Competition

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

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

Equilibria:

$$N_1^* = 0, \quad N_2^* = 0$$

$$N_1^* = K_1, \quad N_2^* = 0$$

$$N_1^* = 0, \quad N_2^* = K_2$$

$$N_1^* = \frac{K_1 - \alpha_{12} K_2}{1 - \alpha_{12}\alpha_{21}}, \quad \frac{K_2 - \alpha_{21} K_1}{1 - \alpha_{12}\alpha_{21}}$$

Jacobian matrix:

$$J = \begin{bmatrix} \frac{r_1}{K_1}\left(K_1 - 2N_1^* - \alpha_{12} N_2^*\right) & -\frac{r_1}{K_1}\alpha_{12} N_1^* \\ -\frac{r_2}{K_2}\alpha_{21} N_2^* & \frac{r_2}{K_2}\left(K_2 - 2N_2^* - \alpha_{21} N_1^*\right) \end{bmatrix}$$

Invasibility and local stability of boundary equilibria

Invasion criteria

Species 1 can invade if

$$\alpha_{12} K_2 < K_1$$

Species 2 can invade if

$$\alpha_{21} K_1 < K_2$$

Local stability criteria

$(N_1^*, N_2^*) = (0, K_2)$ locally stable if

$$\alpha_{12} K_2 > K_1$$

$(N_1^*, N_2^*) = (K_1, 0)$ locally stable if

$$\alpha_{21} K_1 > K_2$$

Stability of boundary equilibria $\Rightarrow$ No invasibility

Instability of boundary equilibria $\Rightarrow$ Mutual invasibility

Invasibility and stability of boundary and coexistence equilibria

Boundary equilibria	Invasion Criteria	Coexistence equilibrium
$(0, K_2)$ stable if	Species 1 can invade if	(N_1^*, N_2^*) stable if
$\alpha_{12}K_2 > K_1$	$\alpha_{12}K_2 < K_1$	$\alpha_{12}K_2 < K_1$
$(K_1, 0)$ stable if	Species 2 can invade if	and
$\alpha_{21}K_1 > K_2$	$\alpha_{21}K_1 < K_2$	$\alpha_{21}K_1 < K_2$

Stability of boundary equilibria $\Rightarrow$ No invasibility $\Rightarrow$ No coexistence

Instability of boundary equilibria $\Rightarrow$ Mutual invasibility $\Rightarrow$ Stable coexistence

Competition: long-term outcomes

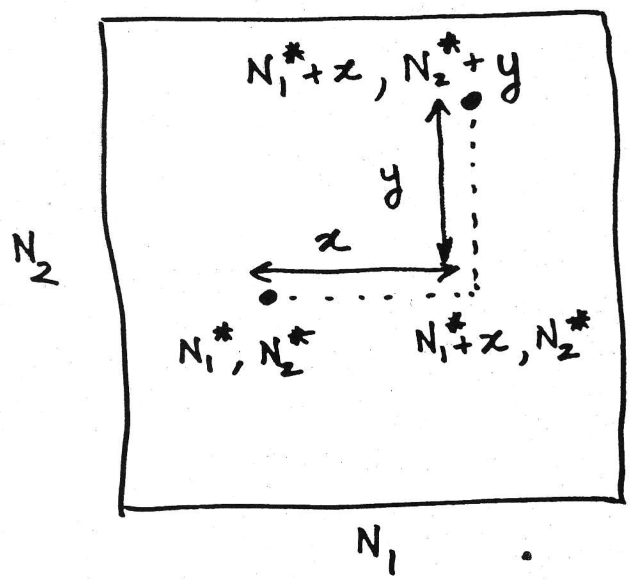
Boundary equilibria	Conditions	Outcome
Both unstable	$\alpha_{12} K_2 < K_1$ $\alpha_{21} K_1 < K_2$	Coexistence
One unstable	$\alpha_{12} K_2 < K_1$ $\alpha_{21} K_1 > K_2$ or $\alpha_{12} K_2 > K_1$ $\alpha_{21} K_1 < K_2$	Competitive dominance
Both stable	$\alpha_{12} K_2 > K_1$ $\alpha_{21} K_1 > K_2$	Priority effect

Local stability analysis for 2-dimensional systems

Consider a small perturbation to the equilibrium (N_1^*, N_2^*) defined as:

$$x = N_1 - N_1^* \quad \text{and} \quad y = N_2 - N_2^*$$

$$\Rightarrow N_1 = N_1^* + x \quad \text{and} \quad N_2 = N_2^* + y$$



$$\frac{dx}{dt} = ?$$

$$\frac{dy}{dt} = ?$$

Then, $\dfrac{dN_1}{dt} = \dfrac{d\,(N_1^* + x)}{dt} = f_1\left(N_1^* + x,\ N_2^* + y\right)$

$$\Rightarrow \frac{dx}{dt} = f_1\left(N_1^* + x,\ N_2^* + y\right)$$

Similarly, $\dfrac{dN_2}{dt} = \dfrac{d\,(N_2^* + y)}{dt} = f_2\left(N_1^* + x,\ N_2^* + y\right)$

$$\Rightarrow \frac{dy}{dt} = f_2\left(N_1^* + x,\ N_2^* + y\right)$$

Taylor series expansion for a function of two variables

$$F(x,y) \approx F(x^\star,y^\star) + \left[\frac{\partial F}{\partial x}|_{x^\star,y^\star}(x-x^\star) + \frac{\partial F}{\partial y}|_{x^\star,y^\star}(y-y^\star)\right] +$$

$$\frac{1}{2!}\left[\frac{\partial^2 F}{\partial x^2}|_{x^\star,y^\star}(x-x^\star)^2 + \frac{\partial^2 F}{\partial y^2}|_{x^\star,y^\star}(y-y^\star)^2\right] + \ldots$$

Ignore higher order terms

$$F(x,y) \approx F(x^\star,y^\star) + \left[\frac{\partial F}{\partial x}|_{x^\star,y^\star}(x-x^\star) + \frac{\partial F}{\partial y}|_{x^\star,y^\star}(y-y^\star)\right]$$

Do the Taylor expansion and ignore the higher-order terms.

Then,

$$f_1(N_1^*+x, N_2^*+y) \approx f_1(N_1^*, N_2^*) + \underbrace{\left.\frac{\partial f_1}{\partial N_1}\right|_{N_1^* N_2^*}}^{J_{11}} x + \underbrace{\left.\frac{\partial f_1}{\partial N_2}\right|_{N_1^* N_2^*}}^{J_{12}} y$$

$$f_2(N_1^*+x, N_2^*+y) \approx f_2(N_1^*, N_2^*) + \underbrace{\left.\frac{\partial f_2}{\partial N_1}\right|_{N_1^* N_2^*}}_{J_{21}} x + \underbrace{\left.\frac{\partial f_2}{\partial N_2}\right|_{N_1^* N_2^*}}_{J_{22}} y$$

Note: $f_1(N_1^*, N_2^*) = f_2(N_1^*, N_2^*) = 0$

Let $J_{11} = \left.\frac{\partial f_1}{\partial N_1}\right|_{N_1^* N_2^*}$, $\quad J_{12} = \left.\frac{\partial f_1}{\partial N_2}\right|_{N_1^* N_2^*}$

$J_{21} = \left.\frac{\partial f_2}{\partial N_1}\right|_{N_1^* N_2^*}$, $\quad J_{22} = \left.\frac{\partial f_2}{\partial N_2}\right|_{N_1^* N_2^*}$

Recall, $\frac{dx}{dt} = f_1(N_1^*+x, N_2^*+y)$

$\frac{dy}{dt} = f_2(N_1^*+x, N_2^*+y)$

So $\frac{dx}{dt} = J_{11}x + J_{12}y$

$\frac{dy}{dt} = J_{21}x + J_{22}y$

Equations for the perturbation in the two directions:

$$\frac{dx}{d\tau} = J_{11} x + J_{12} y$$

$$\frac{dy}{d\tau} = J_{21} x + J_{22} y$$

$\vdots$

$$\lambda x_0 = J_{11} x_0 + J_{12} y_0$$

$$\lambda y_0 = J_{21} x_0 + J_{22} y_0$$

$\vdots$

Characteristic equation:

$$\lambda^2 \underbrace{- (J_{11} + J_{22})}_{A_1} \lambda + \underbrace{J_{11} J_{22} - J_{12} J_{21}}_{A_2} = 0$$

$$\Rightarrow \lambda^2 + A_1 \lambda + A_2 = 0$$

Characteristic equation :

$$\lambda^2 - \underbrace{(J_{11} + J_{22})}_{A_1} \lambda + \underbrace{J_{11} J_{22} - J_{12} J_{21}}_{A_2} = 0$$

$$\Rightarrow \lambda^2 + A_1 \lambda + A_2 = 0$$

Eigenvalues :

$$\lambda_{1,2} = \frac{J_{11} + J_{22}}{2} \pm \sqrt{\frac{(J_{11} + J_{22})^2 - 4(J_{11} J_{22} - J_{12} J_{21})}{2}}$$

Compact form :

$$\lambda_1 = \frac{1}{2}\left(-A_1 + \sqrt{A_1^2 - 4A_2}\right)$$

$$\lambda_2 = \frac{1}{2}\left(-A_1 - \sqrt{A_1^2 - 4A_2}\right)$$

$$A_1 = -(J_{11} + J_{22})$$

$$A_2 = J_{11} J_{22} - J_{12} J_{21}$$