Continuous time dynamical systems
(Review of the second part of Math 361, Winter 2001)

Basic problem:

$x_1(t), ..., x_n(t)$ dynamic variables (e.g. population size of species i at time t); dynamics given by a set of n equations

$$\frac{dx_1}{dt} = F_1\left(x_1(t), ..., x_n(t)\right)$$
$$...$$
$$\frac{dx_n}{dt} = F_n\left(x_1(t), ..., x_n(t)\right)$$

where $F_1, ..., F_n$ are functions of n variables. The general problem is to find solutions $x_1(t), ..., x_n(t)$ (i.e. the dynamics) satisfying this system of equations, subject to some initial conditions, e.g. $x_1(0), ..., x_n(0)$. Usually, the time dependence in the variables x_i is suppressed for notational convenience, so that system becomes

$$\frac{dx_1}{dt} = F_1\left(x_1, ..., x_n\right)$$
$$...$$
$$\frac{dx_n}{dt} = F_n\left(x_1, ..., x_n\right)$$

This is a generally non-linear system of first-order autonomous differential equations (non-linear: the functions F_i may be non-linear; first-order: only the functions x_i and their derivatives occur in these equations; autonomous: there is no explicit time dependence in the functions F_i, only an implicit time dependence through the time dependence of the x_i.)

Example:

$$\frac{dx_1}{dt} = \lambda x_1.$$

Here $n = 1$, and $F_1(x_1) = \lambda x_1$ is linear. Given the initial condition $x_1(0) = x_0$, the solution is

$$x_1(t) = x_0 \cdot \exp[\lambda t].$$

Note that $x_1(t) \to 0$ or $x_1(t) \to \infty$ depending on whether $\lambda < 0$ or $\lambda > 0$.

I. Linear differential equations:

If the F_i are linear real-valued functions

$$F_i(x_1, ..., x_n) = a_{i1}x_1 + ... + a_{in}x_n, \ i = 1, ..., n,$$

(where we assume the a_{ij} to be real numbers), then the system of differential equations is given by the matrix multiplication

$$\begin{pmatrix} \frac{dx_1}{dt} \\ ... \\ \frac{dx_n}{dt} \end{pmatrix} = A \cdot \begin{pmatrix} x_1(t) \\ ... \\ x_n(t) \end{pmatrix},$$

where A is the matrix

$$A = \begin{pmatrix} a_{11} & ... & a_{1n} \\ ... & .. & ... \\ a_{n1} & .. & a_{nn} \end{pmatrix}.$$

In 'most' cases, the matrix A has n eigenvalues $\lambda_1, ..., \lambda_n$ with corresponding eigenvectors $w_1, ..., w_n$:

$$A \cdot w_i = \lambda_i w_i, \ i = 1, ..., n.$$

The general solution for the dynamical system is:

$$\begin{pmatrix} x_1(t) \\ ... \\ x_n(t) \end{pmatrix} = b_1 \cdot \exp[\lambda_1 t] \cdot w_1 + ... + b_n \cdot \exp[\lambda_n t] \cdot w_n,$$

where the initial condition is

$$\begin{pmatrix} x_1(0) \\ ... \\ x_n(0) \end{pmatrix} = b_1 w_1 + ... + b_n w_n.$$

In the long term, i.e. for $t \longrightarrow \infty$, there are two qualitatively distinct cases:

Let λ be the eigenvalue of A with the largest real part (i.e., the *dominant eigenvalue*), and let w be the corresponding eigenvector.

Then, if λ is a real number, (i.e., if the imaginary part $\text{Im}\,\lambda = 0$), then w can be chosen to be real-valued, and the long term behaviour is given by

$$\begin{pmatrix} x_1(t) \\ ... \\ x_n(t) \end{pmatrix} = b \cdot \exp[\lambda t] \cdot w \text{ for } t \to \infty$$

(where bw is the component of the initial condition in the direction of the eigenvector w). Thus, if λ is real, the dynamic variables will eventually grow exponentially at a rate λ, and the vector of variables will be a multiple of w.

If λ is not real, $\lambda = r + is =$ with $\varphi \neq 0$ (hence $s \neq 0$), then $w = u + iv$ with $v \neq 0$, and the complex conjugate $\overline{\lambda} = r - is$ is also an eigenvalue of A with corresponding eigenvector $w = u - iv$. The real valued solution will eventually converge to oscillating behaviour with exponentially growing (or decreasing)

amplitude: $\begin{pmatrix} x_1(t) \\ ... \\ x_n(t) \end{pmatrix} = b_1 \cdot \exp[rt] \cdot [(\cos(ts) \cdot u - \sin(ts) \cdot v)] + b_2 \cdot \exp[rt] \cdot$

$[(\sin(ts) \cdot u + \cos(ts) \cdot v)]$ for $t \to \infty$, where $c = \sqrt{r^2 + s^2}$ is the absolute value of λ, and where b_1 and b_2 are determined from the initial condition.

In particular, all solutions $\begin{pmatrix} x_1(t) \\ ... \\ x_n(t) \end{pmatrix}$ will converge to the 0- vector $\begin{pmatrix} 0 \\ ... \\ 0 \end{pmatrix}$

if and only if all eigenvalues of A have negative real parts.

Special cases:

1. In the example given above, $\frac{dx_1}{dt} = \lambda x_1$, the matrix A simply consists of the number λ, which is its sole eigenvalue (with eigenvector 1).

2. Consider 2-dimensional systems of linear differential equations

$$\begin{pmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{pmatrix} = A \cdot \begin{pmatrix} x \\ y \end{pmatrix}$$

with

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}, \quad a_{ij} \text{ real.}$$

Then either both eigenvalues of A are real, or they are a pair of complex conjugate numbers with non-zero imaginary part. In the first case, the point $(x, y) = (0, 0)$ is called an unstable node, a saddle point, or a stable node depending on whether both eigenvalues are > 0, one eigenvalue is > 0 and one is < 0, or both eigenvalues are < 0, respectively. In this case, solutions will converge to $(0, 0)$ as $t \to \infty$ independent of starting conditions if and only if $(0, 0)$ is a stable node.

In the second case, the point $(x, y) = (0, 0)$ is an unstable focus or a stable focus depending on whether the real part of the eigenvalue is positive or negative. In this case, real -valued solutions will exhibit oscillations, and they will converge to $(0, 0)$ as $t \to \infty$ independent of starting conditions if and only if $(0, 0)$ is a stable focus.

II. Non-linear differential equations:

If the functions F_i in (1) are non-linear, then the general approach is to first look for equilibrium states and then perform a linear stability analysis.

A point $(x_1^*, ..., x_n^*)$ is called an equilibrium for the dynamical system (1) if

$$F_i(x_1^*, ..., x_n^*) = 0 \text{ for } i = 1, ..., n.$$

Given an equilibrium state $(x_1^*, ..., x_n^*)$, the dynamics of a vector of small deviations $D_i(t) = x_i(t) - x_i^*$ from this equilibrium is given by

$$\begin{pmatrix} \frac{dD_1}{dt} \\ ... \\ \frac{dD_n}{dt} \end{pmatrix} = J \cdot \begin{pmatrix} D_1(t) \\ ... \\ D_n(t) \end{pmatrix},$$

where J is the *Jacobian matrix* of partial derivatives evaluated at the equilibrium

$$J = \begin{pmatrix} \frac{\partial F_1}{\partial x_1}(x_1^*, ..., x_n^*) & ... & \frac{\partial F_1}{\partial x_n}(x_1^*, ..., x_n^*) \\ ... & & ... \\ \frac{\partial F_n}{\partial x_1}(x_1^*, ..., x_n^*) & ... & \frac{\partial F_n}{\partial x_n}(x_1^*, ..., x_n^*) \end{pmatrix}.$$

This dynamical equation holds approximately as long as $|D_i(t)| \ll 1$ are small.

The equilibrium is called *locally stable* if and only if

$$\begin{pmatrix} D_1(t) \\ ... \\ D_n(t) \end{pmatrix} \rightarrow \begin{pmatrix} 0 \\ ... \\ 0 \end{pmatrix} \text{ for } t \rightarrow \infty$$

for any initial condition $(D_1(0), ..., D_n(0))$ with $|D_i(0)| \ll 1$ for all i.

It follows from the linear theory that the equilibrium is locally stable if and only if all eigenvalues of the Jacobian J have negative real parts.

Examples:

1. The logistic equation for competition in a single species has the form

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) = F(x).$$

The equation $F(x^*) = 0$ has to solutions: $x^* = 0$ and $x^* = K$. The Jacobian is simply given by dF/dx, and we have $dF/dx(0) > 0$ and $dF/dx(K) < 0$. Therefore, $x^* = 0$ is unstable, and $x^* = K$ is stable.

Note that the logistic equation can be solved analytically as

$$x(t) = \frac{K}{1 - (\frac{K}{x_0} - 1)\exp[-rt]},$$

where $x(0) = x_0$ is the initial condition. Note also that this system exhibits convergence to $x^* = K$ from almost all initial conditions. In particular, this

system always exhibits equilibrium dynamics, and in particular does not exhibit oscillatory behaviour. *This is true for any 1-dimensional differential equation of the type considered above: all solutions to such equations either converge towards an equilibrium state, or they diverge towards $\pm\infty$, as $t \to \infty$.*

To get oscillatory behaviour in 1-dimensional systems, we need to have an explicit dependence of the function F on time (e.g. by assuming that parameters are sinusoidal functions of time), or we need delay density dependence, so that e.g. in the logistic equation the per capita growth rate at time t does not depend on the present population size $x(t)$, but on the population size at some time in the past, i.e. on $x(t - T)$ (for example, T might be the time it takes an egg to develop into an adult individual). The delay logistic equation

$$\frac{dx}{dt} = rx(t)\left(1 - \frac{x(t-T)}{K}\right)$$

typically exhibits oscillations of period approximately $4T$.

2. Lotka-Volterra equations for competition between two species are extensions of the logistic equation and have the form

$$\begin{aligned}
\frac{dx_1}{dt} &= r_1 x_1 \left(1 - \frac{x_1 - \alpha_{12} x_2}{K_1}\right) \\
\frac{dx_2}{dt} &= r_2 x_2 \left(1 - \frac{x_2 - \alpha_{21} x_1}{K_2}\right)
\end{aligned}$$

These equations can be studied using direction fields and phase plane analysis. To do this, one plots the two isoclines

$$x_1 = 0, \quad x_2 = \frac{x_1 - K_1}{\alpha_{12}}$$

for the growth rate in species 1, and

$$x_2 = 0, \quad x_2 = K_2 - \alpha_{21} x_1$$

for the growth rate in species 2, in the phase plane with x_1 as the horizontal axis and x_2 as the vertical axis. Equilibrium points are given as intersections of the isoclines. There is a positive equilibrium (x^*, y^*) with $x^* > 0$ and $y^* > 0$ if and only if the two isoclines $x_2 = \frac{x_1 - K_1}{\alpha_{12}}$ and $x_2 = K_2 - \alpha_{21} x_1$ intersect in the positive quadrant of the phase plane. The directions of change in the various regions delimited by the isoclines can be found by noting that dx_1/dt is negative for points (x, y) lying above the isocline $x_2 = \frac{x_1 - K_1}{\alpha_{12}}$, and positive otherwise. A similar statement hods for dx_1/dt with respect to the isocline $x_2 = K_2 - \alpha_{21} x_1$. Depending on the configuration of the isoclines, one can then see that either one species outcompetes the other species independently of the initial conditions (isoclines do not intersect in positive quadrant), or one species outcompetes the other species but which species wins depends on the initial conditions (isoclines intersect in positive quadrant, with $K_2 < K_1/\alpha_{12}$), or the two species coexist at a stable equilibrium (isoclines intersect in positive

quadrant, with $K_2 > K_1/\alpha_{12}$). Thus, the dynamical behaviour of the system can be determined from phase plane analysis, a type of analysis which is also important for Poincaré-Bendixson theory (s. below). Note that the various equilibria and their stability can also be found analytically using linear stability analysis based on Jacobian matrices.

Linear stability analysis can also be used to determine general conditions under which generalized Lotka-Volterra equations for interactions between n species have a locally stable equilibrium at which all interacting species coexist.

3. The basic Lotka-Volterra predator-prey equations have the form:

$$
\begin{aligned}
\frac{dx}{dt} &= rx - bxy \\
\frac{dy}{dt} &= -cy + dxy
\end{aligned}
$$

Here x is prey population size and y is predator population size, and it is assumed that the attack rate is proportional to the product xy (mass action), so the rate at which prey is killed is bxy, while the rate at which new predators are born is dxy, with $b > 0$ and $d > 0$ some parameters.

The Jacobian of this system at the equilibrium $(c/d, r/b)$ has two purely imaginary eigenvalues, and hence the linearized system exhibits neutral oscillations. It can be shown that the same is true for the full, non-linear system: prey and predator populations will undergo periodic changes, with the amplitude and frequency of the oscillations depending on initial conditions.

In class we have seen various examples of how the configuration of equilibrium points of a dynamical system and/or their stability can change as parameters are varied (e.g. model for cell differentiation along a morphogenetic gradient). One of the most important types of bifurcations is the so-called *Hopf bifurcation*, which occurs when a stable focus loses its stability and becomes an unstable focus as a bifurcation parameter is varied. During a Hopf bifurcation, the eigenvalues of the Jacobian at the equilibrium under consideration change from being a pair of complex conjugate numbers with negative real parts and non-zero imaginary part to being a pair of complex conjugate eigenvalues with positive real parts and non-zero imaginary parts. At the bifurcation point, the Jacobian has purely imaginary (non-zero) eigenvalues, and hence the linearized system exhibits neutral oscillations at the bifurcation point.

The *Hopf bifurcation theorem* states that when a system exhibits a Hopf bifurcation, then, for a range of parameter values in the neighborhood of the bifurcation point, the system admits a unique closed limit cycle as solution (for a precise statement of the Hopf bifurcation theory see textbook p. 342).

Example: predator-prey system of the form

$$
\begin{aligned}
\frac{dx}{dt} &= x(1-x) - \frac{xy}{x+d} \\
\frac{dy}{dt} &= r\left(1 - \frac{y}{x}\right)
\end{aligned}
$$

6

This system has an interior equilibrium

$$(x^*, y^*) = \left(\frac{1}{2} \left(-d + \sqrt{d^2 + 4d} \right), \frac{1}{2} \left(-d + \sqrt{d^2 + 4d} \right) \right),$$

and the Jacobian at this equilibrium is

$$J = \begin{pmatrix} x^* \left[\frac{x^*}{(x^*+d)^2} - 1 \right] & \frac{-x^*}{x^*+d} \\ r & -r \end{pmatrix}$$

Its determinant is

$$\det(J) = \frac{rx^*}{x^* + d} \left(1 - \frac{x^*}{x^* + d} \right) + rx^* > 0.$$

Therefore, for small values of $|tr(J)|$, the eigenvalues

$$\lambda_{1,2} = \frac{tr(J) \pm \sqrt{tr(J)^2 - 4 \det(J)}}{2}$$

will have non-zero-imaginary part, and hence a Hopf bifurcation will occur as $tr(J)$ increases through 0 (with $|tr(J)|$ being kept small. Since

$$tr(J) = \left(1 - \sqrt{d^2 + 4d} \right) \frac{2 + d - \sqrt{d^2 + 4d}}{2} - r,$$

for a fixed r ($0 < r < 1$) a Hopf bifurcation will occur as d is increased through a critical value $\widehat{d}$, the bifurcation point. For values of $d < \widehat{d}$, the equilibrium is a stable focus, and for values of $d > \widehat{d}$, the equilibrium is an unstable focus.

The Hopf bifurcation theorem then states that for a range of values d in the neighborhood of $\widehat{d}$, the system has a unique limit cycle. However, the Hopf bifurcation theorem does not tell us whether this range of values lies below or above $\widehat{d}$, and it does not say anything about the local stability of the limit cycle, i.e. about whether trajectories that are started close by, but not on the limit cycle, will converge towards the limit cycle.
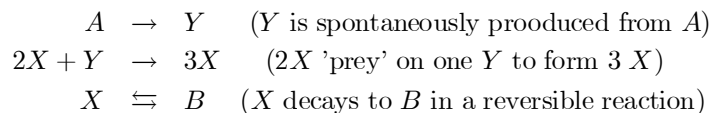
To get this kind of information it is often possible to apply the *Poincaré-Bendixson theorem*, which states that if the phase space of a 2-dimensional system of differential equations contains a bounded region that traps the flow of the system and that contains an unstable focus, then the system must have a limit cycle. Moreover, this limit cycle must be stable if it is unique. (For a detailed formulation of this theorem see p. 328 in the textbook.) To find a trapping region as in the Poincaré-Bendixson theorem, it is important to consider the geometry of the 0-isoclines of the differential equations.

Examples:

1. By studying the isoclines of the predator-prey system above, one can prove that there is a region trapping the flow and containing the positive equilibrium. If this equilibrium is an unstable focus, we can therefore apply the Poincaré-Bendixson theorem and conclude that there is a limit cycle. Since the

7

equilibrium is an unstable focus for $d > \widehat{d}$, we then conclude that the range of d values for which a limit cycle exists according to the Hopf bifurcation theorem must lie above the bifurcation point $\widehat{d}$. Moreover, since the limit cycle existing for this range of d-values is unique by the Hopf bifurcation theorem, it is also stable according to the Poincaré-Bendixson theorem. Overall, we conclude that as the stable focus loses its stability due to a Hopf bifurcation, the system has a stable limit cycle for a range of d-values beyond the bifurcation point.

2. Consider the following chemical reactions between reservoir substances A and B and two reactants ('chemical species') X and Y:

$$
\begin{aligned}
A &\rightarrow Y & (Y \text{ is spontaneously prooduced from } A) \\
2X + Y &\rightarrow 3X & (2X \text{ 'prey' on one } Y \text{ to form 3 } X) \\
X &\leftrightarrows B & (X \text{ decays to } B \text{ in a reversible reaction})
\end{aligned}
$$

For simplicity it is assumed that the rate constants for these three reactions are equal to 1. Therefore, according to the law of mass action, the first reaction occurs at a rate a, where a is the concentration of the substance A (which is assumed to be constant), the second reaction occurs at a rate x^2y, where x and y are the concentrations of the substances X and Y, and the two reactions corresponding to the third step occur at rate x and b, where b is the concentration of the substance B (which is also assumed to be constant). This leads to the following system of differential equations:

$$
\begin{aligned}
\frac{dx}{dt} &= -2x^2y + 3x^2y - x + b = x^2y - x + b \\
\frac{dy}{dt} &= a - x^2y
\end{aligned}
$$

Using similar arguments as in the previous example, one can show that for small values of b a Hopf bifurcation occurs as a decreases from large to small values, with the bifurcation point approximately at $a = 1$. Moreover, by considering the isoclines $x^2y - x + b = 0$ and $a - x^2y = 0$, one can construct a trapping region around the equilibrium, from which one concludes that as the stable focus gives way to an unstable focus during the Hopf bifurcation, the system exhibits a stable limit cycle for a range of a-values below the bifurcation point.