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PERMANENT COEXISTENCE FOR AN INTRAGUILD PREDATION MODEL WITH PREDATOR STAGE STRUCTURE

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The question of long-term survival of a collection of interacting species in an ecological community is of upmost importance to humans and of great interest to ecologists. Using permanence theory, we investigate a unique blend of predation and competition known as intraguild predation or IGP—a top predator feeds on an intermediate predator and competes with that predator for a shared resource. IGP is a simple example of omnivory which is quite ubiquitous in natural systems [1]. We use a differential equations model of IGP with nonlinear functional and numerical responses in which the top predator's life history includes stage structure [2] and investigate the conditions on the parameters required to show that the system is permanently coexistent.

Keywords: Omnivory, Intraguild predation, Permanent coexistence, Stage structure.

INTRODUCTION

Permanence theory is 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 get too close to the boundary (zero density) of the state space [3]. That is, a system with state variables $\mathbf{x}(t)$ is permanently coexistent or permanent if and only if there is a compact region $D_1 \subset D$ such that given any $\mathbf{x}(t_0) = \mathbf{x}_0 \in D$ there is a $T = T(\mathbf{x})$ such that $\mathbf{x}(t) \in D_1$ for $t > T$. This technique was applied to an IGP model without stage structure by Vance [4]. However, the addition of stage structure stipulates that the boundary is no longer invariant and a relaxed definition of permanent coexistence must be introduced. We show under what parameter conditions the relaxed version of permanent coexistence is ensured.

INTRAGUILD PREDATION MODEL

Consider density R of a resource growing logistically in the absence of predators, density C of an intermediate predator (consumer) depending solely upon the resource, density P_1 of juvenile individuals of a top predator that preys upon the resource, and density P_2 of adult individuals of a top predator that preys upon the resource and the consumer (see Figure 1). Then the model for population interaction is given by the system of ordinary differential equations

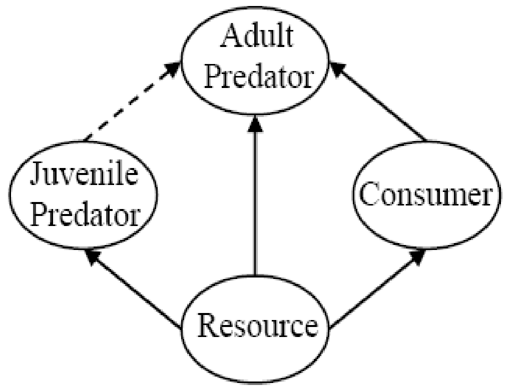

Figure 1. Top predator stage structure.

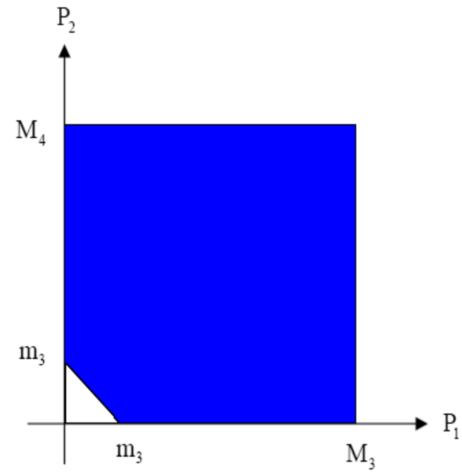

Figure 2. Permanence definition for stage.

$$\frac{dP_2}{dt} = \alpha_P P_1 - \mu_P P_2$$
$$\frac{dP_1}{dt} = \frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C}P_2 - (\alpha_P + \mu_P)P_1$$
$$\frac{dC}{dt} = C\left[\frac{e_{RC}\lambda_{RC}R}{1+\lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P_2}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C} - \mu_C\right]$$
$$\frac{dR}{dt} = R\left[r\left(1-\frac{R}{K}\right) - \frac{\lambda_{RC}C}{1+\lambda_{RC}h_{RC}R} - \frac{\lambda_{RC}P_1}{1+\lambda_{RP}h_{RP}R} - \frac{\lambda_{RP}P_2}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C}\right]$$

defined on $D = \mathbb{R}_+ \times \mathbb{R}_+^4$. The parameters are defined as follows: e's are conversion efficiencies, h's are handling times, λ's are search rates, μ's are mortality rates and α is a maturation rate.

PERMANENT COEXISTENCE

The boundary of the state space is not invariant—required for analysis using Average Lyapunov functions [4], [5]. It is quite easy to show existence and uniqueness of solutions to the system for all $t \geq 0$ and that solutions are pointing into $\mathbb{R}_+^4$ on the bounding hypersurfaces. However, this new scenario requires us to alter the definition of permanent coexistence. Since we have two state variables P_1 and P_2 that must both be zero in order for the top predator species to be extinct, we require that $m \leq P_1(t) + P_2(t)$ for $t > T$ and some $m > 0$. For a graphical depiction see Figure 2.

So under minimal conditions on the parameters, all solutions of the system that initiate in $\mathbb{R}_+^4$ are uniformly bounded and enter a region $B = \left\{(P_2, P_1, C, R) \in \mathbb{R}_+^4 : 0 \leq P_2 + P_1 + C + R \leq M\right\}$. Also, we assume that the Ω-limit set of every orbit in $\partial\mathbb{R}_+^4$ is an equilibrium point. See [6] for details to show this condition using a Poincare-Bendixson argument. We say that an equilibrium $\overline{\mathbf{x}}$ is saturated if $f_i(\overline{\mathbf{x}}) \leq 0$ for all i with $\overline{x}_i = 0$ where f_i is the growth function of the ith species. We then compute the boundary equilibria and show under what conditions they are not saturated.

RESULTS

Notice that our model attempts to counter the consumer inferiority by decreasing predation upon the consumer. Also, the alternative stable states of IGP models always involve the resource [7]. Therefore, the extinction of the resource is of little concern. So we assume that the consumer and resource densities are uniformly bounded away from zero. That is, there exists $m_1, m_2 > 0$ and $T_1 \geq 0$ such that $m_1 \leq R(t)$ and $m_2 \leq C(t)$ for $t \geq T_1$.

Then if $$\alpha_P > \frac{(\mu_P)^2}{b - \mu_P}$$

where $b > 0$ is such that

$$\frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \geq b.$$

Then the system is permanently coexistent. For numerical confirmations see [2]. For proofs of the above statements see [9].

CONCLUSION

These conditions place restrictions on how large or small parameters can be and provide an ecologically sound and mathematically tractable criterion for long-term species coexistence. However, these parameter restrictions are more limiting than we observe in natural ecosystems with intraguild predation (see [8]), so further investigation is warranted.

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