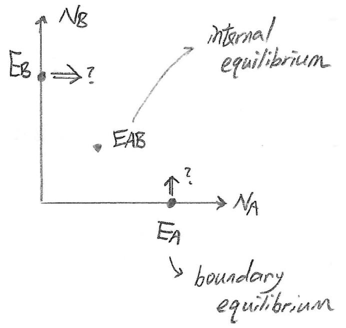
2021.11.16 Competition (Analytical analysis)

$$\begin{cases} \dfrac{dN_A}{dt} = N_A(r_A - \alpha_{AA}N_A - \alpha_{AB}N_B) \\[2ex] \dfrac{dN_B}{dt} = N_B(r_B - \alpha_{BA}N_A - \alpha_{BB}N_B) \end{cases}$$

◎ Invasion analysis

- Can a species "invade" the equilibrium of the other species?
- If both species can invade the boundary equilibrium of the other species, this is called "Mutual invasibility" and coexistence is possible.
- We call this the invasion growth rate (IGR), or, growth rate when rare, a positive IGR means the species can "bounce back" when rare (a criterion for its persistence)

$$IGR_i = \lim_{N_i \to 0} \frac{1}{N_i}\frac{dN_i}{dt}\Bigg|_{N_j^*} \quad \begin{aligned} &> 0 \Rightarrow \text{can invade} \\ &< 0 \Rightarrow \text{cannot invade} \end{aligned}$$



« N_A invading E_B »

Monoculture of N_B = $E_B = \dfrac{r_B}{\alpha_{BB}}$

No intra　　only inter

$$IGR_A = \lim_{N_A \to 0} \frac{1}{N_A}\frac{dN_A}{dt}\Bigg|_{E_B} = (r_A - \alpha_{AA}\underbrace{N_A}_{0} - \alpha_{AB}\underbrace{N_B}_{r_B/\alpha_{BB}})\Bigg|_{E_B} = r_A - r_B\left(\frac{\alpha_{AB}}{\alpha_{BB}}\right)$$

$\Rightarrow$ for N_A to invade : $r_A - r_B\dfrac{\alpha_{AB}}{\alpha_{BB}} > 0 \Rightarrow \dfrac{r_A}{\alpha_{AB}} > \dfrac{r_B}{\alpha_{BB}} \Rightarrow \dfrac{\alpha_{AB}}{r_A} < \dfrac{\alpha_{BB}}{r_B}$

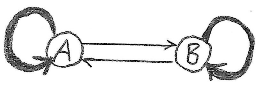
« N_B invading E_A »

Monoculture of N_B = $E_A = \dfrac{r_A}{\alpha_{AA}}$

$$IGR_B = \lim_{N_B \to 0} \frac{1}{N_B}\frac{dN_B}{dt}\Bigg|_{E_A} = (r_B - \alpha_{BA}\underbrace{N_A}_{r_A/\alpha_{AA}} - \alpha_{BB}\underbrace{N_B}_{0})\Bigg|_{E_A} = r_B - r_A\left(\frac{\alpha_{BA}}{\alpha_{AA}}\right)$$

$\Rightarrow$ for N_B to invade : $r_B - r_A\dfrac{\alpha_{BA}}{\alpha_{AA}} > 0 \Rightarrow \dfrac{\alpha_{BA}}{r_B} < \dfrac{\alpha_{AA}}{r_A}$

for coexistence (mutual invasibility)
$$\begin{cases} \dfrac{\alpha_{AB}}{r_A} < \dfrac{\alpha_{BB}}{r_B} \\[2ex] \dfrac{\alpha_{BA}}{r_B} < \dfrac{\alpha_{AA}}{r_A} \end{cases}$$



Same coexistence criteria as graphical method: each species IMPOSE stronger impact ON conspecifics than on heterospecifics

• Potential downside of IGR: ① doesn't tell you the stability of internal equilibrium
② not all models allow such analysis (e.g. Allee effect)

① $IGR_A > 0$, $IGR_B < 0$: A win
② $IGR_A < 0$, $IGR_B > 0$: B win
③ $IGR_A > 0$, $IGR_B > 0$: coexistence
④ $IGR_A < 0$, $IGR_B < 0$: priority effect

ⓒ Local stability analysis

Again, think about displacements & its dynamics,

$\varepsilon_A = N_A - N_A^*$, $\varepsilon_B = N_B - N_B^*$

$$\frac{d\varepsilon_A}{dt} = \frac{dN_A}{dt} - \underbrace{\frac{dN_A^*}{dt}}_{=0} = f_A(N_A, N_B) = f_A(N_A^* + \varepsilon_A, N_B^* + \varepsilon_B)$$

※ Recall: Taylor expansion

$$f(a+\Delta x) = f(a) + \Delta x f'(a) + \frac{\Delta x^2}{2!} f''(a) + \ldots$$

※ Multivariate Taylor expansion:

$$f(a_x+\Delta x, a_y+\Delta y) = f(a_x, a_y) + \Delta x \frac{\partial f}{\partial x}\Big|_a + \Delta y \frac{\partial f}{\partial y}\Big|_a + \frac{\Delta x^2}{2!}\frac{\partial^2 f}{\partial x^2}\Big|_a + \frac{\Delta y^2}{2!}\frac{\partial^2 f}{\partial y^2}\Big|_a + 2\frac{\Delta x \Delta y}{2!}\frac{\partial^2 f}{\partial x \partial y}\Big|_a + \ldots$$

$$= \underbrace{f_A(N_A^*, N_B^*)}_{=0} + \varepsilon_A \cdot \frac{\partial f_A}{\partial N_A}\Big|_{(*)} + \varepsilon_B \frac{\partial f_A}{\partial N_B}\Big|_{(*)} + HOT$$

$$\frac{d\varepsilon_B}{dt} = f_B(N_A^* + \varepsilon_A, N_B^* + \varepsilon_B) = \underbrace{f_B(N_A^*, N_B^*)}_{=0} + \varepsilon_A \cdot \frac{\partial f_B}{\partial N_A}\Big|_{(*)} + \varepsilon_B \cdot \frac{\partial f_B}{\partial N_B}\Big|_{(*)} + HOT$$

$$\frac{d}{dt}\begin{pmatrix}\varepsilon_A \\ \varepsilon_B\end{pmatrix} = \underbrace{\begin{pmatrix} \frac{\partial f_A}{\partial N_A}\Big|_{(*)} & \frac{\partial f_A}{\partial N_B}\Big|_{(*)} \\ \frac{\partial f_B}{\partial N_A}\Big|_{(*)} & \frac{\partial f_B}{\partial N_B}\Big|_{(*)} \end{pmatrix}}_{\text{matrix of first-order partial derivatives of functions}} \begin{pmatrix}\varepsilon_A \\ \varepsilon_B\end{pmatrix} = \underbrace{\begin{pmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{pmatrix}\begin{pmatrix}\varepsilon_A \\ \varepsilon_B\end{pmatrix}}_{\text{linear dynamic system}}$$

matrix of first-order partial derivatives of functions

« Jacobian Matrix »

- This is a <u>linear dynamic system</u> $\left(\frac{d\vec{\varepsilon}}{dt} = J\vec{\varepsilon}\right)$

Assume solution is : $\begin{pmatrix}\varepsilon_A \\ \varepsilon_B\end{pmatrix} = \begin{pmatrix}C \\ D\end{pmatrix} e^{\lambda t}$, with C, D, λ yet to be determined, substitute

$$\Rightarrow \frac{d}{dt}\begin{pmatrix}\varepsilon_A \\ \varepsilon_B\end{pmatrix} = \lambda \cancel{e^{\lambda t}} \begin{pmatrix}C \\ D\end{pmatrix} = \begin{pmatrix}J_{11} & J_{12} \\ J_{21} & J_{22}\end{pmatrix}\begin{pmatrix}C \\ D\end{pmatrix}\cancel{e^{\lambda t}}$$

$$\Rightarrow \begin{pmatrix}J_{11} & J_{12} \\ J_{21} & J_{22}\end{pmatrix}\begin{pmatrix}C \\ D\end{pmatrix} = \lambda\begin{pmatrix}C \\ D\end{pmatrix} \Rightarrow \text{Eigenvalue problem !!}$$

$J\vec{u} = \lambda\vec{u}$

$\downarrow$

$(J - I\lambda)\vec{u} = \vec{0}$

$$\Rightarrow \begin{pmatrix}J_{11}-\lambda & J_{12} \\ J_{21} & J_{22}-\lambda\end{pmatrix}\begin{pmatrix}C \\ D\end{pmatrix} = \begin{pmatrix}0 \\ 0\end{pmatrix}$$

$\Rightarrow$ for non-trivial solution of $\begin{pmatrix}C \\ D\end{pmatrix}$, $\det\begin{pmatrix}J_{11}-\lambda & J_{12} \\ J_{21} & J_{22}-\lambda\end{pmatrix} = 0$

get two eigenvalues λ_1 & λ_2 with corresponding eigenvectors $\begin{pmatrix}C_1 \\ D_1\end{pmatrix}$ & $\begin{pmatrix}C_2 \\ D_2\end{pmatrix}$

have two specific solutions, their linear combination is also a solution :

$\rightarrow \frac{d}{dt}(w_1\vec{x}_1 + w_2\vec{x}_2)$
$= w_1\frac{d\vec{x}_1}{dt} + w_2\frac{d\vec{x}_2}{dt}$
$= w_1 A\vec{x}_1 + w_2 A\vec{x}_2$
$= A(w_1\vec{x}_1 + w_2\vec{x}_2)$

$\Rightarrow$ General solution : $\underline{\begin{pmatrix}\varepsilon_A \\ \varepsilon_B\end{pmatrix} = w_1\begin{pmatrix}C_1 \\ D_1\end{pmatrix}e^{\lambda_1 t} + w_2\begin{pmatrix}C_2 \\ D_2\end{pmatrix}e^{\lambda_2 t}}$

corresponding eigenvector

eigenvalue

※ Recall: Solve by diagonalization

<u>All eigenvalue < 0 gives stability</u>

find $J = ADA^{-1}$ & $\vec{\varepsilon} = A\vec{y}$

$$\frac{d\vec{\varepsilon}}{dt} = A\frac{d\vec{y}}{dt} = JA\vec{y} \rightarrow \frac{d\vec{y}}{dt} = A^{-1}JA\vec{y} = D\vec{y} \rightarrow \vec{\varepsilon} = A\begin{pmatrix}w_1 e^{\lambda_1 t} \\ w_2 e^{\lambda_2 t}\end{pmatrix}$$

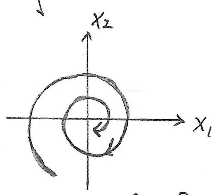
- <u>What about complex numbers as eigenvalues ?</u>

$\lambda_1 = a + bi$; $a, b \in \mathbb{R}$

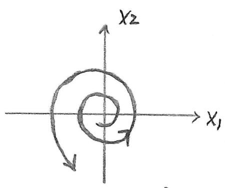
※ Euler's equation : $e^{i\theta} = \cos\theta + i\sin\theta$

$$e^{\lambda t} = e^{(a+bi)t} = e^{at}\cdot e^{bti} = e^{at}\,[\cos(bt) + i\sin(bt)]$$

spiral



« $a < 0$ »



« $a > 0$ »

« Example » $\frac{d\vec{x}}{dt} = \begin{pmatrix} -1 & 1 \\ -2 & -1 \end{pmatrix} \vec{x}$

※ Recall : explicit general solution : $\vec{X}(t) = Ae^{Dt}A^{-1}\vec{X_0}$

$$= A\begin{pmatrix} e^{\lambda_1 t} & 0 \\ 0 & e^{\lambda_2 t} \end{pmatrix} A^{-1}\vec{X_0}$$

$$\begin{pmatrix} C_1 e^{\lambda_1 t} & C_2 e^{\lambda_2 t} \\ D_1 e^{\lambda_1 t} & D_2 e^{\lambda_2 t} \end{pmatrix}\begin{pmatrix} w_1 \\ w_2 \end{pmatrix}$$

Characteristic equation : $(1+\lambda)^2 + 2 = 0$

$$\lambda^2 + 2\lambda + 3 = 0 \rightsquigarrow \lambda = -1 \pm \sqrt{2}\,i$$

eigenvector : $\begin{pmatrix} -1 & 1 \\ -2 & -1 \end{pmatrix}\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = (-1+\sqrt{2}\,i)\begin{pmatrix} u_1 \\ u_2 \end{pmatrix}$

$$\Rightarrow \begin{cases} -u_1 + u_2 = -u_1 + \sqrt{2}\,u_1 i \\ -2u_1 - u_2 = -u_2 + \sqrt{2}\,u_2 i \end{cases} \Rightarrow \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \begin{pmatrix} 1 \\ \sqrt{2}\,i \end{pmatrix}$$

$$A = \begin{pmatrix} 1 & 1 \\ \sqrt{2}i & -\sqrt{2}i \end{pmatrix} ; \quad A^{-1} = \frac{1}{-2\sqrt{2}\,i}\begin{pmatrix} -\sqrt{2}i & -1 \\ -\sqrt{2}i & 1 \end{pmatrix} = \frac{1}{2}\begin{pmatrix} 1 & \frac{1}{\sqrt{2}i} \\ 1 & \frac{-1}{\sqrt{2}i} \end{pmatrix}$$

$$e^{Dt} = \begin{bmatrix} e^{(-1+\sqrt{2}i)t} & 0 \\ 0 & e^{(-1-\sqrt{2}i)t} \end{bmatrix} = e^{-t}\begin{bmatrix} \cos\sqrt{2}t + i\sin\sqrt{2}t & 0 \\ 0 & \cos\sqrt{2}t - i\sin\sqrt{2}t \end{bmatrix}$$

$$e^{Dt}A^{-1} = \frac{e^{-t}}{2}\begin{bmatrix} \cos\sqrt{2}t + i\sin\sqrt{2}t & \frac{1}{\sqrt{2}i}\cos\sqrt{2}t + \frac{1}{\sqrt{2}}\sin\sqrt{2}t \\ \cos\sqrt{2}t - i\sin\sqrt{2}t & -\frac{1}{\sqrt{2}i}\cos\sqrt{2}t + \frac{1}{\sqrt{2}}\sin\sqrt{2}t \end{bmatrix}$$

$$Ae^{Dt}A^{-1} = \frac{e^{-t}}{2}\begin{bmatrix} 2\cos\sqrt{2}t & \frac{2}{\sqrt{2}}\sin\sqrt{2}t \\ -2\sqrt{2}\sin\sqrt{2}t & 2\cos\sqrt{2}t \end{bmatrix} = e^{-t}\begin{bmatrix} \cos\sqrt{2}t & \frac{1}{\sqrt{2}}\sin\sqrt{2}t \\ -\sqrt{2}\sin\sqrt{2}t & \cos\sqrt{2}t \end{bmatrix} *$$

Beauty of Euler equation, i all gone !!

※ General solution for $\frac{d\vec{x}}{dt} = \begin{pmatrix} a & b \\ c & d \end{pmatrix}\vec{x}$ with eigenvalue $\alpha \pm \beta i$

$$\vec{X}(t) = e^{\alpha t} \cdot \begin{bmatrix} \cos(\beta t) + \frac{(a-d)}{2\beta}\sin(\beta t) & \frac{b}{\beta}\sin(\beta t) \\ \frac{c}{\beta}\sin(\beta t) & \cos(\beta t) - \frac{(a-d)}{2\beta}\sin(\beta t) \end{bmatrix}\vec{X_0}$$

Summary: To determine stability of an equilibrium for $\begin{cases} \frac{dN_A}{dt} = f_A(N_A, N_B) \\ \frac{dN_B}{dt} = f_B(N_A, N_B) \end{cases}$

1. Use ZNGIs to find equilibrium E
2. Calculate partial derivatives to get Jacobian matrix & evaluate at E

$$J_E = \left.\begin{pmatrix} \frac{\partial f_A}{\partial N_A} & \frac{\partial f_A}{\partial N_B} \\ \frac{\partial f_B}{\partial N_A} & \frac{\partial f_B}{\partial N_B} \end{pmatrix}\right|_E$$

3. Get eigenvalues of J_E
4. For E to be stable, ALL eigenvalues should have NEGATIVE REAL parts

locally stable, linearizing the system near equilibrium

@ Apply local stability analysis to Lotka-Volterra competition model

$$\begin{cases} J_{11} = \frac{\partial f_A}{\partial N_A} = (r_A - \alpha_{AA} N_A - \alpha_{AB} N_B) + N_A \cdot (-\alpha_{AA}) \\ J_{12} = \frac{\partial f_A}{\partial N_B} = N_A \cdot (-\alpha_{AB}) \\ J_{21} = \frac{\partial f_B}{\partial N_A} = N_B \cdot (-\alpha_{BA}) \\ J_{22} = \frac{\partial f_B}{\partial N_B} = (r_B - \alpha_{BA} N_A - \alpha_{BB} N_B) + N_B (-\alpha_{BB}) \end{cases}$$

1. E_0 $(N_A^* = 0, N_B^* = 0)$

$J_0 = \begin{bmatrix} r_A & 0 \\ 0 & r_B \end{bmatrix}$, has eigenvalue $\lambda = r_A, r_B > 0$ ⇒ E_0 is always unstable

2. E_A $(N_A^* = \frac{r_A}{\alpha_{AA}}, N_B^* = 0)$

$J_A = \begin{bmatrix} -\alpha_{AA} N_A^* & -\alpha_{AB} N_A^* \\ 0 & r_B - \alpha_{BA} N_A^* \end{bmatrix}$, has eigenvalue $\lambda = -r_A, r_B - \alpha_{BA} \cdot \frac{r_A}{\alpha_{AA}}$

⇒ E_A is locally stable if $r_B - \alpha_{BA} \cdot \frac{r_A}{\alpha_{AA}} < 0$ ⇒ if $\frac{\alpha_{AA}}{r_A} < \frac{\alpha_{BA}}{r_B}$

case 1 & 4

3. E_B ($N_A^* = 0$, $N_B^* = \frac{r_B}{\alpha_{BB}}$)

$$J_B = \begin{bmatrix} r_A - \alpha_{AB} N_B^* & 0 \\ -\alpha_{BA} N_B^* & -\alpha_{BB} N_B^* \end{bmatrix}, \text{ has eigenvalue } \lambda = r_A - \alpha_{AB}\frac{r_B}{\alpha_{BB}}, \ -r_B$$

$\Rightarrow$ E_B is stable if $r_A - \alpha_{AB}\frac{r_B}{\alpha_{BB}} < 0 \Rightarrow$ if $\frac{\alpha_{BB}}{r_B} < \frac{\alpha_{AB}}{r_B}$

case 2 & 4

4. E_{AB} ($N_A^* = \dfrac{r_A r_B \left(\frac{\alpha_{BB}}{r_B} - \frac{\alpha_{AB}}{r_A}\right)}{\alpha_{AA}\alpha_{BB} - \alpha_{AB}\alpha_{BA}}$, $N_B^* = \dfrac{r_A r_B \left(\frac{\alpha_{AA}}{r_A} - \frac{\alpha_{BA}}{r_B}\right)}{\alpha_{AA}\alpha_{BB} - \alpha_{AB}\alpha_{BA}}$)

$$J_{AB} = \begin{bmatrix} -\alpha_{AA} N_A^* & -\alpha_{AB} N_A^* \\ -\alpha_{BA} N_B^* & -\alpha_{BB} N_B^* \end{bmatrix}$$

$\Rightarrow$ characteristic equation : $(-\alpha_{AA}N_A^* - \lambda)(-\alpha_{BB}N_B^* - \lambda) - \alpha_{BA}\alpha_{AB}N_A^* N_B^* = 0$

$\Rightarrow$ $\lambda^2 + (\alpha_{AA}N_A^* + \alpha_{BB}N_B^*)\lambda + N_A^* N_B^* (\alpha_{AA}\alpha_{BB} - \alpha_{AB}\alpha_{BA}) = 0$

E_{AB} is stable if both eigenvalues have negative real parts

Recall: if quadratic function has root x_1 & x_2 for $ax^2+bx+c=0$

then $x_1 + x_2 = \frac{-b}{a}$, $x_1 x_2 = \frac{c}{a}$ (根与係数)

$\lambda_1 + \lambda_2 = -(\alpha_{AA}N_A^* + \alpha_{BB}N_B^*) < 0$

$\lambda_1 \lambda_2 = N_A^* N_B^* (\alpha_{AA}\alpha_{BB} - \alpha_{AB}\alpha_{BA}) > 0$

$\Rightarrow$ E_{AB} is stable if $\begin{cases} N_A^* \ \& \ N_B^* > 0 & \longrightarrow \text{feasibility (should check beforehand)} \\ \alpha_{AA}\alpha_{BB} > \alpha_{AB}\alpha_{BA} & \longrightarrow \text{Stabilization (intra > inter)} \end{cases}$

$\Rightarrow$ $\left.\begin{aligned} \frac{\alpha_{AA}}{r_A} &> \frac{\alpha_{BA}}{r_B} \\ \frac{\alpha_{BB}}{r_B} &> \frac{\alpha_{AB}}{r_A} \end{aligned}\right\}$ gives a feasible & stable E_{AB}

$\alpha_{AA}\alpha_{BB} > \alpha_{AB}\alpha_{BA}$

guaranteed by the above two conditions (those are all you need)

stabilization by itself is necessary BUT not sufficient for coexistence

because the equilibrium also needs to be feasible

« Summary »

α_{AA} vs. α_{BA}

α_{BB} vs. α_{AB}

$\alpha_{AA} > \alpha_{BA}$, $\alpha_{BB} > \alpha_{AB}$

E_A unstable ; E_B unstable

E_{AB} feasible & stable

$IGR_A > 0$, $IGR_B > 0$

« Coexist »

$\alpha_{AA} < \alpha_{BA}$, $\alpha_{BB} > \alpha_{AB}$

E_A stable ; E_B unstable

E_{AB} unfeasible

$IGR_A > 0$, $IGR_B < 0$

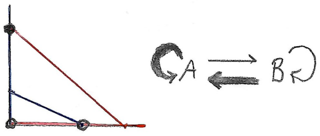
« A win »

$\alpha_{AA} > \alpha_{BA}$, $\alpha_{BB} < \alpha_{AB}$

E_A unstable ; E_B stable

E_{AB} unfeasible

$IGR_A < 0$, $IGR_B > 0$



« B win »

$\alpha_{AA} < \alpha_{BA}$, $\alpha_{BB} < \alpha_{AB}$

E_A stable ; E_B stable

E_{AB} feasible but unstable

$IGR_A < 0$, $IGR_B < 0$

« Priority effect »

For Lotka-Volterra, invasion analysis directly gives the necessary and sufficient condition for coexistence (so would the graphical method), local stability analysis (requires feasibility knowledge) gives the necessary but insufficient stabilization condition.

For Lotka-Volterra, mutual invasibility (ensuring coexistence) also ensures the existence (feasibility) and stability of the coexistence state