Populations in competition [EK 6.3 and problem 6.15]

Two species N_1 and N_2 live in the same environment and compete for resources. A Lotka-Volterra type model for the time evolution:

$$\begin{cases} \dfrac{dN_1}{dt} = r_1 N_1\left(1-\dfrac{N_1}{K_1} - \dfrac{\beta_{12}N_2}{K_1}\right) = F_1(N_1,N_2) \\[2ex] \dfrac{dN_2}{dt} = r_2 N_2\left(1-\dfrac{N_2}{K_2} - \dfrac{\beta_{21}N_1}{K_2}\right) = F_2(N_1,N_2) \end{cases}$$

$\underbrace{r_i N_i\left(1-\dfrac{N_i}{K_i}\right)}$: logistic growth, K_1, K_2 carrying capacities

$\underbrace{\dfrac{\beta_{12}N_2}{K_1},\ \dfrac{\beta_{21}N_1}{K_2}}$: $N_1N_2 \sim$ number of random encounters, negative because of competition of resources, β_{12} and β_{21} measure decline in populations due to competition.

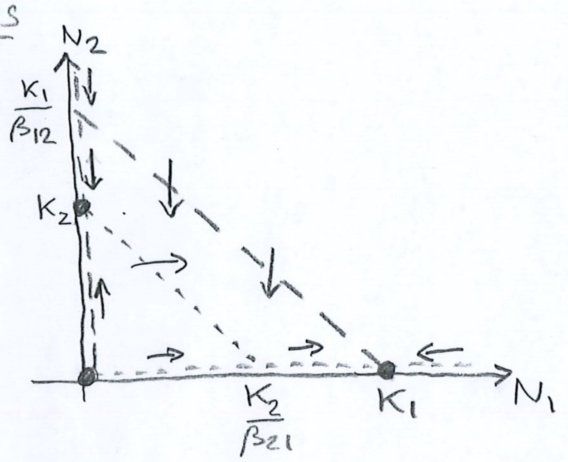
Phase plane analysis

N_1 nullclines $\quad r_1N_1\left(1-\dfrac{N_1}{K_1}-\dfrac{\beta_{12}N_2}{K_1}\right)=0 \Rightarrow \underbrace{N_1=0}_{\text{coord. axis}}$ or $\underbrace{N_1+\beta_{12}N_2=K_1}_{\text{line through } (K_1,0) \text{ and } (0,\frac{K_1}{\beta_{12}})}$

N_2 nullclines $\quad r_2N_2\left(1-\dfrac{N_2}{K_2}-\dfrac{\beta_{21}N_1}{K_2}\right)=0 \Rightarrow N_2=0$ or $\underbrace{N_2+\beta_{21}N_1=K_2}_{\text{through } (\frac{K_2}{\beta_{21}},0) \text{ and } (0,K_2)}$

4 cases

I



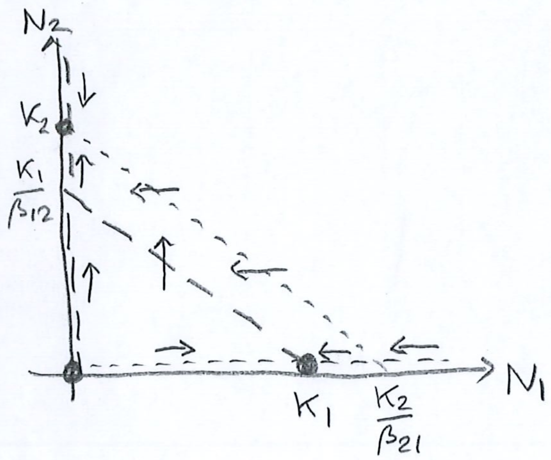
$K_1 > \dfrac{K_2}{\beta_{21}}$, $\dfrac{K_1}{\beta_{12}} > K_2$

3 steady states

$(0,0)$, $(K_1,0)$, $(0,K_2)$

Draw $\bar{F}$ on nullclines in the usual way

II

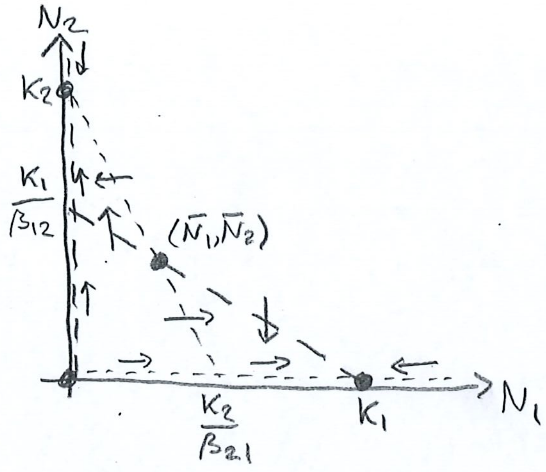


$K_1 < \dfrac{K_2}{\beta_{21}}$, $\dfrac{K_1}{\beta_{12}} < K_2$

3 steady states

$(0,0)$, $(K_1,0)$, $(0,K_2)$

III



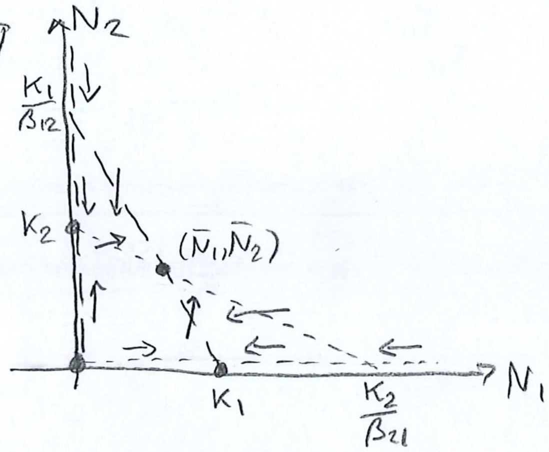
$$K_1 > \frac{K_2}{\beta_{21}}, \quad \frac{K_1}{\beta_{12}} < K_2$$

4 steady states

$(0,0), (K_1,0), (0,K_2), (\bar{N}_1,\bar{N}_2)$

$$\left.\begin{aligned} \bar{N}_1 + \beta_{12}\bar{N}_2 &= K_1 \\ \bar{N}_2 + \beta_{21}\bar{N}_1 &= K_2 \end{aligned}\right\} \Rightarrow (\bar{N}_1, \bar{N}_2) = \left(\frac{K_1 - \beta_{12}K_2}{1-\beta_{12}\beta_{21}}, \frac{K_2 - \beta_{21}K_1}{1-\beta_{12}\beta_{21}} \right)$$

IV



$$K_1 < \frac{K_2}{\beta_{21}}, \quad \frac{K_1}{\beta_{12}} > K_2$$

Same 4 steady states as in case III

Jacobian

$$J(N_1,N_2) = \begin{pmatrix} \frac{r_1}{K_1}(K_1 - 2N_1 - \beta_{12}N_2) & -\frac{r_1\beta_{12}}{K_1}N_1 \\ -\frac{r_2\beta_{21}}{K_2}N_2 & \frac{r_2}{K_2}(K_2 - 2N_2 - \beta_{21}N_1) \end{pmatrix} \Rightarrow$$

$$J(0,0) = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix} \Rightarrow \lambda_1 = r_1 > 0, \ \lambda_2 = r_2 > 0 \ \text{unstable}$$

$$J(K_1,0) = \begin{pmatrix} -r_1 & -r_1\beta_{12} \\ 0 & \underbrace{\frac{r_2\beta_{21}}{K_2}\left(\frac{K_2}{\beta_{21}} - K_1\right)}_{=\lambda_2} \end{pmatrix} \Rightarrow \lambda_1 = -r_1 < 0, \ \lambda_2 \begin{cases} > 0 \text{ in II, IV} \Rightarrow \text{saddle (unstable)} \\ < 0 \text{ in I, III} \Rightarrow \text{stable} \end{cases}$$

$$J(0,K_2) = \begin{pmatrix} \overbrace{\frac{r_1\beta_{12}}{K_1}\left(\frac{K_1}{\beta_{12}} - K_2\right)}^{=\lambda_1} & 0 \\ -r_2\beta_{21} & -r_2 \end{pmatrix} \Rightarrow \lambda_2 = -r_2 < 0, \ \lambda_1 \begin{cases} > 0, \text{ I, IV} \Rightarrow \text{saddle} \\ < 0, \text{ II, III} \Rightarrow \text{stable} \end{cases}$$

(Case III, IV)

$$J(\bar N_1,\bar N_2)=\begin{pmatrix} -\frac{r_1\bar N_1}{K_1} & -\frac{r_1\bar N_1\beta_{12}}{K_1} \\ -\frac{r_2\bar N_2\beta_{21}}{K_2} & -\frac{r_2\bar N_2}{K_2}\end{pmatrix}=J$$

$$\lambda_1+\lambda_2=\mathrm{Tr}\,J=-\frac{r_1\bar N_1}{K_1}-\frac{r_2\bar N_2}{K_2}<0$$

$$\lambda_1\lambda_2=\det J=\frac{r_1r_2\bar N_1\bar N_2}{K_1K_2}(1-\beta_{12}\beta_{21})\begin{cases}<0 \text{ in III}\\ >0 \text{ in IV}\end{cases}$$

(Note: III $K_1K_2>\frac{K_2}{\beta_{21}}\cdot\frac{K_1}{\beta_{12}}\Rightarrow\beta_{12}\beta_{21}>1$, opposite in IV)

$\Rightarrow(\bar N_1,\bar N_2)$ saddle point in III ($\lambda_1>0,\lambda_2<0$) and stable in IV.

Spiral in IV? $\mathrm{disc}\,J=(\mathrm{Tr}\,J)^2-4\det J=\left(\frac{r_1\bar N_1}{K_1}+\frac{r_2\bar N_2}{K_2}\right)^2-\frac{4r_1r_2\bar N_1\bar N_2(1-\beta_{12}\beta_{21})}{K_1K_2}=$

$$=\left(\frac{r_1\bar N_1}{K_1}-\frac{r_2\bar N_2}{K_2}\right)^2+\frac{4r_1r_2\bar N_1\bar N_2\beta_{12}\beta_{21}}{K_1K_2}>0\Rightarrow\lambda_{1,2}\text{ real}$$

$\Rightarrow$ no spiral

Table with steady states

	I	II	III	IV
(0,0)	unstable	unstable	unstable	unstable
$(K_1,0)$	stable	saddle	stable	saddle
$(0,K_2)$	saddle	stable	stable	saddle
$(\bar N_1,\bar N_2)$	—	—	saddle	stable

Interpretations

Case I, II: Only one population survives (N_1 in case I, N_2 in case II), independently of initial values (if >0). The population more negatively influenced by competition vanishes.

Case III: Both are very negatively influenced by competition (large β_{12},β_{21}), only one survives in the long run, which one depends on the initial conditions

Case IV: Less intense competition (small β_{12},β_{21}), both survive with balanced populations. Less similar species?

Note: the boundary between the two regions in III (the "stable manifold" of $(\bar N_1,\bar N_2)$), is tricky to determine

See Maple plots of the 4 cases, $r_1=r_2=K_1=K_2=1$ in all cases and:

	I	II	III	IV
β_{12}	3/4	4/3	4/3	3/4
β_{21}	3/2	2/3	3/2	2/3

Populations in competition, phase spaces

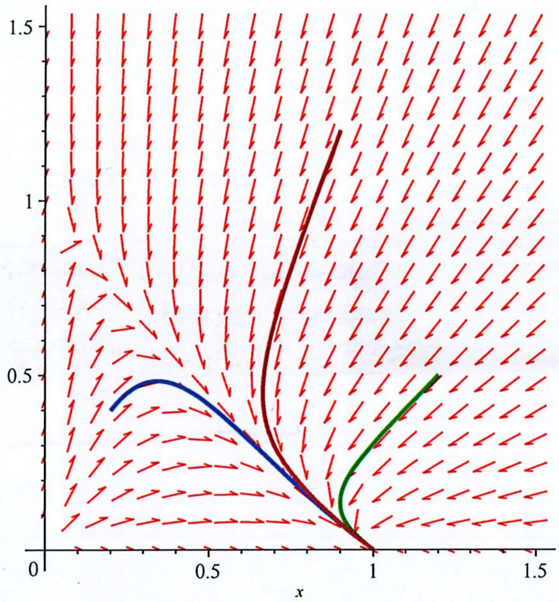
$r_1 = r_2 = K_1 = K_2 = 1$

> with(DEtools) :

> $sys1 := \left\{ diff(x(t), t) = x(t) \cdot \left(1 - x(t) - \frac{3 \cdot y(t)}{4}\right), diff(y(t), t) = y(t) \cdot \left(1 - y(t) - \frac{3 \cdot x(t)}{2}\right) \right\}$

$$sys1 := \left\{ \frac{d}{dt}\, x(t) = x(t)\left(1 - x(t) - \frac{3\, y(t)}{4}\right), \frac{d}{dt}\, y(t) = y(t)\left(1 - y(t) - \frac{3\, x(t)}{2}\right) \right\} \quad (1)$$

> DEplot(sys1, [x(t), y(t)], t = 0..15, [[x(0) = 0.2, y(0) = 0.4], [x(0) = 1.2, y(0) = 0.5], [x(0) = 0.9, y(0) = 1.2]], x = 0..1.5, y = 0..1.5, linecolor = [blue, green, brown], numpoints = 1000)

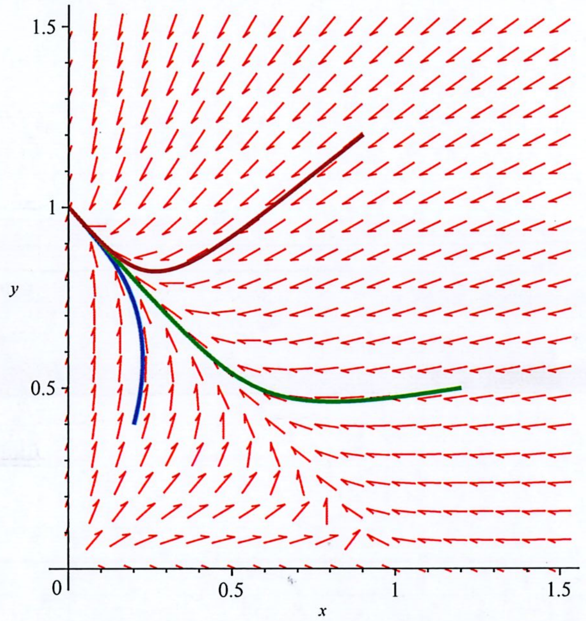


Case I $\beta_{12} = \frac{3}{4} < 1$, $\beta_{21} = \frac{3}{2} > 1$

> $sys2 := \left\{ diff(x(t), t) = x(t) \cdot \left(1 - x(t) - \frac{4 \cdot y(t)}{3}\right), diff(y(t), t) = y(t) \cdot \left(1 - y(t) - \frac{2 \cdot x(t)}{3}\right) \right\}$

$$sys2 := \left\{ \frac{d}{dt}\, x(t) = x(t)\left(1 - x(t) - \frac{4\, y(t)}{3}\right), \frac{d}{dt}\, y(t) = y(t)\left(1 - y(t) - \frac{2\, x(t)}{3}\right) \right\} \quad (2)$$

> DEplot(sys2, [x(t), y(t)], t = 0..15, [[x(0) = 0.2, y(0) = 0.4], [x(0) = 1.2, y(0) = 0.5], [x(0) = 0.9, y(0) = 1.2]], x = 0..1.5, y = 0..1.5, linecolor = [blue, green, brown], numpoints = 1000)

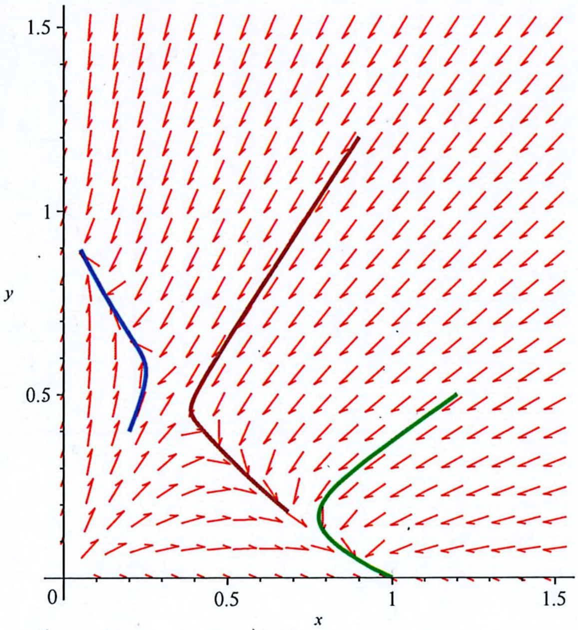


Case II $\beta_{12} = \frac{4}{3} > 1$, $\beta_{21} = \frac{2}{3} < 1$

> $sys3 := \left\{ diff(x(t), t) = x(t) \cdot \left(1 - x(t) - \frac{4 \cdot y(t)}{3}\right), diff(y(t), t) = y(t) \cdot \left(1 - y(t) - \frac{3 \cdot x(t)}{2}\right) \right\}$

$$sys3 := \left\{ \frac{d}{dt}\, x(t) = x(t)\left(1 - x(t) - \frac{4\, y(t)}{3}\right), \frac{d}{dt}\, y(t) = y(t)\left(1 - y(t) - \frac{3\, x(t)}{2}\right) \right\} \quad (3)$$

> DEplot(sys3, [x(t), y(t)], t = 0..15, [[x(0) = 0.2, y(0) = 0.4], [x(0) = 1.2, y(0) = 0.5], [x(0) = 0.9, y(0) = 1.2]], x = 0..1.5, y = 0..1.5, linecolor = [blue, green, brown], numpoints = 1000)

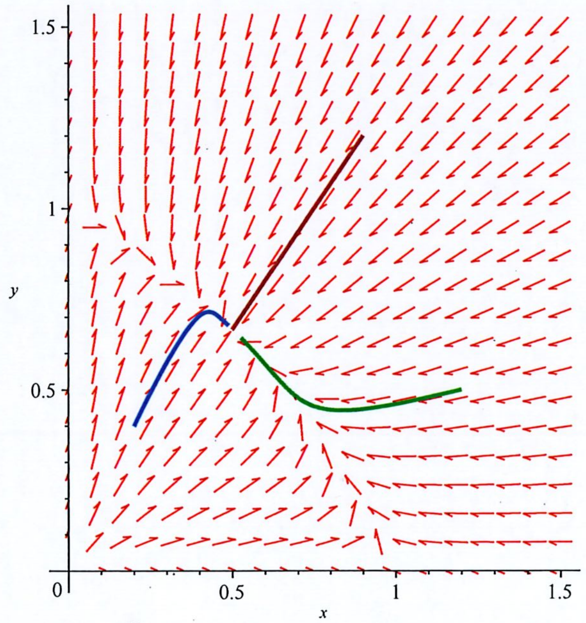


Case III $\beta_{12} = \frac{4}{3} > 1$, $\beta_{21} = \frac{3}{2} > 1$, $(\bar{N}_1, \bar{N}_2) = \left(\frac{1}{3}, \frac{1}{2}\right)$

> $sys4 := \left\{ diff(x(t), t) = x(t) \cdot \left(1 - x(t) - \frac{3 \cdot y(t)}{4}\right), diff(y(t), t) = y(t) \cdot \left(1 - y(t) - \frac{2 \cdot x(t)}{3}\right) \right\}$

$$sys4 := \left\{ \frac{d}{dt}\, x(t) = x(t)\left(1 - x(t) - \frac{3\, y(t)}{4}\right), \frac{d}{dt}\, y(t) = y(t)\left(1 - y(t) - \frac{2\, x(t)}{3}\right) \right\} \quad (4)$$

> DEplot(sys4, [x(t), y(t)], t = 0..15, [[x(0) = 0.2, y(0) = 0.4], [x(0) = 1.2, y(0) = 0.5], [x(0) = 0.9, y(0) = 1.2]], x = 0..1.5, y = 0..1.5, linecolor = [blue, green, brown], numpoints = 1000)



Case IV $\beta_{12} = \frac{3}{4} < 1$, $\beta_{21} = \frac{2}{3} < 1$, $(\bar{N}_1, \bar{N}_2) = \left(\frac{1}{2}, \frac{2}{3}\right)$

Modeling spread of infectious diseases

S = numberof susceptible for a disease
I = number of infective
R = number of removed (immune, deceased, ...)
N = total population

For epidemic models, vital dynamics (births and deaths not due to the disease) do no enter the model. We assume

$$S + I + R = N = \text{constant}$$

Individuals go from S to I, and then in different models from I to S or I to R, and maybe from R back to S.

$\frac{dI}{dt}$ should include a term with new infected, $f(S,I)$. If susceptible and infective meet in a random way, $f(S,I) = \beta SI$ ($\beta > 0$ constant) is a reasonable model, this is similar to the non-linear term in Lotka-Volterra. For S or I fixed, βSI is linear in the other. Maybe a more realistic f should have some saturating properties (compare logistic growth)? But βSI is used in the classical Kermack-MacKendrick models.

A first model is the SI-model (no class R):

$$\begin{cases} \frac{dS}{dt} = -\beta SI \\ \frac{dI}{dt} = \beta SI \end{cases}$$

Susceptible S move to I and stay there.

With $S + I = N$, $S = N - I \Rightarrow$

$$\frac{dI}{dt} = \beta I(N-I) = \beta NI\left(1 - \frac{I}{N}\right)$$

, the logistic eq., recall $y' = ry\left(1 - \frac{y}{B}\right)$, with carrying capacity $B = N$ and $r = \beta N$. The solution is

$$I(t) = \frac{BI(0)}{I(0) + (B - I(0))\underbrace{e^{-rt}}_{\to 0,\, t\to\infty}} \to B = N,\ t \to \infty$$

So after some time the entire population is infected.

More interesting models next seminar