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The competitive Lotka-Volterra system

Verfasst von:

Karoline Schindler

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Betreuer:	Univ.Prof.Dr. Josef Hofbauer

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Contents

Abstract

We want to give an overview on the global dynamics of the competitive Lotka-Volterra system. In the first chapter we will give a short introduction to dynamical systems. In chapter two we will use the theory of chapter one to investigate the competitive Lotka-Volterra system. We are especially interrested in its long-term behavior and its stability. Furthermore we will study the carrying simplex Σ of the system.
For the two-dimensional case the long-term behavior is well understood. For the three-dimensional case the global dynamics are more complex, as periodic orbits can occur. For the three-dimensional competitive Lotka-Volterra systems we have 33 stable nullcline classes [10]. We will rule out periodic orbits in the stable nullcline classes 1-25 [10], 32 and 33 [8]. For the stable nullcline classes 26-31, we will give a criteria to predict the occurence of Hopf-bifurcations, and hence periodic orbits [10]. However it is still not clear how many limit cycles may appear.
As a last point we will try do generalize some result of the two- and three-dimensional system, for a system with arbitrary dimension n.

Wir wollen eine Überblick über das globale Verhalten von Lotka-Volterra Systemes mit Konkurrenz geben. Im ersten Kapitel werden wir eine kurze Einführung in Dynamische Systeme geben. In zweiten Kapitel werden wir die Theorie aus Kapitel eins nutzen, um das Lotka-Volterra System mit Konkurrenz zu untersuchen. Wir interessieren uns insbesondere für das Langzeit-Verhalten und die Stabilität des Systems. Außerdem werden wir die Carrying Simplex Σ des Systems analysieren.
Für den zwei-dimensionalen Fall ist das Langzeit-Verhalten leicht verständlich. Für den drei-dimensionalen Fall ist das globale Verhalten komplexer, da periodische Orbits auftreten können. Für das drei-dimensionale Lotka-Volterra System mit Konkurrenz gibt es 33 stabile Nullklinen-Klassen [10]. Wir können in den Klassen 1-25 [10], 32 und 33 [8] periodische Orbits ausschließen. Für die stabilen Nullklinen-Klassen 36-31, werden wir ein Kriterium angeben, um das Auftreten von Hopf-Bifurkationen und somit periodischer Orbits vorherzusagt [10]. Es bleibt jedoch noch immer unklar, wie viele Grenzzyklen auftreten können.
Zu guter Letzt werden wir noch versuchen einige Resultate des zwei- und drei-dimensionalen Systems für Systeme mit beliebiger Dimension n zu verallgemeinern.

Introduction

We will first introduce some basic results about dynamical systems, following 'An Introduction to Dynamical Systems, Continuous and Discrete' by R. C. Robinson [3] and 'The Theory of Evolution and Dynamical Systems' by J. Hofbauer and K. Sigmund [2].

1 The flow

In general a differential equation in $\mathbb{R}^n$ is given by

$$\dot{x} = F(x),$$

where x is a point in $\mathbb{R}^n$ and $F(x)$ is a vector field in $\mathbb{R}^n$. For every initial condition, x_0, there exists a unique solution to the differential equation (1).

Theorem 1 (Existence and uniqueness of solutions)**.** *[3] Consider a differential equation*

$$\dot{x} = F(x).$$

Assume that both $F(x)$ and $\frac{\partial F_i}{\partial x_j}(x)$ are continuous for x in some open set U in $\mathbb{R}^n$, and that x_0 is a point in U.

(a) Then there exists a solution $x(t)$ defined for some time interval $-\tau < t < \tau$ such that $x(0) = x_0$. Moreover, the solution is unique in the sense, that if $x(t)$ and $y(t)$ are two such solutions with $x(0) = y(0) = x_0$, then they must be equal on the largest interval of time about $t = 0$ where both solutions are defined. Let $\phi(t; x_0)$ be this unique solution with $\phi(0; x_0) = x_0$.

(b) The solution $\phi(t; x_0)$ depends continuously on the initial condition x_0. Moreover, let $T > 0$ be a time for which $\phi(t; x_0)$ is defined for $0 \leq t \leq T$. Let $\varepsilon > 0$ be any bound on the distance between solutions. Then, there exists a $\delta > 0$ which measures the distance between allowable initial conditions, such that if $\|y_0 - x_0\| < \delta$, then $\phi(t; y_0)$ is defined for $0 \leq t \leq T$ and $\|\phi(t; y_0) - \phi(t; x_0)\| < \varepsilon$ for $0 \leq t \leq T$.

(c) In fact, the solution $\phi(t; x_0)$ depends differentiably on the initial condition x_0.

Definition 1. *[3] The function $\phi(t; x_0)$, which gives the solution as a function of the time t and initial condition x_0, is called the* flow of the differential equation. *For each fixed point x_0, the function $\phi(t; x_0)$ is a parameterized curve in the higher dimensional space $\mathbb{R}^n$. The set of points on this curve is called the* orbit *or* trajectory with initial condition x_0.

Three typ of solutions $x(t)$ can occur [2]:

(a) If $x(t) \equiv x$ for all $t \in \mathbb{R}$, i.e. if $x(t)$ is a constant, then x is called an *equilibrium*. These points are characterized by $F(x) = 0$. They are also called rest points, or fixed points. If one starts at such a point, one remains there forever.

(b) If $x(T) = x$ for some $T > 0$, but $x(t) \neq x$ for all $t \in (0,T)$, then x is called a *periodic point* and T is called the *period*. All other points on the orbit are periodic with period T. The motion describes an endless oscillation. Topologically, i.e. up to a continuous transformation, the orbit looks like a circle and the solution travels round and round.

(c) If $t \to x(t)$ is injective, then the orbit never intersects itself. The orbit may be bent, knotted and twisted, but topologically it looks like a line.

It is important to note that two trajectories can not cross or intersect each other, as we will state in the next lemma:

Lemma 2. *[3] Assume that the differential equation*

$$\dot{x} = F(x)$$

satisfies the assumptions required to give unique solutions for differential equations. Assume that there are two initial conditions x_0 and y_0 such that the trajectories intersect for some times along the two trajectories, $\phi(t_0;x_0) = \phi(t_1;y_0)$. Then, by the group property, $y_0 = \phi(t_0 - t_1;x_0)$, so x_0 and y_0 must be on the same trajectory.

Definition 2. *[3] Let $\phi(t;x)$ be the flow of a system of differential equations defined on $\mathbb{R}^n$. A set S is said to be* positively invariant *provided that $\phi(t;x_0)$ is in S for any point x_0 in S and any $t \geq 0$. Similarly, it is* negatively invariant *provided that the same property is true for all $t \leq 0$. Finally, the set S is said to be* invariant *provided that it is both positively and negatively invariant.*

2 Limit sets

We are interested in the long-term behavior of trajectories.

Definition 3. *[2] The* ω-limit set of x_0 *is defined as:*

$$\omega(x_0) = \{y \in \mathbb{R}^n : \phi(t_k;x_0) \to y \textit{ for some sequence } t_k \to +\infty\}.$$

So the ω-limit of x_0 is the set of all limit points of $\phi(t;x_0)$, for $t \to +\infty$.

Definition 4. *[2] Similarly, the* α-limit set of x_0 *is defined as:*

$$\omega(x_0) = \{y \in \mathbb{R}^n : \phi(t_k;x_0) \to y \textit{ for some sequence } t_k \to -\infty\}.$$

The ω-limit of a point x may be empty.

Theorem 3. *[3] Assume that $\phi(t;x_0)$ is a trajectory. Then, the following properties of the ω-limit set are true:*

(a) The limit set depends only on the trajectory and not on the particular point, so $\omega(x_0) = \omega(\phi(t;x_0))$ for any real time t.

(b) The $\omega(x_0)$ is invariant: if $z_0 \in \omega(x_0)$, then the orbit $\phi(t;z_0)$ is in $\omega(x_0)$ for all positive and negative t.

(c) The $\omega(x)$ is closed (i.e., $\omega(x_0)$ contains all its limit points).

(d) If y_0 is a point in $\omega(x_0)$, then $\omega(y_0) \subset \omega(x_0)$.

In addition, assume that the trajectory $\phi(t;x_0)$ stays bounded for $t \geq 0$ (i.e., there is a constant $C > 0$ such that $\|\phi(t;x_0)\| \leq C$ for $t \geq 0$). Then, properties (e) and (f) are true.

(e) The $\omega(x_0)$ is non-empty.

(f) The $\omega(x_0)$ is connected; it is not made up of more than one piece.

Similar properties hold for the α-limit set if $\phi(t;x_0)$ stays bounded for $t \leq 0$.

3 Theorem of Poincaré-Bendixson

Flows in $\mathbb{R}^2$ are particularly simple because of the Jordan curve theorem.

Theorem 4 (Jordan curve theorem)**.** *[2] Any periodic orbit γ in the plane devides the plane into two disjoint connected sets, the interior and the exterior. Two points in the interior (or the exterior)can be connected by a path which never intersects γ, but every path between the interior and the exterior has to cross γ*

Consequently follows:

Theorem 5 (Theorem of Poincaré-Bendixson)**.** *[2] Let $\dot{x} = F(x)$ be an ordinary differential equation defined on an open set $G \subseteq \mathbb{R}^2$. Let $\omega(x)$ be a non-empty compact ω-limit set. Then, if $\omega(x)$ contains no fixed point, it must be a periodic orbit.*

4 Lyapunov function

The following theorem helps us do get a handle on ω-limits even if we do not know the solution.

Theorem 6. *[2] Let $\dot{x} = F(x)$ be a time-independent ordinary differential equation defined on some subset $U \in \mathbb{R}^n$. Let $L : G \to \mathbb{R}$ be continuously differentiable. If for some solution $t \to x(t)$, the derivation $\dot{L}$ of the map $t \to L(x(t))$ satisfies the inequality $\dot{L} \geq 0$ (or $\dot{L} \leq 0$), then $\omega(x) \cap U$ (and $\alpha(x) \cap U$) is contained in the set $\{x \in U : \dot{L}(x) \cap 0\}$.*

There is no general way to find such a Lyapunov function L.

Definition 5. *[3] Assume $\hat{x}$ is a fixed point for the differential equation $\dot{x} = F(x)$. A real-valued function L is called a* weak Lyapunov function *for the differential equation provided there is a neighborhood U of $\hat{x}$ on which L is defined and*

(a) $L(x) > L(\hat{x})$ for all $x \in U$, $x \neq \hat{x}$, and

(b) $\dot{L}(x) \leq 0$ for all $x \in U$.

The function L is called a Lyapunov function *or* strict Lyapunov function *on an open neighborhood U provided it is a weak Lyapunov function which satisfies $\dot{L}(x) < 0$ for all $x \in U$, $x \neq \hat{x}$.*

5 Stability of fixed points

We recall:

Definition 6. *[3] A point $\hat{x}$ is called a* fixed point, *provided that $F(\hat{x}) = 0$. The solution starting at a fixed point has zero velocity, so it just stays there and $\phi(t;\hat{x}) = \hat{x}$ for all t. This justifies the name of a fixed point. Traditionally, such a point was called an* equilibrium point, *because the forces were in equilibrium and the mass did not move.*

5.1 Stability types

Definition 7. *[3] A fixed point $\hat{x}$ is called (Lyapunov) stable, provided that for any $\varepsilon > 0$, there exists a $\delta > 0$ such that, if $\|x_0 - \hat{x}\| < \delta$, then $\|\phi(t;x_0) - \hat{x}\| < \varepsilon$ for all $t \geq 0$.*

Definition 8. *[3] A fixed point $\hat{x}$ is called* asymtotically stable, *provided that it is (Lyapunov) stable and that there exists an $\delta_1 > 0$ such that $\omega(x_0) = \{\hat{x}\}$ for all $\|x_0 - \hat{x}\| < \delta_1$ (i.e., $\|\phi(t;x_0) - \hat{x}\|$ goes to 0 as t goes to infinity for all $\|x_0 - \hat{x}\| < \delta_1$). A asymptotically stable fixed point is also called a* sink. *We also use the word* attracting *to mean asymtotically stable.*

Definition 9. *[2] The set of points x with $x(t) \to \hat{x}$ as $t \to \infty$ is called* basin of attraction *of $\hat{x}$. It is an open invariant set. If the basin of attraction is the whole state space (or at least its interior) then $\hat{x}$ is said to be* globally stable.

Definition 10. *[3] A fixed point is called* repelling *or a* source, *provided that it is asymtotically stable backward in time (i.e., for any $\varepsilon > 0$, there is a $\delta > 0$ such that if $\|x_0 - \hat{x}\| < \delta$ then $\|\phi(t;x_0 - \hat{x}\| < \varepsilon$ for all $t \leq 0$ and there exists a $\delta_1 > 0$ such that $\alpha(x_0) = \{\hat{x}\}$ for all $\|x_0 - \hat{x}\| < \delta_1$).*

Definition 11. *[3] A fixed point $\hat{x}$ is called* unstable, *provided that it is not (Lyapunov) stable (i.e., there exists an $\varepsilon_1 > 0$ such that for any $\delta > 0$ there is some point x_δ with $\|x_\delta - \hat{x}\| < \delta$ and a time $t_1 > 0$ depending on the point x_δ with $\|\phi(t;x_\delta) - \hat{x}\| > \varepsilon_1$).*

Definition 12. *[3] A fixed point is called* hyperbolic, *provided that none of the eigenvalues of the linearized equations at the fixed point have real part* 0.

6 Local behavior near fixed points

We now want to show that a lot of information of the stability of a flow near a fixed point can be read off by linearizing the system around the fixed point.

6.1 Linear differential equations

For linear systems the following theorem gives a criterion on the eigenvalues that ensure asymptotic stability of the origin.

Theorem 7. *[2] Consider the linear differential equation*

$$\dot{x} = Ax.$$

(a) If all of the eigenvalues λ of A have negative real part, then the origin is asymptotically stable. In this case, $\{0\}$ is the ω-limit of every orbit.

(b) If all of the eigenvalues λ of A have positive real part, then the origin is a source. In this case $\{0\}$ is the α-limit of every orbit.

(c) If some eigenvalues have positive and some negative real part, but none has real part 0*, then the origin is a saddle. The orbits whose ω-limit is $\{0\}$ form a linear submanifold of $\mathbb{R}^n$ called the* stable manifold*; those whose α-limit is $\{0\}$ form the* unstable manifold*; and these subspaces span $\mathbb{R}^n$.*

For two-dimensional differential equations, from theorem 7 follows:

Lemma 8. *[3] Let A be a $2x2$ matrix with determinant* $\det A$ *and trace* $\operatorname{tr} A$.

(a) If $\det A < 0$*, then the linear system is a saddle, and therefore unstable.*

(b) If $\det A > 0$ *and* $\operatorname{tr} A > 0$*, then the linear system is a source and therefore unstable.*

(c) If $\det A > 0$ *and* $\operatorname{tr} A < 0$*, then the linear system is a sink and therefore asymptotically stable.*

(d) If $\det A = 0$*, then one or more of the eigenvalues is* 0.

6.2 Linearization

Let us now contemplate the local behavior of the solution of

$$\dot{x} = F(x) \tag{1}$$

near a point z in $\mathbb{R}^n$.

If z is not an equilibrium of $\dot{x} = F(x)$:

Lemma 9 (Straightening out of vector fields)**.** *[5] Suppose $F(z) \neq 0$. Then there is a local coordinate transformation $y = \varphi(x)$ such that $\dot{x} = F(x)$ is transformed to $\dot{y} = (1, 0, \ldots, 0)$.*

If z is a fixed point of $\dot{x} = F(x)$, we determine the *Jacobian matrix* $DF|_z = A$ of first order partial derivatives [2]:

$$A = \begin{pmatrix} \frac{\partial F_1}{\partial x_1}(z) & \dots & \frac{\partial F_1}{\partial x_n}(z) \\ \vdots & \ddots & \vdots \\ \frac{\partial F_n}{\partial x_1}(z) & \dots & \frac{\partial F_n}{\partial x_n}(z) \end{pmatrix}$$

The linear equation

$$\dot{y} = Ay \tag{2}$$

can be solved explicitly.

The next theorem will show that the orbits of the ordinary differential equation (1) near a hyperbolic fixed point $\hat{x}$, locally look like those of the linear equation (2) near 0.

Theorem 10 (Hartman-Grobman)**.** *[2] Let $x(t)$ be the solution of (1) and $y(t)$ be the solution of (2). For any hyperbolic equilibrium z of (1), there exists a neighborhood U and a homeomorphism h from U to some neighborhood V of the origin, such that $y_0 = h(x_0)$ implies $y(t) = h(x(t))$ for all $t \in \mathbb{R}$ with $x(t) \in U$.*

It follows:

Lemma 11. *Consider a differential equation $\dot{x} = F(x)$ in n variables, with a hyperbolic fixed point $\hat{x}$. Assume that F, $\frac{\partial F_i}{\partial x_j}(x)$ and $\frac{\partial^2 F_i}{\partial x_j \partial x_k}(x)$ are all continuous. Then, the stability type of the fixed point for the non-linear system is the same as that for the linearized system at that fixed point.*

(a) If all of the eigenvalues λ of $DF|_{\hat{x}}$ have negative real part, then $\hat{x}$ is asmptotically stable. In this case, $\{\hat{x}\}$ is the ω-limit of every orbit.

(b) If all of the eigenvalues λ of $DF|_{\hat{x}}$ have positive real part, then $\hat{x}$ is a source. In this case $\{\hat{x}\}$ is the α-limit of every orbit.

(c) If some eigenvalues of $DF|_{\hat{x}}$ have positive and some negative real part, but none has real part 0, then $\hat{x}$ is a saddle. The orbits whose ω-limit is $\{\hat{x}\}$ form a submanifold of $\mathbb{R}^n$ called the stable manifold*; those whose α-limit is $\{\hat{x}\}$ form the* unstable manifold*; and these subspaces span $\mathbb{R}^n$.*

The competitive Lotka-Volterra system

To model the interactions of n competitive species we use the competitive Lotka-Volterra system.

Definition 13.

$$F_i(x) = \dot{x}_i = x_i\left(b_i - \sum_{i=1}^{n} a_{ij}x_j\right), i \in \{1,\ldots,n\}, \tag{3}$$

where each x_i represents the population density of one species and b_i, a_{ij} with $j \in \{1,\ldots,n\}$ are constants depending on the environment.
When $b_i > 0$ and $a_{ij} > 0$ for all $i, j \in \{1,\ldots,n\}$ the Lotka-Volterra System is called competitive.

The state space of system (3) is represented by the non-negative vectors $\mathbb{R}^n_+ = \{(x_1,\ldots,x_n) \in \mathbb{R}^n$ with $x_i \geq 0$ for all $i \in \{1,\ldots,n\}\}$, since population densities have to be non-negative.
Each k-dimensional face of $\mathbb{R}^n_+$ is invariant under system (3).

7 The carrying simplex

The assumptions $b_i > 0$ and $a_{ii} > 0$ for all $i \in \{1,\ldots,n\}$, made in definiton 13 ensure that each species is self-regulating. Therefore system (3) restricted to the i-th coordinate axis gives the logistic equation:

$$\dot{x}_i = x_i(b_i - a_{ii}x_i) \tag{4}$$

The fixed points of the logistic equation (4) are found by solving $x_i(b_i - a_{ii}x_i) = 0$. They are given by 0 and $\frac{b_i}{a_{ii}}$.

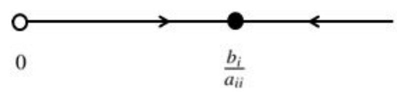

Figure 1: Logistic Equation with carrying capacity $\frac{b_i}{a_{ii}}$.

For $0 < x_i < \frac{b_i}{a_{ii}}$, $\dot{x}_i > 0$ and therefore the density increases. For $x_i > \frac{b_i}{a_{ii}}$, $\dot{x}_i < 0$ and the density decreases. This means there is a repulsion at 0 (growth of small populations) and a repulsion at infinity (competition of large populations).

The population density balances at the attracting fixed point $R_i := \frac{b_i}{a_{ii}}$. We call $\frac{b_i}{a_{ii}}$ the *carrying capacity* of species i.

Due to the invariance of system (3), R_i is also a fixed point of the full system and we call R_i the i-th axial fixed point.

The idea of a 'carrying capacity' can be generalizied for the n-dimensional system (3). Thus, for $x \in \mathbb{R}^n_+$ of sufficiently small magnitude $F(x) \in \mathbb{R}^n_+$ and for $x \in \mathbb{R}^n_+$ of sufficiently large magnitude $-F(x) \in \mathbb{R}^n_+$.
It is easy to see that 0 is a repelling fixed point of system (3) and that the basin of repulsion of 0 is bounded in $\mathbb{R}^n_+$. Intuitively the carrying simplex Σ is defined as the boundary of that basin.

To be precise:

Definition 14. *[9] Define $B(0) = \{x \in \mathbb{R}^n_+ : \alpha(x) = 0\}$, then $\Sigma = \partial B(0)$ where $\alpha(x)$ denotes the α-limit set of the trajectory through x and $\partial B(0)$ denotes the boundary of $B(0)$ taken in $\mathbb{R}^n_+$.*

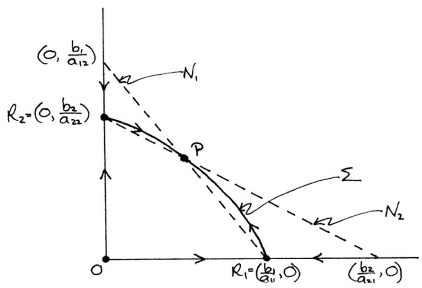

Figure 2: The carrying simplex for a two-dimensional competitive Lotka-Volterra system

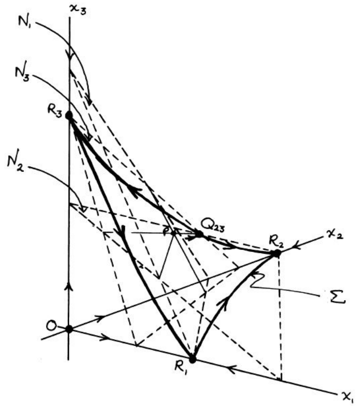

Figure 3: The carrying simplex for a three-dimensional competitive Lotka-Volterra system

7.1 Theorem of Hirsch

For the theorem of Hirsch some notation is needed [7]:

- A vector x is called *positive* if $x \in \mathbb{R}^n_+$.
- A vector x is called *strictly positive* if $x \in int\mathbb{R}^n_+$.
- Two points $u, v \in \mathbb{R}^n$ are *related* if either $u - v$ or $v - u$ is strictly positive.
- A set S is called *balanced* if no two distinct points of S are related.
- The *unit simplex* in $\mathbb{R}^n$ is defined by $\Delta := \{x \in \mathbb{R}^n_+ : \sum_{i=1}^n x_i = 1\}$.

Theorem 12 (Theorem of Hirsch)**.** *[1] Given system (3), every trajectory in $\mathbb{R}^n_+ \setminus \{0\}$ is asymptotic to one in Σ, and Σ is a balanced Lipschitz submanifold, homeomorphic to the unit simplex in $\mathbb{R}^n_+$ by radial projection.*

Σ is balanced, then the trajectories intersect Σ in at most one point. The invariance of Σ follows immediately.

This means that the ω-limit sets of system (3) are exactly those of system (3) restricted to Σ.
For $n = 2$, Σ is a curve. All trajectories in system (5) converge to a fixed point. Therefore, also the limit sets of Σ have to be fixed points.
For $n = 3$, Σ is a two-dimensional surface. By Poincaré-Bendixson the ω-Limit sets of system (8) restricted to Σ are either fixed points, periodic orbits, or connected sets composed of a finite number of fixed points together with homoclinic and heteroclinic orbits connecting these.

8 Two-dimensonal competitive Lotka-Volterra systems

For $n = 2$, system (3) reduces to:

$$\begin{aligned} F_1 = \dot{x}_1 = x_1\,(b_1 - a_{11}x_1 - a_{12}x_2) \\ F_2 = \dot{x}_2 = x_2\,(b_2 - a_{21}x_1 - a_{22}x_2) \end{aligned} \tag{5}$$

with $b_i > 0, a_{ij} > 0$ for $i, j \in \{1, 2\}$.

The state space of system (5) is represented by $\mathbb{R}^2_+$.

8.1 Analysis of the two-dimensional competitive Lotka-Volterra system

The nullclines of system (5) are given by:

$$\dot{x}_i = 0 \iff x_i\,(b_i - a_{i1}x_1 - a_{i2}x_2) = 0 \iff \begin{cases} x_i = 0 \\ \text{or } a_{i1}x_1 + a_{i2}x_2 = b_i \end{cases}$$

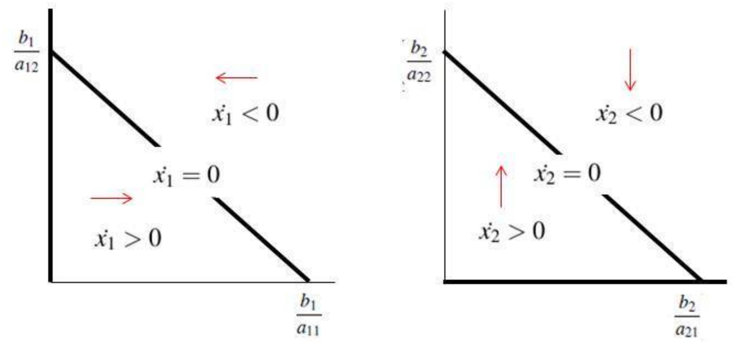

Figure 4: Nullclines for two-dimensional competitive Lotka-Volterra systems

The i-th nullcline therefore consists of the i-th coorinate axis together with the line $N_i = \{(x_1, x_2) : a_{i1}x_1 + a_{i2}x_2 = b_i\}$.

The fixed points of system (5) lie on the intersections of the two nullclines and are generally given by:

- the origin 0,
- the axial fixed points $R_1 = \left(\frac{b_1}{a_{11}}, 0\right)$ and $R_2 = \left(0, \frac{b_2}{a_{22}}\right)$,
- the interior fixed point $P = N_1 \cap N_2$.

Definition 15. *[10] The* nullcline configuration of system (5) *is given by the value of*

$$\operatorname{sgn}\left(\frac{b_i}{a_{ii}} - \frac{b_j}{a_{ji}}\right) = \operatorname{sgn}\left(a_{ji}\frac{b_i}{a_{ii}} - b_j\right) = \operatorname{sgn}((AR_i)_j - b_j),\ for\ i \neq j, \quad i, j \in \{1, 2\};$$

modulo permutation of the indices.

Furthermore $a_{ji}\frac{b_i}{a_{ii}} - b_j = -\frac{\dot{x}_j}{x_j}|_{R_i}$. $\frac{\dot{x}_j}{x_j}|_{R_i}$ is called the *invasion parameter* of species j at the fixed point R_i. If $\frac{\dot{x}_j}{x_j}|_{R_i} > 0$, then species j can invade at R_i and the fixed point R_i is a saddle point. If $\frac{\dot{x}_j}{x_j}|_{R_i} < 0$, then species j can not invade at R_i and the fixed point R_i is stable.

The configuration of the lines N_i determine the dynamic behavior of the flow as shown in figure 5. We see that system (5) admits an interior fixed point P only if $sgn\left(\frac{b_1}{a_{11}} - \frac{b_2}{a_{21}}\right) = sgn\left(\frac{b_2}{a_{22}} - \frac{b_1}{a_{12}}\right)$.

For cases c) and d) (with an internal fixed point) the nullclines divide $\mathbb{R}^n_+$ into four regions:

(R1) $\dot{x}_1 < 0$ and $\dot{x}_2 < 0$

(R2) case c) $\dot{x}_1 < 0$ and $\dot{x}_2 > 0$ or case d) $\dot{x}_1 > 0$ and $\dot{x}_2 < 0$

(R3) $\dot{x}_1 > 0$ and $\dot{x}_2 > 0$

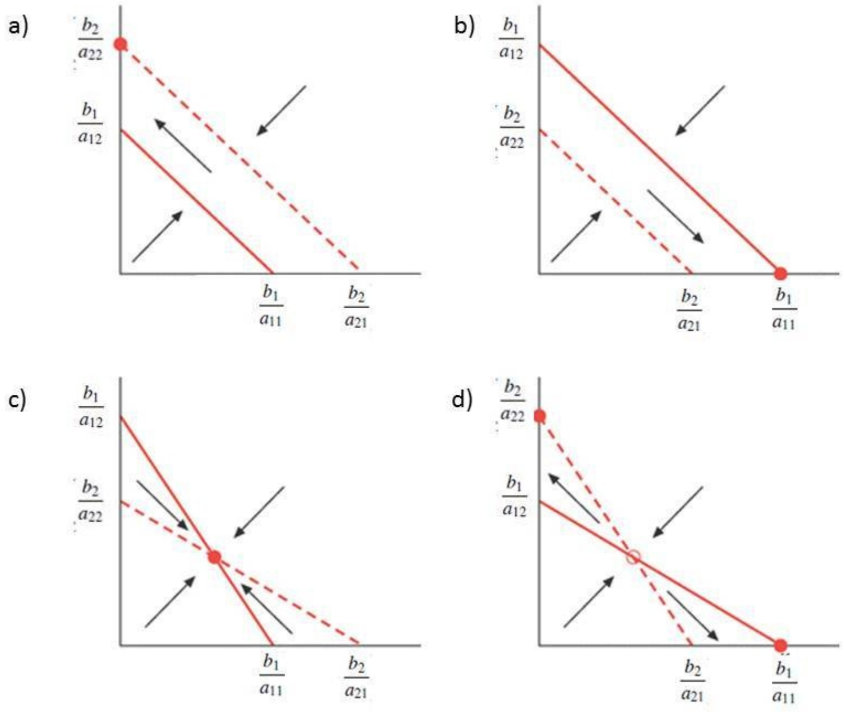

Figure 5: Dynamic behavior of two-dimensional competitive Lotka-Volterra systems

(R4) case c) $\dot{x}_1 > 0$ and $\dot{x}_2 < 0$ or case d) $\dot{x}_1 < 0$ and $\dot{x}_2 > 0$

For $\dot{x}_1 = 0$ the vector field is vertical and for $\dot{x}_2 = 0$ it is horizontal. The orbits from regions R1 and R3 can enter regions R2 and R4. Regions R2 and R4 are forward invariant.

The interior fixed point is given by:

$$P = (\hat{x}_1, \hat{x}_2) = \left(\frac{b_1 a_{22} - b_2 a_{12}}{a_{11}a_{22} - a_{12}a_{21}}, \frac{b_2 a_{11} - b_1 a_{21}}{a_{11}a_{22} - a_{12}a_{21}} \right).$$

The Jacobian matrix of system (5) at P is:

$$DF|_P = \begin{pmatrix} -a_{11}\hat{x}_1 & -a_{12}\hat{x}_1 \\ -a_{21}\hat{x}_2 & -a_{22}\hat{x}_2 \end{pmatrix}.$$

The trace, $trDF|_P < 0$ because $a_{ii} > 0$ for $i \in \{1,2\}$.

8.1.1 The stable case (Coexistence)

If

$$\frac{b_1}{a_{11}} - \frac{b_2}{a_{21}} < 0 \text{ and } \frac{b_2}{a_{22}} - \frac{b_1}{a_{12}} < 0,$$

then for $DF|_P$ it is easy to see that:

$$\det DF|_P > 0.$$

Therefore by lemma 8 it follows that P is globally asymptotically stable on $int\mathbb{R}^2_+$ and P is the ω-limit of every orbit.

8.1.2 The unstable case (Bistability)

If

$$\frac{b_1}{a_{11}} - \frac{b_2}{a_{21}} > 0 \text{ and } \frac{b_2}{a_{22}} - \frac{b_1}{a_{12}} > 0,$$

then for DF_P it is easy to see that:

$$\det DF|_P < 0.$$

By lemma 8 it follows that P is a saddle point. The points R_1 and R_2 are stable fixed points.

8.1.3 The one survival case

Cases a) and b) have the same nullcline configuration (permutation of indices 1 and 2). The nullclines divide $\mathbb{R}^n_+$ into three regions:

(R1) $\dot{x}_1 < 0$ and $\dot{x}_2 < 0$

(R2) case a) $\dot{x}_1 < 0$ and $\dot{x}_2 > 0$ or case b) $\dot{x}_1 > 0$ and $\dot{x}_2 < 0$

(R3) $\dot{x}_1 > 0$ and $\dot{x}_2 > 0$

For $\dot{x}_1 = 0$ the vector field is vertical and for $\dot{x}_2 = 0$ it is horizontal. So every orbit from regions R1 and R3 enters R2. Region R2 is forward invariant, which means that no solution can leave.

Therefore:

$$\frac{b_1}{a_{11}} - \frac{b_2}{a_{21}} > 0 \text{ and } \frac{b_2}{a_{22}} - \frac{b_1}{a_{12}} < 0 \iff x_2 \text{ will die out and } R_1 \text{ is globally stable}$$
$$\frac{b_1}{a_{11}} - \frac{b_2}{a_{21}} < 0 \text{ and } \frac{b_2}{a_{22}} - \frac{b_1}{a_{12}} > 0 \iff x_1 \text{ will die out and } R_2 \text{ is globally stable}$$

8.1.4 The degenerate case

It is also possible that the nullclines coincide, then $\frac{b_1}{a_{11}} = \frac{b_2}{a_{21}}$ and $\frac{b_2}{a_{22}} = \frac{b_1}{a_{12}}$.

Then the Lyapunov function of system (5), given by $L = x_1 x_2^{-\frac{b_1}{b_2}}$, is a constant of motion.

Proof.

$$\begin{aligned}\dot{L} &= \frac{\partial L}{\partial x_1}\dot{x}_1 + \frac{\partial L}{\partial x_2}\dot{x}_2 \\ &= x_1 x_2^{-\frac{b_1}{b_2}}\left[(b_1 - a_{11}x_1 - a_{12}x_2) - \frac{b_1}{b_2}(b_2 - a_{21}x_1 - a_{22}x_2)\right]\end{aligned}$$

Now:

$$\begin{aligned}\dot{L} = 0 &\Leftrightarrow (b_1 - a_{11}x_1 - a_{12}x_2) = \frac{b_1}{b_2}(b_2 - a_{21}x_1 - a_{22}x_2) \\ &\Leftrightarrow \frac{a_{11}}{b_1}x_1 + \frac{a_{12}}{b_1}x_2 = \frac{a_{21}}{b_2}x_1 + \frac{a_{22}}{b_2}x_2\end{aligned}$$

□

We have a line of degenerated fixed points in $\mathbb{R}^2_+$. Each trajectory will converge to one of the fixed points, depending on its initial conditions.

8.2 Stable nullcline classes for two-dimensional competitive Lotka-Volterra systems

Definition 16. *[10] Let F, G be two-dimensional competitive Lotka-Volterra systems. We say the F and G are nullcline equivalent if and only if they have the same nullcline configurations. The equivalence classes under this relationship are called the* nullcline classes*. F is* nullcline stable *if and only if F has a neighbourhood of equivalents. The* stable nullcline classes *are those nullcline classes with nullcline stable elements.*

Theorem 13. *[10] System (5) is nullcline stable if and only if* $\operatorname{sgn}((AR_i)_j - b_j) \neq 0$, *for $i \neq j$.*

Theorem 14. *[10] There are* 3 *stable nullcline classes for system (5).*

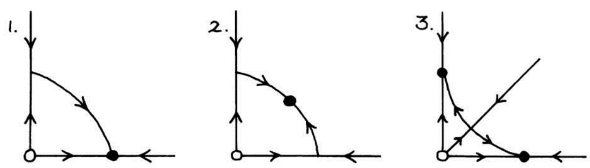

Figure 6: The stable nullcline classes of system (5). A fixed point is represented by a closed dot • if it attracts, by an open dot ∘ if it repels, and by the intersection of its hyperbolic manifolds if it is a saddle.

8.3 Carrying simplex for two-dimensional competitive Lotka-Volterra systems

By theorem 12 we know that for the two-dimensional competitive Lotka-Volterra system the carrying simplex is a curve and the limit sets must be fixed points. So Σ consists of the trajectories joining the R_i and P.
By [17], Σ is the graph of a continuous and strictly decreasing function $\psi : [0, \frac{b_1}{a_{11}}] \to [0, \frac{b_2}{a_{22}}]$ such that $\psi(0) = \frac{b_2}{a_{22}}$ and $\psi(\frac{b_1}{a_{11}}) = 0$.

E. C. Zeeman and M. L. Zeeman [9] claim that for system (5), if $a_{11}a_{22} - a_{12}a_{21} \neq 0$, then Σ is either convex or concave and if $a_{11}a_{22} - a_{12}a_{21} = 0$, then Σ is linear. A. Tineo [6] states that this result was partially wrong.

If Σ is linear, then Σ must be the linie connecting R_1 and R_2. This line is given by:

$$\frac{a_{11}}{b_1}x_1 + \frac{a_{22}}{b_2}x_2 = 1. \tag{6}$$

Σ is linear, if equation (6) is invariant. This means, that every solution starting at some point S on (6) remains on (6) for all time $t, t \to \pm\infty$. Therefore, the directional derivative $\frac{a_{11}}{b_1}\dot{x}_1 + \frac{a_{22}}{b_2}\dot{x}_2$ of (6) at a point $S = \left(x_1, \frac{b_2}{a_{22}} - \frac{b_2 a_{11}}{a_{11} b_1}x_1\right)$ of (6) has to be 0.

$$\begin{aligned}
0 &= (\frac{a_{11}}{b_1}\dot{x}_1 + \frac{a_{22}}{b_2}\dot{x}_2)|_S \\
&= \frac{a_{11}}{b_1}x_1[b_1 - a_{11}x_1 - a_{12}(\frac{b_2}{a_{12}} - \frac{b_2 a_{11}}{a_{22} b_1}x_1)] + \frac{a_{22}}{b_2}(1 - \frac{a_{11}}{b_1}x_1)[b_2 - a_{21}x_1 - a_{22}(\frac{b_2}{a_{12}} - \frac{b_2 a_{11}}{a_{22} b_1}x_1)] \\
&= (x_1 - \frac{a_{11}}{b_1}x_1^2)\frac{a_{11}(b_1 a_{22} - a_{12} b_2) + a_{22}(a_{11} b_2 - b_1 a_{21})}{b_2 a_{11}}
\end{aligned}$$

This holds true if and only if $x_1 = 0$, $x_1 = \frac{b_1}{a_{11}}$ or $Q := a_{11}(b_1 a_{22} - a_{12} b_2) + a_{22}(a_{11} b_2 - b_1 a_{21}) = 0$.

A. Tineo shows that ψ is concave (resp. convex) if $Q > 0$ (resp. $Q < 0$) and ψ is linear if $Q = 0$.

For simplification, A. Tineo [6] rewrites system (5) as:

$$\begin{aligned}
\dot{x}_1 &= x_1(1 - x_1 - \alpha x_2) \\
\dot{x}_2 &= p x_2(1 - \beta x_1 - x_2),
\end{aligned} \tag{7}$$

with $\alpha = \frac{a_{12} b_2}{b_1 a_{22}}$, $\beta = \frac{b_1 a_{21}}{a_{11} b_2}$ and $p = \frac{b_2}{b_1}$.

$\psi : [0,1] \to [0,1]$ denotes the carrying simplex of system (7).

We define:

$$q = 1 - \alpha + p(1 - \beta).$$

8.3.1 The stable case

Assume:

$$\alpha < 1, \qquad \beta < 1.$$

Then $q > 0$. System (7) has an interior fixed point $P = (\hat{x}_1, \hat{x}_2)$ and there exists a solution (u,v) of (7) defined on $\mathbb{R}$ such that $u' > 0 > v'$, $\lim_{t\to-\infty}(u(t),v(t)) = (0,1)$, $\lim_{t\to+\infty}(u(t),v(t)) = (\hat{x_1},\hat{x}_2)$ and $\psi(u(t)) = v(t)$. $\psi \in C^\infty(0,\hat{x}_1)$.

Theorem 15. *[6] If $\alpha,\beta < 1$, then $\psi''(x_1) < 0$ for all $x_1 \notin \{0,\hat{x}_1,1\}$. In particular, ψ is strictly concave.*

For prove see [6].

8.3.2 The unstable case

Assume:

$$\alpha > 1, \qquad \beta > 1.$$

Then $q < 0$ and system (7) has an interior fixed point $P = (\hat{x}_1,\hat{x}_2)$. Furthermore, there exists a solution (u,v) of (7) defined on $\mathbb{R}$ such that $u' < 0 < v'$, $\lim_{t\to+\infty}(u(t),v(t)) = (0,1)$, $\lim_{t\to-\infty}(u(t),v(t)) = (\hat{x}_1,\hat{x}_2)$ and $\psi(u(t)) = v(t)$. $\psi \in C^\infty(0,\hat{x}_1)$.

Theorem 16. *[6] If $\alpha,\beta > 1$, then $\psi''(x_1) > 0$ for all $x_1 \notin \{0,\hat{x}_1,1\}$. In particular, ψ is strictly convex.*

For proof see [6].

8.3.3 The one survivial case

Assume:

$$(1-\alpha)(1-\beta) \le 0, \qquad (\alpha,\beta) \ne (1,1).$$

Without loss of generality, we may further assume:

$$\alpha \le 1 \le \beta.$$

There exists a solution (u,v) of (7) defined on $\mathbb{R}$ such that $u' < 0 < v'$, $\lim_{t\to-\infty}(u(t),v(t)) = (0,1)$, $\lim_{t\to+\infty}(u(t),v(t)) = (1,0)$ and $\psi(u(t)) = v(t)$.

Let $\Gamma = v/(u-1)$ and define:

$$m = \begin{cases} \alpha^{-1}[1+p(1-\beta)] \text{ if } 1+p(1-\beta) > 0 \\ 0 \text{ if } 1+p(1-\beta) \le 0. \end{cases}$$

Corollary 17. *[6] If $\alpha \le 1 \le \beta$ holds then, $\psi \in C^1[0,1]$ and $\psi'(1) = -m$.*

Theorem 18. *[6] Assume $\alpha \leq 1 \leq \beta$ holds. If $q > 0$ (resp. $q < 0$), then $-m < \Gamma < -1$ and $-\Gamma' \leq 0$ (resp. $-1 < \Gamma < -m$ and $-\Gamma' \geq 0$).*

Whenever $q = 0$:

Theorem 19. *[6] If $q = 0$, then $\psi(x_1) = 1 - x_1$ (linear).*

So Σ is linear for the degenerate case, given by:

$$\alpha = 1, \qquad \beta = 1.$$

9 Three-dimensional competitive Lotka-Volterra systems

The three-dimensional competitive Lotka-Volterra system is given by:

$$F(x) = \dot{x}_i = x_i \left(b_i - \sum_{i=1}^{n} a_{ij} x_j \right), \tag{8}$$

with $b_i > 0, a_{ij} > 0$ for $i, j \in \{1, 2, 3\}$.

The state space of system (8) is represented by $\mathbb{R}^3_+$.

9.1 Analysis of the three-dimensional competitive Lotka-Volterra system

The nullclines of system (8) are given by:

$$\dot{x}_i = 0 \iff x_i(b_i - (Ax)_i) = 0 \iff \begin{cases} x_i = 0 \\ \text{or } (Ax)_i = b_i \end{cases}$$

The i-th nullcline therefore consists of the i-th coorinate axis together with the plane $N_i = \{(x_1, x_2, x_3) : (Ax)_i = b_i\}$.

The fixed points of system (8) lie on the intersections of all three nullclines and are generally given by:

- the origin 0,
- the axial fixed points R_i,
- the planar fixed points Q_{ij}, where the plane N_i and N_j meet on the coordinate plane $x_k = 0$, i, j, k are distinct,
- the interior fixed point $P = N_1 \cap N_2 \cap N_3$.

The planar fixed points Q_{ij} and the interior fixed point P do not nescessarily lie in $\mathbb{R}^3_+$.

Theorem 20. *[10] The configuration of the planes $N_i, i \in \{1,2,3\}$ determines the dynamic behavior of the flow at the fixed points R_i and Q_{ij} (whenever $Q_{ij} \in \mathbb{R}^3_+$).*

Nullcline configuration

Analog to definition 15 we define the nullcline configurations of system (8).

Definition 17. *[10] The* nullcline configuration of system (8) *is given by the values of* $\operatorname{sgn}((AR_i)_j - b_j)$ *and* $\operatorname{sgn}((AQ_{ij})_k - b_k)$*, for distinct i, j, k; modulo permutation of the indices.*

Analog to the two-dimensional system, $(AR_i)_j - b_j = -\frac{\dot{x}_j}{x_j}|_{R_i}$. Again the invasion parameter $\frac{\dot{x}_j}{x_j}|_{R_i}$ tells us whether or not species j can invade at R_i.
$(AQ_{ij})_k - b_k = -\frac{\dot{x}_k}{x_k}|_{Q_{ij}}$. $\frac{\dot{x}_k}{x_k}|_{Q_{ij}}$ is the invasion parameter of species k at Q_{ij}. It tells us whether or not species k can invade at Q_{ij}.

9.2 Stable nullcline classes for three-dim. competitive Lotka-Volterra systems

We now want to take a look at the stable nullcline classes of system (8).

Lemma 21. *[10] System (8) is nullcline stable if and only if* $\operatorname{sgn}((AR_i)_j) - b_j) \neq 0$ *and* $\operatorname{sgn}((AQ_{ij})_k) - b_k) \neq 0$

Theorem 22. *[10] There are* 33 *stable nullcline classes for system (8).*

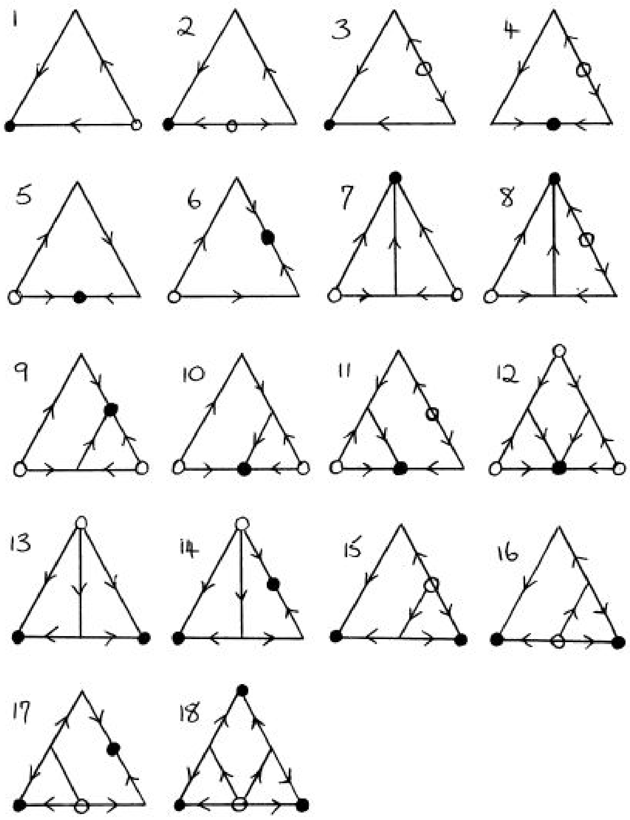

Figure 7: The phase portraits on Σ of the three-dimensional stable nullcline classes without interior fixed point. A fixed point is represented by a closed dot $\bullet$ if it attracts on Σ, by an open dot $\circ$ if it repels on Σ, and by the intersection of its hyperbolic manifolds if it is a saddle on Σ.

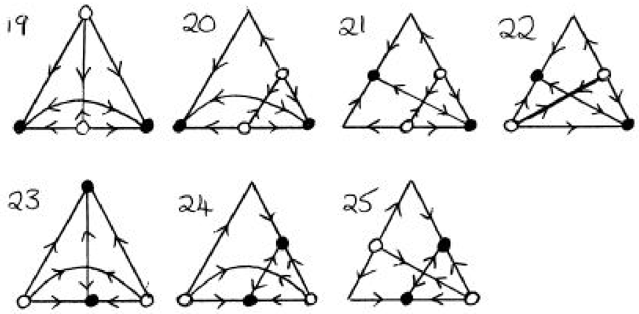

Figure 8: The phase portraits on Σ of the three-dimensional stable nullcline classes with interior saddle point.A fixed point is represented by a closed dot $\bullet$ if it attracts on Σ, by an open dot $\circ$ if it repels on Σ, and by the intersection of its hyperbolic manifolds if it is a saddle on Σ.

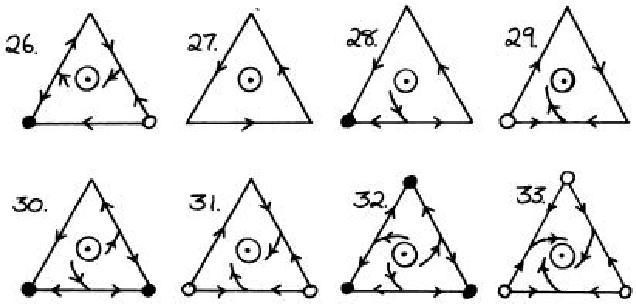

Figure 9: The phase portraits on Σ of the three-dimensional stable nullcline classes with interior fixed point of undetermined type. A fixed point is represented by a closed dot $\bullet$ if it attracts on Σ, by an open dot $\circ$ if it repels on Σ, and by the intersection of its hyperbolic manifolds if it is a saddle on Σ. $\odot$ represents a region of unknown dynamics.

9.3 Periodic orbits for three-dimensional competitive Lotka-Volterra systems

We have shown in section 8.1, that there are no non-trivial periodic orbits in system (5). The same does not hold true for the three-dimensional competitive Lotka-Volterra system.

9.3.1 Stable nullcline classes 1-25

We can however rule out periodic orbits in the stable nullcline classes 1-25.

Theorem 23. *[10] There are no periodic orbits in stable nullcline classes 1-25.*

Proof. [10] The nullcline configurations $1-18$ are those in which the planes N_i do not meet in $int\mathbb{R}^3_+$, so there is no interior fixed point. Thus we can apply Poincaré-Bendixson theory to the flow on Σ to conclude that there are no periodic orbits.
Now let $\dot{x} = F(x)$ be any system from classes $19-25$ and consider its restriction to Σ. There is an interior fixed point P, together with two attracting and two repelling fixed points on $\partial\Sigma$. At each repellor, ther must be a trajectory separating the basins of attraction of the two attractors. The ω-limit set of this trajectory is either P, or a periodic orbit γ, attracting from one side. Similarly, at each attractor there is a trajectory separating the basins of repulsion of the repellors, whose α-limit set can not γ. Thus there are no periodic orbits, and P is a saddle. $\square$

The ecological significance of this theorem is that for nullcline classes $1-25$ there can be no stable coexistence, not even of an oscillatory nature. At least one species will go extinct.

9.3.2 Stable nullcline classes 32 and 33

Furthermore [7] shows, that there are no isolated periodic orbits in the stable nullcline classes 32 and 33.

Theorem 24. *Given system (8) with all $a_{ij}, b_i > 0$, if R_1, R_2 and R_3 are all local attractors (repellors) on Σ, then there are no periodic orbits.*

This theorem applies to the stable nullcline classes 12,18,32 and 33.

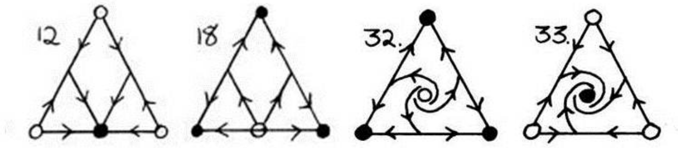

Figure 10: The phase portraits on Σ of the stable nullcline classes with R_1, R_2 and R_3 all local attractors (repellors) on Σ. A fixed point is represented by a closed dot $\bullet$ if it attracts on Σ, by an open dot $\circ$ if it repels on Σ, and by the intersection of its hyperbolic manifolds if it is a saddle on Σ.

To prove theorem 24, P. van den Driessche and M. L. Zeeman use the following backgroud knowledge to rule out periodic orbits:

Theorem 25 (Busenberg and van den Driessche)**.** *[7] Let $f : \mathbb{R}^3 \to \mathbb{R}^3$ be a Lipschitz vector field and let $\gamma(t)$ be a closed piecewise C^1 curve bounding an orientable C^1 surface $S \subset \mathbb{R}^3$ with unit normal vector n. If there exists a vector field $g : \mathbb{R}^3 \to \mathbb{R}^3$, defined and C^1 in a neighborhood of S such that*

(a) $g \cdot f \leq 0$ (≥ 0) *on* γ*,*

(b) $(\mathrm{curl} g) \cdot n \geq 0$ (≤ 0) *on S,*

(c) either $g \cdot f \neq 0$ *on* γ *or* $(\mathrm{curl} g) \cdot n \neq 0$ *on S,*

then $\gamma(t)$ is not a cycle of $\dot{x} = f(x)$ traversed in the positive direction with respect to n.

By noting that the unit vector n can be chosen in either of the two opposite directions, it follows:

Corollary 26. *[7] Let $f, \gamma(t), S$ and n be as in theorem 25. If there exists a vector field $g : \mathbb{R}^3 \to \mathbb{R}^3$, defined and C^1 in a neighborhood of S such that:*

(a) $g \cdot f \equiv 0$ *on* γ*,*

(b) $(\mathrm{curl} g) \cdot n \geq 0$ *or* $(\mathrm{curl} g) \cdot n \leq 0$*, but* $(\mathrm{curl} g) \cdot n \neq 0$ *on S, then $\gamma(t)$ is not a cycle (non-trivial closed piecewise smooth curve composed of a finite union of solution trajecories) of* $\dot{x} = f(x)$*.*

With the help of corollary 26 we can now prove theorem 24:

Proof. [7] Suppose that system (8) has a non-trivial periodic orbit $\gamma(t)$. Then $\gamma(t)$ lies in $int\Sigma$ by theorem 12, and hence encloses a region S of $int\Sigma$. As we have noted in section 7.1, Σ is actually C^1 and balanced, so for $x \in S$, the tangent plane T_xS to S at x exists and is balanced.
Suppose that the normal vector $n = (n_1, n_2, n_3)$ to S at x can not be chosen positive. We may assume, without loss of generality, that $n_1 > 0, n_2 \geq 0$, and $n_3 < 0$. Therefore

$$(n_1, n_2, n_3) \cdot (-n_3, -n_3, (n_1 + n_2)) = 0$$

So $(-n_3, -n_3, (n_1 + n_2)) \in T_xS$. This contradicts the fact that T_xS is balanced. Thus the normal vector n can be chosen to be positive.
Suppose that R_1, R_2 and R_3 are all attracting on Σ then:

$$\begin{aligned} b_2a_{11} - b_1a_{21} &< 0 \\ b_3a_{11} - b_1a_{31} &< 0 \\ b_1a_{22} - b_2a_{12} &< 0 \\ b_3a_{22} - b_2a_{32} &< 0 \\ b_1a_{33} - b_3a_{13} &< 0 \\ b_2a_{33} - b_3a_{23} &< 0 \end{aligned} \tag{9}$$

Let f denote the right-hand side of system (8) and define $g : int\mathbb{R}^3_+ \to \mathbb{R}^3$ by

$$g(x) = f(x) \times \nu(x) \,\text{where}\, \nu(x) = \frac{1}{x_1x_2x_3}\begin{pmatrix} b_1x_1 \\ b_2x_2 \\ b_3x_3 \end{pmatrix}.$$

Then

$$g \cdot f = (f \times \nu) \cdot f \equiv 0 \,\text{on}\, int\mathbb{R}^3_+,$$

which is hypothesis (a) of theorem 26. Now, writing

$$f = \begin{pmatrix} x_1L_1 \\ x_2L_2 \\ x_3L_3 \end{pmatrix} \,\text{where}\, L_i = b_i - \sum_{j=1}^{3} a_{ij}x_j,$$

straightforward computations yield

$$g = \begin{pmatrix} \frac{1}{x_1}(b_3L_2 - b_2L_3) \\ \frac{1}{x_2}(b_1L_3 - b_3L_1) \\ \frac{1}{x_3}(b_2L_1 - b_1L_2) \end{pmatrix}$$

and

$$curlg = \begin{pmatrix} \frac{1}{x_3}(b_1a_{22} - b_2a_{12}) + \frac{1}{x_2}(b_1a_{33} - b_3a_{13}) \\ \frac{1}{x_1}(b_2a_{33} - b_3a_{23}) + \frac{1}{x_3}(b_2a_{11} - b_1a_{21}) \\ \frac{1}{x_2}(b_3a_{11} - b_1a_{31}) + \frac{1}{x_1}(b_3a_{22} - b_2a_{32}) \end{pmatrix}. \tag{10}$$

The signs of the six terms in *curlg* are given by inequalities (9), and since $x_i > 0$ on $int\mathbb{R}^3_+$ for each i, each component of (10) is strictly negative. So hypothesis (b) of corollary 26 follows from the fact that n is positive and non-zero. Thus we may conclude from corollary 26 that $\gamma(t)$ is not a periodic orbit of system (8).
If R_1, R_2 and R_3 are all repelling on Σ, then inequalities (9) are all reversed and the proof follows similarly. □

From theorem 24 now follows:

Corollary 27. *[7] Given system (8) with all $a_{ij}, b_i > 0$, if R_1, R_2 and R_3 are all local attractors on Σ, then almost all trajectories converge to one of the fixed points $R_i, i \in \{1,2,3\}$, meaning there are no other attracting fixed points.*

Corollary 28. *[7] Given system (8) with all $a_{ij}, b_i > 0$ and with fixed point $P \in \mathrm{int}\Sigma$, if R_1, R_2 and R_3 are all local repellors, then P is globally asymptotically stable in* $\mathrm{int}\mathbb{R}^3_+$.

Ecologically corollary 27 can be interpreted as such: If each species can resist invasion at its carrying capacity then there can be no long-term coexistence of all three or even two species. This means two species go extinct while the third survives at its carrying capacity. Which one survives depends on the initial conditions.
Corollary 28 has the following ecological interpretation: None of the species can resist invasion by the other species. If there is an interior fixed point then non of the species will go exstinct and there is no long-term oscillatory behavior. So if the initial populations are strictly positive, all three species coexist at the interior fixed point P.

9.3.3 Stable nullcline classes 26-31

It is now left to show if periodic orbits do occur in the stable nullcline classes 26-31.

M.L. Zeeman [10] shows that in order to study the dynamic behavior in the nullcline classes 26-31, it is enough to consider those systems given by:

$$\dot{x}_i = F_i(x) = x_i(A(1-x))_i, \textit{ where } \det A = -\det(DF_P) > 0.$$

This can further be rewritten as:

$$\dot{x}_i = x_i(TA(1-x))_i$$

where $T = (t_{ij})$ is a diagonal matrix with strictly positive diagonal entries.

Families of systems corresponding to fixed nullclines can now be defined as follows:

Definition 18. *[10] If $\dot{x}_i = F_i(x) = x_i(A(1-x))_i$ and $T = (t_{ij})$ is a 3×3 diagonal matrix, define F^T by $F_i^T(x) = x_i(TA(1-x))_i$. Define the family $\mathscr{F}(F)$ through F by $\mathscr{F}(F) = \{F^T : t_{ii}, i = 1,2,3\}$.*

By varying the diagonal entries of T one by one, we can study $\mathscr{F}(F)$ as a one-parameter family.

Theorem 29. *[10] For every F, there is a positive diagonal matrix T such that $F^T|\Sigma$ is topologically equivalent to a two-dimensional Lotka-Volterra system.*

The fact, that there are no periodic orbits in the two-dimensional Lotka-Volterra system, leads us to the next corollary:

Corollary 30. *[10] For generic F, there is a three-dimensional Lotka-Volterra system having the same nullclines as F, without periodic orbits.*

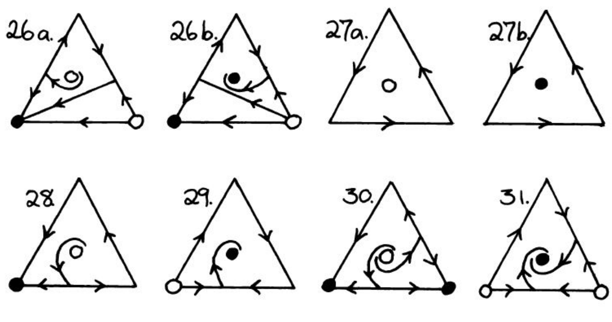

Figure 11: The phase portraits on Σ of representatives without periodic orbits form the three-dimensional stable nullcline classes 26-31.

So the nullclines alone are not enough to show whether or not periodic orbits occur. However M.L. Zeeman [10] shows that the nullclines can be used to predict the occurrence of Hopf-bifurcations and consequently, periodic orbits within a given family.

The prediction of Hopf-bifurcations depends on the signs of the determinants of the principal 2×2 minors

$$A_{jk} = \begin{pmatrix} a_{jj} & a_{jk} \\ a_{kj} & a_{kk} \end{pmatrix} \, with\, j \neq k$$

of any matrix A in the family.
A_{jk} represents the behavior of the system restricted to the $j-k$th coorinate plane. From section 8.1 we recall, that if the j-th and k-th nullcline intersect at Q_{jk} on $\partial\Sigma$, then $\det(A_{jk}) > 0 \Leftrightarrow Q_{jk}$ attracts on the plane, and hence on $\partial\Sigma$ and $\det(A_{jk}) < 0 \Leftrightarrow Q_{jk}$ is a saddle on the plane, and hence repels on $\partial\Sigma$.

Theorem 31. *[10] Let $\dot{x}_i = F_i(x) = x_i(A(1-x))_i, i \in \{1,2,3\}$, with $\det A > 0$. If $\det(A_{jk}) < 0$ whenever $j \neq k$, then P repels on Σ*

There are families of systems in classes 27-31 satisfying the hypotheses of theorem 31, but non in class 26.

Theorem 32. *[10] Let $\dot{x}_i = F_i(x) = x_i(A(1-x))_i, i \in \{1,2,3\}$, with $\det A > 0$. If $\det(A_{jk}), j \neq k$ are not all of the same sign,, then the family of systems $\mathscr{F}(F)$ admits a Hopf-bifurcation. Moreover, we can exhibit a particularly simple one-parameter subfamily of $\mathscr{F}(F)$ which admits a Hopf-bifurcation.*

Corollary 33. *[10] Within stable nullcline class 26, the family of systems corresponding to every set of nullcines admits a Hopf-bifurcation, and consequently, periodic orbits.*

Proof. [10] Any system in class 26 has a planar fixed point repelling on $\partial\Sigma$, and another attracting on $\partial\Sigma$, and thus has principal minors with determinants of opposite signs. $\square$

There are families of systems in the stable nullcline classes 27-31, that satisfy the hypothesis of theorem 32. However, it is still open how many limit cycles may occur.

J. Hofbauer and J. W.-H. So [12] give an example with two limit cycles surrounding the interior equilibrium in stable nullcline class 27 (with a heteroclinic cycle). Z. Lu and Y. Luo [13] have constructed two limit cycles in classes 26, 28 and 29 (without a heteroclinic cycle).
Furthermore the following conjecture was made in [12]: The number of limit cycles in the three-dimensional Lotka-Volterra system is at most two. This is proven wrong: Lu and Luo [15] give a counterexample with three limit cycles in class 27 (with a heteroclinic cycle). M. Gyllenberg, P. Yan and Y. Wang [14] construct three limit cycles for class 29 (without a heteroclinic cycle). Four limit cycles are constructed in [18] and [19].
D. Xiao and W. Li [16] have proven that the number of limit cycles of the three-dimensional competitive Lotka-Volterra systems is finite if the system does not have a heteroclinic cycle.

9.4 The model of May-Leonard

$$\begin{cases} \dot{x}_1 = x_1(1 - x_1 - \alpha x_2 - \beta x_3) \\ \dot{x}_2 = x_2(1 - \beta x_1 - x_2 - \alpha x_3), \\ \dot{x}_3 = x_3(1 - \alpha x_1 - \beta x_2 - x_3) \end{cases} \tag{11}$$

where α, β are non-negative coefficients, $0 < \beta < 1 < \alpha$.

The possible equilibria are:

- $P = \frac{(1,1,1)}{1+\alpha+\beta}$
- $Q_{12} = \frac{(1-\alpha,1-\beta,0)}{1-\alpha\beta}, Q_{23} = \frac{(0,1-\alpha,1-\beta)}{1-\alpha\beta}$ and $Q_{31} = \frac{(1-\beta,0,1-\alpha)}{1-\alpha\beta}$
- $R_1 = (1,0,0), R_2 = (0,1,0)$ and $R_3 = (0,0,1)$
- $0 = (0,0,0)$

From $1 < \alpha$ follows that Q_{ij} $(i, j \in \{1,2,3\}, i \neq j)$ do not lie in $\mathbb{R}^3_+$. Therefore system (11) is an example of stable nullcline class 27.

We will investigate the model by constructing its Lyapunov function [2]:

$$L = \frac{R}{S^3}$$

with $S = (x_1 + x_2 + x_3), R = x_1 x_2 x_3$.

Then:

$$\begin{aligned} \dot{S} &= \dot{x}_1 + \dot{x}_2 + \dot{x}_3 \\ &= x_1 + x_2 + x_3 - \left[x_1^2 + x_2^2 + x_3^2 + (\alpha + \beta)(x_1x_2 + x_2x_3 + x_3x_1)\right] \\ &= S(1 - S) - (\alpha + \beta - 2)(x_1x_2 + x_2x_3 + x_3x_1) \\ \dot{R} &= \dot{x}_1x_2x_3 + x_1\dot{x}_2x_3 + x_1x_2\dot{x}_3 \\ &= R[3 - (1 + \alpha + \beta)S] \\ &= R[3(1 - S) - (\alpha + \beta - 2)S] \end{aligned}$$

We compute:

$$\begin{aligned} \dot{L} &= \frac{\dot{R}S - 3\dot{S}R}{S^4} \\ &= \frac{R}{S^4}(-(\alpha + \beta - 2))\left[S^2 - 3(x_1x_2 + x_2x_3 + x_3x_1)\right] \\ &= \frac{R}{S^4}\frac{-(\alpha + \beta - 2)}{2}\left[(x_1 - x_2)^2 + (x_2 - x_3)^2 + (x_3 - x_1)^2\right] \end{aligned}$$

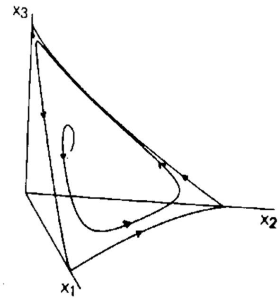

Figure 12: The May-Leonard model for $\alpha+\beta>2$ and $0<\beta<1<\alpha$.

For $\alpha+\beta=2$, $\dot{L}=0$ if and only if $(1-S)=0$. All trajectories will converge to this plane $x_1+x_2+x_3=1$ and the Lyapunov function on this plane is constant.

For $\alpha+\beta>2$, $\dot{L}\leq 0$ and $\dot{L}=0$ only if $x_1=x_2=x_3$. An orbit that is not on $x_1=x_2=x_3$ converges to the boundary. R_1, R_2 and R_3 are all saddle points. The ω-limit is a heteroclinic cycle.

For $\alpha+\beta<2$, $\dot{L}\geq 0$. In order to minimize the Lyapunov function, all trajectories will converge to one point on $x_1=x_2=x_3$.

9.5 Nonconvexity of the carrying simplex for three-dimensional competitive Lotka-Volterra systems

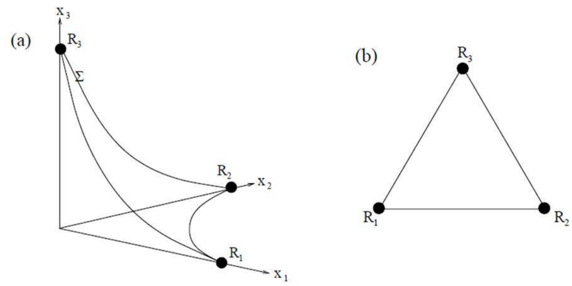

Figure 13: The carrying simplex for the three-dimensional competitive Lotka-Volterra system:(a) as it sits in $\mathbb{R}^3_+$, (b) projected onto Δ and then extracted from $\mathbb{R}^3_+$ and viewed as a flat triangle.

We can now use Theorem 12 to picture Σ of system (8) as a flat two-dimensional manifold, homeomorphic to the unit simplex $\Delta\in\mathbb{R}^3_+$.

Apart from P and 0 all fixed point lie on $\partial\Sigma$, but P and the Q_{ij} do not necessarily lie in $\mathbb{R}^3_+$.

In section 8.3 we discussed whether the carrying simplex of the two-dimensional competitive Lotka-Volterra system is convex or not. Zeeman and Zeeman [9] have shown by example that for the three-dimensional competitive system Σ is not necessarily convex.

Example:

Consider the system

$$\begin{cases} \dot{x}_1 = x_1(10 - 3x_1 - 5x_2 - 2x_3) \\ \dot{x}_2 = x_2(10 - 4x_1 - 3x_2 - 3x_3) \\ \dot{x}_3 = x_3(10 - 2x_1 - 1x_2 - 7x_3) \end{cases} \tag{12}$$

System (12) has fixed point $P = (1,1,1)$. By setting $x_i = 0$, we get a two-dimensional competitive Lotka-Volterra system with carrying simplex $\Sigma_i = \Sigma \cap \{x_i = 0\}$. Σ now consists of $\Sigma_i, i \in \{1,2,3\}$ in the coordinate planes.
For $x_i = 0$, we define $A_i = \begin{pmatrix} a_{jj} & a_{jk} \\ a_{kj} & a_{kk} \end{pmatrix}$ and $B_i = (b_j, b_k)$ where $j < k$ and i, j, k are distinct.

For $x_1 = 0$:

$$A_1 = \begin{pmatrix} 3 & 3 \\ 1 & 7 \end{pmatrix}, B_1 = (10,10) \Rightarrow Q_{23} = \frac{10}{9}(0,2,1) \text{ attracts on } \Sigma \text{ because } \det A_1 > 0$$

For $x_2 = 0$:

$$A_2 = \begin{pmatrix} 3 & 2 \\ 2 & 7 \end{pmatrix}, B_2 = (10,10) \Rightarrow Q_{13} = \frac{10}{17}(5,0,1) \text{ attracts on } \Sigma \text{ because } \det A_2 > 0$$

For $x_3 = 0$:

$$A_3 = \begin{pmatrix} 3 & 5 \\ 4 & 3 \end{pmatrix}, B_3 = (10,10) \Rightarrow Q_{12} = \frac{10}{11}(2,1,0) \text{ repels on } \Sigma \text{ because } \det A_3 < 0$$

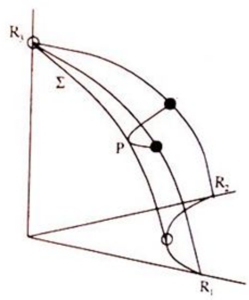

Figure 14: The carrying simplex Σ of system (12). A fixed point is represented by a closed dot $\bullet$ if it attracts, by an open dot $\circ$ if it repels.

Hence Σ is not convex as a surface in $\mathbb{R}^3$.

10 Competitive Lotka-Volterra systems of arbitrary dimension n

We now want to know if any of the results shown in section 8 and 9 generalize for the competitive Lotka-Volterra system with arbitrary dimension n.

In section 8.1 we have seen that for the two-dimensional system (5), all but one species go exstinct if there is no fixed point in $int\mathbb{R}^2_+$. The other species stabilises at its carrying capacity. M. L. Zeeman [11] generalizes the result for arbitrary dimension n.

Theorem 34. *[11] If system (3) satisfies the inequalities*

$$\frac{b_j}{a_{jj}} < \frac{b_i}{a_{ij}} \forall i < j, \text{ and } \frac{b_j}{a_{jj}} > \frac{b_i}{a_{ij}} \forall i > j, \tag{13}$$

then the axial fixed point

$$R_1 = (\frac{b_1}{a_{11}}, 0, \ldots, 0)$$

is globally attracting on $\mathrm{int}\mathbb{R}^n_+$.

From theorem 34 follows by allowing to relabel the axis:

Corollary 35. *[11] If there is a permutation π of the indices $\{1, \ldots, n\}$, after which system (3) satisfies inequalities (13), the $R_{\pi^{-1}(1)}$ is globally attracting on* $\mathrm{int}\mathbb{R}^n_+$ *under the original system.*

Ecologically this means that all but one species go extinct, whilst the remaining species stabilises at its carrying capacity.
For proof see [11].

We now want do know if corollary 28 can also be generalized. In [7] the question is answered by a counterexample from J. Hofbauer:

$$F(x) = \dot{x}_i = x_i \left(b_i - \sum_{i=1}^{4} a_{ij} x_j \right), i \in \{1, \ldots, 4\}, \tag{14}$$

where $A = (a_{ij})$ is the circulant matrix

$$A = \begin{pmatrix} 1 & 1-a & 1-b & 1-c \\ 1-c & 1 & 1-a & 1-b \\ 1-b & 1-c & 1 & 1-a \\ 1-a & 1-b & 1-c & 1 \end{pmatrix},$$

$b_i = 4 - a - b - c$ for $i \in \{1, \ldots, 4\}$, and $a, b, c \in \{0, 1\}$. By [1], system (14) has a three-dimensional carrying simplex Σ, with vertices at the four axial fixed points R_i.
By geometric analysis, each R_i is locally repelling on Σ. System (14) has an interior fixed point $P = (1, 1, 1, 1)^T$.
We now linearize system (14):

$$DF|_P = -A.$$

Its eigenvalues are given by:

$$a+b+c-4,\ -b\pm(a-c)i,\ b-(a+c).$$

If $b<(a+c)$ then all the eigenvalues have negative real part and P is a local attractor, but if $b>(a+c)$ then P is neither locally nor globally attracting.
So we have shown that corollary 28 does not generalize to dimension 4.

Lebenslauf

Persönliche Daten

Name:	Karoline Schindler
Geburtsort:	Eisenstadt, Österreich
Nationalität:	Österreich

Ausbildung

1993 - 1997	Volksschule Au am Leithaberge
1997 - 2001	Don Bosco Gymnasium Unterwaltersdorf
2001 - 2006	Handelsakademie Eisenstadt Fachrichtung Entrepreneurship und Management Ausbildungsschwerpunkt: Digital Business
9. Juni 2006	Matura
WS 06/07-WS 12/13	Studium an der Universität Wien, Mathematik (Diplom)

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