Nonlinear Systems of ODE: Dimensional Analysis, Equilibrium Points, and Stability

MATH 469, Texas A&M University

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This lecture will focus on the competition model

$$\begin{aligned} \frac{dy_1}{dt} &= r_1 y_1 (1 - \frac{y_1 + s_1 y_2}{K_1}); \quad y_1(0) = y_{1_0} \\ \frac{dy_2}{dt} &= r_2 y_2 (1 - \frac{s_2 y_1 + y_2}{K_2}); \quad y_2(0) = y_{2_0}, \end{aligned}$$

and we'll begin by non-dimensionalizing it. For this, we introduce three dimensionless variables

$$au=rac{t}{A};$$
 $Y_1(au)=rac{y_1(t)}{B};$ $Y_2(au)=rac{y_2(t)}{C}.$

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The constant A will be chosen with the dimension time, and the constants B and C will both be chosen with dimension biomass.

First, using the chain rule, we compute

$$\frac{dy_1}{dt} = B\frac{d}{dt}Y_1(\tau) = B\frac{d}{d\tau}Y_1(\tau)\frac{d\tau}{dt} = \frac{B}{A}\frac{dY_1}{d\tau}$$
$$\frac{dy_2}{dt} = C\frac{d}{dt}Y_2(\tau) = C\frac{d}{d\tau}Y_2(\tau)\frac{d\tau}{dt} = \frac{C}{A}\frac{dY_2}{d\tau}$$

If we now substitute these dimensionless variables into the competition model, we get

$$\frac{B}{A}\frac{dY_1}{dt} = r_1 BY_1 (1 - \frac{BY_1 + s_1 CY_2}{K_1}); \quad Y_1(0) = \frac{y_{1_0}}{B}$$
$$\frac{C}{A}\frac{dY_2}{dt} = r_2 CY_2 (1 - \frac{s_2 BY_1 + CY_2}{K_2}); \quad Y_2(0) = \frac{y_{2_0}}{C}.$$

We multiply by A and divide by B to arrive at

$$\frac{dY_1}{dt} = r_1 A Y_1 (1 - \frac{BY_1 + s_1 C Y_2}{K_1}); \quad Y_1(0) = \frac{y_{1_0}}{B}$$
$$\frac{dY_2}{dt} = r_2 A Y_2 (1 - \frac{s_2 B Y_1 + C Y_2}{K_2}); \quad Y_2(0) = \frac{y_{2_0}}{C}.$$

As always, our goal is to choose the constants A, B, and C in a way that simplifies the system, while also ensuring that they have the correct dimensions. We'll take

$$A=\frac{1}{r_1};\quad B=K_1;\quad C=K_2.$$

The system becomes

$$\frac{dY_1}{dt} = Y_1(1 - Y_1 - \frac{s_1K_2}{K_1}Y_2); \quad Y_1(0) = \frac{y_{10}}{K_1}$$
$$\frac{dY_2}{dt} = \frac{r_2}{r_1}Y_2(1 - \frac{s_2K_1}{K_2}Y_1 - Y_2); \quad Y_2(0) = \frac{y_{20}}{K_2}.$$

Recall that one of the things that we accomplish with non-dimensionalization is that we identify useful combinations of parameters. In this case, we set

$$a = \frac{s_1 K_2}{K_1}; \quad b = \frac{r_2}{r_1}; \quad c = \frac{s_2 K_1}{K_2}.$$

This allows us to write our system in the form we'll use for analysis,

$$\begin{aligned} \frac{dY_1}{dt} &= Y_1(1 - Y_1 - aY_2); \quad Y_1(0) = \frac{y_{1_0}}{K_1} \\ \frac{dY_2}{dt} &= bY_2(1 - cY_1 - Y_2); \quad Y_2(0) = \frac{y_{2_0}}{K_2}. \end{aligned}$$

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For a first-order autonomous system of ODE

$$rac{dec y}{dt} = ec f(ec y); \quad ec y(0) = ec y_0,$$

we say that $\hat{y} \in \mathbb{R}^n$ is an equilibrium point if

$$\vec{f}(\hat{y}) = 0.$$

As with single equations, if $\vec{y_0} = \hat{y}$, the constant function $\vec{y}(t) = \hat{y}$ for all $t \in \mathbb{R}$ is a solution to the system (because both sides of the equation are 0).

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Example. Let's find all equilibrium points for the non-dimensionalized competition model,

$$egin{aligned} & rac{dy_1}{dt} = y_1(1-y_1-ay_2) \ & rac{dy_2}{dt} = by_2(1-cy_1-y_2). \end{aligned}$$

We need to find $\hat{y} = \begin{pmatrix} \hat{y}_1 \\ \hat{y}_2 \end{pmatrix}$ so that

$$egin{aligned} 0 &= \hat{y}_1 ig(1 - \hat{y}_1 - a \hat{y}_2 ig) \ 0 &= b \hat{y}_2 ig(1 - c \hat{y}_1 - \hat{y}_2 ig). \end{aligned}$$

For the first equation, we can either have $\hat{y}_1 = 0$ or $\hat{y}_1 = 1 - a\hat{y}_2$. If we substitute $\hat{y}_1 = 0$ into the second equation, we get

$$0 = b\hat{y}_2(1 - \hat{y}_2) \implies \hat{y}_2 = 0, 1.$$

This gives us our first two equilibrium points: $\begin{pmatrix} 0 \\ 0 \end{pmatrix}$ and $\begin{pmatrix} 0 \\ 1 \end{pmatrix}$.

Next, we substitute $\hat{y}_1 = 1 - a\hat{y}_2$ into the second equation, giving

$$0 = b\hat{y}_2(1 - c(1 - a\hat{y}_2) - \hat{y}_2).$$

We see that $\hat{y}_2 = 0$ solves this equation, and for the second solution we have

$$0=1-c+(ac-1)\hat{y}_2\implies \hat{y}_2=\frac{1-c}{1-ac}.$$

In order to find the values of \hat{y}_1 associated with these values of \hat{y}_2 , we substitute back into $\hat{y}_1 = 1 - a\hat{y}_2$. For $\hat{y}_2 = 0$, we see that $\hat{y}_1 = 1$, while for $\hat{y}_2 = \frac{1-c}{1-ac}$, we compute

$$\hat{y}_1 = 1 - a \frac{1-c}{1-ac} = \frac{1-ac-a+ac}{1-ac} = \frac{1-a}{1-ac}.$$

This gives us our next two equilibrium points: $\binom{1}{0}$ and $\binom{\frac{1-a}{1-ac}}{\frac{1-a}{1-ac}}$

In total, we have four equilibrium points

$$\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \quad \begin{pmatrix} 0 \\ 1 \end{pmatrix}, \quad \begin{pmatrix} 1 \\ 0 \end{pmatrix}, \quad \begin{pmatrix} \frac{1-a}{1-ac} \\ \frac{1-c}{1-ac} \end{pmatrix}.$$

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Recalling that we scaled y_1 by dividing by K_1 , and scaled y_2 by dividing by K_2 , we see that we can interpret these equilibrium points in the original variables as described on the next slide.

 $\begin{pmatrix} 0 \\ 0 \end{pmatrix}$: Both species die out;

 $\begin{pmatrix} 0\\ K_2 \end{pmatrix}$: Species y_1 dies out and species y_2 goes to its carrying capacity;

 $\binom{K_1}{0}$: Species y_2 dies out and species y_1 goes to its carrying capacity;

 $(\frac{\frac{K_1 - s_1 K_2}{1 - s_1 s_2}}{\frac{K_2 - s_2 K_1}{1 - s_1 s_2}}): \text{ If } K_1 - s_1 K_2, \ K_2 - s_2 K_1, \text{ and } 1 - s_1 s_2 \text{ are all positive,}$

the two species reach an equilibrium in which neither dies out. In principle, the same statement is true if these quantities are all negative, but we'll see below that that case isn't as interesting.

For the fourth equilibrium point, let's interpret what positivity of these quantities $K_1 - s_1K_2$, $K_2 - s_2K_1$, and $1 - s_1s_2$ corresponds with. First, s_1K_2 denotes the amount resources available to species y_1 that species y_2 consumes at its carrying capacity. The requirement that $K_1 - s_1K_2 > 0$ asserts that species y_2 cannot use up the entirety of these resources, even at its carrying capacity.

The condition $K_2 - s_2 K_1 > 0$ can be interpreted similarly, with the roles of the species reversed.

For the condition $1 - s_1 s_2 > 0$, recall our example in which y_1 corresponds with a population of rabbits and y_2 corresponds with a population of deer. Focusing on resources available to rabbits (and possibly available to the deer), suppose each individual in the deer population uses up twice the amount of these resources as an individual in the rabbit population. Then $s_1 = 2$.

Correspondingly, we might expect that if we focus on resources available to the deer (and possibly available to the rabbits), then each individual in the rabbit population will use up half as much of these resources as an individual in the deer population. I.e., we would have $s_2 = \frac{1}{2}$.

In this case, we would have $s_1s_2 = 1$.

But suppose individuals in the deer population have access to resources unavailable to the rabbits. Then it might be the case that an individual rabbit uses less than half the resources of an individual deer. In that case, we would have $s_2 < \frac{1}{2}$, and so $s_1s_2 < 1$.

Generally, the condition $1 - s_1 s_2 > 0$ indicates that at least one of the species has access to resources that are unavailable to the other species.

Suppose $\hat{y} \in \mathbb{R}^n$ is an equilibrium point for the ODE system

$$rac{dec y}{dt}=ec f(ec y); \quad ec y(0)=ec y_0.$$

I.e., $\vec{f}(\hat{y}) = 0$. As usual, we want to understand what will happen if we start with $\vec{y_0}$ near \hat{y} . To understand this, we write

$$\vec{y}(t) = \hat{y} + \vec{z}(t), \qquad (*)$$

and we'll analyze the behavior of $\vec{z}(t)$ as t increases. If we substitute (*) into our ODE system, and assume \vec{f} is differentiable at \hat{y} , we get

$$\frac{d\vec{z}}{dt} = \vec{f}(\hat{y} + \vec{z}) = \vec{f}(\hat{y}) + \vec{f}'(\hat{y})\vec{z} + \vec{\epsilon}(\vec{z};\hat{y}),$$

where

$$\lim_{\vec{z}|\to 0}\frac{|\vec{\epsilon}(\vec{z};\hat{y})|}{|\vec{z}|}=0.$$

Using the relation $\vec{f}(\hat{y}) = 0$ and observing that $\vec{\epsilon}(\vec{z}; \hat{y})$ is small relative to $\vec{f'}(\hat{y})\vec{z}$, we obtain the linearized equation

$$\frac{d\vec{z}}{dt} = \vec{f}'(\hat{y})\vec{z}; \quad \vec{z}(0) = \vec{y}_0 - \hat{y}.$$
 (**)

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This is a first-order linear system of ODE with constant coefficients, and so we know how to solve it using the eigenvalues and eigenvectors of $\vec{f'}(\hat{y})$.

Let $\{\lambda_j\}_{j=1}^n$ denote the eigenvalues of $\vec{f'}(\hat{y})$, and assume these values are distinct. In this case, we can associate the eigenvalues with a linearly independent collection of eigenvectors $\{\vec{v_i}\}_{i=1}^n$.

Using these eigenvalues and eigenvectors, we can express the general solution to (**) as

$$ec{z}(t) = \sum_{j=1}^n c_j e^{\lambda_j t} ec{v}_j,$$

for some constants $\{c_j\}_{j=1}^n$.

Even if the entries of $\vec{f'}(\hat{y})$ are all real, it may have complex eigenvalues,

$$\lambda_j = \mathrm{Re}\lambda_j + i\mathrm{Im}\lambda_j.$$

In this case, the complex modulus of $e^{\lambda_j t}$ is

$$\begin{split} |e^{\lambda_j t}| &= |e^{t \operatorname{Re} \lambda_j + it \operatorname{Im} \lambda_j}| = |e^{t \operatorname{Re} \lambda_j} e^{it \operatorname{Im} \lambda_j}| \\ &= |e^{t \operatorname{Re} \lambda_j}||e^{it \operatorname{Im} \lambda_j}| = e^{t \operatorname{Re} \lambda_j}. \end{split}$$

In obtaining the final equality on the previous page, we observed that $e^{t{\rm Re}\lambda}$ is always a positive real number, and

$$|e^{it\mathrm{Im}\lambda_j}|^2=e^{it\mathrm{Im}\lambda_j}e^{-it\mathrm{Im}\lambda_j}=1\implies |e^{it\mathrm{Im}\lambda_j}|=1.$$

We see that:

- If Reλ_j < 0 for all j = 1, 2, ..., n, then ŷ will be asymptotically stable;</p>
- If Reλ_j > 0 for at least one j ∈ {1,2,...,n}, then ŷ will be unstable.
- If Reλ_j ≤ 0 for all j = 1, 2, ..., n, and Reλ_j = 0 for at least one j ∈ {1, 2, ..., n}, then this test for stability is inconclusive.

These conditions remain valid if the eigenvalues $\{\lambda_j\}_{j=1}^n$ are not distinct.

Example. For the non-dimensionalized competition model

$$egin{aligned} & rac{dy_1}{dt} = y_1(1-y_1-ay_2) \ & rac{dy_2}{dt} = by_2(1-cy_1-y_2), \end{aligned}$$

with a, b, c > 0, analyze the stability of each of the four equilibrium points

$$\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \quad \begin{pmatrix} 0 \\ 1 \end{pmatrix}, \quad \begin{pmatrix} 1 \\ 0 \end{pmatrix}, \quad \begin{pmatrix} \frac{1-a}{1-ac} \\ \frac{1-c}{1-ac} \end{pmatrix}.$$

We begin by computing the Jacobian matrix $\vec{f'}(\vec{y})$. First:

$$ec{f}(ec{y}) = egin{pmatrix} f_1(y_1, y_2) \ f_2(y_1, y_2) \end{pmatrix} = egin{pmatrix} y_1 - y_1^2 - ay_1y_2 \ by_2 - bcy_1y_2 - by_2^2 \end{pmatrix}.$$

This allows us to compute

$$ec{f'}(ec{y}) = \left(egin{array}{cc} 1-2y_1-ay_2 & -ay_1 \ -bcy_2 & b-bcy_1-2by_2 \end{array}
ight).$$

We can now use this to evaluate each of the four equilibrium points. For $\hat{y} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$, we have

$$ec{f'}(0,0)=\left(egin{array}{cc} 1 & 0 \ 0 & b \end{array}
ight).$$

The eigenvalues are 1 and *b*, which are both positive values, so this equilibrium point is unstable.

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For
$$\hat{y}=inom{0}{1}$$
, we have $ec{f'}(0,1)=inom{1-a}{-bc}inom{0}{-b}$.

The eigenvalues of this matrix are 1 - a and -b. Since -b < 0, the only condition that this imposes is

$$1-a<0\implies a>1.$$

In terms of the original parameters, this asserts that the equilibrium point $\begin{pmatrix} 0\\ K_2 \end{pmatrix}$ will be asymptotically stable provided

$$a=\frac{s_1K_2}{K_1}>1\implies s_1K_2>K_1.$$

I.e., the second species will win if at its carrying capacity it uses more resources than are available to the first species.

Here, keep in mind that when talking about stability, we're always talking about solutions that start near the equilibrium point. Strictly speaking, this tells us that if $s_1K_2 > K_1$, and the populations are initially near $\binom{0}{K_2}$, then the second species will win.

Recall that the Jacobian matrix is

$$ec{f'}(ec{y}) = \left(egin{array}{cc} 1 - 2y_1 - ay_2 & -ay_1 \ -bcy_2 & b - bcy_1 - 2by_2 \end{array}
ight).$$

For $\hat{y} = \begin{pmatrix} 1 \\ 0 \end{pmatrix}$, we have

$$ar{f'}(1,0)=\left(egin{array}{cc} -1 & -a \ 0 & b-bc \end{array}
ight).$$

The eigenvalues are -1 and b(1-c). Since -1 is negative, the only condition this imposes is

$$b(1-c) < 0 \implies c > 1.$$

In terms of the original parameters, this asserts that the equilibrium point $\binom{K_1}{0}$ will be asymptotically stable provided

$$c=\frac{s_2K_1}{K_2}>1\implies s_2K_1>K_2.$$

We can interpret this precisely as we did the previous equilibrium point, with the roles of the two species reversed.

Recall again the Jacobian matrix

$$ec{f'}(ec{y})=\left(egin{array}{cc} 1-2y_1-ay_2&-ay_1\ -bcy_2&b-bcy_1-2by_2\end{array}
ight).$$

For the last equilibrium point $\hat{y} = \begin{pmatrix} \frac{1-a}{1-ac} \\ \frac{1-c}{1-ac} \end{pmatrix}$, it's helpful to recall that the equations we solved to find these values were

$$1 - \hat{y}_1 - a\hat{y}_2 = 0$$

1 - c $\hat{y}_1 - \hat{y}_2 = 0$.

If we use these relations while evaluating $\vec{f}'(\hat{y})$, we obtain

$$ec{f'}(\hat{y}) = \left(egin{array}{ccc} 1 - 2 \hat{y}_1 - a \hat{y}_2 & -a \hat{y}_1 \ -b c \hat{y}_2 & b - b c \hat{y}_1 - 2 b \hat{y}_2 \end{array}
ight) = \left(egin{array}{ccc} - \hat{y}_1 & -a \hat{y}_1 \ -b c \hat{y}_2 & -b \hat{y}_2 \end{array}
ight)$$

In this case, we compute the eigenvalues by writing

$$\det egin{pmatrix} -\hat{y}_1-\lambda & -a\hat{y}_1 \ -bc\hat{y}_2 & -b\hat{y}_2-\lambda \end{pmatrix} = (-\hat{y}_1-\lambda)(-b\hat{y}_2-\lambda) - abc\hat{y}_1\hat{y}_2 \ = \lambda^2 + (\hat{y}_1+b\hat{y}_2)\lambda + b(1-ac)\hat{y}_1\hat{y}_2 = 0. \end{cases}$$

Solving this with the quadratic formula, we find

$$\lambda_{\pm} = rac{-(\hat{y}_1 + b\hat{y}_2) \pm \sqrt{(\hat{y}_1 + b\hat{y}_2)^2 - 4b(1 - ac)\hat{y}_1\hat{y}_2}}{2}.$$

We need to determine conditions under which both λ_{-} and λ_{+} will be negative, and since $\lambda_{-} \leq \lambda_{+}$, we only need to check λ_{+} . For this, notice that λ_{+} will be negative as long as

$$4b(1-ac)\hat{y}_1\hat{y}_2 > 0,$$

because in that case the radical will be smaller than $(\hat{y}_1 + b\hat{y}_2)$.

We see that our condition for stability is simply

$$1 - ac > 0.$$

In our original coordinates, this is

$$1 - \frac{s_1 K_2}{K_1} \frac{s_2 K_1}{K_2} = 1 - s_1 s_2 > 0 \implies s_1 s_2 < 1.$$

This is precisely the condition already discussed above in the context of the signs of the populations associated with this equilibrium point. Notice that the instability of this equilibrium point in the case $s_1s_2 > 1$ is why it was described above as uninteresting.

On this next slide, we'll summarize these observations.

We found the following:

- $\hat{y} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$ is always unstable;
- If $s_2K_1 > K_2$, then $\hat{y} = \begin{pmatrix} 1 \\ 0 \end{pmatrix}$ is asymptotically stable;
- If $s_1K_2 > K_1$, then $\hat{y} = \begin{pmatrix} 0 \\ 1 \end{pmatrix}$ is asymptotically stable;
- If $s_2K_1 < K_2$, $s_1K_2 < K_1$, and $1 s_1s_2 > 0$, then there is an equilibrium point $\hat{y} = \begin{pmatrix} \frac{1-a}{1-ac} \\ \frac{1-c}{1-ac} \end{pmatrix}$ with two positive populations, and it is asymptotically stable.

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