assumptions:

- The escape response $f_P(P_t)$ is only a function of the parasitoid density, and hence, excludes Type II and III functional responses.
- The function $f_P(P_t)$ is is a *continuously differentiable* and a *monotonically decreasing* function with $f_P(0) = 1$. Thus, the fraction of hosts escaping parasitism decreases with increasing parasitoid density P_t.
- Parasitism occurs after hosts have been subjected to intrinsic growth limitation (Fig. 1). In this case, $RH_t f_H(H_t)$ is the host density vulnerable to parasitism, and f_P and $1 - f_P$ are the unparasitized and parasitized host fractions, respectively, at the end of the vulnerable period.

The consumer-resource model (17) has a fixed point $(H_t, P_t) = (K, 0)$ that excludes the parasitoid. However, we are primarily interested in another fixed point $(H_t, P_t) = (H^*, P^*)$ where $H^* > 0$ & $P^* > 0$ allowing coexistence of both species. Setting $H_{t+1} = H_t = H^*$, $P_{t+1} = P_t = P^*$ in (17) shows that this fixed point is the solution to

$$\frac{1}{R} = f_H(H^*) f_P(P^*), \quad H^* = \frac{P^* f_P(P^*)}{k(1 - f_P(P^*))}. \tag{18}$$

A. Stability analysis of the parasitoid-free fixed point

To assess the stability of a fixed point we first obtain the corresponding Jacobian matrix A by linearizing the nonlinearities on the right-hand-side of (17) around the given fixed point. For the fixed point $(H_t, P_t) = (K, 0)$ corresponding to parasitoid extinction and the host density at the carrying capacity K, we obtain

$$A = \begin{bmatrix} a_{00} & a_{01} \\ a_{10} & a_{11} \end{bmatrix} \tag{19}$$

where the entries of the matrix are given by

$$a_{00} = \frac{\partial RH_t f_H(H_t) f_P(P_t)}{\partial H_t}\Big|_{H_t=K, P_t=0} = 1 + S_H(K), \qquad a_{01} = \frac{\partial RH_t f_H(H_t) f_P(P_t)}{\partial P_t}\Big|_{H_t=K, P_t=0} = H^* f_P'(0) \tag{20a}$$

$$a_{10} = k\frac{\partial RH_t f_H(H_t)\left(1 - f_P(P_t)\right)}{\partial H_t}\Big|_{H_t=K, P_t=0} = 0, \qquad a_{11} = k\frac{\partial RH_t f_H(H_t)\left(1 - f_P(P_t)\right)}{\partial P_t}\Big|_{H_t=K, P_t=0} = -ka_{01}, \tag{20b}$$

and

$$f_P'(0) := \frac{df_P(P_t)}{dP_t}|_{P_t=0}. \tag{21}$$

The stability of the fixed point is determined by the Jury conditions, i.e., the fixed point is stable, if and only if, all the following inequalities hold

$$1-tr(A)+det(A)>0, \quad 1+tr(A)+det(A)>0, \quad 1-det(A)>0 \tag{22}$$

[32], where tr and det denote the trace and determinant of A, respectively. This analysis shows that the fixed point $(H_t,P_t)=(K,0)$ is stable, if and only if,

$$1+kKf_P'(0)\,(1+S_H(K))>0, \quad -S_H(K)(1+kKf_P'(0))>0, \quad (2+S_H(K))(1-kKf_P'(0))>0, \tag{23}$$

that, in turn, implies stability, if and only if,

$$-2<S_H(K)<0, \quad -1<kKf_P'(0)\leq 0. \tag{24}$$

Recall that the first inequality in (24) is the same as (11), while the second inequality arises from the fact that when $H_t=K$

$$\lim_{P_t\to 0}\frac{P_{t+1}}{P_t} = -kKf_P'(0), \tag{25}$$

and $-kKf_P'(0)<1$ leads to parasitoid extinction starting from small parasitoid densities. This result leads to a condition for parasitoid establishment: $-kKf_P'(0)>1$ is a necessary and sufficient condition for parasitoids to grow from small numbers.

B. Stability analysis of the coexistence fixed point

Repeating the stability analysis for the coexistence fixed point $(H_t,P_t)=(H^*,P^*)$ where both densities $H^*>0$, $P^*>0$ satisfy (18) results in the Jacobian matrix A with entries

$$a_{00}=1+S_H(H^*), \quad a_{01}=\frac{H^*}{P^*}S_P(P^*), \quad a_{10}=k(1+S_H(H^*))\left(\frac{1}{f_P(P^*)}-1\right), \quad a_{11}=-ka_{01}, \tag{26}$$

and as per the Jury conditions, a stable host-parasitoid coexistence occurs, if and only if,

$$1-f_P(P^*)+S_P(P^*)>-S_H(H^*)S_P(P^*), \tag{27a}$$

$$S_H(H^*)(-1+f_p(P^*)-S_P(P^*))-(1-f_P(P^*))\,S_P(P^*)>0, \tag{27b}$$

$$S_H(H^*)(1-f_p(P^*)-S_P(P^*))+2\,(1-f_P(P^*))-S_P(P^*)\,(1+f_P(P^*))>0, \tag{27c}$$

where S_H and S_P are the dimensionless log sensitivities of the functions f_H and f_P, respectively,

$$S_H(H^*) := \frac{x}{f_H(x)}\frac{df_H(x)}{dx}|_{x=H^*}<0, \quad S_P(P^*) := \frac{x}{f_P(x)}\frac{df_P(x)}{dx}|_{x=P^*}<0. \tag{28}$$

We investigate these inequalities in further detail for different scenarios highlighting new results, and connecting them with known results.

C. Absence of self-limitation in host growth

In the absence of any intrinsic self-limitation in host growth

$$f_H(H_t)=1 \Longrightarrow S_H=0, \tag{29}$$

from (18) the coexistence fixed point is given as the unique solution to

$$\frac{1}{R}=f_P(P^*), \quad H^*=\frac{P^*}{k(R-1)}. \tag{30}$$

Using $S_H = 0$, and given that $f_P(P^*) < 1$, $S_P(P^*) < 0$, the last two inequalities in (27) are always true, and stability is tied to the first inequality (27a). In this case, the coexistence fixed point is stable, if and only if,

$$1 - f_P(P^*) + S_P(P^*) > 0. \tag{31}$$

For the Nicholson-Bailey model

$$f_P(P^*) = e^{-cP^*}, \quad S_P(P^*) = -cP^*, \tag{32}$$

inequality (31) is always violated for any $P^* > 0$, and hence the unstable Nicholson-Bailey fixed point. We next review three complimentary scenarios that drive stability and relate them to (31).

Parasitoid interference: Interference between parasitoids can be captured using a density-dependent attack rate

$$c = c_m P_t^{-m}, \quad c_m > 0, \quad 0 < m < 1, \tag{33}$$

and this power-law-based decrease in search efficiency with parasitoid density has been empirically observed for many parasitoids [33]. This leads to

$$f(P_t) = e^{-c_m P_t^{1-m}} \Longrightarrow S_P(P_t) = -(1-m)c_m P_t^{1-m}. \tag{34}$$

Using the fact that at equilibrium $f(P^*) = e^{-c_m (P^*)^{1-m}} = 1/R$, inequality (31) simplifies to

$$1 - f_P(P^*) + S_P(P^*) > 0 \Longrightarrow 1 - \frac{1}{R} - (1-m)c_m (P^*)^{1-m} > 0 \Longrightarrow 1 - \frac{1}{R} - (1-m)\log R > 0, \tag{35}$$

resulting in a stable species coexistence when

$$1 - \frac{R-1}{R\log R} < m < 1. \tag{36}$$

For example, when $R = 2$ this range is $0.28 < m < 1$, and shrinks to $0.68 < m < 1$ for $R = 20$.

Fractional host refuge: One known mechanism that stabilizes the Nicholson-Bailey fixed point is when a given fraction μ of hosts are protected from parasitism [6]. In this case, the functional response and its log sensitivity take the form

$$f(P_t) = \mu + (1-\mu)e^{-cP_t} \Longrightarrow S_P(P_t) = -\frac{(1-\mu)cP_t e^{-cP_t}}{\mu + (1-\mu)e^{-cP_t}}, \tag{37}$$

respectively. When $f_H(H_t) = 1$ and $\mu < 1/R$, the resulting model has a unique-trivial fixed point given by

$$H^* = \frac{\log\left(\frac{(1-\mu)R}{(1-\mu R)}\right)}{(R-1)kc_p}, \quad P^* = \frac{\log\left(\frac{(1-\mu)R}{(1-\mu R)}\right)}{c_p}. \tag{38}$$

that is asymptotically stable for a range of refuge fractions

$$\mu^* < \mu < 1/R, \tag{39}$$

where μ^* is the unique solution of

$$\frac{R-1}{R(1-\mu^* R)} = \log\left(\frac{R(1-\mu^*)}{1-\mu^* R}\right) \tag{40}$$

[18]. As recently shown in [26], when $R \approx 1$, the range (39) can be approximated by

$$\frac{1}{2R} < \mu < \frac{1}{R}. \tag{41}$$

Variation in host risk: The concept of host refuge can be generalized by considering an arbitrary distribution of parasitism risk across the host population [7]–[12]. Assuming the attack rate c in the Nicholson-Bailey model to be a random variable with a probability distribution function (pdf) $p(x)$ results in the escape response

$$f(P_t) = \int_{x=0}^{\infty} p(x) \exp(-xP_t). \tag{42}$$

Considering $p(x)$ to be a Gamma distribution with mean c and coefficient of variation CV (standard deviation divided by the mean) transforms (42) to

$$f(P_t) = \frac{1}{(1+cCV^2P_t)^{1/CV^2}} \Longrightarrow S_P(P^*) = -\frac{cP^*}{1+CV^2cP^*}. \tag{43}$$

Note that when $CV = 1$

$$1 - f_P(P^*) + S_P(P^*) = 0 \tag{44}$$

and inequality (31) is satisfied for any $P^* > 0$, if and only if, $CV > 1$. Thus, sufficient variability in host susceptibility to parasitism that leads to aggregation of parasitoid attacks to high-risk hosts leads to stable population dynamics [34]–[36]. Further works have shown that when $R \approx 1$, then $CV > 1$ is necessary and sufficient for stability independent of the form of $p(x)$. However, for larger values of R the shape of the risk distribution, $p(x)$ requiring zero modal risk is needed for stability [37].

D. The Beverton-Holt model

As can be seen from (12), for the Beverton-Holt model where $q = 1$,

$$-1 < S_H(H^*) < 0, \tag{45}$$

in which case a necessary and sufficient condition for stable coexistence is

$$1 - f_P(P^*) + S_P(P^*) > -S_H(H^*)S_P(P^*) \tag{46}$$

as the last two inequalities in (27) are always satisfied. Since both the log sensitivities are negative,

$$1 - f_P(P^*) + S_P(P^*) > 0 \tag{47}$$

is a sufficient condition for stable coexistence.

IV. Limits of host density suppression for constant parasitoid attack rate

In this section, we investigate model (17) with an arbitrary form of density-dependent in host growth and escape response $f(P_t) = e^{-cP_t}$ as in the Nicholson-Bailey model. Recall that parasitoid establishment (the ability of the consumer to grow from small densities) requires

$$-kK\frac{df_P(P_t)}{dP_t}|_{P_t=0} > 1 \implies c > \frac{1}{kK}. \tag{48}$$

Using (32), one can map the stability region as determined by the inequalities (27) as a function of S_H and cP^* (Fig. 2). In this figure, the y-axis $S_H = 0$ corresponds to the unstable Nicholson-Bailey model. The stabilizing effect of self-limitation in host growth is clearly seen in the figure, where making S_H negative leads to stable population dynamics, with further negative values again destabilizing the system. The range of stabilizing values of S_H shrinks with increasing levels of parasitoids (Fig. 2). Here the instability-stability boundary on the right and left arise from inequalities (27a) and (27c), respectively, and these boundaries converge to $S_H = -1$ in the limit $cP^* \to \infty$.

Note that in this case, a sufficiently large parasitoid attack rate will drive the host density much below the carrying capacity with $f_H \approx 1$, reducing the model to the unstable Nicholson-Bailey model. This point is illustrated in Fig. 3 for both Beverton-Holt and Ricker models of self-limitation in host growth, where sufficiently large attack rates destabilize the system by crossing the boundary defined by the inequality (27a). This sets up an interesting question: what is the fundamental limit to which the host density can be suppressed below its parasitoid-free density and how does this depend on the form of f_H?

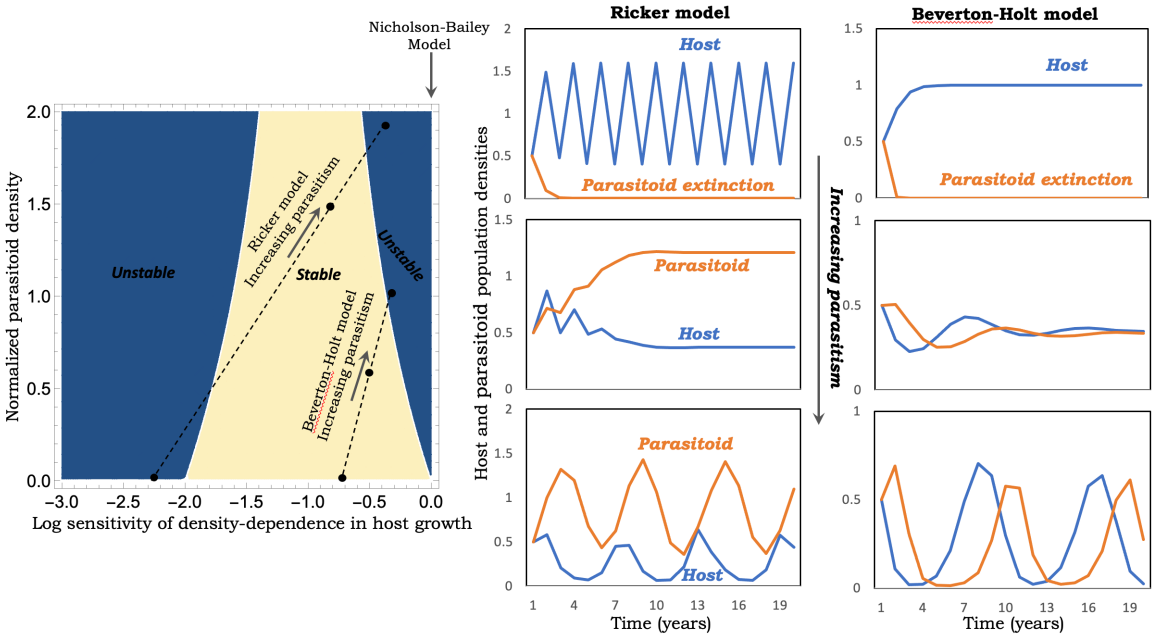

Fig. 2: Region of stable host-parasitoid coexistence for the model (17) as given by (27) for the Nicholson-Bailey escape response $f(P_t) = e^{-cP_t}$. Here the stability region is mapped in terms of $S_H(H^*)$ (the strength of density-dependence in host growth) on the x-axis and the parasitoid level cP^* on the y-axis. Stability arises for a range of values of $S_H(H^*)$ with the instability-stability boundaries on the right and left defined by inequalities (27a) and (27c), respectively. The figure shows the path traced by Berverton-Holt and Ricker models of intrinsic host population dynamics, for increasing levels of parasitoid attack rates that decrease the host density, and ultimately destabilize the system dynamics. Parameters are taken as $k = K = 1$, $R = 4$ for the Berverton-Holt model, and $R = 9.5$ for the Ricker model. Population trajectories corresponding to the black circles on the stability region are shown on the right for increasing parasitoid attack rates. Note for the Ricker model the host population dynamics is unstable in the parasitoid's absence. The inclusion of the parasitoid stabilizes the population dynamics, which is again destabilized for a sufficiently large attack rate.

Mathematically, this limit can be determined from the stability-instability boundary as given by (27a)

$$1 - f_P(P^*) + S_P(P^*) = -S_H(H^*)S_P(P^*) \tag{49}$$

where at equilibrium

$$f_P(P^*) = e^{-cP^*} = \frac{1}{Rf_H(H^*)} \Longrightarrow cP^* = \log Rf_H(H^*) \tag{50}$$

and

$$S_P(P^*) = -cP^* = -\log Rf_H(H^*). \tag{51}$$

For a given functional from f_H, the minimal value of H^* conditioned on stable host-parasitoid coexistence can be obtained by substituting (50)-(51) in (49) and solving for H^*. Quantifying the limit of host suppression as the ratio H^*/K - the minimal achievable stable host density normalized to its parasitoid-free density, our analysis shows that the limits decrease with increasing R (Fig. 3). Intriguingly, when $R \approx 1$, for f_H of the form (5), this limit is always one-third independent of the value of q (Fig. 3), and hence true for both Berverton-Holt and Ricker models (see Appendix for detailed proof). However, differences emerge for larger values of R - decay in the limit is much more gradual for the Ricker model as compared to the Beverton-Holt model (Fig. 3). When f_H takes the form (14) then

this limit of host suppression is

$$\left(\frac{1}{1+2q}\right)^{1/q} \tag{52}$$

when $R \approx 1$ (see Appendix for proof), and the limit increases to one as $q \to \infty$ (Fig. 3).

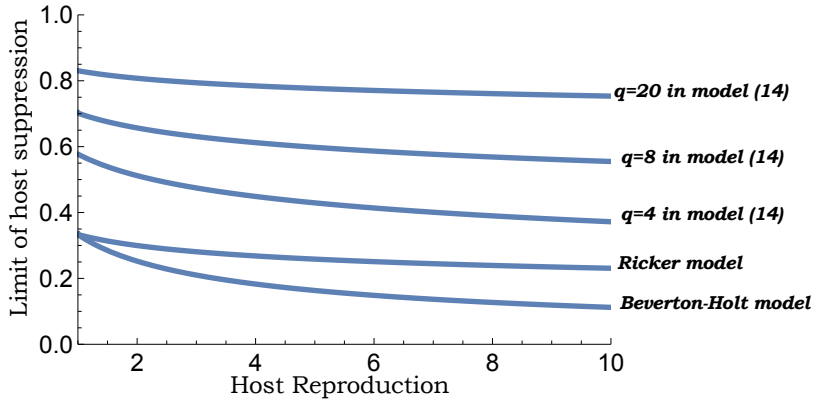

Fig. 3: The limit of host suppression as quantified by the ratio of lowest possible host density with and without parasitoid conditioned on stable species coexistence. The limit is obtained from (49) as a function of host reproduction R for different models of parasitoid-free host population dynamics. The different models include the Beverton-Holt and Ricker models ($q = 1$ and $q \to \infty$ in (5), respectively), and (14) for different values of q.

V. Inclusion of stabilizing factors

We next explore the stabilizing effects of host growth self-limitation in combination with other stabilizing factors, such as host refuge. Such refuges can arise from a variety of scenarios, such as spatial occlusion of some hosts preventing access to parasitoids [38], or some hosts having higher immune response to parasitism [39]–[42]. Towards that end we consider the espace response (37) resulting in the model

$$H_{t+1} = RH_t f_H(H_t)\left(\mu + (1-\mu)e^{-cP_t}\right) \tag{53a}$$

$$P_{t+1} = kRH_t f_H(H_t)(1-\mu)e^{-cP_t}, \tag{53b}$$

with parasitoid establishment requiring

$$-kK\frac{df_P(P_t)}{dP_t}|_{P_t=0} > 1 \implies c > \frac{1}{(1-\mu)kK}. \tag{54}$$

The stabilization region in terms of $S_H(H^*)$ and cP^* is shown to considerably expand as a function of increasing refuge fraction μ (Fig. 4). While there are subtle changes to the left instability-stability boundary, the right-hand boundary shifts further right and disappears for sufficiently large refuge μ. The disappearance can be understood from the fact that when $\mu > 0.5$, then inequality (27a) always holds as $1 - f_P(P^*) + S_P(P^*) > 0$. The stability regions in terms of μ and attack rate c is illustrated in Fig. 5. Note that the region allowing stable coexistence expands for the Berveton-Holt model with increasing R. In contrast, this region contracts with increasing R for $\mu \approx 0$ for the Ricker model but expands for higher values of μ. The observed large regions of stable coexistence in the presence of fractional refuge and different forms of host growth self-limitation are consistent with experimental studies implicating refuges in the stability of host-parasitoid interactions [43]–[47].

Finally, we also explore the stability region in the case of parasitoid interference where the escape response takes the form (34). In this case, we also see an expansion in the stability region with increasing values of m. A key difference from the case of host refuge is that while the stability region in that case expands by moving the right-hand boundary further right (Fig. 5), in the case of parasitoid inference this boundary shifts upwards (Fig. 6).

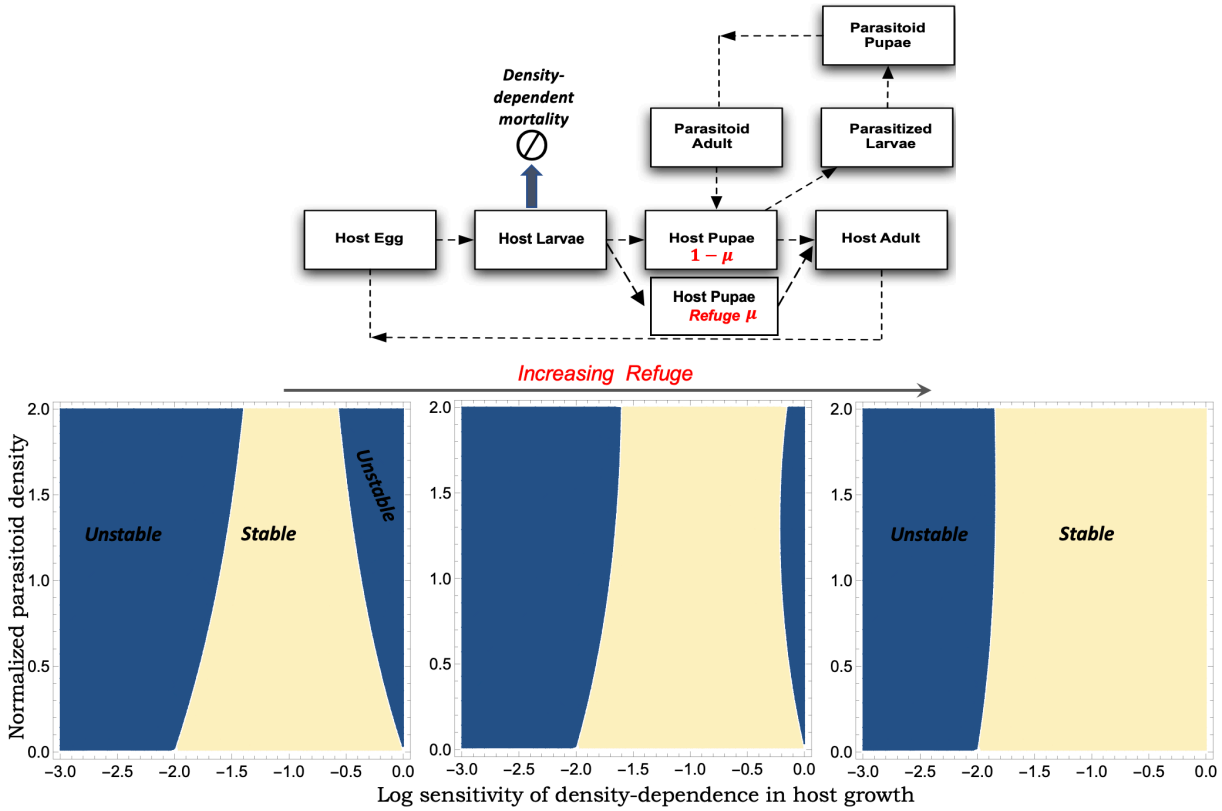

Fig. 4: Schematic of the insect life cycles as in Fig. 1, but showing a fraction μ of hosts protected from parasitism (i.e., in a refuge). The stability region as given by inequalities (27) for increasing values of μ. The left-most plot corresponds to $\mu = 0$ and is the same as in Fig. 2. The middle and right-most plots correspond to $\mu = 0.15$ and $\mu = 0.5$, respectively.

VI. Conculsion

In this contribution, we have systematically analyzed the population dynamics of host-parasitoid interactions for arbitrary forms of density-dependent host growth and specific forms of escape responses. Our key contribution is to derive necessary and sufficient conditions for the stable coexistence of both species that are mapped out in Fig. 2. When parasitoids parasitize hosts randomly as per a Type I functional response, the stabilizing effect of host growth self-limitation is seen in Fig. 2, with stability ensuing for a range of values of S_H (the strength of density dependence in host growth).

When this strength of density dependence is sufficiently weak such that $-1 < S_H$ (as in the Beverton-Holt model or if the host density is operating sufficiently below its carrying capacity), then stability can be tied to a single inequality (46), with the stability region expanding with more negative values of S_H. As the equilibrium host density $H^* \to 0$ then from (12) & (15) the strength $S_H(H^*) \to 0$, and (46) is violated for the Nicholson-Bailey escape response as in that case

$$1 - f_P(P^*) + S_P(P^*) < 0. \tag{55}$$

This instability for sufficiently large parasitism sets set up a limit of host density suppression that has fundamental consequences for biological control measures that use natural enemies such as parasitoids for reducing the density of arthropod pests [33], [48]–[54], A key result of this paper is that for a broad class of intrinsic host population dynamic models given by (5), we show that this limit is one-third of the hosts parasitoid-free density independent of q for slow-growing hosts ($R \approx 1$)(Fig. 3). However, for fast-growing hosts, this will depend on the specific value

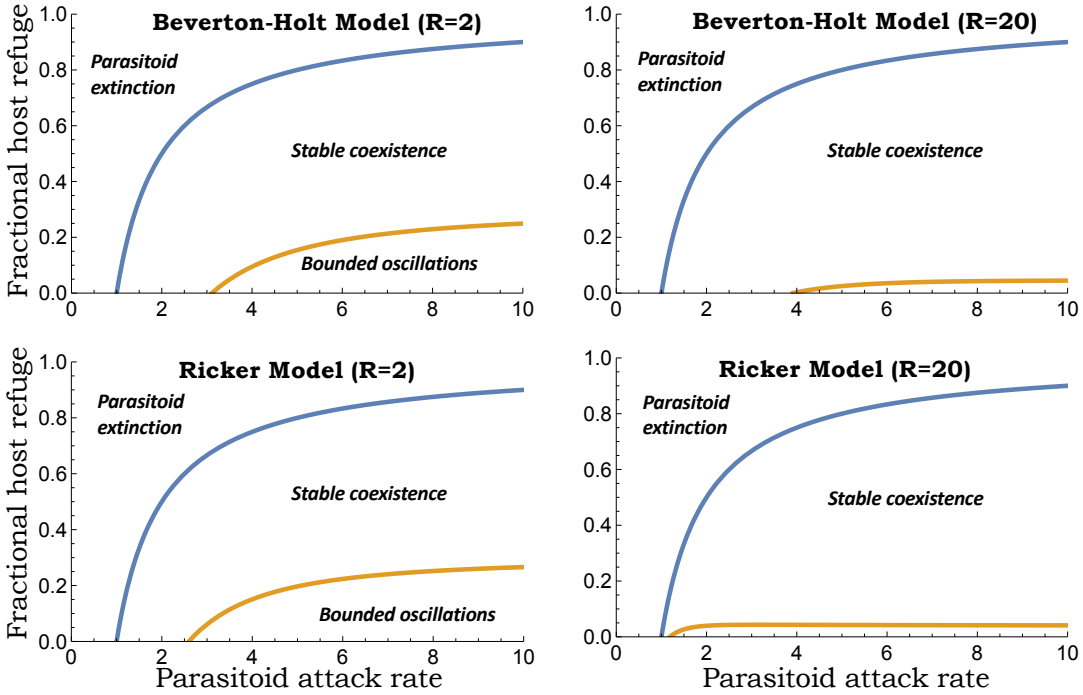

Fig. 5: The region of stable host-parasitoid population dynamic for model (53) in terms of the fractional host refuge μ and parasitoid attack rate c. The regions are plotted for $R = 2$ (left) and $R = 10$ (right) where f_H takes the form of the Beverton-Holt model (top) and the Ricker model (bottom). The blue line corresponds to (54), and the region above leads to parasitoid extinction. Stable consumer-resource coexistence occurs in the region in between the blue and orange lines, with the region below the orange line leading to bounded oscillations in population densities. Other paramters taken as $K = k = 1$. Note that when the host density is sufficiently suppressed for high attack rates, the stability regions for Berverton-Holt and Ricker models become similar for a given R due to the weakening effect of self-limitation in host growth.

of q. For example, for $R = 10$ this limit is $\approx 10\%$ for the Beverton-Holt model ($q = 1$) and $\approx 25\%$ for the Ricker model ($q \to \infty$). In contrast, when density-dependent host growth takes the form as in (14) then this limit always depends on q, and increases with increasing q (Fig. 3). These results argue that the form of density-dependent host growth is important for the success of any biological control program and must be taken into account.

We further expanded these results to consider additional stabilizing factors, such as host refuge and parasitoid interference, that alter the model's escape response. The expansion in the coexistence stability region by coupling these factors with density-dependent host growth is seen in Figs. 3-5. When these factors are present such that inequality (47) holds, then stable parasitoid presence is ensured for high parasitism levels that will lead to better suppression of host density.

While this work has focused on the question of stable coexistence, future work will consider spatial dynamics connecting metapopulations, and explore how spatial effects alter the fundamental limits of biological control [55]–[59]. It will also be important to explicitly consider parasitoid extinction in stochastic formulations of these models with both environment fluctuations in parameters, such as the host reproduction R, and demographic stochasticity. Given the nonlinearities present in these models, the analysis will depend on both stochastic simulations and several closure schemes developed for analyzing population dynamic models [60]–[66]. Finally, it will be important to expand this analysis to Type II and Type III functional responses, which would require semi-discrete formulations that mechanistically capture the continuous changes in population densities during the host's vulnerable stage [17], [67], [68].

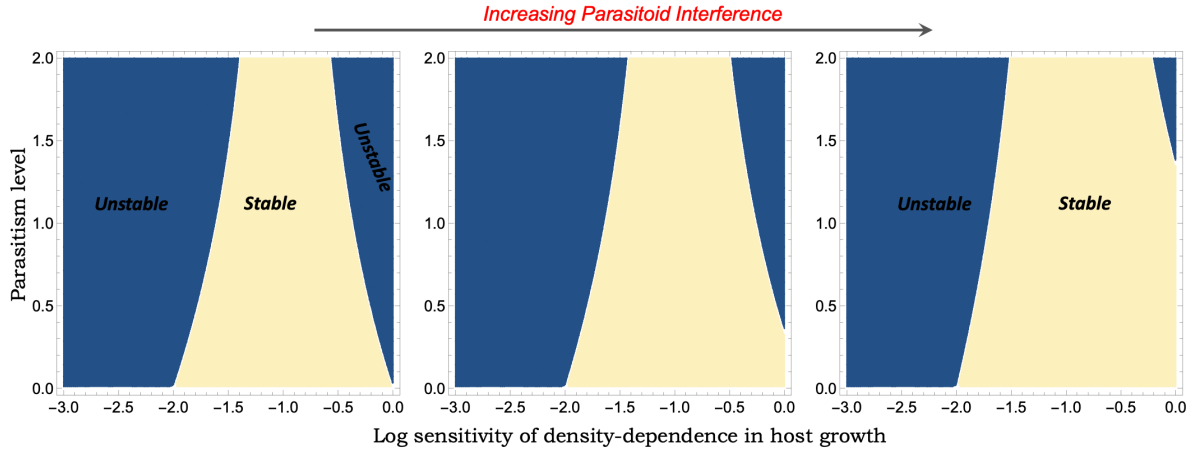

Fig. 6: The region of stable host-parasitoid population dynamic for model (17) with escape response (34) capturing density-dependent attack rate due to interference between parasitoids. Here the x- and y-axis are $S_H(H^*)$ and $c\,(P^*)^{1-m}$, respectively. The plots from the left to right correspond to $m=0$, $m=0.1$, and $m=0.45$, respectively.

APPENDIX

We consider the escape response $f(P_t)=e^{-cP_t}$ as in the Nicholson-Bailey model where at equilibrium

$$f_P(P^*)=\frac{1}{Rf_H(H^*)}\Longrightarrow cP^*=\log Rf_H(H^*). \tag{56}$$

The population dynamics is destabilized for sufficient large parasitoid attack c, and at the stability-instability boundary

$$\frac{1-e^{-cP^*}-cP^*}{cP^*}=-S_H(H^*). \tag{57}$$

From (56), in the limit $R\to 1$, $P^*\to 0$, and the left-hand-side of (57) reduces to

$$\lim_{P^*\to 0}\frac{1-e^{-cP^*}-cP^*}{cP^*}=\frac{cP^*}{2}=\frac{\log Rf_H(H^*)}{2}=\frac{\log R+\log f_H(H^*)}{2}. \tag{58}$$

For f_H of the form (5), when $R\approx 1$

$$\log f_H(H^*)=-q\log\left(1+\frac{\left(R^{\frac{1}{q}}-1\right)H^*}{K}\right)\approx -q\frac{\left(R^{\frac{1}{q}}-1\right)H^*}{K}\approx -\frac{(R-1)H^*}{K}. \tag{59}$$

Note here we have used the fact that when $R\approx 1$, then $R^{\frac{1}{q}}-1\approx (R-1)/q$. Similarly, using (12) we can approximate $S_H(H^*)$ when $R\approx 1$ as

$$S_H(H^*)=-q\left(1-\frac{1}{1+\left(R^{\frac{1}{q}}-1\right)\frac{H^*}{K}}\right)\approx -q\left(R^{\frac{1}{q}}-1\right)\frac{H^*}{K}\approx -(R-1)\frac{H^*}{K}. \tag{60}$$

Substituting (58)-(60) back in (57), and using $\log R\approx R-1$ yields

$$\frac{\log R+\log f_H(H^*)}{2}=(R-1)\frac{H^*}{K}\implies (R-1)-\frac{(R-1)H^*}{K}=2(R-1)\frac{H^*}{K}\implies \frac{H^*}{K}=\frac{1}{3}. \tag{61}$$

Thus, independent of the value of q, for $R\approx 1$, at the stability-instability boundary the host density is one-third of its parasitoid-free density.

Repeating a similar analysis for $R \approx 1$ but with f_H of the form (14) yields

$$\log f_H(H^*) = -\log\left(1+(R-1)\left(\frac{H^*}{K}\right)^q\right) \approx -(R-1)\left(\frac{H^*}{K}\right)^q, \tag{62}$$

and from (15)

$$S_H(H^*) = -q\left(1-\frac{1}{1+(R-1)\left(\frac{H^*}{K}\right)^q}\right) \approx -q(R-1)\left(\frac{H^*}{K}\right)^q, \tag{63}$$

which results in the following minimal host density

$$\frac{\log R+\log f_H(H^*)}{2} = q(R-1)\left(\frac{H^*}{K}\right)^q \implies (R-1)-(R-1)\left(\frac{H^*}{K}\right)^q = 2q(R-1)\left(\frac{H^*}{K}\right)^q \implies \frac{H^*}{K} = \left(\frac{1}{1+2q}\right)^{1/q}. \tag{64}$$

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