Multidimensional systems

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Multidimensional dynamics

A multidimensional dynamic system has more than one state-variable, and therefore more than one corresponding differential equation.
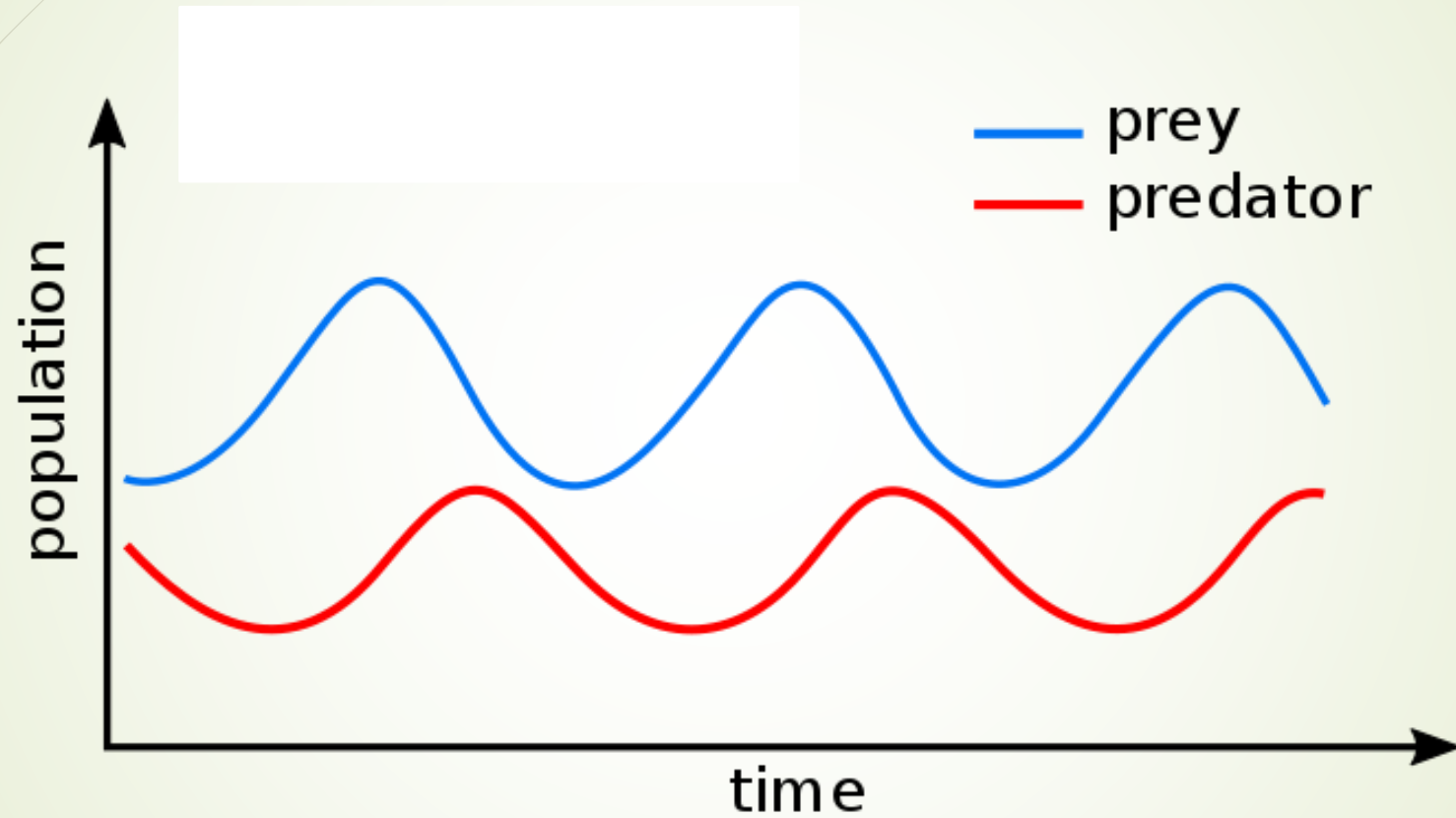
$$\begin{cases} \dfrac{dx_1}{dt} = f_1(x_1, x_2, \ldots, x_n, \ldots) \\[2mm] \dfrac{dx_2}{dt} = f_2(x_1, x_2, \ldots, x_n, \ldots) \\[2mm] \qquad\qquad \vdots \\[2mm] \dfrac{dx_n}{dt} = f_n(x_1, x_2, \ldots, x_n, \ldots) \end{cases}$$

Vector notation:

$$\frac{d\mathbf{x}}{dt} = \mathbf{f}(\mathbf{x}) \qquad \mathbf{x} = \begin{pmatrix} x_1 \\ x_2 \\ \vdots \\ x_n \end{pmatrix}$$

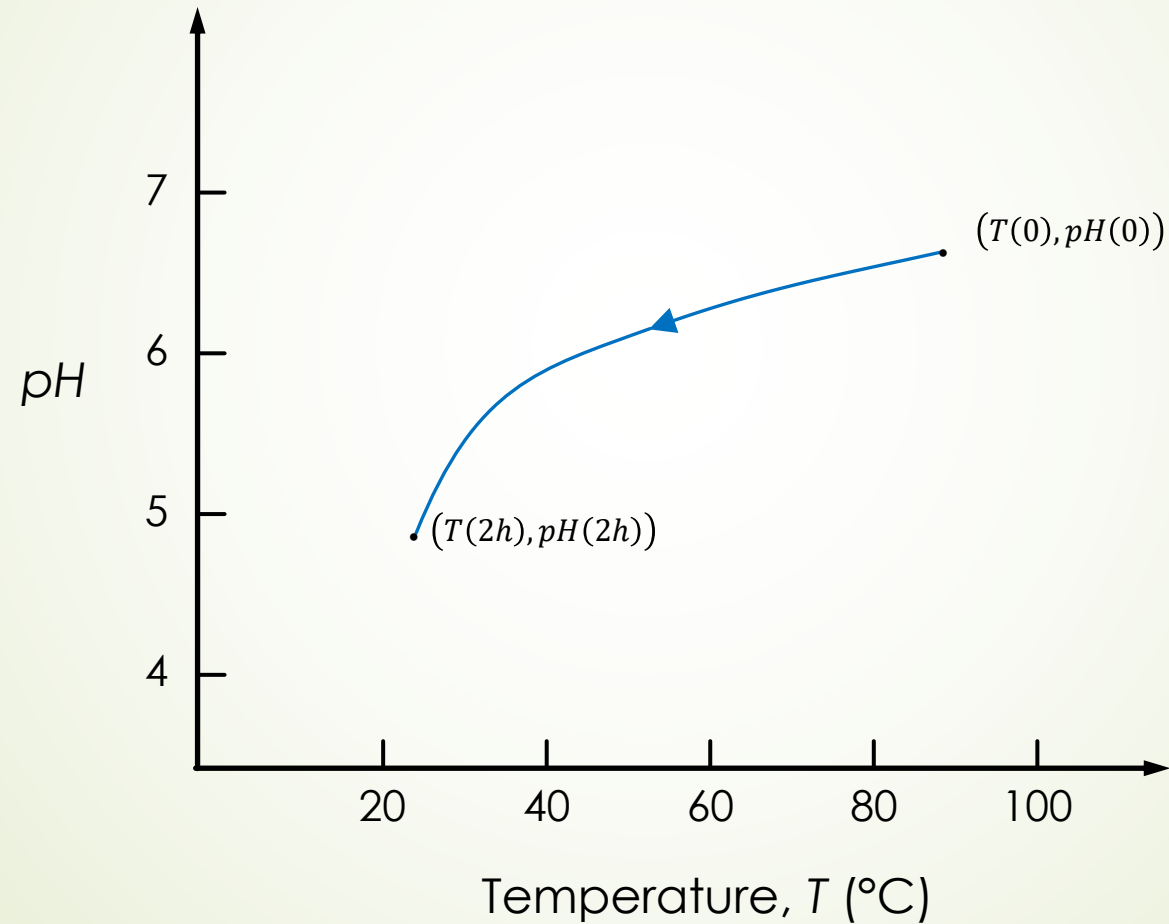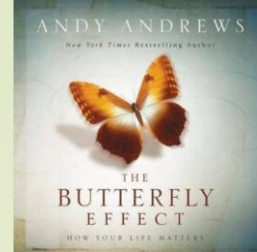n = number of dimensions

Time series

The phase space, trajectories

- It is common, and useful, to depict the dynamics of a 2- or 3-dimensional system in its corresponding *phase space*.

- The phase space has as many dimensions as the dynamics system, with each state variable corresponding to one of the coordinate axes.

- At any point in time, the current state of the system corresponds to a specific point in phase space.

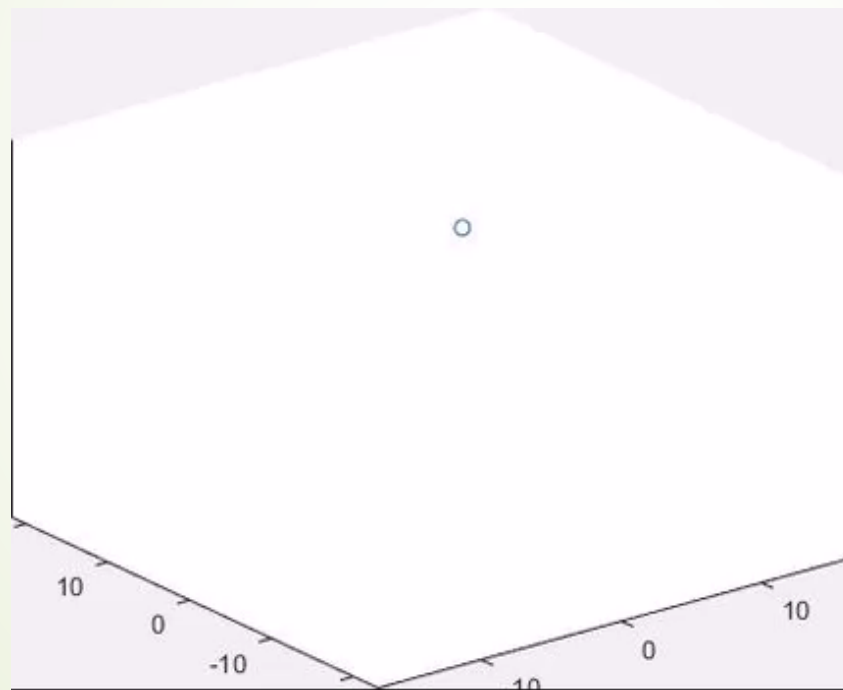- Moving through time, the systems follows a *trajectory* in phase space.

2D

x_2

$(x_1(t), x_2(t))$

$(x_1(0), x_2(0))$

x_1

3D

x_3

x_2

$(x_1(t), x_2(t), x_3(t))$

$(x_1(0), x_2(0), x_3(0))$

x_1
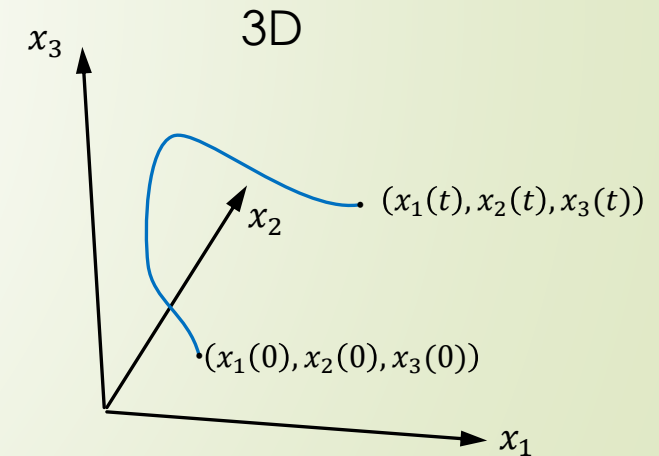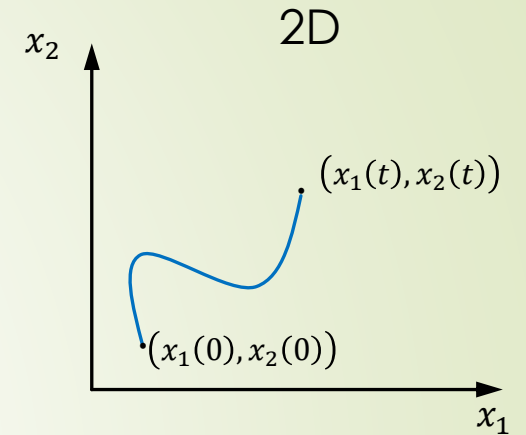
Coffee cup dynamics (2D)

Lorenz attractor (3D)

Atmospheric/ weather dynamics

$$\frac{dx}{dt} = \sigma(y\text{-}x)$$

$$\frac{dy}{dt} = x(\rho - z) - y$$

$$\frac{dz}{dt} = xy - \beta z$$

Logistic growth

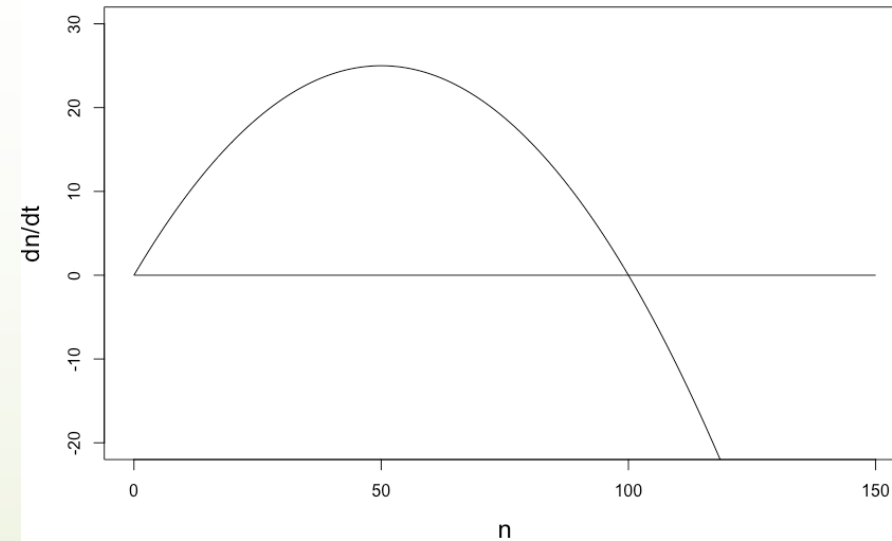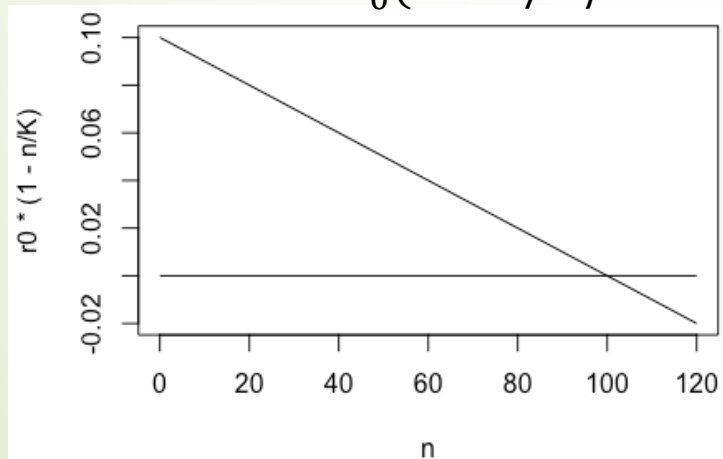Population growth can not go on for ever.

It is reasonable to assume that the birth rate will decrease with population density, that the death rate will increase with population density, or all of the above.

In conclusion, the per capita growth rate $(r = b - d)$ will decrease with population size n.

The simplest assumption is a linear function:

$$\frac{dn}{dt} = rn = r_0 n(1 - n/K)$$

$$r = r_0(1 - n/K)$$

The Lotka-Volterra competition equations (2D)

$$\begin{cases} \dfrac{dn_1}{dt} = r_1 n_1 \left(1 - \dfrac{n_1 + \alpha_{12} n_2}{K_1} \right) \\[2em] \dfrac{dn_2}{dt} = r_2 n_2 \left(1 - \dfrac{n_2 + \alpha_{21} n_1}{K_2} \right) \end{cases}$$

α_{ij} = competition coefficient.

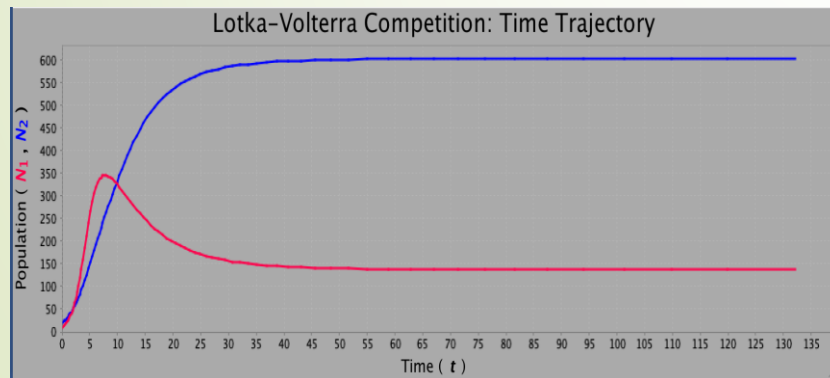   = How much population j competes with population i.

Competition coefficients are usually, but not always, below 1.
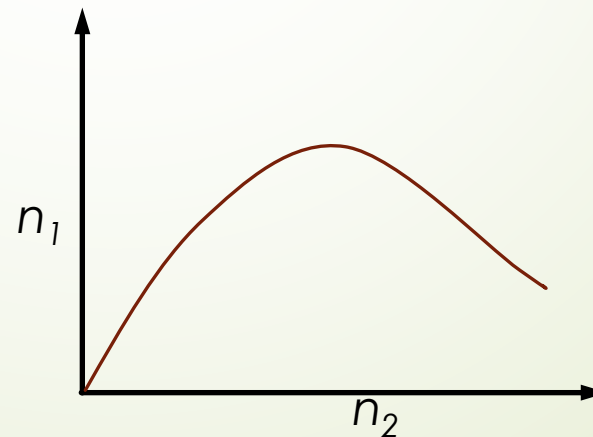
Model analyses

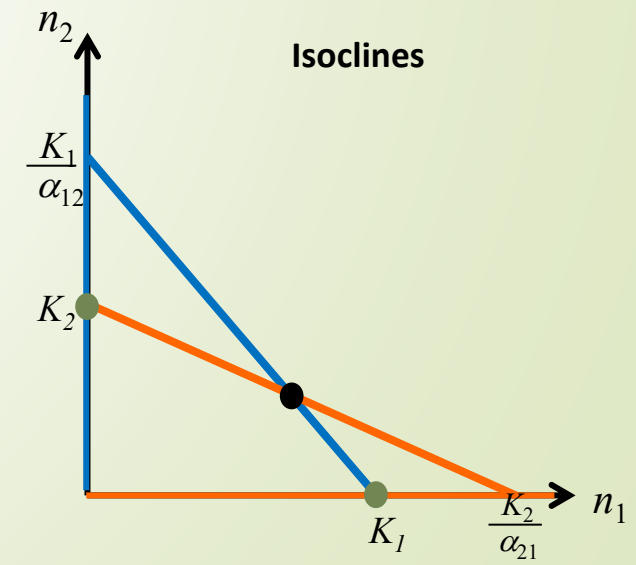- Numerical analyses and simulations.

- Mathematical analyses

Temporal dynamics

Lotka–Volterra Competition: Time Trajectory

Dynamics in state/ phase space

n_1

n_2

Isoclines

Isoclines (null-clines)

- The system *equilibrium* can be hard to solve

- Useful technique: Solve one differential equation at a time (equal to zero).

- The solutions are points in phase space where the corresponding population has zero growth.

<u>n_1 isoclines:</u>

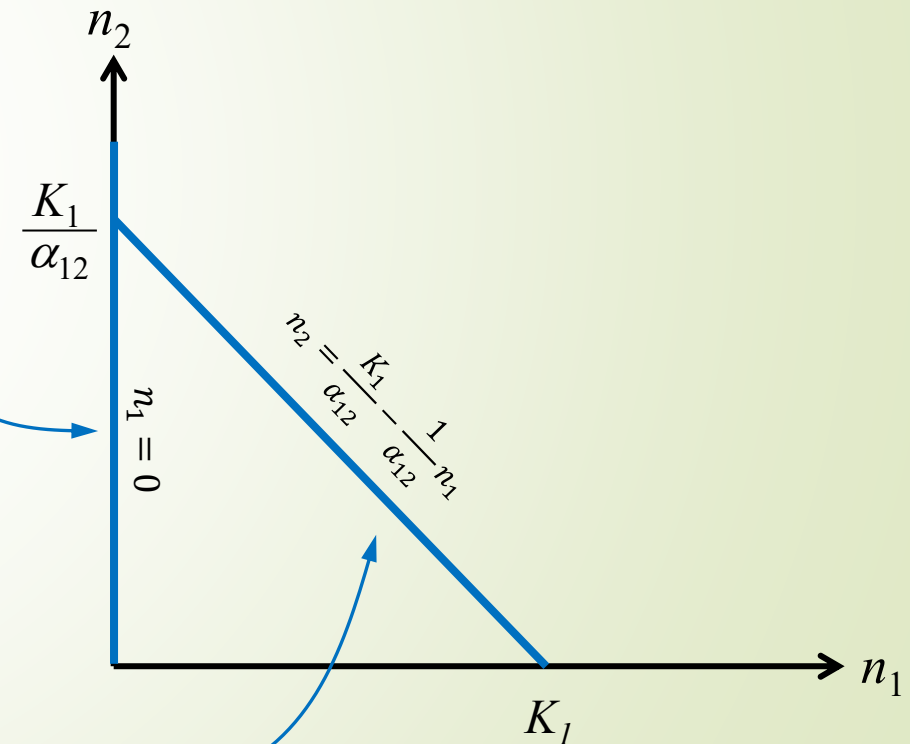$$\frac{dn_1}{dt} = r_1 n_1 \left(1 - \frac{n_1 + \alpha_{12} n_2}{K_1} \right) = 0$$

Trivial solution: $r_1 n_1 = 0 \Rightarrow n_1 = 0$

Non-trivial solution: $1 - \frac{n_1 + \alpha_{12} n_2}{K_1} = 0 \Leftrightarrow$

$K_1 = n_1 + \alpha_{12} n_2 \Leftrightarrow n_2 = \frac{1}{\alpha_{12}} (K_1 - n_1) \Leftrightarrow$

$n_2 = \frac{K_1}{\alpha_{12}} - \frac{1}{\alpha_{12}} n_1$

This is a straight line!

Isoclines (null-clines)

- The isoclines are points in phase space where the corresponding population has zero growth.
- Everywhere else, the population is either increasing or decreasing.
- To go from positive growth to negative growth, you have to pass an isocline.
- The isoclines divide the phase space into regions of either positive or negative growth.

$$\frac{dn_1}{dt} = r_1 n_1 \left(1 - \frac{n_1 + \alpha_{12} n_2}{K_1} \right) = 0$$

Trivial solution: $n_1 = 0$

Non-trivial solution: $n_2 = \frac{K_1}{\alpha_{12}} - \frac{1}{\alpha_{12}} n_1$

n_2

$\frac{K_1}{\alpha_{12}}$

n_1 decreases
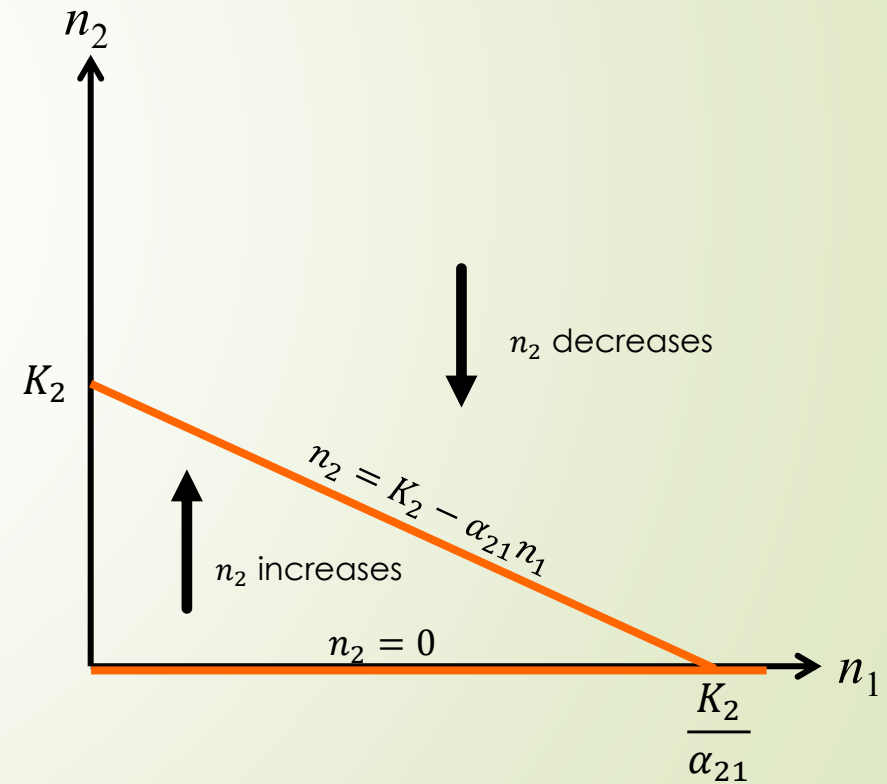
n_1 increases

n_1

K_1
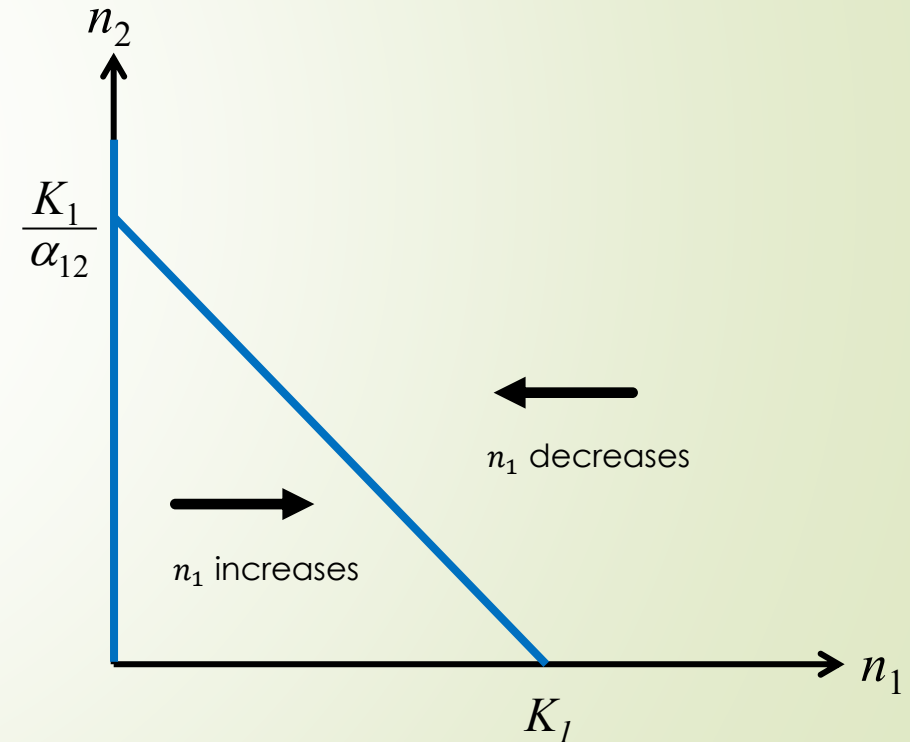
Isoclines (null-clines)

n_2 isoclines:

$$\frac{dn_2}{dt} = r_2 n_2 \left(1 - \frac{n_2 + \alpha_{21} n_1}{K_2} \right) = 0$$
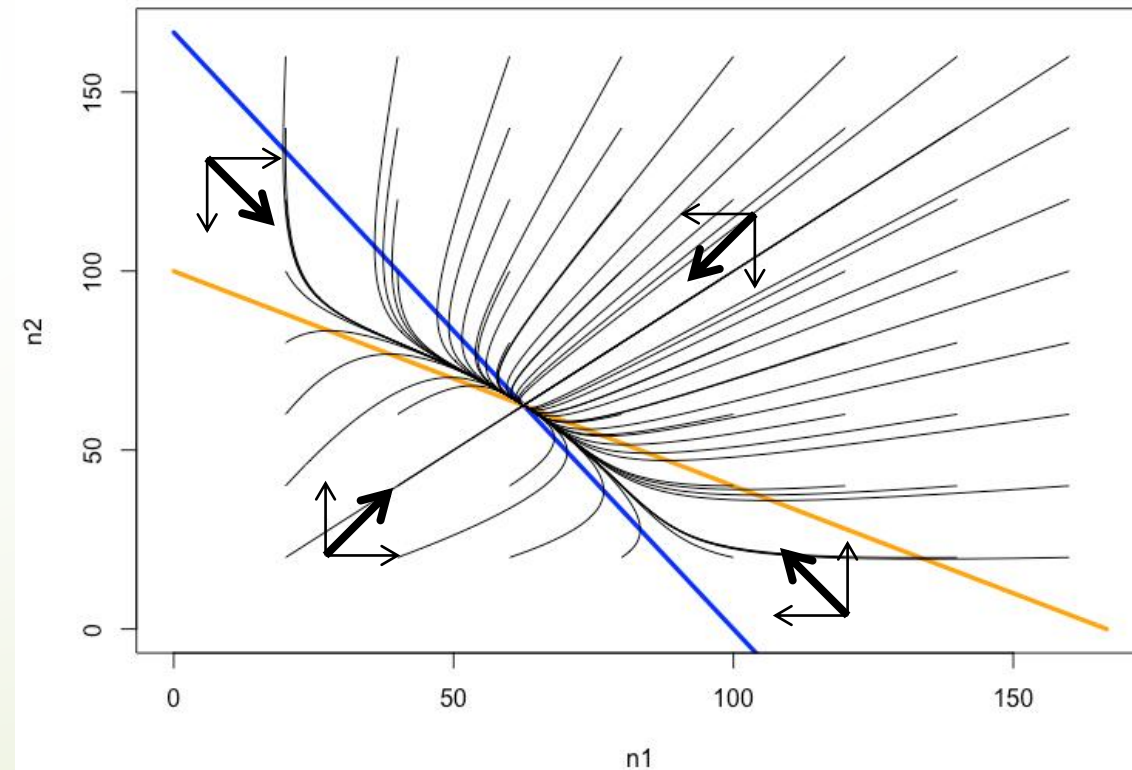
Trivial solution: $n_2 = 0$

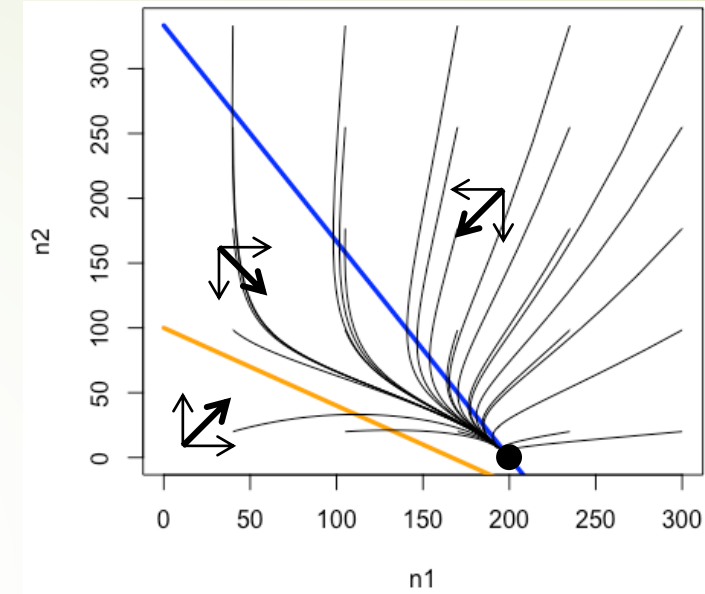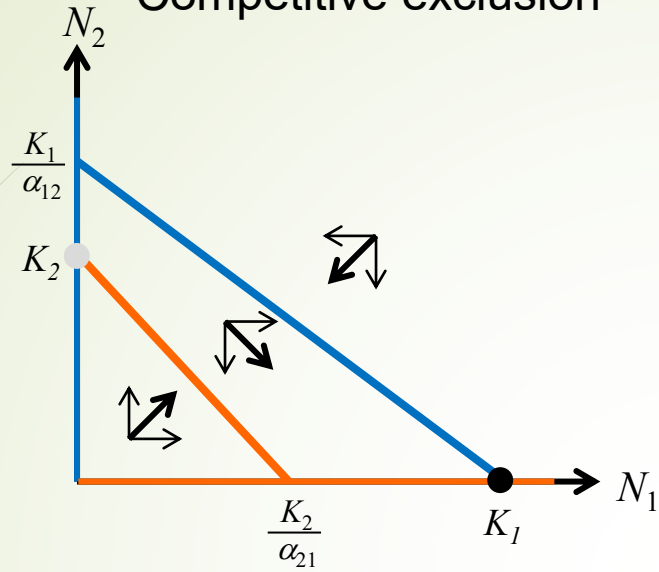Non-trivial solution: $n_2 = K_2 - \alpha_{21} n_1$

Isocline interpretation

- Putting everything together gives a general picture of the system dynamics

- Equilibrium points can be found where two isoclines of different types meet

- Whether an equilibrium is stable or not can generally not be seen from the isoclines, but they can give some hints.
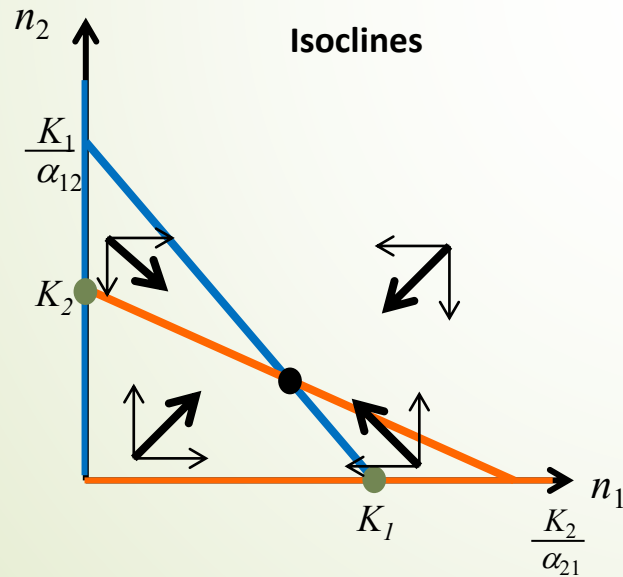
Competitive exclusion

Unstable equilibrium
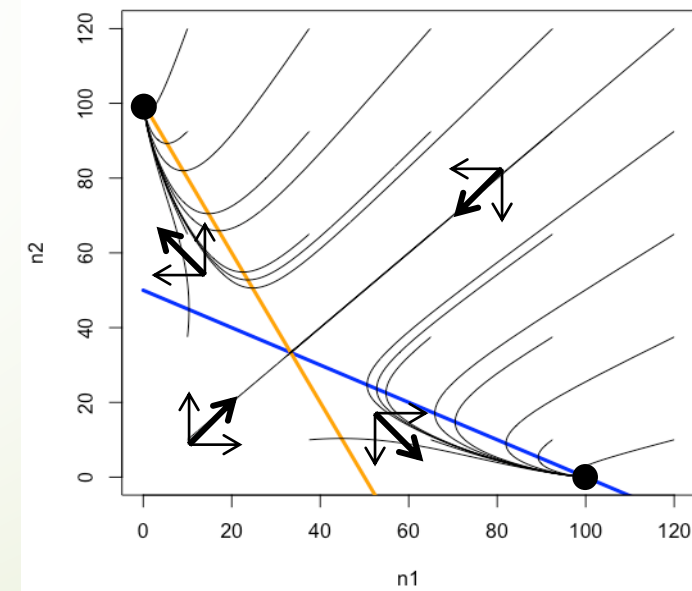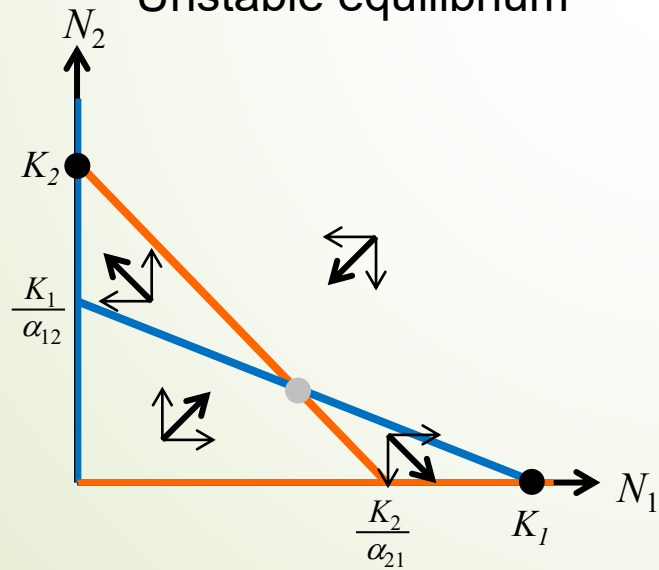
Exponential growth

- A simple example is that of exponential growth, applicable to bacterial growth in a test tube (and many other things).

- The underlying assumption is that all individuals give birth at a fixed rate b and die at a fixed rate d.

- If the population has n individuals, the total population growth rate is Births – Deaths = $\underbrace{bn - dn}_{r} = (b - d)n = rn$

- The parameter r is the *per capita* growth rate, the growth rate per individual.

$$\frac{dn}{dt} = rn$$
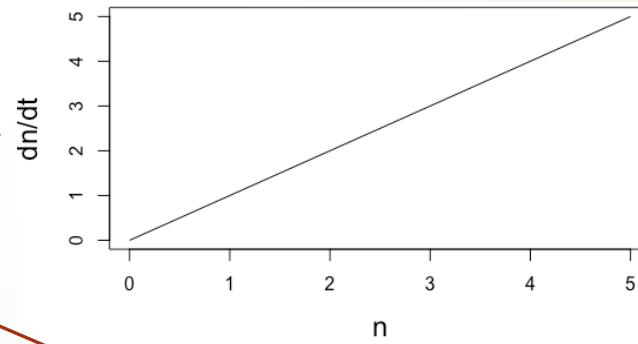
- Solution:

$$n(t) = n(0)e^{rt}$$
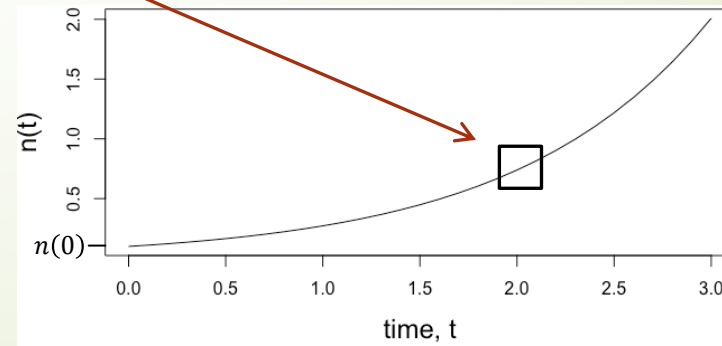
The Lotka-Volterra predator-prey equations (2D)

$$\begin{cases} \dfrac{dn}{dt} = f_n(n,p) = rn - anp \\[2em] \dfrac{dp}{dt} = f_p(n,p) = \varsigma anp - \mu p \end{cases}$$

Exponential growth

Prey caught per time unit

Converting prey to predators

Background mortality of predators

Prey isocline

$$f_n(n,p) = rn - anp = 0$$

Trivial solution: $n = 0$

Non-trivial solution:

$$r - ap = 0 \Rightarrow p = \frac{r}{a}$$

Predator isocline

$$f_p(n,p) = canp - \mu p = 0$$

Trivial solution: $p = 0$

Non-trivial solution:

$$can - \mu = 0 \Rightarrow n = \frac{\mu}{ca}$$

Stability???

p

$(n^*, p^*) = \left(\dfrac{\mu}{ca}, \dfrac{r}{a} \right)$

$\dfrac{r}{a}$

$\dfrac{\mu}{ca}$

n

prey isocline
predator isocline
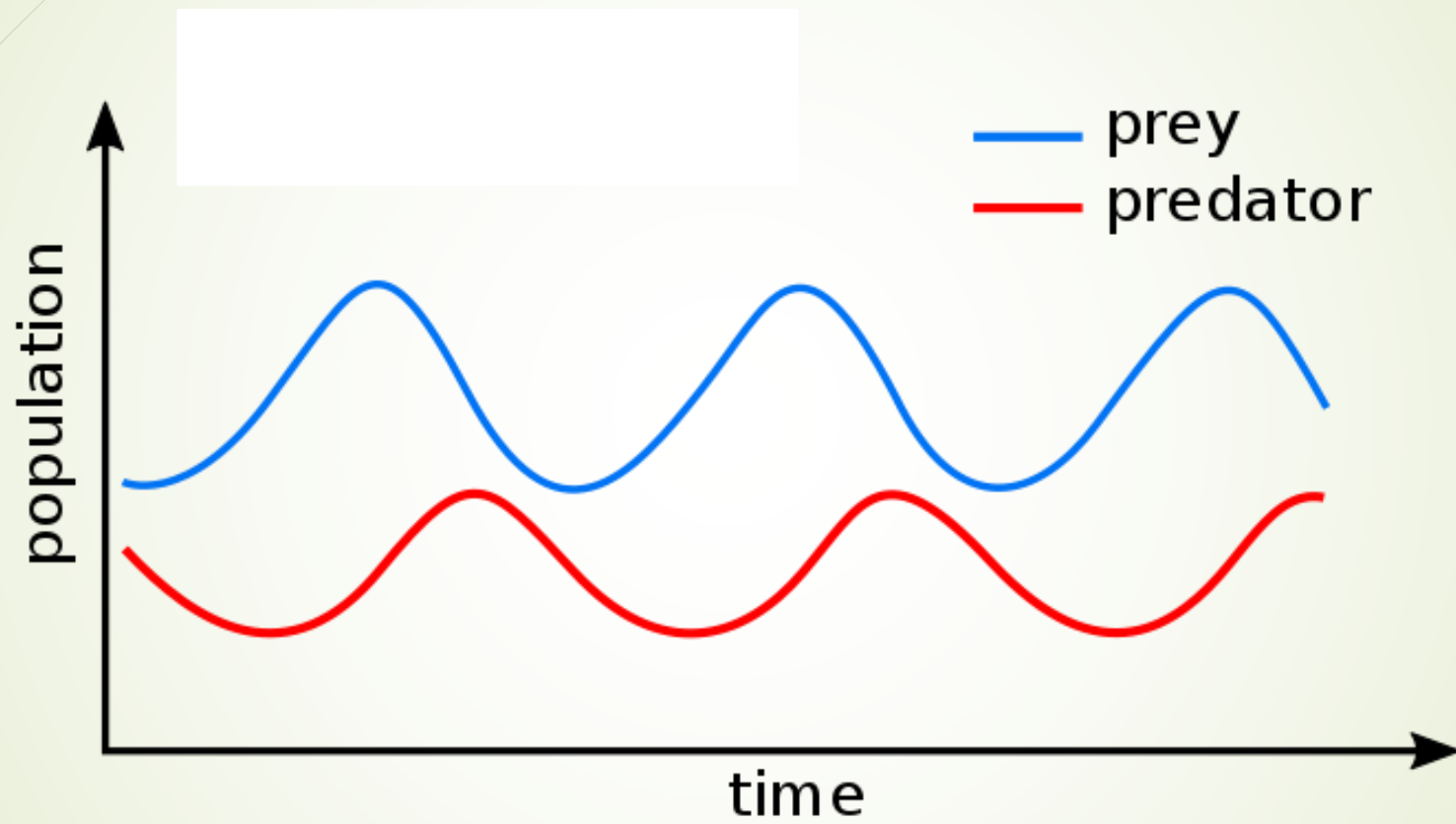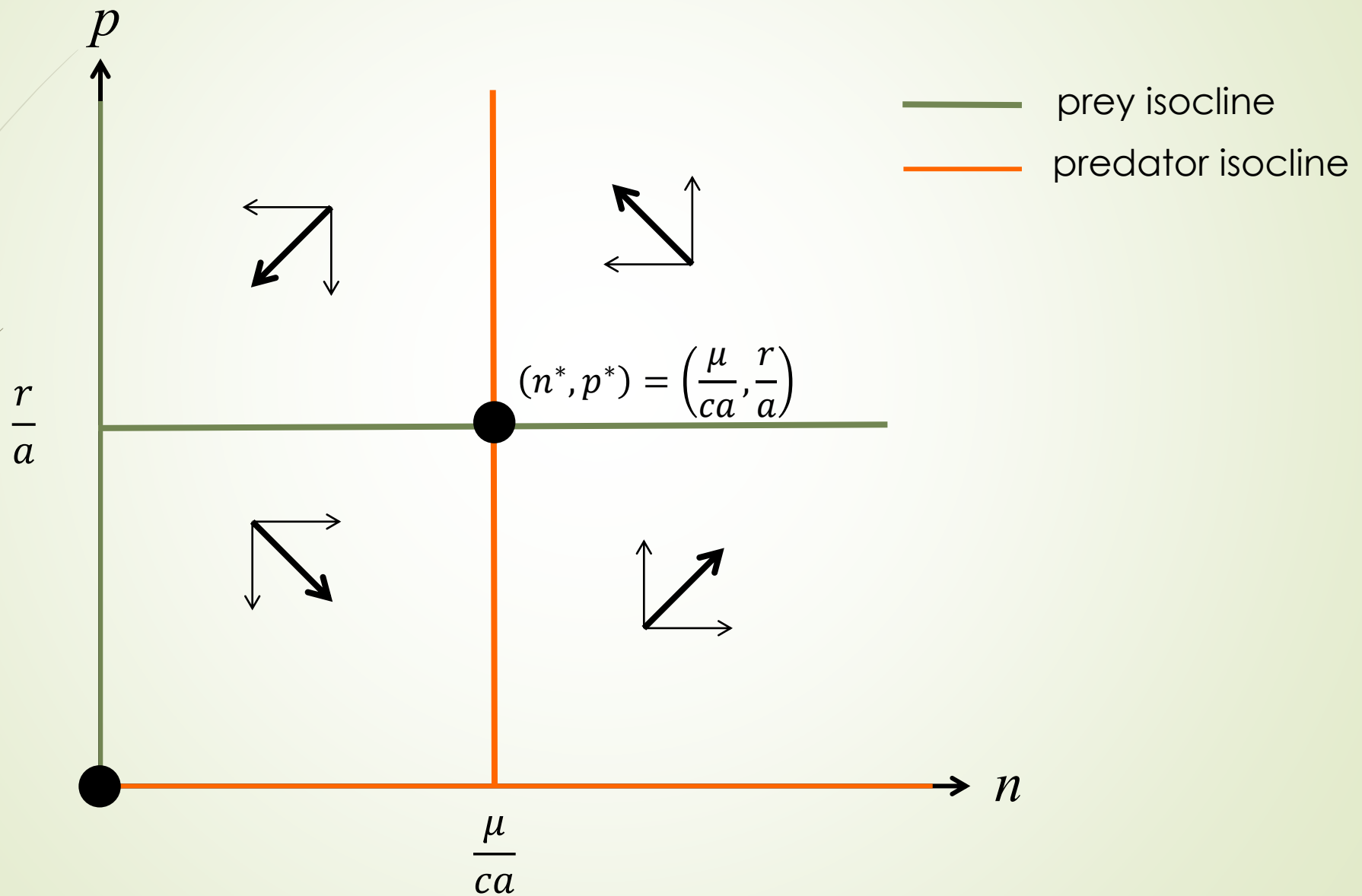
General condition for stability, 1D

- Given an arbitrary differential equation $\dfrac{dn}{dt} = f(n)$

- We find equilibrium points by solving $f(n^*) = 0$

- An equilibrium n^* is stable *if* $\boxed{f'(n^*) < 0}$
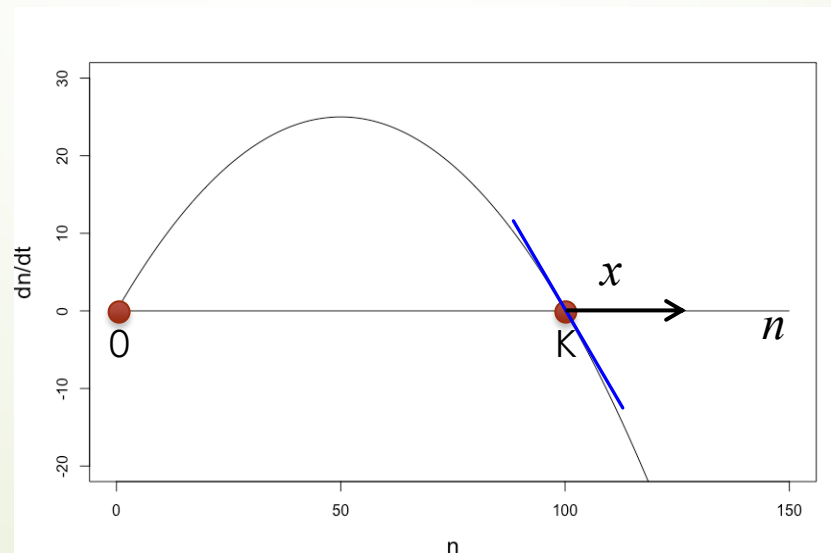
Stability in multi-D?

- Given an arbitrary dynamic system
$$\begin{cases} \dfrac{dx_1}{dt} = f_1(x_1, x_2) \\ \dfrac{dx_2}{dt} = f_2(x_1, x_2) \end{cases}$$
2D system here to save space

- We find equilibrium states by solving
$$\begin{cases} f_1(x_1^*, x_2^*) = 0 \\ f_2(x_1^*, x_2^*) = 0 \end{cases}$$

- But what about the slope? We have two (or, more generally, *n*) functions, and two (*n*) variables.

- There are actually four (*nxn*) slopes.

A few words on partial derivatives

Taking the derivative of a function of several variables is ambiguous. For which variable should we take the derivative? And what about the interpretation as a slope???

A function of two variables, $f(x,y)$, can be interpreted as a surface.

For each point on the surface, there are several possible slopes, depending on the direction you're taking.

The partial derivative with respect to x is written $\frac{\partial f}{\partial x}$. It can be interpreted as the slope of the surface parallel to the x-axis. It is calculated by 'pretending' that all other variables (y) are constant.

Likewise, the partial derivative with respect to y is written $\frac{\partial f}{\partial y}$ and can be interpreted as the slope of the surface parallel to the y-axis. It is calculated by 'pretending' that x is a constant.

Example:

$$f(x,y) = 2x - x^3y$$

$$\frac{\partial f}{\partial x} = 2 - 3x^2y$$

$$\frac{\partial f}{\partial y} = -x^3$$

$f(x,y)$
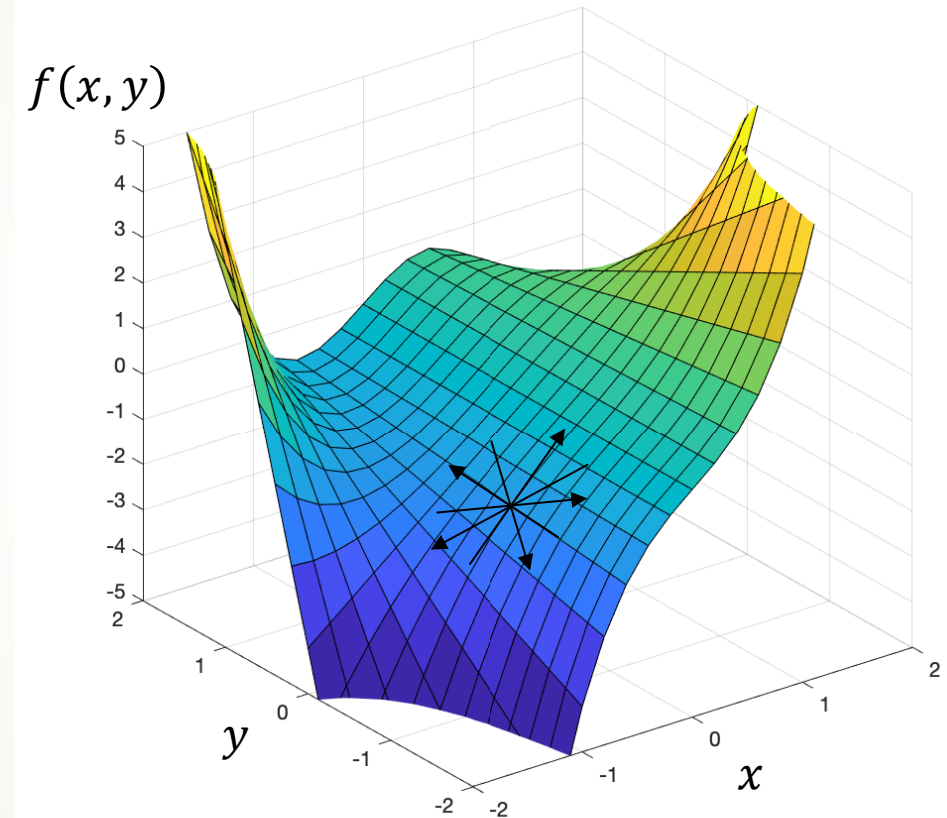
Stability in multi-D???

- To determine the stability of an equilibrium, one should calculate the *Jacobian matrix* of that equilibrium.

$$\begin{cases} \dfrac{dx_1}{dt} = f_1(x_1, x_2) \\ \dfrac{dx_2}{dt} = f_2(x_1, x_2) \end{cases} \qquad J = \begin{pmatrix} \dfrac{\partial f_1}{\partial x_1} & \dfrac{\partial f_1}{\partial x_2} \\ \dfrac{\partial f_2}{\partial x_1} & \dfrac{\partial f_2}{\partial x_2} \end{pmatrix}$$

All derivatives are evaluated at the equilibrium point, (n^*, p^*)

- If all *eigenvalues* of the Jacobian matrix have a <u>negative real part</u>, the equilibrium is stable.

The Jacobian of the Lotka-Volterra predator-prey equations

$$\begin{cases} \dfrac{dn}{dt} = f_n(n,p) = rn - anp \\ \dfrac{dp}{dt} = f_p(n,p) = canp - \mu p \end{cases}$$

$$\frac{\partial f_n}{\partial n} = r - ap \qquad \frac{\partial f_n}{\partial p} = -an$$

$$\frac{\partial f_p}{\partial n} = cap \qquad \frac{\partial f_p}{\partial p} = can - \mu$$

Equilibrium: $(n^*, p^*) = \left(\dfrac{\mu}{ca}, \dfrac{r}{a}\right)$

Jacobian: $J = \begin{pmatrix} r - ap^* & -an^* \\ cap^* & can^* - \mu \end{pmatrix} = \begin{pmatrix} r - \dfrac{ar}{a} & -\dfrac{a\mu}{ca} \\ \dfrac{car}{a} & \dfrac{ca\mu}{ca} - \mu \end{pmatrix} = \begin{pmatrix} 0 & -\dfrac{\mu}{c} \\ cr & 0 \end{pmatrix}$

Eigenvalues of 2x2-matrices: $\lambda_{1,2} = T \pm \sqrt{T^2 - D}$

$T = trace(J) = tr(J) = 0 + 0 = 0$

$D = determinant(J) = \det(J) = 0 - \left(-\dfrac{\mu}{c}\right)(cr) = \mu r$

$\lambda_{1,2} = T \pm \sqrt{T^2 - D} = \pm\sqrt{-\mu r} = \pm i\sqrt{\mu r}$

Conclusions???

$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$

$tr(A) = a_{11} + a_{22}$

$\det(A) = a_{11}a_{22} - a_{12}a_{21}$

General stability conditions for multidimensional systems

- Given an arbitrary dynamic system
$$\begin{cases} \dfrac{dx_1}{dt} = f_1(x_1, x_2) \\ \dfrac{dx_2}{dt} = f_2(x_1, x_2) \end{cases}$$

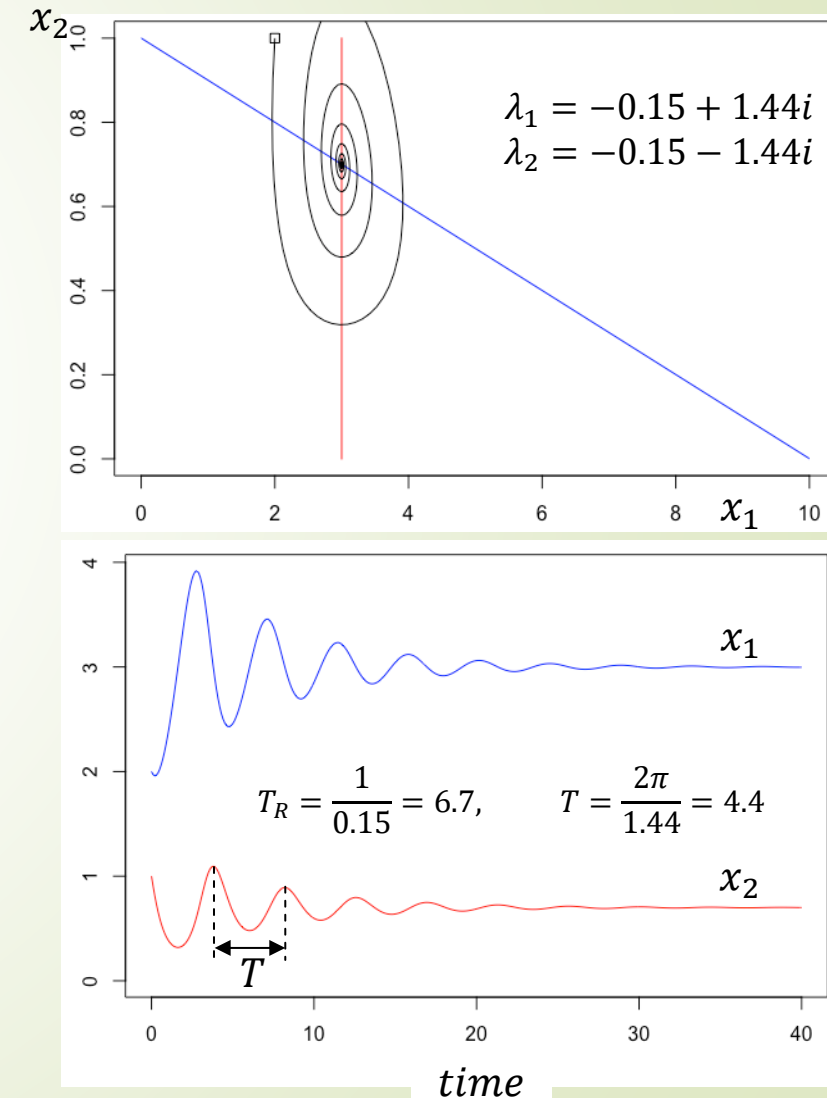2D system here to save space

- We find equilibrium states (x_1^*, x_2^*) by solving
$$\begin{cases} f_1(x_1^*, x_2^*) = 0 \\ f_2(x_1^*, x_2^*) = 0 \end{cases}$$

- The corresponding Jacobian matrix is calculated as
$$J = \begin{pmatrix} \dfrac{\partial f_1}{\partial x_1} & \dfrac{\partial f_1}{\partial x_2} \\ \dfrac{\partial f_2}{\partial x_1} & \dfrac{\partial f_2}{\partial x_2} \end{pmatrix}$$

All derivatives taken at the equilibrium point (x_1^*, x_2^*)

- An equilibrium $\mathbf{x}^*$ is stable *if* all eigenvalues of J have negative real part.
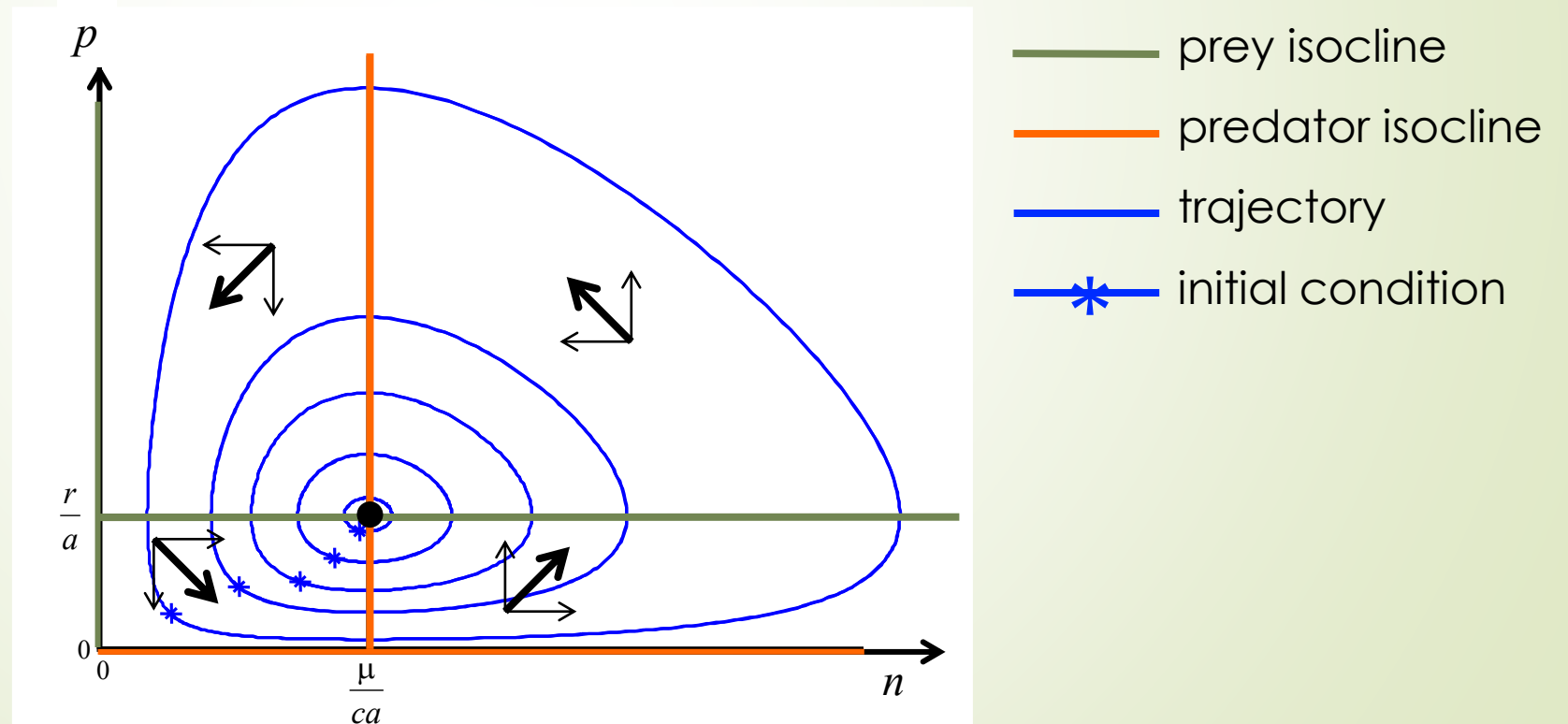
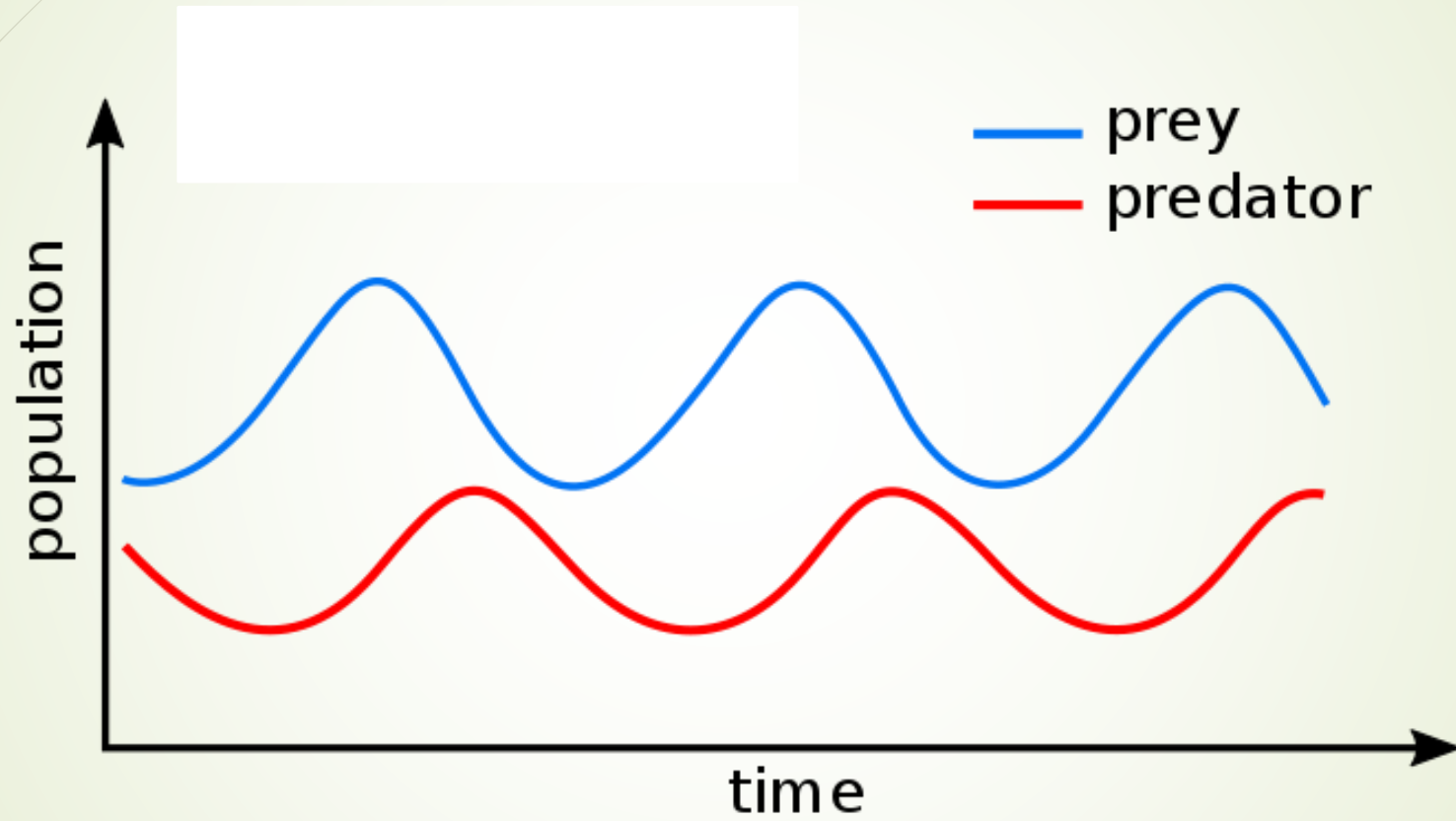# Interpreting the eigenvalues, $\lambda_1, \lambda_2, \ldots$

- The rate of the return to equilibrium is determined by the magnitude of the largest real part (the one closest to zero)

- The *return time* is calculated as $T_R = -\dfrac{1}{Re(\lambda)}$, where λ is the eigenvalue with the largest real part, the *dominant* eigenvalue.

- If any eigenvalues have a non-zero imaginary part, that indicates spiraling or periodic dynamics close to the equilibrium. The *period* of the cycles can be approximated as $T = \dfrac{2\pi}{|Im(\lambda)|}$, where $|Im(\lambda)|$ is the absolute value of the imaginary part of the eigenvalue.

$$\lambda_1 = -0.15 + 1.44i$$
$$\lambda_2 = -0.15 - 1.44i$$

x_2

x_1

x_1

x_2

$$T_R = \frac{1}{0.15} = 6.7, \qquad T = \frac{2\pi}{1.44} = 4.4$$

T

time

Neutral stability

- No matter where you start (*), the Lotka-Volterra predator-prey system makes a loop and comes back to exactly the same place.

- It will not return to equilibrium, but not move away from it either. It is a boundary case, called neutral stability.

The Lotka-Volterra competition equations (2D)

$$
\begin{cases}
\dfrac{dn_1}{dt} = r_1 n_1 \left(1 - \dfrac{n_1 + \alpha_{12} n_2}{K_1} \right) \\[2em]
\dfrac{dn_2}{dt} = r_2 n_2 \left(1 - \dfrac{n_2 + \alpha_{21} n_1}{K_2} \right)
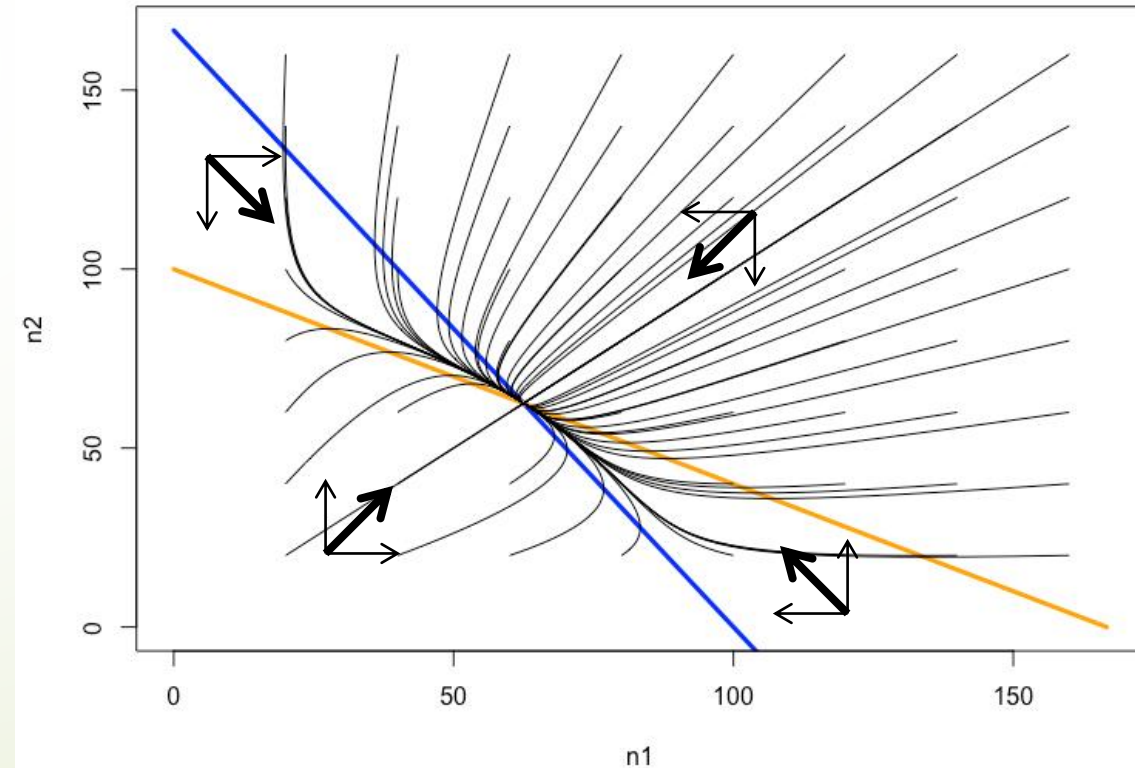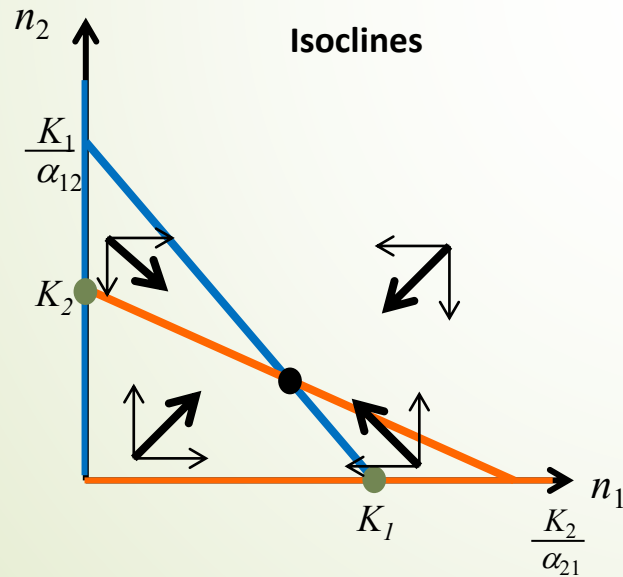\end{cases}
$$

α_{ij} = competition coefficient.

= How much population j competes with population i.

Competition coefficients are usually, but not always, below 1.

Isocline interpretation

- Putting everything together gives a general picture of the system dynamics

- Equilibrium points can be found where two isoclines of different types meet

- Whether an equilibrium is stable or not can generally not be seen from the isoclines, but they can give some hints.

Isoclines

The Lotka-Volterra competition equations (2D)

$$\begin{cases} \dfrac{dn_1}{dt} = r_1 n_1 \left(1 - \dfrac{n_1 + \alpha_{12} n_2}{K_1} \right) \\ \dfrac{dn_2}{dt} = r_2 n_2 \left(1 - \dfrac{n_2 + \alpha_{21} n_1}{K_2} \right) \end{cases}$$

α_{ij} = competition coefficient.

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Competition coefficients are usually, but not always, below 1.

the Jacobian J has entries $J_{ij} = \partial f_i / \partial n_j$:

$$J(n_1, n_2) = \begin{pmatrix} \dfrac{\partial f_1}{\partial n_1} & \dfrac{\partial f_1}{\partial n_2} \\ \dfrac{\partial f_2}{\partial n_1} & \dfrac{\partial f_2}{\partial n_2} \end{pmatrix} = \begin{pmatrix} r_1 \left[1 - \dfrac{2n_1 + \alpha_{12} n_2}{K_1} \right] & -\dfrac{r_1 \alpha_{12}}{K_1} n_1 \\ -\dfrac{r_2 \alpha_{21}}{K_2} n_2 & r_2 \left[1 - \dfrac{2n_2 + \alpha_{21} n_1}{K_2} \right] \end{pmatrix}.$$

The Lotka-Volterra competition equations (2D)

$$\begin{cases} \dfrac{dn_1}{dt} = r_1 n_1 \left(1 - \dfrac{n_1 + \alpha_{12} n_2}{K_1} \right) \\[4mm] \dfrac{dn_2}{dt} = r_2 n_2 \left(1 - \dfrac{n_2 + \alpha_{21} n_1}{K_2} \right) \end{cases}$$
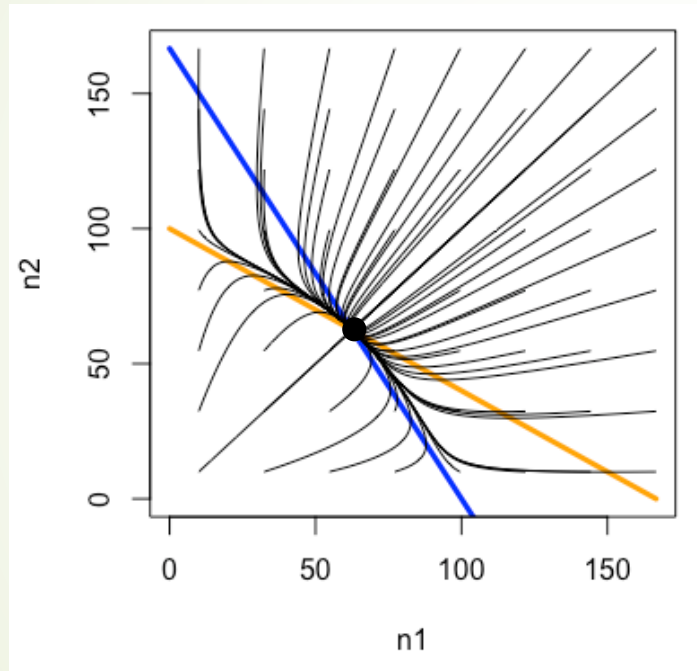
We also need equilibrium points:

$$1 - \frac{n_1^* + \alpha_{12} n_2^*}{K_1} = 0 \quad \Rightarrow \quad n_1^* + \alpha_{12} n_2^* = K_1$$

$$1 - \frac{n_2^* + \alpha_{21} n_1^*}{K_2} = 0 \quad \Rightarrow \quad \alpha_{21} n_1^* + n_2^* = K_2$$

Solve for zero and substitute n_1^* into n_2^* equation

$$n_2^* = \frac{K_2 - \alpha_{21} K_1}{1 - \alpha_{12} \alpha_{21}}$$

$$n_1^* = \frac{K_1 - \alpha_{12} K_2}{1 - \alpha_{12} \alpha_{21}}$$

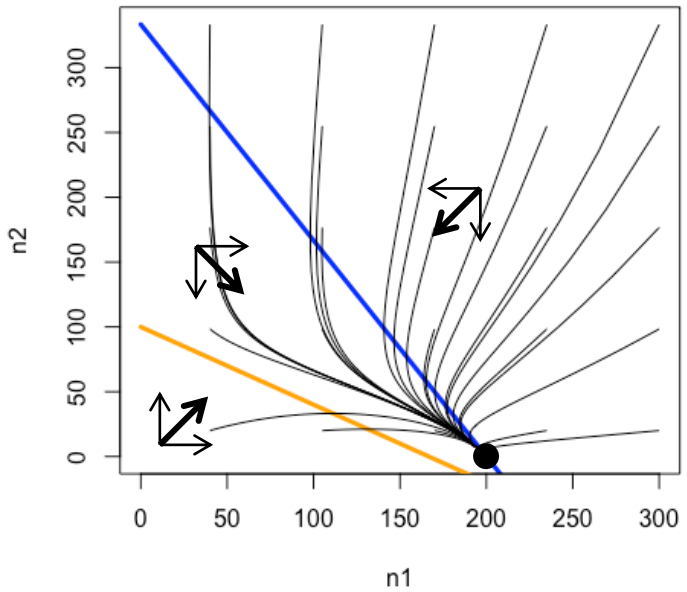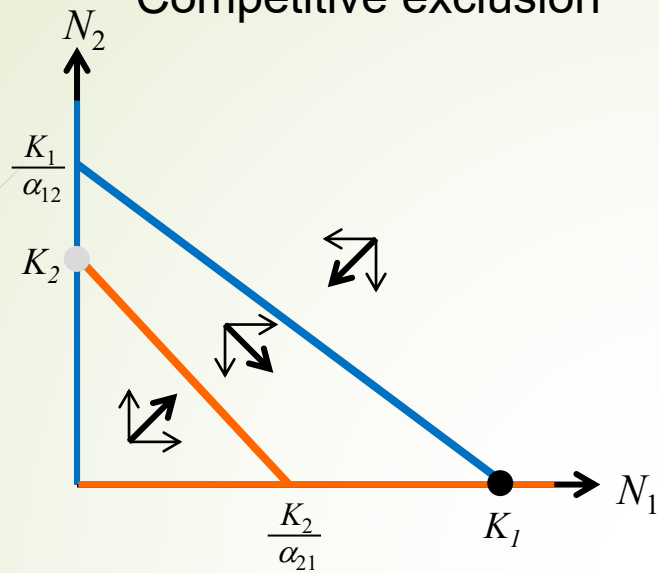$$J = \begin{pmatrix} -0.62 & -0.38 \\ -0.38 & -0.62 \end{pmatrix}$$

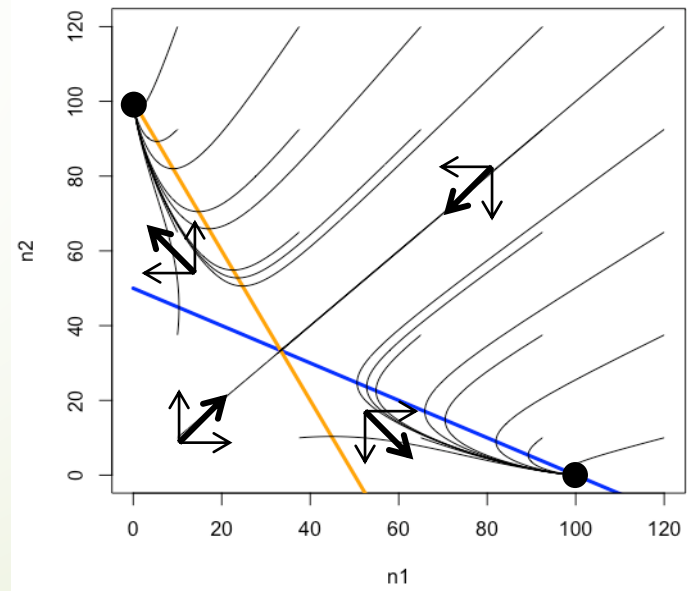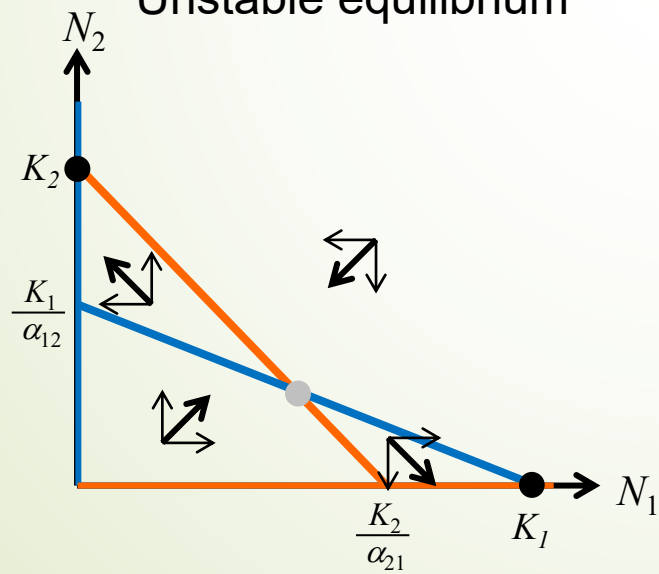$$\lambda_1 = -0.25$$

$$\lambda_2 = -1$$

α_{ij} = competition coefficient.
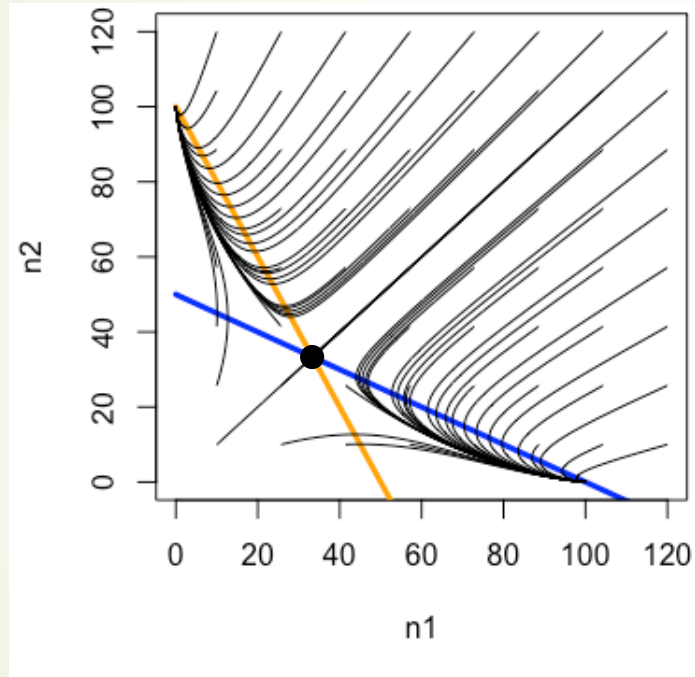   = How much population j competes with population i.

Competition coefficients are usually, but not always, below 1.

Competitive exclusion

Unstable equilibrium

$$J = \begin{pmatrix} -0.33 & -0.67 \\ -0.67 & -0.33 \end{pmatrix}$$

$$\lambda_1 = 0.33$$

$$\lambda_2 = -1$$

α_{ij} = competition coefficient.
= How much population j competes with population i.

What if competition coefficients above 1.

General stability conditions for multidimensional systems

■ Given an arbitrary dynamic system
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2D system here to save space

■ We find equilibrium states (x_1^*, x_2^*) by solving
$$\begin{cases} f_1(x_1^*, x_2^*) = 0 \\ f_2(x_1^*, x_2^*) = 0 \end{cases}$$

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$$J = \begin{pmatrix} \dfrac{\partial f_1}{\partial x_1} & \dfrac{\partial f_1}{\partial x_2} \\ \dfrac{\partial f_2}{\partial x_1} & \dfrac{\partial f_2}{\partial x_2} \end{pmatrix}$$
All derivatives taken at the equilibrium point (x_1^*, x_2^*)

■ An equilibrium $\mathbf{x}^*$ is stable *if* all eigenvalues of J have negative real part.

Interpreting the eigenvalues, $\lambda_1, \lambda_2, \dots$

- The rate of the return to equilibrium is determined by the magnitude of the largest real part (the one closest to zero)

- The *return time* is calculated as $T_R = -\frac{1}{Re(\lambda)}$, where λ is the eigenvalue with the largest real part, the *dominant* eigenvalue.

- If any eigenvalues have a non-zero imaginary part, that indicates spiraling or periodic dynamics close to the equilibrium. The *period* of the cycles can be approximated as $T = \frac{2\pi}{|Im(\lambda)|}$, where $|Im(\lambda)|$ is the absolute value of the imaginary part of the eigenvalue.

$\lambda_1 = -0.15 + 1.44i$
$\lambda_2 = -0.15 - 1.44i$

$T_R = \frac{1}{0.15} = 6.7, \qquad T = \frac{2\pi}{1.44} = 4.4$