APPENDIX B: ANALYSIS OF A STAGE STRUCTURED MODEL

I develop a stage-structured model that incorporates the key biological features of the host-parasitoid system: unidirectional IGP with the IGPrey being the superior resource competitor (i.e., the IGPrey has a higher attack rate than the IGPredator), superparasitism in the IGPredator, and a temporal refuge in the IGPrey. The host has three stages: eggs (E), nymphs (N) and adults (A). The parasitoids each have larval (L_i) and adult (P_i)$(i = 1, 2)$ stages. Both parasitoids attack host eggs. Parasitoid 2 (IGPredator) engages in both superparasitism and IGP. Since all three species have overlapping generations a continuous-time model is appropriate. The quantity T is the time period of seasonal variation (one year), T_R is the time period during only the IGPrey is present (the refuge), and $T - T_R$ is the time period when both IGPrey and IGPredator co-occur. The dynamics are given by:

Refuge period (resource and IGPrey) ($0 \leq t \leq T_R$)

$$\frac{dE}{dt} = rA - m_E E - a_1 E P_1 - d_E E$$

$$\frac{dN}{dt} = m_E E - m_N N - d_N N - q N^2$$

$$\frac{dA}{dt} = m_N N - d_A A$$

$$\frac{dL_1}{dt} = e_1 a_1 E P_1 - m_{L_1} L_1 - d_{L_1} L_1$$

$$\frac{dP_1}{dt} = m_{L_1} L_1 - d_{P_1} P_1$$

Non-refuge period (resource, IGPrey, IGPredator) ($T_R \leq t \leq T$)

$$\frac{dE}{dt} = rA - m_E E - a_1 E P_1 - a_2 E P_2 - d_E E$$

$$\frac{dN}{dt} = m_E E - m_N N - d_N N - q N^2$$

$$\frac{dA}{dt} = m_N N - d_A A$$

$$\frac{dL_1}{dt} = e_1 a_1 E P_1 - m_{L_1} L_1 - \alpha_1 L_1 P_2 - d_{L_1} L_1$$

$$\frac{dP_1}{dt} = m_{L_1} L_1 - d_{P_1} P_1$$

$$\frac{dL_2}{dt} = e_2 a_2 E P_2 - m_{L_2} L_2 - \alpha_2 L_2 P_2 - d_{L_2} L_2$$

$$\frac{dP_2}{dt} = m_{L_2} L_2 + f_1 \alpha_1 L_1 P_2 + f_2 \alpha_2 L_2 P_2 - d_{P_2} P_2$$

The parameter r is the per capita rate of host reproduction, m_E is the host egg maturation rate, m_N is the nymphal maturation rate, and d_X is the density-independent mortality rate of stage X of host. Host self limitation occurs via density-dependent mortality, the strength of which is determined by q. The parameter a_i is the attack rate of parasitoid i on host eggs ($i = 1, 2$), α_1 is the attack rate of parasitoid 2 (IGPredator) on host eggs previously parasitized by parasitoid 1 (IGPrey) that contain larvae of parasitoid 1 (multiparasitism leading to IGP), and α_2 is the attack rate of parasitoid 2 on host eggs parasitized by other conspecific females (superparasitism leading to intra-specific competition in the IGPredator). The parameter e_i is the number of parasitoid i offspring resulting from primary parasitism, f_1 is the number of IGPredator offspring resulting from multiparasitism, and and f_2 is the number of IGPredator offspring resulting from superparasitism. The parameters m_{L_i}, d_{L_i} and d_{P_i} are, respectively, the larval maturation rate, the larval mortality rate and the adult mortality rate of parasitoid i ($i = 1, 2$).

Since the model does not lend itself to analytical results, I numerically simulated long-term dynamics for 365,000 time steps (corresponding to a time span of 1000 years) using the method of Runge-Kutta step 4 (Press *et al.* 2001). In Appendix C I analyze an unstructured version of the model that yields analytical results for both mutual invasibility and long-term coexistence.

Figure 1 illustrates the long-term outcomes of the model for a set of parameters that reflect the biology of the host-parasitoid system. For instance, the invulnerable adult host is long-lived relative to the egg and nymphal stages, while the adult parasitoids are short-lived relative to their larval stages (Amarasekare 2000a); nymphal stages of the host suffer little mortality relative to the larval stages of the parasitoids (Amarasekare 1998). The IGPrey has a higher attack rate on unparasitized hosts than the IGPredator, and a temporal refuge from IGP that is about four months in duration (Amarasekare 1998, 2000a, b).

A variant of the stage structured model that converts superparasitized and multiparasitized larvae into larval IGPredator density rather than adult IGPredator density has no qualitative effect on coexistence or abundance patterns of coexisting species; it has the quantitative effect of increasing the resource productivity thresholds for the IGPrey's exclusion and the IGPredator's invasion which, when the IGPredator suffers a net cost from superparasitism, can increase the productivity region that allows coexistence (P. Amarasekare, unpublished manuscript).

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