



CHALMERS
UNIVERSITY OF TECHNOLOGY

Critical Transitions in Generalised Lotka-Volterra Systems With Random Interaction Strengths and Positive Self-Growth

Master's thesis in Complex Adaptive Systems

KARL NYMAN

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Department of Applied Physics
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Abstract

With better understanding of what causes complex systems to undergo critical transitions, unwanted consequences can be avoided or turned into opportunities [23]. In this thesis I add to that understanding by investigating criticality in an example complex system called the generalised Lotka-Volterra equations. Exploration of this system also adds nuance to May's comment in the diversity-complexity debate [16]. I restrict myself to positive self-growth and random interactions between species and investigate how system behaviour changes as the average interaction strength σ increases, using computer simulations and analytical methods. In line with May's thesis I find that large systems undergo critical transitions for lower σ than small systems, but the route to system instability or collapse goes through an intermediate state where species frequently go extinct and the system is dynamically close to instability. Structurally on the other hand, the system is resilient to changes to σ , except when roughly half of the initial amount of species has gone extinct, at which point either limit cycle behaviour sets in or system collapse occurs. The ecological realism of the model is difficult to justify, but as an example of a complex system exhibiting criticality it has many insights to offer.

Keywords: complex system, diversity-stability debate, structural stability, critical transitions, generalised Lotka-Volterra equations, Hopf bifurcation, extinction, collapse.

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List of symbols

Symbol	Description
n	The number of species.
A^{-1}	The inverse of a matrix A .
$\det(A)$	The determinant of a matrix A .
$\text{tr}(A)$	The trace of a matrix A .
A^T	The transpose of a matrix A .
$\text{adj}(A)$	The adjugate of a matrix A .
$A_{i,j}$	The element on the i :th row and the j :th column of A .
$K_{i,j}$	The minor; The determinant of the matrix resulting from removing row i and column j from some matrix A .
C^1	The class of continuously differentiable functions.
J	The Jacobian of a C^1 function f with elements $J_{i,j} = \frac{\partial}{\partial x_j} f_i$.
I	The identity matrix.
C	The connectivity of a system of interacting species.
σ	The average interaction strength of species.
σ_e	A σ for which an extinction occurs.
σ_{e1}	The σ for which the first extinction occurs.
σ_c	A σ for which a collapse occurs.
x_i	The population size of species i .
\dot{x}_i	Time derivative $\frac{d}{dt}$ of the size of population i .
r_i	Self-growth of species i .
$\delta_{i,j}$	The Kronecker delta. $\delta_{i,j} = 1$ if $i = j$ and 0 otherwise.
x^*	A stationary point.
	For a vector x and scalar c :
\geq	$x_i \geq c, \forall i$
\leq	$x_i \leq c, \forall i$
$>$	$x_i > c, \forall i$
$<$	$x_i < c, \forall i$
$=$	$x_i = c, \forall i$

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1

Introduction

1.1 Background

How do complex systems behave close to points of transition? This fundamental question of complex systems was brought back into the spotlight in 2012 in a review article titled Anticipating Critical Transitions [23]. If one can anticipate how complex systems behave close to critical transitions - point where system behaviour may change drastically - then the transition can either be prevented, or adverse effects can be mitigated [23].

One step towards understanding critical transitions is to analyse example systems which may be specific, but still exhibit behaviour general to more systems. If such systems can be understood, then perhaps more can be learned about other complex systems. The generalised Lotka-Volterra is one such example system which is often used to model interactions between species in ecosystems, and that is the system investigated in this thesis.

Why should the generalised Lotka-Volterra system be considered? Its relevance can be traced from a historical so-called diversity-stability debate [15, 19, 5, 20, 17]. Before the 1970:ies it was generally thought that a large number of interacting species in an ecosystem increases system stability [20, 5], or put differently: diversity begets stability in ecosystems. However, in 1972 Robert May turned the debate on its head by arguing that stable systems cannot be both large and have strongly interacting species [16], the converse to the previous assumption. May, inspired by Gardner and Ashby [7], based his argument on the stability of equilibrium points of dynamical systems, which can be used for modelling ecosystems. He did however make some, perhaps unrealistic, assumptions and this is what motivates the study of the generalised Lotka-Volterra equations.

One critical assumption made by May, also used in recent advances by Allesina [2], is that equilibrium points exist and fulfil quite specific criteria. In this thesis I consider a fairly general system capable of generating such equilibrium points, namely the generalised Lotka-Volterra system, and investigate how the system behaves when the complexity, represented by the average interaction strength, is varied.

I thus aim to answer two questions simultaneously. Firstly, I investigate how a May-like analysis changes if a critical assumption is relaxed using a model system. Secondly, I seek to learn what kind of critical transitions can occur in such a system and how the system behaves close to critical points.

I would like to point out that I am not the first to question May's assumption of the existence of feasible equilibria in non-linear systems. Apart from my supervisor

Assistant Professor Kolbjørn Tunstrøm and his colleague Professor Martin Nilsson Jacobi who introduced me to the idea, Dr Inman Harvey brought forth criticism against May's assumption in 2011 [12]. He demonstrated that there exist multiple equilibria in some example non-linear systems and that the consideration of one single equilibrium point is insufficient to describe system behaviour. He did not, however, consider the generalised Lotka-Volterra system as I do in this thesis.

1.2 Objectives and aims

The primary aim of this thesis is to answer the question: Is the stability analysis of complex systems of interacting species made by May applicable to the generalised Lotka-Volterra equations? If not, how does it differ?

A secondary aim is to investigate which critical points exist in the generalised Lotka-Volterra equations with random interaction strengths as the average interaction strength is increased, and how the system behaves close to these points.

1.3 Limitations

I do not consider time dependence of system parameters or stochasticity. I assume that the interaction strengths between species are zero in the mean. Furthermore, I do not perform simulations for systems larger than 150 species. I will put emphasis on the equilibria of the system and their stability and focus less on the dynamical behaviour of the system, i.e. how the system evolves in time other than close to stable equilibria.

1.4 Methods

A combination of analytical and computer based methods will be used in trying to answer the questions of this thesis. The computer methods consist of simulating the model system by solving ordinary differential equations. The analytical methods come from basic linear algebra and dynamical systems theory.

1.5 Outline of the report

In the second chapter of this thesis I introduce terminology and some basic results and concepts of dynamical systems and linear algebra. In the chapter that follows, I return to the topic of the thesis with a review of selected previous work models concerning the stability of ecosystems. In the fourth chapter, I describe the generalised Lotka-Volterra equations, the equations around which this thesis is centred, in detail. The fifth chapter presents graphical results on critical points in the generalised Lotka-Volterra equations, along with brief discussions, and is intended to give an introduction to critical points in this particular system. In the sixth chapter, I attempt to explain the observations of chapter four, and add to the understanding of the critical points of the generalised Lotka-Volterra equations by presenting some

general and limit results. The seventh chapter describes the methods used in the simulation of the system, parameter choices and how I have chosen to tackle numerical problems and classification of event. The last two chapters contain a discussion of the methods and results of the thesis and draw conclusions connecting to the objectives of the thesis.

2

Prerequisites

In the first section of this thesis I introduce terminology and basic concepts used in this thesis. In the second section of this chapter I give some background on ordinary differential equations and dynamical systems. If you are already familiar with these concepts, you can read this section briefly only to get acquainted with the terminology.

2.1 Terminology

In this section I establish terminology used throughout the thesis. The meaning of symbols can be found in the table of symbols.

Vector notation: Vectors are not denoted in any specific way; for instance with vector bars or bold font. The vector "x" is thus denoted x . The number of components of the vector should be clear from the context.

Largest and smallest eigenvalue: The largest eigenvalue of a matrix A is here taken to mean the eigenvalue with the largest real part. Similarly, the smallest eigenvalue is taken to mean the eigenvalue with the smallest real part.

ODE: An ordinary differential equation (ODE) is an equation which contains functions of one independent variable and its derivatives. A set of ODE:s, which may be connected, is called a system of ODE:s. In this report *ODE* will also be taken to mean *a system of ODE:s*.

Dynamical system: A dynamical system is here taken to mean a system in which a function describes how a state varies in time. Any ODE can be said to represent a dynamical system.

Inequalities: Inequality symbols between a vector x and a scalar c mean the following in this thesis: $x \geq c$ means that $x_i \geq c$ for all i except some for which $x_i = c$. $x > c$ means that $x_i > c, \forall i$. The symbols $<$ and \leq have corresponding meanings. $x = c$ means that $x_i = c, \forall i$.

Comparison of complex eigenvalues: Whenever I compare a complex number with another number, unless otherwise stated, I compare the real parts of the numbers. E.g. $\lambda > \gamma$ means $Re(\lambda) > Re(\gamma)$.

Extinction: A species is said to be extinct if its equilibrium population size is 0. If the system is parametrised with some parameter σ , then a species is said to go extinct if it has a 0 equilibrium population size at the current value of σ , but had a positive equilibrium population size for a slightly smaller σ .

Resurrection: If a species population size equilibrium changes with some parameter σ , then if it is extinct for σ_0 but ceases to be extinct for some slightly larger $\sigma_1 > \sigma_0$, then a resurrection has occurred.

Units: All quantities in this report are assumed to have dimension 1 and units are usually not specified.

Structural stability: A system is structurally stable if the qualitative behaviour of the system, e.g. existence of stable equilibria or limit cycles, is not affected by small perturbations in its parameters. In this thesis I use the term loosely, such that extinction, which effectively changes which equilibrium the system converges to, is still considered structurally stable.

Dynamical stability: I use dynamical stability as an umbrella term for different notions of stability referring to system sensitivity to initial conditions. In specific, if the solution to a system is at an equilibrium, then if it stays close to the equilibrium after being perturbed it is dynamically stable. I will mention different notions of dynamical stability in Section 2.2.4.

All elements in a set: When I refer to elements in a set, e.g. denoted as A_i , then it is implicit that the elements are indexed such that $i \in \{1, 2, \dots, n\}$, where n is the number of elements in a set. The number of elements should be clear from the context. When writing $\forall i$ (for all) or $\exists i$ (there exists some), then I implicitly mean that $i \in \{1, 2, \dots, n\}$.

2.2 Concepts in dynamical systems

Here, I introduce some basic concepts in differential equations and stability analysis required for following through the thesis.

2.2.1 A system of ordinary differential equations

A system of ordinary differential equations with n unknown variables represented by a vector $x(t)$ dependent on one variable t is described by a general first order ODE as:

$$\dot{x} = F(x, t), x(0) = x_0 \quad (2.1)$$

where $(\dot{\cdot})$ denotes a time derivative, $F(x, t)$ is a vector valued function and x_0 is a vector of initial values.

2.2.2 Equilibrium point

A point x^* is an equilibrium point if $\dot{x}|_{x=x^*} = F(x^*) = 0$ for some dynamical system such as the one in Equation (2.1).

2.2.3 Basin of attraction

The basin of attraction of an attractor A (e.g. an attracting equilibrium point) is the set of initial conditions which converge to A as time goes to plus infinity. An intuitively appealing example is the following. Consider a volcano with a concave crater. The bottom of the crater is an attracting point for objects subject to gravity. All points inside the crater constitute the basin of attraction for the attracting point, since if one places a marble (experiencing friction) anywhere in the crater, it will eventually converge to the bottom of the crater. Any point on the volcano not in the crater is not part of the basin of attraction of the bottom of the crater. (The analogy fails slightly, since if the marble has non-zero kinetic energy and reaches the bottom of the crater, it will escape the "attracting point", which is not allowed according to the definition of an attractor).

2.2.4 Notions of stability

There are several notions of stability. If nothing else is stated, by stability around an equilibrium point I mean *asymptotic* stability, which is slightly stronger than Lyapunov stability. A distinction between different forms of stability is given below. If $F(x^*)$ is continuous and x^* is an equilibrium point, then x^* is asymptotically stable if it is Lyapunov stable and $\exists \delta > 0$ such that if $\|x(0) - x^*\| < \delta$ then $\lim_{t \rightarrow \infty} \|x(t) - x^*\| = 0$. Lyapunov stability for an equilibrium point x^* is in turn defined as follows: If for any $\epsilon > 0$ there exists a $\delta(\epsilon) > 0$ such that if $\|x(0) - x^*\| < \delta$ implies that for any $t \geq 0$ $\|x(t) - x^*\| < \epsilon$ then x^* is Lyapunov stable.

One way to analyse the stability of an equilibrium points is by means of linear stability analysis. In linear stability analysis, one considers a dynamical system as in Equation 2.1. For non-linear systems the Hartman–Grobman theorem [10, 11] states that the local behaviour of a dynamical system close to an equilibrium point is qualitatively the same as its linearisation, given that no eigenvalues have real part equal to 0. Such equilibria are called hyperbolic. It follows from this that if the eigenvalues of the linearisation of the right hand side of Equation (2.1) at an equilibrium point has only negative real parts, then it is asymptotically stable.

2.3 Smoothness of eigenvalues and matrices and relations with determinants

In this section I present a set of properties of and facts about eigenvalues and matrices that are used in this thesis. I specifically show a relation between eigenvalues and determinants, and results regarding smoothness of eigenvalues and inverse matrices.

2.3.1 Eigenvalues and determinants

A well known result which relates the eigenvalues of a matrix to its determinant is:

Theorem 2.3.1. *Let A be an $n \times n$ matrix with eigenvalues $\lambda_i, i = 1, 2, \dots, n$, not necessarily unique. Then:*

$$\prod_{i=1}^n \lambda_i = \det(A). \quad (2.2)$$

For a proof, see appendix A.

A corollary which will be of use in this thesis is:

Corollary 2.3.1.1. *Given a square matrix A , $\det(A) = 0 \iff \lambda_i = 0 \exists i$.*

So if the eigenvalues vary continuously with some parameter, then a necessary condition for a real eigenvalue to change sign is that $\det(A) = 0$. This is only a necessary, not a sufficient, condition for real eigenvalues. Complex eigenvalues may change sign (of their real parts) without $\det(A) = 0$ and real eigenvalues do not need to change sign in spite of $\det(A) = 0$.

2.3.2 Continuity and smoothness of eigenvalues

A well known theorem is that if the elements of the matrix vary continuously then the eigenvalues of a matrix vary continuously as well:

Theorem 2.3.2. *Let A be a square matrix. Then if $A_{i,j}(\sigma)$ are continuous functions of σ , then eigenvalues λ of A vary continuously in σ .*

Sketch of a proof: The eigenvalues λ of A are solutions to the characteristic polynomial $\det(A - I\lambda) = 0$, where I is the identity matrix. Note that the elements of $A - \lambda I$ also vary continuously with σ .

The determinant function maps the elements of $A_{i,j}(\sigma)$ to a polynomial in λ :

$$p(\lambda, A_{i,j}(\sigma)) = \sum_{k=0}^n a_k \lambda^k$$

such that the coefficients a_k are constructed from additions and multiplications of elements $A_{i,j}$, where n is the degree of the polynomial. Hence, the mapping is continuous.

A classical result states that the zeros λ_i of a polynomial $p(\lambda) = \sum_k a_k \lambda^k$ vary continuously if its coefficients a_k vary continuously, as long as $a_n \neq 0$ (see for instance [28]). Another way of expressing it is that the function which maps a characteristic polynomial to its roots is continuous if the leading coefficient is non-zero. Since the characteristic polynomial is monic, $a_n \neq 0$ in this case.

Therefore, since function composition is continuous, the function mapping a matrix $A(\sigma)$ to its eigenvalues is continuous. \square

A stronger result is that a simple eigenvalue λ_i of a differentiable square matrix $A(\sigma)$ in a variable σ is also differentiable in σ . This was proven by Lax (although he does not make any claims to be the first one to prove it)[14].

2.3.3 Smoothness of the matrix inverse

In this section I show that the inverse matrix is smooth in the coefficients of the matrix, as long as the matrix is invertible. More precisely:

Theorem 2.3.3. *If $A(\sigma)$ is an $n \times n$ matrix whose entries $A_{i,j}(\sigma)$ are smooth functions, then the inverse $A^{-1}(\sigma)$ is also smooth to the same order as $A_{i,j}$, except where $\det(A) = 0$.*

Proof. The inverse of $A(\sigma)$ is given by $A^{-1}(\sigma) = \frac{1}{\det(A(\sigma))} \text{adj}(A(\sigma))$, where $\det(A(\sigma))$ is the determinant of $A(\sigma)$ and $\text{adj}(A(\sigma))$ is the adjugate of $A(\sigma)$. $\text{adj}(A(\sigma)) = p(\{A_{i,j}(\sigma)\}_{1 \leq i,j \leq n}) \equiv p$, where p is a polynomial in $\{A_{i,j}(\sigma)\}_{1 \leq i,j \leq n}$. Since all $A_{i,j}(\sigma)$ are smooth functions in σ , p is also a smooth function in σ . By an analogous argument $\det(A(\sigma)) = q(\{A_{i,j}(\sigma)\}_{1 \leq i,j \leq n}) \equiv q$ where q is a smooth function in σ . Therefore $A^{-1}(\sigma) = \frac{p}{q}$ is a smooth function in σ as long as $q \neq 0$. In conclusion, $A^{-1}(\sigma)$ is smooth in σ at every point where A is invertible. \square

2.4 Summary

In this chapter, I have introduced terminology, introduced the concepts of ordinary differential equations and notions of stability, and I have showed some basic theorems regarding eigenvalues and the smoothness of matrix inverses. In the next chapter I will present previous work related to this thesis.

3

Previous studies on the stability of ecosystems

In this chapter I aim to give a review of previous work on the stability of ecosystem models and Lotka-Volterra systems with relevance to this thesis. In Section 3.1 I restate May's result for equilibria in large complex systems with random interaction strengths and in Section 3.2 I describe results of Allesina and Tang for systems with specific interaction types, e.g. mutualistic interactions. Finally, in Section 3.3 I present models which aim to relax May's assumption of existence of very specific equilibrium points.

3.1 May's result on the stability of large complex systems

In his 1972 paper May considers the stability around equilibrium points of non-linear ODE:s, under certain assumptions [16]. One assumption is that an equilibrium exists. A second assumption is that the self-interactions are -1 for all species at the equilibrium. A third assumption, which has been relaxed by Allesina and Tang [2], is that all interactions between species are drawn from a random distribution with zero mean and some specified average interaction strength. A fourth assumption is that only a randomly chosen fraction of species are connected, by which it means that they have non-zero interaction strength. In this section I will first restate May's results and then comment on May's assumptions.

May considers a system of n species, interacting in a way which can be described by some possibly non-linear ODE. At some assumed equilibrium x^* , the ODE can be linearised such that its equilibrium can be described by the eigenvalues of the Jacobian J at x^* . May assumes that at the equilibrium each species is self-sustaining in absence of interactions with other species, such that if perturbed it will return to equilibrium with some characteristic damping time, which May sets to -1 such that $J_{i,i} = -1, \forall i$.

Then May introduces interactions between species at the equilibrium, represented by off-diagonal elements of the Jacobian $J_{i,j}, i \neq j$. The random elements are drawn independently from some distribution with zero mean and standard deviation σ , associated with the average interaction strength ¹.

¹The standard deviation $\sigma = \frac{1}{m} \sqrt{\sum_{i=1}^m (X_i - \mu)^2}$ is associated with the average interaction strength $d_{avg} = \frac{1}{m} \sum_{i=1}^m \sqrt{(X_i - \mu)^2}$, where X_i are random variables from the same distribution,

He then invokes Wigner's semicircle law, which states that the density of eigenvalues for a large (in the limit as $n \rightarrow \infty$) Hermitian matrix with all elements drawn from a zero-mean distribution with standard deviation σ converges to a semi-circle with radius $2\sigma\sqrt{n}$ centred around 0. Then the density of eigenvalues in an interval dx is

$$p(x) = \frac{1}{2\pi\sigma^2 n} \sqrt{4n\sigma^2 - x^2} dx, -2\sigma\sqrt{n} \leq x \leq 2\sigma\sqrt{n}.$$

Invoking some transformation, May claims that the radius is given by $\sqrt{n}\sigma$ in the asymmetric case (instead of $2\sqrt{n}\sigma$ in the symmetric case). Consequently, the largest eigenvalue $\lambda_{max} = \sqrt{n}\sigma$. May comments that the matrix he considers is not Hermitian, but argues that the result should apply to the real part of the eigenvalues still. The importance of the lack of hermiticity decreased as Girko and later Tao and Vu [9, 26] showed that the relation for the largest eigenvalue result holds for increasingly wider classes of non-Hermitian random matrices. They specifically showed that for certain non-Hermitian random matrices a circular law holds, which states that eigenvalues are distributed uniformly on a disk in the complex plane with radius $n\sigma$.

May then states that the Jacobian J can be written as $J = B - I$ where B is a random matrix with diagonal elements 0 and off-diagonal elements drawn from a distribution with mean 0 and average interaction strength σ and I is the identity matrix. The subtraction of the identity matrix gives that $J_{i,i} = -1$ and that all eigenvalues are shifted by -1 . The shift stems from that if $\det(B - \lambda I) = 0$, then λ are eigenvalues of B and any $\lambda' = \lambda - 1$ is an eigenvalue of $B - I$ since it satisfies

$$\det(B - I - \lambda' I) = \det(B - I - \lambda I + I) = \det(B - \lambda I) = 0.$$

The density of eigenvalues of the matrix B are given by the circular law in the previous paragraph, and so the largest eigenvalue of J is $\sqrt{n}\sigma - 1$. This gives the criterion for stability

$$Re(\lambda)_{max} = \sqrt{n}\sigma - 1 < 0 \iff \sigma < n^{-1/2}.$$

Next, May lets only a fraction C of species have non-zero interaction strengths. The "effective variance" of the elements of the matrix off-diagonal elements is then reduced to $\sigma\sqrt{C}$. This gives a new stability criterion $\sigma < (nC)^{-1/2}$. From this expression May argues that simultaneously large (large n) **and** complex (large $\sigma\sqrt{C}$) systems can not be stable, which is his main thesis.

May's result is concise, but leaves many questions. One is whether equilibria with negative Jacobian elements for any σ exist in real or model systems. This question is addressed in this thesis, and was tackled previously by Tregonning. Tregonning's work will be presented in another section, but in the next section the question of how special kinds of interaction matrices affect stability is answered.

Before moving to the next section, I would like to note that May did in later work depart from the assumption of an equilibrium of a general non-linear system. He

m is the number of variables and μ is the mean of the distribution, in the sense that they are both measures of distance from the mean and $\sigma' > \sigma \iff d'_{avg} > d_{avg}$ for variables from two distributions X' and X .

even considered the three species competitive generalised Lotka-Volterra equations, but did not scale the off-diagonal elements to perform a structural stability analysis, nor did he comment his result on stability of complex and large systems [18].

3.2 May-like systems with specific interactions

In 2012 Allesina and Tang continued in May's tracks and considered systems with diagonal elements of the Jacobian $J_{i,i} = -1$ at an assumed equilibrium point x^* , but with specific kinds of interactions [2]. Of the kinds of interaction they investigated, I will only present mutualistic systems $J_{i,j} > 0, \forall i, j$, competitive systems $J_{i,j} < 0, \forall i, j$ and predator-prey systems in which $\text{sign}(J_{i,j}) = -\text{sign}(J_{j,i}), \forall i, j$, where $\text{sign}(y) = +1$ is the sign of y (with $\text{sign}(0) \equiv 0$).

For all kinds of systems, Allesina and Tang let each pair of off-diagonal elements be non-zero with probability C . In case of mutualistic systems, for connected (non-zero) interaction pairs they draw both $J_{i,j}$ and $J_{j,i}$ independently from a half-normal distribution $|\mathcal{N} \sim (0, \sigma^2)|$. For competitive systems they draw each connected pair from $-|\mathcal{N}(0, \sigma^2)|$. In predator-prey systems they draw $J_{i,j}$ from $|\mathcal{N}(0, \sigma^2)|$ and $J_{j,i}$ from $|\mathcal{N} \sim (0, \sigma^2)|$ with probability $1/2$ and with reversed signs of $J_{i,j}$ and $J_{j,i}$ with probability $1/2$.

The eigenvalues λ of mutualistic and competitive matrices in the case of zero diagonals are related as $\lambda_{\text{competitive}} = -\lambda_{\text{mutualistic}}$ so it is only necessary to investigate one of the cases. By cleverly observing that for zero diagonal mutualistic matrices the all-ones vector is an eigenvector to J , Allesina and Tang found that the major eigenvalue was given by

$$\lambda_{\max} = (n-1)C\mathbb{E}(|X|).$$

Shifting the eigenvalues by -1 and letting $X \sim \mathcal{N}(0, \sigma^2)$ gives the stability criterion

$$\sigma < \sqrt{\pi}/(\sqrt{2}(n-1)C) \approx 1.25/((n-1)C).$$

In the competitive case the analogous eigenvalue becomes the minor eigenvalue due to the sign change, so the major eigenvalue needs to be found some other way. After some machinery, Allesina and Tang found that in the large n limit the stability criterion is

$$\sigma < \frac{1}{(1 + \frac{2(1-C)}{\pi-2C})\sqrt{nC(1-2C/\pi)} + C\sqrt{2/\pi}}.$$

It is worth noting that the connectivity is not just a scale parameter of n in this expression. In fact, for small C the instability occurs for smaller σ compared to the random case, and for large C for bigger σ . For instance, in the large n limit when the term $C\sqrt{2/\pi}$ can be neglected, the stability criterion is $\sigma < 0.64/\sqrt{nC}$ for $C = 0.1$, and $\sigma < 1.66/\sqrt{nC}$ for $C = 1$. Allesina and Tang did not comment on this in their paper.

For predator-prey systems, Allesina and Tang used a result of Sommers which states that asymmetric matrices with Gaussian elements $J_{i,j} \sim \mathcal{N}(0, 1/n)$ have eigenvalues uniformly distributed in ellipses with real axis $1+\tau$ and imaginary axis $1-\tau$, where $-1 \leq \tau \leq 1$ is parameter related to correlation and n is the size of the

matrix [24]. The result holds in the limit as $n \rightarrow \infty$. $\tau = -1$ implies that the matrix is (anti)symmetric, $\tau = +1$ implies that it is symmetric, and $\tau = 0$ implies that the matrix is asymmetric. Allesina and Tang conjecture that the result holds for a wider class of distributions of elements. Drawing elements from $\pm|N(0, \sigma)|$ such that elements have opposing sign gives $\tau = -\mathbb{E}^2[|X|]/\sigma^2$ and real half-axis $\sigma\sqrt{nC}(1 - \mathbb{E}^2[|X|]/\sigma^2)$. If shifting eigenvalues by -1 like May does, a criterion for stability becomes $\sigma < 1/(\sqrt{nC}(1 - 2/\pi)) \approx 2.75/\sqrt{nC}$. This implies that system instability occurs for larger σ than in the random case.

The stability criteria for mutualistic, competitive and predator-prey networks can be compared with the results of this thesis.

Allesina and Tang report lastly in the supplemental information in their paper that the generalised Lotka-Volterra equations can be made to meet the criteria for their analysis. They consider a scaling of each off-diagonal element by a positive parameter $\sigma_{i,j}$ and wish to meet the -1 diagonal criterion. To this end, they show that the self-growth factor needs to be updated in a non-constant, which also preserves the equilibrium point. The precise expression for the update is given by Equation (A.1) in the appendix, but it is recommended that the reader becomes familiar with the generalised Lotka-Volterra equations presented in the next chapter before looking at the transformation.

One might ask if this transformation of the self-growth and consequent preservation of equilibrium is reasonable. If the average interaction strength between species is changed for a given system, would it not be reasonable if the self-growth for each species remain the same, and that the equilibrium point changes? This is precisely what is done in the model of this thesis and whose behaviour is investigated.

Some other authors have also questioned the assumed existence of an equilibrium point which satisfies the requirement of constant negative diagonal entries of the Jacobian, but from a different angle. Their work is the topic of the next section.

3.3 Existence and generation of feasible and stable equilibria

Shortly after May published his 1972 paper, Roberts published a paper which would lead to a cascade of publications on the topic of what kinds of equilibria occur in ecosystems with random interactions between species [21]. The series of publications is an inspiration to the approach taken in this thesis.

In Roberts first 1974 paper, he proposes that equilibria should only be considered for stability if they also fulfil the requirement of feasibility. Feasibility in Roberts' terminology, which will be used only throughout this section, means strictly positive population sizes. Note that that this definition differs from the one used in the rest of this thesis, in that it does not consider population 0 feasible. Roberts considers the generalised Lotka-Volterra equations for n species

$$\dot{x}_i = x_i(r_i + \sum_{j=1}^n A_{i,j}x_j),$$

where x_i is the population size of species i , \dot{x}_i is the time derivative of population

size i and $A_{i,j}$ is the interaction between species i and j , with all self-growth factors $r_i = c$, where c is a positive constant, and self-interaction terms $A_{i,i} = -1$ for species i . The generalised Lotka-Volterra Equations will be presented in more detail in chapter 4.

Roberts lets all inter-species interaction terms $A_{i,j}$ be either $+\sigma$ or $-\sigma$, where the sign is random with equal probability. His main result is that when generating such systems, the equilibria tend to be stable as long as they are also feasible, for a given σ . The only σ for which feasible systems tend to be unstable are those for which the portion of systems that are feasible is also low. Critical to his argument is that for larger n this effect is more pronounced. Reasons for this will be touched on in chapter 5. He also argues that species with negative population sizes are the source of instability in the system, so excluding these species would falsify the thesis that ecosystems with strong interactions tend to be unstable. Roberts does not however comment on the fact that excluding species with negative population sizes also reduces the number of species in the system.

Gilpin responded to Roberts' paper, questioning his assumption of all species being self-sustaining [8]. Gilpin lets all r_i and $A_{i,i}$ be ± 1 with equal probability instead of having all $r_i = +1$ and $A_{i,i} = -1$. The percentage of feasible solutions decreases with increasing n as in Roberts' model, but differently from Roberts, Gilpin means that unfeasible configurations also classify as unstable since negative species are likely to go extinct for such solutions. He further discredits Roberts' model for being biologically unreasonable and non-robust, since his (Gilpin's) related model shows in agreement with May that the percentage of unstable solutions decrease with increasing system size.

In 1979 Tregonning entered the debate alongside Roberts [27] presenting a model for how stable and feasible can come into being. They heed the advice of Gilpin and consider models where r_i and $A_{i,i}$ may be both $+$ and -1 to produce random realisations of systems, whose stability and feasibility is "highly improbable" in their words. They then remove the species with the most negative equilibrium population, arguing that that species would go extinct first. Each time they remove a species they increase the average interaction strength by a factor $m/(m-1)$ where m is the number of species before removal. This they claim is to obtain a constant "May" number $\sigma\sqrt{mC}$. They continue removing species this way and report that whenever a solution would become feasible it would also be stable. After removal of an average of half of the initial species count, they obtained a feasible and stable solution. Although May's stability analysis is not strictly applicable for this kind of system, it is worth noting that Tregonning and Roberts initially used $\sigma = 1/4$, $n = 50$ and $C = 0.2$ in their simulations. This gives that σ was $3/4$ of the average interaction strength required for collapse, as predicted by May.

The following year Tregonning and Roberts return [22]. This time they investigate the stability of subsystems of systems generated by the method of their 1979 paper. For a given stable and feasible system of size n , they remove q species from the system and check for feasibility. This is done for 20 randomly chosen configurations of $n - q$ species with replacement. They find that for these systems, a high proportion of subsystems are also feasible, as compared to an initially unfeasible and randomly generated solution. This they argue is a characteristic of their so-called

"naturally evolved" solutions; that they are robust to removal of species.

3.4 Summary

In this chapter I have introduced Robert May's model of the stability of systems of randomly interacting species around equilibria and demonstrated why the model concludes that complex systems can not be both large and stable. I have also presented Allesina and Tang's extension to May's model, in which they allow species to have other distributions of interactions than random zero-mean Gaussians. Lastly, I showed a series of papers by Gilpin, Roberts and Tregonning taking a different approach to the question of existence of stable ecosystem, namely that of generating equilibria of model systems and considering only feasible and stable subsets. In the next Chapter I will present the generalised Lotka-Volterra equations used by the latter authors, which is a general model of ecosystems used throughout this thesis.

4

The Generalised Lotka-Volterra Equations

In this chapter I introduce the generalised Lotka-Volterra (GLV) equations and some of their characteristics. The system of equations can be used as a simple and abstract model for interacting species, among other things. It can be treated analytically, owing to the closed form expression for equilibrium points and its Jacobian, but is still capable of generating complex behaviour, such as chaos and limit cycles. At the end of this chapter I give an expression for the rate of growth of equilibrium points in a parameter σ . I also show how the spectrum of the Jacobian can be split into one part containing the eigenvalues of extinct species and one part containing the eigenvalues of the non-extinct subset of species.

4.1 Description of the GLV

Here, I first give a formal definition of the generalised Lotka-Volterra equations and then I give them an ecological interpretation.

4.1.1 A definition of the GLV

The generalised Lotka-Volterra equations are autonomous and deterministic and are defined in this thesis as:

$$\dot{x}_i(t) = x_i(t)(r_i + \sum_{k=1}^n A_{i,k}x_k(t)), x_i(0) = x_{i,0} \quad (4.1)$$

for $i = 1, 2, \dots, n$, where n is the number of species, r_i is the self-growth of species i , $A_{i,j}$ is the effect that species j has on species i , $x_i(t)$ is the size of population i , $\dot{x}_i(t)$ is the time derivative of species i , t is the time variable and $x_{i,0}$ is the initial population of species i . Although populations are usually measured in integer numbers, $x_i(t)$ are real and can be interpreted as density, biomass or some other measure which correlates with the number of species. The matrix A is called the community matrix and contains all information of how one species interact with another. The explicit time dependence is often dropped, so that x is taken to mean $x(t)$.

4.1.2 Interpretations of the GLV

One way to interpret Equation (4.1) is that that x_i varies according to

$$\dot{x}_i = x_i F_i(x_1, x_2, \dots, x_n), \quad (4.2)$$

where F_i is some function describing the rate of change of species i . r_i is a constant rate of growth independent of the abundance of other species. The sum $\sum_{k=1}^n A_{i,k}x_k$ is a sum of terms $A_{i,k}x_k$, which describe the influence of species x_k on the growth of species i . $A_{i,k}$ describes the rate of change of x_i per unit of x_k . $A_{i,k} > 0$ means that the presence of species x_k enhances the growth of species i and $A_{i,k} < 0$ means that it decreases the growth of species i . If x_k is small, it affects the growth of species i little and if it is large it affects species i more.

In absence of interaction in between species, the ODE becomes decoupled and the growth of species i is determined by:

$$\dot{x}_i = r_i x_i + A_{i,i} x_i^2. \quad (4.3)$$

If $A_{i,i} < 0$ and $r_i > 0$ then $-r_i/A_{i,i}$ becomes the carrying capacity of species i , since all i equilibrate to $x_i = -r_i/A_{i,i}$.

From an ecological point of view, negative species is not realistic. Therefore, as is common practice I do not consider negative x_i valid solutions. Solutions x obeying $x \geq 0$ are called feasible solutions. Equilibria x^* for which $x^* > 0$ are called interior solutions as opposed to solutions which have some component $x_i = 0$.

Interactions pairs $A_{i,j}$ and $A_{j,i}$ can be labelled *mutualistic*, *competitive* or *predator-prey* to describe how species i and j affect each other. If $A_{i,j} > 0$ and $A_{j,i} > 0$, then the species are in a symbiotic relationship where the abundance of one species reinforces the other and the interaction is called mutualistic. If instead $A_{i,j} < 0$ and $A_{j,i} < 0$ then the species compete with each other and the interaction is called competitive. If one species' interaction coefficient is positive and the other's is negative, then the interaction is called predator-prey.

It follows from Equation (4.1) that x_i cannot cross 0 such that solutions with a positive initial condition remain non-negative and solutions with negative initial condition remain non-positive.

4.2 Equilibrium points of the GLV

In this section I present the equilibrium points of Equation (4.1) and the Jacobian at the equilibria and I mention some facts regarding its eigenvalues.

4.2.1 General results for equilibria

There are 2^n equilibria for the generalised Lotka-Volterra Equations, each corresponding to a different set of species for which $x_i^* = 0$. The remaining equilibria need to simultaneously satisfy $x_i^* = r_i + \sum_{k=1}^n A_{i,k}x_k^*$, or if we denote the matrix of non-extinct species \tilde{A} and the self-growth vector of non-extinct species \tilde{r} , then the vector of non-extinct species \tilde{x}^* must satisfy $\tilde{x}^* = -\tilde{A}^{-1}\tilde{r}$. It is difficult to give an explicit expression for \tilde{x}^* because of the inverse \tilde{A}^{-1} . However, a compact expression is found if one expresses \tilde{A}^{-1} in terms of minors.

I drop the tilde and let x^* denote the interior point of some system. A^{-1} can be expressed in terms of a determinant $\det(A)$ and adjugate $\text{adj}(A)$ as $A^{-1} = \frac{1}{\det(A)}\text{adj}(A)$, where the i, j :th component of $\text{adj}(A)$ is defined as $\text{adj}(A)_{i,k} = (-1)^{i+k}K_{k,i}$,

where $K_{i,k}$ is the i, k minor of A . The minor of A is the determinant of the matrix obtained if row i and column k is removed from A . The determinant can also be expressed in terms of minors by Laplace's formula: $\det(A) = \sum_{j=1}^n (-1)^{i+j} A_{j,i} K_{j,i}$. We have that $x^* = -A^{-1}r$ so that:

$$\begin{aligned} x_i^* &= \sum_{k=1}^n A_{i,k}^{-1} r_k \\ &= \frac{1}{\det(A)} \sum_{k=1}^n (-1)^{i+k} r_k K_{k,i} \\ &= \frac{\sum_{k=1}^n (-1)^{i+k} K_{k,i} r_k}{\sum_{j=1}^n (-1)^{i+j} K_{j,i} A_{j,i}}. \end{aligned} \quad (4.4)$$

4.2.2 Rate of growth of x^* in σ

If one assumes that $A = \sigma B - I$, where B is a matrix with 0 diagonal and independent $\mathcal{N}(0, 1)$ random variables, then at an internal equilibrium x^* the following relation holds simultaneously for all i :

$$\begin{aligned} 0 &= r_i + \sum_{k=1}^n A_{i,k} x_k^* \\ x_i^* &= -\frac{r_i}{A_{i,i}} - \frac{1}{A_{i,i}} \sigma \sum_{k=1, k \neq i}^n B_{i,k} x_k^* \end{aligned} \quad (4.5)$$

where r is the self-growth rate and $A_{i,i} = -1, \forall i$. A and x^* are polynomial in σ and A^{-1} is a ratio of polynomials, so as long as A^{-1} and in turn x^* exist one can take the σ derivative of x^* . One may take the simple derivative with respect to σ , since x^* is time independent. Doing so gives:

$$\frac{dx_i^*}{d\sigma} = \frac{-1}{A_{i,i}} \left(\sum_{k=1, k \neq i}^n B_{i,k} x_k^* + \sigma \sum_{k=1, k \neq i}^n B_{i,k} \frac{dx_k^*}{d\sigma} \right). \quad (4.6)$$

On matrix form the system of equations above can be written, where $\text{diag}(a)$ is a square matrix with diagonal elements $A_{i,i}$ and off-diagonal elements 0, and I the identity matrix:

$$\begin{aligned} \frac{dx^*}{d\sigma} &= -\text{diag}(a) \left(\sigma B \frac{dx^*}{d\sigma} + Bx^* \right) \\ (-\text{diag}(a) - \sigma B) \frac{dx^*}{d\sigma} &= Bx^* \\ \frac{dx^*}{d\sigma} &= -(\text{diag}(a) + \sigma B)^{-1} Bx^* \\ \frac{dx^*}{d\sigma} &= (\text{diag}(a) + \sigma B)^{-1} B A^{-1} r \end{aligned} \quad (4.7)$$

where I use that $x^* = -A^{-1}r$. As is often assumed in this thesis $A_{i,i}$ are identical and equal to -1 . In that case the equation assumes the compact form: $\frac{dx^*}{d\sigma} = A^{-1} B A^{-1} r$.

The differential equation can then be rewritten to express the explicit σ dependence:

$$\frac{dx^*}{d\sigma} = (\sigma B - I)^{-1} B (\sigma B - I)^{-1} r. \quad (4.8)$$

We will return to this equation later in the thesis.

I would like to remark that it is possible to generalise Equation (4.8) to higher order derivatives. Take the n :th derivative of both sides with respect to σ in Equation (4.5) and it follows immediately that:

$$\frac{d^n x^*}{d\sigma^n} = B \frac{d^{n-1} x^*}{d\sigma^{n-1}} + \sigma B \frac{d^n x^*}{d\sigma^n} \quad (4.9)$$

such that

$$\frac{d^n x^*}{d\sigma^n} = (I - \sigma B)^{-1} B \frac{d^{n-1} x^*}{d\sigma^{n-1}} \quad (4.10)$$

where $\frac{d^{n-1} x^*}{d\sigma^{n-1}}$ are known recursively (I define $\frac{d^0 x^*}{d\sigma^0} \equiv x^*$). This expression shows that x^* is infinitely many times differentiable in σ given that $\sigma B - I$ is nonsingular.

4.2.3 Stability of the equilibria

The stability of the equilibria is given by the eigenvalues of the Jacobian, whose i, j :th component is given by:

$$\begin{aligned} J_{ij} &= \frac{\partial}{\partial x_j} (x_i (r_i + \sum_{k=1}^n A_{i,k} x_k)) \\ &= \frac{\partial x_i}{\partial x_j} (r_i + \sum_{k=1}^n A_{i,k} x_k) + x_i \left(\frac{\partial}{\partial x_j} \sum_{k=1}^n A_{i,k} x_k \right) \\ &= \delta_{i,j} (r_i + \sum_{k=1}^n A_{i,k} x_k) + x_i A_{i,k} \delta_{k,j} \\ &= \delta_{i,j} (r_i + \sum_{k=1}^n a_{i,k} x_k) + x_i a_{i,j} \end{aligned} \quad (4.11)$$

where $\delta_{i,j}$ is the Kronecker delta, r_i is the self-growth of species i and $A_{i,j}$ is the effect of species j on species i . The eigenvalues of J at some equilibrium point x^* are then the λ satisfying:

$$\det(J - \lambda I) = 0 \quad (4.12)$$

where I denotes the identity matrix.

The eigenvalues of the Jacobian can be split naturally into two sets: the eigenvalues of the extinct species ($x_i^* = 0$) and the non-extinct species ($x_i^* \neq 0$). This follows from Theorem 4.2.1 that I will present next. As a preparation, observe that if $x_i = 0$, then the i :th row of J has non-zero elements only on the diagonal.

Theorem 4.2.1. *Consider an n species system (4.1) with m extinct species having indices $E = (e_1, e_2, \dots, e_m)$. Assume that an equilibrium point x^* exists where $x_i^* = 0$ for $i \in E$ and $x_i^* \neq 0$ otherwise. Then m eigenvalues are given by $\lambda_i = r_i + \sum_{k=1}^n A_{i,k} x_k^*$ and the $n - m$ remaining eigenvalues are the eigenvalues of the interior equilibrium \tilde{x}^* of the system of non-extinct species.*

Proof. Laplace's formula for the determinant is $\det(A) = \sum_{j=1}^n (-1)^{i+j} A_{i,j} K_{i,j}$, where A is a square matrix, n is the size of A and $K_{i,j}$ is a minor, which is the determinant of the matrix that remains when removing rows i and j from A . i may be chosen arbitrarily. The eigenvalues λ of the Jacobian J of (4.1) are given by solutions to the characteristic equation $\det(J - \lambda I) = 0$ where I is the identity matrix. Evaluate the determinant with Laplace's formula at row e_1 . The only non-zero element in the row lies on the diagonal, where $i + j$ is even, and hence $\det(J - \lambda I) = (J_{e_1, e_1} - \lambda) K_{e_1, e_1}$. Next, evaluate K_{e_1, e_1} along row e_2 . Repeat this procedure until column e_m . Then $\det(J - \lambda I) = M \prod_{k=1}^m (J_{e_k, e_k} - \lambda)$, where M is the determinant of the matrix remaining when columns and rows E have been removed from A . Hence, m eigenvalues are given by J_{e_i, e_i} , $e_i \in E$ and the remaining $n - m$ eigenvalues are given by the characteristic equation of the interior equilibrium of the system of $n - m$ non-extinct species. \square

The interior equilibrium of a system of species, if it exists, is obtained from Equation (4.11) by observing that the first term vanishes for every species at the interior equilibrium. The Jacobian for such a system is consequently given by:

$$J_{ij} = x_i^* A_{i,j} \quad (4.13)$$

on component form or:

$$J = \text{diag}(x_i^*) A_{i,j} \quad (4.14)$$

on matrix form, where $\text{diag}(x^*)$ is a square matrix with diagonal elements x_i^* and off-diagonal elements 0, and $x^* = -A^{-1}r$ is the interior equilibrium.

The Jacobian of the interior equilibrium of this model is almost the same as in May's model, in which it is $J_{i,j} = A_{i,j}$, with the difference that here the rows of A are scaled by the elements of x^* .

4.3 Summary

In this chapter I have introduced the generalised Lotka-Volterra equations and made a heuristic interpretation of them. I have given an expression for their equilibrium points, which have m species set to population size 0 and the remaining $n - m$ species being an interior solution to the system where the m species are removed. Here, n is the number of species of the full system and $0 \leq m \leq n$. This splitting up of the species in the equilibria also translates to eigenvalues. In the following chapter I will give an introduction to the critical points of the generalised Lotka-Volterra equation, building on the results of this chapter, which will hopefully spur your interest.

5

Introduction to critical points in the GLV

In this chapter I aim to give an introduction to the possible kinds of critical points in the model of this thesis as the average interaction strength σ is varied. I do this by treating the mechanisms briefly in text and by providing several figures showing examples. The critical phenomena extinction, collapse, resurrection and instability are presented here, but will be treated more in depth in subsequent chapters. All figures of this chapter are located in a section at the end of this chapter.

Throughout this section and in the Figures shown I assume that $r_i = 1, \forall i$ and $A_{i,i} = -1, \forall i$, and that off-diagonal elements of the community matrix A are scaled by a non-negative parameter σ .

5.1 Critical points in GLV

Critical points refer to values of parameters in a model which cause the system to abruptly change behaviour [23]. One example of a critical point may be a critical temperature above which the global climate may enter a new regime [6]. Another example is when an insect population abruptly changes steady state population as system parameters are varied [25].

If one is interested in no characteristics other than existence and stability of equilibria of the form of generalised Lotka-Volterra equations in this thesis, then there are four kinds of critical transitions; extinction, resurrection, collapse and positive eigenvalue. Since σ is the only parameter that is varied, the critical points are expressed in terms of σ .

Extinction is one critical point which occurs when the equilibrium of a species turns exactly zero. A sufficient and necessary requirement for extinction at $\sigma = \sigma_e$ is composed by two requirements. Firstly, $\lambda_i(\sigma_0) = 0, \exists i$ (which is equivalent to $x_i^* = 0, \exists i$) needs to hold. Secondly, the species must have been non-extinct ($x_i^* > 0$) for some slightly smaller $\sigma_e^- \equiv \lim_{\epsilon \rightarrow 0^+} \sigma_e - \epsilon$.

Another kind of critical point is resurrection, which occurs if a species has previously turned extinct at some σ_e and then gets a positive population size at some $\sigma > \sigma_e$.

The third critical point is collapse, which occurs if a previously stable and feasible equilibrium point ceases to exist. This happens if $\det(A) = 0$ for some σ , since this is equivalent to $Ax + r = 0$ lacking a solution.

The fourth, and most difficult to describe, kind of critical transition is that of

instability. The instability may result in explosive growth of populations, limit cycles or chaos.

In the remainder of this chapter I present examples illustrating the different critical transitions.

5.2 Extinction in GLV systems

Extinctions occur when the system has a stable and feasible interior equilibrium point for some initial sigma σ_e consisting of n species, but for some $\sigma_1 > \sigma_e$ gets that one of its species i has a zero equilibrium population $x_i^* = 0$. Extinction can be shown in several ways. In Figure 5.14, which shows equilibrium population sizes normalised to 1 for increasing σ , extinction is manifested by population sizes going to zero and staying there. This happens just above $\sigma = 0.04$ in this system of initially 80 species.

Extinction can also be manifested as that one eigenvalue reaches 0, as seen repeatedly in Figure 5.20. The curves show the real part of the eigenvalues of a system of 20 non-extinct species initially. Since there is no evident ordering of eigenvalues when computing them numerically, I have chosen to colour them in order of size. This makes the curves change colour repeatedly as their size rank changes with σ . With a little imagination one can however see that there are distinct curves which vary continuously. In particular, at $\sigma \approx 0.08$ one curve rises to 0 and then sharply decreases. This corresponds to that one species goes extinct, making the eigenvalues of the system the union of the eigenvalues of the $(n - 1)$ species subsystem and the eigenvalue associated with the extinct species, as was shown in Section 4.2.3. Eventually, the decreasing curve intersects with another curve, which takes on the lead as the largest eigenvalue, rises to zero and then sharply begins to decrease. This repeated extinction process is also manifests itself if one only considers the largest real part of eigenvalues, as is done in Figure 5.11 for an initially 80 species system. Although the resolution in σ is smaller, which makes it difficult to discern the repeated extinctions with maximum eigenvalues close to zero, a comparison with Figure 5.20 should clarify the mechanism. The red lines in Figure 5.11 will be discussed later in the context of system collapse.

It is natural to ask where the bifurcations of real parts of eigenvalues come from in 5.20, where one eigenvalue appears to split onto two distinct eigenvalues or vice versa. The explanation is simply that a complex conjugate eigenvalue pair reaches the real line and split into two distinct eigenvalues, or that two real eigenvalues merge and split into two conjugate eigenvalues (with identical real part).

It is important to emphasise, that if an eigenvalue is identically 0 then its real part is also 0, but the converse does not necessarily hold true. This means that the real part of an eigenvalue reaching 0 does not imply extinction, although this is often the case and always so in Figure 5.11 and Figure 5.20.

In the next chapter, we will deal with extinction more in depth: When does the first extinction occur? What happens with eigenvalues close to extinction? How frequent is extinction for increasing σ , and which species goes extinct first?

5.3 Collapse in GLV systems

Another kind of critical point is collapse of the system. Collapse in this context means that the system lacks a solution and that prior to the point of collapse the population equilibrium grows rapidly. A collapse occurs when $r + Ax^* = 0$ lacks a solution, which happens when the interaction matrix A is not invertible, as described in the introduction of this chapter. This manifests itself in that species grow unboundedly, but also in that eigenvalues tend to decrease rapidly. The reason for this is loosely speaking that the Jacobian J depends on $\det(A)$ as $J \propto \frac{-1}{\det(A)^{n-1}}$. The resulting plummeting of eigenvalues close to the point of a collapse is illustrated in Figure 5.12. In this system of initially 80 species eigenvalues are initially on the order of magnitude 1 but as the σ of collapse is approached at about $\sigma = 14.2$, most eigenvalues dip rapidly.

In the next chapter we will learn when collapse occurs and why systems tend to collapse first after $n/2$ species have gone extinct, where n is the initial number of species.

5.4 Resurrection in GLV systems

Resurrection occurs if one species which has been extinct for some σ_0 gets a positive population size for some σ_1 . One example of resurrection is seen in Figure 5.21, in which the species equilibrium population versus σ plot has been zoomed in onto a region where one species emerges from the 0 axis. The initial number of species was 80 in this simulation run, and this was the only occurrence of resurrection as σ was increased.

Resurrection will not be discussed in detail in this thesis, but will be of importance in the treatment of uniqueness of stable and feasible points in the next chapter.

5.5 Instability of solutions in GLV systems

One kind of critical point is when the system ceases to have stable equilibrium points, or at least tend not to converge to the equilibria. There can be several causes of instability, but presence of an eigenvalue with positive real part for some equilibrium point is a requirement.

One example of when the system enters a limit cycle is shown in Figure 5.3. The shape of the oscillations is reminiscent of the oscillations in the classical two-species Lotka-Volterra system. An example of what looks like chaotic behaviour is seen in Figure 5.4. The chaos appears intermittent, with fast oscillations in some time frames and slower oscillations in other time frames. In both figures the number of species was $n = 80$, in the figure with the limit cycle $\sigma = 0.1348$ and in the chaotic behaviour figure $\sigma = 0.1434$.

In this thesis I will not go in depth into the nature of limit cycles and chaotic behaviour, but I will discuss briefly under what circumstances the phenomena occur.

5.6 The σ of first extinction in GLV systems

A question which deserves particular attention is when the first extinction occurs. In the next chapter I will show that if extinctions do not occur, then the system is likely to collapse close to the σ of instability in May's model. Therefore, extinctions must occur before the σ of collapse in May's model to obtain the extinction pattern demonstrated in e.g. Figure 5.20.

Figure 5.23 shows the average σ for the first extinction σ_{e1} in the model of this thesis, here called "non-May", and the σ of instability in May's model σ_c for population sizes between 20 and 149 and full connectivity $C = 1$. The equation for the critical σ in May's model according to Girko's circular circle law assumed to be valid for $n \rightarrow \infty$ is included as a reference. The figure shows that at least for the selected n , the average σ_{e1} occurs before the average σ_c in May's model. It appears like the rate of decrease of the ratio between σ_c and σ_{e1} decreases for increasingly large n . For small n , the empirical average σ_c appears to overestimate the prediction by Girko's circular law. This is not surprising, since Girko's law holds with probability 1 only in the $n \rightarrow \infty$ limit. Furthermore, the variance in σ_c is greater for small n in both the May and non-May model. Figure 5.22 shows σ_c and σ_{e1} versus n , but with connectivity $C = 0.5$. The qualitative behaviour is the same as in the full connectivity case and the ratio between σ_c and σ_{e1} appears to be roughly the same on the average. It appears as if the curves are scaled by $C^{-1/2}$ as Girko's circular law predicts.

In the next chapter I provide an explanation for why a first extinction occurs and show the distribution of the σ for the first extinction.

5.7 Repeated extinctions

In the previous section I presented evidence for that for large systems with random interactions tend to have a first extinction. But as can be seen in for instance Figure 5.14 more than one species tend to go extinct. Figure 5.10 shows the number of extinct species at a stable and feasible equilibrium for increasing σ for a typical system of 80 species. The first extinction begins at $\sigma = 0.041$ and then the number of extinct species rises approximately linearly until collapse at $\sigma = 0.163$. A linear least squares fit gives a slope of 4.06 extinct species per 100 σ with $R^2 = 0.99$. The fit is made on data from the last σ of non-extinction to the σ of collapse σ_c . I would like to point out that in most cases the linear fit is not as good, but still good. Worth noting is also that the number of extinct species at collapse (46) is close to half of the number of species in the system. This will be explored further in the next chapter.

5.8 How eigenvalues change with σ

It is illustrative to see how the distribution of eigenvalues in the complex plane tends to change as σ is increased. Figures 5.5, 5.6 and 5.7 show the eigenvalues $\lambda_i, i = 1, 2, \dots, n$ of the Jacobian of an $n = 80$ species system at the equilibrium for

$\sigma = 0.022, 0.048$ and 0.098 . When viewing these figures it is good to keep in mind that for $\sigma = 0$ all eigenvalues $\lambda_i = -1, \forall i$. In Figure 5.5 all eigenvalues are in a blob which narrows toward the real axis, meaning that eigenvalues closer to the real axis tend to have smaller imaginary parts. In Figure 5.6 the eigenvalues to the left of -1 are more spread out and close to the real axis the tip of the eigenvalue cloud is close to zero. The red symbol is the eigenvalue attributed to a species which has gone extinct. This extinction occurred when one the eigenvalue cloud expanded and one eigenvalue became 0. In Figure 5.7 several species have gone extinct, as indicated by the red symbols. The eigenvalues are more spread out, and although not clearly apparent, the average of the real parts of eigenvalues has decreased.

Figures 5.1 and 5.2 show how the eigenvalue distribution in May's model differs from the distribution in the model of this thesis. In Figure 5.1 the eigenvalues in a May $n = 50$ species system appear to spread out in increasingly larger disks as σ increases, approximately within the boundary of Girko's circular law (valid in the $n \rightarrow \infty$ limit), drawn as red circles. In the model of this system, the eigenvalues become stretched out along the real axis compared with May's model, as seen in Figure 5.2. The eigenvalues closer to the imaginary axis tend to have smaller imaginary parts compared with eigenvalues father from the imaginary axis and it appears like the eigenvalue with real part is also real.

5.9 Summary

Now that we have seen how eigenvalues change with σ and been introduced to the mechanics of extinction, collapse, resurrection and unstable system behaviour we are ready to answer the questions posed in this chapter. This will be done in the following chapter.

5.10 Figures

In this section all figures of this chapter are collected.

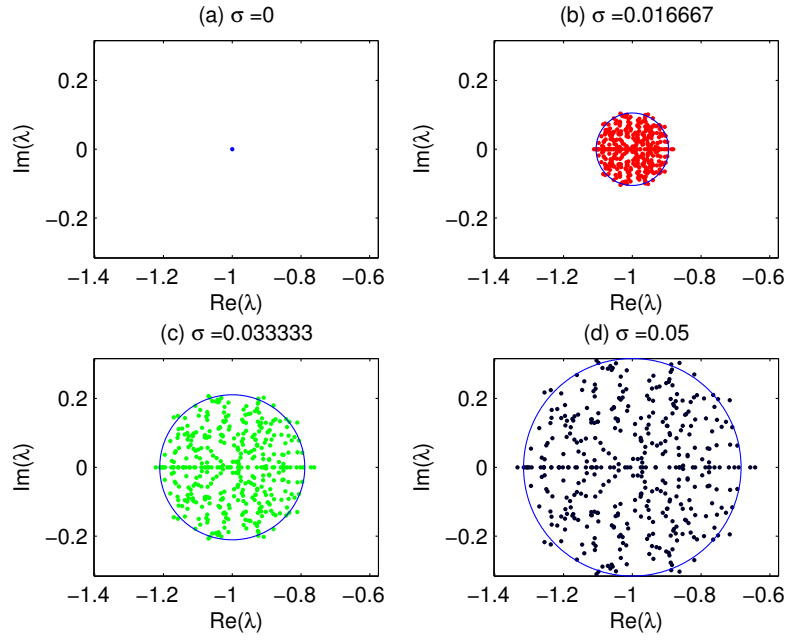


Figure 5.1: Eigenvalues of the Jacobian $J = \sigma B - I$ in May's model, where I is the identity matrix, $B_{i,i} = 0$, $B_{i,j} \sim \mathcal{N}(0, 1)$, $i \neq j$ and independent and σ is a parameter. The number of species $n = 40$. The dots are eigenvalues of ten realisations of B , for a given σ . Solid circles enclose disks $\sigma = \sqrt{n}$ which all eigenvalues lie inside with probability 1 in the limit $n \rightarrow \infty$ (for one realisation). The network of species is fully connected $C = 1$.

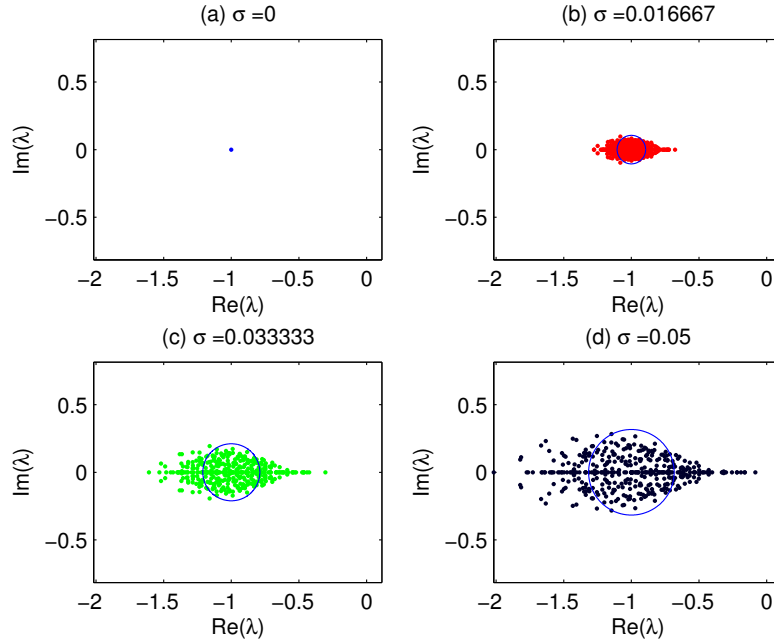


Figure 5.2: Eigenvalues of the Jacobian $J = \text{diag}(x^*)(\sigma B - I)$ of an equilibrium point x^* of the GLV, where I is the identity matrix, $B_{i,i} = 0$, $B_{i,j} \sim \mathcal{N}(0, 1)$, $i \neq j$ and independent and σ is a parameter. The number of species $n = 40$. The dots are eigenvalues of ten realisations of B , for a given σ . Solid circles enclose disks $\sigma = \sqrt{n}$ which all eigenvalues lie inside with probability 1 in the limit $n \rightarrow \infty$ (for one realisation) in May's model. The network of species is fully connected $C = 1$.

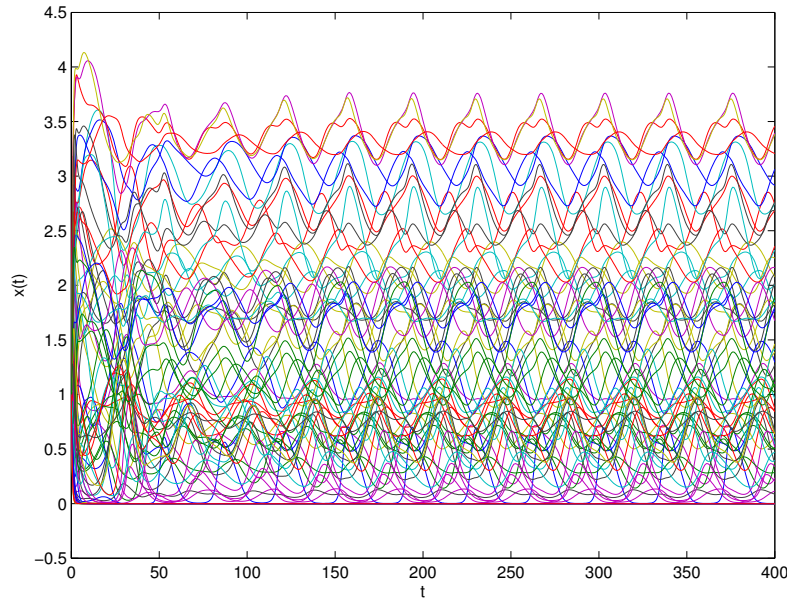


Figure 5.3: The system converging to a limit cycle. $x(t)$ is a vector of species populations and t is a time unit. The initial number of species is $n = 80$, $\sigma = 0.1348$ and $x_i(0) = 1, \forall i$.

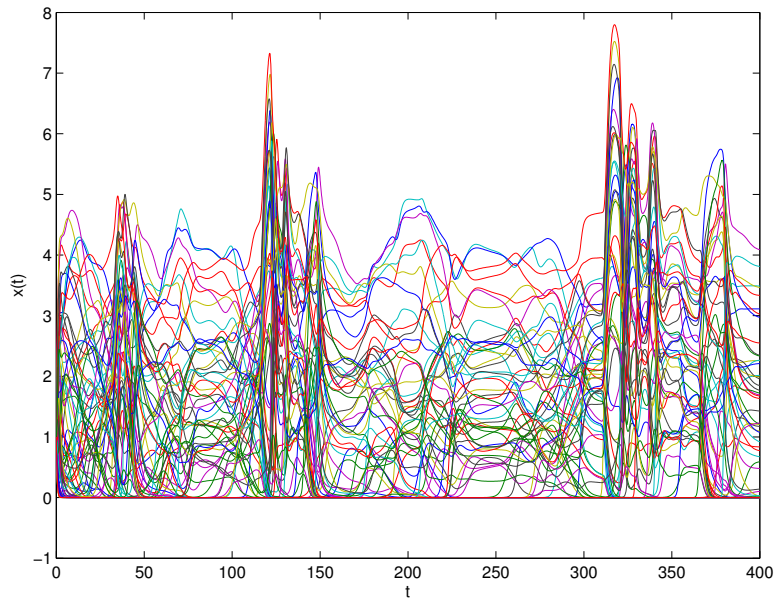


Figure 5.4: The system exhibiting chaotic behaviour. $x(t)$ is a vector of species populations and t is a time unit. The initial number of species is $n = 80$, $\sigma = 0.1434$ and $x_i(0) = 1, \forall i$.

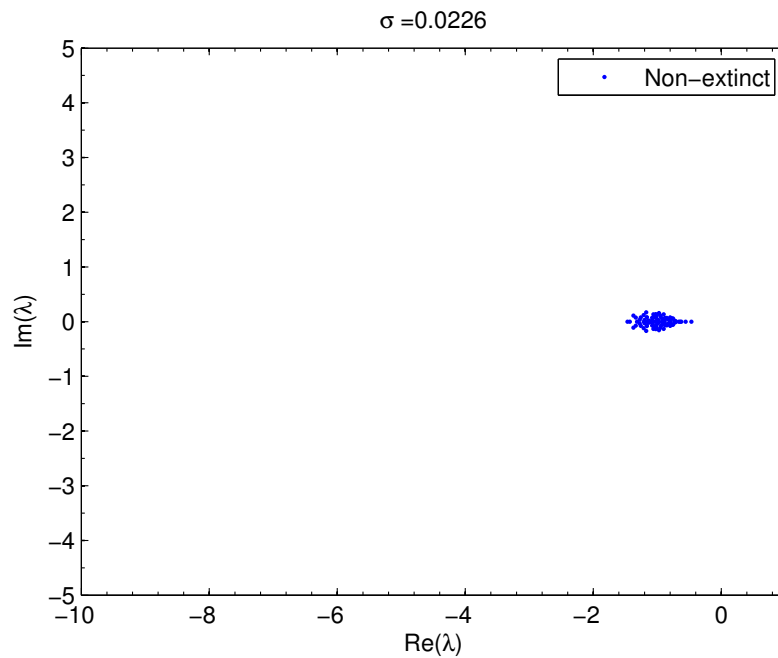


Figure 5.5: Eigenvalue plot at an equilibrium point x^* that the system has converged to. $n = 80$, $\sigma = 0.0226$. No species are extinct at x^* . This is the same realisation of the interaction matrix as in figures (5.6) and (5.7).

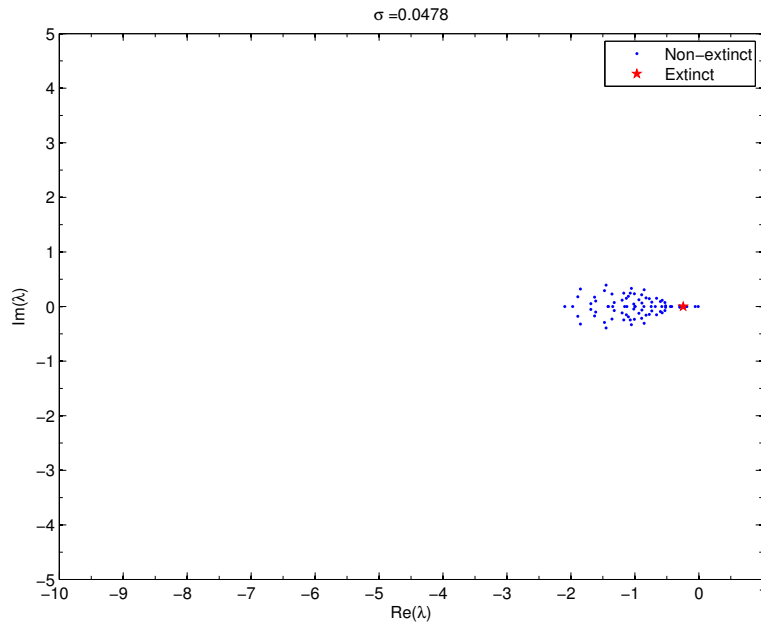


Figure 5.6: Eigenvalue plot at an equilibrium point x^* that the system has converged to. $n = 80$, $\sigma = 0.02$. No species are extinct at x^* . This is the same realisation of the interaction matrix as in figures (5.5) and (5.7).

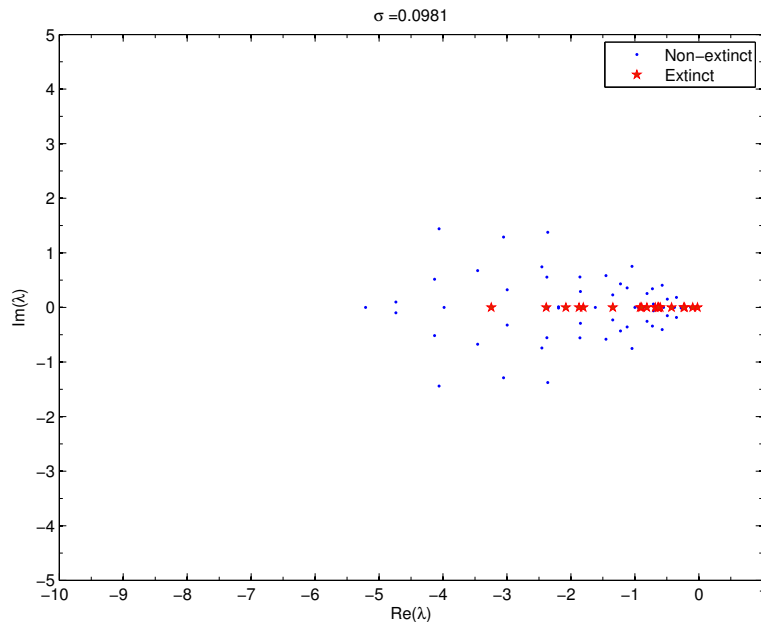


Figure 5.7: Eigenvalue plot at an equilibrium point x^* that the system has converged to. $n = 80$, $\sigma = 0.0981$. Eigenvalues associated with extinct species are marked as red stars. This is the same realisation of the interaction matrix as in figures (5.5) and (5.6). The plot window is cropped, so some eigenvalues are not visible. All eigenvalues are in the negative real plane, however.

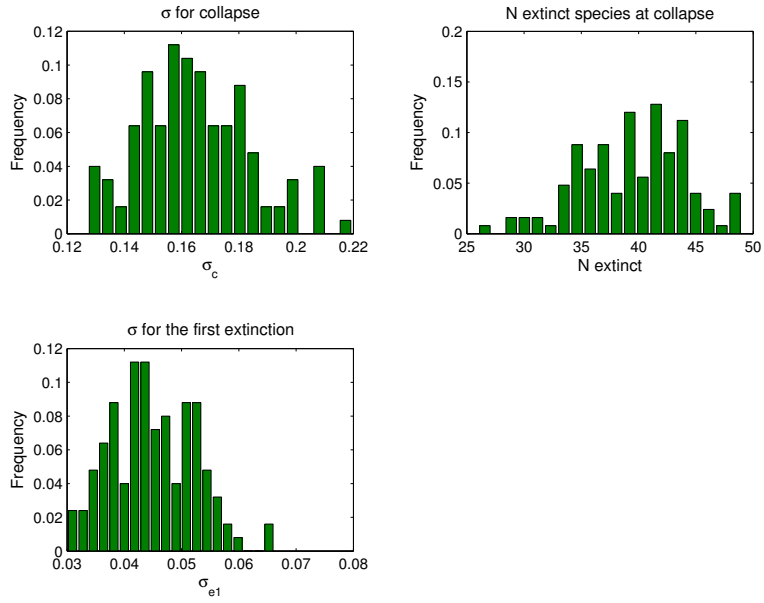


Figure 5.8: The σ of collapse σ_c , number of extinct species $N_{extinct}$ at collapse and the σ of the first extinction σ_{e1} for 125 runs where the system was allowed to equilibrate for increasingly large σ . The initial number of species was $n = 80$. The sample mean and sample standard deviations are: $\bar{\sigma}_c = 0.1648$ and $s_{\sigma_c} = 0.0197$, $\bar{N}_{extinct} = 39.5$ and $s_{N_{extinct}} = 4.62$, and $\bar{\sigma}_{e1} = 0.0450$ and $s_{\sigma_{e1}} = 0.0074$. In total 150 runs were made, of which 125 ended in collapse, 24 did not converge for some σ and one was aborted due to the solver having a negative solution.

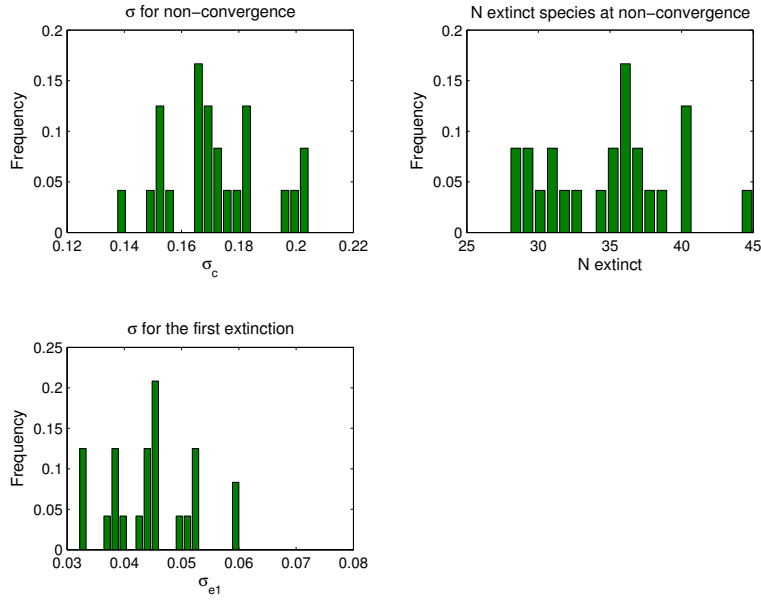


Figure 5.9: The first σ for which the system does not converge σ_c , the number of extinct species $N_{extinct}$ at the σ of non-convergence and the σ of the first extinction σ_{e1} for 24 runs where the system was allowed to equilibrate for increasingly large σ . The initial number of species was $n = 80$. The sample mean and sample standard deviations are: $\bar{\sigma}_c = 0.1720$ and $s_{\sigma_c} = 0.0175$, $\bar{N}_{extinct} = 34.78$ and $s_{N_{extinct}} = 4.43$, and $\bar{\sigma}_{e1} = 0.0445$ and $s_{\sigma_{e1}} = 0.0077$. In total 150 runs were made, of which 125 ended in collapse, 24 did not converge for some σ and one was aborted due to the solver having a negative solution.

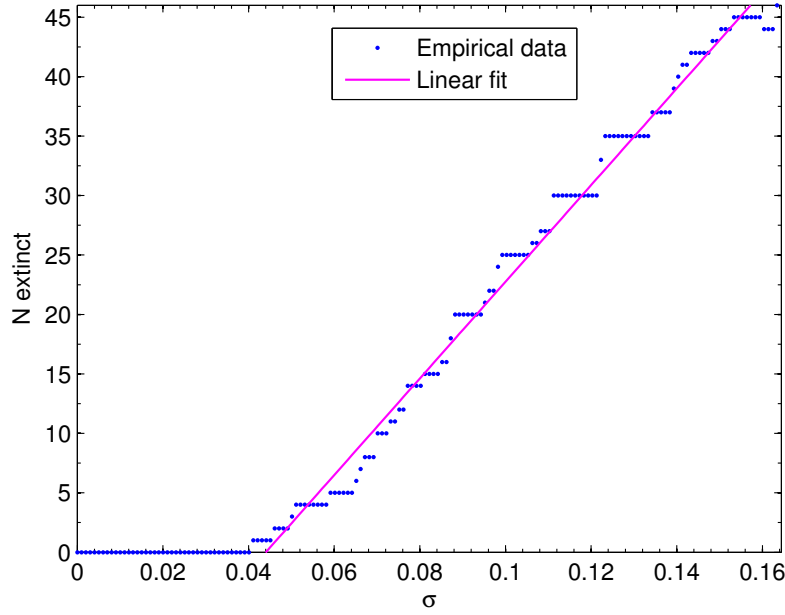


Figure 5.10: The number of extinct species at a stable equilibrium x^* for σ between 0 and 0.1434. The initial number of species was $n = 80$. A species i is considered extinct if $x_i < 10^{-5}$. The magenta line shows a linear fit with slope 4.06 extinct species per 100 σ , vertical axis intercept -17.9 and $R^2 = 0.99$. The fit is made on data from the last σ of non-extinction to the σ of collapse σ_c .

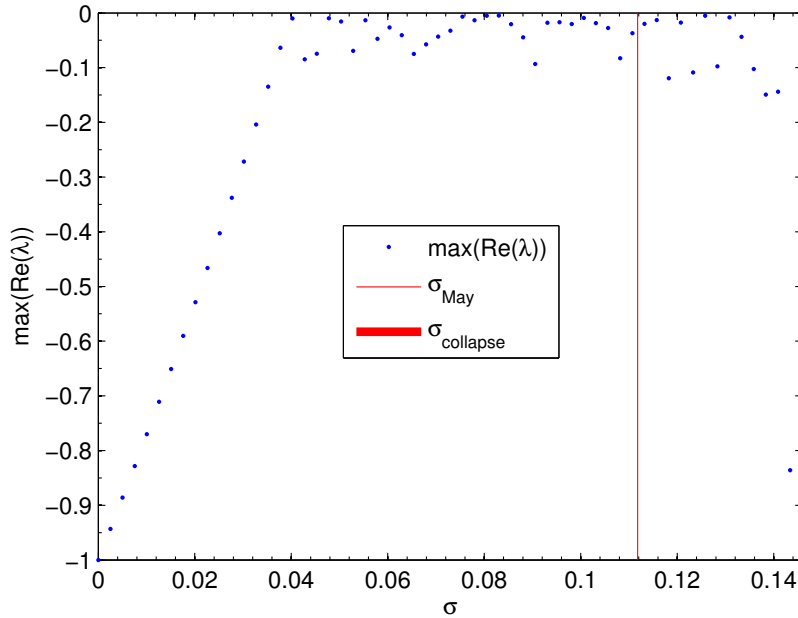


Figure 5.11: The maximum real part of all eigenvalues at an equilibrium x^* denoted by blue dots. $n = 80$. The thin red line shows the σ for which a May system is predicted to go unstable. The thick red line demarcates the σ for which the system collapses.

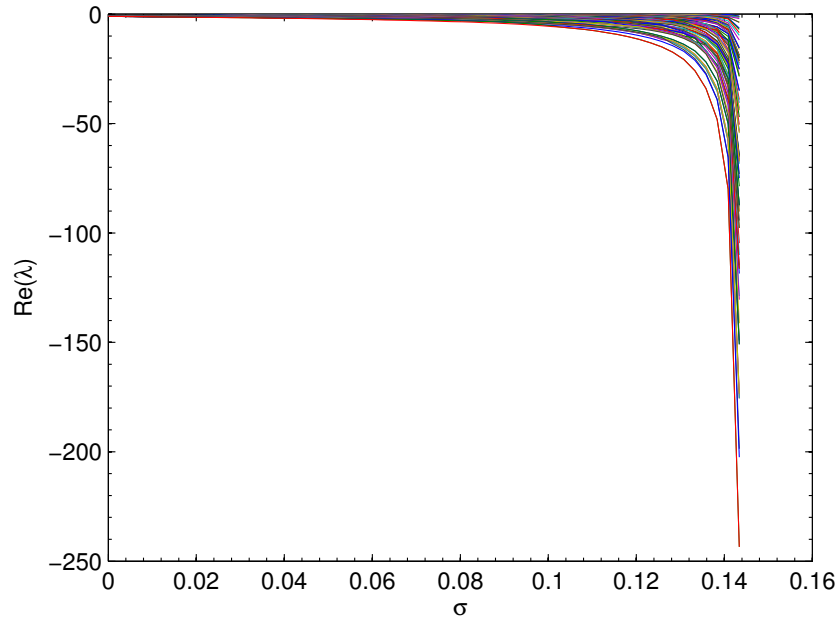


Figure 5.12: The real part of eigenvalues λ of the Jacobian J at an equilibrium point x^* up until $\sigma = 0.1434$ after which the system collapses. The initial number of species was $n = 80$.

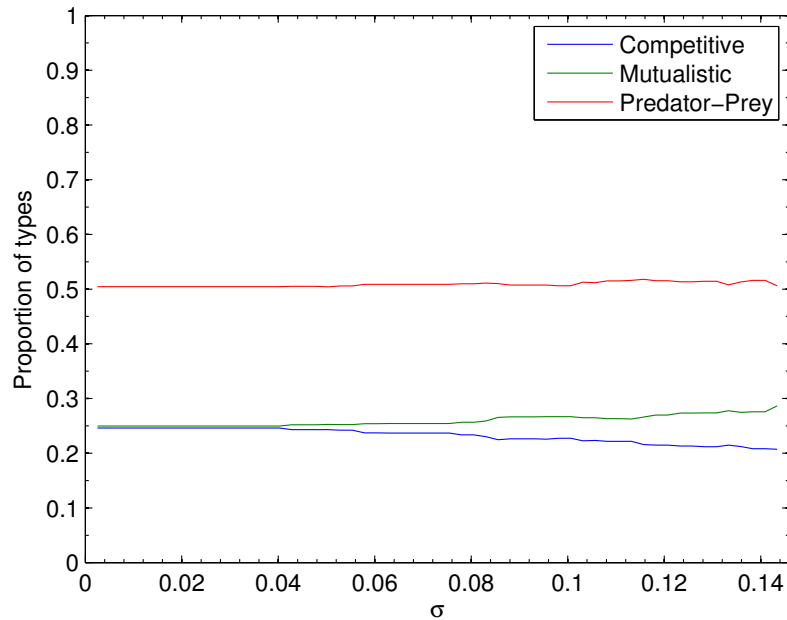


Figure 5.13: Proportion of different interaction types for increasing σ . As a species goes extinct the composition of mutualistic, competitive and predator-prey interactions may change, as is observed. Initial number of species was $n = 80$.

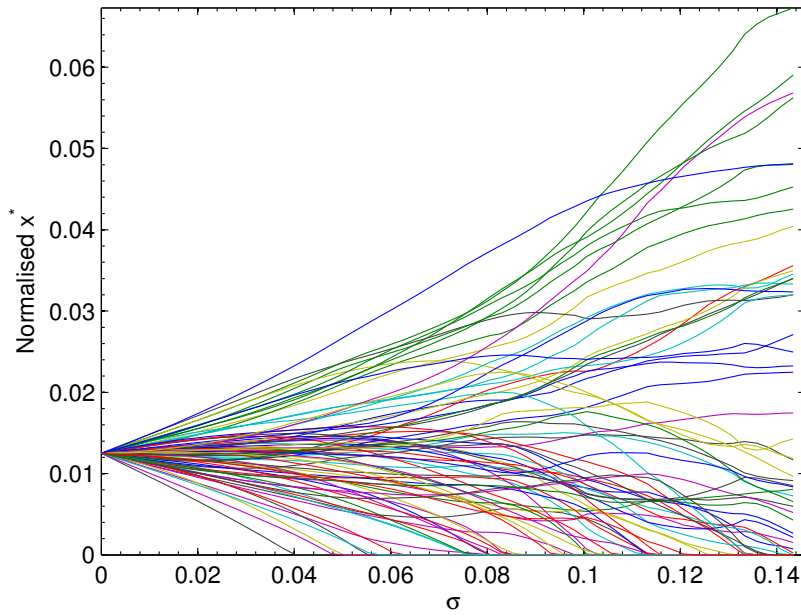


Figure 5.14: All components of the equilibrium point $x^*(\sigma)$ that the system converges to for each σ , until collapse occurs at $\sigma = 0.1434$. The equilibrium point $x^*(\sigma)$ is normalised such that $|x^*(\sigma)| = 1$.

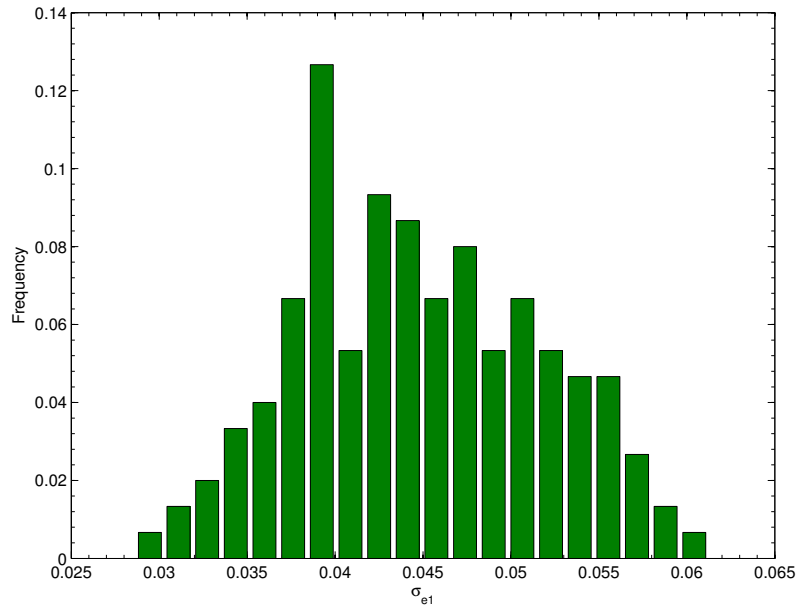


Figure 5.15: The first σ of extinction σ_{e1} for Neumann series expansions to order two from 150 realisations of the interaction matrix. The series is convergent since the eigenvalues of the interaction matrix were less than one. Sample mean and standard deviations were $\sigma_{e1}^- = 0.0448$ and $s_{\sigma_{e1}} = 0.0069$. The initial number of species was $n = 80$.

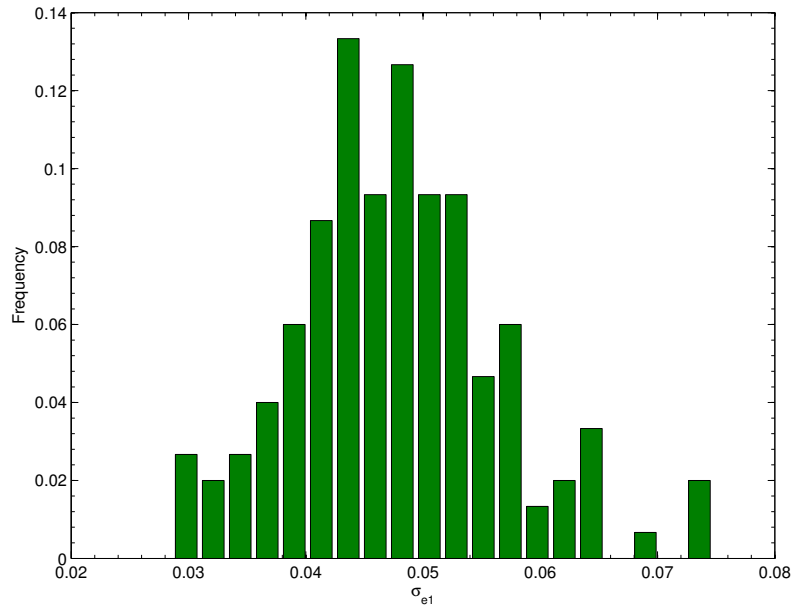


Figure 5.16: The first σ of extinction σ_{e1} for Neumann series expansions to order one from 150 realisations of the interaction matrix. The series is convergent since the eigenvalues of the interaction matrix were less than one. Sample mean and standard deviations were $\bar{\sigma}_{e1} = 0.0447$ and $s_{\sigma_{e1}} = 0.0089$. The initial number of species was $n = 80$.

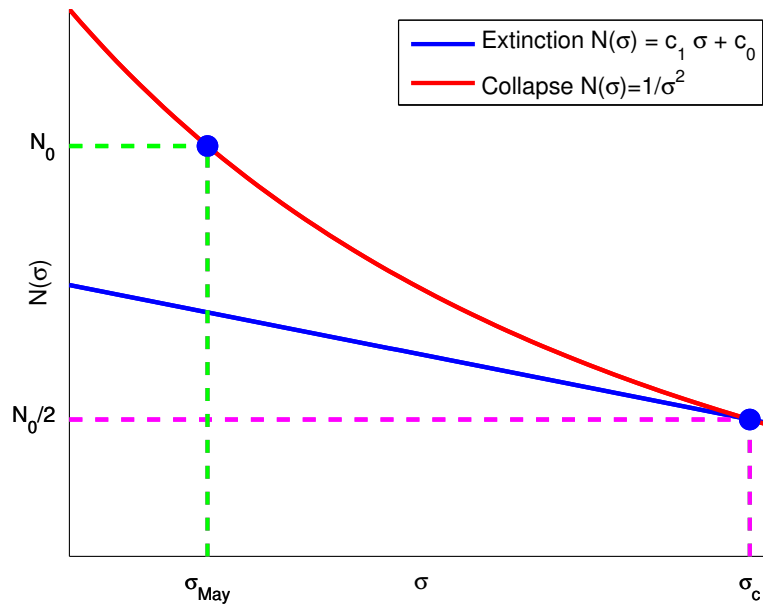


Figure 5.17: Conceptual explanation for why extinction occurs after approximately half of the species have gone extinct. By assumption the number of non-extinct species N decreases linearly. The number of species required for instability in May's model, and often collapse in the model of this thesis, is $\max(\operatorname{Re}(\lambda)) = 0$, where λ is an eigenvalue of a matrix A of N species whose off-diagonal elements are a zero-mean i.i.d. elements and the diagonal consists of all elements -1 . This required number of species decreases as $\frac{1}{\sigma^2}$ for large N . For a discussion on the relation between $\max(\operatorname{Re}(\lambda)) = 0$ and collapse, see Section 6.5. The blue dots show the intersections which give rise to the critical σ .

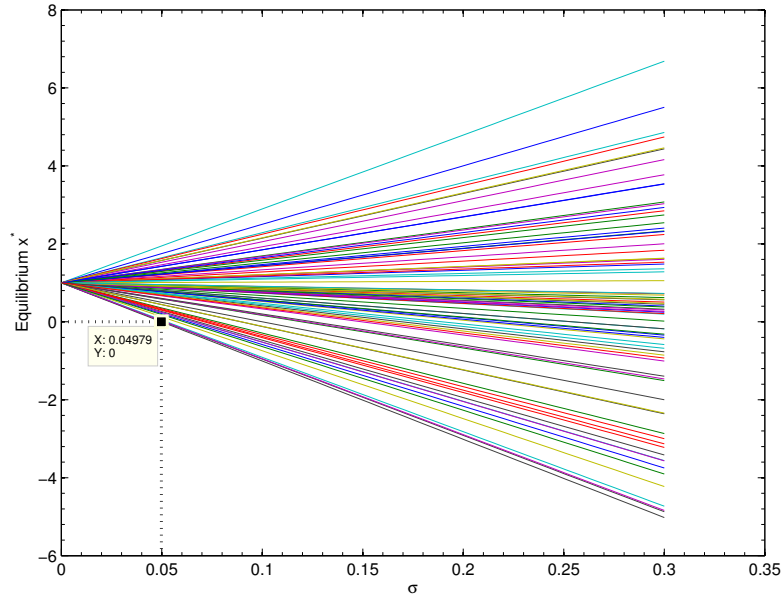


Figure 5.18: Neumann expansion to first order in σB of the interior $n = 80$ species equilibrium point: $x^* = -A^{-1}r = (I - \sigma B)^{-1}r \approx r + \sigma Br$. The marker shows where the first component intersects with the 0 line.

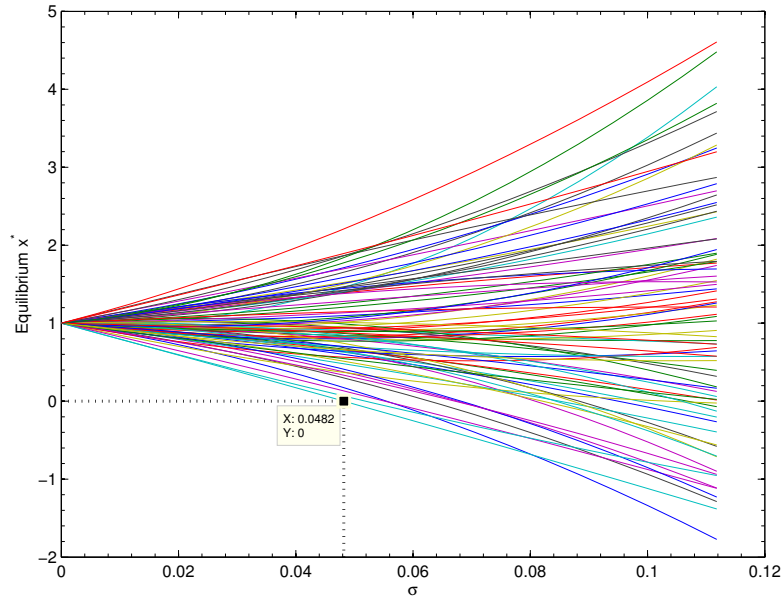


Figure 5.19: Neumann expansion to second order in σB of the interior $n = 80$ species equilibrium point: $x^* = -A^{-1}r = (I - \sigma B)^{-1}r \approx (I + \sigma B + \sigma^2 B^2)r$. The marker shows where the first component intersects with the 0 line.

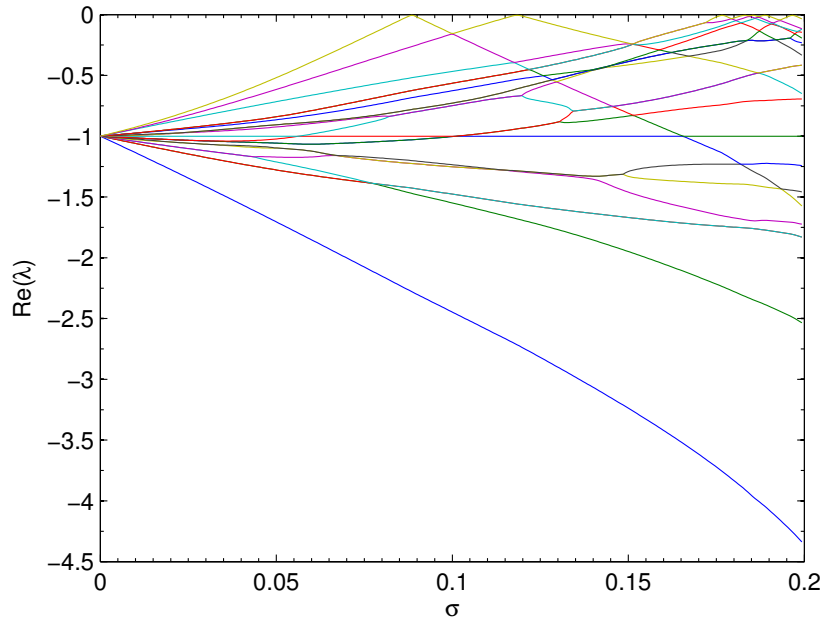


Figure 5.20: The real part of eigenvalues λ of the Jacobian J at an equilibrium point x^* . The initial number of species was $n = 20$.

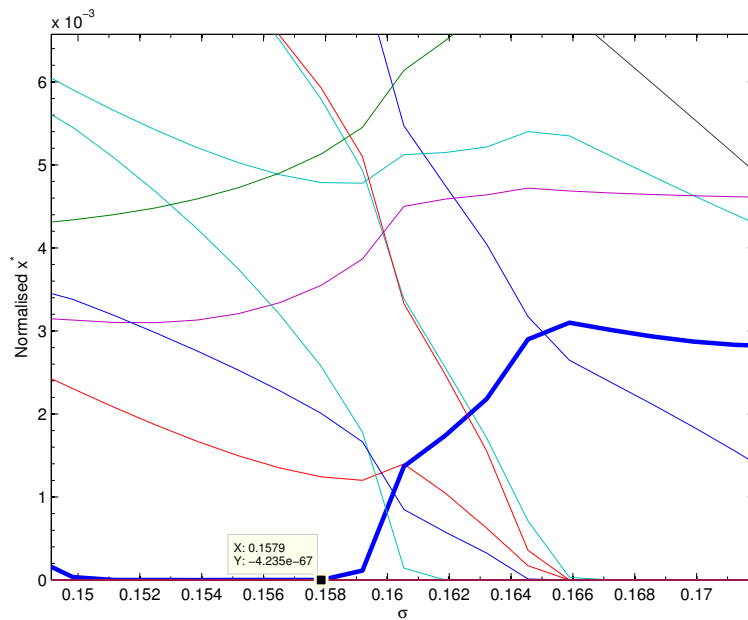


Figure 5.21: Zoom in on an example of resurrection in a system of initially $n = 80$ species. The thick blue line is the equilibrium population size of a species which goes extinct around $\sigma = 0.151$ and gets resurrected around $\sigma = 0.158$. The population sizes of the equilibrium point $x^*(\sigma)$ are normalised such that $|x^*(\sigma)| = 1$.

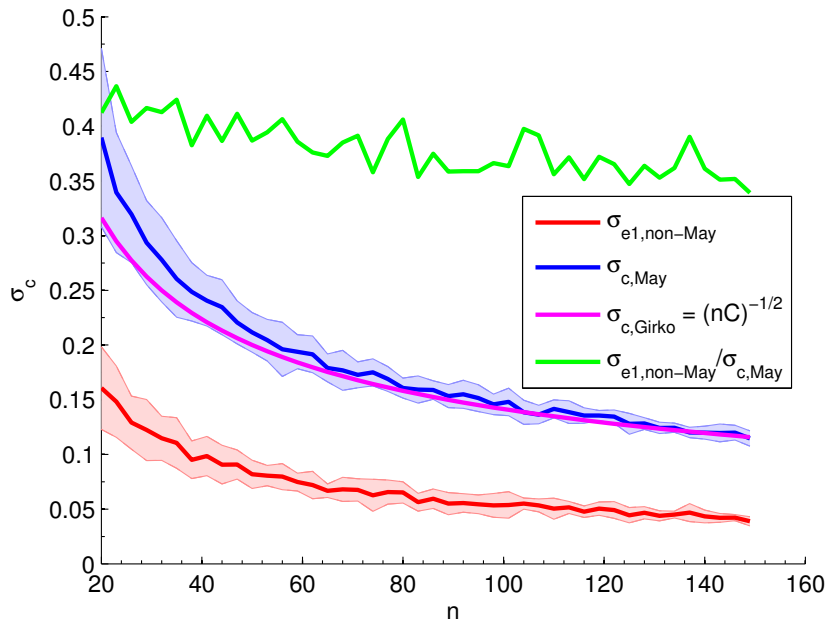


Figure 5.22: Critical σ for instability in May's model and σ for first extinction in the model of this thesis. The connectivity was $C = 0.5$. The number of species n was spaced in intervals of three between 20 and 149. Error bars give the standard deviation of the sample σ_c for a given n . The prediction for σ_c in the large n limit is given as a magenta curve. The green curve is the ratio between the average σ_c for the May model and the other model. The number of averaging rounds was different for different σ . For details see Section 7.4.1.

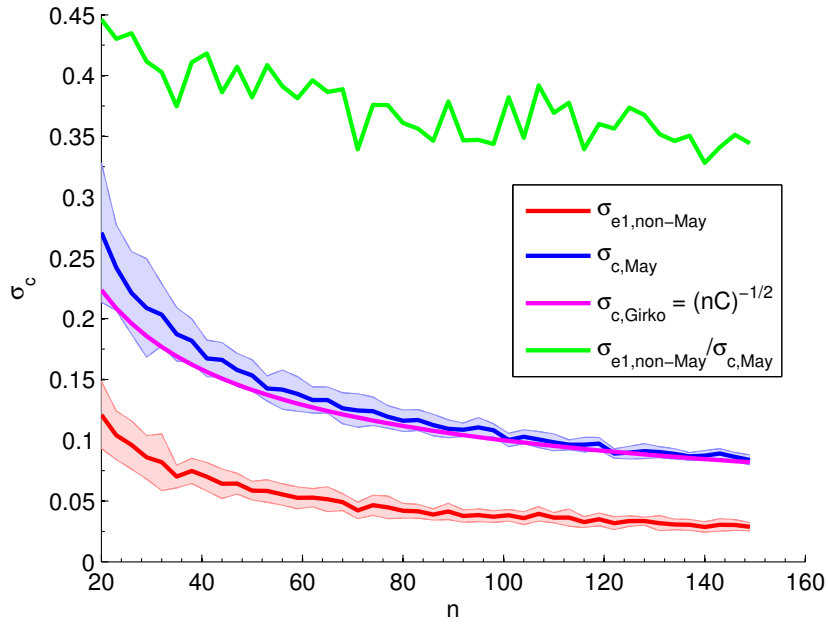


Figure 5.23: Critical σ for instability in May's model and σ for first extinction in the model of this thesis. The connectivity was $C = 1$. The number of species n was spaced in intervals of three between 20 and 149. Error bars give the standard deviation of the sample σ_c for a given n . The prediction for σ_c in the large n limit is given as a magenta curve. The green curve is the ratio between the average σ_c for the May model and the other model. The number of averaging rounds was different for different σ . For details see Section 7.4.1.

6

Understanding Critical Transitions in the GLV

In this chapter I go deeper into the mechanisms of critical points such as extinction and collapse in generalised Lotka-Volterra (GLV) model systems. The chapter can naturally be divided into three parts. First, I describe all possible equilibria for a two species system and discuss the possible system behaviour as the average interaction strength parameter σ is varied. I then try to explain the possible critical points introduced in the previous chapter. In the last part I present an assortment of unrelated results for the system, such as the uniqueness of solutions under some assumptions (which are shown not to always hold) and a criterion for which species go extinct first.

Throughout this chapter, I assume that the self-growth is identical for all species ($r_i = r_j, \forall i, j$) and that all diagonal elements of the community matrix A are identical ($A_{i,i} = A_{j,j}, \forall i, j$). In some cases, when specified, I further assume that $r_i = A_{i,i} = 1, \forall i$. Why this assumption preserves the qualitative behaviour of the system is motivated in Section 6.4.2.

6.1 Understanding a two species system

I start out the course of trying to explain how GLV systems behave by exhausting the possible behaviour close to equilibrium points of a two species GLV system. Since a two species system is exactly solvable, one can gain insights which might aid the understanding of larger systems for which explicit solutions do not exist or are unwieldy.

6.1.1 The equilibria, eigenvalues and determinants

In the following section I present equilibrium points, eigenvalues and determinants of the community matrix A and the Jacobian and discuss how they affect system behaviour. Derivations can be found in Section A.3.1 of the appendix. I assume that the self-growth vector $r_i = 1, \forall i$ and that $A_{i,i} = -d, d > 0$. A similar analysis, but with a different focus, was made by Baigent [3].

Let $A = \begin{bmatrix} -d & a \\ b & -d \end{bmatrix}$. For the moment, let a and b be fixed real numbers. Later they will be parametrized by a parameter σ and also viewed as random variables.

The determinant of A becomes:

$$\det(A) = d^2 - ab. \quad (6.1)$$

Define $D \equiv \det(A)$. Then:

$$A^{-1} = \frac{1}{D} \begin{bmatrix} -d & -a \\ -b & -d \end{bmatrix} \quad (6.2)$$

and

$$x^* = -A^{-1}r = \frac{1}{D} \begin{bmatrix} a + d \\ b + d \end{bmatrix} \quad (6.3)$$

where x^* is the interior equilibrium point. $D \neq 0$ is assumed. Otherwise x^* does not exist. The Jacobian then becomes:

$$J = \text{diag}(x^*)A = \frac{1}{D} \begin{bmatrix} -d^2 - ad & a^2 + ad \\ b^2 + bd & -d^2 - bd \end{bmatrix} \quad (6.4)$$

where $\text{diag}(x^*)$ is a square matrix with elements x_i^* on the diagonals and 0 on the off-diagonal.

$$\det(J) = \frac{1}{D^2}(d^2(a+d)(b+d) - ab(a+d)(b+d)) = \frac{1}{D}(a+d)(b+d). \quad (6.5)$$

One of the eigenvalues of the Jacobian is $\lambda_1 = -1$. The second eigenvalue is $-\det(J)$.

We are now ready to introduce a dependence on a parameter σ on a and b by the transformation $a \rightarrow \sigma a, b \rightarrow \sigma b$. If a and b are viewed as outcomes of independent $N(0, 1)$ variables, then σa and σb can be viewed as outcomes of $N(0, \sigma)$ variables. Then we have that:

$$D = \det(A) = d^2 - \sigma^2 ab \quad (6.6)$$

and

$$\lambda_2 = -\det(J) = -\frac{1}{D}(\sigma a + d)(\sigma b + d). \quad (6.7)$$

Now we can exhaust possible behaviour of the system by investigating three cases: $a, b > 0$, $a, b < 0$ and $(a > 0, b < 0 \text{ or } a < 0, b > 0)$. Due to symmetry it is sufficient to investigate only $a > 0, b < 0$ but not $a < 0, b > 0$.

In the showcase of system behaviour in Chapter 5, σ was started out to be 0 and then increased in small steps. In the same vein I will talk about "increasing" σ , although the system does not have to "start" at any particular σ .

It will be shown in Section 6.4.1 that the $x^* = 0$ equilibrium is unstable with all eigenvalues $\lambda_i = r_i > 0$, why this equilibrium will not be further mentioned in this section.

6.1.1.1 Case $a > 0, b > 0$ (mutualism)

In this case $\lambda_2 < 0$ as long as $D > 0$ and so no species can go extinct (before the system collapses at least). System collapse occurs when $D = 0$ at $\sigma = d/\sqrt{(ab)}$.

Before system collapse, the eigenvalues of the interior equilibrium point are $\lambda_1 = -d$ and $\lambda_2 = -\frac{1}{D}(|a| + d)(|b| + d) < 0$ so point is stable. x^* is similarly seen to be positive, so the equilibrium point is feasible.

What happens for $\sigma > d/\sqrt{ab}$? Then $D < 0$ and $x^* < 0$ 6.3, so the interior equilibrium is unfeasible.

What happens with the equilibrium with one extinct species? Consider $x_1^* = 0$ and $x_2^* = 1/d$. Then according to Equation (4.11) $\lambda_1 = 1 + \sigma a/d > 0$ and $\lambda_2 = -1$, so the equilibrium is feasible but non-attracting for all σ , since one eigenvalue is positive. The same holds for $x_1 \neq 0$ and $x_2 = 0$.

6.1.1.2 Case $a < 0, b < 0$ (competition)

For both a and b negative extinction can occur since $J = 0$ if either $\sigma = -d/a = d/|a|$ or $\sigma = -d/b = d/|b|$. Collapse is also possible, since $D = 0$ for $\sigma = d/\sqrt{(ab)}$.

As in the $a > 0, b > 0$ case, the interior equilibrium point is seen to be both feasible and stable before extinction.

One may ask if collapse can occur before extinction. This is not possible by the following argument. Consider first the case $a = b$. Then the critical σ for extinction is $\sigma_e = -d/a = d/|a|$ and for collapse $\sigma_c = d/|a|$. In this case extinction and collapse occurs simultaneously in some sense, since $x^* = \frac{1}{(d+\sigma a)(d-\sigma a)} \begin{bmatrix} d + \sigma a \\ d + \sigma a \end{bmatrix}$ and $\lambda_2 = -(d - \sigma|a|)/(d + \sigma|a|)$. If a and b are drawn from independent continuous random variables, as is often the case in this thesis, then the probability that $a = b$ is 0, so this case is not of much importance.

Disregarding the case of equality of a and b assume without loss of generality that $a < b$. Then the critical σ for extinction is $\sigma_e = -d/a = d/\sqrt{a^2}$ and for collapse $\sigma_c = d/\sqrt{ab}$. Since $|a| < |b|$ extinction must occur first.

There are two equilibria where one species is extinct, but due to symmetry it is sufficient to investigate only $x_1^* = 0$. Case $x_1^* = 0$ and $x_2^* = 1/d$ the eigenvalues are $\lambda_1 = -1$ and $\lambda_2 = 1 - \sigma|a|/d$. If $|a| > |b|$, then $\lambda_2 > 0$ before extinction and the equilibrium point is unstable. If $|a| < |b|$ instead, then $\sigma|a| > \sigma|b|$ so that $\lambda_2 = 1 - \sigma|a|/d > 1 - \sigma|b|/d > 0$ before extinction. Hence the equilibrium point is always unstable before extinction.

After extinction, the $x_1^* = 0$ and $x_2^* = 1/d$ equilibrium point behaves differently depending on which one of a or b is the largest in absolute value. If $|a| > |b|$ then $\lambda_2 = 1 - \sigma|a|/d < 0$ such that the equilibrium is stable. If however $|a| < |b|$, then $\lambda_2 > 0$ at the point of extinction $\sigma = 1 - \sigma|b|/d$. For sufficiently large σ , such that $1 - \sigma|a|/d < 0$, both single-species equilibria become attracting.

6.1.1.3 Case $a < 0, b > 0$ (predator-prey)

In this case $D = d^2 + \sigma^2|a||b| > 0$, so collapse cannot occur. Extinction happens for $\sigma = d/|a|$ however.

Before extinction the interior equilibrium is feasible and stable by an argument analogous to the $a, b > 0$ case.

After extinction, the previous interior equilibrium point is no longer feasible, since $x_1^* = \frac{1}{D}(d - \sigma|a|) < 0$.

The $x_1^* = 0, x_2^* = 1/d$ equilibrium point is unstable before extinction, since $\lambda_2 = 1 - \sigma|a|/d > 0$ then. After extinction this equilibrium point becomes stable however. The $x_1^* = 1/d, x_2^* = 0$ equilibrium point never is stable since $\lambda_2 = 1 + \sigma|b|/d > 0$.

6.1.2 Summary of two species cases

In summary, for all two species systems the interior equilibrium point is stable initially, but eventually either extinction or collapse occurs. The all-extinct equilibrium is always unstable and all non-interior equilibrium points are unstable initially.

In case of mutualism ($a, b > 0$) the interior equilibrium is stable until it becomes unfeasible at $\sigma = d/\sqrt{ab}$ through a collapse.

In case of predator-prey ($a < 0, b > 0$) the interior equilibrium point becomes unstable at a point of extinction which occurs at $\sigma = d/|a|$. Thereafter the system remains stable in the $x_1^* = 0, x_2^* \neq 0$ equilibrium for arbitrarily large σ .

In the competition case ($a, b < 0$) extinction always occurs before collapse, and at $\sigma = \min(d/|a|, d/|b|)$. Thereafter, the species with the least negative interaction coefficient survives and remains stable for arbitrarily large σ .

What can be learned about the two species case is that there are two principal behaviours of the system; it either collapses or one species goes extinct and the other lives on. Interesting is that there does not always exist a σ for which there exists no stable feasible equilibria, so the system does not necessarily have to "fail".

6.1.3 Statistical predictions

One may wonder if there exists an expected σ for which collapse or extinction occurs if elements a and b are drawn randomly. In the previous section (Section 6.1.2) I showed that one of the two outcomes always occur for some σ (given that both $a, b \neq 0$).

In search of an expected σ for when one of the two events occur, one can consider each interaction type separately rather than considering a random matrix in its entirety. In 25% of cases $a, b > 0$, and then a and b can be considered drawn from some independent random variables $|Y|$ and $|Z|$, where $Y \sim \mathcal{N}(0, 1)$ and $Z \sim \mathcal{N}(0, 1)$. In 25% of cases $a, b < 0$, in which case a and b are drawn from $-|Y|$ and $-|Z|$. Similarly, in 50% of cases, either a is drawn from $|Y|$ and b is drawn from $-|Z|$ or the opposite.

In the mutualist $a, b > 0$ case, only collapse can occur. The expected σ for collapse is given by $\sigma_{mut} = \mathbb{E}[\sigma] = d\mathbb{E}[1/\sqrt{a}]\mathbb{E}[1/\sqrt{b}]$, since a and b are both positive and independent. The expectation $\mathbb{E}[1/\sqrt{b}] = \int_0^\infty \frac{1}{\sqrt{x}} e^{-x^2/2} dx$ is evaluated by Mathematica to $\Gamma(1/4)/(2^{1/4}\sqrt{\pi})$, where $\Gamma(\cdot)$ is the gamma function. Thus $\sigma_{mut} = -d \cdot \Gamma(1/4)^2/(2^{1/2}\pi) \approx 2.96$ for $d = -1$.

It should be noted however, that $Var[\sigma_{mut}] = \mathbb{E}[\sigma_{mut}^2] - \mathbb{E}[\sigma_{mut}]^2$ is infinite. This is because $\mathbb{E}[\sigma_{mut}^2] = \mathbb{E}[d^2 \frac{1}{a} \frac{1}{b}] = d^2 \mathbb{E}[\frac{1}{b}]^2$ which is divergent since $\mathbb{E}[\frac{1}{b}] = \int_0^\infty \frac{1}{x} e^{-x^2/2} dx$ does not converge in the lower integration limit. This caveat implies that the values of sampled σ_{mut} may vary greatly.

I demonstrated in the previous paragraph that $\mathbb{E}[\frac{1}{b}]$ is infinite. This implies that the expectation of σ for extinction in the predator-prey case ($a < 0, b > 0$) or ($a > 0, b < 0$) is infinite as well, such that the critical σ in the predator case $\sigma_{pp} = \infty$. In the case of competition the σ for extinction is given by $\sigma_{comp} = \mathbb{E}[\min(d/|a|, d/|b|)]$. If this expectation exists, then it should be given by extreme value theory, in which one studies the distribution of the maximum or minimum of an ensemble of random

variables. I have not been able to find a closed form expression, but numerical tests suggest that $\sigma_{comp} \approx 1.4$ for $d = 1$.

We can conclude that there does not exist an expected σ for which the first critical occurrence, extinction or collapse, occurs. This is because it is infinite in the predator-prey case. However, the expected critical σ for collapse σ_c has a finite value $\sigma_c \approx 2.96$.

6.2 Other kinds of critical behaviour in higher dimensions

In the two species case, both eigenvalues are necessarily real. This is not the case for higher dimensions, since eigenvalues can then appear in complex conjugate pairs. Then the system can become unstable not only by collapse or extinction, but also by a pair of complex eigenvalues crossing the imaginary axis in what is called a Hopf bifurcation. This was the case when the system entered first limit cycle behaviour, and then what looks like intermittent chaos in figures 5.3 and 5.4.

I have not studied Hopf bifurcations or non-equilibrium behaviour in depth, but I can share a two observations. Just as two imaginary eigenvalues can cross the imaginary axis to the real half plane they can also return to the negative half plane. This happened during one simulation of an 80 species system. For small σ the system showed the usual linear extinction pattern as shown in Figure 5.10 but suddenly did not converge to a stable equilibrium and instead entered first limit cycle behaviour and then intermittent chaos, as shown in figures 5.3 and 5.4 (the images are from the same run, but different σ). For even greater σ the system resumed limit cycle behaviour and eventually converged to a stable equilibrium once more. Interestingly enough, the number of extinct species continued along the same line as before limit cycle and chaos behaviour happened and in the end collapsed when approximately half of species had gone extinct.

Another observation is that eigenvalues approaching the imaginary axis tend to be real more often than imaginary. This is suggested by the eigenvalue plot in Figure 5.6. A more quantitative indication of this is that out of 150 simulation runs with systems of 80 species, 125 of them included no limit cycle or chaotic behaviour in contrast to 24 runs which did. And in both cases the average number of extinctions were numerous (on average 39 and 35 respectively). The 24 runs were aborted the first time that the system did not converge to one equilibrium point and the 125 runs were aborted when the system collapsed. One round was discarded since a negative solution was obtained by the solver. Data from these 150 simulation runs were used to estimate the distributions of critical σ and the average number of extinct species at collapse and can be seen in figures 5.9 and 5.8, which are the topic of the next section.

6.3 Explaining critical values of the model

In this section I try to explain why a system of species tend to have its first extinction close to a particular σ , why it tends to collapse when roughly half of the species are alive and why it tends to collapse for a particular σ . Figures in Chapter 5 showed that extinction tend to occur at an even rate after the first extinction at σ_{e1} . They also showed that when roughly half of the species had died out the system collapsed at σ_c . Figure 5.8 quantifies these phenomena. It shows that for 125 simulations of systems of 80 species when the first instability was due to collapse, the average σ_{e1} was 0.0450, the average σ_c was 0.1648 and the average number of extinct species at collapse was 39.5. It also shows that there is a spread in the three quantities, but that the distributions appear unimodal. I will first try to explain why σ_{e1} is as it is.

6.3.1 The first σ of extinction σ_{e1}

As suggested by Figure 5.8, the average first σ of extinction is 0.045. One way to explain this is to consider a series expansion of the equilibrium solution. I use that $(I - \sigma B)^{-1} = \sum_{i=0}^{\infty} (\sigma B)^i$ which is convergent as long as $\max |\lambda| < 1$, where λ are the eigenvalues of σB and I is the identity matrix. Incidentally, for $B = A + I$ where A is the interaction matrix of our model, $\max |\lambda| \approx \sqrt{n} = \sigma_{c,May}$ if B is fully connected according to Girko's circular law for reasonably large matrices. Thus, the series is convergent for σ less than the expected σ for instability in May's model $\sigma_{c,May}$. Then we have that the equilibrium x^* is given by:

$$x^* = -A^{-1}r = (I - \sigma B)^{-1}r = \left(\sum_{i=0}^{\infty} \sigma^i B^i\right)r \quad (6.8)$$

For small σ truncation to first order should be valid, yielding:

$$x^* \approx I + \sigma Br \quad (6.9)$$

Letting $r_i = 1, \forall i$, we have that $x_i^* = 1 + \sigma \sum_{j=1}^n B_{i,j}$. Figure 5.18 shows a first order expansion for an 80 species system. The second order expansion in Figure 5.19 looks qualitatively more similar to a typical exact solution as shown in Figure 5.14, which is expected. The smallest component of x^* does however appear linear up until the intersection with 0 also for the second order expansion.

If the $B_{i,j}$ are jointly independent $\mathcal{N}(0,1)$ variables, then $Z_i = \sum_{j=1}^n B_{i,j}$ is $\mathcal{N}(0, n-1)$ distributed and Z_i are jointly independent for all i . Since the intercepts of x_i are given by $\sigma_{e,i} = -1/\sum_{j=1}^n B_{i,j}$ the σ for the first extinction is random and given by $\sigma_{e1} = -\min(1/Z_i)$ under the condition that $Z_i < 0$. It might be possible to find a closed form expression for the expectation of σ_{e1} using extreme value theory, but I have not looked into that. The sample mean from 150 samples for 80 species systems is $\sigma_{e1} = 0.0466$ and the sample standard deviation was 0.0088. This is slightly different from the empirical estimate of the mean for the full system 0.0450, which reflects that the series approximation is not exact. The figures are still similar.

There is one thing with this example which helps to explain why the average σ for extinction is infinite in the two species case, and why the variation in the average

is large for small n , as observed in Figure 5.23. First of all, for a first σ of extinction to exist, out of n observations of the row sums at least one is required to be negative, such that $z_i < 0, \exists i$. Since Z_i have zero mean and are independent of the number of negative observations N out of n trials is binomially distributed $N \sim \text{Bin}(\frac{1}{2}, n)$. So the probability of having no negative observations is $P(N = 0) = \frac{1}{2^n}$. For small n this probability is relatively large, as was noticed for the two-species system, for which numerical estimation of the mean impossible. For large n however, this probability shrinks exponentially, and it is possible that $P(N = 0)$ becomes sufficiently small for large n such that a limit distribution for σ_{e1} exists.

One can expect that the fewer negative elements there are to choose from, the larger the variation in σ_{e1} . This could explain the large variance in σ_{e1} observed in Figure 5.23.

In conclusion, we have that σ_{e1} is a random quantity $\sigma_{e1} = |\min(\frac{1}{Z_i})|$ where $i = 1, 2, \dots, N$ and $N \sim \text{Bin}(\frac{1}{2}, n)$ is a random variable as well, and $Z_i \sim -|\mathcal{N}(0, n-1)|$. It remains an open problem to find a closed form expression for the cumulative distribution function of this random variable, if it exists.

One can observe that the expression for the σ_{e1} from the linearisation agrees with the exact expression in the two species case and that the problem from the two species case holds still: For finite n , there is a non-negligible probability that no observations of z_i are negative, in which case σ_{e1} is ill defined as the minimum of an empty set. Numerical simulations suggest that there exists a well defined mean for σ_{e1} and yet it is difficult to see from the analytical expression for σ_{e1} how such a mean can exist for finite n . It would be interesting to see this apparent paradox solved.

6.3.2 The σ of collapse σ_c

Figure 5.8 shows an empirical distribution of sigma for collapse σ_c , from 125 sample rounds of $n = 80$ species systems with sample average is $\sigma_{c,obs} = 0.1648$. One explanation for this value of σ_c can be given under the assumption that Girko's circular law holds sufficiently well for an n under consideration and the assumption that the community matrix elements $\sigma A_{i,j}$ are randomly and independently distributed $\mathcal{N}(0, \sigma^2)$ in spite of extinctions (this is not the case as shown later). Under these assumptions, the average $\bar{\sigma}_c$ should be $\sigma_c \approx 0.1571$, if using the empirical number of surviving species $N = 40.5$. It is not really valid to say that $\bar{\sigma}_c = (\bar{N})^{-1/2}$, but we get a decent estimate as long as the spread in N is not too big. Barred variables denote averages. The estimate is in the region of the observed average $\hat{\sigma}_c$.

I hypothesise that the biggest contribution to the discrepancy between $\hat{\sigma}_c$ and $\sigma_{c,obs}$ comes from that the elements of A can not be considered independent $\mathcal{N}(0, \sigma^2)$. In fact, species have been eliminated selectively, as seen in Figure 5.13 which shows that mutualistic interactions tend to increase and competitive interactions tend to decrease. A digression into the causes for this is made in Section 6.4.8. Before that, the cause of the system becoming extinct when approximately $n/2$ species have gone extinct is discussed in the next section.

6.3.3 Why extinction occurs for $n/2$ extinct species

Figure 5.8 shows that the system tends to go extinct when approximately $n/2$ species have gone extinct. One explanation for why this happens can be given under three assumptions. One is that Girko's circular law holds for all numbers of non-extinct species $N(\sigma)$ under consideration or at least gives a lower bound on σ_c . The second one is that the off-diagonal elements of the community matrix A can be considered identically and independently $\mathcal{N}(0, 1)$ distributed, in spite of extinction of species. A third assumption is that the number of extinct species increases linearly starting from the σ of first extinction σ_{e1} . The third assumption is supported by Figure 5.10 (and similar figures from simulations).

Under these three assumptions, one can observe that the Circular law prediction of the number of species required for collapse $N_{circular}(\sigma) = \frac{1}{\sigma^2}$ is larger than the number of non-extinct species $N(\sigma)$ at the σ for the first extinction. As σ is increased, the gap between $N_{circular}(\sigma)$ and $N(\sigma)$ decreases until it reaches 0 for the critical σ for collapse σ_c . The idea is illustrated in Figure 5.17.

This proposed mechanism behind extinction of roughly $n/2$ species before collapse, however, does not provide any explanation for why the curves intersect for σ_c . That is a result of the rate of extinction, which I have not studied in depth. The reason for the particular rate of species extinction remains an open question.

6.4 Other results for the GLV

In this section I present an assortment of results which do not directly connect to the objectives of this thesis, but which add to the understanding of the GLV.

6.4.1 Instability of the all species extinct equilibrium

Here, I show that the equilibrium consisting of all species being extinct is unstable if $r_i > 0, \forall i$.

The GLV system 4.1 has a trivial equilibrium $x^* = 0$. The Jacobian at the equilibrium is $J_{i,j} = \delta_{i,j}r_i$ (from Equation 4.11). Since the matrix is diagonal, its eigenvalues are given by $\lambda_i = r_i, \forall i$. Hence, as long as $r_i \leq 0, \exists i$ the equilibrium is not guaranteed to be stable. In addition, if $r_i > 0, \exists i$ then instability is guaranteed. This is heuristically reasonable, since if $r_i > 0$ for species i , then that species in absence of influence from other species will want to increase linearly at a rate r_i , if close to $x = 0$.

6.4.2 Insignificance of the choice of r_i and $A_{i,i}$

If one assumes that $r_i = R > 0, \forall i$, $A_{i,i} = -d < 0, \forall i$ in the GLV (4.1) and that $A_{i,j}, i \neq j$ all are scaled by a common parameter σ , then the parameters and variables of GLV can be rescaled, showing that R and d can be set to any positive constants without changing the qualitative behaviour of the equations. Rescaling of equations is common practice, and a similar rescaling was done by Baigent [3].

Consider the GLV with the above assumptions:

$$\begin{aligned}\dot{x}_i &= x_i(R - dx_i + \sigma \sum_{k=1}^n A_{i,k}x_k) \\ \frac{dx}{dtR} &= x_i(1 - \frac{d}{R}x_i + \sigma \sum_{k=1}^n A_{i,k}x_k).\end{aligned}\tag{6.10}$$

The constant d should not be confused with the differential operator $\frac{d}{dt}$. With the substitutions $tR = \tau$ and $y_i = x_i \frac{R}{d}$ the equations take the form:

$$\frac{d}{R} \frac{dx}{d\tau} = \frac{d}{R} y_i(1 - y_i + \sigma \frac{d}{R} \sum_{k=1}^n A_{i,k}y_k).\tag{6.11}$$

The substitution $\sigma \frac{d}{R} = \gamma$ gives the final form of the equations:

$$\frac{dx}{d\tau} = y_i(1 - y_i + \gamma \sum_{k=1}^n A_{i,k}y_k).\tag{6.12}$$

This shows that R and d can be chosen to be 1 without changing the qualitative behaviour of the equations. Even if all r_i and $A_{i,i}$ are not identical, similar rescaling can be done for instance to improve numerical properties.

6.4.3 Coincidence of extinction and zero eigenvalues

In Section 2.3.1, I established that $\lambda_i = 0 \iff \det(A) = 0$ for some eigenvalue λ_i of some matrix A . Consider now the Jacobian (4.11) of the n species GLV at an interior equilibrium x^* point and its eigenvalues λ_i . Then the determinant of the Jacobian can be written as:

$$\begin{aligned}\det(J) &= \\ &= \det(\text{diag}(x^*)A) \\ &= \det(\text{diag}(x^*))\det(A) \\ &= \det(A) \prod_{i=1}^n x_i^*\end{aligned}\tag{6.13}$$

where $\text{diag}(x^*)$ is a square matrix with elements x_i^* on the diagonal and 0 on the off-diagonals. Since an interior equilibrium point is assumed to exist, $\det(A) \neq 0$. Hence, because $\det(J) = 0 \iff \lambda_i = 0, \exists i$ it holds that $\lambda_i = 0, \exists i \iff x_i = 0, \exists i$.

6.4.4 The equilibria after a collapse

Under the assumption that the system collapses for some critical σ_c , how does the system behave for $\sigma > \sigma_c$? To answer this question, consider the expression for the i :th element of the interior equilibrium point (with $r_i = 1, \forall i$):

$$x_i^* = -A^{-1}r = -\frac{1}{\det(A)} \sum_{j=1}^n \text{adj}(A)_{i,j} = \frac{p_i(\sigma)}{q(\sigma)}\tag{6.14}$$

where $\text{adj}(A)$ is the adjugate of A , n is the number of species in the (non-extinct) system, $p_i(\sigma) = \sum_{j=1}^n \text{adj}(A)_{i,j}$ and $q(\sigma) = \det(A)$. Note that n is the number of species in some subsystem of all species, not necessarily the entire system. $p_i(\sigma)$ and $q(\sigma)$ are introduced to emphasise that they are both polynomials in σ .

Next, I show under what circumstances x_i^* changes sign as a result of collapse. By the Fundamental theorem of algebra, $p(\sigma) = \prod_{i=1}^{n-1} (\sigma - z_{p,i})$ and $q(\sigma) = \prod_{i=1}^n (\sigma - z_{q,i})$ where $z_{p,i}$ and $z_{q,i}$ are the complex roots to respective polynomials¹. Since all coefficients are real, complex roots appear in complex conjugate pairs. Assume first that $p_i(\sigma)$ and $q(\sigma)$ share a real root of multiplicities m_{p_i} and m_q . Then if $m_{p_i} \geq m_q$ there is no collapse for that root. If otherwise $m_{p_i} < m_q$ collapse occurs. If $m_q - m_{p_i}$ is even x_i^* does not flip sign as σ crosses the root. If instead $m_q - m_{p_i}$ is odd, then x_i^* does flip sign. The case when $p_i(\sigma)$ and $q(\sigma)$ do not share roots is covered by setting $m_{p_i} = 0$.

I hypothesise that it is rare for $p_i(\sigma)$ and $q(\sigma)$ to have double roots or to share roots in the model of this thesis with random interactions, so that x_i^* does flip sign at σ_c . In that case, any x_i^* that was positive before the sign change will change sign and the old interior feasible point will become unfeasible. If all n components x_i^* become positive once more for some greater $\sigma > \sigma_c$ through sign changes in $p_i(\sigma)$ and/or $q(\sigma)$ then x^* becomes feasible again. In order for it to be a solution which the system can converge to, all eigenvalues of the full system need also be negative.

That it is rare for $p_i(\sigma)$ and $q(\sigma)$ to share roots if their coefficients are combinations of outcomes of random variables is not self-evident. This is because the coefficients are not independent, as seen from Equation 4.4. Nevertheless, I have not observed in any simulations that double roots exist other than for isolated σ , which have measure 0 in the space of all possible σ .

In the simulations I don't simulate any longer until the first collapse, if there is one. It is however good to see why feasible equilibria tend to become unfeasible immediately after a collapse.

6.4.5 Uniqueness of the solution under assumptions

In this section I show that for a GLV system (4.1) of n species with a stable interior equilibrium point, there cannot exist a subsystem of dimension $m < n$ with a stable interior equilibrium point under a set of assumptions:

- U1** Extinct species are not resurrected.
- U2** All self-growth terms are equal and positive $r_i = r_j > 0, \forall i, j$.
- U3** No two species become simultaneously extinct for the same σ .
- U4** When an extinction occurs, the eigenvalue associated with that species is negative for slightly larger σ .
- U5** Eigenvalues with non-zero imaginary part cannot cross the real axis (that is: instability implies extinction).

¹That $p_i(\sigma)$ has degree $n - 1$ follows from that $p_i(\sigma) = \sum_{j=1}^n \text{adj}(A)_{i,j} \sigma^{n-j} = \sum_{j=1}^n (-1)^{i+j} K_{j,i}(\sigma) \sigma^{n-j}$ where $K_{j,i}(\sigma)$ is a minor of size $(n - 1) \times (n - 1)$ and $\text{adj}(A)$ is the adjugate A .

U6 The system has not experienced collapse.

In addition, I show that if one starts with an n species system for which a stable equilibrium exists, then this equilibrium is the unique equilibrium for any subsystem of $m \leq n$ species, where the $n - m$ species not included in the system are extinct. Assumption U1 will be discussed in Section 6.4.7 and the other assumptions will be discussed in Section 6.4.6.

Assumption U6 ensures that the equilibrium and in turn all eigenvalues vary continuously with σ , which is crucial in showing uniqueness.

Consider a GLV system of n species (Equation (4.1)), for which the off-diagonal elements of the community matrix A are scaled by a parameter $\sigma \geq 0$. I show that no stable equilibria containing extinct species exist in case that $\sigma = 0$. The same idea will be used to show uniqueness for larger σ .

When $\sigma = 0$, the system is stable with equilibrium $x_i^* = r_i/A_{i,i}, \forall i$ and eigenvalues $\lambda_i = -A_{i,i}/r_i, \forall i$. Assume that there exists a stable and feasible equilibrium \tilde{x} for which $\tilde{x}_i = 0$ for one species i and $\tilde{x}_j > 0, \forall j \neq i$. For a system with one extinct species i , one eigenvalue of the system is given by

$$\lambda_i = r_i + A_{i,i}x_i + \sigma \sum_{k=1, k \neq i}^n A_{i,k}x_k$$

and the other eigenvalues are those of the subsystem of non-extinct species (by Theorem (4.2.1)). Since $x_i = 0$ and $\sigma = 0$, the eigenvalue is $\lambda_i = r_i > 0$, so the equilibrium is unstable, contrary to the assumption.

Consider now the system for some $\sigma > 0$ such that no extinction has occurred (in the full system). The condition for species j to go extinct (from being non-extinct) is equivalent to that

$$\lambda_j = r_j + A_{j,j}x_j + \sigma \sum_{k=1, k \neq j}^n A_{j,k}x_k = 0$$

(see Section 6.4.3). By assumption U3 only one species can become extinct at a time. This makes the machinery simpler, although it is not certain that the assumption is necessary for the main result. If extinction is possible, let species l be the species that goes extinct first. (As we will see in the next section, if extinction is not possible, then no eigenvalues can get positive real parts with increasing σ by assumption U5 and there are no alternative feasible and stable solutions).

Assume first that species $i = l$ such that it is the first to go extinct in the original equilibrium x^* . The case $i \neq l$ will be addressed soon. We know from Section 2.3.2 that the eigenvalues of the system vary continuously in σ and are interested in for what σ the equilibrium \tilde{x} can become stable. For \tilde{x} to be stable, λ_i must transition from being positive to negative and pass 0 in the process. If this is possible, then there exists some σ_i for which

$$r_i + \sigma_i \sum_{k \neq i} A_{i,k}x_k = 0.$$

But this is precisely the condition for the full system equilibrium x^* to have $x_i = 0$. The full system equilibrium x^* for which $x_i = 0$ must coincide with \tilde{x} , where

quantities marked with tilde (\sim) are those of the subsystem of species with species i removed, since at x^* all species $k \neq i$ need to equilibrate without influence of species i . This is equivalent to solving $\tilde{r} + \tilde{A}\tilde{x} = 0$, whose solution is \tilde{x} . In conclusion, this shows that if i is the first species to go extinct, \tilde{x} cannot be a stable equilibrium different from x^* for $\sigma \leq \sigma_i$.

Consider the case that i is not the first species to go extinct in the full system, but instead species $l \neq i$ goes extinct first at $\sigma_l < \sigma_0$. Then $\lambda_i > 0$ for $\sigma \leq \sigma_l$, so the equilibrium is not stable. When species l goes extinct at σ_l the previously interior equilibrium x^* ceases to be an interior equilibrium, so the assumption of x^* being interior fails. Since by assumption U1 resurrection is not possible, the point will remain not-interior for all $\sigma > \sigma_l$.

Removing more than one species at once for a fixed σ cannot produce a stable solution, since at $\sigma = 0$ all eigenvalues associated with those species i would be r_i . Increasing σ successively can not stabilise the equilibrium, without one single species going extinct in the full system. This is because the associated eigenvalues λ_i would all have to become negative, and assuming (U3) that they all become negative for distinct σ , the last eigenvalue to become negative would have to satisfy the extinction criterion for a single species, as described in the previous paragraphs.

Thus far I have only considered the case when the n species equilibrium x^* starts as at $\sigma = 0$. Next, I show that the case when some subset of species has gone extinct (at some larger σ) works as the full species system. More precisely, I show that there cannot exist interior stable solutions for subsystems of $m < (n-1)$ species, where the system of $n-1$ species is the result of extinction of one species in the original n species system. Let σ_l be the σ for which species l in the n species system goes extinct such that $x_l = 0$. The equilibria of the system of $(n-1)$ species where species l has been excluded behave precisely like the full n species system with x_l fixed to 0, except that the latter has one more eigenvalue

$$\lambda_l = r_l + \sigma \sum_{k \neq l} A_{l,k} x_k.$$

By assumption U4, λ_l became negative for σ slightly larger than σ_l (more precisely for $\lim_{\epsilon \rightarrow 0} \sigma_l + \epsilon$), and by assumption U1 the species can not be resurrected. Therefore, under these assumptions λ_l remains negative for all $\sigma > \sigma_l$ and species l has no influence on the subsystem of non-extinct species.

Under the assumption that $\lambda_l < 0$ for $\sigma > \sigma_l$, consider now the $n-1$ species subsystem in which species l is excluded. I will show that there exists no stable interior solution to any subsystem of $m < (n-1)$ species for $\sigma \leq \sigma_l$. By contradiction: Assume that the subsystem with species q removed is stable. Then one eigenvalue is given by

$$\lambda_q = r_q + \sigma_l \sum_{k \neq q} A_{q,k} x_k.$$

and it is negative. But this is a contradiction. In the full n -species system, if q were the species to be removed instead of l , then λ_q would be given by

$$\lambda_q = r_q + \sigma A_{q,l} x_l + \sigma \sum_{k \neq q, l} A_{q,k} x_k.$$

Since l was the first species to become extinct, λ_q would have had to be positive for $\sigma < \sigma_l$. For $\sigma = \sigma_l$ the population of species $x_l = 0$, so that

$$r_q + \sigma A_{q,l}x_l + \sigma \sum_{k \neq q,l} A_{q,k}x_k = r_q + \sigma \sum_{k \neq q,l} A_{q,k}x_k.$$

But this quantity, which implies extinction of species q if equal to 0, cannot be 0 since only one species is assumed to become extinct for a single σ and hence the quantity cannot have undergone a sign change. It must therefore be positive, and the assumption that the subsystem for which species q is removed is stable must be false.

This shows that, under the assumption, if there exists a stable and feasible solution of a system of $n - 1$ species for a given σ , then there exists no stable interior solution to any subsystem of $m < (n - 1)$ species. Then by induction the same argument holds for any subsystem containing more than one species.

Uniqueness follows from that extinction without resurrection only allows there to be at most one feasible system of p species, where $p \leq n$. Figure 6.1 illustrates this fact. It shows that as soon as the system has one species i go extinct, then the only possible equilibria for the system are those with species i extinct. This is because any equilibria where i is non-extinct cannot be reached, since that would require the resurrection of species i .

In the next section I discuss the validity of assumptions U2 to U6.

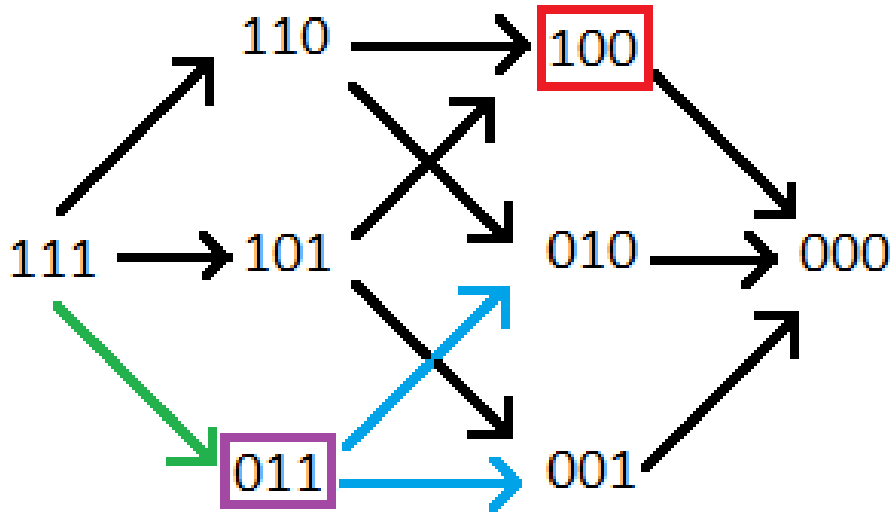


Figure 6.1: Extinction of species without resurrection. A sequence XXX represents the state of a system of three species. $X = 1$ means that a species is non-extinct and $X = 0$ means that a species is extinct. If assuming that resurrection is not possible, then the arrows indicate which states the system can go from and to. If the system started in 111 with all species alive and the first species went extinct (green arrow), then 011 is the current state (magenta box). The system can now move to some states with fewer species (blue arrows) but the system 100 (red box) is unreachable.

6.4.6 Assumptions in showing uniqueness

The result of uniqueness of a stable and feasible equilibrium relies on a set of assumptions. In this section I discuss if and when assumptions U2 to U5 are valid. I also discuss the case of system collapse. Assumption U1 is discussed in the next section.

Assumption U2: That all species have self-growth r_i identical and positive is an integral assumption of all simulations in this thesis and is thus is not an additional assumption imposed for showing uniqueness. Its biological validity can however be questioned.

Assumption U3: The assumption that the σ for extinction for all species is unique makes showing uniqueness easier, but relaxing it would probably not invalidate uniqueness. It is important for assumption U4, however, although problems might arise concerning smoothness. In any case, since coefficients of the system equations are real and random, it is unlikely that any two species will go extinct precisely simultaneously.

Assumption U4: When a species l goes extinct, the eigenvalue

$$\lambda_l = r_l + \sigma \sum_{k \neq l} A_{l,k} x_k$$

becomes 0 for $\sigma = \sigma_l$. For σ slightly larger than σ_l , the eigenvalue can either become positive, negative, or remain zero. In case the eigenvalue becomes negative, the eigenvalue can not make an equilibrium unstable. If the eigenvalue becomes non-negative, then this is not guaranteed however. Next, I motivate why it is that the eigenvalue tend to become negative, although it is not a proof.

By a theorem of Lax [14], if a matrix J has all distinct eigenvalues and its coefficients vary continuously in a parameter σ (which they do in this case), then the eigenvalues vary smoothly. This can be observed, for instance in figure 5.12, where the eigenvalues appear to vary smoothly everywhere except where two complex eigenvalues meet or split up (and when a species goes extinct, in which case the system considered is a different one). The theorem implies that as long as λ_l has a negative linear term in the Taylor series with respect to σ at the point of extinction σ_l , then the eigenvalue will be negative right after the extinction due to smoothness and dominance of the linear term for small deviations in σ .

By the same argument the eigenvalues can not have been positive right before extinction, and thus cannot be right after extinction either. The possibility the linear term vanishes at σ_l I consider unlikely and pathological, but I can not prove it impossible.

I also consider it unlikely that there are two identical eigenvalues at σ_l because of the randomness of interaction coefficients. Neither this can I show is impossible, however.

Assumption U5: This assumption, which states that eigenvalues only cross the imaginary axis at the origin, is not necessary for showing uniqueness of a stable and feasible equilibrium conditioned on that one exists, obviously. It is however elucidating to observe that if a pair of complex eigenvalues crosses the imaginary axis to the real plane, then any subsystems with some species removed can only potentially become stable if an extinction occurs, or if the complex eigenvalue pair

returns to the left half plane. When or if the complex eigenvalues return to the left half plane I have not found any way to predict. The Routh-Hurwitz criterion can always be applied, but doesn't give an easily interpretable criterion for when all eigenvalues have negative real parts in large systems.

Assumption U6: As mentioned before, the assumption that the system has not undergone collapse is essential for the assumption of continuity of the equilibrium point and the eigenvalues in σ . If a collapse occurs, the equilibrium x^* becomes unbounded, and immediately after the collapse changes sign. If collapse is allowed, then the eigenvalues of extinct species can change sign in other ways than through extinction. Similarly, equilibria can become unfeasible in other ways than through extinction of a species. What happens in such cases is discussed in Section 6.4.4.

6.4.7 Uniqueness of equilibria in practice

One may question how reasonable the assumption of no resurrection is; resurrection is in fact possible, as demonstrated in Figure 5.21. The example of a competitive two-species system showed that it is possible to have multiple stable and feasible equilibria, although to switch between them resurrection would be necessary. A simple generalisation can be made as a counterexample to uniqueness of solutions for a given σ . Consider an n -species competitive system and the equilibrium when species i is non-extinct and at its carrying capacity and all other species are extinct. Then one eigenvalue $\lambda_i = -r_i$ and the rest are given by

$$\lambda_j = r_j - \sigma A_{j,i} x_i = r_j - \sigma A_{j,i} r_i / A_{i,i}, \forall i \neq j.$$

Since $A_{i,i} < 0$, $A_{j,i} < 0$, $r_i > 0$ and $r_j > 0$ by assumption, there exists some σ_0 such that all $\lambda_j < 0$ and consequently all eigenvalues are negative and the equilibrium is stable. This can be made to hold for all species i , such that there exists some σ_0 for which there are n feasible and stable equilibria. The switching between equilibria would require simultaneous extinction and resurrection of species, but this is easily obtained by selecting initial conditions to be in the basin of attraction of a desired equilibrium.

Evidently, uniqueness fails if resurrection is allowed. A relevant question is how often this occurs in practice for the GLV system considered in this thesis which starts with the unique equilibrium $x^* = 1$ for $\sigma = 0$ and then has σ increased successively. I mean that this should not happen very often. The eigenvalue associated with an extinct species i is

$$\lambda_i = r_i + \sigma \sum_{k=1, k \neq i}^n A_{i,k} x_k.$$

When species i goes extinct $\lambda_i = r_i + \sigma \sum_{k=1, k \neq i}^n A_{i,k} x_k = 0$ so the sum over k must be less than $-r_i$. The following is no rigorous argument, but I hypothesise that species which go extinct tend to have many negative interactions $A_{i,j}$. Then, as the abundance of species x_k increases λ_i will tend to decrease. The only way species i can be resurrected is if the configuration of x_i^* changes such that the sum $\sigma \sum_{k=1, k \neq i}^n A_{i,k} x_k$ begins to increase. It is possible, as evidenced, but not likely if many $A_{i,j}$ are negative.

I ran five simulations for a system of 80 species to check if the number of negative interactions were higher among extinct species. Each species was given a rank based on the number of negative interactions. In total over the five simulation runs, 196 extinctions occurred and in each case the species that became extinct had the highest number of negative elements (with possible ties). However, as the number of rows with a high fraction of negative elements decrease when species go extinct, resurrection should be more likely. The simulations show that resurrection is indeed more common when more species have gone extinct (that there are many extinct species that can be resurrected should also increase the likelihood of resurrection however).

So although one can not count on there being one unique feasible and stable equilibrium, the rarity of resurrection means that the equilibrium often is unique in practice.

6.4.8 Which species goes extinct first

One may wonder which species goes extinct first, if any. A tempting guess is that species with many and/or negative interactions tend to go extinct first, but such a guess can be difficult to justify. In the following paragraph I will give criteria that the species that goes extinct first needs to fulfil.

Define a quantity $Q_i = r_i + \sum_{k=1}^n A_{i,k}x_k$ for each species i . $Q_i = 0, \forall i$ when x is the interior equilibrium point x^* . Let the off-diagonal elements be scaled by a positive parameter σ , such that $A_{i,j} \rightarrow \sigma A_{i,j}$ for $i \neq j$ and $Q_i = r_i + A_{i,i}x_i + \sigma \sum_{k \neq i} A_{i,k}x_k$. A requirement for the interior point to transition to a point on the boundary, that is to go extinct, is that $x_i = 0, \exists i$. For all σ prior to that, $Q_i = 0, \forall i$ must hold.

Let us now assume that extinction is possible for some $\sigma > 0$ and that it happens for one single species j before the others. Assume also that no collapse occurs before extinction, such that $x_i < \infty$ for all $\sigma < \sigma_e$, where σ_e is σ at the first extinction. For simplicity of argument, let $r_i = r_j, \forall i, j$ and $a_{i,i} < 0, \forall i$ as is usually done in this thesis.

Before extinction $Q_i = 0, \forall i$, so consider two species i and j :

$$\begin{cases} Q_i = r_i + A_{i,i}x_i + \sigma A_{i,j}x_j + \sigma \sum_{k \neq i,j} A_{i,k}x_k \\ Q_j = r_j + A_{j,j}x_j + \sigma A_{j,i}x_i + \sigma \sum_{k \neq i,j} A_{j,k}x_k \end{cases} \quad (6.15)$$

where $\sum_{k \neq i,j}$ is a sum over $k \in \{1, 2, \dots, n\} \setminus \{i, j\}$. They both equal zero, so we may set them equal to each other and cancel out $r_i = r_j$.

$$\begin{aligned} A_{i,i}x_i + \sigma A_{i,j}x_j + \sigma \sum_{k \neq i,j} A_{i,k}x_k &= A_{j,j}x_j + \sigma A_{j,i}x_i + \sigma \sum_{k \neq i,j} A_{j,k}x_k \\ (A_{i,i} - \sigma A_{j,i})x_i &= (A_{j,j} - \sigma A_{i,j})x_j + \sigma \sum_{k \neq i,j} (A_{j,k} - A_{i,k})x_k \\ x_i &= \frac{1}{(\sigma A_{j,i} - A_{i,i})} [(\sigma A_{i,j} - A_{j,j})x_j + \sigma \sum_{k \neq i,j} (A_{i,k} - A_{j,k})x_k] \end{aligned} \quad (6.16)$$

where in the last step I assume that $\sigma A_{j,i} - A_{i,i} \neq 0$. In the next paragraph I argue why this is reasonable.

Neglecting the specific case that the right hand side of row two in Equation (6.16) equals zero for precisely the same σ as the denominator $\sigma A_{j,i} - A_{i,i} = 0$, $\sigma A_{j,i} - A_{i,i} = 0$ implies that x_i is not finite (has collapsed), which is assumed not be the case before extinction. Since $\sigma A_{j,i} - A_{i,i} > 0$ for $A_{i,i} < 0$ and $\sigma = 0$, under the assumption that no collapse occurs before extinction we have that $\sigma A_{j,i} - A_{i,i} > 0$ for $\sigma < \sigma_e$.

Recall that j is the index of the species which goes extinct first. At the point of extinction $x_j = 0$ and $x_i > 0, \forall i \neq j$, so the following relation must hold simultaneously for all i :

$$x_i = \frac{\sigma}{(\sigma A_{j,i} - A_{i,i})} \sum_{k \neq i,j} (A_{i,k} - A_{j,k}) x_k > 0. \quad (6.17)$$

If the inequality does not hold then at least one assumption is violated. In the previous paragraph, I concluded that $\sigma A_{j,i} - A_{i,i} > 0$ for $\sigma < \sigma_e$, so the only way for the inequality not to hold is for $\sum_{k \neq i,j} (A_{i,k} - A_{j,k}) x_k \leq 0$. Since all $x_k > 0$ by assumption when considering a specific i , for the inequality to hold the average of differences $(A_{i,k} - A_{j,k})$ weighed by x_k must be positive.

Since x_k is in general given by a complicated expression, it is not possible to tell only from the interaction strengths which species qualifies as the first to become extinct. A few things can be said however. No other species i must dominate j in the sense that $A_{i,k} > A_{j,k}, \forall k$. The species j will likely have smaller interaction strengths than on average for all inequalities (6.17) and if interaction strengths are drawn randomly from a zero mean distribution then j should include "many" negative interaction strengths. The effect of a "large" species k on j should be especially small compared to the effect of k on other species $i \neq j$. From the expression $Q_j = r_j + A_{j,j}x_j + \sum_{k \neq j} A_{j,k}x_k$ it is obvious that $A_{j,k} < 0, \exists k$ for extinction to be possible.

In summary, a species j which is the first to go extinct must have small (or more negative) interaction strengths with other species k on average weighed by x_k at equilibrium compared to other species $i \neq j$. A specific criterion that must be satisfied for all other species i is (6.17).

6.5 Distribution of real eigenvalues for random matrices

At some places in this thesis I combine the result that $\det(A) = 0 \iff \lambda_i = 0, \exists i$ and Girko's circular law which roughly states that the eigenvalues of an $n \times n$ matrix A are uniformly distributed in a disk with radius $\sqrt{\sigma n}$, where A have *i.i.d* $\mathcal{N}(0, \sigma^2)$ off-diagonal elements (in the limit of large n). Girko's law implies that if A has diagonal elements -1 , then the largest real part of the eigenvalues is 0 with probability 1 if $\sigma = \frac{1}{\sqrt{n}}$. It does not however say that the eigenvalue with the largest real part is real! In fact, one might falsely believe that the probability of finding a single real eigenvalue is 0, since eigenvalues are uniformly distributed in a disk in the complex plane and the real line has Lebesgue measure 0 in the plane [4].

Edelman, Kostlan and Shub showed that this is not true, at least not for matrices with zero-mean normal off-diagonal elements [4]. In fact, they showed that the real

eigenvalues of such a matrix (with zero mea diagonal) are uniformly distributed in $[-\sqrt{\sigma^2 n}, -\sqrt{\sigma^2 n}]$ and that the expected number of real zeros in the limit of large n tends to $\sqrt{\frac{2n\sigma^2}{\pi}}$ (I have rescaled the matrix in their paper by $\sigma\sqrt{n}$).

So in essence, it is not flawed to assume that if the largest real part of eigenvalues is 0, then if the eigenvalue is not real, there is likely to exist an almost equally large real eigenvalue close by. This means that $\det(A) = 0$ can be expected to happen for only slightly larger σ than the σ for which the first eigenvalue gets a positive real part.

6.6 Asymptotic distribution of feasible equilibria

In previous sections, I have discussed how the feasible and stable equilibria of the system come into place and that extinction occurs when the full system of species becomes unfeasible. In this section I aim to show that the probability of having a feasible equilibrium for large σ is rare and that its rarity scales with the size of the system and is related to the fraction of species removed. First, I argue that the equilibria of a system can be approximated for large σ . Then, I discuss the statistical properties of feasibility.

Consider the ordinary system (4.1) in this thesis with $r_i = 1, \forall i$, $A_{i,i} = -1, \forall i$, $\dot{x}_i = x_i(r_i + A_{i,i}x_i + \sigma \sum_{k=1, k \neq i}^n A_{i,k}x_k)$. An internal equilibrium (excluding extinct species) is given by:

$$x^* = -A^{-1}r = -(\sigma B - I)^{-1}r = -\frac{1}{\sigma}(B - \frac{I}{\sigma})^{-1}r \quad (6.18)$$

where $B \equiv A + I$ and σ is assumed positive. We have from Section 2.3.3 that the matrix inverse of a matrix A is smooth wherever $\det(A) \neq 0$. This means (from continuity) that, as long as B^{-1} exist in an open neighbourhood D of B^{-1} , sufficiently small changes to the elements of B produces arbitrarily small changes to B^{-1} . In this case we can let $B - \frac{1}{\sigma}I \equiv G = B + E$, where E is a matrix of perturbations $\epsilon_{i,j}$. Then by continuity for any $\delta > 0$ there exists some $\epsilon \equiv \|E\|_{max} > 0$ such that $\|G^{-1} - B^{-1}\|_{max} < \delta$, where $\|\cdot\|_{max}$ is the maximum norm.

$E = \frac{1}{\sigma}I$, ϵ can be made arbitrarily small by making σ arbitrarily big. So under the assumption that B^{-1} exists in an open neighbourhood there exists some, possibly very large, σ such that $(\sigma B - I)^{-1} \approx B^{-1}$ in some sense. In the space of real and random coefficients the probability of B being non-invertible has measure 0, and I conjecture that so does the probability of picking B arbitrarily close to a singularity. Therefore, under this assumption I conclude that this large σ approximation is with probability 1 valid. Note that the "farther" B is from being non-invertible, the better should the approximation be.

Assuming for large σ that $x^* \approx \frac{1}{\sigma}B^{-1}r$, what is the probability that x^* is feasible for any subsystem of species (with some set of rows and columns of B and r removed and corresponding components $x = 0$), and for the entire set of subsystems to be feasible? In answering this question I will make a few assumptions:

I will assume that the elements of B^{-1} are i.i.d. random variables from a distribution symmetric about a mean μ . This is certainly not true, since for a random

matrix B , B^{-1} is a deterministic combination of elements of B , so independence is violated. I cannot justify this assumption, but I will assume that it is a reasonably good assumption since it gives good predictions; it "works". Under the assumption that $B_{i,j}^{-1}$ are i.i.d., numerical simulations suggest that the fraction of negative elements appears normal and symmetric, so this assumption does not seem unjustified.

I will also assume that the row sums of submatrices of B^{-1} resulting from removing rows and columns of B are independent. They would not necessarily be so, even if the elements of B^{-1} were i.i.d., but once more, it seems to be a reasonably good assumption. As usual, I assume also that $r_i = 1, \forall i$.

For a subsystem in which k species have been removed, it is required that $x_i \geq 0, \forall x_i$ for the equilibrium point to be feasible. So if we let Z_i denote the row sum of row i , $i = 1, \dots, n - k$, where the rows are appropriately relabelled when rows and columns are removed, then for the point to be feasible we need that $Z_i \leq 0, \forall i$, which occurs with probability:

$$P(Z_1 \leq 0, Z_2 \leq 0, \dots, Z_{n-k} \leq 0) = P(Z_1 \leq 0)P(Z_2 \leq 0) \dots P(Z_{n-k} \leq 0) = p^{n-k} \quad (6.19)$$

where I have used independence of row sums, and where p denotes the probability that one row is non-negative (what I also call "success"). For zero-mean symmetric Z_i the probability of success is $p = \frac{1}{2}$. For a general normal distribution $p = \Phi(-\mu_{Z_i}/\sigma_{Z_i})$, where Φ is the CDF of the normal distribution, μ_{Z_i} is the mean of the distribution and $\sigma_{Z_i}^2$ the variance.

Since there are $\binom{n}{k}$ ways of removing k rows (and corresponding columns) from n rows, the expected number of feasible solutions is $\binom{n}{k}p^{n-k}$ if k rows are removed. For this to be guaranteed to hold, the probabilities of getting a feasible solution from each possible configuration must be independent, which it is not as I have pointed out. I assume it holds nonetheless. By normalising over all possible choices of k we get a distribution over the probability of finding a feasible solution when k rows have been removed:

$$f(k) = \frac{1}{C} \sum_{k=0}^n \binom{n}{k} p^{n-k}, \quad (6.20)$$

where C is a normalisation constant and $0 < p < 1$. In Section A.4 I compute C to be $(p+1)^n$ and derive the other quantities which we will encounter in this section.

A natural guess would be that $p = \frac{1}{2}$ for the row sums of the inverse matrix B^{-1} to be negative, since one could imagine that there would be no bias toward either positive or negative numbers. This does however not appear to be the case. In lack of any arguments for a particular value of p one can estimate it from experimental data. This was done for 200 realisations of size $n = 10$ matrices B^{-1} , for which the feasibility of all equilibrium points was determined. In Figure 6.2 the portion of feasible points having k row-column pairs removed is shown, along with the theoretical distribution in which the maximum likelihood estimator $\hat{p} = 0.5077$ has been used. The qualitative agreement is good, lending support to that the assumptions hold.

The expected number of row-column pairs removed is $\mathbb{E}[X] = \frac{n}{p+1}$ and the perhaps more interesting expected *proportion* of row-column pairs removed is $\mathbb{E}[X/n] = \frac{1}{p+1}$. This says that a feasible point is most likely found when $\frac{1}{p+1}$ species are set to

0, or conversely, for a system where $\frac{p}{p+1}$ species remain. The proportion of feasible points is given by the sum of expected number of feasible points for k species set to 0, which is $\sum_{k=0}^n \binom{n}{k} p^{n-k} = C = (p+1)^n$ divided by the total number of equilibria 2^n . This gives the expression:

$$f_{feasible} = \frac{(p+1)^n}{2^n} \quad (6.21)$$

This fraction decreases for increasing n if $p < 1$, although the absolute number of feasible points increases. Two interesting special cases are $p = 0$ and $p = 1$. The case $p = 0$ corresponds to a mutualistic system, where all row sums are guaranteed to be positive. Then the only feasible point is $x^* = 0$. The case $p = 1$ corresponds to pure competition, in which case all equilibria are feasible in the large σ limit.

The perhaps most interesting result of this section is that there is a low probability to find feasible equilibrium points for large submatrices (meaning small k) for large σ , as shown in Figure 6.2. Although we can not say anything about the stability of equilibria with this analysis, we can at least say that the probability of finding a feasible and large equilibrium for large σ is low. This is an argument for why species tend to go extinct for increasingly large σ increases, although I have not investigated whether the "large σ regime" is reached in any of the simulations carried out in this thesis.

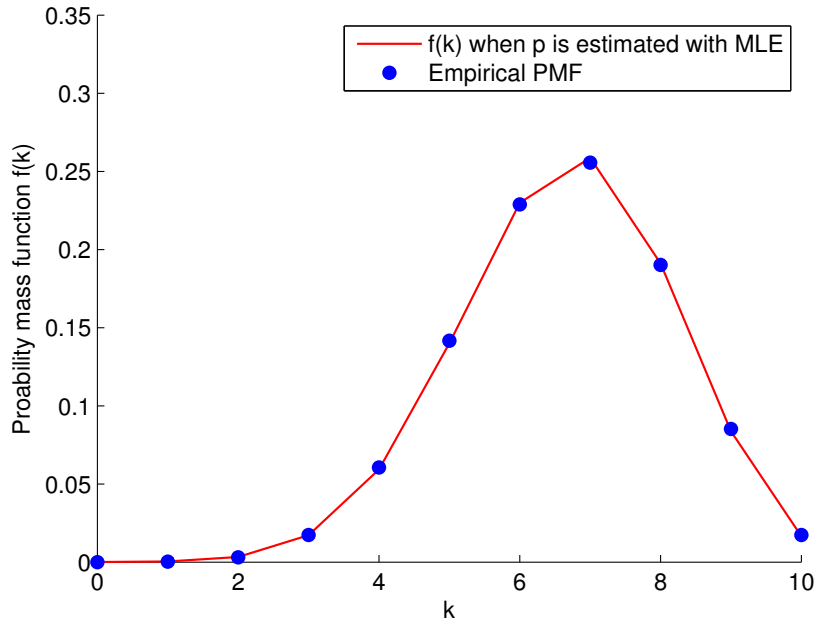


Figure 6.2: Frequency of feasible equilibria per number of species removed, in the large σ limit for a system with $n = 10$ species. Blue dots show empirical relative frequencies of feasible equilibria from 200 randomly generated community matrices. The red line shows the theoretical probability mass function (PMF) $f(k) = \frac{1}{(\hat{p}+1)^n} \binom{n}{k} \hat{p}^{n-k}$, where \hat{p} is the maximum likelihood estimate (MLE) of the probability that one equilibrium solution component x_i^* is feasible, based on the empirical data.

6.7 Summary

The findings of this chapter has led closer to an understanding of critical points in Lotka-Volterra systems. The introductory two species example showed how extinction and collapse can occur and highlighted the problem of finding an expected parameter value of σ for which critical points occur if system parameters are randomly chosen. I then provided suggestions for why the expected first σ of extinction and the first σ for collapse for large systems have the values that they do, but the description is not complete. In the remaining part of the chapter I present general facts about the stability and critical points of the system, which in part explains how the system behaves as the average interaction strength parameter σ is changed.

7

Methods for Simulation

In this chapter I present methods used in simulation, for instance to solve differential equations, detect unstable solutions and detect when species have gone extinct. I also discuss problems in the methodology and describe how I have chosen to tackle these problems. One section at the end is devoted to explaining in particular how data was obtained for the plots showing the relationship between system size and critical σ in the model of this thesis and May's model.

7.1 A method for solving ODE:s

Almost all the results in this report are based on the solving the GLV, which are a system of ODE:s. The solver used was `ode23s` in Matlab. It is a stiff, low accuracy solver using a Rosenbrock method of order (2,3). The solver was chosen to be able to handle stiffness, which may arise when the system exhibits chaotic behaviour. The method uses an adaptive time step.

For all solutions to differential equations in this thesis I use an absolute error tolerance of 10^{-3} and a relative error tolerance of 10^{-7} .

7.2 Detecting events in the solution

To detect when the solution of the system fulfils certain criteria, such as having equilibrated or diverged to infinity, one has to use approximate methods. One reason for this is numerical limitations, as in the case of determining if a solution has converged or not, and another is a difficulty to quantify when an event has occurred, e.g. if the system has entered a limit cycles. In the following sections I describe the criteria used for detecting the different events.

7.2.1 Detecting when an equilibrium has been reached

A fact to consider is that a solution which approaches an equilibrium asymptotically does not reach it in finite time. This imposes a practical constraint when trying to classify if an equilibrium point has been reached or not. One way to work around this used in this thesis is to set an absolute tolerance parameter δ_{eq} and saying that any solution, whose maximum difference in any component of a solution vector between two consecutive time steps is less than δ_{eq} has converged to an equilibrium.

This has several caveats. One is that if one uses a sufficiently small time step between consecutive evaluations, then the convergence criterion will be met for any

continuous solution, no matter how far it is from equilibrium. The time step between consecutive solution iterates also affects at which time the solution is considered to have reached an equilibrium.

Another caveat is that solutions with components which approach close to an equilibrium for some time t_0 might move far away from it at some later time $t_1 > t_0$. This has been showed to be possible for purely competitive Lotka-Volterra systems [1]. This problem cannot be escaped; one simply has to assume that not all components of a solution simultaneously go below the equilibrium threshold and later increase in number.

A third problem is how to choose δ_{eq} . I set it $\delta_{eq} = 10^{-7}$, such that convergence would be possible in a time span of 400 time units in most instances, without accepting too fluctuating solutions as being convergent. When eigenvalues are close to zero the solution converges slowly, as described in Section 7.5. Therefore I choose to accept solutions as convergent if they at the end of the time span has a smaller deviation between consecutive time steps than 10^{-2} .

7.2.2 Detecting chaotic and limit cycle solutions

I choose not to make any distinction between solutions which are both bounded during the time span of simulation and do not converge to an equilibrium point. Therefore, both limit cycles attracting α -orbits (at $t \rightarrow \infty$) and chaotic non-exploding solutions are included. To classify such a solution, I require that the deviation between the last two time steps at the end of the simulation time span must be greater than or equal to 10^{-2} (complementing the criterion for an equilibrated solution).

I simulated a large number of systems and found that this criterion identified few systems as false positives (the solutions did indeed appear to exhibit chaotic or limit cycle behaviour).

7.2.3 Detecting collapse and explosions

A criterion for considering collapse as having occurred is that at least one component of the solution must have reached above a certain threshold, set to 10^4 and that the absolute value of the determinant of the community matrix A must be smaller than a critical threshold set to 10^{-3} . This is to differentiate the collapses from other divergent solutions, which typically do not also have a small determinant. It is of course possible that the solution to have small determinant and still diverge not as a consequence of collapse, but in this case I consider the solution close to collapse in all relevant aspects anyway.

Explosions are defined negatively as a solution having reached a large maximum amplitude, without having a sufficiently small $\det(A)$ at the previous iteration.

7.2.4 Detecting negative solutions

Occasionally, the numerical solver would return negative solutions, in spite of this not being possible in theory if initial conditions are strictly positive. In these rare cases I discarded the solution, with the motivation that their exclusion probably

does not affect statistics greatly. As an example, over a set of 150 simulations of an 80 species system only one solution was aborted due to having a negative solution.

7.3 Choosing initial conditions

How to select initial conditions in simulations is not a trivial question. All equilibria and other attractors have basins of attractions, such that if the state of the system is situated in the basin at some time t_0 , then it will converge to the equilibrium or the attractor. Therefore, different initial conditions can lead the system to converge to different attractors or even diverge.

Several authors have concerned themselves with the possible behaviour of purely competitive and mutualistic systems [1, 13, 29, 3], where it has been shown for instance that competitive systems are bounded and that all orbits converge to a carrying simplex. None have to my knowledge found any results that hold in general for Lotka-Volterra systems. In lack of general results, to completely exhaust the space of initial conditions for a given parameter set (including σ) is the only option to know all possible behaviour. But this is clearly intractable, even if one confines the system to some finite subset of initial conditions in the non-negative subset of \mathbb{R} . Therefore a pragmatic approach is necessary.

One option is to let the system initialise in the old equilibrium when σ is perturbed slightly. This can be motivated from a biological perspective in that a system continually adapts to some externally imposed change reflected in a change of parameters. But it limits the scope of the results. Are we not interested in learning about the stability of any system, without prior assumption on initial conditions?

A way out of this would be to select initial values randomly (from some subset of the positive real space which one has to motivate). The drawback of this approach is that it restricts reproducibility of results and the ability to compare systems starting in different initial conditions. Say that we wish to investigate how the system behaviour changes if σ is increased slightly. If the initial conditions in one case are $x(0) = 10^{-6}$ and $x(0) = 10^6$ in another case, then the system might exhibit very different behaviour in spite of the systems being similar.

A third approach, although not perfect, is to use the same initial point for all problems. In this thesis I do this and choose the initial condition $x(0) = 1$, which coincides with the only stable and feasible equilibrium for $\sigma = 0$. This enables comparison between different runs and σ , but explores only a tiny subspace of system behaviour. Starting the system in a point with all species equally populous can also be argued to make the least assumptions about the system.

7.4 Classifying species as being extinct

Ideally, a species is extinct only if its equilibrium population is 0. In practice, no solution can reach zero in finite time with exponential convergence. Therefore it is necessary to set a threshold for when a system is to be considered extinct. For the results of this thesis I considered a species extinct if its population size went below 10^{-5} . This gave a fairly good correspondence between the σ for which species went

extinct and the σ for which the real part of eigenvalues turned sharply (see Figure 5.11).

7.4.1 Obtaining data for the σ versus n plot

The data shown in Figure 5.23 and Figure 5.22 was obtained as follows. For each value of n , a binary search was made in the interval $[0, 10]$ to find the smallest σ yielding a positive eigenvalue, in the May case of the interaction matrix A , and in the other case of the interior equilibrium Jacobian $J = x^*A$. It was assumed A and J respectively would have at least one positive eigenvalue for $\sigma_1 > \sigma_0$ if they would have one positive eigenvalue for σ_0 . A minimum difference between consecutive σ in the binary search was set to 10^{-5} , giving a maximum error $2 \cdot 10^{-5}$ in the estimates of σ_c . This error was considered negligible compared to the variance of the true σ_c for the tested n , but should have a greater effect for larger n since the variance appears to decrease with n .

For the same reason, that the variance in σ_c appears larger for smaller n , more averaging rounds N_{avg} were used for small n , according to the following formula: $N_{avg}(n) = \text{round}(N_{min}(n/m)^\alpha)$, where N_{min} is the smallest allowed number of averages for any n , $m = \max(n)$ is the largest tested n , and $\alpha < 0$ is an exponent. The parameters were set to $N_{min} = 20$ and $\alpha = -3/4$.

In the figures, only the standard deviations for the σ_c are shown, and not the standard deviation of the averages. Confidence intervals for the ratio between the two σ_c can be obtained by a Fieller test, but was not done here. The same interaction matrix A was used for estimating $\sigma_{c,May}$ and $\sigma_{c,non-May}$ for each n and averaging round.

7.5 Convergence to equilibria for small negative eigenvalues

Consider a general system of ODE:s with a stable interior equilibrium point x^* . Let λ_{min} be the smallest eigenvalue of the Jacobian J at x^* . Close to the equilibrium point, a perturbed solution $\delta x(t)$ in the eigendirection of the eigenvector with eigenvalue λ_{min} behaves as $\delta x(t) = \delta x(0)e^{(\lambda_{min} - \lambda_{min}t)}$, where $\delta x(0)$ is the initial perturbation. This implies that if λ_{min} is decreased by a factor c , then the characteristic time to convergence is increased by a factor c .

This has consequences when trying to numerically have the system converge to a stable equilibrium point. Assume that one starts the system in the basin of attraction of some stable equilibrium point. Assume also that one sets a tolerance T on how much the solution can deviate from the equilibrium point (in e.g. the Euclidean or maximum norm) in order for it to be considered to have converged. Then in the limit $\lambda_{min} \rightarrow 0$ the time for convergence $t \rightarrow \infty$. Hence, T and λ_{min} put limits on the time of convergence such that smaller T and λ_{min} require longer simulation times.

To handle the increase in the time until convergence for decreasing λ_{min} a maximum evaluation time $t_{max} = 400$ time units was used. If the system had not

converged after t_{max} , then $x(t_{max})$ was taken to be an approximation to x^* . A consequence of accepting points which have not converged as being equilibria is that the Jacobian will not be correctly calculated and hence the eigenvalues will not be the eigenvalues of the actual equilibrium point. Furthermore, there will be a delay (in σ) for when a species is classified as extinct, since convergence to 0 might only be fast enough when the maximum real part of any eigenvalue of the system moves away from 0.

7.6 Summary

In this chapter I have presented the methods used for simulating the system of equations in this thesis. I have discussed the problem of choosing parameters and initial conditions, and when applicable motivated my choices.

8

Discussion

In this chapter I discuss the assumptions made in this model and their plausibility from both a mathematical and ecological perspective. I also connect to the objectives of this thesis; How the results of this thesis relate to those of Robert May and what can be said about the critical points of the Lotka-Volterra equations of this thesis in which the average interaction strength is varied.

8.1 Assumptions in the model

Are the assumptions of the model justified? One can answer this question from either an ecological or a mathematical perspective.

One assumption that can be questioned from both perspectives is that of identical and positive self-growth r_i for all species. This means that in a system of species, all species grow in absence of others. This description does not fit a typical predator, which typically is in need of the existence of a prey to survive. In a food chain, one can imagine that only the bottom layer species, or possibly omnivores both consuming other species and some external food source (not considered part of the ecosystem of species), have positive self-growth. That the self-growth should be equal for all species is also a simplifying assumption that can be criticised also from a mathematical perspective. Small deviations from equal self-growth should not make a big difference to the system dynamics, but it is possible that large deviations requires another analysis to be made.

The assumption of equal and negative self-interaction $A_{i,i}$ might also be a crude assumption. That the self-interaction is negative is not very controversial since competition for resources within one species is likely to increase with the abundance of that species. That the self-interaction should be identical is however harder to justify, and as for the self-growths r_i , a new analysis would have to be made to cover the case of non-identical self-interaction.

One reason for the choice of r_i and $A_{i,i}$ was to make the system similar to one of May's systems valid for small values of σ , which is stable in absence of interactions. There is however no reason to believe that a system in absence of interactions should have a stable equilibrium. Therefore, a more realistic assumption would be to start with some positive average interaction strength σ and set r and $A_{i,i}$ as to obtain a stable system fulfilling the criteria of May's equilibria and then varying the parameter σ (both to be smaller and bigger).

8.2 Ecological implications

Next, I discuss ecological implications of the results of this thesis. Before doing this however, I would like to point out that the model is highly abstract and idealised. While this makes it clear to analyse, it might omit features in real world systems crucial for system behaviour [19].

8.2.1 Implausibility of collapse

One thing about the model which speaks against its plausibility as a realistic ecosystem model is the existence of collapse. No real world system would have its species populations diverge toward infinity. Even though an increase in the total number of species can be expected in some circumstances, there should mechanisms which bring down extremely large populations. A simple remedy which could eliminate collapses, is to introduce a quartic self-interaction term, as proposed by Professor Martin Nilsson Jacobi and Assistant Professor Kolbjørn Tunstrøm. It would then be difficult, if even possible to find a closed form of the equilibria however, and it is not easy to motivate the addition from an ecological point of view.

8.2.2 Does May's conclusion apply to the GLV?

If one does take the model for what it is and neglect the mathematically convenient assumptions currently made, then one can interpret the results of this thesis to say something about ecosystem system behaviour.

The main question of this thesis: "Does May's analysis and conclusions also apply to the example non-linear model system the generalised Lotka-Volterra equations?", can be given both a positive or a negative answer depending on what one means by stability. If one means that instability occurs when an equilibrium consisting of a set of non-extinct species ceases to be stable and feasible, then the answer is yes. This occurs for the first σ of extinction, which almost always is smaller than May's predicted σ for instability.

One could however mean that the extinction of one species and a continued existence of a stable and feasible equilibrium consisting of the remaining surviving species does not mean that the system is unstable, since the system still manages to stabilise to *some* equilibrium. In that case, species go extinct in increasing numbers for larger mean interaction strengths and as such manage to cope with the increasing mean interaction strength. Eventually, the system does however become unstable, either through a limit cycle or system collapse.

In the case of transition into a limit cycle one can discuss whether this is equivalent to system "failure"; the species do remain bounded and vary predictably in cycles. Requiring that all populations remain precisely constant in time might be a too narrow definition of stability [19]. If accepting limit cycle behaviour as a viable ecological state, then one can question whether May's requirement of negative real parts of eigenvalues of the Jacobian does imply "stability" in the wider sense. In case one does require stability in the conventional sense, then the system does become

unstable for large interaction strengths also for the GLV system, as hypothesised by May.

System collapse is more difficult to translate into instability in May's sense. It is true that for σ larger than the σ for collapse, the previously stable solution becomes unstable and the system fails to converge to some stable state. But the instability does not arise as the result of one eigenvalue of the system transitioning smoothly from having negative to positive real part. It occurs because the equilibrium, in spite of being stable, grows unboundedly and then sharply (in σ) ceases to exist. This kind of transition does not exhibit the "critical slowing down" so often associated with critical transitions [23]. Critical slowing down means that recovery from small perturbations takes longer time the closer to a critical point the system is. In dynamical systems language this means that one eigenvalue has a negative but close to zero real part. A warning signal for collapse would instead be quick convergence to increasingly large equilibria. One complication is that for the GLV at the σ of collapse, at least for a large number of species, there are often eigenvalues close to 0, which slow down convergence to the equilibrium, possibly masking the collapse as a smooth eigenvalue sign change.

If one wholly accepts collapse as a kind of instability, then May's thesis does hold: Complex (strongly interacting) systems tend to be unstable, and for smaller σ for larger systems. The instability does however occur later than in May's model (if one allows extinction and considers the size of the system to be the initial size of the system).

8.2.3 Resilience of the GLV

The repeated extinction of species as exemplified in Figure 5.11 has interesting interpretations. On the one hand side, the ability of the system to counter an increase in average interaction strength σ by letting some species become extinct can be viewed as a kind of "structural resilience"; For small perturbations of σ the system remains stable at the expense of "sacrificing" (for positive perturbations) or reintroducing (for negative perturbations) one species.

On the other hand side, between the σ of first extinction and the σ of collapse the eigenvalue with the largest real part is close to 0. This means that perturbations of the population densities die out slowly, at least in some eigendirection(s) and that the system is close to instability in that sense. From this point of view the system is not very resilient to perturbations.

The combination of the two interpretations of resilience give the somewhat paradoxical description of the system as being insensitive to changes in the environment (σ), but sensitive to disruption of the equilibrium.

8.2.4 Recovery from instability

As was mentioned in Section 6.2, it occurred on one occasion that the system went into limit cycle behaviour for some σ , but resumed convergent equilibrium behaviour

for even greater σ . If the GLV is assumed to be an accurate model of ecosystems, then this implies that increasing average interaction strength not only can cause instability, but that it can also stabilise a system (at the price of having more species go extinct possibly).

8.3 Comparison with Tregonning's model

In their 1979 paper [27], Tregonning and Roberts found feasible and stable point by a process where they randomly generated coefficients r_i and $A_{i,j}$, checked if there were any species with negative equilibrium solutions, and if there were, removed the species with the most negative solution. They repeated this process until they found a feasible (and stable) equilibrium. They found that after removing on average half of the species the system would have a stable and feasible point.

The parallels to the model of this thesis; repeated removal of species and abrupt change when on average half of the species are removed, are apparent. They might be superficial however, since their approach differs significantly from that of this thesis. For one thing, Tregonning and Roberts allowed for negative self-growths r_i , which I do not.

Secondly, the species which has the most negative equilibrium population in their model does not need to be the one which would go extinct first in the model of this thesis, had the average interaction strength σ been increased from 0. Although the relative order of species extinction might not matter much, this is still a difference between the models.

Thirdly, Tregonning and Roberts changed the average interaction strength by a factor σ each time a species was extinct, independent of the initial interaction strength. This means that although the average interaction strength is increased in absolute numbers in their model, as in the model of this thesis, the interaction strength for a given number of species depends on the interaction strength chosen for the initial random system. This is not the case for the model system of this thesis, in which a stable and feasible equilibrium will be found regardless of which σ is chosen, given that one such exists.

The most notable difference between the models is however that in the model of this thesis, when approximately half of species have gone extinct feasible and stable equilibria cease to exist, as opposed to the model of Tregonning and Roberts, in which a feasible and stable equilibrium appears! That Tregonning and Roberts find a stable and feasible equilibrium when approximately half of species have been removed should be dependent on the initial σ . Two particular choices of initial σ for a system of n species are $\sigma = 0$ and σ close to infinity. If σ were 0 in their model, the interaction strength would not be changed by species extinction. Furthermore, a stable and feasible equilibrium would be found when all species with non-negative self-growth would have been eliminated (on average half of species, incidentally). If σ would be close to infinity on the other hand, it is unlikely that any moderate number of species removals would give a stable and feasible equilibrium, since the system would always have a σ beyond collapse in the model of this thesis.

In conclusion, although the model of Tregonning and Roberts and the model of this thesis bear superficial resemblance, they are indeed fundamentally different and

I do not see how their respective implications can be meaningfully compared.

8.4 Limitations from choice of initial condition

In Section 7.3 I discussed in length the difficulties choosing initial values for the solution of differential equations. I would like to emphasise that the inability to survey the entire space of initial conditions limits the implications one can draw from the results in this thesis. It has been proven for competitive systems that an invariant subspace attracts all orbits [29], but unfortunately I am not aware of any such result for general Lotka-Volterra equations. Therefore, since choosing initial conditions differently can give different system behaviour, it is important to keep in mind that the results of this report pertain to the special case that all species start with equal population sizes 1.

8.5 A weakness in the methodology

One weakness in the methodology is that most simulations in the report were made for one number of species 80. It would be good to test and show results for more number of species. In general, when testing for a smaller number of species the same general behaviour is found as in larger species system, but the results are less consistent due to increased variability.

8.6 Summary

The discussion in this chapter has covered the plausibility of assumptions made in this thesis and what can be said about the system from an ecological implications. In conclusion, I find it difficult to motivate assumptions from an ecological perspective, but choose to adopt them for mathematical convenience and for limiting the scope of the analysis. A main point from the discussion of ecological implications is that Robert May's analysis hold in essence; sufficiently complex (strongly interacting) systems tend to become unstable and it happens for lower interaction strengths for larger systems. However, the system enters a regime before the point of collapse or instability, in which species go extinct frequently, while retaining stability of the system. The model of Tregonning and Roberts is however difficult to relate to the model of this thesis, in spite of the superficial resemblance between the models.

9

Summary and Conclusions

In this thesis, I have investigated critical points of a special class of generalised Lotka-Volterra systems (GLV), where self-growth is identically 1 for all species, self-interactions are identically -1 for all species and the species interactions are outcomes of random independent Gaussian variables with zero mean and variance parametrised by a variable σ^2 . For this system I have emphasised checking for instability of equilibria, when species have gone extinct and when solutions have ceased to exist, rather than on the nature of instability, e.g. basins of attraction or limit cycle/chaotic behaviour. As a basis and benchmark I have used Robert May's analysis of the stability of large and complex systems from his 1972 paper [16].

I have found that the GLV system considered can resist instability resulting from increased interaction strengths by letting species go extinct. Extinction begins for lower interaction strengths than in May's model, but system collapse or instability in the form of limit cycles is delayed compared with May's model. System collapse means that feasible and stable solutions to the system cease to exist, and the typical "critical slowing down" warning signal often observed close to critical points does not apply for this kind of critical point.

I have presented some explanations for why few equilibria tend to be simultaneously feasible and stable in the GLV and for why critical behaviour typically occurs for certain average interaction strengths σ and number of extinct species N . More research is needed however, to fully understand the mechanisms behind the critical behaviour.

9.1 Conclusions

Connecting to the objectives of this thesis one can say that May's thesis that large systems cannot be simultaneously complex and stable in essence holds true for the example system GLV investigated in this thesis. There is more however, to the behaviour of the system than that the system becomes unstable as soon as one equilibrium under consideration becomes unstable, as claimed by May. The multiple equilibria of the system enables it to adapt to increasing complexity, to some extent, by having some species go extinct. Collapse is a kind of critical point not very well described by May's analysis, since the instability does not occur as a result of the real part of one eigenvalue smoothly becoming positive.

As an example complex system exhibiting critical behaviour, the GLV does offer insights. The critical behaviour when repeated extinction occurs is interesting, since the system is structurally resilient in the sense that it can withstand perturbations of

a parameter and yet dynamically non-resilient in that the system has an eigenvalue with a real part close to zero. The lack of critical slowing down warning signals close to the collapse critical point is also an unexpected aspect of the system. One thing that enables the rich behaviour of the GLV is the multitude of equilibria, such that the system stability is contingent not only on the stability of one equilibrium. The feasibility constraint present in the GLV also sets it apart from many other dynamical systems.

The GLV lends itself well to mathematical analysis due to its simplicity and linearity of the equilibria. The bareness and simplicity of the model might reduce its relevance as a realistic model of ecosystems. Therefore, ecological implications of the model should be interpreted with caution. As a generic mathematical model however, it exhibits rich and diverse critical behaviour. The success in mapping out the critical behaviour in this model calls for exploration of other generic dynamical systems capable of critical behaviour, to create a larger portfolio of knowledge to be used in the quest of gaining greater understanding of criticality in complex systems.

9.2 Open questions and future work

In this thesis I barely scratch the surface of what can be known about both the GLV and complex systems with critical behaviour. Concerning the GLV much research has been made on either small dimensional examples or narrow classes of species interaction such as competitive systems, but little research has been done on large systems with arbitrary or random interactions. In this respect the model of this thesis can be extended in many ways, e.g. by allowing for negative self-interaction, food-web interaction structure, non-zero average interaction strength or a greater selection of initial values.

Concerning other complex systems, the GLV studied in this thesis is only one example from which one can not draw general conclusions regarding complex systems. If more systems are studied, one might be able to find differences and similarities between systems and perhaps find general results regarding the nature of critical transitions.

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A

Appendix 1

In this appendix lengthy derivations are presented.

A.1 Relation between the eigenvalues and the determinant of a matrix

Proof of theorem 2.3.1. Every square matrix A has a Jordan normal form, such that $A = QKQ^T$, where Q is some change of basis matrix and K is an upper triangular matrix. Note that $Q^T = Q^{-1}$. The proof follows from a combination of elementary results:

The determinant is invariant under a change of basis: This fact follows from that:

$$\det(A) = \det(Q) \det(K) \det(Q^T) = \det(Q)(1/\det(Q)) \det(K) = \det(K)$$

where the multiplication law of determinants has been used.

The determinant of a triangular matrix equals the product of diagonal elements: Laplace expansion of the determinant of an $n \times n$ matrix U gives that

$$\det(U) = \sum_{j=1}^n (-1)^{i+j} U_{i,j} M_{i,j}$$

where $M_{i,j}$ is the minor (the determinant of U when row i and column j are removed) and the row i may be chosen at will. Hence, if U is triangular (upper or lower) then

$$\det(U) = \prod_{i=1}^n U_{i,i}.$$

The eigenvalues of a triangular matrix equal the diagonal elements: The eigenvalues λ of a matrix U are the solutions to $\det(U - \lambda I) = 0$, where I is the identity matrix. If U is triangular, then so is $U - \lambda I$, and

$$\det(U - \lambda I) = \prod_{i=1}^n (U_{i,i} - \lambda).$$

Thus $U_{i,i}$ are the solutions to $\det(U - \lambda I) = 0$ and $\lambda_i = U_{i,i}, \forall i$.

The eigenvalues are invariant under a change of basis: Assume λ is an eigenvalue of a matrix A . Then $\det(A - \lambda I) = 0$. Under a change of basis $K = QAQ^T$:

$$\begin{aligned} \det(K - \lambda I) &= \det(QAQ^T - \lambda I) \\ &= \det(Q(AQ^{-1} - Q^{-1}\lambda I)) \\ &= \det(Q(A - Q^{-1}\lambda IQ)Q^{-1}) \\ &= \det(Q) \det(A - \lambda Q^{-1}Q) \det(Q^{-1}) \\ &= (\det(Q)/\det(Q)) \det(A - \lambda I) \\ &= \det(A - \lambda I) = 0 \end{aligned}$$

showing that the eigenvalues of K and A are identical.

Using the above results, we have that if K is the Jordan normal form of some matrix A then: $\det(A) = \det(K) = \prod_{i=1}^n \lambda_i$, where all λ_i are an eigenvalues of both A and K . \square

A.2 Transformation of r to preserve constant diagonal of the Jacobian

Allesina and Tang considered the generalised Lotka-Volterra equations (4.1) (with a slightly different naming of constants) and showed how the self-growth factors r_i needs to be transformed in order to preserve constant diagonal elements of the Jacobian, if the off-diagonal elements are scaled by factors $\sigma_{i,j}$. The expression, for $\sigma_{i,j} \equiv \sigma, \forall i, j$ is:

$$r'_i = r_i \sigma + x_i^* A_{i,i} (\sigma - 1) \quad (\text{A.1})$$

where r'_i and r_i are the new and old self-growth factors respectively, x_i^* is the (interior) equilibrium population, $A_{i,i}$ is the self-interaction of species, all for species i , and σ is the scaling of off-diagonal elements.

A.3 Identical self-growth R

Often in this report the assumption is made that all self-growth rates are identical, i.e. $r_i = r_j, \forall i, j$. Here I show that scaling all elements of such a self-growth vector by a parameter R scales all eigenvalues by R .

Assume x^* is an equilibrium interior point for some $r_i = R, \forall i$ and that λ is an eigenvalue of the Jacobian $J = \text{diag}(x^*)A$ at that equilibrium point, where $\text{diag}(x^*)$ is a square matrix with elements x_i^* on the diagonal and 0 on the off-diagonals. Then λ satisfies:

$$\det(J - \lambda I) = 0 \quad (\text{A.2})$$

Now let $r' = Rr$ such that $x' = -A^{-1}Rr = Rx^*$ is an interior equilibrium point of $\dot{x} = x(Rr + Ax)$. Then the Jacobian J' at x' is given by $J' = \text{diag}(Rx^*)A =$

$R \cdot \text{diag}(x^*)A = RJ$. Hence any eigenvalue λ' of J' must satisfy

$$\begin{aligned}\det(J' - \lambda'I) &= 0 \\ \det(RJ - \lambda'I) &= 0 \\ (Rn) \det(J - (\lambda'/R)I) &= 0\end{aligned}\tag{A.3}$$

under the assumption that $R \neq 0$ and where n is the number of species in the system. If $R = 0$ then $J' = 0$ where 0 is the zero matrix and hence $\lambda'_i = 0, \forall i$. Thus $\lambda' = 0 = R\lambda$ for any λ as claimed. A comparison with A.2 shows that $\lambda'/R = \lambda$ for $R \neq 0$ and hence $\lambda' = R\lambda$ as claimed.

A.3.1 Analytical solution of a two species system

In this section the determinant of the interaction matrix A , the determinant of the Jacobian J of the GLV equations at the internal equilibrium point x^* and the eigenvalues of J are derived.

I assume that $r_i = 1, \forall i$ and that the diagonal elements of A are all $-d$. Let $A = \begin{bmatrix} -d & a \\ b & -d \end{bmatrix}$. Consequently:

$$\det(A) = d^2 - ab.\tag{A.4}$$

Let $D \equiv \det(A)$. Then:

$$A^{-1} = \frac{1}{D} \begin{bmatrix} -d & -a \\ -b & -d \end{bmatrix}\tag{A.5}$$

$$x^* = -A^{-1}r = \frac{1}{D} \begin{bmatrix} a + d \\ b + d \end{bmatrix}\tag{A.6}$$

$$J = \text{diag}(x^*)A = \frac{1}{D} \begin{bmatrix} -d^2 - ad & a^2 + ad \\ b^2 + bd & -d^2 - bd \end{bmatrix}\tag{A.7}$$

This is under the assumption that $D \neq 0$. Otherwise x^* does not exist. x^* is the interior equilibrium point. The determinant of J becomes:

$$\det(J) = \frac{1}{D^2}(d^2(a+d)(b+d) - ab(a+d)(b+d)) = \frac{1}{D}(a+d)(b+d).\tag{A.8}$$

The eigenvalues λ for a 2×2 matrix J are:

$$\frac{1}{2}[\text{tr}(J) \pm \sqrt{(\text{tr}(J))^2 - 4\det(J)}]\tag{A.9}$$

Since in this case $\text{tr}(J) = -\frac{1}{D}d(2d + a + b)$ we have:

$$\begin{aligned}\lambda &= \frac{1}{2}\left[-\frac{1}{D}d(2d + a + b) \pm \sqrt{\frac{1}{D^2}(d^2(2d + a + b)^2 - \frac{1}{D}4(a+d)(b+d))}\right] \\ &= \frac{1}{2D}\left[-d(2d + a + b) \pm \sqrt{d^2(2d + a + b)^2 - 4D(a+d)(b+d)}\right].\end{aligned}\tag{A.10}$$

The expression under the square root can be simplified as follows:

$$\begin{aligned}
& d^2(4d^2 + 4d(a+b) + (a+b)^2) - 4d^2(a+d)(b+d) + 4ab(a+d)(b+d) = \\
& d^2(4d^2 + 4d(a+b) + (a+b)^2) - 4d^2(ab + d(a+b) + d^2) + 4ab(ab + d(a+b) + d^2) = \\
& d^2((a+b)^2) + 4ab(ab + d(a+b)) = \\
& d^2((a+b)^2) + (2ab)^2 + 2(2ab)d(a+b) = \\
& (2ab + d(a+b))^2.
\end{aligned} \tag{A.11}$$

Then the eigenvalues become:

$$\lambda = \frac{1}{2D}[-d(2d + a + b) \pm (2ab + d(a + b))] \tag{A.12}$$

such that:

$$\begin{cases} \lambda_1 = \frac{1}{2D}[-d(2d + a + b) + (2ab + d(a + b))] = \frac{-2(d^2 - ab)}{2(d^2 - ab)} = -1 \\ \lambda_2 = \frac{1}{2D}[-d(2d + a + b) - (2ab + d(a + b))] = \frac{1}{2D}2(-d^2 - d(a + b) - ab) = -\det(J) \end{cases} \tag{A.13}$$

where $\det(J)$ is given in (A.7).

If one scales all off-diagonal elements by some parameter $\sigma > 0$ by letting $a \rightarrow \sigma a, b \rightarrow \sigma b$ then $\det(A)$ becomes:

$$\det(A) = d^2 - \sigma^2 ab \tag{A.14}$$

and $\det(J)$ becomes

$$\det(J) = \frac{1}{D}(\sigma a + d)(\sigma b + d). \tag{A.15}$$

This leads to $\lambda_1 = -1$ and $\lambda_2 = \frac{1}{d^2 - \sigma^2 ab}(\sigma a + d)(\sigma b + d)$.

A.3.2 One constant eigenvalue

Here, I show that $-R$ always is an eigenvalue of the Jacobian (4.11) at an interior equilibrium, if assuming that $r_i = R$ and $A_{i,i} = -d, \forall i \in 1, 2, \dots, n$. Let I denote the identity matrix. For simplicity of notation, I do not distinguish between the full system and the reduced system and let n denote the number of species of any reduced system. The assumption that A is invertible is included in the assumption of existence of an internal equilibrium point.

We have that $-R$ is an eigenvalue of $J = \text{diag}(x^*)A$, where $\text{diag}(x^*)$ is a square matrix with elements x_i^* on the diagonals and 0 on the off-diagonals, if and only if

$$\det(J - (-R)I) = 0 \tag{A.16}$$

Assuming that A^{-1} exists the condition can be written

$$\begin{aligned}
& \det(\text{diag}(x^*)A + RA^{-1}A) = 0 \\
& \det((\text{diag}(x^*) + RA^{-1})A) = 0 \\
& \det(\text{diag}(x^*) + RA^{-1}) \det(A) = 0
\end{aligned} \tag{A.17}$$

where the last step follows from the multiplication rule for determinants. Since A is assumed non-singular $\det(A) \neq 0$ and it is required that

$$\det((\text{diag}(x^*) + RA^{-1}) = 0. \quad (\text{A.18})$$

Since the i :th diagonal element of $\text{diag}(x^*)$ is $-R \sum_{k=1}^n A_{i,k}^{-1}$ the matrix $((\text{diag}(x^*) + RA^{-1})$ has the following structure:

$$= R \begin{bmatrix} RA_{1,1}^{-1} - \sum_{k=1}^n RA_{1,k}^{-1} & RA_{1,2}^{-1} & \dots & RA_{1,n}^{-1} \\ RA_{2,1}^{-1} & RA_{2,2}^{-1} - \sum_{k=1}^n RA_{2,k}^{-1} & & RA_{2,n}^{-1} \\ \vdots & & \ddots & \vdots \\ RA_{n,1}^{-1} & \dots & & RA_{n,n}^{-1} - \sum_{k=1}^n RA_{n,k}^{-1} \end{bmatrix} \quad (\text{A.19})$$

$$= R \begin{bmatrix} -\sum_{k=1, k \neq 1}^n A_{1,k}^{-1} & A_{1,2}^{-1} & \dots & A_{1,n}^{-1} \\ A_{2,1}^{-1} & -\sum_{k=1, k \neq 2}^n A_{2,k}^{-1} & & A_{2,n}^{-1} \\ \vdots & & \ddots & \vdots \\ A_{n,1}^{-1} & \dots & & -\sum_{k=1, k \neq n}^n A_{n,k}^{-1} \end{bmatrix}$$

From this expression it is obvious that the sum of all columns or rows is the zero vector which means that the matrix is rank-deficient. This in turn implies that the determinant is 0, which concludes the proposition that $-R$ is an eigenvalue of any Jacobian satisfying the above assumptions.

A.4 Derivations for the distribution in Section 6.6

Consider the distribution $f(k) = \frac{1}{C} \sum_{k=0}^n \binom{n}{k} p^{n-k}$, where p is the probability of success, k is the number of elements removed, n is the total number of elements and C is a normalisation constant. I later derive the expectation of a random variable with this distribution, but first I derive the normalisation constant.

By the binomial theorem $(a+b)^n = \sum_{k=0}^n \binom{n}{k} a^k b^{n-k}$. If we set $a = 1$ and $b = p$ we get that

$$(p+1)^n = \sum_{k=0}^n \binom{n}{k} p^{n-k}, \quad (\text{A.20})$$

so that $C = (p+1)^n$. I next derive the expectation of a random variable X with this distribution.

Taking the derivative with respect to p of Equation (A.20) gives that

$$\begin{aligned}
n(p+1)^{n-1} &= \sum_{k=0}^n \binom{n}{k} (n-k)p^{n-k-1} \\
np(p+1)^{n-1} &= \sum_{k=0}^n \binom{n}{k} np^{n-k} - \sum_{k=0}^n \binom{n}{k} kp^{n-k} \\
\sum_{k=0}^n \binom{n}{k} kp^{n-k} &= n(p+1)^n - np(p+1)^{n-1} \\
\sum_{k=0}^n \binom{n}{k} kp^{n-k} &= n(p+1)^n \left(1 - \frac{p}{p+1}\right) \\
\sum_{k=0}^n \binom{n}{k} kp^{n-k} &= n(p+1)^n \left(\frac{1}{p+1}\right).
\end{aligned} \tag{A.21}$$

Now, we identify the left hand side as $C\mathbb{E}[X]$, where $\mathbb{E}[X]$ is the expectation of a random variable X with this distribution. Dividing by C , we get that:

$$\mathbb{E}[X] = \frac{n}{p+1}. \tag{A.22}$$

If we instead are interested in the expected proportion of elements removed, we get $\mathbb{E}[X/n] = \frac{1}{p+1}$, which is decreasing in p and $\frac{2}{3}$ in case $p = \frac{1}{2}$. If we furthermore seek the expected proportion of feasible solutions (see Section 6.6), then we sum over the expected number of solutions per number of removed rows k and divide by the total number of solutions 2^n to get:

$$\frac{\sum_{k=0}^n \binom{n}{k} p^{n-k}}{2^n} = \frac{(p+1)^n}{2^n}, \tag{A.23}$$

which converges to 0 as $n \rightarrow \infty$, if $p < 1$. In the special case of $p = 1$ we get the proportion 1. This corresponds to purely competitive systems, for which the row sums are guaranteed to be negative. On the other extreme $p = 0$, we get that only $\frac{1}{2^n}$ solutions are feasible (which is the solution $x^* = 0$).

If p is not known, a solution is to try to infer it from data. One method for doing so is called the maximum likelihood method, in which one seeks to find an estimate of some parameter p which maximises the likelihood function $\mathcal{L}(p; x_1, x_2, \dots, x_m) = \prod_{i=1}^m f(k_i|p)$, where x_1, x_2, \dots, x_m are outcomes of i.i.d variables following some hypothesised distribution.

Sometimes, as is the case now, it is more convenient to maximise the logarithm of the likelihood function. I take the derivative of $\log(\mathcal{L})$ with respect to p and get:

$$\begin{aligned}
\frac{d}{dp} \log(\mathcal{L}) &= \frac{d}{dp} \sum_{i=1}^m \left(\log \binom{n}{k_i} + (n - k_i) \log(p) - n \log(p+1) \right) \\
&= \left(mn - \sum_{i=1}^m k_i \right) \frac{1}{p} - mn \frac{1}{p+1}.
\end{aligned} \tag{A.24}$$

In order to find the p which maximises the likelihood, I set the derivative to 0 and

solve for p :

$$\begin{aligned}
0 &= (mn - \sum_{i=1}^m k_i) \frac{1}{p} - mn \frac{1}{p+1} \\
0 &= (p+1)(n - \bar{k}) - np \\
0 &= -p\bar{k} + (n - \bar{k}) \\
p &= \frac{n - \bar{k}}{\bar{k}}
\end{aligned} \tag{A.25}$$

where $\bar{k} \equiv \frac{1}{m} \sum_{i=1}^m k_i$ is the sample mean. This gives the minimum likelihood estimator (MLE) $\hat{p} = \frac{n - \bar{k}}{\bar{k}}$. Apparently \bar{k} is a sufficient statistic and incidentally the MLE is identical to the method of moments estimator.