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Matrix stability concepts for the Lotka-Volterra model

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Abstract

In the area of applied mathematics, particularly in mathematical ecology, one model is of main importance and that is the Lotka-Volterra model. In order to gain more understanding in the field of theoretical population dynamics in a biological community of n interacting species, we can analyse the asymptotic stability in the linear approximation of a system of ODEs. Another motivation for the analysis of such a multi-component system (i.e., intra- and interspecific relations in a community of interacting species) is to obtain insight in the stability of the system by the very definition of its matrix entries.
In the first chapter we concern ourselves with a short introduction to dynamical systems. In chapter two and three we recap the stability theory of fixed points. In chapter four we give an introduction to the Lotka-Volterra equation and analyse the two dimensional system. In chapter five we introduce matrix stability concepts, special notions like *VL-stability*, *total stability*, *D-stability* and *P-matrix* arise in this context. We turn our attention to the relations and logical implications between these concepts. In chapter six we give examples of the three dimensional Lotka-Volterra model and analyse the dynamical behaviour. In chapter seven we introduce a method to verify if a given 3×3 matrix is *totally stable*.
In chapter eight we are investigating the conditions for *VL-stability* of a three dimensional matrix.

Abstract

Im Gebiet der Angewandten Mathematik, speziell in der Mathematischen Ökologie, ist ein Modell von besonderer Bedeutung, nämlich das Lotka-Volterra Modell. Um Einblicke in die Dynamik einer biologischen Gemeinschaft von n interagierenden Spezies zu erhalten, können wir die asymptotische Stabilität von Fixpunkten des linearisierten Systems untersuchen. Ein anderer Zugang um ein solches System mit Wechselwirkungen innerhalb derselben Spezies und zwischen verschiedenen Spezies, zu untersuchen, ist es, Aussagen über die Stabilität aufgrund der bloßen Matrixeinträge machen zu können.

Im ersten Kapitel ist eine kurze Einführung von fundamentalen Definitionen und Sätzen aus dem Gebiet der Differentialgleichungen zu finden. In den Kapiteln zwei und drei wiederholen wir die Stabilität von Fixpunkten. In Kapitel vier wird das Lotka-Volterra Modell vorgestellt und das zweidimensionale Konkurrenz Modell untersucht. In Kapitel fünf werden die Matrixstabilitätskonzepte *VL-Stabilität, totale Stabilität, D-Stabilität* und die *P-Matrizen* eingeführt. Wir werden die Beziehungen und logischen Implikationen zwischen diesen Konzepten untersuchen. In Kapitel sechs geben wir Beispiele für das dreidimensionale Lotka-Volterra Modell und untersuchen die Dynamik des Systems. In Kapitel sieben stellen wir eine Methode vor um eine 3×3 Matrix auf *totale Stabilität* zu untersuchen.

In Kapitel acht beschäftigen wir uns mit der Frage wann eine dreidimensionale Matrix *VL-stabil* ist.

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1 Introduction

The main references used in this chapter are 'An Introduction to Dynamical Systems, Continuous and Discrete' by Robinson [12] and 'The Theory of Evolution and Dynamical Systems, Mathematical Aspects of Selection' by Hofbauer and Sigmund [5].

Autonomous differential equations

Let us consider *autonomous* (or *time-independent*) differential equations.

Definition 1.1. *Let U be an open subset of $\mathbb{R}^n$. For $F : U \mapsto \mathbb{R}^n$, a system of the form*

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

is called an autonomous differential equation, because the right-hand side does not depend on the time t. The right-hand side is called a vector field on $U \subset \mathbb{R}^n$.

Theorem 1.2 (Existence and uniqueness of solutions)**.** *[12] Let us consider the differential equation $\dot{x} = F(x)$. Assume that both $F(x)$ and $\dfrac{\partial F_i(x)}{\partial x_j}$ are continuous for x in an open set $U \subset \mathbb{R}^n$, 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 the 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 such that $\phi(t; x_0)$ is defined for $0 \leq t \leq T$. Let $\epsilon > 0$ be any bound on the distance between solutions. Then, there exists a $\delta > 0$ which measures the distance between allowable initial conditions, in the following sense: if $\|y_0 - x_0\| < \delta$, then $\phi(t; y_0)$ is defined for $0 \leq t \leq T$ and $\|\phi(t; y_0) - \phi(t; x_0)\| < \epsilon$ for $0 \leq t \leq T$.

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

The Flow

Definition 1.3. *[12] 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 parametrized 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.*

[5] There are three types of solutions $\phi(t; x_0)$ that can occur:

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

(ii) If $\phi(T; x_0) = x_0$ for some $T > 0$, but $\phi(t; x_0) \neq x_0$ for all $t \in (0, T)$, then x_0 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 periodic oscillation. Topologically, i.e., up to a continuous transformation, the orbit looks like a circle and the solution travels round and round.

(iii) If $t \mapsto \phi(t; x_0)$ is injective, then the orbit never intersects itself. The orbit may be bent, knotted and twisted, but topologically it looks like a line.

Remark 1.4. *Two trajectories cannot cross or intersect each other.*

The explanation is given in the next lemma.

Lemma 1.5. *[12] 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 1.6. *[12] 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.*

Limit sets

The difficulty with most differential equations is the fact that in most cases we do not know how to compute the solutions. There are two ways how to handle this situation: to calculate approximate orbits numerically or to analyse the qualitative behaviour. Since we are interested in the long time behaviour of dynamical systems, we will stick to the analysis of the qualitative behaviour. The asymptotic features of a solution are described in its ω-limit.

Definition 1.7. *[5] The ω-limit set of x_0 is defined as:*

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

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

Definition 1.8. *[5] The α- limit set of x_0 is defined as:*

$$\alpha(x_0) = \{y \in \mathbb{R}^n \mid \phi(t_k; x_0) \to y \text{ for some sequence } t_k \to -\infty\}$$

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

Theorem 1.9. *[12] Assume that $\phi(t; x_0)$ is a trajectory. Then, the following properties of the ω-limit set are true:*

(i) 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.

(ii) 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.

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

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

Furthermore, 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, the following properties are true.

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

(vi) 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 $t \leq 0$.

Ljapunov function

Definition 1.10. *Assume $\hat{x}$ is a fixed point for the differential equation $\dot{x} = F(x)$. A real-valued function L is called a weak Ljapunov function for the differential equation provided there is a neighbourhood U of $\hat{x}$ on which L is defined and*

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

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

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

Theorem 1.11. *Let $\dot{x} = F(x)$ be a time - independent ordinary differential equation defined on some subset $U \subseteq \mathbb{R}^n$. Let $L : U \to \mathbb{R}$ be a continuously differentiable function. 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 $\{x \in U \mid \dot{L}(x) = 0\}$.*

Unfortunately, there is no recipe how to find such a Ljapunov function L.

2 Stability of fixed points

Here we will recap the basic stability terms for fixed points.

Definition 2.1. *[12] 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.*

Stability types

Definition 2.2. *[12] A fixed point $\hat{x}$ is said to be (Ljapunov) stable, provided that any solution $\phi(t; x_0)$ stays near $\hat{x}$ for all $t \geq 0$ if the initial condition x_0 starts near enough $\hat{x}$. More precisely, a fixed point $\hat{x}$ is called (Ljapunov) stable, provided that for any $\epsilon > 0$, there exists a $\delta > 0$ such that, if $\|x_0 - \hat{x}\| < \delta$, then $\|\phi(t; x_0) - \hat{x}\| < \epsilon$ for all $t \geq 0$.*

Definition 2.3. *[12] A fixed point $\hat{x}$ is called asymptotically stable, provided that it is (Ljapunov) stable and that there exists a $\delta_1 > 0$ 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 zero as t goes to infinity for all $\|x_0 - \hat{x}\| < \delta_1$). An asymptotically stable fixed point is also called a sink. We also use the word attracting for asymptotically stable points.*

Definition 2.4. *[12] The set of points x with $\phi(t; x_0) \to \hat{x}$ 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 2.5. *[12] A fixed point is called repelling or a source, provided that it is asymptotically stable backward in time (i.e., (i) for any $\epsilon > 0$, there is a $\delta > 0$ such that if $\|x_0 - \hat{x}\| < \delta$ then $\|\phi(t; x_0) - \hat{x}\| < \epsilon$ for all $t \leq 0$ and (ii) there exists a $\delta_1 > 0$ such that $\alpha(x_0) = \{\hat{x}\}$ for all $\|x_0 - \hat{x}\| < \delta_1$).*

Definition 2.6. *A fixed point $\hat{x}$ is called unstable, provided that it is not (Ljapunov) stable (i.e., there exists an $\epsilon_1 > 0$ 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 $\|\phi(t_1; x_\delta) - \hat{x}\| > \epsilon_1$).*

Definition 2.7. *[5] A fixed point is said to be hyperbolic, provided that none of the eigenvalues of the linearised equations at the fixed point have 0 as real part of eigenvalues. It follows that hyperbolic equilibria are sources, saddles and sinks.*

Just as a fixed point can be (Ljapunov) stable or asymptotically stable, so a periodic orbit can have different types of stability.

Definition 2.8. *[12] A periodic orbit $\gamma = \{\phi(t; x_0) \,|\, 0 \le t \le T\}$ is called orbitally (Ljapunov) stable, provided that for any $\epsilon > 0$, there exists a $\delta > 0$ such that, if x_0 is an initial condition within a distance δ of γ, then $\phi(t; x_0)$ is within a distance ϵ of γ for all $t \ge 0$.*

Definition 2.9. *[12] A periodic orbit $\gamma = \{\phi(t; x_0) \,|\, 0 \le t \le T\}$ is called orbitally asymptotically stable, provided it is orbitally (Ljapunov) stable and that there exists a $\delta_1 > 0$ such that any initial condition $x_0$within δ_1 of γ has the distance between $\phi(t; x_0)$ and γ go to zero as t goes to infinity, i.e., $\omega(x_0) = \gamma$. An orbitally asymptotically stable periodic orbit is also called an attracting periodic orbit or an attractor.*

Definition 2.10. *[5] A periodic orbit is called a limit cycle if $\omega(x_0) = \gamma$ holds, for at least one $x_0 \notin \gamma$.*

3 Local behaviour near fixed points

Since we are interested in the qualitative behaviour of a dynamical system, we can gain a lot of insight in the stability of the fixed points by linearising the system around the fixed point.

Linear differential equations

The following theorem gives a criterion on the eigenvalues that ensures asymptotic stability of the origin.

Theorem 3.1. *[5] Consider the linear differential equation*

$$\dot{x} = Ax$$

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

(ii) If all 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.

(iii) 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 subspace of $\mathbb{R}^n$ called the stable subspace; those whose α-limit is $\{0\}$ form the unstable subspace; and these subspaces span $\mathbb{R}^n$.

For a two dimensional differential equation system, the determinant and the trace can be used to describe the stability type of the fixed point:

Lemma 3.2. *[12] Let A be a 2×2 matrix with determinant $\det(A)$ and trace $\operatorname{tr}(A)$.*

(i) If $\det(A) < 0$, then the origin is a saddle, and therefore unstable.

(ii) If $\det(A) > 0$ and $\operatorname{tr}(A) > 0$, then the origin is a source and unstable.

a)If $\det(A)^2 - 4\operatorname{tr}(A) > 0$, then the origin is an unstable node.
b)If $\det(A)^2 - 4\operatorname{tr}(A) = 0$, then the origin is an degenerate unstable node.
c)If $\det(A)^2 - 4\operatorname{tr}(A) < 0$, then the origin is an unstable focus.

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

a)If $\det(A)^2 - 4\operatorname{tr}(A) > 0$, then the origin is a stable node.
b)If $\det(A)^2 - 4\operatorname{tr}(A) = 0$, then the origin is a degenerate stable node.
c)If $\det(A)^2 - 4\operatorname{tr}(A) < 0$, then the origin is a stable focus.

(iv) If $\det(A) = 0$, then one or more of the eigenvalues are equal to zero. In this case there is a line of fixed points.

Linearisation

Let us now consider the local behaviour of the solution of

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

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

If $\hat{x}$ is not an equilibrium of $\dot{x} = F(x)$, then contemplate:

Theorem 3.3. *[16] Suppose $F(\hat{x}) \neq 0$. Then there is a local coordinate transformation $y = \varphi(x)$ such that $\dot{x} = F(x)$ is transformed to $\dot{y} = (1, 0, ..., 0)$.*

If $\hat{x}$ is a fixed point of $\dot{x} = F(x)$, we determine the Jacobian matrix $J(\hat{x}) = DF|_{\hat{x}}$ of the first order partial derivatives:

$$J(\hat{x}) = \begin{bmatrix} \frac{\partial F_1}{\partial x_1}(\hat{x}) & \dots & \frac{\partial F_1}{\partial x_n}(\hat{x}) \\ \vdots & \ddots & \vdots \\ \frac{\partial F_n}{\partial x_1}(\hat{x}) & \dots & \frac{\partial F_n}{\partial x_n}(\hat{x}) \end{bmatrix}$$

The linear equation

$$\dot{y} = J(\hat{x})y$$

can be solved explicitly. The next theorem will show that the orbits of the ordinary differential equation $\dot{x} = F(x)$ near a hyperbolic fixed point $\hat{x}$, locally look like those of the linear equation $\dot{y} = J(\hat{x})y$ near 0.

Theorem 3.4. *(Hartman-Grobman) [16] Let $\phi(t; x_0)$ be the solution of $\dot{x} = F(x)$ and $\psi(t; y_0)$ be the solution of $\dot{y} = J(\hat{x})y$. For any hyperbolic equilibrium $\hat{x}$ of $\dot{x} = F(x)$, there exists a neighbourhood U of $\hat{x}$ and a homeomorphism h from U to some neighbourhood V of the origin $\mathbf{0}$, such that $y_0 = h(x_0)$ implies $\psi(t; y_0) = h(\phi(t; x_0))$ for all $t \in \mathbb{R}$ with $\phi(t; x_0) \in U$.*

Theorem 3.5. *[12] Consider a differential equation $\dot{x} = F(x)$ in n variables, with a fixed point $\hat{x}$. Assume that F, $\frac{\partial F_i}{\partial x_j}(x)$ are all continuous. Then, the stability type of the fixed point for the nonlinear system is the same as that for the linearised system at that fixed point.*

(i) If the real parts of all eigenvalues of $DF|_{\hat{x}}$ are negative, then $\hat{x}$ is asymptotically stable for the nonlinear equation.

(ii) If at least one eigenvalue of $DF|_{\hat{x}}$ have positive real part, then $\hat{x}$ is unstable for the nonlinear equation..

(iii) If one of the eigenvalues of $DF|_{\hat{x}}$ has a zero real part, then the linearised system does not determine the stability type of the fixed point.

4 The general Lotka-Volterra equation

In mathematical ecology the Lotka-Volterra model is of fundamental importance for the analysis of the mutual reactions and effects between and within a system of interacting species. The species can encounter each other in three different ways. They can have a positive effect and benefit each other, this is called a mutualistic system. They can interact as predator and prey, which means that one species is taking advantage of the other species. This is called a predator-prey model. The third kind of interaction is competition, which we will further examine. The general Lotka-Volterra equation for n populations or species is modeled by the system

$$F_i(x) = \dot{x}_i = x_i \left(r_i + \sum_{j=1}^{n} a_{ij} x_j \right) \quad i = 1, \dots, n \tag{1}$$

where each $x_i(t)$ represents the population size of the i-th species at time t. The r_i are intrinsic growth (or decay) rates, and the a_{ij} describe the effect of the j-th upon the i-th population, which is positive if it enhances and negative if it inhibits the growth. The matrix $A = (a_{ij})$ is called the *interaction matrix*.
The state space of system (1) is the positive orthant represented by

$$\mathbb{R}^n_+ = \{x = (x_1, \dots, x_n) \in \mathbb{R}^n \mid x_i \geq 0 \text{ for } i = 1, \dots, n\}.$$

The boundary points of $\mathbb{R}^n_+$ lie on the coordinate planes $x_i = 0$, which correspond to the states where species i is absent. These "faces" are invariant, since $x_i(t) \equiv 0$ is the unique solution of the i-th equation of (1) satisfying $x_i(0) = 0$. In such a model, a missing species cannot "immigrate". Thus the boundary bd $\mathbb{R}^n_+$, and consequently $\mathbb{R}^n_+$ itself, are invariant under (1). So is the interior int $\mathbb{R}^n_+$, which means that if $x_i(0) > 0$ then $x_i(t) > 0$ for all t. The density $x_i(t)$ may approach 0, however, which means extinction. It is known that all possible two dimensional cases can be classified. Below we will see all possible cases for the two dimensional competition model that can occur. In higher dimensions, many open questions remain. We will see that even interaction of three species may lead to some kind of chaotic motion where the long-term outcome is unpredictable.

For ecological equations of the type $\dot{x}_i = x_i f_i(x)$ on $\mathbb{R}^n_+$ we can introduce the definition of a saturated fixed point.

Definition 4.1. *A fixed point $\hat{x}$ is a (strictly) saturated fixed point, if*

$$\hat{x}_i > 0 \Rightarrow f_i(\hat{x}) = 0 \qquad \textit{and}$$

$$\hat{x}_i = 0 \Rightarrow f_i(\hat{x}) \leq 0 \qquad (f_i(\hat{x}) < 0).$$

In other words, saturated means that no other species can invade the prevailing species a this fixed point.

Interior equilibria

The fixed points of (1) in int $\mathbb{R}^n_+$ are the solutions of the linear equations

$$r_i + \sum_{j=1}^{n} a_{ij} x_j = 0 \quad i = 1, \ldots, n \tag{2}$$

whose components are positive. (The equilibria on the boundary faces of $\mathbb{R}^n_+$ can be found in a similar way: one has only to note hat the restriction of (1) to any such face is again of Lotka-Volterra type.)

Theorem 4.2. *[5] Int $\mathbb{R}^n_+$ contains α- or ω- limit points if and only if (1) admits an interior equilibrium.*

The competitive Lotka-Volterra model

The competitive Lotka-Volterra system for n species is given by

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

We can see that this equation differs from (1) just in the minus sign. We will use this notation only in this chapter.
The mutual competition between the species dictates that $a_{ij} > 0$ for all $i \neq j$. In addition, each species is assumed to be self-regulating, and, in the absence of other species, to have a positive density independent growth rate constant; thus $a_{ii}, r_i > 0$ for all i.
The restriction of system (3) to the i-th coordinate axis is the logistic equation $\dot{x}_i = x_i(r_i - a_{ii}x_i)$, which has a fixed point E_i at the carrying capacity $K_i = \frac{r_i}{a_{ii}}$. Since each coordinate subspace of $\mathbb{R}^n$ is invariant under system (3), each E_i is a fixed point of the full system.

Two dimensional competitive Lotka-Volterra system

The two dimensional competitive Lotka-Volterra system is given by

$$\begin{aligned} \dot{x}_1 &= x_1(r_1 - a_{11}x_1 - a_{12}x_2) \\ \dot{x}_2 &= x_2(r_2 - a_{21}x_1 - a_{22}x_2) \end{aligned} \tag{4}$$

We will later examine the dynamical behaviour of the system by using the Jacobian matrix in order to gain insight in the stability of the fixed points. Another way of discussing the stability of fixed points, is the geometric approach, i.e., drawing the phase portrait.
We can start by examining the relationship between a vector field and a system of differential equations in the plane. For the system of differential equations given by

$$\begin{aligned} \dot{x} &= f(x, y) \\ \dot{y} &= g(x, y) \end{aligned}$$

the vector field is given by

$$F(x,y) = \begin{pmatrix} f(x,y) \\ g(x,y) \end{pmatrix}$$

The idea is that with every point (x, y) in the plane, there is associated a vector $F(x, y)$ with base point at (x, y). Thus, there is a collection of vectors (arrows) on the plane, with the magnitude and direction of the vector changing from point to point. A trajectory of the system goes along a curve such that the velocity vector of the curve at each point is the vector field at that same point. The basic geometric approach to determining the phase portrait is to find the fixed points, and then determine the signs of $\dot{x}$ and $\dot{y}$ in different regions of the plane. Since these time derivatives can change sign only at the points where they equal zero, we find the curves where $\dot{x} = 0$ and $\dot{y} = 0$. These curves are called *nullclines*, since they are curves on which one component of the vector field for the system of differential equation is zero (i.e., is either vertical or horizontal). They are sometimes called *isoclines* because the vector field has the same direction along one of these curves. This information is used to draw the phase portrait for the nonlinear system of differential equations. As we already know, the fixed points of the system are the intersection points of the particular nullclines of each species.

For the competitive Lotka-Volterra model, we can say: In the absence of all other species, the remaining species has *logistic growth* given by the equation

$$\dot{x} = rx(1 - \frac{x}{K})$$

where r and K are positive constants.
In the two dimensional Lotka-Volterra model, we have the following situation on the axes:

$$\dot{x}_1 = r_1 x_1 (1 - \frac{x_1}{\frac{r_1}{a_{11}}}) \text{ and } \dot{x}_2 = r_2 x_2 (1 - \frac{x_2}{\frac{r_2}{a_{22}}})$$

We have four fixed points, namely $0 = (0, 0)$, $E_1 = (K_1, 0)$, $E_2 = (0, K_2)$ and the interior fixed point $\hat{x} = (\frac{a_{12}r_2 - a_{22}r_1}{a_{12}a_{21} - a_{11}a_{22}}, \frac{-a_{11}r_2 + a_{21}r_1}{a_{12}a_{21} - a_{11}a_{22}})$, where $K_1 = \frac{r_1}{a_{11}}$ and $K_2 = \frac{r_2}{a_{22}}$.

The equilibria E_1 and E_2 describe the capacities of the system for the species 1 and 2, respectively. They represent the number of individuals the ecological system is capable of bearing. If the population density is above the capacity, the ecological environment cannot sustain the excess of individuals and the density of the respective species will decline until it reaches the capacity K_i. If the population density is under the capacity, it will grow until it reaches the capacity K_i and then it stops growing.

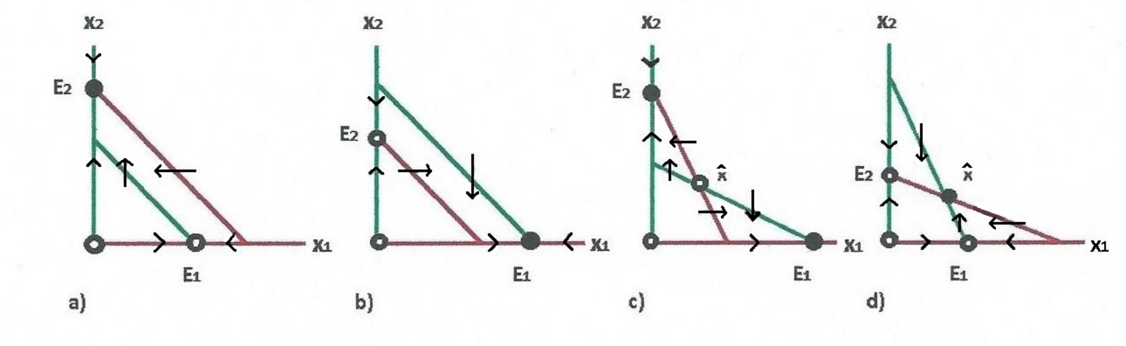


Figure 1: Possible cases for a two dimensional Lotka-Volterra competition model.

a) and b) depict dominance of species 2 over 1, respectively 1 over 2,
c) shows bistability ($\det(A) < 0$) and d) represents coexistence of the two species ($\det(A) > 0$). Solid circles represent a stable fixed point, open circles are unstable fixed points. The green lines are the nullclines $\dot{x}_1 = 0$ and the red lines are the nullclines $\dot{x}_2 = 0$.

By means of the Jacobian matrix

$$J(x) = DF|_x = \begin{pmatrix} r_1 - 2a_{11}x_1 - a_{12}x_2 & -a_{12}x_1 \\ -a_{21}x_2 & r_2 - a_{21}x_1 - 2a_{22}x_2 \end{pmatrix}$$

we can analyse the stability of the fixed points. We know that a fixed point is asymptotically stable if all eigenvalues of the Jacobian matrix have negative real part, with respect to the fixed point. In further calculations we will show how the cases $a) - d)$ from Figure 1 are obtained.

$J(0) = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix}$ has eigenvalues $\lambda_1 = r_1$ and $\lambda_2 = r_2$. According to initial definition, each r_i is positive, hence the origin $0 = (0, 0)$ is a source and thereby unstable.

$J(E_1) = \begin{pmatrix} -r_1 & -\frac{a_{12}r_1}{a_{11}} \\ 0 & r_2 - \frac{a_{21}r_1}{a_{11}} \end{pmatrix}$ has eigenvalues $\lambda_1 = -r_1$ and $\lambda_2 = r_2 - \frac{a_{21}r_1}{a_{11}}$.

In order to check when E_1 is stable, we have to examine for which values λ_2 is negative. Hence,

$$\lambda_2 = r_2 - \frac{a_{21}r_1}{a_{11}} = r_2 - K_1a_{12} < 0 \;\Leftrightarrow\; K_1 > \frac{r_2}{a_{21}}.$$

$J(E_2) = \begin{pmatrix} r_1 - \frac{a_{12}r_2}{a_{22}} & 0 \\ -\frac{a_{21}r_2}{a_{22}} & -r_2 \end{pmatrix}$ has eigenvalues $\lambda_1 = r_1 - \frac{a_{12}r_2}{a_{22}}$ and $\lambda_2 = -r_2$.

Examine for which values λ_1 is negative. The fixed point E_2 is stable for $K_2 > \frac{r_1}{a_{12}}$.

$$\lambda_1 = r_1 - \frac{a_{12}r_2}{a_{22}} = r_1 - K_2a_{12} < 0 \;\Leftrightarrow\; K_2 > \frac{r_1}{a_{12}}$$

The Jacobian for the interior equilibrium $\hat{x}$ is given by

$$J(\hat{x}) = -\mathrm{diag}(\hat{x}) \cdot A = \begin{pmatrix} -\hat{x}_1 a_{11} & -\hat{x}_1 a_{12} \\ -\hat{x}_2 a_{21} & -\hat{x}_2 a_{22} \end{pmatrix}$$

According to Theorem 3.2, we can investigate the stability of a fixed point by means of the trace and the determinant.

For asymptotic stability of the interior fixed point $\hat{x}$ we need to show that $\mathrm{tr}(J(\hat{x})) < 0$ and $\det(J(\hat{x})) > 0$ holds.

$$\mathrm{tr}(J(\hat{x})) = -\hat{x}_1 a_{11} - \hat{x}_2 a_{22} < 0 \text{ since } \hat{x}_1, \hat{x}_2, a_{11}, a_{22} > 0.$$

Consider now the determinant

$$\begin{aligned} \det J(\hat{x}) &= \det(\mathrm{diag}(\hat{x})) \cdot \det(A) \\ &= \hat{x}_1 \hat{x}_2 \cdot \det(A) \end{aligned}$$

The determinant is positive if and only if $\det(A) > 0$.

In summary, we can classify cases a) - d) from Figure 1.

a) $K_2 > \frac{r_1}{a_{12}}$ and $K_1 < \frac{r_2}{a_{21}}$ means species 2 dominates species 1.

b) $K_2 < \frac{r_1}{a_{12}}$ and $K_1 > \frac{r_2}{a_{21}}$ represents domination of species 1 over species 2.

c) $K_2 > \frac{r_1}{a_{12}}$ and $K_1 > \frac{r_2}{a_{21}}$ stands for bistability of species 1 and species 2.
In this case $\det(A) < 0$ holds.

d) $K_2 < \frac{r_1}{a_{12}}$ and $K_1 < \frac{r_2}{a_{21}}$ denotes coexistence of both species.
Here we have $\det(A) > 0$.

In the next chapter, we will see that we can discuss the stability of fixed points of two dimensional and three dimensional systems without checking where the null-clines intercept the ordinate and abscissa. We will concentrate on the entries of the interaction matrix.

5 Matrix stability concepts

The main references used in this section are 'The Theory of Evolution and Dynamical Systems, Mathematical Aspects of Selection' by Hofbauer and Sigmund [5] and 'Matrix Diagonal Stability in Systems and Computation' by Kaszkurewicz and Bhaya [6]. In this chapter we will embrace the relationship between stability properties of the Lotka-Volterra equation and the algebraic properties of the interaction matrix $A = (a_{ij})$.

At the end of the nineteenth century, the Russian mathematician Ljapunov showed that the differential equation

$$\frac{d}{dt}\, x(t) = Ax(t)$$

is asymptotically stable (i.e., all trajectories converge to zero) if and only if there exists a symmetric positive definite matrix X such that the matrix

$$XA + A^T X \quad \text{is negative definite.}$$

Around the same time, Hurwitz characterised stability in terms of the coefficients of the characteristic polynomial of the matrix A on the right-hand side of the differential equation above. This fact is used nowadays to say that a real square matrix is stable if all its eigenvalues lie in the open left half of the complex plane. One can use the Routh-Hurwitz criterion to determine if a matrix is stable. The following theorems will give the Routh-Hurwitz stability conditions for a two dimensional and a three dimensional matrix A.

Theorem 5.1. *A 2×2 matrix A is stable if and only if* $\mathrm{tr}(A) = a_{11} + a_{22} < 0$ *and* $\det(A) = a_{11}a_{22} - a_{12}a_{21} > 0$.

Theorem 5.2. *A 3×3 matrix A is stable if and only if* $\mathrm{tr}(A) < 0$, $\det(A) < 0$ *and* $\det(A) > M \cdot \mathrm{tr}(A)$ *holds, where M is the sum of the 2×2 principal minors $A_i = a_{jj}a_{kk} - a_{jk}a_{kj}$.*

Ljapunov stability

Definition 5.3. *A matrix A is called stable, if all eigenvalues of A have negative real part.*

Definition 5.4. *A matrix A is called semistable, if all eigenvalues of A have non-positive real part.*

Theorem 5.5. *[8] A matrix $A \in \mathbb{R}^{n\times n}$ is stable if and only if there exists a symmetric positive definite solution $X = X^T > 0$ to the Ljapunov equation*

$$XA + A^T X = C \tag{5}$$

where $C = C^T$ is negative definite.

Proof: $\boxed{\Rightarrow}$: Assume A is stable, i.e., all eigenvalues of A have negative real part. Then there exists a constant $c > 0$ such that

$$\|e^{tA}\| < e^{-ct} \tag{6}$$

for all elements of e^{tA}.

Define

$$X := -\int_0^\infty e^{tA^T} C e^{tA} dt$$

as a solution to (5). Because of (6), the integral exists and is finite.
We can verify that $X = -\displaystyle\int_0^\infty e^{tA^T} C e^{tA} dt$ is a solution to (5).

$$\begin{aligned}
XA + A^T X &= -\int_0^\infty e^{tA^T} C e^{tA} A \, dt - \int_0^\infty A^T e^{tA^T} C e^{tA} dt \\
&= -\int_0^\infty \left(e^{tA^T} C e^{tA} A + A^T e^{tA^T} C e^{tA}\right) \\
&= -\int_0^\infty \left(\frac{d}{dt}(e^{tA^T} C e^{tA})\right) dt \\
&= -e^{tA^T} C e^{tA}\Big|_0^\infty \\
&= \underbrace{-\lim_{t\to\infty}(e^{tA^T} C e^{tA})}_{\to 0} + \underbrace{e^{0\cdot A^T}}_{=I} C e^{0\cdot A} \\
&= C
\end{aligned}$$

Now let $v \neq 0$ be arbitrary in $\mathbb{R}^n$. Then

$$v^T X v = \int_0^\infty (e^{tA} v)^T (-C)(e^{tA} v) dt.$$

Since $-C > 0$ and e^{tA} is nonsingular for all t, the integrand is positive.
Hence $v^T \, X \, v > 0$ for all $v \neq 0$ and thus X is positive definite.

$\boxed{\Leftarrow}$: Suppose $X = X^T > 0$ and let λ be an eigenvalue of A with corresponding eigenvector y. There are two cases we have to distinguish. First, λ can be a real number and second, the eigenvalue can be complex with $\lambda = \alpha + i\beta,\ \beta \neq 0$.
Consider the case when λ is real. Then

$$\begin{aligned}
0 > y^T C y &= y^T X A y + y^T A^T X y \\
&= y^T X A y + (Ay)^T X y \\
&= y^T X \lambda y + (\lambda y)^T X y \\
&= \langle y, \lambda X y\rangle + \langle \lambda y, X y\rangle \\
&= (\lambda + \lambda)\langle y, X y\rangle
\end{aligned}$$

Since $y^T X y > 0$, we must have $2\lambda < 0$.

Contemplate now $\lambda = \alpha + i\beta$. Thus, $y \in \mathbb{C}^n$. Due to the fact that we are dealing with a complex eigenvalue, we will use a conjugated transpose or Hermitian transpose, which is denoted by H. For a real-valued matrix A, it holds $A^H = A^T$.

Then,

$$\begin{aligned} 0 > y^H C y &= y^H X A y + y^H A^H X y \\ &= y^H X A y + (Ay)^H X y \\ &= y^H X \lambda y + (\lambda y)^H X y \\ &= \langle y, \lambda\, Xy \rangle + \langle \lambda y, Xy \rangle \\ &= (\bar{\lambda} + \lambda)\langle y, Xy \rangle \\ &= (\alpha - i\beta + \alpha + i\beta)\langle y, Xy \rangle \\ &= 2\alpha \langle y, Xy \rangle \end{aligned}$$

As $y^H X y > 0$, we must have $2\alpha = 2\Re(\lambda) < 0$.

Since λ was arbitrary, it follows that A is stable. □

VL-stability and global stability

In this section we will examine the strongest stability concept, namely those guaranteeing global asymptotic stability. The basic notation and definitions that are used throughout this work are established below. Unless otherwise stated, we will use this terminology.

Definition 5.6. *[5] A matrix A is called Volterra-Ljapunov stable, VL-stable, Ljapunov diagonally stable, diagonally stable or dissipative, if there exists a positive diagonal matrix $D > 0$ such that the symmetric matrix $DA + A^T D$ is negative definite, i.e., if there exist positive numbers d_i such that*

$$\sum_i \sum_j d_i a_{ij} x_i x_j < 0 \quad \textit{for all} \quad x \neq 0. \tag{7}$$

i.e.,

$$\langle DAx, x \rangle \; < 0 \quad \textit{for all} \quad x \neq 0.$$

Volterra [14] formulated the definition of *VL-stability* in terms of a quadratic form and called it *dissipativity.*

Definition 5.7. *A matrix A is called VL-semistable if there exists a positive diagonal matrix $D > 0$ such that the symmetric matrix $DA + A^T D$ is negative semidefinite, i.e., if there exist positive numbers d_i such that*

$$\sum_i \sum_j d_i a_{ij} x_i x_j \leq 0 \quad \textit{for all} \quad x \in \mathbb{R}^n. \tag{8}$$

We can state now the next theorem which is of great importance.

Theorem 5.8. *[5] If a matrix A is VL-stable, then for every $r \in \mathbb{R}^n$ the Lotka-Volterra equation $\dot{x}_i = x_i(r_i + \sum_{j=1}^{n} a_{ij}x_j)$ has one globally stable fixed point. If the Lotka-Volterra equation admits an interior fixed point $\bar{x}$, then $\bar{x}$ is globally stable.*

Proof: (7) implies the existence of a saturated fixed point $\bar{x}$, see Theorem 5.30. Let $V(x)$ be the standard Ljapunov function proposed by Volterra,

$$V(x) = \sum_{i=1}^{n} d_i(\bar{x}_i \log x_i - x_i) \tag{9}$$

It has a unique global maximum at the point $\bar{x}$ and is defined for all x with $supp(x) \supseteq supp(\bar{x})$. Now

$$\begin{aligned}\dot{V}(x) &= \sum_i d_i(\bar{x}_i - x_i)\frac{\dot{x}_i}{x_i} = \sum_i d_i(\bar{x}_i - x_i)(r_i + \sum_j a_{ij}x_j) \\ &= -\sum_{i,j} d_i a_{ij}(x_i - \bar{x}_i)(x_j - \bar{x}_i) + \sum_i d_i(\bar{x}_i - x_i)(r_i + \sum_j a_{ij}\bar{x}_j)\end{aligned}$$

By (7) the first sum is positive for $x \neq \bar{x}$. In the second sum all terms with $\bar{x}_i > 0$ vanish since $\bar{x}$ is a fixed point, and the remaining terms are nonnegative since $\bar{x}$ is saturated. Thus $\bar{x}$ is globally stable. □

The next results will clearly reflect the invariance of *VL-stability* under inversion (A^{-1}), transposition (A^T) and multiplication by diagonal matrices DAD' with $D, D' > 0$.

Theorem 5.9. *[6] If A is VL-stable, then A^{-1} is VL-stable.*

Proof: Since A is *VL-stable*, there exists a positive definite diagonal matrix $D > 0$ such that $DA + A^T D$ is negative definite, i.e., $DA + A^T D = -Q < 0$ and further A is invertible. Pre-multiplying by the matrix $(A^{-1})^T$ and post-multiplying by the matrix A^{-1} yields

$$\begin{aligned}(A^{-1})^T DAA^{-1} + (A^{-1})^T A^T DA^{-1} &= (A^{-1})^T D \underbrace{AA^{-1}}_{=I} + \underbrace{(A^T)^{-1}A^T}_{=I} DA^{-1} \\ &= (A^{-1})^T D + DA^{-1} \\ &= -(A^{-1})^T QA^{-1} < 0\end{aligned}$$

and this completes the proof. □

Theorem 5.10. *[6] If A is VL-stable, then A^T is VL-stable.*

Proof: Since A is *VL-stable*, there exists a positive diagonal matrix D such that $\langle DAx, x\rangle = \langle x, A^T Dx\rangle \; < 0, \; \forall x \neq 0$. Set $x = D^{-1}z$ which maintains the negative definiteness of the quadratic form $\langle D^{-1}z, A^T DD^{-1}z\rangle = \langle z, D^{-1}A^T z\rangle < 0, \forall z \neq 0$, which shows that A^T is *VL-stable.* □

Theorem 5.11. *[5] If A is VL-stable and D, D' are positive diagonal matrices, then DAD' is VL-stable.*

Proof: We will show that in two steps, in fact by showing A is *VL-stable* $\Rightarrow$ AD' is *VL-stable* and AD' is *VL-stable* $\Rightarrow$ DAD' is *VL-stable.*
Assuming A is *VL-stable*, then there exists a positive diagonal matrix P, such that $PA + A^T P < 0$. We can pre- and post-multiply $PA + A^T P < 0$ with D' and obtain:

$$\begin{aligned} PA + A^T P &< 0 \\ \underbrace{D'P}_{=:M} AD' + D'A^T PD' &< 0 \\ MAD' + (AD')^T M &< 0 \end{aligned}$$

Because M is a positive diagonal matrix it follows that AD' is *VL-stable.*

According to Theorem 5.10, AD' is *VL-stable* implies $(AD')^T = D'A^T$ is *VL-stable.* From analogous computation as above, we obtain that $D'A^T D$ is *VL-stable* and hence DAD' is *VL-stable.* □

Definition 5.12. *A principal submatrix A_I of an $n \times n$ matrix A is a matrix (a_{ij}) with $i, j \in I \subseteq \{1, \ldots, n\}$. If I is of the form $\{1, 2, \ldots, k\}$, $k = 1, \ldots n$, then A_I is said to be a leading principal submatrix. The minors are the corresponding determinants.*

Theorem 5.13. *[2] [6] If A is VL-stable, then so are all principal submatrices of A.*

Proof: If A is *VL-stable*, then there exists a positive diagonal matrix P such that $Q := PA + A^T P < 0$. Since any principal submatrix of Q is negative definite, as can be seen by specialisation of the associated quadratic form, it follows that any principal submatrix is itself *VL-stable.* □

The next theorem gives us algebraic conditions for the *VL-stability* of a 2×2 interaction matrix.

Theorem 5.14. *A 2×2 matrix A is VL-stable*

$$\Leftrightarrow$$

$$a_{11} < 0,\ a_{22} < 0 \text{ and } \det(A) > 0.$$

Proof: $\boxed{\Rightarrow}$: By assumption A is *VL-stable* and hence the symmetric matrix

$$DA + A^T D = \begin{pmatrix} 2d_1 a_{11} & d_1 a_{12} + d_2 a_{21} \\ d_1 a_{12} + d_2 a_{21} & 2d_2 a_{22} \end{pmatrix}$$

is negative definite. One important property of negative definite matrices is the alternating sign of the leading principal minors, starting with negative sign. The second leading principal minor, which is also the determinant of the matrix, is positive. It holds:

$$|(DA + A^T D)_{1,1}| = |2d_1 a_{11}| = 2d_1 a_{11} < 0 \quad \Rightarrow a_{11} < 0. \quad \checkmark$$

$$\det(DA + A^T D) = 4a_{11}a_{22}d_1 d_2 - (a_{12}d_1 + a_{21}d_2)^2 > 0 \quad \Rightarrow a_{22} < 0. \quad \checkmark$$

From Theorem 5.5 we know that *VL-stability* implies *stability*, which means that every eigenvalue of A has negative real part. Furthermore, we know that the determinant of a matrix is the product of its eigenvalues. Let λ_1 and λ_2 be the two eigenvalues of A. We have $\det(A) = \underbrace{\lambda_1}_{<0} \cdot \underbrace{\lambda_2}_{<0} > 0.$ $\checkmark$
This consideration is also valid, if the eigenvalues were complex.

$\boxed{\Leftarrow}$: [4] We want to find D such that $DA + A^T D$ is negative definite, i.e., we need to show that

$$d_1 a_{11} < 0,\ d_2 a_{22} < 0 \tag{10}$$

and

$$4a_{11}a_{22}d_1 d_2 - (a_{12}d_1 + a_{21}d_2)^2 > 0 \tag{11}$$

(10) is true due to our precondition $a_{11} < 0,\ a_{22} < 0$.

For (11) there are three cases; a) $a_{12}a_{21} = 0$, b) $a_{12}a_{21} > 0$ and c) $a_{12}a_{21} < 0$.

In case a) either $a_{12} = 0$ or $a_{21} = 0$ or both are equal to zero. Suppose $a_{12} = 0$. Condition (11) becomes

$$d_2(4d_1 a_{11}a_{22} - d_2 a_{21}^2) > 0. \tag{12}$$

Clearly, it is possible to choose positive numbers d_1 and d_2 so that (12) is satisfied. Similar arguments apply when $a_{21} = 0$ or both are equal to zero.

In case b) $a_{12}a_{21} > 0$, either $a_{12} < 0$ and $a_{21} < 0$ or $a_{12} > 0$ and $a_{21} > 0$.

These subcases are known as competition and mutualism, respectively. Condition (11) can be rewritten as:

$$4d_1d_2(a_{11}a_{22} - a_{12}a_{21}) - (d_1a_{12} - d_2a_{21})^2 > 0. \tag{13}$$

Choose positive numbers d_1 and d_2 so that

$$d_1a_{12} - d_2a_{21} = 0, \tag{14}$$

which is possible as $a_{12}a_{21} > 0$. We obtain that

$$4d_1d_2(a_{11}a_{22} - a_{12}a_{21}) > 0$$

since $\det(A) = a_{11}a_{22} - a_{12}a_{21} > 0$ by assumption.

Case c) is a predator-prey interaction: a_{12} and a_{21} are non-zero and have opposite signs. Hence it is possible to select positive numbers d_1 and d_2 so that

$$d_1a_{12} + d_2a_{21} = 0.$$

We obtain

$$4a_{11}\, a_{22}d_1\, d_2 > 0.$$

□

For $n = 3$ see §8.

Theorem 5.15. *[15] Suppose that A is an $n \times n$ matrix. Then A is VL-stable if one of the following conditions is satisfied:*

(i) A is negative diagonally dominant, i.e., there exists a set of n positive numbers $\pi_i > 0$ $(i = 1, \dots, n)$ such that

$$-a_{ii}\pi_i > \sum_{j \neq i} |a_{ij}|\pi_j \quad i = 1, \dots, n$$

(ii) $A + A^T$ is negative definite, i.e., $x^T Ax < 0$ for all $x \neq 0$.

Proof: (i) Suppose that A is negative diagonally dominant. Then we define the matrix $\bar{A} = (\bar{a}_{ij})$ satisfying $\bar{a}_{ii} = a_{ii}$ and $\bar{a}_{ij} = |a_{ij}|$ for $i, j = 1, \dots, n,\ i \neq j$. Because of the negative diagonal dominance, there exists $\pi = (\pi_1, \dots, \pi_n) > 0$ such that $\bar{A}\pi < 0$. This implies that $\bar{A}$ is *VL-stable* [11]. Hence,

$$0 > |x|^T(D\bar{A} + \bar{A}^T D)|x| \geq x^T(DA + A^T D)x \text{ for any } x \in \mathbb{R}^n,\ x \neq 0.$$

(ii) Use the identity matrix I for the positive diagonal matrix D.
Then, $IA + A^T I = A + A^T < 0 \quad \Rightarrow A$ is *VL-stable.* □

D-stability and total stability

Motivation for D-stable matrices:

Let $\hat{x}$ be the interior fixed point of the Lotka-Volterra equation

$$\dot{x}_i = x_i(r_i + \sum_{j=1}^{n} a_{ij}x_j)$$

i.e., $r = -A\hat{x}$ holds. We can rewrite the L-V equation as

$$\dot{x}_i = x_i \sum_{j=1}^{n} a_{ij}(x_j - \hat{x}_j)$$

The Jacobian matrix is given by

$$J(x) = \begin{pmatrix} a_{11}(2x_1 - \hat{x}_1) + \sum_{j=2}^{n} a_{1j}(x_j - \hat{x}_j) & x_1 a_{12} & \dots & x_1 a_{1n} \\ x_2 a_{21} & a_{22}(2x_2 - \hat{x}_2) + \sum_{j\neq 2}^{n} a_{1j}(x_j - \hat{x}_j) & \cdots & x_2 a_{2n} \\ \vdots & \vdots & & \vdots \\ x_n a_{n1} & x_n a_{n2} & \dots & \begin{matrix} a_{nn}(2x_n - \hat{x}_n) \\ + \sum_{j=1}^{n-1} + a_{1j}(x_j - \hat{x}_j) \end{matrix} \end{pmatrix}$$

and we obtain for the interior fixed point $\hat{x}$

$$J(\hat{x}) = \begin{pmatrix} \hat{x}_1 a_{11} & \hat{x}_1 a_{12} & \dots & \hat{x}_1 a_{1n} \\ \hat{x}_2 a_{21} & \hat{x}_2 a_{22} & \cdots & \hat{x}_2 a_{2n} \\ \vdots & \vdots & & \vdots \\ \hat{x}_n a_{n1} & \hat{x}_n a_{n2} & \dots & \hat{x}_n a_{nn} \end{pmatrix} = diag(\hat{x}) \cdot A$$

and hence depends on the rates r_i.

In order to ensure the asymptotic stability of the interior fixed point (regardless where it is in the positive orthant), the interaction matrix A should be *D-stable.*

Definition 5.16. *A matrix A is called D-stable, if DA is stable for any positive diagonal matrix D, i.e., all eigenvalues of DA have negative real part.*

Definition 5.17. *A matrix A is called D-semistable, if DA is semistable for any positive diagonal matrix D, i.e., all eigenvalues of DA have nonpositive real part.*

The next theorem is important, as we will refer to it in further computations.

Theorem 5.18. *A 2×2 matrix A is D-stable*

$$\Leftrightarrow$$

$$a_{11} \leq 0,\ a_{22} < 0 \text{ (or vice versa) and } \det(A) > 0.$$

Proof: $\boxed{\Leftarrow}$: We can apply the Routh-Hurwitz Theorem, which states that a 2×2 matrix A is stable if and only if $\operatorname{tr}(A) < 0$ and $\det(A) > 0$ holds. We want to show that $\operatorname{tr}(DA) < 0$ and $\det(DA) > 0$ is valid.
Consider the trace $\operatorname{tr}(DA) = a_{11}d_1 + a_{22}d_2$. Since $a_{11} \leq 0$ and $a_{22} < 0$ we obtain $\operatorname{tr}(DA) < 0$.
We have $\det(DA) = \det(D)\ \det(A)$ is positive, because $\det(D) > 0$ and $\det(A) > 0$.

$\boxed{\Rightarrow}$: Since DA is stable, we know that $\operatorname{tr}(DA) < 0$ and $\det(DA) > 0$ is true.

$$\operatorname{tr}(DA) = a_{11}d_1 + a_{22}d_2 < 0 \quad \forall d_1, d_2 > 0 \Rightarrow\ a_{11} \leq 0,\ a_{22} \leq 0 \text{ but not both} = 0.$$

$$\det(DA) = \underbrace{\det(D)}_{>0}\ \det(A) > 0 \quad \Rightarrow\ \det(A) > 0.$$

□

Definition 5.19. *A matrix A is called totally stable, if every principal submatrix of A is D-stable.*

Theorem 5.20. *If A is VL-stable, then A is D-stable.*

Proof: According to Theorem 5.11, A *VL-stable* implies AD and DA are *VL-stable* for $D > 0$ diagonal matrix and hence stable, i.e., A is *D-stable.* □

Example 5.21. *(cf. Example 8.12) While VL-stability implies D-stability, the converse does not hold, since, e.g., the matrix*

$$A = \begin{pmatrix} -1 & -2 & 0 \\ -1 & -2 & -5 \\ 0 & 2 & -4 \end{pmatrix}$$

is D-stable but not VL-stable.

As per Theorem 5.13, A *VL-stable* implies every principal submatrix of A is itself *VL-stable.* If we consider the the principal submatrix $A_{1,2} = \begin{pmatrix} -1 & -2 \\ -1 & -2 \end{pmatrix}$, we see that the determinant $\det(A_{1,2}) = 0$ and this violates the condition of Theorem 5.14.

Theorem 5.22. *[2] [6] If A is D-stable, then all principal submatrices of A are D-semistable.*

Proof: Given P positive diagonal and a submatrix $A_{i_1,\ldots,i_l}$ (the subscripts indicate the rows and columns of A that make up the submatrix), let L be the limit of DA as the d_i with $i \notin \{i_1, \ldots, i_l\}$ decrease to zero. Every eigenvalue of $D_{i_1,\ldots,i_l}A_{i_1,\ldots,i_l}$ is an eigenvalue of L. But L is semistable, because A is *D-stable* and the eigenvalues of DA depend continuously on the d_i. □

Theorem 5.23. *If A is a VL-stable matrix, then A is a totally stable matrix.*

Proof: According to Theorem 5.13, any principal submatrix of a *VL-stable* matrix is itself *VL-stable* and hence, by Theorem 5.20, *D-stable* as well. It follows that any *VL-stable* matrix is *totally stable.* $\square$

Example 5.24. *The converse does not hold, since we can find a totally stable matrix which is not VL-stable. See Example 8.13 and Example 8.14.*

In the chapters §7 and §8 we will introduce convenient ways to check if a given 3×3 matrix is *totally stable* or *VL-stable.*

How these kinds of stabilities relate to each other?

In summary:

$$\boxed{A \text{ is } \textit{VL-stable}} \Rightarrow \boxed{A \text{ is } \textit{totally stable}} \Rightarrow \boxed{A \text{ is } \textit{D-stable}} \Rightarrow \boxed{A \text{ is } \textit{stable}}$$

In two dimensions we have equivalence between *VL-stability* and *total stability.*

To give a résumé, if the Lotka-Volterra equation admits an interior fixed point $\hat{x}$, and the interaction matrix is *VL-stable*, then $\hat{x}$ is globally stable. If the interaction matrix is *D-stable*, then $\hat{x}$ is locally asymptotically stable. It remains unsettled, if *D-stability* ensures global stability.

P-matrices

Another set of matrices that is of great importance for us, are the *P-matrices.*

Definition 5.25. *A matrix A is said to be a P-matrix, if all its principal minors are positive.*

Theorem 5.26. *[5] The following properties are equivalent:*

(P1) *A is a P-matrix.*

(P2) *For every diagonal matrix $D \geq 0$, $A + D$ is a P-matrix.*

(P3) *For all $x \neq 0$, there exists an i such that $x_i(Ax)_i > 0$.*

(P4) *For all $x \neq 0$, there exists a diagonal matrix $D > 0$ such that $x \cdot DAx = Dx \cdot Ax > 0$.*

(P5) *Every real eigenvalue of a principal submatrix of A is positive.*

Theorem 5.27. *[15] If a matrix A is VL-stable, then -A is a P-matrix.*

Proof: If A is *VL-stable*, then by definition there exists a diagonal matrix $D > 0$ such that $DA + A^T D < 0$, i.e., $-DA$ is a *P-matrix*. The principal minors of $-DA$ are equal to the product of the corresponding principal minors of $-A$ and D, since D is a diagonal matrix. Therefore, every principal minor of $-A$ is positive, that is, $-A$ is a *P-matrix*, because D is positive definite. $\square$

Theorem 5.28. *If a matrix A is totally stable, then -A is a P-matrix.*

Proof: If A is *totally stable*, then A is also stable, i.e., A has only eigenvalues with negative real part. Consider the principal submatrices A_I, with $I = \{1, \ldots, n\}$ of A. The determinant can be expressed as the product of eigenvalues.

Let the dimension of a principal submatrix be odd, $n = 2k - 1$.

$$\det(A_I) = \underbrace{\lambda_1}_{<0} \cdots \underbrace{\lambda_n}_{<0} < 0 \quad \Rightarrow \quad \det(-A_I) = \underbrace{(-1)^{2k-1}}_{<0} \underbrace{\det(A_I)}_{<0} > 0.$$

Consider an even dimension of a principal submatrix, $n = 2k$.

$$\det(A_I) = \underbrace{\lambda_1}_{<0} \cdots \underbrace{\lambda_n}_{<0} > 0 \quad \Rightarrow \quad \det(-A_I) = \underbrace{(-1)^{2k}}_{>0} \underbrace{\det(A_I)}_{>0} > 0.$$

This calculation is also valid, if the eigenvalues were complex.

Hence, $-A$ is a *P-matrix*. $\square$

Remark 5.29. *For a 2×2 matrix A it holds, A is VL-stable $\Leftrightarrow$ $-A$ is a P-matrix.*

The question why *P-matrices* are so important for ecological systems is answered in the next theorem.

Theorem 5.30. *[5] The Lotka-Volterra equation $\dot{x}_i = x_i(r_i + \sum_{j=1}^{n} a_{ij}x_j)$ has a unique saturated rest point for every $r \in \mathbb{R}^n$ if and only if $-A$ is a P-matrix.*

If the Lotka-Volterra equation, with interaction matrix A and $-A$ is a *P-matrix*, admits an interior fixed point, then there is no solution that converges to a point on the boundary.
If the Lotka-Volterra equation doesn't have an interior fixed point, then there must be a saturated fixed point on the boundary of $\mathbb{R}^n_+$.

6 Three dimensional Lotka-Volterra models

In this chapter we will deal with two examples of the Lotka-Volterra model. We will examine a three species cyclic competition model and a two-prey, one-predator model. In the next two subsections we will look more closely at the relation between the entries of the interaction matrix and the dynamical behaviour of the respective system. The sources that were used to prepare this chapter are [5] and 'Nonlinear Aspects of Competition Between Three Species' by May and Leonard [10].

The May-Leonard model

Algebraic conditions

The following example is given as an exercise in [5] and concerns the cyclic competition system in [10].

Example 6.1. *The matrix* $A = \begin{pmatrix} -1 & -\alpha & -\beta \\ -\beta & -1 & -\alpha \\ -\alpha & -\beta & -1 \end{pmatrix}$ *with* $\alpha, \beta > 0$ *is the interaction matrix of a 3 species competition model. The following equalities hold:*

a) $\quad$ *A is VL-stable* $\Leftrightarrow$ $-1 < \alpha + \beta < 2$.
b) $-A$ *is a P-matrix* $\Leftrightarrow$ $-1 < \alpha + \beta$ *and* $\alpha\beta < 1$.

Proof: a) $\boxed{\Rightarrow}$: We know that for a matrix A holds: A is *VL-stable* $\Rightarrow$ A is *stable*, i.e., every eigenvalue of A has negative real part.

In most cases it is a difficult task to find the eigenvalues of a matrix. For cyclic symmetry as in our case it is pretty easy. In [5] there is a formula presented for the eigenvalues and eigenvectors of a cyclic matrix.
An $n \times n$-matrix is said to be *circulant* if it is of the form

$$\begin{pmatrix} c_0 & c_1 & c_2 & \cdots & c_{n-2} & c_{n-1} \\ c_{n-1} & c_0 & c_1 & \cdots & c_{n-3} & c_{n-2} \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ c_2 & c_3 & c_4 & \cdots & c_0 & c_1 \\ c_1 & c_2 & c_3 & \cdots & c_{n-1} & c_0 \end{pmatrix}$$

where a cyclic permutation sends the elements of each row into those of the next one. The eigenvalues are given via

$$\gamma_k = \sum_{j=0}^{n-1} c_j \lambda^{jk} \quad k = 0, ..., n-1 \tag{15}$$

and the eigenvectors are

$$y_k = (1, \lambda^k, \lambda^{2k}, ..., \lambda^{(n-1)k})$$

where λ is the n-th root of unity

$$\lambda = e^{\frac{2\pi i}{n}}.$$

Now let us return to our matrix and calculate the three eigenvalues.

$$\begin{aligned}
\gamma_0 &= c_0\lambda^{0\cdot 0} + c_1\lambda^{1\cdot 0} + c_2\lambda^{2\cdot 0} \\
&= -1 \cdot 1 - \alpha \cdot 1 - \beta \cdot 1 \\
&= -1 - \alpha - \beta
\end{aligned}$$

$$\begin{aligned}
\gamma_1 &= c_0\lambda^{0\cdot 1} + c_1\lambda^{1\cdot 1} + c_2\lambda^{2\cdot 1} \\
&= -1 - \alpha e^{\frac{2\pi}{3}} - \beta e^{\frac{4\pi}{3}} \\
&= -1 - \alpha(\cos(\frac{2\pi}{3}) + i\sin(\frac{2\pi}{3})) - \beta(\cos(\frac{4\pi}{3}) + i\sin(\frac{4\pi}{3})) \\
&= -1 + \frac{\alpha+\beta}{2} + i\frac{\sqrt{3}}{2}(\beta - \alpha)
\end{aligned}$$

$$\begin{aligned}
\gamma_2 &= c_0\lambda^{0\cdot 2} + c_1\lambda^{1\cdot 2} + c_2\lambda^{2\cdot 2} \\
&= -1 - \alpha e^{\frac{4\pi}{3}} - \beta e^{\frac{8\pi}{3}} \\
&= -1 - \alpha(\cos(\frac{4\pi}{3}) + i\sin(\frac{4\pi}{3})) - \beta(\cos(\frac{8\pi}{3}) + i\sin(\frac{8\pi}{3})) \\
&= -1 + \frac{\alpha+\beta}{2} - i\frac{\sqrt{3}}{2}(\beta - \alpha)
\end{aligned}$$

We can see that the second and third eigenvalue have the same real part. Due to the fact that we have a *VL-stable* matrix, we know every eigenvalue has negative real part.

$$-1 - (\alpha+\beta) < 0 \Rightarrow \boxed{\alpha + \beta > -1} \quad \checkmark$$

$$\begin{gathered}
-1 + \frac{\alpha+\beta}{2} < 0 \;/ \cdot 2 \\
-2 + \alpha + \beta < 0 \\
\Rightarrow \boxed{\alpha + \beta < 2} \quad \checkmark
\end{gathered}$$

a) $\boxed{\Leftarrow}$: Recap the definition of *VL-stability*:
An $n \times n$-matrix A is VL-stable $\Leftrightarrow$ $\exists D > 0$ diagonal matrix such that the symmetric matrix $DA + A^T D$ is negative definite. In our example the symmetric matrix is of the form

$$DA + A^T D = \begin{pmatrix} -2d_1 & -(\alpha d_1 + \beta d_2) & -(\alpha d_3 + \beta d_1) \\ -(\alpha d_1 + \beta d_2) & -2d_2 & -(\alpha d_2 + \beta d_3) \\ -(\alpha d_3 + \beta d_1) & -(\alpha d_2 + \beta d_3) & -2d_3 \end{pmatrix}.$$

We choose the matrix D as the identity matrix and obtain

$$A + A^T = \begin{pmatrix} -2 & -(\alpha + \beta) & -(\alpha + \beta) \\ -(\alpha + \beta) & -2 & -(\alpha + \beta) \\ -(\alpha + \beta) & -(\alpha + \beta) & -2 \end{pmatrix}.$$

Our task is now to show negative definiteness and we will achieve this by using the alternating sign of the leading principal minors, starting with negative sign.

$$|(A + A^T)_{1,1}| = |-2| = -2 \ < \ 0. \quad \checkmark$$

$$|(A + A^T)_{1,2}| = \begin{vmatrix} -2 & -(\alpha + \beta) \\ -(\alpha + \beta) & -2 \end{vmatrix} = 4 - (\alpha + \beta)^2 \underbrace{>}_{-1<\alpha+\beta<2} 0. \quad \checkmark$$

$$\det(A + A^T) = -2(\alpha + \beta)^3 + 6(\alpha + \beta)^2 - 8$$

$$= -2 \underbrace{(\alpha + \beta - 2)^2}_{> 0} \underbrace{(\alpha + \beta + 1)}_{\substack{>0 \\ \text{because of} \\ \alpha+\beta>-1}} < \ 0. \quad \checkmark$$

$$\Rightarrow A \text{ is } \textit{VL-stable.}$$

b) $\boxed{\Leftrightarrow}$: Want to show, every principal minor of $-A$ is positive.

The 1×1 principal minors:

$$|(-A)_{1,1}| = |(-A)_{2,2}| = |(-A)_{3,3}| = |1| = 1. \quad \checkmark$$

Here are the 2×2 principal minors:

$$|(-A)_{1,2}| = |(-A)_{1,3}| = |(-A)_{2,3}| = \begin{vmatrix} 1 & \alpha \\ \beta & 1 \end{vmatrix} = 1 - \alpha\beta \underbrace{>}_{\alpha\beta<1} 0. \quad \checkmark$$

The determinant:

$$\det(-A) = \alpha^3 + \beta^3 - 3\alpha\beta + 1 = \underbrace{(\alpha+\beta+1)}_{\substack{>0 \\ \alpha+\beta>-1}} \underbrace{(\alpha^2+\beta^2-\alpha-\beta-\alpha\beta+1)}_{=\frac{1}{2}[(\alpha-\beta)^2+(1-\alpha)^2+(1-\beta)^2\,]>0} > 0. \quad \checkmark$$

We have shown that every principal minor is positive and from that we can conclude that -A is a *P-matrix*.

$\square$

In this example we can easily see that *VL-stability* is stronger than *P-matrix*. The condition of *VL-stability* implies the condition of *P-matrix*. We can geometrically illustrate this fact.

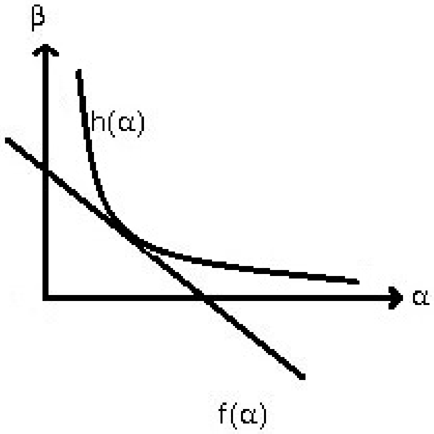


Figure 2: *VL-stabilitiy* $\Rightarrow$ *P-matrix*
$f(\alpha) = \beta < 2 - \alpha \quad \Rightarrow \quad h(\alpha) = \beta < \frac{1}{\alpha}$

Remark 6.2. *In view of the proof for a) and Theorem 5.23 we can conclude, that in this special example we have equivalence between VL-stability, total stability, D-stability and stability.*

Dynamical behaviour

Now, that we have proved the algebraic conditions, we can investigate the dynamics of this specific Lotka-Volterra competition model. The upcoming analysis of the dynamical behaviour of the May-Leonard model was taken from [5].

The Lotka-Volterra equation $\dot{x}_i = x_i(r_i + \sum_{j=1}^{3} a_{ij}x_j)$ with $A = \begin{pmatrix} -1 & -\alpha & -\beta \\ -\beta & -1 & -\alpha \\ -\alpha & -\beta & -1 \end{pmatrix}$ can be written as

$$\begin{aligned} \dot{x}_1 &= x_1(1 - x_1 - \alpha x_2 - \beta x_3) \\ \dot{x}_2 &= x_2(1 - \beta x_1 - x_2 - \alpha x_3) \\ \dot{x}_3 &= x_3(1 - \alpha x_1 - \beta x_2 - x_3) \end{aligned} \tag{16}$$

where we choose $r = (1, 1, 1)^T$.

For three or more competing species one can observe curious behaviour, which can be explained by the May-Leonard model. It may look for some time as if species 1 were bound to be the unique survivor. Then, suddenly, its density drops, species 2 takes its place and seems to dominate the "ecosystem"; after some time, it in turn collapses, however, and leaves the field to species 3, which appears to be the ultimate winner; but then, species 1 suddenly rallies and outcompetes its rivals, and so another "round" starts. The species supersede each other in cyclic fashion. An observer may get the impression that one species is better adapted and the other two doomed to extinction, until suddenly, without exterior cue, another revolution occurs. We will examine such a behaviour for system (16) with $0 < \beta < 1 < \alpha$.
Our system has eight fixed points.

Three two-species fixed points:

Set $x_3 = 0$
$\dot{x}_1 = 0$ holds for $x_1 = 0$ or for $1 - x_1 - \alpha x_2 - \beta x_3 = 0 \Rightarrow x_2 = -\frac{1}{\alpha}x_1 + \frac{1}{\alpha}$
$\dot{x}_2 = 0$ holds for $x_2 = 0$ or for $1 - \beta x_1 - x_2 - \alpha x_3 = 0 \Rightarrow x_2 = -\beta x_1 + 1$.

We obtain $x_1 = \frac{1-\alpha}{1-\alpha\beta}$ and $x_2 = \frac{1-\beta}{1-\alpha\beta}$. So the fixed point of species one and species two in absence of species 3 is $E_{12} = (\frac{1-\alpha}{1-\alpha\beta}, \frac{1-\beta}{1-\alpha\beta}, 0)$.

The remaining two-species fixed points can be obtained in the same way.
They are $E_{13} = (\frac{1-\beta}{1-\alpha\beta}, 0, \frac{1-\alpha}{1-\alpha\beta})$ and $E_{23} = (0, \frac{1-\alpha}{1-\alpha\beta}, \frac{1-\beta}{1-\alpha\beta})$.

Three one-species fixed points:
$E_1 = (1, 0, 0)$
$E_2 = (0, 1, 0)$
$E_3 = (0, 0, 1)$

One fixed point where no one survives, i.e., every species goes to extinction:
The origin $\mathbf{0} = (0, 0, 0)$.

One three-species fixed point, this is the interior fixed point denoted by $\hat{x}$:

$\hat{x} = \frac{1}{1+\alpha+\beta}(1, 1, 1)$ for $x_1 = x_2 = x_3$

As mentioned above, we can analyse the stability by using the Jacobian matrix J for each fixed point.

$$J = DF|_x = \begin{pmatrix} 1 - 2x_1 - \alpha x_2 - \beta x_3 & -\alpha x_1 & -\beta x_1 \\ -\beta x_2 & 1 - \beta x_1 - 2x_2 - \alpha x_3 & -\alpha x_2 \\ -\alpha x_3 & -\beta x_3 & 1 - \alpha x_1 - \beta x_2 - 2x_3 \end{pmatrix}$$

A fixed point is stable, if the Jacobian matrix with respect to the fixed point has only eigenvalues with negative real part.

$$J(0) = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}$$

has one eigenvalue, namely $\lambda_{1,2,3} = 1 > 0$. Hence, the origin $\mathbf{0} = (0, 0, 0)$ is a source and therefore unstable.

$$J(E_1) = \begin{pmatrix} -1 & -\alpha & -\beta \\ 0 & 1 - \beta & 0 \\ 0 & 0 & 1 - \alpha \end{pmatrix}$$

has three distinct eigenvalues, $\lambda_1 = -1 < 0$, $\lambda_2 = 1 - \beta > 0$, $\lambda_3 = 1 - \alpha < 0$. The fixed point $E_1 = (1, 0, 0)$ is a saddle point and therefore unstable.
The eigenvalues of the Jacobian matrix with respect to the other two edge fixed points E_2 and E_3 are the same like those for E_1, so we can conclude that they are also unstable.

The Jacobian matrix with respect to the interior fixed point $\hat{x}$ is given by

$$J(\hat{x}) = diag(\hat{x}) \cdot A = \begin{pmatrix} \frac{1}{1+\alpha+\beta} & 0 & 0 \\ 0 & \frac{1}{1+\alpha+\beta} & 0 \\ 0 & 0 & \frac{1}{1+\alpha+\beta} \end{pmatrix} \begin{pmatrix} -1 & -\alpha & -\beta \\ -\beta & -1 & -\alpha \\ -\alpha & -\beta & -1 \end{pmatrix}$$

$$= \frac{1}{1+\alpha+\beta} \begin{pmatrix} -1 & -\alpha & -\beta \\ -\beta & -1 & -\alpha \\ -\alpha & -\beta & -1 \end{pmatrix}$$

In order to obtain the eigenvalues we can apply (15), the formula for the eigenvalues of a cyclic matrix. Hereby we immediately obtain the eigenvalues

$\lambda_1 = -1$
$\lambda_2 = -1 + \frac{\alpha+\beta}{2} + i\frac{\sqrt{3}}{2}(\beta - \alpha)$

$\lambda_3 = -1 + \frac{\alpha+\beta}{2} - i\frac{\sqrt{3}}{2}(\beta - \alpha)$

The first eigenvalue is obviously negative, the second and third eigenvalue have the same real part. We will examine the sign in order to gain information about the stability of the inner fixed point $\hat{x}$.

$$-1 + \frac{\alpha+\beta}{2} = \begin{cases} \text{asymptotically stable for } < 0, & \text{iff } -1 < \alpha+\beta < 2 \\ \text{stable for } = 0, & \text{iff } \quad \alpha+\beta = 2 \\ \text{unstable for } > 0, & \text{iff } \quad \alpha+\beta > 2 \end{cases}$$

The three two-species fixed points E_{12}, E_{13} and E_{23} can be neglected, because with the restriction $0 < \beta < 1 < \alpha$ they are not in $\mathbb{R}^n_+$ and therefore they are biologically irrelevant.

In the following we will examine the dynamics of the May-Leonard model with a Ljapunov function, as well. We can start by investigating the case where $\alpha + \beta > 2$ holds. The restriction of (16) to the face $x_3 = 0$ yields a competition equation for x_1 and x_2, which we have studied above. In the absence of species 3, species 2 will outcompete species 1, see Figure 1 a). This implies that the stable manifold of E_2 is the two dimensional set $\{(x_1, x_2, x_3) \,|\, x_1 \geq 0,\, x_2 \geq 0,\, x_3 = 0\}$, while the unstable manifold of E_1 consists of a single orbit o_2 converging to E_2.
On the other boundary faces, the situation is similar: on the plane $x_1 = 0$, there is an orbit o_3 with α-limit E_2 and ω-limit E_3, and on $x_2 = 0$, there is an orbit o_1 from E_3 to E_1. We denote by F the set consisting of the three saddles E_1, E_2 and E_3 and three connecting orbits o_1, o_2 and o_3. See Figure 3 a) below. We shall show that for the case $\alpha + \beta > 2$ all orbits in int $\mathbb{R}^n_+$ (with the exception of those on the diagonal) have F as $\omega-$limit. The state thus remains for a long time close to the rest point E_1, then travels along o_2 to the vicinity of the rest point E_2, lingers there for a still

longer time then jumps over to the rest point E_3 and so on, in cyclic fits and starts. To verify this, we shall use the functions

$$S = x_1 + x_2 + x_3 \tag{17}$$

and

$$P = x_1 x_2 x_3. \tag{18}$$

to construct a Ljapunov function

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

One has

$$\begin{aligned} \dot{S} &= x_1 + x_2 + x_3 - [x_1^2 + x_2^2 + x_3^2 + (\alpha+\beta)(x_1x_2 + x_2x_3 + x_3x_1)] \\ &= S(1-S) - (\alpha+\beta-2)(x_1x_2 + x_1x_3 + x_2x_3) \end{aligned} \tag{19}$$

and

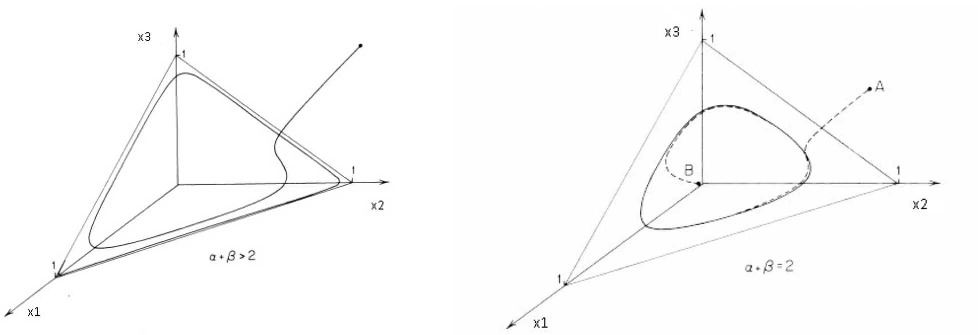
$$\begin{aligned} \dot{P} &= \dot{x}_1 x_2 x_3 + x_1 \dot{x}_2 x_3 + x_1 x_2 \dot{x}_3 \\ &= P\ \left(3 - (1+\alpha+\beta)S\,\right) \\ &= P\ \left[3(1-S) - (\alpha+\beta-2)S\,\right] \end{aligned} \tag{20}$$

(19) implies $\dot{S} \le S(1-S)$, so that no population can explode. A straightforward computation yields

$$\dot{L} = \left(\frac{P}{S^3}\right)^{\cdot} = S^{-4}P(1 - \frac{\alpha+\beta}{2})[(x_1-x_2)^2 + (x_2-x_3)^2 + (x_3-x_1)^2] \le 0.$$

The theorem of Ljapunov then implies that any orbit which is not on the (invariant) diagonal $x_1 = x_2 = x_3$ converges to the boundary (the set where P vanishes). But we have already investigated the behaviour there: the only candidate for an $\omega-$limit is the set F.
Of course such an ω-limit can never occur "in reality". Since lim inf $x_i(t) = 0$, one of the species will sooner or later vanish, and then one of the remaining species will outcompete the other one. Still, the model is of biological interest, as it suggests a surprising mechanism for sudden upheavals in ecological communities.

[10]



(a) (b)

Figure 3: The May-Leonard model with $a)$ $\alpha + \beta > 2$ and $b)$ $\alpha + \beta = 2$

$a)$ This figure illustrates the behaviour of the three competing populations x_1, x_2, x_3 with $\alpha + \beta > 2$. For the Ljapunov function holds $\dot{L} \leq 0$ 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. The fixed points E_1, E_2 and E_3 are saddle points. The ω-limit is a heteroclinic cycle.

$b)$ This figure depicts the three dimensional x_1, x_2, x_3 population space for $\alpha + \beta = 2$ and shows the limit cycle (solid curve) at the intersection of the $x_1 + x_2 + x_3 = 1$ and one particular hyperboloid, namely $x_1 x_2 x_3 = 0.02$. The dashed lines indicate the manner in which the system asymptotically tends to this limit cycle from the initial point $A = (0.2, 1, 0.8)$ and the point $B = (0.05, 0.01, 0.04)$.

Hence, for $\alpha + \beta < 2$ the inner fixed point $\hat{x}$ is globally stable, for $\alpha + \beta = 2$ all orbits lie on cones with $(PS^{-3}) = const$ and tend to periodic orbits, and finally for $\alpha + \beta > 2$ each orbit approaches the boundary.

In Theorem 5.8 the function $V(x) = \sum_{i=1}^{n} d_i(\bar{x}_i \log x_i - x_i)$ was introduced as a Ljapunov function for the general Lotka-Volterra model.

We will use this function and show, that we can actually apply it for system (16). In the proof $a)\boxed{\Leftarrow}$ of Theorem 6.1, we assumed $d_1 = d_2 = d_3 = 1$.

The time derivative of $V(x) = \sum_{i=1}^{n} (\bar{x}_i \log x_i - x_i)$ is given by

$$\begin{aligned}
\dot{V}(x) &= \sum_{i=1}^{3} \left(\frac{\bar{x}_i}{x_i} - 1 \right) \dot{x}_i = \sum_{i=1}^{3} \left(\frac{\bar{x}_i}{x_i} - 1 \right) x_i \left(r_i + \sum_{j=1}^{3} a_{ij} x_j \right) \\
&= \sum_{i=1}^{3} (\bar{x}_i - x_i) \left(r_i + \sum_{j=1}^{3} a_{ij} x_j \right) \\
&= (\bar{x}_1 - x_1)\ (\bar{x}_1 + \alpha\bar{x}_2 + \beta\bar{x}_3 - x_1 - \alpha x_2 - \beta x_3) + \\
&\quad + (\bar{x}_2 - x_2)\ (\beta\bar{x}_1 + \bar{x}_2 + \alpha\bar{x}_3 - \beta x_1 - x_2 - \alpha x_3) + \\
&\quad + (\bar{x}_3 - x_3)\ (\alpha\bar{x}_1 + \beta\bar{x}_2 + \bar{x}_3 - \alpha x_1 - \beta x_2 - x_3) \\
&= (\bar{x}_1 - x_1)^2 + (\bar{x}_2 - x_2)^2 + (\bar{x}_3 - x_3)^2 + \\
&\quad + (\alpha + \beta)\ ((\bar{x}_1 - x_1)(\bar{x}_2 - x_2) + (\bar{x}_1 - x_1)(\bar{x}_3 - x_3) + (\bar{x}_2 - x_2)(\bar{x}_3 - x_3)) \\
&= (\bar{x}_1 - x_1)^2 + (\bar{x}_2 - x_2)^2 + (\bar{x}_3 - x_3)^2 + \\
&\quad + (\alpha + \beta)\ \frac{[(\bar{x}_1 - x_1) + (\bar{x}_2 - x_2) + (\bar{x}_3 - x_3)]^2 - (\bar{x}_1 - x_1)^2 - (\bar{x}_2 - x_2)^2 - (\bar{x}_3 - x_3)^2}{2} \\
&= \frac{2 - (\alpha + \beta)}{2}\ \left((\bar{x}_1 - x_1)^2 + (\bar{x}_2 - x_2)^2 + (\bar{x}_3 - x_3)^2 \right) + \\
&\quad + \frac{\alpha + \beta}{2}\ ((\bar{x}_1 - x_1) + (\bar{x}_2 - x_2) + (\bar{x}_3 - x_3))^2
\end{aligned}$$

We can see that for $\alpha + \beta = 2$ we have $\dot{V}(x) \geq 0\ \forall x$ and $\dot{V}(x) = 0$ on the plane $\sum_{i=1}^{3} x_i = \sum_{i=1}^{3} \bar{x}_i$. In the case $0 < \alpha + \beta < 2$, it holds $\dot{V}(x) \geq 0$ for all x.

For $\alpha + \beta > 2$ we can conclude, that $V(x)$ is not a Ljapunov function for the system (16), since the summands of $\dot{V}(x)$ do not have the same sign.

Two-prey, one-predator Lotka-Volterra model

In order to expand our understanding of species interaction, we can also examine a system with two prey and one predator species. We will also introduce an interesting relationship between the structure of a matrix, in particular the entries and the existence of a unique saturated rest point of a Lotka-Volterra system.

Algebraic conditions

The next lemma is an exercise taken from [5], to which we can refer in an upcoming proof.

Lemma 6.3. *A two-prey, one-predator system whose interaction matrix is a P-matrix is totally stable.*

Proof: We will prove this Lemma by applying Theorem 7.1 Let A be such an interaction matrix, with $-A$ is a *P-matrix.*

$$A = \begin{pmatrix} -b_{11} & -b_{12} & -b_{13} \\ -b_{21} & -b_{22} & -b_{23} \\ b_{31} & b_{32} & -b_{33} \end{pmatrix} \text{ with } b_{ij} > 0,\ i,j \in \{1,2,3\}.$$

Because of the *P-matrix* property we know that every principal minor is positive. We can use that fact in our further calculations. Let us check every principal minor of $-A$. There are seven of them.

Here are the three 1×1 principal minors:

$$|b_{11}| = b_{11} > 0, \quad |b_{22}| = b_{22} > 0, \quad |b_{33}| = b_{33} > 0$$

Here are the three 2×2 principal minors:

$$-A_1 = \begin{vmatrix} b_{22} & b_{23} \\ -b_{32} & b_{33} \end{vmatrix} = b_{22}b_{33} + b_{23}b_{32} > 0$$

$$-A_2 = \begin{vmatrix} b_{11} & b_{13} \\ -b_{31} & b_{33} \end{vmatrix} = b_{11}b_{33} + b_{13}b_{31} > 0$$

$$\begin{aligned} -A_3 = \begin{vmatrix} b_{11} & b_{12} \\ b_{21} & b_{11} \end{vmatrix} &= b_{11}b_{22} - b_{12}b_{21} > 0 \\ &\Rightarrow b_{11}b_{22} > b_{12}b_{21} \end{aligned}$$

The determinant:

$$\begin{aligned}\det(-A) &= b_{11}b_{22}b_{33} - b_{12}b_{23}b_{31} - b_{13}b_{21}b_{32} \\ &\quad + b_{22}b_{13}b_{31} + b_{11}b_{23}b_{32} - b_{12}b_{21}b_{33} \\ \\ &= (b_{11}b_{22} - b_{12}b_{21})b_{33} + (b_{22}b_{13} - b_{12}b_{23})b_{31} \\ &\quad + (b_{11}b_{23} - b_{13}b_{21})b_{32} \\ &\quad > \ 0\end{aligned}$$

We can now apply Theorem 7.1

$$-b_{11} < 0. \checkmark \quad - b_{22} < 0. \checkmark \quad - b_{22} < 0. \checkmark$$

$$\det(-A) = (-1)^3 \det(A) = -\det(A) > 0 \ \Rightarrow \ \det(A) < 0. \checkmark$$

The 2×2 principal minors of $-A$ and A have the same sign. They are > 0. ✓

The last requirement we have to show is that

$$\begin{aligned}&\sqrt{b_{11}(b_{22}b_{33} + b_{23}b_{32})} + \sqrt{b_{22}(b_{11}b_{33} + b_{13}b_{31})} + \sqrt{b_{33}(b_{11}b_{22} - b_{12}b_{21})} \\ &> \sqrt{b_{11}b_{22}b_{33} - b_{12}b_{23}b_{31} - b_{13}b_{21}b_{32} + b_{22}b_{13}b_{31} + b_{11}b_{23}b_{32} - b_{12}b_{21}b_{33}}\end{aligned}$$

holds.

We can square the whole inequality and obtain:

$$\begin{aligned}&b_{11}b_{22}b_{33} + b_{11}b_{23}b_{32} + b_{11}b_{22}b_{33} + b_{22}b_{13}b_{31} + b_{11}b_{22}b_{33} - b_{12}b_{21}b_{33} + \\ &+ 2\sqrt{b_{11}(b_{22}b_{33} + b_{23}b_{32})}\sqrt{b_{22}(b_{11}b_{33} + b_{13}b_{31})} + \\ &+ 2\sqrt{b_{11}(b_{22}b_{33} + b_{23}b_{32})}\sqrt{b_{33}(b_{11}b_{22} - b_{12}b_{21})} + \\ &+ 2\sqrt{b_{22}(b_{11}b_{33} + b_{13}b_{31})}\sqrt{b_{33}(b_{11}b_{22} - b_{12}b_{21})} \\ &> b_{11}b_{22}b_{33} - b_{12}b_{23}b_{31} - b_{13}b_{21}b_{32} + b_{22}b_{13}b_{31} + b_{11}b_{23}b_{32} - b_{12}b_{21}b_{33}\end{aligned}$$

This leads to

$$\begin{aligned}&2b_{11}b_{22}b_{33} + b_{12}b_{23}b_{31} + b_{13}b_{21}b_{32} + \\ &+ 2\sqrt{b_{11}(b_{22}b_{33} + b_{23}b_{32})}\sqrt{b_{22}(b_{11}b_{33} + b_{13}b_{31})} + \\ &+ 2\sqrt{b_{11}(b_{22}b_{33} + b_{23}b_{32})}\sqrt{b_{33}(b_{11}b_{22} - b_{12}b_{21})} + \\ &+ 2\sqrt{b_{22}(b_{11}b_{33} + b_{13}b_{31})}\sqrt{b_{33}(b_{11}b_{22} - b_{12}b_{21})} \ > \ 0\end{aligned}$$

As we know, all b_{ij} are positive and all radicands are also positive, so on the left-hand side we have only positive terms. We satisfied all conditions of Theorem 7.1.

i.e., we have shown that

$$\sqrt{b_{11}(b_{22}b_{33}+b_{23}b_{32})}+\sqrt{b_{22}(b_{11}b_{33}+b_{13}b_{31})}+\sqrt{b_{33}(b_{11}b_{22}-b_{12}b_{21})}+$$

$$-\sqrt{b_{11}b_{22}b_{33}-b_{12}b_{23}b_{31}-b_{13}b_{21}b_{32}+b_{22}b_{13}b_{31}+b_{11}b_{23}b_{32}-b_{12}b_{21}b_{33}} > 0$$

holds. □

The next theorem is an exercise from [5] as well. We can use the previous lemma to prove the following.

Theorem 6.4. *Consider two-prey, one-predator systems*

$$-A_\varepsilon = \begin{pmatrix} a & b & 1 \\ c & d & 1 \\ -1 & -1 & \varepsilon \end{pmatrix} \text{ with } (a,b,c,d,\varepsilon > 0).$$

a) A_ε *is VL-stable for every* $\varepsilon > 0 \quad \Rightarrow \quad 4ad \geq (b+c)^2$.
A_ε *is VL-stable for every* $\varepsilon > 0 \quad \Leftarrow \quad 4ad > (b+c)^2$.

b) $(i), (ii)$ *and* (iii) *are equivalent*

(i) $-A_\varepsilon$ *is a P-matrix for every* $\varepsilon > 0$
(ii) A_ε *is totally stable for every* $\varepsilon > 0$
(iii) $ad > bc$ *and* $a + d \geq b + c$

We can also construct matrices A which are totally stable but not VL-stable. (See Example 8.14).

Before we start with the proof, we can briefly show that

$$4ad > (b+c)^2 \;\Rightarrow\; ad > bc \text{ and } a+d > b+c$$

holds. This can be verified by using the inequality of arithmetic and geometric means, which postulates the following relationship for real, non-negative numbers x_i, where $i = 1, \dots, n$

$$\frac{x_1 + \ldots + x_n}{n} \geq (x_1 \cdots x_n)^{\frac{1}{n}}.$$

Equality holds if and only if $x_1 = \ldots = x_n$.

$$\begin{aligned} 4ad &> (b+c)^2 \\ ad &> \frac{(b+c)^2}{4} \geq bc \\ &\Rightarrow ad > bc \end{aligned}$$

$$4ad > (b+c)^2 \quad /\sqrt{}$$

$$2\,\frac{a+d}{2} \geq 2\sqrt{ad} \;> b+c$$

$$a+d \geq 2\sqrt{ad} > 2\,\frac{b+c}{2} \geq 2\sqrt{bc}$$

$$\Rightarrow a+d > b+c$$

Thus, we have

$$\frac{a+d}{2} \geq \sqrt{ad} > \frac{b+c}{2} \geq \sqrt{bc}.$$

From $a+d = b+c$ and the condition for *VL-stability* it follows $a = d$.

Proof: a) $\boxed{\Rightarrow}$: An $n \times n$ matrix A is VL-stable $\Leftrightarrow$ $\exists D > 0$ diagonal matrix such that the symmetric matrix $DA + A^T D$ is negative definite. In our example we have, that

$$DA_\varepsilon + A_\varepsilon^T D = \begin{pmatrix} -2ad_1 & -(bd_1+cd_2) & d_3-d_1 \\ -(bd_1+cd_2) & -2dd_2 & d_3-d_2 \\ d_3-d_1 & d_3-d_2 & -2\varepsilon d_3 \end{pmatrix}$$

is negative definite. This is equivalent to $-(DA_\varepsilon + A_\varepsilon^T D)$ is positive definite.
One property of positive definite matrices is that every principal minor is positive.

Consider the 2×2 principal minors of $-(DA_\varepsilon + A_\varepsilon^T D)$.

$$|(-(DA_\varepsilon + A_\varepsilon^T D))_{2,3}| = \begin{vmatrix} 2dd_2 & d_2-d_3 \\ d_2-d_3 & 2\varepsilon d_3 \end{vmatrix} = 4d\varepsilon d_2 d_3 - (d_2-d_3)^2 > 0.$$

Note that d_i depends on ε. But as $\varepsilon \to 0$, this implies $d_2 = d_3$.

$$|(-(DA_\varepsilon + A_\varepsilon^T D))_{1,3}| = \begin{vmatrix} 2ad_1 & d_1-d_3 \\ d_1-d_3 & 2\varepsilon d_3 \end{vmatrix} = 4a\varepsilon d_1 d_3 - (d_1-d_3)^2 > 0.$$

Hence, for $\varepsilon \to 0$ it follows $d_1 = d_3$.

$$|(-(DA_\varepsilon + A_\varepsilon^T D))_{1,2}| = \begin{vmatrix} 2ad_1 & (bd_1+cd_2) \\ (bd_1+cd_2) & 2dd_2 \end{vmatrix} = 4add_1d_2 - (bd_1+cd_2)^2 > 0.$$

Since the above implies $d_1 = d_2$ for small ε, we obtain:

$$= 4add_1d_1 - (bd_1+cd_1)^2 > 0$$

$$= 4add_1^2 - ((b+c)d_1)^2 > 0$$

$$= 4add_1^2 - (b+c)^2 d_1^2 > 0$$

$$= (4ad - (b+c)^2)d_1^2 \; > 0$$

$$= 4ad - (b+c)^2 \geq \; 0, \quad \text{i.e.,} \quad 4ad \geq (b+c)^2 \quad \text{holds.}$$

Remark 6.5. *We can ask ourselves what will happen for $\varepsilon = 0$? We will denote this case by A_0 and examine it.*

Is A_0 still *VL-stable*? The answer to this question is no, since the diagonal entries of a *VL-stable* matrix have to be negative.
We will see that A_0 is *VL-semistable*, because we can show A_0 is in the closure of the set of *VL-stable* matrices. The closure of the set of *VL-stable* matrices can be described by $\overline{VL} = \{A \in \mathbb{R}^{n\times n} \,|\, \exists D > 0 \text{ diagonal matrix } : DA + A^T D \leq 0\}$.

As we know, the closure is a closed set and a closed set can be defined as a set which contains all its limit points. Thus, we can find a convergent sequence A_n, $n \in \mathbb{N}$ in $\overline{VL}$ whose limit is A_0 and is contained in $\overline{VL}$.

$$A_n = \begin{pmatrix} -a & -b & -1 \\ -c & -d & -1 \\ 1 & 1 & \frac{1}{n} \end{pmatrix} \quad \longrightarrow \quad A_0 = \begin{pmatrix} -a & -b & -1 \\ -c & -d & -1 \\ 1 & 1 & 0 \end{pmatrix} \quad \text{for } n \to \infty$$

We can apply the Frobeniusnorm and obtain $\lim\limits_{n\to\infty} \|A_n\|_F = \|A_0\|_F$.

$\boxed{\Leftarrow}$: We want to show, $4ad > (b+c)^2$ implies A_ε is *VL-stable*, i.e., the matrix $DA_\varepsilon + A_\varepsilon^T D$ is negative definite for some $D > 0$ diagonal.

Assume, D is the identity matrix.

$$(A_\varepsilon + A_\varepsilon^T) = -\begin{pmatrix} 2a & b+c & 0 \\ b+c & 2d & 0 \\ 0 & 0 & 2\varepsilon \end{pmatrix}$$

Show, the leading principal minors have alternating sign, starting with negative sign.

$$|(A_\varepsilon + A_\varepsilon^T)_{1,1}| = -2a < 0 \;, \quad a > 0.$$

$$|(A_\varepsilon + A_\varepsilon^T)_{1,2}| = \begin{vmatrix} 2a & b+c \\ b+c & 2d \end{vmatrix} = 4ad - (b+c)^2 \underset{4ad > (b+c)^2}{>} 0.$$

$$\det(A_\varepsilon + A_\varepsilon^T) = -(4ad - (b+c)^2)\, 2\varepsilon \underset{4ad > (b+c)^2}{<} 0.$$

Showed, the matrix $DA_\varepsilon + A_\varepsilon^T D$ is negative definite for some $D > 0$.

$$\Rightarrow A_\varepsilon \text{ is VL-stable.}$$

Remark 6.6. *At this point we will temporary pause and reconsider the propositions made in a). We have seen that if A_ε is VL-stable for every $\varepsilon > 0$ it follows that $4ad \geq (b+c)^2$ holds. Conversely, we have that $4ad > (b+c)^2$ implies VL-stability. As there is a gap in this statement, we will try to find conditions for $a, b, c, d > 0$ to complete this assertion. In order to obtain some further restrictions, we are going to apply a method which is presented in Theorem 8.1 and concerns testing for VL-stability. We will pursue this consideration in chapter § 8.*

Now, we will continue with the proof of Theorem 6.4.

b) The following are equivalent:

(i) $\quad -A_\varepsilon$ is a P-matrix for every $\varepsilon > 0$

(ii) $\quad A_\varepsilon$ is totally stable for every $\varepsilon > 0$

(iii) $\quad ad > bc$ and $a + d \geq b + c$

$(i) \Rightarrow (ii)$: Lemma 6.3
$(ii) \Rightarrow (i)$: Theorem 5.28
$(i) \Leftrightarrow (iii)$: Every principal minor of $-A$ is positive:

$$A_3 = \begin{vmatrix} a & b \\ c & d \end{vmatrix} = ad - bc > 0 \Leftrightarrow ad > bc \checkmark$$

$$\begin{vmatrix} a & b & 1 \\ c & d & 1 \\ -1 & -1 & \varepsilon \end{vmatrix} = (ad - bc)\varepsilon + a + d - b - c > 0 \quad \forall \varepsilon > 0$$

$$\Leftrightarrow a + d \geq b + c \checkmark$$

$\square$

Dynamical behaviour

Now we can investigate the dynamics of the system with interaction matrix A_ε. How we can apply the introduced theorems?

The Lotka-Volterra system with respect to A_ε can be described by these three equations

$$\begin{aligned} \dot{x}_1 &= x_1(\ a+b+1-ax_1-bx_2-x_3) \\ \dot{x}_2 &= x_2(\ c+d+1-cx_1-dx_2-x_3) \\ \dot{x}_3 &= x_3(\varepsilon-2+x_1+x_2-\varepsilon x_3) \end{aligned} \tag{21}$$

where we choose $r = (a+b+1, c+d+1, \varepsilon-2)^T$.

For this choice of r the system has an interior fixed point $\hat{x} = (1,1,1)^T$.
It is globally stable if condition a) of Theorem 6.4 holds and locally stable if b) of Theorem 6.4 holds.

As this is a two prey-one, predator system, we see that the intrinsic rates for the two prey species x_1 and x_2 are positive, while for the predator the intrinsic rate is negative. This means, that without the prey populations the predator would go extinct.

From previous considerations we know, that the matrix A_ε is a *P-matrix* and from Theorem 5.30 that the interior fixed point is a unique saturated fixed point.

Gilpin model - chaotic behaviour

In the previous chapters we dealt with "nice" examples, where the dynamical behaviour was predictable and the solutions settled down to equilibria or to cycles. In two dimensions, all cases can be classified and we know, there is no chaotic motion possible. Unfortunately, we cannot claim that for higher dimensions, as there many open questions remain. Numerical simulations showed that even for three interacting species chaotic behaviour is attainable. The asymptotic behaviour of the solutions consists of highly irregular oscillations and depends in a very sensitive way upon the initial conditions. Therefore, we are not able to forecast the long term outcome.

The next example of a two-prey, one-predator interaction will illustrate such circumstances. It was presented by Gilpin in 'Spiral Chaos in a Predator-Prey Model' [3].

Example 6.7.

$$\begin{aligned} \dot{x}_1 &= x_1(\quad 1-x_1-x_2-10\,x_3) \\ \dot{x}_2 &= x_2(\quad 1-1,5\,x_1-x_2-x_3) \\ \dot{x}_3 &= x_3(-1+5\,x_1+0,5\,x_2) \end{aligned} \tag{22}$$

We can easily verify that $-A$ is not even a *P-matrix*, if we would consider competition within the predator species, for example $\varepsilon = 0.001$. In this example one principal minor $\det(A_{1,2})$ is negative. Therefore, we can have very interesting dynamical behaviour if just one requirement is violated.

Here we can see the chaotic motion for the Gilpin system, where x_1 and x_2 are the prey and x_3 represents the predator.

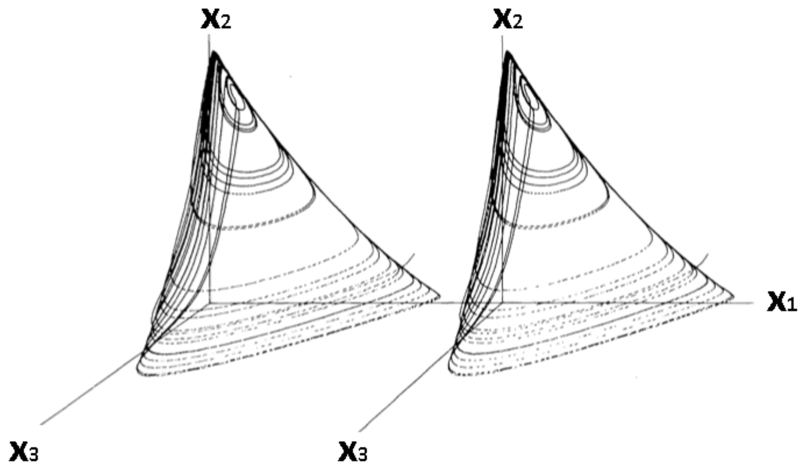


Figure 4: [3] Nonperiodic oscillations

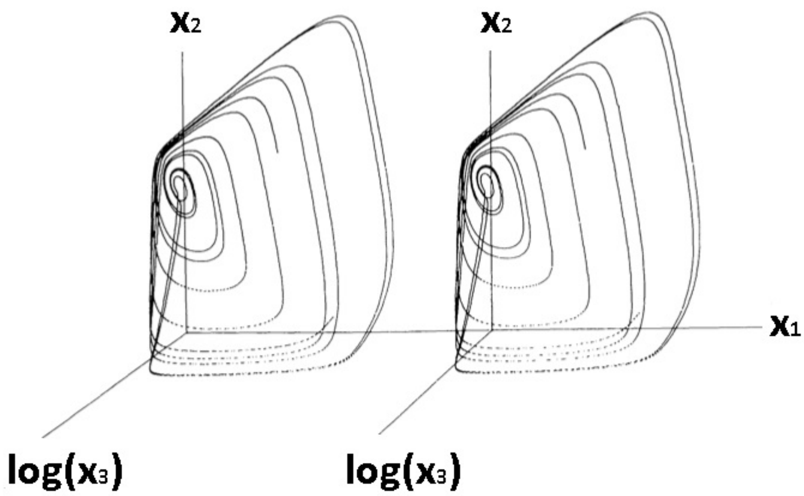


Figure 5: [3] Stereoscopic state space trajectories of system (22).
Both figures, Figure 4 and Figure 5, have the same parameter values and the same initial conditions. The lower plot shows that there are no discontinuous behaviours at low predator densities that might have arisen as computer artifacts. The trajectory is dashed where it moves most rapidly.

We can observe the dynamics also from a third perspective:

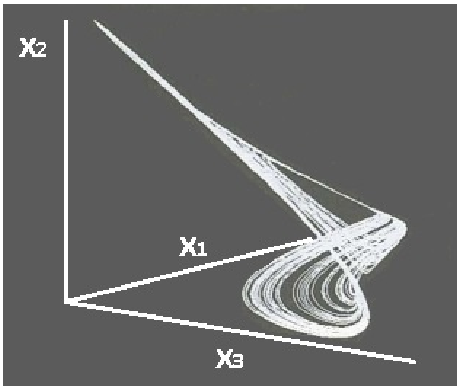


Figure 6: [13] In the absence of predation, species 1 would outcompete species 2. But the first species is also the predator's preferred lunch. When it comes abundant the population of the the other prey species recovers.

7 Testing for total stability

The next theorem provides us with a method to examine if a 3×3 matrix is *totally stable.*

Theorem 7.1. *A 3×3 matrix A is totally stable*

$$\Leftrightarrow$$

(i) $a_{ii} < 0$*,*

(ii) the 2 × 2 minors $A_i = a_{jj}a_{kk} - a_{kj}a_{jk}$ *are positive,*

(iii) $\det(A) < 0$,

(iv) $\sqrt{-a_{11}A_1} + \sqrt{-a_{22}A_2} + \sqrt{-a_{33}A_3} > \sqrt{-\det(A)}$

The proof is based on the proof that is given by Cain [1].

Proof: $\boxed{\Leftarrow}$: A *totally stable* matrix is itself *D-stable* and every principal submatrix is also *D-stable.* We will begin the proof by showing *D-stability* of the whole matrix, i.e., DA is stable for every positive diagonal matrix $D = \mathrm{diag}(d_1, d_2, d_3) > 0$.

Consider $b_{ii} = -a_{ii} = |a_{ii}|,\ i \in \{1, 2, 3\}$.

Applying the Routh-Hurwitz Theorem, see Theorem 5.2, to the characteristic polynomial of DA,

$$char(\lambda) = \lambda^3 - \mathrm{tr}(DA)\lambda^2 + ((DA)_1 + (DA)_2 + (DA)_3)\lambda - \det(DA),$$

we obtain the following statement:

$$\text{The matrix } DA \text{ is stable } \Leftrightarrow \begin{array}{l} (a)\ a_{ii}d_i < 0, \\ (b)\ \mathrm{tr}(DA) < 0, \\ (c)\ \det(DA) < 0, \\ (d)\ \det(DA) > \mathrm{tr}(DA)[(DA)_1 + (DA)_2 + (DA)_3]. \end{array}$$

We will now verify the points $(a), (b), (c)$ and (d).

(a) is fulfilled, $a_{11}d_1 = -b_{11}d_1 < 0$, because $b_{11} > 0$ and $d_1 > 0$. For $a_{22}d_2$ and $a_{33}d_3$ we can use the same argument.
(b) is also valid, because $\mathrm{tr}(DA) = -b_{11}d_1 - b_{22}d_2 - b_{33}d_3 < 0$.
(c) holds, because $\det(DA) = d_1\,d_2\,d_3\,\underbrace{\det(A)}_{<0} < 0$.
(d) We want to show that $\det(DA) > \mathrm{tr}(DA)[(DA)_1 + (DA)_2 + (DA)_3]$ is true. Rewrite it as

$$d_1\,d_2\,d_3\ \det(A) > (-b_{11}d_1 - b_{22}d_2 - b_{33}d_3)(A_1\,d_2\,d_3 + A_2\,d_1\,d_3 + A_3\,d_1\,d_2)$$

$$d_1\,d_2\,d_3\ \det(A) - (-b_{11}d_1 - b_{22}d_2 - b_{33}d_3)(A_1\,d_2\,d_3 + A_2\,d_1\,d_3 + A_3\,d_1\,d_2) > 0$$

$$\det(A) + \frac{(b_{11}d_1 + b_{22}d_2 + b_{33}d_3)(A_1\,d_2\,d_3 + A_2\,d_1\,d_3 + A_3\,d_1\,d_2)}{d_1\,d_2\,d_3} > 0 \tag{23}$$

Set

$$f(d_1, d_2, d_3) = \frac{(b_{11}d_1 + b_{22}d_2 + b_{33}d_3)(A_1\,d_2\,d_3 + A_2\,d_1\,d_3 + A_3\,d_1\,d_2)}{d_1\,d_2\,d_3}.$$

We can now return to our precondition (iv) and reform it to obtain a more suitable term for our purpose. We have

$$\sqrt{-a_{11}A_1} + \sqrt{-a_{22}A_2} + \sqrt{-a_{33}A_3} > \sqrt{-\det(A)} \qquad /^2$$

and since we have positive expressions on both sides, we can square the left-hand and the right-hand side. We obtain

$$\begin{aligned} &- a_{11}A_1 - a_{22}A_2 - a_{33}A_3 + 2\sqrt{-a_{11}A_1}\,\sqrt{-a_{22}A_2} \\ &+ 2\sqrt{-a_{11}A_1}\,\sqrt{-a_{33}A_3} + 2\sqrt{-a_{22}A_2}\,\sqrt{-a_{33}A_3} \qquad > -\det(A) \end{aligned}$$

$$\begin{aligned}&\det(A) - a_{11}A_1 - a_{22}A_2 - a_{33}A_3 + 2\sqrt{-a_{11}A_1}\sqrt{-a_{22}A_2}\\&+ 2\sqrt{-a_{11}A_1}\sqrt{-a_{33}A_3} + 2\sqrt{-a_{22}A_2}\sqrt{-a_{33}A_3} \qquad > 0\end{aligned}$$

$$\begin{aligned}&\det(A) + b_{11}A_1 + b_{22}A_2 + b_{33}A_3 + 2\sqrt{b_{11}A_1}\sqrt{b_{22}A_2}\\&+ 2\sqrt{b_{11}A_1}\sqrt{b_{33}A_3} + 2\sqrt{b_{22}A_2}\sqrt{b_{33}A_3} \qquad > 0\end{aligned} \tag{24}$$

We can now compare (23) to our precondition (24), and we see that we have to examine the relation between $f(d_1, d_2, d_3)$ and $b_{11}A_1 + b_{22}A_2 + b_{33}A_3 + 2\sqrt{b_{11}A_1}\sqrt{b_{22}A_2} + 2\sqrt{b_{11}A_1}\sqrt{b_{33}A_3} + 2\sqrt{b_{22}A_2}\sqrt{b_{33}A_3}$.

For convenience we will use $\Delta = \sqrt{b_{11}A_1} + \sqrt{b_{22}A_2} + \sqrt{b_{33}A_3}$.

A straightforward computation shows that

$$\begin{aligned}d_1\, d_2\, d_3(\, f(d_1, d_2, d_3) - \Delta^2) &= b_{11}A_1\, d_1\, d_2\, d_3 + b_{11}A_2 d_1^2\, d_3 + b_{11}A_3\, d_1^2\, d_2\\&+ b_{22}A_1\, d_2^2\, d_3 + b_{22}A_2\, d_1\, d_2\, d_3 + b_{22}A_3\, d_1\, d_2^2\\&+ b_{33}A_1\, d_2\, d_3^2 + b_{33}A_2\, d_1\, d_3^2 + b_{33}A_3\, d_1\, d_2\, d_3\\&- b_{11}A_1\, d_1\, d_2\, d_3 - b_{22}A_2\, d_1\, d_2\, d_3 - b_{33}A_3\, d_1\, d_2\, d_3\\&- 2\sqrt{b_{11}A_1}\sqrt{b_{22}A_2} d_1\, d_2\, d_3\\&- 2\sqrt{b_{11}A_1}\sqrt{b_{33}A_3} d_1\, d_2\, d_3\\&- 2\sqrt{b_{22}A_2}\sqrt{b_{33}A_3}\, d_1\, d_2\, d_3\\&\\&= d_3(\sqrt{b_{11}A_2} d_1 - \sqrt{b_{22}A_1} d_2)^2\\&+ d_2(\sqrt{b_{11}A_3} d_1 - \sqrt{b_{33}A_1} d_3)^2\\&+ d_1(\sqrt{b_{22}A_3} d_2 - \sqrt{b_{33}A_2} d_3)^2\end{aligned}$$

We have proved that (d) is also fulfilled and further that the matrix A is *D-stable.*

Remark 7.2. *We can write*

$$f(d_1, d_2, d_3) = \left(\sum_i b_{ii} d_i\right)\left(\sum_i A_i \cdot \frac{1}{d_i}\right) \geq \left(\sum_i \sqrt{b_{ii}Ai}\right)^2$$

by using the Cauchy-Schwarz inequality

$$\sum_i x_i^2 \cdot \sum_i y_i^2 \geq \left(\sum_i x_i y_i\right)^2.$$

In order to ensure *total stability* our next step is to show that every principal submatrix of A is *D-stable* as well. We can apply Theorem 5.18 for *D-stability* of 2×2 matrices on the submatrix $A_{2,3}$, whose determinant is denoted by A_1. We see that $A_{2,3}$ is *D-stable* since $a_{22}, a_{33} < 0$ and $\det(A_{2,3}) = A_1 > 0$ are our preconditions. We can use the same argument for the remaining 2×2 submatrices $A_{1,2}$ and $A_{1,3}$.

For the 1×1 submatrices $(DA)_{1,1}, (DA)_{2,2}, (DA)_{3,3}$ we need to show that they have negative eigenvalues, which is not very difficult, since $a_{11}, a_{22}, a_{33} < 0$ holds.

$\boxed{\Rightarrow}$: Suppose A is *totally stable*, then $-\det(A) < f(d_1, d_2, d_3)$ holds. We also know, that $f(d_1, d_2, d_3) \geq \Delta^2$ is valid. From that we can write $-\det(A) < \Delta^2 \leq f(d_1, d_2, d_3)$ and we see that (iv) is shown.
(i) is true, since from $d_i a_{ii} < 0 \;\Rightarrow a_{ii} < 0 \;\; i = 1, 2, 3$
(ii) The principal minors A_1, A_2, A_3 are positive, since every principal submatrix of A is *D-stable*, particularly for the 2×2 submatrices we have two eigenvalues with negative real part and hence A_i is positive, $\; i = 1, 2, 3$.
(iii) is fulfilled, because from $\det(DA) = d_1\, d_2\, d_3 \det(A) < 0 \;\Rightarrow\; \det(A) < 0$. □

From the previous theorem we can derive a slightly different way to verify *D-stability.*

Let A be a 3×3 matrix. We say that a_{ii} and A_i, $(i = 1, 2, 3)$, 1 and $\det(A)$ are supplementary principal minors of each other. In addition, we say that A is of *type 1* if some principal minor of A vanishes without its supplement vanishing also. Otherwise, A is of *type 2*.

Corollary 7.3. *[1]* *A is D-stable*

$$\Leftrightarrow$$

(i) $a_{ii} \leq 0, \quad a_{11} + a_{22} + a_{33} < 0$

(ii) $A_i = a_{jj}a_{kk} - a_{kj}a_{jk} \geq 0, \quad A_1 + A_2 + A_3 > 0$

(iii) $det(A) < 0,$

(iv) $\sqrt{-a_{11}A_1} + \sqrt{-a_{22}A_2} + \sqrt{-a_{33}A_3} \geq \sqrt{-\det(A)}$ *if A is of type*1

$\sqrt{-a_{11}A_1} + \sqrt{-a_{22}A_2} + \sqrt{-a_{33}A_3} > \sqrt{-\det(A)}$ *if A is of type*2

The proof is given by Cain [1].

8 Testing for VL-stability

As mentioned in the previous chapters, we will give now the introduction in the method to verify if a given 3×3 matrix is *VL-stable* or not. In order to be consistent with the terminology and the obtained results we will give the theorem slightly rephrased by Kaszkurewicz and Bhaya [6] and furthermore the original text given by Kraaijevanger [7].

Theorem 8.1. *[6] A* 3×3 *matrix* $A = (a_{ij})$ *is VL-stable if and only if* $-A$ *has the following properties*
(i) $-A$ *is a P-matrix and*
(ii) Each of the four numbers 1, ω_1, ω_2, ω_3 *is smaller than the sum of the other three (or, equivalently,* $\max(1, \omega_1, \omega_2, \omega_3) < \frac{1}{2}(1 + \omega_1 + \omega_2 + \omega_3)$*)*
where $\omega_i = \sqrt{-a_{ii}((-A)^{-1})_{ii}}$, $i = 1, 2, 3$.

Before we proceed with the proof of this theorem, we can examine the relation between the condition (ii) of Theorem 8.1 for *VL-stability* and (iv) of Theorem 7.1 for *total stability.*

Consider (iv)

$$\sqrt{-a_{11}A_1} + \sqrt{-a_{22}A_2} + \sqrt{-a_{33}A_3} > \sqrt{-\det(A)} \tag{25}$$

where $a_{ii} < 0$, $A_i > 0$ for $i = 1, 2, 3$ and $\det(A) < 0$.

We can divide inequality (25) by $\sqrt{-\det(A)}$ and obtain:

$$\sqrt{\frac{a_{11}A_1}{\det(A)}} + \sqrt{\frac{a_{22}A_2}{\det(A)}} + \sqrt{\frac{a_{33}A_3}{\det(A)}} > 1 \tag{26}$$

Let us briefly repeat the inverse of a 3×3 matrix A.

$$A^{-1} = \frac{1}{\det(A)} \begin{pmatrix} A_1 & -a_{12}a_{33} + a_{32}a_{13} & a_{12}a_{23} - a_{22}a_{13} \\ -a_{21}a_{33} + a_{31}a_{23} & A_2 & -a_{11}a_{23} + a_{21}a_{13} \\ a_{21}a_{32} - a_{31}a_{22} & -a_{11}a_{32} + a_{12}a_{31} & A_3 \end{pmatrix}$$

Now consider (26) and take the diagonal entries of the inverse matrix into account.

$$\sqrt{a_{11}(A^{-1})_{11}} + \sqrt{a_{22}(A^{-1})_{22}} + \sqrt{a_{33}(A^{-1})_{33}} > 1 \tag{27}$$

We see, the summand $\sqrt{a_{ii}(A^{-1})_{ii}}$ with $i = 1, 2, 3$ equals to the ω_i's from condition (ii) of Theorem 8.1., i.e., $\omega_1 + \omega_2 + \omega_3 > 1$.

The following text is prepared by means of Kraaijevanger [7]. Kraaijevanger made use of positive stability in his work.

Definition 8.2. *A matrix A is called positive stable, if all eigenvalues of A have positive real part.*

Definition 8.3. *[7] A matrix A is said to be Ljapunov diagonally stable if there exists a diagonal matrix $D > 0$ such that $DA + A^T D > 0$. This is equivalent to $-A$ is VL-stable.*

There are several characterizations for *VL-stability*. We will present Kraaijevanger's main theorem from [7] where he used the *Hadamard product* $A \circ B$ of two matrices $A = (a_{ij})$ and $B = (b_{ij})$ of the same size, defined by $A \circ B = (a_{ij}b_{ij})$.

Theorem 8.4. *[7] The following statements are equivalent for a matrix A:*
(L1) A is diagonally stable
(L2) $A \circ S$ is a P-matrix for all $S = S^T = (s_{ij}) \geq 0,\ s_{ii} \neq 0$
(L3) $A \circ S$ is a P-matrix for all $S = S^T = (s_{ij}) \geq 0,\ s_{ii} = 1$

The proof of this theorem is based on the following four results and is given later.

Theorem 8.5. *A matrix A is diagonally stable if and only if*
(L4) AS has at least one positive diagonal element for all $S = S^T = (s_{ij}) \geq 0, S \neq 0$.

Theorem 8.6. *(cf.5.26) [11] A matrix A is a P-matrix if and only if for each real vector $x = (x_i) \neq 0$ there exists an index i with $x_i(Ax)_i > 0$.*

Theorem 8.7. *Let $P = (p_{ij})$ and $Q = (q_{ij})$ be two symmetric matrices of the same size. If $P > 0$ and $Q \geq 0$, $(q_{ii}) \neq 0$ then $P \circ Q > 0$.*

An immediate consequence of the previous theorem is the following:

Corollary 8.8. *If A is diagonally stable, then so is $A \circ S$ for all $S = S^T = (s_{ij}) \geq 0, (s_{ii}) \neq 0$.*

Proof: Suppose $D > 0$ is a diagonal matrix such that $DA + A^T D > 0$. It follows from Theorem 8.7 that for any S as above we have $D(A \circ S) + (A \circ S)^T D = (DA + A^T D) \circ S > 0$ □

Proof: [of Theorem 8.4] Since the implication $(L2) \Rightarrow (L3)$ is trivial, it is sufficient to prove the implications $(L1) \Rightarrow (L2)$ and $(L3) \Rightarrow (L1)$.

$(L1) \Rightarrow (L2)$: This follows immediately from Corollary 8.8 and the fact that any diagonally stable matrix is a *P-matrix*.

$(L3) \Rightarrow (L1)$: Suppose $(L3)$ holds, and let $S = S^T = (s_{i,j}) \geq 0$, $S \neq 0$, be given. Introducing the diagonal matrix $D = diag(d_i)$, $d_i = \sqrt{s_{ii}}$, we can write $S = D\tilde{S}D$, where $\tilde{S} = \tilde{S}^T = (\tilde{s}_{i,j}) \geq 0$, $\tilde{s}_{ii} = 1$. In view of $(L3)$ (with S replaced by $\tilde{S}$), $A \circ \tilde{S}$ is a *P-matrix*. Theorem 8.6 (with A replaced by $A \circ \tilde{S}$ and $x = (d_i)$) shows that there exists an index i with $d_i \sum_j (A \circ \tilde{S})_{ij} d_j > 0$, i.e., $\sum_j a_{ij} s_{ij} > 0$, i.e., $(AS)_{ii} > 0$. An application of Theorem 8.5 completes the proof. □

Theorem 8.9. *[7] A matrix A is diagonally stable if and only if it satisfies one of the following equivalent conditions, (cf. Theorem 8.4):*
$(L2')$ A is a P-matrix satisfying $\det(A \circ S) > 0$ *for all* $S = S^T = (s_{ij}) \geq 0,\ s_{ii} \neq 0$
$(L3')$ A is a P-matrix satisfying $\det(A \circ S) > 0$ *for all* $S = S^T = (s_{ij}) \geq 0,\ s_{ii} = 1$

The following theorem gives us for $n = 3$ a very nice way to test if a given matrix is *VL-stable*, i.e., *diagonally stable.*

Theorem 8.10. *[7] A 3×3 matrix $A = (a_{ij})$ is diagonally stable if and only if*
(i) A is a P-matrix and
(ii) Each of the four number 1, ω_1, ω_2, ω_3 is smaller than the sum of the other three (or, equivalently, max$(1, \omega_1, \omega_2, \omega_3) < \frac{1}{2}(1 + \omega_1 + \omega_2 + \omega_3)$)
where $\omega_i = \sqrt{a_{ii}(A^{-1})_{ii}}$, $i = 1, 2, 3$.

Proof: By Theorem 8.9, A is diagonally stable if and only if $(L3')$ holds. It is easy to see that the matrix $S = S_{a,b,c}$ defined by

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

is positive semidefinite if and only if $(a, b, c) \in \Omega$, where $\Omega \subset \mathbb{R}^3$ is given by

$$\Omega = \{(a, b, c) : |a| \leq 1, |b| \leq 1, |c| \leq 1, a^2 + b^2 + c^2 - 2abc \leq 1\}.$$

Hence, it is sufficient to prove that for a *P-matrix* A, condition (ii) is equivalent to

$$f(a, b, c) \ > \ 0 \text{ for all } (a, b, c) \in \Omega \tag{28}$$

where $f : \Omega \to \mathbb{R}$ is defined by

$$\begin{aligned} f(a, b, c) &= \det(A \circ S_{a,b,c}) \\ &= a_{11}a_{22}a_{33} - a_{12}a_{21}a_{33}a^2 - a_{13}a_{22}a_{31}b^2 \\ &\quad - a_{11}a_{23}a_{32}c^2 + (a_{12}a_{23}a_{31} + a_{13}a_{21}a_{32})abc. \end{aligned}$$

A simple calculation shows that for any $(a, b, c) \in \Omega$, the condition $\partial f/\partial a = \partial f/\partial b = \partial f/\partial c = 0$ implies

$$\begin{aligned} f(a, b, c) &= a_{33}(a_{11}a_{22} - a_{12}a_{21}a^2) \\ &\geq a_{33} \min(a_{11}a_{22}, a_{11}a_{22} - a_{12}a_{21}) > 0. \end{aligned}$$

Hence (28) is equivalent to

$$f(a,b,c) > 0 \text{ for all } (a,b,c) \in \partial\Omega \tag{29}$$

where $\partial\Omega$ denotes the boundary of Ω. This boundary can be parametrized by $a = \cos\ \alpha$, $b = \cos\ \beta$, $c = \cos(\alpha \pm \beta)$ (where $\alpha, \beta \in [0,\pi]$) and therefore also by $a = \cos\ \alpha$, $b = \cos\ \beta$, $c = \cos(\alpha + \beta)$ (where $\alpha \in [0,\pi]$ and $\beta \in [-\pi,\pi]$).
Since

$$f(\cos\ \alpha, \cos\ \beta, \cos(\alpha+\beta)) = \frac{\det\ \mathrm{A}}{4}\ g(\alpha,\beta)$$

where

$$g(\alpha,\beta) = C_1 + C_2\ \cos(2\alpha) + C_3\ \cos(2\beta) + C_4\ \cos(2\alpha+2\beta), \text{ with}$$

$$C_1 = 1 + \omega_1^2 + \omega_2^2 + \omega_3^2$$

$$C_2 = 1 - \omega_1^2 - \omega_2^2 + \omega_3^2$$

$$C_3 = 1 - \omega_1^2 + \omega_2^2 - \omega_3^2$$

$$C_4 = 1 + \omega_1^2 - \omega_2^2 - \omega_3^2$$

it follows that (29) is equivalent to

$$g(\alpha,\beta) > 0 \quad (\text{for all } \alpha,\beta). \tag{30}$$

Rewriting $g(\alpha,\beta)$ as

$$g(\alpha,\beta) = C_1 + C_2\ \cos(2\alpha) + [C_3 + C_4\ \cos(2\alpha)]\cos(2\beta) - C_4\ \sin(2\alpha)\sin(2\beta),$$

we see that for any fixed α we have

$$\begin{aligned}\min_{\beta} g(\alpha,\beta) &= C_1 + C_2\ \cos(2\alpha) - \sqrt{[C_3 + C_4\ \cos(2\alpha)]^2 + [C_4\ \sin(2\alpha)]^2} \\ &= C_1 + C_2\ \cos(2\alpha) - \sqrt{C_3^2 + C_4^2 + 2\,C_3C_4\ \cos(2\alpha)}.\end{aligned}$$

Hence (30) is equivalent to

$$\sqrt{C_3^2 + C_4^2 + 2\,C_3\,C_4 t}\ <\ C_1 + C_2\,t \quad \text{for all } t \in [-1,1].$$

Since $C_1 > 0$, it is easy to see that we may replace the left- and right-hand sides of the above inequality by their squares, leading to the equivalent condition

$$p(t) > 0 \quad \text{for all } t \in [-1, 1] \tag{31}$$

where

$$p(t) = \gamma_2\, t^2 + \gamma_1\, t + \gamma_0,$$

$$\gamma_2 = C_2^2 = (1 - \omega_1^2 - \omega_2^2 + \omega_3^2)^2,$$

$$\gamma_1 = 2\,(C_1 C_2 - C_3 C_4) = 8\,(\omega_3^2 - \omega_1^2 \omega_2^2),$$

$$\gamma_0 = C_1^2 - C_3^2 - C_4^2 = 8\,(\omega_3^2 + \omega_1^2 \omega_2^2) - \gamma_2.$$

Note that $p(-1) = \gamma_2 - \gamma_1 + \gamma_0 = 16\,\omega_1^2\,\omega_2^2 > 0$ and $p(1) = \gamma_2 + \gamma_1 + \gamma_0 = 16\,\omega_3^2 > 0$. Hence (31) is fulfilled if $\gamma_2 = 0$.
If $\gamma_2 > 0$, then p has a minimum $\mu = \dfrac{(4\gamma_0\gamma_2 - \gamma_1^2)}{4\gamma_2}$ at $t = -\dfrac{\gamma_1}{2\gamma_2}$. We conclude that (31) is equivalent to

$$|\gamma_1| < 2\gamma_2 \;\Rightarrow\; \gamma_1^2 < 4\gamma_0\,\gamma_2. \tag{32}$$

Note that $|\gamma_1| < 2\gamma_2$ is equivalent to $-4\gamma_2 < \gamma_1 - 2\gamma_2 < 0$ and that $\gamma_1^2 < 4\,\gamma_0\gamma_2$ is equivalent to $(\gamma_1 - 2\gamma_2)^2 < 4\,\gamma_2(\gamma_2 - \gamma_1 + \gamma_0)$. Using $\gamma_2 - \gamma_1 + \gamma_0 = 16\,\omega_1^2\,\omega_2^2$ once more, we see that (32) is equivalent to

$$-4\gamma_2 < \gamma_1 - 2\gamma_2 < 0 \;\Rightarrow\; \gamma_1 - 2\gamma_2 > -8\,\omega_1\,\omega_2\sqrt{\gamma_2},$$

which can be reduced to

$$\gamma_1 \le -2\gamma_2 \quad \vee \quad \gamma_1 > 2\gamma_2 - 8\,\omega_1\,\omega_2\sqrt{\gamma_2}. \tag{33}$$

In the following we will show that (33) is equivalent to

$$\sqrt{\gamma_2} < 2\,(\omega_1\,\omega_2 + \omega_3). \tag{34}$$

We distinguish two cases:

<u>*Case 1:*</u> Suppose $\gamma_2 \le 4\,\omega_1^2\,\omega_2^2$.

Then (34) trivially holds. Furthermore, (33) holds as well, since $\gamma_2 \le 4\,\omega_1^2\,\omega_2^2$ and $\gamma_1 > -2\gamma_2$ imply $\gamma_1 > 2\gamma_2 - 8\,\omega_1\,\omega_2\sqrt{\gamma_2}$.

<u>*Case 2:*</u> Suppose $\gamma_2 > 4\,\omega_1^2\,\omega_2^2$.

Then $\gamma_1 + 2\gamma_2 = 8\,\omega_3^2 - 8\,\omega_1^2\,\omega_2^2 + 2\gamma_2 > 8\,\omega_3^2 > 0$, so that $\gamma_1 > -2\gamma_2$.
Hence (33) reduces to $\gamma_1 > 2\gamma_2 - 8\,\omega_1\,\omega_2\sqrt{\gamma_2}$, i.e., $8\,\omega_3^2 > 2\,(\sqrt{\gamma_2} - 2\,\omega_1\,\omega_2)^2$, i.e., $\sqrt{\gamma_2} < 2\,(\omega_1\,\omega_2 + \omega_3)$.
Finally, to see that (34) is equivalent to (ii), one may square the left-and right-hand sides of (34) and reorder terms to obtain

$$(\omega_1+\omega_2+\omega_3-1)(\omega_1+\omega_2-\omega_3+1)\times(\omega_1-\omega_2+\omega_3+1)(-\omega_1+\omega_2+\omega_3+1) > 0. \tag{35}$$

Note that the sum of any two factors of the above product is positive, implying that (35) is equivalent to the positivity of each of the four factors, i.e., (ii). $\square$

At this point we will give an answer to the question that came up in Remark 6.6, concerning the gap between the necessary and sufficient conditions in Theorem 6.4, part a). The idea is to apply Theorem 8.1 to the matrix A_ε. I thank my advisor for his insistence and his help.

Consider

$$-A_\varepsilon = \begin{pmatrix} a & b & 1 \\ c & d & 1 \\ -1 & -1 & \varepsilon \end{pmatrix} \text{ with } a,b,c,d,\varepsilon > 0.$$

Recall the proposition:

$$A_\varepsilon \textit{ VL-stable} \text{ for every } \varepsilon > 0 \;\Rightarrow\; 4ad \geq (b+c)^2$$
$$A_\varepsilon \textit{ VL-stable} \text{ for every } \varepsilon > 0 \Leftarrow\; 4ad > (b+c)^2.$$

We will start by deriving again the first implication.
In view of Theorem 8.1, we have to investigate the inequalities

$$\begin{aligned} \text{I:}\quad & \omega_1 < 1+\omega_2+\omega_3 \\ \text{II:}\quad & \omega_2 < 1+\omega_1+\omega_3 \\ \text{III:}\quad & \omega_3 < 1+\omega_1+\omega_2 \\ \text{IV:}\quad & 1 < \omega_1+\omega_2+\omega_3 \end{aligned}$$

where $\omega_1 = \sqrt{\frac{a(1+d\varepsilon)}{(ad-bc)\varepsilon+a+d-b-c}}$, $\omega_2 = \sqrt{\frac{d(1+a\varepsilon)}{(ad-bc)\varepsilon+a+d-b-c}}$, $\omega_3 = \sqrt{\frac{(ad-bc)\varepsilon}{(ad-bc)\varepsilon+a+d-b-c}}$.

Remember, $\omega_i = \sqrt{-a_{ii}((-A)^{-1})_{ii}}$. The inverse of $-A_\varepsilon$ is given by

$$(-A_\varepsilon)^{-1} = \frac{1}{(ad-bc)\varepsilon+a+d-b-c}\begin{pmatrix} 1+d\varepsilon & -1-b\varepsilon & b-d \\ -1-c\varepsilon & 1+a\varepsilon & c-a \\ d-c & a-b & ad-bc \end{pmatrix}$$

with $a,b,c,d > 0$ for all $\varepsilon > 0$.

We rewrite inequality I by multiplying with the common denominator:

$$\sqrt{a(1+d\varepsilon)} \; < \sqrt{(ad-bc)\varepsilon + a + d - b - c} \; + \sqrt{d(1+a\varepsilon)} + \sqrt{(ad-bc)\varepsilon}.$$

If this holds for all $\varepsilon > 0$ then we obtain for $\varepsilon \to 0$: (*w.l.o.g.* we assume $a \geq d$)

$$\begin{aligned}
\sqrt{a} &\leq \sqrt{a+d-b-c} + \sqrt{d} \\
\sqrt{a} - \sqrt{d} &\leq \sqrt{a+d-b-c} \qquad /^2 \\
a - 2\sqrt{ad} + d &\leq a + d - b - c \\
2\sqrt{ad} &\geq b + c \qquad /^2 \\
4ad &\geq (b+c)^2
\end{aligned}$$

Thus, by applying Theorem 8.1 to the matrix A_ε, we obtain the required necessary condition for *VL-stability*. In analogous manner as above, we get from inequality II the condition for *VL-stability* in the case $a \leq d$.

We now proceed to the converse implication. As we already know, inequality I is given by $\omega_1 < 1 + \omega_2 + \omega_3$ and this is equivalent to

$$\sqrt{a(1+d\varepsilon)} \; < \; \sqrt{(ad-bc)\varepsilon + a + d - b - c} + \sqrt{d(1+a\varepsilon)} + \sqrt{(ad-bc)\varepsilon}.$$

We want to show that this inequality holds for every $\varepsilon > 0$. Again we can assume $a \geq d$ (otherwise $\omega_1 \leq \omega_2$ and inequality I holds trivially). Then we have

$$\sqrt{a + ad\varepsilon} - \sqrt{d + ad\varepsilon} \; < \; \sqrt{(ad-bc)\varepsilon + a + d - b - c} + \sqrt{(ad-bc)\varepsilon}$$

where we can rewrite the left-hand side with

$$(a + ad\varepsilon) - (d + ad\varepsilon) = (\sqrt{a + ad\varepsilon} - \sqrt{d + ad\varepsilon})(\sqrt{a + ad\varepsilon} + \sqrt{d + ad\varepsilon})$$

as

$$\underbrace{\frac{a-d}{\sqrt{a+ad\varepsilon} + \sqrt{d+ad\varepsilon}}}_{\text{decreasing in } \varepsilon} \; < \; \underbrace{\sqrt{(ad-bc)\varepsilon + a + d - b - c} + \sqrt{(ad-bc)\varepsilon}}_{\text{increasing in } \varepsilon}$$

$$\Leftrightarrow$$

$$\frac{a-d}{\sqrt{a} + \sqrt{d}} \; \leq \; \sqrt{a+d-b-c}.$$

We can handle inequality II (for $a \leq d$) in the same way. For inequality III just note that $\omega_3 \leq 1$.

Inequality IV reads

$$\sqrt{(ad-bc)\varepsilon+a+d-b-c} \;<\sqrt{a+ad\varepsilon}+\sqrt{d+ad\varepsilon}+\sqrt{(ad-bc)\varepsilon}$$

and is equivalent to

$$\sqrt{(ad-bc)\varepsilon+a+d-b-c}-\sqrt{(ad-bc)\varepsilon} \;<\sqrt{a+ad\varepsilon}+\sqrt{d+ad\varepsilon}$$

and, by the same trick as above, to

$$\frac{a+d-b-c}{\sqrt{(ad-bc)\varepsilon}+\sqrt{(ad-bc)\varepsilon+a+d-b-c}}< \;\sqrt{a+ad\varepsilon}+\sqrt{d+ad\varepsilon}.$$

The left-hand side is again a decreasing function of ε and the right-hand side is increasing in ε. Hence we have to check only the values at $\varepsilon=0$:

$$\begin{aligned}\sqrt{a+d-b-c} &\le \sqrt{a}+\sqrt{d} \qquad /^2\\ a+d-b-c &\le a+2\sqrt{ad}+d\\ 2\sqrt{ad}+b+c &\ge 0\end{aligned}$$

Therefore we have shown the following characterisation (which closes the open question from Remark 6.6 and also corrects the statement in Exercise 21.6.11 on p. 209 of [5]):

Theorem 8.11.

$$A_\varepsilon \textit{ is VL-stable } \quad \forall\varepsilon\; >0 \;\Leftrightarrow\; 4ad\ge(b+c)^2 \;\;\wedge\;\; ad>bc.$$

Now we can discuss the previous mentioned Example 5.21 and Example 5.24 properly.

Example 8.12. *(cf. Example 5.21) We stated VL-stability implies D-stability. A simple counterexample for the converse statement is the matrix*

$$A=\begin{pmatrix}-1&-2&0\\-1&-2&-5\\0&2&-4\end{pmatrix}$$

which is D-stable but not VL-stable.

The answer why A is not *VL-stable*, is because $-A$ is not a *P-matrix*.
To check if a given 3×3 matrix is *D-stable*, we can use Corollary 7.3. The diagonal elements $-1,-2,-4$ are nonpositive. The determinant -10 is negative, all 2×2 minors $A_1=18$, $A_2=4$ and $A_3=0$ are nonnegative.
The required inequality is also fulfilled $\sqrt{18}+\sqrt{8}+\sqrt{0}\ge\sqrt{10}$, i.e., $7,07\ge3,16$.

The next example was presented by Logofet in [9].

Example 8.13. *(cf. Example 5.24) This interaction matrix represents a competition system. The matrix is totally stable but not VL-stable.*

$$A = \begin{pmatrix} -1 & -0,3 & -2 \\ -0,95 & -1 & -1,92 \\ -0,49 & -0,495 & -1 \end{pmatrix}$$

Consider the inverse

$$(-A)^{-1} = \begin{pmatrix} 6,75749 & 94,0054 & -194,005 \\ -1,25341 & 2,7248 & -2,7248 \\ -2,69074 & -47,4114 & 97,4114 \end{pmatrix}$$

The matrix A is totally stable because it satisfies the requirements of Theorem 7.1. The diagonal entries are negative, the determinant $-0,00734$ is negative, all 2×2 principal minors $A_1 = 0,05$, $A_2 = 0,02$ and $A_3 = 0,71$ are positive and the inequality is also fulfilled $\sqrt{0,05} + \sqrt{0,02} + \sqrt{0,71} > \sqrt{0,00734}$, i.e., $1,21 > 0,09$.

This is nothing else but checking if inequality $\omega_1 + \omega_2 + \omega_3 > 1$ is valid. We have $\omega_1 = \sqrt{1 \cdot 6,75749} = 2,5996$, $\omega_2 = \sqrt{1 \cdot 2,7248} = 1,6507, \omega_3 = \sqrt{1 \cdot 97,4114} = 9,8697$. Thus, $2,5996 + 1,6507 + 9,8697 > 1$ is true, i.e., $14,12 > 1$.

Let us explain why this matrix is not *VL-stable*.

In order to check if a matrix A is *VL-stable*, we have to verify that $-A$ is a *P-matrix* and the correctness of the following inequalities:

$$\begin{aligned} \text{I:} &\quad \omega_1 < 1 + \omega_2 + \omega_3 \\ \text{II:} &\quad \omega_2 < 1 + \omega_1 + \omega_3 \\ \text{III:} &\quad \omega_3 < 1 + \omega_1 + \omega_2 \\ \text{IV:} &\quad 1 < \omega_1 + \omega_2 + \omega_3 \end{aligned}$$

Point (i) from Theorem 8.1 is achieved ($-A$ is a *P-matrix*), but point (ii) is violated, since $\omega_3 < 1 + \omega_1 + \omega_2$ is not true, i.e., $9,8697 > 1 + 2,5996 + 1,6507 = 5,2503$.

The final example is the interaction matrix of a two-prey, one-predator system, which is *totally stable* but not *VL-stable*.

Example 8.14. *(cf. Theorem 6.4)* $\begin{pmatrix} -2 & -1 & -1 \\ -4 & -3 & -1 \\ 1 & 1 & -0,001 \end{pmatrix}$

For *total stability* we will again use inequality $\omega_1 + \omega_2 + \omega_3 > 1$.

The inverse is given by

$$(-A)^{-1} = \begin{pmatrix} 501,5 & -500,5 & -1000 \\ -502 & 501 & 1000 \\ -500 & 500 & 1000 \end{pmatrix}$$

The omegas are $\omega_1 = \sqrt{2 \cdot 501,5} = 31,67$, $\omega_2 = \sqrt{3 \cdot 501} = 38,77$ and $\omega_3 = \sqrt{0,001 \cdot 1000} = 1$. Thus, $31,67 + 38,77 + 1 > 1$, i.e., $71,44 > 1$ is true and hence A is totally stable.

The matrix A is not *VL-stable*, because inequality II is not fulfilled, since $38,77 > 1 + 31,67 + 1 = 33,67$.

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