11 Ecological interactions

11.1 General Lotka–Volterra model on a plane and types of ecological interactions

Finally I am in a position to start discussion of simple mathematical models of species interactions in a uniform fashion. For this let me start the discussion with the general form of the Lotka–Volterra model for two interacting species. Let $N_1(t)$ and $N_2(t)$ denote the species population sizes at time t, and all the interactions are modeled using the law of mass action. This implies that I can write

$$\dot{N}_1 = N_1(b_1 + a_{11}N_1 + a_{12}N_2),$$
$$\dot{N}_2 = N_2(b_2 + a_{21}N_1 + a_{22}N_2),$$

where $b_1, b_2, a_{11}, a_{12}, a_{21}, a_{22}$ are constants (non necessarily positive). The constants b_1, b_2 describe the *Malthusian growth* ($b_i > 0$) or *decay* ($b_i < 0$), the constants a_{11} and a_{12} refer to the *intraspecific competition* in the case $a_{ii} < 0$, and constants a_{12} and a_{21} describe the species interactions (*interspecific competitions* in a broad sense). In particular, two species can be in the following relationships:

- *Neutralism.* This corresponds to the case $a_{12} = a_{21} = 0$, i.e., there is no direct influence of any of the species on the other one.

- *Amensalism* is an interaction when one of the species clearly has a negative effect on another without getting any significant influence back. For the parameters of the system this means that, say, $a_{12} < 0$ and $a_{21} = 0$.

- *Commensalism.* Here one species benefits without affecting the other. It implies that, e.g., $a_{12} > 0$ and $a_{21} = 0$ (in this case species 1 is a *commensal*, the one that benefits, and species 2 is a *host*).

- *Competition* is a mutually detrimental interaction, $a_{12} < 0, a_{21} < 0$.

- *Antagonism.* In antagonism one species benefits at the expense of the other, $a_{12} < 0, a_{21} > 0$. Different terms can be used in this case, e.g., *consumer–resource* interaction, or *host–parasite* interaction, or *prey–predator* interaction.

- *Mutualism* leads to mutual benefit of interacting species (*symbiosis*, which is sometimes considered as a synonym, is a more general term, which may refer to any mutual interaction of two species), and hence $a_{12} > 0, a_{21} > 0$.

Sometimes matrix $\boldsymbol{A} = (a_{ij})_{2 \times 2}$ of the parameters describing the intra- and interspecific interactions is called the *interaction matrix*. I already discussed at length the predator–prey Lotka–Volterra model, in which, $b_1 > 0, b_2 < 0, a_{11} = a_{22} = 0, a_{12} < 0, a_{21} > 0$. In this lecture I will look at some other interesting cases. It should be clear how to extend the system for the case of three, four, or more interacting species.

11.2 Lotka–Volterra predator–prey model with intraspecific competition

Recall that Lotka–Volterra predator–prey model that I analyzed is *structurally unstable*, i.e., a small perturbation of this system would lead to a topologically nonequivalent system (this phrase means "would lead to a system that possesses a topologically nonequivalent phase portrait, no matter how small perturbation is"). Consider a modification of this model that includes both prey and predator intraspecific competitions:

$$\dot{N} = aN\left(1 - \frac{N}{K_1}\right) - bNP,$$

$$\dot{P} = -dP\left(1 + \frac{P}{K_2}\right) + cNP,$$

where $a, b, c, d, K_1, K_2 > 0$ and $N(t)$ and $P(t)$ are prey and predator populations at time t respectively (actually, the predator intraspecific competition is redundant here, the same result is obtained putting formally $K_2 = \infty$). By switching to non-dimensional variable, I find that

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

where

$$N(t) = \frac{ax(\tau)}{c}, \quad P(t) = \frac{ay(\tau)}{b}, \quad \tau = at, \quad \gamma = \frac{d}{a}, \quad \alpha = \frac{a}{cK_1}, \quad \beta = \frac{d}{aK_2}.$$

For the biologically motivated models the phase space is $\mathbf{R}_+^2 = \{(x, y): x \geq 0, y \geq 0\}$, therefore I do not consider the orbit structure in other parts of the plane. An important point, however, is to show that the chosen biologically realistic state space is *positively invariant*, i.e., if the initial conditions belong to our state space, then the positive semi-orbit starting at this point will stay in the phase space for any $t \to +\infty$ (I can similarly define a *negatively invariant* set). In my case it is a simple matter since the axis are invariant and consist of the orbits. This follows from the fact that $x = 0$ is a solution (plug it in the first equation) and $y = 0$ is a solution (plug it in the second equation). Since the axis are composed of the orbits and other orbits cannot intersect them I can conclude that $\mathbf{R}_+^2$ is both positively and negatively invariant, and hence simply *invariant*.

In $\mathbf{R}_+^2$ system (1) can have up to three equilibria:

$$\hat{\boldsymbol{x}}_0 = (0, 0), \quad \hat{\boldsymbol{x}}_1 = \left(\frac{1}{\alpha}, 0\right), \quad \hat{\boldsymbol{x}}_2 = \left(\frac{\gamma + \beta}{1 + \alpha\beta}, \frac{1 - \gamma\alpha}{1 + \alpha\beta}\right),$$

and $\hat{\boldsymbol{x}}_2 \in \mathbf{R}_+^2$ only if $\gamma\alpha < 1$.

The Jacobi matrix of (1) has the form

$$\boldsymbol{f}'(x, y) = \begin{bmatrix} 1 - y - 2\alpha x & -x \\ y & -\gamma - 2\beta y + x \end{bmatrix}.$$

By analyzing eigenvalues of the Jacobi matrix, I find that $\hat{\boldsymbol{x}}_0$ is always a saddle point, with x-axis being the unstable manifold, and y-axis being the stable manifold. For $\hat{\boldsymbol{x}}_1$ one has

$$\boldsymbol{f}'(\hat{\boldsymbol{x}}_1) = \begin{bmatrix} -1 & -\dfrac{1}{\alpha} \\ 0 & \dfrac{1 - \gamma\alpha}{\alpha} \end{bmatrix},$$

therefore this point is a saddle if $\alpha\gamma < 1$ and stable node if $\alpha\gamma > 1$, for $\alpha\gamma = 1$ I have one eigenvalue equal to zero, and therefore a bifurcation occurs, the exact type of this bifurcation will be determineed by looking at the third equilibrium. Note that when $\hat{\boldsymbol{x}}_1$ is a saddle then the stable manifolds are on the x-axis, and the unstable manifold is tangent to straight line with the direction $(1, \gamma\alpha - 1 - \alpha)$, i.e., has a negative slope.

Now assume that $\hat{\boldsymbol{x}}_2 = (\hat{x}_2, \hat{y}_2)$ be the coordinates of the third equilibrium in case $\alpha\gamma < 1$. That is, they solve the system

$$\alpha x + y = 1,$$
$$x - \beta y = \gamma,$$

and I know that $\hat{x}_2 > 0, \hat{y}_2 > 0$. Using the fact that, e.g.,

$$\frac{\partial f_1}{\partial x} = (1 - \alpha x - y) - \alpha x,$$

I find that

$$\operatorname{tr} \boldsymbol{f}'(\hat{\boldsymbol{x}}_2) = -\alpha\hat{x}_2 - \beta\hat{y}_2 < 0,$$

and

$$\det \boldsymbol{f}'(\hat{\boldsymbol{x}}_2) = \hat{x}_2\hat{y}_2(1 + \alpha\beta) > 0,$$

which implies that $\hat{\boldsymbol{x}}_2$ is asymptotically stable and either stable node or stable focus depending on the exact parameter values. I also notice that if $\alpha\gamma = 1$ then the coordinates of $\hat{\boldsymbol{x}}_2$ are precisely $(\alpha^{-1}, 0)$, i.e., they coincide with the coordinates of $\hat{\boldsymbol{x}}_1$. This implies, given that both $\hat{\boldsymbol{x}}_1$ and $\hat{\boldsymbol{x}}_2$ exist for any parameter values (but not always in $\mathbf{R}_+^2$) that the local bifurcation that occurs for $\alpha\gamma = 1$ is exactly the *transcritical bifurcation*, at which these two equilibria collide and exchange the stability properties.

To figure out the global behavior of the orbits I need to look at the mutual positioning of the null-clines, which are given here as

$$x = 0, \quad y = 0, \quad l_1 = \{(x,y)\colon y = 1 - \alpha x\}, \quad l_2 = \{(x,y)\colon \beta y = x - \gamma\},$$

where I named only those different from the coordinate axis. I will use the proposition from the previous lecture, in which it was stated that the monotone orbits in a bounded open set either approach the boundary of this set or converge to an equilibrium.

Consider first $\alpha\gamma > 1$. l_1 has a negative slope and intersect x-axis at the equilibrium with $x = 1/\alpha$, l_2 has a positive slope and intersects x-axis at $x = \gamma > 1/\alpha$ due to the assumption. Therefore these null-clines divide $\mathbf{R}_+^2$ into three sets, let me call them U_1, U_2, U_3 starting from left to right (see the figure). Assume that $\boldsymbol{x}_0 \in U_3$. According to the proposition the orbit $\gamma(\boldsymbol{x}_0)$ has to cross l_2, because in this set $\dot{x} < 0$ and there are no equilibria to converge to. In U_2 I have that $\dot{x} < 0, \dot{y} < 0$, therefore the only two possibilities are to converge to $\hat{\boldsymbol{x}}_1$ or to cross l_1. Finally, in U_2 there is no other option for the orbits other than converge to $\hat{\boldsymbol{x}}_1$, and I conclude that for the case $\alpha\gamma > 1$ the equilibrium $\hat{\boldsymbol{x}}_1$ is *globally asymptotically stable*, meaning that for *almost all* initial conditions from $\mathbf{R}_+^2$ I have $\boldsymbol{x}(t; \boldsymbol{x}_0) \to \hat{\boldsymbol{x}}_1$.

Now let $\alpha\gamma < 1$. Then l_1 and l_2 intersect at $\hat{\boldsymbol{x}}_2$, and $\mathbf{R}_+^2$ is divided into four sets U_1, U_2, U_3, U_4 going in a clockwise fashion. Now I can argue that the orbits either approach $\hat{\boldsymbol{x}}_2$ or cross boundaries of our sets in the order $U_4 \to U_3 \to U_2 \to U_1 \to U_4$. This means that there is a *theoretical* possibility to have a closed orbits that corresponds, as I discussed earlier for Lotka–Volterra model, to periodic oscillations in prey and predator populations. At this point I am just going to state that there are
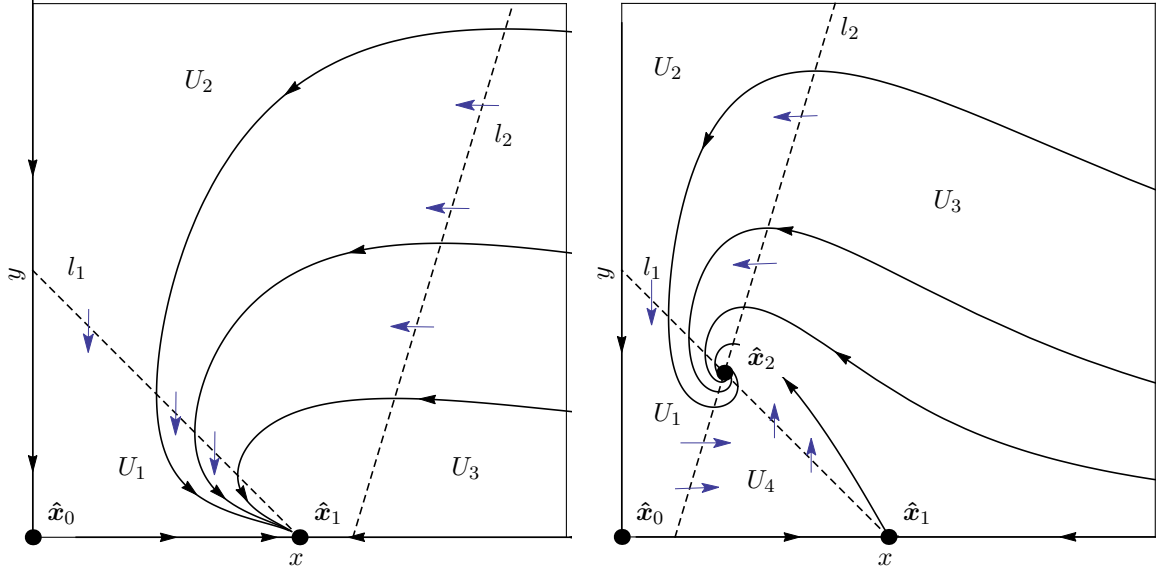
Figure 1: Topologically non-equivalent phase portraits of the prey–predator model with intraspecific competition. The left one corresponds to $\alpha\gamma > 1$, and the right one corresponds to the case $\alpha\gamma < 1$

no closed orbits in this system, a proof will be given later. Therefore, I conclude that in case $\alpha\gamma < 1$ equilibrium $\hat{\boldsymbol{x}}_2$ is globally asymptotically stable.

As a general conclusion I have that system (1) allows two structurally stable topologically non-equivalent phase portraits, the transcritical bifurcation occurs when $\alpha\gamma = 1$, and each of these parameters can be taken as a bifurcation parameter. Parameter β does not influence the topological picture.

In biological terms I have two very different outcomes:

- If $\alpha\gamma > 1$, i.e., when

$$\frac{d}{cK_1} > 1,$$

  which corresponds to a high mortality rate for the predator, or a low carrying capacity for the prey, or a low effectiveness of the predator to transform prey biomass into predator biomass, then the predator goes extinct whereas the prey population stabilizes at $N(t) = K_1$.

- If $\alpha\gamma < 1$, i.e., when

$$\frac{d}{cK_1} < 1,$$

  which means that either prey has a large carrying capacity, or the predator has a low mortality rate, or a high effectiveness in prey consumption, then the prey and predator coexist at the equilibrium $\hat{\boldsymbol{x}}_2$, whose coordinates should be written in the original dimensional parameters.

Finally, it is not necessary for this example, but usually very useful to do is to sketch in the parameter space the domains of topologically non-equivalent behaviors. Here is how it look for our case, where β does not change anything, and hence there are only two parameters changes in which lead to bifurcations:
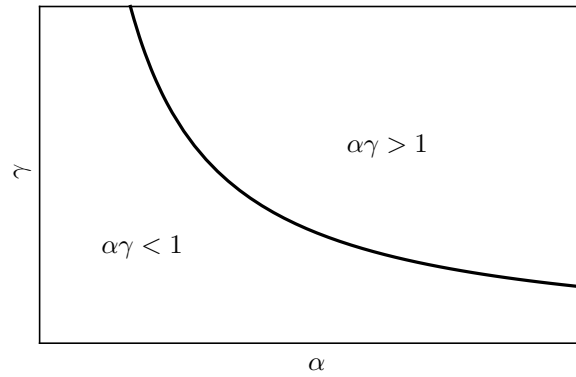
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Figure 2: Parametric portrait of the predator–prey system with intraspecific competition. There is only one bifurcation boundary on which transcritical bifurcation of $\hat{\boldsymbol{x}}_1$ occurs

  The *parametric portrait* as shown above together with phase portraits for each domain in the parametric portrait as shown in the previous figure constitute together a *bifurcation diagram* of the system, obtaining which is the ultimate goal of analysis of nonlinear parameter dependent autonomous ODE systems. Unfortunately in many many cases, only partial information about the corresponding bifurcation diagram is available.