THESIS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

Stability and complexity of ecosystems

Global interaction constraints, landscape, and extinctions

SUSANNE PETTERSSON

Department of Space, Earth and Environment
Division of Physical Resource Theory
CHALMERS UNIVERSITY OF TECHNOLOGY

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SUSANNE PETTERSSON

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Department of Space, Earth and Environment
Division of Physical Resource Theory
Chalmers University of Technology
SE-412 96 Göteborg
Sweden
Telephone: +46 (0)31-772 1000

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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 fortuitous fluctuations as well as migration, climate, and evolution, in a human time-frame ecosystems are relatively stable. Stability of an ecosystem can refer to many different aspects but in general denotes an ability to uphold 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 and specifically General Lotka-Volterra equations 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 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. Further, these stability aspects are found to hold when spatial extension is modelled explicitly. With spatial extension homogeneous landscapes are shown to enhance robustness by a larger spectrum of dynamics and in the limit of high dispersal heterogeneous landscapes can facilitate much higher complexity. 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 local and global features of ecosystems which determine response behaviour and stabilising dynamics to a high degree, important when analysing systems and assessing their vulnerability in face of environmental pressures.

Keywords: Ecosystems, Complexity, Stability, Extinctions, Collapse, Dynamical systems, Population dynamics, spatial heterogeneity, dispersal

APPENDED PUBLICATIONS

This thesis is based upon the following papers:

Paper A S. Pettersson, V. M. Savage, and M. Nilsson Jacobi (2020). Predicting collapse of complex ecological systems: quantifying the stability–complexity continuum. *Journal of the Royal Society Interface* **17** (166), p. 20190391.

Paper B S. Pettersson, V. M. Savage, and M. N. Jacobi (2020). Stability of ecosystems enhanced by species-interaction constraints. *Physical Review E* **102** (6), p. 062405.

Paper C S. Pettersson and M. Nilsson Jacobi (2021). Spatial heterogeneity enhance robustness of large multi-species ecosystems. *PLoS computational biology* **17** (10), e1008899.

Paper D A. Vikrant, S. Pettersson, and M. Nilsson Jacobi (2022). Spatial coherence and the persistence of high diversity in spatially heterogeneous landscapes. *Ecology and Evolution* **12** (6), e9004.

Author contributions

Paper A: MNJ conceived the idea. SP performed simulations and wrote original draft. MNJ and SP produced analytic results. MNJ, SP and VMS interpreted the results and worked on paper.

Paper B: MNJ and SP conceived the idea. SP performed simulations and wrote original draft. MNJ and SP produced analytic results. MNJ, SP and VMS interpreted the results and worked on paper.

Paper C: SP and MNJ conceived the idea. SP performed simulations and wrote original draft. MNJ and SP interpreted the results and worked on paper.

Paper D: SP and AV conceived the idea, contributed equally to simulation, analysis and original draft. SP produced analytical results. MNJ, AV, and SP interpreted results and worked on paper.

To the ether

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Contents

Abstract **i**

Appended publications **iii**

Acknowledgements **vii**

1 Introduction **1**
1.1 Motivation, aim and contribution 3
1.2 Disposition of thesis 4

2 Background **5**
2.1 Stability 5
2.2 Dynamical models 6
2.3 Networks and topology 10
2.4 May's framework 12
2.5 Spatial extension and dispersal 14

3 Present work **17**
3.1 Paper A 18
3.2 Paper B 24
3.3 Paper C 27
3.4 Paper D 33

4 Discussion, conclusions and outlook **39**

References **45**

Paper A **55**

Paper B **83**

Paper C **93**

Paper D **111**

CHAPTER 1

Introduction

The world of living organisms, their interrelations, rhythms and harmonies have interested humans since time immemorial. We have sought to learn of our natural surroundings both to 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 sustains itself and acts under changing circumstances as important goals. Important that is, if we wish to keep natures harmonies while continuing to utilise 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 biodiversity, and specifically their conditions and mechanisms. The early paradigm view was that complex ecosystems 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. Alfred J. Lotka and Vito 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 random matrix theory [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 [10]. 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.

One of the blatant departures 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 in fact observe highly diverse stable ecosystems we might speculate that a key to stability is the structure of interactions lacking in May's model. Thus comparing specific structures of interaction to the random model has been a fruitful way to test their stabilising effects [11, 12]. Many features conducive to ecosystems stability have been found by such comparisons, examples include trophic structures [13], compartmentalisation [14], large number of weak interactions [15], and allometric species properties [16, 17]. Some features are contested such as nestedness sometimes shown to be stabilising [18], sometimes not [19]. In other studies features are shown to be either stabilising or destabilising depending on parameter choices [20]. However, despite the stabilising effects of such features, complexity as destabilising rather than stabilising in most cases still remain.

Another rather blatant departure from real ecosystems present in May's model but also in the dynamical models including more realistic species interaction structures and functions, is the lack of space. Ecosystem features such as species interaction strengths and abundances are thought of as averages of an ecosystem spread out in space, with the assumption that intrinsic differences in such features are not operative for system behaviour.

In contrast to this assumption meta-community studies modelling a species community as local populations connected by dispersal, have found asynchronous species abundances within the system to prevent extinctions [21]. The local populations act as buffers. With the same reasoning, high dispersal leading to synchronisation of local populations have been found to increase the risk of extinction [22]. Although such studies include either single or few species they do highlight a possible stabilising effect unaccounted for in ecosystem models without spatial dimension.

An active research area is now combining the insights from these two strands of modelling and filling the gap between high diversity spaceless models and low diversity spatial models. We now know that intermediate dispersal rates promotes higher diversity, mirroring its conduciveness to prevent extinctions in single species models [23, 24]. It has also been found that chaotic dynamics supported only in spatial extension can allow an ecosystem as a whole to have higher complexity than predicted possible by May [23].

1.1 Motivation, aim and contribution

With humanities increasing ability and propensity to utilise and affect the worlds ecosystems the instrumental value of knowledge of ecosystem functioning is increasing. In order to for example manage our fishing without depleting the stocks [25] or make informed judgements on boundaries of nature reserves [26], and an abundance of other issues, knowledge of functioning, response behaviours, transition points, and conditions for stability and biodiversity of ecosystems is desirable. On top of this enormous instrumental value tough, I believe gaining knowledge of the conditions and ways of our fellow life has intrinsic value. It is simply fascinating to know about the world around.

May's paper has been hugely influential in the field of theoretical ecology. Since it's conception to this day May's work has functioned as a reference point either expanding the model [26–30] comparing against it [31–34], confirming its conclusions [35–37], refuting them [38–40], discussing it [41–43], or highlighting it's shortcomings as a model for real ecosystems [13]. But May's framework used a specific way of defining stability. In reality there are multitude of ways an ecosystem can be said to be stable, some stability concepts enhancing, some decreasing for the same ecosystem features [44].

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.

The issue of stability concepts is raised in Papers A and B, where we show

that including several stability concepts in the analysis of May's model leads to a new mechanism of stability and consequences for ecosystem behaviour and diversity. Specifically, in paper A we find that single species extinctions always occur at lower complexities than May predicted which introduces an additional phase of novel ecosystem response behaviour. Paper B in addition locates global species interaction structures with a large effect on the new phase of single species extinctions. In Paper C and D we extend the model to space and bring the insights from Paper A and B to a spatial setting. We investigate homogeneous space in paper C which is found to widen the response behaviour of an ecosystem leading to additional ways to stay stable. In paper D we have heterogeneous space with high dispersal of species making it possible for an ecosystem to sustain both higher local and global complexity.

1.2 Disposition of thesis

The thesis consists of three content chapters and four 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 four 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 future research.

CHAPTER 2

Background

In this chapter I present concepts, definitions and dynamical models used in my research, starting with the most common stability concepts in section 2.1. In section 2.2 I introduce dynamical models of ecosystems and technical definitions of the stability concepts from section 2.1. In section 2.3 I present the interactions of ecosystem represented as matrices and the representation of interaction structures. Section 2.4 is dedicated to May's framework and it's relation to the research field of theoretical ecology. In the final section 2.5 I show how we introduce spatial dimensions and dispersal in the model.

2.1 Stability

The complexity of ecosystems makes the concept of stability an impossible phenomena to capture in a single definition. All would agree that an ecosystem returning to the same state after a disturbance is stable, likewise a devastating loss of all species after a disturbance would render it unstable. But there are countless ways a complex system can react between these two extremes. For example, would an ecosystem that recovers from a disturbance such as 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 abundances but after several years? Or, all species returning to almost the same abundances while one goes extinct? All such different ecosystem responses and behaviours have led to a multitude of stability classifications such as resilient and robust. Although, even with stability broken down in this way what is regarded as stable is not always apparent. In the examples above, the two first scenarios are generally said to be stable, 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.

Out of the many stability concepts the most commonly used are robustness, resilience, invasibility and variability. Robustness is the ability of a

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.

system to uphold characteristic features of interest when perturbed or pressured. Because of the unspecific definition robustness can be measured in different ways, one example is a system's propensity for cascading secondary extinctions after a species removal [40]. Resilience is the ability of a system to return to the same state after a perturbation [45], sometimes including the time of return [46]. An ecosystem is termed invasible if it is susceptible to successful establishment of foreign species [47] and variability is a measure of fluctuations in species abundances [41]. 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, whether it be oscillating dynamics or fixed abundances, and fluctuations around it. In this thesis an ecosystem state will refer to such an equilibrium state.

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

$$\frac{d\,x_i}{d\,t} = R_i(x_i) + \sum_{j=1}^{N} G_{ij}(x_i, ..., x_N), \tag{2.1}$$

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 interac-

tions) with differing functions for when a species acts as prey or predator [48, 49]. 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 [50]. 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

$$\frac{d\,x_i}{d\,t} = x_i\,f_i(x) \tag{2.2}$$

where $\boldsymbol{f} = \boldsymbol{r} + A\boldsymbol{x}$. 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 predators not being able to reap the benefits 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

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

where the diagonal of A 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 oscillating species abundances), chaotic dynamics and fixed-points where the species abundances do not change over time. The focus for larger systems has for the most part been on the stability of fixed points, because of the connection to May´s stability analysis discussed in section 2.4 and for analytical tractability.

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

are

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

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 (since the linear systems of non-extinct species have unique solutions). These fixed points can be either stable or unstable. A natural assumption often made when the system is interpreted as an ecosystem is that all species are extant (non-extinct) $x_i > 0$ for all i. Such a fixed point is called feasible. Regions of feasibility have now been rigorously mapped [51–53] and in paper I we will show that dropping the assumption of feasibility changes the behaviour of the ecosystem, radically transforming the stability analysis.

All papers in this thesis makes use of 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, $J_{ij} = \frac{\frac{dx_i}{dt}}{dx_j}$. The Jacobian for the system in 3.1 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. If the return time is not measured but rather the ability to return is thought of as resilient, a stable fixed-point is a resilient state.

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 [51, 54]. 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 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 [51] the size of a region without extinction in the space of intrinsic growth rates $\boldsymbol{r}$ is used to measure structural stability. In papers A, B and C, but specifically in paper A we define structural stability in terms of an interaction strength parameter, but also generalise the findings to structural parameters in general.

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 A and B.

2.2.3 Persistence

The third stability concept we use is persistence. Persistence is measured as the fraction of extant 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 extant. 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 has a large influence on the stability of a system modelled as a dynamical system. The interaction network is represented by the matrix A in equation 3.1. Each species in the ecosystem has a row in A and the columns are the possible interaction partners (usually all species, 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 effect on one but none on the other (ammensalism), or positive effect on one but none on the other (commensalism). The effect 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 [13]. 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 [20]. A typical feature in pollination networks is nestedness [18], 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.

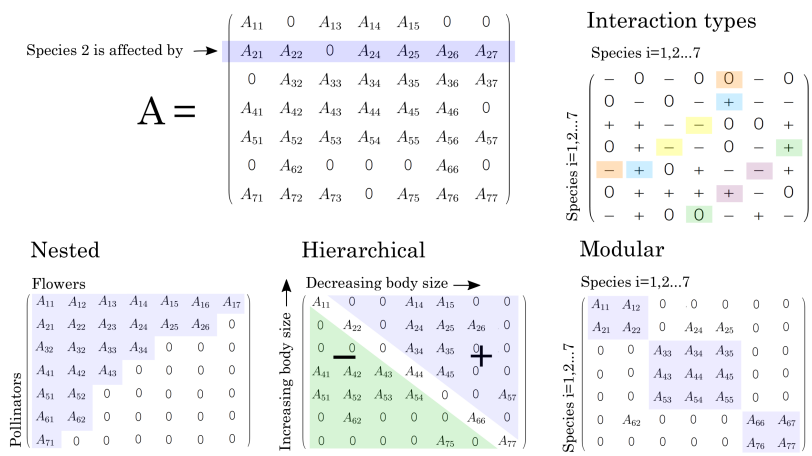

Figure 2.1: Matrix representations of interaction networks of species. The top right panel displays the sign structure of the five different interaction types mutualism (blue), competitive (yellow), predator/prey (purple), ammensalism (pink) and, commensalism (green). Bottom matrices are visualised with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

2.4 May's framework

The contributions of papers A and B mean to elucidate and reevaluate 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 (mainly for paper A and B) and the influence of May's paper on the field of theoretical ecology can be seen in figure 2.3.

May's 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 with mean zero. This is ingenious since the spectrum (all eigenvalues) of a random matrix is known from random matrix theory [9]. 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 an $N \times N$ 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 highly diverse and 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 [27], 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 extant. 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 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. 3.1, 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 [55], but are in general considered too simple to model species, for example there would be no limiting carrying capacities which would allow for 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 that the real part of the spectrum stays negative. It is quite interesting that such an analysis was not done until rather recently [53, 56]. They found that indeed the stability almost never changes (the risk of instability if J_M is stable decreases exponentially with diversity), even though the spectra of the two Jacobians J_M and J are radically different as seen in figure 2.2. A third approach would be to change perspective and interpret the random matrix A as already including fixed point abundances. Although, inclusion of fixed-point abundances generally introduces structure. Yet another structure not accounted for in a random A.

Why more attention was not given to these points in the debate, with their possibility to undermine the 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 extant (also assumed in [56]). This gap has now been filled [51–53] and is the issue investigated from different angles in papers A and B. Insights from these papers then build the basic framework for papers C and D.

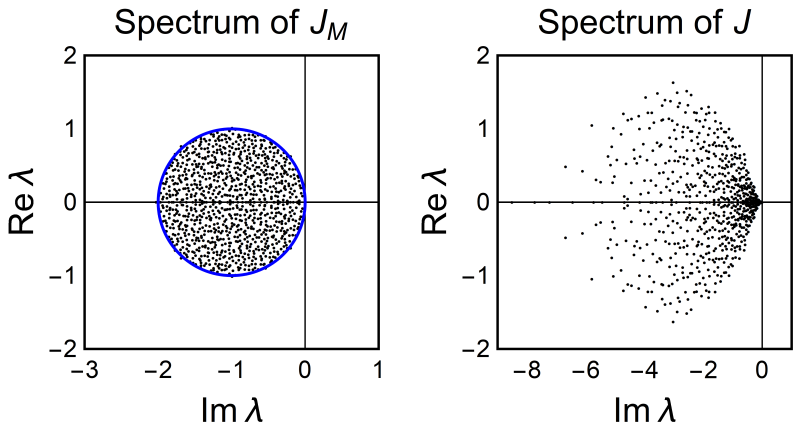

Figure 2.2: The difference between the two spectra of J (including species abundances) and J_M (excluding species abundances) at May's stability boundary σ_M is clearly visible. Note though, that all the real parts of the eigenvalues are negative for both spectra.

2.5 Spatial extension and dispersal

A crucial assumption in modelling an ecosystem as a dynamical system described by the GLV equations regardless of interaction matrix topology and feasibility, is the lack of heterogeneity within the system. All ecosystems have spatial extension making local heterogeneity possible in for example abiotic conditions, which can lead to differences in local interaction and/or abundances. The interaction strengths in the interaction matrix in the GLV as well as the resulting abundances are usually interpreted as averages of a spatially extended ecosystem.

A way of taking head to internal heterogeneity is extending the GLV model by adding spatial dimensions and diffusion. Diffusion in such a model is then meant to model dispersal and migration of species within the system. The most general form of the GLV equations extended to continuous flat space with diffusion are

$$\begin{aligned}\frac{\partial x_i(\mathbf{v},t)}{\partial t} &= r_i(\mathbf{v})x_i(\mathbf{v},t)\left(1-\frac{x_i(\mathbf{v},t)}{K_i(\mathbf{v})}\right)\\ &\quad + x_i(\mathbf{v},t)\sum_{j=1}^{N}A_{ij}(\mathbf{v})x_j(\mathbf{v},t)\\ &\quad + \sum_{p=1}^{d}\sum_{q=1}^{d}\frac{\partial}{\partial v_p}\left[D_{i,pq}(x_i,\mathbf{v})\frac{\partial x_i(\mathbf{v},t)}{\partial v_q}\right],\end{aligned} \tag{2.9}$$

where the species abundances $x_i(\mathbf{v}, t)$, now depend on both time and space, $\mathbf{v}$. Intrinsic growth rates, carrying capacities and interaction matrix are $r_i(\mathbf{v})$, $K_i(\mathbf{v})$ and $A_{ij}(\mathbf{v})$ for species i respectively as in the regular GLV model but also dependent on space. $D_{i,pq}(x_i, \mathbf{v})$ is the diffusion rate which can vary between species and is a function of species abundances and spatial location. The number of spatial dimensions is d.

The model in Eq. 2.9 is general and most studies simplify it in different ways, for example assuming constant diffusion rates in space and independence of abundances $D_{i,pq}(x_i, \mathbf{v}) \longrightarrow D_i$ and using discrete space instead of continuous. In a discrete space setting the system has patches/sites with diffusion in between. The species abundances are then averages for each patch, but can differ between patches. There are many ways to discretise the Laplace operator, $\frac{\partial^2}{\partial v_p v_q}$, which is diffusion with constant diffusion rates. One way is shown below for one and two spatial dimensions, $(d = 1, 2)$

$$\begin{aligned} \frac{\partial^2 x_i(\mathbf{v}, t)}{\partial v_p \partial v_q} &\approx \frac{x_{i,\alpha+1\beta} + x_{i,\alpha-1\beta} + x_{i,\alpha\beta+1} + x_{i,\alpha\beta-1} - 4x_{i,\alpha\beta}}{h^2} \\ \frac{\partial^2 x_i(\mathbf{v}, t)}{\partial v^2} &\approx \frac{x_{i,\alpha+1} + x_{i,\alpha-1} - 2x_{i,\alpha}}{h}, \end{aligned} \tag{2.10}$$

where h is the distance between patches. With the above mentioned simplifications Eq.2.9 in two dimensions simplifies to

$$\begin{aligned} \frac{\partial x_{i,\alpha\beta}}{\partial t} = r_{i,\alpha\beta} x_{i,\alpha\beta} \left(1 - \frac{x_{i,\alpha\beta}}{K_{i,\alpha\beta}}\right) + x_{i,\alpha\beta} \sum_{j=1}^{N} A_{ij,\alpha\beta} x_{j,\alpha\beta} \\ + D_i \big(x_{i,\alpha+1\beta} + x_{i,\alpha-1\beta} + x_{i,\alpha\beta+1} \\ + x_{i,\alpha\beta-1} - 4x_{i,\alpha\beta}\big)/h^2, \end{aligned} \tag{2.11}$$

where α and β are indices for the spatial dimensions.

By varying the parameters of the model in Eq.2.11 it can represent a variety of different natural settings. For example low diffusion rates but constant r_i, K_i, and A_{ij} is a homogeneous ecosystem with local communities with limited exchange. This scenario is used in paper C to investigate stability aspects when allowing abundances to differ within a system. With high diffusion rates but different interaction matrices for different spatial locations we can simulate a well connected ecosystem including different types of habitats, this scenario is used in paper D.

Diffusion is of course not the only way of modelling dispersal and migration. Drift is another way which can account for asymmetric movement [57].

Stability Concept	Dynamics: Other functions (ex. Holling type II)	Dynamics: Extended GLV	Dynamics: GLV					Topology
Type of interaction								
Only equilibrium		AE:[30]				Paper A [53],[59] C:[34] A:[37],[56],[61]	Paper B A:[20]	
Local stability	[48] A:[36] [18] [54]	A:[52] C:[33]	Paper C Paper D R:[86] AE:[26] C:[32] [11] R:[58],[38] A:[35],[12]	[53] A:[47] assembly	AE:[27] AE:[28]			
Permanence			A:[35]					
Structural stability	R:[83] R:[84] [54]		Paper C		[51]	Paper A C:[31]	Paper B	
Persistence	[14],[17] [49] R:[16],[84] [18] [19] [54] [58]		Paper C Paper D AE:[29] [13] A:[88]			Paper A C:[31]	Paper B	
Feasibility	[54]	A:[52]	Paper C Paper D R:[86]	[53]	[51]	Paper A [53],[59] A:[34],[37],[60] [61]	Paper B	R:[40]
Ext.Cascade	[85] R:[84]							
Return time			[46]					
Variability	[15] R:[16]	[43] Paper C						

Food-web | Competitive | Structure | [ ] Discussing May
Mutualism | Random | Mixture or multiple | 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 [10]. 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

In modern science no model or method so far can capture all aspects of systems as complex as ecosystems. To handle such systems instead many different models and simplifications are used. Out of the myriad of results regarding ecosystem behaviour and properties gained in this manner a greater understanding of the full complex system will hopefully emerge. The papers I present in this thesis I hope contributes to this myriad, building our understanding of ecosystem stability, response behaviour and diversity.

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]. Many simplifications are utilised in May's exposition to obtain his stability limit, some previously mentioned such as random structure and the lack of spatial extension. Another more subtle simplification is that stability concepts are lumped together due to the assumption that all species are extant.

The sections on paper A and B in this chapter presents our work outlining response behaviours, stability limits and measures when the assumption of feasibility is relaxed and the three stability concepts (local stability, structural stability and persistence) are separately taken into account. In paper A this is done with the basic interaction structures known in the literature. In paper B with structures we hypothesise to be conducive to structural stability.

Our work in paper C and D presented in the following sections uses the findings from the previous papers as background knowledge while expanding the model with spatial dimensions and diffusion. In paper C we use a homogeneous landscape with varying diffusion rates while in paper D the landscape is heterogeneous and the diffusion is high.

3.1 Paper A

Motivation

In preliminary investigations of the GLV model we found that the assumption of all species to be extant 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 [14, 58], since persistence is based on extinctions and measures the fraction of extant 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 [32] and expanding the limit to cover more cases [27], 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 [52, 53, 59, 60].

Research questions and method

The research questions in paper A are, what types of behaviours can a system exhibit in response to external perturbations 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

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

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.

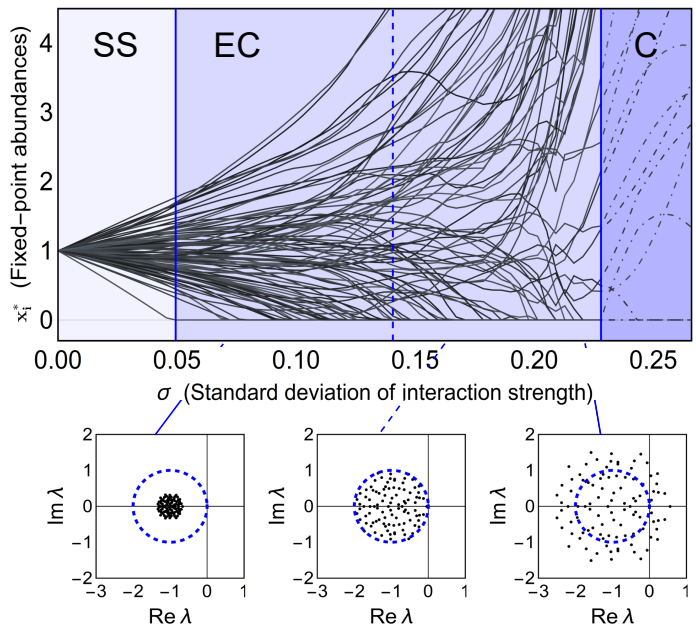

Figure 3.1: Effects on stability of increasing interaction strength in a complex system. Example simulation of a system with initial number of species, $N = 100$, connectance (fraction of realised species interactions), $c = 0.5$, $r_i = K_i = 1$, and $\mu = 0$ for the mean of the distribution of inter-specific 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 extant, $x_i^* > 0$. 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.

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 treat the species abundances as stochastic variables, X_i, and find and use their probability density function, $f_X(x)$, and cumulative distribution function, $F_X(x)$. With $f(x)$, $F(x)$ and order statistics (supplementary material paper A) we obtain the distribution of the minimum of the set of abundances,

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

where the standard deviation and mean of $f_X(x)$ are found to be $\sigma_+ = \sigma\sqrt{cN(1-(1-c)\mu^2)}$ and $\mu_+ = cN\mu$ 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 extant species) and combining it with May's boundary for the 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.

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 species 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.

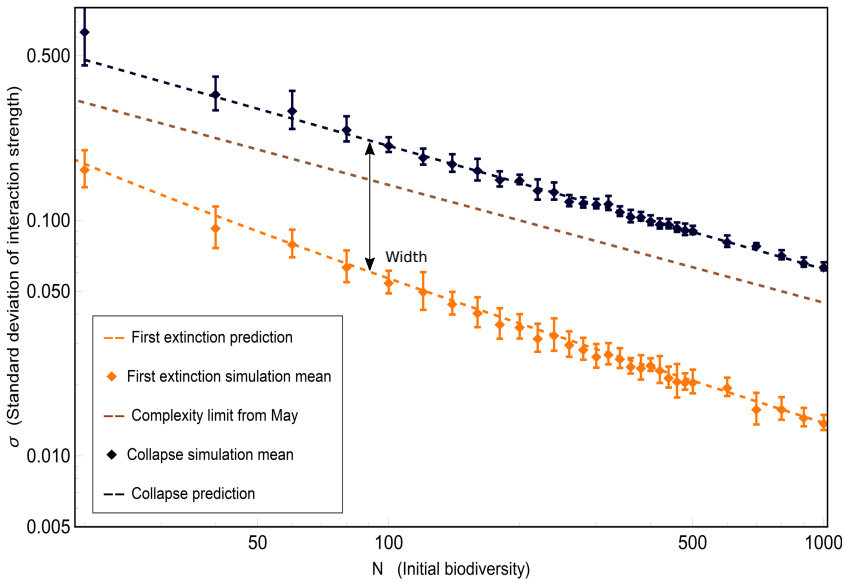

Figure 3.2: Stability predictions for complex systems. In the parameter-space of the standard deviation of interaction strength, there are three phases of behaviour: Strict Stability (SS), Extinction Continuum (EC), and Collapse (C). Here we demonstrate that these phases hold across a large range of 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.

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 [61]. 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 previ-

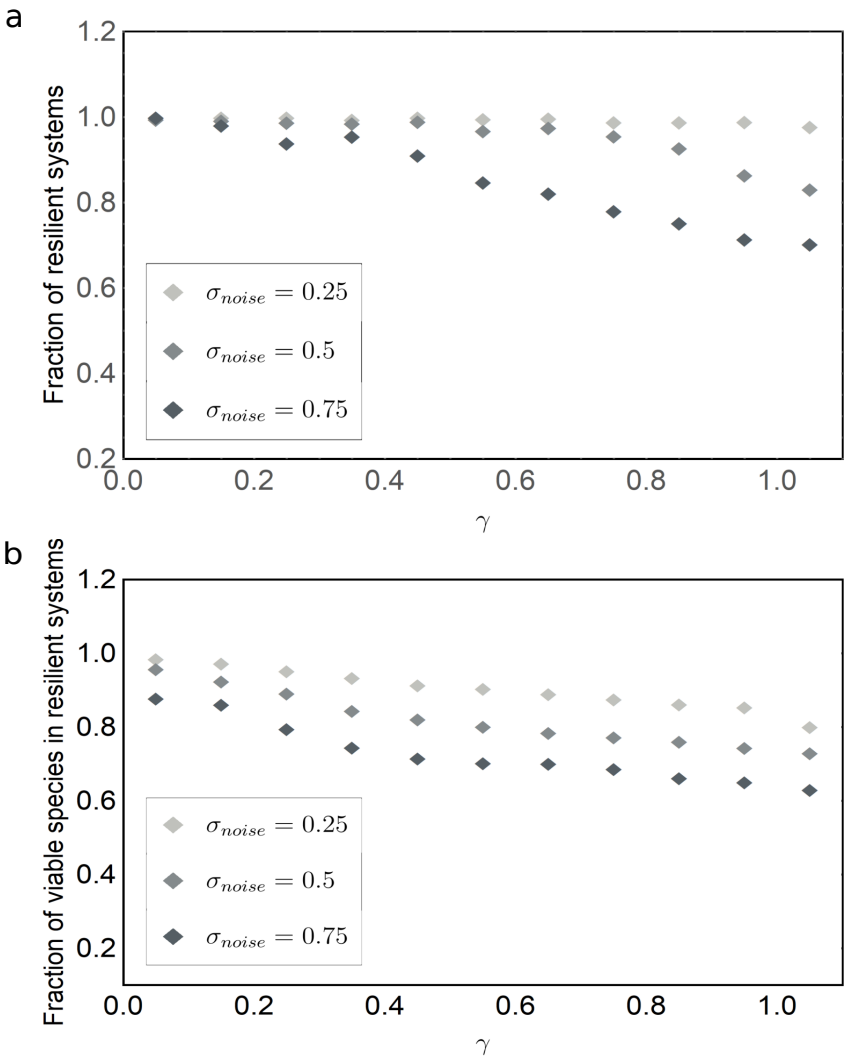

Figure 3.3: Predicting collapse. The plot shows in the top panel the fraction of systems for a certain γ that found a locally stable fixed point after perturbations. The systems with varying γ values were generated from random systems with $N = 70$ and $N = 100$, connectance $c = 0.5$, intrinsic growth 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 extant 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.

ous 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 [62–64], 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 [65]. 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 x_i^*, $g_i^* = \sum_{j=1}^{N} \alpha_{ij} x_j^*$, with g_i^* for example representing a vector of functional traits and α_{ij} a transition matrix). 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 B

Motivation, research questions and method

The stabilising mechanism found in paper A in terms of single species extinctions, was also found to apply to systems with additional biological structure found in the literature, such as predator-prey. 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 B: Are there ecologically relevant interaction structures that significantly change the size or eliminate the Extinction Continuum? We continue in the same framework as paper A, using the GLV dynamical model in Eq. 3.1 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, since the abundances are partly 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 A to an exact expression for the variance (σ_+^2) of the distribution of the species abundances, the stability 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

exact expression for the variance derived in paper B is

$$\sigma_+(c,N,\sigma)^2 = \sum_{p=1}^{\infty}\left(cN\sigma^2\right)^p = \frac{cN\sigma^2}{1-cN\sigma^2}, \tag{3.5}$$

whereas in paper A the first order approximation $\sigma_+(c,N,\sigma)^2 = cN\sigma^2$ was used. The extended expression for the variance in systems with row sum constraints we found to be,

$$\begin{aligned}\sigma_+(c,N,\sigma,\xi)^2 &= \sum_{p=1}^{\infty}\left[\left(cN\sigma^2\right)^p \sum_{q=0}^{p-1}\binom{p-1}{q}(1-\xi)^{2q}\,\xi^{2(p-q)}\right] \\ &= \frac{cN\sigma^2\xi^2}{1-cN\sigma^2\left((1-\xi)^2+\xi^2\right)},\end{aligned} \tag{3.6}$$

which can be seen to reduce to the variance for systems without constraint (Eq. 3.5) when $\xi = 1$. 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 and intense Extinction Continuum and eventual collapse at $\sigma_c \approx 1/\sqrt{cn}$.

Discussion

We show examples in paper B 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. It is a constraint 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 [66] or allometric [67] 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 energy consumption is

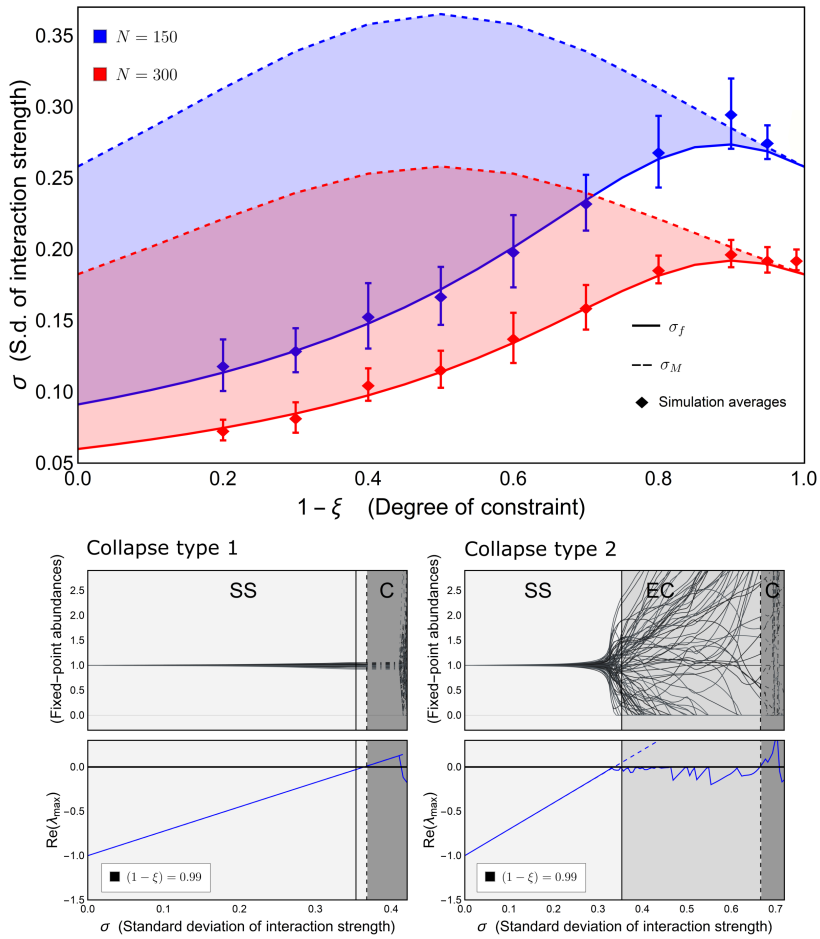

Figure 3.4: Decreasing the Extinction Continuum. The top plot shows averages from simulations of standard deviation of interaction strengths for first extinction σ_f, with one standard deviation errorbars, for increasing row sum constraint $(1-\xi)$. Theoretical predictions of first extinction are shown 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.

approximately equal for all species, smaller species making up for their smaller energy consumption/individual by larger numbers [68]. This connection has not been fully explored (interpreting x_i as energy use) and is left for future study, but it does point to the ecological plausibility of such global constraint which we have shown to 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 [28]. 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 A and 2.2. This means that a sign of system vulnerability to species extinctions demonstrated in [53] as $\mathrm{Re}(\lambda_{max}) \approx \min(x_i)$, no longer holds for systems with global constraints such as the row-sum constraint.

3.3 Paper C

Motivation

One of the more dramatic simplifications of the GLV model is the exclusion of spatial extension. Spatial extension is of course always present in real ecosystems and allow for differentiation in both abiotic factors and populations within an ecosystem. The usual interpretation of parameters such as interaction strengths, intrinsic growth rates, carrying capacities and abundances of species in the GLV model are that they are averages of a spatially extended ecosystem. The assumption is then that fluctuations or differences within a system in these parameters do not qualitatively affect stability aspects of the system. This is a large assumption. It has long been known for example that the stability of a meta-community is greatly enhanced when abundances in local populations are not synchronised [21, 22]. This because a local decline or extinction in a population can be reversed with the help of migration/dispersal from other local populations where the abundance is higher.

Meta-community studies are primary examples where local differences in abundances have a large role to play and stability evaluation would be significantly altered if average abundances are used. Meta-community studies have mostly been performed on single or few species communities [21,

22, 69, 70] but they point to a mechanism that most likely has an impact in high diversity ecosystems. With all the knowledge gained from spatially unresolved systems, an investigation into the stability aspects of high diversity ecosystems with spatial extension relating to those results therefore seems vital.

In the realm of high diversity spatially extended ecosystems it has been noted in recent studies that chaotic dynamics can be sustained over long periods of time promoting higher diversity [23, 24]. Mechanism for this were found both to be the buffering effect of local populations as with the meta-communities and the impact of different habitats within the ecosystem where some act as sources of higher diversity for the entire system. Chaotic dynamics is one piece of the puzzle, remaining to be investigated are the effects of spatial extension on robustness, resilience, stability limits, and biodiversity with other types of dynamics.

Research question and method

The research questions for paper C were: How does spatial extension affect robustness, diversity, and stability limits of an ecosystem in a homogeneous landscape connected by dispersal compared to spatially unresolved models? How does the rate of dispersal affect the same aspects? Do different dispersal rates for different species affect stability?

To answer these questions we use a spatially extended GLV model with diffusion in discrete space. To look at the bare impact of spatial extension and its effect on stability we investigate a homogeneous landscape, in effect we use the same intrinsic growth rates r_i, carrying capacities K_i for each species, and use the same interaction matrix A_{ij}, in all discrete patches. This means we are still using averages of the whole ecosystem for these parameters. Species abundances and dynamics on the other hand, we allow to vary across the landscape. The equations representing this set-up are

$$\begin{aligned}\frac{\partial x_{i,\alpha\beta}}{\partial t} &= r_i x_{i,\alpha\beta}\left(1-\frac{x_{i,\alpha\beta}}{K_i}\right)+\sigma x_{i,\alpha\beta}\sum_{j=1}^{N}A_{ij}x_{j,\alpha\beta}\\ &\quad + D_i\left(x_{i,\alpha+1\beta}+x_{i,\alpha-1\beta}+x_{i,\alpha\beta+1}\right.\\ &\quad \left.+x_{i,\alpha\beta-1}-4x_{i,\alpha\beta}\right)/h^2,\end{aligned} \tag{3.7}$$

where α and β are indices for the spatial dimensions. The distance between patches was set to one, $h = 1$. The interaction strengths in A_{ij} were non-zero with probability $c = 0.5$ and when non-zero drawn from a normal distribution with mean -0.5 and variance 1. As in paper A and B the interaction strength variance (complexity) is regulated by the parameter σ^2. The diffusion rates D_i for each species were drawn from a uniform distribution with a

mean which we varied from 10^{-5} (low diffusion) to 1 (high diffusion), with standard deviations in the same order of magnitude. Although we varied the diffusion rates between species (within the same magnitude) to simulate different dispersal rates, we kept them constant in space for each species.

We performed a sweep over σ and diffusion rates D_i, while gathering statistics over four system aspects relating to stability, and cataloguing dynamical behaviour. The four aspects were A) number of system patches with oscillating dynamics, B) level of synchronisation between patches if oscillating dynamics, C) amplitude if oscillations, and D) diversity. In contrast to paper A an B we expanded the dynamics to include oscillations in abundances. In these cases we do not look specifically at resilience (local stability), although oscillatory dynamics found had large basins of attraction making the oscillatory "state" resilient, however this was not systematically tested. All fixed-points are locally stable as in paper A and B. With the inclusion of oscillations, focus in Paper C was instead on robustness (structural stability), that is keeping ecosystem properties after perturbations, diversity, and the upholding or not of stability limits.

Results

The repertoire of dynamical behaviour increases dramatically when adding the possibility of different dynamics in patches connected by dispersal. This effect is most dramatic at low and intermediate dispersal rates. Not surprisingly, and as many previous studies have mentioned, at high dispersal the dynamics in the patches synchronise thereby lowering the amount of available dynamics. At low and intermediate dispersal the system can have combinations of different fixed-points, different oscillation patterns, and combinations of fixed-points and oscillations. In addition, the same oscillatory pattern can be phase-shifted and vary in amplitude across space. Spatial extension is also seen to promote oscillatory dynamics at all dispersal rates.

We found the increase in possibilities to be a source of robustness. For example, a perturbation in σ for a spatially unresolved GLV in the Extinction Continuum would lead to extinctions. In a spatially resolved systems local patches might experience extinctions but be in different fixed points, preserving global biodiversity. A prominent feature enhancing robustness and thereby diversity is the ability for the system to experience local oscillations if perturbed instead of switching to a fixed point with lower species richness as in the EC. If such oscillations are out of phase the global system effectively stays in the same state. A state which would have bifurcated into an unstable fixed point in the non-spatial GLV. An example of this is shown in Fig. 3.5. Diversity can likewise be preserved with a switch to synchronised oscillations when the diffusion rate i higher, albeit very high diffusion rates

can synchronise the dynamics to a highly volatile oscillation pattern also found in the non-spatial GLV. The overall increase in robustness is most easily visualised with the four aspects of systems stability mentioned earlier oscillations, synchronisation, amplitude and diversity. These properties are visualised in σ and D parameter-space in Fig. 3.6.

From figure 3.6 we see directly in the diversity diagram that diversity is higher with dispersal across the whole σ span, with a small extra increase at low and medium dispersal rates. Oscillations are present throughout the σ span, albeit more prevalent at large σ. Synchronisation is as expected present at high dispersal rates, making low to intermediate dispersal better at keeping global species abundances in a "fixed-point" state due to asynchronous local oscillations. An additional feature is seen in the amplitude diagram, if there are oscillations not only are systems more likely to oscillate out of phase at low and intermediate dispersal rates, they also have lower amplitudes. This makes such systems more stable in the "variability" stability measure mentioned in table 2.1 in section 2.1. Together these diagrams show the increase in robustness and diversity for spatially extended systems.

The enhanced robustness accompanying oscillations make it possible for a system to cross previous collapse boundary without much change in species abundances. Fig. 3.5 is also an example of this.

Discussion

In paper C we show the change in stability aspects due to spatial extension of an ecosystem in a homogeneous landscape. It is clear that aspects of stability are missed when looking at an average of the species abundances of a spatially extended ecosystem. We find an increase in robustness, higher diversity and the ability to traverse previous collapse boundaries.

In light of the results for spatially resolved systems from paper C one might rightly ask if the insights gained from spatially unresolved systems are now obliterated. Despite the stability differences between them there are properties that still remain. For example even though robustness is enhanced such that a system perturbed can remain in a similar state by local oscillations, if pressured sufficiently single species extinctions will eventually occur. The Extinction Continuum still exists as seen from the diversity diagram in Fig. 3.6. For small σ prior to the first extinction boundary the behaviour of the spatially extended and regular GLV are identical (there exists only a unique fixed point). The effect of spatial extension becomes more pronounced the higher the complexity (larger γ from paper A).

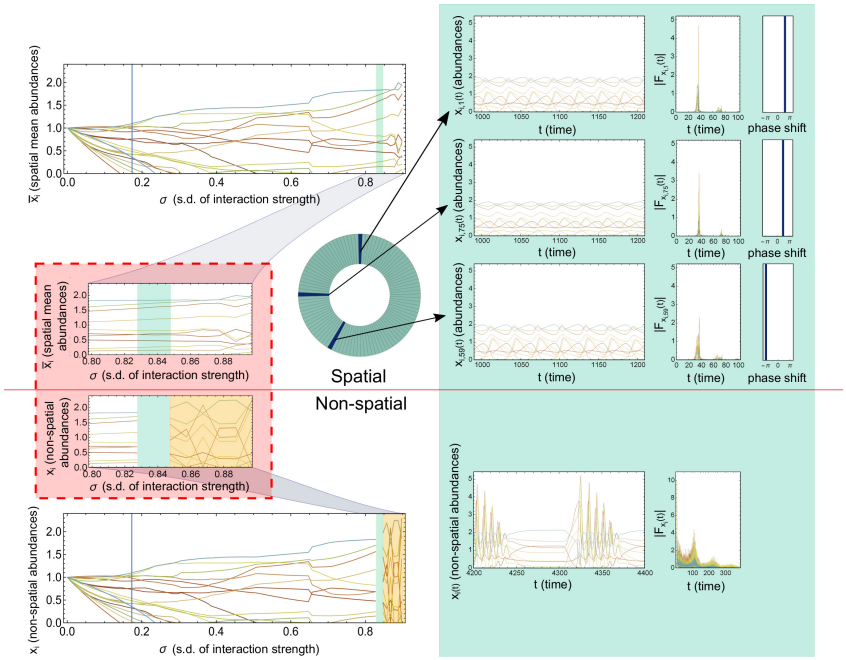

Figure 3.5: Unsynchronised local oscillations stabilise. The figure shows an example of a system of $N = 20$ maximum number of species with out-of-phase oscillations when σ is larger than the feasibility limit and diffusion rates are small ($\mu_D = 10^{-2}$, $\sigma_D = 0.4\mu_D$). On the left side on top we show global average fixed point or oscillation species abundances for a system with small diffusion. On the bottom we show fixed point abundances for a system with the same interaction matrix but with no spatial dimension (non-spatial GLV). Both the global average abundances for the spatial system and the non-spatial are shown for σ ranging from zero to collapse values with an enlargement of the latter part in the red box. The Green shading in the plots indicate a region where the only stable fixed point for the non-spatial GLV is with 3 species going extinct. On the other hand the global average abundances show no change at all (green area in top left plots). With higher σ in the orange region of the non-spatial GLV (bottom left plot) the system is seen to be structurally unstable, while the spatial system on top shows little if any structural instability. These systems behave almost the same with and without a connected space until σ is large enough approaching collapse values. To the right on the green background are shown example dynamics (for σ in the green marked area in the left plots), in different grid-points for the spatial system (top) and for a oscillatory solution for the non-spatial system (bottom). We see in the spatial system oscillatory dynamics in each grid-point example with the same Fourier spectra, but differing phases (the panels to the right). Together the different phases and amplitudes but same frequencies of the local abundance oscillations average to the values corresponding to an unstable fixed point of the non-spatial GLV. For the non-spatial system there is a oscillatory pattern, note however the increase in sharpness in both frequency and amplitude as well as some species going extinct and reappearing, which is not a biologically realistic or stable solution for a ecological system.

The conundrum of natural complex diverse ecosystems that remains regardless of the interaction structure in the interaction network of the non-spatial GLV also remains in the spatially extended GLV in a homogeneous landscape. Although, since spatial extension comes into effect at high complexity, with the addition of spatial habitat heterogeneity or external connectedness spatial extension might still be a resolution to the long held complexity paradox.

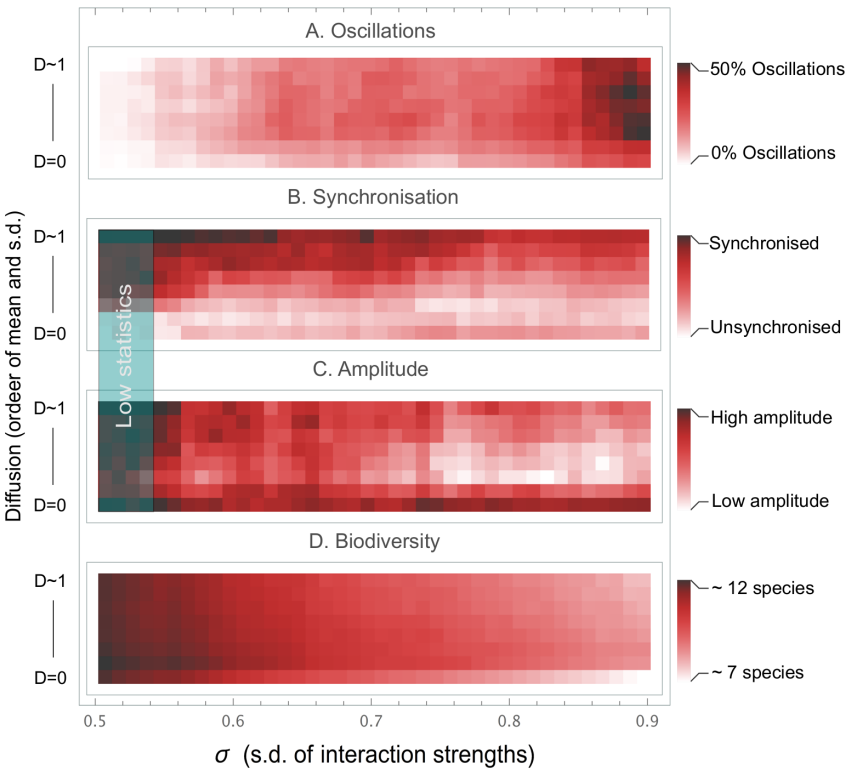

Figure 3.6: Parameter-space Diffusion magnitude vs. s.d. of interaction strength. The figure shows statistics for 70 systems in diffusion magnitude vs. standard deviation parameter-space for panel A) Number of grid-points with oscillatory patterns, panel B) Average maximum phase shift for a species between grid-points if oscillations (degree of synchronisation), panel C) Average amplitude if oscillations, and panel D) Average diversity (n). The lowest diffusion in the diagrams is zero, corresponding to completely disconnected space (non-spatial GLV) and the largest $D_i \sim 1$ ($\mu_D = 1, \sigma_D = b\mu_D, 0.3 < b < 0.4$). Worthy of noting is the lower degree of oscillations and the lower diversity in the non-spatial systems. It is also clear that oscillations are present in almost the entire non-feasible region.

3.4 Paper D

Motivation

From paper C and other similar studies using GLV with diffusion we find that the possibility of internal dynamical and abundance heterogeneity has a positive effect on many aspects of stability and diversity [24]. Expanding spatial heterogeneity to include heterogeneity in habitat types (affecting species interactions) within an ecosystem is another property purported to influence diversity. According to the Area Heterogeneity Trade-Off (AHTO), for a given area spatial heterogeneity has a positive influence on diversity except for very high heterogeneity which correspond to very small areas per habitat. In contrast to this hypothesis however, an empirical study show a positive influence on diversity also for the highest levels of heterogeneity [71]. Other GLV studies including spatial heterogeneity in interactions have found, an increase in diversity for chaotic dynamics at intermediate diffusion rates [23], and in the context of stability of communities indicate that high dispersal can shift May's complexity limit (assuming feasibility) to higher complexities [26]. However, the link between dispersal effects in heterogeneous landscapes and species richness/diversity remains unexplored.

Intermediate diffusion has been shown to promote stability and diversity in a number of studies [21, 72], while high diffusion despite it's positive shift of May's limit, leads to synchronisation (coherence) of species abundances across the ecosystem which has been thought of as detrimental for diversity because of a higher risk of extinctions [22]. The high dispersal limit is therefore much less explored than spatial models with low and intermediate dispersal. Nevertheless, habitat heterogeneity with high dispersal represents a scenario akin to for example tropical lowland forests like the Amazon. For example a recent phylogenetic study suggested that on evolutionary timescales, the entire Amazon basin should be considered as the meta-community for local or regional tree communities [73]. A rigorous investigation of diversity in the high dispersal limit of heterogeneous landscapes is therefore needed.

Research question and method

The main research question of paper D is: what is the relationship between spatial heterogeneity and diversity in landscapes with high dispersal?

The type of spatial heterogeneity we use in paper D is heterogeneity in interaction structures and/or interaction strengths of interspecies interactions. Interaction heterogeneity can be thought of as a consequence of abiotic factors, as for example soil depth or humidity. It is known that interspecies interactions can have highly non-linear dependencies on abiotic factors

such as temperature and humidity [74, 75], they have also been found to better explain biodiversity responses along climate gradients than the abiotic factors themselves [75].

To model spatially heterogeneous landscapes with high dispersal we use the GLV equations on a lattice with diffusion as in equation 2.11, with the difference that we now vary the interaction matrices in space $A_{ij} \to A_{ij,\alpha\beta}$. This gives the following equations

$$\begin{aligned}\frac{\partial x_{i,\alpha\beta}}{\partial t} &= r_i x_{i,\alpha\beta}\left(1-\frac{x_{i,\alpha\beta}}{K_i}\right)+x_{i,\alpha\beta}\sum_{j=1}^{N}A_{ij,\alpha\beta}x_{j,\alpha\beta}\\ &+D\left(x_{i,\alpha+1\beta}+x_{i,\alpha-1\beta}+x_{i,\alpha\beta+1}\right.\\ &\left.+x_{i,\alpha\beta-1}-4x_{i,\alpha\beta}\right)/h^2,\end{aligned} \tag{3.8}$$

where we again set $h = 1$. The diffusion constants are kept equal for all species and across the grid and high enough to ensure coherence (synchronisation) in space. Intrinsic growth rates and carrying capacities are set to one for all species and across space. The interaction matrices are either completely independent, with random matrices at each patch or have the same non-zero elements and with correlated interaction strengths with correlations $\rho \in [0,1]$. We also implemented two types of correlations either all patches had correlated interaction strengths or patches were only correlated with nearest neighbour.

Results

The first result was that a spatially extended system with spatial interaction heterogeneity modelled by Eq. 3.8 can in the high dispersal limit be represented by a regular non-spatial GLV. Regardless of the type or amount of correlation, from completely random interaction matrices between patches to all correlated with $\rho = 0.95$, the non-spatial GLV with an effective interaction matrix (average over all patches, $\bar{A}_{ij} = \sum_{\alpha}^{G}\sum_{\beta}^{G} A_{ij,\alpha\beta}/G$ with G number of patches), captured the entire system's dynamics

$$\frac{dx_i}{dt} = r_i x_i\left(1-\frac{x_i}{K_i}\right)+x_i\sum_{j=1}^{N}\bar{A}_{ij}x_j. \tag{3.9}$$

This creates a bridge between the spatially extended and spatially unresolved systems' properties, valid in the high dispersal limit where dynamics across space is coherent. The interesting part is then the properties of the effective interaction matrix for the system as a whole $\bar{A}_{ij}$. The variance and mean of the effective matrix determines the stability aspects of the ecosystem, in effect whether it resides in the EC or not, or where in the EC (its γ). Important

to note however, is that the effective interaction matrix is only a representation and does not realistically portray the interactions among species in the ecosystem, which are better captured by the local interaction matrices $A_{ij,\alpha\beta}$. This is especially important in ecosystems with high heterogeneity. The variance of the effective interaction matrix for all cases of heterogeneity are found using the formulas in supplementary material paper D. For the case of random interaction matrices with connectance c, variance σ^2, and mean μ in G number of patches we get

$$\begin{aligned} E[\bar{A}_{ij}] &= c\mu \\ &= \bar{\mu} \\ Var[\bar{A}_{ij}] &= \frac{c}{G}(\sigma^2 + \mu^2(1-c)) \\ &= \bar{\sigma}^2. \end{aligned} \tag{3.10}$$

From this we see that in the limit of a large G the variance of the effective matrix effectively goes to zero. This is a quite unrealistic but illustrative example that can harbour infinite local complexity and diversity.

For the case of interaction matrices with connectance c, variance σ^2, mean μ and correlation ρ between all G patches we find

$$\begin{aligned} Var[\bar{A}_{ij\rho}] &= \frac{\sigma^2}{G}\left(1+(G-1)\rho\right) \\ &= \bar{\sigma}^2_{\rho}. \end{aligned} \tag{3.11}$$

With correlations between all patches we find that in the limit of large G the variance instead saturates at $\sigma^2\rho$. How this affects the maximum possible biodiversity for different values of ρ is shown in Fig 3.7.

For the case of nearest neighbour correlated, $\rho_{nn} \in [0,1]$, interaction strengths we get

$$\begin{aligned} Var[\bar{A}_{ij\rho_{nn}}] &= \frac{\sigma^2\left(G + 2\sum_{\eta=1}^{G-1}\rho^{\eta}(G-\eta)\right)}{G^2} \\ &= \bar{\sigma}^2_{\rho_{nn}}. \end{aligned} \tag{3.12}$$

The correlation between neighbours falls off exponentially resulting in a correlation of $\rho_{2nn} = \rho^2_{nn}$ for the next nearest neighbours, $\rho_{3nn} = \rho^3_{nn}$ for the third nearest neighbours and so on. At a certain number of habitats, the variance saturates at a level below the ρ_{nn}, with an effective dynamics that corresponds to the fully correlated case with some correlation ρ. In the limit of a large number of habitats $G \longrightarrow \infty$, we get $\bar{\sigma}_{\rho_{nn}} \xrightarrow{\infty} 0$.

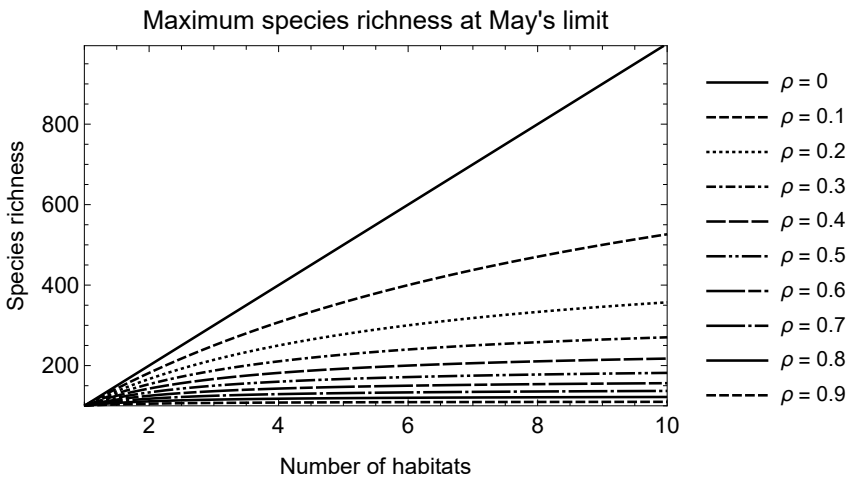

Figure 3.7: Maximum species richness increases with number of habitats and decreasing correlation. For given values of ρ, the plot shows the maximum species richness at May's limit, $\sigma_M = 1/\sqrt{cN}$, as the number of habitats is increased. Starting with a species pool of $N_{init} = 100$ for one habitat, the maximum species richness as habitats increase is $N = N_{init}/\bar{\sigma}^2_\rho$. Thus, the function for maximum species richness in terms of number of habitats, G, is $N = N_{init} G\left(1+(G-1)\rho\right)/\sigma^2$. For all systems with nonzero correlations the maximum species richness will saturate at some level. However, the uncorrelated habitats can harbour indefinitely large species richness as the number of habitats goes to infinity.

In all cases we find that more spatial heterogeneity leads to a smaller variance in the effective interaction matrix which in turn makes the system more stable or allows for a larger diversity. Results from simulations for different values of ρ for interaction matrices with interaction strength means $\mu = 0$ and $\mu = -0.5$ are shown in Fig. 3.8.

Discussion

In paper D we find clear indications of a positive effect of spatial heterogeneity on diversity. The more heterogeneity the higher the diversity the system can sustain. This might seem like a trivial insight for global diversity in a heterogeneous landscape, one can easily imagine different species residing in different areas resulting in low local diversity but high global diversity. Our systems on the other hand are in the high dispersal limit where global and local diversity are equal, meaning high diversity in every part of the system. This maybe able to shed some light on the debate around how forests such

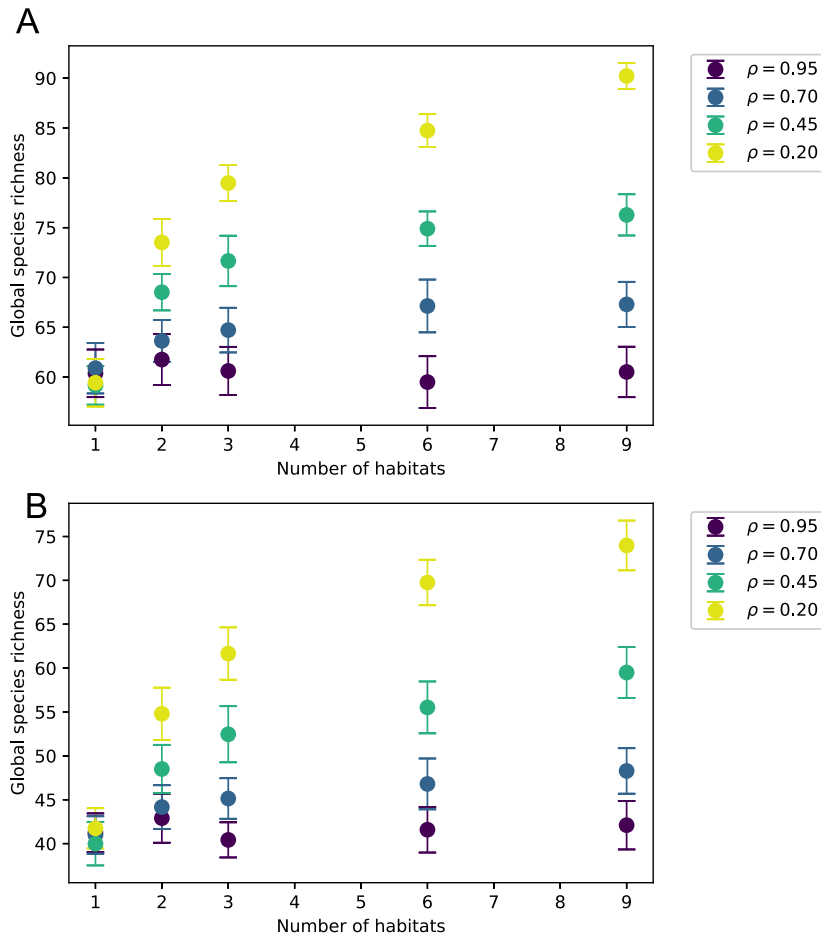

Figure 3.8: Relationship between habitat heterogeneity and species richness. For a given value of ρ, the plots show the mean species richness (with one standard deviation error bars) resulting from different number of habitats distributed over nine spatial patches. A given number of habitats corresponds to an equivalent number of correlated random interaction matrices such that the means are computed over 50 realizations of these matrices. The two panels correspond to (A) Mean interaction strength = 0. (B) Mean interaction strength = -0.5.

as the amazon can support high local diversity of species such as trees [76, 77].

In paper C we found that spatial heterogeneity in abundances and dynamics in a homogeneous landscape increases system robustness, diversity and ability to cross previous stability limits. This effect was highest at low to

intermediate levels of dispersal. Although our systems in the high dispersal limit can have astounding local diversity due to spatial interaction heterogeneity the system is less robust because of the coherent dynamics. Spatial interaction heterogeneity together with intermediate dispersal we might speculate will lead to robust systems with high global diversity. However, there seems to be a trade-off between robustness and local diversity.

Our results also reveal a possible solution to the complexity-diversity paradox highlighted by May. Including more biologically realistic structures in the interaction matrices together with realistic spatial heterogeneity might well lead to a model able to sustain the high diversity we find in real ecosystems.

CHAPTER 4

Discussion, conclusions and outlook

In this thesis I present work adding to the understanding of ecosystem stability, response behaviours and diversity using both non-spatial and spatial dynamical models. The choice to work with a non-spatial model in paper A and B was almost given by the research question itself. We observed phenomena when simply implementing May's non-spatial model, that has been extensively used and referenced for over 50 years, which were not visible in published studies using it. Because May's model has functioned as a reference point for stability of 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 studies at the time [52, 53, 59].

In paper C and D we added a spatial dimension, inspired by metacommunity studies showing stabilising effects of spatial heterogeneity in abundances [21, 22] and intriguing preliminary results when combining interaction matrices. Although additional stabilising mechanisms were found in the spatial setting the insights from the non-spatial representation in paper A and B were not overridden but rather extended and complexified. Together the papers and my thesis main 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, the stabilising effect of heterogeneous local dynamics including local oscillations 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 phase of resilience and structural instability by mapping all transition points.
- It shows that in the high dispersal limit a heterogeneous system's dynamics can be found by a non-spatial GLV with an effective interaction matrix
- It provides an analytical expression in the high dispersal limit that shows that higher interaction heterogeneity within a system leads to higher global and local diversity
- It shows that the mechanism of single species extinctions to avoid collapse does not vanish with spatial extension

The results from this thesis are added to the vast knowledge now gained on stability by a large array of ecosystem models. The GLV model and GLV with spatial extension used in this thesis are insightful tools due to their simplicity and generality in analysis. Simplifications have to be done when modelling complex systems, but GLV dynamics have many times been accused of being too simple to capture the complex dynamics of a real ecosystem. Both quantitative and qualitative. Not without warrant, as mentioned earlier the interactions are averages over time and space. Space is included to an extent in our spatial GLV but for example seasonal changes are assumed to have no impact. The constant interactions exclude prey switching and handling time as well as predator learning (Holling type II and III), known phenomena in natural ecosystems. Besides these issues in the model itself, generally all species are given positive intrinsic growth rates and the intraspecific interactions are assumed negative. Positive growth rates are a natural assumption for primary producers but a quite precarious one for consumers. Negative intraspecific interactions are needed in the GLV for stability [78] but their existence in nature a contested issue [46, 79] and recent models suggest that age-structure of species might render them unnecessary for stability [80].

Despite the issues raised in the previous paragraph the GLV model has shown promise both qualitatively and quantitatively. In [81] abundances of an observed system could be predicted by GLV dynamics, with an interaction network based on empirical data of pairwise interaction experiments; It has been shown that more comprehensive models can be mapped onto the GLV with the right parameter calibration [82], making it possible to use the simple GLV model for analysis and prediction [25]; Comparisons to data of theoretical predictions from the GLV can inform where natural communities differ the most from model interaction networks and thereby hint at evolutionary selected properties [54].

Comprehensive or not, ecological models and their predictions should

be handled in the context of the field of theoretical ecology which includes simplifications of many variations. The risk for model specific results must be held in mind. For example allowing for adaptive foraging, so that interactions among species can change have been shown to reverse the stability-complexity relationship [83, 84], or sometimes reverse it depending on timescale or modularity [85] in comparison to the GLV. Although shown for models without spatial extension it is likely that an effect of for example variable interaction strengths will appear also in spatial models. Another example of reversal is expanding to higher order interactions including multiple species [86], although experiments on small microbial communities have found no stabilising effect from higher order interactions [87]. It is not an easy solvable problem to evaluate which features can be simplified without losing the connection to real systems or how to model if most simplifications have a large impact on results.

The problem of evaluation of all ecosystem models, but especially models with interaction networks, 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 [88], especially non-trophic interactions. Despite trophic interactions being the "easiest" to measure with the help of gut-contents, there are examples where gut contents and observations do not agree [89]. One of the difficulties of measuring regarding all types of interactions is that it is very time consuming, an aspect making it even more troublesome validating models with spatial heterogeneity. Then, either an average over an entire ecosystem is needed, not just data from a local area. Or, the spatial heterogeneity (interaction correlations) within the ecosystem need to be estimated. The intraspecific interactions, which as mentioned have a large stabilising role in the GLV models (spatial and otherwise), are notoriously hard to observe/measure [78]. On the bright side both experimental and natural data looking at single or few species dispersal and synchronisation of local abundances have been collected for a number of species [21, 69, 70, 72, 90]. Although generalising these results to high diversity systems is not given, and similar data for high diversity systems are naturally harder to gather.

The second reason comparison to data is limited is shared with many complex systems. It is hard to do controlled experiments to validate theory. Even if we find the means to track natural diverse ecosystem abundances and interactions, it is rather unethical to disturb such a system in a controlled manner to for example see if species go extinct. Another way is of course an experimental set-up. Such 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 [91], we also find experiments on single species synchronisation and colonisation [69, 72] as

well as the role of spatial heterogeneity [71] and how diversity affects stability in microcosms [92], among others. These are very important contributions but as of yet they are too few and particular for accurate generalisations to high diversity ecosystems to be drawn.

A way of getting around experimental set-up and controlled disturbances to natural systems are "natural experiments". Such experiments are "performed" when a system tracked and measured goes through a change. Sadly, because of environmental changes and human impacts, many such examples exist [93–97]. Some of these cases can even be regarded as ecosystem collapses, in effect irreversible changes in species, biomass, structure or functioning. Although a great source of "experiments", causes for ecosystem disruptions are usually many and interconnected, effects are diverse and full coverage of all species and their interactions are often lacking. This data is indeed invaluable to inform ecosystem management [93], but as for validation of high diversity population models are seldom comprehensive or specific enough.

Thus, it is not an easy task to validate or invalidate many of the theoretical predictions. But the game is not lost, large efforts are being made to collect data from different ecosystems around the globe as well as locating where those efforts are best placed for largest impact [98]. In addition new techniques such as remote sensing of biomass can open new avenues of validation. Remote sensing can for example be used to approximate vegetation biomass [99, 100] together with knowledge of faunal biomass linked to the vegetation [101, 102] or by other means [103] total biomass can be approximated. Although biomass is not species resolved data it might help to cover large areas with less manpower.

It is also encouraging to see large amounts of experimental and natural data gathered in nearby fields such as biodiversity and ecosystem functioning (BEF) and biodiversity and ecosystem services (BES) [104]. From this we now know that for example biodiversity is conducive to ecosystem functioning. Studies looking at species abundance distributions, species area distributions and related concepts, also commonly compare against data. Despite some criticism for not spanning large enough areas or enough scales to test theory properly [56, 105], there are some datasets that are comprehensive enough for rigorous theory testing [105].

Besides advancing data gathering, advances in modelling are enabling the use of different types of data to fill some data-gaps. Examples are integrated population models [106] and state space models [107] to predict future abundances and biologically relevant parameters of single species. Spreading the data-intake even further to take advantage of the knowledge of life-histories, phylogenetics and leakage of data between similar species has been shown to improve predictions of abundances drastically [108]. Such models do

incorporate dynamics but no network of interacting species. They might therefore be unable to account for structural instability of communities which can mean drastic changes due to small disturbances. A combination of such models and network models could lead to interesting results both for theorists and practitioners.

The issue of prediction and trusting model results is of course put to a head in conservation ecology. Conservationist should be careful and perhaps consult several models for indicators of for example collapse and vulnerability, such as γ from paper A, feasibility domain [109], increase in autocorrelation time and abundance fluctuations [62], analyzing covariation and frequency distribution of relevant response and effect traits [110] among many others. Or, justifying the use of simple working models by calibrating against more intricate ones [25]. Choosing and using all these models is not an easy task for conservationists and more collaboration between network theorists and practitioners to inform one another and identify suitable "easy" to measure proxies would be desirable [98].

I believe we should also try to "theoretically" increase the belief in theoretical ecological models. One way would be to construct individual based agent-based models to confirm aggregated ones such as the GLV. In the same line of thinking performing a rigorous comparison of stability results between all types of models simple and comprehensive would also be valuable in guiding interpretation of all results. An example connected to this thesis could be adding to the spatial model the possibility of species to switch or regulate their interactions with other species depending on circumstance, as for example in prey-switching in accordance with prey abundance. This could be compared to results from the spatial GLV with uncorrelated local random interaction matrices, which can be seen as a crude version of this phenomena (although constant interactions within a local area). In addition the spatial model where interactions are chosen in a more biologically informed manner would add another version to compare and evaluate against as well as producing novel stability results.

There is, as usually concluded, much left for future investigations. But, in the midst of all that can and remains to be done in understanding ecosystem stability I am glad to have with thesis contributed an eddy to the river of knowledge.

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