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Functional Extinctions of Species in Ecological Networks

Torbjörn Säterberg

LINKÖPING UNIVERSITY

Department of Physics, Chemistry and Biology
Division of Theory and Modelling
Linköping University
SE – 581 83 Linköping, Sweden
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Till Olof och Hilma!

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Summary

Current rates of extinctions are estimated to be around 1000 times higher than background rates that would occur without anthropogenic impacts. These extinction rates refer to the traditional view of extinctions, i.e. numerical extinctions. This thesis is about another type of extinctions: functional extinctions. Those occur when the abundance of a species is too small to uphold the species' ecologically interactive role. I have taken a theoretical approach and used dynamical models to investigate functional extinctions and threshold values for species' mortality rates in ecological networks. More specifically, I have derived threshold values for focal species mortality rates at which another species or the focal species itself goes numerically extinct (Paper I-II), or transgresses some predefined threshold abundance (Paper III). If an increased mortality rate of a focal species causes another species to go numerically extinct, the focal species can be regarded as functionally extinct, since its abundance is no longer large enough to uphold its ecologically interactive role. Such functional extinctions are investigated in the first papers (Paper I-II). In the following paper, limits for both increased and decreased mortality rates of species are explored (Paper III). Paper III also extends the basic theoretical idea developed in paper I-II into a more applied setting. In this paper I develop a time series approach aimed at estimating fishing mortalities associated with a low risk that any species in a community transgresses some predefined critical abundance threshold. In the last paper (Paper IV) the community wide effect of changes in the abundance of species is investigated.

In the first paper (Paper I) I investigate threshold levels for the mortality rate of species in ecological networks. When an increased mortality rate of a focal species causes another species to go extinct, the focal species can be characterized as functional extinct, even though it still exists. Such functional extinctions have been observed in a few systems, but their frequency and general patterns have been unexplored. Using a new analytical method the patterns and frequency of functional extinctions in theoretical and empirical ecological networks are explored. It is found that the species most likely to be the first to go extinct is not the species whose mortality rate is increased, but instead another species in the network. The species which goes extinct is often not even directly linked to the species whose mortality rate is increased, but instead indirectly linked. Further, it is found that large-bodied species at the top of food chains can only be exposed to small increases in mortality rate and small decreases in abundance before going functionally extinct compared to small-bodied species lower in the food chains. These results illustrate the potential importance of functional extinctions in ecological networks and lend support to arguments advocating a more community-oriented approach in conservation biology, with target levels for populations based on ecological functionality rather than the mere persistence of species.

In Paper II I use the approach developed in Paper I to explore the frequency and patterns of functional extinctions in ecological networks with varying proportions of mutualistic and antagonistic (predator-prey) interactions. The general results from Paper I are also found in Paper II; that is, an increased mortality rate of one focal species often first

leads to an extinction of another species rather than to an extinction of the focal species itself.

Further, the frequency of functional extinctions is higher in networks containing a mixture of interaction types than in networks with only antagonistic interactions. Overall, this study generalizes the findings of paper I for networks containing a variety of interaction types.

To make the theoretical approaches developed in paper I-II operational in a management setting I develop a time series approach aimed at estimating ecologically sustainable fishing mortalities in a multispecies fisheries context (Paper III). An ecologically sustainable fishing mortality is here defined as a long-term fishing mortality associated with a multispecies objective which infers a low risk that any species, either the focal species itself or another species, in a community transgresses a critical biomass limit, below which the risk of recruitment failure is high. The approach is exemplified using a statistical food web model of the dominating fish stocks in the Baltic Sea. For the most abundant fish stock a counterintuitive result is found; it is more likely that the multispecies objective is met if its mortality caused by fishing is increased compared to if it is decreased. Further, simultaneous changes of the fishing mortality of a number of interacting species in the food web model shows a much narrower region of possible sustainable fishing mortalities than a single species approach, something that is not captured by current stock assessment models. Altogether these results are governed by indirect effects propagating in the community and pinpoint the need to adopt community dynamical approaches in fisheries management.

The population sizes of many species in the world are declining. Negative population trends are particularly pronounced in large-bodied herbivores and carnivores, species known to play important regulatory roles in many ecosystems. Although this indicates that the ecological consequence of declining populations of species might be profound, its impact on ecosystem stability remains largely unexplored. In paper IV it is therefore explored how declining populations of rare and common species affects the resilience – recovery rate – of ecological networks. An analytical approximation shows that network resilience is a function of the harmonic mean of the species' abundances. This means that network resilience is especially sensitive to declining abundances of rare species. Consistent with this analytically derived result, a clear and positive relationship between resilience and the abundance of the rarest species in a broad spectrum of dynamical models of ecological networks is found. Together these results illustrate the potentially negative consequences of declining populations of rare species for the stability of the ecological systems in which they are embedded, and provide ecological arguments for the protection and management of rare species.

Populärvetenskaplig sammanfattning

Forskning har visat att populationsstorlekarna, dvs. antalet individer som lever i ett specifikt område, minskar hos många arter. Oavsett vad som orsakar minskningen av en arts populationsstorlek, så skulle en fortsatt minskning till slut kunna leda till ett lokalt artutdöende. Den här avhandlingen handlar om en annan typ av utdöenden: funktionella utdöenden. Dessa sker när en arts populationsstorlek är för liten för att upprätthålla artens ekologiska funktion. Eftersom arter påverkar varandra på olika sätt i ett ekosystem så kan en förändring i populationsstorleken hos en art få konsekvenser för andra arter. Till exempel så har överfiske av toppredatorer (t.ex. torsk) visats indirekt påverka andra organismer längre ned i näringskedjan (t.ex. växtplankton) i vissa marina system. En förändring av en arts populationsstorlek kan därmed leda till förändringar i andra arters populationsstorlekar. Men hur mycket kan en arts populationsstorlek förändras innan det får stora effekter på hela ekosystemet? Hur många bin behövs det till exempel för att pollinera ett fält? Hur stort fisketryck kan man utsätta en viss art för innan det får förödande konsekvenser för hela ekosystemet? Avhandlingen handlar om sådana tröskelnivåer, dvs. hur stor en arts populationsstorlek behöver vara och hur mycket man kan påverka en art innan den förlorar sin ekologiska funktion. Sådana tröskelnivåer undersöks här teoretiskt med hjälp av matematiska modeller. Dessa matematiska modeller beskriver hur starkt arter interagerar med varandra och hur arternas populationsstorlekar förändras över tid. Med hjälp av dessa modeller så kan man till exempel simulera hur system påverkas av olika typer av störningar; exempelvis klimatförändringar, förändringar av fisketryck och övergödning. I avhandlingens första artiklar (Artikel I-II) så antas störningen vara av generell karaktär och påverkar arter genom en förändring i deras mortalitet, vilket är ett mått på proportionen av individer i en population som dör per tidsenhet. För att vara mer specifik så undersöks det hur mycket en arts mortalitet kan förändras, innan den själv, eller någon annan art i det ekologiska samhället dör ut. Om en ökad mortalitet hos en art leder till ett utdöende av en annan art så kan arten som utsätts för den ökade mortaliteten ses som funktionellt utdöd. Sådana funktionella utdöenden undersöks i avhandlingens första artiklar (Artikel I-II). I artikel III så utvecklas ett statistiskt ramverk för att uppskatta ekologiskt hållbara fisketryck. Ett ekologiskt hållbart fisketryck definieras här som ett fisketryck som medför en låg risk att någon art i systemet går under en kritisk biomassa gräns – en gräns under vilken risken för reproduktionsproblem är hög. Den sista artikeln (Artikel IV) är av något annorlunda karaktär än de andra. I den undersöks det hur ekologiska nätverk, dvs. system med arter som interagerar med varandra, påverkas av förändringar i arters populationsstorlekar.

När en ökad mortalitet hos en art leder till ett utdöende av en annan art så kan arten som utsätts för den ökade mortaliteten ses som funktionellt utdöd. Sådana funktionella utdöenden har observerats i ett antal system, men den möjliga frekvensen och mönstren av sådana funktionella utdöenden har inte utforskats i detalj. Med hjälp av matematiska modeller av några empiriskt observerade och teoretiskt genererade nätverk, så undersöks mönstren och frekvensen av sådana funktionella utdöenden i avhandlingens första artikel (Artikel I). Resultaten visar att det oftast är någon annan art och inte arten själv som är den första att dö ut till följd av en ökad mortalitet. Ofta är det till och med så att arten som dör ut inte ens är direkt kopplad till arten vars mortalitet ökades.

Överlag så illustrerar denna artikel därför den potentiella betydelsen av funktionella utdöenden och indirekta effekter i ekologiska system. Artikeln styrker därmed argument för ett holistiskt och ekologiskt orienterat förhållningssätt inom bevarandebiologin, med målnivåer för populationer baserade på ekologisk funktion i stället för ett ensidigt fokus på bevarande av arten som sådan.

I den andra artikeln (Artikel II) så används metoden som utvecklades i den första artikeln (Artikel I) för att undersöka frekvensen och mönstren av funktionella utdöenden i ekologiska nätverk med olika typer av interaktioner mellan arter. Det generella resultatet från artikel I återfinns i artikel II. En ökad mortalitet hos en art leder ofta indirekt till ett utdöende av en annan art.

För att göra den teoretiska metodiken som används i de första artiklarna (Artikel I-II) användbar i tillämpade frågeställningar så är det nödvändigt att använda så mycket information om ett system som möjligt. I artikel III så utvecklas därför en tidsseriemetod som skulle kunna användas för att uppskatta ekologiskt hållbara fisketryck i system med interagerande arter. Ett ekologiskt hållbart fisketryck definieras här som ett fisketryck som medför en låg risk att någon art i systemet går under en kritisk biomassa gräns – en gräns under vilken risken för reproduktionsproblem är hög. Metoden exemplifieras med en statistisk flerartsmodell som är baserad på tidsseriedata för de dominerande fiskarterna i Östersjön. Resultaten visar att en flerartsmodell ger andra rekommendationer för hållbara fisketryck än vad en enartsmodell ger. Överlag så pekar resultaten i denna studie därför på vikten av att införa dynamiska flerartsmodeller inom fiskerinäringen.

Populationsstorlekarna hos många av världens arter minskar. Mest uttalad är minskningen av stora rovdjur och växtätare. Det är väl känt att dessa stora djur ofta har en betydande ekologisk roll. Trots att detta tyder på att en minskning av populationsstorlekarna hos dessa typer av djur skulle kunna ha en stor effekt på ekosystemen i vilka de lever, så vet man relativt lite om effekterna av sådana populationsstorleksminskningar. I artikel IV så undersöks därför hur minskningar av ovanliga respektive vanliga arters populationsstorlekar påverkar resiliensen – återhämtningstakten- i ekologiska system. En matematisk approximation visar att systemens resiliens huvudsakligen styrs av förändringar i de ovanligaste arternas populationsstorlekar. Detta resultat konfirmeras med hjälp av numeriska metoder. Överlag så tyder resultaten därmed på att ovanliga arter kan ha en betydande roll för ekosystems stabilitet och sammansättning. Studien ger därmed ett ekologiskt argument för bevarande av ovanliga arter i ekosystem.

List of papers

- I. Säterberg, T., S. Sellman & B. Ebenman. (2013).
High frequency of functional extinctions in ecological networks.
Nature, 499, 468-470.¹
- II. Sellman, S., T. Säterberg & B. Ebenman. (2015).
Pattern of functional extinctions in ecological networks with a variety of interaction types.
Theoretical Ecology, 9, 83-94.²
- III. Säterberg, T., M. Casini & A. Gårdmark.
Ecologically sustainable fishing mortalities – A multispecies approach for fisheries management.
Manuscript.
- IV. Säterberg, T., T. Jonsson, J. Yearsley, S. Berg & B. Ebenman.
Declining populations of rare species decreases ecosystem resilience
Manuscript.

Contributions to papers:

Paper I: TS & BE designed the project; TS, BE & SS performed research; TS analysed data; TS & BE wrote the paper with contributions from SS.

Paper II: SS, TS & BE designed the project; SS & TS developed code; SS & TS analysed data; BE, SS & TS wrote the paper.

Paper III: TS designed the project with contribution from AG; TS developed code and analysed data; MC gathered data; TS wrote the paper with contributions from AG & MC.

Paper IV: BE, TJ & TS designed the project; SB, BE, TJ, TS and JY performed research; TS developed code and analysed data; BE wrote the paper with contributions from TJ, TS & JY.

TS - Torbjörn Säterberg; BE - Bo Ebenman; SS – Stefan Sellman; AG – Anna Gårdmark; MC – Michele Casini; TJ – Tomas Jonsson; JY - Jon Yearsley; SB – Sofia Berg

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PART 1 – OVERVIEW

Functional Extinctions of Species in Ecological Networks

Torbjörn Säterberg

1. Introduction

Current rates of extinctions are estimated to be around 1000 times higher than background rates that would occur without anthropogenic impacts (Pimm et al. 2014). These extinction rates refer to the traditional view of extinctions, i.e. numerical extinctions. This thesis is about another type of extinctions: functional extinctions. Those occur when the abundance of a species is too small to uphold the species' ecologically interactive role (Soulé et al. 2003; Soulé et al. 2005; Estes et al. 2010). A school book example of a functional extinction of a species stems from the kelp-forest ecosystems around the Aleuthian Islands in northern Alaska. Because of hunting and fur trade the number of sea otters declined in this system (Estes and Palmisano 1974). In turn this led to a complete collapse of the ecosystem caused by a trophic cascade: the diminishing sea otters led to an increase in its preferred prey, sea urchins, whom in turn overgrazed the kelp-forest - leaving a barren sea floor. Notably, there appears to be a threshold abundance of sea otters above which the system tend to stay in a healthy state (Estes et al. 2010). This abundance threshold can be referred to as a species' ecologically effective population size, below which it can be considered functionally extinct. This example provides a good starting point to what this thesis is about: threshold levels for species mortality rates and densities.

Functional extinctions and ecologically effective population sizes of single species have only been observed in a few ecosystems (e.g. McConkey and Drake 2006; Estes, Tinker et al. 2010; Cury et al. 2011). But, extensive field observations (Estes et al. 2011; Möllman and Diekmann 2012; Myers et al. 2007; Baum and Worm 2009; Frank et al. 2005; Casini et al. 2008; Ripple et al. 2014) and experiments (Shurin et al. 2002; Borer et al. 2005; Sanders et al. 2013; Sanders et al. 2015) suggest the existence of trophic cascades (indirect effects caused by changed predator abundance) and regime shifts (abrupt shifts in the whole ecosystem) in a whole range of ecosystems. These empirical observation thus suggest that functional extinctions might occur in many ecosystems. To this end, I have in this thesis taken a theoretical approach and used dynamical models to theoretically explore the patterns and potential frequency of such functional extinctions in ecological networks, i.e. in systems with a large number of interacting species.

1.1 Ecological networks

An ecological network is a description of the interactions among species in an ecosystem, i.e. the biotic (living) part of an ecosystem (Montoya et al. 2006). The interactions among species can be represented as a binary network of who interacts with whom (Fig. 1A), but also in what way (Fig. 1C) and how strongly species interact with each other (Fig. 1B). If the strength of species interactions is considered, the dynamics of the ecological network can be described by a set of coupled equations. One such very basic description of the dynamics of interacting species is the generalized Lotka-Volterra model. In this model, the population growth rate of species is dependent on species' intrinsic growth/mortality rates and interactions among species. Three of the papers in this thesis are based on this very basic approach of modeling community dynamics.

Traditionally, most research on ecological networks has focused on food webs (Vázquez et al. 2015), i.e. the network of species describing who feeds on whom. This might not be so surprising since all organisms are dependent on energy for survival. However, other type of ecological networks, e.g. mutualistic networks (Saavedra et al. 2011; Rohr et al. 2014; Bascompte et al. 2003; Thébault and Fontainé 2010; Olesen et al. 2007), competitive networks (Fowler 2010; Ruokolainen and Fowler 2008; Ruokolainen et al. 2007) or combinations thereof (Sauve et al. 2014; Mougi and Kondoh 2012; Mougi and Kondoh 2012; Pocock et al. 2012; Kéfi et al. 2015), have recently received an increased amount of attention. Ecological networks have been investigated in terms of press perturbations (Bender et al. 1984), i.e. sustained changes in some component of a community. How such perturbations propagate within an ecological network is dependent on the strength and the specific way that species interact.

1.2 Species interactions and community dynamics

At the core of ecological networks is the pairwise interactions among species. The strength with which an individual of one species affect the population growth rate of another species can be described by a function. So called functional responses (Fig. 2), have been thoroughly investigated for predator-prey interactions (Jeschke et al. 2002). Holling (1959) originally defined three basic type of equations describing the number of prey taken per individual predator, per unit of time (Fig. 2). At its most basic form a functional response can be described as a type I functional response. Here, the number of prey taken by an individual predator is a linear function of prey abundance. The type I functional response can be extended to allow for predator saturation at high prey densities - a type II functional response. The third basic type of functional response is the functional response of type III, where the number of prey taken per predator is a sigmoidal function of prey abundance (Fig. 2). Since the seminal work by Holling (1959) a number of different more mechanistically based

functional responses have been suggested (e.g. Jeschke et al. 2002; Englund et al. 2011; Rall et al. 2012). These include, for example, temperature (Englund et al. 2011) and body size (Rall et al. 2012) dependent functional responses. Even though species interactions most likely are non-linear in nature (Jeschke et al. 2004), most papers in this thesis are based on functional responses of type I. Further, interactions for prey densities found in multispecies natural settings might, at least in some systems, be approximately linear (Novak 2010; Wootton and Emmerson 2005).

Figure 2. A schematic illustration of the three major types of functional responses: type I, type II and type III. Type I, in which the number of prey taken per individual predator per unit of time is a linear function of prey density, has mainly been used in this thesis.

Traditional models describing the dynamics of ecological networks have assumed parameters randomly drawn from certain intervals (e.g. May 1972; Pimm 1979; Pimm 1980; Yodzis 1988). However, since the seminal work by Yodzis & Innes (1992), the idea of constraining parameters based on body masses of species has received increasing popularity. The model by Yodzis & Innes (1992) has for example been used to parametrize multi trophic networks generated by the Niche-model, which is a model describing the network of who eats whom (Williams and Martinez 2000; Brose et al. 2006; Berlow et al. 2009). This model has been extensively used to derive theory based on numerical simulations (e.g. Binzer et al. 2011; Curtsdotter et al. 2011; Berlow et al. 2009; Brose et al. 2006). Recently, this framework has also been extended to mechanistically model the effect of temperature on community dynamics (Gilbert et al. 2014; Vasseur et al. 2005; O'Connor et al. 2011), using metabolic theory of ecology (Brown et al. 2004). All these studies suggest that body size scaling could be a fruitful way of parameterizing ecological models. However, all of these approaches of relating model parameters to species specific characteristics, i.e. body mass, have mainly had a focus of predator-prey interactions. Other type of interactions might be important for community stability (Kéfi et al. 2012; Mougi and Kondoh 2012; Mougi and Kondoh 2014) and thus also for the propagation of potential perturbations within a community.

1.3 Time series approaches

Another potential way of parameterizing and describing the dynamics of ecological networks is to use a time series approach. Unfortunately these approaches require long time series, but they do provide a good coupling between ecological theory and empirical research (e.g. Ives et al. 2003; Francis et al. 2014). Depending on the specific research question such approaches can be used to forecast the state of specific systems, but also to derive general ecological theory (Ives et al. 2003). In recent years, non-parametric time series approaches have been developed. Their main advantage is their ability to predict the state of non-linear systems (e.g. Deyle et al. 2016; Perretti et al. 2013; Sugihara et al. 2012; Ye et al. 2015), but whether or not such models provide better forecast than simple linear autoregressive models is an open question (Ward et al. 2014). Linear models, like multivariate autoregressive models (Ives et al. 2003; Hampton et al. 2013), can easily be fitted to time series data, and have successfully predicted fish dynamics in some marine ecosystems (Lindegren et al. 2009; Lindegren et al. 2014; Bell et al. 2014). Importantly, this method can also include the effect of extrinsic environmental variables, which for sure is very important in almost any ecological system. Further, these models can be used to simulate the response of communities to press perturbations (Ives 1995) and have also given reasonable predictions to long-term sustained changes in environmental variables (Ives et al. 1999; Beisner et al. 2003).

1.4 Theoretical approaches for studying press perturbations

Paine (1966) showed in an intertidal community that the removal of a single predator can lead to an extinction cascade. Since then theoretical (Pimm 1979; Pimm 1980; Berlow et al. 2009; Ebenman and Jonsson 2005) as well as empirical research (Wootton 2004; Schmitz et al. 2000; Borer et al. 2005; Shurin et al. 2002) has investigated the potential effects of removing species from ecological communities. In a theoretical setting, species removal experiments have both been conducted using a topological approach (Fig. 1A) (e.g. Dunne et al. 2002), or by using dynamical models (e.g. Curtsdotter et al. 2011; Ebenman et al. 2004; Berlow et al. 2009). In a food web context, the topological approach only captures bottom up effects (species losing all their prey will go extinct), whereas the dynamical approach can reveal both bottom-up and top-down effects (Eklöf and Ebenman 2006; Curtsdotter et al. 2011). When it comes to less severe perturbations some research has focused on community sensitivity analysis (Berg et al. 2011). This framework focuses on how the equilibrium or resilience – the rate of return to equilibrium following temporary disturbances - of a community is affected by small changes in model parameters (see Tab. 1). One community sensitivity analysis is based on the negative inverse of the Jacobian matrix, whose elements gives the total direct and indirect response of species' equilibrium abundances to small additive sustained changes in the equilibrium abundance of other species. This approach has given quite puzzling results since even the sign of the responses might be hard to predict if the pairwise interactions among species are measured with error (Yodzis 1988), and the sign of the response to such perturbations might be even harder to predict for large systems (Novak et al. 2011). Furthermore, other research has also shown that indirect effects propagating in a community might very likely reverse the direct effect that one species has on another species (Montoya et

al. 2009). These studies thus point at the importance of good estimates of pairwise interactions, but also at the counterintuitive and potentially strong indirect effects which might propagate within ecological communities.

Table 1. *Some types of press perturbations exposed to single species in dynamical models of ecological communities.*

Perturbation	Response	References	Used in Paper
Enforced extinction	Number of secondary extinctions	(Pimm 1979; Fowler 2010; Ebenman and Jonsson 2005)	-
	Changes in the biomass of species	(Berlow et al. 2009)	-
Sustained changes in mortality	Extinction of a species in an ecological network	(Säterberg et al. 2013; Sellman et al. 2015)	I-II
	Changes in the biomass of species	(Smith et al. 2011; Ives 1995)	III
Small sustained changes in:			
species' intrinsic rates of increase	Changes in resilience or equilibrium abundances of species	(Berg et al. 2011)	-
species' equilibrium abundances	Changes in equilibrium abundances of species	(Yodzis 1988; Novak et al. 2011)	-
	Changes in resilience	-	IV
per capita interaction strengths	Changes in resilience or equilibrium abundances of species	(Berg et al. 2011)	-

1.5 Stability concepts

Related to perturbations of ecological networks is the concept of stability. The robustness of a community to primary enforced extinctions, so called species deletion stability (Pimm 1980; Ebenman and Jonsson 2005), is one measure of ecological stability. But, stability is a multifaceted concept within ecology (Ives and Carpenter 2007; McCann 2000) and can for example be measured in terms of variability in population sizes (e.g. Gudmundson et al. 2015; Karlsson et al. 2007), but also in terms of the qualitative dynamical behavior of a dynamical system. One of the more traditional concepts of stability within theoretical ecology is local stability (e.g. May 1972). This is a qualitative definition of stability and infers that the system will return to equilibrium following a small temporary disturbance. The rate at which the system returns to equilibrium following a temporary disturbance - its' resilience - is determined by the dominant eigenvalue of the Jacobian matrix evaluated at the equilibrium. Related to local stability is the basin of attraction, which is the region in the multidimensional state-space which has the equilibrium as an attractor (Takeuchi 1996; van Nes and Scheffer 2007).

In contrast to a locally stable equilibrium, a globally stable equilibrium has the whole, or at least the interior, of state space as basin of attraction (Takeuchi 1996). Permanence is one global stability concept and it infers that no matter how strongly the abundances of species in a community are perturbed - as far as they are not driven to extinction - they will end up in a compact set in the interior of state space. The boundary equilibria of the system acts as repellors and constrain the species' abundances within the positive orthant of state-space (Law and Morton 1996). However, one practical problem with permanence, just as some other global stability criteria (Logofet 2005), is that it gets computationally unfeasible for large systems.

2. Aims

The general aim of this thesis is to: (i) investigate threshold levels for species mortality rates in ecological networks and; (ii) to investigate the dynamical response of ecological networks to sustained perturbations. The approach is theoretical and I use coupled dynamical models to explore threshold levels for species mortality rates (Paper I-III) and the effect of changes in equilibrium abundance of species on community dynamics (Paper IV).

Specific aims:

Aims of paper I

In this paper I develop an approach to find critical mortality rates leading to extinctions of some species in an ecological network. The main aims with this paper are to:

- (i) Investigate how likely it is that an increased mortality rate of one species leads to extinction of another species in the network.
- (ii) Investigate the patterns of such functional extinctions within ecological networks.

Aims of paper II

In paper I, models are mainly represented by antagonistic interactions. In paper II, the aim is therefore to further investigate how the results from paper I are affected by varying the degree of mutualistic and antagonistic interactions in an ecological network. The specific aims with paper II are to:

- (i) Investigate how the frequency of functional extinctions in an ecological network is affected by different proportions of mutualistic- and antagonistic interactions.
- (ii) Investigate how the degree of intra-specific competition among species affects the frequency of functional extinctions.

Aims of paper III

In order to make the analytical and deterministic approach used in paper I-II applicable in real systems I develop a stochastic framework for investigating critical mortality levels. The approach is based on time series data and has a potential applied usage in fisheries management. Two specific aims with this paper are to:

- (i) Develop a stochastic model for estimating ecologically sustainable fishing mortalities.
- (ii) Investigate how fishing mortality limits are affected by taking a holistic multispecies approach compared to a single species approach.

Aims of paper IV

The last paper stands out from the other papers since it does not investigate the effects of changed mortality rates of species, but rather how ecological networks are affected by changes in the abundance of species. More specifically, the aim with this study is to:

- (i) Investigate how resilience of ecological networks is affected by small additive changes in the abundance of focal species, and how this is related to focal species' initial abundances.

3. Results & discussion

All results in this thesis illustrate the potential importance of adopting community-oriented approaches for conservation biology and management of natural resources. This result is clearly demonstrated both from a theoretical standpoint (Paper I, II & IV), and also in a somewhat more applied setting (Paper III).

Paper I

In 2003 Solé and co-workers (Soulé et al. 2003) gave a strong case for the existence of ecological effective population sizes of species in ecological communities. By their definition an ecologically effective population size of a species is a population size that maintain critical interactions and help ensure against ecosystem degradation. Below this population size threshold a species can be considered ecologically or functionally extinct (Jackson et al. 2001; Estes et al. 2010). The abundance of a species should thus be large enough to uphold the species ecologically interactive role. In the same vein, a theoretical framework for investigating functional extinctions and ecologically effective population sizes in ecological networks is derived in paper I. Specifically, an analytical method is developed to find how much the mortality rate of single focal species can be increased before any species in an ecological network goes extinct. If an increased mortality rate of a focal species first leads to extinction of another species rather than to extinction of the focal species itself, the focal species can be regarded as functionally extinct, even though it still exists. Using a number of different natural and computer generated networks I find that there is a high risk of functional extinctions within those systems (Fig. 3). Further, the species going extinct due to a changed mortality of a focal species is often not even directly linked to the focal species whose mortality rate is changed, i.e. it is neither a predator nor prey to the focal species (Fig. 3). These result suggest that single species approaches to conservation might not be sufficient if the ecological role of a species is considered, since other species might go extinct due to changed mortality and abundance of certain focal species (Sanders et al. 2013; Koh et al. 2004). It further suggests critical mortality rates for some species, above which interdependent species might be lost. These mortality rate thresholds are shown to be related to species' average body masses. Species with large average body mass - those that in general occupy high trophic levels - can be exposed to smaller absolute changes in the mortality rate compared to species with a smaller body mass, before an extinction occurs in the ecological network. Further, a small change in the mortality rate of a species is also related to a small changes in its equilibrium abundance. This suggests that ecological networks could be more sensitive to changes in the mortality rate and abundances of top predators than to changes in the mortality rate and abundances of species at the base of food webs.

Figure 3. This figure shows that an increased mortality of one focal species (in black) often leads to an extinction of another species (grey and white) rather than to an extinction of the species itself (adapted from Säterberg et al. 2013, Nature). The figure shows the proportion of extinctions affecting the focal species itself (black), directly linked species (grey) and indirectly linked species (white) in (a) theoretically generated food webs and (b) natural food webs. The same general result, i.e. that an increased mortality rate of one species often first leads to an extinction of another species rather than to an extinction of the species itself, is found in both paper I and paper II.

In order to investigate which species that are most likely to go functionally extinct following an increase in their mortality rate, a number of species specific traits are investigated. Among those traits it is found that the total biomass of a species is an important predictor. This result is in line with another theoretical study showing that the complete removal of single species causes larger biomass changes of other species in the community, if the initially removed species has a high biomass compared to if it has a low biomass (Berlow et al. 2009). Similarly, complex models of marine communities suggest that maximum sustainable yield fishing of forage fish species with a large biomass leads to large effects on other species in the community (Smith et al. 2011).

In paper I it is assumed that stressors only affect one species at a time. However, stressors like fishing, climate change and pollution, can be expected to strike more broadly. To this end, simultaneous stressors - in terms of fishing mortalities - are investigated in paper III.

Paper II

Paper II is a follow up study to paper I. Here, it is investigated how robust the results from paper I are to differences in species interaction types in ecological networks. Model networks with different proportions of mutualistic interactions and antagonistic interactions (Mougi and Kondoh 2012) are built and the method developed in paper I is used to explore the frequency and patterns of functional extinctions in these systems. Overall, a high frequency of functional extinctions is found in these systems as well, corroborating the results from paper I.

In paper II it is additionally explored how the effect of different proportions of mutualistic and antagonistic interactions, and the degree of intraspecific competition among species affect the frequency of functional extinctions within these systems. It is found that the frequency of functional extinctions is higher in networks with a mixture of interaction types compared to networks with only antagonistic interactions. Furthermore, an increased degree of intra-specific competition leads to lower frequencies of functional extinctions within the networks and a decreased trophic distance (number of links) between the focal species, whose mortality rate is increased, and the species which goes numerically extinct. This result is in agreement with the general theoretical result that an increased degree of self-regulation among species tends to stabilize ecological networks (May 1972; Neutel et al. 2002; Thébault et al. 2007; Allesina and Tang 2012; Mougi and Kondoh 2012). However, it is in this study specifically found that an increased degree of self-regulation among species tend to localize the impact of press perturbations. It should further be noted that even though an increased degree of intra-specific competition tends to decrease the number of functional extinctions, there is still a large number of functional extinctions occurring, even when the average intraspecific interaction strength is about 20-30 times stronger than inter-specific interactions. This means that even if intra-specific effects were relatively strong compared to inter-specific interactions, the indirect effect caused by perturbations to single species could anyway be large in species-rich ecological systems.

Paper III

To be able to make predictions for specific ecological systems, data driven models are needed. Therefore, paper III extends the approach from paper I-II into a more applied setting. A time series approach is developed in order to estimate ecologically sustainable fishing mortalities. An ecologically sustainable fishing mortality is here defined as a long-term mean fishing mortality associated with a low risk that any species, either the focal species itself or another species, in the ecological community goes below a critical biomass limit. A statistical multispecies model based on time series of the three dominating fish species in the Baltic Sea, is used to exemplify the approach. In contrast to paper I & II, the model used in this paper accounts for extrinsic environmental variables as well as stochastic variation in population sizes (see Fig. 5), which are all important to account for in a management setting.

By using this method of estimating ecologically sustainable fishing mortalities it is found that, in order to attain a low risk that any species transgresses its critical biomass limit, it might in some cases be more beneficial to increase the fishing mortality of certain species than what it is to decrease it. Further, simultaneous changes of the mean fishing mortality of all the three fish species in the multispecies model shows a much narrower region of simultaneous

sustainable fishing mortalities compared a single species model. Overall, this study points to the importance of adopting multispecies models in fisheries management. Such an approach can disclose counterintuitive effects that a single species approach might not reveal.

Paper IV

In the first papers of this thesis (Paper I-III) the ecological effects of changing the mortality rate of species is explored. In contrast paper IV explores the community wide effects of changes in the abundance of species. More specifically, paper IV explores the relative importance of rare and common species in ecological networks. It is found that changes in the abundance of rare species have a large effect on network resilience – the recovery rate following temporary disturbance. This result is arrived at by an analytical approximation showing that network resilience is a function of the harmonic mean of species' abundances, meaning that changes in the abundance of a rare species has a larger effect on resilience than changes in the abundance of a common species. This analytical result is corroborated by extensive numerical investigations of a number of natural and computer generated ecological networks. Specifically, the sensitivity of resilience to additive changes in the density of species is negatively related to species abundances in those systems (Fig. 4).

Figure 4. *This figure illustrates the major result found in paper IV. The resilience – the recovery rate following temporary disturbance - of ecological networks is more sensitive to changes in the abundance of rare species than what it is to changes in the abundance of common species.*

So overall, this study suggests that rare species might have an important role for the dynamics of ecological networks. A small absolute change in rare species' abundances tend to affect the dynamics more than a small change in the abundances of common species. But, which species are rare in natural systems? In terms of numerical abundance, rare species are expected to be found at the top of food webs (Brown et al. 2004). Diminished abundances of such species have been shown to lead to extinctions of other species in models of ecological communities (Paper I) and to have large community wide effects in a wide range of ecosystem (e.g. Estes et al. 2011; Baum et al. 2003; Myers et al. 2007). This suggests that such species might be of extra conservation concern.

An important question is of course why rare species could be important for the dynamics of an ecological network. One idea is that rare species interact strongly, on per capita basis, with other species and thus that an additive change in the abundance of a rare species will lead to a larger community wide effect than an additive change in the abundance of a common species. A recent empirical work indicate that this might be the case since individuals of rare species interact more strongly, both through direct and indirect effects, with other species than more common species (Wood et al. 2010).

Overall, this study illustrates the potentially negative consequence of declining populations of rare species for the stability of the ecological systems in which they are embedded, and thus provide ecological arguments for the protection and management of rare species.

Concluding remark

Overall, this thesis points at the importance of adopting a community-oriented approach for conservation biology and management of natural resources. Using mathematical models of a variety of ecological networks it is here found that if a focal species is perturbed it is often another species that goes extinct rather than the focal species itself. This result can be set in contrast to some of the current concepts within conservation biology - like population viability analysis and minimum viable population sizes - which focuses on the conservation of single species and often neglects the dynamical effects of species interactions (Sabo 2008). Further, for fisheries management the same single species focus is often the case (e.g. Möllmann et al. 2014; Worm et al. 2009).

Most analyses in this thesis assume that perturbations affect one species at a time (Except Paper III). Simultaneous perturbations to a number of species in a community might lead to another outcome. It has for example been shown that the cascading effects of primary enforced extinctions might sometimes be counteracted by enforcing another species within a community to extinction (Sahasrabudhe and Motter 2011). Due to indirect effects caused by perturbations of a given species compensatory perturbations might therefore sometimes counterbalance the effect caused by a primary perturbation. However, this does of course depend on how and where a specific stressor affects a system. Many marine ecosystem have, for example, been selectively overfished. In many cases overfishing has started with long-lived top predators and continued with overfishing of short-lived species like planktivorous fishes and invertebrates; something called fishing down the food web (Pauly et al. 1998). The historical selectivity patterns of fisheries might thus mainly have been pointed towards certain functional groups, rather than towards single species. Such a practice might be even worse for an ecological community since the functional redundancy of multiple species with similar ecological roles might be lost (see e.g. Myers et al. 2007; McClanahan et al. 2011). To this end, some advocate for balanced harvesting (Garcia et al. 2012; Zhou et al. 2010), which infers that a small proportion of the abundances of a wide range of species is removed simultaneously. This might be a fruitful way towards a sustainable management of resources because selective perturbations to species might very well lead to unwanted and strong indirect effects - even extinctions - in ecological networks.

4 Methods

4.1 Community dynamics

Coupled dynamical models have been used to explore the community wide effects caused by changes in the mortality rate (Paper I-III) and changes in the equilibrium abundance of species (Paper IV). Continuous time Lotka-Volterra models have mainly been used in three of the papers (Paper I-II & IV), whereas multivariate autoregressive models (MAR-models) are used to model community dynamics in paper III.

4.1.1 Lotka-Volterra models

Continuous time Lotka-Volterra models are described by the following equation:

$$\frac{dN_i}{dt} = N_i (r_i + \sum_j \alpha_{ij} N_j) \quad (1)$$

Where N_i represent the density of species i in a community with n species, r_i is the intrinsic growth or mortality rate of species i , and α_{ij} is the per capita or per unit biomass effect of species j on species i .

In matrix notation the equilibrium of a Lotka-Volterra system (eq. 1) is given by:

$$\hat{\mathbf{N}} = -\mathbf{A}^{-1}\mathbf{r} \quad (2)$$

Where $\hat{\mathbf{N}}$ is a column vector with species' equilibrium densities, $\mathbf{A}^{-1}$, is the inverse interaction matrix with elements describing the direct and indirect effects of a change in species j 's intrinsic growth rate on species i 's equilibrium abundance; and $\mathbf{r}$ is a column vector with intrinsic growth rates of all species.

In this thesis I have used two basic approaches to parameterize these models: (i) By drawing parameters from some preset intervals (Paper I-II) or (ii) by relating some of the parameters in the model to the average body mass of species (Paper I & IV).

Many biological characteristics of organisms have been shown to be related to organism's body masses (Peters 1984; Brown et al. 2004; Woodward et al. 2005). In general these relationships tend to follow some power function:

$$Y = Y_0 M^a \quad (3)$$

Where Y is the biological characteristic, Y_0 is a scaling constant, M is body mass of the organism or average body mass of the species and, a , is scaling exponent. Typically a tends to be some multiple of a quarter. These allometric relationships have for example been shown to predict intrinsic growth rates of species (Blueweiss et al. 1978), species natural mortality rates

(McCoy and Gillooly 2008) and ingestion rates (Peters 1984). These type of relationships can thus be used to relate some parameters in a Lotka-Volterra model to species average body mass (Berg et al. 2011; Säterberg et al. 2013; Lewis and Law 2007; Lewis et al. 2008). So, given a network with known feeding interactions and average body masses it is possible derive a dynamical description of a networks with parameters inferred from the average body masses of species.

4.1.2 Multivariate autoregressive models

Multivariate autoregressive models (MAR-models) can easily be fitted to time series of species abundances using a variety of approaches (e.g. maximum likelihood or generalized least square). MAR-models are neatly introduced by Ives et al. (2003), and have been used extensively to infer species interactions from time series of different organisms (e.g. Ives et al. 2003; Mutshinda et al. 2009; Hampton et al. 2013; Lindegren et al. 2009). The multivariate autoregressive modeling framework is based on discrete Gompertz models:

$$N_{i,t} = N_{i,t-1} \exp\{a_i - \ln(N_{i,t-1}) + \sum_{j=1}^S b_{ij} \ln(N_{j,t-1})\} \quad (4)$$

Where $N_{i,t}$ is the abundance of species i at time t , a_i is the specific growth rate of species i , b_{ij} are interaction strengths.

On a log scale, this model simplifies to a linear difference equation:

$$x_{i,t} = a_i + \sum_{j=1}^S b_{ij} * x_{j,t-1} \quad (5)$$

where $x_{i,t} = \ln N_{i,t}$. A stochastic version of the same model is a multivariate AR(1) process given by:

$$x_{i,t} = a_i + \sum_{j=1}^S b_{ij} * x_{j,t-1} + e_{i,t} \quad (6)$$

where $e_{i,t}$ are multivariate normally distributed process errors with mean vector $\mathbf{0}$ and a covariance matrix, Σ_E , assumed to affect the per capita growth rate of species. In matrix form eq. 6 is given by:

$$\mathbf{X}_t = \mathbf{A} + \mathbf{B}\mathbf{X}_{t-1} + \mathbf{E}_t \quad (7)$$

One important thing with this model is that it can be extended to include other environmental variables assumed to have an effect on community dynamics (Ives et al. 2003). In paper III I investigate the effect of changing the fishing mortality on community dynamics using this modelling framework. Fishing mortality and additional environmental covariates are therefore included in the modelling set up. If the time series of species abundances, i.e. $\mathbf{X}_t$, is mean adjusted (i.e. centered around zero) and fishing mortality and other environmental covariates are also mean adjusted, the model (eq. 7) can be described as follows:

$$\mathbf{X}_t = \mathbf{B}\mathbf{X}_{t-1} + \mathbf{C}\mathbf{U}_t + \mathbf{D}\mathbf{F}_t + \mathbf{E}_t \quad (8)$$

Where $\mathbf{C}$ is a $S \times m$ matrix with elements (i, j) giving the per unit effect of environmental covariate j on the per capita growth rate of species i , $\mathbf{U}_t$ is a $m \times 1$ vector with environmental

covariates at time t , $\mathbf{D}$ is a $S \times S$ diagonal matrix with the per unit effect of fishing mortality on species' growth rates and $\mathbf{F}_t$ is a $S \times 1$ vector with fishing mortalities at time t .

Conditional on $\mathbf{U}_t$ and $\mathbf{F}_t$, the endogenous part, $\mathbf{X}_t$, is a stationary process given that all eigenvalues of the interaction matrix $\mathbf{B}$ lie within the unit circle (Tsay 2014). The mean and covariance of the stationary process, with environmental covariates and fishing mortalities held at their mean values, is given by:

$$\boldsymbol{\mu}_x = (\mathbf{I} - \mathbf{B})^{-1}(\mathbf{C}\boldsymbol{\mu}_U + \mathbf{D}\boldsymbol{\mu}_F) \quad (9)$$

$$\text{Vec}(\mathbf{V}_x) = (\mathbf{I} - \mathbf{B} \otimes \mathbf{B})^{-1} \text{Vec}(\boldsymbol{\Sigma}_E + \mathbf{C}\boldsymbol{\Sigma}_U\mathbf{C}^T)$$

Where $\boldsymbol{\mu}_x$ is the mean vector of the stationary distribution, $\mathbf{V}_x$ is the covariance matrix of the stationary distribution, $\mathbf{I}$, is the identity matrix, $\otimes$ refers to the tensor product and “Vec” is the vector form of a matrix in which columns of the matrix are packed on top of each other, with the first column of the matrix on top. $\boldsymbol{\mu}_U$ and $\boldsymbol{\mu}_F$ refers to the mean vectors of environmental covariates and fishing mortalities, respectively. Environmental covariates affect the stationary covariance by the term $\mathbf{C}\boldsymbol{\Sigma}_U\mathbf{C}^T$, in which $\boldsymbol{\Sigma}_U$ is the covariance of the environmental covariates. This stationary distribution is used to estimate ecologically sustainable fishing mortalities in Paper III.

4.2 Network structures

Throughout this thesis I have parameterized both empirically observed (Paper I & Paper III-IV) and computer generated network structures (Paper I-II & IV). The network structures used in this thesis are summarized in table 2.

Table 2. This table summarize all ecological networks used in this thesis. *S* stands for the number of species in the community, *C*, is the connectance of the network, i.e. the proportion of possible interactions that are realized (links/S^2).

Network	Paper	S	C	Reference network structure	Reference Body masses	Reference Parameterisation
Sequentially assembled networks	I & IV	50	0.12 ± 0.02	(Säterberg et al. 2013)	-	(Lewis and Law 2007; Säterberg et al. 2013)
Cascade model	II	50	0.3	(Mougi and Kondoh 2012)	-	(Mougi and Kondoh 2012)
Bipartite network	II	50	0.3	(Mougi and Kondoh 2012)	-	(Mougi and Kondoh 2012)
Rectangular food webs	I	9	0.17	(Säterberg et al. 2013)	-	(Säterberg et al. 2013)
Baltic Sea	I & IV	9	0.19	(Berg et al. 2011)	(Berg et al. 2011)	(Säterberg et al. 2013)
Baltic Sea fish community	III	3	0.33	-	-	Paper III
Lake Vättern	I & IV	11	0.18	(Berg et al. 2011)	(Berg et al. 2011)	(Säterberg et al. 2013)
Montane Forest	I & IV	28	0.06	(Cohen et al. 1990)	(Jonsson 1998)	(Säterberg et al. 2013)
Broadstrone Stream	I & IV	28	0.20	(Woodward et al. 2005)	(Brose et al. 2005)	(Säterberg et al. 2013)
Celtic Sea fish community	I	67	0.08	(Barnes et al. 2008)	(Barnes et al. 2008)	(Säterberg et al. 2013)
Skipwith Pond	I & IV	33	0.32	(Warren 1989)	(Brose et al. 2005)	(Säterberg et al. 2013)
Trelease Woods	I & IV	24	0.09	(Cohen et al. 1990)	(Jonsson 1998)	(Säterberg et al. 2013)
Tropic Sea	I & IV	19	0.14	(Cohen et al. 1990)	(Jonsson, 1998)	(Säterberg et al. 2013)

4.3 Approaches for studying perturbations to species

Perturbations to species are introduced in two ways in this thesis: (i) by imposing large sustained press perturbations to species or (ii) by using community sensitivity analysis, which measure community wide effects caused by small changes in some model parameter. In this thesis I have induced large press perturbations through sustained changes in the mortality rate of species (Paper I-III) and community sensitivity analysis has been adopted to explore the effect of small sustained changes in the equilibrium abundance of species (Paper IV).

4.3.1 Large press perturbations

Large press perturbations are conducted using both Lotka-Volterra and MAR-models. The conceptual difference between the assumed responses of these models to press perturbations can be seen in Fig. 5. In the first papers (Paper I-II), I have used Lotka-Volterra models to investigate the effects of sustained changes in the intrinsic rate of increase of species. A gradual sustained change in the intrinsic rate of increase of species in a Lotka-Volterra model leads to a linear response (eq. 12) in all species' equilibrium abundances (Fig. 5A). How each species equilibrium abundance respond to a gradual change in the intrinsic growth rate of a certain focal species is determined by the inverse interaction matrix of the model (eq. 2). Thus, by changing the intrinsic growth rate parameter species equilibrium abundances respond in a deterministic and linear way using the Lotka-Volterra model (Fig. 5A). This should be set in contrast to the stochastic MAR-model's response to a gradual change in mean fishing mortality (Paper III), as seen in Fig. 5B. If the MAR-model is stationary it fluctuates around a certain mean, and if simulated over infinite time it gives a normal distribution with an analytically expressed variance (eq. 9). This distribution is shown in Fig. 5B. If it is assumed that the stationarity is not lost due to a change in the mean of the fishery induced mortality, then the response of the model to a change in mean fishing mortality can be predicted by eq. 9. Similar to the equilibrium of Lotka-Volterra models, the response of the stationary mean to a change in mean fishing mortality of a MAR-model is predicted by its inverse interaction matrix (eq. 9).

Figure 5. A schematic figure illustrating the response of the equilibrium of the Lotka-Volterra model (A) and the mean of a MAR-model (B), to a gradual change in one species mortality. In the Lotka-Volterra model (A), an extra mortality rate, ϵ_3 , is imposed on species no. 3. This leads to a linear change in the equilibrium abundance of all species in the system. Here, the extra mortality added to species 3 first leads to an extinction of species 2 (Paper I & II). **B)** The methodological approach used in Paper III. A gradual change in the mean fishing mortality of one species, μ_{F3} , leads to a shift in the mean of the stationary distribution of a stochastic model. Instead of investigating how large mortality rate that is needed to cause an extinction (Paper I & II), paper III instead investigates the probability that any species goes below its associated critical biomass level (not shown in this figure). This probability is found using the cumulative distribution function of the stationary distribution of the MAR-model.

4.3.1.1 Deriving mortality rates leading to an extinction in ecological networks

Given a feasible Lotka-Volterra model (eq. 1 & eq. 2) it is possible to derive the extra mortality rate induced to one focal species, leading to an extinction of any species in an ecological network. Starting at a feasible and locally stable equilibrium (eq. 2), the per capita intrinsic growth rate of species j can be changed to a new value:

$$r'_j = r_j - \varepsilon_j \quad (10)$$

Where, ε_j , is an extra mortality rate added to species j . In matrix notation this gives a new interior equilibrium:

$$\hat{\mathbf{N}}' = -\mathbf{A}^{-1}(\mathbf{r} - \varepsilon_j \mathbf{e}_j) \quad (11)$$

Where $\mathbf{e}_j$ is a vector with a 1 in the j :th row and zero elsewhere.

The new equilibrium of species i is then given by:

$$\hat{N}'_i = \hat{N}_i + \varepsilon_j \gamma_{ij} \quad (12)$$

Where γ_{ij} is the (i,j) :th element of $\mathbf{A}^{-1}$. Setting $\hat{N}'_i = 0$ in eq. 12 gives $\varepsilon_j(i) = -\hat{N}_i / \gamma_{ij}$. This is the added mortality rate to species j that will lead to an extinction of species i . It is possible to find, for every species j , the smallest added mortality, ε_j , that will lead to an extinction within the ecological network. For every species j this is given by:

$$\varepsilon_j = \min_i(\varepsilon_j(i): \varepsilon_j(i) > 0) \quad (13)$$

This is the minimum added mortality rate to species j that will lead to an extinction within the ecological community. If the species going extinct is another species rather than the species whose mortality rate is increased (species j), species j can be regarded as functionally extinct.

Thus, starting at a feasible and locally stable equilibrium point an extra mortality rate that is large enough to cause an extinction within the ecological community is added to a certain focal species. The new equilibrium (eq. 11) might be unstable. This could lead to other extinctions within the community, or to another qualitative dynamical behavior of the system. Furthermore, the system might become unstable before the extinction occurs, i.e. if the added mortality is smaller than the added mortality needed to cause an extinction within the community. A local stability analysis (Tab. 3) indicate that the equilibrium of many of the ecological networks used in this thesis are stable just before the extinction occurs, and when the extinction occurs many equilibria of these systems lose their stability.

Table 3. *The proportion of ecological networks exposed to an added mortality rate that are locally stable just before an extinction occurs and after the extinction. The subdivision of the second table is based on the different parameter combinations and network types used in paper II. The three first columns of this table indicate: (i) the proportion of mutualistic links in the system; (ii) the degree of self-regulation among species in the system; and (iii) the network type.*

Systems used in Paper I				
			Stable before	Stable after
Baltic Sea			0.56	0.23
Broadstone Stream			1.0	0.48
Lake Vättern			0.90	0.43
Mountane Forest			1	0.50
Skipwith Pond			1	0.48
Tropic Sea			0.81	0.37
Trelease Woods			1	0.5
Celtic Sea			0.91	0.51
Sequentially assembled webs			0.91	0.46

Systems used in Paper II				
Prop. mutualistic links	Degree of self-regulation	Netw_type	Stable before	Stable after
Antagonistic	Low	Cascade	0.95	0.44
Antagonistic	Low	Bipartite	0.99	0.51
Antagonistic	Intermediate	Cascade	0.98	0.47
Antagonistic	Intermediate	Bipartite	1.0	0.48
Antagonistic	High	Cascade	1.0	0.50
Antagonistic	High	Bipartite	1.0	0.49
Low	Low	Cascade	0.75	0.32
Low	Low	Bipartite	0.59	0.28
Low	Intermediate	Cascade	0.81	0.41
Low	Intermediate	Bipartite	0.77	0.37
Low	High	Cascade	0.98	0.51
Low	High	Bipartite	0.94	0.48
High	Low	Cascade	0.83	0.37
High	Low	Bipartite	0.72	0.36
High	Intermediate	Cascade	0.97	0.47
High	Intermediate	Bipartite	0.89	0.45
High	High	Cascade	1.0	0.49
High	High	Bipartite	0.97	0.47

4.3.1.2 Deriving ecologically sustainable fishing mortalities

Ecologically sustainable fishing mortalities are estimated using the stationary distribution of MAR-models (eq. 9). The analytical expression for the mean of the stationary distribution of the MAR-model (eq. 9) predicts how a changed mean fishing mortality affects species abundances through indirect effects. A change in the mean fishing mortality of a species thus leads to a shift in the stationary distribution (exemplified in Fig. 5B). Each fish stock is further assumed to have an associated lower critical biomass limit, below which the risk of recruitment failure is high. By using the stationary distribution of the MAR-model (eq. 9) it is possible to derive the probability that any species in a community transgresses its critical biomass limit, given a certain mean fishing mortality. Mean fishing mortalities associated with such a probability, which is smaller than a maximum risk a manager might be willing to take, can be defined as ecologically sustainable fishing mortalities. Mathematically this can be expressed as an objective function (Fig. 6):

$$\varphi(\mu'_F) = \alpha - P(\mu'_F) \quad (14)$$

Where α is a constant giving the predefined maximum acceptable risk that a manager might be willing to take, and $P(\mu'_F)$ is the probability that any species fluctuates below its Blim, given a vector of mean fishing mortalities, μ'_F .

Figure 6. This figure shows the objective function used to estimate ecologically sustainable fishing mortalities in Paper III. A positive value of this multispecies objective function is associated with an ecologically sustainable fishing mortality, whereas negative values infer unsustainable fishing mortalities. The breakpoints (A & C), where the multi species objective function is zero, reflects the limits for ecologically sustainable fishing mortalities.

4.3.2 Community sensitivity analysis

Community sensitivity analysis can be used to investigate the response of the equilibrium or the resilience of a model to small sustained changes in any model parameter (Berg et al. 2011). In a Lotka-Volterra model this could be through small sustained changes in the intrinsic rates of increase, per capita interaction strengths or the equilibrium abundance of species. In this thesis, community sensitivity analysis is used to investigate the sensitivity of resilience to changes in the equilibrium abundances of species (Paper IV). This is done in order to investigate the robustness of an analytical derived approximation saying that rare species, i.e. species with a low equilibrium abundance, primarily govern resilience in systems close instability (i.e. in systems with resilience close to zero).

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PART 2 – PAPERS

- I. Säterberg, T., S. Sellman & B. Ebenman. (2013).
High frequency of functional extinctions in ecological networks.
Nature, 499, 468-470.¹
- II. Sellman, S., T. Säterberg & B. Ebenman. (2015).
Pattern of functional extinctions in ecological networks with a variety of interaction types.
Theoretical Ecology, 9, 83-94.²
- III. Säterberg, T., M. Casini & A. Gårdmark.
Ecologically sustainable fishing mortalities – A multispecies approach for fisheries management.
Manuscript.
- IV. Säterberg, T., T. Jonsson, J. Yearsley, S. Berg & B. Ebenman.
Declining populations of rare species decreases ecosystem resilience
Manuscript.

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Papers

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