

PhD mini course: introduction to bifurcation analysis

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Abstract

This pdf document provides the textual background in the mini course on bifurcation analysis, by George van Voorn. It is the companion material by the powerpoint presentations posted on the site www.bio.vu.nl/thb. Goal of this manuscript is to explain some of the basics of bifurcation theory to PhD-students at the group. The emphasis is strongly on the biological interpretation of bifurcations; mathematics are reduced to an absolute minimum. Some expert things are covered as well, with the goal that it is possible for the reader to understand results of model analyses at the group in sufficient detail.

Keywords: bifurcation analysis, equilibria, ODE systems.

1 Introduction

In scientific fields as diverse as fluid mechanics, electronics, chemistry and theoretical ecology, there is the application of what is referred to as bifurcation analysis; the analysis of a system of ordinary differential equations (ODE's) under parameter variation. Performing a local bifurcation analysis is often a powerful way to analyse the properties of such systems, since it predicts what kind of behaviour (system is in equilibrium, or there is cycling) occurs where in parameter space. With local bifurcations linearisation in state space at the critical point of the parameter space provides sufficient information. For a good introduction on the basics of local bifurcation analysis the reader is referred to Guckenheimer and Holmes (1985), Wiggins (1990) and Kuznetsov (2004), be it these are all very mathematical in their approach.

This mini course has been developed to provide PhD students in the field of theoretical biology, or anybody else interested in the subject, enough background on the subject of bifurcation analysis to understand basic results in this field. The main goal is then that the results can be understood in terms of biology. It is assumed that the participant has some background in mathematics in general and specifically in ordinary differential equations.

The course has been made such that it should be feasible to do it in a single day. For that reason, as much mathematical background as possible has been eliminated. Instead, pictures are provided. The single goal is to give the participant some understanding of results, obtained by others. Please note, that this course can therefore not ever function as the substitute for a decent mathematical background.

2 Simple one-dimensional ODE systems

Under the assumption the reader understands what an ordinary differential equation (ODE) is, let us introduce some notation. A typical one-dimensional ODE is written as

$$\dot{x} = f(x) , \tag{1}$$

where x is the variable subject to change. Note, that when x depends on time t , we call Equation 1 an autonomous system. For the remainder of the manuscript we assume all ODE's to be time-dependent.

If we know the value of x at time $t = 0$, we have an initial value problem

$$\dot{x} = f(x) , \quad x(0) = x_0 , \tag{2}$$

where x_0 is the known value. When we plot the change in x during time we have an orbit. All orbits together with the direction of arrows gives a phase portrait.

2.1 Equilibria

It is possible that for $t \rightarrow \infty$ all orbits converge to a single value of x , denoted as x^* . We call this value a stable equilibrium of Eqn. (1). Equilibria can also be unstable; orbits then

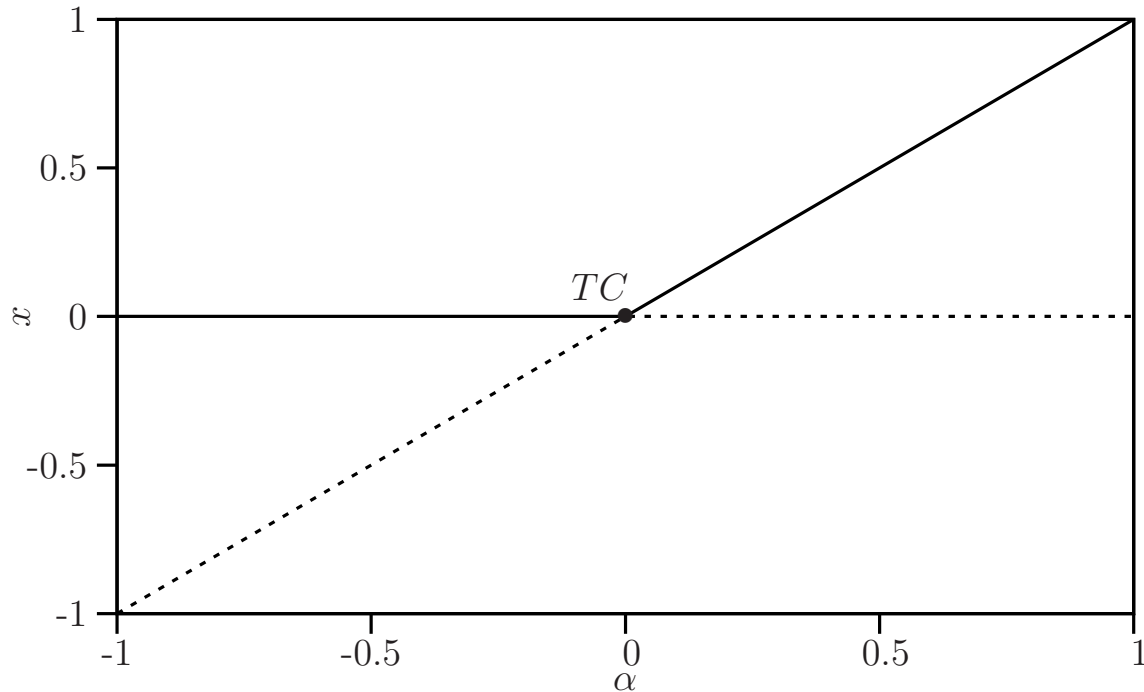


Figure 1: Transcritical bifurcation point for a one-dimensional system.

go into the direction away from x^* . Of course, when time is reversed the equilibrium can be perceived as stable again.

To find an equilibrium all one has to do is set Eqn. (1) equal to zero and solve the resulting equation. To investigate the stability of the found equilibria linearisation is needed, i.e. we need to differentiate the function. Now, if $f'(x) < 0$, the equilibrium is stable. Vice versa, if $f'(x) > 0$ the equilibrium is unstable. If $f'(x) = 0$ we cannot say anything about the equilibrium at this point.

2.2 Bifurcation analysis

Consider an ODE that depends on one or more parameters α

$$\dot{x} = f(x, \alpha), \tag{3}$$

where, for simplicity, we assume α to be one parameter only. There is the possibility that under variation of α nothing interesting happens to Eqn. (3). There is only a quantitatively different behaviour (shifted equilibria, e.g.). Let us define Eqn. (3) to be *structurally stable* in the case there are no qualitative changes occurring. However, the ODE might change qualitatively. At that point, bifurcations will have occurred.

2.3 Transcritical bifurcation

Let us study the following example

$$\dot{x} = x(\alpha - x) . \tag{4}$$

In this case we have two equilibria

$$x = 0 , \quad x = \alpha , \tag{5}$$

of which one is stable and the other one is unstable. The stability can be checked by taking the derivative $f'(x) = \alpha - 2x$. For $\alpha < 0$ the equilibrium $x = 0$ is stable, while for $\alpha > 0$ this equilibrium is unstable. For the non-trivial equilibrium $x \neq 0$ the opposite is true. Note that the stable equilibrium functions as an attractor, while the unstable equilibrium functions as a *separatrix*.

What happens at $\alpha = 0$? Note, that we have only one equilibrium $x = 0$ then. This equilibrium is stable. This point we call a transcritical bifurcation. At this point, the two equilibria exchange stability (see Figure 1). From a biological perspective we associate this behaviour with the invasion of a species x . The transcritical bifurcation is said to be the invasion boundary of this species. For $\alpha < 0$ the stable equilibrium is zero, which means the species does not survive (for infinite time; it might stick around a while though before it inevitably disappears). For $\alpha > 0$ the stable equilibrium is larger than zero, which means a population can be maintained always.

2.4 Tangent bifurcation

Let us study a second example, now written as

$$\dot{x} = (x^2 - \alpha) . \tag{6}$$

This system is qualitatively different from Eqn. (4). We have the following equilibria

$$x = -\sqrt{\alpha} , \quad x = \sqrt{\alpha} , \tag{7}$$

under the assumption $\alpha > 0$. Note, that these equilibria have disappeared for values of $\alpha < 0$. Again, one equilibrium is attracting, while the other equilibrium is unstable.

What happens at $\alpha = 0$? The two equilibria merge (there is only the equilibrium $x = 0$) into one stable equilibrium (see Figure 2). For values of $\alpha < 0$ there are no equilibria at all. Of course, in most systems there will be another attractor somewhere. In a biological setting, this other attractor will often be $x = 0$, while the two equilibria involved in the tangent bifurcation are both positive. We then interpret the tangent bifurcation as a sudden extinction of the species, as opposed to the transcritical bifurcation, which shows a graduate decline for decreasing α .

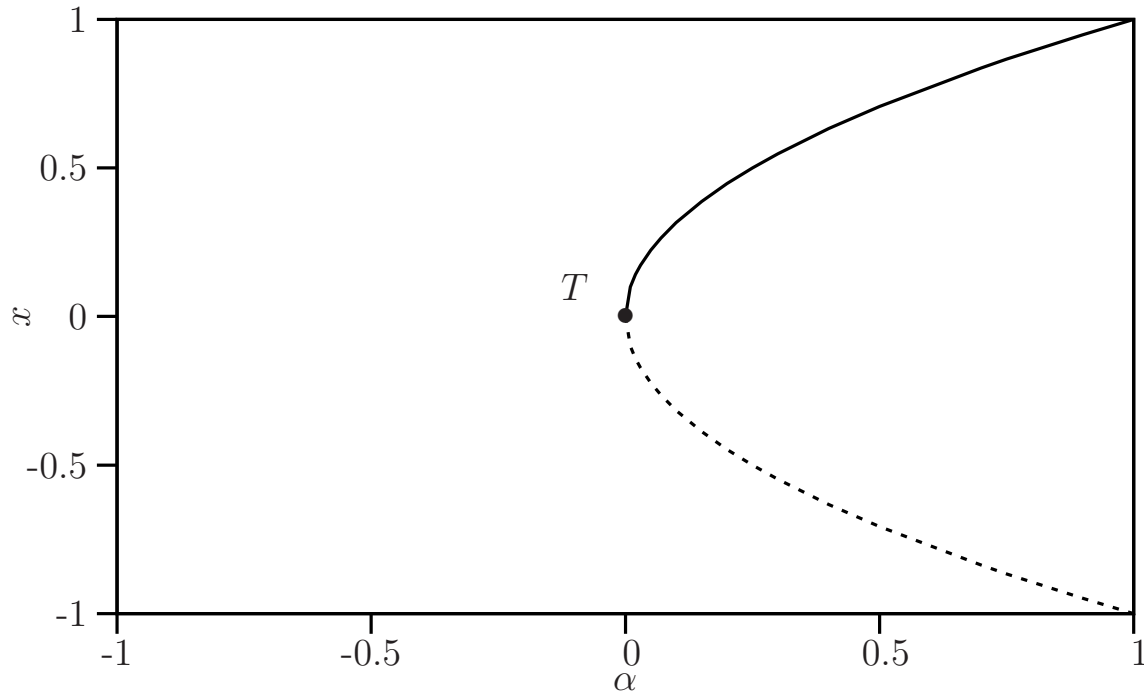


Figure 2: Tangent bifurcation point for a one-dimensional system.

3 Two-dimensional ODE systems

Many of the basic principles discussed apply also for two-dimensional systems. Let us define a two-dimensional system

$$\dot{x} = f(x, y, \alpha), \tag{8a}$$

$$\dot{y} = g(x, y, \alpha), \tag{8b}$$

where biologically we mostly interpret x as prey or resource and y as predator or consumer. Equilibria can also be found by taking the equations equal to zero. Note however, that we now have three possibilities for the stability of an equilibrium. Next to the stable and unstable equilibrium, there is the saddle equilibrium. A two-dimensional stable equilibrium is attracting in two directions, while a two-dimensional unstable equilibrium is repelling in two directions. A saddle point is attracting in one direction and repelling in the other direction. In the less formal literature saddles are often considered just unstable equilibria.

A second remark is that also the dynamics of the system around the equilibria can differ. The attracting or repelling can occur via straight orbits (a node) or via spiralling orbits (a spiral or focus). Note, that it is not possible to have a saddle focus in two dimensions. It is possible though in three or higher dimensional systems.

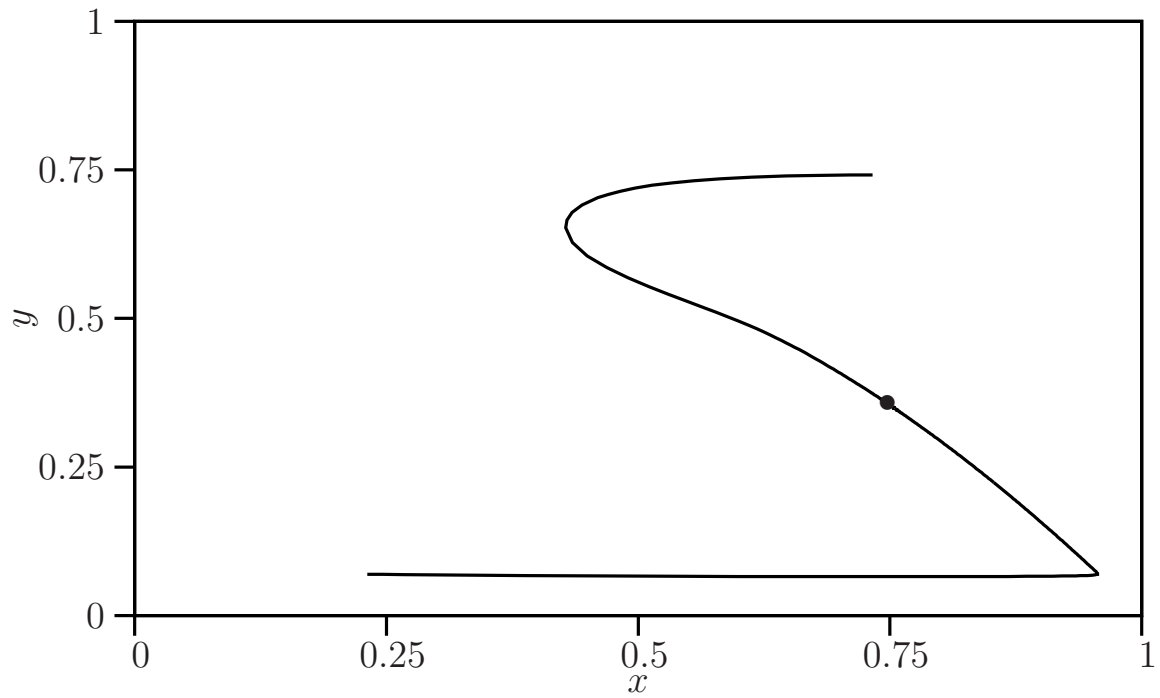


Figure 3: Example of a node. In this case the manifolds clearly differ in attraction strength.

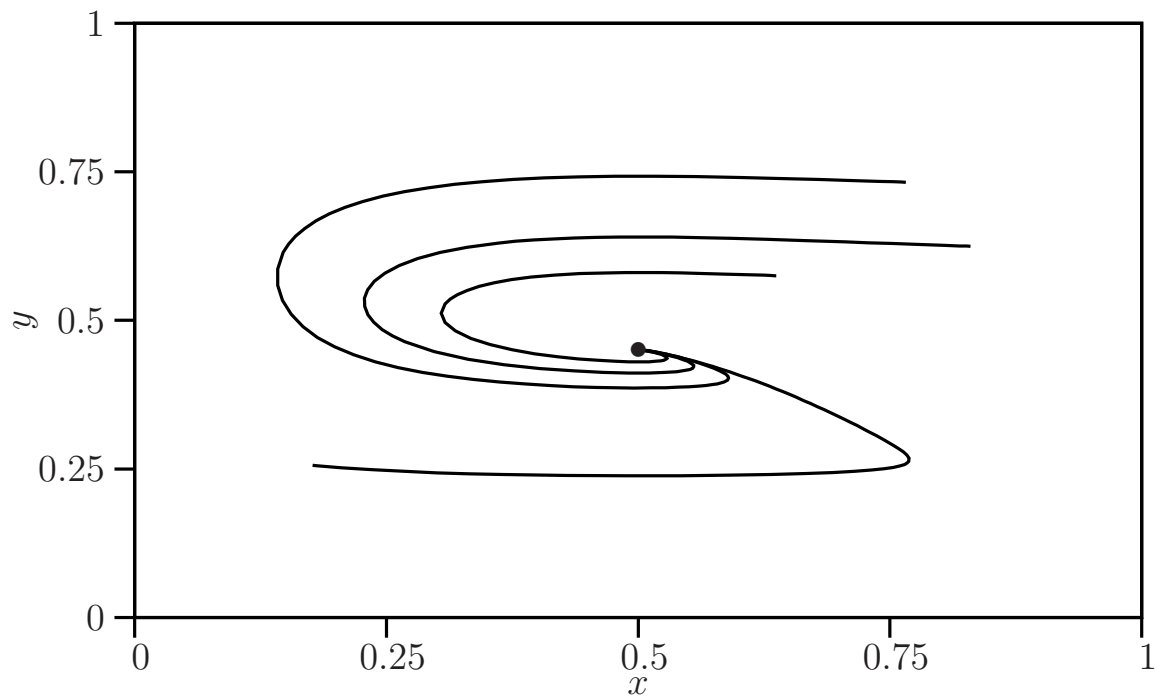


Figure 4: Example of a focus, or spiral. Notice the spiralling towards the equilibrium, as opposed to attraction in one direction only

3.1 Jacobian matrix, eigenvectors

How do we discriminate between these options? The best way is to first determine the *Jacobian matrix* of the system. This matrix is composed of the partial derivatives of both functions in Eqn. (8), written as

$$\mathbf{J} = \begin{pmatrix} \frac{df}{dx} & \frac{df}{dy} \\ \frac{dg}{dx} & \frac{dg}{dy} \end{pmatrix}. \quad (9)$$

From this matrix we can derive the so-called eigenvalues and eigenvectors using

$$\mathbf{J}\mathbf{v} = \lambda\mathbf{v}, \quad (10)$$

where λ is the eigenvalue and \mathbf{v} the eigenvector. In the case of a two-dimensional system we have

$$\begin{pmatrix} \frac{df}{dx} & \frac{df}{dy} \\ \frac{dg}{dx} & \frac{dg}{dy} \end{pmatrix} \cdot \begin{pmatrix} v_x \\ v_y \end{pmatrix} = \lambda \begin{pmatrix} v_x \\ v_y \end{pmatrix}, \quad (11)$$

with two sets of solutions for λ, v_x, v_y . The eigenvectors are linearisations along which the orbits enter or exit the surroundings of the equilibrium. The eigenvalues give information on the direction and the strength of the attracting or repelling of the orbits.

Note, that the eigenvalues can be complex numbers. If they are we have a spiral equilibrium. In the case where the eigenvalues are real numbers, we have a node. In the case of $\lambda_1, \lambda_2 < 0$ we have a stable node or focus. Equally, for $\lambda_1, \lambda_2 > 0$ we have an unstable node or focus. And finally, for $\lambda_1 < 0, \lambda_2 > 0$ the equilibrium is a saddle.

Figure 3 gives an example of a node. Apparently one eigenvalue is much more attracting than the other direction, which leads to an S-like shape. Figure 4 then depicts a spiral in the same system, but with other parameter values. All orbits clearly enter via the same direction (this is a stable manifold, which will be discussed further on).

Though both pictures differ quantitatively, their stability properties are alike. As such the differences are of limited interest.

An easier way to determine whether an equilibrium is a node or a focus, stable, unstable or saddle, is by evaluating the *trace* and the *determinant*

$$tr(\mathbf{J}) = \frac{df}{dx} + \frac{dg}{dy}, \quad (12)$$

$$det(\mathbf{J}) = \frac{df}{dx} \frac{dg}{dy} - \frac{df}{dy} \frac{dg}{dx}, \quad (13)$$

for the Jacobian matrix \mathbf{J} at the equilibrium. We have a saddle when $det(\mathbf{J}) < 0$. For $det(\mathbf{J}) > 0$ we have to evaluate the trace as well. If $tr(\mathbf{J}) < 0$ the equilibrium is stable, if $tr(\mathbf{J}) > 0$ the equilibrium is unstable. For $(tr(\mathbf{J}))^2 < 4det(\mathbf{J})$ we have a spiral, otherwise we have a node. These results are compiled in Figure 5.

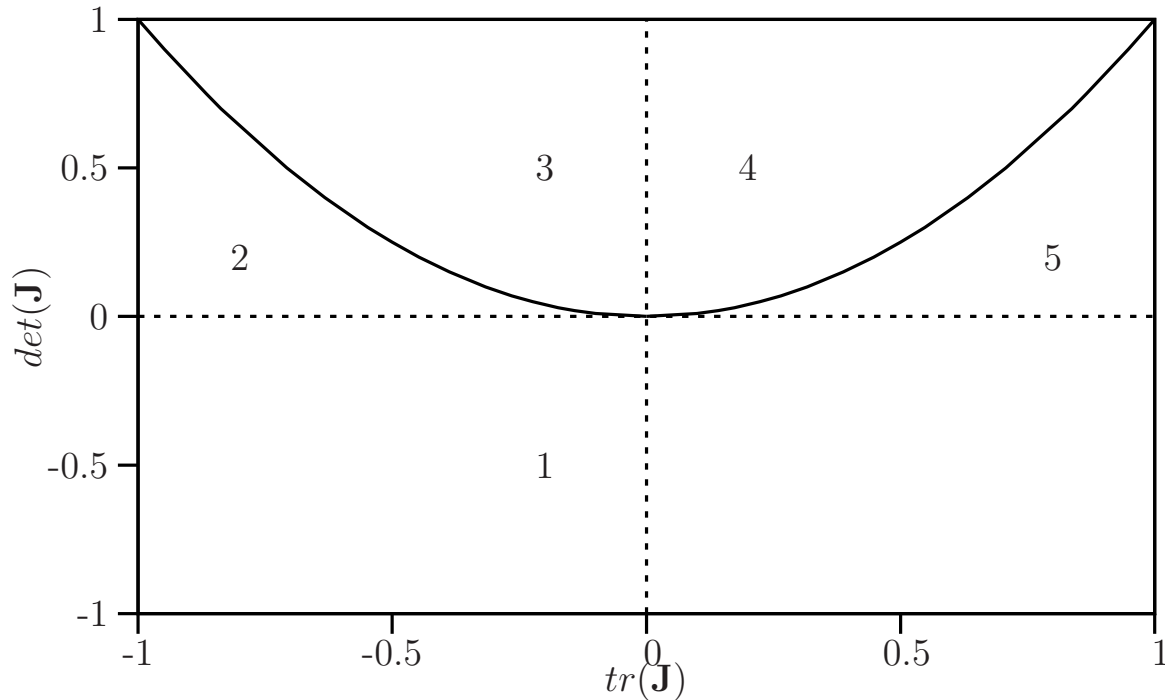


Figure 5: Diagram of $tr(\mathbf{J})$ plotted against $det(\mathbf{J})$. Regions are 1. Saddle, 2. Stable node, 3. Stable spiral, 4. Unstable spiral, 5. Unstable node.

3.2 Isocline analysis

One type of analysis of two-dimensional models applied regularly is an analysis of the isoclines of the system. To obtain an isocline, one simply has to put one of the equations of System (8) equal to zero. Note that when both equations are put to zero we have the equilibria.

Isoclines only give information about the vector field of a system. It does not show the directions orbit go into, though often it coincides. Isoclines can give hints about the behaviour of a system, but this information is very limited.

Figures 6 and 7 give some example of isoclines. Compare these pictures with Figures 3 and 4, respectively. Convince yourself that the isoclines give you an impression, but do not give you a detailed picture of the dynamics of the system.

3.3 Manifolds

Manifolds, in the practical sense (this is not the formal definition), are phase space boundaries that indicate the direction of orbits. Manifolds can easily be confused with isoclines. However, they provide more information about system dynamics, since they precisely show the attractors and separatrices in the system. The drawback is they are almost impossible to calculate. The only program currently able to do so for some one- and two-dimensional systems is DSTOOL.

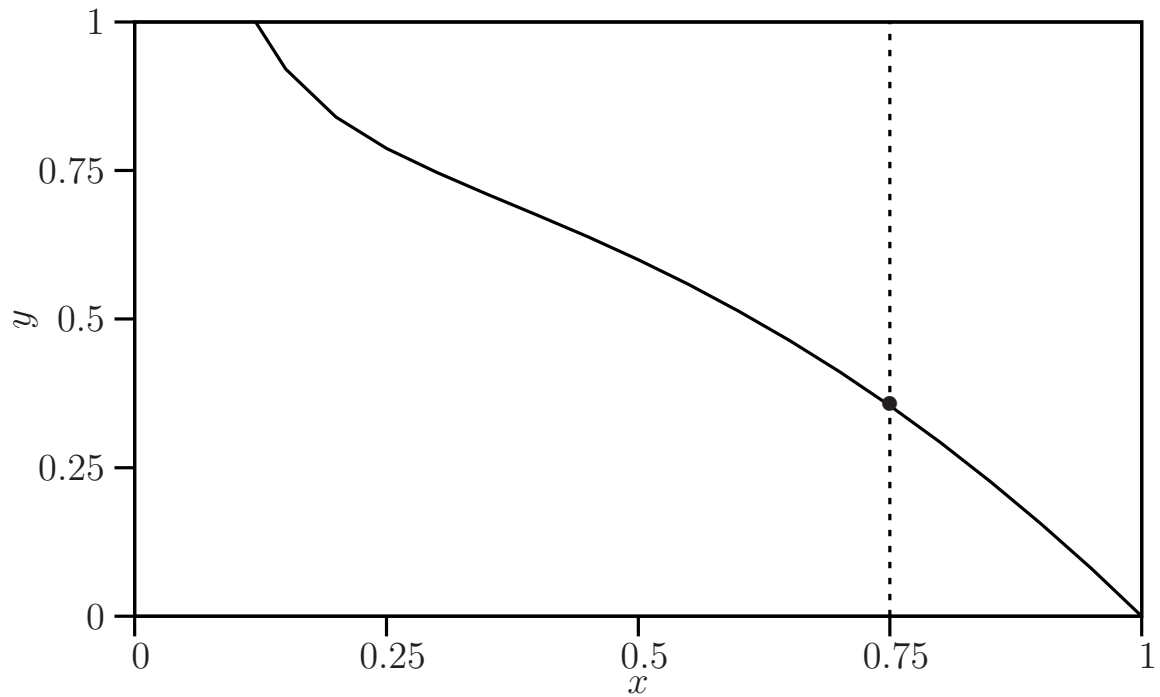


Figure 6: Isoclines for the node in Fig. 3.

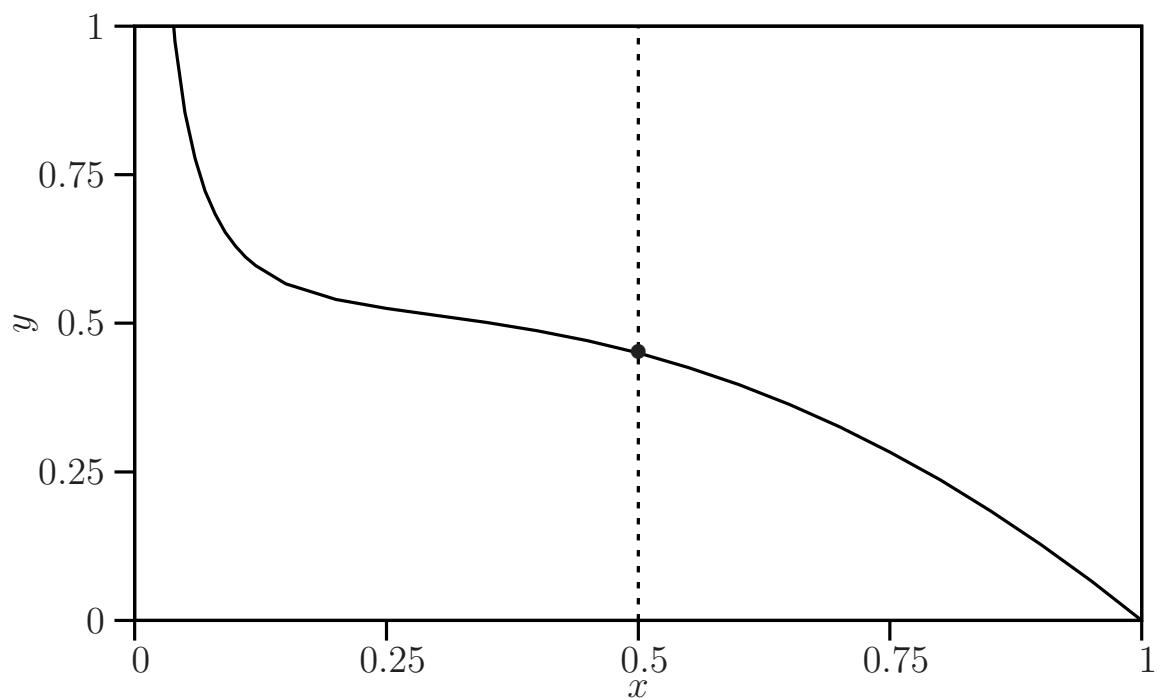


Figure 7: Isoclines for the focus in Fig. 4.

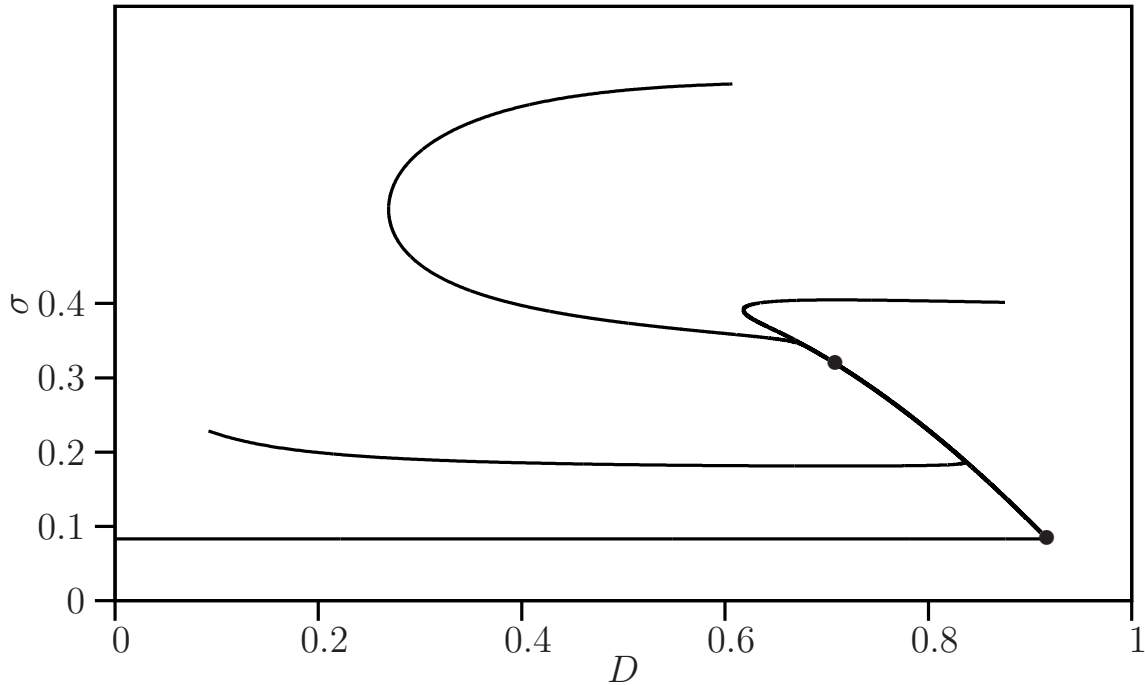


Figure 8: Temporary figure manifolds.

Around an equilibrium, the manifolds are the eigenvectors of this equilibrium, again in a practical sense. As such, manifolds that are associated with unstable eigenvectors automatically function as separatrices in two-dimensional models. For focus cases this is a little bit more complicated. Since with a spiral there are two complex eigenvectors the stable manifold of the focus equilibrium just spirals inwards to or outwards from the equilibrium point.

Figures 8 and 9 give an example of manifolds in a two-dimensional system. Let us compare these figures with Figure 4. The latter figure gives information only about the vector field, while the two pictures that include manifolds clearly give an idea of the system dynamics. Also, comparing Figure 8 with 9 reveals that all positive solutions go to or near to the equilibrium in Figure 8, while Figure 9 shows that there is a separatrix in the system, leading to dependence on initial conditions.

Manifolds of the same or different equilibria can be connected to each other. We then get unique point-to-point connecting orbits (homoclinic or heteroclinic orbits). We will discuss those in a later section.

4 Bifurcations in two-dimensional systems

In the section on one-dimensional systems we discussed two bifurcation points that can occur in such systems. These bifurcations can also occur in two- and higher-dimensional systems. We can often continue such bifurcation points in two dimensions, giving a bifur-

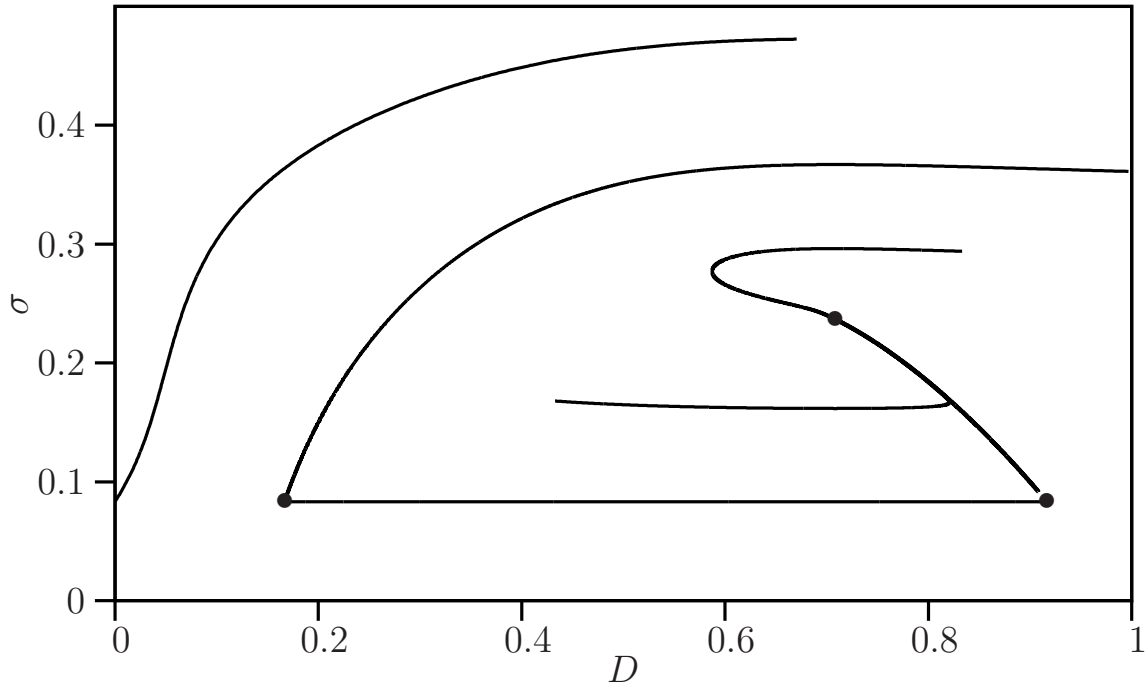


Figure 9: Temporary figure manifolds.

cation curve. Mostly we only depict these bifurcation curves in two-parameter dimensions then.

4.1 Tangent and transcritical bifurcation (2D)

For a tangent or transcritical bifurcation to occur in a two-dimensional system one of the eigenvalues has to be equal to zero. Tangent bifurcation curves are denoted with T , transcritical bifurcation curves with TC . In biological models the x -axis almost always has a transcritical curve.

Many of the models used at the Theoretical Biology Group at the Vrije Universiteit display series of transcritical bifurcations occurring on the x -axis at different values of α . Biologically we can interpret these as a series of invasions of different species. Figure 10 gives an example of this in a two-dimensional model. Imagine we increase K gradually. At $K = 0$ already there is an invasion of species X . Species Y , feeding on species X , can only invade when K is increased further to $K \approx 6$.

The tangent bifurcation of course is more dramatic. We will see an example of the tangent bifurcation in the three-dimensional system discussed in Section 5.

4.2 Hopf bifurcation

One new bifurcation that can occur in a two-dimensional system is the so-called Andronov-Hopf bifurcation, mostly just referred to as Hopf bifurcation. In order for a Hopf bifurcation

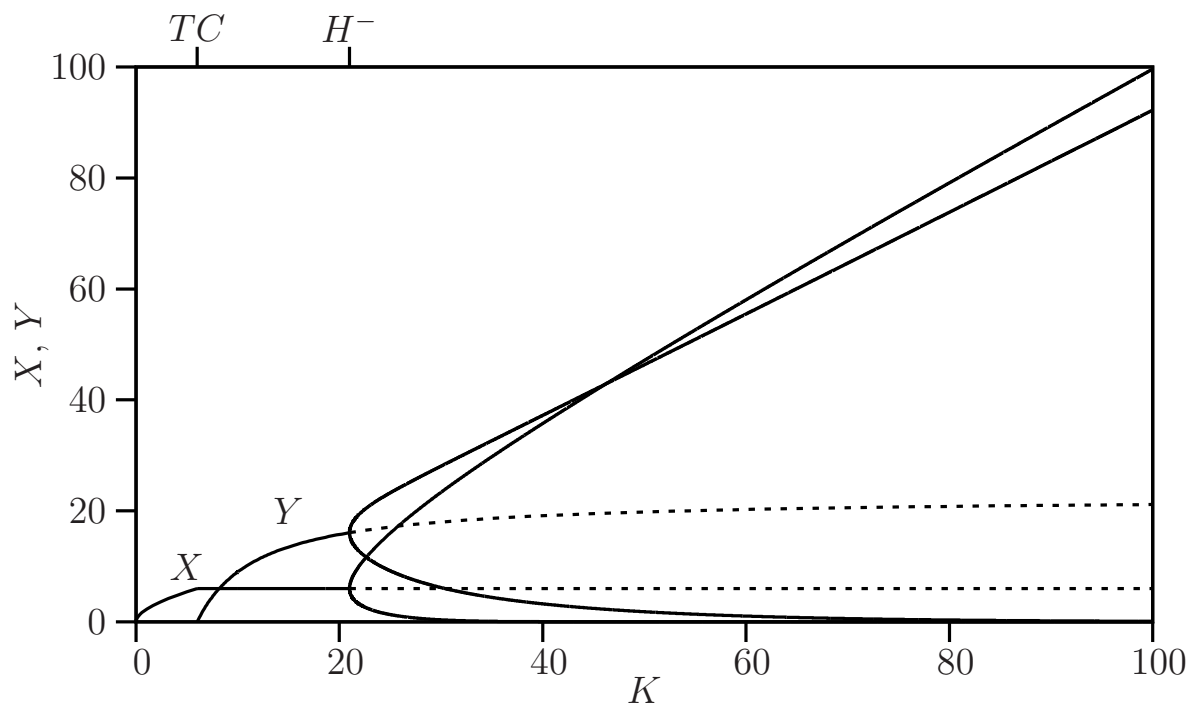


Figure 10: One-parameter bifurcation diagram of a system with species X and Y and with bifurcation parameter K . Parameters are $R = 0.5$, $A = 0.5$, $B = 9$, $C = 0.4$, $D = 0.08$. The first transcritical bifurcation occurs at the origin, with the invasion of X . Then, at $K \approx 6$, also Y invades. The latter situation is referred to as coexistence of X and Y . At $K \approx 20$ a Hopf bifurcation H^- occurs, and a stable limit cycle is born. The minimal and maximal values of X and Y are also depicted were the unstable equilibrium is shown as dashed curves.

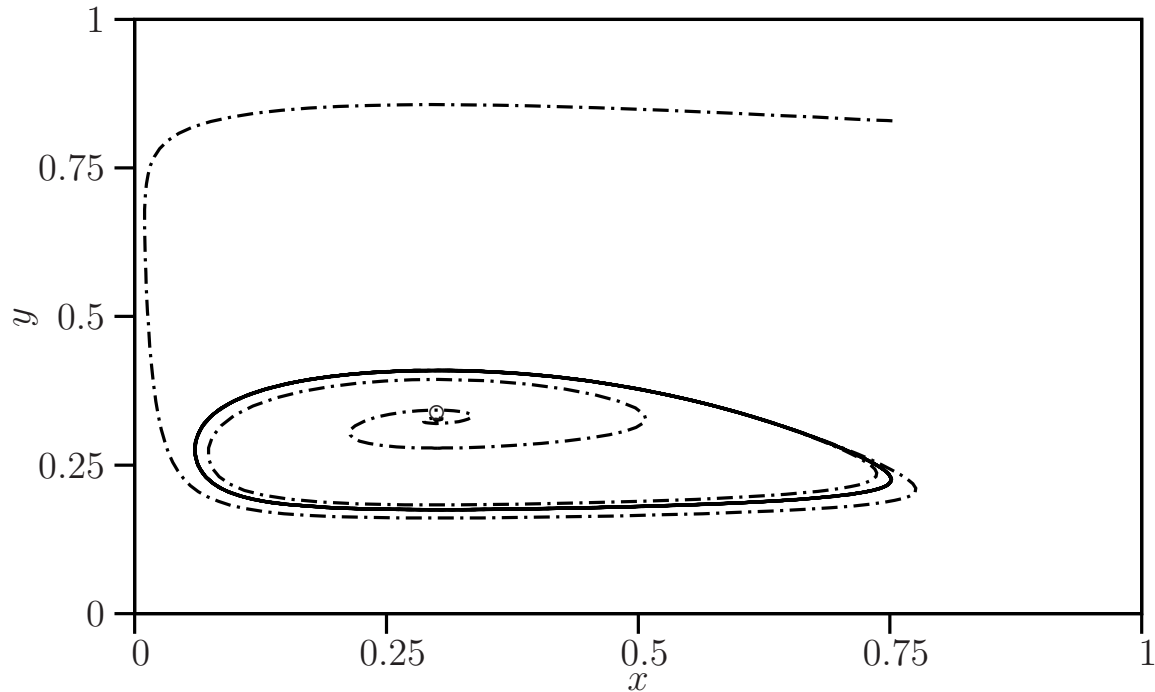


Figure 11: Limit cycle after the occurrence of a supercritical Hopf bifurcation. The empty dot indicates the unstable equilibrium. A Hopf bifurcation where a stable limit cycle is born is denoted as H^- , see also Figure 10. The dashed curves are orbits, shown to demonstrate the stability of the limit cycle.

to occur the eigenvalues must form a complex pair, so there must be a focus. Then, when the real parts of both eigenvalues are equal to zero, while they have a complementary imaginary part, a Hopf bifurcation occurs ($\Re(\lambda) = 0$, $\Im(\lambda) \neq 0$, $\Im(\lambda_1) = -\Im(\lambda_2)$). A Hopf bifurcation can also be defined as a point where $\det(\mathbf{J}) = 0$, $\text{tr}(\mathbf{J}) = 0$.

At the Hopf bifurcation point the involved equilibrium becomes unstable when it was stable (supercritical) or stable when it was unstable (subcritical). Also, a periodic solution, a limit cycle, is born that inherits the stability properties that the equilibrium had before the occurrence of the bifurcation. See Figure 11 for a phase plot where a limit cycle is depicted. Figure 10 then shows a one-parameter bifurcation diagram, where the equilibrium becomes unstable at $K \approx 20$. Depicted in the diagram are also the minimal and maximal values of the limit cycles, that increase for larger values of K . In the depicted example, the limit cycle has become the stable attractor of the system, while the equilibrium is unstable.

In the case when a stable point becomes unstable, while a stable limit cycle is born, we have a supercritical Hopf bifurcation. When an unstable limit cycle is born, while the equilibrium becomes stable, we have a subcritical Hopf bifurcation. One can calculate the so-called *Lyapunov exponent* to determine the type of Hopf bifurcation, but this requires a lot of calculating, and we will not discuss it here.

4.3 Paradox of enrichment

Limit cycles occurring in biological systems are often associated with an increased extinction probability, and as such the Hopf bifurcation can be called a *destabilising* occurrence in these models. The basis for this goes back to one much debated issue in the theoretical ecological literature: the ‘paradox of enrichment’ by Rosenzweig (1971).

In 1963 a paper was published by Rosenzweig and MacArthur that discussed a two-dimensional predator-prey model that displayed some interesting properties. In the model the prey x has logistic growth, while the predator y feeds on the prey following a Holling type II functional response (Holling, 1959)

$$\dot{x} = Rx\left(1 - \frac{x}{K}\right) - \frac{Axy}{B+x}, \quad (14a)$$

$$\dot{y} = C\frac{Axy}{B+x} - Dy, \quad (14b)$$

where R is intrinsic growth rate, K is carrying capacity, A and B are constants for attack rate on and handling time of prey, C is yield on eaten prey biomass and D is the death rate of the predator. The system is analysed in more detail in the Appendix A. The Jacobian of this model is written as

$$\mathbf{J} = \begin{pmatrix} R\left(1 - \frac{x}{K}\right) - \frac{Rx}{K} - \frac{Ay}{B+x} + \frac{Axy}{(B+x)^2} & -\frac{Ax}{B+x} \\ \frac{CAy}{B+x} - \frac{CAxy}{(B+x)^2} & \frac{CAy}{B+x} - D \end{pmatrix}. \quad (15)$$

Rosenzweig and MacArthur published isocline diagrams that showed that an increase in food availability for the prey ($K >$) did not lead to more prey biomass. For that, let us look at the expressions for the isoclines, obtained by putting Eqn. (14) equal to zero

$$x = \frac{DB}{CA - D}, \quad (16a)$$

$$y = -\frac{R(x - K)(B + x)}{KA}. \quad (16b)$$

The expression for the prey biomass does not depend on K . Instead the predator biomass would increase. For increased values of K a Hopf bifurcation would eventually occur, leading to larger and larger limit cycles. In the follow-up paper by Rosenzweig he argued this to be a paradoxical effect - an increase in food availability leads to the extinction of species (Figure 10 once again has a nice demonstration role)

Since then many an experiment and theoretical work has been done to either prove this result wrong or to confirm it. It is safe to say that, despite the simplicity of the model, hard evidence is lacking to deny or confirm the existence of this phenomenon. Recently things have even been complicated by authors that have found a Hopf bifurcation occurring in measured chemostat systems (Fussman et al., 2000).

4.4 Limit cycle bifurcations

We have already discussed in the section on Hopf bifurcations how limit cycles can be born. However, it has not yet been said that for limit cycles all the same principles apply as for equilibria. Imagine cutting through a limit cycle - one will see the same pictures again as for equilibria. Note that there is one extra feature: limit cycles go round and have one eigenvector (called multiplier μ , to discriminate between the eigenvalue λ of equilibria) that is either 1 or -1 . This multiplier is associated with the rotation of the cycle.

The stability properties that apply for equilibria also apply for limit cycles. Note however, that there is always one $|\mu| = 1$ for rotation. For shorter notation we do not write this down. A limit cycle with only multipliers $|\mu| < 1$ is stable, while a limit cycle with only multipliers $|\mu| > 1$ is unstable. A saddle cycle has multipliers $|\mu|$ both larger and smaller than 1. So, for example, if we have a two-dimensional system with a stable limit cycle for a given parameter set, this system then must have $\Re(\lambda_1) = \Re(\lambda_2)$, $\Im(\lambda_1) = -\Im(\lambda_2)$, $\Re(\lambda) \neq 0$, $\Im(\lambda) \neq 0$, $|\mu_1| = 1$ and $0 < |\mu_2| < 1$.

It will not surprise you perhaps that the bifurcations that can occur for equilibria can also occur for limit cycles. Limit cycles can undergo tangent bifurcations T_c that result in the birth of saddle cycles. The system then displays both a stable or unstable limit cycle and a saddle cycle. The other way around two cycles can collide and then disappear.

A transcritical bifurcation for cycles TC_c occurs when the cycle hits some invariant plane, mostly just one of the axes. Both the transcritical and tangent bifurcation in cycles will be demonstrated later on.

The Hopf bifurcation can also occur for a limit cycle, in which case it is called a Neimark-Sacker bifurcation. Just think of the intersection through the cycle and imagine a spiral towards the point. At the Neimark-Sacker bifurcation, a 'limit cycle' is born while the point becomes unstable. Zoom back from the intersection to the whole picture, and the limit cycle is unstable, while there is a stable torus around it. This torus is *invariant*, meaning orbits starting inside cannot go outside or vice versa. Personal remark: until now I've never encountered a Neimark-Sacker bifurcation in a biological model I've used.

The new type of bifurcation for limit cycles is the flip bifurcation. Note that until now the multipliers have been denoted as $|\mu|$ instead of μ . It is important to understand that the manifolds of a limit cycle can be perceived as 'ribbons' around the limit cycle. There are two possibilities how these manifolds can be folded around the limit cycle. For that, imagine we start at a point u_0 a small step away from the limit cycle and in the direction of $\mu \neq 1$, and we follow the limit cycle for one turn. We can either end up on the same side of the cycle (at $u_1 = \mu \cdot u_0$, then $\mu = 1$) or on the opposite side (in which case $\mu = -1$). A bifurcation where a switch occurs from $\mu = 1$ to $\mu = -1$ is a flip bifurcation.

The flip bifurcation is also referred to as period doubling. The reason for that is that the time it takes to go from point u_0 to the neighbourhood of u_0 again is doubled. We will revisit flip bifurcations in the section on chaos.

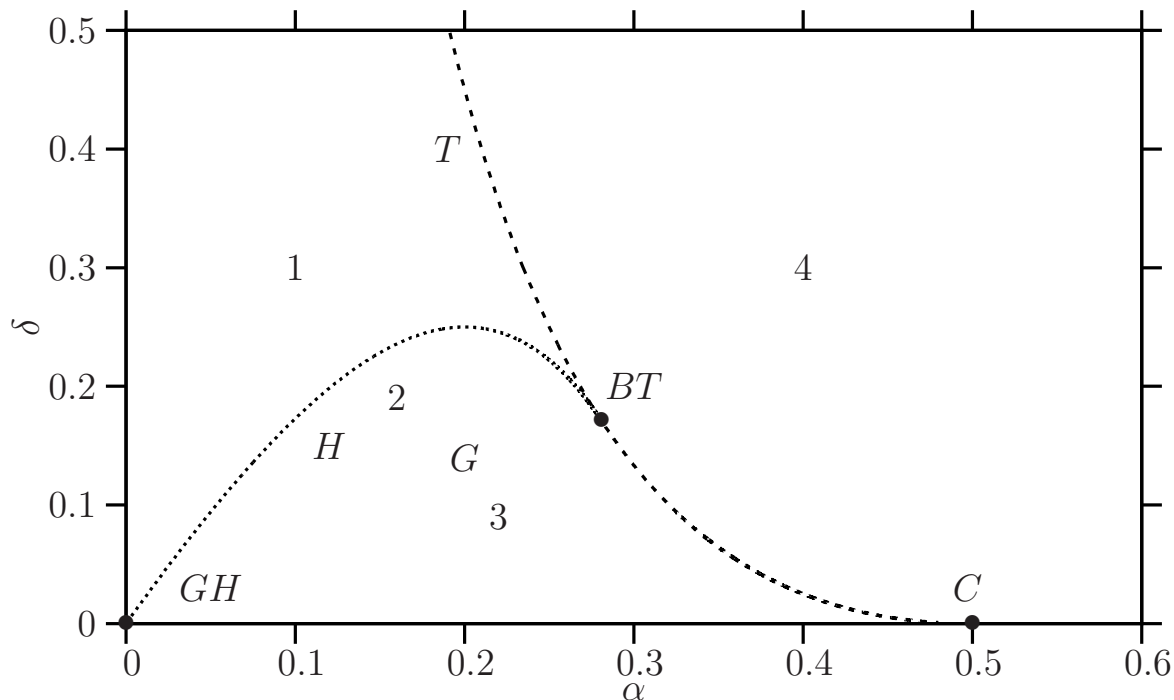


Figure 12: Bogdanov-Takens point in the two-dimensional Bazykin model (see text).

4.5 Co-dimension two points

It was mentioned earlier that we can follow bifurcation points in two-dimensional space and that we get bifurcation curves then. Now, imagine that such bifurcation curves can intersect and that these bifurcations interfere with one another. This happens at so-called co-dimension two bifurcation points.

We know from Section 2 what happens when one eigenvalue becomes zero. What happens when two eigenvalues become zero simultaneously? It is possible that in a two-dimensional system there occur a tangent and a Hopf bifurcation curve and that these curves intersect. Remember that for a tangent bifurcation one eigenvalue must be zero, and that for a Hopf bifurcation the real part of two eigenvalues must be zero. Hence, when they cross both eigenvalues will be zero (also the imaginary part). The special point where this happens is called a Bogdanov-Takens (or double-zero) point (often denoted BT , except for scholars from the University of Groningen, where professor Takens still works, and this point is called Takens-Bogdanov). The BT point is such a co-dimension two point (codim 2).

A classical Bogdanov-Takens bifurcation occurs in the model by Bazykin (1998)

$$\begin{cases} \dot{x} &= x - \frac{xy}{1+\alpha x}, \\ \dot{y} &= \frac{xy}{1+\alpha x} - 2y - \delta y^2, \end{cases} \quad (17)$$

where the predator y has a non-linear death term (usually interpreted as mortality through fighting or cannibalism). Figure 12 displays the BT point as an intersection of the Hopf

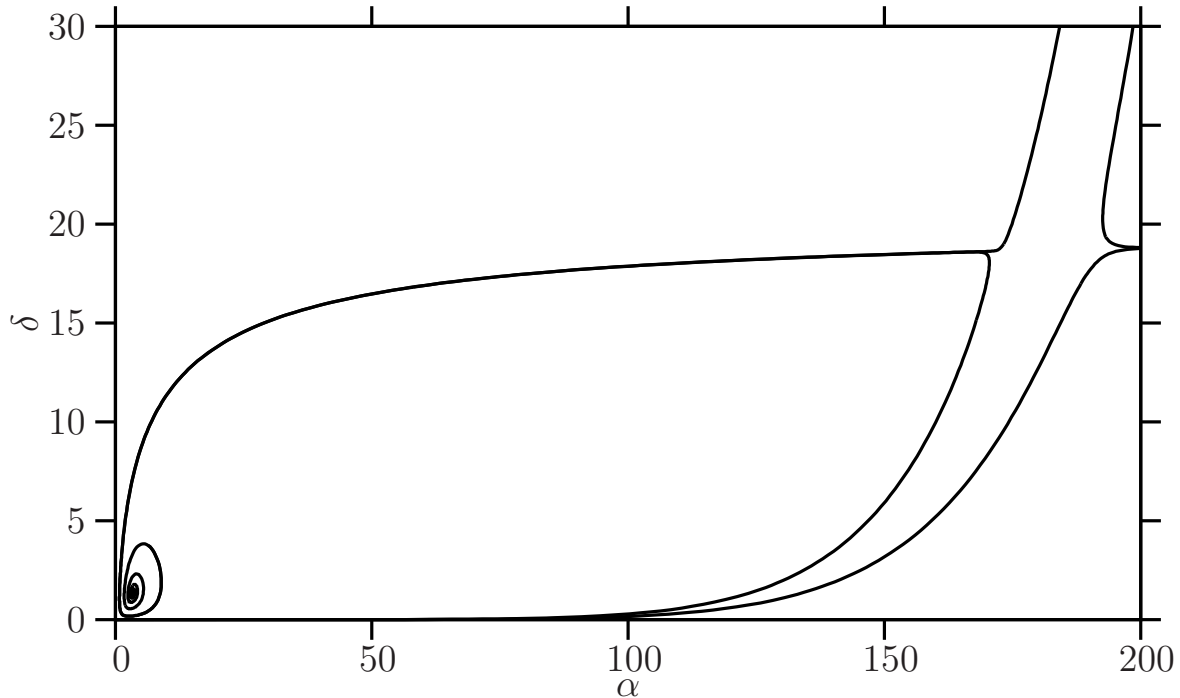


Figure 13: Characteristic phase portrait of region 1 in Figure 12. The equilibrium nearest to the origin is attracting.

and the tangent bifurcation curves. Note that there are four regions where dynamics are qualitatively different, and that the region, denoted by 3, has a boundary that is somewhere around G . We will discuss this in the next section.

The same Figure also displays two more codim 2 points: the cusp C and the generalised Hopf GH bifurcation points. At a cusp, two tangent bifurcation points collide and disappear (as such it is a ‘tangent bifurcation of tangent bifurcations’). At a generalised Hopf (also called Bautin point, denoted as B) an equilibrium with a stable limit cycle (H^-) turns into an equilibrium with an unstable limit cycle (H^+).

4.6 Global bifurcations

In the previous section we have looked at the local bifurcation curves involved in a BT bifurcation point. The occurrence of a BT point also automatically means the occurrence of a homoclinic bifurcation. In this section we will discuss such a homoclinic connection and the implications on system dynamics (or, why is it important to know?!).

As mentioned earlier, it is possible that the manifolds of an equilibrium or pair of equilibria become connected for a specific set of parameter values. We then have either a homo- or heteroclinic connection to a point. Now, it was also mentioned implicitly that in a system with a Bogdanov-Takens point the transition of dynamics from region 2 to region 3 in Figure 12 is not indicated by the occurrence of a local bifurcation. How does it work

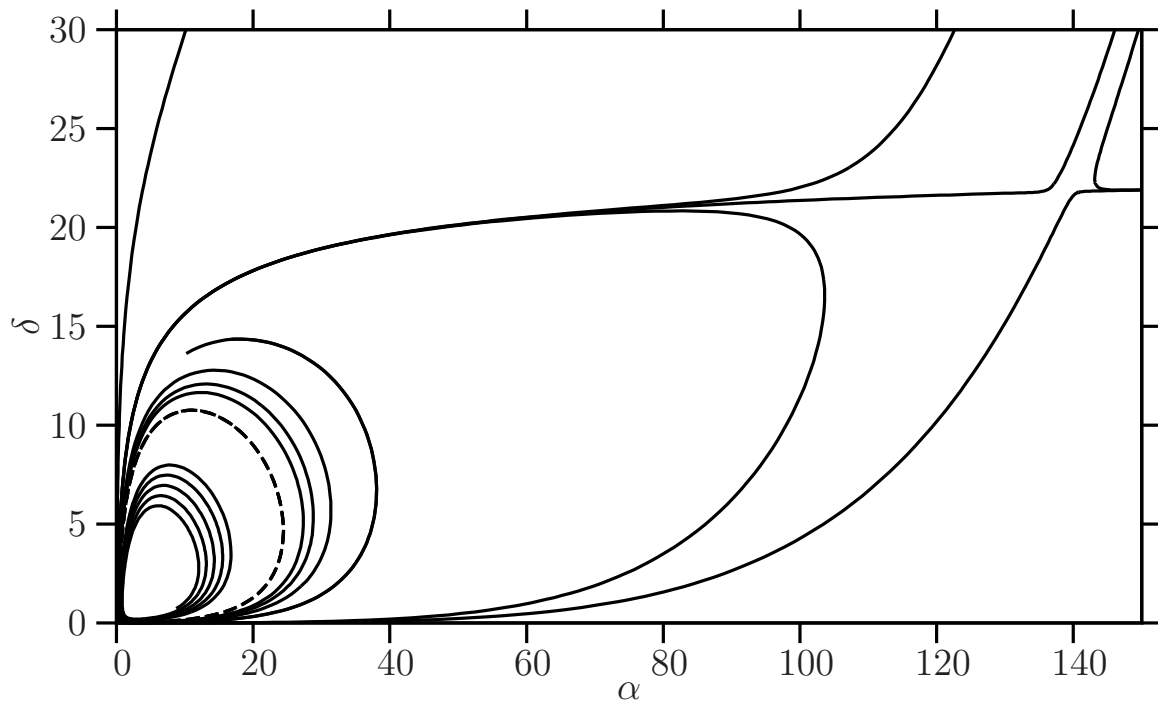


Figure 14: Characteristic phase portrait of region 2 in Figure 12, with dotted the stable limit cycle.

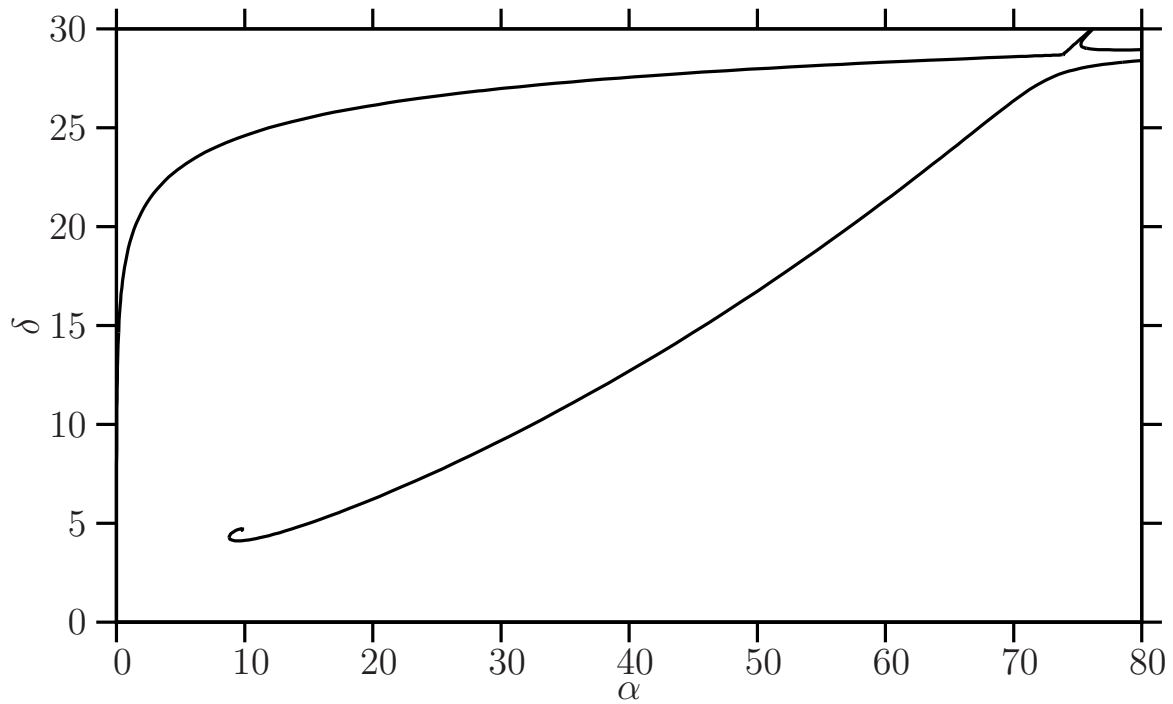


Figure 15: Characteristic phase portrait of region 3 in Figure 12. There are two unstable equilibria.

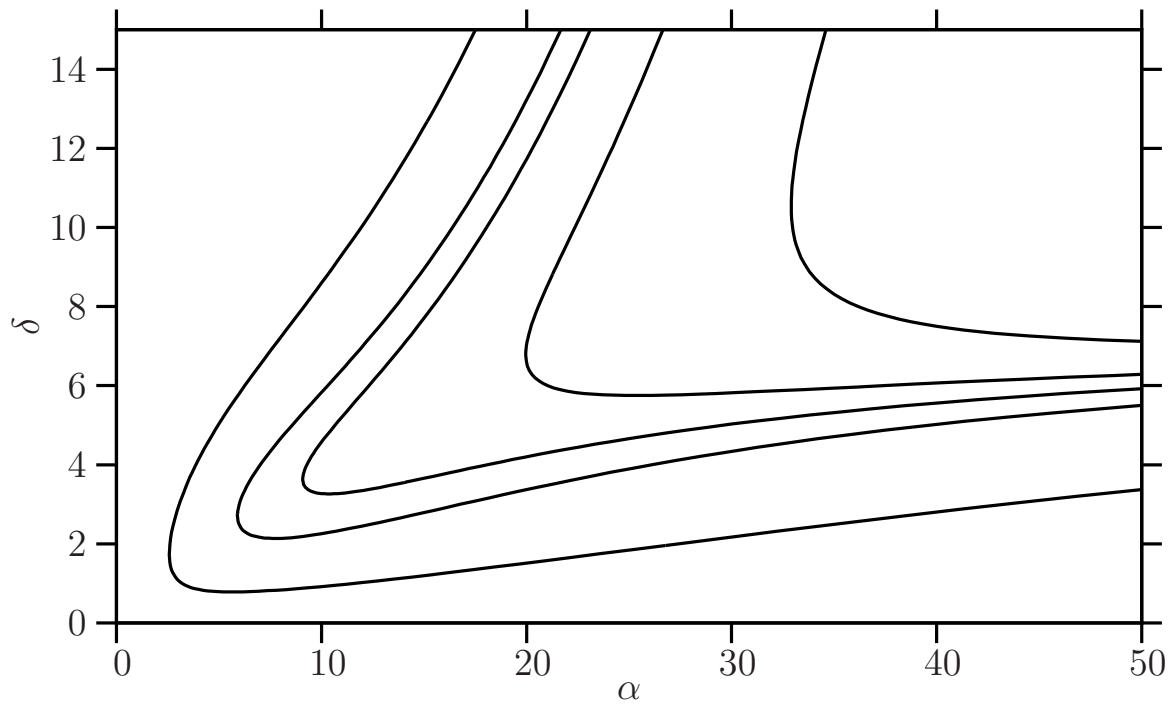


Figure 16: Characteristic phase portrait of region 4 in Figure 12. Both equilibria have disappeared through a fold bifurcation.

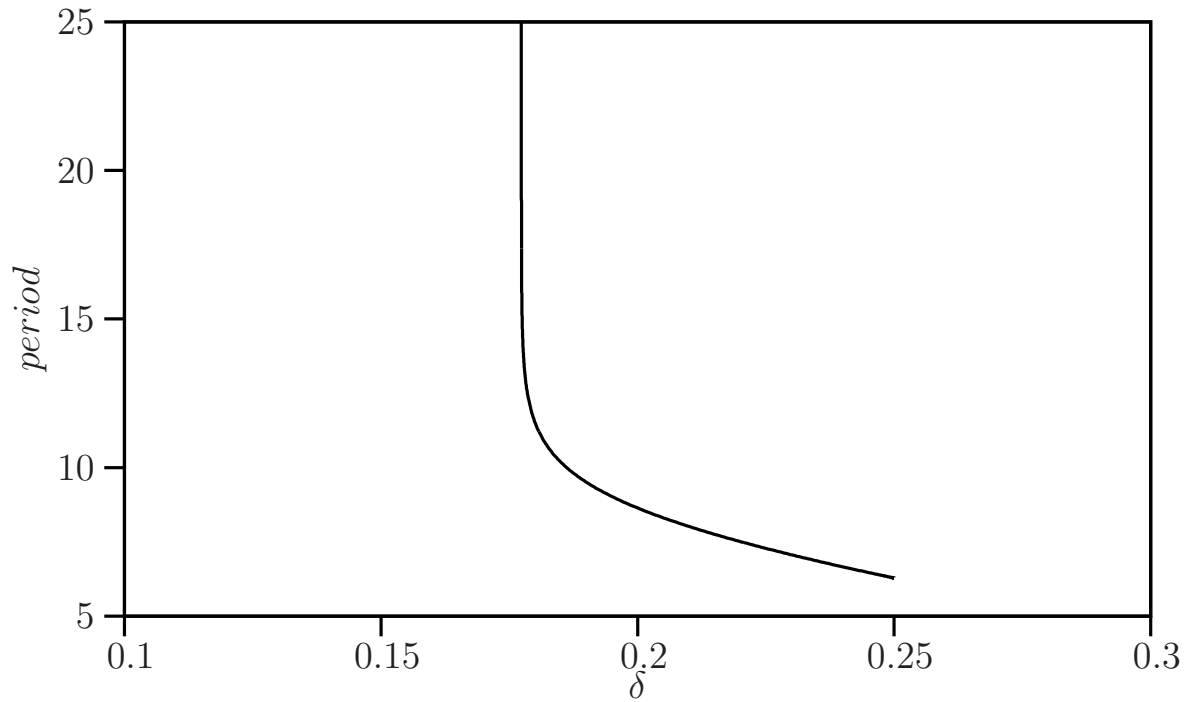


Figure 17: The existence of a homoclinic point-to-point connecting orbit in the Bazykin model for $\alpha = 0.2, \delta \approx 0.1773572$.

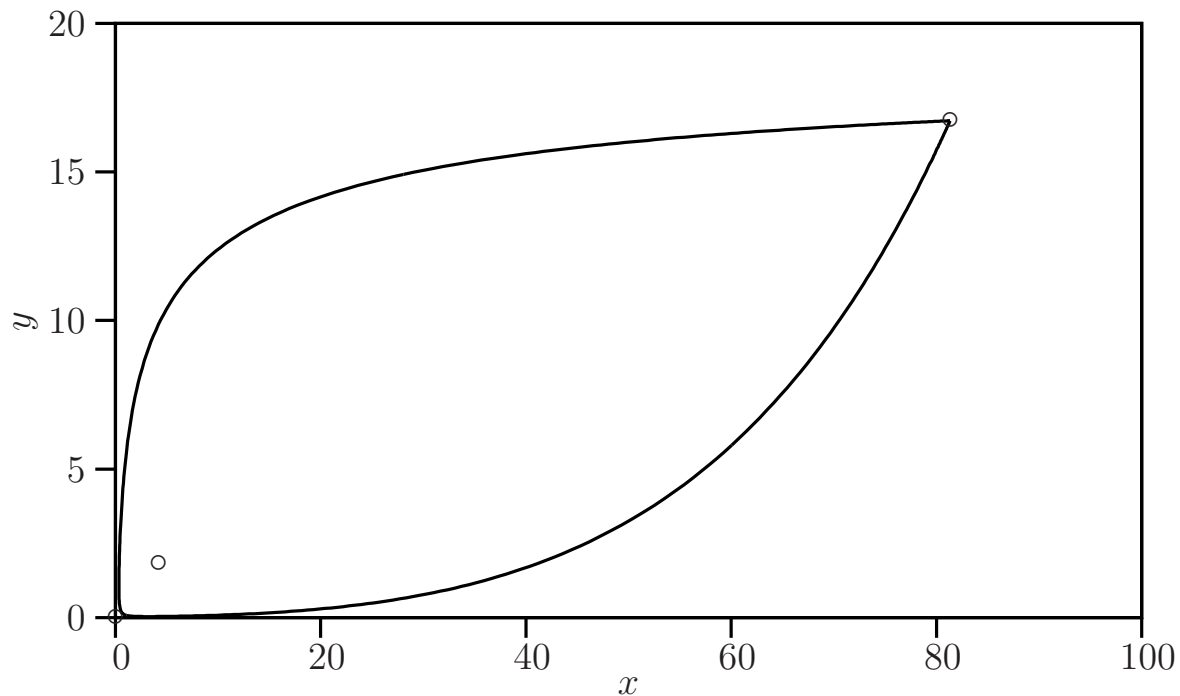


Figure 18: This Figure clearly shows that the limit cycle revolving the unstable equilibrium $x \approx 4.1719405$, $y \approx 1.8066354$ collides with the saddle equilibrium point $x \approx 81.3321337$, $y \approx 16.725386$ at $\alpha = 0.2$, $\delta \approx 0.1773572$.

then?

Let us expand on the example of the Bazykin model. Imagine starting in Figure 12 on the Hopf bifurcation point for $\alpha = 0.2$ and keep α fixed. If we move down through this picture and track the period of the limit cycle we get Figure 17. What happens is displayed in Figure 18. There we see the limit cycle has grown such that it approaches the saddle equilibrium $\tilde{x} \approx 81.3321337$, $\tilde{y} \approx 16.725386$ for the parameter set $\alpha = 0.2$, $\delta \approx 0.1773572$.

Now, let us take a closer look at Figure 19, similar to Figure 12. There we continue the homoclinic connecting orbit, depicted as curve G^\neq . As such, the boundaries of region 3 in Figure 12 become clear. The biological interpretation of this region is nothing less than extinction, since the limit cycle is destroyed and thus the only attractor in the system has disappeared.

The above example nicely demonstrates why a local bifurcation analysis of the model still only gives a limited understanding of the system. If we did not know about this global bifurcation, we might think there is coexistence in the whole region of 2 and 3, or we might get puzzled by the strange transition in dynamics between regions 2/3 and region 4.

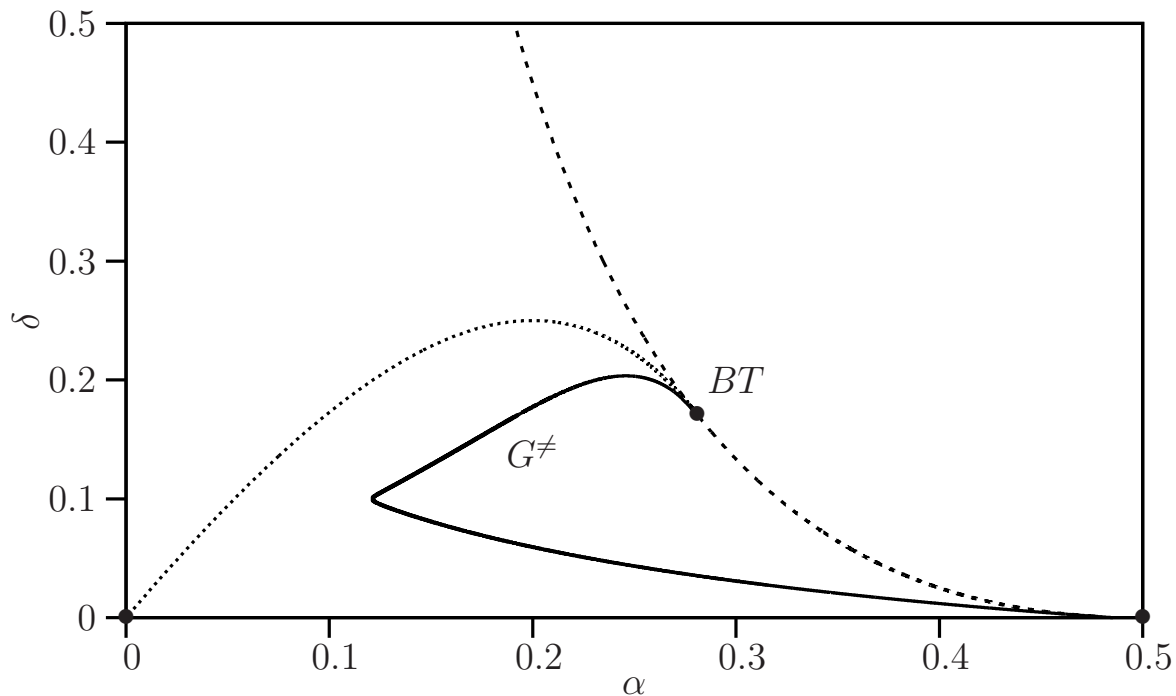


Figure 19: Continuation of the homoclinic point-to-point connecting orbit in the Bazykin model in α , δ .

4.7 Normal forms

It is not my intention to scare any reader with large mathematical formulas, which is the reason why in this subsection the so-called *normal form* of a bifurcation point is only mentioned. A normal form of a point in space is actually the linearisation of that point, much like the Jacobian matrix but with more terms (second-order derivatives, and more).

For regular points in phase space it is not interesting to study the normal form, but normal forms can give important information about bifurcation points, especially for points of higher co-dimension, like the Bogdanov-Takens bifurcation. The important thing here is that the higher the co-dimension of a point, the more linearisation terms are required. So for a regular tangent bifurcation only the first and second-order derivatives are important, while for some bifurcation points the sixth-order term is needed to correctly understand its dynamics.

The ‘unfolding’ of the *BT* point in the Bazykin model in the previous sections can be better understood when a normal form analysis is done of this point. However, the discussion of this analysis is far beyond the scope of this manuscript. The reader is referred to Kuznetsov (2004, p. 316 and further, p. 327, and p. 376).

5 Three and higher-dimensional systems

In three-dimensional systems, all bifurcations we have discussed already can occur, and a lot more. More interesting however, is the occurrence of chaos. In this section, we will discuss the three-dimensional version of the Rosenzweig-MacArthur model (in short RM model) to demonstrate the occurrence of local bifurcations, chaos and global connecting orbits. The local bifurcations and the chaos patterns in the RM model are well described by many authors (Hogeweg and Hesper, 1978; Gilpin, 1979; Hastings and Powell, 1991; Kuznetsov et al., 1992; Kuznetsov et al., 1995; McCann and Yodzis, 1995; Kuznetsov and Rinaldi, 1996; De Feo and Rinaldi, 1998; Deng, 2001; Kuznetsov et al., 2001; Deng and Hines, 2002; Deng and Hines, 2003; Deng, 2004). Most of the information on global bifurcations in the RM model is covered in the work by Martin Boer (Boer et al., 1999; Boer, 2000; Boer et al., 2001), with the co-notation this work is not finished yet and more progress is expected in the near future.

5.1 The Rosenzweig-MacArthur model

The three-dimensional Rosenzweig-MacArthur model is written as

$$\dot{X} = RX\left(1 - \frac{X}{K}\right) - \frac{A_1XY}{B_1 + X}, \quad (18a)$$

$$\dot{Y} = C_1 \frac{A_1XY}{B_1 + X} - D_1Y - \frac{A_2YZ}{B_2 + Y}, \quad (18b)$$

$$\dot{Z} = C_2 \frac{A_2YZ}{B_2 + Y} - D_2Z, \quad (18c)$$

where K carrying capacity, R intrinsic growth rate, A_i/B_i parameters associated with handling and attack rates, C_i yield and D_i death rates. Rescaling makes the system dimensionless

$$\dot{x} = x(1 - x) - f_1, \quad (19a)$$

$$\dot{y} = f_1 - d_1y - f_2, \quad (19b)$$

$$\dot{z} = f_2 - d_2z, \quad (19c)$$

where

$$f_1 = \frac{a_1xy}{1 + b_1x}, \quad (20a)$$

$$f_2 = \frac{a_2yz}{1 + b_2y}. \quad (20b)$$

Mostly the two death rates d_i are used as default bifurcation parameters. The other parameters then are $a_1 = 5$, $a_2 = 0.1$, $b_1 = 3$, and $b_2 = 2$.

The equilibria of System 19a are

$$E_1 = (0, 0, 0) , \quad (21a)$$

$$E_2 = (1, 0, 0) , \quad (21b)$$

$$E_3 = \left(\frac{d_1}{a_1 - b_1 d_1} , \frac{a_1 - d_1(b_1 + 1)}{(a_1 - b_1 d_1)^2} , 0 \right) , \quad (21c)$$

$$E_4 = (\bar{x}, \bar{y}, \bar{z}) , \quad (21d)$$

where

$$\bar{x} = \frac{b_1 - 1 + \sqrt{(b_1 + 1)^2 - \frac{4a_1 b_1 d_2}{a_2 - b_2 d_2}}}{2b_1} , \quad (22a)$$

$$\bar{y} = \frac{d_2}{a_2 - b_2 d_2} , \quad (22b)$$

$$\bar{z} = \frac{f_1(\bar{x}) - d_1}{a_2 - b_2 d_2} . \quad (22c)$$

for $0.16 \leq d_1 \leq 0.32$, $0.0075 \leq d_2 \leq 0.015$.

5.2 Local bifurcation picture

The stability of the equilibria, and the local bifurcation analysis of the RM model, are described in detail by Kuznetsov and Rinaldi (1996). We will shortly discuss some of the basic results.

In Figure 21 most of the local bifurcations are displayed. Also compare Figure 20, where x_3 (or the maximal and minimal value for limit cycles) are plotted against d_1 , for a better understanding of the location of the bifurcations in phase space. Starting at point M , a bifurcation point of higher co-dimension, we see a transcritical bifurcation curve TC_e . This is a transcritical bifurcation of the equilibrium. Along this curve the non-trivial equilibrium invades the positive quadrant. There is also a Hopf bifurcation curve H_p , where the p stands for planar. This is a Hopf bifurcation for a lower dimensional system, with $x_3 = 0$. The tangent bifurcation curve T_e indicates where two equilibria collide and disappear. Figure 20 clearly shows that for $d_2 \gtrsim 0.017391$ there cannot be coexistence of this system. Finally, there is a Hopf bifurcation for the non-trivial equilibrium (again see Figure 20 for more detail).

Note that the Hopf bifurcation curve starting in M is a H^+ , which means the equilibrium becomes stable. From the bifurcation point an unstable limit cycle can be continued. Interesting enough the limit cycle also undergoes bifurcations. First the cycle goes through a tangent bifurcation T_c . Then, the limit cycle hits the invariant plane $x_3 = 0$, where it exchanges stability properties. This transcritical bifurcation of the limit cycle TC_c can also be traced back to point M . Note, that this gives an idea of why this is called unfolding.

Back to the bifurcations of the equilibria in Figure 20, we find continuation of the stable equilibrium results in another Hopf bifurcation being found, this time a H^- . At this point,

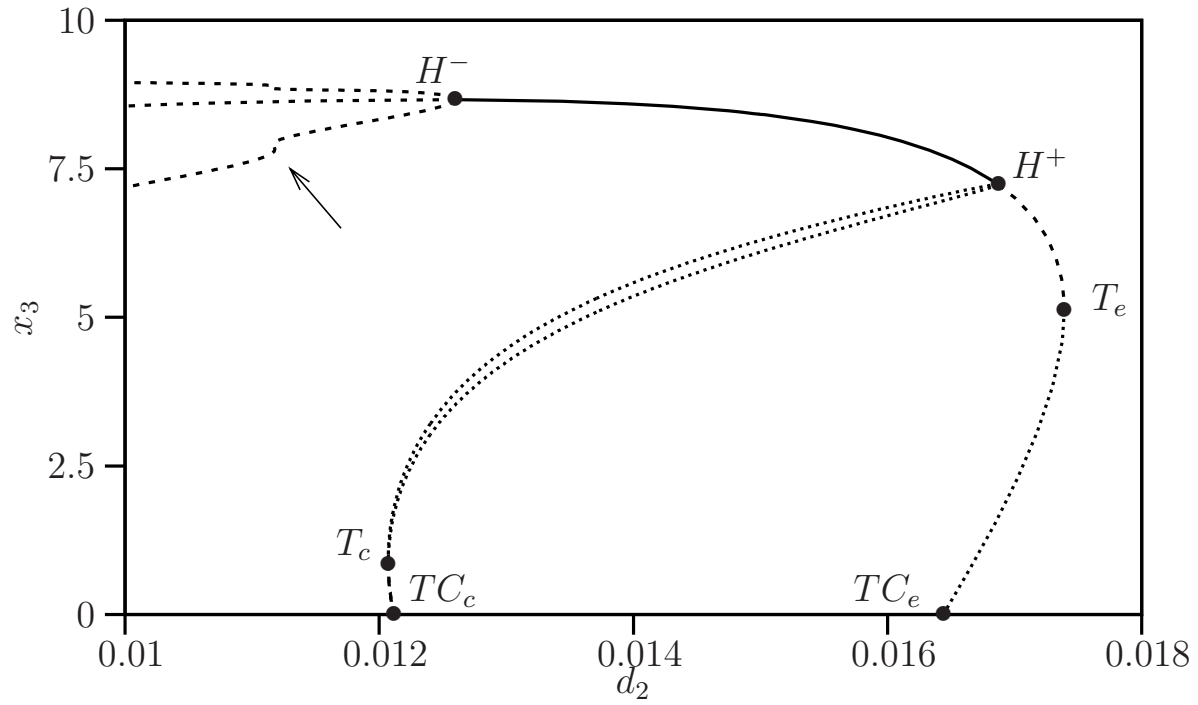


Figure 20: One-parameter local bifurcation diagram of the RM model, with d_2 as free parameter ($d_1 = 0.015$). See text for all details.

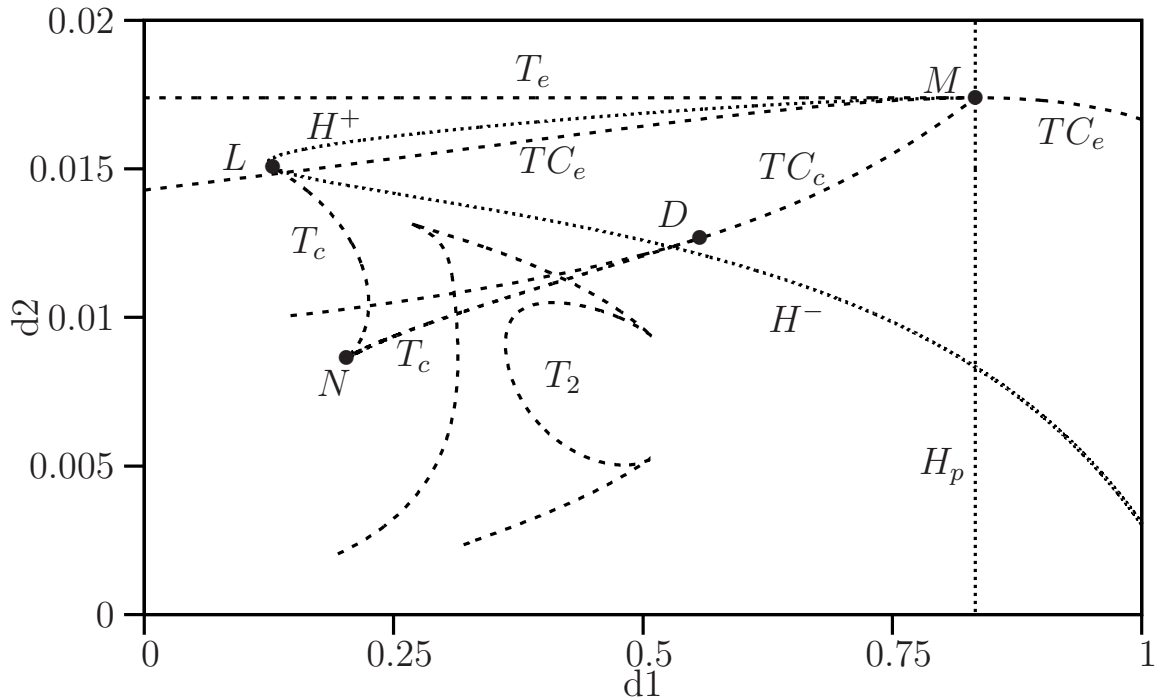


Figure 21: Two-parameter local bifurcation diagram of the RM model. The free parameters are d_1 and d_2 . See text for explanation.

the equilibrium becomes unstable and a stable limit cycle is born. This is then the system attractor.

We are not done yet. In Figure 21 we see that the two Hopf bifurcation curves can be continued to the same point L , a generalised Hopf bifurcation. Near L , on the curve H^- , also a tangent bifurcation T_c of the cycle takes place. The same happens at point D on the TC_c . Both T_c curves can be continued until they eliminate each other in the cusp point N (referred to as A in Kuznetsov and Rinaldi, 1996). We will revisit these tangent curves later on.

5.3 Chaos: local and global bifurcations

The occurrence of chaos in model systems is well known, but what is it exactly? For that, let us look at Figure 20 again, at the stable limit cycle born in H^- . The arrow there indicates where period doubling of the limit cycle starts. The cycles born through this period doubling have not been continued, but this period doubling is an ongoing process. In the section on limit cycle bifurcations we have discussed the flip bifurcation; remember that at the flip bifurcation the period of the cycle doubled.

Now, with continuation in the direction of smaller d_1 , a whole serie of flip bifurcations is undergone, until there is an unlimited number of limit cycles (none of them stable, however). There, if we start at a point in the three-dimensional space bounded by the inner- and outermost limit cycles we will never come back exactly at that point again. Remember, we have undergone an unlimited number of flip bifurcations, and thus have period infinity! When this occurs we have chaos, and the path of undergone flip bifurcations is a ‘route to chaos’.

There are some interesting questions now. Firstly, since chaos means there is no stability, does this imply biological extinction? The answer is no, for several reasons. First of all, the region of chaos for a given parameter set does not need to include the whole phase space. It is feasible there is another attractor somewhere else. Secondly, the chaotic region itself is bounded, and starting in the chaotic region means that the biomasses will continue to vary forever. However, they will not be attracted to zero. As such, one can interpret this as biological coexistence, be it of an unstable type.

A second question is: how is the chaotic region bounded in parameter space? For that, we have to recall what has been discussed on global bifurcations. The work by Martin Boer shows that the chaotic region is ‘cut off’ by a cycle-to-cycle connection bifurcation. The results are too specific to discuss in detail, but the existence has been shown of a connecting orbit starting on the unstable manifold of a cycle and returning to the cycle via the stable manifold. This homoclinic bifurcation bounds the region of chaos in the RM model, and probably similar bifurcations occur in other models as well. Currently it is still very hard to find these bifurcations, but progress has been made (see for instance Dieci and Rebaza, 2004, and my own work with Bob Kooi and Yuri Kuznetsov).

The tangent bifurcations T_c mentioned in the previous section also play an interesting role in this tale. Apart from a homoclinic cycle-to-cycle connection there is also a heteroclinic point-to-cycle connection (actually, it is quite likely there exists an infinite number

of homo- and heteroclinic connections). This heteroclinic connection is destroyed with the tangent bifurcations.

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A Using the Jacobian matrix

Let us revisit the Jacobian matrix of the Rosenzweig-MacArthur model (Rosenzweig and MacArthur, 1963) with parameters $R = 0.5$, $A = 0.5$, $B = 9$, $C = 0.4$, $D = 0.08$

$$\mathbf{J} = \begin{pmatrix} 0.5 - \frac{x}{K} - \frac{0.5y}{9+x} + \frac{0.5xy}{(9+x)^2} & -\frac{0.5x}{9+x} \\ \frac{0.2y}{9+x} - \frac{0.2xy}{(9+x)^2} & \frac{0.2x}{9+x} - 0.08 \end{pmatrix}. \quad (23)$$

If we take $K = 3$, and substitute the biologically relevant equilibrium ($x = 3, y = 0$), we get

$$\mathbf{J} = \begin{pmatrix} -0.5 & -0.125 \\ 0 & -0.03 \end{pmatrix}. \quad (24)$$

If we take $K = 10$, and substitute the biologically non-trivial positive equilibrium ($x = 6, y = 6$), we get

$$\mathbf{J} = \begin{pmatrix} -0.22 & -0.2 \\ 0.048 & 0 \end{pmatrix}. \quad (25)$$

Finally, we take $K = 25$, and substitute the non-trivial equilibrium ($x = 6, y = 11.4$) again, we get

$$\mathbf{J} = \begin{pmatrix} 0.032 & -0.2 \\ 0.0912 & 0 \end{pmatrix}. \quad (26)$$

Let us now evaluate the determinant and the trace of these three Jacobian matrices. In the case of $K = 3$ we have $\det(\mathbf{J}) = 0.015$, $\text{tr}(\mathbf{J}) = -0.53$. Looking at Fig 5 we see it is a stable node. In the case of $K = 10$ we have $\det(\mathbf{J}) = 0.0096$, $\text{tr}(\mathbf{J}) = -0.22$. Looking in the diagram reveals that we are in the neighbourhood of switching from a stable node to a stable spiral. From the point of view of bifurcation analysis this difference bears no relevance however. We can safely conclude we have a stable equilibrium.

In the case of $K = 25$ we have $\det(\mathbf{J}) = 0.01824$, $\text{tr}(\mathbf{J}) = 0.032$. Because of the switch in the trace from negative to positive we now have an unstable spiral. Somewhere in the range $10 < K < 25$ the Hopf bifurcation has occurs. Solving the trace equal to zero would give the correct K .