Lecture Notes for Lecture 13 of Dr. Z.'s Dynamical Systems in Biology

These notes are based on Chapters 2 and 3 of Leah Edelsetein-Keshet's classic textbook "Mathematical Models in Biology".

How to Find the Steady-Sates of First order Non-Linear k-dimensional Vector Recurrences?

Recall that a first-order k-dimensional vector recurrence has the format:

$$\mathbf{x}(n+1) = \mathbf{F}(\mathbf{x}(n) \quad ,$$

where $\mathbf{x}(n)$ is a (column) vector with k components, and $\mathbf{F}$ is a mapping from $R^k \to R^k$.

$$[x_1, \dots, x_k] \to [f_1(x_1, \dots, x_k), \dots, f_k(x_1, \dots, x_k)] \quad ,$$

for some **multivariable** functions, of the k variables $x_1, \dots, x_k$, $f_1, \dots, f_k$.

Such vectors $\mathbf{x}_0$ (if they exist) must satisfy the equation

$$\mathbf{x}^{(0)} \;=\; \mathbf{F}(\mathbf{x}^{(0)})] \quad .$$

Splled-out if

$$\mathbf{x}^{(0)} \;=\; [x_1^{(0)}, \dots, x_k^{(0)}] \quad .$$

we have to solve a system of k equations with k unknowns.

$$\begin{aligned}
x_1^{(0)} &= f_1(x_1^{(0)}, \dots, x_k^{(0)}) \\
x_2^{(0)} &= f_2(x_1^{(0)}, \dots, x_k^{(0)}) \\
&\dots \\
x_k^{(0)} &= f_k(x_1^{(0)}, \dots, x_k^{(0)})
\end{aligned}$$

Problem 13.1: Find all the steady-states of the system

$$a_1(n+1) = \frac{a_1(n)}{2a_1(n) + 3a_2(n)} \quad ,$$

$$a_2(n+1) = \frac{a_2(n)}{3a_1(n) + 2a_2(n)} \quad .$$

Solution of 13.1: The **underlying transformation** $R^2 \to R^2$ is

$$(x, y) \to \left(\frac{x}{2x+3y} \quad , \quad \frac{y}{3x+2y} \right) \quad .$$

We have to solve the system of equations

$$x = \frac{x}{2x+3y} \quad , \quad y = \frac{y}{3x+xy} \quad .$$

Moving everything to the left and leaving 0 at the right in both equations, we have

$$x\left(1 - \frac{1}{2x+3y}\right) = 0 \quad , \quad y\left(1 - \frac{1}{3x+2y}\right) = 0 \quad .$$

From the first equation either $x = 0$ or $2x + 3y = 1$. Plugging in $x = 0$ in the second equation we get $\frac{1}{2y} = 1$ hence $2y = 1$ hence $y = \frac{1}{2}$. So $(0, \frac{1}{2})$ is one steady-state.

From the second equation either $y = 0$ or $3x + 2y = 1$. $(0,0)$ is not possible since then the transformation is undefined. So $(\frac{1}{2}, 0)$ is another steady-state. Finally, if neither $x = 0$ nor $y = 0$ then

$$2x + 3y = 1 \quad , \quad 3x + 2y = 1 \quad ,$$

whose solution is $x = \frac{1}{5}$, $y = \frac{1}{5}$. Hence $(\frac{1}{5}, \frac{1}{5})$ is yet another steady-state.

Solution of 13.1: There are three steady-states: $(\frac{1}{2}, 0)$, $(0, \frac{1}{2})$ $(\frac{1}{5}, \frac{1}{5})$.

How to find whether a steady-state is stable?

The first, and easiest, if you have a computer is to find the orbit starting at a nearby point and see if it converges to it. You can use `ORB` in the Maple file tt DMB14.txt, but there is a more rigorous, reliable way, but first we need to recall the important notion of the **Jacobian Matrix** of a transformation $\mathbf{F} : R^k \to R^k$.

Definition: The **Jacobian Matrix** of the transformation

$$[x_1, \dots, x_k] \to [f_1(x_1, \dots, x_k), \dots, f_k(x_1, \dots, x_k)] \quad ,$$

is the $k \times k$ matrix of functions

$$\begin{bmatrix} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} & \dots & \frac{\partial f_1}{\partial x_k} \\ \frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} & \dots & \frac{\partial f_2}{\partial x_k} \\ \dots & \dots & \dots & \dots \\ \frac{\partial f_k}{\partial x_1} & \frac{\partial f_k}{\partial x_2} & \dots & \frac{\partial f_k}{\partial x_k} \end{bmatrix}$$

How to decide whether a steady state is stable?

Step 1: Find the Jacobian matrix, it is a certain matrix of (multi-variable) functions.

Step 2: Plug-in the candidate steady-state, getting a **numerical** $k \times k$ matrix.

Step 3: Find all the eigenvalues of this matrix. If their **absolute values** are all less than 1 then it is **stable**. If even one of the eignevalues have absolute value larger than 1 then it is **unstable**. If some of the eigenvalues have absolute value 1 and the other ones less than 1 it is **semi-stable**.

Explanation: For a linear transformation

$$\mathbf{x} \to A\mathbf{x} \quad ,$$

where A is a $k \times k$ matrix, the zero vector $\mathbf{0}$ is a steady-state. From Linear Algebra we know that such a matrix can be **diagonalized**

$$A = UDU^{-1}$$

where D is a diagonal matrix with the eigenvalues. Now

$$A^k = UD^kU^{-1} \quad ,$$

and if any of the eigenvalues of A (entries of D) has absolute value larger than 1 this would explode as $k \to \infty$.

So much for a **linear transformation**,

But remember from multi-variable calculus, the multi-variable Taylor expansion around a point $(a_1, \ldots, a_k)$

$$F(x_1, \ldots x_k) = F(a_1, \ldots, a_k) + \frac{\partial F}{\partial x_1}(x_1 - a_1) + \frac{\partial F}{\partial x_2}(x_2 - a_2) + \ldots + \frac{\partial F}{\partial x_k}(x_k - a_k) \quad ,$$

plus higher-degree terms. Near a steady-state $(a_1, \ldots, a_k)$ $x_1 - a_1, \ldots, x_k - a_k$ are small so we can ignore higher-degree terms.

Applying it to $F = f_1 \ldots f_k$, we have, ignoring higher-degree terms

$$f_1(x_1, \ldots x_k) - f_1(a_1, \ldots, a_k) = \frac{\partial f_1}{\partial x_1}(x_1 - a_1) + \frac{\partial f_1}{\partial x_2}(x_2 - a_2) + \ldots + \frac{\partial f_1}{\partial x_k}(x_k - a_k) \quad ,$$

$$f_2(x_1, \ldots x_k) - f_2(a_1, \ldots, a_k) = \frac{\partial f_2}{\partial x_1}(x_1 - a_1) + \frac{\partial f_2}{\partial x_2}(x_2 - a_2) + \ldots + \frac{\partial f_2}{\partial x_k}(x_k - a_k) \quad ,$$

$$\ldots$$

$$f_k(x_1, \ldots x_k) - f_k(a_1, \ldots, a_k) = \frac{\partial f_k}{\partial x_1}(x_1 - a_1) + \frac{\partial f_k}{\partial x_2}(x_2 - a_2) + \ldots + \frac{\partial f_k}{\partial x_k}(x_k - a_k) \quad .$$

So, since $\mathbf{F}(\mathbf{a}) = \mathbf{a}$ (remember $\mathbf{a}$ is s steady-state)

$$\mathbf{F}(\mathbf{x}) - \mathbf{F}(\mathbf{a}) = A(\mathbf{x} - \mathbf{a}) \quad ,$$

where A is the (numerical) matrix obtained by plugging-in the candidate steady-state to the Jacobian matrix. From the linear case we know that in order for it to be stable all the eigenvalues must have absolute values less than 1.

Problem 13.2: Find all the stable steady-states of the first-order vector recurrence.

$$a_1(n+1) = \frac{a_1(n)}{2a_1(n) + 3a_2(n)} \quad ,$$

$$a_2(n+1) = \frac{a_2(n)}{3a_1(n) + 2a_2(n)} \quad .$$

Solution of 13.2: We first need the steady-states. That was done in the above problem. The underlying transformation was

$$(x, y) \to \left(\frac{x}{2x+3y} \quad , \quad \frac{y}{3x+2y} \right) \quad .$$

The steady-states were $(\frac{1}{2}, 0)$, $(0, \frac{1}{2})$ $(\frac{1}{5}, \frac{1}{5})$.

The Jacobian matrix is

$$\begin{bmatrix} \frac{\partial}{\partial x}\left(\frac{x}{2x+3y}\right) & \frac{\partial}{\partial y}\left(\frac{x}{2x+3y}\right) \\ \frac{\partial}{\partial x}\left(\frac{y}{3x+2y}\right) & \frac{\partial}{\partial y}\left(\frac{y}{3x+2y}\right) \end{bmatrix}$$

Using the quotient rule (you do it!) we get

$$J(x, y) = \begin{bmatrix} \frac{3y}{(2x+3y)^2} & -\frac{3x}{(2x+3y)^2} \\ -\frac{3y}{(3x+2y)^2} & \frac{3x}{(3x+2y)^2} \end{bmatrix}$$

Now is is time to investigate the three steady-states. For the point $(\frac{1}{2}, 0)$, we have

$$J(\frac{1}{2}, 0) = \begin{bmatrix} 0 & -\frac{3}{2} \\ 0 & \frac{2}{3} \end{bmatrix}$$

The eigenvalues are the solutions of the characteristic equation

$$-\lambda(\frac{2}{3} - \lambda) = 0 \quad ,$$

so the eigenvalues are 0 and $\frac{2}{3}$ both of which have absolute value less than 1 so the point $(\frac{1}{2}, 0)$ is stable.

For the point $(0, \frac{1}{2})$, we have

$$J(0, \frac{1}{2}) = \begin{bmatrix} \frac{2}{3} & 0 \\ -\frac{3}{2} & 0 \end{bmatrix}$$

the eigenvalues are also 0 and $\frac{2}{3}$ both of which have absolute value less than 1 so the point $(0, \frac{1}{2})$ is also stable.

Regarding the steady-state $(\frac{1}{5}, \frac{1}{5})$, we have

$$J(\frac{1}{5}, \frac{1}{5}) = \begin{bmatrix} \frac{3}{5} & -\frac{3}{5} \\ -\frac{3}{5} & \frac{3}{5} \end{bmatrix} \quad .$$

The characteristic equation is

$$\left(\lambda - \frac{3}{5}\right)^2 - \left(\frac{3}{5}\right)^2 = 0 \quad .$$

Expanding

$$\lambda^2 - \frac{6}{5}\lambda = 0 \quad .$$

Factoring

$$(\lambda - \frac{6}{5})\lambda = 0 \quad .$$

So the eigenvalues are 0 and $\frac{6}{5}$. Since the absolute value of $\frac{6}{5}$ is larger than 1 this is **unstable**.

Sol. of 13.2: There are two stable steady-states $(\frac{1}{2}, 0)$ and $(0, \frac{1}{2})$.

Host-Parasitoid Systems

- $N(n)$ is the density of host species in generation n
- $P(n)$ is the density of parasitoid species in generation n
- λ is host-reproduction rate.
- c is the average number of viable eggs laid by a parasitoid on a single host.
- $f(N(n), P(n))$ is the fraction of hosts not parasitized.

Then we have the two-dimensional vector first-order recurrence

$$N(n+1) = \lambda N(n) f(N(n), P(n)) \quad ,$$

$$P(n+1) = cN(n)(1 - f(N(n), P(n))) \quad .$$

The Nicholson-Bailey model

You take $f(N(n), P(n)) = e^{-aP(n)}$ (so it does not depend on $N(n)$, and a is another numerical parameter.

$$N(n+1) = \lambda N(n) e^{-aP(n)}$$

$$P(n+1) = cN(n)(1 - e^{-aP(n)}) \quad .$$

This is **not** a good model, since it has no stable steady-states.

The Modified Nicholson-Bailey model

It has three parameters, a, r, K.

$$N(n+1) = \lambda N(n) exp(r(1 - N(n)/K)) - aP(n))$$

$$P(n+1) = N(n)(1 - e^{-aP(n)}) \quad .$$

It is impossible to find the steady-states by hand, but you can find them with a computer, and it has steady stable-states for a wide range of realistic parameter values.