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Appendix B Locations and stabilities of the equilibrium points

Let $P_{R_1R_2}$ denote the coexistence equilibrium of the subsystem where only R_1 and R_2 are present (assuming it exists). Let $P_{R_iN_j}$ denote the coexistence equilibrium of the subsystem where only R_i and N_j are present. Let P_{3,N_j} denote the coexistence equilibrium of the subsystem where only R_1, R_2 and N_j are present (assuming it exists). Let P_4 denote the coexistence equilibrium where the densities of all four species are positive. We refer to $P_{R_1R_2}$, $P_{R_iN_j}$, and P_{3,N_j} as boundary equilibria. In the following, we denote the entries of the two-species equilibria using overbars (e.g., $\bar{R}_1$), the entries of the three-species equilibria using hats (e.g., $\hat{R}_1$), and the entries of the four species equilibria using asterisks (e.g., R_1^*).

Appendix B.1 Definition and stability of the two-species equilibria

There are five two-species equilibria. To be biologically relevant the equilibrium densities of both species must be positive. The boundary equilibrium where R_1 and R_2 coexist is

$$P_{R_1R_2} = \{\bar{R}_1, \bar{R}_2\} = \left\{ \frac{1}{1-\alpha^2}\left(\frac{r_1}{k_1} - \frac{r_2\alpha q}{k_2}\right), \frac{1}{1-\alpha^2}\left(\frac{r_2}{k_2} - \frac{r_1\alpha/q}{k_1}\right) \right\}. \qquad \text{(B1)}$$

This equilibrium can be invaded by N_j if $0 < b_{j1}c_{j1}\bar{R}_1 + b_{j2}c_{j2}\bar{R}_2 - d_j$ where $\bar{R}_i$ is the equilibrium density of R_i at $P_{R_1R_2}$.

The four remaining two-species equilibria each involve one predator species and one prey species. The boundary equilibrium where R_i and N_j coexist is

$$P_{R_iN_j} = \{\bar{R}_i, \bar{N}_j\} = \left\{ \frac{d_j}{b_{ji}c_{ji}}, \frac{r_i}{c_{ji}}\left[1 - \frac{d_jk_i}{b_{ji}c_{ji}r_i}\right] \right\}. \qquad \text{(B2)}$$

Table B1: Stability conditions for two-species boundary equilibria

Eq.	Stability Condition (prey invasion) (predator invasion)	Resource Partitioning $\Delta, \bar{\Delta} > 0$	$\bar{\Delta}, \Delta < 0$
$P_{R_1N_1}$	$r_2\left(1-\frac{d_1k_2}{b_{11}c_{11}r_2}\alpha/q\right)-\frac{c_{12}r_1}{c_{11}}\left(1-\frac{d_1k_1}{b_{11}c_{11}r_1}\right)$	$\pm$	$+$
	$b_{21}c_{21}d_1-b_{11}c_{11}d_2$	$+$	$-$
$P_{R_2N_1}$	$r_1\left(1-\frac{d_1k_1}{b_{12}c_{12}r_1}\alpha q\right)-\frac{c_{11}r_2}{c_{12}}\left(1-\frac{d_1k_2}{b_{12}c_{12}r_2}\right)$	$+$	$\pm$
	$b_{22}c_{22}d_1-b_{12}c_{12}d_2$	$-$	$+$
$P_{R_2N_2}$	$r_1\left(1-\frac{d_2k_1}{b_{22}c_{22}r_1}\alpha q\right)-\frac{c_{21}r_2}{c_{22}}\left(1-\frac{d_2k_2}{b_{22}c_{22}r_2}\right)$	$\pm$	$+$
	$b_{12}c_{12}d_2-b_{22}c_{22}d_1$	$+$	$-$
$P_{R_1N_2}$	$r_2\left(1-\frac{d_2k_2}{b_{21}c_{21}r_2}\alpha/q\right)-\frac{c_{22}r_1}{c_{21}}\left(1-\frac{d_2k_1}{b_{21}c_{21}r_1}\right)$	$+$	$\pm$
	$b_{11}c_{11}d_2-b_{21}c_{21}d_1$	$-$	$+$

Legend: $+$ can invade, $-$ cannot invade, and $\pm$ invasion depends on parameters

Let N_k and R_h denote the two species not present at $P_{R_iN_j}$. N_k can invade if

$$b_{ki}c_{ki}d_j - b_{ji}c_{ji}d_k > 0. \tag{B3}$$

R_h can invade if

$$r_h\left(1-\frac{d_jk_h}{b_{ji}c_{ji}r_h}\alpha_{hi}\right)-\frac{c_{jh}r_i}{c_{ji}}\left(1-\frac{d_jk_i}{b_{ji}c_{ji}r_i}\right) > 0. \tag{B4}$$

The stabilities of the four 1-predator,1-prey equilibria are shown in Table B1. Note that the stabilities depend on the signs of Δ and $\bar{\Delta}$. In Table B1, $+$ implies invasion by that species is possible, $-$ implies invasion is not possible by that species, and $\pm$ implies either outcome is possible.

Note that if both of the above two inequalities are reversed for a particular the 1-predator,1-prey equilibrium, then that equilibrium cannot be invaded. It is possible to choose parameter values such that there are two uninvasible 1-predator,1-prey equilibria. This occurs in two cases: (i) all invasion conditions for $P_{R_1N_1}$ and $P_{R_2N_2}$ are negative or (ii) all invasion conditions for $P_{R_1N_2}$ and $P_{R_2N_1}$ are negative. In both cases the system exhibits bistability and four-species coexistence is not possible.

Appendix B.2 Definition and stability of the three-species equilibria

There are two three-species equilibria. The equilibrium where R_1, R_2 and N_j coexist is

$$P_{3,N_j} = \{\hat{R}_1, \hat{R}_2, \hat{N}_j\} = \left\{ \frac{c_{j2}(r_1 b_{j2} c_{j2} - d_j k_1 \alpha q) - c_{j1}(r_2 b_{j2} c_{j2} - d_j k_2)}{c_{j1} k_2 (b_{j1} c_{j1} - b_{j2} c_{j2} \alpha / q) + c_{j2} k_1 (b_{j2} c_{j2} - b_{j1} c_{j1} \alpha q)}, \right.$$
$$\frac{c_{j1}(r_2 b_{j1} c_{j1} - d_j k_2 \alpha / q) - c_{j2}(r_1 b_{j1} c_{j1} - d_j k_1)}{c_{j1} k_2 (b_{j1} c_{j1} - b_{j2} c_{j2} \alpha / q) + c_{j2} k_1 (b_{j2} c_{j2} - b_{j1} c_{j1} \alpha q)},$$
$$\left. \frac{r_2 k_1 (b_{j2} c_{j2} - b_{j1} c_{j1} \alpha q) + r_1 k_2 (b_{j1} c_{j1} - b_{j2} c_{j2} \alpha / q) - k_1 k_2 d_j (1 - \alpha^2)}{c_{j1} k_2 (b_{j1} c_{j1} - b_{j2} c_{j2} \alpha / q) + c_{j2} k_1 (b_{j2} c_{j2} - b_{j1} c_{j1} \alpha q)} \right\}. \tag{B5}$$

We denote the denominator of the entries of P_{3,N_j} by $\sigma_j = c_{j1} k_2 (b_{j1} c_{j1} - b_{j2} c_{j2} \alpha / q) + c_{j2} k_1 (b_{j2} c_{j2} - b_{j1} c_{j1} \alpha q)$. As shown in appendix D, stable coexistence of all three species occurs when $\sigma_j > 0$ and $\alpha < 1$. If $\sigma_j < 0$, then stable coexistence is not possible because P_{3,N_j} is a saddle with one eigenvalue with positive real part. P_{3,N_j} can be invaded by the predator not present at equilibrium, N_k, if

$$b_{k1} c_{k1} \hat{R}_1 + b_{k2} c_{k2} \hat{R}_2 - d_k > 0. \tag{B6}$$

Appendix B.3 Definition and stability of the four-species equilibrium

The four-species coexistence equilibrium is

$$P_4 = \{R_1^*, R_2^*, N_1^*, N_2^*\} = \left\{ \frac{b_{12} c_{12} d_2 - b_{22} c_{22} d_1}{\bar{\Delta}}, \frac{b_{21} c_{21} d_1 - b_{11} c_{11} d_2}{\bar{\Delta}}, \right.$$
$$\frac{r_2 c_{21} - r_1 c_{22}}{\Delta} + \frac{c_{22} k_1 - c_{21} k_2 \alpha / q}{\Delta} R_1^* - \frac{c_{21} k_2 - c_{22} k_1 \alpha q}{\Delta} R_2^*,$$
$$\left. \frac{r_1 c_{12} - r_2 c_{11}}{\Delta} + \frac{c_{11} k_2 - c_{12} k_1 \alpha q}{\Delta} R_2^* - \frac{c_{12} k_1 - c_{11} k_2 \alpha / q}{\Delta} R_1^* \right\}.$$

Each N_j entry of P_4 is positive if (1) the other three species can coexist (i.e., P_{3,N_k} has positive entries and $\sigma_k > 0$) and the three-species subsystem can be invaded by N_j or (2) N_j can invade one of the two-species equilibria at which it is absent, e.g., N_1 can invade P_{R_1,N_2} or P_{R_2,N_2}. The proof of this statement follows.

Theorem 1. *Assume Δ and $\bar{\Delta}$ have the same sign.*
(i) If P_{3,N_2} has positive entries, $\sigma_2 > 0$, and N_1 can invade P_{3,N_2}, then the N_1 entry of P_4 is positive. Similarly, if P_{3,N_1} has positive entries, $\sigma_1 > 0$, and N_2 can invade P_{3,N_1}, then the N_2 entry of P_4 is positive.
(ii) Assume $P_{R_i N_j}$ has positive entries for all i and j. All entries of P_4 are positive only if N_1 can invade $P_{R_i N_2}$ and N_2 can invade $P_{R_h N_1}$ for $i \neq h$.

Proof. Proof of (i): We will prove the statement for the N_1 entry. The proof for the N_2 entry is nearly identical. Denote the condition for N_1 to invade P_{3,N_2}, i.e., the left hand side of equation (B6), by C_1. Note that $C_1 = N_2^* \Delta \bar{\Delta} \sigma_2$ where N_2^* is the equilibrium density of N_2 at P_4. Since we assume Δ and $\bar{\Delta}$ have the same sign, $\sigma_2 > 0$, and P_{3,N_2} has positive entries, C_1 and N_2 have the same sign. Hence, invasion ($C_1 > 0$) implies $N_2^* > 0$.

Proof of (ii) We will prove the result by way of a proof by contradiction. Via Table B1, we have that if N_1 can invade $P_{R_2N_2}$ then N_2 cannot invade $P_{R_2N_1}$. Similarly, if N_1 can invade $P_{R_1N_2}$ then N_2 cannot invade $P_{R_1N_1}$. Assume the entries of P_4 are positive and N_1 can invade both $P_{R_1N_2}$ and $P_{R_2N_2}$. This implies that $A_1 = (b_{12}c_{12}d_2 - d_1 b_{22}c_{22}) > 0$ and $A_2 = (b_{11}c_{11}d_2 - b_{21}c_{21}d_1) > 0$. Because $R_1^* = A_1/\bar{\Delta}$ and $R_2^* = -A_2/\bar{\Delta}$, it must be the case that either R_1^* or R_2^* is negative, which contradicts our assumption that P_4 has positive entries. Via an identical argument, if N_1 can invade both $P_{R_1N_2}$ and $P_{R_2N_2}$, then either R_1^* or R_2^* is negative. $\square$

Equilibrium Stability: We now present some limited results about the stability of P_4. Figure 4 of the main text shows the locations of the Hopf bifurcation curves for the numerical examples in Figures 1 and 2. Our two main findings are that (1) four-species coexistence is not possible if Δ and $\bar{\Delta}$ have opposite signs and (2) cycles are more likely to occur when interspecific prey competition is sufficiently high (α close to one) and asymmetric ($q \neq 1$). We also show that stable coexistence is guaranteed when $b_{11}/b_{21} = b_{12}/b_{22}$ and α is sufficiently small.

The Jacobian evaluated at P_4 is

$$J|_{P_4} = \begin{pmatrix} -R_1^*k_1 & -R_1^*k_1\alpha q & -c_{11}R_1^* & -c_{21}R_1^* \\ -R_2^*k_2\alpha/q & -R_2^*k_2 & -c_{12}R_2^* & -c_{22}R_2^* \\ b_{11}c_{11}N_1^* & b_{12}c_{12}N_1^* & 0 & 0 \\ b_{21}c_{21}N_2^* & b_{22}c_{22}N_2^* & 0 & 0 \end{pmatrix}. \tag{B7}$$

The determinant of the Jacobian is $N_1^*N_2^*R_1^*R_2^*\Delta\bar{\Delta}$. Stable or cyclic coexistence of all species only occurs in our Lotka-Volterra model when the determinant of the Jacobian is positive. Consequently, coexistence is not possible if Δ and $\bar{\Delta}$ have opposite signs. When Δ and $\bar{\Delta}$ have the same sign, stable or cyclic coexistence are possible.

The characteristic polynomial for the Jacobian is

$$p(\lambda) = \lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 \tag{B8}$$

where

$$\begin{aligned} a_1 &= k_1R_1^* + k_2R_2^* \\ a_2 &= R_1^*R_2^*k_1k_2(1-\alpha^2) + N_1^*R_1^*b_{11}c_{11}^2 + N_1^*R_2^*b_{12}c_{12}^2 + N_2^*R_1^*b_{21}c_{21}^2 + N_2^*R_2^*b_{22}c_{22}^2 \\ a_3 &= -R_1^*R_2^*\alpha(k_1q + k_2/q)(N_1^*b_{11}c_{11}c_{12} + N_2^*b_{21}c_{21}c_{22}) \\ &\quad + R_1^*R_2^*(N_1^*k_2b_{11}c_{11}^2 + N_1^*k_1b_{12}c_{12}^2 + N_2^*k_1b_{22}c_{22}^2 + N_2^*k_2b_{21}c_{21}^2) \\ a_4 &= N_1^*N_2^*R_1^*R_2^*\Delta\bar{\Delta}. \end{aligned} \tag{B9}$$

The number of roots with positive real part is given by the number of sign changes in the sequence $\{A_0, A_1, A_2, A_3, A_4\}$ where $A_0 = 1$, $A_1 = a_1$, $A_2 = a_1(a_1a_2 - a_3)$, $A_3 = (a_1a_2 - a_3)(a_1a_2a_3 - a_3^2 - a_1^2a_4)$, and $A_4 = a_4$. By inspection, A_0, and A_1 are positive. A_2 is positive under our assumption that $\alpha \leq 1$. A_4 has the same sign as $\Delta\bar{\Delta}$, which is positive since we assume Δ and $\bar{\Delta}$ have the same sign. Thus, the occurrence of cycles is determined by the sign of A_3: cycles arise when A_3 is negative and stable coexistence occurs when A_3 is positive. After collecting powers of α and q, we have

$$a_1a_2a_3 - a_3^2 - a_1^2a_4 = (c_1 + c_2)\alpha^3 - c_3\alpha^2 - c_4\alpha^2q^2 - c_5\alpha^2q^{-2} + (c_6 + c_7)\alpha + c_8 \tag{B10}$$

where c_i is positive for $i \leq 5$; $c_1 = O(q)$; $c_2 = O(q^{-1})$; c_3, c_4, c_5, and c_8 do not depend on α or q; $c_6 = O(q)$; and $c_7 = O(q^{-1})$. The signs of the $O(\alpha^2q^2)$ and $O(\alpha^2q^{-2})$ terms in equation (B10) suggest that cycles will arise when interspecific prey competition is sufficiently high (α is close to one) and sufficiently asymmetric (q is sufficiently larger or smaller than 1).

Using a Lyapunov function, we now show that stable coexistence is guaranteed if $b_{11}/b_{21} = b_{12}/b_{22}$ and $\alpha < 2q\sqrt{b_{11}c_{11}b_{12}c_{12}k_1k_2}/(c_{11}b_{11}k_1q^2 + c_{12}b_{12}k_2)$.

Theorem 2. *If $b_{11}/b_{21} = b_{12}/b_{22}$, then P_4 is globally Lyapunov stable when*

$$(b_{12}k_2\alpha/q + b_{11}k_1\alpha q)^2 - 4b_{12}b_{11}k_1k_2 < 0. \tag{B11}$$

Proof. Let $P_4 = (R_1^*, R_2^*, N_1^*, N_2^*)$. Our Lyapunov function is

$$\begin{aligned} V(R_1, R_2, N_1, N_2) = {} & c_1\left[R_1 - R_1^* - R_1^*\ln(R_1) + R_1^*\ln(R_1^*)\right] \\ & + c_2\left[R_2 - R_2^* - R_2^*\ln(R_2) + R_2^*\ln(R_2^*)\right] \\ & + c_3\left[N_1 - N_1^* - N_1^*\ln(N_1) + N_1^*\ln(N_1^*)\right] \\ & + c_4\left[N_2 - N_2^* - N_2^*\ln(N_1) + N_2^*\ln(N_2^*)\right] \end{aligned} \tag{B12}$$

for some constants $c_i > 0$. Note that $V(R_1, R_2, N_1, N_2) \geq 0$ for all positive values of R_1, R_2, N_1, and N_2 and equality holds only at P_4. Since $dR_i/dt(P_4) = 0$ and $dN_j/dt(P_4) = 0$, we can write dV/dt as

$$\begin{aligned} \frac{dV}{dt} = {} & c_1(R_1 - R_1^*)\left[\frac{dR_1}{dt} - \frac{dR_1}{dt}(P_4)\right] - c_2(R_2 - R_2^*)\left[\frac{dR_2}{dt} - \frac{dR_2}{dt}(P_4)\right] \\ & - c_3(N_1 - N_1^*)\left[\frac{dN_1}{dt} - \frac{dN_1}{dt}(P_4)\right] - c_4(N_2 - N_2^*)\left[\frac{dN_2}{dt} - \frac{dN_2}{dt}(P_4)\right]. \end{aligned} \tag{B13}$$

After algebraic manipulation we have

$$\begin{aligned} \frac{dV}{dt} = {} & -c_1k_1(R_1 - R_1^*)^2 - c_2k_2(R_2 - R_2^*)^2 - (c_2k_2\alpha/q + c_1k_1\alpha q)(R_1 - R_1^*)(R_2 - R_2^*) \\ & + (R_1 - R_1^*)(N_1 - N_1^*)(c_3b_{11}c_{11} - c_1c_{11}) + (R_1 - R_1^*)(N_2 - N_2^*)(c_4b_{21}c_{21} - c_1c_{21}) \\ & + (R_2 - R_2^*)(N_1 - N_1^*)(c_3b_{12}c_{12} - c_2c_{12}) + (R_2 - R_2^*)(N_2 - N_2^*)(c_4b_{22}c_{22} - c_2c_{22}) \end{aligned} \tag{B14}$$

The terms in the bottom two lines are zero when the coefficients c_i satisfy

$$\frac{c_3}{c_4} = \frac{b_{11}}{b_{21}} = \frac{b_{12}}{b_{22}}, \qquad c_1 = b_{11}c_3, \qquad c_2 = b_{12}c_3. \tag{B15}$$

Recall that we assume $b_{11}/b_{21} = b_{12}/b_{22}$. Setting $c_3 = 1$ yields

$$\frac{dV}{dt} = -b_{11}k_1(R_1 - R_1^*)^2 - b_{12}k_2(R_2 - R_2^*)^2 - (b_{12}k_2\alpha/q + b_{11}k_1\alpha q)(R_1 - R_1^*)(R_2 - R_2^*)$$

We want the conditions under which $dV/dt \leq 0$ for all positive R_1 and R_2. Let $x = (R_1 - R_1^*)$, $y = (R_1 - R_1^*)$, and $c = b_{12}k_2\alpha/q + b_{11}k_1\alpha q$. Then the condition $dV/dt \leq 0$ for all positive R_1 and R_2 is the same as determining when the conditions on c are such that there does not exist a real solution to $0 = b_{11}k_1x^2 + b_{12}k_2y^2 + cxy$. Via the quadratic formula, this occurs when $c^2 - 4b_{11}b_{12}k_1k_2 < 0$. Substituting for c yields the result. □