Next logical step: consider dynamics of more than one species. We start with models of 2 interacting species. We consider, so-called, “box models” where species are assumed to be “well mixed”. Models that include spatial movement of species are no discussed in this course. (Ordinary vs. partial diff. equations.)

1. **Lotka-Volterra predator-prey model: “heuristic” derivation.**

Consider 2 species, prey \( u \), and predator \( v \).

Population of prey without predator grows \((a > 0 \text{ is a const.})\):

\[
\frac{du}{dt} = au; \quad u(0) = u_0;
\]

population of predator without prey decays \((b > 0 \text{ is a const.})\):

\[
\frac{dv}{dt} = -bv; \quad v(0) = v_0.
\]

If they co-exist in the same environment:

rate of change of \( u = + \text{growth} - \text{effect of predator-prey encounters} \)

rate of change of \( v = - \text{decay} + \text{effect of predator-prey encounters} \)

How to describe the effect of encounters? **Law of Mass Action!**
According to Law of Mass Action the probability of encounters of 2 species is proportional to the product of population densities of these species. Proportionality coefficients depend of various factors. Thus, we arrive at the system of equations ($a, b, n, m > 0$ are const.):

$$\frac{du}{dt} = au - nuv,$$

$$\frac{dv}{dt} = -bv + muv;$$

$$u(0) = u_0, \quad v(0) = v_0.$$

Possible model modifications: logistic growth for prey (instead of exponential), etc.

2. **Competition model: derivation.** "Heuristic" derivation: consider two species that consume the same resource. Assume that each species population in the absence of the other is described by the logistic equation (here $u$ and $v$ are population densities of the two species):

$$\frac{du}{dt} = k_1u - \alpha_1u^2,$$

$$\frac{dv}{dt} = k_2v - \alpha_2v^2.$$

When the other species is present:

- rate of change of $u = + \text{ growth} - \text{ competition between } u$
  - competition between $u$ and $v$
- rate of change of $v = + \text{ growth} - \text{ competition between } v$
  - competition between $u$ and $v$

Thus, using once again the Law of Mass Action, we write:

$$\frac{du}{dt} = k_1u - \alpha_1u^2 - \beta_1uv,$$

$$\frac{dv}{dt} = k_2v - \alpha_2v^2 - \beta_2uv;$$

$$u(0) = u_0, \quad v(0) = v_0.$$
Another way to derive: Consider a well stirred batch reactor. Let \( u \) and \( v \) be the population densities of two types of bacteria in a chemostat, and \( c \) be the food concentration. The same food is consumed by both types of bacteria. Assume that growth rate coefficient for each bacteria type is a linear function of \( c \): \( K_i = K_i(c) = \kappa_i c \ (i = 1, 2) \).

Then we have a system of equations

\[
\begin{align*}
\frac{du}{dt} &= \kappa_1 cu, \\
\frac{dv}{dt} &= \kappa_2 cv, \\
\frac{dc}{dt} &= -a_1 \kappa_1 cu - a_2 \kappa_2 cv,
\end{align*}
\]

where \( 1/a_i \ (i = 1, 2) \) are, so-called, yield factors. Initial conditions are

\[
u(0) = u_0, \quad v(0) = v_0, \quad c(0) = c_0.
\]

The above system can be reduced to two equations as follows. Let us multiply the first equation by \( a_1 \), the second — by \( a_2 \), and add the three equations. We obtain,

\[
a_1 \frac{du}{dt} + a_2 \frac{dv}{dt} + \frac{dc}{dt} = \frac{d(a_1 u + a_2 v + c)}{dt} = 0.
\]

Integrating this equation, we get for any \( t \):

\[
a_1 u(t) + a_2 v(t) + c(t) = \text{const},
\]

and from the initial conditions:

\[
a_1 u(t) + a_2 v(t) + c(t) = a_1 u_0 + a_2 v_0 + c_0 \quad \text{(conservation of mass!)}.\]

From the above we express

\[
c(t) = a_1 u_0 + a_2 v_0 + c_0 - a_1 u(t) - a_2 v(t) = A - a_1 u - a_2 v,
\]

and substitute this expression in the original equations for \( u \) and \( v \) to obtain the system:

\[
\frac{du}{dt} = \kappa_1 cu = \kappa_1 u(A - a_1 u - a_2 v)
\]
\[ du = k_1u - \alpha_1u^2 - \beta_1uv; \]
\[ dv \frac{dt}{dt} = \kappa_2cv = \kappa_2v(A - a_1u - a_2v) \]
\[ = k_2v - \alpha_2v^2 - \beta_2uv; \]

where \( k_i = \kappa_iA, \alpha_1 = \kappa_ia_1, \alpha_2 = \kappa_2a_2, \beta_1 = \kappa_1a_2, \) and \( \beta_2 = \kappa_2a_1. \)

In the future, for the analysis, we will write this system in yet another form.

3. SIR model. It is common to start with a schematic representation:

\[
\begin{array}{c}
S \rightarrow I \rightarrow R
\end{array}
\]

Which processes affect the rates of change of respective populations?

What are the assumptions?

Law of Mass Action!

For “box models” it does not matter whether we use the population densities or actual populations: numerical values of coefficients will be different but qualitative behavior is going to be the same! Let us use notations \( S, I, \) and \( R \) for susceptible, infected, and recovered. Then,

\[ \frac{dS}{dt} = -\alpha IS, \]
\[ \frac{dI}{dt} = +\alpha IS - \beta I, \]
\[ \frac{dR}{dt} = +\beta I, \]

\[ S(0) = S_0, \quad I(0) = I_0, \quad R(0) = 0 \quad \text{without immunization.} \]

Remark 1. It can be easily checked that in this system the total population is conserved: at any instant of time

\[ S(t) + I(t) + R(t) = S_0 + I_0 = N_{\text{total}} = \text{const.} \]
Remark 2. If deaths are included in the model, we get the system:

\[
\begin{align*}
\frac{dS}{dt} &= -\alpha IS - \delta_1 S, \\
\frac{dI}{dt} &= +\alpha IS - \beta I - \delta_2 I, \\
\frac{dR}{dt} &= +\beta I - \delta_1 R,
\end{align*}
\]

\[S(0) = S_0, \quad I(0) = I_0, \quad R(0) = 0.\]

We note that the SIR system is, in fact, a combination of a closed system of 2 equations for \(S\) and \(I\) (this system can be solved independently of \(R\)) and the differential relation for \(R\) (i.e., when \(I\) is known, \(R\) is obtained by simple integration). So, we actually have to analyze the system of 2 equations:

\[
\begin{align*}
\frac{dS}{dt} &= -\alpha IS, \\
\frac{dI}{dt} &= +\alpha IS - \beta I.
\end{align*}
\]

If recovered can become susceptible again we arrive at the, so-called, SIRS model.

4. SIRS model. Schematic representation:

![Schematic representation of SIRS model](image)

Corresponding model system will now be in the form:

\[
\begin{align*}
\frac{dS}{dt} &= -\alpha IS + \gamma R, \\
\frac{dI}{dt} &= +\alpha IS - \beta I,
\end{align*}
\]
\[
\frac{dR}{dt} = +\beta I - \gamma R,
\]

\[S(0) = S_0, \quad I(0) = I_0, \quad R(0) = R_0 \quad \text{in general case.}\]

Using the fact that in this model (without deaths) the total population, \(N\), is once again conserved, we can reduce the above 3-dimensional system to a system of 2 equations. We express \(R\) in terms of \(S\) and \(I\) as follows. For \(N = S_0 + I_0 + R_0 = \text{const known}\), we have:

\[R(t) = N - I(t) - S(t).\]

Substituting this into equations for \(S\) and \(I\) we, finally, obtain:

\[\frac{dS}{dt} = -\alpha IS + \gamma (N - I - S),\]

\[\frac{dI}{dt} = +\alpha IS - \beta I,\]

\[S(0) = S_0, \quad I(0) = I_0.\]

4. **General systems of two nonlinear differential equations.** It can be easily seen that all the models introduced above can be written in the following general form:

\[\frac{du}{dt} = f(u, v),\]

\[\frac{dv}{dt} = g(u, v),\]

\[u(0) = u_0, \quad v(0) = v_0 \quad \text{known.}\]

Functions \(f(u, v)\) and \(g(u, v)\) describe the “rules” of species interactions and behavior.

Our goal is to describe possible types of solutions: we want to know when the populations will grow to certain values, go extinct, oscillate, etc., and how will these types of solutions depend on numerical values of model parameters?
Let us extend the approach that worked previously for scalar (single) non-linear differential equations to systems of two (and later, to systems of three and more) differential equations.

5. Model solutions and phase plane. Geometry of the model system. Assume that the solution of a system is somehow known: \( u = u(t), \ v = v(t) \). Consider a \((u,v)\)–plane, which we call a phase plane. Then the point with coordinates \((u(t), v(t))\) (where time \(t\) is changing) will trace a curve on this plane.

If the solution goes to a steady state (i.e., as \( t \to \infty \), \((u(t), v(t)) \to (\bar{u}, \bar{v})\)) then the point on the phase plane corresponding to a solution will eventually
If the solution oscillates (i.e., the values of \((u(t), v(t))\) periodically repeat themselves with certain period \(T\)) then the point on the phase plane will trace a closed loop.

The velocity vector \(\vec{w}\) related to motion of a point \((u(t), v(t))\) on the plane (this vector is tangential to the, so-called, trajectory of the moving point, it shows the direction of point’s motion and its length shows how fast the point is moving) is defined as follows:

\[
\vec{w} = \left(\frac{du}{dt}, \frac{dv}{dt}\right) = (f(u,v), g(u,v)).
\]

The above expression means that the system of differential equations specifies the, so-called, vector field on the phase plane: with every point \((u, v)\) we associate a vector \((f(u,v), g(u,v))\). These vectors show the direction and speed of motion of a solution point, that is currently located at position \((u, v)\), as time increases.

Sometimes it is convenient to show only the direction of motion at every point of the phase plane and not how fast the solution changes along the phase trajectory. Then instead of velocity vector field one may show the, so-called, direction field: all the vectors associated with different locations in the phase plane will have the same length and will possibly differ only by
direction. To normalize the vectors with coordinates \((f(u, v), g(u, v))\) (i.e., to make them all be of the same length \(L\)) the following formula may be used: the new “normalized” vectors will have coordinates:

\[
(F(u, v), G(u, v)) = \left( \frac{L f(u, v)}{\sqrt{f^2(u, v) + g^2(u, v)}}, \frac{L g(u, v)}{\sqrt{f^2(u, v) + g^2(u, v)}} \right).
\]

Same as in the case of the scalar equation, steady states \((\bar{u}, \bar{v})\) are the constant solutions that satisfy the following system of equations (since \(d\bar{u}/dt = 0\) and \(d\bar{v}/dt = 0\)):

\[
0 = f(\bar{u}, \bar{v}), \quad 0 = g(\bar{u}, \bar{v}).
\]

In terms of behavior on the phase plane we have that if the point corresponds to a steady state, it will not move since the velocity vector at this point has zero entries: \((f(\bar{u}, \bar{v}), g(\bar{u}, \bar{v})) = (0, 0)\) (and thus, no direction of motion is defined, and the speed of motion is zero).

The prescribed initial condition hits one of the trajectories on the phase plane and follows it as time increases. For us it is important to know where it will go. If the initial condition corresponds to a steady state, then the solution will stay at this steady state forever. It turns out that if the initial condition is not at a steady state, only a few possibilities may occur on the phase plane: (a) solution tends to a stable steady state, (b) moves away (to infinity), (c) belongs to a limit cycle, (d) tends to a limit cycle, (e) moves away from a limit cycle, (f) what else?
Important! No chaos for continuous systems of 2 equations, i.e., no chaos on the phase plane! We need 3 equations to produce chaos.

Our goal will be to characterize possible types of solution behavior in the vicinity of the steady states, which will lead to identification of several distinct types of steady states (also called equilibrium points). Then, using some additional information on general behavior of phase trajectories away from steady states (e.g., the fact that trajectories can only intersect at steady states), we will be able to qualitatively characterize the global behavior of solutions (not only near the steady states).

In what follows we will extensively use the idea of a null-cline. The curves in the phase plane whose \((u, v)\) coordinates satisfy the equation \(f(u, v) = 0\) are called \(u\) null-clines. Special feature: solution trajectories intersect these null-clines vertically (since on these curves the \(u\)-component of velocity vectors is zero). Similarly, curves in the phase plane whose \((u, v)\) coordinates satisfy the equation \(g(u, v) = 0\) are called \(v\) null-clines. Their special feature: solution trajectories intersect these null-clines horizontally (since on these curves the \(v\)-component of velocity vectors is zero). Evidently, the steady states correspond to points of intersection of \(u\) null-clines and \(v\) null-clines.