Peter A. Abrams and Michael H. Cortez. 2015. The many potential indirect interactions between predators that share competing prey. Ecological Monographs VOL: pp-pp.

Appendix D Effects of press perturbations on predator densities

Here we are interested in how controlled changes in the density of one predator affect the equilibrium density of the other predator. Mathematically, these effects are determined by dropping the equation for the controlled predator in model (1) and solving the resulting three-species system with the density of the controlled predator treated as a parameter. With a slight abuse in notation, we denote these press equilibria by $P_{3,N_j}(N_k)$, where N_k $(k \neq j)$ is the density of the controlled species. For example, if we are interested in the effects of controlled changes in the density of N_1 on the equilibrium density of N_2, then we drop the dN_1/dt equation and solve for the equilibrium of the three-species system (with only R_1, R_2, and N_2) with N_1 treated as a parameter. For a given controlled density of N_1, the equilibrium point is denoted by $P_{3,N_2}(N_1)$.

The indirect effects inferred using these press perturbations are the same as those calculated using method 2 so long as neither predator exhibits a hydra effect in the full system (model (1)). When a predator does exhibit a hydra effect in the four-species model (1), then maintaining the density of that species at a fixed value destabilizes the system (see below). This means that (i) this approach is not informative when a predator exhibits a hydra effect in the full system and (ii) maintaining the density of the hydra-effect species at a particular value will cause one or more other species to go extinct. Below we introduce the press equilibria and then determine the stability of the equilibria.

The press equilibrium where the density of N_2 is controlled is

$$\begin{aligned}
P_{3,N_1}(N_2) =&(\hat{R}_1, \hat{R}_2, \hat{N}_1)\\
=&\{[b_{12}c_{12}(r_1c_{12} - c_{11}r_2) + d_1(c_{11}k_2 - c_{12}k_1\alpha q) - N_2b_{12}c_{12}\Delta]/\sigma_1,\\
&[b_{11}c_{11}(r_2c_{11} - r_1c_{12}) + d_1(c_{12}k_1 - c_{11}k_2\alpha/q) + N_2b_{11}c_{11}\Delta]/\sigma_1,\\
&[k_1r_2(b_{12}c_{12} - b_{11}c_{11}\alpha q) + k_2r_1(b_{11}c_{11} - b_{12}c_{12}\alpha/q)\\
&- N_2c_{22}k_1(b_{12}c_{12} - b_{11}c_{11}\alpha q) - N_2c_{21}k_2(b_{11}c_{11} - b_{12}c_{12}\alpha/q)\\
&- d_1k_1k_2(1-\alpha^2)]/\sigma_1\}
\end{aligned} \tag{D1}$$

$$\sigma_1 = c_{11}k_2(b_{11}c_{11} - b_{12}c_{12}\alpha/q) + c_{12}k_1(b_{12}c_{12} - b_{11}c_{11}\alpha q) \tag{D2}$$

Note that $\sigma_1 = -\Delta\bar{\Delta}\partial N_2^*/\partial d_2$; see equation (C4). The press equilibrium where the density of N_1 is controlled is

$$\begin{aligned}
P_{3,N_2}(N_1) =&(\hat{R}_1, \hat{R}_2, \hat{N}_2)\\
=&\{[b_{22}c_{22}(r_1c_{22} - c_{21}r_2) + d_2(c_{21}k_2 - c_{22}k_1\alpha q) - N_1b_{22}c_{22}\Delta]/\sigma_2,\\
&[b_{21}c_{21}(r_2c_{21} - r_1c_{22}) + d_2(c_{22}k_1 - c_{21}k_2\alpha/q) + N_1b_{21}c_{21}\Delta]/\sigma_2,\\
&[k_1r_2(b_{22}c_{22} - b_{21}c_{21}\alpha q) + k_2r_1(b_{21}c_{21} - b_{22}c_{22}\alpha/q)\\
&- N_1c_{12}k_1(b_{22}c_{22} - b_{21}c_{21}\alpha q) - N_1c_{11}k_2(b_{21}c_{21} - b_{22}c_{22}\alpha/q)\\
&- d_2k_1k_2(1-\alpha^2)]/\sigma_2\}
\end{aligned} \tag{D3}$$

$$\sigma_2 = c_{21}k_2(b_{21}c_{21} - b_{22}c_{22}\alpha/q) + c_{22}k_1(b_{22}c_{22} - b_{21}c_{21}\alpha q) \tag{D4}$$

Note that $\sigma_2 = -\Delta\bar{\Delta}\partial N_1^*/\partial d_1$; see equation (C3).

The effects of a controlled change in one species' density on the equilibrium density of the other are determined by differentiating the N_1 term in $P_{3,N_1}(N_2)$ with respect to N_2 and differentiating the N_2 term in $P_{3,N_2}(N_1)$ with respect to N_1. Those derivatives are

$$\begin{aligned}
\frac{\partial \hat{N}_1}{\partial N_2} &= -\frac{c_{22}k_1(b_{12}c_{12} - b_{11}c_{11}\alpha q) + c_{21}k_2(b_{11}c_{11} - b_{12}c_{12}\alpha/q)}{c_{11}k_2(b_{11}c_{11} - b_{12}c_{12}\alpha/q) + c_{12}k_1(b_{12}c_{12} - b_{11}c_{11}\alpha q)}\\
\frac{\partial \hat{N}_2}{\partial N_1} &= -\frac{c_{12}k_1(b_{22}c_{22} - b_{21}c_{21}\alpha q) + c_{11}k_2(b_{21}c_{21} - b_{22}c_{22}\alpha/q)}{c_{21}k_2(b_{21}c_{21} - b_{22}c_{22}\alpha/q) + c_{22}k_1(b_{22}c_{22} - b_{21}c_{21}\alpha q)}.
\end{aligned} \tag{D5}$$

Note that the right hand sides of those equations are equal to the right hand sides of the derivatives in equations (6) and (7), respectively, in the main text (after setting $b_{ji} = 1$).

We now show that the press equilibria are stable as long as the controlled species does not exhibit a hydra effect in model (1). Throughout we assume Δ and $\bar{\Delta}$ have the same sign. First, consider the press equilibrium $P_{3,N_1}(N_2)$. The Jacobian evaluated at $P_{3,N_1}(N_2)$ is

$$J_{3,N_1} = \begin{pmatrix} -k_1\hat{R}_1 & -k_1\hat{R}_1\alpha q & -c_{11}\hat{R}_1 \\ -k_2\hat{R}_2\alpha/q & -k_2\hat{R}_2 & -c_{12}\hat{R}_2 \\ b_{11}c_{11}\hat{N}_1 & b_{12}c_{12}\hat{N}_1 & 0 \end{pmatrix}. \tag{D6}$$

The characteristic polynomial for J_{3,N_1} is $p(\lambda) = \lambda^3 + a_1\lambda^2 + a_2\lambda + a_3$ where

$$\begin{aligned} a_1 &= k_1\hat{R}_1 + k_2\hat{R}_2 \\ a_2 &= \hat{N}_1(b_{11}c_{11}c_{11}\hat{R}_1 + b_{12}c_{12}c_{12}\hat{R}_2) + k_1k_2\hat{R}_1\hat{R}_2(1-\alpha^2) \\ a_3 &= -\det(J_{3,N_1}) = \hat{R}_1\hat{R}_2\hat{N}_1\sigma_1. \end{aligned} \tag{D7}$$

The number of eigenvalues of J_{3,N_1} with positive real part is given by the number of sign changes in the sequence

$$\{1, a_1, a_1(a_1a_2 - a_3), a_3\}. \tag{D8}$$

The first and second terms of the sequence are positive. The difference $a_1a_2 - a_3$ in the third term simplifies to

$$\begin{aligned} a_1a_2 - a_3 =& \hat{R}_1\hat{R}_2^2k_1k_2^2(1-\alpha^2) + \hat{R}_1^2\hat{R}_2k_1^2k_2(1-\alpha^2) + \hat{R}_2^2\hat{N}_1b_{12}c_{12}c_{12}k_2 \\ &+ \hat{R}_2^2\hat{N}_1b_{11}c_{11}c_{11} + \hat{R}_1\hat{R}_2\hat{N}_1(b_{11}c_{11}c_{12}k_1\alpha q + b_{12}c_{12}c_{11}k_2\alpha/q) \end{aligned} \tag{D9}$$

This is always positive if $\alpha \leq 1$. Note that if values of α larger than one are allowed, then for sufficiently large values of α the third term can change signs and become negative. The fourth term has the same sign as σ_1.

If $\sigma_1 > 0$, then predator N_1 does not exhibit a hydra effect in the full model (1). In this case, if $\alpha \leq 1$, then all entries of the sequence (D8) are positive. This means that $P_{3,N_1}(N_2)$ is stable and stable coexistence of all species is possible. If $\sigma_1 < 0$, then predator N_2 does exhibit a hydra effect in model (1). In this case, all entries of the sequence (D8) are positive except for the last entry, implying $P_{3,N_1}(N_2)$ is a saddle. This means that stable or cyclic coexistence of all species is not possible and that trajectories will converge to a boundary equilibrium where one or more species are extinct. Note that we use 'coexistence' to refer to the coexistence of all four of the original species. It is often the case that introducing a specialist top predator that consumes N_i, which has a hydra effect, causes extinction of one of the prey, but the two original predators still coexist.

For the press equilibrium $P_{3,N_2}(N_2)$, the analysis and conclusions are identical after making the substitutions $c_{j1} \to c_{k1}$ and $b_{j1} \to b_{k1}$ where $j \neq k$ and $\sigma_1 \to \sigma_2$. Hence, for $\alpha \leq 1$, stable coexistence occurs when predator N_2 does not exhibit a hydra effect in the original model ($\sigma_2 > 0$). When $\sigma_2 > 0$, predator N_2 exhibits a hydra effect in the original model (1) and stable coexistence of all four species at $P_{3,N_2}(N_2)$ is not possible.