12 More on ecological interactions

12.1 Competition model with intraspecific competition

Consider a mathematical model that describes interactions of two populations competing for the same resource, assuming that also intraspecific competition is at play:

$$\dot{N}_1 = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - bN_1N_2,$$
$$\dot{N}_2 = r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - cN_1N_2,$$

note mutually negative influence of the populations on each other. By passing to dimensionless variables (you should write down the change of variables) I arrive at

$$\begin{aligned} \dot{x} &= x(1 - y - \alpha x), \\ \dot{y} &= y(\gamma - x - \beta y), \end{aligned} \tag{1}$$

which always has three equilibria in $\mathbf{R}^2_+$:

$$\hat{\boldsymbol{x}}_0 = (0,0), \quad \hat{\boldsymbol{x}}_1 = (1/\alpha, 0), \quad \hat{\boldsymbol{x}}_2 = (0, \gamma/\beta).$$

Additionally, if $\alpha\gamma > 1, \beta > \gamma$ or $\alpha\gamma < 1, \beta < \gamma$ there is an internal equilibrium

$$\hat{\boldsymbol{x}}_3 = (\hat{x}_3, \hat{y}_3) = \left(\frac{\beta - \gamma}{\alpha\beta - 1}, \frac{\alpha\gamma - 1}{\alpha\beta - 1}\right).$$

Point $\hat{\boldsymbol{x}}_0$ is an unstable node with eigenvalues 1 and γ, $\hat{\boldsymbol{x}}_1$ is a saddle if $\alpha\gamma > 1$ and an asymptotically stable node if $\alpha\gamma < 1$, $\hat{\boldsymbol{x}}_1$ is a saddle if $\beta > \gamma$ and asymptotically stable node if $\beta < \gamma$. Finally, if $\hat{\boldsymbol{x}}_3 \in \mathbf{R}^2_+$, then

$$\operatorname{tr} \boldsymbol{f}'(\hat{\boldsymbol{x}}_3) = -\alpha\hat{x}_3 - \beta\hat{y}_3 < 0, \quad \det \boldsymbol{f}'(\hat{\boldsymbol{x}}_3) = (\alpha\beta - 1)\hat{x}_3\hat{y}_3,$$

which implies that $\hat{\boldsymbol{x}}_3$ is stable if $\alpha\beta > 1$ and is a saddle if $\alpha\beta < 1$ if $\hat{\boldsymbol{x}}_3 \in \mathbf{R}^2_+$. The last condition is equivalent to $\alpha\gamma < 1, \beta < \gamma$ and $\alpha\gamma > 1, \beta > \gamma$ respectively.

The null-clines of interest here are

$$l_1 = \{(x,y) \colon y = 1 - \alpha x\}, \quad l_2 = \{(x,y) \colon \beta y = \gamma - x\},$$

which can be in four different mutual positions (see the figure below). If $\beta < \gamma$ and $\alpha\gamma > 1$ then $\hat{\boldsymbol{x}}_2$ is stable, $\hat{\boldsymbol{x}}_1$ unstable, $\hat{\boldsymbol{x}}_3 \notin \mathbf{R}^2_+$, and the analysis of null-clines implies that the phase portrait look like portrait (1) in the figure below. Species 2 outcompetes Species 1. If $\beta > \gamma$ and $\alpha\gamma < 1$ then the situation is similar in the sense that now species 2 wins the race, $\hat{\boldsymbol{x}}_1$ is an asymptotically globally stable equilibrium. Now assume that $\alpha\gamma > 1$ and $\beta > \gamma$, then $\hat{\boldsymbol{x}}_3 \in \mathbf{R}^2_+$ and asymptotically stable, all other points are unstable, and the analysis of null-clines yields that all the orbits converge to $\hat{\boldsymbol{x}}_3$, in this case we have species coexistence (Panel (3) in the figure). Finally, if $\alpha\gamma < 1$ and $\beta < \gamma$ then $\hat{\boldsymbol{x}}_3 \in \mathbf{R}^2_+$ and unstable, whereas both equilibria on the axes are stable (see case (4) in the figure). This is the so-called *bistable* situation, when the final outcome of the competition is determined not only by the parameter values, but also by the initial conditions.

Math 484/684: Mathematical modeling of biological processes by Artem Novozhilov
e-mail: artem.novozhilov@ndsu.edu. Fall 2015

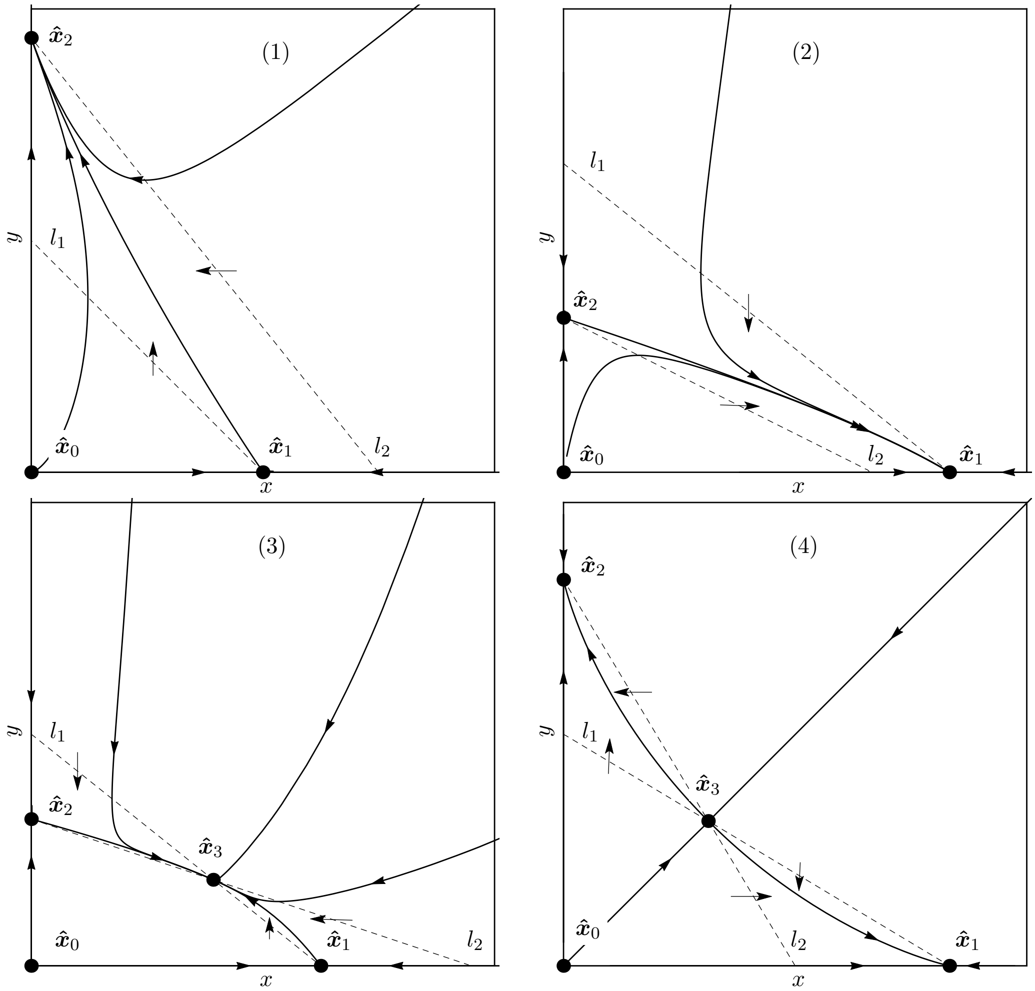

Figure 1: Four topologically non-equivalent phase portraits of the model (1)

I can summarize all the information in the parametric portrait of the model, which is now actually three-dimensional, since all three parameters play the role in the determining the dynamics of the system. In such cases it is usually convenient to fix one parameter, and consider "slices" of the full parametric portrait for this fixed value. In this case it is very convenient to fix γ, then I obtain the following parametric portrait in the space (α, β). You should represent the same parametric portrait for α fixed in (β, γ) space, and for β fixed in (α, γ) space. Recall that the parametric portrait together with the phase portraits for each topologically non-equivalent domain are called *bifurcation diagram*.

12.2 Principle of competitive exclusion

Which (biological) conclusions can be obtained from the (mathematical) analysis of the model? This model was used actually to predict the fate of a mosquito imported to the US, but I personally would

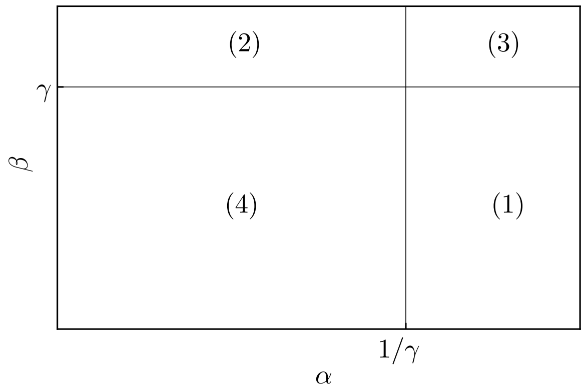

Figure 2: Parametric portrait of the model (1). The numbers of domains coincide with the numbers of topologically non-equivalent phase portraits in the previous figure

be quite careful with such quantitative predictions (here is reference for the paper[1], you should totally read it, it only two pages long). On the other hand, in three of four domains in the parametric portrait only one species survives the competition. This modeling conclusion was tested experimentally by Georgy Gause, who published his findings in the book *The Struggle for Existence*[2].

Gause formulated the *principle of competitive exclusion*, which states that

> *two species competing for the same resources cannot coexist if other ecological factors are constant*

Here is a mathematical incarnation of this principle when the species depend linearly on available resources (the principle need not be valid when the dependence is nonlinear).

Proposition 1. *If d bounded populations depend linearly on k resources, and $k < d$, then at least one population dies out.*

Proof. The assumption on the linear dependence translates into the equations

$$\frac{\dot{x}_i}{x_i} = b_{i1}R_1 + \ldots + b_{ik}R_k - \alpha_i, \quad i = 1, \ldots, d,$$

where x_i is the population size of the i-th population, α_i are the death rates, R_j is the abundance of the j-th resource, and b_{ij} describes the effectiveness of consumption of the j-th resource by the i-th population.

Since $d > k$ then the system of equations

$$b_{1j}c_1 + \ldots + b_{dj}c_d = 0, \quad j = 1, \ldots, k,$$

has a nontrivial solution, which I denote $\boldsymbol{c} = (c_1, \ldots, c_d)^\top$. Let (assuming a generic case)

$$\alpha = c_1\alpha_1 + \ldots + c_d\alpha_d \neq 0,$$

[1]Livdahl, T., & Willey, M. (1991). Prospects for an Invasion: Competition Between *Aedes albopictus* and Native *Aedes triseriatus*. Science, 253, 189-191

[2]Gause, G. F. (2003). *The struggle for existence.* Courier Dover Publications, also available online at http://www.ggause.com/Contgau.htm

such that $\alpha > 0$ (I can always guarantee this because together with $\boldsymbol{c}$, $-\boldsymbol{c}$ is also a solution). I have

$$c_1\frac{\dot{x}_1}{x_1} + \ldots + c_d\frac{\dot{x}_d}{x_d} = -\alpha,$$

which, by using the fact that $\frac{\dot{x}_i}{x_i} = \frac{\mathrm{d}\log x_i}{\mathrm{d}t}$ and integrating from 0 to some constant T, gives

$$\big(x_1(T)\big)^{c_1} \cdot \ldots \cdot \big(x_d(T)\big)^{c_d} = Ce^{-\alpha T}$$

for some constant $C \in \mathbf{R}$. For $T \to \infty$ I have that the right-hand side tends to zero, hence for at least one of the population, say x_i, I must have

$$\liminf_{T\to\infty} x_i(T) = 0,$$

which means that the i-th population goes extinct. ■

From a biological point of view the principle of competitive exclusion is still debatable, because there are quite a few instances in nature when two or more populations competing for the same resources are able to survive in a long term.

12.3 Cooperative systems

I would like to be as general as possible in this section. Analysis of many concrete mathematical models is left as an exercise.

Definition 2. *A system $\dot{\boldsymbol{x}} = \boldsymbol{f}(\boldsymbol{x})$, $\boldsymbol{x}(t) \in U \subseteq \mathbf{R}^d$, is called cooperative in U if*

$$\frac{\partial f_i}{\partial x_j}(\boldsymbol{x}) \geq 0$$

for all $\boldsymbol{x} \in U$ and $j \neq i$. It is called strictly cooperative in U if

$$\frac{\partial f_i}{\partial x_j}(\boldsymbol{x}) > 0$$

holds for all $\boldsymbol{x} \in U$ and $j \neq i$.

This means that the growth rate of each population does not decrease when the population sizes of other species increase. This clearly describes the mutualistic interaction, especially in the strict case.

Proposition 3. *Let two-dimensional system*

$$\dot{\boldsymbol{x}} = \boldsymbol{f}(\boldsymbol{x}), \quad \boldsymbol{x}(t) \in U \subseteq \mathbf{R}^2,\ \boldsymbol{f}\colon U \longrightarrow \mathbf{R}^2$$

be strictly cooperative in U. Then all the orbits converge either to an equilibrium or to a boundary of U (including ∞).

Proof. Denote $U_i, i = 1, 2, 3, 4$ the quadrants of $\mathbf{R}^2$ in the usual counterclockwise fashion. If $\dot{\boldsymbol{x}} \in \overline{U}_1$ for some $t = t_0$, where $\overline{U}_1$ means the closure of the set, then $\dot{\boldsymbol{x}} \in U_1$ for all $t > t_0$. This can be seen from the fact that

$$\ddot{x}_1 = \frac{\partial f_1}{\partial x_1}(\boldsymbol{x})\dot{x}_1 + \frac{\partial f_1}{\partial x_2}(\boldsymbol{x})\dot{x}_2,$$

assumption of being strictly cooperative, and the fact that if both $\dot{x}_1 = \dot{x}_2 = 0$ then we are at an equilibrium. Similarly for U_3. If $\dot{\boldsymbol{x}} \in U_2$ or $\dot{\boldsymbol{x}} \in U_4$ then the sign of derivatives can change only once, and thus both of the components are eventually monotone. ■

Note that the time reversal will turn a cooperative system into a competitive one:

Definition 4. *A system* $\dot{\boldsymbol{x}} = \boldsymbol{f}(\boldsymbol{x})$, $\boldsymbol{x}(t) \in U \subseteq \mathbf{R}^d$, *is called competitive in* U *if*

$$\frac{\partial f_i}{\partial x_j}(\boldsymbol{x}) \leq 0$$

for all $\boldsymbol{x} \in U$ *and* $j \neq i$. *It is called strictly competitive in* U *if*

$$\frac{\partial f_i}{\partial x_j}(\boldsymbol{x}) < 0$$

holds for all $\boldsymbol{x} \in U$ *and* $j \neq i$.

This implies that

Proposition 5. *Let two-dimensional system*

$$\dot{\boldsymbol{x}} = \boldsymbol{f}(\boldsymbol{x}), \quad \boldsymbol{x}(t) \in U \subseteq \mathbf{R}^2,\ \boldsymbol{f}\colon U \longrightarrow \mathbf{R}^2$$

be strictly competitive in U. *Then all the orbits converge either to an equilibrium or to a boundary of* U *(including* ∞*).*

In particular, if one assumes a limited growth (i.e., $f_1(\boldsymbol{x}) < 0$ for large enough x_1 and $f_2(\boldsymbol{x}) < 0$ for large enough x_2) then every solution of a strictly cooperative system converges to a fixed point.

Cooperative and competitive systems are examples of *monotone dynamical systems*, for which an extensive theory exists.