CHAPTER 8

Competition Between Two Populations

Consider two competing populations N_1 and N_2:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{12}\frac{N_2}{K_1}\right), \tag{8.1}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} - b_{21}\frac{N_1}{K_2}\right). \tag{8.2}$$

We introduce nondimensionalized variables:

$$x_1 = \frac{N_1}{K_1},\ \ x_2 = \frac{N_2}{K_2},\ \ \tau = r_1 t, \tag{8.3}$$

and

$$r = \frac{r_2}{r_1},\ \ \beta_{12} = b_{12}\frac{K_2}{K_1},\ \ \beta_{21} = b_{21}\frac{K_1}{K_2}. \tag{8.4}$$

Then,

$$\frac{dx_1}{d\tau} = x_1(1 - x_1 - \beta_{12}x_2) = f(x_1, x_2), \tag{8.5}$$

$$\frac{dx_2}{d\tau} = r x_2(1 - x_2 - \beta_{21}x_1) = g(x_1, x_2). \tag{8.6}$$

Drawing null clines, it is easy to see that $\big(x_1^* = x_2^* = 0\big)$, $\big(x_1^* = 1, x_2^* = 0\big)$, $\big(x_1^* = 0, x_2^* = 1\big)$, and

$$\left(x_1^* = \frac{1-\beta_{12}}{1-\beta_{12}\beta_{21}},\ x_2^* = \frac{1-\beta_{21}}{1-\beta_{12}\beta_{21}}\right),$$

are four fixed points. Furthermore, the last fixed point is in the positve quadrant if both $\beta_{12}, \beta_{21} < 1$, or both $\beta_{12}, \beta_{21} > 1$. In other words, if one of the β's is greater than 1, and the other less than 1, then there is no fixed point in the first quadrant.

We now carry out linear stability analysis. We are interested in the Jacobian matrix:

$$A = \begin{pmatrix} \frac{\partial f}{\partial x_1} & \frac{\partial f}{\partial x_2} \\ \frac{\partial g}{\partial x_1} & \frac{\partial g}{\partial x_2} \end{pmatrix}_{(x_1^*, x_2^*)} = \begin{pmatrix} 1 - 2x_1 - \beta_{12}x_2 & -\beta_{12}x_1 \\ -r\beta_{21}x_2 & r(1 - 2x_2 - \beta_{21}x_1) \end{pmatrix}_{(x_1^*, x_2^*)}. \tag{8.7}$$

Now applying this to the four fixed points.

At (0.0) we have $\lambda_1 = 1$, $\lambda_2 = r$. It is unstable.

At $(1, 0)$, we have $\lambda_1 = -1$, $\lambda_2 = r(1 - \beta_{21})$. Therefore, it is stable if $\beta_{21} > 1$ and unstable if $\beta_{21} < 1$.

Then at $(0, 1)$ we have a similar result: it is stable if $\beta_{12} > 1$ and unstable if $\beta_{12} < 1$.

Finally, for the positive fixed point:

$$A = \left(1 - \beta_{12}\beta_{21}\right)^{-1} \begin{pmatrix} \beta_{12} - 1 & \beta_{12}(\beta_{12} - 1) \\ r\beta_{21}(\beta_{21} - 1) & r(\beta_{21} - 1) \end{pmatrix} \tag{8.8}$$

We see that its trace

$$\text{Tr}[A] = \beta_{12} - 1 + r(\beta_{21} - 1), \tag{8.9}$$

and its determinant

$$\det[A] = r(1 - \beta_{12}\beta_{21})^{-1}(\beta_{12} - 1)(\beta_{21} - 1). \tag{8.10}$$

Therefore, if both $\beta_{12}, \beta_{21} > 1$, then Tr$[A] > 0$ and det$[A] < 0$. Thus the positive fixed point is a saddle.

If both $\beta_{12}, \beta_{21} < 1$, then Tr$[A] < 0$ and det$[A] > 0$, and the positive fixed point is stable.

A large β means strong competition; a smaller β means weaker competition. Therefore, only when the two populations have equal balanced strength, there is the possibility for co-existence. Then both are strong competitors, the initial situation matters.

8.1 Sustained population oscillations

Let us now consider the following population dynamics for a pair of species X and Y:

$$\frac{dx}{dt} = a_1 - a_2 x + b_2 x^2 y, \quad \frac{dy}{dt} = b_1 - b_2 x^2 y. \tag{8.11}$$

This dynamics can be either an ecological population system with constant immigrations for X and Y, and a predator-prey interaction between X and Y:

$$\xrightarrow{a_1} X \xrightarrow{a_2}, \ \xrightarrow{b_1} Y, \ 2X + Y \xrightarrow{b_2} 3X. \tag{8.12}$$

Just as the case of Lotka-Volterra nonlinear chemical reaction system which corresponds to a predator-prey ecological dynamics, Eq. 8.12 can be also interpreted as a system of chemical reactions with autocatalysis.

Introducing non-dimensionalization with

$$u = \sqrt{\frac{b_2}{a_2}}x, \ v = \sqrt{\frac{b_2}{a_2}}y, \ \tau = a_2 t, \ \alpha = \frac{a_1}{a_2}\sqrt{\frac{b_2}{a_2}}, \ \beta = \frac{b_1}{a_2}\sqrt{\frac{b_2}{a_2}}, \tag{8.13}$$

we have

$$\frac{du}{d\tau} = \alpha - u + u^2 v = f(u,v), \quad \frac{dv}{d\tau} = \beta - u^2 v = g(u,v). \tag{8.14}$$

The system has a positive fixed point at

$$u^* = \alpha + \beta; \quad v^* = \frac{\beta}{(\alpha+\beta)^2}. \tag{8.15}$$

Linear analysis gives the "community matrix"

$$A = \begin{pmatrix} \dfrac{\beta-\alpha}{\alpha+\beta} & (\alpha+\beta)^2 \\ -\dfrac{2\beta}{\alpha+\beta} & -(\alpha+\beta)^2 \end{pmatrix}, \tag{8.16}$$

with determinant and trace:

$$\det[A] = \left(\frac{\partial f}{\partial u}\frac{\partial g}{\partial v} - \frac{\partial f}{\partial v}\frac{\partial g}{\partial u}\right)_{(u^*,v^*)} = \big(\alpha+\beta\big)^2 > 0; \tag{8.17}$$

$$\text{Tr}[A] = \left(\frac{\partial f}{\partial u} + \frac{\partial g}{\partial v}\right)_{(u^*,v^*)} = \frac{\beta-\alpha}{\alpha+\beta} - (\alpha+\beta)^2. \tag{8.18}$$

Actually, the two eigenvalues has an imaginary component:

$$\lambda^2 - \lambda\,\text{Tr}[A] + \det[A] = 0, \tag{8.19}$$

whose discriminator is

$$\Delta = \big(\text{Tr}[A]\big)^2 - 4\det[A]. \tag{8.20}$$

Hence, when $\text{Tr}[A] \approx 0$, the $\Delta \approx -4(\alpha+\beta)^2 < 0$.

When the $\text{Tr}[A] > 0$, the (u^*, v^*) is unstable. What happens to the dynamics? It turns out that one can show that there is a *bounding box*.* Then there is the celebrated Poincaré-Bendixson theorem.

There will be *Hopf bifurcation*. There are two types of Hopf bifurcation: *supercritical* and *subcritical*. The former corresponds to a stable fixed point becomes unstable and the emergence of a stable limit cycle; the latter corresponds to a stable fixed point becomes unstable and the disappearance of a unstable limit cycle.

8.2 Transcritical bifurcation, Hopf bifurcation, and polar coordinates

The canonical form of transcritical bifurcation is

$$\frac{dx}{dt} = \mu x - x^2. \tag{8.21}$$

It has two fixed points, at $x_1^* = 0$ and $x_2^* = \mu$. The important things to note about this equation, however, is that change has to be smooth. In other words, when μ changes from -10^{-100} to $+10^{-100}$, even though the x_2^* switched, mathematically, from unstable to become stable, the dynamics for any reasonable x, e.g., $x \sim 10^{-5}$, does not change at all. The change is very "localized"; in fact, both x_1^* and x_2^* are at $x = 0$ when $\mu = 0$. The fixed point at this critical condition is *semi-stable*.

We now consider this example

$$\begin{aligned} \frac{dx}{dt} &= \Big(\mu - x^2 - y^2\Big)x - \omega y, \\ \frac{dx}{dt} &= \Big(\mu - x^2 - y^2\Big)y + \omega x. \end{aligned} \tag{8.22}$$

This planar system can be transformed into polar coordinates as

$$\frac{dr}{dt} = \big(\mu - r^2\big)r, \quad \frac{d\theta}{dt} = \omega, \tag{8.23}$$

in which $r \geq 0$. Therefore, for $\mu < 0$, it has only a single fixed point at $r = 0$, which is stable. However, for $\mu > 0$, it has a unstable fixed point at $r = 0$ but a stable "fixed" $r = \sqrt{\mu}$, which corresponds to a limit cycle. This is called supercritical Hopf bifurcation. When $\mu = 0$, the system has a stable fixed point at $r = 0$. If we change the t to $-t$ in (8.22), then the Hopf bifurcation becomes subcritical: There is a unstable limit cycle which circles around a stable fixed point.

If the equation for $\frac{dr}{dt}$ in (8.23) were for $r \in \mathbb{R}$, then it would have a transcritical bifurcation. Therefore, a Hopf bifurcation can be heuristically understood as a transcritical bifurcation in r. See L. Perko, "Differential Equations and Dynamical Systems" (Springer, 2001), Sec. 4.4.

* A bounding box can be constructed as follows: When $u > \alpha + \beta$, and $v > 0$, the vector field (f, g) has $\big(u^2v - u + \alpha, \beta - u^2v\big)$: It is pointing toward lower-right, and steeper than the line $x + y = C$. When this line intersects with $u = \alpha + \beta$, we construct a horizontal line on which all the vector field has to point downward. This horozontal line interacts with the nullcline $g = 0$, at which a vertical line is drawn, on which all the vector fields pointing rightward. It is easy to check that the x and y axes are part of the bounding box.

The Lorenz system has a subcritical Hopf bifurcation at $r = r_c$.