Linköping Studies in Science and Technology.

Dissertations, No 1609

Extinctions in Ecological Communities – direct and indirect effects of perturbation on biodiversity

Alva Curtsdotter

Linköping University
INSTITUTE OF TECHNOLOGY

Department of Physics, Chemistry and Biology
Division of Theory and Modelling
Linköping University
SE – 581 83 Linköping, Sweden
Linköping, August 2014

Linköping Studies in Science and Technology. Dissertations, No 1609

Curtsdotter, A. 2014. Extinctions in Ecological Communities – direct and indirect effects of perturbation on biodiversity

ISBN 978-91-7519-278-9

ISSN 0345-7524

Copyright © Alva Curtsdotter unless otherwise noted

Front cover: Designed by Staffan Sunnerud.

Photo: Coral reef in the Red Sea, ©IBorisoff, distributed via istockphoto.com

Printed by LiU-Tryck

Linköping, Sweden 2014

Also available at LiU Electronic Press

<http://www.ep.liu.se>

*To my Mother and Father.
It's all because of you.
Thank you!*

“Doing science is not such a barrier to feeling or such a dehumanizing influence as is often made out. It does not take the beauty from nature. The only rules of scientific method are honest observations and accurate logic. To be great science it must also be guided by a judgment, almost an instinct, for what is worth studying. No one should feel that honesty and accuracy guided by imagination have any power to take away nature’s beauty.”

Robert H. MacArthur (1930-1972)
in the introduction to his book
Geographical Ecology: Patterns in the
Distribution of Species, published 1972.

TABLE OF CONTENTS

Summary	i
Populärvetenskaplig sammanfattning	iii
List of papers	v

PART 1 - OVERVIEW

1. Introduction	1
1.1 Species extinctions	1
1.2 Species interactions	2
1.3 Direct and indirect effects of perturbation	4
1.4 Approaches for studying extinction responses to perturbation	6
2. Aims	8
2.1 Aims of Paper I	8
2.2 Aims of Paper II	8
2.3 Aims of Paper III	9
2.4 Aims of Paper IV	9
2.5 Aims of Paper V	9
3. Approaches and Methods	10
3.1 Community interaction structure	10
3.1.1 Niche model food webs	10
3.1.2 Probabilistic niche model food webs	11
3.1.3 Pyramidal model food webs	11
3.1.4 Natural food webs	11
3.1.5 Competition communities	14
3.2 Temporal community dynamics	14
3.2.1 Rosenzweig-McArthur model	14
3.2.2 Allometric trophic network model	15
3.3 Spatio-temporal community dynamics	18
3.4 Direct and indirect interactions in the models	19

3.5 Perturbations	22
3.5.1 Primary extinctions	22
3.5.2 Climate change – increased mean annual temperature	23
3.5.3 Climate change – increased environmental variation	24
3.6 Measures of the extinction response	25
3.6.1 Quantifying secondary extinction cascades	25
3.6.2 Quantifying total species loss	27
4. Main results and implications	28
4.1 Paper I	28
4.2 Paper II	28
4.3 Paper III	29
4.4 Paper IV	29
4.5 Paper V	30
5. Discussion	31
5.1 Competition	31
5.1.1 Basal interspecific competition, species richness and extinction risk	31
5.1.2 Basal interspecific competition in an eco-evolutionary and spatial context	31
5.1.3 Extinction risk and the pattern of interspecific competition strengths	32
5.1.4 Consumer’s intraspecific competition and extinction risk	33
5.2 Trophic interactions	34
5.2.1 The functional response	34
5.2.2 Rewiring of predator-prey interactions	35
5.3 A note on interactions not included	36
5.4 A note on diversity and stability	38
5.5 Conclusions	40
5.6 An outlook for the future	41
Acknowledgments	43
References	44

TABLE OF CONTENTS continued

FIGURES AND TABLES IN PART 1

Figure 1 Direct and indirect interactions	3
Figure 2 Food web topology	10
Figure 3 The functional response of predators	15
Figure 4 Allometric relationships	17
Figure 5 Indirect interactions	21
Figure 6 Measures of secondary extinction cascades	26
Table 1 Community properties	12

PART 2 - PAPERS

Paper I	Robustness to secondary extinctions: Comparing trait-based sequential deletions in static and dynamic food webs
Paper II	The interaction between species traits and community properties determine food web resistance to species loss
Paper III	The strength of interspecific competition modulates the eco-evolutionary response to global warming
Paper IV	Species-rich ecosystems are vulnerable to cascading extinctions in an increasingly variable world
Paper V	Adaptive rewiring aggravates the effects of species loss in ecological networks

SUMMARY

In the dawning of what may become Earth's 6th mass extinction the topic of this thesis, understanding extinction processes and what determines the magnitude of species loss, has become only too relevant. The number of known extinctions (~850) during the last centuries translates to extinction rates elevated above the background rate, matching those of previous mass extinction events. The main drivers of these extinctions have been human land use, introduction of exotic species and overexploitation. Under continued anthropogenic pressure and climate change, the current extinction rates are predicted to increase tenfold.

Large perturbations, such as the extinction drivers mentioned above, affects species directly, causing a change in their abundance. As species are not isolated, but connected to each other through a multitude of interactions, the change in abundance of one species can in turn affect others. Thus, in addition to the direct effect, a perturbation can affect a species indirectly through the ecological network in which the species is embedded. With this thesis, I wish to contribute to our basic understanding of these indirect effects and the role they play in determining the magnitude of species loss. All the studies included here are so called *in silico* experiments, using mathematical models to describe ecological communities and computer simulations to observe the response of these communities to perturbation.

When a perturbation is severe enough, a species will be driven to extinction. The loss of a species from a system is in itself a large perturbation, and may result in further extinctions, so called secondary extinctions. The traits of the species initially lost, can be a potential predictor of the magnitude of secondary species loss. In Paper I of this thesis, I show that when making such predictions, it is important to incorporate temporally dynamic species interactions and abundances, in order not to underestimate the importance of certain species, such as top predators.

I further show that species traits alone are not particularly good predictors of secondary extinction risk (Paper I), but that in combination with community level properties they are (Paper II). Indeed, there seems to be an interaction such that the specific property making a community prone to secondary species loss, depends on what kind of species was lost in the primary extinction. As different types of perturbation put different types of species at risk of (primary) extinction, this means that the specific property making a community prone to secondary species loss, will depend on the type of perturbation the community is subjected to.

One of the predicted main drivers of future species extinction is climate change. If the local climate becomes adverse, a species can either migrate to new and better areas or

stay and evolve. Both these processes will be important in determining the magnitude of species loss under climate change. However, migration and evolution do not occur in vacuum – the biotic community in which these processes play out may modulate their effect on biodiversity. In paper III, I show that the strength of competition between species modulates the effect of both dispersal and evolution on the magnitude of species loss* under climate change. The three-way interaction between interspecific competition, evolution and dispersal, creates a complex pattern of biodiversity responses, in which both evolution and dispersal can either increase or decrease the magnitude of species loss. Thus, when species interactions are incorporated, it is clear that even though migration and evolution may alleviate the impact of climate change for some species, they may indirectly aggravate the situation for others.

In Paper III, the aspect of climate change incorporated in the model is an increase in mean annual temperature. But climate change is also predicted to increase environmental variability. Paper IV shows that species-rich communities are more sensitive to high environmental variability than species-poor ones. The smaller population sizes in the species-rich communities increased the extinction risk connected to population fluctuations driven by the variable environment. Hence, systems such as tropical forests and coral reefs are predicted to be particularly sensitive to the increased variability that may follow with climate change.

In Paper IV, primary extinctions of primary producers result in extinction cascades of consumer species, when they lose their prey. However, in reality a consumer species might be able to switch to another prey, and such flexibility has both been observed and suggested as a potential rescue mechanism. But what is beneficial for an individual predator in the short-term can become detrimental to the ecological community in the long-term. Paper V shows that consumer flexibility often led to consumers continuously overexploiting their new prey, in the worst case to the point of system collapse. Thus, the suggested rescue mechanism aggravated the effect of initial species loss, rather than ameliorating it.

Overall, the research presented here, underscores the importance of including population dynamics and biotic interactions when studying the effects of perturbation on biodiversity. Many of the results are complex, hard to foresee or even counter-intuitive, arising from the indirect effects of the perturbation being translated through the living web of species interactions.

* In papers III-V, I do not differentiate between primary and secondary species loss, but look at the sum of the two, i.e. the total species loss.

Idag står vi inför en biodiversitetskris som vi själva har skapat. Över hälften av all landyta är ägnad åt jord- och skogsbruk, vilket tillsammans med överexploatering (jakt och fiske), introduktion av främmande arter samt föroreningar redan har orsakat över 800 artutdöenden de senaste århundrandena. Detta motsvarar utdöendetakter (artutdöenden/tidsenhet) i nivå med de 5 massutdöenden som livet på jorden tidigare genomgått (t ex när dinosaurierna dog ut). Utöver de artförluster som redan skett, är mer än 20 000 arter utrotningshotade, varav ca 4 500 kritiskt hotade. Därför förväntas den nuvarande utdöendetakten öka tiofaldigt under fortsatt mänskligt tryck på biosfären, i kombination med global klimatförändring. Denna biodiversitetskris är inte bara tragisk i sig, utan hotar även att allvarligt påverka tillhandahållandet av ekosystemtjänster. Dessa ekosystemtjänster är kritiska för vårt uppehälle och inkluderar t ex vatten- och luftrening, jordbildning, pollinering, mat- och virkesproduktion.

De ovan nämnda faktorer som driver förlusten av global biodiversitet kan inkluderas inom begreppet störning. En störning kommer att direkt påverka en arts abundans (individantal), genom effekter på individernas tillväxt, fortplantning eller överlevnad. Men en störning kan också påverka en art indirekt. Arter ingår nämligen i ekologiska samhällen, dvs system av växter, djur och andra organismer som interagerar med varandra. Dessa interaktioner kan t ex vara födointeraktioner (en organism äter en annan), tjänster såsom försvar eller pollen-/fröspredning eller konkurrens om föda, boplatser, ljus eller andra resurser. Därför kommer abundansförändringen av en art påverka andra arter som den interagerar med, och på så vis kan en störning fortplanta sig genom interaktionsnätverket.

Forskningen i denna avhandling syftar till att bättre förstå hur ekologiska samhällen fungerar och vad som påverkar risken för artutdöenden i samband med en störning. Närmare bestämt har jag studerat hur effekten av störning påverkas av olika egenskaper hos det ekologiska samhället, t ex antalet arter i samhället eller hur stark konkurrensen mellan primärproducenterna (växterna) är. Eftersom mitt ämnesområde är teoretisk ekologi, har de ekologiska samhällena beskrivits med hjälp av matematiska modeller och effekten av störning har undersökts med hjälp av datorsimuleringar.

I de första två studierna (Paper I & II) i avhandlingen, har jag fokuserat på sekundära utdöenden. Detta är utdöenden som sker till följd av en primär artförlust, vilken i sin tur är orsakad av en störning. Jag fann att mängden sekundära utdöenden beror på en interaktion mellan system- och artegenskaper. När växter och herbivorer (växtätare) dog ut primärt, var det strukturen (t ex andelen rovdjur i systemet) hos det ekologiska samhället som avgjorde mängden sekundära utdöenden. När det istället var toppredatorer (rovdjur högst upp i näringskedjan) som dog ut primärt, var det

dynamiska egenskaper (t ex rovdjurens inomartskonkurrens) som var avgörande. Olika störningar hotar olika typer av arter, t ex drabbar jakt och fiske rovdjur och rovfiskar mest, medan övergödning drabbar konkurrenssvaga växter mest. I ljuset av resultaten från Paper I & II innebär detta att beroende på vilken störning som ett system utsätts för, kommer det vara olika systemegenskaper som styr risken för sekundära utdöenden.

I de följande studierna (Paper III-IV) utsatte vi våra modellsystem för klimatförändring, antingen i form av en ökning i medeltemperatur (Paper III) eller som en förhöjd miljövariation (Paper IV-V). I Paper III studerade jag enkla växtsamhällen, och hur styrkan på konkurrensen mellan växterna påverkade risken för artutdöenden under klimatförändring. Denna studie skiljer sig från de andra fyra i avhandlingen, genom att den inkluderar evolution och spridning. Således kan arter undkomma klimatförändringen genom att anpassa sig på plats eller sprida sig till områden med bättre klimat. Jag fann att stark konkurrens mellan växterna skapade spridningsbarriärer i landskapet, vilket ofta ledde till katastrofala artförluster när klimatet förändrades. Jag fann även att styrkan på konkurrensen påverkade effekten av evolution och spridning. Även om spridning och evolution kan mildra effekten av klimatförändring för vissa arter, kan de indirekt förvärra situationen för andra, t ex genom att öka risken för konkurrensuteslutning (en art konkurrerar ut en annan).

I Paper IV fann vi att risken för artutdöenden var större i artrika system än i artfattiga system, när miljön är mycket variabel (t ex stora svängningar i temperatur). Populationsstorlekarna i artrika system var mindre, vilket gjorde att arterna lättare dog ut i samband med populationssvängningar. Det innebär att t ex tropiska skogar och korallrev kan vara särskilt känsliga för en ökad miljövariation i samband med klimatförändring. Utdöenderisken ökade också om herbivorer och rovdjur var specialister. Det senare indikerar att utdöenden på konsumentnivå ofta var sekundära. Utdöenderisken borde således kunna minska om konsumenter kunde börja äta andra arter efter att deras vanliga byten dött ut. Detta undersökte vi i Paper V, men fann att en sådan flexibilitet hos konsumenterna oftast ledde till att de överexploaterade sina nya byten, vilket ledde till att utdöenderisken totalt sett ökade istället för att minska som förväntat.

Många av resultaten i den här avhandlingen var komplexa och svårförutsägbara, eftersom de uppstod när störningen filtrerades genom nätverket av artinteraktioner. Sammantaget understryker de därför betydelsen av störningars indirekta effekter på ekologiska system.

LIST OF PAPERS

- I. Curtsdotter, A., A. Binzer, U. Brose, F. Castro, B. Ebenman, A. Eklöf, J. O. Riede, A. Thierry & B. C. Rall. (2011).
Robustness to secondary extinctions: Comparing trait-based sequential deletions in static and dynamic food webs.
Basic and Applied Ecology, 12, 571-580.[†]

- II. Curtsdotter, A., A. Binzer, U. Brose & B. Ebenman. (2014).
The interaction between species traits and community properties determine food web resistance to species loss.
Manuscript.

- III. Curtsdotter, A., P. Münger, J. Norberg, A. Åkesson & B. Ebenman. (2014).
The strength of interspecific competition modulates the eco-evolutionary response to global warming.
Manuscript.

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

- V. Gilljam, D., A. Curtsdotter & B. Ebenman. (2014).
Adaptive rewiring aggravates the effects of species loss in ecological networks.
Submitted manuscript.[‡]

[†] Reprinted with permission from Elsevier.

[‡] Under revision for Nature Communications.

CONTRIBUTIONS TO PAPERS

A. Curtsdotter contributed to project design in Paper I-III & V, performed research for Paper I-V, analyzed data for Paper I-III, made a major contribution to the writing of Paper I-III and a minor contribution to the writing of Paper IV-V.

The research performed for Paper I-II was developing project-specific C++ code, which was added to the already implemented modeling framework of U. Brose's research group at University of Göttingen, Germany. The research performed for Paper III, was model development and the implementation of the model in MATLAB code. The research for Paper IV was mainly performed as project discussions. The research for Paper V includes model and MATLAB code development in the early stages of the project, and project discussions in the later stages.

PAPERS OUTSIDE THE THESIS

- VI. Binzer, A., U. Brose, A. Curtsdotter, A. Eklöf, B. C. Rall, J. O. Riede & F. de Castro. (2011).
The susceptibility of species to extinctions in model communities.
Basic and Applied Ecology, 12, 590-599.

- VII. Riede, J. O., A. Binzer, U. Brose, F. de Castro, A. Curtsdotter, B. C. Rall & A. Eklöf. (2011).
Size-based food web characteristics govern the response to species extinctions.
Basic and Applied Ecology, 12, 581-589.

- VIII. Digel C., A. Curtsdotter, J. Riede, B. Klarner & U. Brose. (2014).
Unravelling the complex structure of forest soil food webs: higher omnivory and more trophic levels.
Oikos, Early View online.

OVERVIEW

**Extinctions in Ecological Communities –
direct and indirect effects of perturbation on biodiversity**

Alva Curtsdotter

1. Introduction

The research presented in this thesis, will add to our understanding of how species interactions influence the amount of extinctions that occur within an ecological community, when it is subjected to perturbation. The chosen research approach is theoretical, using mathematical models to describe ecological communities and computer simulations to observe the response of these communities to perturbation. This research is rather of a basic than of an applied nature; but in addition to this knowledge being valuable in itself, a general understanding of extinction processes is valuable for natural management and conservation.

1.1 Species extinctions

The topic of species extinctions is today only too relevant. The number of known extinctions (~850, (“IUCN 2013” 2014)) during the last centuries, translates to an extinction rate 100-1000 times above the background extinction rate (Millenium Ecosystem Assessment 2005, Pereira et al. 2010, Pimm et al. 2014). Among the most important extinction drivers are human land use, overexploitation and the introduction of exotic species (“IUCN 2013” 2014). Continued anthropogenic pressure, with the addition of rapid climate change, yields predictions of even higher extinction rates for the future (Sala et al. 2000, Millenium Ecosystem Assessment 2005, Pereira et al. 2010). The threats against biodiversity are severe and escalating (Pereira et al. 2010), and unless the trends are reversed we will hit the mass extinction threshold (loss of $\frac{3}{4}$ of extant species richness) in as little as 300-12 000 years (Barnosky et al. 2011). The looming biodiversity crisis is not only tragic in its own right, but also threatens our own livelihood (Hooper et al. 2012). The human species is ultimately dependent on a number of ecosystem services, such as soil formation, water and air purification, food production and pollination (Costanza et al. 1998). How robust the provisioning of these services will be as biodiversity dwindles is still uncertain, but it is self-evident that at some point of biodiversity loss this provisioning must suffer as well (Balvanera et al. 2006, Cardinale et al. 2012).

Species’ threat status, with regard to their risk of extinction, is listed by the IUCN, based on assessments of the species’ state and trend in population size and geographical distribution. These assessments are data-demanding and therefore time-consuming, leaving the lion share of described species yet not assessed. Currently, around 70 000 animal and plant species have been assessed (“IUCN 2013” 2014), while the described number of land plant species is approximately 400 000 and animal species is about 1.9 million (Pimm et al. 2014). As valuable as the IUCN Red List is, there is a need for a more general approach to assessing threat of extinction. In this vein, several species traits have been investigated to see whether they correlate with extinction risk; among these high trophic level, large body size, diet specialization,

rarity, small geographic range size and slow growth rate are examples of traits found to correlate with extinction risk (McKinney 1997, Purvis et al. 2000, Koh et al. 2004, Munday 2004, Cardillo et al. 2005).

These traits do not only represent properties intrinsic to a species itself, but also properties reflecting interspecific interactions. Diet specialization and other strict interspecific dependencies are a prime example. Highly specialized species are under double threat, as perturbations affecting a sole prey, obligate host or mutualistic partner are of as great concern as a perturbation affecting the specialist directly (Koh et al. 2004, Dunn et al. 2009, Colwell et al. 2012). Another example is provided by species at high trophic levels. These species can be at risk for many reasons, some of them relating directly to their position in the interaction network, as in the case of biomagnification of toxic substances along the food chain (Gray 2002). Furthermore, the length of a food chain may be limited by energetic constraints (Post 2002). In such a case, top predators may be living on the edge of what is energetically feasible, which would render them sensitive to any disturbances that diminishes the community's capability of energy production and transfer (Binzer et al. 2011).

1.2 Species interactions

In general, the impact of any perturbation on a species is likely to in part depend on the species' biotic context (Wootton 1994, Tylianakis et al. 2008). Species are connected to each other through a multitude of interactions: predation, parasitism, mutualism, competition, amensalism and commensalism (Pianka 1999, Stiling 2001, Ricklefs 2008). Through these physical interactions species affect each other directly, positively or negatively depending on the type of interaction (Fig. 1 A-E). But because of the complexity of the interaction network indirect effects also arise; sometimes of such magnitude and sign as to make the net effect of one species on another the opposite of the direct effect (Wootton 1994, Pianka 1999)(Fig. 1 F-H). In the classic trophic cascade of a tri-trophic food chain, a top-predator controls the abundance of an intermediate predator, creating a positive indirect effect of the top-predator on the basal resource (Wootton 1994, Prugh et al. 2009, Ripple et al. 2014). This indirect effect may be so strong, that even in the case of intra-guild predation it outweighs the direct negative effect of predation of the top-predator on the basal resource (Polis et al. 1989, Holt and Huxel 2007, Elmhagen et al. 2010). Another twist to the classic cascade is that simply the presence of a top-predator can alter the behavior or even physiology of the intermediate predator as to result in predation alleviation of the basal resource (interaction modification sensu Wootton 1994) (Schmitz et al. 1997, Werner and Peacor 2003, Sheriff et al. 2009, Steffan and Snyder 2009). Thus, an indirect interaction arises when the impact of one species on another is mediated by a third, and additional examples include: exploitative competition, apparent competition and competitive mutualism (Wootton 1994, Pianka 1999) (see also section 3.4).

Figure 1 | Illustrations of direct (A-E) and indirect (F-H) interactions. Species can have positive (+), negative (-) or no effect (0) on each other; see box in upper corner. Examples: (A) Trophic interactions, such as a top-predator feeding on herbivore. (B) Insect pollination of flowering plants. (C) Plant competition for light etc. (D) Ungulates trample the soil and stir up insects, benefitting cattle egrets. (E) Skew competition between plants through allelopathy; the shrub exudes chemicals which kill nearby grass plants. (F) Tri-trophic chain of plant, herbivore and top-predator. The plant and the top-predator indirectly affect each other positively (dashed line), through their effect on herbivore abundance. (G) Intra-guild predation: both lynx and fox feed on hare, but the lynx also kills foxes, indirectly benefitting the hare. (H) Presence of lions decreases cheetahs' hunting activity, benefitting the cheetahs' prey.

However, some interactions are neither physical nor mediated by another species; instead the effect of one species on another is mediated through the abiotic environment. It is debatable whether these interactions should be classed as direct or indirect, but it is unarguable that among them we find interactions of great importance, e.g. habitat facilitation, habitat formation (foundation species) and ecosystem engineering (Dayton 1972, Jones et al. 1996, Stachowicz 2001, Ellison et al. 2005, Brooker et al. 2008, Cuddington et al. 2009).

1.3 Direct and indirect effects of perturbation

Just as species affect each other both directly and indirectly, so can a perturbation affect species directly and indirectly (Frank et al. 2005, Parmesan 2006, Tylianakis et al. 2008, Casini et al. 2009, Kirby and Beaugrand 2009, Blois et al. 2013). Here, a perturbation is any event or process that substantially affects species' abundances, such as extreme events or high variability of the climate, harvesting, pollution, habitat destruction etc. Perturbations affect species' abundances directly by altering the species' vital rates, for example their survival, growth or reproduction (Roberts and Hawkins 1999, Connell et al. 1999, Parmesan et al. 2000, Bennett et al. 2002, Harley et al. 2006, Rohr et al. 2006, Turvey et al. 2007). As species affect each other directly and indirectly through the interaction network, the direct impact of a perturbation on one species' abundance will translate to an indirect effect of the perturbation on another (Connell et al. 1999, Parmesan et al. 2000, Jackson et al. 2001, Tylianakis et al. 2008, Casini et al. 2009, Blois et al. 2013). The perturbation can even affect the strength of the inter-specific interaction directly, by changing a species' behavior or its quality as a resource (Sanford 1999, Post et al. 1999, Salminen et al. 2002, Didham et al. 2007, Touchon and Warkentin 2009). For example, changing phenology of resource species, in response to climate change, can create a trophic mismatch between the resource peak biomass and the peak energetic requirement of its predator (Parmesan 2006, Post and Forchhammer 2008, Hegland et al. 2009, Both et al. 2009). Climate can also influence activity and other aspects of predator behavior, and thereby affect the *per capita* predation pressure (Sanford 1999, Post et al. 1999, Touchon and Warkentin 2009).

If a perturbation is severe, it may drive a species to local or global extinction. This primary extinction may be followed by secondary extinctions, caused not by the initial perturbation directly but indirectly as a result of the primary species loss (Ebenman and Jonsson 2005). Such secondary extinctions occur due to species' interactions and interdependencies; a predator may have lost its prey, a parasite its host or a mutualist its partner (Dunne et al. 2002a, Memmott et al. 2004, Colwell et al. 2012). These are examples of loss of direct interaction partners, but the same goes for indirect interaction partners. A prey may be overexploited by its predator when top-down control of that predator is lost; a species may be out-competed because intra-guild or

top-down control of a stronger competitor is lost; or a species may lose its habitat because the foundation species or eco-system engineer is lost (Paine 1966, Estes and Palmisano 1974, Estes et al. 1998, Ripple et al. 2014). One might think that the first species driven to extinction by a perturbation would be the one most sensitive to the perturbation's direct effect. Certainly, this may often be the case, but a recent study suggests that extinctions due to interaction-mediated indirect perturbation effects may be much more frequent than previously thought (Säterberg et al. 2013).

Species loss, whether primary or secondary, can also affect a system's sensitivity to further perturbation. As species loss goes on, it is accompanied by the erosion of diversity-related mechanisms stabilizing ecosystem function, e.g. redundancy, response diversity and compensation (Chapin III et al. 2000, Elmqvist et al. 2003, Folke et al. 2004, Gonzalez and Loreau 2009, Laliberté et al. 2010, Kaneryd et al. 2012 [Paper IV]). However, not only the number of species going extinct but their identity and traits will be important for the system's continued stability. If species go extinct in order of their sensitivity to perturbation, the community may actually become more resistant, as the average perturbation tolerance of remaining species is higher (Ives and Carpenter 2007). On the other hand, it may make the community more susceptible to other disturbances, such as invasion (Lyons and Schwartz 2001, Zavaleta and Hulvey 2004). Furthermore, species may not only differ in sensitivity, but also in their importance for community stability, for example by contributing to a more robust structure and/or more stable population dynamics (Bascompte et al. 2005, Zavaleta et al. 2009, Saavedra et al. 2011). If this community importance of species is correlated with their perturbation vulnerability, the community would instead become increasingly sensitive as it disassembled (Gilbert 2009, Zavaleta et al. 2009, Saavedra et al. 2011).

Finally, the perturbation response is not always linear. Instead the community may show an initial inertia, leading an observer to believe the system is more resistant than it is (Jørgensen et al. 2007). All the while, the system's perturbation resistance erodes, and as it reaches a critical level the system can experience a major shift in community composition and function. (Scheffer et al. 2001, Folke et al. 2004). For example, an ecological community can be quite robust to primary extinctions up to a certain threshold, after which secondary extinction cascades are triggered (Dunne et al. 2002a, Allesina et al. 2009; see also Gilljam et al. 2014 [Paper V]). This is similar to how ecosystems, following a period of seeming inertia, can abruptly change state or regime in response to perturbations, such as fishing, disease, land use change, climate change and eutrophication (Scheffer et al. 2001, deYoung et al. 2008). Examples of such abrupt shifts include clear vs turbid water states in lakes (Blindow et al. 1993), coral vs algal dominance on reefs (Mumby et al. 2007) and woodland vs grassland domination in terrestrial systems (Van Langevelde et al. 2003). The reversibility of these shifts is sometimes hindered by hysteresis in the perturbation response (Scheffer and Carpenter 2003, Schröder et al. 2005). It seems that the initial inertia, the abrupt shift and/or

hysteresis can be caused by positive feedbacks between the system state and the species it benefits, including effects on species interactions (Scheffer et al. 2001, Norström et al. 2009, Huss et al. 2013). Overall, this goes to show, that when studying responses to perturbation, there is indeed good reason to do so in a community setting of species interactions (see also Gårdmark et al. 2012).

1.4 Approaches for studying extinction responses to perturbation

Studying the effects of perturbation on ecological communities falls under the large umbrella of research regarding the stability of ecological communities, one of the main topics in theoretical ecology. Here, community stability can take many shapes, such as local and global stability (whether the community returns to its abundance equilibrium point after a small or large perturbation), resilience (rate of return to the equilibrium point), permanence (long term community persistence despite the lack of a stable equilibrium point, i.e. cyclic or chaotic population dynamics), resistance (resistance to perturbation, e.g. many extinctions = low resistance), robustness (the magnitude of perturbation needed to cause a certain magnitude of response; often the response is species loss) and biomass stability (temporal and spatial stability in population or aggregate community biomass) (see Borrvall 2006 for a concise introduction; also Ives and Carpenter 2007). When studying extinction responses to perturbation, resistance and robustness are the most commonly used stability measures. Other stability measures, specific for this sub-discipline of stability research, include the number of extinctions, extinction risk, decrease in species richness, risk curves etc.

In this line of research, the theoretical approach is for obvious reasons quite common. Large-scale experimental studies of extinction responses cannot be justified on ethical grounds, although some “natural” large-scale experiments come about through non-scientific human endeavors. Overfishing, and elimination/exclusion of large terrestrial predators, constitutes examples of such “natural” experiments (Jackson et al. 2001, Ripple et al. 2014). Indeed, the entire biodiversity crisis could be seen as a very ill-advised extinction experiment on the biosphere scale. Scientific experiments on smaller scale (e.g. smaller plots, meso- and microcosms) are however quite viable; they are ethically defensible, practically feasible and can, despite the small scale, still capture a substantial amount of biological complexity (Paine 1966, Jiang and Morin 2004, 2007, Suttle et al. 2007, O’Gorman and Emmerson 2009, Worsfold et al. 2009). Of course, all approaches have their drawbacks, and with the small-scale experiments the main criticisms regard temporal and spatial scale (Raffaelli 2005). Experiments with micro- or mesocosms or small plots, may not reflect the response of real, large-scale systems, if the response to perturbation is scale-dependent. It seems that spatial scale can indeed be very important (Hewitt et al. 2007), but before dismissing small scale experiments it should be remembered that a small absolute scale (i.e. size) does not necessarily mean a small ecological scale. As Raffaelli puts it: “...a 1m² plot for a rocky

shore limpet may be equivalent to a 10,000 km² plot for a polar bear” (Raffaelli 2005). Similar considerations of the system and its constituent species apply for the temporal scale (Yodzis 1988). But already organisms such as grasses, herbs or invertebrates may have generation times long enough to necessitate experiments to last several years in order to observe the final outcome; including more and/or larger (longer-lived) species increases the necessary duration to several decades (Yodzis 1988, Raffaelli and Moller 2000, Suttle et al. 2007, Haddad et al. 2011).

In this light, the theoretical approach (analytical or numerical) comes with several advantages. Firstly, there are no ethical concerns. Secondly, large spatial scales and spatial heterogeneity can be included. Thirdly, responses over long temporal scales can be investigated; in a simulation ten thousand years can be run in a matter of minutes to days. Furthermore, experimental control increases from observation at large scale to experimental approaches at small-intermediate scale to theoretical approaches. Control and simplicity facilitate our mechanistic understanding of extinction responses to perturbation, and the isolated mechanisms studied in these simplified systems should still operate in a more complex and realistic context. But the theoretical approach also has its weaknesses and limitations. In simulation studies, the qualitative outcome may depend on the initial conditions of the simulated system, if the system has multiple equilibria or attractors. Also, while simulation studies can encompass large scales, they will have limits for system time and size (species richness as well as space), determined by available computation power. Furthermore, control and simplicity usually comes at the expense of realism, and the importance of a mechanism, relative to other, cannot be known when studied in isolation. In conclusion, all approaches come with advantages as well as disadvantages; there is no “best” approach. Instead the approaches complement each other as tools to increase our understanding of extinction processes in perturbed ecological systems.

2. Aims

The overall aim of the thesis is to increase our understanding of how the magnitude of the extinction response, following a perturbation of an ecological community, is affected by the biotic community itself. In each of the papers presented herein, we have chosen to focus on a few selected aspects of the biotic community, ranging from simple, topological species traits to structural and dynamical properties of the community itself. In the following sections I outline the aims for each paper.

2.1 Aims of Paper I

In this study, we subject food webs to sequential species removals, mimicking non-random species extinctions. Species are removed by order of their trait value, with regard to such traits as trophic role, number of interactions and body mass. We record the resulting number of secondary extinction, and measure stability as robustness. We wish to know:

- 1) Can the magnitude of secondary species loss be predicted by the traits of the species lost in the primary (perturbation caused) extinctions?
- 2) How does the ex- or inclusion of temporal population dynamics affect the predictive power of species traits with regard to robustness?

2.2 Aims of Paper II

We use the data from Paper I and investigate the effect of community level properties on the magnitude of secondary species loss. The community level properties cover a large range of topological (structural), allometrical (body mass related) and dynamical (relating to interaction strengths and abundances) measures. We perform this analysis independently for each trait-based removal sequence. We wish to know:

- 1) Are different community properties identified for the different removal sequences, i.e. is resistance to species loss governed by an interaction between the community properties and the traits of the species primarily lost?

2.3 Aims of Paper III

In Paper III, we subject spatially explicit competition communities, with temperature dependent species growth rates, to an increase in mean temperature, mimicking global climate change. We investigate the interactive effects of interspecific competition, dispersal and evolution on the magnitude of species loss. We wish to know:

- 1) If and how the strength of interspecific competition affects biodiversity following climate change?
- 2) If and how the strength of interspecific competition modulates the effects of adaptation and dispersal on the biodiversity outcome of climate change?

2.4 Aims of Paper IV

Another aspect of climate change is changed patterns of climatic variability. Here, we subject food webs to high environmental variation, affecting species' vital rates. Given this perturbation, we wish to know:

- 1) How is the risk and extent of extinction affected by local species richness?
- 2) How is the risk and extent of extinction affected by the degree of correlation among species in their response to climatic variability?
- 3) How is the risk and extent of extinction affected by whether predators are generalists or specialists, i.e. how feeding effort is allocated among their prey?

2.5 Aims of Paper V

In Paper V, as in Paper IV, we expose food webs to high environmental variation. Here, we investigate a suggested rescue mechanism: the rewiring of consumers to novel prey after the loss of their original prey species. More specifically, we wish to know:

- 1) How does extinction risk depend on the proportion of consumers able to rewire?
- 2) How does extinction risk depend on the functional response of rewiring consumers?
- 3) How does extinction risk depend on the efficiency of consumers following rewiring to novel prey?

3. Approaches and Methods

For this research, I have simplified ecological communities by modeling them as competition communities and/or food webs. In the following sections I will present the approaches taken for modeling community structure, dynamics and perturbations and for measuring the extinction response. Although these model communities are simple, as compared to real ecosystems, they still include substantial complexity. In the final section, I will therefore sketch out which direct and indirect interaction effects these models can potentially capture and, by extension, what direct and indirect effects of perturbation can occur.

3.1 Community interaction structure

In all papers, except Paper III, the ecological community is modeled as a local food web. Three food web-generating algorithms were used, in addition to empirical food web structures (Fig 2.).

3.1.1 Niche model food webs

The food webs in Papers I & II were generated using the niche model algorithm (Williams and Martinez 2000). This algorithm is considered to generate realistic food web structures (Williams and Martinez 2000, 2008) and is widely used in theoretical food web research. The niche model creates an interaction network structure with a pre-specified species richness, S , and connectance, C . The connectance is the connection probability of species pairs in the web; here $C=L/S^2$, where L is the total number of links (interactions) in the network. Our niche model webs have 10-60 species, and a connectance of 0.05-0.30. The connectance range is within observed connectance values in natural food webs (Dunne et al. 2002b, Digel et al. 2011).

Figure 2 | Examples of food web topology: (A) generated by the probabilistic niche model [$S=24$, $C=0.16$], (B) a pyramidal model web [$S=24$, $C=0.14$] and (C) an empirical web, Montane Forest [$S=28$, $C=0.06$, see Paper V]. Black circles are basal species, dark grey are intermediate species, and light grey are top species.

Species can be primary producers, herbivores, omnivores or carnivores, and there is no constraint on the number of trophic levels. Measures of the structure of these interaction networks were used in the analysis of Paper II. These are presented in Table 1, together with the dynamical and allometrical properties of these webs, which are explained in section 3.2. Observe that the structural measures are based on the trophic links only (not competition, see section 3.2) as these are the only links created by the niche model (or any of the other food web algorithms presented here).

3.1.2 Probabilistic niche model food webs

In Paper V an extensions of the niche model was used: the probabilistic niche model (PNM) algorithm (Williams et al. 2010). In the original niche model, a species is constrained to feed on other species that are within a contiguous interval along a one-dimensional trophic niche space. The PNM relaxes this strict assumption, allowing for realistic diet gaps (Williams and Martinez 2008). The food webs contain 12-24 species, with connectance of 0.02-0.37. Again, species can be primary producers, herbivores, omnivores or carnivores, and the number of trophic levels is not constrained.

3.1.3 Pyramidal model food webs

In Papers IV & V a simple algorithm generating pyramidal food webs of 6-24 species was used (Kaneryd et al. 2012). In Paper IV connectance is set to 0.14, and in Paper V it ranges from 0.05-30. The pyramidal algorithm is not mechanistic as the niche models, but rather phenomenological. However, as most current food web algorithms underestimate the proportion of herbivores (Williams and Martinez 2008), the pyramidal model may still be more realistic than the niche models with regard to food web geometry, i.e. the proportion of species with different trophic roles (1° producers, 1° and 2° consumers). Species in these food webs can be either primary producers, primary consumers (herbivores) or secondary consumers (omni- or carnivores), and the ratio of species with each trophic role is 3:2:1.

3.1.4 Natural food webs

In addition to the model food webs, Paper V also includes a set of four empirical food web structures. These include a lotic (running fresh-water) system, Broadstone Stream (Woodward et al. 2010), a marine coastal system, Kelp bed, and a terrestrial forest system, Montane Forest (Cohen et al. 2011), and a plant container fresh-water system, Phytotelmata (Kitching 2009). In these webs, (trophic) species richness is 17-28 and connectance 0.06-0.17. Competition was implemented as in the PNM webs.

Table 1 (on the following spread) | Community properties in the niche model webs (see Paper II). Boxes show the interquartile range and whiskers extend up to 1.5 times the interquartile range from the box. Numbers on the sides of the box plots indicate the minimum and maximum value plotted.

Food web properties:		Description:	Ranges:
Topological			
Species richness (S)		Number of species in the food web.	$S\ 11[-\dots\dots\dots]59$
Connectance (C)		Probability of 2 species interacting. Defined as L/S^2 , where L is the total number of links in the web.	$C\ 0.04[-\dots\dots\dots]0.3$
Link density (LD)		Defined as L/S . Note that mean degree = $2 * LD$. Degree is the number of interactions a species has.	$LD\ 0.9[-\dots\dots\dots]11$
Slope of the degree distribution (sDD)		The frequency distribution of cumulative species degree; y is the proportion of species that have a degree of x or higher. A shallow slope indicates an even distribution of links between species.	$sDD\ -0.3[-\dots\dots\dots] -0.05$
Assortativity/Degree correlation (DC)		The correlation of degree (nr of links) of interacting species. Positive value means species with similar degree interact, negative value means species with dissimilar degree interact.	$DC\ -0.2[-\dots\dots\dots]0.3$
Modularity (MOD)		Occurrence of interaction sub-groups in the food web. Here measured as relative modularity, i.e. [the modularity of the food web]/[the modularity expected given S and C].	$MOD\ -0.2[-\dots\dots\dots]0.7$
Apparent competition (MAC)		Proportion of the 3-species motif apparent competition (2 species sharing a consumer).	$MAC\ 0.2[-\dots\dots\dots]0.5$
Exploitative competition (MEC)		Proportion of the 3-species motif exploitative competition (2 species sharing a resource).	$MEC\ 0.07[-\dots\dots\dots]0.3$
Tri-trophic chain (MTC)		Proportion of the 3-species motif tri-trophic food chain.	$MTC\ 0.09[-\dots\dots\dots]0.4$
Intra-guild predation (MIGP)		Proportion of the 3-species motif intra-guild predation (a predator-prey pair sharing a resource). All motif proportions are proportions of the total number of the 4 3-species motifs.	$MIGP\ 0[-\dots\dots\dots]0.4$
Maximum similarity (MS)		Mean over all species' maximum value of trophic similarity. Trophic similarity of a species pair is the similarity of 2 species' predator and prey sets, as measured by the Jaccard similarity index.	$MS\ 0.7[-\dots\dots\dots]1.6$
Trophic height (TH)		The maximum value of trophic height in the food web.	$TH\ 2.8[-\dots\dots\dots]7.3$
Basal species (pB)		Proportion of species at the base of the food web (primary producers).	$pB\ 0.02[-\dots\dots\dots]0.4$

Herbivores (pH)	Proportion of species that are strict herbivores (feeding only on the basal species).
Carnivores (pC)	Proportion of species that are strict carnivores (not feeding on basal species).
Omnivores (pO)	Proportion of omnivores (i.e. species that feed on basal species as well as on consumers).
Allometrical		
Trophic level - Body mass (sTH, iTH)	Slope (sTH) and intercept (iTH) of the relationship between trophic height and body mass.
Body mass - Generality (sG, iG)	Slope (sTH) and intercept (iTH) of the relationship between body mass and generality.
Body mass - Vulnerability (sV, iV)	Slope (sTH) and intercept (iTH) of the relationship between body mass and vulnerability.
Body mass - Abundance (sA, iA)	Slope (sTH) and intercept (iTH) of the relationship between body mass and abundance.
Dynamical		
Functional response (FR)	Shape of predator response to prey abundance, from hyperbolic type II (FR=2) to sigmoid, "weak" type III (2<FR<3).
Interference (INT)	Strength of intra-specific predator interference.
Median interaction strength (mdIS)	Median of the population level interaction strengths of all trophic interactions.
SD of interaction strengths (sdIS)	Standard deviation of the population level interaction strengths of all trophic interactions.
CV of interaction strengths (cvIS)	Coefficient of variation of the population level interaction strengths of all trophic interactions.
Kurtosis of interaction strengths (kIS)	Kurtosis of the population level interaction strengths of all trophic interactions.
Trophic diversity (TD)	A measure of how trophically dissimilar species in a food web are. Dissimilarity of 2 species is based on prey and predator interactions and the strength of these interactions.

3.1.5 Competition communities

In the competition communities of Paper III all 8 primary producer species compete with all other, in a weakly asymmetrical manner. As the model used in this study was explicit with regard to space, there were several local communities. The number of species actually present at each locality before perturbation was determined by the eco-evolutionary processes and ranged from 1 to 8.

3.2 Temporal community dynamics

3.2.1 Rosenzweig-McArthur model

Two different models of multi-species temporal population dynamics were used. The Rosenzweig-McArthur model is an extension of the classic Lotka-Volterra predator-prey model (Rosenzweig and MacArthur 1963). It is used in Papers IV & V and takes the following form for primary producers:

$$\frac{dN_i}{dt} = N_i \left(b_i - \sum_j a_{ij} N_j \right) - N_i^q \sum_j \left(\frac{h_{ij} \alpha_{ij} N_j}{1 + T \sum_k h_{kj} \alpha_{kj} N_k^q} \right) \quad (1)$$

and the following form for consumers:

$$\frac{dN_i}{dt} = N_i \left(-b_i - a_{ii} N_i + \sum_j \left(e \frac{h_{ji} \alpha_{ji} N_j^q}{1 + T \sum_k h_{ki} \alpha_{ki} N_k^q} \right) \right) - N_i^q \sum_j \left(\frac{h_{ij} \alpha_{ij} N_j}{1 + T \sum_k h_{kj} \alpha_{kj} N_k^q} \right) \quad (2)$$

The equation describes the rate of change in abundance (population density, N_i) of species i as a function of an intrinsic demographic rate, b_i , and the intra- and interspecific interactions. b_i is a growth rate for primary producers and a mortality rate for consumers. Both producers and consumers are limited by intra-specific competition, a_{ii} , and primary producers also have inter-specific competition, a_{ij} .

The trophic interaction depends on the predator's preference, h , for its prey, the attack rate, α , handling time, T , the capture coefficient, q , and in the case of the predator it further depends on the conversion efficiency, e . All the preference terms, h_{ij} , for a certain predator i , must sum to 1, as they can be seen as how large a share of the total feeding effort the predator spends on a certain prey, j . The conversion efficiency, e , describes how large a share of the prey biomass that is converted into predator biomass; the rest is lost to metabolism and excretion. The attack rate, α , the capture exponent (also known as the Hill exponent), q , and handling time, T , determine the shape of the functional response, i.e. how a predator individual's efficiency changes

with prey abundance (Holling 1959) (Fig. 3). In Paper IV a Type II functional response is used; in Paper V both a Type II and a Type III response is used.

In the parameterization of this model, we assume a trend of increasing average species body mass with increasing trophic position, as often seen natural systems (Riede et al. 2011b). This assumption is expressed in decreasing absolute values of species growth or mortality rate, b_i , with increasing trophic level: $|b_{\text{primary producers}}| > |b_{\text{primary consumers}}| > |b_{\text{secondary consumers}}|$. Parameter values are chosen as to be ecologically reasonable and to give good model behaviour with regard to the population dynamics.

Figure 3 | The functional response of a predator to the abundance of a single prey, for Hollings type II (black line), for Hollings type III (dashed line), and for a response curve intermediate between type II and III (dotted line). Note how the type III response yields a lower *per capita* (or *per biomass unit*) predation pressure at the lowest prey abundances (density or biomass), but a higher predation pressure at higher prey abundances. At even higher prey abundances, the type II & III curves will saturate at the same level. (A) Functional response as modelled in Paper IV & V [section 3.2.1]. Parameters are $h=1$, $\alpha=1.5$ and $T=0.2$. (B) Functional response as modelled in Paper I & II [section 3.2.2]. Parameters are $h=1$, $B_0=0.5$, $a=0.1$ and $B_j=1$. The legend in (A) applies also for (B), but note the difference in scale between the two y-axes.

3.2.2 Allometric trophic network model

In Paper I & II the Allometric Trophic Network model (ATN) is used (Brose et al. 2006, Binzer et al. 2011). It is an extension of the model of Yodzis & Innes (Yodzis and Innes 1992), and it takes the following form for primary producers:

$$\frac{dB_i}{dt} = B_i r_i \left(1 - \frac{B_i}{K_i} \right) - \sum_j \frac{x_j y_j B_j F_{ji}}{e_{ji}} \quad (3)$$

and the following form for consumers:

$$\frac{dB_i}{dt} = -x_i B_i + \sum_k x_i y_i B_i F_{ik} - \sum_j \frac{x_j y_j B_j F_{ji}}{e_{ji}} \quad (4)$$

Again, the equation describes the rate of change in abundance (biomass, B_i) of species i as a function of an intrinsic demographic rate and the intra- and interspecific interactions. Producers have a growth rate r_i and consumers have a mortality (metabolic rate) x_i . Producer growth is limited by a species-specific carrying capacity, K_i . All basal species have the same K_i value, namely $K_{sys}/(nr \text{ of basal species})$, and K_{sys} is the same for all systems no matter their total or basal species richness. Thus, in a static way (independent of species abundances), there is also inter-specific competition between basal species. But there are important difference between the ATN and the other models with regard to the basal inter-specific competition. Firstly, competitive exclusion, for example following the loss of top-down control, is not possible since the competition is symmetrical and static. Secondly, since the K_i values are not updated in the case of a basal species extinction, the interspecific competition can not result in any compensatory responses on the basal level. Thus, we assume that historically strong competition has resulted in niche partitioning and the current “active” inter-specific competition is weak, i.e. the community is structured by “the ghost of competition past”. Consumers also have self-limitation in the form of intra-specific predator interference competition, which is implemented in the functional response (see below).

The trophic interaction depends on the predator’s metabolic rate, x , and maximum consumption rate, y , the functional response, F , and in the case of the predator it further depends on the conversion efficiency, e . The functional response is described by:

$$F_{ji} = \frac{h_j B_i^q}{B_0^q + a B_j + \sum_k h_j B_k^q} \quad (5)$$

Where h is the preference (feeding effort) of predator j on prey i , B_0 is the half-saturation density, a is the intra-specific interference competition, and q is the capture coefficient (Fig. 3).

In this model, body mass is explicitly modelled and, just as in the previous model, increases with species' trophic position. The allometric community properties, used in the analysis of Paper II, are functions of these body masses (Fig. 4). Some of the model parameters are also functions of species body mass, namely the growth rate, r_i , the metabolic rate, x_i , and the maximum consumption rate, y_i . The other parameters are given values that are ecologically reasonable and create good model behaviour.

Figure 4 | Allometric relationships for a model food web. (A) The relationship between species' trophic level and body mass. Species' trophic level is a result of the food web structure (here generated by the niche model). Each species is assigned a body mass, according to a linear function of trophic level. However, some variability around this function is incorporated. Thus, the fit between species' trophic level and body mass is not perfect. Slope = 1.6, intercept = -1.8. (B) The relationship between species' abundance (prior to perturbation) and body mass. Slope = -0.8, intercept = -0.4. (C) The relationship between species' generality (number of prey) and body mass. Slope = 1.7, intercept = 0.6. (D) The relationship between species' vulnerability (number of predators) and body mass. Slope = -0.7, intercept = 8.5. See Table 1 for the distribution of these slope and intercept values for all the niche model webs used in Paper I & II.

3.3 Spatio-temporal community dynamics

The most complex model is found in Paper III, and it includes ecological as well as evolutionary temporal and spatial population dynamics (Norberg et al. 2012). This model is based on standard equations of quantitative genetics (Kirkpatrick and Barton 1997, Case and Taper 2000) and describes the rate of change in the abundance (population density, N_i) and the evolving trait (temperature optimum, $\bar{Z}_i$) of the population of species i at spatial location x and time t :

$$\frac{\partial N_i}{\partial t} = g_i N_i + \frac{p_i V_i}{2} \frac{\partial^2 g_i}{\partial \bar{Z}_i^2} N_i + D_i \frac{\partial^2 N_i}{\partial x^2} \quad (6a)$$

$$\frac{\partial \bar{Z}_i}{\partial t} = p_i V_i \frac{\partial g_i}{\partial \bar{Z}_i} + D_i \left(\frac{\partial^2 \bar{Z}_i}{\partial x^2} + 2 \frac{\partial \log N_i}{\partial x} \frac{\partial \bar{Z}_i}{\partial x} \right) \quad (6b)$$

The change in abundance depends on local population dynamics, genetic load and dispersal, while the change in the evolving temperature optimum depends on directional selection and gene flow. Local population dynamics are described by the fitness function g , which takes the form of Lotka-Volterra competition dynamics:

$$g_i(x, t) = r_i - \sum_{j=1}^S a_{ij} N_j \quad (7)$$

where r_i is a temperature dependent growth rate, and a_{ij} describes the strength of intra- and interspecific competition. Genetic load corrects for the assumption made for the population's growth rate, r_i , that all individuals in the population has the mean genotype $\bar{Z}_i$. At very low abundances this genetic variation, described by the term V_i , tends to decrease. This is corrected for by p_i , which is a function of N_i . Dispersal depends on the intrinsic dispersal rate D_i and the abundances of neighboring populations. Directional selection depends on the genetic variance, V_i , again adjusted by p_i , and on the difference between the local temperature and the population temperature optimum. Gene flow is the genetic aspect of dispersal and depends on the trait values and relative abundances of neighboring populations.

The species in this model are assumed to be herbaceous primary producers, with a body mass of around 1 g (dry-weight) (McCoy and Gillooly 2008). Species growth rates are here body mass dependent (in addition to their temperature dependence) (Niklas and Enquist 2001). Other parameter values are chosen as to be ecologically reasonable and to produce good model behaviour.

3.4 Direct and indirect interactions in the models

In the introduction, several direct and indirect types of species interactions were mentioned. These are present in natural communities, but they are not all present in the models used here. Firstly, the only direct interactions present in the model are predator-prey interactions (including herbivory) and/or competition. Direct mutualism, facilitation, commensalism, amensalism and parasitism are not included. Of the indirect interactions, only the “interaction chain” type (*sensu* Wootton 1994) are included. Interaction modification (also called trait-mediated indirect interactions) is not included, nor is the environment-mediated effects of ecosystem engineers and foundation species.

Despite this simplification in the description of natural communities, dynamical food web models can still boast a substantial range of potential indirect effects (Fig. 5). Two species using the same resource will indirectly interact through exploitative competition, as they both depress the abundance of the resource (Fig. 5A) (Wootton 1994). On the other hand, two weakly competing species may benefit each other if they both compete more strongly with a third species, which in turn competes strongly with them (Fig. 5C) (Case 1999, Pianka 1999). This indirect (competitive) mutualism is evidenced by secondary extinctions occurring in competitive communities consisting of a single trophic level (Fowler 2010). Furthermore, the competition between two resource species can make their consumers benefit each other. If one consumer depresses the abundance of its resource, the negative impact of competition on the other resource decreases, which in turn benefits its consumer (Fig. 5F) (Davidson et al. 1984, Vandermeer et al. 1985).

Another situation is when two resources share a common predator. As they both affect the consumer’s abundance positively, the resource species indirectly affect each other negatively, so called apparent competition (Fig. 5B) (Holt 1977). But there are cases when shared predation actually can be positive for a resource, for example when the predator has a prey switching behavior, such that the predator feed disproportionately on the more abundant or preferred prey (Miller et al. 2006, Valdovinos et al. 2010). In such cases, the rare or less preferred prey is benefited by the presence of the alternative prey, as a disproportionate amount of the predation pressure is averted (Fig. 5D).

The models also capture classic trophic cascades. In a tri-trophic food chain, the top-predator and the basal species are involved in food-chain mutualism. The basal species has a positive effect on the herbivore, i.e. the top-predator’s prey, and the top-predator has a negative effect on the herbivore, i.e. the basal species’ consumer (Fig. 5G). However, if the food chain has four instead of three species, the positive influence of the top-predator will now fall on the herbivore, by reducing the abundance of the

intermediate predator. The relation between basal species and top-predator is now asymmetrical as the basal species still exerts a positive indirect effect on the top-predator, which in turn has a negative indirect effect on the basal species (Fig. 5G). The importance of these trophic cascades is evidenced by the effects of top-predator loss. It has been documented in several cases, how the released intermediate consumers, whether they are herbivores or carnivores, drive down the abundances of their resources, sometimes to extinction (Elmhagen and Rushton 2007, Casini et al. 2008, Prugh et al. 2009, Elmhagen et al. 2010, Estes et al. 2011, Ripple et al. 2014). Furthermore, trophic cascades are per definition vertical, but through intra-guild competition, their effect can continue in the horizontal direction (Fig. 5E). Top-down control of a species, will benefit its competitors, and if the species is a strong competitor the loss of top-down control can result in competitive exclusions (Paine 1966, Chase et al. 2002, van Veen et al. 2005, Brose 2008). In this way, predation can be positive for co-existence, but of course, predation may also have the opposite effect: “predation is often expected to make coexistence more difficult by virtue of making existence more difficult” (Chase et al. 2002).

The examples of indirect interactions presented here have quite short pathways, but they can of course be longer (see Sanders et al. 2013 for an empirical example). From a mathematical point of view, the sign of an indirect interaction (of the interaction chain type) between two species, is simply the product of the direct interactions along a pathway (in which no species occur more than once) between them (Case 1999, Pianka 1999). When negative direct interactions are concerned, the indirect effect of species A on species B will be positive if the number of links in the chain between them is even, while it will be negative if the number of links is odd. In contrast, direct positive interactions along the path of an indirect interaction do not change the sign of the indirect interaction. However, determining the sign of the indirect effect of one species on another becomes more complicated if the species have more than one possible path between them (Fig. 5H). If there are multiple indirect interaction chains between two

Figure 5 | Illustrations of interaction chains (indirect interactions). Full lines are direct interactions; dashed lines are indirect interactions. In these examples, the direct and indirect effect of one species on another is either positive (+) or negative (-), see box in upper corner. Examples: (A) Two predators sharing a prey affect each other negatively. (B) Two prey species (plants) sharing a predator (herbivore) affect each other negatively. (C) Two species (the smaller trees) compete weakly with each other, but indirectly benefit each other by competing more strongly with a third species (large middle tree). (D) The eagle prefers the fish prey; in its presence the goose suffers very little eagle predation. Thus the goose benefits from the fish, while the fish either suffers from the goose presence or is not affected by it. (E) Two consumer's benefit each other by suppressing the competitor of each other's prey. (F) By suppressing its prey, the consumer benefits the prey's competitor. (G) The sign of the indirect interaction between wolverine and lynx cannot be determined as there are multiple pathways of different signs between them (e.g. lynx affects wolverine negatively by suppressing hare, while lynx benefits wolverine by suppressing capercaillie). For the indirect effect to be known, the strength of the direct interactions must be known. (H) Indirect interactions in food chains of odd and even length.

OVERVIEW

(A) Exploitative competition

(B) Apparent competition

(C) Competitive mutualism

(D) Prey switching

(E) Consumer-mediated co-existence

(F) Facilitation

(G) Indirect interactions in 3- and 4-species food chains

(H) Multiple indirect interaction chains

species, and if these chains are of different signs, it cannot be determined whether the net indirect effect is positive or negative, without knowing both sign and strength of the involved direct interactions (Case 1999). The presence of these direct and indirect interactions enables many possible indirect effects of a perturbation. Whether the net effect is negative or positive for a specific species will depend on the sign and magnitude of the direct and indirect interactions the species is involved in, the direction in which the perturbation affects these interactions, and the sign and magnitude of the perturbation's direct effect on the species directly.

3.5 Perturbations

3.5.1 Primary extinctions

When a perturbation is severe enough it leads to the extinction of a species. This extinction can be seen as a perturbation in itself, as it may trigger further species loss, so called secondary extinctions (Ebenman and Jonsson 2005). There are two main approaches to modeling primary species loss, either single species deletions (Eklöf and Ebenman 2006, Thebault et al. 2007, Fowler 2010) or sequential species deletions (Dunne et al. 2002b, Memmott et al. 2004, Curtsdotter et al. 2011 [Paper I]). In the first case, one species is removed (or deleted) from the community and the response is observed. After that the community may be “restarted” from its pre-deletion condition, and another species is removed. By comparing the magnitude of secondary species loss, following the primary extinction of each species in turn, and relating this magnitude to traits of the species primarily lost, conclusions may be drawn concerning the importance of certain species (traits) (Borrvall et al. 2000, Eklöf and Ebenman 2006). Here, a species is considered more important, the more secondary species loss that follow in its wake.

In the second approach, species are ranked by trait value (the trait can be body mass, trophic position, number of links etc) and the highest (or lowest) ranked species is removed. The response is recorded, the ranking is updated (as the primary and/or secondary extinctions may have changes species' trait values) and the species that now has the highest (or lowest) rank is removed, without the community being “rebooted” between removals. These sequences can either be defined with a specific perturbation in mind, ranking species according to their sensitivity to this perturbation (Srinivasan et al. 2007, de Visser et al. 2011), or they can be defined according to a general species trait (Solé and Montoya 2001, Curtsdotter et al. 2011 [Paper I]). By comparing the magnitude (and timing) of secondary extinction resulting from different deletion sequences, conclusions can be drawn as to how sensitive communities are to certain types of disturbances or about the relative importance of species (traits). In both approaches, comparisons of the magnitude of secondary species loss in different food webs (or other ecological communities) can be made. By relating this magnitude to

properties of the community, conclusions can instead be drawn concerning what makes a community prone to lose species in secondary extinction cascades (Dunne et al. 2002a, Thebault et al. 2007, Riede et al. 2011a).

Species removal analyses can be performed both in topological and dynamical settings. In the topological approach, there are no population dynamics, only a network structure depicting which species interact with each other. In most cases, these network depictions are binary, i.e. there are no interaction strengths, and by definition secondary extinction occurs when a consumer has lost all of its prey species or a mutualist all of its partners etc. (Dunne et al. 2002a, Memmott et al. 2004). In the dynamic approach, interactions are weighted by interaction strengths and populations grow and decline over time. In this case, secondary extinction occurs when populations decline to zero or, for example to implicitly include demographic stochasticity, an extinction threshold above zero (Eklöf and Ebenman 2006, Thebault et al. 2007, Berg 2013). In contrast to the topological approach, in the dynamical setting top-down (in addition to bottom-up) secondary extinction cascades could potentially occur (Curtisdotter et al. 2011 [Paper I]).

In Papers I & II we modeled perturbation as sequential deletions, using species body mass, degree (number of trophic interactions), generality (number of species preyed upon) and vulnerability (number of predators being preyed upon by) as sequence-defining traits. In Paper I the focus was on the species traits, and both the topological and dynamical approach was used. In Paper II community properties were also included in the analysis, but only data from the dynamical approach.

3.5.2 Climate change – increased mean annual temperature

In Paper III the perturbation was explicitly modeled as climate change. There are many different aspects of climate change, and its nature also varies between regions and over different spatial scales (IPCC 2013, Garcia et al. 2014). Here, we chose to focus on a general, large-scale pattern, namely the increase in global annual mean temperature. The magnitude of this increase is predicted, and observed, to be greater at higher latitudes in the northern hemisphere than at lower latitudes (IPCC 2013). For this reason, species at high latitudes may be more at risk of extinction because of climate change than species at low latitudes. This should be particularly true for polar species as they are already living in an edge habitat; there is no place colder to go when the polar region heats up.

However, the opposite has also been suggested, as extinction risk under climate change does not only depend on the magnitude of change but also on species vulnerability (Huey et al. 2009). Generally, species at low latitudes have narrower temperature tolerance curves, than species at high latitudes (Deutsch et al. 2008, Sunday et al. 2011).

Most likely, this is because of lower temperature variability at low latitudes than at high latitudes with their strongly seasonal environments. Furthermore, temperature tolerance curves tend to be skewed, with tolerances decreasing faster with a positive deviation from the temperature optimum than with a negative deviation (Martin and Huey 2008). Again, most likely because of the large environmental variation, high latitude species tend to live in habitat with mean temperatures quite far below the species temperature optimum; species must be able to cope with temperatures high above the habitat mean temperature (Deutsch et al. 2008). On the other hand, in more stable environments species can survive in habitats with temperatures close to the species' optimum temperature (Deutsch et al. 2008); there is little risk that temperatures will ever become critically high, crossing the species upper tolerance limit. Thus, both the relative position of experienced to optimum temperatures and the width of the tolerance curve, points to tropical species being at higher risk of extinction under climate change than boreal or polar species.

In Paper III we incorporate the latitudinal trends with regard to increasing mean temperatures as well as to the observed patterns of species' temperature tolerance curves. We record the relative change in both global and regional species richness as the temperature increases.

3.5.3 Climate change – increased environmental variation

Not only mean values of climatic variables, but also variability, may change as the global temperature rises (IPCC 2013). Extreme weather events, both with regard to temperature, precipitation and wind conditions are predicted to increase in frequency and severity (Easterling 2000, Mann and Emanuel 2006). Climatic patterns may change in more subtle ways as well, for example shifting timing of precipitation (Suttle et al. 2007) or changing temporal auto-correlation (Wigley et al. 1998, Pounds et al. 1999, Pol et al. 2011).

Environmental variability can increase species extinction risk, by causing large fluctuations in abundance (Lande 1993, Ripa and Lundberg 1996, 2000, Lögdberg and Wennergren 2012). This is especially dangerous if species abundances are low; the smaller the population the smaller fluctuation it takes to drive the species over the zero line (Kaneryd et al. 2012 [Paper IV]). Furthermore, taking demographic stochasticity and Allee effects into account means the actual fluctuation size needed to cause extinction is even smaller (Adler and Drake 2008). Another negative aspect of environmental variation is that it may cause a decrease in long-term growth rates; this is true even if positive deviations, resulting in higher than average per capita growth rates, are as common as negative deviations, resulting in lower than average per capita growth rates (Lande 1993). The key to this seeming conundrum lies in the fact that population growth rate does not only depend on the per capita growth rate but also on

number of individuals, i.e. population size. And apparently, population declines are faster than population recovery (Lande 1993). However, environmental variation has also been suggested as a co-existence mechanism, especially if species show high response diversity (Chesson and Huntly 1997). In this case, conditions favoring one species disfavor another, and vice versa.

In Papers IV & V, we model the perturbation as high short-term variability affecting species growth/mortality rates and study what it may mean for species extinction risk. Positive and negative deviations are equally likely, and there is no auto-correlation (i.e. the noise color is white). To allow for the potentially stabilizing mechanism of response diversity, we investigate scenarios with low (as well as high) correlation among species with regard to their response to the variability.

3.6 Measures of the extinction response

As mentioned in the introduction, stability can be measured in a vast number of ways. In this thesis I have used measures of robustness and resistance to species loss and I have calculated the risk of extinction and the relative change in species richness following a perturbation. Here, these measures are presented and discussed.

3.6.1 Quantifying secondary extinction cascades

In Paper I, we used the robustness measure R_{50} , which is specifically suited for measuring robustness in sequential deletion studies (Dunne et al. 2002a). It is defined as the fraction of S (the initial species richness) that has to be removed (i.e. be lost in primary extinctions) in order to result in a total species loss (primary + secondary extinctions) of 50% (see Fig. 6A). Minimum robustness is $1/S$, in which case a single primary extinction results in the loss of $\geq 50\%$ of the initial species richness. Maximum robustness is 0.5, in which case no secondary extinctions occurred. The choice of a 50% threshold is quite arbitrary, and the conclusions regarding the relative importance of species traits for food web robustness could potentially depend on the chosen threshold. However, in those cases where several threshold values have been investigated the conclusions based on R_{50} seem to be quite robust, at least for thresholds of 10-60% (Srinivasan et al. 2007, de Visser et al. 2011, Berg 2013).

The R_{50} measure has been the response variable of choice in sequential deletion studies ever since Jennifer Dunne's influential paper in 2002 (Dunne et al. 2002a, 2004, Srinivasan et al. 2007, Coll et al. 2008, Dunne and Williams 2009, de Visser et al. 2011). Others have chosen the same approach, but with a different threshold level (Staniczenko et al. 2010, Thierry et al. 2011). But no matter the threshold, this method has the weakness that it is essentially a "snapshot" in time. For example, two food webs could have similar R_{50} values, but in one the majority of the secondary extinction

happened earlier than in the other, and should be considered more sensitive. Such aspects of timing, this method cannot capture.

The measure of extinction area (EA), suggested by Allesina and Pascual (2009), is better in capturing the aspect of timing in secondary extinction cascades. It is the area under the curve, when plotting number of primary extinctions vs accumulative total species loss (see Fig. 6B). Therefore, it captures the entire sequential deletion process and it captures the timing of secondary species loss. In contrast to R_{50} , extinction area is a measure of resistance rather than robustness. Minimum resistance is $EA = 1$, in which case complete system collapse followed a single primary extinction. Maximum resistance is when $EA = (S+1)/2S$, which tends to 0.5 for large values of initial species richness. Maximum resistance means no secondary extinctions occurred. In Paper II, in which we used extinction area to calculate resistance to species loss, we transformed the EA values in order to get a resistance measure with a more straightforward interpretation: 0 and 1 for minimum and maximum resistance, respectively.

Figure 6 | Example of the response measures R_{50} (A) and Extinction area (B) for the same data. In both graphs the number of primary extinctions is on the x-axis. For R_{50} , the y-axis shows the cumulative number of secondary extinctions. For Extinction area (EA), the y-axis shows the cumulative number of total (primary + secondary) extinctions. The R_{50} is the number of primary extinctions that the community can suffer before 50% of initial species richness is lost (the point where the curve intersects with the dotted line; the dashed line indicates 100% species loss). The EA is the discretized area under the curve in (B), i.e. the area of the grey bars. All species are lost at primary extinction number 7; in the case of EA the curve must be extended to the final species richness (here 10).

3.6.2 Quantifying total species loss

A simple and straightforward measure of species loss is extinction risk (Kaneryd et al. 2012 [Paper IV]). Here, this is calculated as the proportion of the initial species richness that is lost in extinction during a simulation (i.e. a certain period of time). This measure, used in Papers IV and V, does not discriminate between primary and secondary extinctions. But by comparing the time to extinction for different trophic levels, we can make some inference as to the mechanisms behind extinctions and hence to their primary or secondary “nature”.

In local communities with no species invasions or evolution of new species, the change in species richness can only be negative, and the extinction risk is a suitable measure. But when the study system contains several local communities and community composition differs between these communities, the change in local species richness following a perturbation could either increase or decrease (Norberg et al. 2012). This is the case in Paper III, and we therefore use a relative measure of species richness after perturbation: zero means there is no change in species richness, negative values mean species richness decreased following the perturbation, and positive values mean species richness increased. As simple and easy to interpret as this measure seems, there is one thing to bear in mind: the species richness after perturbation is for most local communities the sum of extinction of locally native species and the immigration of locally non-native species. Thus, a local extinction can be “hidden” by a numerically compensating invasion. A zero change in species richness can therefore mean anything from the survival of all locally native species to the complete loss of native richness, fully replaced by non-native immigrants.

4. Main results and implications

Overall, the research results underscore the importance of including population dynamics and biotic interactions when studying the effects of perturbation on biodiversity. Many of the results are complex, hard to foresee or even counter-intuitive, arising from the indirect effects of the perturbation being translated through the living web of species interactions.

4.1 Paper I

To a certain extent, this study corroborates previous findings of the importance of species at low trophic levels and with many interactions (Dunne et al. 2002a, Srinivasan et al. 2007, Staniczenko et al. 2010, de Visser et al. 2011). However, these previous studies were topological (not including population dynamics), and our comparison between topological and dynamical approaches reveals some important issues. Firstly, a topological approach will underestimate the magnitude of secondary species loss in general, and for top-down sequences in particular. Importantly, in the dynamical approach we find that the extinction of top-predators causes secondary extinction cascades on par with the extinction of low-level consumers. Secondly, we find that the topological approach largely underestimates the variation in robustness within removal sequences, i.e. between food web variation. All in all, the results points to the importance of including population dynamics when studying extinction responses to perturbation. We must also conclude that food web robustness to species loss cannot be well predicted solely by the traits of the species involved in the primary extinctions.

4.2 Paper II

Even though species traits alone were shown not to be good predictors of the extent of secondary extinctions, the combination of species traits and community properties is. It seems that depending on the traits of the species lost in the primary extinction, different secondary extinction cascades are triggered. To a large extent, the direction of this extinction cascade will determine which community properties are important for resistance. In bottom-up extinction cascades, food web structure governs resistance to species loss; in top-down cascades it is instead dynamical properties that play an important role. This species-community interaction has a critical implication for the identification communities prone to secondary species loss. Different anthropogenic perturbations are likely to put different types of species at risk; for example, larger-bodied animals run greater risk of overexploitation (Isaac and Cowlishaw 2004, Cardillo et al. 2005), while weak competitors among the primary producers indirectly suffer from eutrophication (Bobbink et al. 2010). Thus, the property defining a sensitive community can be dependent on the type of disturbance it is subjected to.

4.3 Paper III

The magnitude of species loss from competition communities, in response to an increase in annual mean temperature, increases with the strength of interspecific competition. In effect, strong competition creates impenetrable local communities, resulting in dispersal barriers in the landscape. Unless dispersal is very high, so that barriers can be overcome, or local adaptation is very fast, so that species have no need to emigrate, catastrophic biodiversity losses of >90% of initial species richness occur. By extension, this also highlights the potentially devastating effects of both natural dispersal barriers (e.g. mountain ranges, deserts, large water bodies) and anthropogenic ones (e.g. degraded and fragmented habitat through human land use). Furthermore, interspecific competition modulates the effect of adaptation and dispersal, giving rise to a range of different relationships between these variables and global species richness. Overall, it is clear that there is a three-way interaction between dispersal, adaptation and competition affecting the biodiversity outcome of climate change, sometimes in counter-intuitive ways. This response complexity is rather discouraging, as general predictions will be very hard to make.

4.4 Paper IV

Under high environmental variability, high species richness increases extinction risk, especially when the response to climatic variability is weakly correlated among species. The environmental variability drives primary producers to extinction, triggering bottom-up extinction cascades that are most extensive in food webs with specialist consumers. Thus, our study suggests that biodiversity hotspots, such as many tropical rain forests and coral reefs, are also the ones that may experience most extinctions if climatic variability increases under climate change. These results also provide a perspective on the hypothesis that environmental variability confers co-existence (Chesson 1986). This hypothesis hinges on an assumption of non-linearity, such that species have a competitive advantage when rare (Chesson and Huntly 1997, Gravel et al. 2011). However, there should be many instances when the “advantage when rare”-assumption is not fulfilled (Adler and Drake 2008). We show that in such case, not only does environmental variability fail to promote co-existence; on the contrary, it increases the risk of competitive exclusion.

4.5 Paper V

In Paper IV, the most severe effect of environmental variability on consumers was indirect, namely the loss of prey through perturbation-triggered extinctions of primary producers. Hence, if consumers are flexible, i.e. able to rewire to novel prey species if all of the consumer's original prey have gone extinct, their survival chances should increase and food web resistance with it. However, here we show that extinction risk increases with an increasing fraction of flexible consumers, especially when consumers have a Type II (hyperbolic) functional response. Only when almost all consumer species have a sigmoidal type III functional response does rewiring lead to increased network persistence. When flexible consumers are less efficient in exploiting novel prey than original prey, their effect is less detrimental. In essence, what is beneficial for individual consumers in the short-term may prove fatal to food web persistence in the long-term. Similar patterns have been observed empirically (Springer et al. 2003), and we further argue that the human species is an example of a particularly flexible and efficient consumer, as evidenced by the world's fisheries (Pauly et al. 1998). Our results imply that as we begin to rewire to fish species at low trophic levels, we risk triggering extensive extinction cascades, eventually causing large changes in the structure and dynamics of marine ecosystems.

5. Discussion

Competition and trophic interactions are two of the most fundamental interactions in nature (Ricklefs 2008). They are ubiquitous and can be important structuring forces in natural communities (Silvertown 2004). Here I will discuss their importance in relation to perturbation, with a focus on and starting point in the results found in the papers of this thesis. Furthermore, I also briefly discuss the potential importance of a few interaction types *not* included in the thesis, positive interactions such as mutualism and facilitation, and interaction modification or trait-mediated indirect effects.

5.1 Competition

5.1.1 Basal interspecific competition, species richness and extinction risk

Resource and interference competition among primary producers may be of particular importance for how sensitive communities are to certain perturbations. In Paper IV, the high extinction risk in species-rich communities faced with high environmental variation is in fact driven by interspecific competition at the basal level. As the number of species increases, so does the number of basal species. In the model used, all basal species compete with each other and there is no trade-off in per capita competition strength as basal species number increases. As a result, the population size of each basal species decreases as total species richness increases. In a variable environment, low abundance increases the likelihood of the species' extinction. Thus, faced with the same magnitude of environmental variation, a greater number of basal species are lost from the species-rich than the species-poor communities. As also seen in Paper I, basal species loss is detrimental with secondary extinction cascading upwards through the food web. In conclusion, the strength of interspecific competition may determine at least one aspect of communities' sensitivity to environmental variability: with stronger competition, sensitivity should increase and the slope of the diversity-stability relationship should become increasingly more negative.

5.1.2 Basal interspecific competition in an eco-evolutionary and spatial context

Inter-specific competition is also found to be of great importance in a spatial context (Paper III). Firstly, competition was a major structuring force prior to climate change, with species distributions being limited more by strong competitive interactions than by low rates of dispersal and evolution. Secondly, the dispersal barriers posed by strong inter-specific competition led to catastrophic levels of species loss, as all species were forced to stay in their original habitat. Could they not evolve fast enough, the populations perished. Even when the rate of evolution was high, and biodiversity loss was more moderate, did strongly competitive communities experience substantially more extinctions than weakly competitive ones. Thirdly, competitive exclusion

contributed to biodiversity loss under climate change, both in strongly and weakly competitive communities (observed through visual inspection of time series; data not shown). In the first case, species cannot co-exist and an established, well-adapted species at high abundance is uninvasible. However, if the rate of local adaptation is too slow, the native species will become mal-adapted as the climatic conditions change. Its growth rate and local abundance decreases, and it becomes susceptible to invasion, and inevitably exclusion. In the second case, all 8 species can, and sometimes do, co-exist at the same locality. However, this co-existence seems to hinge on all species being well-adapted to the locality. A species rendered mal-adapted from climate change, but not so badly as to be driven to extinction by the abiotic perturbation alone, can be pushed over the edge by the arrival of a better adapted invading species. These results highlight a potential dilemma; if species cannot track suitable climate through dispersal, for example because native communities are closed to invasion, we should expect substantial biodiversity loss. But on the other hand, if communities are open to invasion, we should expect species loss because of the combined abiotic and biotic pressure on native species. In real communities, we might expect invasibility and native species loss accelerating as the native community crumbles under increasing abiotic and biotic pressure, akin to the hypothesis of invasional meltdown (Simberloff and Holle 1999, Adams et al. 2003, Ackerman et al. 2014).

Lastly, the strength of inter-specific competition modulates the effect that dispersal and adaptation have on the biodiversity outcome of climate change. This happens for at least three reasons: 1) the initial community structure differs between strongly and weakly competitive communities, 2) a process, e.g. dispersal, can be of different importance under climate change in strongly and weakly competitive communities, and 3) competitive interactions determine whether the benefits of dispersal and/or evolution (climate tracking and adaptation) outweighs the risks (competitive exclusion).

5.1.3 Extinction risk and the pattern of interspecific competition strengths

In all 5 papers of this thesis, all primary producers have been assumed to compete with each other. If another assumption is made, as in the competition model of limiting similarity, the outcome could have been different. In the limiting similarity model, each species is assumed to compete only with the two species most similar to itself with regard to resource use. In this case, species abundances do not depend on species richness (Hughes and Roughgarden 2000), and the trend in Paper IV of extinction risk increasing with species richness might not be observed.

Other types of competition relate to the variability among interaction strengths. In Paper I,II & V, basal species have “diffuse” competition, i.e. all species compete symmetrically with each other ($a_{ij} = a_{ji}$, for all i and j), while in Papers III & IV competition is “random”, i.e. pair wise interaction strengths are asymmetrical ($a_{ij} \neq a_{ji}$)

[“diffuse” and “random” sensu (Hughes and Roughgarden 2000)]. This asymmetry can have profound effects on community stability. The chance of many species co-existing decreases with increasing variance among competitive interaction strengths, as it does with increasing mean strength (Kokkoris et al. 2002). Thus, a narrower (broader) spectrum of interaction strengths may have decreased (increased) extinction risk stemming from competitive exclusion in the spatially explicit competition communities of Paper III. As exemplified in the previous section, this risk is involved in the risk-benefit balance of dispersal and local adaptation. Hence, this must by extension mean that the pattern of interaction strengths can influence the relationship between global species loss under climate change and the rates of dispersal and evolution.

In a similar vein, (Fowler 2013) found that secondary extinction risk was higher in food webs when basal species competed asymmetrically instead of symmetrically (i.e. diffuse competition). Particularly, there were no secondary extinctions of basal species when competition was symmetrical. In contrast, basal species were quite frequently lost when competition was asymmetrical, especially following the primary extinction of an herbivore or basal species. These results may be related to competitive mutualism and consumer-mediated co-existence. Firstly, competitive mutualism, as defined by (Pianka 1999) does not exist under diffuse competition. Secondly, greater asymmetry (variance) decreases the likelihood of co-existence (Kokkoris et al. 2002), which means that the potential importance of interaction based co-existence mechanisms increases. Self-evidently, the more co-existence hinges on such indirect interactions, the more vulnerable must communities be to species loss.

5.1.4 Consumer’s intraspecific competition and extinction risk

But it is not only competition on the basal level that affects community stability – consumer’s intra-specific competition does too. To my knowledge, most community models in this field assume a relatively strong intra-specific competition at the basal level, but assumptions for consumer levels vary. Here, we show that stronger consumer interference competition increases food web resistance to top predator loss (Paper II) and that strong self-limitation on the consumer level decreases extinction risk in food webs subjected to high environmental variation (Paper IV). Similarly, we found in early simulations for Paper V that strong intra-specific competition of flexible consumers lessened the risk of overexploitation of novel prey following a rewiring (data not shown). These results are in line with previous findings of consumer intra-specific competition increasing resistance to single primary extinctions in food webs (Thebault et al. 2007) and increasing dynamical stability (resilience: Saunders 1978, Sterner et al. 1997; population variability: Rall et al. 2008).

The weaker predation pressure of self-limited consumers leads to weaker top-down control, i.e. more donor controlled systems. In such systems, consumer-mediated co-

existence would be rare, and the loss of top-predators would be unlikely to cause any secondary extinctions. Indeed, this is what Pimm (1984) found, and what the results of Paper II indicate. Again, it seems that co-existence based on indirect species interactions can become an Achilles' heel when natural communities are perturbed.

Finally, the result in Paper IV deserves a special note, as it is quite contrary to expectation: consumer densities and extinction risk both decrease with stronger self-limitation. But the environmental variability has a relatively small direct effect on the consumers, and thus the smaller population size conferred by strong self-limitation does not increase primary extinction risk. Thus, the observed decrease in extinction risk could be caused by fewer secondary extinctions of consumers. But why this would be the case is hard to elucidate, as producer densities and extinction risk are surprisingly little affected by the strength of consumers' intra-specific competition. Unless more complicated cascades than pure bottom-up ones are involved, the increased extinction risk for consumers with weaker intra-specific competition is hard to explain. I believe this topic deserves further study.

5.2 Trophic interactions

5.2.1 The functional response

The functional response of predators to the abundance of their prey has a large impact on stability. Holling's functional response of type II is known to destabilize population dynamics, i.e. cause population fluctuations, while the type III response is stabilizing (Oaten and Murdoch 1975, Williams and Martinez 2004, Brose et al. 2006, Rall et al. 2008). There are functional responses intermediate between type II and III (see Fig. 3), and apparently the destabilizing effect of the pure type II response can be dampened by a quite small sigmoidal tendency of the response curve (Williams and Martinez 2004). In line with the effects on population stability, the type II functional response also decreases persistence (Brose et al. 2006, Rall et al. 2008).

Similarly, we find that the type of functional response has a large impact on the extinction response of perturbed food webs. In Paper II, the functional response is an important predictor of food web resistance to the loss of consumer species, no matter their trophic level. In line with Williams and Martinez (2004), resistance increased and saturated after a small deviation from pure type II to a slightly sigmoidal response curve. As there was no "control" simulation without species removals, it is hard to say whether this is due to "spontaneous" primary extinctions caused by unstable population dynamics or because food webs with type II dynamics actually experience more secondary extinctions following the species removals. However, the greater importance of the functional response following the extinction of top predators,

suggests that at least in this case, a sigmoidal functional response decreases the amount of secondary extinctions.

In addition to dampening dangerous population fluctuations, a sigmoidal functional response also decreases the risk of consumers overexploiting their prey at very low abundances. All else being equal, a type III consumer is more efficient than a type II consumer at high prey abundances (until the response saturates), and less efficient at low abundances (until prey abundance is null). For a type II consumer, the *per capita* effect of predator on prey is actually highest at low prey abundances. This is the key to its dynamical instability, and also enables the consumer to drive its prey extinct when the prey is at very low abundances, whether this low abundance is caused by unstable predator-prey dynamics or environmental variability. I therefore suggest that when a top-predator is lost, there is a greater risk of meso-predator release leading to prey overexploitation and extinction, when the meso-predator has a type II functional response (Paper II). Similarly, with more type II consumers in the food web, species extinction risk increases in a variable environment (Paper V). This trend is seen both with and without rewiring, but is more pronounced the larger the proportion of flexible consumers is. Rewiring type II consumers can eat their way through the food web, continuously overexploiting each novel prey, in the worst case causing the entire food web to collapse. Almost all consumers must have a type III functional response for rewiring to decrease extinction risk.

5.2.2 Rewiring of predator-prey interactions

In Paper IV, the main reason for the extinction of consumers in a variable environment was indirect, through the loss of prey species. As expected, consumers with specialist preferences were particularly sensitive to prey loss (here, specialists depend largely on one preferred prey, while generalists divide feeding effort equally among their prey). Under such circumstances, re-allocation of preferences among remaining prey following partial prey loss, or rewiring to novel prey following complete prey loss, should decrease secondary extinction risk of consumers and thus be positive for overall food web persistence. In topological models, the effect of rewiring on robustness varies from positive to null, depending on food web connectance and at which level of energy (prey) loss secondary extinction of the consumer is assumed to take place (Thierry et al. 2011). Likewise, Staniczenko et al. (2010) found robustness increased if consumers could add to their diets, prey species whose predators had gone extinct. In our dynamical study (Paper V), the effect of rewiring on persistence varies from positive to negative, depending on the functional response (as discussed above), but with the overall tendency being that of increased extinction risk. However, the detrimental effect of rewiring is somewhat dampened when consumers are less efficient in consuming novel prey than they were in consuming their original prey. This is analogous to the effect of strong intra-specific

consumer competition mentioned in an earlier section (5.1.4). In both cases, the risk of the rewiring consumer overexploiting its novel prey is reduced thanks to a weaker predation pressure, either because *per capita* interaction strength or predator abundance is lower.

Consumer rewiring can be seen as an extreme case of adaptive foraging. A consumer with adaptive (or optimal) foraging behavior will allocate feeding effort to abundant prey and away from rare prey. This is generally found to be stabilizing, including increased robustness to species loss (see Valdovinos et al. 2010 for a review). A main mechanism for the increased stability (increased persistence and robustness), is that adaptive foragers allow the recovery of rare prey. Indeed, in this sense adaptive foraging is similar to the functional response of type III, both in mechanism and effect. However, the stabilizing effect of adaptive foraging depends on the adaptive behavior being sufficiently fast in responding to changing prey abundances (Kondoh 2003). The rewiring used in Paper V can be seen as adaptive foraging, with a (too) slow adaptive speed. In reality, I would expect consumers to rewire (or reallocate feeding effort) before having driven the prey to extinction. But the consumer may drive down prey abundances quite dramatically before switching (Springer et al. 2003), in which case the prey will still be at risk of extinction, due to increased vulnerability to environmental and demographic stochasticity.

Not only consumers, but also prey, can show adaptive trophic behavior (Valdovinos et al. 2010). Instead of optimizing food intake, the adaptive behavior of prey has the purpose of avoiding being taken in; animal prey can choose to actively avoid predators (Lima and Dill 1990) and plants can increase their chemical defenses (Chen 2008). Just as adaptive foraging, adaptive resource responses can be stabilizing, at least if they are predator specific (Kondoh 2007), by allowing the recovery of rare predators (Valdovinos et al. 2010). On the other hand, if the prey's response is general and affects all of its consumers whether they are abundant or not, an analog to apparent competition arises (Valdovinos et al. 2010). In this thesis, no adaptive resource behavior has been studied, but it would be an interesting area to explore – especially as (to my knowledge) very little, if any, research in the vein of investigating the effect of adaptive resource behavior on the extinction responses to perturbation has been attempted.

5.3 A note on interactions not included

As mentioned previously, ecological communities have here been modeled as competition communities and food webs, which means that the interaction types included are competition and/or trophic interactions. These are antagonistic interactions, on which community ecology has long focused (Stiling 2001). But the importance and ubiquity of positive interactions, such as mutualism and facilitation are

being increasingly acknowledged (Stachowicz 2001, Brooker et al. 2008). I would be surprised if they were not also found to be important in relation to perturbation responses. Mutualists may be at particular risk of secondary extinction (co-extinction), as both partners are as critically dependent on each other, as a consumer is on its prey (Dunn et al. 2009, Colwell et al. 2012). In line with this, Koh et al. (2004) estimated that there are 6300 co-endangered species, i.e. species affiliated with directly endangered species through parasitic, mutualistic or other dependent interactions. But on the other hand, Memmott et al. (2004) found that mutualistic plant-pollinator webs were more robust to species loss than food webs, thanks to pollinator redundancy and the nested network structure. In the networks of Memmott's study links were binary, as interaction strengths were unknown. However, also quantitative mutualistic networks seem to be robust to species loss, although robustness thresholds (as found by Dunne et al. [2002a] for food webs) apparently can arise (Kaiser-Bunbury et al. 2010).

Simple mutualistic models can be quite unstable, e.g. positive feedbacks between mutualistic partners can cause runaway dynamics. However, this inherent instability can be counter-acted by negative interactions, for example intra-specific competition (Case 1999). Mougi and Kondoh (2012) also showed that when mixing mutualistic and trophic interactions (with self-limitation of all species), local stability was highest for intermediate-high ratios of mutualist interactions. Thus, the time is perhaps ripe for merging food web ecology with the study of mutualist networks. Even though we have some knowledge on each network type, the effect on stability when merging the two is still largely unexplored. There is one recent example, showing that the results from networks of single interaction types are not always transferrable to networks of multiple interaction types (Sauve et al. 2014). The nested structure of mutualistic networks and the compartmentalized structure of food webs, have been shown to increase these networks' persistence and resilience (Okuyama and Holland 2008, Thébault and Fontaine 2010, Stouffer and Bascompte 2011). But the stabilizing effect of these network structures is much weakened, when mutualistic and antagonistic networks are merged (Sauve et al. 2014). In a similar vein, it would be interesting to study the effect of consumer flexibility in merged networks, as the effect is de-stabilizing in dynamical food webs (Gilljam et al. 2014 [Paper V]) but stabilizing in mutualistic networks (Kaiser-Bunbury et al. 2010, Ramos-Jiliberto et al. 2012)

In addition to direct, positive interactions we have also excluded an important indirect interaction type: the interaction modification (Wootton 1994, Werner and Peacor 2003). In this indirect interaction, the strength of a direct interaction between two species depends on the presence of a third. For example, the presence of a plant species may decrease predation pressure on a prey by making it harder to find (Wootton 1994, Stachowicz 2001). Similarly, a (top-)predator may decrease predation pressure from meso-predators or herbivores, as these in turn change behavior to avoid

being eaten (Lima and Dill 1990, Lima 1998, Werner and Peacor 2003). These trait-mediated trophic cascades may be at least as important as the classic (density-mediated) trophic cascades (Schmitz et al. 1997, 2004, Peacor and Werner 2001, Steffan and Snyder 2009), and have indeed been implied in some striking trophic cascades in natural systems following top-predator loss (Ripple and Beschta 2004, Johnson et al. 2007). Thus, interaction modification may have far-reaching consequences for community stability (Goudard and Loreau 2008, Kéfi et al. 2012) and structure (Peacor et al. 2012), both in the presence and absence of perturbation, and poses an interesting area of research.

5.4 A note on diversity and stability

How species richness affects the stability of natural systems is perhaps one of the oldest questions in ecology. The early view was that species richness conferred stability (Odum 1953, MacArthur 1955, Elton 1958). Large population fluctuations in simple, often human-modified systems led both Odum and Elton to the conclusions that species richness confers stability (Odum 1953, Elton 1958). Similarly, MacArthur argued that stability increased with the “amount of choice of the energy has in following the paths up through the food web” (MacArthur 1955). The turning point came when May theoretically demonstrated, that the likelihood of a community being locally stable decreased with species richness when interaction patterns were random (May 1973, McCann 2000). These results conflicted with the observation that natural communities are very species-rich and still persist. Hence, May encouraged ecologists to find the non-random properties of real communities that confer stability. The diversity-stability has been going on ever since, with research results showing everything from positive to neutral to negative relationships (Pimm 1984, McCann 2000, Ives and Carpenter 2007). Similarly, I find contrasting results regarding the effect of species richness on the risk of extinction.

In Paper IV, species richness significantly increased species’ extinction risk. But for none of the deletion sequences investigated in Paper II was species richness among the community properties that explained resistance to species loss. Not even when using species richness as the single predictor does it have any explanatory power (early analyses of the data in Paper II; data not shown). What can explain these contrasting results? The results of Paper IV hinges on 1) that high species richness means high basal species richness, 2) that high basal species richness means low basal species population size, and 3) that environmental stochasticity drives low abundance population to extinction. In Paper II, basal population size should decrease with basal species richness because of intra-specific competition, but the correlation of basal to total species richness is weak ($r \approx 0.25$; data not shown). Furthermore, there is no stochasticity to drive or contribute to neither primary nor secondary extinctions, and

therefore the inherent risk conferred by being rare is much smaller (Ebenman et al. 2004).

The controversy regarding the effect of diversity on stability has partly been due to the many different definitions of stability (Pimm 1984), as different aspects of community stability have different relationships with diversity (Ives and Carpenter 2007, Kaneryd et al. 2012 [Paper IV]). But we see here, that even when the same stability measure is used (resistance), the diversity-stability relationship can differ depending on what type of disturbance the community is subjected to. To complicate matters further, it may also depend on the correlation structure of community properties (e.g. correlation between basal and total species richness) and the type of dynamics of the community (type of basal species competition). Indeed, I find it interesting to speculate whether unacknowledged differences in interaction patterns might be behind some part of the controversy regarding the effect of diversity on stability (see for example Kokkoris et al. 2002, Neutel and Thorne 2014, Tang et al. 2014). It is clear at least that differences in the type, strength and variation of inter- and intra-specific competition has implications for how extinction risk relates to diversity (Hughes and Roughgarden 2000, Kokkoris et al. 2002, Thebault et al. 2007, Kaneryd et al. 2012 [Paper IV], Fowler 2013; Curtsdotter et al. 2014 [Paper II]).

5.5 Conclusions

Overall, the research results underscore the importance of including population dynamics and biotic interactions when studying the effects of perturbation on biodiversity. Many of the results are complex, hard to foresee or even counter-intuitive, arising from the indirect effects of the perturbation being translated through the living web of species interactions. These are the main conclusions of each paper:

- ❖ When studying robustness of food webs to species loss, it is important to include population dynamics, as top-down processes can be equally important as bottom-up processes.
- ❖ The community properties governing food web resistance depend on what species are lost in the primary extinctions. As different anthropogenic disturbances puts different types of species at risk, the properties defining a sensitive community will depend on the disturbance it is subjected to.
- ❖ Strong inter-specific competition increases global species loss under climate change, and the strength of inter-specific competition modulates the effect of evolution and dispersal on species' survival.
- ❖ In the face of high environmental variability, extinction risk increases with higher species richness, higher response diversity and higher degree of consumer specialization.
- ❖ The suggested rescue mechanism of consumer rewiring, aggravated species loss in a variable environment, due to consumers overexploiting novel prey. Only when consumers were inefficient at low prey abundances (Holling's functional response type III) did rewiring increase food web resistance.

5.6 An outlook for the future

In the scientific literature, I have come across the following quote:

“I would not give a fig for the simplicity this side of complexity, but I would give my life for the simplicity on the other side of complexity”

– Oliver Wendell Holmes (either Sr. 1809-1894 or Jr. 1841-1935)

Considering the person(s) to which the quote is attributed, I doubt it originally related to ecology, but it has stuck with me as being very appropriate for this science. In early ecology, it seems to me that we looked for rather simple answers. Perhaps we still do, although I believe there is now a general acknowledgement that there is no one correct answer, but instead that the answer is context dependent. Lawton (1999) even stated that “community ecology is a mess, with so much contingency that useful generalisations are hard to find”. Accordingly, MacArthur (1984) noted that “many take refuge in nature’s complexity as a justification to oppose any search for patterns”, although he was most certainly not one of the “many”. My belief is that we are still fighting our way through the vast complexity of ecological systems – and that we can find the other side.

Instead of a few general and independent rules, I believe the simplicity we can hope for is to understand and formulate under which circumstances certain species traits, processes, or community properties are important for certain community functions. In turn, this would allow us to identify ‘keystone species’ as well as the properties of vulnerable communities; the identities of both are likely to change over time and space. I would also presume that such understanding must be on an abstract, mechanistic level, and linked to real systems by knowledge of species’ physiology and abiotic environment, and how these determine species’ vital rates as well as the type, presence and strength of species interactions. Efforts in this direction have been made (e.g. Brown et al. 2004, Kearney and Porter 2006, Eklöf et al. 2013) and molecular genetics may come to play a very important role (Moritz and Cicero 2004, Kesanakurti et al. 2011, García-Robledo et al. 2013, Wirta et al. 2014).

To reach the understanding on the other side of ecological complexity would be my ultimate goal, although I would say we are still far from it; likely it will not be reached until well beyond my life time. One very important implication of this is, that we cannot wait for complete understanding of ecological systems before we take action to protect them against the many anthropogenic threats they face today. Indeed, there is no reason to wait; even though there are large uncertainties regarding the exact quantitative response of biodiversity to global change, there is little uncertainty that we must expect great biodiversity loss, and associated loss of ecosystem function, if we do not change our course (Chapin Iii et al. 2000, Rockström et al. 2009, Barnosky et al.

2011, Bellard et al. 2012, Hoekstra and Wiedmann 2014). I make myself no illusions; just as reaching ecological understanding will require long time, so will changing humanity's view on and use of the biosphere. With regard to the latter, I'm not certain that we will. But I believe neither is impossible. If you can forgive me another quote, I will put it in the words of a Norwegian explorer:

“The difficult is what takes a little time; the impossible is what takes a little longer.”

– Fridtjof Nansen (1861-1930)

Acknowledgements

I wish to thank my supervisor Bo Ebenman for the opportunity to work in this field, and for guidance and support throughout. Your wide ecological knowledge, your great grasp of the literature, your eye for interesting questions, and your skill in singling out the most relevant and interesting from a complex result have all been invaluable and I hope I have managed to learn from it. Thanks also to my second supervisor Peter Münger for crucial support in programming and mathematical modeling; your technical skills in combination with your ability to communicate them in a less technical way makes you such a wonderful support for a theoretical ecologist. A special thanks to David Gilljam, whom I have shared office with this entire time, for help on programming issues, inspiring discussions and for a certain knack of knowing when to and when not to listen to a talkative roomie.

I wish to thank everyone who has been part of the theoretical ecology group during my time here; you all make it such a warm and friendly environment to work in. It means a lot. The same goes for the entire biology department, although my presence in our lunch room has been a bit so and so lately (I blame it all on the thesis; my inclination for cooking of course has nothing to do with it).

There are also persons outside of Linköping University that has contributed to my time as PhD student, and whom I view as friends as well as colleagues, many of which I've met through the SIZEMIC network. A special thanks to Amrei Binzer, Björn Rall and Ulrich Brose for great hospitality during my work visits to Göttingen and for fun collaborations.

I also wish to thank family and friends. In consideration of my upbringing (according to me) and my personality (according to my parents) I'm not sure I could have become anything but a researcher. And it's not bad for dayjob. All my friends in the dance group bring joy and bling to my life, the most wonderful counterbalance to the more strict and intellectual work of a theoretical ecologist. Finally, a thanks to all family and friends who bring love and happiness to my life; (wo)man does not live by bread alone.

References

- Ackerman, J. D., W. Falcón, J. Molinari, C. Vega, I. Espino, and A. A. Cuevas. 2014. Biotic resistance and invasional meltdown: consequences of acquired interspecific interactions for an invasive orchid, *Spathoglottis plicata* in Puerto Rico. *Biological Invasions*:1–13.
- Adams, M. J., C. A. Pearl, and R. Bruce Bury. 2003. Indirect facilitation of an anuran invasion by non-native fishes. *Ecology Letters* 6:343–351.
- Adler, P. B., and J. M. Drake. 2008. Environmental Variation, Stochastic Extinction, and Competitive Coexistence. *The American Naturalist* 172:E186–E195.
- Allesina, S., A. Bodini, and M. Pascual. 2009. Functional links and robustness in food webs. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:1701–1709.
- Allesina, S., and M. Pascual. 2009. Googling Food Webs: Can an Eigenvector Measure Species' Importance for Coextinctions? *PLOS Computational Biology* 5:1–6.
- Balvanera, P., A. B. Pfisterer, N. Buchmann, J.-S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* 9:1146–1156.
- Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L. Lindsey, K. C. Maguire, B. Mersey, and E. A. Ferrer. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471:51–57.
- Bascompte, J., C. J. Melián, and E. Sala. 2005. Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences of the United States of America* 102:5443–5447.
- Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters* 15:365–377.
- Bennett, E. L., E. J. Milner-Gulland, M. Bakarr, H. E. Eves, J. G. Robinson, and D. S. Wilkie. 2002. Hunting the world's wildlife to extinction. *Oryx* 36:328–329.
- Berg, S. 2013. Community Robustness Analysis : Theoretical Approaches to Identifying Keystone Structures in Ecological Communities. Dissertation, Linköping.
- Binzer, A., U. Brose, A. Curtsdotter, A. Eklöf, B. C. Rall, J. O. Riede, and F. de Castro. 2011. The susceptibility of species to extinctions in model communities. *Basic and Applied Ecology* 12:590–599.

- Blindow, I., G. Andersson, A. Hargeby, and S. Johansson. 1993. Long-term pattern of alternative stable states in two shallow eutrophic lakes. *Freshwater Biology* 30:159–167.
- Blois, J. L., P. L. Zarnetske, M. C. Fitzpatrick, and S. Finnegan. 2013. Climate Change and the Past, Present, and Future of Biotic Interactions. *Science* 341:499–504.
- Bobbink, R., K. Hicks, J. Galloway, T. Spranger, R. Alkemade, M. Ashmore, M. Bustamante, S. Cinderby, E. Davidson, F. Dentener, B. Emmett, J.-W. Erismann, M. Fenn, F. Gilliam, A. Nordin, L. Pardo, and W. De Vries. 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications* 20:30–59.
- Borrvall, C. 2006. Biodiversity and Species Extinctions in Model Food Webs. Dissertation, Linköping.
- Borrvall, C., B. Ebenman, and T. Jonsson. 2000. Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters* 3:131–136.
- Both, C., M. Van Asch, R. G. Bijlsma, A. B. Van Den Burg, and M. E. Visser. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology* 78:73–83.
- Brooker, R. W., F. T. Maestre, R. M. Callaway, C. L. Lortie, L. A. Cavieres, G. Kunstler, P. Liancourt, K. Tielbörger, J. M. J. Travis, F. Anthelme, C. Armas, L. Coll, E. Corcket, S. Delzon, E. Forey, Z. Kikvidze, J. Olofsson, F. Pugnaire, C. L. Quiroz, P. Saccone, K. Schiffrers, M. Seifan, B. Touzard, and R. Michalet. 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* 96:18–34.
- Brose, U. 2008. Complex food webs prevent competitive exclusion among producer species. *Proceedings of the Royal Society B: Biological Sciences* 275:2507–2514.
- Brose, U., R. Williams, and N. Martinez. 2006. Allometric scaling enhances stability in complex food webs. *Ecology Letters* 9:1228–1236.
- Brown, J., J. Gillooly, A. Allen, V. Savage, and G. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
- Cardillo, M., G. Mace, K. Jones, J. Bielby, O. Bininda-Emonds, W. Sechrest, C. Orme, and A. Purvis. 2005. Multiple causes of high extinction risk in large mammal species. *Science* 309:1239–1241.
- Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, D. A. Wardle, A. P. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A. Larigauderie, D. S. Srivastava, and S. Naeem. 2012. Biodiversity loss and its impact on humanity. *Nature* 486:59–67.
- Case, T. J. 1999. *An Illustrated Guide to Theoretical Ecology*. Oxford University Press, New York, U.S.A. and Oxford, United Kingdom.

- Case, T. J., and M. L. Taper. 2000. Interspecific Competition, Environmental Gradients, Gene Flow, and the Coevolution of Species' Borders. *The American Naturalist* 155:583–605.
- Casini, M., J. Hjelm, J.-C. Molinero, J. Lövgren, M. Cardinale, V. Bartolino, A. Belgrano, and G. Kornilovs. 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proceedings of the National Academy of Sciences* 106:197–202.
- Casini, M., J. Lövgren, J. Hjelm, M. Cardinale, J.-C. Molinero, and G. Kornilovs. 2008. Multi-level trophic cascades in a heavily exploited open marine ecosystem. *Proceedings of the Royal Society B: Biological Sciences* 275:1793–1801.
- Chapin III, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Díaz. 2000. Consequences of changing biodiversity. *Nature* 405:234–242.
- Chase, J. M., P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, R. M. Nisbet, and T. J. Case. 2002. The interaction between predation and competition: a review and synthesis. *Ecology Letters* 5:302–315.
- Chen, M.-S. 2008. Inducible direct plant defense against insect herbivores: A review. *Insect Science* 15:101–114.
- Chesson, P., and N. Huntly. 1997. The Roles of Harsh and Fluctuating Conditions in the Dynamics of Ecological Communities. *The American Naturalist* 150:519–553.
- Chesson, P. L. 1986. Environmental variation and the coexistence of species. Pages 240–254 in J. M. Diamond and T. J. Case, editors. *Community ecology*. Harper & Row, New York, U.S.A.
- Cohen, J., F. Briand, C. Newman, and Z. J. Palka. 1990. *Community Food Webs: Data and Theory*. Springer, Berlin and Heidelberg, Germany.
- Coll, M., H. Lotze, and T. Romanuk. 2008. Structural degradation in Mediterranean Sea food webs: Testing ecological hypotheses using stochastic and mass-balance modelling. *Ecosystems* 11:939–960.
- Colwell, R. K., R. R. Dunn, and N. C. Harris. 2012. Coextinction and Persistence of Dependent Species in a Changing World. *Annual Review of Ecology, Evolution, and Systematics* 43:183–203.
- Connell, D. W., P. Lam, B. Richardson, and R. Wu. 1999. *Introduction to Ecotoxicology*. 1st edition. Wiley-Blackwell, Oxford, United Kingdom and Malden, U.S.A.
- Costanza, R., R. d' Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. O'Neill, J. Paruelo, R. G. Raskin, P. Sutton, and

- M. van den Belt. 1998. The value of the world's ecosystem services and natural capital. *Ecological Economics* 25:3–15.
- Cuddington, K., W. G. Wilson, and A. Hastings. 2009. Ecosystem Engineers: Feedback and Population Dynamics. *The American Naturalist* 173:488–498.
- Curtsdotter, A., A. Binzer, U. Brose, F. de Castro, B. Ebenman, A. Eklöf, J. O. Riede, A. Thierry, and B. C. Rall. 2011. Robustness to secondary extinctions: Comparing trait-based sequential deletions in static and dynamic food webs. *Basic and Applied Ecology* 12:571–580.
- Davidson, D. W., R. S. Inouye, and J. H. Brown. 1984. Granivory in a Desert Ecosystem: Experimental Evidence for Indirect Facilitation of Ants by Rodents. *Ecology* 65:1780–1786.
- Dayton, P. 1972. Toward an understanding of community resilience and the potential effects of enrichment to the benthos at McMurdo Sound, Antarctica. *in* B. Parker, editor. *Proceedings of the Colloquium on Conservation Problems in Antarctica*. Allen Press, Lawrence, Kansas, U.S.A.
- Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences* 105:6668–6672.
- deYoung, B., M. Barange, G. Beaugrand, R. Harris, R. I. Perry, M. Scheffer, and F. Werner. 2008. Regime shifts in marine ecosystems: detection, prediction and management. *Trends in Ecology & Evolution* 23:402–409.
- Didham, R. K., J. M. Tylianakis, N. J. Gemmell, T. A. Rand, and R. M. Ewers. 2007. Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology & Evolution* 22:489–496.
- Digel, C., J. O. Riede, and U. Brose. 2011. Body sizes, cumulative and allometric degree distributions across natural food webs. *Oikos* 120:503–509.
- Dunn, R. R., N. C. Harris, R. K. Colwell, L. P. Koh, and N. S. Sodhi. 2009. The sixth mass coextinction: are most endangered species parasites and mutualists? *Proceedings of the Royal Society B: Biological Sciences* 276:3037–3045.
- Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002a. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters* 5:558–567.
- Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002b. Food-web structure and network theory: the role of connectance and size. *Proceedings of the National Academy of Sciences, USA* 99:12917–12922.

- Dunne, J., and R. Williams. 2009. Cascading extinctions and community collapse in model food webs. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:1711–1723.
- Dunne, J., R. Williams, and N. Martinez. 2004. Network structure and robustness of marine food webs. *Marine Ecology: Progress Series* 273:291–302.
- Easterling, D. R. 2000. Climate Extremes: Observations, Modeling, and Impacts. *Science* 289:2068–2074.
- Ebenman, B., and T. Jonsson. 2005. Using community viability analysis to identify fragile systems and keystone species. *Trends in Ecology & Evolution* 20:568–575.
- Ebenman, B., R. Law, and C. Borrvall. 2004. Community Viability Analysis: The Response of Ecological Communities to Species Loss. *Ecology* 85:2591–2600.
- Eklöf, A., and B. Ebenman. 2006. Species loss and secondary extinctions in simple and complex model communities. *Journal of Animal Ecology* 75:239–246.
- Eklöf, A., U. Jacob, J. Kopp, J. Bosch, R. Castro-Urgal, N. P. Chacoff, B. Dalsgaard, C. de Sassi, M. Galetti, P. R. Guimarães, S. B. Lomáscolo, A. M. Martín González, M. A. Pizo, R. Rader, A. Rodrigo, J. M. Tylianakis, D. P. Vázquez, and S. Allesina. 2013. The dimensionality of ecological networks. *Ecology Letters* 16:577–583.
- Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. Von Holle, and J. R. Webster. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3:479–486.
- Elmhagen, B., G. Ludwig, S. P. Rushton, P. Helle, and H. Lindén. 2010. Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. *Journal of Animal Ecology* 79:785–794.
- Elmhagen, B., and S. P. Rushton. 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecology Letters* 10:197–206.
- Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* 1:488–494.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. Methuen, London, United Kingdom.

- Estes, J. A., and J. F. Palmisano. 1974. Sea otters: Their role in structuring nearshore communities. *Science* 185:1058–1060.
- Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic Downgrading of Planet Earth. *Science* 333:301–306.
- Estes, J., M. Tinker, T. Williams, and D. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282:473–476.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. *Annual Review of Ecology, Evolution, and Systematics* 35:557–581.
- Fowler, M. S. 2010. Extinction cascades and the distribution of species interactions. *Oikos* 119:864–873.
- Fowler, M. S. 2013. The form of direct interspecific competition modifies secondary extinction patterns in multi-trophic food webs. *Oikos* 122:1730–1738.
- Frank, K. T., B. Petrie, J. S. Choi, and W. C. Leggett. 2005. Trophic Cascades in a Formerly Cod-Dominated Ecosystem. *Science* 308:1621–1623.
- Garcia, R. A., M. Cabeza, C. Rahbek, and M. B. Araújo. 2014. Multiple Dimensions of Climate Change and Their Implications for Biodiversity. *Science* 344:1247579.
- García-Robledo, C., D. L. Erickson, C. L. Staines, T. L. Erwin, and W. J. Kress. 2013. Tropical Plant–Herbivore Networks: Reconstructing Species Interactions Using DNA Barcodes. *PLoS ONE* 8:e52967.
- Gårdmark, A., M. Lindegren, S. Neuenfeldt, T. Blenckner, O. Heikinheimo, B. Müller-Karulis, S. Niiranen, M. T. Tomczak, E. Aro, A. Wikström, and C. Möllmann. 2012. Biological ensemble modeling to evaluate potential futures of living marine resources. *Ecological Applications* 23:742–754.
- Gilbert, A. 2009. Connectance indicates the robustness of food webs when subjected to species loss. *Ecological Indicators* 9:72–80.
- Gonzalez, A., and M. Loreau. 2009. The Causes and Consequences of Compensatory Dynamics in Ecological Communities. *Annual Review of Ecology, Evolution, and Systematics* 40:393–414.
- Goudard, A., and M. Loreau. 2008. Nontrophic Interactions, Biodiversity, and Ecosystem Functioning: An Interaction Web Model. *The American Naturalist* 171:91–106.

- Gravel, D., F. Guichard, and M. E. Hochberg. 2011. Species coexistence in a variable world. *Ecology Letters* 14:828–839.
- Gray, J. S. 2002. Biomagnification in marine systems: the perspective of an ecologist. *Marine Pollution Bulletin* 45:46–52.
- Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad, and D. Tilman. 2011. Plant diversity and the stability of foodwebs. *Ecology Letters* 14:42–46.
- Harley, C. D. G., A. Randall Hughes, K. M. Hultgren, B. G. Miner, C. J. B. Sorte, C. S. Thornber, L. F. Rodriguez, L. Tomanek, and S. L. Williams. 2006. The impacts of climate change in coastal marine systems. *Ecology Letters* 9:228–241.
- Hegland, S. J., A. Nielsen, A. Lázaro, A.-L. Bjerknes, and Ø. Totland. 2009. How does climate warming affect plant-pollinator interactions? *Ecology Letters* 12:184–195.
- Hewitt, J. E., S. F. Thrush, P. K. Dayton, and E. Bonsdorff. 2007. The Effect of Spatial and Temporal Heterogeneity on the Design and Analysis of Empirical Studies of Scale-Dependent Systems. *The American Naturalist* 169:398–408.
- Hoekstra, A. Y., and T. O. Wiedmann. 2014. Humanity’s unsustainable environmental footprint. *Science* 344:1114–1117.
- Holling, C. S. 1959. The Components of Predation as Revealed by a Study of Small-Mammal Predation of the European Pine Sawfly. *The Canadian Entomologist* 91:293–320.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–229.
- Holt, R. D., and G. R. Huxel. 2007. Alternative prey and the dynamics of intraguild predation: theoretical perspectives. *Ecology* 88:2706–2712.
- Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, and M. I. O’Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486:105–108.
- Huey, R. B., C. A. Deutsch, J. J. Tewksbury, L. J. Vitt, P. E. Hertz, H. J. Á. Pérez, and T. Garland. 2009. Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society B: Biological Sciences* 276:1939–1948.
- Hughes, J. B., and J. Roughgarden. 2000. Species Diversity and Biomass Stability. *The American Naturalist* 155:618–627.
- Huss, M., A. M. de Roos, A. V. Leeuwen, Michele Casini, and A. Gårdmark. 2013. Cohort Dynamics Give Rise to Alternative Stable Community States. *The American Naturalist* 182:374–392.
- IPCC. 2013. Climate Change 2013: The Physical Science Basis. Working Group 1 Contribution to the Fifth Assessment Report of the Intergovernmental

- Panel on Climate Change. (T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, Eds.). Cambridge University Press, Cambridge, United Kingdom and New York, N.Y., U.S.A.
- Isaac, N. J. B., and G. Cowlshaw. 2004. How species respond to multiple extinction threats. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271:1135–1141.
- Ives, A. R., and S. R. Carpenter. 2007. Stability and diversity of ecosystems. *Science* 317:58–62.
- Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical Overfishing and the Recent Collapse of Coastal Ecosystems. *Science* 293:629–637.
- Jiang, L., and P. J. Morin. 2004. Temperature-dependent interactions explain unexpected responses to environmental warming in communities of competitors. *Journal of Animal Ecology* 73:569–576.
- Jiang, L., and P. J. Morin. 2007. Temperature fluctuation facilitates coexistence of competing species in experimental microbial communities. *Journal of Animal Ecology* 76:660–668.
- Johnson, C. N., J. L. Isaac, and D. O. Fisher. 2007. Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proceedings of the Royal Society B: Biological Sciences* 274:341–346.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1996. Organisms as Ecosystem Engineers. Pages 130–147 *Ecosystem Management*. Springer, New York, U.S.A.
- Jørgensen, C., K. Enberg, E. S. Dunlop, R. Arlinghaus, D. S. Boukal, K. Brander, B. Ernande, A. G. Gårdmark, F. Johnston, S. Matsumura, H. Pardoe, K. Raab, A. Silva, A. Vainikka, U. Dieckmann, M. Heino, and A. D. Rijnsdorp. 2007. Ecology: Managing Evolving Fish Stocks. *Science* 318:1247–1248.
- Kaiser-Bunbury, C. N., S. Muff, J. Memmott, C. B. Müller, and A. Caflisch. 2010. The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecology Letters* 13:442–452.
- Kaneryd, L., C. Borrvall, S. Berg, A. Curtsdotter, A. Eklöf, C. Hauzy, T. Jonsson, P. Münger, M. Setzer, T. Säterberg, and B. Ebenman. 2012. Species-rich ecosystems are vulnerable to cascading extinctions in an increasingly variable world. *Ecology and Evolution* 2:858–874.

- Kearney, M., and W. P. Porter. 2006. Ecologists have already started rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21:481–482.
- Kéfi, S., E. L. Berlow, E. A. Wieters, S. A. Navarrete, O. L. Petchey, S. A. Wood, A. Boit, L. N. Joppa, K. D. Lafferty, R. J. Williams, N. D. Martinez, B. A. Menge, C. A. Blanchette, A. C. Iles, and U. Brose. 2012. More than a meal... integrating non-feeding interactions into food webs. *Ecology Letters* 15:291–300.
- Kesanakurti, P. R., A. J. Fazekas, K. S. Burgess, D. M. Percy, S. G. Newmaster, S. W. Graham, S. C. H. Barrett, M. Hajibabaei, and B. C. Husband. 2011. Spatial patterns of plant diversity below-ground as revealed by DNA barcoding. *Molecular Ecology* 20:1289–1302.
- Kirby, R. R., and G. Beaugrand. 2009. Trophic amplification of climate warming. *Proceedings of the Royal Society B: Biological Sciences*:4095–4103.
- Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a Species' Range. *The American Naturalist* 150:1–23.
- Kitching, R. L. 2000. *Food Webs and Container Habitats: The Natural History and Ecology of Phytotelmata*. 1st edition. Cambridge University Press, Cambridge, United Kingdom.
- Koh, L. P., R. R. Dunn, N. S. Sodhi, R. K. Colwell, H. C. Proctor, and V. S. Smith. 2004. Species Coextinctions and the Biodiversity Crisis. *Science* 305:1632–1634.
- Kokkoris, G. D., V. A. A. Jansen, M. Loreau, and A. Y. Troumbis. 2002. Variability in interaction strength and implications for biodiversity. *Journal of Animal Ecology* 71:362–371.
- Kondoh, M. 2003. Foraging Adaptation and the Relationship Between Food-Web Complexity and Stability. *Science* 299:1388–1391.
- Kondoh, M. 2007. Anti-predator defence and the complexity-stability relationship of food webs. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 274:1617–1624.
- Laliberté, E., J. A. Wells, F. DeClerck, D. J. Metcalfe, C. P. Catterall, C. Queiroz, I. Aubin, S. P. Bonser, Y. Ding, J. M. Fraterrigo, S. McNamara, J. W. Morgan, D. S. Merlos, P. A. Veski, and M. M. Mayfield. 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters* 13:76–86.
- Lande, R. 1993. Risks of Population Extinction from Demographic and Environmental Stochasticity and Random Catastrophes. *The American Naturalist* 142:911–927.
- Van Langevelde, F., C. A. D. M. Van De Vijver, L. Kumar, J. Van De Koppel, N. De Ridder, J. Van Andel, A. K. Skidmore, J. W. Hearne, L. Stroosnijder, W. J.

- Bond, H. H. T. Prins, and M. Rietkerk. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84:337–350.
- Lawton, J. H. 1999. Are There General Laws in Ecology? *Oikos* 84:177–192.
- Lima, S. L. 1998. Nonlethal Effects in the Ecology of Predator-Prey Interactions. *BioScience* 48:25–34.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Lögdberg, F., and U. Wennergren. 2012. Spectral color, synchrony, and extinction risk. *Theoretical Ecology* 5:545–554.
- Lyons, K. G., and M. W. Schwartz. 2001. Rare species loss alters ecosystem function – invasion resistance. *Ecology Letters* 4:358–365.
- MacArthur, R. 1955. Fluctuations of Animal Populations and a Measure of Community Stability. *Ecology* 36:533–536.
- MacArthur, R. H. 1984. *Geographical Ecology. Patterns of the Distribution of Species*. Princeton University Press, Princeton, N.J., U.S.A.
- Mann, M. E., and K. A. Emanuel. 2006. Atlantic hurricane trends linked to climate change. *Eos, Transactions American Geophysical Union* 87:233–241.
- Martin, T. L., and R. B. Huey. 2008. Why “Suboptimal” Is Optimal: Jensen’s Inequality and Ectotherm Thermal Preferences. *The American Naturalist* 171:E102–E118.
- May, R. M. 1973. *Complexity and stability in model ecosystems*. Princeton University Press, Princeton, N. J., U.S.A.
- McCann, K. S. 2000. The diversity-stability debate. *Nature* 405:228–233.
- McCoy, M. W., and J. F. Gillooly. 2008. Predicting natural mortality rates of plants and animals 11:710–716.
- McKinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics* 28:495–516.
- Memmott, J., N. M. Waser, and M. V. Price. 2004. Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271:2605–2611.
- Millenium Ecosystem Assessment. 2005. *Ecosystems and Human Well-being: Biodiversity Synthesis*. World Resources Institute.
- Miller, D. A., J. B. Grand, T. F. Fondell, and M. Anthony. 2006. Predator functional response and prey survival: direct and indirect interactions affecting a marked prey population. *Journal of Animal Ecology* 75:101–110.
- Moritz, C., and C. Cicero. 2004. DNA Barcoding: Promise and Pitfalls. *PLoS Biol* 2:e354.

- Mougi, A., and M. Kondoh. 2012. Diversity of Interaction Types and Ecological Community Stability. *Science* 337:349–351.
- Mumby, P. J., A. Hastings, and H. J. Edwards. 2007. Thresholds and the resilience of Caribbean coral reefs. *Nature* 450:98–101.
- Munday, P. L. 2004. Habitat loss, resource specialization, and extinction on coral reefs. *Global Change Biology* 10:1642–1647.
- Neutel, A.-M., and M. A. S. Thorne. 2014. Interaction strengths in balanced carbon cycles and the absence of a relation between ecosystem complexity and stability. *Ecology Letters* 17:651–661.
- Niklas, K. J., and B. J. Enquist. 2001. Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proceedings of the National Academy of Sciences* 98:2922–2927.
- Norberg, J., M. C. Urban, M. Vellend, C. A. Klausmeier, and N. Loeuille. 2012. Eco-evolutionary responses of biodiversity to climate change. *Nature Climate Change* 2:747–751.
- Norström, A. V., M. Nyström, J. Lokrantz, and C. Folke. 2009. Alternative states on coral reefs: beyond coral-macroalgal phase shifts. *Marine Ecology Progress Series* 376:295–306.
- O’Gorman, E. J., and M. C. Emmerson. 2009. Perturbations to trophic interactions and the stability of complex food webs. *Proceedings of the National Academy of Sciences* 106:13393–13398.
- Oaten, A., and W. W. Murdoch. 1975. Switching, Functional Response, and Stability in Predator-Prey Systems. *The American Naturalist* 109:299–318.
- Odum, E. P. 1953. *Fundamentals of ecology*. Saunders, Philadelphia, U.S.A.
- Okuyama, T., and J. N. Holland. 2008. Network structural properties mediate the stability of mutualistic communities. *Ecology Letters* 11:208–216.
- Paine, R. T. 1966. Food Web Complexity and Species Diversity. *The American Naturalist* 100:65–75.
- Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics* 37:637–669.
- Parmesan, C., T. L. Root, and M. R. Willig. 2000. Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society* 81:443–450.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres. 1998. Fishing Down Marine Food Webs. *Science* 279:860–863.
- Peacor, S. D., K. L. Pangle, L. Schiesari, and E. E. Werner. 2012. Scaling-up anti-predator phenotypic responses of prey: impacts over multiple generations in a complex aquatic community. *Proceedings of the Royal Society B: Biological Sciences* 279:122–128.

- Peacor, S. D., and E. E. Werner. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. *Proceedings of the National Academy of Sciences* 98:3904–3908.
- Pereira, H. M., P. W. Leadley, V. Proença, R. Alkemade, J. P. W. Scharlemann, J. F. Fernandez-Manjarrés, M. B. Araújo, P. Balvanera, R. Biggs, W. W. L. Cheung, L. Chini, H. D. Cooper, E. L. Gilman, S. Guénette, G. C. Hurtt, H. P. Huntington, G. M. Mace, T. Oberdorff, C. Revenga, P. Rodrigues, R. J. Scholes, U. R. Sumaila, and M. Walpole. 2010. Scenarios for Global Biodiversity in the 21st Century. *Science* 330:1496–1501.
- Pianka, E. R. 1999. *Evolutionary Ecology*. 6th edition. Benjamin Cummings, San Francisco, U.S.A.
- Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature* 307:321–326.
- Pimm, S. L., C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P. H. Raven, C. M. Roberts, and J. O. Sexton. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344:1246752.
- Pol, M. van de, Y. Vindenes, B.-E. Sæther, S. Engen, B. J. Ens, K. Oosterbeek, and J. M. Tinbergen. 2011. Poor environmental tracking can make extinction risk insensitive to the colour of environmental noise. *Proceedings of the Royal Society B: Biological Sciences* 278:3713–3722.
- Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The Ecology and Evolution of Intraguild Predation: Potential Competitors That Eat Each Other. *Annual Review of Ecology and Systematics* 20:297–330.
- Post, D. M. 2002. The long and short of food-chain length. *Trends in Ecology & Evolution* 17:269–277.
- Post, E., and M. C. Forchhammer. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions: Biological Sciences* 363:2369–2375.
- Post, E., R. O. Peterson, N. C. Stenseth, and B. E. McLaren. 1999. Ecosystem consequences of wolf behavioural response to climate. *Nature* 401:905–907.
- Pounds, J. A., M. P. L. Fogden, and J. H. Campbell. 1999. Biological response to climate change on a tropical mountain. *Nature* 398:611–615.
- Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The Rise of the Mesopredator. *BioScience* 59:779–791.
- Purvis, A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace. 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267:1947–1952.

- Raffaelli, D., and H. Moller. 2000. Manipulative field experiments in animal ecology: do they promise more than they can deliver? *Advances in Ecological Research* 30:298–337.
- Raffaelli, J. M. 2005. Introduction to Section 7: Environmental Change, Perturbations and Food Webs. *in* P. de Ruiter, V. Wolters, and J. C. Moore, editors. *Dynamic food webs: multispecies assemblages, ecosystem development and environmental change*. Academic Press, Burlington, USA.
- Rall, B., C. Guill, and U. Brose. 2008. Food-web connectance and predator interference dampen the paradox of enrichment. *Oikos* 117:202–213.
- Ramos-Jiliberto, R., F. S. Valdovinos, P. Moisset de Espanés, and J. D. Flores. 2012. Topological plasticity increases robustness of mutualistic networks. *Journal of Animal Ecology* 81:896–904.
- Ricklefs, R. E. 2008. *The Economy of Nature*. 6th edition. W. H. Freeman, New York, U.S.A.
- Riede, J. O., A. Binzer, U. Brose, F. de Castro, A. Curtsdotter, B. C. Rall, and A. Eklöf. 2011a. Size-based food web characteristics govern the response to species extinctions. *Basic and Applied Ecology* 12:581–589.
- Riede, J. O., U. Brose, B. Ebenman, U. Jacob, R. Thompson, C. R. Townsend, and T. Jonsson. 2011b. Stepping in Elton’s footprints: a general scaling model for body masses and trophic levels across ecosystems. *Ecology Letters* 14:169–178.
- Ripa, J., and P. Lundberg. 1996. Noise Colour and the Risk of Population Extinctions. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 263:1751–1753.
- Ripa, J., and P. Lundberg. 2000. The route to extinction in variable environments. *Oikos* 90:89–96.
- Ripple, W. J., and R. L. Beschta. 2004. Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems? *BioScience* 54:755–766.
- Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and Ecological Effects of the World’s Largest Carnivores. *Science* 343:1241484.
- Roberts, C. M., and J. P. Hawkins. 1999. Extinction risk in the sea. *Trends in Ecology & Evolution* 14:241–246.
- Rockström, J., W. Steffen, K. Noone, Å. Persson, F. S. Chapin, E. F. Lambin, T. M. Lenton, M. Scheffer, C. Folke, H. J. Schellnhuber, B. Nykvist, C. A. de Wit, T. Hughes, S. van der Leeuw, H. Rodhe, S. Sörlin, P. K. Snyder, R. Costanza, U. Svedin, M. Falkenmark, L. Karlberg, R. W. Corell, V. J. Fabry, J. Hansen, B. Walker, D. Liverman, K. Richardson, P. Crutzen, and

- J. A. Foley. 2009. A safe operating space for humanity. *Nature* 461:472–475.
- Rohr, J. R., J. L. Kerby, and A. Sih. 2006. Community ecology as a framework for predicting contaminant effects. *Trends in Ecology & Evolution* 21:606–613.
- Rosenzweig, M. L., and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. *American Naturalist* 97:209–223.
- Saavedra, S., D. B. Stouffer, B. Uzzi, and J. Bascompte. 2011. Strong contributors to network persistence are the most vulnerable to extinction. *Nature* 478:233–235.
- Sala, O. E., F. S. Chapin III, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global Biodiversity Scenarios for the Year 2100. *Science* 287:1770–1774.
- Salminen, J., T. Korkama, and R. Stroömmmer. 2002. Interaction modification among decomposers impairs ecosystem processes in lead-polluted soil. *Environmental Toxicology and Chemistry* 21:2301–2309.
- Sanders, D., L. Sutter, and F. J. F. van Veen. 2013. The loss of indirect interactions leads to cascading extinctions of carnivores. *Ecology Letters* 16:664–669.
- Sanford, E. 1999. Regulation of Keystone Predation by Small Changes in Ocean Temperature. *Science* 283:2095–2097.
- Säterberg, T., S. Sellman, and B. Ebenman. 2013. High frequency of functional extinctions in ecological networks. *Nature* 499:468–470.
- Saunders, P. T. 1978. Population dynamics and the length of food chains. *Nature* 272:189–190.
- Sauve, A. M. C., C. Fontaine, and E. Thébault. 2014. Structure–stability relationships in networks combining mutualistic and antagonistic interactions. *Oikos* 123:378–384.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–596.
- Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution* 18:648–656.
- Schmitz, O. J., A. P. Beckerman, and K. M. O’Brien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78:1388–1399.
- Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* 7:153–163.

- Schröder, A., L. Persson, and A. M. De Roos. 2005. Direct experimental evidence for alternative stable states: a review. *Oikos* 110:3–19.
- Sheriff, M. J., C. J. Krebs, and R. Boonstra. 2009. The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares. *Journal of Animal Ecology* 78:1249–1258.
- Silvertown, J. 2004. The ghost of competition past in the phylogeny of island endemic plants. *Journal of Ecology* 92:168–173.
- Simberloff, D., and B. V. Holle. 1999. Positive Interactions of Nonindigenous Species: Invasional Meltdown? *Biological Invasions* 1:21–32.
- Solé, R. V., and M. Montoya. 2001. Complexity and fragility in ecological networks. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 268:2039–2045.
- Springer, A. M., J. A. Estes, G. B. van Vliet, T. M. Williams, D. F. Doak, E. M. Danner, K. A. Forney, and B. Pfister. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences* 100:12223–12228.
- Srinivasan, U., J. Dunne, J. Harte, and N. Martinez. 2007. Response of complex food webs to realistic extinction sequences. *Ecology* 88:671–682.
- Stachowicz, J. J. 2001. Mutualism, Facilitation, and the Structure of Ecological Communities. *BioScience* 51:235–246.
- Staniczenko, P., O. Lewis, N. Jones, and F. Reed-Tsochas. 2010. Structural dynamics and robustness of food webs. *Ecology Letters* 13:891–899.
- Steffan, S. A., and W. E. Snyder. 2009. Cascading diversity effects transmitted exclusively by behavioral interactions. *Ecology* 91:2242–2252.
- Sterner, R. W., A. Bajpai, and T. Adams. 1997. The enigma of food chain length: absence of theoretical evidence for dynamical constraints. *Ecology* 78:2258–2262.
- Stiling, P. 2001. *Ecology: Theories and Applications*. 4th edition. Prentice Hall, Upper Saddle River, NJ, U.S.A.
- Stouffer, D. B., and J. Bascompte. 2011. Compartmentalization Increases Food-Web Persistence. *Proceedings of the National Academy of Sciences* 108:3648–3652.
- Sunday, J. M., A. E. Bates, and N. K. Dulvy. 2011. Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B: Biological Sciences* 278:1823–1830.
- Suttle, K. B., M. A. Thomsen, and M. E. Power. 2007. Species Interactions Reverse Grassland Responses to Changing Climate. *Science* 315:640–642.

- Tang, S., S. Pawar, and S. Allesina. 2014. Correlation between interaction strengths drives stability in large ecological networks. *Ecology Letters*:Early View Online.
- The IUCN Red List of Threatened Species. Version 2013.2. 2014, May 23. . <http://www.iucnredlist.org>.
- Thébault, E., and C. Fontaine. 2010. Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. *Science* 329:853–856.
- Thébault, E., V. Huber, and M. Loreau. 2007. Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure. *Oikos* 116:163–173.
- Thierry, A., A. P. Beckerman, P. H. Warren, R. J. Williams, A. J. Cole, and O. L. Petchey. 2011. Adaptive foraging and the rewiring of size-structured food webs following extinctions. *Basic and Applied Ecology* 12:562–570.
- Touchon, J. C., and K. M. Warkentin. 2009. Negative synergism of rainfall patterns and predators affects frog egg survival. *Journal of Animal Ecology* 78:715–723.
- Turvey, S. T., R. L. Pitman, B. L. Taylor, J. Barlow, T. Akamatsu, L. A. Barrett, X. Zhao, R. R. Reeves, B. S. Stewart, K. Wang, Z. Wei, X. Zhang, L. T. Pusser, M. Richlen, J. R. Brandon, and D. Wang. 2007. First human-caused extinction of a cetacean species? *Biology Letters* 3:537–540.
- Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11:1351–1363.
- Valdovinos, F. S., R. Ramos-Jiliberto, L. Garay-Narváez, P. Urbani, and J. A. Dunne. 2010. Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecology Letters* 13:1546–1559.
- Vandermeer, J., B. Hazlett, and B. Rathcke. 1985. Indirect facilitation and mutualism. Pages 326–343 *in* D. H. Boucher, editor. *The biology of mutualism*. Croom Helm Ltd., Beckenham. United Kingdom.
- Van Veen, F., P. van Holland, and H. Godfray. 2005. Stable coexistence in insect communities due to density- and trait-mediated indirect effects. *Ecology* 86:3182–3189.
- De Visser, S. N., B. P. Freymann, and H. Olff. 2011. The Serengeti food web: empirical quantification and analysis of topological changes under increasing human impact. *Journal of Animal Ecology* 80:484–494.
- Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100.

- Wigley, T. M. L., R. L. Smith, and B. D. Santer. 1998. Anthropogenic Influence on the Autocorrelation Structure of Hemispheric-Mean Temperatures. *Science* 282:1676–1679.
- Williams, R. J., A. Anandanadesan, and D. Purves. 2010. The Probabilistic Niche Model Reveals the Niche Structure and Role of Body Size in a Complex Food Web. *PLoS ONE* 5:e12092.
- Williams, R. J., and N. D. Martinez. 2000. Simple rules yield complex food webs. *Nature* 404:180–183.
- Williams, R. J., and N. D. Martinez. 2008. Success and its limits among structural models of complex food webs. *Journal of Animal Ecology* 77:512–519.
- Williams, R., and N. Martinez. 2004. Stabilization of chaotic and non-permanent food-web dynamics. *European Physical Journal B* 38:297–303.
- Wirta, H. K., P. D. Hebert, R. Kaartinen, S. W. Prosser, G. Várkonyi, and T. Roslin. 2014. Complementary molecular information changes our perception of food web structure. *Proceedings of the National Academy of Sciences* 111:1885–1890.
- Woodward, G., J. Blanchard, R. B. Lauridsen, F. K. Edwards, J. I. Jones, D. Figueroa, P. H. Warren, and O. L. Petchey. 2010. Individual-based food webs: species identity, body size and sampling effects. *Advances in Ecological Research* 43:211–266.
- Wootton, J. T. 1994. The Nature and Consequences of Indirect Effects in Ecological Communities. *Annual Review of Ecology and Systematics* 25:443–466.
- Worsfold, N. T., P. H. Warren, and O. L. Petchey. 2009. Context-dependent effects of predator removal from experimental microcosm communities. *Oikos* 118:1319–1326.
- Yodzis, P. 1988. The Indeterminacy of Ecological Interactions as Perceived Through Perturbation Experiments. *Ecology* 69:508–515.
- Yodzis, P., and S. Innes. 1992. Body Size and Consumer-Resource Dynamics. *The American Naturalist* 139:1151–1175.
- Zavaleta, E., J. Pasari, J. Moore, D. Hernández, K. B. Suttle, and C. C. Wilmers. 2009. Ecosystem Responses to Community Disassembly. *Annals of the New York Academy of Sciences* 1162:311–333.
- Zavaleta, E. S., and K. B. Hulvey. 2004. Realistic Species Losses Disproportionately Reduce Grassland Resistance to Biological Invaders. *Science* 306:1175–1177.

Papers

The articles associated with this thesis have been removed for copyright reasons. For more details about these see:

<http://urn.kb.se/resolve?urn=urn:nbn:se:liu:diva-108906>