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Structure and Stability of Ecological Networks

The role of dynamic dimensionality and species variability in
resource use

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“Everything is both simpler than we can imagine, and more complicated than we can conceive.”

Johan Wolfgang von Goethe

“Big fish eat little fish”
Enok Gilljam (2016)

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Summary

The main focus of this thesis is on the response of ecological communities to environmental variability and species loss. My approach is theoretical; I use mathematical models of networks where species population dynamics are described by ordinary differential equations. A common theme of the papers in my thesis is variation – variable link structure (Paper I) and within-species variation in resource use (Paper III and IV). To explore how such variation affect the stability of ecological communities in variable environments, I use numerical methods evaluating for example community persistence (the proportion of species surviving over time; Paper I, II and IV). I also develop a new method for quantifying the dynamical dimensionality of an ecological community based on eigenvalue analysis and investigate its effect on community persistence in stochastic environments (Paper II). Moreover, if we are to gain trustworthy model output, it is of course of major importance to create study systems that reflect the structures of natural systems. To this end, I also study highly resolved, individual based empirical food web data sets (Paper III, IV).

In Paper I, the effects of adaptive rewiring induced by resource loss on the persistence of ecological networks is investigated. Loss of one species in an ecosystem can trigger extinctions of other dependent species. For instance, specialist predators will go extinct following the loss of their only prey unless they can change their diet. It has therefore been suggested that an ability of consumers to rewire to novel prey should mitigate the consequences of species loss by reducing the risk of cascading extinction. Using a new modelling approach on natural and computer-generated food webs I find that, on the contrary, rewiring often aggravates the effects of species loss. This is because rewiring can lead to overexploitation of resources, which eventually causes extinction cascades. Such a scenario is particularly likely if prey species cannot escape predation when rare and if predators are efficient in exploiting novel prey. Indeed, rewiring is a two-edged sword; it might be advantageous for individual predators in the short term, yet harmful for long-term system persistence.

The persistence of an ecological community in a variable world depends on the strength of environmental variation pushing the community away from equilibrium compared to the strength of the deterministic feedbacks, caused by interactions among and within species, pulling the community towards the equilibrium. However, it is not clear which characteristics of a community that promote its persistence in a variable world. In Paper II, using a modelling approach on natural and computer-generated food webs, I show that community persistence is strongly and positively related to its dynamic dimensionality (DD), as measured by the inverse participation ratio (IPR) of the real part of the eigenvalues of the community matrix. A high DD means that the real parts of the eigenvalues are of similar magnitude and the system will therefore approach equilibrium from all directions at a similar rate. On the other hand, when DD is low, one of the eigenvalues has a large magnitude of the real part compared to the others and the deterministic forces pulling the system towards equilibrium is

therefore weak in many directions compared to the stochastic forces pushing the system away from the equilibrium. As a consequence the risk of crossing extinction thresholds and boundaries separating basins of attractions increases, and hence persistence decreases, as DD decreases. Given the forecasted increase in climate variability caused by global warming, Paper II suggests that the dynamic dimensionality of ecological systems is likely to become an increasingly important property for their persistence.

In Paper III, I investigate patterns in the size structure of one marine and six running freshwater food webs: that is, how the trophic structure of such ecological networks is governed by the body size of its interacting entities. The data for these food webs are interactions between individuals, including the taxonomic identity and body mass of the prey and the predator. Using these detailed data, I describe how patterns in diet variation and predator variation scales with the body mass of predators or prey, using both a species- and a size-class-based approach. I also compare patterns of size structure derived from analysis of individual-based data with those patterns that result when data are aggregated into species (or size class-based) averages. This comparison shows that analysis based on species averaging can obscure interesting patterns in the size structure of ecological communities. For example, I find that the strength of the relationship between prey body mass and predator body mass is consistently underestimated when species averages are used instead of the individual level data. In some cases, no relationship is found when species averages are used, but when individual-level data are used instead, clear and significant patterns are revealed. Further, when data are grouped into size classes, the strength of the relationship between prey body and predator body mass is weaker compared to what is found using species-aggregated data. I also discuss potential sampling effects arising from size-class-based approaches, which are not always seen in taxonomical approaches. These results have potentially important implications for parameterisation of models of ecological communities and hence for predictions concerning their dynamics and response to different kinds of disturbances.

Paper IV continues the analysis of the highly resolved individual-based empirical data set used in Paper III and investigates patterns and effects of within- and between species resource specialisation in ecological communities. Within-species size variation can be considerable. For instance, in fishes and reptiles, where growth is continuous, individuals pass through a wide spectrum of sizes, possibly more than four orders of magnitude, during the independent part of their life cycle. Given that the size of an organism is correlated with many of its fundamental ecological properties, it should come as no surprise that an individual's size affects the type of prey it can consume and what predators will attack it (Paper III). In Paper IV, I quantify within- and between species differences in predator species' prey preferences in natural food webs and subsequently explore its consequences for dynamical dimensionality (Paper II) and community stability in stage structured food web models. Among the natural food webs there are webs where species overlap widely in their resource use while the

resource use of size-classes within species differs. There are also webs where differences in resource use among species is relatively large and the niches of size-classes within species are more similar. Model systems with the former structure are found to have lower dynamical dimensionality and to be less stable compared to systems with the latter structure. Thus, although differential resource use among individuals within a species is likely to decrease the intensity of intraspecific competition and favor individuals specializing on less exploited resources it can destabilize the community in which the individuals are embedded.

Populärvetenskaplig sammanfattning

Denna avhandlings huvudfokus ligger på ekologiska samhällens respons på miljömässig variation och förlust av arter. Mitt tillvägagångssätt är teoretiskt; jag använder mig av matematiska modeller för att beskriva nätverk där arters populationsdynamik bestäms av ordinära differentialekvationer. Ett genomgående tema i avhandlingens artiklar är variation – variabel länkstruktur (artikel I) och variation inom arter i deras utnyttjande av resurser (artikel III och IV). För att undersöka hur sådan variation påverkar ekologiska samhällens stabilitet i en variabel omvärld, använder jag numeriska metoder som utvärderar till exempel ett samhälls persistens (proportionen arter som överlever en given tid; artikel I, II och IV). Jag utvecklar också en ny metod baserad på egenvärdesanalys för att kvantifiera ett ekologiskt samhälls dynamiska dimensionalitet och undersöker sedan dess effekt på samhälls persistens i en stokastisk miljö (artikel II). Om vi vill kunna lita på resultaten från våra teoretiska modeller, så är det naturligtvis viktigt att skapa studiesystem som efterliknar naturliga system i så stor mån som möjligt. Därför studerar jag också högt upplösta, individ-baserade empiriska näringsvävs-data (artikel III, IV).

I artikel I undersöks effekterna av konsumentarters förmåga att utnyttja nya resurser efter förlust av alla ursprungliga resurser (så kallad 'adaptive rewiring') för persistensen av ekologiska nätverk. En förlust av en art i ett ekosystem kan orsaka utdöenden av andra, beroende arter. Specialiserade predatorer kommer till exempel att dö ut om de förlorar sitt enda byte, förutsatt att de inte har förmågan att ändra sin diet. Det har därför föreslagits att om konsumentarter kan ändra sin diet till helt nya byten, så kommer detta att lindra konsekvenserna av förlorade arter genom att minska risken för utdöendekaskader. Genom att använda ett nytt tillvägagångssätt för att modellera naturliga och dator-genererade näringsvävar, visar jag att oftast så inträffar det motsatta – adaptive rewiring förvärrar konsekvenserna av artförluster. Detta beror på att adaptive rewiring kan leda till överutnyttjande av resurser, vilket till slut orsakar utdöendekaskader. Ett sådant scenario är speciellt troligt om bytesarter inte kan undkomma predation då de är ovanliga och om predatorer utnyttjar nya byten effektivt. Adaptive rewiring kan därför sägas ha två sidor; det kan vara kortsiktigt fördelaktigt för en individuell predator, men ändå långsiktigt negativt för hela systemets persistens.

Ett ekologiskt samhälls persistens i en variabel omvärld beror på styrkan av den stokastiska variationen som tvingar samhället bort från jämviktspunkten, jämfört med styrkan av de deterministiska krafterna orsakade av interaktioner inom och mellan arter som drar samhället mot jämviktspunkten. Det är dock oklart vilka karaktärer hos ett samhälle som främjar dess persistens i en variabel miljö. I artikel II använder jag modeller av naturliga och dator-genererade näringsvävar för att visa att ett ekologiskt samhälls persistens är starkt positivt kopplat till dess dynamiska dimensionalitet (DD). DD mäts med IPR-värdet (inverse participation ratio) av realdelarna av samhällsmatrisens egenvärden. En hög DD innebär att magnituden av egenvärdenas

realdelar är av liknande storlek och systemet kommer då att återgå mot jämviktspunkten med liknande hastighet från alla riktningar. Å andra sidan, när DD är lågt, så har ett egenvärdes realdel en stor magnitud jämfört med de andra och de deterministiska krafterna som drar systemet mot jämviktspunkten är därför svaga i många riktningar jämfört med de stokastiska krafterna som tvingar systemet bort från jämviktspunkten. Då ökar risken för systemet att korsar arters utdöendetrösklar eller för att förflytta sig till en annan attraktionspunkt, och därmed minskar persistensen då DD minskar. Eftersom miljövariationen förutsägs öka på grund av global uppvärmning, så föreslår artikel II att den dynamiska dimensionaliteten av ekologiska system är en karaktär som kommer att få ökad betydelse för systemens persistens.

I artikel III undersöker jag mönster i storleksstrukturen hos en marin och sex rinnande sötvattensnäringssvävar, eller mer precist, hur den trofiska strukturen i sådana ekologiska nätverk styrs av kroppsstorleken hos de interagerande enheterna. Näringssvävarna är baserade på empiriska data av individuella predationshändelser, där den taxonomiska tillhörigheten och kroppsstorleken hos både predatoren och dess byte är tillgängliga. Genom att använda denna detaljerade information, beskriver jag bland annat hur variation i diet och variation i predation beror av predatorns eller bytets kroppsstorlek, både ur ett taxonomiskt- och storlekklass-baserat perspektiv. Jag jämför också mönster i storleksstruktur från en individbaserad analys med de mönster som erhålls då data aggregeras till arters (eller storlekklassers) medelvärden. Denna jämförelse visar att en analys baserad på arters medelvärden kan dölja intressanta mönster i ett ekologiskt samhälles storleksstruktur. Till exempel så visar jag att styrkan på sambandet mellan ett bytes kropps massa och predatorns kropps massa är konsekvent underskattad då arters medelvärden används istället för data på individnivå. Det kan också vara så att inget samband alls upptäcks då arters medelvärden används, men då individbaserade data istället används så framkommer tydliga och signifikanta mönster. Dessutom är styrkan på sambandet mellan bytets kropps massa och predatorns kropps massa svagare då data grupperas baserat på storlekklasser istället för på taxonomisk tillhörighet. Jag diskuterar också potentiella samplingseffekter som tydliggörs då data är ordnade i storlekklasser, men som inte alltid syns med ett taxonomiskt tillvägagångssätt. Resultaten i artikel III har potentiellt stor betydelse för parameterisering av modeller av ekologiska samhällen och därför också för förutsägelser gällande modellernas dynamik och reaktion på olika typer av störningar.

I artikel IV utvecklas analysen av de högt upplösta, individ-baserade empiriska näringsvävs-data som används i artikel III och mönster och effekter av resursspecialisering inom och mellan arter analyseras. Inomartsvariation i storleken hos en art kan vara betydande. Bland till exempel fiskar och reptiler, där tillväxt är kontinuerlig, passerar individer under sin självständiga del av livs cykeln genom ett stort storleksspektrum, ibland mer än fyra tiopotenser. Givet att en organisms storlek är korrelerad med många av dess fundamentala ekologiska egenskaper, så är det inte någon överraskning att en individs storlek påverkar både vilken typ av byten den föredrar och vilka predatorer den själv har (artikel III). I artikel IV kvantifierar jag

skillnader i predatorers bytespreferenser inom och mellan arter i naturliga näringsvävar och undersöker därefter konsekvenser av detta för dynamisk dimensionalitet (artikel II) och stabilitet i stadiestrukturerade näringsvävsmodeller. Bland de undersökta naturliga systemen finns näringsvävar där arters diet överlappar stort medan dieten hos storleksklasser inom arter är olika. Det finns också näringsvävar där skillnaden i arters diet är relativt stor och där nischerna hos storleksklasser inom arter är mer lika. Modell-system med den förra strukturen har lägre dynamisk dimensionalitet och lägre stabilitet jämfört med system med den senare strukturen. Även om skillnader i bytespreferenser hos individer inom en art sannolikt sänker inomartskonkurrensens intensitet och favoriserar individer som specialiserar sig på resurser som utnyttjas mindre, så kan sådana skillnader destabilisera det ekologiska samhället där individerna finns.

List of papers

- I. Gilljam, D., A. Curtsdotter, B. Ebenman. 2015.
Adaptive rewiring aggravates the effects of species loss in ecosystems.
Nature Communications, 6:8412.¹
- II. Gilljam, D. and B. Ebenman. 2016.
High dynamic dimensionality promotes the persistence of ecological networks in a variable world.
Manuscript.
- III. Gilljam, D., A. Thierry, F. K. Edwards, D. Figueroa, A. T. Ibbotson, J. I. Jones, R. B. Lauridsen, O. L. Petchey, G. Woodward, B. Ebenman. 2011.
Seeing double: size-based and taxonomic views of food web structure.
Advances in Ecological Research, 45:67–133.²
- IV. Gilljam, D. and B. Ebenman. 2016.
Patterns of resource utilisation within and between species affect the dynamic dimensionality and stability of ecological communities
Manuscript.

Contributions to papers:

Paper I: **DG**, **BE** and **AC** designed and performed research; **DG** developed the code and analysed the data; **DG** wrote the paper together with **BE** with contributions from **AC**.

Paper II: **DG** and **BE** designed and performed research; **DG** developed the code and analysed the data; **DG** wrote the paper together with **BE**.

Paper III: **DG**, **BE**, **OP** and **AT** designed and performed research; **DG** developed the code and analysed the data; **DG** and **AT** wrote the paper with contributions from **BE**, **OP** and **GW**.

Paper IV: **DG** and **BE** designed and performed research; **DG** developed the code and analysed the data; **DG** wrote the paper together with **BE**.

DG – David Gilljam; **AC** – Alva Curtsdotter; **BE** – Bo Ebenman; **OP** – Owen Petchey; **AT** – Aaron Thierry; **GW** – Guy Woodward

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PART 1 – OVERVIEW

Structure and Stability of Ecological Networks

The role of dynamic dimensionality and
species variability in resource use

David Gilljam

1. Introduction

A balance of nature?

A central and much discussed question in ecology is what properties of ecosystems that promote the long-term coexistence of numerous interacting species, that is, properties conferring a 'balance of nature' (May 1973a, Pimm 1984, 1991, Haydon 1994, Neubert and Caswell 1997, McCann 2000, Neutel et al. 2002, Montoya et al. 2006, Ives and Carpenter 2007, Otto et al. 2007). Especially, understanding the ecological processes and mechanisms that links diversity and stability in natural ecosystems has been at the heart of community ecology for more than half a century (McCann 2000, Namba 2015). The traditional view was that complexity, like many species and interactions between species, enhances stability (Odum 1953, MacArthur 1955, Elton 1958), a view primarily based on observational studies of natural and experimental empirical systems. For example, Elton (1958) noted more violent population fluctuations in simple compared to more diverse terrestrial communities, which led him to suggest that complex communities with many species prevented populations from undergoing explosive growth. However in 1972, Robert May published a seminal theoretical study in which he showed that an ecological network with randomly interacting species, resting at an equilibrium point, is inherently unstable if complex enough (May 1972). As this study completely contradicted the prevailing, and after all quite intuitive view, May challenged other ecologists to try to find the mechanisms and ecological structures that promotes the existence of large, complex natural ecosystems. Ever since, the 'diversity-stability debate' has been continuously ongoing (McCann 2000, Namba 2015). Some of the more prominent findings have been that realistic, non-random interaction patterns and food web structures can both stabilise and destabilise food webs (e.g. Yodzis 1981, de Ruiter et al. 1995, Solé and Montoya 2001, Neutel et al. 2002, Allesina and Tang 2012, Tang et al. 2014). For example, Allesina and Tang (2012) extended May's findings and showed that predator-prey interactions are stabilising while mutualistic- and competitive interactions are destabilising. Interestingly, if a realistic food web structure is imposed or if the majority of interactions are weak, Allesina and Tang (2012) found that the probability of stability in predator-prey networks decreased, contrary to what has been proposed in earlier studies (e.g. Yodzis 1981, McCann et al. 1998). There is also a large interest in how other topological characteristics, like modularity and nestedness (Bastolla et al. 2009, Thébault and Fontaine 2010, Stouffer and Bascompte 2011, James et al. 2012, Staniczenko et al. 2013, Suweis et al. 2013, Rohr et al. 2014) or adaptive trophic behaviour (e.g. Kondoh 2003a, Valdovinos et al. 2010), allometric degree distributions (e.g. Otto et al. 2007) and interaction type mixing (Mougi and Kondoh 2012, Sellman et al. 2015) affect the stability of ecological networks.

One reason for the difficulties in finding general diversity-stability relationships is the varying levels of biological organisation at which complexity or stability is quantified. For example, measures involving stability at the ecosystem level are not generally independent from species level measures, but neither are they completely dependent

(Tilman 1996). Another, and perhaps greater, source of confusion, is the many different definitions of complexity and stability used throughout the literature (Pimm 1984, Grimm and Wissel 1997, Ives and Carpenter 2007). In an inventory of 70 stability concepts, Grimm and Wissel (1997) found 163 different definitions. One area of research that attracts many theoretical ecologists concerns local (asymptotic- or neighbourhood) stability analysis of networks (May 1972, 1973a, Allesina and Tang 2012). A system's behaviour around an equilibrium point, $\mathbf{N}^*$, can be characterised by the eigenvalues of its community (Jacobian) matrix. If all eigenvalues have negative real parts, the equilibrium is locally stable and small perturbations will decay with time (May 1973a). In fact, if the long term behaviour of a system (in a deterministic setting) is our only concern, then only the sign of the real part of the largest (dominant) eigenvalue is needed to characterise local stability. The dominant eigenvalue determines the system's asymptotic behaviour following a perturbation; if it is negative, perturbations will decay and if it is positive, perturbations will continue to grow.

However, in a stochastic environment where species are continuously perturbed, short term dynamics and thus non-dominant eigenvalues should also be of importance. In a stochastic environment, there is no fixed equilibrium point $\mathbf{N}^*$ but rather an 'equilibrium cloud' in phase space described by the equilibrium time-independent probability distribution $f^*(\mathbf{N})$, the centre of which equals $\mathbf{N}^*$ (May 1973b). The size and shape of the cloud is determined by the strength of interactions among species, the variance of the environment and the correlation in species' response to the environmental variation (May 1973b, Ripa and Ives 2003). Around $\mathbf{N}^*$, there are two forces at play; the stabilising deterministic population interactions acting to restore populations to their equilibrium values and the destabilising stochastic environmental fluctuations pushing population sizes from the equilibrium, 'diffusing the cloud' (May 1973b). In a system which 'deterministically' recovers along all dimensions (directions) at similar rates, the risk of species going extinct due to destabilising environmental fluctuations is likely to be lower compared to a system in which recovery is fast along one dimension (direction) and slow along the others. The former system could be characterised as having a higher *dynamic dimensionality* (DD) (Roughgarden 1998, p. 339). A high DD means that the real-part of the eigenvalues are of similar magnitude and that the system therefore approaches the equilibrium from all directions at a similar rate. On the other hand, when DD is low one (or a few) of the eigenvalues has a large magnitude compared to the others and the deterministic forces pulling the system towards equilibrium is therefore weak in many directions compared to the stochastic forces pushing the system away from the equilibrium (see Local stability analysis and dynamic dimensionality in Materials and Methods).

More recently, the importance of gaining a deeper understanding about how ecosystem complexity, stability and function are related has been acknowledged in many other fields than just within ecology, such as economics (Gómez-Baggethun et al. 2010) or social sciences (Potschin and Haines-Young 2006). Ironically, this is largely because anthropogenic pressures on natural systems, such as habitat destruction and

fragmentation, overexploitation of natural resources, invasive species and accelerated climate change, now is being recognised as causes for ecosystem functioning loss (Hooper et al. 2012, Isbell et al. 2015) and increased species extinction rates (Pereira et al. 2010, Pimm et al. 2014, Ceballos et al. 2015). The fact that current anthropogenic pressures have such dire consequences for the diversity and functioning of ecosystems – systems which we are part of and are greatly dependent upon – now place the understanding of the ‘balance of nature’ into a much broader context than simply in the minds of curious ecologists.

Food webs

Throughout this thesis, the focus is on trophic interactions between species in ecological communities, that is, food webs (Fig 1). A classical food web in its simplest form is just a random adjacency matrix, where rows and columns of the matrix represent species and filled (empty) cells indicate presence (absence) of a trophic interaction between one species and another. Trophic interactions are however rarely random in nature and as an attempt to describe who eats whom in an ecological community, a number of algorithms for predicting the topology and structural properties of natural systems have been developed (Cohen et al. 1990, Williams and Martinez 2000, Cattin et al. 2004, Stouffer et al. 2006, Petchey et al. 2008, Allesina et al. 2008, Williams et al. 2010). Theoretical models for generating artificial food webs share the advantage of being able to produce, in principle, unlimited amounts of food web realisations with, for example, a predefined number of species and number of interactions. Of course, the drawback is their varying success in accurately describing the topology of natural communities (see Williams and Martinez (2008) for a comparison of some of the models). Preferably, food webs based on empirical observations, directly mirroring ecological communities (hereafter ‘natural food webs’ or ‘natural networks’) would be used instead of their computer-generated counterparts. However, the quality of the natural food webs available in the primary literature is also varying. For example, a natural food web may not precisely describe an ecological community because not all trophic interactions might have been observed, or nodes in the network are not resolved to the species level or might represent trophic species, i.e. functional or taxonomical groups that share resource and consumer nodes (Dunne et al. 2002).

Figure 1 | Example topologies of computer generated- and natural food webs used in the thesis. Upper row shows two example food web realisations of the pyramidal- (left) and PNM algorithms (right) used in Paper I and II. Bottom row shows two natural food webs; Broadstone stream (left) used in Paper I, III and IV, and a container habitat (Phytotelmata, right) used in Paper I and II. Black, grey and white nodes represent basal, intermediate and top species, respectively. Links show trophic (predator-prey) interactions. The vertical position of a species indicates its relative trophic height.

Adaptive trophic behaviour

Adaptive Trophic Behaviour (ATB) is defined as "the fitness-enhancing changes in individuals' feeding related traits due to variation in their trophic environment" (Valdovinos et al. 2010). Suggested traits that have implications for population dynamics and stability are the adaptive behaviour of prey in response to predation risk (Abrams 2000) and optimal diet choice of predators (Křivan and Sikder 1999). Recently, ATB has come to the fore as a mechanism that is tightly coupled with the stability and persistence of complex ecological networks (Kondoh 2003a, 2003b, 2006, 2007, Beckerman et al. 2006, Uchida et al. 2007, Uchida and Drossel 2007, Petchey et al. 2008, Staniczenko et al. 2010, Berec et al. 2010, Thierry et al. 2011, Heckmann et al. 2012), where the overwhelming majority of studies conclude that ATB promotes network complexity and increases the stability of their dynamics (but see Berec et al. (2010) and Paper I). One particular form of ATB is Adaptive foraging (AF). AF is a proposed mechanism to increased permanence and persistence in food webs with consumers of functional type I or II (Kondoh 2003a, 2003b, 2006, Heckmann et al. 2012) (but see Berec et al. 2010 for an exception). Adaptive foragers focus feeding efforts on resources with relatively high abundance in order to maximise energy gain. Provided that other resources are sufficiently abundant, predation pressure on rare resources is relaxed and these are allowed to recover and avoid extinction (Uchida et al. 2007, Uchida and Drossel 2007).

In ecological networks, loss or declining abundance of one species can trigger extinctions of other dependent species (Pimm 1980, Ebenman et al. 2004, Koh et al. 2004, Sanders et al. 2013, Säterberg et al. 2013), in the worst case leading to a complete system collapse (Estes and Palmisano 1974). Both top-down driven (Estes et al. 2011) and bottom-up driven secondary extinctions (Koh et al. 2004) have been documented in ecological communities. Looking at bottom-up driven secondary extinctions, the loss of a plant species might cause extinctions of herbivores specializing on that particular plant (Koh et al. 2004, Fonseca 2009, Pearse and Altermatt 2013). Likewise, specialized parasites might go secondarily extinct following the loss of their host

species (Koh et al. 2004). The possible frequency and extent of such secondary extinctions as well as mechanisms that might prevent them is attracting considerable current interest (for recent reviews see Colwell et al. 2012, Brodie et al. 2014). A possible mechanisms that may buffer against bottom-up driven secondary extinctions in ecological networks are the forming of new feeding links (rewiring). In food webs (or plant-pollinator networks) a predator (pollinator) species might switch to a new prey (plant) species following the extinction of its original prey (plant) species (Pearse and Altermatt 2013). It has been suggested that such rewiring should promote network persistence and decrease the risk of cascading extinctions (Staniczenko et al. 2010, Valdovinos et al. 2010, 2013, Thierry et al. 2011, Ramos-Jiliberto et al. 2012, Pearse and Altermatt 2013). Earlier studies on rewiring in ecological networks are mainly based on a static (topological) approach that do not consider population dynamics (e.g. Staniczenko et al. 2010, Kaiser-Bunbury et al. 2010b, Thierry et al. 2011). Such an approach precludes an exploration of the effects of top-down processes and hence the potentially negative effects of rewiring. The ability of a consumer to expand its diet by rewiring to novel resources is a mechanism that could increase the risk of extinction cascades to propagate through a network (Fig. 2).

Figure 2 | The ability of consumer species to expand diets by rewiring to novel resources is a mechanism that allows extinction cascades to propagate through a network. Worst case scenarios after a stochastic extinction of a resource in a 6 species food web consisting of 2 separate sub-webs (A), with (B-E) or without (F-H) adaptive consumers. The consumer who lost its preferred prey (thick arrows) selects a new preferred prey, which causes a secondary extinction due to over-exploitation (B). This forces the consumer who now lost all its original prey to adaptively rewire to a novel prey (C), which connects the two isolated sub-webs and causes another extinction from over-exploitation. As a consequence, the entire system collapses (D-E). In (F) the consumer who lost its preferred prey goes secondarily extinct because of lack of resources, which in turn causes a final extinction of the top predator (G). (H) shows the three remaining species in the system without adaptive consumers. Here, the smaller sub-web is unaffected by the extinction cascade.

Individuals within food webs

When dealing with the apparently bewildering complexity encountered in nature, ecologists have traditionally viewed multispecies systems (communities, food webs, ecosystems) through some kind of simplifying prism, usually by focusing on taxonomy or body size. The analogy of the ‘entangled bank’ was first coined by Charles Darwin in *The Origin of Species* (Darwin 1859), and modern ecology has unveiled evermore complex networks of interactions since Camerano (1880) first depiction of a recognisable food web over a century ago. However, variation in traits among individuals within a species is ubiquitous, reflecting both genetic variation, phenotypic plasticity and ontogenetic development (Bolnick et al. 2011). Some differences in traits are obvious, such as sex or colour, while others, for example related to behaviour or physiology, are less apparent. In community ecology, functional traits are of particular interests, as these are characters that are relevant for a species’ interactions with other species and with the environment, in essence defining its functional role and performance within the community (Díaz and Cabido 2001, McGill et al. 2006, Miller and Rudolf 2011, Violle et al. 2012, Siefert et al. 2015). The ecological consequences of intraspecific variation in such traits have been found to be significant (however not always coherent), as it can influence central ecological processes at different levels of biological organisation (Gibert et al. 2015). For example, it affects population productivity and stability (Agashe et al. 2009), species coexistence and diversity (Lankau and Strauss 2007, Fridley and Grime 2009, Clark 2010), community assembly (Jung et al. 2010, Long et al. 2011), stability (Zhang et al. 2013) and functionality (Crutsinger et al. 2006). (For recent reviews, see Bolnick et al. 2011, Violle et al. 2012, Siefert et al. 2015).

Intraspecific variation in traits related to resource utilization, like body size, have been documented in many species, here illustrated using individual based data on feeding interactions from the Broadstone Stream running freshwater system (Fig. 3, [Paper I & III]). The role of different factors – like strength of intra- and interspecific competition – in modulating the extent of individual specialization in resource use have received a lot of attention (for recent reviews, see Bolnick et al. 2011, Araújo et al. 2011), however the consequences of such intraspecific variation in resource use for the dynamics and stability of ecological communities are less well-studied. An exception being cases where individual specialization in resource use is due to trait differences among individuals related to their age or life-stage, notably differences in their body sizes (De Roos et al. 2008, Guill 2009, de Roos and Persson 2013, van Leeuwen et al. 2013, 2014, Gårdmark et al. 2015). One line of research focuses entirely on the body size of individuals without any consideration of taxonomy, so called size spectra models of the dynamics of ecological communities (Law et al. 2009, Hartvig et al. 2011).

Figure 3 | The Broadstone stream food web, illustrated using individual feeding events.

Predator individuals (filled nodes) and their respective prey items (open nodes), connected by links (grey lines). Predator taxa are separated vertically by their relative trophic height and their mean logged body mass (mg) is given within parenthesis. Resource taxa (taxa comprised of only prey individuals) have the lowest trophic height and their abbreviations are positioned at the respective mean logged body mass (mg). Note the large overlap in the body sizes of individuals of different species and in the body size of the prey individuals of predator individuals of different species. Moreover, large individuals of an on average smaller species sometimes feed on small individuals of an on average larger species. See Fig. 1 for comparison with a classical species centric food web. For clarity, the figure includes 25% of the total number of feeding events in the data set (randomly drawn), and a small jitter is added to the Y-axis.

Indeed, body size is an important ecological trait with considerable variation both within and among species. The size range of all living organisms spans over 23 orders of magnitude, with for example the blue whale weighing over 10^8 g and the smallest phytoplankton less than 10^{-15} g (McMahon and Bonner 1983, Peters 1983, Barnes et al. 2010). In species with continuous growth during the entire independent part of their

life cycle – such as in fishes, reptiles or plants – individuals can pass through a wide spectrum of body sizes, sometimes larger than four orders of magnitude (Werner and Gilliam 1984, Ebenman 1987; Ebenman and Persson 1988). Many fundamental ecological properties are related to the size of an organism (Peters 1983, Ebenman and Persson 1988; Brown et al. 2004, Woodward et al. 2005a), for instance, the size of an individual will in part determine the size of resources it can consume and which predators it has. Indeed, a predator’s body mass has been shown to be a good predictor for its diet, both at the species (e.g. Cohen and Newman 1985, Warren and Lawton 1987, Lawton 1989, Cohen et al. 1993; Neubert et al. 2000; Brose et al. 2006; Petchey et al. 2008; Riede et al. 2011) and at the individual level (e.g. Barnes et al. 2010, Woodward et al. 2010, Gilljam et al. 2011).

2. General aims

The main focus of this thesis is on the response of ecological communities to environmental variability and species loss. My approach is theoretical; I use mathematical models of networks where species population dynamics are described by ordinary differential equations. A common theme of the papers in my thesis is variation – variable link structure (Paper I) and within-species variation in resource use (Paper III and IV). To explore how such variation affect the stability of ecological communities in variable environments, I use numerical methods evaluating for example community persistence (the proportion of species surviving over time; Paper I, II and IV). I also develop a new method for quantifying the dynamical dimensionality of an ecological community based on eigenvalue analysis and investigate its effect on community persistence in stochastic environments (Paper II). Moreover, if we are to gain trustworthy model output, it is of course of major importance to create study systems that reflect the structures of natural systems. To this end, I also study highly resolved, individual based empirical food web data sets and investigate how our perception of food web structure depends on the quality of the data from which it is derived (Paper III) and how the community niche structure is partitioned within and between species (Paper IV).

3. Main results, discussion and implications

Overall, the research results in this thesis highlight the importance of accounting for variability when investigating the structure and stability of ecological networks. Both when it comes to topological variability, such as the rewiring of trophic links, and when it comes to intraspecific variability in for example resource use. Accounting for such variation sometimes reveal ‘conflicts’ between fitness of individuals and long-term persistence of the systems where individuals are embedded.

Paper I

Paper I shows that an ability of consumer species to adapt to the loss of resources by rewiring to novel resources do not rescue ecosystems from cascading extinctions (Fig. 4), which has been the prevailing view in community ecology (e.g. Staniczenko et al. 2010, Thierry et al. 2011, Ramos-Jiliberto et al. 2012). We arrive at this conclusion by using a food web modelling framework on natural and theoretical ecological networks, which considers population dynamics and thus allows both positive as well as potentially negative effects of rewiring to be captured.

Rewiring of trophic links following species loss in ecological network models without considering population dynamics will never increase the risk of secondary extinctions, because the potential negative top-down effect following the forming of a novel interaction is not considered. The new interaction instead act as an insurance, with the possibility to save species bereaved of resources from starvation. The magnitude of the increase in robustness because of rewiring then depends on the identity and order of the species going extinct, the criteria for rewiring and the complexity of the network (Staniczenko et al. 2010, Kaiser-Bunbury et al. 2010, Thierry et al. 2011). However, Paper I shows that adaptively rewiring consumers can increase the top-down load on remaining resources in an ecological network and may thus trigger additional resource extinctions. Such a scenario is particularly likely if resource species cannot escape predation when rare and if consumers are efficient in exploiting novel prey (Fig. 4). The ability of a consumer to expand its diet by rewiring to novel resources is a mechanism that allows secondary extinctions to propagate through a network. In the worst case, a ‘bouncing’ cascade can be released as adaptively rewiring consumers drive new resource extinctions, which in turn force new rewiring and so on. Adaptive rewiring can thus be seen as an additional perturbation to the network, as the rewiring consumer species in effect turns into a native invader (Carey et al. 2012).

In the short-term, adaptive rewiring can be advantageous for the individual consumer species, yet Paper I show that it is harmful for long-term network persistence. A dramatic example is provided by the sequential collapse of marine mammals in the North Pacific Ocean induced by prey switching (rewiring) killer whales. Following sharp declines in the great whales caused by large-scale commercial whaling, the killer whale switched to pinnipeds thereby decimating the populations of these species severely, which in turn lead to yet another prey switch to sea otters. The resulting decline in the sea otter populations finally led to local collapse of species-rich kelp forest ecosystems (Estes et al. 1998, Springer et al. 2003).

This finding has a bearing on the interaction of human harvesters with natural populations in that human harvesters are examples of especially flexible and efficient consumers (Pauly et al. 1998, Brashares et al. 2004, Smith et al. 2011, Bonhommeau et al. 2013). Our study indicates that under such circumstances rewiring can potentially trigger extensive extinction cascades causing large changes in the structure and dynamics of ecosystems.

Figure 4 (Paper I) | Rewiring increases risk of cascading extinction. The proportion of species going extinct in natural food webs as a function of the fraction of adaptive consumers and the fraction of consumers with a type II and type III functional response. Type II consumers are more effective at capturing rare prey. Dark colour indicates high proportion extinct species. Column 1 shows the topologies of the natural webs. Column 2 and column 3 denote low and high rewiring cost, respectively. S denotes number of species and C denotes connectance. Green, blue and red nodes represent basal, intermediate and top species, respectively. See Paper I for details on the study.

Figure 5 (Paper II) | High dynamic dimensionality increases the persistence of ecological networks in variable environments.

[Figure 5 text] The persistence of pyramidal (green) and PNM (orange) model food webs and the natural Phytotelmata food web (blue) as a function of the normalised dynamic dimensionality of the networks. Persistence is the proportion of the original species that remains after 10000 time units. Columns represent different degrees of correlation (ρ) in the response of species to environmental variation and rows represent different degrees of environmental autocorrelation ($\gamma=0$, white noise; $\gamma=0.5$, red noise). Trend lines are from logistic GLMMs with type of food web and functional response as nested random effects for the model intercept and slope. See Paper II for details on the study.

Paper II

In Robert May's (1973) pioneering work on stability and complexity in model ecosystems, a mathematical framework for describing population dynamics exposed to environmental stochasticity is presented. May elegantly explains how the persistence of an ecological community in a variable world depends on the strength of environmental variation pushing the community away from equilibrium compared to the strength of the deterministic feedbacks, caused by interactions among and within species, pulling the community towards the equilibrium. What characteristics of a community that tip the balance of these forces in favour of persistence is however not clear. Paper II shows that long-term persistence of interacting species in a variable environment is positively related to the dynamic dimensionality [DD] (Roughgarden 1998) of the community, as measured by the inverse participation ratio of the eigenvalues (real parts) of the community matrix (Fig. 5). A high DD means that the eigenvalues are of similar magnitude and that the system therefore approaches the equilibrium from all directions at a similar rate. On the other hand, when DD is low one (or a few) of the eigenvalues has a large magnitude compared to the others and the deterministic forces pulling the system towards equilibrium is therefore weak in many directions compared to the stochastic forces pushing the system away from the equilibrium. As a consequence the risk of crossing extinction thresholds increases, and hence persistence decreases, as DD decreases.

The effect of dynamic dimensionality on persistence tends to be somewhat stronger when species are highly correlated in their response to environmental variation (Fig. 5). For a given dynamic dimensionality, persistence also tends to be higher when correlation among species is high. A possible reason for this is that highly correlated responses counteracts compensatory dynamics driven by competition among primary producer species and therefore leads to less negative correlation in their abundances (see Kaneryd et al. 2012). Moreover, there is a stronger relationship between DD and persistence when there is no temporal autocorrelation (white noise) compared to when positive autocorrelation is present (red noise), suggesting that DD might be more important for the persistence of terrestrial communities than for marine communities (Steele 1985, Vasseur and Yodzis 2004).

The findings of Paper II illustrates the potential importance of dynamic dimensionality of ecosystems for their persistence in a variable world and by extension for their vulnerability to changes in the strength and patterns of climate variability caused by

global warming. As shown here the dynamic dimensionality of an ecological community is determined by the distribution of the magnitudes of the eigenvalues of the community matrix. The magnitudes of these eigenvalues are themselves determined by network topology, types (predator-prey, mutualistic, competitive) and strengths of species interactions together with the demographic rates of species (May 1972, Neutel et al. 2002, Allesina and Tang 2012, Tang et al. 2014, Allesina et al. 2015). This suggests that there exist relationships between dynamic dimensionality and patterns of interactions in ecological networks. Finding these relationships would help in identifying robust and vulnerable systems.

Paper III

Compared to Paper I and II, Paper III has a different approach when it comes to analysing ecological communities. Instead of looking at the effects of food web structure and flexibility on community stability, Paper III investigates how our perception of food web structure depends on the quality of the data from which it is derived. Specifically, Paper III uses highly resolved natural food web data sets to investigate how the trophic structure of one marine and six running freshwater systems is governed by the body size of interacting individuals. The data sets hold specific information on predator feeding events, including the taxonomic identity and body mass of the predator and its prey. By comparing patterns of size structure derived from analysis of individual-based data with those patterns that result when data are aggregated into species (or size class-based) averages, Paper III shows that analysis based on species averaging can obscure interesting patterns in the size structure of ecological communities. For example, we find that the strength of the relationship between prey body mass and predator body mass is consistently underestimated when species averages are used instead of the individual level data (Fig. 6). In some cases, no relationship is found when species averages are used, but when individual-level data are used clear and significant patterns are revealed. Further, when data are grouped into size classes, the strength of the relationship between prey body and predator body mass is weaker compared to what is found using species-aggregated data.

The overall conclusion drawn from Paper III is that considering trophic interactions at the scale of individuals – which, after all, is the level at which interactions do occur – instead of at the scale of species, often changes our perception of patterns in size structure in ecological communities. The main reason for this result is that intraspecific size variation in predators and prey is taken into account when using individual level data. For example, the size range of prey species used of predators often change markedly during their life cycles (Woodward and Warren 2007, Woodward et al. 2010, Hartvig et al. 2011) which is something that is not accounted for when using species averages. The results has implications for the parameterisation of models of ecological communities and hence for predictions concerning their dynamics and response to different kinds of disturbances. In for example species-oriented food web modelling approaches, all individuals within a species are considered equal and assigned the same body size and ecological parameters like intrinsic growth rates and per capita

interaction strengths are assumed to be functions of this body size (using allometric scaling relationships) (Yodzis and Innes 1992, Jonsson and Ebenman 1998, Brose et al. 2006a, 2006b, 2006b, Otto et al. 2007). Specifically, both empirical work (Emmerson and Raffaelli 2004, Wootton and Emmerson 2005) and theory based on metabolic considerations (Lewis et al. 2008, O’Gorman et al. 2010) suggest that the per capita strength of interaction between predator and prey should depend on the ratio between their respective body masses (predator-prey body mass ratios, PPMR). Thus, it has been argued that the distribution of species body masses and patterns of PPMR in food webs should have important consequences for their dynamics and stability (de Ruiter et al. 1995, Neutel et al. 2002, Emmerson and Raffaelli 2004, Brose et al. 2006a, 2006b, Otto et al. 2007).

Figure 6 | Species averaging underestimates the strength of the relationship between predator and prey body mass. Prey body mass versus predator body mass in the seven natural food webs included in Paper III. Left panel shows feeding events for the individual-level data and right panel shows species averages. Trend lines are from linear mixed effect models per study system (identified by colour/abbreviation). All system trend lines in the left panel have a steeper slope than their respective counterpart in the right panel. The dashed line indicates where prey size equals predator size. See Paper III for details on the study

Paper IV

Paper IV combines the dynamical food web modelling approach used in Paper I and II with the approach of analysing empirical food web data sets that is used in Paper III. First, we quantify the niche structure – the resource use within and between species – of aquatic natural food webs where data on individual feeding events are available. In particular, we quantify the contribution of variation in resource within species (WSC) and differences in resource use among species (BSC) to the total niche width of a community (n^2) and find that the within-species component in the large majority of cases is the dominant component of the total niche width of the communities; in 11 out of 13 systems, WSC/n^2 is larger than 0.5. That is, diet overlap with respect to prey size of predator species is generally large. The most likely explanation to this is that, in

aquatic systems where gape limited predation is prevalent, the preferred prey of predator individuals is to a large extent a function of the size of the prey and predator individual itself (e.g. Barnes et al. 2008, Woodward et al. 2010, Gilljam et al. 2011 [Paper III]), and to a lesser extent dependent on the taxonomic identity of the predator and the prey. As predator species' individuals pass through a large size-spectrum during their life-cycle, so does the maximum size of the prey it can consume (Gilljam et al. 2011 [Paper III]). Specific size-classes of predator species with overlapping diets will thus be competing for resources, while others will not. Or if seen at the individual level, similarly sized individuals will compete for similarly sized prey, while individuals with large difference in size will compete less. A size-class based analysis (Gilljam et al. 2011 [Paper III]) would most likely result in a smaller 'within size-class component' to n^2 ratio, compared to the taxonomically based analysis we perform here. Taxonomic identity as a determining factor for who eats whom in aquatic environments should however not be completely ignored (Naisbit et al. 2011, 2012).

Figure 7 | Effects of within and between species variation in resource use on dynamic dimensionality and community stability. Dynamic dimensionality and stability for two stage-structured food web scenarios having large (A) and small (B) WSC/n^2 , respectively. **(a)** Dynamic dimensionality, **(b)** community displacement from equilibrium state and **(c)** resilience and reactivity. System stability is high if resilience is high and reactivity is low, and if the mean (Mean(D)) and standard deviation (Sd(D)) of the community displacement from the equilibrium state is small (Euclidian distance, D, between equilibrium state and actual state in phase space is small). Values in **(b)** are logged to clarify differences between scenarios. Boxplots show medians (horizontal lines), means (diamonds) and 1st and 3rd quartiles. Whiskers extend from the box to the highest and lowest value within 1.5 times the inter-quartile range. Results are based on **(a, c)** 200 replicate food webs per scenario and on **(b)** replicates (out of 200) without any extinctions ($n_A=86$ and $n_B=183$) during model simulation over time. See Paper IV for details on the study.

Next, to explore how differences in niche structures of communities affect their dynamic dimensionality and stability, we construct two simple food web modules

reflecting the extreme scenarios found among the natural systems and analyse their dynamics. Here we find that stage-structured food webs where life-stages use the same resources and species use different resources (WSC/n^2 is small) have higher dynamic dimensionality (Paper II) and are more stable than food webs where life-stages differ in their resource use and species use the same resources (WSC/n^2 is large) (Fig. 7). These findings suggest that niche separation of life-stages within species can lead to decreased dynamic dimensionality and stability of the ecological community of which they are parts. This is in line with Rudolf and Lafferty (2011) who used a modelling approach to show that ontogenetic specialisation of predator species for specific prey decreases network robustness as predator species life-stages become more vulnerable to resource loss. Then loss of one of these prey species will cause secondary extinction of the consumer species in question. On the other hand, if the different life stages use the same several prey species, the loss of one of these prey species do not necessarily cause the extinction of the consumer species. To conclude, although individual specialization in resource use is likely to decrease the intensity of competition within species and increase the fitness of individuals it can lead to increased risk of species extinction and decreased stability of the communities in which the individuals are embedded. Decreased intraspecific competition in general tends to have a destabilizing effect on communities (May 1972, Neutel et al. 2002, Allesina and Tang 2012).

4. Concluding remarks

The main focus of this thesis is on the response of ecological communities to a changing environment and species loss. A common theme of the papers is variation – variable link structure and within-species variation in resource use. Overall, the research results highlight the importance of accounting for variability when investigating the structure and stability of ecological networks. Accounting for such variation sometimes reveal ‘conflicts’ between fitness of individuals and long-term persistence of the systems where individuals are embedded. Moreover, I develop a new method for quantifying the dynamical dimensionality of an ecological community based on eigenvalue analysis of the community matrix and investigate its effect on community persistence in stochastic environments.

More precisely, the main conclusions of the four papers included in this thesis are:

- I. An ability of consumer species to adapt to the loss of resources by rewiring to novel resources do not rescue ecosystems from cascading extinctions, which has been the prevailing view in community ecology. On the contrary, adaptive rewiring aggravates the effects of species loss. We arrive at this conclusion by using a framework that allows positive as well as potentially negative effects of rewiring to be captured.
- II. Long-term persistence of interacting species in a variable environment is positively related to the dynamic dimensionality of the community, as measured by the inverse participation ratio of the eigenvalues (real parts) of the community matrix.
- III. Considering trophic interactions at the scale of individuals – which, after all, is the level at which interactions do occur – instead of at the scale of species, often changes our perception of patterns in size structure in ecological communities.
- IV. Consumer species in aquatic natural food webs often overlap widely in their resource use. Model systems where species overlap widely in their resource use while the resource use of life-stages within species differs have lower dynamic dimensionality and are less stable compared to systems where differences in resource use among species is relatively large and the niches of life-stages within species are more similar.

5. Materials and methods

Ecological networks: computer-generated- and natural food webs

In summary, the thesis includes a broad spectrum of antagonistic network types and topologies, both natural and computer-generated (Table 1). Paper I and II use three types of computer-generated large antagonistic food webs; pyramidal (Kaneryd et al. 2012, Gilljam et al. 2015), probabilistic niche model (PNM) (Williams et al. 2010) and bipartite webs (Gilljam et al. 2015). Paper IV uses smaller, two trophic level food web modules with stage-structure added to consumer species. To increase generalism and realism, all papers includes natural food webs from different types of habitats; Paper I and II use natural food webs resolved at the species (sometimes genus or ‘trophic’) level and Paper III and IV use natural food webs resolved at the level of individuals. Computer-generated and natural food webs vary in size from 8 to 24 and 5 to 59 species, and in connectance (probability of two species interacting) from 0.05 to 0.3 and 0.03 to 0.24, respectively.

Table 1 | Food webs included in the thesis.

Food web	Type or habitat	Resolution	Paper	Reference
Pyramidal	Computer generated	S	I, II	Kaneryd et al. 2012; Gilljam et al. 2015
PNM	Computer generated	S	I, II	Williams et al. 2010
Bipartite	Computer generated	S	I	Gilljam et al. 2015; Thébault & Fontaine 2010
Bipartite stage structured	Computer generated	S	IV	Unpublished
Broadstone stream	Running freshwater	S, I	I, III, IV	Woodward et al 2010
Kelp bed community	Marine	S	I	Cohen 1990
Montane forest	Terrestrial	S	I	Cohen 1990
Phytotelmata	Freshwater	S	I, II	Kitching 2000
Afon Hirnant	Running freshwater	I	III	Woodward et al 2010
Celtic Sea	Marine	I	III, IV	Barnes et al. 2008; Woodward et al. 2010
Coilaco river	Running freshwater	I	III	Figueroa 2007
Guampoe river	Running freshwater	I	III	Figueroa 2007
Trancura river	Running freshwater	I	III	Figueroa 2007
Tadnoll brook	Running freshwater	I	III, IV	Edwards et al 2009; Woodward et al. 2010
Off the Bay of Biscay	Marine	I	IV	Barnes et al. 2008
Antarctic Peninsula	Marine	I	IV	Barnes et al. 2008
Strait of Georgia	Marine	I	IV	Barnes et al. 2008
Apalachicola Bay	Marine	I	IV	Barnes et al. 2008
Atlantic Ocean	Marine	I	IV	Barnes et al. 2008
Western North Pacific	Marine	I	IV	Barnes et al. 2008
Catalan Sea	Marine	I	IV	Barnes et al. 2008
French Polynesian EEZ	Marine	I	IV	Barnes et al. 2008
Greenland	Marine	I	IV	Barnes et al. 2008
W. Greenland	Marine	I	IV	Barnes et al. 2008

[Table 1 notes] Resolution indicates at which level information on interactions are available; between species (S) or between individuals (I). Nodes in the species level natural networks represents true species (or sometimes genus) or trophic species, i.e. functional or taxonomical groups that share resource and consumer nodes. For details, see the specific papers.

Pyramidal food webs

We generate pyramidal model food webs where species are distributed over three relatively discrete trophic levels - primary producers, primary consumers and secondary consumers – in agreement with the pattern found in natural webs (Johnson et al. 2014). The ratio between the numbers of species at the different trophic levels is 3:2:1. Trophic links are distributed randomly, but with some constraints: consumers must feed on at least one resource from the trophic level directly below themselves and cannibalism is not allowed. Secondary consumers can be omnivorous, that is, feeding not only on the primary consumers but also on the primary producers.

Probabilistic niche model (PNM) food webs

Niche models like the PNM have been widely used to generate antagonistic networks. The PNM uses a Gaussian formulation for the probability that species i eats species j . That is, there is always a non-zero probability that a species feeds on another species, and the closer the niche position of the resource is to the optimal diet position of the consumer, the higher the probability. This allows for gaps in the diet width of consumers. There are no constraints on trophic links except that cannibalism is not allowed.

Bipartite food webs

A set of antagonistic bipartite model (BPM) networks are also included, where species are distributed over two discrete trophic levels; primary producers and primary consumers. In Paper I, the degree of nestedness in these networks is varied using the methods developed by Thébault and Fontaine (2010). In Paper IV, 6-species bipartite network modules with stage-structured consumers are analysed.

Natural food webs

In total, 21 natural food webs are studied in the thesis, including terrestrial, freshwater and marine systems (Table 1). In Paper I and II, natural systems are used where nodes in the networks represents true species (or sometimes genus) or trophic species, i.e. functional or taxonomical groups that share resource and consumer nodes. In Paper III and IV, highly resolved natural food webs where data is available at the level of individuals are used. More precisely, the food web datasets analysed consist of information on individual predation events, where the taxonomic identity and the body mass of both the predator and its prey are known.

Network dynamics

Paper I and II includes population dynamics over time for interacting species, using a generalised Rosenzweig-MacArthur model (Rosenzweig and MacArthur 1963), which is an extension of the classical Lotka-Volterra predator-prey model. Here, the functional response of predators to the densities of their prey can be of type I (linear)

or non-linear of type II (hyperbolic) or III (sigmoidal) (Holling 1959). Direct interspecific competition is present in primary producer species only. Population dynamics is described by

$$\begin{aligned} \frac{dN_i}{dt} = & N_i b_i(t) - N_i \sum_{j \in L(i)} a_{ij} N_j - N_i \sum_{j \in C(i)} \left(N_j \frac{h_{ij} \alpha_{ij} N_i^{q_{ij}-1}}{1 + \sum_{n \in R(j)} T_{nj} h_{nj} \alpha_{nj} N_n^{q_{nj}}} \right) \\ & + N_i \sum_{j \in R(i)} \left(e_{ji} \frac{h_{ji} \alpha_{ji} N_j^{q_{ji}}}{1 + \sum_{n \in R(i)} T_{ni} h_{ni} \alpha_{ni} N_n^{q_{ni}}} \right) \end{aligned} \quad (1)$$

where dN_i/dt is the rate of change of the density of species i with respect to time in a network with S species, $b_i(t)$ is the per capita growth (mortality) rate for primary producers (consumers) of species i at time t . Competitive interactions are contained in the first sum, where a_{ij} and a_{ii} ($j=i$) is the per capita strength of inter- and intra-specific competition, respectively. The second and third sum describe the loss and gain of species i 's density due to consumption. $L(i)$ is the set of species being competitors to species i , $C(i)$ is the set of species being consumers of resource species i , $R(j)$ is the set of species being resources of consumer species j and $R(i)$ is the set of species being resources of consumer species i . Further, h_{ij} is the 'preference' (feeding effort) and a_{ij} is the intrinsic attack rate of consumer species j on resource species i . For each consumer species prey preferences sums up to 1. T_{ij} is the time needed for consumer i to catch and consume resource j (handling time), e_{ij} is the rate at which resource j is converted into new consumer i (conversion efficiency) and q_{ij} (capture exponent) is an interaction specific positive constant. The capture exponent (q) and handling time (T) determine the type of functional response: $q=1$ and $T=0$ gives a type I (linear) functional response; $q=1$ and $T>0$ gives a hyperbolic type II functional response and increasing q gradually from 1 to 2 gives an increasingly sigmoidal type III functional response.

Adding stage structure

In Paper IV, stage-structure is accounted for by adding a juvenile and an adult stage to consumer species, with life-stage dynamics implemented following (Pimm and Rice 1987). Here only a type I (linear) functional response is used and the number of trophic levels is kept at two. Then, Eq. 1 can be reduced to the following set of ordinary differential equations, describing population dynamics for resources species (Eq. 2), juvenile consumers (Eq. 3) and adult consumers (Eq. 4), respectively:

$$\frac{dR_i}{dt} = R_i b_i(t) - R_i \sum_{j \in L(i)} a_{ij} R_j - R_i \sum_{j \in C^{J,A}(i)} (C_j h_{ij} \alpha_{ij}) \quad (2)$$

$$\frac{dC_i^J}{dt} = C_i^J \left(b_i(t) - a_{ii} C_i^J + (1 - k_i) \sum_{j \in R^J(i)} (e_{ji} h_{ji} \alpha_{ji} R_j) - k_i \sum_{j \in R^A(i)} (e_{ji} h_{ji} \alpha_{ji} R_j) - c_i \right) + f_i^A C_i^A \quad (3)$$

$$\frac{dC_i^A}{dt} = C_i^A \left(b_i(t) - a_{ii}C_i^A + \sum_{j \in R^A(i)} (e_{ji}h_{ji}\alpha_{ji}R_j) \right) + C_i^J \left(c_i + k_i \sum_{j \in R^J(i)} (e_{ji}h_{ji}\alpha_{ji}R_j) \right) \quad (4)$$

Here dR_i/dt , dC_i^J/dt and dC_i^A/dt is the rate of change of the density of resource species i , juveniles (J) and adults (A) of consumer species i , respectively, $b_i(t)$ is the intrinsic per capita growth (mortality) rate of resource (life-stage of consumer) species i at time t , a_{ij} and a_{ii} is the per capita strength of inter- and intra-specific competition, respectively. $L(i)$ is the set of species being competitors to species i , $C^{J,A}(i)$ is the set of juvenile- and adult consumers of resource species i and $R^J(i)$ and $R^A(i)$ is the set of species being resources of juvenile- and adult life-stages of consumer species i respectively. Further, h_{ij} is the ‘preference’ (feeding effort) of juvenile- and adult life-stages of consumer species j for resource species i , α_{ji} is the intrinsic attack rate of juvenile- and adult life-stages of consumer species j on resource species i and e_{ij} is the conversion efficiency. Finally, k is the fraction of consumed resources spent on development and $(1-k)$ is the fraction of consumed food spent on maintenance (reducing juvenile mortality), c is the resource independent per capita development rate of juvenile stages (background maturation rate) and f is the per capita production of recruits of adult consumers (an approximation of the stock-recruitment function, Pimm and Rice 1987).

Model realism and generality

Parameter values are assigned as to be ecologically reasonable. Species mean intrinsic mortality or growth rates are ordered such that $|b_{\text{primary producers}}| > |b_{\text{primary consumers}}| > |b_{\text{secondary consumers}}|$. This is because the body mass of species often increases with trophic level (Jonsson et al. 2005, Gilljam et al. 2011, Riede et al. 2011) and larger body mass often confers lower mortality rates (Roff 1992). To increase the generality of results, model parameters are randomly drawn from uniform intervals and different types of scenarios are explored using many replicates. Paper I also employs a Latin Hypercube Sampling design (McKay et al. 1979), which even further expands the parameter space explored while still keeping simulations computationally feasible. Parameters describing network topology (e.g. connectance) as well as species vital rates and interactions are randomly drawn from predefined intervals. Details on parameter ranges used can be found in the specific papers in this thesis.

Adaptive rewiring

In Paper I, consumer species have the ability to adapt to the loss of a prey species (Fig 8). It is plausible that extinction thresholds, set by processes like demographic stochasticity and Allee effects, could be higher than the density thresholds causing consumers to rewire. We therefore assume that rewiring and compensatory change in feeding efforts takes place in connection with the extinction of preferred prey species, and not before. Hence, an adaptive consumer adjusts its resource preferences (feeding efforts), h_{ij} , when a resource in its original set of resources goes extinct. Finally, each time an adaptive consumer loses its last resource it rewires to a completely new resource from a trophic level below itself, thus forming a novel trophic link. The new

resource is randomly chosen from the set of resources belonging to the consumer which has the most similar set of prey as that of the rewiring consumer itself.

Fig 8 | The response of adaptive consumers to resource species loss. A, Redistribution of feeding efforts and B, rewiring. A, Consumer (b) loses its preferred resource (3) and redistributes its feeding efforts by selecting another of its original resources (4) as the preferred one. B, Consumer (c) loses its last original resource and rewires (green arrow) to a previously unexploited resource (3). The new resource is randomly assigned from the set of resources

belonging to the consumer which has the most similar set of prey (here consumer (b)) as that of the rewiring consumer itself (here consumer (c)). Consumer similarity, J , with respect to their sets of prey, $R_a = \{1, 2\}$, $R_b = \{3, 4, 5\}$ and $R_c = \{4\}$, is quantified using the Jaccard index of similarity; $J(c, b) = (|c \cap b|) / (|c \cup b|) = 0.33$ and $J(c, a) = (|c \cap a|) / (|c \cup a|) = 0$

Exposing food webs to environmental variability

To explore the effects of environmental variability on community persistence (proportion species surviving for a given period of time), we expose food web models to white (no temporal autocorrelation, Paper I and IV) and red (positive temporal autocorrelation, Paper II) noise. Moreover, we investigate the effects of varying degree of correlation among species in their response to environmental fluctuations, ρ , (Paper I and II) and the effects of varying the strength (variance, σ^2) of environmental variability (Paper II), on community persistence.

Environmental variability is introduced in species' intrinsic growth or mortality rates as $b_i(t) = \bar{b}_i(1 + \varepsilon_i(t))$ where $\bar{b}_i$ is the mean per capita growth or mortality rate of species i and $\varepsilon_i(t)$ is a stochastic process. In Paper I, the resulting stochastic time series are uniformly distributed on the interval $[-1, 1]$ and extreme values are as likely as the mean value of 0. The correlation among species in their response to environmental fluctuations, ρ , is generated as in Kaneryd et al. (2012). In Paper II and IV, we use a $1/f$ noise-generating method (Lögberg and Wennergren 2012), where the mean, variance, σ^2 , temporal autocorrelation (spectral exponent, i.e. environmental noise colour), γ , and correlation in species response to the environmental variability, ρ , of ε_i are controlled. For the values of γ used here, the resulting stochastic time series are approximately Gaussian, that is, extreme values are not as frequent as values close to the mean.

Patterns of size structure and within-species variability

In Paper III and IV, highly resolved natural food webs where data is available at the level of individuals are used (Table 1). More precisely, the food web datasets analysed consist of information on individual predation events, where the taxonomic identity and the body mass of both the predator and its prey are available. Such detailed information makes it possible to analyse how the trophic structure of ecological networks is governed by the body size of its interacting entities. Further, if the individual-level data is ‘artificially’ aggregated, we can investigate how our perception of the trophic structure of ecological networks depend on the level of resolution of the data at hand or on the type of aggregation used (Fig. 9, Paper III).

Figure 9 | An illustration of the framework used in Paper III. We use the letters A–F to depict aggregations into different levels of resolution and groupings. The raw data of individual predator–prey interactions (A) are aggregated using a taxonomic based approach to generate different levels of resolution (A–D) or binned into body size classes using a size-class-based approach to provide groups (E and F) which can be contrasted with the taxonomic aggregations. Comparisons of for example the relationship between predator- and prey mass can then be made, either between the levels of resolution or between the two approaches to grouping (all possible comparisons are denoted by dashed and dotted arrows, respectively). The data shown in this example are from Broadstone Stream, depicting the predator mass to prey mass relationship. Log₁₀ predator body mass is on the x-axis and log₁₀ prey body mass is on the y-axis, the line denotes the one-to-one relationship where predator mass equals prey mass. Solid arrows illustrate along which axis the aggregations were conducted, that is, no aggregation for the individual-level data (A—highest resolution); aggregation

along the x-axis (focal axis) for resolution B and grouping E; and aggregation along both the x- and y-axes (non-focal axis) for resolution C and D, and grouping F. See Paper III for details on the study.

Paper IV continues the analysis of the highly resolved individual-based empirical data set used in Paper III and investigates patterns and effects of within- and between species resource specialisation. Using the method originally developed by Roughgarden (1972, 1974), we partition the community niche width (total variation in body size of all prey items of all predators in the community, w^2) into two components. One is the variance in body size of prey items consumed by a species averaged over all species (WSC) and the other is the variance of the average of prey body sizes of the different consumer species (BSC) (Fig. 10). Note that $w^2 = WSC + BSC$ and that WSC/w^2 is the proportion of the total community niche width (w^2) due to within-species variation in resource use (WSC). Small values indicate low overlap in resource use among species and large values indicate high overlap in resource use among species.

Figure 10 | An illustration of intra- and interspecific components of resource use for a community with three consumer species. The whole niche width of the community, w^2 , can be split into two components. The within species component (WSC) is the average variance in body mass of prey items utilized within a species, σ^2_v . The between species component (BSC) is the variance of the mean prey body sizes (y_i) of the different consumer species.

Local stability analysis and dynamic dimensionality

If linearised around the equilibrium point, the behaviour of a set of non-linear ordinary differential equations after an initial perturbation can be described by the equation (Yodzis 1989 p. 116, Case 2000 p. 298)

$$\mathbf{n}(t) = \sum_{i=1}^S h_i \mathbf{v}_i e^{\lambda_i t} \quad (5)$$

Here, $\mathbf{n}(t)$ is a vector of the deviations of the species densities from the equilibrium densities at time t after the initial perturbation, S is the number of dimensions (species) and $\mathbf{v}_i$ and λ_i are the eigenvectors and corresponding eigenvalues of the Jacobian (community) matrix, respectively. h_i are integration constants which depend on the initial perturbation, $\mathbf{n}(0)$. If all λ have negative real parts, then the equilibrium is locally stable and deviations will decay with time (May 1973a). Further, the dominant eigenvalue, λ_{max} , (having the largest real part) will determine the system's asymptotic

decay rate of deviations (its *resilience*, Neubert and Caswell 1997) because the term in eq. (5) containing $\lambda_{\max}$ will decay the slowest. If any λ have imaginary parts, the system will oscillate following a perturbation.

Systems with different community matrices can have equal eigenvalues, both for real and complex solutions, and thus the same resilience (they asymptotically approach zero at the same rate). They can however initially behave differently after a perturbation, i.e. one system can exhibit transient growth of deviations while the other do not (Neubert and Caswell 1997, Hastings 2004). The systems which exhibits transients where the deviation from equilibrium grows initially are *reactive* (Neubert and Caswell 1997). In a varying environment, a locally stable reactive system would be more likely to suffer species extinctions following a perturbation, compared to a locally stable non-reactive system. This is because the transient growth of the reactive system will amplify the initial perturbation, thereby temporarily moving the system even farther away from the equilibrium point and thus potentially closer to any species extinction threshold.

If we are interested in the long term behaviour of a system, in a deterministic setting, then only the sign (and the magnitude) of the dominant eigenvalue is needed to characterise local stability. However in a stochastic environment where species are continuously perturbed, short term dynamics and thus non-dominant eigenvalues should also be of importance for community persistence. In a stochastic environment, there is no fixed equilibrium point $\mathbf{N}^*$ but rather an ‘equilibrium cloud’ in phase space described by the equilibrium time-independent probability distribution $f^*(\mathbf{N})$, the centre of which equals $\mathbf{N}^*$ (May 1973b). The size and shape of the cloud is determined by the strength of interactions among species, the variance of the environment and the correlation in species’ response to the environmental variation (May 1973b, Ripa and Ives 2003). Around $\mathbf{N}^*$, there are two forces at play; the stabilising deterministic population interactions acting to restore populations to their equilibrium values and the destabilising stochastic environmental fluctuations pushing population sizes from the equilibrium, ‘diffusing the cloud’ (May 1973a, 1973b).

If exemplified using a two species system, eq. (5) can be written as

$$\begin{Bmatrix} n_1 \\ n_2 \end{Bmatrix} (t) = h_1 \begin{Bmatrix} v_1 \\ v_2 \end{Bmatrix}_1 e^{\lambda_1 t} + h_2 \begin{Bmatrix} v_1 \\ v_2 \end{Bmatrix}_2 e^{\lambda_2 t} \quad (6)$$

The integration constants h_1 and h_2 can be found by solving eq. (6) at time $t = 0$ (that is when $\mathbf{n}$ equals the size of the perturbation):

$$\begin{Bmatrix} n_1 \\ n_2 \end{Bmatrix} (0) = h_1 \begin{Bmatrix} v_1 \\ v_2 \end{Bmatrix}_1 + h_2 \begin{Bmatrix} v_1 \\ v_2 \end{Bmatrix}_2 \quad (7)$$

Solving eq. (7) is easily done as the eigenvectors $\mathbf{v}_i$ are known.

In eq. (6) it is more easily seen that the stabilising (assuming $\text{real}(\lambda_1, \lambda_2) < 0$) deterministic interactions governing a particular species’ short-term displacement from the equilibrium (n_1, n_2) , at time t after a perturbation $\mathbf{n}(0)$, is a function of all

eigenvalues (λ_1, λ_2) and the corresponding row (element) of all eigenvectors $(v_{1,2})_1$ and $(v_{1,2})_2$. For example, the displacement of species 1 at time 1 after a perturbation would be

$$n_1(1) = h_1(v_1)_1 e^{\lambda_1} + h_2(v_1)_2 e^{\lambda_2} \quad (8)$$

where $(v_1)_{1,2}$ denotes the first row of the eigenvector 1 and 2 respectively.

In a system which ‘deterministically’ acts to recover along both dimensions (directions) at similar rates, the risk of species going extinct due to destabilising environmental fluctuations is likely to be lower compared to a system which recover along one dimension (direction) very quickly and along the other very slowly. The former system could be characterised as having a higher *dynamic dimensionality* (Roughgarden 1998, p. 339, [Paper II]). Dynamic dimensionality can be quantified as the inverse participation ratio (inverse Simpson index) of the eigenvalues (real parts) of the Jacobian (community) matrix of the system (see Paper II for details). A high DD means that the real-part of the eigenvalues are of similar magnitude and that the system therefore approaches the equilibrium from all directions at a similar rate (Fig. 11). On the other hand, when DD is low one (or a few) of the eigenvalues has a large magnitude compared to the others and the deterministic forces pulling the system towards equilibrium is therefore weak in many directions compared to the stochastic forces pushing the system away from the equilibrium. As a consequence the risk of crossing extinction thresholds increases, and hence persistence and time to first extinction decreases, as DD decreases.

Figure 11 | Phase-plane of two species competition systems illustrating the effects of dynamic dimensionality on species variability and recovery pattern. Columns represent degree of dynamic dimensionality (left – high, right – low). Small dots show species densities during a 1000 time unit stochastic simulation (95% of the dots are contained within the grey ellipsoids) and large, dark dots highlight the deterministic recovery following one possible perturbation. Dynamic dimensionality (DD) is given by the inverse participation ratio (IPR) of the magnitudes of the real-part of the eigenvalues (λ) of the Jacobian (community) matrix $\mathbf{J} = \mathbf{N}^* \mathbf{A}$. Here, $\mathbf{N}^*$ is the deterministic equilibrium point of the system and $\mathbf{A}$ is the interaction matrix ($\mathbf{A}_{\text{IPR high}} = [-1, -0.15; -0.15, -1]$; $\mathbf{A}_{\text{IPR low}} = [-1, -0.85; -0.85, -1]$). The eigenvectors $\mathbf{v}_1 = \{0.71, 0.71\}$ and $\mathbf{v}_2 = \{-0.71, 0.71\}$ (left panel), and $\mathbf{v}_1 = \{-0.71, -0.71\}$ and $\mathbf{v}_2 = \{0.71, -0.71\}$ (right panel) are shown by the dashed lines. λ -values are positioned next to their corresponding eigenvector. Per capita growth/mortality rates used are $b = [1; 1]$. Environmental white noise here affects population dynamics additively, i.e. its effect is not proportional to species' intrinsic growth rates or population densities.

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PART 2 – PAPERS

- I. Gilljam, D., A. Curtsdotter, B. Ebenman. 2015.
Adaptive rewiring aggravates the effects of species loss in ecosystems.
Nature Communications, 6:8412.¹
- II. Gilljam, D. and B. Ebenman. 2016.
High dynamic dimensionality promotes the persistence of ecological networks in a variable world.
Manuscript.
- III. Gilljam, D., A. Thierry, F. K. Edwards, D. Figueroa, A. T. Ibbotson, J. I. Jones, R. B. Lauridsen, O. L. Petchey, G. Woodward, B. Ebenman. 2011.
Seeing double: size-based and taxonomic views of food web structure.
Advances in Ecological Research, 45:67–133.²
- IV. Gilljam, D. and B. Ebenman. 2016.
Patterns of resource utilisation within and between species affect the dynamic dimensionality and stability of ecological communities
Manuscript.

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