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T VI: Nonlinear Dynamics and Complex Systems

(Prof. E. Frey)

Problem Set 3: Limit-cycles, spirals and star nodes.

Aufgabe 1 *Rock-Paper-Scissors: Rock crushes scissors, scissors cut paper and paper wraps rock*

1.) In recent experiments on heterogeneous cell cultures the feature of "cyclic dominance" analog to the Rock-Paper-Scissors game was found: Bacteria of species A produce antibiotics, that kill wild type bacteria of species B. A and a third species C are immune to antibiotics, since they lack a membrane protein for nutrient uptake, which also transports antibiotics into the cytosol. Production of antibiotics is costly while reduced nutrient uptake slows reproduction. In summary, each species is superior with respect to one and dominant with respect to the other species in its environment: A kills B, B grows faster than C, and C outperforms A.
For a mathematical model of cyclic dominance consider relative cell densities a, b and c. Dominant species kill their victims with rate σ. When the total cell density $\rho := a+b+c$ is low, all species reproduce with rate μ. Growth is limited since the habitat has a finite total carrying capacity, normalized to 1. Dynamics of the system are governed by the equations:

$$\begin{aligned}\dot{a} &= a[\mu(1-\rho) - \sigma c]\ , \\ \dot{b} &= b[\mu(1-\rho) - \sigma a]\ , \\ \dot{c} &= c[\mu(1-\rho) - \sigma b]\ .\end{aligned}$$

a) Write down the underlying chemical reaction equations of the species involved and argue the dimensionality of the model above.

b) Determine all fixed points of the system and explain their biological significance.

c) Linearize the system about the non-trivial fixed point and classify it. Is biodiversity (coexistence of all three species) stable in this model? Use Fig.2 of the first reference listed to get an impression of the dynamics in the corresponding phase space. In a later problem set we will learn how to determine the manifold on which the dynamics takes place.

d) Show that the time derivative of $L = \frac{abc}{\rho^3}$ (a Liapunov function) is always less or equal to zero. Where is it zero? What does that tell you about the long time limit of the system? Argue the role of fluctuations qualitatively.

2.) Now consider another three strategy model which is defined by the following chemical reaction equations:

$$\begin{aligned} A+B &\xrightarrow{k} A+A \qquad & A+B &\xrightarrow{r} B+B \\ B+C &\xrightarrow{k} B+B \qquad & B+C &\xrightarrow{r} C+C \\ C+A &\xrightarrow{k} C+C \qquad & C+A &\xrightarrow{r} A+A \end{aligned}$$

In addition mutation shall be possible:

$$\begin{aligned} A &\xrightarrow{\mu} B, \quad B \xrightarrow{\mu} C, \quad C \xrightarrow{\mu} A \\ A &\xrightarrow{\mu} C, \quad B \xrightarrow{\mu} A, \quad C \xrightarrow{\mu} B. \end{aligned}$$

e) Formulate the corresponding non-linear equations for the concentrations a, b and c. Show that the total concentration ($a+b+c=1$) of species is conserved. What is the dimensionality of the model?

f) Find the non-trivial fixed point, perform a linear expansion around that fixed point and determine the eigenvalues of the corresponding matrix. Sketch the phase portrait near that fixed point with and without mutations. Argue qualitatively the role of fluctuations for the case without mutation.

g) Sum up your findings and compare model 1.) and 2.) carefully.

Note: For the influence of fluctuations and spatial degrees of freedom on model 1.) see refs. [1–3].

Aufgabe 2 *Cell cycle*

Tyson [4] proposed an elegant model of the cell division cycle, based on interactions between the proteins *cdc2* and *cyclin*. He showed that the model's mathematical essence is contained in the following set of dimensionless equations:

$$\dot{u} = b(v-u)(\alpha+u^2) - u, \quad \dot{v} = c - u,$$

where u is proportional to the concentration of the active form of a *cdc2-cyclin* complex, and v is proportional to the total *cyclin* concentration (monomers and dimers). The parameters $b \gg 1$ and $\alpha \ll 1$ are fixed and satisfy $8\alpha b < 1$, and c is adjustable.

a) Sketch the nullclines.

b) Show that the system exhibits relaxation oscillations for $c_1 < c < c_2$, where c_1 and c_2 are to be determined approximately. (It is hard to find c_1 and c_2 exactly, but a good approximation can be achieved if you assume $8\alpha b \ll 1$.)

c) Check the condition for c found in b.) now numerically (e.g. with the help of mathematica) and plot the phase space for interesting values of c.

Aufgabe 3 *Parameter domain analysis*

Hanusse [5] showed that two species reaction models can exhibit limit cycle periodic oscillations only if the reactions are tri-molecular. The simplest such reaction mechanism is

$$X \rightleftharpoons A, \quad b \rightarrow Y, \quad 2X+Y \rightarrow 3X,$$

which, using the law of mass action, results in nondimensionalized equations for u and v, the dimensionless concentrations of X and Y, given by

$$\dot{u} = a - u + u^2 v, \quad \dot{v} = b - u^2 v,$$

where a and b are positive constants.

a) Construct a trapping region for the system.

b) Determine the parameter domain where limit cycle solutions exist. Use Mathematica or a similar program to create a stream plot for some specific parameter combination, giving rise to limit cycle solutions and plot two trajectories.

c) Assume $a, b > 0$. Use the numerical capabilities of Mathematica (or whatever program you favor) and partition the parameter space according to the type and stability of the fixed point.

Literatur

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