

# Permanent Coexistence for an Intraguild Predation Model with Type II Responses

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**Abstract**—Permanence theory provides a mathematical framework for investigating long-term species survival where species densities are allowed to vary in any way (e.g. equilibrium, chaos, etc.) as long as the densities do not remain too close to the boundary (zero density) of the state space. We apply permanence theory to an intraguild predation model with nonlinear Holling Type II functional responses. Intraguild predation is the simplest example of omnivory--feeding on more than one trophic level--and consists of three species interacting through a unique blend of predation and competition. Our analysis shows that three restrictions must be placed on the model parameters in order to guarantee coexistence. The biological interpretations resulting from the parameter restrictions are also included.

**Keywords**—Functional Response, Intraguild Predation, Omnivory, Permanent Coexistence.

## I. INTRODUCTION

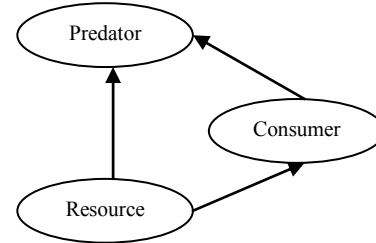
THE long-term survival of species should be of great importance to humans since our survival depends upon understanding natural systems. We investigate an intraguild predation or IGP model in this work. IGP refers to a top predator and an intermediate consumer that compete for a resource in a similar way, but also engage in direct predator-prey interactions [1], [2]. The larger classification of omnivory has been well documented throughout the literature [1]–[3].

An IGP model with linear functional and numerical responses was investigated by Vance [4] using permanence theory. We will use nonlinear Holling Type II functional responses because they are more realistic. This is due to the fact that predator rates of consumption become saturated as victim densities increase. The search for robust mechanisms that can explain permanence of tightly linked omnivory systems remains an important challenge [5]. We use a lower semicontinuous average Lyapunov function to deal with these nonlinear responses.

## II. INTRAGUILD PREDATION MODEL

Omnivorous interactions can be very complex, so we restrict ourselves to the asymmetrical classification of IGP as given by [2]. The asymmetric classification refers to the fact

that



the

Fig. 1 Asymmetrical intraguild predation. Arrows indicate that one species (base of arrow) is eaten by another species (point).

consumer (C) does not feed on the predator (P), but the predator feeds on the consumer (see Figure 1). Our nonlinear response IGP model is given by the following system of differential equations:

$$\begin{aligned} \frac{dP}{dt} &= P \left[ \frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} - m_P \right] \\ \frac{dC}{dt} &= C \left[ \frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} - m_C \right] \\ \frac{dR}{dt} &= R \left[ r \left( 1 - \frac{R}{K} \right) - \frac{\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{RP}P}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \right] \end{aligned} \quad (1)$$

similar to Křivan and Diehl [5].

Parameter  $\lambda_{ij}$  is the search rate of species  $j$  for species  $i$ ,  $e_{ij}$  is the efficiency with which species  $i$  is converted to new offspring of species  $j$ , and  $h_{ij}$  is the time spent by species  $j$  handling species  $i$ .  $K$  is the resource carrying capacity and  $r$  is the intrinsic rate of increase of the resource. The natural mortality rates of the predator and consumer are  $m_p$  and  $m_c$ .

TABLE I  
LIST OF VARIABLES AND PARAMETERS

Symbol	Meaning
$P(t)$	Predator density at time $t$
$C(t)$	Consumer density at time $t$
$R(t)$	Resource density at time $t$
$r$	Resource intrinsic rate of increase
$K$	Resource carrying capacity
$e_{ij}$	Efficiency with which species $i$ is converted to new offspring of species $j$
$\lambda_{ij}$	Search rate of species $j$ for species $i$
$h_{ij}$	Time spent by species $j$ handling species $i$

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respectively. See Table I for a list of variables and parameters.

III. KOLMOGOROV MODELS

Consider a specific form of differential equations that is typically used in modeling the population densities of interacting species. The n-species Kolmogorov model has the form

$$\frac{dx_i}{dt} = x_i f_i(\mathbf{x}), \quad 1 \leq i \leq n \quad (2)$$

where  $\mathbf{x} = \{x_i\}$ . Since we are dealing with species densities, we will restrict ourselves to the non-negative cone in  $\mathbb{R}^n$  denoted  $\mathbb{R}_+^n = \{\mathbf{x} \in \mathbb{R}^n : x_i \geq 0, 1 \leq i \leq n\}$ . Then, the bounding hypersurfaces are  $H_i = \{\mathbf{x} \in \mathbb{R}_+^n : x_i = 0\}$ .

**Definition 1:** A region R is invariant for (2) if  $\mathbf{x}_0 \in R$  and  $\mathbf{x}(t)$  is the solution to (2) with  $\mathbf{x}(t_0) = \mathbf{x}_0$ , then  $\mathbf{x}(t) \in R$  for all  $t > t_0$ .

Clearly, our IGP model (1) is of Kolmogorov type and the bounding hypersurfaces are invariant by a result given by Vance [4]. This in turn implies that  $P(t), C(t), R(t) \geq 0$  for all  $t \geq 0$ .

We will need the following lemma on differential inequalities throughout this work. This lemma is similar to one given by Birkhoff and Rota [6].

**Lemma 1:** Let S be a differentiable function on [a,b].

Part A: If S satisfies the differential inequality

$$\dot{S}(t) \leq \lambda S(t), \quad a \leq t \leq b \quad (3)$$

where  $\lambda > 0$  is a constant, then

$$S(t) \leq S(a)e^{\lambda(t-a)}, \quad a \leq t \leq b. \quad (4)$$

Part B: If S satisfies the differential inequality

$$\dot{S}(t) + \lambda S(t) \leq M_1, \quad a \leq t \leq b \quad (5)$$

where  $M_1 > 0$  and  $\lambda > 0$  are constants, then

$$S(t) \leq \frac{M_1}{\lambda} + \left( S(a) - \frac{M_1}{\lambda} \right) e^{\lambda(a-t)}, \quad a \leq t \leq b. \quad (6)$$

Part C: If S satisfies the differential inequality

$$\dot{S}(t) \leq (M_1 + M_2 e^{\lambda t}) S(t), \quad a \leq t \leq b \quad (7)$$

where  $M_1 > 0, M_2 > 0$ , and  $\lambda > 0$  are constants, then

$$S(t) \leq S(a) e^{M_1(t-a) + \frac{M_2}{\lambda}(e^{\lambda t} - e^{\lambda a})}, \quad a \leq t \leq b. \quad (8)$$

*Proof:* The first result is proved similar to the second result except for multiplying both sides of (3) by  $e^{-\lambda t}$ . For the second result, we multiply both sides of (5) by  $e^{\lambda t}$  to get

$$[\dot{S} + \lambda S]e^{\lambda t} \leq e^{\lambda t} M_1.$$

Rearranging, we get

$$0 \geq e^{\lambda t} [\dot{S} + \lambda S - M_1] = \frac{d}{dt} \left\{ S(t)e^{\lambda t} - \frac{M_1}{\lambda} e^{\lambda t} \right\}.$$

Thus, the function  $\left( S(t) - \frac{M_1}{\lambda} \right) e^{\lambda t}$  has a nonpositive

derivative and so is nonincreasing for  $a \leq t \leq b$ . Therefore,

$$\left( S(t) - \frac{M_1}{\lambda} \right) e^{\lambda t} \leq \left( S(a) - \frac{M_1}{\lambda} \right) e^{\lambda a}$$

and rearranging yields

$$S(t) \leq \frac{M_1}{\lambda} + \left( S(a) - \frac{M_1}{\lambda} \right) e^{\lambda(a-t)}.$$

For Part C, multiply both sides of (7) by

$$e^{\left( M_1 t + \frac{M_2}{\lambda} e^{\lambda t} \right)}$$

to get  $0 \geq e^{-\left( M_1 t + \frac{M_2}{\lambda} e^{\lambda t} \right)} [\dot{S} - (M_1 + M_2 e^{\lambda t}) S(t)]$

$$= \frac{d}{dt} \left\{ e^{-\left( M_1 t + \frac{M_2}{\lambda} e^{\lambda t} \right)} S(t) \right\}.$$

Hence,  $S(t) \leq S(a) e^{M_1(t-a) + \frac{M_2}{\lambda}(e^{\lambda t} - e^{\lambda a})}$ , completing the proof.

IV. SOLUTION TO SYSTEM

In order to investigate long term species survival, we need to show the existence and uniqueness of a solution to our differential equation model. To do this we specify some initial conditions:

$$P(0) = c_1 > 0, \quad C(0) = c_2 > 0, \quad R(0) = c_3 > 0.$$

The differential equation with the initial conditions forms an initial value problem:

$$\frac{d\mathbf{g}}{dt} = \mathbf{g}(\mathbf{x}), \quad \mathbf{g}(0) = \mathbf{c} \quad (9)$$

on  $D = \mathbb{R}_+ \cap \mathbb{R}_+^3$  with the understood definitions for  $\mathbf{g}, \mathbf{x}$ , and  $\mathbf{c}$ . Since  $\mathbf{g}$  and its partial derivatives are all continuous with respect to P, C, and R for all positive t, P, C, and R by an existence and uniqueness theorem [7] our initial value problem (9) has exactly one solution in D.

Now we show by means of a theorem that this solution exists for all  $t \geq 0$ .

**Theorem 1:** The initial value problem (9) has a unique solution in  $\mathbb{R}_+^3$  for all  $t \geq 0$ .

*Proof:* Recall from above that  $P(t), C(t), R(t) \geq 0$  for all  $t \geq 0$ . Then, we have the differential inequality

$$\frac{dR(t)}{dt} \leq R(t)r(1 - R(t)/K).$$

However, the initial value problem

$$\frac{du(t)}{dt} = u(t)r(1 - u(t) / K), \quad u(0) = u_0$$

has the unique solution

$$u(t) = \frac{K}{1 + \left(\frac{K}{u_0} - 1\right)e^{-rt}}$$

Then, applying a theorem on differential inequalities [8], we have that  $R(t) \leq u(t)$  for  $0 \leq t \leq \infty$ . If in addition, we let  $K_{\max} = \max\{u_0, K\}$  then,  $u(t) \leq K_{\max}$  and we have

$$R(t) \leq K_{\max} \text{ for } 0 \leq t \leq \infty. \quad (10)$$

$$\begin{aligned} \text{Also, } \frac{dC(t)}{dt} &\leq \frac{e_{RC}\lambda_{RC}R(t)}{1 + h_{RC}\lambda_{RC}R(t)}C(t) \\ &\leq e_{RC}\lambda_{RC}R(t)C(t) \\ &\leq e_{RC}\lambda_{RC}R_{\max}C(t) \text{ for } 0 \leq t \leq \infty. \end{aligned}$$

If we define  $\Gamma = e_{RC}\lambda_{RC}R_{\max}$ , then by Lemma 1 Part A

$$\begin{aligned} C(t) &\leq C(0)e^{\Gamma(t-0)} \\ &= c_2e^{\Gamma t}. \end{aligned} \quad (11)$$

This exponential function does not reach infinity in finite time.

Finally,

$$\begin{aligned} \frac{dP(t)}{dt} &\leq \frac{e_{RP}\lambda_{RP}R(t) + e_{CP}\lambda_{CP}C(t)}{1 + h_{RP}\lambda_{RP}R(t) + h_{CP}\lambda_{CP}C(t)}P(t) \\ &\leq e_{RP}\lambda_{RP}R(t) + e_{CP}\lambda_{CP}C(t)P(t). \end{aligned}$$

Since  $R(t) \leq K_{\max}$  and  $C(t) \leq c_2e^{\Gamma t}$ , we have that

$$\frac{dP(t)}{dt} \leq (\Gamma + e_{CP}\lambda_{CP}c_2e^{\Gamma t})P(t).$$

If we define  $\Phi = e_{CP}\lambda_{CP}c_2$  and  $\Lambda = \frac{\Phi}{\Gamma}$ , then by Lemma 1

Part C

$$P(t) \leq c_1e^{\Gamma t + \Lambda(e^{\Gamma t} - 1)}. \quad (12)$$

This exponential function does not reach infinity in finite time.

So, by a global existence and uniqueness lemma [9] and inequalities (10), (11), and (12) a unique solution for the initial value problem (9) exists for all  $0 \leq t \leq \infty$ . This completes the proof.

### V. PERMANENT COEXISTENCE

In this section we show that our IGP model with nonlinear Holling Type II responses is permanently coexistent under certain parameter restrictions. Several definitions of permanent coexistence or permanence have been used throughout the literature [10]–[15]. We use the definition given by Hutson [16].

**Definition 2:** We say that an orbit of (9) is ultimately in  $M \subset \mathbb{R}_+^3$  if and only if there exists  $T(\mathbf{x}) < \infty$  such that

$\mathbf{x}(t) \in M$  for  $t \geq T(\mathbf{x})$ . Also, we use the notation  $A - B$  to denote set difference for two sets  $A$  and  $B$ .

The following definition will also be using in our analysis.

**Definition 3:** An equilibrium point  $\bar{\mathbf{x}}$  is saturated if  $f_i(\bar{\mathbf{x}}) \leq 0$  for all  $i$  with  $\bar{x}_i = 0$ .

Note that every equilibrium point in the interior of the state space is saturated. For an equilibrium point on the boundary, saturated means that the dynamics do not “call for” the missing species [15].

**Definition 4:** The system (9) is permanently coexistent if and only if there exists a compact set  $M \subset \mathbb{R}_+^3$  such that orbits are ultimately in  $M$  for all  $\mathbf{x} \in \mathbb{R}_+^3$ .

Our proof on permanent coexistence will be based on the following theorem from Hutson [16] which is an extension of a result by Hofbauer [17].

**Theorem 2:** Let  $B \subset \mathbb{R}_+^3$  be compact and  $S$  a compact subset of  $B$ . Assume that  $S$  and  $B - S$  are invariant. Suppose that there is a  $C^1$  function  $P : B \rightarrow \mathbb{R}_+$  which is such that  $P(\mathbf{x}) = 0$  if and only if  $\mathbf{x} \in S$ . Take  $\Psi(\mathbf{x}) = \dot{P}(\mathbf{x}) / P(\mathbf{x})$  and assume that  $\Psi(\mathbf{x})$  is bounded below on  $B - S$ . Define its lower semi-continuous extension to  $S$ , still denoted by  $\Psi(\mathbf{x})$ , by setting

$$\Psi(\mathbf{x}) = \liminf_{y \rightarrow \mathbf{x}, y \in B - S} \Psi(\mathbf{y}) \quad (\mathbf{x} \in S)$$

and assume that for

$$\mathbf{x} \in \bar{\Omega}(S), \quad \sup_{t \geq 0} \int_0^t \Psi(\mathbf{x}(t)) dt > 0. \quad (13)$$

Then there is a compact invariant set  $M$  with  $d(M, S) > 0$  which is such that every orbit generated by (9) with  $\mathbf{x} \in \mathbb{R}_+^3$  is ultimately in  $M$ . That is, the system (9) is permanently coexistent.

The function  $P$  is known as an Average Lyapunov function [16]. Note that (13) holds if  $\Psi > 0$  on  $\bar{\Omega}(S)$ . Also, note that the function  $P(\mathbf{x})$  should not be confused with the state variable  $P(t)$ .

We begin our analysis by showing that system (1) has uniformly bounded orbits and enters a compact region of  $\mathbb{R}_+^3$ .

**Theorem 3:** Provided that  $e_{RP} < e_{CP}e_{RC}$ , all solutions of the system (1) that initiate in  $\mathbb{R}_+^3$  are uniformly bounded and enter a certain region  $B$  defined by

$$B = \{(P, C, R) \in \mathbb{R}_+^3 : 0 < P + C + R < M\}$$

where  $M_2 = \max \left\{ \frac{M_1}{\lambda}, \frac{M_1}{e_{CP}\lambda}, \frac{M_1}{e_{CP}e_{RC}\lambda} \right\}$ ,

$$M_1 = \frac{Ke_{CP}e_{RC}(r + \lambda)^2}{4r}, \text{ and } 0 < \lambda < \min \{m_C, m_P\}.$$

*Proof:* Recall that we have already stated that the components of all solutions of the system that initiate in  $\mathbb{R}_+^3$  are bounded below by zero. Now, define

$$S(t) = e_{CP}e_{RC}R + e_{CP}C + P.$$

Taking the time derivative along a solution of the system we have the following inequality fulfilled for each  $\lambda > 0$ :

$$\begin{aligned} \dot{S}(t) + \lambda S(t) &= (e_{CP}e_{RC}r + e_{CP}e_{RC}\lambda)R - \left( \frac{e_{CP}e_{RC}r}{K} \right)R^2 \\ &+ (e_{CR} - e_{CP}e_{RC}) \left( \frac{\lambda_{RP}}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \right)RP \\ &+ (\lambda e_{CP} - e_{CP}m_C)C + (\lambda - m_P)P \\ &\leq (e_{CP}e_{RC}r + e_{CP}e_{RC}\lambda)R - \left( \frac{e_{CP}e_{RC}r}{K} \right)R^2 \end{aligned}$$

since  $e_{RP} < e_{CP}e_{RC}$  and we choose  $\lambda < \min \{m_C, m_P\}$ .

Because the right hand side is a parabola that opens downward, it is bounded for all  $(P, C, R) \in \mathbb{R}_+^3$ . Specifically, the right hand side is bounded by  $M_1$ . Thus, we find an  $M_1 > 0$  with  $\dot{S}(t) + \lambda S(t) \leq M_1$ . Applying Lemma 1 Part B, we obtain

$$0 \leq S \leq \frac{M_1}{\lambda} + \left( S(P(0), C(0), P(0)) - \frac{M_1}{\lambda} \right) e^{-\lambda t}$$

and as  $t \rightarrow \infty$ ,  $0 \leq e_{CP}e_{RC}R + e_{CP}C + P \leq M_1 / \lambda$ .

Now let  $M_2$  be defined as above, then

$$0 \leq P + C + R \leq M_2.$$

Thus, there is a compact neighborhood  $B \in \mathbb{R}_+^3$  such that for sufficiently large  $T = T(c_1, c_2, c_3)$ ,  $(P(t), C(t), R(t))$  is in B for all  $t \geq T$ , where  $(P(t), C(t), R(t))$  is a solution to (1) that initiates in  $\mathbb{R}_+^3$ . This completes the proof.

Since we have global existence and uniqueness of a solution,  $\mathbb{R}_+^3$  and the compact set B from Theorem 3 are invariant. Now define the set  $S = B \cap \partial\mathbb{R}_+^3$ .

**Lemma 2:** The sets S and B - S are invariant.

*Proof:* Assume that  $\mathbf{x}_0 \in S$  and  $\mathbf{x}(t)$  is a solution of (1) with  $\mathbf{x}(t_0) = \mathbf{x}_0$ . Since B and  $\partial\mathbb{R}_+^3$  are invariant, then  $\mathbf{x}(t) \in B$  and  $\mathbf{x}(t) \in \partial\mathbb{R}_+^3$  for all  $t > t_0$ . Thus,  $S = B \cap \partial\mathbb{R}_+^3$  is invariant.

Now assume that  $\mathbf{x}_0 \in B - S$  and  $\mathbf{x}(t)$  is a solution of (1) with  $\mathbf{x}(t_0) = \mathbf{x}_0$ . Since S and B are invariant we have global existence and uniqueness of solutions, then  $\mathbf{x}(t) \in B$  and  $\mathbf{x}(t) \notin S$  for all  $t > t_0$ . Hence, B - S is invariant, completing the proof.

Now we show that the  $\Omega$ -limit set of every orbit in  $\partial\mathbb{R}_+^3$  is an equilibrium point. The zero equilibrium is unstable due to the fact that r and K are positive. Also, it is well known that solutions to the logistic equation quickly reach the fixed carrying capacity K [18]. However, for the predator-prey subsystems, there may be periodic orbits.

We use a lemma from Hsu [19] which is based on an application of the Poincaré-Bendixson Theorem and the Dulac Criterion [20] to show that a positive stable equilibrium of a predator-prey system is globally stable, thus eliminating the possibility of periodic orbits. Consider the predator-prey model

$$\begin{aligned} \frac{dx}{dt} &= xg(x) - yp(x) \\ \frac{dy}{dt} &= y[e_{xy}p(x) - m_y] \end{aligned} \tag{14}$$

where y represents the predator density and x represents the prey density and

$$\begin{aligned} g(x) &= r \left( 1 - \frac{x}{K} \right) \\ p(x) &= \frac{\lambda_{xy}x}{1+x} \end{aligned}$$

To investigate global stability, we compute the variational matrix evaluated at the positive equilibrium  $(x^*, y^*)$ ,

$$H(x^*) = x^* g'(x^*) + g(x^*) - \frac{x^* g(x^*) p'(x^*)}{p(x^*)}.$$

Then the equilibrium is (locally) asymptotically stable if  $H(x^*) \leq 0$  [19]. Graphically, this means that if the prey isoline  $y = \frac{xg(x)}{p(x)}$  is decreasing at  $x^*$ , then  $(x^*, y^*)$  is asymptotically stable. To give conditions under which local stability of  $(x^*, y^*)$  implies global stability of  $(x^*, y^*)$  we give the following Lemma without proof from Hsu [19].

**Lemma 3:** Assume the equilibrium  $(x^*, y^*)$  of (14) is stable

and  $\frac{d^2}{dx^2} \left( \frac{xg(x)}{p(x)} \right) < 0, 0 \leq x \leq K$ . Then  $(x^*, y^*)$  is globally stable.

So we prove the following lemma on the  $\Omega$ -limit set of every orbit in  $\partial\mathbb{R}_+^3$ .

**Lemma 4:** Let the conditions of Lemma 3 hold for the two equilibria  $(\bar{C}, \bar{R})$  and  $(\bar{P}, \bar{R})$  of the appropriate subsystems of (1), that is

$$H(\bar{R}) = \frac{rm_C(\lambda_{RC}(K-1)\xi_1 - 2m_C)}{\lambda_{RC}K\xi_1(m_C + \lambda_{RC}\xi_1)} \leq 0 \tag{15}$$

$$\frac{d^2}{dx^2} \left( \frac{xg(x)}{p(x)} \right) = -\frac{2r}{\lambda_{RC}K} < 0$$

and

$$H(\bar{R}) = \frac{rm_P(\lambda_{RP}(K-1)\xi_2 - 2m_P)}{\lambda_{RP}K\xi_2(m_P + \lambda_{RP}\xi_2)} \leq 0 \tag{16}$$

$$\frac{d^2}{dx^2} \left( \frac{xg(x)}{p(x)} \right) = -\frac{2r}{\lambda_{RP}K} < 0$$

respectively, where

$$\begin{aligned} \xi_1 &= e_{RC} - m_C h_{RC} \\ \xi_2 &= e_{RP} - m_P h_{RP}. \end{aligned}$$

Then for the system (1), the  $\Omega$ -limit set of every orbit in  $\partial\mathbb{R}_+^3$  is an equilibrium point.

*Proof:* From the above comments, we see that the  $\Omega$ -limit set of every orbit on each axis is an equilibrium point. Since the above conditions hold, each stable equilibrium in the bounding hyperplanes is globally stable. That is, the  $\Omega$ -limit set of every orbit in each bounding hyperplane is an equilibrium point. This completes the proof.

Notice that conditions on the curvature are trivially satisfied for our system (1) because we assume  $r, K, \lambda_{RC}, \lambda_{RP} > 0$ .

Now, we use Theorem 2 to determine conditions that guarantee permanent coexistence of the system (1).

**Theorem 4:** Assume that the following conditions hold:

- (H1) The solutions of (1) in  $\mathbb{R}_+^3$  are uniformly bounded.
- (H2) The  $\Omega$ -limit set of every orbit on  $\partial\mathbb{R}_+^3$  consists of equilibrium points.
- (H3) No boundary equilibrium is saturated.

Then the system (1) is permanently coexistent. The conditions for no saturated boundary equilibria are:

- 1) a, b, b', c and d hold **or**
- 2) a, b, and d hold, but not b' **or**
- 3) a, b', and c hold, but not b

where

$$a) r > 0 \tag{17}$$

$$b) \frac{e_{RP}\lambda_{RP}K}{1 + \lambda_{RP}h_{RP}K} - m_P > 0 \tag{18}$$

$$b') \frac{e_{RC}\lambda_{RC}K}{1 + \lambda_{RC}h_{RC}K} - m_C > 0 \tag{19}$$

$$c) \frac{\lambda_{RC}K\xi_1(\lambda_{RP}e_{RP}m_C + \lambda_{CP}e_{CP}e_{RC}r)}{K(\lambda_{RC})^2\xi_1^2 - \lambda_{CP}e_{RC}h_{CP}m_Cr + \lambda_{RC}K\xi_1\nu} \tag{20}$$

$$\begin{aligned} & - \frac{\lambda_{CP}e_{CP}e_{RC}m_Cr}{K(\lambda_{RC})^2\xi_1^2 - \lambda_{CP}e_{RC}h_{CP}m_Cr + \lambda_{RC}K\xi_1\nu} - m_P > 0 \\ d) & \frac{\lambda_{RC}e_{RC}m_P}{\lambda_{RP}e_{RP} + \lambda_{RC}h_{RC}m_P - \lambda_{RP}h_{RP}m_P} \\ & \frac{r\lambda_{CP}(\lambda_{RP}h_{RP}Km_P + m_P + \lambda_{RP}e_{RP}K)}{K(\lambda_{RP})^2\xi_2^2} - m_C > 0 \end{aligned} \tag{21}$$

and

$$\begin{aligned} \xi_1 &= e_{RC} - m_C h_{RC} \\ \xi_2 &= e_{RP} - m_P h_{RP} \\ \xi_3 &= e_{CP} - m_P h_{CP} \\ \nu &= \lambda_{RP}h_{RP}m_C + r\lambda_{CP}h_{CP}e_{RC}. \end{aligned}$$

*Proof:* We break the proof up into two parts. In Part I, we find the equilibria of system (1). For Part II, we use Theorem 2 to show permanence.

Part I: From the form of the equations in (1), we see that  $\mathbf{F}_0 = (0, 0, 0)^T$  is a boundary equilibrium point in  $\mathbb{R}_+^3$ . The only possible one species equilibrium is  $\mathbf{F}_R = (0, 0, K)^T$ . The two species equilibria involve the resource and consumer,  $\mathbf{F}_{RC}$ , and the resource and predator,  $\mathbf{F}_{RP}$ :

$$\mathbf{F}_{RC} = \left( 0, \frac{re_{RC}(K\lambda_{RC}\xi_1 - m_C)}{K(\lambda_{RC})^2\xi_1^2}, \frac{m_C}{\lambda_{RC}\xi_1} \right)^T = (0, \bar{C}, \bar{R}_C)^T$$

$$\mathbf{F}_{RP} = \left( \frac{re_{RP}(K\lambda_{RP}\xi_2 - m_P)}{K(\lambda_{RP})^2\xi_2^2}, 0, \frac{m_P}{\lambda_{RP}\xi_2} \right)^T = (\bar{P}, 0, \bar{R}_P)^T$$

with the understood definitions of  $\bar{P}, \bar{C}, \bar{R}_P$ , and  $\bar{R}_C$ .

The equilibrium with the resource absent is never positive and thus does not exist. Notice that boundary equilibrium  $\mathbf{F}_{RC}$  exists in  $\mathbb{R}_+^3$  if and only if b' holds. This is due to the fact that

$$\begin{aligned} & \frac{e_{RC}\lambda_{RC}K}{1 + \lambda_{RC}h_{RC}K} - m_C > 0 \\ \Rightarrow & e_{RC} > m_C \left( h_{RC} + \frac{1}{K\lambda_{RC}} \right) > m_C h_{RC}. \end{aligned}$$

Similarly, boundary equilibrium  $\mathbf{F}_{RP}$  exists in  $\mathbb{R}_+^3$  if and only if b holds.

Part II: Let  $\mathbf{x}(t) = (P(t), C(t), R(t))^T$  and

$$P(\mathbf{x}) = x_1^{p_1} x_2^{p_2} x_3^{p_3} (x_1 + x_2)^e. \tag{22}$$

Clearly,  $P(\mathbf{x}) = 0$  for  $\mathbf{x} \in \partial\mathbb{R}_+^3$  and  $P(\mathbf{x}) > 0$  for  $\mathbf{x} \in \text{int}(\mathbb{R}_+^3)$ . Also,

$$\begin{aligned} \dot{P}(\mathbf{x}) &= p_1 x_1^{p_1-1} \dot{x}_1 (x_2^{p_2} x_3^{p_3} (x_1 + x_2)^\varepsilon) \\ &+ x_1^{p_1} (p_2 x_2^{p_2-1} \dot{x}_2 x_3^{p_3} (x_1 + x_2)^\varepsilon) \\ &+ x_2^{p_2} (p_3 x_3^{p_3-1} \dot{x}_3 (x_1 + x_2)^\varepsilon) \\ &+ x_3^{p_3} \varepsilon (x_1 + x_2)^{\varepsilon-1} (\dot{x}_1 + \dot{x}_2)) \\ &= x_1^{p_1} x_2^{p_2} x_3^{p_3} (x_1 + x_2)^\varepsilon (p_1 f_1(\mathbf{x}) + p_2 f_2(\mathbf{x}) \\ &+ p_3 f_3(\mathbf{x}) + \varepsilon \left( \frac{x_1 f_1(\mathbf{x}) + x_2 f_2(\mathbf{x})}{x_1 + x_2} \right)) = P(\mathbf{x}) \Psi(\mathbf{x}) \end{aligned}$$

where

$$\Psi(\mathbf{x}) = \sum_{i=1}^3 p_i f_i(\mathbf{x}) + \varepsilon \left( \frac{x_1 f_1(\mathbf{x}) + x_2 f_2(\mathbf{x})}{x_1 + x_2} \right) \quad (23)$$

in  $\text{int}(\mathbb{R}_+^3)$ .

However, the last term in  $\Psi$  does not admit a continuous extension to the  $x_3$ -axis. To correct this, we take the lower semicontinuous extension and the last term in (23) becomes

$$\Psi(0, 0, x_3) = \varepsilon \min(f_1(0, 0, x_3), f_2(0, 0, x_3)).$$

By (H2), condition (13) reduces to

$$\Psi(\mathbf{x}) > 0 \quad (24)$$

for all equilibrium points in  $\partial\mathbb{R}_+^3$  for a suitable choice of  $\varepsilon \geq 0, p_1, p_2, p_3 > 0$ . For  $\mathbf{F}_{RC}$  and  $\mathbf{F}_{RP}$ , (24) becomes,

$$\begin{aligned} p_1 f_1(0, \bar{C}, \bar{R}_C) &> 0 \\ p_2 f_2(\bar{P}, 0, \bar{R}_P) &> 0 \end{aligned} \quad (25)$$

respectively. But, we assumed that no boundary equilibria are saturated. That is  $f_1(\mathbf{F}_{RC})$  equals condition c) and  $f_2(\mathbf{F}_{RP})$  equals condition d). Thus, we have that (25) holds for any  $p_1, p_2 > 0$ .

At  $\mathbf{F}_0$  and  $\mathbf{F}_R$ , (25) yields:

$$\begin{aligned} 0 < p_1 f_1(\mathbf{0}) + p_2 f_2(\mathbf{0}) \\ + p_3 f_3(\mathbf{0}) + \varepsilon \min(f_1(\mathbf{0}), f_2(\mathbf{0})) \end{aligned} \quad (26)$$

$$\begin{aligned} 0 < p_1 f_1(0, 0, K) + p_2 f_2(0, 0, K) + p_3 f_3(0, 0, K) \\ + \varepsilon \min(f_1(0, 0, K), f_2(0, 0, K)). \end{aligned} \quad (27)$$

Since  $r > 0$  we have that  $\mathbf{F}_0$  is not saturated. In order for  $\mathbf{F}_R$  not to be saturated, we need either  $f_1(0, 0, K)$  equal to condition b) or  $f_2(0, 0, K)$  equal to condition b') or both, since  $\bar{P} = \bar{C} = 0$ . So in either case, we can first choose  $p_1 > 0, p_2 > 0$ , and  $\varepsilon = 0$  such that (27) holds. Since  $f_3(\mathbf{0}) > 0$ , then for large  $p_3$ , (24) holds too. Hence, by Theorem 2 the system (1) is permanent.

## VI. BIOLOGICAL INTERPRETATIONS

In this section we will provide interpretations for what the parameter restrictions mean biologically. It has been shown by

Křivan and Diehl [5] that the consumer must be the superior competitor for the shared resource for an IGP model with Type II functional responses.

The following analysis is similar to that done in [5]. Theorem 3 requires that  $e_{RP} < e_{CP} e_{RC}$ . That is, the consumer provides a high benefit to the predator, relative to the basal resource and thus, the predator gains significantly from its consumption of the consumer.

Conditions b) and b') can be rewritten as

$$\frac{e_{RP}}{h_{RP}} > m_P \left( 1 + \frac{h_{RP}}{\lambda_{RP} K} \right) > m_P \quad (28)$$

and

$$\frac{e_{RC}}{h_{RC}} > m_C \left( 1 + \frac{h_{RC}}{\lambda_{RC} K} \right) > m_C \quad (29)$$

respectively. Condition (28) states that the profitability of resources for predators (the energy return per handling time) must exceed predator mortality by a sufficient amount. Similarly, (29) states that the profitability of resources for consumers must exceed consumer mortality by a sufficient amount. Also, we see that  $\xi_1 > 0$  and  $\xi_2 > 0$ .

Equation (15) and (16) can be rewritten as

$$\frac{e_{RC}}{h_{RC}} < m_C \left( 1 + \frac{2h_{RC}}{\lambda_{RC}(K-1)} \right)$$

and

$$\frac{e_{RP}}{h_{RP}} < m_P \left( 1 + \frac{2h_{RP}}{\lambda_{RP}(K-1)} \right)$$

respectively. That is, the profitability of resources for consumer must not be too high. Otherwise, the predator is driven to extinction. Similarly, the profitability of resources for predators must not be too high, so that the consumer is not driven to extinction.

Solving for K in (15) and (16) yields

$$K \leq \frac{2m_C}{\lambda_{RC}\xi_1}, K \leq \frac{2m_P}{\lambda_{RP}\xi_2}.$$

Since,  $\xi_1, \xi_2 > 0$ , these conditions state that there must be an upper bound on K for coexistence of species.

In conclusion, we have the following:

- B1) The predator should gain significantly from its consumption of the consumer.
- B2) The consumer should be superior at exploitative competition for the shared resource.
- B3) Along gradients in resource productivity, coexistence is most likely at intermediate levels of productivity.

## VII. CONCLUSION

In this paper we have analyzed the conditions under which our IGP model with Type II responses is permanent, or in a realistic biological sense, the coexistence of species is ensured. In summary, permanence requires that the solutions of system (1) are uniformly bounded in  $\mathbb{R}_+^3$ , the  $\Omega$ -limit set

of every orbit on  $\partial\mathbb{R}_+^3$  consists of equilibrium points, and no boundary equilibrium can be saturated. Biologically, these conditions imply that the predator should gain significantly from its consumption of the consumer, the consumer should be superior at exploitative competition for the shared resource, and along gradients in resource productivity, coexistence is most likely at intermediate levels of productivity.

The permanence of models with migration dynamics, symmetrical interactions, and additional species is still an open question. One limiting factor is that most available theory assumes that the boundary of the state space is invariant. Therefore, it would be useful to investigate these more complicated models and provide the theory to analyze the permanence of these models.

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