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Extinctions and Ecosystem Stability

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ABSTRACT

Human society's expansion and demand for both biotic and abiotic natural resources exert a large pressure on ecosystems around the globe. Ecosystems are complex networks of species interacting with each other and their physical surroundings. Although they are in constant change due to incidental/fortuitous fluctuations as well as climate, migration and, evolution, in a human time-frame ecosystems are relatively stable, upholding certain qualities and functions. Stability of an ecosystem can refer to many different aspects but in general denotes an ability to keep the perceived qualities and functions in the face of external disturbances.

This thesis builds on the long heritage of trying to understand stability of ecosystems, and the more recent use of dynamical modelling for this purpose. A contested issue in ecosystem research is the role of complexity in facilitating stability. Complexity being an intuitive but not strictly defined concept including among others number of species, amount of interactions and structure of interactions. Irrespective of the role of complexity for ecosystem stability there is general agreement that there are limits to stability, in terms of some property, at which point an ecosystem if perturbed/pressured beyond it will transition to a qualitative different state.

This thesis shows that, contrary to previous conception, there are more limits of stability than one. The new limits revise the important transition points of an ecosystem and differentiate between different types of stability, which in turn have differing responses to disturbances of equal magnitude. Species extinctions are found as a mechanism to prevent collapse of an entire community and collapse is found to be divided into two types. The thesis also exposes certain types of constraints on the structures of interactions among species that have a large influence on the stability limits. Together these results give indication of important structures of ecosystems which determine response behaviour to a high degree, important when analysing systems and assessing their vulnerability in an uncertain environment.

Keywords: ecosystems, complexity, stability, dynamical systems, Generalised Lotka-Volterra, interaction structure, structural stability, local stability

APPENDED PUBLICATIONS

Paper I S. Pettersson, V. Savage and M. Nilsson Jacobi (2019). *Predicting Collapse of Complex Ecological Systems: Quantifying the Extinction Continuum.* In review. Prepublished at bioRxiv `http://biorxiv.org/cgi/content/short/713578v1`.

Author contributions: MNJ conceived the project; SP performed simulations and wrote the paper; MNJ and SP produced the analytic results; All authors MNJ, SP, VMS, interpreted results and worked on the manuscript.

Paper II S. Pettersson, V. Savage and M. Nilsson Jacobi (2019). *Stability of Ecosystems Enhanced by Biological Constraint.* Working paper.

Author contributions: MNJ conceived the project; SP performed simulations and wrote the paper; MNJ and SP produced the analytic results; All authors MNJ, SP, VMS, interpreted results and worked on the manuscript.

To the Ether

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Thanks to my supervisor Martin, co-author Van, lovely office sharers Florence and Laura, and all other inspiring colleagues at Physical Resource Theory. Days would not be as fun without the everlasting discussions.

CONTENTS

CHAPTER 1

Introduction

The world of living organisms, their interrelations, rhythms and harmonies have interested humans since time immemorial. We have sought to learn from living nature the properties of our surroundings to both survive and utilise it, as well as understand ourselves as humans in relation to it. Today, our enormous capacity to harness natural resources, shaping our surroundings in the process, adds inquiries into how living nature acts under changing circumstances as an important goal. Important that is, if we wish to understand how to keep natures harmonies and continue utilising its products.

Ecosystem is the word we use today for the living nature around us, coined by Arthur Tansly in 1935 [1]. It is defined as the complex of living organisms, their physical environment, and all their interrelationships in a particular unit of space. Despite our long history of interest in living nature Ecology as a discipline is rather young. It transitioned from a more descriptive science to its modern form, in terms of a search for mechanisms of synthesis, functioning and, degradation during the late 19th and 20th centuries. Partly because humanity's influence on ecosystems was already quite apparent in the wake of the industrial revolution.

With humanity's increasing impact in mind, a focus in modern ecology is on ecosystem stability, and specifically its reasons and mechanisms. The early paradigm view was that complex ecosystem with a large number of species and interactions among them, are more stable than less complex ones. This was theorised to be because of less reliance on specific keystone species [2] and functional redundancies [3] – the more species and interactions the more room for the system to manoeuvre if perturbed or pressured. Observations also seemed in favour of this view, complex ecosystems were not seen to fluctuate in species abundances as radically as less diverse systems.

For example, agricultural mono-cultures appeared more prone to pest invasions than complex tropical forests like the Amazon [4]. In addition, mathematics was entering ecology and arguments based on the stability of interaction modules including a few species extrapolated to larger systems and information theory, were used to posit a positive relationship between stability and complexity [5].

The introduction of mathematics into ecology was pioneered by MacArthur and Wilson. In their "Theory of Island biogeography" for example, they used curves of emigration and immigration and argued that ecosystems will equilibrate at the intersection, which can then be used to predict biodiversity [6]. Another influential mathematical approach was the application of dynamical systems theory and differential equations to model species populations. Lotka and Volterra separately and simultaneously found cycles of fluctuating predator and prey populations in a two species model [7, 8], made famous under the epithet the Lotka-Volterra model. Although useful to illuminate possible dynamical behaviours of interactions between a few species, the dynamical models become intractable when systems grow to the size of entire ecosystems.

In 1972 Robert May expanded population dynamics beyond a few species, while retaining a means of analysis by the use of statistics of random numbers [9]. He posited a random network of interactions among species, where the strengths of the interactions and which species were to interact, were randomly chosen. With this model he showed that complexity, in terms of species diversity, amount of interaction and strength of interactions will destabilise a system. This was in opposition to the ruling paradigm of positive stability-complexity connection and spurred a still ongoing debate of the role of complexity in ecosystem stability.

The most blatant departure from real ecosystems in May's model is also the feature giving it strength in terms of analysis, the random interaction structure. Since we do observe large stable ecosystems the structure of interactions can be seen with all its clarity as key to stability. Thus comparing specific structures of interaction to the random model has been a fruitful way to test their stabilising effects [10, 11]. With the increase in computer power ecosystem stability has been explored along many different avenues, but since it's conception May's work has functioned as a reference point for the field of ecology either expanding the model [12–16] comparing against it [17–20], confirming its conclusions [21–23], refuting them [24–26], discussing it [27–29], or highlighting it's shortcomings as a model for real ecosystems [30].

1.1 Motivation and Aim

I believe unravelling the mysteries of the natural world and increasing our understanding of the functioning of complex systems, such as the worlds ecosystems has an intrinsic value. However, with humanities increasing ability and propensity to expand, utilise and affect the worlds ecosystems the instrumental value of this knowledge is increasing. In order to for example manage our fishing without depleting the stocks [31] or make informed judgements on boundaries of nature reserves [13], and an abundance of other issues, knowledge of functioning, response behaviours and, transition points of ecosystems is desirable.

Many features of ecosystems having stabilising effects have been found with the help of theoretical models, examples include hierarchical structures [30], compartmentalisation [32], large number of weak interactions [33], and allometric species properties [34, 35]. Some features are contested such as nestedness sometimes shown to be stabilising [36], sometimes not [37]. Other studies including stabilising features in conjunction have shown less stability when combined than in isolation [38]. The picture of ecosystems stability is additionally complexified by the multitude of ways a system can be said to be stable, some stability concepts enhancing, some decreasing for the same ecosystem features [39]. Because of the difficulties in analysing the overwhelming complexity of the ecosystems, there is a tendency to focus on one stability concept or feature at a time, missing possible synergies.

The aim of this thesis is to add to the knowledge of ecosystem response behaviours by expanding the stability analysis of two of the most influential models in theoretical ecology, May and General Lotka Volterra. This by including several concepts of stability in the analysis and finding structures of species interactions that influence them.

1.2 Disposition of thesis

The thesis consists of three additional chapters and two appended papers. Chapter 2 gives the necessary background for the papers, in terms of theory, concepts and research context. Chapter 3 contains motivation for the two papers as well as summaries of results and discussions. In chapter 4 the results of the entire thesis is discussed together with conclusions and an outlook for my future research.

CHAPTER 2

Background

The issue I wish to address in this thesis is the stability of ecosystems in relation to species interaction structures. To close in on this issue some background is needed as to what type of ecosystem behaviour stability in our work refers to, how species interactions are represented and what modelling method is used. All this will be clarified and put into a research context in this chapter.

In section 2.1 I introduce the most common stability concepts, section 2.2 introduces dynamical models of ecosystems and technical implementations of the stability concepts form section 2.1 which we use in our work. In section 2.3 I present the interactions of ecosystem represented as matrices and structures of interactions. Last but definitively not least, in section 2.4 May's framework is presented and related to the research field of theoretical ecology.

2.1 Stability

The concept of stability of an ecosystem is no easy thing. It spreads into a multitude of different behaviours and definitions both because of our own conception of what stability implies and the complexity and openness of ecosystems. For example, would an ecosystem that recovers from a drought but with the abundance of some species drastically reduced while others increased be said to be stable? How about returning to the former state but after several years? Or, returning to almost the same state but with one species less? There is of course no final judgement, the two first are generally said to be stable but capturing different concepts of stability, the first system robust the second resilient. The third on the other hand would by some be labelled robust, keeping its general appearance, while others would classify the loss of a species as a mark of instability.

Stability concept	Definition
Robustness	Ability to uphold characteristic/important features when perturbed
Resilience	Return/return time to equilibrium state after perturbation
Invasibility	A new species ability to invade
Variability	The variation of species abundances over time
Permanence	Change in any system characteristic except extinctions

Table 2.1: The table lists the most common concepts of stability in ecology.

The most commonly used concepts of stability are robustness, resilience, invasibility and variability. Robustness is the ability of a system to uphold characteristic features of interest when perturbed or pressured. Because of the unspecific definition robustness can be measured in a multitude of ways, one example is a system's propensity for cascading secondary extinctions after a species removal [26]. Resilience is the ability of a system to return to the same state after a perturbation [40], sometimes including the time of return [41]. An ecosystem is termed invasibile if it is susceptible to successful establishment of foreign species [42] and variability is a measure of fluctuations in species abundances [27]. In table 2.1 stability concepts are listed with short descriptions.

A subtlety when employing stability concepts is that they in turn refer to concepts of state. Ecosystems are not static, species abundances and interactions fluctuate, because of fortuitous reasons or more ordered, for example seasonal ones. A usual way to handle this is to think of some equilibrium "normal" state and fluctuations around it. This means stability can be liable to the tolerance of the magnitude of fluctuations, as well as some stability aspects inherent in fluctuations overlooked. Nevertheless, in many cases an equilibrium state is a fitting simplification and one I will employ the rest of the thesis.

2.2 Dynamical models

A common way to investigate ecosystem stability, and the approach used in this thesis, is dynamical modelling (population dynamics), using differential equations to model species abundances over time.

The most general form can be stated as

$$\frac{dx_i}{dt} = R_i(x_i) + \sum_{i=1}^{N} G_{ij}(x_i, ..., x_N), \tag{2.1}$$

where x_i are species abundances, R_i and G_{ij} are functions for intrinsic growth rate and the interactions among species respectively for each species $i = 1, 2...N$. R_i and G_{ij} are in some cases split up, for example dividing R_i into separate breeding and mortality functions. Similarly G_{ij} is sometimes split up when treating food-webs (only including predator and prey interactions) with differing functions for when a species acts as prey or predator [43, 44]. For example, using a function for predation which takes the predators limited capacity of processing food into account called Holling type II, or Holling type III adding extra difficulty of finding prey when their abundance is low [45]. Making each interaction type explicit with a specific function can capture dynamics more realistically, although the cost is in analytical tractability.

One of the most widely used dynamical models is the Generalized Lotka Volterra (GLV) set of differential equations

$$\frac{dx_i}{dt} = x_i f_i(x) \tag{2.2}$$

where $\boldsymbol{f} = \boldsymbol{r} + B\boldsymbol{x}$. Here $\boldsymbol{r}$ is a vector of intrinsic growth rates (assuming $R_i(x_i)$ to be linear) and A is an adjacency matrix coding the interactions among species, discussed in more detail in section 2.3. This general dynamical model thus assumes static interactions among species which do not depend on abundances, such as a predator's shifting of preferred prey if prey abundances change or as in Holling type II not being able to benefit of a large increase in prey because of food processing limitations.

In terms of presentation it can be useful to explicitly separate the intraspecific interactions (diagonal of A), which is competition within a species, from the other interaction terms in the matrix. Giving the equation in its usual appearance

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + x_i \sum_{i=1}^{N} A_{ij} x_j, \tag{2.3}$$

where the diagonal of A_{ii} is set to zero. The intraspecific interaction term $-1/K_i$ makes a species self-stabilising by inhibiting exponential growth in the absence of interactions with other species (in case of positive r_i). K_i is called the carrying capacity, setting the limit for a species abundance.

The GLV equations allow for different types of dynamics, including limit cycles (patterns of rising and falling species abundances), chaotic dynamics and fixed-points where the species abundances do not change over time. The focus for larger systems has mainly been on the stability of fixed points, mainly because of the connection to Mays stability analysis discussed in section 2.4.

The equilibrium state of an ecosystem in theoretical ecology usually refers to fixed points of a dynamical model. For the GLV equations the fixed points are

$$\begin{aligned} x_i^* &= 0 \\ &\text{or} \\ x_i^* &= \frac{K_i}{r_i}\left(r_i + \sum_{i=1}^{N} A_{ij} x_j^*\right) \end{aligned} \tag{2.4}$$

as can be seen from these solutions different extinction patterns, where $x_i^* = 0$ means a species i is extinct, leads to 2^N fixed-point solutions for a system of with N species. These fixed points can be either stable or unstable. A natural assumption usually made when the system is interpreted as an ecosystem is that all species are viable (non-extinct) $x_i > 0$ for all i. Such a fixed point is called feasible, and we will show that the assumption of feasibility excludes certain stability concepts and radically transforms the stability analysis.

In paper I and II we combine three stability concepts when analysing the GLV model, local stability, structural stability and persistence. The first two are technically defined versions of resilience and robustness respectively, while the third is mainly a technical measure not corresponding to any of the stability concepts listed in table 2.1. The three stability concepts are presented below.

2.2.1 Local stability

The most common type of stability for a fixed-point of a dynamical model is local stability, which is the return to the exact same state (species abundances) after a perturbation. Local stability is based on a linearisation around the fixed-point, therefore the epithet "local", which leads to a differential equation for a small perturbation $\delta \boldsymbol{x}$ from the fixed-point

$$\delta \dot{\boldsymbol{x}} = J\delta \boldsymbol{x}, \tag{2.5}$$

where J is the Jacobian of the system. The Jacobian for the system in 2.3 is

$$J_{ij} = \delta_{ij}\left(r_i - 2\frac{r_i}{K_i}x_i + \sum_{k=1}^{N} A_{ik}x_k\right) + x_i A_{ij}, \tag{2.6}$$

where δ is the Kronecker delta (equal to one when $i = j$ and zero otherwise). Assuming we are in a fixed point where all $x_i^* \neq 0$ the Jacobian can be reduced to the more common form

$$J = X(A - D), \tag{2.7}$$

where X and D are diagonal matrices with x_i^* and r_i/K_i on the diagonal respectively.

The solutions of equation 2.5 for perturbations around a fixed point are $\delta z_j \sim e^{\lambda_j t}$ in the diagonal basis, giving the perturbations as $\delta x_i = \sum_{j=1}^{N} \alpha_{ij}\delta z_j$, where $\boldsymbol{\alpha}_j$ are eigenvectors of the Jacobian and columns in the matrix α_{ij} and, λ_j are the eigenvalues. From these solutions we see that the real part of the eigenvalues need to be negative for a fixed point to be locally stable. If any of the real parts are positive, perturbations will increase exponentially in time and the fixed-point will not return to the same state.

As mentioned in the section 2.1, in some studies resilience refers to the time for a system to return to its initial state after a perturbation. In such cases resilience is measured by the magnitude of the least negative real part of the eigenvalues. Less negative eigenvalues lead to longer times for the perturbations to die out.

2.2.2 Structural stability

Structural stability is one way of representing robustness. In theoretical ecology it is defined as the size of the parameter region of a system where the fixed points are qualitatively similar [46]. Qualitatively similar is not strictly defined but in general means not too large changes in species abundances, moving from fixed point to another type of dynamics (cycles, chaos etc.) or switching to a fixed point with extinct species. The parameters in this case refer to intrinsic growth rates, carrying capacities, average interaction strengths, increase in amount

Stability concept	**Definition**
Local stability	System returns to fixed-point after small perturbations in species abundances
Persistence	Fraction of species out of an initial number of species present at the fixed-point
Structural stability	size of parameter region which leave the system fixed-point qualitatively unchanged

Table 2.2: The table lists the three stability concepts we utilise in papers I and II.

of interactions between species or shift in interaction structure. Structural stability thus measures how likely a system is to change radically in response external perturbations. An example could be how likely it is that an ecosystem will change qualitatively if experiencing a flood or, a permanent shift in some external factor such as currents leading to more nutrients (all intrinsic growth rates increase). For example in [47] the size of a region without extinction in the space of intrinsic growth rates $\boldsymbol{r}$ is used to measure structural stability. In both papers I and II, but specifically in paper I we define structural stability in terms of an interaction strength parameter, but also generalise the findings to structural parameters in general.

2.2.3 Persistence

The third stability concept we use in papers I and II is persistence. Persistence is measured as the fraction of viable species at a fixed-point for a specific choice of model parameters (r_i, c, K_i etc.) compared to an initial starting amount, N. This measure has mainly been used in simulation studies, although in some cases in comparison with empirical systems. In the latter context if a stability analysis of an actual system has a persistence smaller than 1, something is missing in the analysis or representation of the system since obviously all species in the measured ecosystem are viable. Or, an empirical system is said to be more stable if it has a larger persistence when parametrised and represented as a dynamical system.

2.3 Networks and topology

The structure of the network of species interactions is mainly what determines the stability of a system modelled as a dynamical system. The interaction network is represented by the matrix A in equation 2.3. Each species in the ecosystem has a row in A and the columns are the possible interaction partners (usually all species, including itself, making A an $N \times N$ matrix, where N is the number of species). An interaction between two species is represented by a non-zero entry in the intersecting rows and columns of the two species, see figure 2.1.

There are different types of interactions between two species, either the interaction can benefit both species (mutualistic), be detrimental to both species (competitive), benefiting one but detrimental to the other (predator-prey, parasitism), having negative affect on one but none on the other (ammensalism), or positive affect on one but none on the other (commensalism). The affect on a species is coded for by the sign and magnitude of the entries in its row in the interaction matrix, see figure 2.1. Since the interaction matrix can code for interactions of any type, flower-pollinator, competition for light, symbiosis of bacteria and plant (although assuming all are fixed averages with the same functional form), the interaction matrix does not inherently have a unit. The entries of A can represent for example magnitudes and directions of biomass, or energy (which are the usual ones).

In addition to type of interaction between any two species the network matrix as a whole can have a range of topologies, meaning structures of the interactions. For example a food-web is generally not flat, where anyone species can prey on any other, but structured into hierarchies [30]. Plants, absorbing energy from the sun are classified as primary producers. Herbivores, eating the primary producers classified as primary consumers, predators eating primary consumers are called secondary consumers and so on. Predators also tend to prey on animals in a range around their own size and more often on prey smaller than themselves, adding to the structure of the network. Other types of topologies include modular, which means species having more and stronger interactions within subgroups of the whole system [38]. A typical feature in pollination networks is nestedness [36], meaning specialist pollinators tend to interact with flowers that are subsets of the interaction partners of less specialist pollinators. Schematics of network topologies in matrix form are shown in figure2.1.

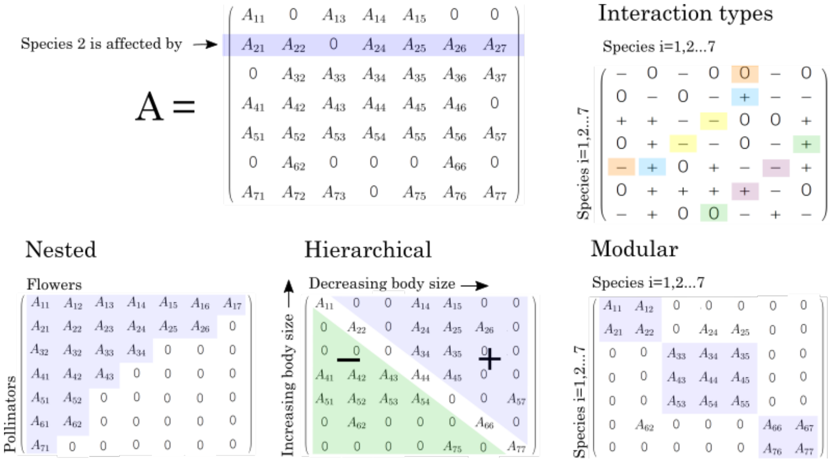


Figure 2.1: Matrix representations of interaction networks of species. The top right panel displays the sign structure of the five different interaction types mutualism (blue), competitive (yellow), predator/prey (purple), ammensalism (pink) and, commensalism (green). Bottom matrices show schematics of the different topological interaction structures: nested, hierarchical and modular.

2.4 May's framework

The specific contributions in our papers mean to elucidate some aspects of the "point of reference"-paper of May and in this way theoretically expand the response behaviour of a system when perturbed. A visualisation of the research context and the influence of May's paper on the field of theoretical ecology can be seen in figure 2.3.

The model in its original formulation is based in dynamical systems theory, uses the concept of linearisation around a fixed point and local stability, but does not specify a system (any dynamics). Instead the form of the Jacobian was proposed directly as

$$J_M = \sigma A - I. \tag{2.8}$$

The ingenious step in May's analysis was to assume the interaction matrix A is a random matrix, meaning interaction partners are randomly chosen and the non-zero entries are drawn from some distribution. This is ingenious since the spectrum (all eigenvalues) of a random matrix is known from random matrix theory [48]. This spectrum only depends on aggregated knowledge such as the mean and variance of the distribution of the entries of A and its connectance

c, which is the fraction of all possible links in the network which are realised. In May's framework an entry is drawn with probability c from a distribution with mean $\mu = 0$ and variance 1. The variance is set to one so that the parameter σ in equation 2.8 can be used for tuning the variance of A.

The spectrum of a $N \times N$ random matrix (with mean $\mu = 0$ and variance σ) is a uniform disc in the complex plane centred at zero with radius $\sigma\sqrt{cN}$. For local stability all real parts of eigenvalues have to be negative. With a shift in the spectrum from the identity matrix in Eq. 2.8 together with the radius $\sigma\sqrt{cN}$ this means a stability boundary can be located at $\sigma = 1/\sqrt{cN}$.

From the model the conclusion can thus be drawn that there is a limit to how complex a system can be (in terms of the parameters σ, c and N) and still retain stability. Since we do see large dense stable systems in nature, and random structure of A is not a very plausible biological structure of an ecosystem, May remarked, it must be some extra structure that acts to stabilise a system. He therefore proposed that random interaction matrices be used as null models to compare to matrices with specific structures in order to evaluate their stability impact. In the years since many such studies have been done and indeed some features, such as predator/pray structure have been found to be stabilising [12], in the sense that it increases the limit of complexity before loss of stability. It is still intrinsic in the model though, that complexity at some point leads to loss of stability. The fact that complexity could play a destabilising role was the main point that ignited the ongoing stability-complexity debate in ecological research.

The Jacobian proposed by May, J_M has a close resemblance to the Jacobian from the GLV equations, J, in Eq. 2.6 (when setting $r_i = K_i$) under the assumption that all species are viable. With the obvious difference that J includes fixed-point abundances while J_M does not. Since it is from the Jacobian J_M that the whole complexity debate started, and was used as a general argument that complexity can lead to instability, it is interesting to evaluate which kind of systems J_M can be a Jacobian of.

A first aspect is the randomness referred to earlier and treated in more detail in chapter 4. A second aspect is the lack of anything referring to the state of a system e.i species abundances, which is one reason why the conclusions can be said to be a representative of all systems. A first approach is to consider dynamics that would lead to such a Jacobian, devoid of species abundances. The Jacobian being derivatives (with respect to x_i) of Eq. 2.3, the only way to not end up with x_i in the solution is if the differential equations of the dynamical model are linear in x_i or constant. Such dynamics has been used to model quasi-species [49], but are in general considered too simple to model species, for example there would be no limiting carrying capacities allowing infinite growth.

If no reasonable model of species growth and interactions can lead to a Jacobian as in equation 2.7, a second approach is to assume that the inclusion of species abundances does not affect the stability, i.e the spectrum. It is quite interesting that such an analysis was not done until rather recently [50, 51]. They found that indeed the stability does not change, even though the spectra of the two Jacobians J_M and J are radically different as seen in figure 2.2. Why more attention was not given to these points in the debate, with their possibility to undermine the whole model, is hard to tell. There is one remaining issue even after the establishment of the stability with and without the inclusion of x_i, which is the assumption that all species are viable (also assumed in [50, 51]). This is the gap we found and have investigated from different angles in papers I and II.

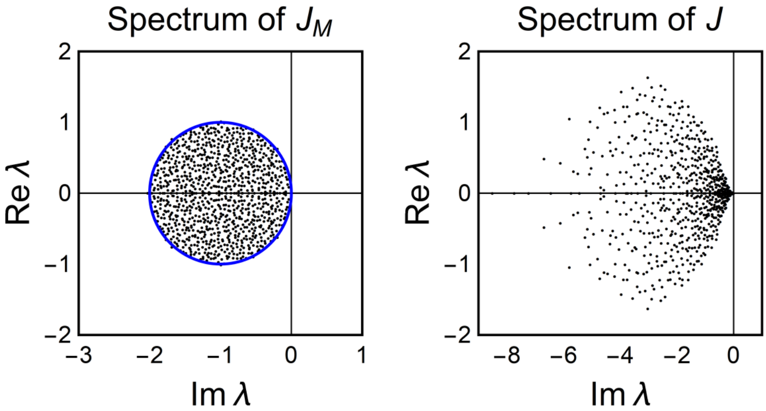
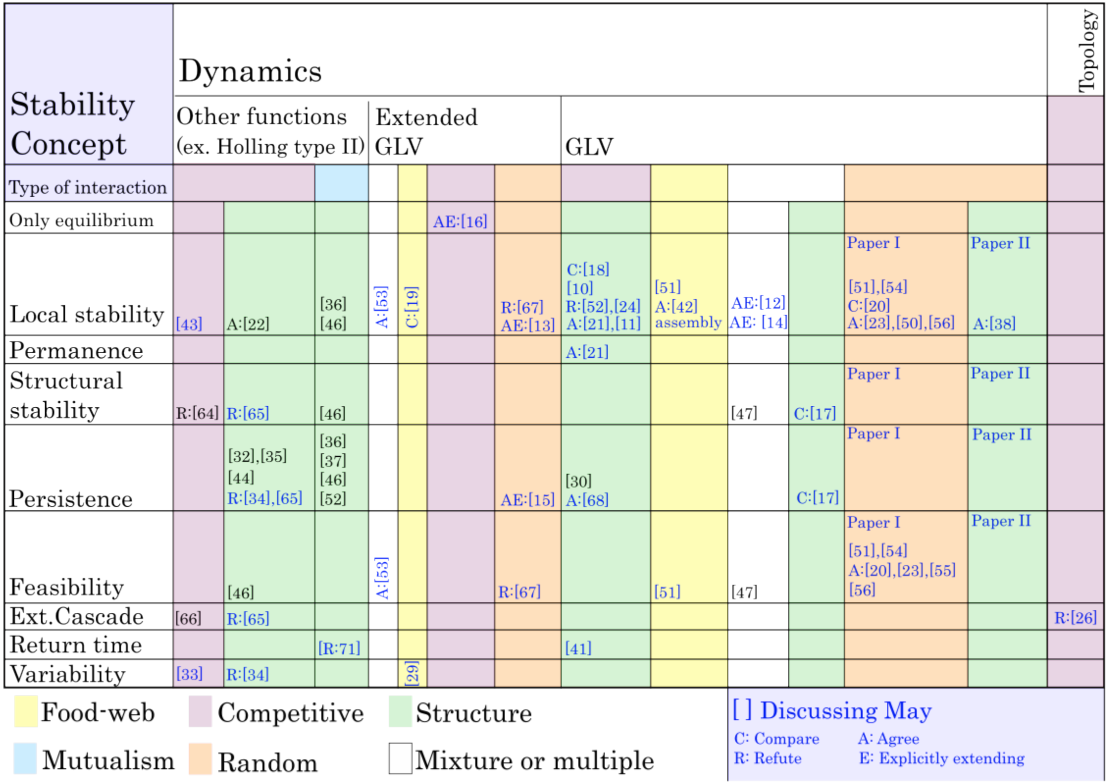


Figure 2.2: The difference between the two spectra of J (including species abundances) and J_M (excluding species abundances) at May's stability boundary σ_M is clearly visible. Note though, that all the real parts of the eigenvalues are negative for both spectra.



Stability Concept	Dynamics													Topology
	Other functions (ex. Holling type II)			Extended GLV			GLV							
Type of interaction	🟪	🟩	🟦 🟩	⬜	🟨	🟪	🟧	🟪 🟩	🟨	⬜	🟩	🟧	🟩	🟪
Only equilibrium						AE:[16]								
Local stability	[43]	A:[22]	[36] [46]	A:[53]	C:[19]		R:[67] AE:[13]	C:[18] [10] R:[52],[24] A:[21],[11]	[51] A:[42] assembly	AE:[12] AE: [14]		Paper I [51],[54] C:[20] A:[23],[50],[56]	Paper II A:[38]	
Permanence								A:[21]						
Structural stability	R:[64]	R:[65]	[46]							[47]	C:[17]	Paper I	Paper II	
Persistence		[32],[35] [44] R:[34],[65]	[36] [37] [46] [52]				AE:[15]	[30] A:[68]			C:[17]	Paper I	Paper II	
Feasibility		[46]		A:[53]			R:[67]		[51]	[47]		Paper I [51],[54] A:[20],[23],[55] [56]	Paper II	
Ext.Cascade	[66]	R:[65]												R:[26]
Return time			[R:71]					[41]						
Variability	[33]	R:[34]			[29]									

🟨 Food-web 🟪 Competitive 🟩 Structure
🟦 Mutualism 🟧 Random ⬜ Mixture or multiple

[ ] Discussing May
C: Compare A: Agree
R: Refute E: Explicitly extending

Figure 2.3: This table gives an overview of the research field of theoretical ecology, including the influence of May's 1972 paper [9]. The colours of the columns in the row "Type of interaction" classifies the studies in their respective columns. Absence of colour indicates either a mixture or that several types were used. The "Structure" refers to additional topological structure such as modularity, nestedness, hierarchy etc. explicitly included in the interaction matrices. Note that the category "Other functions", denoting other type of functional responses than the GLV model, also introduces structure to the interactions but not in the same manner. The column "Topology" refers to studies only looking at the interaction network, for example studying change in connectance due to species deletions. Blue citations are studies that in some way discuss May's stability limit, in which way specified by the different letters C (Compare), A (Agree), R (Refute) and E (Explicitly extending). As a last comment, this table is necessarily skewed, with more detail closer to my own work and incomplete since the field is broad and diverse, and categorisation tend to lead to some overlap between categories.

CHAPTER 3

Present work

There is no doubt that May's paper has had a major impact on ecological research, both by elucidating aspects of complexity other than revealed by empirical observation [2, 4], as well as effects when increasing the size of a system in theoretical investigations [5]. It has also shaped the way stability and the limits of stability are thought to function in real ecosystems.

In May's framework the view of ecosystem stability is, that for a range of parameters c,N and σ (but usually represented by the standard deviation of interaction strengths σ), the system is locally stable (and implicitly structurally stable) with a single boundary to where it is not. What happens on the other side of the boundary is not specified but a bifurcation, meaning a qualitative shift in dynamics, is implied and has often been interpreted as collapse. Thus, the view of stability transported onto real ecosystems is divided into two phases of stability, either a system is both resilient and robust or neither.

A real ecosystem is generally assumed to be in the stable range and therefore believed able to withstand perturbations or changes, in both species abundances and structural features. This belief however is purely theoretical and not substantiated by observation. A separation of the two stability concepts in analysis can lead to other phases of stability and, an expansion of the of responses an ecosystem can exhibit when perturbed. The stability concepts are lumped together in May's analysis due to the assumption of viability of all species. This chapter presents our current work outlining response behaviours, stability limits and measures, for when this assumption is relaxed and the three stability concepts (local stability, structural stability and persistence) are taken into account.

3.1 Paper I

Motivation

In preliminary investigations of the GLV model we found that the assumption of all species to be non-extinct was routinely violated within the supposed stable range, implying the systems were not structurally stable as previously believed. This was substantiated by the existence of studies using persistence as a stability measure [32, 52], since persistence is based on extinctions and measures the fraction of non-extinct species at a fixed-point for a certain set of parameters. Although, no comparison to the stability range was done in these studies. Other studies were using May's stability limit to compare with empirical systems [18] and expanding the limit to cover more cases [12], all under the assumption that a feasible system can always be found. These inconsistencies were becoming apparent in the literature with a call for rigorous investigations into feasibility [51, 53–55].

Research questions and method

The research questions in paper I are, what types of behaviours can a system exhibit in response to external perturbations, both in species abundances and structural parameters? What are the parameter ranges for the different types of responses? and how can we relate these parameter ranges to real systems? To address these questions we use the GLV dynamical model and include all three mentioned concepts of stability (structural stability, local stability and, persistence) in the analysis. The GLV model that we use

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \sigma x_i \sum_{i=1}^{N} A_{ij} x_j, \tag{3.1}$$

where x_i are the species abundances, r_i the intrinsic growth rates, K_i carrying capacities, and A an $N \times N$ interaction matrix. The off-diagonal entries of A are drawn from a normal distribution with mean zero and variance of one, with probability c. The intraspecific interactions are not included in A (its diagonal is zero) but represented by the quadratic x_i term. The standard deviation of the interaction strengths can be varied with the parameter σ. Setting $r_i = K_i = 1$ we obtain the dynamical system with a Jacobian closest in form to the Jacobian proposed by May. With this model we can both theoretically (using linear algebra and order statistics) and with simulations map regions in parameter space with varying system stability characteristics and relate the findings to May's results.

Results

The first thing established was the generality of extinctions in the GLV model with random interaction matrices in the previously designated "stable" parameter region. The extinctions were found to occur in successive single species events when increasing the parameter σ, rather than mass extinctions at some parameter values, as shown for an example simulation in figure 3.1. The abundances of the remaining species after an extinction (after a perturbation) only adjusts slightly and the community remains locally stable.

We derived the parameter boundary at which the first extinction event occurs σ_f. In the derivation we find and use the distributions of the species abundances. With these distributions and order statistics we obtain the distribution of the minimum of the set of abundances, $x_i \in Z$,

$$\begin{aligned} f_{min}(x) &= N(1-F(x))^{N-1} f(x) \\ &= \frac{N e^{-(x-\mu_+)^2/2\sigma_+^2}}{\sigma_+\sqrt{2\pi}} \left(\frac{1}{2} - \frac{1}{\sqrt{\pi}} \int_0^{\frac{x-\mu_+}{\sigma_+\sqrt{2}}} e^{-t^2} dt \right)^{N-1}, \end{aligned} \tag{3.2}$$

where $f(x)$ is the distribution of species abundances x_i with cumulative distribution function $F(x)$. σ_+ and μ_+ are standard deviation and mean of $f(x)$ respectively. The first extinction event σ_f is located at the σ for which the mean of $f_{min}(x)$ is zero.

We also located a second boundary, σ_c,where the system loses stability altogether. We did this by predicting the persistence, based on the reduced interaction matrix (only including interactions for viable species) and combining it with May's boundary for the a reduced system

$$\sigma_c = \frac{1}{\sqrt{cNp_c}}, \tag{3.3}$$

where p_c is the persistence at the collapse boundary. The predictions of σ_f and σ_c are shown in figure 3.2 together with simulation averages.

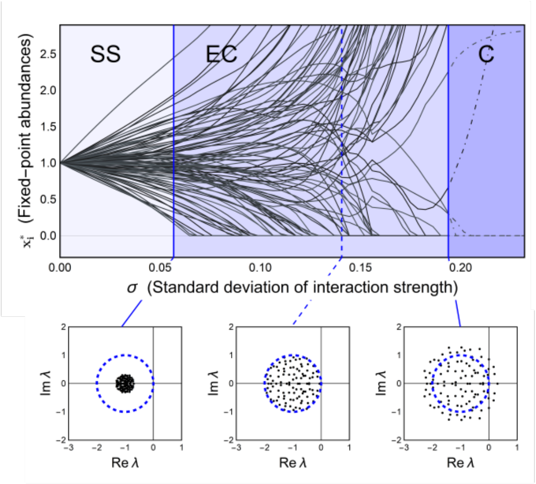


Figure 3.1: Effects on stability of increasing interaction strength in a complex system. Example simulation of a system with initial number of species, $N = 100$, connectance (fraction of realised species interactions), $c = 0.5$, $r_i = K_i = 1$, and $\mu = 0$ for the mean of the distribution of inter-specific interaction. The plot shows the species abundances (top) and the spectrum (bottom panels) at locally stable fixed-points for increasing values of the standard deviation of interaction strength, σ. The first extinction event and collapse are indicated by the blue lines, and the dashed blue line indicates σ_M. Up to the first extinction the system is in the Strict Stability (SS) phase, where the system is locally and structurally stable with all $N = 100$ species non-extinct, $x_i^* > 0$. Between the first extinction and collapse the system is in the Extinction Continuum (EC), with successive single species extinctions preventing collapse. The last phase is Collapse (C), where no nearby similar stable fixed-points exist. The bottom panels show the spectrum of the general Jacobian used by May j_M at three the points of interest first σ_f, σ_M and σ_c, with the circle indicating the radius of stability. Note how the σ_M both overestimates the first extinction event and underestimates collapse.

None of the two boundaries derived coincide with the boundary $\sigma_M = 1/\sqrt{cN}$ previously thought to mark the loss of stability. Thus we uncovered a phase between the two boundaries, the Extinction Continuum (EC), where a system is locally stable but not structurally stable, or stated in the general stability terms resilient but not robust.

Since determining the parameter-distance to the collapse boundary is not possible solely based on macro properties such as number of spe-

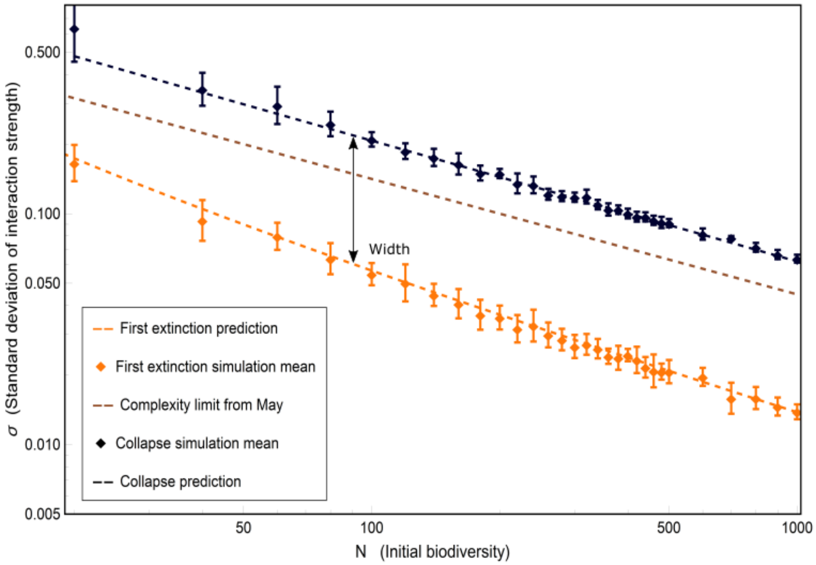


Figure 3.2: Stability predictions for complex systems. In the parameter-space of the standard deviation of interaction strength, there are three phases of behaviour: Strict Stability (SS), Extinction Continuum (EC), and Collapse (C). Here we demonstrate that these phases hold across a large range of system sizes N. The plot shows simulation averages of first extinction events (orange dots) with one standard deviation error bars, our theoretical prediction of first extinction (orange dashed line), the complexity limit introduced by May (brown line), simulation averages of collapse (black dots) with one standard deviation error bars, and our theoretical collapse prediction (black dashed line). The width of the Extinction Continuum is indicated by the arrow, note the increase in width for larger systems. All simulations shown were run with, $r_i = K_i = 1$, $\mu = 0$ for the distribution of inter-specific interactions and a value of $c = 0.5$ for connectance in the interaction matrix A.

cies n, standard deviation of interaction strength σ, and connectance c, we constructed a metric, $\gamma \in [0,1]$, from the reduced interaction matrix to place a system in the Extinction Continuum. The metric in addition to indicating the parameter-distance to collapse captures the level of structural instability (figure 3.3), interpreted as the size of σ perturbation that would lead to an extinction.

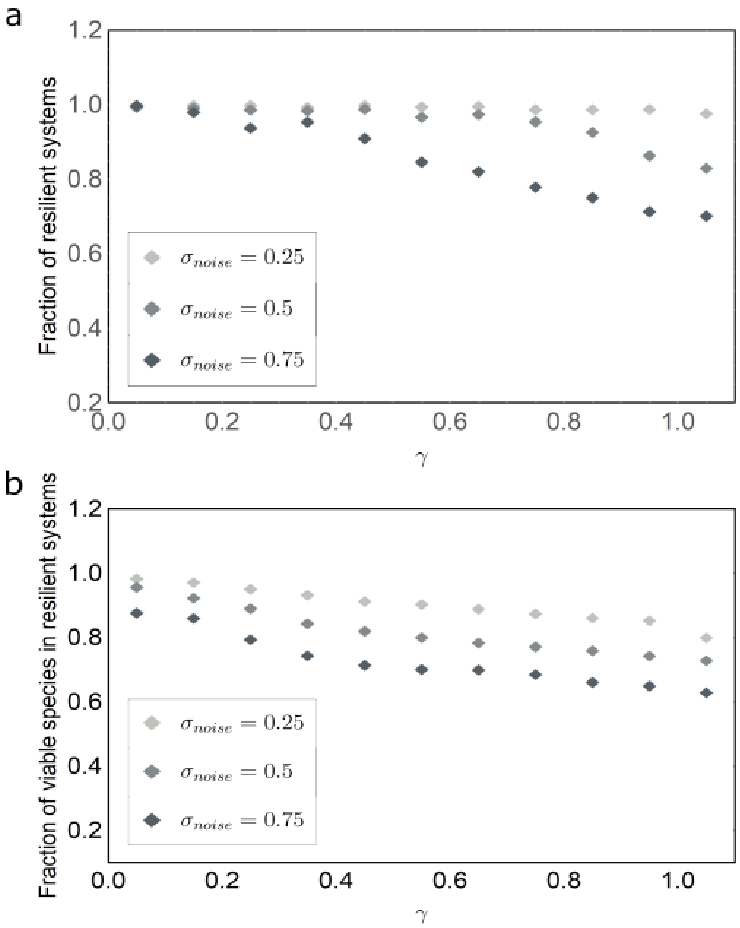


Figure 3.3: Predicting collapse. The plot shows in the top panel the fraction of systems for a certain γ that found a locally stable fixed point after perturbations. The systems with varying γ values were generated from random systems with $N = 70$ and $N = 100$, connectance $c = 0.5$, intrinsic growth rates and carrying capacities $r_i = K_i = 1$, and interaction strengths from a Normal distribution with $\mu = 0$, by specifying their standard deviation of interaction strength σ. Note that γ reaches values larger than one, this is because it is inferred from the reduced interaction matrix. The bottom panel shows the fraction of non-extinct species at the new fixed-point for systems that found a stable state after perturbation. Here even for small perturbations in the Extinction Continuum some species go extinct for the system to find a new locally stable fixed-point. Together the plots demonstrate that a larger γ indicates collapse both in terms of a substantial loss of species (more structurally unstable) and a higher probability of loss of local stability.

Discussion

A noteworthy aspect of the collapse boundary, σ_c, is its location approximately at $\sigma_c = 1/\sqrt{cn}$ (with a slight upward bias), where n is the number of viable species in the remaining community. This is because the entries in the interaction matrix of the reduced community with n species, are still distributed according to the normal distribution with a variance of one and a small but now positive mean. Random matrix theory relying only on aggregate statistics is not incorrect. However, correlations are formed by the non-random extinction events [56]. Thus, the interaction matrices of communities in the Extinction Continuum are no longer completely random.

The new collapse boundary σ_c, in addition expels some of the previous vagueness of a system's behaviour if pushed beyond it. As mentioned, $\sigma_M = 1/\sqrt{cN}$ was seen as a boundary to any type of qualitative change, including single species extinctions. From our analysis we established that systems crossing $\sigma_c = 1/\sqrt{cn}$ will experience more radical change and either transition to limit cycles, chaos or lose a substantial number of species, thereby living up to its name of collapse boundary.

The location of two boundaries adds an extra phase to the picture of ecosystem stability, where a system is locally stable but not structurally stable. This phase, the Extinction Continuum (EC), reveals a new stabilising mechanism where systems can use extinctions to avoid collapse. Since extinctions are far more common than collapse in real ecosystems, this phase might be more ecologically realistic than the previous binary phases.

A system's approach to collapse is radically changed by the existence of the EC. This also means the behaviour of the eigenvalue with least negative real part is radically different. The standard way of predicting collapse is by critical slowdown [57–59], which means a system takes longer to return to its equilibrium state after a perturbation, when approaching collapse. This corresponds to the eigenvalue with least negative real part approaching zero. In the light of this, the behaviour in the Extinction Continuum is very interesting, since the least negative real part of the eigenvalues fluctuates just below zero, implying critical slowdown in the entire phase [60]. Thus, the extra information of γ locating a system in the EC is needed to measure the closeness to collapse. Although, the approach to zero only involves one eigenvalue at a time in the EC, while at the actual collapse a collection of eigenvalues have real parts approaching zero. This means, in the approach to collapse the critical slowing down must be present in many directions in the n-dimensional space of species abundances.

The fluctuating just below zero of the real part of the least negative eigenvalue in the Extinction Continuum is curious in another aspect than extending critical slow down. Since the spectrum is the same regardless of which vector basis is chosen for the Jacobian, this behaviour is carried over to all other choices of basis (linear combinations of $^*_i$, $g^*_i = \sum_{i=1}^{N} \alpha_i x^*_i$ representing for example functional traits). This is curious since the fluctuations will appear to come out of thin air in other bases, since they do not correlate with magnitudes of the new variables g^*_i as with species extinctions in x^*_i. This is of course due to us enforcing a "sticky" boundary, keeping species with abundance zero at zero. Species extinctions might be an obvious sticky-boundary, but it is an interesting phenomena that could be present in other less obvious but ecologically important partitionings of a system, for example trait based representations, leading to seemingly abrupt stability changes in real systems.

3.2 Paper II

Motivation, research questions and method

The stabilising mechanism found in paper I in terms of single species extinctions, was also found to apply to systems with additional biological structure found in the literature. This naturally spurred the question if there does exist interaction structures that could impact the parameter range of the Extinction Continuum or erase it altogether. This is the main research question of paper II: Are there ecologically relevant interaction structures that significantly change the size or eliminate the Extinction Continuum? We continue in the same framework as paper I, using the GLV dynamical model in equation 2.3 and locate boundaries in parameter space using dynamical systems theory, linear algebra and order statistics.

From the fixed-point expression for the species abundances,

$$\mathbf{x}^* = \left(\sum_{p=0}^{\infty} \sigma^p A^p \right) \mathbf{1}, \tag{3.4}$$

we could hypothesise which kind of constraints/structures in the interaction matrix that would likely lead to significant changes in the range of the Extinction Continuum. Specifically we hypothesised that constraining the variance of the row-sums in the interaction matrix would have a large impact. Thus we constructed an interaction matrix according to $A = (1-\xi)A_c + \xi A_0$, to investigate the change in Extinction Continuum. Here, A_c is a matrix with connectance c and and entries distributed according to $\mathcal{N}(0,1)$ where each row has been shifted so that it sums to zero. A_0 is a random matrix with entries in the exact positions as A_c and distributed according to $\mathcal{N}(0,1)$ and, ξ is a parameter regulating the amount of variance in the row sums of A.

Results

As we expected, by increasing the row-sum constraint, $(1-\xi)$, the first extinction boundary, σ_f, is shifted to larger values. With our construction of A, and an improved derivation of the first extinction boundary from a first order approximation in paper I to an exact expression for the variance of the distribution of the species abundances, the analysis could be extended to account for the row-sum constraint and predict the first extinction and collapse boundaries for systems constrained to any degree. The expression for the variance of the distribution of the species abundances, $f(x)$, in systems with row sum constraints is,

$$\begin{aligned}\sigma_+(c,N,\sigma,\xi)^2 &= \sum_{p=1}^{\infty}\left[\left(cN\sigma^2\right)^p \sum_{q=0}^{p-1}(1-\xi)^{2q}\,\xi^{2(p-q)}\binom{p-1}{q}\right] \\ &= \frac{cN\sigma^2\xi^2}{1-cN\sigma^2\left((1-\xi)^2+\xi^2\right)},\end{aligned} \tag{3.5}$$

which can be seen to reduce to the variance for systems without constraint when $\xi = 1$,

$$\sigma_+(c,N,\sigma)^2 = \sum_{p=1}^{\infty}\left(cN\sigma^2\right)^p = \frac{cN\sigma^2}{1-cN\sigma^2}. \tag{3.6}$$

Our analytical prediction together with simulation averages are shown in figure 3.4.

When increasing the constraint on the row-sums the Extinction Continuum is decreased. Although the first extinction boundary never crosses σ_M, but instead converges to it when $\xi \to 0$. This leads to two types of collapse behaviour in the region of small ξ. The first being when the system collapses before any extinction has occurred, a situation without an Extinction Continuum. The second collapse type displays a rapid (unexpected) plummeting of some species abundances to extinction at σ_M, a short Extinction Continuum and eventual collapse at $\sigma_c \approx 1/\sqrt{c\,n}$.

Discussion

We show examples in paper II of systems with more structure in their interactions, such as predator/prey, for which the Extinction Continuum is seen to remain and the first extinction boundary is almost unchanged. The structure we introduce, in terms of row-sum constraint, has a larger impact because the entries in the expression for the species abundances, stemming from the interaction matrix, can no longer be approximated as independent. We posit such constraint are of a more global character.

The row-sum constraint is a type of global constraint since it requires a balance of a species negative and positive interactions with other species. Other such global constraints are thought to exist in nature, such as energy [61] or allometric [62] constraints. The effects on extinctions and collapse of row-sum constrained systems is maybe extra intriguing because of its resemblance to Damuth's law, stating that species biomass is approximately equal for all species, smaller species making up for there lack of mass by larger numbers [63]. This connection has not been fully explored and is left for future study, but it does point to the ecological plausibility of such global constraint which we have shown have a large impact on a systems dynamical behaviour and approach to collapse.

An additional interesting aspect of the row-sum constraint is that it does not give itself away in the spectrum, in contrast to for example predator/prey structures which stretches the spectrum in the imaginary direction and compresses in the real [14]. This is why it is an interaction structure that affects the first extinction boundary but not σ_M. Systems with a small ξ also have a spectrum that does not change when including species abundances in the Jacobian– except when the standard deviation diverges at σ_M. This is in contrast to un-constrained system where the spectrum is transformed by the abundances, as shown in paper I and 2.2. This means that a sign

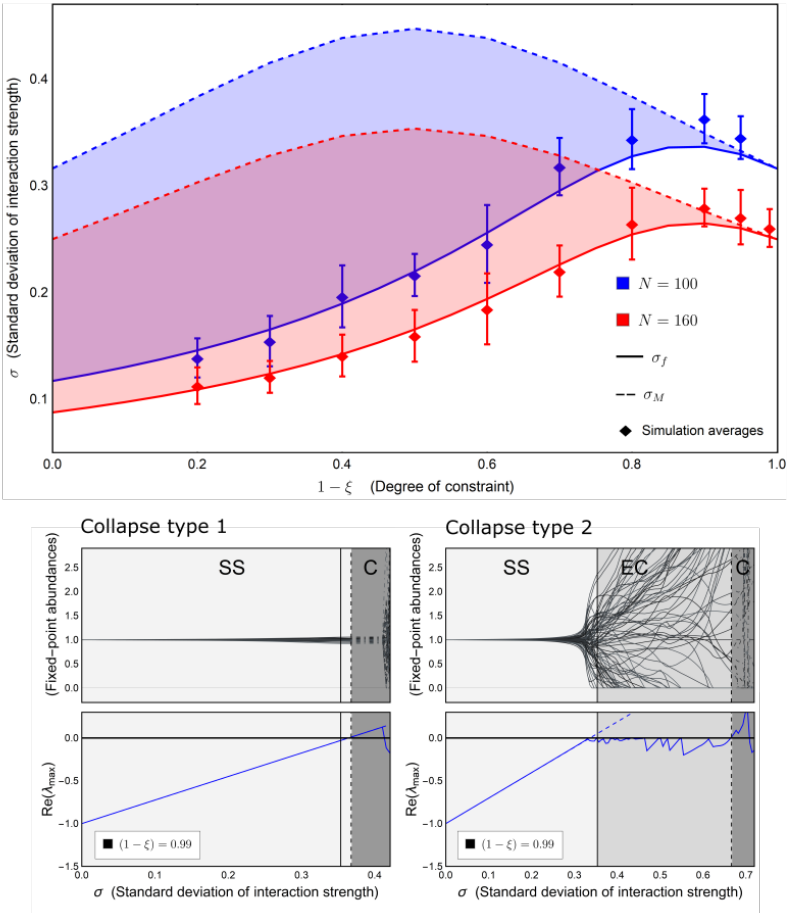


Figure 3.4: Decreasing the Extinction Continuum. The top plot shows averages from simulations of standard deviation of interaction strengths for first extinction σ_f, with one standard deviation errorbars, for increasing row sum constraint $(1-\xi)$. Theoretical predictions of first extinction are shown as full lines and σ_M as striped lines for systems of size $N = 100$ and $N = 160$. The decreasing width for small ξ and convergence to σ_M is clearly seen for both system sizes. The bottom panels show species fixed point abundances (above) and the eigenvalue with smallest negative real part (below) for J (blue line) and J_M (blue striped line) for example simulations of the two collapse types for highly constrained systems ($\xi = 0.01$). The behavioural phases are marked by different shades of grey: Strict Stability (SS) before the first extinction boundary, Extinction Continuum (EC) and, Collapse (C) where no stable nearby fixed-point exists. Note that Collapse type 1 does not have an Extinction Continuum. Collapse type 2 abruptly enters the Extinction Continuum at σ_M and can uphold stability by single species extinctions until eventual collapse.

of system vulnerability to species extinctions demonstrated in [51] as $\mathrm{Re}(\lambda_{max}) \approx \min(x_i)$, no longer holds for systems with global constraints such as the row-sum constraint.

CHAPTER 4

Discussion, conclusions and outlook

In this thesis I present work aimed at expanding the knowledge of ecosystem stability and response behaviours. The choice of model to reach this aim was almost given for our investigation. We observed phenomena when simply implementing a model, that has been extensively used and referenced for over 50 years, which were not visible in studies where it was used. Because May's model has functioned as a reference point of how to think about stability of real ecosystems and their behaviour in response to perturbations, a thorough investigation of the discrepancies we found seemed vital. These discrepancies were also becoming visible in recent studies [51, 53, 54]. In my mind, there is no doubt that all the dynamical stability aspects of this widely used model, in both its original form and in more biologically realistic versions, need to be understood if it is to be used as a model to understand stability of real systems.

The main conclusions of this thesis and contributions to the field of theoretical ecology are

- It shows that a naive implementation of May's stability limit, only including one type of stability, leads to incorrect predictions of ecosystem transition points
- It expands the theoretical repertoire of ecosystem behaviour in response to perturbations, introducing single species extinctions as a stabilising mechanism to avoid collapse and, different types of collapse behaviours.
- It provides a metric of parameter-distance to collapse and, structural stability.
- It shows which interaction structures lead to contraction or elimination of the new phase of resilience and structural instability

by mapping all transition points.

With this thesis more aspects of stability in the GLV model have been elucidated. There are however many issues with the model itself and its explanatory powers. Its simplicity is desirable in its generality of analysis but might give implications that point in the wrong directions. For example allowing for adaptive foraging, so that interactions among species can change have been shown to reverse the stability-complexity relationship [64, 65], or sometimes reverse it depending on timescale or modularity [66]. Another example of reversal is expanding to higher order interactions including multiple species [67]. It is not an easy solvable problem to evaluate which features can be simplified without losing the connection to real systems.

The problem of evaluation lies in the limited capacity to compare against data. Such a comparison is limited in at least two ways, first by the difficulties in measuring the interactions among species [68], especially non-trophic interactions. The intraspecific interactions, which have a large stabilising role in the GLV models, are notoriously hard to observe/measure [69]. The other reason is shared with many complex systems, it is hard to do controlled experiments to validate theory. Although some experiments have been done, including the classic removal experiment [3], which lead to the concept of keystone predator. Another demonstrated the role of interspecific competition [70], although important contributions they are too few and particular for generalisations to be drawn. In addition, very few collapses of ecosystems have been observed since humans started keeping records. One rare example being in the 1993 when the biomass of the Northern Cod fell to 1% of earlier levels. So few recorded collapses is maybe an indication that ecosystems are rather resilient and structurally unstable, since in contrast extinctions are routinely observed.

Thus, it is not an easy task to validate or invalidate many of the theoretical predictions. Despite this, many studies with GLV models do compare to the data available [46, 47, 71]. Another way to "theoretically" increase the belief in these models would be to construct agent-based models to see if the behaviour of the GLV and the Extinction Continuum can be reproduced. This is an avenue worth exploring in the remaining years of my doctoral studies.

Other choices we made in the GLV model, such as only positive intrinsic growth rates (leading to a stable community of independent primary producers when $\sigma = 0$) and revisiting the random structure of an interaction matrix after much effort has been spent since the days of May on understanding structure, is a way of starting again from the basics without being circumscribed by the assumption of feasibility. Once a better understanding has been gained on this basic level, extensions can be done to more realistically structured systems. The next step is to combine more ecologically informed structures based on metabolic theories, hierarchies and clusters in combination with realistically chosen growth rates and global constraints of different kinds.

References

[1] A. G. Tansley (1935). The use and abuse of vegetational concepts and terms. *Ecology* **16** (3), pp. 284–307.

[2] R. T. Paine (1969). A note on trophic complexity and community stability. *The American Naturalist* **103** (929), pp. 91–93.

[3] G. E. Hutchinson (1959). Homage to santa rosalia or why are there so many kinds of animals? *The American Naturalist* **93** (870), pp. 145–159.

[4] C. S. Elton (1958). *The ecology of invasions by animals and plants.* University of Chicago Press. ISBN: 0226206386.

[5] R. MacArthur (1955). Fluctuations of animal populations and a measure of community stability. *ecology* **36** (3), pp. 533–536.

[6] R. H. MacArthur and E. O. Wilson (2001). *The theory of island biogeography.* Vol. 1. Princeton university press. ISBN: 0691088365.

[7] A. J. Lotka (1926). Elements of physical biology. *Science Progress in the Twentieth Century (1919-1933)* **21** (82), pp. 341–343.

[8] V. Volterra (1926). Variations and fluctuations of the number of individuals in animal species living together. *Animal ecology,* pp. 409–448.

[9] R. M. May (1972). Will a large complex system be stable? *Nature* **238** (5364), pp. 413–414.

[10] A.-M. Neutel, J. A. Heesterbeek and P. C. de Ruiter (2002). Stability in real food webs: weak links in long loops. *Science* **296** (5570), pp. 1120–1123.

[11] S. Tang, S. Pawar and S. Allesina (2014). Correlation between interaction strengths drives stability in large ecological networks. *Ecology letters* **17** (9), pp. 1094–1100.

[12] S. Allesina and S. Tang (2012). Stability criteria for complex ecosystems. *Nature* **483** (7388), pp. 205–208.

[13] D. Gravel, F. Massol and M. A. Leibold (2016). Stability and complexity in model meta-ecosystems. *Nature communications* **7**, p. 12457.

[14] S. Allesina and S. Tang (2015). The stability–complexity relationship at age 40: a random matrix perspective. *Population Ecology* **57** (1), pp. 63–75.

[15] S. Sinha and S. Sinha (2005). Evidence of universality for the may-wigner stability theorem for random networks with local dynamics. *Physical Review E* **71** (2), p. 020902.

[16] Y. V. Fyodorov and B. A. Khoruzhenko (2016). Nonlinear analogue of the may wigner instability transition. *Proceedings of the National Academy of Sciences* **113** (25), pp. 6827–6832.

[17] A. Mougi and M. Kondoh (2014). Stability of competition – antagonism – mutualism hybrid community and the role of community network structure. *Journal of theoretical biology* **360**, pp. 54–58.

[18] A.-M. Neutel, J. A. Heesterbeek, J. Van de Koppel, G. Hoenderboom, A. Vos, C. Kaldeway, F. Berendse and P. C. De Ruiter (2007). Reconciling complexity with stability in naturally assembling food webs. *Nature* **449** (7162), pp. 599–602.

[19] D. A. Kessler and N. M. Shnerb (2015). Generalized model of island biodiversity. *Physical Review E* **91** (4), p. 042705.

[20] A. Roberts (1974). The stability of a feasible random ecosystem. *Nature* **251** (5476), p. 607.

[21] X. Chen and J. E. Cohen (2001). Global stability, local stability and permanence in model food webs. *Journal of Theoretical Biology* **212** (2), pp. 223–235.

[22] T. Gross, L. Rudolf, S. A. Levin and U. Dieckmann (2009). Generalized models reveal stabilizing factors in food webs. *Science* **325** (5941), pp. 747–750.

[23] M. E. Gilpin (1975). Stability of feasible predator-prey systems. *Nature* **254** (5496), p. 137.

[24] S. Johnson, V. Domínguez-García, L. Donetti and M. A. Muñoz (2014). Trophic coherence determines food-web stability. *Proceedings of the National Academy of Sciences* **111** (50), pp. 17923–17928.

[25] C. Jacquet, C. Moritz, L. Morissette, P. Legagneux, F. Massol, P. Archambault and D. Gravel (2016). No complexity–stability relationship in empirical ecosystems. *Nature communications* **7**, p. 12573.

[26] J. A. Dunne, R. J. Williams and N. D. Martinez (2002). Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology letters* **5** (4), pp. 558–567.

[27] S. L. Pimm (1984). The complexity and stability of ecosystems. *Nature* **307** (5949), p. 321.

[28] K. S. McCann (2000). The diversity–stability debate. *Nature* **405** (6783), p. 228.

[29] M. Loreau and C. de Mazancourt (2013). Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology letters* **16**, pp. 106–115.

[30] P. Yodzis (1981). The stability of real ecosystems. *Nature* **289** (5799), p. 674.

[31] A. Farcas and A. G. Rossberg (2016). Maximum sustainable yield from interacting fish stocks in an uncertain world: two policy choices and underlying trade-offs. *ICES Journal of Marine Science* **73** (10), pp. 2499–2508.

[32] D. B. Stouffer and J. Bascompte (2011). Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences* **108** (9), pp. 3648–3652.

[33] K. McCann, A. Hastings and G. R. Huxel (1998). Weak trophic interactions and the balance of nature. *Nature* **395** (6704), p. 794.

[34] U. Brose, R. J. Williams and N. D. Martinez (2006). Allometric scaling enhances stability in complex food webs. *Ecology letters* **9** (11), pp. 1228–1236.

[35] S. B. Otto, B. C. Rall and U. Brose (2007). Allometric degree distributions facilitate food-web stability. *Nature* **450** (7173), p. 1226.

[36] U. Bastolla, M. A. Fortuna, A. Pascual-Garcia, A. Ferrera, B. Luque and J. Bascompte (2009). The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* **458** (7241), p. 1018.

[37] A. James, J. W. Pitchford and M. J. Plank (2012). Disentangling nestedness from models of ecological complexity. *Nature* **487** (7406), p. 227.

[38] J. Grilli, T. Rogers and S. Allesina (2016). Modularity and stability in ecological communities. *Nature communications* **7**, p. 12031.

[39] A. R. Ives and S. R. Carpenter (2007). Stability and diversity of ecosystems. *science* **317** (5834), pp. 58–62.

[40] C. S. Holling (1973). Resilience and stability of ecological systems. *Annual review of ecology and systematics* **4** (1), pp. 1–23.

[41] S. L. Pimm and J. Lawton (1977). Number of trophic levels in ecological communities. *Nature* **268** (5618), pp. 329–331.

[42] G. Kokkoris, A. Troumbis and J. Lawton (1999). Patterns of species interaction strength in assembled theoretical competition communities. *Ecology Letters* **2** (2), pp. 70–74.

[43] D. L. DeAngelis, R. Goldstein and R. O'neill (1975). A model for tropic interaction. *Ecology* **56** (4), pp. 881–892.

[44] R. J. Williams (2008). Effects of network and dynamical model structure on species persistence in large model food webs. *Theoretical Ecology* **1** (3), pp. 141–151.

[45] C. S. Holling (1959). The components of predation as revealed by a study of small-mammal predation of the european pine sawfly. *The Canadian Entomologist* **91** (5), pp. 293–320.

[46] R. P. Rohr, S. Saavedra and J. Bascompte (2014). On the structural stability of mutualistic systems. *Science* **345** (6195), p. 1253497.

[47] J. Grilli, M. Adorisio, S. Suweis, G. Barabás, J. R. Banavar, S. Allesina and A. Maritan (2017). Feasibility and coexistence of large ecological communities. *Nature communications* **8**, p. 0.

[48] E. Wigner (1959). Proceedings of the fourth canadian mathematical congress.

[49] P. Schuster and M. Eigen (1979). *The hypercycle; a principle of natural self-organization.* Springer-Verlag.

[50] T. Gibbs, J. Grilli, T. Rogers and S. Allesina (2017). The effect of population abundances on the stability of large random ecosystems. *arXiv preprint arXiv:1708.08837.*

[51] L. Stone (2018). The feasibility and stability of large complex biological networks: a random matrix approach. *Scientific reports* **8** (1), p. 8246.

[52] S. Saavedra, D. B. Stouffer, B. Uzzi and J. Bascompte (2011). Strong contributors to network persistence are the most vulnerable to extinction. *Nature* **478** (7368), p. 233.

[53] M. Dougoud, L. Vinckenbosch, R. P. Rohr, L.-F. Bersier and C. Mazza (2018). The feasibility of equilibria in large ecosystems: a primary but neglected concept in the complexity-stability debate. *PLoS computational biology* **14** (2), e1005988.

[54] C. A. Serván, J. A. Capitán, J. Grilli, K. E. Morrison and S. Allesina (2018). Coexistence of many species in random ecosystems. *Nature ecology evolution*, p. 1.

[55] G. Bunin (2017). Ecological communities with lotka-volterra dynamics. *Physical Review E* **95** (4), p. 042414.

[56] — (2016). Interaction patterns and diversity in assembled ecological communities. *arXiv preprint arXiv:1607.04734.*

[57] L. Dai, D. Vorselen, K. S. Korolev and J. Gore (2012). Generic indicators for loss of resilience before a tipping point leading to population collapse. *Science* **336** (6085), pp. 1175–1177.

[58] A. J. Veraart, E. J. Faassen, V. Dakos, E. H. van Nes, M. Lürling and M. Scheffer (2012). Recovery rates reflect distance to a tipping point in a living system. *Nature* **481** (7381), p. 357.

[59] M. Scheffer, S. R. Carpenter, T. M. Lenton, J. Bascompte, W. Brock, V. Dakos, J. Van de Koppel, I. A. Van de Leemput, S. A. Levin and E. H. Van Nes (2012). Anticipating critical transitions. *science* **338** (6105), pp. 344–348.

[60] V. Dakos and J. Bascompte (2014). Critical slowing down as early warning for the onset of collapse in mutualistic communit-

ies. *Proceedings of the National Academy of Sciences* **111** (49), pp. 17546–17551.

[61] D. Barneche, M. Kulbicki, S. R. Floeter, A. M. Friedlander and A. Allen (2016). Energetic and ecological constraints on population density of reef fishes. *Proceedings of the Royal Society B: Biological Sciences* **283** (1823), p. 20152186.

[62] K. L. Voje, T. F. Hansen, C. K. Egset, G. H. Bolstad and C. Pélabon (2014). Allometric constraints and the evolution of allometry. *Evolution* **68** (3), pp. 866–885.

[63] J. Damuth (1981). Population density and body size in mammals. *Nature* **290** (5808), pp. 699–700.

[64] M. Kondoh (2003). Foraging adaptation and the relationship between food-web complexity and stability. *Science* **299** (5611), pp. 1388–1391. URL: `http://science.sciencemag.org/content/299/5611/1388.long`.

[65] F. S. Valdovinos, R. Ramos-Jiliberto, L. Garay-Narváez, P. Urbani and J. A. Dunne (2010). Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecology Letters* **13** (12), pp. 1546–1559.

[66] S. Nuwagaba, F. Zhang and C. Hui (2017). Robustness of rigid and adaptive networks to species loss. *PloS one* **12** (12), e0189086.

[67] E. Bairey, E. D. Kelsic and R. Kishony (2016). High-order species interactions shape ecosystem diversity. *Nature communications* **7**, p. 12285.

[68] R. T. Paine (1988). Road maps of interactions or grist for theoretical development? *Ecology* **69** (6), pp. 1648–1654.

[69] G. Barabás, M. J. Michalska-Smith and S. Allesina (2017). Self-regulation and the stability of large ecological networks. *Nature ecology evolution* **1** (12), p. 1870.

[70] J. H. Connell (1961). The influence of interspecific competition and other factors on the distribution of the barnacle chthamalus stellatus. *Ecology* **42** (4), pp. 710–723.

[71] T. Okuyama and J. N. Holland (2008). Network structural properties mediate the stability of mutualistic communities. *Ecology Letters* **11** (3), pp. 208–216.