BME 5742 Bio-Systems Modeling and Control

Lecture 13
Linearization Examples 2
Linearization of the Competition and Symbiosis Models

Example 2: Need to linearize the simple Competition Model :

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \frac{N_1}{K_1} - b_{12} \frac{N_2}{K_1})$$

$$\frac{dN_2}{dt} = r_2 N_2 (1 - \frac{N_2}{K_2} - b_{21} \frac{N_1}{K_2})$$

All constants are positive.

Birth Rates: r_1, r_2

Carrying Capacities: K_1, K_2

Example 2: Recall the Competition Model normalization

- Details are not important.
- We can reduce the number of model parameters from 6 to 3.

$$u_1 = \frac{N_1}{K_1} \qquad u_2 = \frac{N_2}{K_2} \qquad \tau = r_1 t$$

Example 2: Recall the normalized Competition Model parameters

$$\rho = \frac{r_2}{r_1} \qquad a_{12} = b_{12}\frac{K_2}{K_1} \qquad a_{21} = b_{21}\frac{K_1}{K_2}$$

Example 2: Recall the normalized Competition model

$$\rho = \frac{r_2}{r_1} \qquad a_{12} = b_{12}\frac{K_2}{K_1} \qquad a_{21} = b_{21}\frac{K_1}{K_2}$$

$$u_1 = \frac{N_1}{K_1} \qquad u_2 = \frac{N_2}{K_2} \qquad \tau = r_1 t$$

$$\frac{du_1}{d\tau} = u_1(1 - u_1 - a_{12}u_2)$$

$$\frac{du_2}{d\tau} = \rho u_2(1 - u_2 - a_{21}u_1)$$

Example 2: Recall the Competition Model equilibria – we will show that equilibria locations don't depend on ρ, but equilibria stability does

$$\frac{du_1}{d\tau} = 0 = u_1(1 - u_1 - a_{12}u_2)$$

$$\frac{du_2}{d\tau} = 0 = \rho u_2(1 - u_2 - a_{21}u_1)$$

4 equilibria:

(0,0) is an unstable equilibrium.

(1,0) is stable if $a_{21}>1$, and unstable if $a_{21}<1$.

Example 2: Recall Competition Model equilibria stability results

$$\frac{du_1}{d\tau} = 0 = u_1(1 - u_1 - a_{12}u_2)$$

$$\frac{du_2}{d\tau} = 0 = \rho u_2(1 - u_2 - a_{21}u_1)$$

(0,1) is stable if $a_{12}>1$.

$((1-a_{12})/(1-a_{12}a_{21}),(1-a_{21})/(1-a_{12}a_{21}))$ exists only if both parameters are simultaneously <1, or simultaneously >1.

Example 2: Recall Competition Model equilibria stability results

$$\frac{du_1}{d\tau} = 0 = u_1(1 - u_1 - a_{12}u_2)$$

$$\frac{du_2}{d\tau} = 0 = \rho u_2(1 - u_2 - a_{21}u_1)$$

Depending on ρ, $((1-a_{12})/(1-a_{12}a_{21}),(1-a_{21})/(1-a_{12}a_{21}))$ is sometimes stable if both "a parameters" are simultaneously <1 ("non-aggressive competition").

Here both (1,0) and (0,1) are unstable.

Example 2: Recall Competition Model equilibria stability results

$$\frac{du_1}{d\tau} = 0 = u_1(1 - u_1 - a_{12}u_2)$$

$$\frac{du_2}{d\tau} = 0 = \rho u_2(1 - u_2 - a_{21}u_1)$$

$((1-a_{12})/(1-a_{12}a_{21}),(1-a_{21})/(1-a_{12}a_{21}))$ is unstable if both parameters a_{12} and a_{21} are simultaneously >1. Here both (1,0) and (0,1) are stable, each has its own domain of attraction (i.e. set of initial states from which solution converge to given equilibrium).

Example 2: Finding the A matrix

$$\frac{du_1}{d\tau} = u_1(1 - u_1 - a_{12}u_2) = f_1(u_1, u_2)$$

$$\frac{du_2}{d\tau} = \rho u_2(1 - u_2 - a_{21}u_1) = f_2(u_1, u_2), \quad x = (u_1, u_2)^T$$

$$A = \begin{pmatrix} \frac{\partial f_1}{\partial u_1} & \frac{\partial f_1}{\partial u_2} \\ \frac{\partial f_2}{\partial u_1} & \frac{\partial f_2}{\partial u_2} \end{pmatrix}\Bigg|_{x_e} = \begin{pmatrix} 1 - 2u_1 - a_{12}u_2 & -a_{12}u_1 \\ -\rho a_{21}u_2 & \rho(1 - a_{21}u_1 - 2u_2) \end{pmatrix}\Bigg|_{x_e}$$

Example 2: Stability of $(0,0)^T$

$$\frac{du_1}{d\tau} = u_1(1 - u_1 - a_{12}u_2) = f_1(u_1, u_2)$$

$$\frac{du_2}{d\tau} = \rho u_2(1 - u_2 - a_{21}u_1) = f_2(u_1, u_2), \quad x_{e1} = (0,0)^T$$

$$A = \begin{pmatrix} 1 - 2u_1 - a_{12}u_2 & -a_{12}u_1 \\ -\rho a_{21}u_2 & \rho(1 - a_{21}u_1 - 2u_2) \end{pmatrix}\Bigg|_{x_e} = \begin{pmatrix} 1 & 0 \\ 0 & \rho \end{pmatrix}$$

$$\det\begin{pmatrix} \lambda - 1 & 0 \\ 0 & \lambda - \rho \end{pmatrix} = 0 \rightarrow \lambda_1 = 1 \quad \lambda_2 = \rho$$

$(0,0)^T$ is always an unstable node

Example 2: Stability of $(0,1)^T$

$$\frac{du_1}{d\tau} = u_1(1-u_1-a_{12}u_2) = f_1(u_1,u_2)$$

$$\frac{du_2}{d\tau} = \rho u_2(1-u_2-a_{21}u_1) = f_2(u_1,u_2), \quad x_{e2} = (0,1)^T$$

$$A = \begin{pmatrix} 1-2u_1-a_{12}u_2 & -a_{12}u_1 \\ -\rho a_{21}u_2 & \rho(1-a_{21}u_1-2u_2) \end{pmatrix}\Bigg|_{x_e} = \begin{pmatrix} 1-a_{12} & 0 \\ -a_{21}\rho & -\rho \end{pmatrix}$$

$$\det\begin{pmatrix} \lambda-(1-a_{12}) & 0 \\ a_{21}\rho & \lambda+\rho \end{pmatrix} = 0 \rightarrow \lambda_1 = 1-a_{12} \quad \lambda_2 = -\rho$$

$(0,1)^T$ is a stable node if $a_{12}>1$. It is an unstable node if $a_{12}<1$.

Example 2: Stability of $(1,0)^T$

$$\frac{du_1}{d\tau} = u_1(1-u_1-a_{12}u_2) = f_1(u_1,u_2)$$

$$\frac{du_2}{d\tau} = \rho u_2(1-u_2-a_{21}u_1) = f_2(u_1,u_2), \quad x_{e3} = (1,0)^T$$

$$A = \begin{pmatrix} 1-2u_1-a_{12}u_2 & -a_{12}u_1 \\ -\rho a_{21}u_2 & \rho(1-a_{21}u_1-2u_2) \end{pmatrix}\Bigg|_{x_e} = \begin{pmatrix} -1 & -a_{12} \\ 0 & \rho(1-a_{21}) \end{pmatrix}$$

$$\det\begin{pmatrix} \lambda+1 & a_{12} \\ 0 & \lambda-\rho(1-a_{21}) \end{pmatrix} = 0 \rightarrow \lambda_1 = -1 \quad \lambda_2 = \rho(1-a_{21})$$

$(1,0)^T$ is a stable node if $a_{21}>1$. It is an unstable node if $a_{21}<1$.

Example 2: Stability of $((1-a_{12})/(1-a_{12}a_{21}),((1-a_{21})/(1-a_{12}a_{21}))^T$

$$\frac{du_1}{d\tau} = u_1(1-u_1-a_{12}u_2) = f_1(u_1,u_2)$$

$$\frac{du_2}{d\tau} = \rho u_2(1-u_2-a_{21}u_1) = f_2(u_1,u_2)$$

$$x_{e4} = \left(\frac{1-a_{12}}{1-a_{12}a_{21}}, \frac{1-a_{21}}{1-a_{12}a_{21}}\right)^T$$

$$A = \begin{pmatrix} 1-2u_1-a_{12}u_2 & -a_{12}u_1 \\ -\rho a_{21}u_2 & \rho(1-a_{21}u_1-2u_2) \end{pmatrix}\Bigg|_{x_e}$$

$$= \frac{1}{1-a_{12}a_{21}}\begin{pmatrix} -1+a_{12} & -a_{12}(1-a_{12}) \\ -\rho a_{21}(1-a_{21}) & \rho(-1+a_{21}) \end{pmatrix}$$

Example 2: Stability of $((1-a_{12})/(1-a_{12}a_{21}),((1-a_{21})/(1-a_{12}a_{21}))^T$

- For the equilibrium point to exist in the first quadrant we must have:
- Simultaneously: $a_{12}>1$ and $a_{21}>1$, or
- Simultaneously: $a_{12}<1$ and $a_{21}<1$

$$x_{e4} = \left(\frac{1-a_{12}}{1-a_{12}a_{21}}, \frac{1-a_{21}}{1-a_{12}a_{21}}\right)^T$$

Example 2: Stability of $((1-a_{12})/(1-a_{12}a_{21}),((1-a_{21})/(1-a_{12}a_{21}))^T$

$$A = \begin{pmatrix} 1-2u_1-a_{12}u_2 & -a_{12}u_1 \\ -\rho a_{21}u_2 & \rho(1-a_{21}u_1-2u_2) \end{pmatrix}\Bigg|_{x_e}$$

$$= \frac{1}{1-a_{12}a_{21}}\begin{pmatrix} -1+a_{12} & -a_{12}(1-a_{12}) \\ -\rho a_{21}(1-a_{21}) & \rho(-1+a_{21}) \end{pmatrix}$$

$$\det\begin{pmatrix} \lambda-(-1+a_{12})/* & a_{12}(1-a_{12})/* \\ \rho a_{21}(1-a_{21})/* & \lambda-\rho(-1+a_{21})/* \end{pmatrix} = 0$$

$$* = 1-a_{12}a_{21}$$

Example 2: Stability of $((1-a_{12})/(1-a_{12}a_{21}),((1-a_{21})/(1-a_{12}a_{21}))^T$

$$\det\begin{pmatrix} \lambda-(-1+a_{12})/* & a_{12}(1-a_{12})/* \\ \rho a_{21}(1-a_{21})/* & \lambda-\rho(-1+a_{21})/* \end{pmatrix}=0$$

$$*=1-a_{12}a_{21}$$

$$\lambda^2-\frac{-1+a_{12}-\rho(-1+a_{21})}{*}\lambda-\frac{a_{12}(1-a_{12})\rho a_{21}(1-a_{21})}{(*)^2}=0$$

All polynomial coefficients must be positive, for the eigenvalues to have both negative real part.

Example 2: Stability of $((1-a_{12})/(1-a_{12}a_{21}),((1-a_{21})/(1-a_{12}a_{21}))^T$

$$\det\begin{pmatrix} \lambda-(-1+a_{12})/* & a_{12}(1-a_{12})/* \\ \rho a_{21}(1-a_{21})/* & \lambda-\rho(-1+a_{21})/* \end{pmatrix}=0$$

$$*=1-a_{12}a_{21}$$

$$\lambda^2-\frac{-1+a_{12}-\rho(-1+a_{21})}{*}\lambda-\frac{a_{12}(1-a_{12})\rho a_{21}(1-a_{21})}{(*)^2}=0$$

For "aggressive competition" (a_{12} and a_{21} both >1), the coefficient of λ is negative → x_{e4} is unstable (could be a node or focus depending on ρ)

Example 2: Stability of $((1-a_{12})/(1-a_{12}a_{21}),((1-a_{21})/(1-a_{12}a_{21}))^T$

$$\det\begin{pmatrix} \lambda-(-1+a_{12})/* & a_{12}(1-a_{12})/* \\ \rho a_{21}(1-a_{21})/* & \lambda-\rho(-1+a_{21})/* \end{pmatrix}=0$$

$$*=1-a_{12}a_{21}$$

$$\lambda^2-\frac{-1+a_{12}-\rho(-1+a_{21})}{*}\lambda-\frac{a_{12}(1-a_{12})\rho a_{21}(1-a_{21})}{(*)^2}=0$$

For "non-aggressive competition" (a_{12} and a_{21} both <1), the coefficient of λ is positive. Depending on ρ the point x_{e4} is supposed to be stable. Where is the error in the calculations?

Example 3: Linearize the Simple Symbiosis Model :

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \frac{N_1}{K_1} + b_{12} \frac{N_2}{K_1})$$

$$\frac{dN_2}{dt} = r_2 N_2 (1 - \frac{N_2}{K_2} + b_{21} \frac{N_1}{K_2})$$

All constants are positive.

Birth Rates: r_1, r_2

Carrying Capacities: K_1, K_2

Example 3: Recall the Symbiosis Model Normalization

- It is done in exactly the same way as the Competition model.
- We can reduce the number of model parameters from 6 to 3.

$$u_1 = \frac{N_1}{K_1} \qquad u_2 = \frac{N_2}{K_2} \qquad \tau = r_1 t$$

Example 3: Recall the Normalized Symbiosis Model Parameters

$$\rho = \frac{r_2}{r_1} \qquad a_{12} = b_{12}\frac{K_2}{K_1} \qquad a_{21} = b_{21}\frac{K_1}{K_2}$$

Example 3: Recall the Normalized Symbiosis Model

$$\rho = \frac{r_2}{r_1} \qquad a_{12} = b_{12}\frac{K_2}{K_1} \qquad a_{21} = b_{21}\frac{K_1}{K_2}$$

$$u_1 = \frac{N_1}{K_1} \qquad u_2 = \frac{N_2}{K_2} \qquad \tau = r_1 t$$

$$\frac{du_1}{d\tau} = u_1(1 - u_1 + a_{12}u_2)$$

$$\frac{du_2}{d\tau} = \rho u_2(1 - u_2 + a_{21}u_1)$$

Example 3: Recall the Symbiosis Model Equilibria

$$\frac{du_1}{d\tau} = 0 = u_1(1 - u_1 + a_{12}u_2)$$

$$\frac{du_2}{d\tau} = 0 = \rho u_2(1 - u_2 + a_{21}u_1)$$

4 equilibria: (Stability properties – without proof)

(0,0),(1,0) and (0,1) are all unstable equilibria.

Example 3: Recall the Symbiosis Model Equilibria

$$\frac{du_1}{d\tau} = 0 = u_1(1 - u_1 + a_{12}u_2)$$

$$\frac{du_2}{d\tau} = 0 = \rho u_2(1 - u_2 + a_{21}u_1)$$

$((1+a_{12})/(1-a_{12}a_{21}),(1+a_{21})/(1-a_{12}a_{21}))$ exists only if $1-a_{21}a_{12}>0$.

Example 3: Recall the Symbiosis Model Equilibria

$$\frac{du_1}{d\tau} = 0 = u_1(1 - u_1 + a_{12}u_2)$$

$$\frac{du_2}{d\tau} = 0 = \rho u_2(1 - u_2 + a_{21}u_1)$$

If $1-a_{12}a_{21}<0$, there are only three unstable equilibrium points. All trajectories go to infinity.

It's an indication that model is unrealistic.

Example 3: Finding the A matrix

$$\frac{du_1}{d\tau} = u_1(1 - u_1 + a_{12}u_2) = f_1(u_1, u_2)$$

$$\frac{du_2}{d\tau} = \rho u_2(1 - u_2 + a_{21}u_1) = f_2(u_1, u_2), \quad x = (u_1, u_2)^T$$

$$A = \begin{pmatrix} \frac{\partial f_1}{\partial u_1} & \frac{\partial f_1}{\partial u_2} \\ \frac{\partial f_2}{\partial u_1} & \frac{\partial f_2}{\partial u_2} \end{pmatrix}\Bigg|_{x_e} = \begin{pmatrix} 1 - 2u_1 + a_{12}u_2 & a_{12}u_1 \\ \rho a_{21}u_2 & \rho(1 + a_{21}u_1 - 2u_2) \end{pmatrix}\Bigg|_{x_e}$$

Example 3: Stability of $(0,0)^T$

$$\frac{du_1}{d\tau} = u_1(1 - u_1 + a_{12}u_2) = f_1(u_1, u_2)$$

$$\frac{du_2}{d\tau} = \rho u_2(1 - u_2 + a_{21}u_1) = f_2(u_1, u_2), \quad x_{e1} = (0,0)^T$$

$$A = \begin{pmatrix} 1 - 2u_1 + a_{12}u_2 & a_{12}u_1 \\ \rho a_{21}u_2 & \rho(1 + a_{21}u_1 - 2u_2) \end{pmatrix}\Bigg|_{x_e} = \begin{pmatrix} 1 & 0 \\ 0 & \rho \end{pmatrix}$$

$$\det\begin{pmatrix} \lambda - 1 & 0 \\ 0 & \lambda - \rho \end{pmatrix} = 0 \rightarrow \lambda_1 = 1 \quad \lambda_2 = \rho$$

$(0,0)^T$ is always an unstable node

Example 3: Stability of $(0,1)^T$

$$\frac{du_1}{d\tau} = u_1(1 - u_1 + a_{12}u_2) = f_1(u_1, u_2)$$

$$\frac{du_2}{d\tau} = \rho u_2(1 - u_2 + a_{21}u_1) = f_2(u_1, u_2), \quad x_{e2} = (0,1)^T$$

$$A = \begin{pmatrix} 1 - 2u_1 + a_{12}u_2 & a_{12}u_1 \\ \rho a_{21}u_2 & \rho(1 + a_{21}u_1 - 2u_2) \end{pmatrix}\Bigg|_{x_e} = \begin{pmatrix} 1 + a_{12} & 0 \\ a_{21}\rho & -\rho \end{pmatrix}$$

$$\det\begin{pmatrix} \lambda - (1 + a_{12}) & 0 \\ -a_{21}\rho & \lambda + \rho \end{pmatrix} = 0 \rightarrow \lambda_1 = 1 + a_{12} \quad \lambda_2 = -\rho$$

$(0,1)^T$ is always an unstable node.

Example 3: Stability of $(1,0)^T$

$$\frac{du_1}{d\tau} = u_1(1 - u_1 + a_{12}u_2) = f_1(u_1, u_2)$$

$$\frac{du_2}{d\tau} = \rho u_2(1 - u_2 + a_{21}u_1) = f_2(u_1, u_2), \quad x_{e3} = (1,0)^T$$

$$A = \begin{pmatrix} 1 - 2u_1 + a_{12}u_2 & a_{12}u_1 \\ \rho a_{21}u_2 & \rho(1 + a_{21}u_1 - 2u_2) \end{pmatrix}\Bigg|_{x_e} = \begin{pmatrix} -1 & a_{12} \\ 0 & \rho(1 + a_{21}) \end{pmatrix}$$

$$\det\begin{pmatrix} \lambda + 1 & -a_{12} \\ 0 & \lambda - \rho(1 + a_{21}) \end{pmatrix} = 0 \rightarrow \lambda_1 = -1 \quad \lambda_2 = \rho(1 + a_{21})$$

$(1,0)^T$ is always an unstable node.

Example 3: Stability of $((1+a_{12})/(1-a_{12}a_{21}),((1+a_{21})/(1-a_{12}a_{21}))^T$

$$\frac{du_1}{d\tau} = u_1(1-u_1-a_{12}u_2) = f_1(u_1,u_2)$$

$$\frac{du_2}{d\tau} = \rho u_2(1-u_2-a_{21}u_1) = f_2(u_1,u_2)$$

$$x_{e4} = \left(\frac{1+a_{12}}{1-a_{12}a_{21}}, \frac{1+a_{21}}{1-a_{12}a_{21}}\right)^T$$

$$A = \begin{pmatrix} 1-2u_1+a_{12}u_2 & a_{12}u_1 \\ \rho a_{21}u_2 & \rho(1+a_{21}u_1-2u_2) \end{pmatrix}\Bigg|_{x_e}$$

$$= \frac{1}{1-a_{12}a_{21}} \begin{pmatrix} -1-a_{12} & a_{12}(1+a_{12}) \\ \rho a_{21}(1+a_{21}) & -\rho(1+a_{21}) \end{pmatrix}$$

Example 2: Stability of $((1+a_{12})/(1-a_{12}a_{21}),((1+a_{21})/(1-a_{12}a_{21}))^T$

- For the equilibrium point to exist in the first quadrant we must have:
- $1 > a_{12}a_{21}$

$$x_{e4} = \left(\frac{1+a_{12}}{1-a_{12}a_{21}}, \frac{1+a_{21}}{1-a_{12}a_{21}}\right)^T$$

Example 2: Stability of $((1+a_{12})/(1-a_{12}a_{21}),((1+a_{21})/(1-a_{12}a_{21}))^T$

$$A = \begin{pmatrix} 1-2u_1+a_{12}u_2 & a_{12}u_1 \\ \rho a_{21}u_2 & \rho(1+a_{21}u_1-2u_2) \end{pmatrix}\Bigg|_{x_e}$$

$$= \frac{1}{1-a_{12}a_{21}} \begin{pmatrix} -1-a_{12} & a_{12}(1+a_{12}) \\ \rho a_{21}(1+a_{21}) & -\rho(1+a_{21}) \end{pmatrix}$$

$$\det \begin{pmatrix} \lambda+(1+a_{12})/* & -a_{12}(1+a_{12})/* \\ -\rho a_{21}(1+a_{21})/* & \lambda+\rho(1+a_{21})/* \end{pmatrix} = 0$$

$$* = 1-a_{12}a_{21}$$

Example 2: Stability of $((1+a_{12})/(1-a_{12}a_{21}),((1+a_{21})/(1-a_{12}a_{21}))^T$

$$\det\begin{pmatrix} \lambda+(1+a_{12})/* & -a_{12}(1+a_{12})/* \\ -\rho a_{21}(1+a_{21})/* & \lambda+\rho(1+a_{21})/* \end{pmatrix}=0$$

$$*=1-a_{12}a_{21}$$

$$\lambda^2+\frac{1+a_{12}+\rho(1+a_{21})}{*}\lambda+\frac{a_{12}(1+a_{12})\rho a_{21}(1+a_{21})}{(*)^2}=0$$

All polynomial coefficients must be positive, for the eigenvalues to have both negative real part.

Example 2: Stability of $((1+a_{12})/(1-a_{12}a_{21}),((1+a_{21})/(1-a_{12}a_{21}))^T$

$$\det\begin{pmatrix} \lambda+(1+a_{12})/* & -a_{12}(1+a_{12})/* \\ -\rho a_{21}(1+a_{21})/* & \lambda+\rho(1+a_{21})/* \end{pmatrix}=0$$

$$*=1-a_{12}a_{21}$$

$$\lambda^2+\frac{1+a_{12}+\rho(1+a_{21})}{*}\lambda+\frac{a_{12}(1+a_{12})\rho a_{21}(1+a_{21})}{(*)^2}=0$$

For “non-aggressive symbiosis” ($a_{12}a_{21}<1$) the point is stable. It can be a node or a focus depending on ρ