THE DYNAMICS OF THE SCHOENER-POLIS-HOLT MODEL OF INTRA-GUILD PREDATION

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ABSTRACT. Intraguild predation occurs when one species (the intraguild predator) predates on and competes with another species (the intraguild prey). A classic model of this interaction was introduced by Gary Polis and Robert Holt building on a model of competing species by Thomas Schoener. A global analysis reveals that this model exhibits generically six dynamics: extinction of one or both species; coexistence about a globally stable equilibrium; contingent exclusion in which the first established species prevents the establishment of the other species; contingent coexistence in which coexistence or displacement of the intraguild prey depend on initial conditions; exclusion of the intraguild prey; and exclusion of the intraguild predator. Implications for biological control and community ecology are discussed.

1. **Introduction.** Intraguild predation occurs when one species (the intraguild predator) preys on and competes for limiting resources with another species (the intraguild prey). This mixture of predation and competition is observed in a diversity of freshwater, marine, and terrestrial food webs [2, 3]. For example, in freshwater streams, bluegills and insects compete for plankton, and bluegills prey on insects. In deserts, spiders and scorpions compete for insects and prey on one another. In [3, 2], which coined the phrase "intraguild predation," Gary Polis and Robert Holt modeled intraguild predation by modifying a model of competition by Thomas Schoener [5]. If N_1 is the density of the intraguild prey and N_2 is the density of the intraguild predator, then this model is given by

$$\frac{dN_1}{dt} = a_1 b_1 R(N_1, N_2) N_1 - \alpha N_1 N_2 - c_1 N_1 =: F_1(N_1, N_2) \tag{1}$$

$$\frac{dN_2}{dt} = a_2 b_2 R(N_1, N_2) N_2 + \alpha \beta N_1 N_2 - c_2 N_2 =: F_2(N_1, N_2)$$

$$R(N_1, N_2) = \frac{S}{a_1 N_1 + a_2 N_2}$$

where $a_i > 0$ is the rate at which a species finds the resource, $b_1 > 0$ (respectively b_2) is the efficiency at which the intraguild prey (resp. intraguild predator) convert the basal resource into intraguild prey (resp. intraguild predators), $c_i > 0$ is the per-capita death rate, $\alpha > 0$ is the rate at which the intraguild predator encounters the intraguild prey, $\beta > 0$ is the efficiency at which the consumed intraguild prey is converted into intraguild predators, and

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$S > 0$ is the rate at which the resource enters the system. In the absence of intraguild predation (i.e., $\alpha = \beta = 0$), Schoener [5] showed that (generically) one species competitively excluded the other. Holt and Polis [1, 3] illustrated that the inclusion of intraguild predation (i.e., $\alpha > 0$ and $\beta > 0$) could mediate coexistence between the two species, reverse competitive dominance, and generate alternative stable states. In this article, we provide a complete mathematical analysis of a generalization of this model.

An unfortunate feature of the original Schoener model is that the "resource function" $R(N_1, N_2) = \frac{S}{a_1 N_1 + a_2 N_2}$ is not defined at the origin. A modified version of this resource function was presented by Schoener in 1978 and is given by $R(N_1, N_2) = \frac{S}{\gamma + a_1 N_1 + a_2 N_2}$ where γ is the natural "decay rate" of the resource [6]. This resource function has a simple mechanistic interpretation, as it corresponds to the quasi steady state of the equation

$$\frac{dR}{dt} = S - \gamma R - a_1 R N_1 - a_2 R N_2.$$

In this article, we study the dynamics of

$$\begin{aligned}
\frac{dN_1}{dt} &= a_1 b_1 R(N_1, N_2) N_1 - \alpha N_1 N_2 - c_1 N_1 =: F_1(N_1, N_2) \qquad (2)\\
\frac{dN_2}{dt} &= a_2 b_2 R(N_1, N_2) N_2 + \alpha \beta N_1 N_2 - c_2 N_2 =: F_2(N_1, N_2)\\
R(N_1, N_2) &= \frac{S}{\gamma + a_1 N_1 + a_2 N_2}
\end{aligned}$$

under the assumption that $\gamma > 0$. The remainder of the article is structured as follows. In section 2, we state and illustrate our main results. In sections 3 and 4, we prove our main results. In section 5, we discuss the implications of these results for biological control and the structure of ecological communities.

2. **Main results.** To ensure that (2) has solutions defined for all forward time, we begin with a proposition that ensures that all solutions to (2) enter a compact subset of the nonnegative quadrant.

PROPOSITION 2.1. *Let $(N_1(t), N_2(t))$ be a solution to (2) with $N_i(0) \geq 0$ for $i = 1, 2$. Then*

$$\limsup_{t \to \infty} \beta N_1(t) + N_2(t) \leq \frac{S(b_1 \beta + b_2)}{\min\{c_1, c_2\}}.$$

Proof. Let $(N_1(t), N_2(t))$ be a solution to (2) with $N_i(0) \geq 0$ for $i = 1, 2$. Define $Q(t) = \beta N_1(t) + N_2(t)$. Since

$$\frac{S(a_1 b_1 \beta N_1 + a_2 b_2 N_2)}{\gamma + a_1 N_1 + a_2 N_2} \leq \frac{S(a_1 b_1 \beta N_1)}{a_1 N_1} + \frac{S(a_2 b_2 N_2)}{a_2 N_2} \leq S(b_1 \beta + b_2)$$

we get

$$\begin{aligned}
\frac{dQ}{dt} &= R(N_1, N_2)(a_1 b_1 \beta N_1 + a_2 b_2 N_2) - c_1 \beta N_1 - c_2 N_2\\
&\leq S(b_1 \beta + b_2) - \delta(\beta N_1 + N_2)\\
&\leq S(b_1 \beta + b_2) - \delta Q
\end{aligned}$$

where $\delta = min\{c_1, c_2\}$. It follows that $\limsup_{t \to \infty} Q(t) \leq \frac{S(b_1 \beta + b_2)}{\delta}$.

$\square$

Equation (2) always has the equilibrium $(0,0)$. The per-capita growth rate of species i at $(0,0)$ is $\frac{a_i b_i S}{\gamma} - c_i$. When $\frac{a_i b_i S}{\gamma} - c_i > 0$, there is a positive equilibrium on the N_i axis given by $N_i = \frac{b_i S}{c_i} - \frac{\gamma}{a_i}$ at which the resource level is $R = \frac{c_i}{a_i b_i}$. The missing species can invade at these boundary equilibria if its per-capita growth rate at this equilibrium is positive. The per-capita growth rate of the intraguild prey at the intraguild predator equilibrium $(0, \frac{b_2 S}{c_2} - \frac{\gamma}{a_2})$ is given by

$$\Gamma_1 = \frac{c_2^2 b_1 a_1 - c_1 b_2 a_2 c_2 - \alpha b_2^2 S a_2 + \alpha b_2 c_2 \gamma}{b_2 a_2 c_2}.$$

The per-capita growth rate of the intraguild predator at the intraguild prey equilibrium $(\frac{b_1 S}{c_1} - \frac{\gamma}{a_1}, 0)$ is given by

$$\Gamma_2 = \frac{c_1^2 b_2 a_2 - c_2 b_1 a_1 c_1 + \beta \alpha b_1^2 S a_1 - \beta \alpha b_1 c_1 \gamma}{b_1 a_1 c_1}.$$

The following theorem characterizes the behaviors of (2) when both species can invade the origin. The conclusions of this theorem are illustrated in Fig. 1. The proof is given in section 3.

THEOREM 2.1. *Assume $\frac{a_i b_i S}{\gamma} > c_i$, $a_i > 0$, $b_i > 0$, $c_i > 0$, for i =1,2, $\alpha \geq 0$; $\beta \geq 0$; and $\gamma > 0$. Define Γ_i for i = 1,2 as above, and define*

$$
\begin{aligned}
A_1 &= -c_1 a_2 b_2 \beta - a_1 c_2 b_2 + 2a_1 b_1 c_2 \beta + \alpha \beta \gamma b_2 \\
A_2 &= 2c_1 a_2 b_2 - c_1 a_2 b_1 \beta - b_1 \alpha \beta \gamma - a_1 b_1 c_2 \\
B_1 &= 4a_1 \beta a_2 b_2 c_2 \Gamma_1 (-b_2 + b_1 \beta).
\end{aligned}
$$

Then (2) exhibits five types of dynamics:

1. **Global coexistence.** *If $\Gamma_1 > 0$ and $\Gamma_2 > 0$, then there exists a unique equilibrium $(\widehat{N_1}, \widehat{N_2})$ in the positive quadrant, and $\lim_{t \to \infty}(N_1(t), N_2(t)) = (\widehat{N_1}, \widehat{N_2})$ for every solution satisfying $N_1(0) > 0$ and $N_2(0) > 0$.*

2. **Contingent exclusion.** *If $\Gamma_1 < 0$ and $\Gamma_2 < 0$ then there exists a unique equilibrium $(\widehat{N_1}, \widehat{N_2})$ in the positive quadrant with a one dimensional stable manifold S that separates the positive orthant into two connected components. For every solution with $(N_1(0), N_2(0))$ lying below S, we have that $\lim_{t \to \infty}(N_1(t), N_2(t)) = (\frac{b_1 S}{c_1} - \frac{\gamma}{a_1}, 0)$. For every solution with $(N_1(0), N_2(0))$ lying above S, we have that $\lim_{t \to \infty}(N_1(t), N_2(t)) = (0, \frac{b_2 S}{c_2} - \frac{\gamma}{a_2})$.*

3. **Intraguild predator displacement.** *If $\Gamma_1 > 0$ and $\Gamma_2 < 0$, then $\lim_{t \to \infty}(N_1(t), N_2(t)) = (\frac{b_1 S}{c_1} - \frac{\gamma}{a_1}, 0)$ for every solution with $N_1(0) > 0$ and $N_2(0) \geq 0$.*

4. **Intraguild prey displacement.** *If $\Gamma_1 < 0$ and $\Gamma_2 > 0$, and either $b_2 \leq b_1 \beta$ or $A_1 > 0$ or $A_2 > 0$ or $A_1^2 < B_1$, then $\lim_{t \to \infty}(N_1(t), N_2(t)) = (0, \frac{b_2 S}{c_2} - \frac{\gamma}{a_2})$ for every solution with $N_1(0) \geq 0$ and $N_2(0) > 0$.*

5. **Contingent coexistence.** *If $\Gamma_1 < 0$, $\Gamma_2 > 0$, $b_2 > b_1 \beta$, $A_i < 0$ for $i = 1,2$, and $A_1^2 > B_1$, then there exist two positive equilibria (N_1^+, N_2^+) and (N_1^-, N_2^-) with $N_2^- < N_2^+$. (N_1^+, N_2^+) is a saddle with a one-dimensional stable manifold S that separates the positive orthant into an upper and lower region. Moreover, $\lim_{t \to \infty}(N_1(t), N_2(t)) = (N_1^-, N_2^-)$ for every solution with $(N_1(0), N_2(0)) > (0,0)$ lying below S, and $\lim_{t \to \infty}(N_1(t), N_2(t)) = (0, \frac{b_2 S}{c_2} - \frac{\gamma}{a_2})$ for every solution with $(N_1(0), N_2(0)) > (0,0)$ lying above S.*
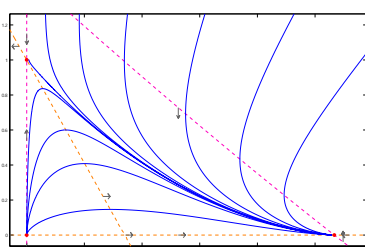
The following proposition characterizes the behavior of (2) when one of the species can not invade the origin. The proof is given in section 4.
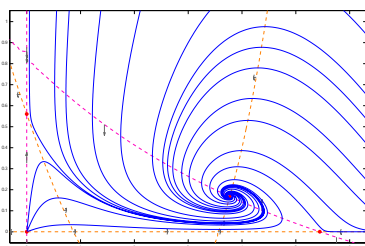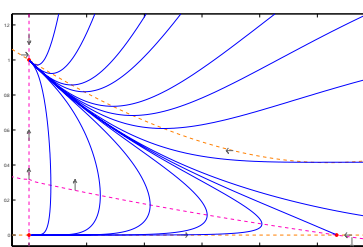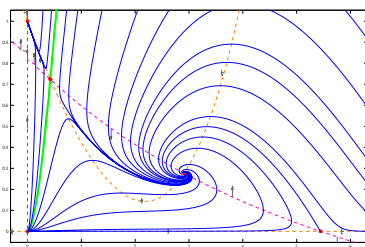
1. Global coexistence
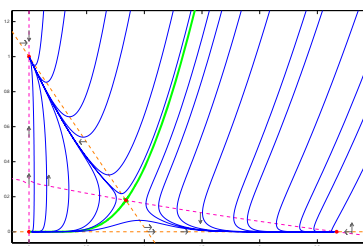
2. Contingent exclusion

3. Intraguild predator displacement

4. Intraguild prey displacement

5. Contingent coexistence

FIGURE 1. The phase portraits in the N_1–N_2 plane corresponding to the conclusions of Theorem 2.1. Solutions (in blue) are plotted along with the nullclines (in red/yellow). In the case of bistability and contingent coexistence, the separatrix of the positive saddle is shown in green.

PROPOSITION 2.2. *Define Γ_2 as above.*

1. **Intraguild prey failure.** *If $\frac{a_1 b_1 S}{\gamma} < c_1$, then $\lim_{t \to \infty} N_1(t) = 0$ for any solution $(N_1(t), N_2(t))$ of (2) with $N_1(0) \geq 0$ and $N_2(0) \geq 0$.*

2. **Intraguild predator failure.** *If $\frac{a_2 b_2 S}{\gamma} < c_2$ and either $\frac{a_1 b_1 S}{\gamma} < c_1$ or $\frac{a_1 b_1 S}{\gamma} > c_2$ with $\Gamma_2 < 0$, then $\lim_{t \to \infty} N_2(t) = 0$ for any solution $(N_1(t), N_2(t))$ of (2) with $N_1(0) \geq 0$ and $N_2(0) \geq 0$.*

3. **Global coexistence.** *If $\frac{a_2 b_2 S}{\gamma} < c_2$, $\frac{a_1 b_1 S}{\gamma} > c_1$ and $\Gamma_2 > 0$, then there exists a unique equilibrium $(\widehat{N}_1, \widehat{N}_2)$ in the positive quadrant, and $\lim_{t \to \infty}(N_1(t), N_2(t)) = (\widehat{N}_1, \widehat{N}_2)$ for every solution satisfying $N_1(0) > 0$ and $N_2(0) > 0$.*

3. **Proof of Theorem 2.1.** Assume that $\frac{a_i b_i S}{\gamma} > c_i$ for $i = 1, 2$. We begin by proving that there are no periodic solutions or heteroclinic loops in the positive quadrant for (2). Recall that the Dulac criterion states that if there exists a positive continuously differentiable real-valued function $\Psi(N_1, N_2)$ on the positive quadrant such that $\frac{\partial \Psi F_1}{\partial N_1} + \frac{\partial \Psi F_2}{\partial N_2} < 0$ in the positive quadrant, then there are no closed orbits or heteroclinic loops in the positive quadrant. Choosing $\Psi(N_1, N_2) = \frac{1}{N_1 N_2}$ yields the desired result. Since (as we shall shortly prove) equation (2) generically has only a finite number of equilibria, Poincaré-Bendixson theory implies that generically every solution $(N_1(t), N_2(t))$ of (2) with $N_i(0) \geq 0$ for $i = 1, 2$ converges to an equilibrium.
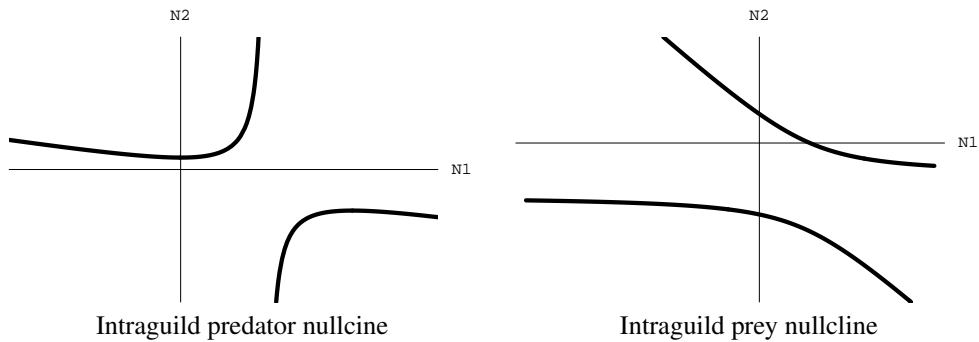

FIGURE 2. Non-trivial nullclines for (2)

To understand the equilibria of (2), we examine the nullclines. The equations, $\frac{dN_i}{dt} = 0$, have a pair of solutions. For each species, one of its nullclines exists on the opposing axis. For example, one nullcline for the prey is the N_2 axis . The nontrivial nullcline for the intraguild predator is the curve

$$N_2 = \frac{b_2 S}{c_2 - \alpha \beta N_1} - \frac{\gamma}{a_2} - \frac{a_1}{a_2} N_1. \tag{3}$$

This intraguild predator nullcline is a hyperbola with a vertical asymptote at $N_2 = \frac{c_2}{\alpha \beta}$ and an oblique asymptote along the line $N_2 = -\frac{\gamma}{a_2} - \frac{a_1}{a_2} N_1$. Since $\frac{b_2 S}{c_2} - \frac{\gamma}{a_2} > 0$, the N_2 intercept of this nullcline is positive. Consequently, the graph of (3) does not intersect the negative quadrant (see Figure 2), and no equilibria can reside in this quadrant. Similarly, the nontrivial intraguild prey nullcline is the curve

$$N_1 = \frac{b_1 S}{c_1 + \alpha N_2} - \frac{\gamma}{a_1} - \frac{a_2}{a_1} N_2. \tag{4}$$

This intraguild prey nullcline has the same oblique asymptote $N_2 = -\frac{\gamma}{a_2} - \frac{a_1}{a_2} N_1$ as the oblique asymptote of (3). It also has a horizonal asymptote at $N_2 = -\frac{c_1}{\alpha}$. Moreover, both components of this intraguild prey nullcline are strictly decreasing as functions of N_1 (see Figure 2).

In addition to the three equilibria on the axes, we can solve the nontrivial nullcline equations (3) and (4) for N_1 and N_2. If $b_2 \neq b_1 \beta$, then this yields the two additional possibilities

for equilibria

$$(N_1^+, N_2^+) = \left(\frac{A_1 - \sqrt{A_1^2 - B_1}}{C_1}, \frac{A_2 + \sqrt{A_2^2 - B_2}}{C_2} \right)$$

$$(N_1^-, N_2^-) = \left(\frac{A_1 + \sqrt{A_1^2 - B_1}}{C_1}, \frac{A_2 - \sqrt{A_2^2 - B_2}}{C_2} \right)$$

where

$$
\begin{aligned}
A_1 &= -c_1 a_2 b_2 \beta - a_1 c_2 b_2 + 2a_1 b_1 c_2 \beta + \alpha \beta \gamma b_2 \\
A_2 &= 2c_1 a_2 b_2 - c_1 a_2 b_1 \beta - b_1 \alpha \beta \gamma - a_1 b_1 c_2 \\
B_1 &= 4a_1 \beta a_2 b_2 c_2 \Gamma_1 (-b_2 + b_1 \beta) \\
B_2 &= 4a_1 b_1 c_1 a_2 \Gamma_2 (b_2 - b_1 \beta) \\
C_1 &= 2a_1 \alpha \beta (-b_2 + b_1 \beta) \\
C_2 &= 2a_2 \alpha (-b_2 + b_1 \beta).
\end{aligned}
$$

We will use the fact that

$$A_i^2 - B_i = b_j^2 \left(D^2 + 4a_1 a_2 S \beta \alpha (-b_2 + b_1 \beta) \right) \text{ where } D = \gamma \alpha \beta - c_1 \beta a_2 + a_1 c_2 \quad (5)$$

for $i, j = 1, 2$ with $i \neq j$. Alternatively, when $b_2 = b_1 \beta$ and $A_i \neq 0$ for $i = 1, 2$, solving (3) and (4) yields

$$(N_1^*, N_2^*) = \left(\frac{a_2 b_2 c_2 \Gamma_1}{\alpha A_1}, -\frac{a_1 b_1 c_1 \Gamma_2}{\alpha A_2} \right).$$

Since $A_2 = -A_1/\beta$ when $b_2 = b_1 \beta$, we have

$$(N_1^*, N_2^*) = \left(\frac{a_2 b_2 c_2 \Gamma_1}{\alpha A_1}, \frac{a_1 b_1 c_1 \beta \Gamma_2}{\alpha A_1} \right). \quad (6)$$

Finally if $b_2 = b_1 \beta$ and $A_i = 0$ for $i = 1$ or 2, there is no solution to (3) and (4).

Let $(\widehat{N_1}, \widehat{N_2})$ be an equilibrium with $\widehat{N_1} > 0$ and $\widehat{N_2} > 0$. This can occur only if $\alpha > 0$ and $\beta > 0$. Linearizing the right-hand side of (2) about $(\widehat{N_1}, \widehat{N_2})$ yields

$$J = \begin{pmatrix} -\frac{\widehat{N_1} a_1^2 b_1 S}{(\gamma + a_1 \widehat{N_1} + a_2 \widehat{N_2})^2} & -\frac{\widehat{N_1} a_1 a_2 b_1 S}{(\gamma + a_1 \widehat{N_1} + a_2 \widehat{N_2})^2} - \alpha \widehat{N_1} \\ -\frac{\widehat{N_2} a_1 a_2 b_2 S}{(\gamma + a_1 \widehat{N_1} + a_2 \widehat{N_2})^2} + \alpha \beta \widehat{N_2} & -\frac{\widehat{N_2} a_2^2 b_2 S}{(\gamma + a_1 \widehat{N_1} + a_2 \widehat{N_2})^2} \end{pmatrix}.$$

The trace of J is negative. Moreover, we claim that $\det J = 0$ if and only if $A_i^2 = B_i$ and $b_2 \neq b_1 \beta$. Indeed, the determinant of J is given by

$$\det J = \alpha \widehat{N_1} \widehat{N_2} \left(\frac{a_1 a_2 S(-b_2 + b_1 \beta)}{(\gamma + a_1 \widehat{N_1} + a_2 \widehat{N_2})^2} + \alpha \beta \right).$$

If $b_2 = b_1 \beta$, then $\det J = \alpha^2 \beta \widehat{N_1} \widehat{N_2} \neq 0$ as $\alpha > 0, \beta > 0$, and $\widehat{N_i} > 0$ for $i = 1, 2$. Alternatively, assume $b_2 \neq b_1 \beta$. Let $\varepsilon = (A_1^2 - B_1)/b_2^2$. Substituting the expressions $(N_1^\pm, N_2^\pm)$ for $(\widehat{N_1}, \widehat{N_2})$ yields

$$\frac{1}{\gamma + a_1 \widehat{N_1} + a_2 \widehat{N_2}} = \frac{2\alpha \beta}{D \pm \sqrt{\varepsilon}}.$$

Substituting the preceding equation into $\det J$ yields

$$\det J = \alpha^2 \beta \widehat{N_1} \widehat{N_2} \left(\frac{4\alpha\beta a_1 a_2 S(-b_2 + b_1\beta)}{2\varepsilon \pm 2D\sqrt{\varepsilon} - 4\alpha\beta a_1 a_2 S(-b_2 + b_1\beta)} + 1 \right).$$

Hence, $\det J = 0$ if and only if $\varepsilon = 0$, equivalently, if and only if $A_1^2 = B_1$. These observations imply that so long as $A_i^2 \neq B_i$ or $b_2 = \beta b_1$, any equilibrium in the positive quadrant is either a sink (i.e., eigenvalues of J have negative real parts) or a saddle (i.e., J has a positive and negative eigenvalue).

Case 1 - Global coexistence. Assume $\Gamma_i > 0$ for $i = 1, 2$. We claim that there is a unique equilibrium in the positive quadrant. To prove this claim and identify the correct expression of this positive equilibrium, we need to consider three cases. For the first case, assume that $b_1\beta > b_2$. Then, $C_1 > 0$ and $C_2 > 0$. Moreover, $\Gamma_i > 0$ and $b_1\beta > b_2$ imply that $B_1 > 0$, and $B_2 < 0$. Hence, $N_2^- < 0 < N_2^+$. Since $A_1^2 > A_1^2 - B_1 = \frac{b_1^2}{b_2^2}(A_2^2 - B_2) > 0$ (cf. (5)), N_1^- and N_1^+ must be real and have the same sign. Moreover, as there are no equilibria in the negative quadrant, N_1^- and N_1^+ are positive. Hence, $(\widehat{N_1}, \widehat{N_2}) = (N_1^+, N_2^+)$ is the unique equilibrium in the positive quadrant. For the second case, assume that $b_1\beta < b_2$. Then, $C_1 < 0$ and $C_2 < 0$. Moreover, $\Gamma_i > 0$ and $b_1\beta < b_2$ imply that $B_1 < 0$, and $B_2 > 0$. Hence, $N_1^- < 0 < N_1^+$. Since $A_2^2 > A_2^2 - B_2 = \frac{b_2^2}{b_1^2}(A_1^2 - B_1) > 0$ (cf. (5)), N_2^- and N_1^+ are real and have the same sign. Moreover, as there are no equilibria in the negative quadrant, N_2^- and N_2^+ are positive. Hence, $(\widehat{N_1}, \widehat{N_2}) = (N_1^+, N_2^+)$ is the unique equilibrium in the positive quadrant. For the third case, assume that $b_1\beta = b_2$. In this case the only equilibrium is given by (N_1^*, N_2^*). Since $\Gamma_i > 0$ for $i = 1, 2$ and there are no equilibria in the negative quadrant, equation (6) implies that (N_1^*, N_2^*) must lie in the positive quadrant.

Let $(\widehat{N_1}, \widehat{N_2})$ denote the unique equilibrium in the positive quadrant. Since we have either $b_2 \neq b_1\beta$ or $A_1^2 - B_1 \neq 0$ at this equilibrium, the equilibrium is either a sink or a saddle. Since the equilibria on the axes are a source (the origin) and two saddles and all solutions starting in the positive quadrant must converge to an equilibrium, the Poincaré-Bendixson theory implies that all solutions starting in the positive quadrant must converge to $(\widehat{N_1}, \widehat{N_2})$.

Case 2: Contingent exclusion. Assume that $\Gamma_1 < 0$ and $\Gamma_2 < 0$. We claim that there is a unique equilibrium in the positive quadrant. To prove this claim and identify the correct expression of this positive equilibrium, we need to consider three cases. For the first case, assume that $b_1\beta > b_2$. Then, $C_1 > 0$ and $C_2 > 0$. Moreover, $\Gamma_i < 0$ and $b_1\beta > b_2$ imply that $B_1 < 0$, and $B_2 > 0$. Hence, $N_1^- > 0 > N_1^+$. As N_2^+ and N_2^- have the same sign and there are no equilibria in the negative quadrant, $(\widehat{N_1}, \widehat{N_2}) = (N_1^-, N_2^-)$ is the unique equilibrium in the positive quadrant. For the second case, assume that $b_1\beta < b_2$. Then, $C_1 < 0$ and $C_2 < 0$. Moreover, $\Gamma_i < 0$ and $b_1\beta < b_2$ imply that $B_1 > 0$ and $B_2 < 0$. Hence, $N_2^- > 0 > N_2^+$. As N_1^+ and N_1^- have the same sign and there are no equilibria in the negative quadrant, $(\widehat{N_1}, \widehat{N_2}) = (N_1^-, N_2^-)$ is the unique equilibrium in the positive quadrant. For the third case, assume that $b_1\beta = b_2$. In this case the only equilibrium is given by (N_1^*, N_2^*). Since $\Gamma_i < 0$ for $i = 1, 2$ and there are no equilibria in the negative quadrant, equation (6) implies that (N_1^*, N_2^*) must lie in the positive quadrant.

Let $(\widehat{N_1}, \widehat{N_2})$ denote the unique equilibrium in the positive quadrant. Since we have either $b_2 \neq b_1\beta$ or $A_1^2 - B_1 \neq 0$ at this equilibrium, this equilibrium is either a sink or a saddle. However, since $(\frac{b_1 S}{c_1} - \frac{\gamma}{a_1}, 0)$ and $(0, \frac{b_2 S}{c_2} - \frac{\gamma}{a_2})$ are sinks and the origin is a source,

$(\widehat{N_1}, \widehat{N_2})$ must be a saddle. Moreover, the stable manifold of $(\widehat{N_1}, \widehat{N_2})$ separates the basins of attraction of $(\frac{b_1 S}{c_1} - \frac{\gamma}{a_1}, 0)$ and $(0, \frac{b_2 S}{c_2} - \frac{\gamma}{a_2})$.

Case 3: Intraguild predator displacement. Assume that $\Gamma_1 > 0$ and $\Gamma_2 < 0$. Since $\Gamma_2 < 0$, the intraguild predator nullcline given by (3) must lie below the N_1 axis at $N_1 = \frac{a_1 b_1 S}{\gamma} - c_1$ and have a vertical asymptote at $N_1 > \frac{a_1 b_1 S}{\gamma} - c_1$. Since the prey nullcline given by (4) is decreasing and passes through the point $(\frac{b_1 S}{c_1} - \frac{\gamma}{a_1}, 0)$ and the predator nullcline has a vertical asymptote at $N_1 > \frac{b_1 S}{c_1} - \frac{\gamma}{a_1}$, these nullclines must intersect at an equilibrium $(\widehat{N_1}, \widehat{N_2})$ with $\widehat{N_1} > 0$ and $\widehat{N_2} < 0$. Using this observation, we claim there are no equilibria in the positive quadrant. To prove this claim, we consider three cases. First, assume that $b_1 \beta > b_2$. Then, $B_1 > 0$ and $B_2 > 0$. Hence, when $A_i^2 - B_i \geq 0$ (i.e., the equilibria are real), $N_1^{\pm}$ have the same sign and $N_2^{\pm}$ have the same sign. Our observation about $(\widehat{N_1}, \widehat{N_2})$ implies that $N_1^{\pm} > 0$ and $N_2^{\pm} < 0$. Hence, there are no equilibria in the positive quadrant. Second, assume that $b_1 \beta < b_2$. Since $C_i < 0$ and $B_i < 0$ for $i = 1, 2$ in this case, we get $N_1^- < 0 < N_1^+$ and $N_2^+ < 0 < N_2^-$. Hence, neither (N_1^-, N_2^-) nor (N_1^+, N_2^+) lie in the nonnegative quadrant. Third, assume that $b_1 \beta = b_2$. Then, (N_1^*, N_2^*) must equal $(\widehat{N_1}, \widehat{N_2})$ and there is no equilibrium in the positive quadrant.

Since $(\frac{b_1 S}{c_1} - \frac{\gamma}{a_1}, 0)$ is a sink, $(0, \frac{b_2 S}{c_2} - \frac{\gamma}{a_2})$ is a saddle, and there are no equilibria in the positive quadrant, the Poincaré-Bendixson theory implies that all solutions in the positive quadrant converge to $(\frac{b_1 S}{c_1} - \frac{\gamma}{a_1}, 0)$.

Cases 4 and 5: Intraguild prey displacement and contingent coexistence. Assume that $\Gamma_1 < 0$ and $\Gamma_2 > 0$. First, consider the case that $b_1 \beta < b_2$. Then $B_i > 0$ and $C_i < 0$ for $i = 1, 2$. Thus, if $A_1^2 - B_1 > 0$ and $A_i < 0$ for $i = 1, 2$, then the two equilibria (N_1^+, N_2^+) and (N_1^-, N_2^-) lie in the positive quadrant. Alternatively, if $A_1^2 - B_1 < 0$ or $A_1 > 0$ or $A_2 > 0$, then there are no equilibria in the positive quadrant. Second, consider the case that $b_1 \beta > b_2$. Then $C_i > 0$ and $B_i < 0$ for $i = 1, 2$. Hence, $N_2^+ > 0 > N_2^-$ and $N_1^- > 0 > N_1^+$. Therefore, there are no equilibria in the positive quadrant. Third, consider the case that $b_1 \beta = b_2$. Since $\Gamma_1 \Gamma_2 < 0$, equation (6) implies that N_1^* and N_2^* are of opposite sign. Therefore, there are no equilibria in the positive quadrant.

Assume that there are no equilibria in the positive quadrant (i.e., $b_1 \beta \geq b_2$ or $A_1^2 < B_1$ or $A_1 > 0$ or $A_2 > 0$). Since $(\frac{b_1 S}{c_1} - \frac{\gamma}{a_1}, 0)$ is a saddle and $(0, \frac{b_2 S}{c_2} - \frac{\gamma}{a_2})$ is a sink, all solutions in the positive quadrant converge to $(0, \frac{b_2 S}{c_2} - \frac{\gamma}{a_2})$. Alternatively assume that there are two positive equilibria $(N_1^{\pm}, N_2^{\pm})$ in the positive quadrant (i.e., $b_1 \beta < b_2$, $A_1^2 > B_1$, and $A_i < 0$ for $i = 1, 2$). Since $A_1^2 > B_1$, these equilibria are either sinks or saddles. By the Poincaré-Hopf Index theorem, one of the positive equilibria is a sink and the other is a saddle. The stable manifold of this saddle must separate the basins of attraction of the boundary sink and the sink in the positive quadrant.

4. Proof of Proposition 2.2.

Case 1: Intraguild prey failure. Suppose that $\frac{a_1 b_1 S}{\gamma} < c_1$. Then, $\frac{dN_1}{dt} \frac{1}{N_1} \leq \frac{a_1 b_1 S}{\gamma} - c_1 < 0$ for $N_1 > 0$ and $N_2 \geq 0$. Hence, $\lim_{t \to \infty} N_1(t) = 0$ for any solution $(N_1(t), N_2(t))$ to (2) with $N_1(0) \geq 0$ and $N_2(0) \geq 0$.

Case 2: Intraguild predator failure. Suppose that $\frac{a_2 b_2 S}{\gamma} < c_2$ and $\frac{a_1 b_1 S}{\gamma} < c_1$. Let $(N_1(t), N_2(t))$ be a solution to (2) with $N_1(0) \geq 0$ and $N_2(0) > 0$. Then, $\lim_{t \to \infty} N_1(t) = 0$. Since $\frac{a_2 b_2 S}{\gamma} < c_2$, there exists a $T > 0$ such that

$$\frac{N_2'(t)}{N_2(t)} \leq \frac{a_2 b_2 S}{\gamma} - c_2 + \alpha \beta N_1(t) < 0$$

for all $t \geq T$. Hence, $\lim_{t \to \infty} N_2(t) = 0$.

Suppose that $\frac{a_2 b_2 S}{\gamma} < c_2$, $\frac{a_1 b_1 S}{\gamma} > c_1$, and $\Gamma_2 < 0$. Then, the intraguild predator nullcline (3) lies below the N_1 axis for $0 \leq N_1 \leq \frac{b_1 S}{c_1} - \frac{\gamma}{a_1}$. Since the intraguild prey nullcline (4) lies below the N_1 axis for $N_1 > \frac{b_1 S}{c_1} - \frac{\gamma}{a_1}$, there is no equilibrium in the positive quadrant. Since the origin is a saddle and $(\frac{b_1 S}{c_1} - \frac{\gamma}{a_1}, 0)$ is a sink, the Poincaré-Bendixson theorem implies that $\lim_{t \to \infty} (N_1(t), N_2(t)) = (\frac{b_1 S}{c_1} - \frac{\gamma}{a_1}, 0)$ for any solution $(N_1(t), N_2(t))$ to (2) with $N_1(0) > 0$ and $N_2(0) \geq 0$.

Case 3: Global coexistence. Suppose that $\frac{a_2 b_2 S}{\gamma} < c_2$, $\frac{a_1 b_1 S}{\gamma} > c_1$, and $\Gamma_2 > 0$. Then, the intraguild predator nullcline (3) has a negative N_2 intercept; has an N_1 intercept, call it N_1^*, in the interval $0 < N_1 < \frac{b_1 S}{c_1} - \frac{\gamma}{a_1}$; is increasing on the interval $N_1^* < N_1 < \frac{c_2}{\alpha \beta}$; and has a vertical asymptote at $N_1 = \frac{c_2}{\alpha \beta}$. Since the intraguild prey nullcline (4) is decreasing and positive on the interval $0 \leq N_1 < \frac{b_1 S}{c_1} - \frac{\gamma}{a_1}$ and has a N_1 intercept at $\frac{b_1 S}{c_1} - \frac{\gamma}{a_1}$, there is a unique intersection $(\widehat{N}_1, \widehat{N}_2)$ of these nullclines in the positive quadrant. Since there are no periodic orbits in the positive quadrant (cf. the first paragraph of the proof of Theorem 2.1) and the origin and $(\frac{b_1 S}{c_1} - \frac{\gamma}{a_1}, 0)$ are saddles, the Poincaré-Bendixson theorem implies that $\lim_{t \to \infty} (N_1(t), N_2(t)) = (\widehat{N}_1, \widehat{N}_2)$ for any solution $(N_1(t), N_2(t))$ to (2) with $N_1(0) > 0$ and $N_2(0) > 0$.

5. **Discussion.** Competition and predation are two fundamental processes in ecological communities that have been studied extensively. Intraguild predation combines these two processes in a unique way: species that compete for common resources also predate on one another. In this article, we analyzed a variation of an intraguild predation model introduced by Polis and Holt [1, 3], which builds on Schoener's model of competing species [5, 6]. Our analysis reveals that there are generically six types of dynamics: extinction of one or both species; coexistence about a globally stable equilibrium; competitive exclusion of the intraguild predator; competitive exclusion of the intraguild prey; contingent exclusion in which the first established species prevents the establishment of the other species; and contingent coexistence in which the species coexist or the intraguild prey is displaced, depending on initial conditions.

As observed by Polis and Holt [2], this model of intraguild predation has important implications for classical biological control where a pest species (in our case, the "resource") is regulated by natural enemies (in our case, the intraguild prey or predator). For example, many agricultural pests, such as lepidoptera or hymenoptera ("the resource species"), are attacked by parasitic wasps and predatory insects. Since these predatory insects also attack pests that contain wasp larvae [4], the predators are intraguild predators, and the wasps are their intraguild prey. The relevance of our analysis to biocontrol stems from the observation that the equilibrium pest abundance equals

$$R(\widehat{N}_1, \widehat{N}_2) = \frac{c_1}{a_1 b_1} - \alpha \widehat{N}_1 \tag{7}$$

at any equilibrium $(\widehat{N}_1, \widehat{N}_2)$ supporting the intraguild prey and predator. Hence, the pest equilibrium

$$R\left(\frac{b_1 S}{c_1} - \frac{\gamma}{a_1}, 0\right) = \frac{c_1}{a_1 b_1}$$

determined by the intraguild prey is smaller than the pest abundance $R(\widehat{N}_1, \widehat{N}_2)$ determined by an equilibrium supporting both species. Thus, intraguild predators coexisting with intraguild prey may disrupt biological control by raising the equilibrium abundance of the

pest. However, this prediction needs to be viewed with caution, as this model does not account for the potentially stabilizing effects of intraguild predation with a dynamic pest species [7].

Our analysis also has various implications for how intraguild predation impacts community structure. Most interestingly, intraguild predation can result in alternative stable states in which community composition depends on the order of species arrivals. In the case of contingent exclusion, the species that arrives first exclusively determines the community composition. Alternatively, in the case of contingent coexistence, there exist alternative states with different levels of species richness. If the intraguild predator arrives first, it prevents the establishment of the intraguild prey. However, if the intraguild prey arrives first, the community can be augmented with the intraguild predator. Our analysis also makes predictions about the effect of environmental productivity on community structure. Assume the intraguild prey can suppress the resource to a lower equilibrium abundance (i.e., $\frac{c_1}{a_1 b_1} < \frac{c_2}{a_2 b_2}$). Then at low productivity (i.e., S just large enough to support both species), the intraguild prey displaces the intraguild prey (i.e., $\Gamma_1 > 0$ and $\Gamma_2 < 0$). Alternatively, at high levels of productivity (i.e. S sufficiently large), a reversal occurs in which the intraguild predator exerts sufficient predatory pressure to displace the intraguild prey (i.e., $\Gamma_1 < 0$, $\Gamma_2 > 0$, and either $b_2 \leq b_1 \beta$ or $B_1 > A_1^2$). Thus, only at intermediate levels of productivity are alternative states or coexistence possible.

In conclusion, simple models of intraguild predation exhibit a diversity of behaviors that have noteworthy ecological ramifications. While providing an illuminating starting point, the biological complexities of the real world require us to understand how stage-structure, nonlinear functional responses, spatial heterogeneity, additional species interactions and environmental stochasticity interact with intraguild predation to modulate the effects observed in these simple models.

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