

APPENDIX C: ANALYSIS OF AN UNSTRUCTURED MODEL

Here I present a model without stage structure that is a special case of a general IGP model that is investigated elsewhere (P. Amarasekare, unpublished manuscript). While its overall conclusions are broadly similar to those of the stage-structured model, this simpler model provides more insight into the influence of key biological parameters on invasibility and long-term coexistence.

The dynamics of the three species system are given by:

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

$$\frac{dR}{dt} = rR - qR^2 - a_1RP_1$$

$$\frac{dP_1}{dt} = e_1a_1RP_1 - d_1P_1$$

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

$$\frac{dR}{dt} = rR - qR^2 - a_1RP_1 - a_2RP_2$$

$$\frac{dP_1}{dt} = e_1a_1RP_1 - d_1P_1 - \alpha_1P_1P_2$$

$$\frac{dP_2}{dt} = e_2a_2RP_2 - d_2P_2 + f_1\alpha_1P_1P_2 + (f_2 - 1)\alpha_2P_2^2$$

where R , P_1 and P_2 are the abundances of the host, IGPrey and IGPredator respectively,

and r is the per capita rate of host reproduction. Host self limitation occurs via

density-dependent mortality, the strength of which is determined by q . The parameters a_1

and a_2 are the attack rates, respectively, of the IGPrey and IGPredator on the resource, α_1

is the attack rate of the IGPredator on the IGPrey (multiparasitism leading to IGP), and α_2

is the attack rate of the IGPredator on itself (superparasitism leading to intra-specific

competition in the IGPredator). The parameter e_i is the number of parasitoid i offspring

resulting from primary parasitism ($i = 1, 2$), f_1 is the number of IGPredator offspring resulting from multiparasitism, and f_2 is the number of IGPredator offspring resulting from superparasitism. Parameters d_1 and d_2 are the background mortality rates, respectively, of the IGPrey and IGPredator.

Invasibility and long-term coexistence when trade-off is augmented by superparasitism in the IGPredator

In the absence of a temporal refuge the system reduces to:

$$\begin{aligned}\frac{dR}{dt} &= rR - qR^2 - a_1RP_1 - a_2RP_2 \\ \frac{dP_1}{dt} &= e_1a_1RP_1 - d_1P_1 - \alpha_1P_1P_2 \\ \frac{dP_2}{dt} &= e_2a_2RP_2 - d_2P_2 + f_1\alpha_1P_1P_2 + (f_2 - 1)\alpha_2P_2^2\end{aligned}\tag{C.1}$$

This system yields 5 sets of equilibria:

(i) the trivial equilibrium with all species extinct:

$$(R^*, P_1^*, P_2^*) = (0, 0, 0),$$

(ii) the resource at carrying capacity and the consumers extinct:

$$(R^*, P_1^*, P_2^*) = \left(\frac{r}{q}, 0, 0\right),$$

(iii) boundary equilibrium with the resource and IGPrey:

$$(R^*, P_1^*, P_2^*) = \left(\frac{d_1}{e_1a_1}, \frac{re_1a_1 - qd_1}{e_1a_1^2}, 0\right),$$

(iv) boundary equilibrium with the resource and IGPredator:

$$(R^*, P_1^*, P_2^*) = \left(\frac{a_2d_2 - r\alpha_2(f_2 - 1)}{e_2a_2^2 - q\alpha_2(f_2 - 1)}, 0, \frac{re_2a_2 - qd_2}{e_2a_2^2 - q\alpha_2(f_2 - 1)}\right) \text{ and,}$$

(v) the coexistence equilibrium:

$$R^* = \frac{a_1(\alpha_1 d_2 + \alpha_2 d_1(f_2 - 1))}{a_1 a_2 \alpha_1 (e_2 - e_1 f_1) + q f_1 \alpha_1^2 + e_1 a_1^2 \alpha_2 (f_2 - 1)},$$

$$P_1^* = \frac{e_1 a_1 (a_2 d_2 - r \alpha_2 (f_2 - 1)) + q(\alpha_1 d_2 + \alpha_2 d_1(f_2 - 1)) - a_2 (r e_2 \alpha_1 + e_2 a_2 d_1)}{a_1 a_2 \alpha_1 (e_2 - e_1 f_1) + q f_1 \alpha_1^2 + e_1 a_1^2 \alpha_2 (f_2 - 1)},$$

$$P_2^* = \frac{a_1 (e_2 a_2 d_1 - e_1 a_1 d_2) + f \alpha_1 (r e_1 a_1 - q d_1)}{a_1 a_2 \alpha_1 (e_2 - e_1 f_1) + q f_1 \alpha_1^2 + e_1 a_1^2 \alpha_2 (f_2 - 1)}.$$

Fig. C1 depicts the changes in equilibrium abundances as a function of resource productivity.

The invasion criterion for each species is obtained by computing the dominant eigenvalue of the Jacobian of Equation (1) evaluated at the appropriate boundary equilibrium.

The IGPrey can invade when rare if:

$$\frac{e_1 a_1 (a_2 d_2 - r \alpha_2 (f_2 - 1)) + q(\alpha_1 d_2 + \alpha_2 d_1(f_2 - 1)) - a_2 (r e_2 \alpha_1 + e_2 a_2 d_1)}{e_2 a_2^2 - q \alpha_2 (f_2 - 1)} > 0.$$

By setting the above invasion criterion to zero one can derive the host productivity threshold (r_{P_1}) for invasibility:

$$r_{P_1} = \frac{a_2 (e_1 a_1 d_2 - e_2 a_2 d_1) + q(\alpha_1 d_2 + d_1 \alpha_2 (f_2 - 1))}{e_2 a_2 \alpha_1 + e_1 a_1 \alpha_2 (f_2 - 1)}.$$

The IGPrey can invade when rare if $r < r_{P_1}$. When $f_2 = 1$ there is no net effect of superparasitism and the productivity threshold for invasion of IGPrey is the same as that for the basic IGP model: $r < r_{P_1} = \frac{a_2 (e_1 a_1 d_2 - e_2 a_2 d_1) + q \alpha_1 d_2}{e_2 a_2 \alpha_1}$. When $f_2 > 1$ the productivity threshold r_{P_1} is *lower* than that in the basic IGP model, i.e., when the IGPredator engages in superparasitism and gains a net benefit from it, the IGPrey is excluded at a *lower* level of productivity than in the absence of superparasitism. When $f_2 < 1$, the productivity

threshold r_{P_1} is *higher* than that in the basic IGP model, i.e., when the IGPredator engages in superparasitism and incurs a net cost from it, the IGPrey is excluded at a *higher* level of productivity than in the absence of superparasitism.

We can also derive the threshold level of f_2 (the benefit to the IGPredator from superparasitism) that allows the IGPrey to invade:

$$f_2 < \frac{a_2(e_1a_1d_2 - e_2a_2d_1) - \alpha_1(e_2a_2 - qd_2) + \alpha_2(re_1a_1 - qd_1)}{\alpha_2(e_1a_1r - qd_1)}.$$

This threshold depends on resource productivity. Interestingly, there is a critical value of f_2 ($f_{2critical} = 1 - \frac{e_2a_2\alpha_1}{e_1a_1\alpha_2}$) at which the IGPrey's invasibility is independent of resource productivity. When $f_2 > f_{2critical}$, the IGPrey's invasibility decreases with increasing productivity, as does its equilibrium abundance. When $f_2 < f_{2critical}$, the IGPrey's invasibility increases with increasing productivity, as does its equilibrium abundance. The IGPrey's invasion criterion is independent of f_1 because IGPrey numbers are low when invading a community where the IGPredator is resident.

The IGPredator can invade when rare if:

$$\frac{a_1(e_2a_2d_1 - e_1a_1d_2) + f\alpha_1(re_1a_1 - qd_1)}{e_1a_1^2} > 0.$$

The productivity threshold (r_{P_2}) is given by:

$$r_{P_2} = \frac{a_1(e_1a_1d_2 - e_2a_2d_1) + qf_1\alpha_1d_1}{e_1a_1f_1\alpha_1}.$$

The IGPredator can invade when rare if $r > r_{P_2}$. Thus, coexistence occurs in the region $r_{P_2} < r < r_{P_1}$. IGPredator's invasibility is independent of f_2 because IGPredator numbers

are low when it is invading a community where the IGPrey is resident. We can derive the threshold level of f_1 that allows the IGPredator to invade:

$$f_1 > \frac{a_1(e_1a_1d_2 - e_2a_2d_1)}{\alpha_1(re_1a_1 - qd_1)}.$$

*Invasibility and long-term coexistence when trade-off is augmented by a temporal refuge
in the IGPrey*

The influence of a temporal refuge on invasibility and coexistence has been investigated in detail elsewhere (P. Amarasekare, unpublished manuscript). Here I briefly illustrate the mechanism by which the refuge augments trade-off mediated coexistence.

When a trade-off is augmented by a temporal refuge with no superparasitism ($\alpha_2 = 0, f_2 = 0$ in the full model above), the IGPrey can invade if its per capita growth rate when rare, averaged over the year, is positive, i.e.,

$$e_1a_1(R_{P_2} - R_{P_1} + \tilde{R}_R) - \alpha_1\tilde{P}_2 > 0$$

where $R(t)$ and $P_2(t)$ are the abundances of resource and IGPredator at time t ,

$R_{P_2} = \int_{t=T_R}^{t=T} R(t)dt$ is the resource abundance set by the IGPredator when resident,

$R_{P_1} = \int_{t=0}^{t=T} R(t)dt$ is the resource abundance set by the IGPrey when resident,

$\tilde{R}_R = \int_{t=0}^{t=T_R} R(t)dt$ is the resource abundance during the refuge period (T_R) when neither

species is resident, and $\tilde{P}_2 = \int_{t=T_R}^{t=T} P_2(t)dt$ is the abundance of the IGPredator when resident.

The other parameters are as defined above.

The IGPredator can invade if its per capita growth rate when rare, averaged over the

year, is positive, i.e.,

$$e_2 a_2 (R_{P_1} - R_{P_2} - R_R(P_1)) + f_1 \alpha_1 \tilde{P}_1 > 0$$

where $P_1(t)$ is the IGPrey abundance at time t , $\tilde{P}_1 = \int_{t=T_R}^{t=T} P_1(t)dt$ is the abundance of the IGPrey when resident, and $R_R(P_1) = \int_{t=0}^{t=T_R} R(t)dt$ is the resource abundance required by the IGPrey to balance reproduction and mortality during the refuge period.

As can be seen, the presence of a refuge increases the IGPrey's invasibility and decreases the IGPredator's invasibility. More importantly, the IGPrey's invasibility increases as the resource availability during the refuge period (\tilde{R}_R) increases. If $\tilde{R}_R > R_R(P_1)$ (i.e., resource availability during the refuge period when neither species is resident exceeds that required by the IGPrey to balance reproduction and mortality), the IGPrey can increase from small numbers during the refuge period and this increases the IGPrey's invasibility above that under a pure trade-off. We know that $\tilde{R}_R > R_R(P_1)$, because in nature the IGPrey can increase when rare given ambient resource levels during the refuge period (Amarasekare 1998, 2000a). Thus, the positive effect of the refuge on the IGPrey's invasibility should be greater than the negative effect of the refuge on the IGPredator's invasibility, and this difference should increase as \tilde{R}_R increases, as would be the case with an experimental augmentation of resource productivity. Fig. C1 gives the long-term abundances from this model as a function of resource productivity.

Invasibility and long-term coexistence when trade-off is augmented by superparasitism in the IGPredator and a temporal refuge in the IGPrey

When superparasitism and a refuge are both operating in concert with a

competition-IGP trade-off, analytical expressions for mutual invasibility criteria are the same as in the previous section. Effects of superparasitism on the IGPrey's invasibility are manifested via the IGPredator's abundance when it is resident (\tilde{P}_2). If the benefit from superparasitism is less than the cost (i.e., $f_2 < 1$), IGPredator's abundance when resident is less than that in the absence of superparasitism. This will reduce the strength of IGP that the IGPrey experiences, and increases its invasibility.

Fig. C1 gives the long-term abundances as a function of resource productivity. By comparing Figs. C1 and C2 with Figs. 1 and 2 in the main text, it can be seen that the results on mutual invasibility and long-term coexistence are broadly similar in models with and without stage structure. The one notable difference is that the unstructured model allows coexistence at higher resource productivities when superparasitism and a refuge both augment trade-off mediated coexistence than when superparasitism or a refuge augments such coexistence, which is not the case with the stage structured model for parameter values that are realistic for the host-parasitoid system.

REFERENCES

- Amarasekare, P. 1998. Coexistence in a spatial context: empirical and theoretical perspectives. Ph.D. thesis, University of California, Irvine, California, USA.
- Amarasekare, P. 2000a. Coexistence of competing parasitoids on a patchily distributed host: local vs. spatial mechanisms. *Ecology* **81**:286-1296.

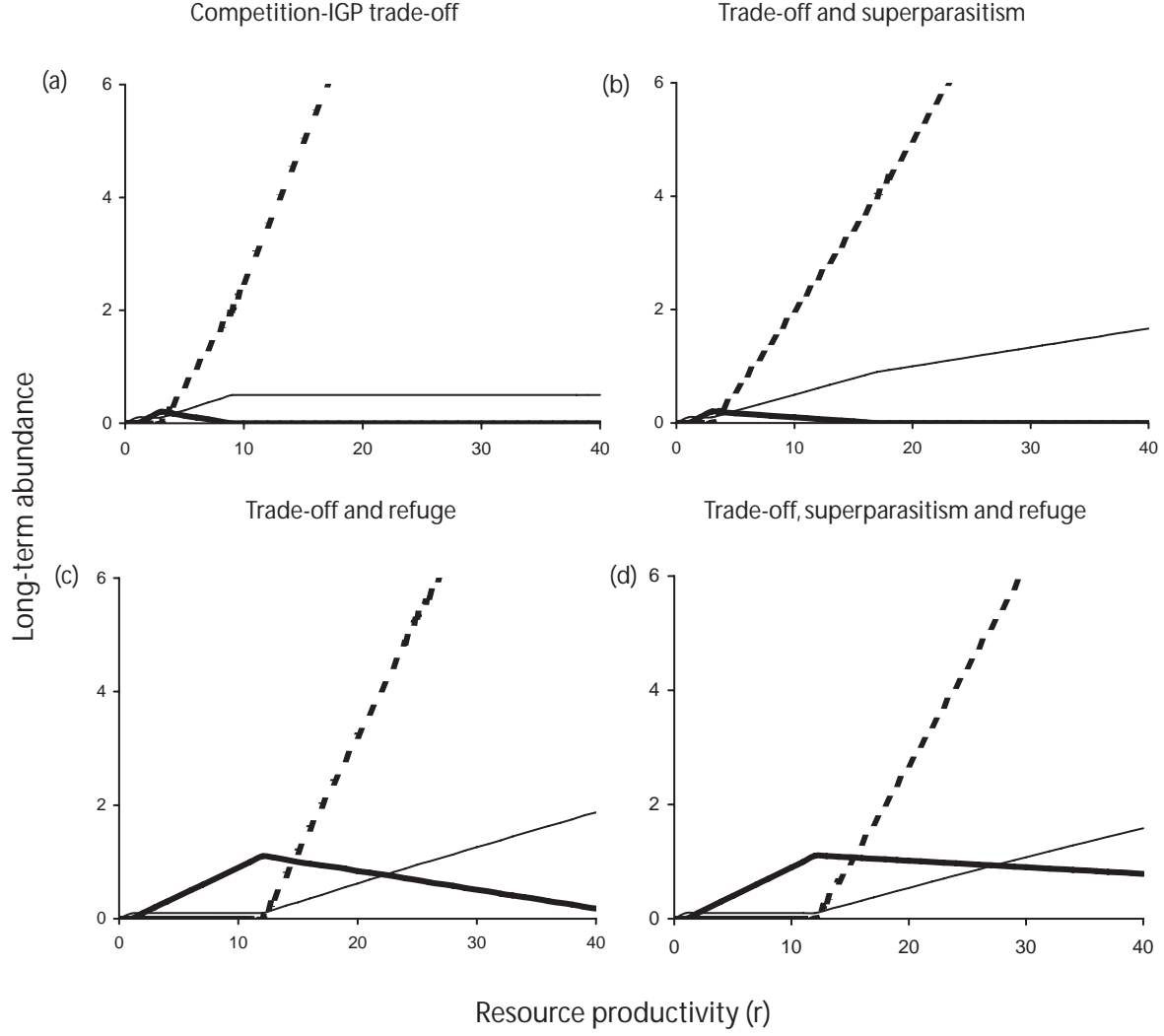


Figure C1: Long-term abundances predicted by the unstructured model for the resource (thin solid line), IGPrey (thick solid line), and IGPredator (dashed line) as a function of resource productivity. Parameter values used are as follows: $a_1 = 10, a_2 = 2, \alpha_1 = 2, \alpha_2 = 2, e_1 = 1.0, e_2 = 1.0, f_1 = 2, f_2 = 0.9, d_1 = 1.0, d_2 = 1.0, q = 10, T_R = 4$ and $T = 12$.

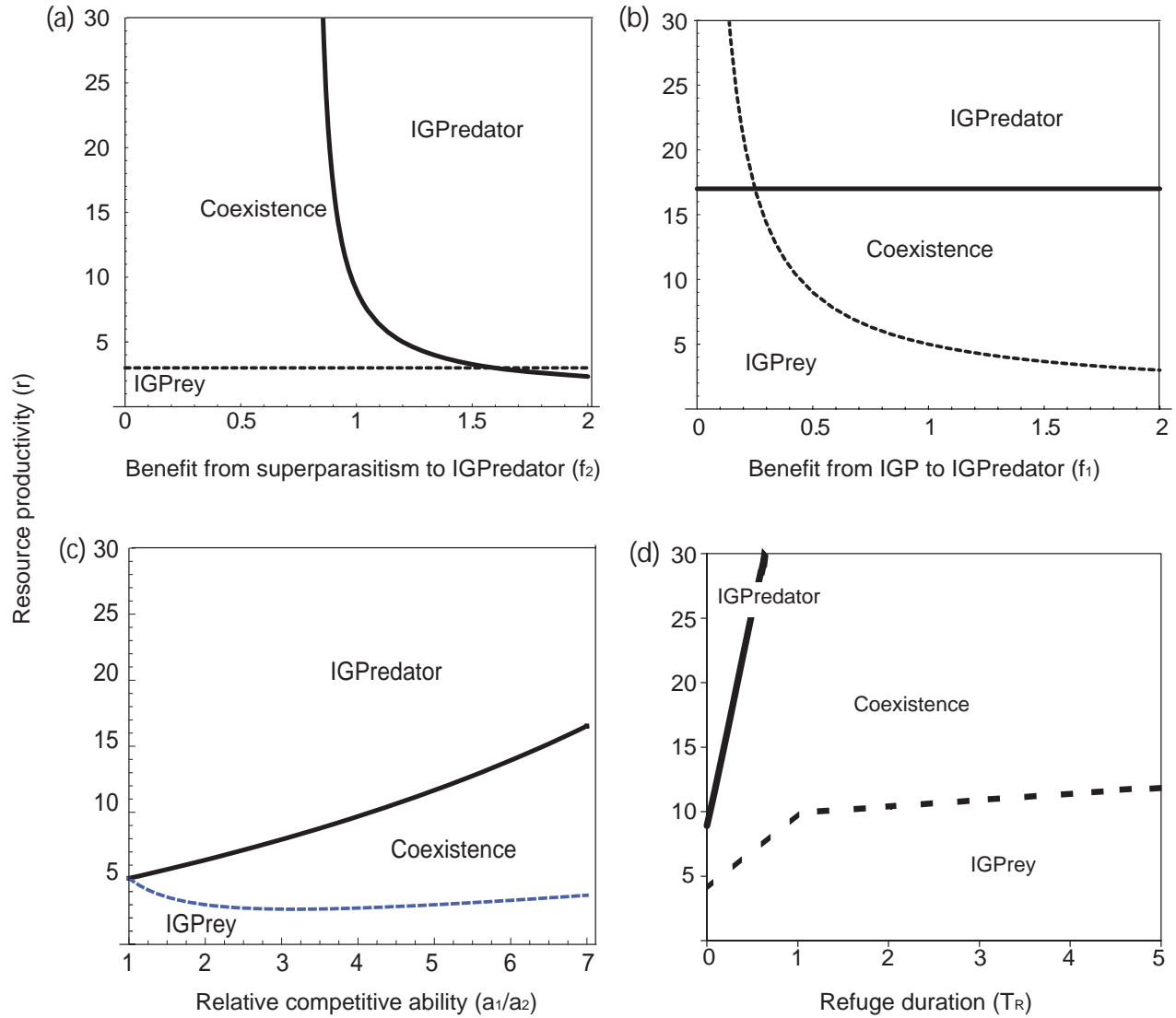


Figure C2. Sensitivity of the IGPrey and IGPredator's invasibility to key biological parameters in the unstructured model. The results are similar to those from the stage structured model (Fig. 2). The IGPrey's invasibility decreases as f_2 increases, while the IGPredator's invasibility is insensitive to variation in f_2 (panel (a)). In contrast, the IGPrey's invasibility is insensitive to variation in f_1 , while the IGPredator's invasibility increases with increasing f_1 (panel (b)). The IGPrey's invasibility increases and the IGPredator's invasibility decreases as the IGPrey's competitive ability increases relative to that of the IGPredator (panel (c)). The IGPrey's invasibility increases sharply with increase in the duration of the temporal refuge, but the IGPredator's invasibility is relatively insensitive to refuge duration (panel (d)). Other parameter values are the same as in Fig. C1.