Lecture Notes for Lecture 17 of Dr. Z.'s Dynamical Systems in Biology

These notes are based on parts of Chapters 4,5, and 6 of Leah Edelstein-Keshet's classic "Mathematical Models in Biology".

A 1-dimensional continuous dynamical system

It is a differential equation, where the unknowns function $x(t)$ of times satisfies the differential equation

$$\frac{dx}{dt} = F(x(t), t)$$

where F is some function of two variables. If F only depends on $x(t)$ (i.e. only depends on time via $x(t)$) it is called autonomous. We will only consider this case, so the format is

$$\frac{dx}{dt} = F(x(t)) \quad .$$

Often you write it as

$$\frac{dx}{dt} = F(x) \quad ,$$

where it is understood that x is a function of t.

For any initial condition $x(t_0) = x_0$ $x(t)$ will evolve as time t goes to infinity. Often it would go to infinity, but sometimes it would tend to some **stable steady-state**, that in the continuous case is more often called **stable equilibrium**.

Def. A number x_0 is called an *equilibrium* if it solves the (algebraic) equation $F(x_0) = 0$.

Problem 17.1: Find all the equilibrium points of the 1D continuous dynamical system

$$\frac{dx}{dt} = (x(t)-1)(x(t)-2)(x(t)-3)(x(t)-4)(x(t)-5) \quad .$$

Sol. of 17.1: We have to solve

$$(x-1)(x-2)(x-3)(x-4)(x-5) = 0 \quad .$$

whose solutions are $x = 1$, $x = 2$, $x = 3$, $x = 4$, $x = 5$.

Ans. to 17.1: The set of equilibrium points of this differential equation is $\{1, 2, 3, 4, 5\}$.

If the quantity (e.g. population of some species) is exactly at an equilibrium point, then it stays there for ever after, so the solution of the initial value differential equation 1 with

- initial condition $x(0) = 1$ is $x(t) = 1$

• initial condition $x(0) = 2$ is $x(t) = 2$

• initial condition $x(0) = 3$ is $x(t) = 3$

etc.

But for some equilibrium points, if you just move a *tiny bit*, you would go very far away. These are **unstable** equilibrium points. For other equilibrium points, if you start at a nearby value (and often pretty far), in the long run it would be attracted to it.

How to decide whether an equilibrium point is stable?

If x_0 is an equilibrium point of $x'(t) = F(x(t))$, in other words $F(x_0) = 0$. Look at $F'(x_0)$.

Stability Criterion

x_0 is *stable* if $F'(x_0) < 0$. It is *unstable* if $F'(x_0) > 0$. It is *semi-stable* if $F'(x_0) = 0$.

Problem 17.2: Find all the stable equilibrium points of the 1D continuous dynamical system

$$\frac{dx}{dt} = (x(t) - 1)(x(t) - 2)(x(t) - 3)(x(t) - 4)(x(t) - 5) \quad .$$

Sol. of 17.2: By the product rule

$$F'(x) = (x-2)(x-3)(x-4)(x-5) + (x-1)(x-3)(x-4)(x-5) + (x-1)(x-2)(x-4)(x-5)$$
$$+(x-1)(x-2)(x-3)(x-5) + (x-1)(x-2)(x-3)(x-4) \quad .$$

please do not expand.

We know from 17.1 that the candidates are $\{1, 2, 3, 4, 5\}$.

When $x = 1$, we have $F'(1) = (1-2)(1-3)(1-4)(1-5) = 24$ since this is **positive**, we know that $x = 1$ is **unstable**.

When $x = 2$, we have $F'(2) = (2-1)(2-3)(3-4)(2-5) = -6$ since this is **negative**, we know that $x = 2$ is **stable**.

When $x = 3$, we have $F'(3) = (3-1)(3-2)(3-4)(3-5) = 2$ since this is **positive**, we know that $x = 3$ is **unstable**.

When $x = 4$, we have $F'(4) = (4-1)(4-2)(4-3)(4-5) = -6$ since this is **negative**, we know that $x = 4$ is **stable**.

When $x = 5$, we have $F'(5) = (5-1)(5-2)(5-3)(5-4) = 24$ since this is **positive**, we know that $x = 3$ is **unstable**.

Ans. to 17.2: The set of stable equilibria is $\{2, 4\}$.

Dynamical Systems in Several Variables (species)

A k-dimensional continuous dynamical system (we only do autonomous ones) is a system of k differential equations, with k unknown functions of time, $x_1(t), \ldots, x_k(t)$ (e.g. the relative occurrence of each species, concentration of nutrients, ratio of infected) of the form

$$\frac{dx_1}{dt} = F_1(x_1(t), \ldots, x_k(t)) \quad ,$$
$$\frac{dx_2}{dt} = F_2(x_1(t), \ldots, x_k(t)) \quad ,$$
$$\ldots$$
$$\frac{dx_k}{dt} = F_k(x_1(t), \ldots, x_k(t)) \quad ,$$

where $F_1, ..., F_k$ are k multi-variable functions of k variables. The **underlying transformation** is

$$\mathbf{F} : R^k \to R^k \quad ,$$

given by

$$\mathbf{F}(x_1, \ldots, x_k) = (F_1(x_1, \ldots x_k), \ldots, F_k(x_1, \ldots x_k)) \quad .$$

How to find the Equilibrium points?

Solve the system of k algebraic (or tanscendental) equations $\mathbf{x} = \mathbf{F}(\mathbf{x})$. In other words

$$F_1(x_1, \ldots, x_k) \;=\; 0 \quad , \quad F_2(x_1, \ldots, x_k) \;=\; 0 \; quad, \quad \ldots F_k(x_1, \ldots, x_k) \;=\; 0 \quad .$$

How to find the Stable Equilibrium points?

Recall that for discrete dynamical systems, we find the Jacobian of the underlying transformation, a certain matrix of **functions**. Then we find all the steady-states, and for each and every one of them we plug into the Jacobian, getting a matrix of **numbers**. Then we look at the eigenvalues. If all of them have absolute value less than 1 then we know it is stable. For the continuous case we do the same **except** that we have a different criterion.

An equilibrium point $\mathbf{x}_0$ is stable if and only if all the eigenvalues of $J(\mathbf{x}_0)$ have negative real part.

If they have non-negative real parts and some of them are purely imaginary (i.e. the real part is 0) then it is a **semi-stable** equilibrium point.

Why is it True?

Again using multi-variable Taylor we get that, near the equilibrium point $\mathbf{x}_0$,

$$\mathbf{F}(\mathbf{x}) - \mathbf{x}_0 = J(\mathbf{x}_0)(\mathbf{x} - \mathbf{x}_0) \quad + \quad TINY \quad .$$

A linear system

$$\mathbf{x}'(t) = L\mathbf{x}(t) \quad ,$$

where L is a numerical matrix, **0** is obviously an equilibrium. By diagonalizing

$$L = UDU^{-1} \quad ,$$

where D is a diagonal matrix consisting of the eigenvalues, By a change of variable $\mathbf{y} = U^{-1}\mathbf{x}$ we have the system

$$\mathbf{y}'(t) = D\mathbf{y}(t) \quad ,$$

spelling it out

$$y_1'(t) = \lambda_1 y_1(t) \quad ,$$

$$y_2'(t) = \lambda_2 y_2(t) \quad ,$$

$$\ldots$$

$$y_k'(t) = \lambda_k y_k(t) \quad ,$$

Hence

$$y_1(t) = e^{\lambda_1 t} \quad , \quad y_k(t) = e^{\lambda_k t} \quad ,$$

If the real part of any of the λ_i-s is positive the corresponding $y_i(t)$ would blow up as t gets larger and larger.

Problem 17.3: Find all equilibrium points of the continuous dynamical system

$$\frac{dx}{dt} = 2 - \frac{5x}{1+4y}$$

$$\frac{dy}{dt} = \frac{5}{9} - \frac{5y}{1+4x}$$

Solution pf 17.3

We have to solve

$$2 - \frac{5x}{1+4y} = 0 \quad , \quad \frac{5}{9} - \frac{5y}{1+4x} = 0 \quad .$$

Cross-multiplying and simplifying we get

$$5x - 8y = 2 \quad , \quad -4x + 9y = 5 \quad ,$$

whose only solution is $(x, y) = (2, 1)$.

Answer to 17.3: The only equilibrium point of the system is $(2, 1)$.

Problem 17.4: Find all stable equilibrium points of the continuous dynamical system

$$\frac{dx}{dt} = 2 - \frac{5x}{1+4y}$$

$$\frac{dy}{dt} = \frac{5}{9} - \frac{5y}{1+4x}$$

The underlying transformation is

$$(x,y) \to (2 - \frac{5x}{1+4y}, \frac{5}{9} - \frac{5y}{1+4x}) \quad .$$

The Jacobian is

$$J(x,y) = \begin{bmatrix} -\frac{5}{1+4y} & \frac{20x}{(1+4y)^2} \\ \frac{20y}{(1+4x)^2} & -\frac{5}{1+4x} \end{bmatrix} \quad .$$

From 17.3 we know that the only equilibrium point is $(2,1)$. Plugging it in we get

$$J(2,1) = \begin{bmatrix} -\frac{5}{1+4\cdot 1} & \frac{20\cdot 2}{(1+4\cdot 1)^2} \\ \frac{20\cdot 1}{(1+4\cdot 2)^2} & -\frac{5}{1+4\cdot 2} \end{bmatrix} \quad .$$

$$\begin{bmatrix} -1 & \frac{8}{5} \\ \frac{20}{81} & -\frac{5}{9} \end{bmatrix}$$

The characteristic equation is

$$(-1-\lambda)(-\frac{5}{9}-\lambda) - \frac{8}{5}\cdot\frac{20}{81} = 0 \quad .$$

Simplifying:

$$\lambda^2 + \frac{14}{9}\lambda + \frac{13}{81} = 0 \quad .$$

Factorizing:

$$(\lambda + \frac{1}{9})(\lambda + \frac{13}{9}) = 0 \quad .$$

So the two eigenvalues are $-\frac{1}{9}$ and $-\frac{13}{9}$. Both are negative real numbers (and hence they have negative real parts, the imaginary part being 0), and we found out that $(2,1)$ is a stable equilibrium point.

Ans. to 17.4: The only stable equilibrium point is $(2,1)$.

Two Important Dynamical Systems in Mathematical Biology

The **Chemostat**: If N is the **bacterial population** and C is the **nutrient**, and a_1, a_2 are two parameters that depend on the particular situation (determined experimentally) then the system is

$$\frac{dN}{dt} = a_1 \cdot \frac{CN}{C+1} - N$$

$$\frac{dC}{dt} = -\frac{CN}{C+1} - C + a_2$$

The equilibrium points are

$$(0, a_2) \quad , \quad (\frac{a_1(a_2 a_1 - a_2 - 1)}{a_1 - 1}, \frac{1}{a_1 - 1}) \quad .$$

$(0, a_2)$ is not stable, but the other one often is.

The (continuous) **SIRS** model, due to Kermack and MacKendrick with population $N = S + I + R$, where S is susceptible but not infected, I is infected, and $R = N - I - S$ is removed. there are biological parameters β, γ, ν and we also consider N as a parameter. The variables are S and I. The two differential equations are:

$$\frac{dS}{dt} = -\beta S\, I + \gamma(N - S - I)$$

$$\frac{dI}{dt} = \beta S\, I \, - \, \nu I$$

The equilibrium points are

$$(N, 0) \quad , \quad (\frac{\nu}{\beta}, \gamma \frac{N - \frac{\nu}{\beta}}{\nu + \gamma}) \quad .$$

In the first one no one is infected (but everyone is susceptible), the second one can only happen if it is positive i.e.

$$N - \frac{\nu}{\beta} > 0 \quad ,$$

i.e.

$$\frac{N\beta}{\nu} > 1 \quad .$$

$$R_0 = \frac{N\beta}{\nu}$$

is a famous number called the *infectious contact number*. It is the *cutoff* . If it is less than 1 no one is infectedm but if it is larger than 1 some pople will be infected.