1) Consider the Lotka- Volterra model for two competing species:

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \alpha_{11} N_1 - \alpha_{12} N_2) \qquad (1)$$

$$\frac{dN_2}{dt} = r_2 N_2 (1 - \alpha_{22} N_2 - \alpha_{21} N_1)$$

a) solve equation (i) for the coexistence equilibrium. Show that there are two situations under which coexistence equilibrium is feasible. Also show that the two cases correspond to stable coexistence and priority effects

When the system is at equilibrium, $\frac{dN_1}{dt} = \frac{dN_2}{dt} = 0$.

So, $\frac{dN_1}{dt} = 0 = r_1 N_1 (1 - \alpha_{11} N_1 - \alpha_{12} N_2) = \frac{dN_2}{dt} = r_2 N_2 (1 - \alpha_{22} N_2 - \alpha_{21} N_1)$

The first trivial case is when $\boxed{N_1 = N_2 = 0}$

Then, we consider eq. by setting $(1 - \alpha_{11} N_1 - \alpha_{12} N_2) = 0 = (1 - \alpha_{22} N_2 - \alpha_{21} N_1)$

By setting $N_2 = 0$ (to the left) and $N_1 = 0$ (to the right), we derive the boundary equilibria - $\boxed{(1/\alpha_{11}, 0) \; ; \; (0, 1/\alpha_{22})}$

Finally, we set $(1 - \alpha_{11} N_1 - \alpha_{12} N_2) = 0 \quad ; N_2 \neq 0$

$$\rightarrow \quad 1 = \alpha_{11} N_1 + \alpha_{12} N_2 \quad \rightarrow \quad N_1^* = \frac{1 - \alpha_{12} N_2}{\alpha_{11}} \qquad (2)$$

Similarly, $N_2^* = \frac{1 - \alpha_{21} N_1}{\alpha_{22}} \qquad (3)$

By substituting Eq. (3) into Eq. (2), we get

$$N_1^* = \frac{1 - \alpha_{12} \left(\frac{1 - \alpha_{21} N_1}{\alpha_{22}} \right)}{\alpha_{11}}$$

$\rightarrow$

$$N_1^* = \frac{1}{\alpha_{11}} - \frac{\alpha_{12}(1-\alpha_{21}N_1)}{\alpha_{11}\alpha_{22}} = \frac{1}{\alpha_{11}} - \frac{\alpha_{12}}{\alpha_{11}\alpha_{22}} + \frac{\alpha_{12}\alpha_{21}N_1}{\alpha_{11}\alpha_{22}}$$

$$\rightarrow \quad N_1^* - \frac{\alpha_{12}\alpha_{21}N_1}{\alpha_{11}\alpha_{22}} = \frac{1}{\alpha_{11}} - \frac{\alpha_{12}}{\alpha_{11}\alpha_{22}} = \frac{\alpha_{22}-\alpha_{12}}{\alpha_{11}\alpha_{22}}$$

$$\rightarrow \quad N_1^*\left(1 - \frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}\right) = \frac{\alpha_{22}-\alpha_{12}}{\alpha_{11}\alpha_{22}}$$

$$\rightarrow \quad N_1^* = \left(\frac{\alpha_{22}-\alpha_{12}}{\alpha_{11}\alpha_{22}}\right) \Big/ \left(1 - \frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}\right) = \frac{\left(\frac{\alpha_{22}-\alpha_{12}}{\alpha_{11}\alpha_{22}}\right)}{\left(\frac{\alpha_{11}\alpha_{22}-\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}\right)}$$

$$\rightarrow \quad N_1^* = \frac{\alpha_{22}-\alpha_{12}}{\cancel{\alpha_{11}\alpha_{22}}} \cdot \frac{\cancel{\alpha_{11}\alpha_{22}}}{\alpha_{11}\alpha_{22}-\alpha_{12}\alpha_{21}} = \frac{\alpha_{22}-\alpha_{12}}{\alpha_{11}\alpha_{22}-\alpha_{12}\alpha_{21}} = N_1^*$$

We can go through the same algebra to arrive at the solution for N_2^*

$$(N_1^*; N_2^*) = \left(\frac{\alpha_{22}-\alpha_{12}}{\alpha_{11}\alpha_{22}-\alpha_{12}\alpha_{21}}, \frac{\alpha_{11}-\alpha_{21}}{\alpha_{11}\alpha_{22}-\alpha_{12}\alpha_{21}}\right), \; \underline{\alpha_{11}\alpha_{22} \neq \alpha_{12}\alpha_{21}} \quad (4)$$

There are two ways for $\left(\frac{\alpha_{ii}-\alpha_{ij}}{\alpha_{ii}\alpha_{jj}-\alpha_{ij}\alpha_{ji}}\right)$ to be a positive number-

a) both denominator & numenator are positive:

$$\alpha_{ii} > \alpha_{ij} \quad ; \quad \alpha_{ii}\alpha_{jj} > \alpha_{ij}\alpha_{ji}$$

→ Since $\alpha_{ii} > \alpha_{ij}$ satisfies the invasibility criterion, this case corresponds to Stable coexistence.

b) both terms are negative:

$$\alpha_{ii} < \alpha_{ij} \quad ; \quad \alpha_{ii}\alpha_{jj} < \alpha_{ij}\alpha_{ji}$$

Since $\alpha_{ii} < \alpha_{ij}$ does not satisfy invasibility criterion, this case corresponds not to stable coexistence, but priority effects.

b) Construct the Jacobian matrix for the Lotka Volterra model.

Recall the model:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \alpha_{11} N_1 - \alpha_{12} N_2\right) = r_1 N_1 - r_1 \alpha_{11} N_1^2 - r_1 N_1 \alpha_{12} N_2$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \alpha_{22} N_2 - \alpha_{21} N_1\right) = r_2 N_2 - r_2 \alpha_{22} N_2^2 - r_2 N_2 \alpha_{21} N_1$$

$$\therefore J = \begin{bmatrix} r_1 - 2 r_1 \alpha_{11} N_1 - r_1 \alpha_{12} N_2 & - r_1 N_1 \alpha_{12} \\ - r_2 N_2 \alpha_{21} & r_2 - 2 r_2 \alpha_{22} N_2 - r_2 \alpha_{21} N_1 \end{bmatrix}$$

We can simplify the J_{11} and J_{22} terms:

$$J_{11} = r_1 - 2 r_1 \alpha_{11} N_1 - r_1 \alpha_{12} N_2 = r_1 \left(1 - \alpha_{11} N_1 - \alpha_{12} N_2\right) - r_1 \alpha_{11} N_1$$

Since we are considering the system nearly at equilibrium, this bracketed term tends to 0, so that

$$J_{11} \approx - r_1 \alpha_{11} N_1 .$$

*Note: $r_1 \left(1 - \alpha_{11} N_1 - \alpha_{12} N_2\right) = \frac{dN}{dt} \frac{1}{N}$, so the whole thing is 0 @ eq.

Thus simplified (and similarly for J_{22}), we get

$$J = \begin{bmatrix} - r_1 \alpha_{11} N_1 & - r_1 N_1 \alpha_{12} \\ - r_2 N_2 \alpha_{21} & - r_2 \alpha_{22} N_2 \end{bmatrix}$$

c) Derive Routh-Hurwitz criteria for the priority effects case. Compare the results with those of the stable coexistence case. Point out major differences and what they say about long-term coexistence. 4

Recall the Interior equilibrium: $\left(\dfrac{\alpha_{22} - \alpha_{21}}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}} , \dfrac{\alpha_{11} - \alpha_{12}}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}} \right)$, $\alpha_{11}\alpha_{22} \neq \alpha_{12}\alpha_{21}$

Recall J: $\begin{bmatrix} -r_1\alpha_{11}N_1 & -r_1N_1\alpha_{12} \\ -r_2\alpha_{21}N_2 & -r_2\alpha_{22}N_2 \end{bmatrix}$

The Routh-Hurwitz criteria are that (N_1^*, N_2^*) is stable if $-(Tr(J)) > 0$ and $Det(J) > 0$

If ~~either~~ $-Tr(J)$ and $Det(J)$ are of opposite signs, the equilibrium is a saddle point.

$A_1 = -Tr(J) = -(-r_1\alpha_{11}N_1 + -r_2\alpha_{22}N_2) = r_1\alpha_{11}N_1 + r_2\alpha_{22}N_2$, which is always positive

so, $A_1 > 0$

$A_2 = Det(J) = (-r_{1}\alpha_{11}N_1)(-r_2\alpha_{22}N_2) - (-r_2\alpha_{21}N_2)(-r_1\alpha_{12}N_1)$

$= r_1N_1N_2r_2(\alpha_{11}\alpha_{22} - \alpha_{21}\alpha_{12})$

We know that for the second equilibrium point (the one considered here), both $\alpha_{22} - \alpha_{21} < 0$ and $\alpha_{22}\alpha_{11} - \alpha_{12}\alpha_{21} < 0$.

Since this second term appears in the equation for A_2, $A_2 < 0$

→ Since $A_1 > 0$ and $A_2 < 0$, the second coexistence case yields a saddle point.

d. Derive an algebraic equation for the eigenvalues when competition involves priority effects. Show that the two Eigenvalues have opposite signs.

Recall J: $\begin{bmatrix} -r_1\alpha_{11}N_1 & -r_1N_1\alpha_{12} \\ -r_2N_2\alpha_{21} & -r_1\alpha_{22}N_2 \end{bmatrix}$

and recall the characteristic polynomial: $0 = \lambda^2 + A_1\lambda + A_2$

From part (c), recall the expressions for A_1 and A_2:

$$A_1 = r_1\alpha_{11}N_1 + r_2\alpha_{22}N_2$$

$$A_2 = r_1r_2N_1N_2(\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21})$$

Applying the quadratic formula to the characteristic polynomial, we get

$$\lambda_{1,2} = \frac{1}{2}\left(-A_1 \pm \sqrt{A_1^2 - 4A_2}\right)$$

$$= \frac{1}{2}\left(-(r_1\alpha_{11}N_1 + r_2\alpha_{22}N_2) \pm \sqrt{(r_1\alpha_{11}N_1 + r_2\alpha_{22}N_2)^2 - 4r_1r_2N_1N_2(\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21})}\right)$$

To show that λ_1 and λ_2 are of different signs, we need to show that the output of the $\pm$ yields one positive and one negative term.

Since we are considering the Priority Effect case where $(\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}) < 0$,

We know that ~~the~~ $\left|\sqrt{(r_1\alpha_{11}N_1 + r_2\alpha_{22}N_2)^2 - 4r_1r_2N_1N_2(\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21})}\right| > \left|\sqrt{(r_1\alpha_{11}N_1 + r_2\alpha_{22}N_2)^2}\right|$

We can rewrite (and simplify) the eigenvalue expression to the form

$$\frac{1}{2}\left(-x \pm \sqrt{x^2 + y}\right), \quad y > 0.$$

Since $\sqrt{x^2+y} > x$, the $\pm$ operation yields one positive and one negative output; therefore, there is a positive and a negative Eigenvalue!

e. Using the Eigenvalue expressions, show that local stability of the coexistence requires two negative eigenvalues.

$$\lambda_{1,2} = \frac{1}{2}\left(-(r_1\alpha_{11}N_1 + r_2\alpha_{22}N_2) \pm \sqrt{(r_1\alpha_{11}N_1 + r_2\alpha_{22}N_2)^2 - 4r_1r_2N_1N_2(\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21})}\right)$$

For coexistence to be stable, $\alpha_{ii} > \alpha_{jj}$; in other words, $\alpha_{jj}\alpha_{ii} - \alpha_{ij}\alpha_{ji} > 0$

We can simplify the Eigenvalue equation to the form

$$\lambda_{1,2} = \frac{1}{2}\left(-x \pm \sqrt{x^2 - y}\right), \quad y > 0$$

Since $\left|\sqrt{x^2-y}\right| < |-x|$, we see that both outcomes of the $\pm$ operation will be negative numbers. Therefore, both eigenvalues will be negative in cases of stable coexistence in the Lotka-Volterra Competition model.

2. Consider a model for two species engaged in a mutualistic interaction

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \alpha_{11} N_1 + m_{12} N_2)$$
$$\frac{dN_2}{dt} = r_2 N_2 (1 - \alpha_{22} N_2 + m_{21} N_1) \quad (2.1)$$

a) Solve for equilibria. Identify the boundary equilibria and the interior (coexistence) equilibria.

1) The first (trivial) equilibrium point is $\underline{(N_1^*, N_2^*) = (0, 0)}$

2) A second set of boundary equilibria occur when $N_1 = 0$ or $N_2 = 0$

$$\frac{dN_1}{dt} = 0 = r_1 N_1 (1 - \alpha_{11} N_1 + \underbrace{m_{12} N_2}_{0}) = r_1 N_1 (1 - \alpha_{11} N_1)$$

$\rightarrow 0 = 1 - \alpha_{11} N_1 \quad \rightarrow N_1^* = 1/\alpha_{11}$

Similarly for N_2^*. So, $\underline{(N_1^*, N_2^*) = (1/\alpha_{11}, 0)}$ and $\underline{(N_1^*, N_2^*) = (0, 1/\alpha_{22})}$

3) To solve for the interior equilibria:

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \alpha_{11} N_1 + m_{12} N_2)$$

$$\therefore (1 - \alpha_{11} N_1 + m_{12} N_2) = 0 \quad \rightarrow \quad N_1^* = \frac{1 + m_{12} N_2}{\alpha_{11}} \quad (2.2)$$

Similarly, $$N_2^* = \frac{1 + m_{21} N_1}{\alpha_{22}} \quad (2.3)$$

Substituting eq (2.3) into eq (2.2), we get

$$N_1^* = \frac{1 + m_{12}\left(\frac{1 + m_{21} N_1}{\alpha_{22}}\right)}{\alpha_{11}} = \frac{1}{\alpha_{11}} + \frac{m_{12}}{\alpha_{11}\alpha_{22}} + \frac{m_{12} m_{21} N_1}{\alpha_{11}\alpha_{22}}$$

$$\rightarrow N_1^* - \frac{m_{12} m_{21} N_1}{\alpha_{11}\alpha_{22}} = N_1^* \left(1 - \frac{m_{12} m_{21}}{\alpha_{11}\alpha_{22}}\right) = \frac{\alpha_{22} + m_{12}}{\alpha_{11}\alpha_{22}} \quad (2.4)$$

$\longrightarrow$

Rewrite eq (2.4) from previous side:

$$N_1^* \left(1 - \frac{m_{12} m_{21}}{\alpha_{11} \alpha_{22}}\right) = \frac{\alpha_{22} + m_{12}}{\alpha_{11} \alpha_{22}}$$

$$\rightarrow \quad N_1^* = \frac{\left(\frac{\alpha_{22} + m_{12}}{\alpha_{11} \alpha_{22}}\right)}{\left(1 - \frac{m_{12} m_{21}}{\alpha_{11} \alpha_{22}}\right)} = \frac{\left(\frac{\alpha_{22} + m_{12}}{\alpha_{11} \alpha_{22}}\right)}{\left(\frac{\alpha_{11}\alpha_{22} - m_{12} m_{21}}{\alpha_{11} \alpha_{22}}\right)} = \frac{\alpha_{22} + m_{12}}{\alpha_{11}\alpha_{22} - m_{12} m_{21}} = N_1^*$$

We follow similar algebra to derive N_2^*. So, the interior equilibrium is

$$(N_1^*, N_2^*) = \left(\frac{\alpha_{22} + m_{12}}{\alpha_{11}\alpha_{22} - m_{12} m_{21}}, \frac{\alpha_{11} + m_{21}}{\alpha_{11}\alpha_{22} - m_{12} m_{21}}\right), \quad \alpha_{11}\alpha_{22} \neq m_{12} m_{21}$$

b) Compute the invasion criterion for each species. Show that each species can always increase when rare when its mutualist is abundant.

To satisfy the invasibility criterion, a species must have a positive per-capita growth rate when it is rare, and the interacting species is at its equilibrium.

I will compute the criterion for Sp. I:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \alpha_{11} N_1 + m_{12} N_2\right)$$

- to get a per-capita eq, $\frac{dN_1}{dt} \cdot \frac{1}{N_1} = r_1 \left(1 - \alpha_{11} N_1 + m_{12} N_2\right)$

- because we are interested in $dN_1/N_1 dt$ when $N \approx 0$, the $(\alpha_{11} N_1)$ term tends to 0. So,

$$\frac{dN_1}{N_1 dt} = r_1 \left(1 + m_{12} N_2\right).$$

- from Q. A, we know that the bondary ~~coor~~ equilibrium is $(N_1^*, N_2^*) = (0, 1/\alpha_{22})$

we can substitute that in to write

$$\frac{dN_1}{N_1 dt} = r_1 \left(1 + m_{12} \frac{1}{\alpha_{22}}\right)$$

- for the value to be positive, $\boxed{\left(1 + m_{12} \cdot \frac{1}{\alpha_{22}}\right) > 0.}$ This will always be true, because it is essentially $(1 + \text{positive number})$.

c) Compute the Jacobian matrix and simplify its elements.

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \alpha_{11} N_1 + m_{12} N_2\right) = r_1 N_1 - \alpha_{11} r_1 N_1^2 + r_1 N_1 m_{12} N_2 \qquad = f_1$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \alpha_{22} N_2 + m_{21} N_1\right) = r_2 N_2 - \alpha_{22} r_2 N_2^2 + r_2 N_2 m_{21} N_1 \qquad = f_2$$

$$J_{11} = \frac{\partial f_1}{\partial N_1} = r_1 - 2\alpha_{11} r_1 N_1 + r_1 N_2 m_{12}$$

$$= r_1 \left(1 - \alpha_{11} N_1 + m_{12} N_2\right) - r_1 \alpha_{11} N_1$$

Near equilibrium, the bracket term tends to 0, so $J_{11} = -r_1 \alpha_{11} N_1$

$$J_{12} = \frac{\partial f_1}{\partial N_2} = r_1 N_1 m_{12}$$

$$J_{22} = \frac{\partial f_2}{\partial N_2} = r_2 - 2\alpha_{22} r_2 N_2 + r_2 N_1 m_{21}$$

$$= r_2 \left(1 - \alpha_{22} N_2 + m_{21} N_1\right) - \alpha_{22} r_2 N_2 \approx -r_2 \alpha_{22} N_2$$

$$J_{21} = \frac{\partial f_2}{\partial N_1} = r_2 N_2 m_{21}$$

$$\therefore \quad J = \begin{bmatrix} -r_1 \alpha_{11} N_1^* & r_1 N_1 m_{12} \\ r_2 N_2 m_{21} & -r_2 \alpha_{22} N_2^* \end{bmatrix}$$

d) Compare this Jacobian with the one for the competition model.

$$J_{comp} = \begin{bmatrix} -r_1 \alpha_{11} N_1^* & -\alpha_{12} r_1 N_1 \\ -\alpha_{21} r_2 N_2 & -r_2 \alpha_{22} N_2^* \end{bmatrix} \qquad J_{mutualism} = \begin{bmatrix} -\alpha_{11} r_1 N_1^* & r_1 N_1 m_{12} \\ r_2 N_2 m_{21} & -r_2 \alpha_{22} N_2^* \end{bmatrix}$$

In the Jacobian for competition, we see only negative effects of a population on itself - this makes senses as there is only negative feedback (competitive inhibition) in the model.

The Jmutualism has positive interspecific but negative intraspecific feedbacks - also consistent with the model.

e) Using the Routh-Hurwitz criteria, evaluate the stability of these coexistence equilibria. (19)

$$J = \begin{bmatrix} -r_1\alpha_{11}N_1 & r_1 m_{12} N_1 \\ r_2 m_{21} N_2 & -r_2\alpha_{22} N_2 \end{bmatrix}$$

$A_1 = -Tr(J) = -\left(-r_1\alpha_{11}N_1 + -r_2\alpha_{22}N_2\right) = r_1\alpha_{11}N_1 + r_2\alpha_{22}N_2,$

So, $A_1 > 0$ always.

$A_2 = Det(J) = (-r_1\alpha_{11}N_1)(-r_2\alpha_{22}N_2) - (r_2 m_{21} N_2)(r_1 m_{12} N_1)$

$= r_1 r_2 N_1 N_2 \left(\alpha_{11}\alpha_{22} - m_{21}m_{12}\right)$

So, $A_2 > 0$ if $\underline{(\alpha_{11}\alpha_{22} - m_{21}m_{12}) > 0.}$ Recall from the equation for internal equilibrium that this is also a condition for having a positive internal equilibrium:

$$(N_1^*, N_2^*) = \left(\frac{\alpha_{22} + m_{12}}{\alpha_{11}\alpha_{22} - m_{12}m_{21}}, \frac{\alpha_{11} m_{21}}{\alpha_{11}\alpha_{22} - m_{12}m_{21}}\right) \quad \alpha_{11}\alpha_{22} \neq m_{12}m_{21}$$

So, if this mutualist system has an internal equilibrium, it is stable, since $\alpha_{11}\alpha_{22} - m_{12}m_{21}$ always >0 for an equilibrium to exist.

f) What is the biological interpretation of this stability criterion, and what is its general significance?

The stability criteria derived above show that *if* there is a positive equilibrium to the system, then it will always be a stable equilibrium. In other words, there is no saddle point.

This makes sense generally, as an equilibrium only occurs if net negative feedbacks exceed net positive feedbacks $(\alpha_{11}\alpha_{22} - m_{12}m_{21} > 0)$. ~~This~~