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Community Robustness Analysis: Theoretical Approaches to Identifying Keystone Structures in Ecological Communities

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*There is a pleasure in the pathless woods,
There is a rapture on the lonely shore,
There is society, where none intrudes,
By the deep sea, and music in its roar:
I love not man the less, but Nature more.*

Lord George Gordon Byron

SUMMARY

Most of the world's ecosystems suffer from stress caused by human activities such as habitat destruction, fragmentation, overexploitation of species and climate change. These factors affect the reproduction and/or survival of individual species as well as interactions between species in ecological communities. Forthcoming effects of this are altered abundances, direct species loss, and indirect cascading extinctions, with yet largely unknown consequences on community structure and functioning. Today, biodiversity loss is of global concern since human society and welfare depend upon resources and services provided by ecosystems. The importance of considering entire ecological communities as a target for conservation and management has been increasingly recognized due to the interdependencies of species. Our ability to make predictions of the response of ecological communities to stress and biodiversity loss is in need of a deeper understanding of how structure and dynamical processes contributes to the functioning and stability of a community. In this thesis I use mathematical theory and dynamical models to study the response of community structure and resilience to a variety of disturbances affecting species and species interactions, ranging from small perturbations (Papers I-II) to large perturbations (species extinctions, Papers III-IV).

In Paper I we develop Community Sensitivity Analysis (CSA) as an analytical tool to study how a small *permanent* perturbation to the intrinsic growth rate, or mortality rate, of species is expected to affect *i*) the resilience (return rate) and *ii*) the structure (distribution of species equilibrium abundances) of an ecological community. Species interactions are described using Lotka-Volterra predator-prey dynamics. We apply CSA on the pelagic food webs of Lake Vättern and the Baltic Sea, respectively, and find that a change in the mortality rate of large-bodied species has a higher impact on community resilience and structure, compared to a perturbation to small-bodied species. However, analyzing the effect of a *proportional change* to the growth or mortality rate of species (elasticity analysis) shows that small-bodied species have proportionally larger effects on species equilibrium abundances, but not on resilience. CSA can also be used to study the effect of permanent (absolute or proportional) changes to inter- and intraspecific interaction strengths. For the two pelagic systems used in this study, CSA reveal that changes in the effect of a prey on its consumer tend to affect community structure and resilience significantly more than changes in the effect of a predator on its prey.

In Paper II we assess the importance of rare species for the structure and resilience of ecological communities. First we show analytically, for a two species predator-prey system, that a change in the intrinsic growth rate of the rare species affect resilience more than a change in the growth rate of the common species. To test the generality of these results we next apply CSA on complex model food webs. In the analysis we distinguish between four trophic groups, each including only species with a similar trophic position, to separate the effect of abundance from the trophic position of species. Using mixed effect models we find

support for our analytical predictions. More precisely, we find a strong negative relationship between the importance (sensitivity) of a species and its equilibrium abundance within all consumer groups and a weaker, but significant, relationship for producer species. The results from this study suggest that rare species can act as keystones through their effect on both community resilience and community structure, regardless of its trophic position.

In Paper III we evaluate the risk of food web collapse caused by different trait-based extinction scenarios. In previous studies, groups of species, e.g. rare species, large-bodied species and top predators, have been identified to be relatively more prone to extinctions and other studies have found that extinctions of such species have comparably small effects on the remaining community. Using mathematical models of species dynamics we study the response of ecological communities to species removal (i.e. the proportion of species needed to be primarily removed to cause a 50% reduction in species richness, R^{50}) when species are sequentially removed from the food web based on eight different traits. We show, contrary to some previous studies of sequential extinction simulations, that communities can be very vulnerable to realistic species loss. We furthermore find that the response of communities seems to depend on whether the extinction sequence follows a bottom-up or top-down direction, making it difficult to identify one particular extinction sequence as the most important/severe sequence.

Finally, in Paper IV we aim to identify traits of species that can be used to identify keystone species, in terms of causing the highest proportion of secondary extinctions following their loss, in food webs with different degree of disassembly. Moreover, we analyze if the loss of a species that triggers a cascade of many secondary extinctions are the same species being identified as a keystones using Community Sensitivity Analysis. To answer these questions we randomly remove species from a set of 100 model communities. We analyze the relationship between the number of secondary extinctions following the randomly removed species and a range of species traits in communities where *i*) 75-100% of the initial number of species remain, *ii*) 50-75% of all species remain, *iii*) 25-50% of all species remain and *iv*) only 0-25% of all species remain. We find that the variation in secondary extinctions explained using species traits increases when the degree of food web disassembly and food web connectance are taken into account. The most important trait varies for different degrees of food web disassembly and also depends on whether basal species can go primarily extinct or not. However, due to correlation between most important traits, we conclude that the key status of different traits is rather robust against structural changes in the model food webs. Interestingly, food webs seem to be most sensitive to a random species loss after the loss of more than 25% of all initial species, suggesting that there is a threshold from which secondary extinctions increases. We also conclude that species being identified as keystones, based on the effect of their loss, are to some extent the same species being identified as having the largest effect on community structure and resilience, respectively, following a small perturbation.

POPULÄRVETENSKAPLIG SAMMANFATTNING

Biologisk mångfald är den imponerande variationsrikedomen av gener, arter och deras livsmiljöer. Tyvärr minskar denna mångfald i en alltmer ökande takt och bidragande faktorer till detta är förstörelse av arters livsmiljöer, överutnyttjande av arter, klimatförändringar och invasiva arter. Förlust av biologisk mångfald kan äventyra människans framtida chanser till välfärd och god hälsa då vi är beroende av de material, resurser och tjänster som olika ekosystem levererar. Då arter interagerar både direkt (exempel predator-byte interaktion) och indirekt (exempel konkurrens med andra arter) med varandra kan störningar av arters tätheter påverka stabiliteten och funktionerna i den näringsväv (ekologiska samhälle) som arter lever i. I denna avhandling presenterar jag fyra studier där jag studerar hur strukturen och resiliensen (återhämtningstid efter en störning) hos olika näringsvävar påverkas när arter utsätts för små störningar (Paper I-II) samt när arter dör ut (Paper III-IV).

I den första studien (Paper I) utvecklar vi en metod som analytiskt uppskattar hur känslig resiliensen samt arters sammanlagda jämviktstätheter är mot små störningar i en arts tillväxt/dödlighet. Vi tillämpar metoden på två pelagiska näringsvävar av Östersjön och Vättern. Resultaten visar att stora arter (stor kroppsvikt) påverkar stabiliteten och strukturen mer i näringsvävarna när dessa utsätts för små störningar, jämfört med småvuxna arter. Känslighetsanalysen kan också tillämpas för att studera hur små förändringar i interaktionsstyrkor mellan eller inom en art påverkar strukturen och resiliensen. För de pelagiska näringsvävarna i Östersjön och Vättern finner vi att en förändring i bytets effekt på predatorn har störst påverkan på resiliensen och strukturen.

I den andra studien (Paper II) visar vi med hjälp av analytiska härledningar samt känslighetsanalys av komplexa näringsvävar att ovanliga arter påverkar resiliensen och jämviktsstrukturen hos arters tätheter mer än vad vanliga arter gör, när dessa utsätts för små störningar. Vi finner att ovanliga arter är viktiga för stabiliteten och strukturen oavsett var i näringskedjan de befinner sig. Att ovanliga arter skulle vara mer betydelsefulla för dynamiken (resiliensen och jämviktstrukturen av arters tätheter) i en näringsväv är inte tidigare påvisat, och studien utgör en viktig grund för kommande prövningar av innebörden av ovanliga arter för balansen i näringsvävar.

I den tredje studien (Paper III) studerar vi hur sårbara näringsvävar är för olika sekvenser av artutdöenden. Vi finner att artrikedomen minskar snabbast när arter dör ut på ett icke slumpmässigt sätt. I verkliga ekosystem har man funnit att vissa grupper av arter har högre utdöenderisk än andra, exempelvis toppredatorer, storvuxna arter och ovanliga arter. Genom att simulera artutdöenden i näringsvävar, där utdöendeordningen är baserad på olika egenskaper hos arten (exempelvis arter med stor kroppsvikt dör ut först eller arter långt ner i näringskedjan dör ut först), kan vi studera om näringsvävar är mer känsliga för förlust av vissa specifika arter. Vi finner att den totala artrikedomen i näringsvävar minskar snabbast (på grund av sekundära utdöenden) när arter med empiriskt identifierade höga

utdöenderisker försvinner från näringsväven, det vill säga, när ovanliga arter, storvuxna arter och arter högt upp i näringskedjan dör ut.

I den fjärde studien (Paper IV) analyserar vi om egenskaper som utmärker nyckelarter förändras i takt med att arter dör ut och strukturen hos näringsväven förändras. En nyckelart är här en art vilkens försvinnande från näringsväven resulterar i att många andra arter också dör ut (s.k. sekundära utdöenden). Vi finner att den enskilt viktigaste egenskapen hos arter som bäst kan förutsäga antalet sekundära utdöenden förändras allteftersom näringsväven bryts ner men beror främst på om primärproducenter ingår i de slumpmässiga primära artutdöendena. Fokuserar vi enbart på primära utdöenden av konsumenter visar resultaten att nyckelartsstatusen hos arter är tämligen robust mot förändringar i näringsvävens struktur. Dessutom finner vi att antalet sekundära artutdöenden är som högst först efter att ca 25 % av alla arter redan dött ut. Detta innebär att näringsvävar kan brytas ner än fortare efter att flera arter redan försvunnit från väven.

Ovanliga arter, arter med stor kroppsvikt och toppkonsumenter är grupper av arter som löper stor risk att dö ut från verkliga ekosystem på grund av pågående globala förändringar och mänsklig påverkan. Sammantaget visar resultaten från denna avhandling att störningar (stora som små) på arter inom dessa grupper har störst påverkan på näringsvävens struktur och stabilitet (resiliens). Detta belyser vikten av ett effektivt bevarandearbete där den globala utarmningen av arter hålls tillbaka och på sikt minskar.

LIST OF PAPERS

- I. **Berg S.**, M. Christianou, T. Jonsson & B. Ebenman (2011) Using sensitivity analysis to identify keystone species and keystone links in size-based food webs. *Oikos* 120:510-519
- II. **Berg S.**, T. Jonsson, C. Hauzy, T. Säterberg, M. Christianou, J. Yearsley & B. Ebenman. (2013) Rare but potentially important: perturbations to uncommon species have disproportionately large impact on ecological communities. *Submitted manuscript*¹
- III. **Berg S.**, A. Pimenov, C. Palmer, M. C. Emmerson & Jonsson, T. (2013) Ecological communities are vulnerable to realistic extinction sequences. *Manuscript*
- IV. **Berg S.**, A. Pimenov, C. Palmer, M. C. Emmerson & Jonsson, T. (2013) Using species traits to predict secondary extinctions during food web disassembly. *Manuscript*

My contributions to the papers:

Paper I: All authors contributed in planning the study, **S.B.** and M.C. performed research, B.E. and M.C. derived analytical results. **S.B.**, B.E. and T.J. wrote the paper.

Paper II: **S.B.**, M.C., B.E., and T.J. designed the project, **S.B.**, B.E., C.H., T.J., T.S. and J.Y. performed research, **S.B.**, C.H. and T.J. analysed the data, B.E. and J.Y. derived analytical results and wrote Box 1. **S.B.**, C.H., T.S wrote Methods and Supplementary Information text, **S.B.**, B.E. and T.J. wrote the initial draft of the main text and C.H., T.S. and J.Y. contributed to manuscript editing.

Paper III: All authors contributed in planning the study. A.P. and **S.B.** ran the simulations and **S.B.** analyzed the data. **S.B.** and T.J. wrote the paper, with contributions from A.P., C.P. and M.C.E.

Paper IV: All authors contributed in planning the study. A.P. and **S.B.** ran the simulations and **S.B.** analyzed the data. **S.B.** and T.J. wrote the paper, with contributions from A.P., C.P. and M.C.E.

¹ Submitted to *Ecology*

PUBLICATIONS NOT INCLUDED IN THIS THESIS

- I. Jacob, U., Thierry, A., Brose, U., Arnts, W.E., **Berg, S.**, Bret, T., Fetzer, I., Jonsson, T., Mintenbeck, K., Möllmann, C., Petchey, O.L., Riede, J.O. & Dunne, J. (2011) The role of body size in complex food webs: a cold case. *Advances in Ecological Research* 45, 181-224

- II. Kaneryd, L., Borrvall., **Berg, S.**, Curtsdotter, A., Eklöf, A., Hauzy, C., Jonsson, T., Münger, P., Setzer, M., Säterberg, T. & Ebenman, B. (2012) Species-rich ecosystems are vulnerable to cascading extinctions in an increasingly variable world. *Ecology and Evolution* 2, 858–874

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INTRODUCTION

Everywhere on earth, most species are adapted to environments of continuous natural habitats. Though, due to massive habitat changes caused by humans (Vitousek *et al.* 1997) and additional factors such as overexploitation, invasive species and climate change, the world is losing species at an exceptionally high rate that is predicted to lead to the earth's sixth mass extinction (Shipper *et al.* 2008; Barnosky *et al.* 2011). Ironically, the effect of human actions on natural systems will affect their ability to provide a range of different ecosystem services that human welfare rest upon, such as provisioning (the production of renewable resources) and regulating services (services that lessen environmental change) (Worm *et al.* 2006; Cardinale *et al.* 2012). A body of studies has recently showed the importance of biodiversity on many aspects such as human health (Fuller *et al.* 2007), economic growth (Guo 2010) (Costanza *et al.* 1997) and ecosystem functioning (Ives & Cardinale 2004; Isbell *et al.* 2011; Hooper *et al.* 2012). The current loss of biodiversity put these services at risk, in fact, it may cause major shifts in ecosystems (Estes *et al.* 2011) and a recent study show that the earth may approaching a planetary-scale transition due to human impact (Barnosky *et al.* 2012). It is thus of immediate importance to learn more about how ecosystems respond to changes in their environments. As biological systems consist of many species that operate on different trophic levels and interact directly and indirectly with each other (e.g. through prey-predators interactions, mutualism and symbiosis), their complexity make them a real challenge to work with and to understand. However, using different approaches, from observations and monitoring of real ecosystems through experiments to analyses of theoretical models, we can gain insights into how these system function and increase our knowledge of how they respond to the ongoing species loss and identify mechanisms that drive these changes. As revealed by both empirical observations and theoretical experiments, it is widely acknowledged that the loss of one species can trigger a cascade of secondary extinctions, operating through the community (Terborgh *et al.* 2001; Borrvall & Ebenman 2006; Estes *et al.* 2011) with consequences on the functioning and stability of ecosystems. Yet, the effects of species loss on community robustness are strongly influenced by the identity of the lost species (Pimm 1979; Cardinale *et al.* 2006). However, the contribution of species to the persistence of ecological communities may differ widely as their importance is defined by the type of ecosystem of which it is a part, the type of process/function studied as well as presence/absence of other species (Worsfold 2009; Isbell *et al.* 2011). That is, the contribution and importance of species is expected to be context dependent. Thus, we need to identify species and species attributes that contribute to buffering ecological communities against stochastic as well as anthropogenic disturbances for various types of ecosystems and processes. In this thesis, I use a theoretical approach to study how perturbations to species affect *i)* the ability of the community to recover from temporary perturbations (Papers I and II), *ii)* the risk of food web collapse (Paper III) and *iii)* number of secondary extinction following one primary loss (Paper IV). The analyses are performed on complex model food webs, in most cases composed of 50 species. In the first two papers I focus on the effect of small perturbations (i.e. press

perturbation on the growth- or mortality rate of species) and in paper III and IV large perturbations (i.e. species losses) are simulated.

Using mathematical models to analyze the response of food webs to anthropogenic pressure will help us to understand the importance of different parameters and structures that can be difficult to study using field experiments. Also, with the help of theoretical approaches, hypothesis can be put forward that can be further evaluated in the field. Taken together, combining the knowledge gained from different areas (e.g. mathematics, theoretical ecology, empirical ecology and data science) may give us the information needed to be able to forecast the future of our ecosystems.

AIMS

The overall aim of this thesis is to develop new tools to identify keystone species necessary for maintaining the structure of ecological communities and the processes going on within them. This is done by studying the effect on ecological communities to various forms of perturbations, ranging from small changes in the mortality rates of species to sequential losses of species from local communities. By analyzing what characteristics that is associated with the species that, if perturbed or lost, causes the greatest change in community structure and stability, potential keystone species can be identified. See below for a more specific description of the objectives of each of the included papers.

- Paper I Development of a new tool, community sensitivity analysis (CSA), to analyze the effect of small changes in species intrinsic growth- or mortality rates on community structure and resilience.
- Paper II Assessing the importance of rare species to community structure and resilience.
- Paper III Evaluating the effect of different trait-based extinction sequences on community robustness (i.e. the risk of food web collapse).
- Paper IV Identify what species traits (if any) that are good predictors of the importance of species for community robustness and analyze if the keystone status of a species change as the structure of the food web change.

FOOD WEBS AND IMPORTANCE OF COMMUNITY STRUCTURE

All living organisms in a specific habitat, the interactions among these organisms as well as their interaction with the physical environment (e.g. water, climate, soil, temperature and humidity), is defined as an ecosystem (Primack 2002). The interdependence of species within an ecosystem can be described in different ecological networks, each describing one type or a mixture of interactions between species (trophic and/or symbiotic). Mutualistic networks describe interactions beneficial for both of the interacting species, for example a pollination network (Memmott, Waser & Price 2004; Bascompte & Jordano 2007; Ramos-Jiliberto et al. 2012). Interactions beneficial for one and negative for the other of the two interacting species build up host-parasite and predator-prey interaction networks (Poulin 2010) and interactions not beneficial for either of the two interacting species (although both species do not need to be equally negatively affected) build up competitive networks (Allesina & Levine 2011). A food web is a predator-prey network that describes all feeding relationships (i.e. who eats whom), ranging from primary producers to top predators (hereafter trophic network, ecological community, food web and system are used synonymously). In this thesis, I focus on networks with two types of interactions; predator-prey interactions and competition interactions. Figure 1 shows a model food web generated using an assembly algorithm (see section Model food webs algorithms), with structural properties similar to what's been observed in empirical food webs. Here, the nodes represent species and the links represents feeding relationships.

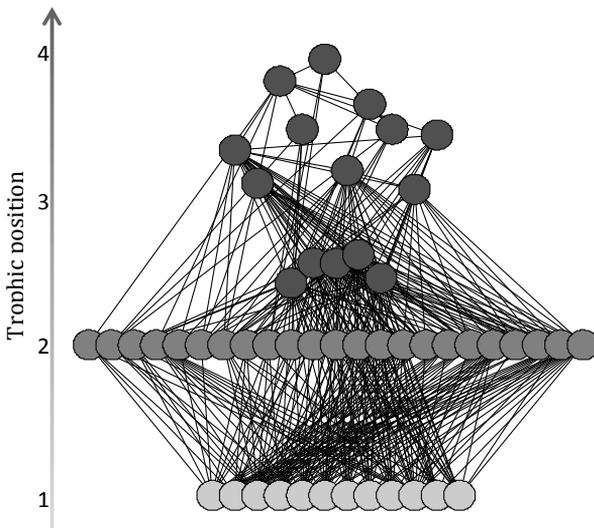


Figure 1. Schematic illustration of a food web where the links represent feeding relationships between the species (nodes). The trophic position of species increases along the y-axis, ranging from primary producers to secondary consumers. The food web is generating using an assembly algorithm (Paper II).

The behavior and stability of ecological communities depends on the topology of the system (Borrvall, Ebenman & Jonsson 2000; Thébault & Fontaine 2010; Stouffer & Bascompte 2011). For example, the architecture of networks that favors stability in trophic networks differs from those that enhance stability in mutualistic networks (Thébault & Fontaine 2010). Additionally, modules or building blocks within communities that are frequently found in natural food webs have been found to make significant contributions to community persistence (Stouffer & Bascompte 2010). Therefore, the structure is of great importance and needs to be considered when studying effects of changes in species environments. To discriminate between different community structures, various food web statistics can be calculated. Table 1 lists a number of properties describing the structure of communities.

Table 1. Food web properties.

Food web properties	
Number of species (S)	Number of trophic levels
Link per species (L/S)	Number of omnivore species
Connectance (L/S^2)	Body size distribution
Predator-prey ratio	Distribution of interaction strengths
Fraction of basal-, intermediate- and top species (B/S, I/S, T/S)*	Degree distribution (the frequency of species with L links)
Proportion of links between B-I	Number of cannibalistic species
Proportions of links between I-T	Mean shortest chain lengths (MSC)
Proportions of links between T-B	Trophic modules**

*Basal species refers to autotrophs, intermediate species refers to species being consumed and consume, top species refers to species with at least one prey but no predators. ** Trophic modules refer to different ways three species can be connected to each other (Stouffer & Bascompte 2010).

Thanks to the massive search for patterns in the structures of empirical observed food webs (see for an early summary (Cohen, Briand & Newman 1990)) ecologists have begun to identify values and ranges of these properties that characterize real communities. An early view was that many properties (e.g. connectance and link diversity) were scale invariant, that is, they had a general value across food webs with different species richness (Riede *et al.* 2010). However, using more highly resolved food webs, Riede *et al.* (2010), found that 16 different food web properties, including connectance and link diversity, are in fact not scale invariant but change with species richness. Information of food web properties describing different types of communities are used when generating model food webs. Finding an algorithm that can generate the structure of ecological communities, similar to those found in real communities, is of high importance as one need to use replicates of food webs in the process of answering questions about how, for example, trophic cascades and stability change with species diversity. Moreover, using model food webs with different food web properties, the importance of different structures on community robustness can be evaluated, for example, are low connected communities less robust than highly connected

communities, or are communities with a certain body-size distribution more robust compared to other body-mass distributions? The answer to such questions can provide insightful information on features that stabilize ecological communities and what structures are more vulnerable to disturbances.

Model food web algorithms

In 1985, Cohen & Newman presented the so called *cascade model* (Cohen & Newman 1985). This model is based on only two parameters, species richness (S) and link density, the total number of links in the food web (L). In the process of creating a food web, species are randomly distributed in a one dimensional hierarchy that is determined by some parameter, e.g. body size, and each species can only feed on species that has a lower position in the hierarchy than themselves. The probability that one species consume a species lower in the hierarchy is equal to the connectance (L/S^2) of the system. This assumption creates a predation matrix that is strictly upper triangular, a shape that is frequently found in many aquatic systems (Woodward, Speirs & Hildrew 2005). Though, in many terrestrial communities it is not uncommon that a species consume a prey that is bigger than itself. In 2000, Williams & Martinez presented a modified version of the cascade model, the *niche model* (William & Martinez 2000). The major difference from Cohen & Newman cascade model is that the species are here restricted to predate on the nearest prey species, those falling within the niche width of the predator. This means, in contrast to the cascade model, that species can predate on prey bigger than themselves which in turn creates a predation matrix that is not strictly upper triangular. The niche model was an improvement in the search of finding a model that could reproduce qualitative patterns from empirical food webs like link density and connectivity. Yet, compared to more recent documentation of empirical food webs, the niche model perform less good in generating a realistic proportion of herbivore species, where the number of such species generally are highly underestimated (William & Martinez 2008).

Both the cascade model and the niche model are phenomenological ways to generate the structure of an ecological system. Though, in 2008, Petchey *et al.* presented a more mechanistic way to construct a food web, the so called *allometric diet breath model* (hereafter ADBM). Here, using the body size of species and optimal foraging theory, the ADBM predicts the diet of each species by estimating the set of prey that maximizes the rate of energy intake for each consumer. Compared to a set of real food webs, the ADBM manage to predict on average 65 % of the links (Petchey *et al.* 2008a).

One challenge when working with the dynamics of ecological communities is to find a parameterization of the system (interaction strength, growth- and mortality rates and equilibrium abundances) that result in feasible, locally stable systems (i.e. a parameterization that allows all species to coexist in a deterministic environment). The above described model food web algorithms can all generate systems with many species,

however, the parameterization of a dynamical model of such large communities to locally stable communities is a challenge that ecologists still try to work out. One way of solving this issue is to incorporate dynamics during the build-up process of the food web structure. *The assembly algorithm* developed by Säterberg (see Paper II) is similar to the approach developed by (Lewis & Law 2007) but use local stability, instead of the permanence criteria, as a measure of food web stability (as permanence becomes to computational demanding as the number of species increases). This assembly algorithm successfully generates large complex feasible and locally stable community configurations. During the assembly process, Lotka-Volterra predator-prey parameters are obtained using metabolic theory, that relates the feeding requirements of consumers to their average species body size (see section *Theoretically predicted interaction strengths*). Starting with a feasible locally stable system consisting of a predefined number of basal species, new species are randomly drawn from one of three trophic-groups (autotroph, herbivore or carnivore species) and are introduced in the food web. All species present in the system with an average body mass falling within the diet breath (defined by consumer/resource body size ratio) of this consumer will be fed upon. For each new species added to the system the equilibrium of the newly invaded system is checked for feasibility and local stability, if not reached the added species is removed and another species is introduced. This process continue until the desired number of coexisting species is reached.

Knowing the structure of an ecological community enables a variety of analysis to take place, for example, how the loss of one node (species) changes food web structure (see section *Topological analyses*). However, if we aim to learn more about how fluctuations in species abundances affect community function and stability, we need to add population dynamics to this structure.

The Lotka-Volterra model

Working with prey and predator interactions, the population dynamics of species are often described using the Lotka-Volterra equation:

$$\frac{dN_i}{dt} = N_i \left(b_i + \sum_{j=1}^n a_{ij} N_j \right) \quad (1)$$

Here dN_i/dt is the rate of change of abundance of species i with respect to time in a community with n species, b_i is the intrinsic per capita growth rate (if i is an autotroph) or mortality rate (if i is a consumer) of species i , and a_{ij} is the per capita effect of species j on the per capita growth rate of species i . The Lotka-Volterra equation is based on some simplified assumptions, for example, the per capita growth rate b is set to a constant, that is, it is density independent, and the relationship between the prey and its predator is proportional to the product of predator and prey densities, that is to say, the predator consumes more of its prey as the prey becomes more abundant without any saturation (i.e.

the functional response is of type I). This latest simplification can though be modified using other functional responses, most often type II or type III (Holling 1959).

There are alternative to describe species dynamics than the traditional Lotka-Volterra model. For example, Yodzis & Innes (1992) presented a two-species consumer-resource model with type II functional response where body size and metabolic categories are used to parameterize the model which describe biomass dynamics (dB/dt) of the two populations (Yodzis & Innes 1992). In 2006, Brose *et al.* extended this model to multispecies systems, allowing both type II and type III functional responses of consumers. This extended version have for example been used to study the impact of body size ratios on community persistence (Brose, William & Martinez 2006; Rall, Guill & Brose 2008). However, one set back using this approach is the difficulties of finding stable food web parameterizations as the non-linear functional response have destabilizing effects (see section below). As a consequence of this, species will in general go extinct from the very beginning of a simulation resulting in difficulties in separating between perturbation-caused extinctions and deterministic extinctions due to the unstable model.

Functional response

The relationship between prey density and number of prey consumed by each predator is called the predator's functional response. Holling (1959) described three different functional responses (see figure 3). Looking at functional response type I, the predator is equally efficient in capturing and consuming prey independent of prey density, i.e. there is a liner relationship between number of prey consumed and prey density, resulting in a neutral stabilizing effect of population dynamics. Though, looking at functional response type II, the predator becomes less and less efficient in capturing and consuming prey as prey density increases (due to the consumer becoming satiated, which in turn is determined by the time it takes for the predator to kill and eat the prey) resulting in a destabilizing effect. Following functional response type III, the predator becomes more efficient in consuming prey individuals (with increasing prey density) at low densities, compared to at high densities where the response saturating, consequently bringing a stabilizing effect when prey density is low, but a destabilizing effect when prey density is high.

As the proportion of a prey population that is consumed by each predator depends on the functional response, the choice of functional response in modeling studies will have consequences for the ability of predators to control prey populations (Pimm 1991; Stiling 2002). Comparing functional response type I-III, type II and III appear to be the most realistic description of a predator's success in finding and consuming prey. Though, functional response type I has been argued to act as a good description when species are close to their equilibrium abundances (Case 2000).

In this thesis, I use model food webs with Lotka-Volterra dynamics and functional response type I. Using this approach, I can use analytical methods to study the effect of perturbations

to complex, locally stable and feasible communities. This can so far not be done using models with functional response type II or III, where smaller food web configurations are used instead (e.g. (Kaneryd *et al.* 2012)).

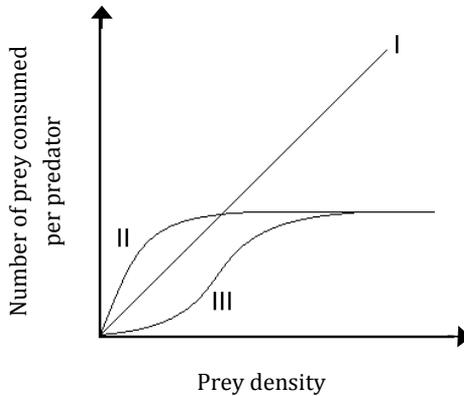


Figure 3. Functional response type I, II and III, the number of prey consumed by each predator relative to prey density.

Interaction strengths

The dynamical response of a community to perturbations is partly determined by the distribution and strength of interactions between and within species in the community. Interaction strengths can be defined in several different ways and three commonly used definitions used by theoretical ecologists are *i)* elements of the Lotka-Volterra interaction matrix (the α_{ij} 's or the per capita effect of one species on the per capita growth rate of another species) *ii)* elements of the community matrix (or the Jacobian matrix, i.e. the per capita direct effects of one species on the population growth rate of another species near its equilibrium) and *iii)* elements of the inverse interaction matrix (the per capita net effects (summarizing both direct and indirect effects) of one species on the equilibrium density of another species) (Berlow *et al.* 2004).

In a Lotka-Volterra system interactions are summarized by the coefficients in the interaction matrix a_{ij} (the per capita effects of species j on the per capita growth rate of species, see equation 1). Earlier research found that complex food webs can be dynamically stable if most of the interactions between species are weak (McCann, Hastings & Huxel 1998; Woodward *et al.* 2005). Other studies indicated that non-random patterning of strong and weak interaction strengths is critical for stability of complex food webs (Berlow *et al.* 2004) and showed that asymmetric interactions in mutualistic networks enhance stability. We know that interaction strengths are crucial for the dynamics of ecosystems, though; one big challenge is to derive realistic interaction strengths to use in our models.

How to estimate interaction strengths

To this date, there are only a few studies that have tried to estimate interaction strengths using experiment in the field. Designing an experiment to measure the Lotka-Volterra predator prey interaction coefficients (α_{ij}) can be done using exclosures where the target species (i.e the predator) is removed and the change in abundance of the focal species (prey species) is observed. Importantly, the response of every species is not fixed, it is a function of time. Removing the target species, the response of the focal species will initially be dominated by direct effects (i.e. the response in prey density caused by removal of the predator) but with time more and more indirect effects (i.e. change in prey density as a result of, among other things, competitive prey species which also lost their predator) will accumulate and after a long time, the response of the focal species will be the sum of both direct and indirect effects, i.e. net effect. Hence to estimate the per capita effect of one predator individual on the per capita growth rate of the prey (α_{ij} , the direct effect), the instantaneous growth rate of the focal species should be measured on as short time as possible (to avoid indirect effects) and divided by the duration of the experiment, to get the growth rate of the focal species, and finally divided by the abundance of the target species to get the per capita effect.

Empirical estimations of interaction strengths

The earliest field experiments performed to estimate interaction coefficients didn't consider time in their formulas, and most likely, both direct and indirect effects was captured in their estimations of per capita effects. An early experiment was performed by Paine (1992), who removed kelp grazers and measured the change in brown algae after 8 month(Paine 1992). Using a number of treatments Paine found a distribution of interaction strengths with a few strong and many weak interactions. These results are consistent with the findings of Raffaelli & Hall (1996). They used data from field experiments in the Ythan estuary in Scotland to estimate the strength of interactions of 36 links, between six consumer species and six prey species. Using the same formula as Paine (1992), the per capita effect of species j on the per capita growth rate of species i was estimated by:

$$\alpha_{ij} = \frac{\frac{\text{treatment density} - \text{control density}}{\text{control density}}}{\text{predator density}}$$

where treatment density was the density of species i in presence of species j , control density was the density of species i in absence of species j , and predator density was the density of species j . They found that 76 % of all the studied links had very small per capita values and only a few ones had large negative per capita values (Raffaelli & Hall 1996). However, it should be acknowledge that it is very unclear what proportion of these interaction coefficients that is direct versus indirect effects. In 2010, O'Gorman *et al.* empirically estimated the interaction coefficients (a_{ij}) in the shallow subtidal of Lough Hyne, using

mesocosm. The direct effect (a_{ij}) was calculated in a similar way as Paine (1992), but here different t (duration of the experiment) was accounted for.

Theoretically predicted interaction strengths

Body size ratio

Estimating interaction strengths in the field is a time-consuming process and ecologists try to find out how to derive realistic interaction strength using theory. Different theoretical approaches have been used when estimating interaction strengths between a prey and its predator. One way is to assume that the interaction strengths are functions of the body size ratio of species (Emmerson & Raffaelli 2004) according to:

$$a_{ij} = \phi \left(\frac{M_j}{M_i} \right)^\theta \quad (2)$$

where M_i is the body mass of species i and M_j is the body mass of species j , ϕ and θ are scaling constants. Using laboratory-based mesocosm, Emmerson & Raffaelli (2004) obtained some empirical support for such a relationship, with a value of θ between 0.5-0.7 and $\phi = 0.0007$. Furthermore, using this formula to parameterize the food web of Ythan Estuary resulted in a dynamically stable food web.

Metabolic theory and body size allometry

Recent studies (O’Gorman *et al.* 2010; Berg *et al.* 2011) have implemented metabolic theory that relates the feeding requirements of individuals ϕ , ($\text{kg} \times \text{ind}^{-1} \times \text{time}^{-1}$) allometrically to body size, M , and assuming that, at equilibrium, the feeding requirements of a consumer population, $\Phi_j = N_j \times \phi_j$, ($\text{kg} \times \text{pop}^{-1} \times \text{time}^{-1}$) is matched by the feeding rate, F_j , of the population (i.e., $\Phi_j = F_j$). Letting $F_j = P_{ij} \times a_{ij} \times B_j \times B_i$, where P_{ij} is the prey-preference, represent the amount of biomass extracted from species i by species j and assuming that the Lotka-Volterra product $a_{ij} \times B_j \times B_i$ represents this feeding rate, we have:

$$a_{ij} \times B_j \times B_i = -F_j \times P_{ij} \quad (3)$$

This suggests that:

$$a_{ij} = \frac{-F_j \times P_{ij}}{B_i \times B_j} = \frac{N_j \times \phi_j \times P_{ij}}{B_i \times B_j} \quad (4)$$

where a_{ij} is the per unit biomass L-V interaction strength of species j on species i , B is the biomass abundance of species i and j , respectively. Using metabolic theory, the per individual feeding requirement of species j , ϕ_j , ($\text{kg} \times \text{ind}^{-1} \times \text{time}^{-1}$) can be allometrically related to body size by the relationship $\phi_j \propto M_j^\alpha$, where M_j is the body size of species j and α is a constant commonly found to be $\frac{3}{4}$ (Peters 1983; Brown & Gillooly 2003). In other words,

metabolic theory suggests that food requirement (kg) *per unit biomass* ($\phi_j = \phi_j/M_j$), per unit time, and thus ingestion or feeding rate (f_j) is given by:

$$\phi_j = \frac{f_j}{M_j} = \frac{c \times M_j^\alpha}{M_j} = c \times M_j^{\alpha-1} \quad (5)$$

where M_j is the body size of species j and α and c are two constants. Feeding rate per population (F_j), is given by:

$$F_j = B_j \times \phi_j = B_j \times c \times M_j^{\alpha-1} \quad (6)$$

The density, N , of a species can also be allometrically related to body size (Peters 1983) by the relationship: $N_j \propto M_j^\gamma \rightarrow B_j \propto M_j^{1+\gamma}$ where γ is a constant often found to be near -1 (in studies of species across trophic levels). Using above derived formulas and assuming that species biomass, B , is proportional to species body mass, the per unit biomass interaction strength (a_{ij}) (assuming that $\alpha=3/4$ and $\gamma=-1$) is given by:

$$a_{ij} = -\frac{F_j \times P_{ij}}{B_i \times B_j} = -\frac{M_j^{1-1} \times c \times M_j^{(3/4)-1} \times P_{ij}}{M_i^{1-1} \times M_j^{1-1}} = -c \times M_j^{-1/4} \times P_{ij} \quad (7)$$

Interestingly, the empirical estimated interaction strengths by O’Gorman *et al.* (2010) for the species in the Lough Hyne system, were found to be significantly correlated to the theoretically predicted interaction strengths using equation 7 (assuming that predators have no active preference, i.e. $P_{ij}=1/s_j$ where s_j is the number of prey species of predator species j).

STABILITY OF ECOSYSTEMS

The diversity-stability debate

Ever since 1950 scientists have looked for factors that could buffer against instability and make a system more or less robust. An early view of ecosystem stability was that diversity begets stability (Odum 1953; MacArthur 1955; Elton 1958). For example, Elton (1958) observed that simplified terrestrial communities seemed to display more and stronger fluctuations in population density than more diverse terrestrial communities. From these observations Elton argued that simple communities were more easily upset than richer ones, which in turn made them more vulnerable to invasions. Moreover, Elton also found a relationship between insect outbreaks and cultivated land where human agricultural practice to some extent had contributed to create more simplified ecological communities. According to Elton, these insects' outbreaks did not occur in more diverse tropical forest which in turn led him to argue that complex communities prevented populations from undergoing explosive outbreaks. This part of Elton's work was closely related to the ideas of MacArthur (1955). He argued that the greater the connectance (the proportion of possible interactions that are realized) the greater the stability. For example, if the abundance of one prey or predator species declined it could cause a dramatic change in the abundances of other species in a community with low connectance. But, if the system is well connected, other species would buffer against this dramatic change. This view has to some extent resurfaced in the insurance hypothesis (Yachi & Loreau 1999) which hypothesizes that there will be less variation in ecosystem properties with increasing species richness as this increases the probability that a failure by any one species can be covered by another species, assuming that there is an uncorrelated responses of species to environmental fluctuations. The early views of Elton and MacArthur were challenged in the 1970's when theoretical results showed that diversity and complexity tend to cause instability in random networks (Gardner & Ashby 1970; May 1972; May 1973). The basis in this argumentation is borrowed from Newtonian physics which manifest that the more diverse and connected a system is, and the longer the pathways for a perturbation to spread and the less stable the system will be. The assumptions behind the models used to obtain these results have been looked into and criticized (DeAngelis 1975; Cohen & Newman 1985). First, the model communities used by Gardner & Ashby (1970) and May (1972) were randomly constructed. DeAngelis (1975) argued that such random networks did not necessarily have the same properties as more realistic non-random communities. He found, for example, if self-regulation of species at higher trophic levels or donor dependence is included in the model, the probability of stability could actually increase with increasing connectance. Moreover, (Yodzis 1981) found that if the interaction strengths between species in food webs of variable sizes are arranged in a specific way to produce plausible community matrices and not randomly distributed as in the case of May's studies, the probability of finding stable communities increased. Despite these objections, the new view presented by May and others became the new paradigm during the 70s and 80s. However, at the end of the 1990's the diversity-stability debate took

a new turn. McCann *et al.* (1998) published a study showing that weak interactions between a consumer and a resource species tend to dampen the fluctuations, which kept both populations away from a density close to zero. By this mechanism, diverse communities could be able to persist through time (McCann, Hastings & Huxel 1998).

One reason why it may be hard to find a general relationship between diversity and stability could be due to the various forms of *stability*, that different researches focus on (Pimm 1991; Grimm & Wissel 1997; Loreau *et al.* 2002). Out of 70 stability concepts (see table 2 for examples) at least 163 definitions have been developed by different authors (Grimm & Wissel 1997). Thus, measuring robustness using a specific stability definition could give rise to a positive diversity-stability relationship while using another definition could result in the opposite pattern (McCann 2000; Ives & Carpenter 2007). A survey done by Ives & Carpenter (2007) of diversity-stability relationships (total 64 relationships) using empirical approaches showed 69% positive relationships and 14% negative relationships. However, these empirical studies have focused on a few number of stability measures (e.g. variability, resistance and invasibility) and more than half of the commonly used theoretical definitions have not been evaluated empirically. In addition, few of these studies have sorted out the underlying mechanism for the positive (and negative) diversity-stability relationships found in the empirical systems. As concluded by Ives & Carpenter (2007), the important task is not to continue the search for generalities in diversity-stability relationships, but to investigate responsible mechanisms. Here, theoretical approaches can be of use provided that they are able to capture the dynamics of empirical systems realistically.

The stability concepts presented in table 2 can all be used to study/measure stability using theoretical approaches. However, which concept is most proper to use depends on the inherent dynamics of the system and the type of perturbation the system experience (if any). When deciding how to measure stability of ecological communities, Ives & Carpenter (2007) argued that the following aspects should to be considered: *i*) does species densities fluctuate without any external disturbance, *ii*) does the system have alternative stable states, *iii*) does the system have one single equilibrium point (i.e. species densities will not fluctuate in the absence of an external disturbance), *iv*) does perturbations occur rarely or frequently and *v*) does the perturbation include species extinctions or invasions of new species.

Table 2. Examples of stability concepts.

Stability concepts	
<i>Non-equilibrium states</i>	
Chaotic or periodic attractor	For systems with nonpoint attractors, an unstable attractors is called chaotic attractor, and stable and regular attractors are called periodic attractors. If the attractor is chaotic, the system is considered to be less stable. Suitable when no external perturbation acts on the system.
Persistence	The ability of a system to maintain itself through time. Generally used for unstable systems before a perturbation occur.
Amplitudes of fluctuations	The lower amplitude-fluctuations in species densities, the higher stability. Suitable when no external perturbation act on the system.
<i>Alternative stable states</i>	
Number of alternative stable states	The fewer alternative states, the higher stability.
Holling's resilience	How much disturbance a system can absorb before switch to a alternative stable state.
<i>Stable equilibrium point</i>	
Resilience	The return rate back to the reference state after a disturbance. Most suitable when perturbations occur rarely.
Reactivity	The maximum short-term rate away from equilibrium followed directly after a perturbation. Most suitable when perturbations occur rarely.
Resistance/constancy	Variability in the change in combined densities for a given period of time. Suitable when perturbations occur frequently.
Functional redundancy	The likeliness that a species can be lost without causing further consequences on community structure and function.
<i>Response to species loss</i>	
Secondary extinctions	The number of species going secondary extinct due to a primary loss.
Compensatory dynamics	Compensatory change in combined densities of all remaining species.
<i>Response to species invasion</i>	
Extent of secondary extinctions	Measure the extent of secondary extinctions following the establishment of invasive species.
Successful establishment	Measure the probability of a successful establishment of invasive species.

Keystone species

As described above, ecologists have for a long time sought to find a general relationship between stability and diversity. This question, to some extent, assumes that it is the total number of species that is important, not the identity or characteristics of individual species. However, within any ecosystem, there can be species that, when perturbed or even lost, may cause more far-reaching consequences on the structure and stability when compared to other species in the community. In 1969, Robert Paine named such species keystone species. According to Paine a keystone is a species that has a far greater impact on its community than one would expect it to have, considering its total biomass or overall numbers (Paine 1969). Scientists have tried to find out if the loss, or decline in population size, of some groups of species is likely to induce a trophic cascade of secondary extinctions more than others. According to (Hambäck *et al.* 2004) predator species have an important role in shaping the structure and composition of ecological communities. There are a number of studies that show how the loss of predators can lead to radical changes in species composition (Terborgh *et al.* 2001; Reiwitz, Estes & Simenstad 2006; Estes *et al.* 2011) of ecological communities, or even cause a local collapse of the ecosystem (Estes & Palmisano 1974). Interestingly, Isbell *et al.* (2011) found, among 147 grassland plants, that 84% of the species promoted ecosystem functioning. The importance of species was found to be linked to four combined factors; 1) place, 2) time (year), 3) type of function and 4) type of environmental impact. This study supports the hypothesis that many species can act as keystone species if considering variation in these factors, that is, different species promoted ecosystem functioning at different places, at different years, for different functions and under different environmental conditions. In this thesis, I make use of the term keystone species. However, my definition of a keystone is somewhat modified to denote species that, when perturbed or forced extinct, have a higher impact on community dynamics and/or structure relative to other species. In paper II we identify rare species as keystones, in terms of their effect on community structure and resilience. Low abundant species, on average, have a higher trophic position compared to more abundant species in real ecosystems (Jonsson, Cohen & Carpenter 2005) as in our model food webs, and as mentioned earlier, top predators have been found to have drastic effects on community robustness when they are lost from ecosystems. Interestingly, we find that rare species have disproportionately large effects on community resilience and structure compared to common species, independent of trophic position, when subjected to a small permanent perturbation to their growth or mortality rate.

Using models of communities, the behavior and response of food webs to perturbations, and the identity of keystone species, can be studied using topological- and dynamical approaches. An introduction to these methods is presented below.

TOPOLOGICAL AND DYNAMICAL APPROCHES

Topological analyses

Topological analyses are based on the structure of the food webs and its properties (see table 1). Here, species densities are usually not considered, only the interaction structure and number of species. Using this information, one can identify differences in structure between, for example, species rich and species poor communities, or between aquatic and terrestrial communities. From here, we want to see whether some patterns/structures are associated with the robustness against species removal when ignoring population dynamics. Using this approach, Solé & Montoya (2001) showed that systems with a skewed link distribution (i.e. with a few highly connected species embedded in a network with many poorly connected species) were very robust against random species removals (that is, food web fragmentation was unusual, meaning that remaining species and modules of species were almost always connected to other species or modules as species were randomly removed). However, when species were removed in a selective way, starting with the most connected species, the system turned out to be highly vulnerable (Solé & Montoya 2001). One thing to bear in mind working with topological species removal experiments are that the results tends to reflect a “best case scenario”. Here, a species goes secondary extinct (i.e. goes extinct due to a primary extinction) only when it has lost its entire set of prey species (Srinivasan *et al.* 2007; Dunne & Williams 2009; de Visser, Freymann & Olf 2011; Jacob *et al.* 2011). This means that the loss of a top predator could never cause any secondary extinctions under this scenario, as no other species is dependent on this top predator as a resource, nor can basal species go secondary extinct as they are autotrophs (see figure 2 for an illustration of this example). Hence, the number of secondary extinct species obtained using a topological estimation will represent the likely minimum number of secondary extinctions caused by one primary loss. One can ask why do scientists still use these approaches. The reason is simple; by ignoring dynamics and interaction strengths, one can work with larger food webs (more species), that are difficult to parameterize and analyze dynamically (Dunne & Williams 2009).

Dynamical analyses

The dynamics of species in an ecological community are influenced by a series of interactions, such as predator-prey interactions and competitive interactions. In this way species interact both directly (e.g. when one species predate on another species) and indirectly (e.g. two consumer species that predate on the same prey species) with each other. The main difference between topological and dynamical approaches is that topological models only focus on the structure of a community (which includes the direct effect of one species on another) whereas a dynamical model also consider indirect effects on species dynamics (e.g. generated from changes in species densities) (Ebenman & Jonsson 2005). This major difference between the topological- and dynamical approach can give rise

to important differences in the predicted outcome of extinction scenarios. See figure 2 for an illustration of secondary extinctions predicted using a dynamical approach and using a topological approach.

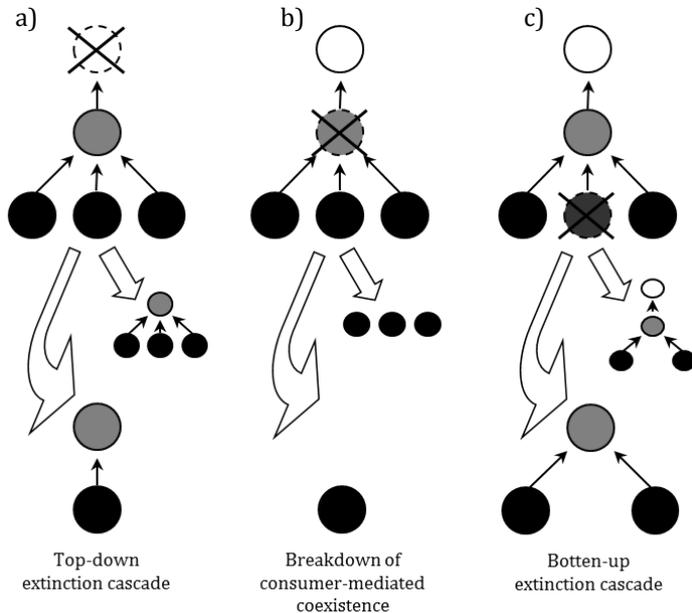


Figure 2. Three illustrations of how food web structure changes (i.e. how many species that goes secondary extinct following one primary species loss) after **a)** loss of a top species (white circles), **b)** loss of an intermediate species (grey circles) and **c)** loss of a basal species (black circles). The small arrows points to the post-extinction community predicted using a topological species extinction model and the big arrows points to the post-extinction community predicted using a dynamical species extinction model (after Ebenman & Jonsson (2005)).

Local and global stability

A system with a locally stable equilibrium will return to this equilibrium following a small perturbation. This criteria makes the concept “local stability” (in literature also called asymptotic stability or neighborhood stability) very simple and useful in computer analysis. A straight forward definition of local stability is that when we have an equilibrium point N^* that is locally stable, all solutions which begin from an initial condition sufficiently close to N^* will converge to N^* as time goes to infinity (Roughgarden 1979). However simple and appealing, it raises the question how close to N^* must the initial condition be for the system to return to equilibrium? To be able to answer this one needs to look for the domain of attraction for a specific equilibrium, which is defined as the region around an equilibrium from which all starting points will move towards the equilibrium in question (see figure 4). Analytical methods to obtain the domain of attraction are rarely available for nonlinear systems, e.g. Lotka-Volterra systems. Furthermore, if the perturbation away from

equilibrium is large, local stability can be compared with global stability. A system that is globally stable will return to equilibrium after any perturbation, no matter the size of this perturbation (Begon, Townsend & Harper 2006).

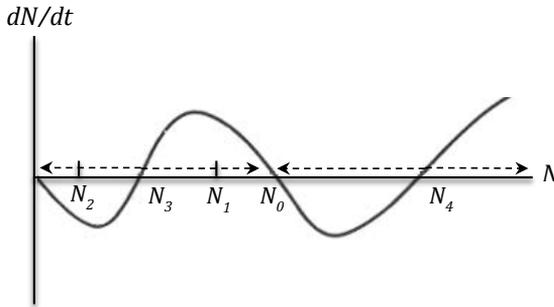


Figure 4. Domains of attraction for a single species. Here, N_0 is locally stable, that is, if N is displaced to N_1 it will return to N_0 . Though, if N is displaced to N_2 it will not go back to N_0 as dN/dt is negative. Both N_3 and N_4 are locally unstable meaning that the slightest initial displacement will make the system move away from these points (Yodzis 1989).

Resilience

Among theoretical ecologists resilience (Λ) is often defined as the rate at which a perturbation is disappearing and the community is returning to equilibrium (Pimm 1991; DeAngelis 1992; Neubert & Caswell 1997). Yet, there is another well-known definition of resilience as well. Holling (1973) defined resilience as a measure of the ability of a system to absorb changes of state variables, driving variables and parameters and still persist (see also resistance and robustness in table 2) (Holling 1973). This alternative definition of resilience has been and is still in focus in several research projects (e.g. (Folke *et al.* 2004; Walker & Salt 2006) but here I only consider resilience as being the rate of return to equilibrium following a perturbation.

The classical theoretical definition of resilience requires that the community is locally stable, otherwise the return rate back to equilibrium cannot be assessed. The most frequently used estimate of resilience is based on the eigenvalues of the system at its equilibrium. More specifically, it is determined by the negative of the real part of the dominant eigenvalue (λ_1) of the Jacobian matrix \mathbf{C} of the community (i.e. $-\text{Re}(\lambda_1(\mathbf{C}))$), provided that $\text{Re}(\lambda_1) < 0$ and that a positive equilibrium exist $N^* > 0$ (Neubert & Caswell 1997). Under Lotka-Volterra dynamics with functional response of type I the Jacobian coefficients can easily be calculated using the interaction coefficients (a_{ij}) and the equilibrium abundances (N^*) of the species:

$$c_{ij} = \alpha_{ij} \times N_i^*$$

Resilience can also be expressed as return time, that is the time it takes for the system to recover a certain fraction of the displacement from the equilibrium after a small perturbation (Yodzis 1989; Pimm 1991; DeAngelis 1992). If the resilience turns out to be high, the system will go back to equilibrium comparably fast, hence giving a comparably low return time (Pimm 1991; Stone, Gabric & Berman 1996). The most recent empirical support of resilience as a measure of recovery rate and indicator of a system approaching instability was found by Veraart *et al.* 2012. Here, using microcosms with cyanobacteria populations, the team found that recovery from small perturbations became slower as the system moved towards a critical point, i.e. towards an unstable system (Veraart *et al.* 2012). In theory this means that a negative eigenvalue of **C** that is still very close to zero, and hence very close to instability, will result in a low recovery rate, and vice versa.

Perturbation analysis using dynamical models

These days only a few places on earth still exist under purely natural conditions. Other places have, to some extent, been affected by humans. Thus, analyzing how ecological communities behave in the presence of perturbations may provide us with useful information and reveal targets for conservation actions. According to (Pascual & Dunne 2006), conservation of functional ecosystems will benefit from a deeper understanding of how structure and dynamical processes contributes to stability in case of a perturbation. In all the included papers in this thesis I make use of different perturbation analyses (i.e. CVA and CSA, see sections below) to identify crucial structures/keystone species for different ecosystem processes when exposed to external disturbances.

Community Viability Analysis (CVA) and sequential losses of species

CVA is a technique used to estimate the number of secondary extinctions taking place in a community as the result of one primary loss. It was initially developed by Ebenman *et al.* (2004) and these authors showed, using quasi collapse risk curves, that the removal of certain species, in this case basal- and intermediate species, resulted in a higher probability of secondary extinctions compared to removal of a top predator. The quasi collapse risk is the probability that the number of species in a food web falls below a certain level within a fixed period of time as the result of one species removal (Ebenman, Law & Borrvall 2004). The technique can further be used to identify crucial food web structures. A community structure is labeled fragile if the loss of this structure, on average, results in many species going secondary extinct (Ebenman & Jonsson 2005). Theoretical single species removal experiments have been applied on a range of different communities to identify vulnerable structures and keystone species (e.g. (Eklöf & Ebenman 2006; Petchey *et al.* 2008b). For example, Eklöf & Ebenman (2006) identified communities with a low connectivity to be less robust against single species removal, compared to communities with a high connectivity. Moreover, well connected species in these model food webs caused the highest number of secondary extinctions.

Dealing with single species experiments, one would like to ask how communities respond to additional or repeated species losses. The interest in this question has resulted in a number of studies, either simulating or empirically monitoring how sequential loss (based on certain traits, e.g. body size and connectance) affect community structure (Larsen, Williams & Kremen 2005; Curtsdotter *et al.* 2011; de Visser, Freymann & Olf 2011). In paper III, we show that realistic extinction scenarios, for example when low abundant species or large-bodied species goes sequentially extinct, cause a relatively fast collapse of the community (i.e. species richness is reduced by half) through secondary extinctions following the primary losses. So far, only two studies (Paper III & Curtsdotter *et al.* 2011) have incorporated dynamics in species response to sequential loss and additional studies will be needed to evaluate the effect on different food web structures.

Community Sensitivity Analysis (CSA)

Originally, sensitivity analysis means a study of the variation in the output of a mathematical model as a result of variation in its input parameters. In contrast to community viability analysis (see above), sensitivity analyses often study the response of small perturbations. In ecology, sensitivity analysis has long been used to analyze how the growth rate of a stage- (or size-) structured population would be affected if there were to be a change in some demographic variables of the species. This analytical technique, presented by Caswell (1978), has been useful in the management of endangered species but also in the work of how to control pests (Caswell 1978; Benton & Grant 1999). Having a stage-structured species, its growth rate is given by the eigenvalue of the projection matrix (see figure 5). From here, we can study how this growth rate (λ) changes as a result of changes in its coefficients (d_{ij}):

$$\frac{\partial \lambda}{\partial d_{ij}} = \sum_{i,j} \frac{\bar{v}_i w_j}{\langle \mathbf{v}, \mathbf{v} \rangle} \quad (5)$$

where d_{ij} is element ij in projection matrix \mathbf{D} , \mathbf{v} and \mathbf{w} are the right and left eigenvectors corresponding to the dominant eigenvalue, v_i and w_j are elements of the respective vectors and \bar{v}_i is the complex conjugate of v_i , $\langle \rangle$ represent the scalar product of the vectors (Brault & Caswell 1993). Performing a sensitivity analysis on an ecological community is not far from Caswell's original concept. Using the same formula (equation 5), we can study how the dominant eigenvalue (λ) of a community model (i.e. resilience) is affected by changes in the elements of the community matrix (i.e. the Jacobian coefficients c_{ij} are used instead of d_{ij} in equ 5) (see also figure 5). However, as the Jacobian coefficients are products of interaction strengths (a_{ij}) and equilibrium abundances (N^*) their ecological interpretation may become somewhat abstract. Thus, in Paper I, we present formulas to study how the resilience is affected by small changes in *i)* predator-prey interactions, *ii)* intra- and interspecific interactions and *iii)* growth- or mortality rates of species. In Paper I, we also derive formulas for assessing the sensitivity of community structure, i.e. the distribution of species equilibrium densities, to small changes in model parameters *i-iii*.

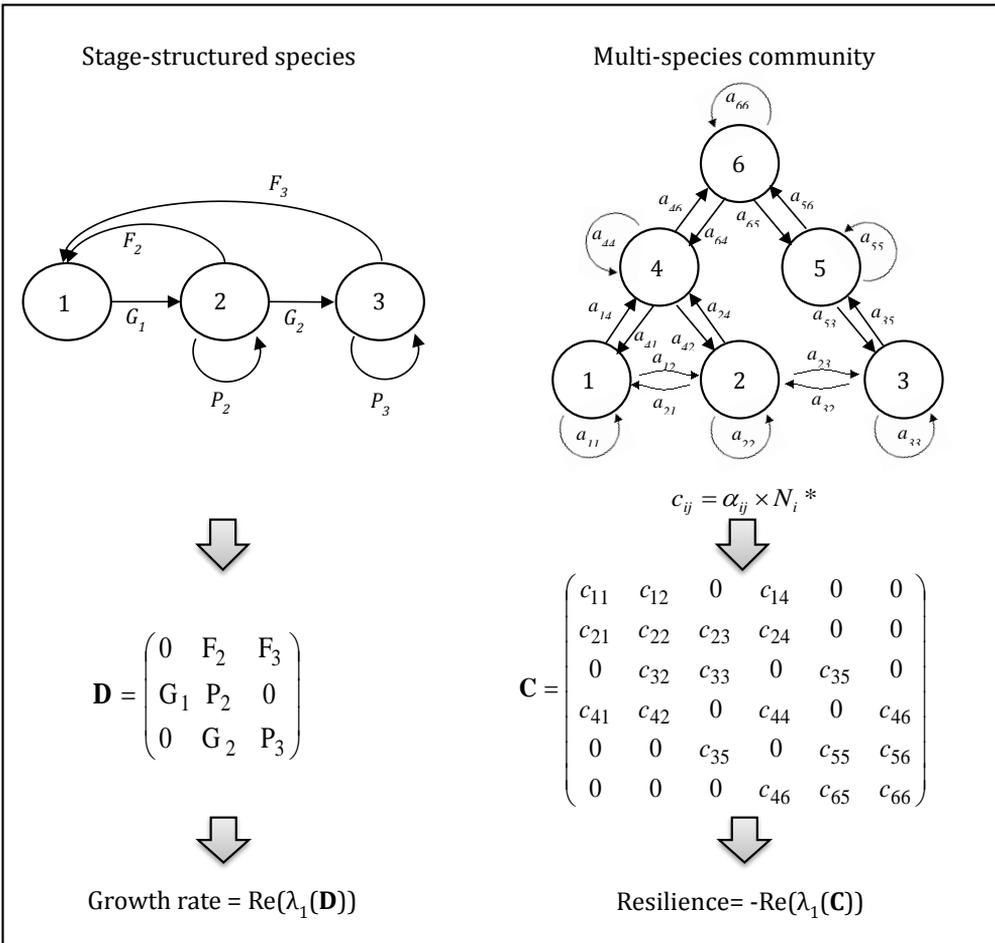


Figure 5. Illustration of a stage-structured single species model next to a multispecies model. Both these configurations can be presented in two matrices, **D** (Lefkovich’s matrix) and **C** (Jacobian matrix), which eigenvalues represents the growth rate of the single species model and community resilience of the multi-species model. For the stage-structured model, the circles represent stage classes, (1) yearlings; (2) juveniles and young adults; (3) reproductive adults, the F_n represent fecundities, the G_n represent probabilities of surviving and growing to the next stage, and the P_n represent the probabilities of surviving and persisting in the same stage (Benton & Grant 1999). For the multi-species model the circles represent six species on different trophic levels (1-3) basal species, (4, 5) herbivore species and (6) carnivore species. The straight arrows, α_{ij} , where i is the prey and j is the predator show the impact each species has on another species, α_{ii} represent the intra-specific competition and α_{ij} on the horizontal arrows represent inter-specific competition.

To sum up, community sensitivity analysis is used to study the response, of community resilience and community structure, to small changes in species intrinsic growth- or mortality rates, and in interactions occurring between and within species. Applying this approach on a

multi-species community, the association between species characteristics and their effect on community resilience and structure, respectively, can be evaluated. Figure 6 show the relationship between body size and the sensitivity values associated with individual species in the pelagic systems of the Baltic Sea and Lake Vättern, respectively. Here it can be seen that large-bodied species is predicted to change community structure and resilience more, if they are perturbed, compared to small-bodied species.

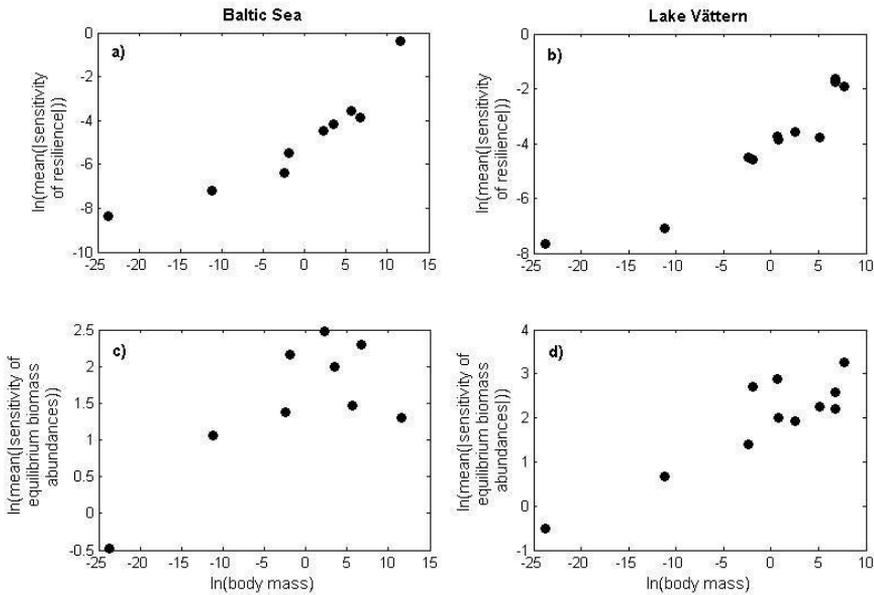


Figure 6. Sensitivity of resilience in **a)** Baltic Sea and **b)** Lake Vättern, and sensitivity of equilibrium abundances in **c)** Baltic Sea and **d)** Lake Vättern, to a change in the intrinsic growth- and mortality rates of species. Regression analysis show for **a)** $R=0.914$, **b)** $R=0.942$, **c)** $R=0.752$ and **d)** $R=0.895$. All relationships has a p -value <0.02 . From paper I.

A similar analysis to community *sensitivity* analysis is community *elasticity* analysis. While sensitivity analysis estimates the impact of an *absolute* change on community stability, elasticity analysis estimates the effect of a *proportional* change instead. To clarify this further, all species have a so called baseline mortality (or original mortality, b_0) before any perturbation starts to act and an additional mortality caused by the perturbation (b_p), i.e. the total mortality (b_t) becomes $b_t=b_0+b_p$. Different perturbations may affect the baseline mortality differently, i.e. in an absolute or a proportional way. If causes of mortality act independently of the value of the baseline mortality, e.g. an external factor affecting all individuals just as much, then this extra mortality rate created by the perturbation can be added to the baseline mortality as a constant $b_t=b_0+b_p=b_0+c$. However, if the perturbation modifies the already existing baseline mortality this produce a proportional change in the baseline mortality according to $b_t=b_0+b_p=b_0+c \times b_0=b_0(1+c)$

MODEL FOOD WEBS AND THE REAL WORLD

Model food webs are simplified descriptions of complex natural networks with species and species interactions being the results of millions of years of evolution. However, data on food web structures and properties (see table 1) from real communities have enabled theoretical ecologists to mimic the structure of real observed ecological communities. Combining food web structure and species dynamics (i.e. species abundances, interaction strengths and growth rates), we can build either explanatory or predictive models of ecological communities and gain insight into how species and food web properties respond and are affected by different kinds of perturbations. The explanatory models are used to test causal hypothesis, for example, is there a relation between body sizes of species and their effect on community resilience? The predictive models, on the other hand, should predict new or future observations, for example, in year 2020, the stock of cod in the Baltic Sea will increase with 20% of its current stock size (Shmueli 2010). In this thesis I analyze explanatory models to investigate what structures are associated with community robustness. Yet every model is based on simplifying assumptions, leading to questions of how realistic these models are in the description of species dynamics and food web structure. In the papers included in this thesis, I describe species dynamics using Lotka-Volterra interactions with a linear functional response (type I, see figure 3). This modeling framework implies that a predator can consume more prey as prey density increases without any saturation limit. Such a linear relationship gives a good estimation of population dynamics close to equilibrium (Case 2000). However, it should be acknowledged that when population densities are far away from equilibrium, functional responses of type II or III may provide a better description of predator foraging behavior. Functional response II and III include that predators consumption of prey species will be limited by a handling time which can be defined as the time it takes for a predator to catch and consume its prey. The reason why type II or III functional response is not used here is the complexities this brings into the equations and the analyses of those equations and the difficulties in finding large complex locally stable food webs.

In real communities, species are influenced by the presence of other species through a range of different interactions which can be beneficial or detrimental (e.g. mutualism, parasitism, competition). In the models developed here, symbiotic interactions are not considered, only competition interactions and predator-prey interactions. For studies of mutualistic network, see e.g. (Fortuna & Bascompte 2006; Bascompte 2009) and for a comparison of structures that enhance stability in ecological communities and mutualistic communities, see Thébaud & Fontaine (2010).

To sum up, the models presented in this thesis is not a perfect representation of real communities. A number of simplifications have been made which make the models manageable to work with, yet at the cost of description details of community dynamics. Still, using these models we can conduct experiments not possible in an empirical setting, for example, due to moral principles (i.e. how will species in the food web respond when

different species face extinction). Additionally, models allow us to examine carefully defined and controlled scenarios and separate the effect of different model parameters which can reveal interesting hypothesis that can be further tested and evaluated using field experiments.

CONCLUDING REMARKS

The aim of this thesis is to study the robustness of food webs to small as well as large perturbations and as part of this develop tools for identification of keystone structures in ecological communities. In the analysis performed in the included papers, species can respond dynamically to changes in species abundances. By the use of Community Sensitivity analysis (developed in Paper I), which analyzes the effect of small perturbations, we identify the importance of rare species for the structure and resilience in complex communities (Paper II). However, due to global change species are also subjected to large perturbations which results in species going extinct. In Paper III, we find that sequential losses of species following a top-down orientated direction, that is, when species high up in the trophic hierarchy are lost more frequently than species with a lower trophic position, results in a higher risk of community collapse. Furthermore, shown in Paper IV, as species are lost from their communities, the number of secondary extinctions following one primary loss increases with the number of primary extinctions and peak before species richness are reduced by half.

Field studies have identified certain groups of species as having a high risk of extinction, including top predators, rare species and large-bodied species. The analysis performed in this thesis identifies and highlights the importance of these groups of species for upholding the stability (resilience) and structure of ecological communities. Taken together, the ongoing species loss may strike hard on our ecosystems with a potential accelerating effect. This calls for caution and conservation of species are not only for ethical reasons but also for ecological reasons.

To finally conclude, the question whether some species are more important for the balance in ecosystems must be answered using a combination of different approaches (including theoretical and empirical approaches). In this thesis, complex ecological communities are analyzed using theoretical approaches. The structures and dynamics of these model communities mostly mimic the structure and dynamics found in aquatic and marine communities. For the future, the search for keystones must also be done in a variety of other networks and descriptions of species dynamics must be adapted to the identity of the system.

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