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Extinctions in complex food webs: drivers and consequences

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Contents

Summary

Biodiversity is declining rapidly throughout the world. The rate of extinctions matches historical extinction waves and is likely to accelerate even further since two main drivers of biodiversity loss, global warming and nutrient enrichment, are predicted to increase in their impact over the coming decades. These extinctions are not only irreversible, diminishing the astounding diversity of life on our planet, but they also pose a direct threat to the health and wellbeing of humans. Thus, understanding the drivers and consequences of extinctions in existing species communities, and how they are affected by climate change and nutrient enrichment, is of vital importance.

In this thesis I examine different aspects of extinctions in food webs, representations of feeding interactions among species in a community. This accounts for the fact that, in nature, species interact and whatever affects one species also affects other species in the same community. Thus, species interactions have to be considered when investigating extinctions. In this thesis I used a dynamic food web model which, based on biological meaningful parameters such as growth, consumption and metabolism, tracks the flow of energy through complex food web structures.

To be able to assess species extinctions in changing environments I established a basic extinction risk for species in recent food webs (chapter 2). I found that the extinction risk of species is mainly governed by energy availability and dynamic stability of the population. Consequently, species that are at a high trophic levels, have few prey species that are of similar size bear, the highest intrinsic risk of extinction. I found that the time to extinction for species is determined by its body size and that small species will go extinct earlier than large ones. This implies that in the field the extinctions of small species will be detected earlier, even if the large species are already doomed to die and will go extinct as well.

In chapter 3 I investigated trophic cascades, which describe the well known positive indirect influence a top species has on the populations of a species two feeding links down by controlling the population of the intermediate species. Many studies on trophic cascades are on isolated food chains since the manipulation of entire species communities is difficult. In chapter 3 I compared the top species influence in an isolated chain and in a chain that was embedded in a food web. In isolated three-species food chains the impact of the top on the basal species was always positive, because it controls the population of the intermediate species. Whereas, when embedded in a food web, the top species impact was much more

variable and could be both positive and negative. Its strength was determined by the body mass and abundance of both the top species and the basal species. At the example of trophic cascades, this demonstrates that accounting for species interactions in a food web context is important for accurately assessing the indirect effects of one species on another.

Warming directly affects growth, metabolism, feeding and death of organisms. Enrichment increases the energy availability in the food web. In chapter 4 I account for the temperature dependency of biological rates and show that warming and enrichment interactively affect the dynamics of populations. At low temperatures, increasing energy input leads to increased population oscillations and therefore species extinctions. Warming decreases the flux of energy to higher trophic levels and thus counteracts the destabilizing effect of enrichment. However, with increasing temperatures the metabolism of species increases faster than their ability to consume food. This leads to extinctions due to starvation. These extinctions at high temperatures can be counteracted by enrichment induced higher energy levels. In combination, these two main drivers of global change and biodiversity loss can have both positive and negative effects on population stability.

In food webs, predator-prey body mass ratios are an important determinant of species persistence. Large body mass ratios decrease the strength of the interaction and increase species persistence. In chapter 5 I found that body-mass ratios, temperature and fertility interactively affect food web connectance, species persistence and link distributions. Body-mass ratios influence the effects of temperature on persistence and determines the interactive effects of temperature and fertility. In food webs in which predator and prey species are roughly of equal size species persistence is increased by warming and reduced by enrichment. In food webs in which predators are substantially larger than their prey persistence is reduced by warming, but can be reduced or increased by enrichment. At high body mass ratios and high temperatures specialist consumers with only few feeding links are more likely to survive than generalist consumers. This influences food web connectance, which is reduced under these conditions. This study shows that the multi-faceted interactions of temperature, fertility and body mass ratios trigger varied responses in complex food webs. However, knowledge of the interactions is a first important step towards disentangling these effects.

This thesis elucidates different aspects of extinctions in food webs. It shows that accounting for the complexity of species interactions is necessary to fully apprehend the dynamics within food webs. Looking at undisturbed food webs and ones affected by warming and enrichment helps grasp the effects of global change on species communities. This thesis also identifies the complex interactive effects of drivers of species extinctions. It contributes to the sorely needed understanding of extinctions in complex species communities.

Zusammenfassung

Die biologische Artenvielfalt unseres Planeten ist in Gefahr. Jeden Tag gehen Arten unwiederbringlich verloren, mit einer Geschwindigkeit, die jetzt schon historischen Aussterbewellen gleicht. Zusätzlich wird vorhergesagt, dass zwei wichtige Auslöser des Artensterbens, Erwärmung und Nährstoffanreicherung, in den kommenden Jahrhunderten weiter an Bedeutung gewinnen werden. Damit wird sich die Geschwindigkeit des Verlustes biologischer Vielfalt weiter erhöhen. Der Verlust von Arten ist dabei nicht nur unwiderruflich, sondern stellt auch eine direkte Bedrohung für die Gesundheit und das Wohlbefinden des Menschen dar. Ein Verständnis der Auslöser und Auswirkungen des Artensterbens, in bestehenden sowie in von globalem Wandel beeinflussten Artengemeinschaften, ist somit von entscheidender Bedeutung.

In der vorliegenden Arbeit habe ich verschiedene Aspekte des Artensterbens untersucht. Dazu konzentrierte ich mich auf Nahrungsnetze, die die Fraßbeziehungen zwischen den Arten einer Gemeinschaft beschreiben. Mit diesem Ansatz berücksichtige ich die Tatsache, dass Arten in natürlichen Systemen miteinander interagieren und sich somit alles was sich auf eine Art auswirkt auch auf anderen Arten auswirkt. Dies ist besonders wichtig in Untersuchungen von Artensterben. In dieser Arbeit benutze ich ein dynamisches Computermodell, das, basierend auf biologisch aussagekräftigen Parametern wie Wachstum, Fraß und Stoffwechsel, den Energiefluss durch komplexe Nahrungsnetzstrukturen verfolgt.

Um das Aussterben von Arten unter sich ändernden Bedingungen beurteilen zu können, ist es nötig das grundlegende Aussterberisiko der Arten in heutigen Nahrungsnetzen zu kennen. Dieses Aussterberisiko habe ich in Kapitel 2 untersucht. Dabei zeigte sich, dass das Aussterberisiko von Arten hauptsächlich durch die Verfügbarkeit von Energie und der dynamischen Stabilität der Population bestimmt wird. Dem ensprechend tragen Arten hoher trophischer Ebenen, mit wenigen Beutearten ähnlicher Größe das höchste inherente Aussterberisiko. Des weiteren zeigte sich, dass die Zeit bis zum Aussterben einer Art wesentlich von deren Körpergröße abhängt. Die bedeutet, dass in Feldbeobachtungen das Aussterben kleiner Arten früher detektiert werden kann als das größerer Arten, die bereits dem Tode geweiht, aber noch nicht ausgestorben sind.

In Kapitel 3 untersuchte ich trophische Kaskaden. Diese beschreiben das Phänomen, dass eine Art durch Fraß an einer anderen Art deren Beute indirekt positive beeinflusst, indem sie sie von Prädationsdruck befreit. Da die Manipulation gesamter Artengemeinschaften äußerst

schwierig ist, beschränken sich viele Studien trophischer Kaskaden auf die Untersuchung isolierter Nahrungsketten. Mein Computermodell aber kann ganze Artengemeinschaften simulieren. In Kapitel 3 zeige ich dramatische Unterschiede zwischen trophischen Kaskaden in isolierten Nahrungsketten und in Nahrungsketten, die in ein Nahrungsnetz eingebettet sind. In isolierten Dreiartenketten war die Auswirkung des Prädators auf die Basalart immer positiv, weil die Population der intermediären Art von ihr kontrolliert wurde und die Basalart damit weniger gefressen wurde. In eingebetteten Nahrungsketten jedoch war die Auswirkung auf die Basalart wesentlich variabler und konnte sowohl positiv, als auch negativ sein. Die Stärke des Einflusses in der eingebetteten Nahrungskette wurde sowohl von der Körpermasse und Abundanz des Prädators, als auch von der Abundanz der Basalart bestimmt. Am Beispiel der trophischen Kaskade konnte ich damit zeigen, dass für eine genaue Beurteilung der indirekten Effekte zwischen Arten die Betrachtung der vielen Beziehungen innerhalb eines Nahrungsnetzes unerlässlich ist.

Steigende Temperaturen wirken sich unmittelbar auf Wachstum, Fraß, Stoffwechsel und den Tod von Tieren aus. In Kapitel 4 berücksichtige ich die Temperaturabhängigkeiten der biologischen Parameter explizit in der Parameterisierung des Computermodelles. Damit konnte ich zeigen, dass steigende Temperaturen und Nährstoffanreicherung gemeinsam und interaktiv die Dynamiken der Populationen beeinflussen. Bei niedrigen Temperaturen führt die durch Nährstoffanreicherung zugeführte zusätzliche Energie zu vermehrten Oszillationen der Population und erhöht damit das Aussterberisiko. Steigende Temperaturen verringern den Energiefluss zu höheren trophischen Ebenen und wirken somit dem destabilisierenden Einfluss von Nährstoffanreicherung entgegen. Mit zunehmenden Temperaturen jedoch steigt der Stoffwechsel einer Art schneller als ihre Fähigkeit Nahrung zu konsumieren. Dies führt dazu, dass Arten ihren Energiebedarf irgendwann nicht mehr decken können und einfach verhungern. Dieses Verhungern bei hohen Temperaturen kann durch mehr Energie (durch Nährstoffanreicherung) verhindert werden. Somit können diese beiden Treiber des globalen Wandels und Artensterbens beide sowohl positive als auch negative Auswirkungen auf die Stabilität von Populationen haben.

Das Größenverhältnis zwischen Räubern und ihrer Beute ist ein wichtiger Faktor für die Persistenz von Arten. Hohe Körpermassenverhältnisse verringern die Stärke der Fraßinteraktion und erhöhen die Überlebenswahrscheinlichkeit der Arten innerhalb eines Nahrungsnetzes. In Kapitel 5 wird deutlich, dass Körpermassenverhältnisse, Temperaturen und Fertilität interaktiv die Überlebenswahrscheinlichkeit von Arten und die Verteilung ihrer Fraßbeziehungen beeinflussen. Außerdem bestimmen sie den finalen Verschaltungsgrad innerhalb des Netzwerkes. Die Körpermassenverhältnisse beeinflussen die interaktiven Effekte von Temperatur und Systemfertilität. In Nahrungsnetze in denen Räuber und ihre Beute in etwa gleich groß sind erhöht sich die Überlebenswahrscheinlichkeit der Arten durch Erwärmung, und sinkt durch Nährstoffanreicherung. In Nahrungsnetzen, in denen

Räuber deutlich größer sind als ihre Beute sinkt die Überlebenswahrscheinlichkeit der Arten durch Erwärmung, kann aber durch Nährstoffanreicherung erhöht oder reduziert werden. In Nahrungsnetzen mit hohen Körpermassenverhältnissen und hohen Temperaturen ist die Überlebenswahrscheinlichkeit für Arten mit wenigen Beutearten (Spezialisten) höher als die für Arten mit vielen Beutearten (Generalisten). Dies beeinflusst den finalen Verschaltungsgrad, der in diesen Nahrungsnetzen sinkt. Diese Studie zeigt, dass die vielfältigen Wechselwirkungen von Temperatur, Fertilität und Körpermassenverhältnisse in komplexen Nahrungsnetzen eine Reihe verschiedener Reaktionen auslösen können. Die Kenntnis dieser Wechselwirkungen ist ein erster, wichtiger Schritt zum Verständnis der Einflüsse von sich ändernden Umweltbedingungen.

Die vorliegende Arbeit beleuchtet verschiedene Aspekte des Aussterbens in Nahrungsnetzen. Sie zeigt, dass die Miteinbeziehung der Interaktionen zwischen Arten notwendig ist um die Dynamiken innerhalb von Nahrungsnetzen zu verstehen. Der Blick auf ungestörte Nahrungsnetze ermöglicht den Vergleich mit von Erwärmung und Nährstoffanreicherung beeinflussten Nahrungsnetzen. Dies ermöglicht es die Auswirkungen des globalen Wandels auf Artengemeinschaften zu verstehen. Diese Arbeit zeigt die komplizierten Wechselwirkungen zwischen verschiedenen Auslösern des Artensterbens. Damit trägt sie zum dringend notwendigen Verständnis von Aussterebereignissen in Nahrungsnetzen bei.

Contributions to the chapters of this thesis

Chapter 2

The susceptibility of species to extinctions in model communities

Amrei Binzer, Ulrich Brose, Alva Curtsdotter, Anna Eklöf, Björn C. Rall, Jens O. Riede, Francisco de Castro

All authors designed the study. The numerical experiment was coded and performed by A.B. and A.C. Data were analyzed by A.B., F.C. and B.C.R. The text was written by A.B., U.B. and F.C.

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Chapter 3

Predator body mass determines the strength of positive and negative trophic cascades in complex food webs

Amrei Binzer, Björn C. Rall, Eric L. Berlow, Ulrich Brose

A.B. and U.B. designed the study, the numerical experiment was coded and performed by A.B., data were analyzed by A.B., B.C.R. and E.L.B, the text was written by A.B. and U.B. with input from E.L.B.

Chapter 4

The dynamics of food chains under climate change and nutrient enrichment

Amrei Binzer, Christian Guill, Ulrich Brose, Björn C. Rall

All authors designed the study, the model was developed and implemented by A.B. and C.G., the numerical experiment was coded and performed by A.B., data were analyzed by A.B. and B.C.R., the text was written by A.B. and U.B.

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Chapter 5

How temperature, energy availability and predator prey body mass ratios help shape complex food webs

Amrei Binzer, Christian Guill, Björn C. Rall, Ulrich Brose

A.B. and U.B. designed the study, the model was developed and implemented by A.B. and C.G. and parameterized by A.B. and B.C.R., the numerical experiment was coded and performed by A.B., data were analyzed by A.B., the text was written by A.B. and U.B.

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Part I.

General introduction

Chapter 1.

Modelling extinctions in complex food webs

The tremendous diversity of life on Earth is astonishing and awe inspiring. However, today global biodiversity is declining ever more rapidly, at rates that match historical extinction waves (Pimm *et al.*, 1995; Regan *et al.*, 2001; Barnosky *et al.*, 2011). Evidence suggests that we are at the beginning or in the middle of a sixth wave of mass extinction (Wake and Vredenburg, 2008; Wagler, 2011). Additionally, the Millennium Ecosystem Report predicts two main drivers of biodiversity loss, global warming and enrichment, to rapidly increase their impacts over coming decades (Millennium Ecosystem Assessment, 2005). These accelerated rates of biodiversity loss may degrade ecological communities beyond retrieval and impair their ability to perform functions and services important for humankind and its well-being (Loreau *et al.*, 2001; Solan *et al.*, 2004; Hooper *et al.*, 2005). Therefore, understanding the drivers and consequences of extinctions in existing species communities, and how they are affected by climate change and nutrient enrichment, is sorely needed and vitally important.

In consequence, in the chapters of this thesis, I examine different aspects of extinctions. I establish a basic extinction risk for species in undisturbed food webs (chapter 2) and then go on to look at how the effects of two major drivers of biodiversity loss, global warming and enrichment, affect species persistence (chapters 4 and 5). Additionally, I investigate aspects of how extinctions might be propagated through food webs in the form of trophic cascades (chapter 3).

In nature, species do not exist in isolation but form complex communities. In these communities, species are linked by interactions which form a complicated network. Because of these interactions, species do not just respond individually to environmental drivers but influence each other. My investigations therefore had to be carried out on the community level using techniques that would accommodate the effects of interactions. I concentrated on feeding interactions because they are fundamental for life as they supply animals with the energy they need to grow and reproduce. Food webs are networks made up of feeding interactions are and representations of the “who eats who” in an ecological community. Investigating them allowed me to look at extinction risk in complex communities and how they respond to the drivers of biodiversity loss. I examined these complex communities using mathematical simulations. To do so experimentally would be virtually impossible as manipulating communities of large numbers of species is very complicated. Modeling, however, allows such manipulation.

The food web model I used combines structural models (the static description of the feeding links among the species in the food web) with a dynamic population model. This is a system of differential equations which quantify the effects of species on each other and with which I can track species biomasses over time. The equations use biologically meaningful parameters such as growth, metabolism, and consumption. By bringing these two parts together I am able to investigate the dynamics of complex species communities and obtain general outcomes that are not specific to any particular ecosystem or ecosystem type. Despite being general, the outcomes are relevant to natural ecosystems because the parameters and their values are biologically realistic. Furthermore, in chapters 4 and 5 I parameterize the models biological parameters with data from the largest and most comprehensive empirical databases compiled so far (Ehnes *et al.*, 2011; Rall *et al.*, 2012). This unique model accounts for the fact that growth, feeding and metabolism of species change with a species body mass, as well as with environmental temperature. This is especially relevant in the context of warming as the linking of the model parameters with temperature helps reveal the mechanisms by which temperature causes extinctions. Thus, this model is capable of identifying complex effects and provides possible mechanistic explanations for extinctions in recent food webs, as well as for food webs affected by climate change.

In the following paragraphs I provide background information on the model and its implementation. I conclude with an outline of the chapters included in this thesis.

Food webs

A brief history

Food web research is not a new field of ecology. As early as 1859 Darwin wrote about the "entangled bank" and remarked on the abundance of species interactions in nature (Darwin, 1859). However, these interactions not only include feeding interactions, but also encompass non-trophic interactions such as habitat provisioning. More than half a century later, Summerhayes and Elton published one of the earliest food webs depicting the feeding interactions of animals on Bear Island, south of Spitsbergen (Summerhayes and Elton, 1923). Subsequently, Elton found general patterns in food webs, such as positive correlations between predator and prey body-masses or predator body masses and their

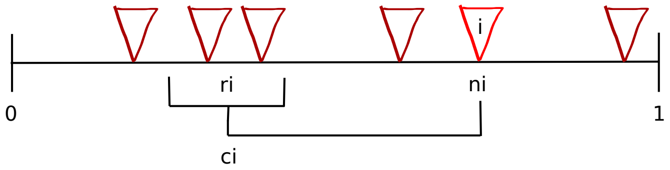

Figure 1.1 – Diagram of the niche model (after (Williams and Martinez, 2000)). The species, represented by triangles, are lined up on the niche axis according to their niche value. Species *i* (bright red) can consume all species that fall within its range *ri*, which is placed on the niche axis by the center value, *ci*.

trophic level, that are still valid today (Elton, 1927; Riede *et al.*, 2011). Since then, the resolution of food webs has steadily increased , not least through modern techniques such as manual and molecular gut content analyses (Woodward and Hildrew, 2001; Eitzinger and Traugott, 2011).

Structural models

Early theoretical studies on food webs simply assumed them to be random networks (May, 1972), but it quickly became apparent that this did not represent natural food webs (Cohen and Newman, 1985), because their structure is far from random (Pascual and Dunne, 2005). So, just as empiricists took on the labor intensive task of assembling food webs from detailed field data, theoretical researchers began looking for rules of assembling artificial species communities which would resemble natural food webs. These artificial food web structures represent the static feeding relationships between species in a community (Solow, 1996) without being specific to any type of real world food web.

The model food webs used in the studies reported in this thesis are based on the niche model (Williams and Martinez, 2000). This model creates a food web structure by distributing the feeding links, L, among the species, S in the food web (see figure 1.1). The species are positioned on a niche axis according to their niche value, n_i. The niche values are randomly drawn from a range between zero and one. This niche axis ensures a hierarchical ordering of the species and is often thought to represent species traits such as body mass. Every species is then assigned a feeding link to all species that lie within its range. r_i. The center, c_i, of the range is randomly chosen and is less than the species niche value. The width of the range is calculated using a beta function to produce the desired connectance of the model food web. The connectance is the probability that any pair of species within the food web will interact and is calculated by dividing the existent number of links by the number of possible links: $C = L/S^2$. This structural food web model allows looping (two or more species feeding on each other) and cannibalism. The food webs created by the niche model closely resemble empirical data from real webs (Williams and Martinez, 2000; Dunne *et al.*, 2004). But they under-estimate the number of herbivores found in more recently reported empirical food webs (Williams and Martinez, 2008). Even though other more recent structural food web models, such as the allometric diet breath model (Petchey *et al.*, 2008), offer a more mechanistic way of building food web structures, the niche model has the the advantage of creating complex network structures by using simple link distribution rules and only two input parameters.

Knowledge of the static structure of food webs and examinations of model food web structures allows a variety of analyses of extinction risks, such as trait based sequential deletions to identify species that are important for the stability of the food web. However, these static observations of extinctions only include bottom-up effects. For example, a species extinction does not affect its prey but only its predators, since they are loosing a prey species. Secondary extinctions only occur when the last prey species goes extinct. This severely underestimates the extinction risk of species (Curtsdotter *et al.*, 2011). However, in real communities, predator driven top-down effect can also influence extinctions (Paine, 1966; Elmhagen and Rushton, 2007; Curtsdotter *et al.*, 2011). Therefore, to gain better understanding about extinctions in food webs, bottom-up and top-down effects clearly both have to be considered. This can be done by accounting for the population dynamics between species.

Population dynamic models

A brief history

The origin of modern population dynamic models lies in the observation that populations of a predator and its prey over time are coupled and fluctuate, often in recognizable, periodic cycles. The most famous textbook example of this is the time series of the Canadian lynx *Lynx canadiensis*, which was compiled using fur acquisition data of the Hudson Bay Company from over 200 years (Elton and Nicholson, 1942). The regular, 10-year cycles displayed by the number of lynx furs were linked to the abundance of its prey, the snowshoe hare *Lepus americanus* (Elton and Nicholson, 1942; Chitty, 1948). The synchrony of population cycles of different species in different parts of Canada was an early indicator of the influence of climatic factors on population dynamics (Elton and Nicholson, 1942).

Mathematical descriptions of such coupled predator-prey pairs were developed early, in the 1920s. Lotka and Volterra independently developed a set of differential equations that use predation to link populations of predators and their prey (Lotka, 1925; Volterra, 1926). In the Lotka-Volterra model, the change in the number of prey is given by its growth minus the predation rate. The number of predators increases with predation and declines by natural death.

More specifically, the prey population, N, grows exponentially in the absence of predation (exponential growth $= rN$, see equation 1.1). The predator population, P, declines in the absence of prey (mP, where m is the populations intrinsic death rate, see equation 1.2). Those two populations are linked by a predation term, aNP, which is proportional to the rate at which predator and prey meet, a. If either N or P are zero, there is no predation. The preys population declines with predation at the rate of predation, whereas the predator population increases with predation modified by a conversion factor, e.

$$\frac{dN}{dt} = rN - aNP \tag{1.1}$$

$$\frac{dP}{dt} = -mP + aNPe \tag{1.2}$$

This simple model tracks numbers of individuals. It forms the backbone of many modern dynamic population models. Its shortcomings, such as the assumption of exponential growth in the absence of predation, or the overly simple predation term, have subsequently been addressed and changed (MacArthur and Rosenzweig, 1963).

Mathematical implementation

The model that I use throughout this thesis is a multi-species version of the predator-prey model developed by Yodzis and Innes (Yodzis and Innes, 1992). Here, I present the differential equations for a predator-prey pair, which instead of tracking individuals, track energy in form of biomass over time (Yodzis and Innes, 1992; Williams and Martinez, 2004*b*). The prey species accumulates biomass by growing and loses biomass to the predator. After accounting for metabolic activity, the predator can build up its own biomass. More precisely, the equations for the change of biomass, B, over time for a species i and its predator j are the following:

$$\dot{B}_i = r_i G_i B_i - B_j F_{ji} \tag{1.3}$$

$$\dot{B}_j = e_{ji}(B_j F_{ji}) - x_j B_j \tag{1.4}$$

Here, the prey i gains biomass by growing and loses biomass due to predation (equation 1.3). The growth is calculated by the species intrinsic maximum growth rate, r_i and the logistic growth term, G_i. Logistic growth, $G_I = (1 - \frac{B_i}{K_i})$, limits the growth of i to a maximum carrying capacity, K_i, which is approached in a saturating curve and reached in the absence of a predator (MacArthur and Rosenzweig, 1963). The predation term is described by the functional response, F_{ji}. The functional response describes the prey-density dependent feeding of j on i. The predator j gains biomass through predation (equation 1.4), which is the biomass the prey loses through predation modified by a factor describing the efficiency with which prey biomass is converted into predator biomass $(0 \leq e_{ji} \leq 1)$. The predator looses biomass through metabolic activity, x_i.

Details of the feeding interactions

The functional response is crucial for determining the feeding dynamics between species. For this reason, it has received considerable attention from researchers (Holling, 1959; MacArthur and Rosenzweig, 1963; Vucic-Pestic *et al.*, 2010; Rall *et al.*, 2012). In 1959, Holling introduced a mechanistic model describing the functional response that remedied the problem of unbounded consumption as implemented in the Lotka-Volterra model (Holling, 1959). His assumption was that the predator has to divide its time between capturing (searching and subduing) and handling (digesting) its prey. Thus, in his model the prey-density dependent feeding of j on i increases with the attack rate a_{ji}, and at high prey densities it saturates at the inverse of the handling time, Th:

$$F_{ji} = \frac{a_{ji} N_i}{1 + a_{ji} Th_{ji} N_i} \tag{1.5}$$

Functional responses can take on many shapes. They can be linear as in the Lotka-Volterra model (type I functional response, the consumption increases linearly with the prey density), hyperbolic (basic type II functional response, the consumption saturates with increasing prey density) or sigmoid (type III functional response, the consumption is low at low prey densities, then increases and saturated at high prey densities).

Real extended equation 1.5 to accommodate this variety and substituted a by bN^q (Real, 1977). This makes the attack rate dependent on the prey density and introduces q, a scaling coefficient, into the equation of the functional response:

$$F_{ji} = \frac{b_{ji} N_i^{q+1}}{1 + b_{ji} Th_{ji} N_i^{q+1}} \tag{1.6}$$

This annotation allows a gradual shift of the functional response between type II $(q = 0)$ and type III $(q = 1)$. The term $q + 1$ is also called the Hill exponent, h.

Attack rate and handling time are usually measured in laboratory or field experiments.

In theoretical studies, a more phenomenological connotation of the functional response is more common. It is derived from two parameters describing the curve of the functional response, the maximum ingestion, y, and the half saturation density, B_0. The maximum ingestion is equivalent to the saturation point of the feeding curve and therefore to $1/Th$. The half saturation density is the prey density at which half the maximum consumption is reached. It is calculated by $1/aTh$ (Real, 1977). This yields the following functional response equation:

$$F_{ji} = \frac{y_i N_i^{q+1}}{B_{0_{ji}}^{q+1} + B_i^{q+1}} \tag{1.7}$$

This equation provides the basic functional responses that in their biomass-based multi-species connotation (Koen-Alonso, 2007) are used in the research chapters of this thesis.

Parameterization

Conveniently, the major parameters of the introduced dynamic population model scale with the body mass of the species (Yodzis and Innes, 1992). This drastically simplifies the parameterization of the model and yields stable food webs (Brose *et al.*, 2006*b*).

Generally, all biological parameters, Y, such as growth and consumption, as well as metabolism should scale with the species body mass, M, according to a certain scaling exponent, b, and parameter specific constant, Y_0 (West *et al.*, 1997; Brown *et al.*, 2004):

$$Y = Y_0 M^b \tag{1.8}$$

In chapters 2 and 3, I use the widely accepted scaling exponent of 3/4 (Yodzis and Innes, 1992; West *et al.*, 1997; Brown *et al.*, 2004; Brose *et al.*, 2006*b*).

In chapters 4 and 5, I use rate specific scaling exponents which are derived from empirical data-bases (Savage *et al.*, 2004; Ehnes *et al.*, 2011; Rall *et al.*, 2012). In the latter two chapters, I also account for temperature dependencies of these biological rates (West *et al.*, 1997; Brown *et al.*, 2004; Ehnes *et al.*, 2011; Rall *et al.*, 2012) that are derived from the same databases. For the implementation please consult the respective chapter.

Theory and empiricism - a fruitful get together

The food web model I used in this thesis thus combines complex food web structure with population dynamics based on feeding interactions. The biological parameters scale with the body size of the species and, in chapters 4 and 5 also with the temperature of the food web. This simplifies the model, but at the same time allows investigation of how fundamental physiological effects scale up to the species community (Clarke, 2006).

The model I use could not have been assembled without constant communication with empiricists. The structure, the dynamical equations and the parameterization are, even if condensed and abstracted, derived from empirical data. This makes models like this ideal tools for deriving general theoretical predictions that can then be tested in the field. They are an example of how fruitful the cooperation between theoreticians and empiricists can be.

It is particularly relevant that the model is rooted in empirical data. This is because continual cross talk back and forth between empiricist and theoretician is key for developing models that can deliver biologically meaningful predictions and mechanistic understanding of the processes that underlie species extinctions. As part of this process, I use the results of the dynamic food web models to develop hypotheses that might be tested experimentally.

Outline of this thesis

The papers included in this thesis address different aspects of extinctions, their drivers and consequences, in food webs. They can broadly be split up in two groups: **Chapter 2** and **Chapter 3** concentrate on extinction risk and the consequences of extinctions in recent food webs. **Chapter 4** and **Chapter 5** explore the consequences of warming and enrichment, two main drivers of biodiversity loss, on the biological parameters of species and how that affects species survival and the remaining food webs.

Species extinctions are a continuous process in food webs. Over the course of time, an estimated 99% of all species has gone extinct (Barnosky, 2009). In **Chapter 2** I explore the intrinsic extinction risk of species depending on network and species parameters. Screening a multitude of food webs with different dynamic parameters, I establish a baseline extinction risk for species in non-perturbed food webs. These basic risk profiles allow disentanglement of intrinsic from disturbance-induced extinction risks in future studies.

Species extinctions can have a multitude of consequences and affect the remaining community in different ways. The extinction of a consumer can have cascading effects on species two feeding links down, causing a trophic cascade. But, can trophic cascades fully be understood by concentrating on the species directly involved or is modeling the full, complex, food web necessary to understand the impact of species loss? In **Chapter 3** I compare the effect of consumer loss in isolated food chains and in food chains that are embedded in a food web to understand whether the food web context is necessary to understand extinction events or not.

Warming directly accelerates biological rates of species, such as growth (Savage *et al.*, 2004), metabolism (Gillooly *et al.*, 2001; Brown *et al.*, 2004; Ehnes *et al.*, 2011) and feeding rates (Vucic-Pestic *et al.*, 2011; Lang *et al.*, 2012; Rall *et al.*, 2012), which are fundamental to the species interactions and therefore the energy distribution in food webs. Enrichment increases the energy input into the system. In **Chapter 4** I parameterized the model of a three species food chain with empirically derived body-mass and temperature scaling relationships. With this I monitor how warming and enrichment induced changes in biological rates separately and interactively affect species population dynamics and ultimately their survival.

In **Chapter 5** I expand this model and combine complex food web structure with the empirically scaled dynamic population model from chapter 4. With this unique model, I investigate the consequences of warming, enrichment and body-mass structure on species persistence and link distributions as well as final food web connectance. This gives a comprehensive overview about how warming and enrichment can affect extinctions in a wide variety of food webs and reveals the far reaching consequences that changes of biological rates can have on the community level.

Part II.

Research chapters

Chapter 2.

The susceptibility of species to extinctions in model communities

Amrei Binzer, Ulrich Brose, Alva Curtsdotter, Anna Eklöf, Björn C. Rall, Jens O. Riede,
Francisco de Castro

Abstract

Despite the fact that the loss of a species from a community has the potential to cause a dramatic decline in biodiversity, for example through cascades of secondary extinctions, little is known about the factors contributing to the extinction risk of any particular species. Here we expand earlier modeling approaches using a dynamic food-web model that accounts for bottom-up as well as top-down effects. We investigate what factors influence a species' extinction risk and time to extinction of the non-persistent species.

We identified three basic properties that affect a species' risk of extinction. The highest extinction risk is born by species with (1) low energy input (e.g. high trophic level), (2) susceptibility to the loss of energy pathways (e.g. specialists with few prey species) and (3) dynamic instability (e.g. low Hill exponent and reliance on homogeneous energy channels when feeding on similarly sized prey).

Interestingly, and different from field studies, we found that the trophic level and not the body mass of a species influences its extinction risk. On the other hand, body mass is the single most important factor determining the time-to-extinction of a species, resulting in small species dying first. This suggests that in the field the trophic level might have more influence on the extinction risk than presently recognized.

Zusammenfassung

Obwohl wir wissen, dass Artensterben durch sekundäre Aussterbefälle weitreichende Verluste von Biodiversität in Artengemeinschaften auslösen kann, ist wenig bekannt über Faktoren, die das Aussterberisiko einer bestimmten Art beeinflussen. Hier erweitern wir frühere theoretische Arbeiten mit Hilfe eines dynamischen Nahrungsnetzmodells, das sowohl top-down als auch bottom-up Effekte berücksichtigt. Wir untersuchen welche Faktoren das Aussterberisiko und die Zeit bis zum Aussterben der nicht persistenten Arten beeinflussen.

Wir identifizierten drei fundamentale Eigenschaften, die sich auf das Aussterberisiko einer Art auswirken. Das höchste Risiko tragen Arten mit (1) niedriger Energiezufuhr (z.B.

mit hohem trophischen Level), (2) Anfälligkeit für den Verlust von Energiepfaden (z.B. Spezialisten mit wenig Beutearten) und (3) dynamischer Instabilität (z.B. mit niedrigem Hill Exponenten und Abhängigkeit von homogenen Energiepfaden durch Fraß an ähnlich großen Beutearten).

Unser Modell zeigt, dass, anders als in Feldstudien festgestellt, nicht die Körpergröße einer Art sondern ihr trophischer Level ihr Aussterberisiko beeinflusst. Für die Zeit bis zum Aussterben auf der anderen Seite ist die Körpergröße der wichtigste bestimmende Faktor. Dies führt dazu, dass die kleinen Arten als Erste aussterben. Somit könnte sich der trophische Level einer Art mehr als bisher angenommen auf ihr Aussterberisiko auswirken.

Keywords | Extinction risk, Allometry, Dynamic modelling

Introduction

Today, global biodiversity is declining at an alarming rate that matches the rate of historical extinction waves (Pimm *et al.*, 1995; Barnosky *et al.*, 2011) and is referred to as the sixth wave of extinction. This is especially critical since every extinction has the potential to trigger secondary extinctions, which might in turn lead to extinction cascades, accelerating the rate of biodiversity loss even further (Pimm, 1980; Berlow *et al.*, 2004; Dunne and Williams, 2009). Declining species numbers, in consequence, endanger an ecosystem's ability to perform certain functions important to mankind (Loreau *et al.*, 2001; Solan *et al.*, 2004; Hooper *et al.*, 2005). This risk of cascading extinctions and degradation of ecological communities makes it vitally important to gather information about the causes of species extinctions. One important task is the development of effective models that can be translated into protection measures for preserving the diversity of natural systems.

There have been a number of studies trying to assess a species' vulnerability to extinction and discussing different individual traits influencing extinction risk (McKinney, 1997; Simberloff, 1998; Purvis *et al.*, 2000). These have identified high trophic levels (Purvis *et al.*, 2000; Jackson *et al.*, 2001), low population density (McKinney, 1997; Purvis *et al.*, 2000), and large body size as an indicator of the species' life history (McKinney, 1997; Jackson *et al.*, 2001) as key factors influencing extinction risk. Unfortunately, many of these studies focus on carnivorous vertebrates, primates (Purvis *et al.*, 2000), birds and mammals (McKinney, 1997) with few invertebrate examples, even though invertebrates contribute far more to global diversity. Hence, the crucial question remains whether these results obtained for certain groups of vertebrates can be generalized. As long as high quality empirical data on extinctions is lacking, modeling approaches promise to be the most effective means to gain knowledge that can be universally applied to fit a multitude of species.

Some prior studies have used different mathematical models to predict future biodiversity. The "field of bullets" model assumed a single, fixed extinction rate for all species, rendering the extinctions independent from one another (Raup, 1992; Nee and May, 1997). This model predicted an exponential decline of biodiversity. Sole and Manrubia (1996) included species interactions into their model, to account for changing extinction risks. This resulted in a clustering of species losses into fewer but larger avalanches that were found to make predictions more difficult. Recently, Ingram and Steel (2010) expanded the field of bullets model and compared the outcome of a version with varying extinction rates ("generalized field of bullets") with one that incorporated food-web topology ("ecology-based field of bullets"). They also found that accounting for food-web dependencies reduces the prediction accuracy of the model. All these studies focused solely on bottom-up effects for extinction risk and did not incorporate top-down processes, which can underestimate the number of secondary extinctions (Ebenman *et al.*, 2004; Eklöf and Ebenman, 2006; Curtsdotter *et al.*, 2011).

Berlow *et al.* (2009) used a dynamic bioenergetic model to investigate the response of one species to the extinction of another. Unlike the other models, theirs accounted for the dynamics in a food web, which include top-down as well as bottom-up effects. They found that the knowledge of individual species traits such as the biomasses of the involved species and the body mass of the extinct species suffice to predict a species' biomass response to an extinction event. Including food web interactions into the model thus makes it easier rather than more difficult to predict the consequences of species extinctions.

Here, we use a dynamic bioenergetic food-web model to assess a species' vulnerability to extinction (extinction risk) and the time-to-extinction (number of time-steps before extinction) of the species dying out. This model does not use explicit extinction rates for the species but uses the dynamic energy flow within the food web over time to calculate changes in biomass densities. We want to explore a species' intrinsic extinction risk, as depending on network and species parameters. We therefore assemble a variety of food webs and combine them with a variety of dynamic parameters, all within the range found in natural communities (see Methods section). Screening this multitude of combinations enables us to identify a species' basic risk profile as applicable without perturbation of the system. In addition to providing a theoretical framework for studies of extinctions, these risk profiles allow disentangling intrinsic from disturbance-induced extinction risks in future studies. Our findings do not focus on one individual system, but take a broader approach that nonetheless can be helpful for nature conservation.

We address the question of a species' extinction risk in two steps: Step 1: What determines the susceptibility of species to extinction? By incorporating food web structure as well as dynamic interactions between species we identify a simple combination of traits that are measurable in the field and thus usable for conservationists. Step 2: What determines the time-to-extinction of the species dying out? Our interest is to see whether it is possible to predict which extinctions will be the first to be observed in the system and which species are “living dead“, doomed to extinction but not yet gone.

Methods

Our data set consists of 1000 size-structured food webs that were dynamically simulated based on an allometric, multi-species version of Yodzis and Innes' (1992) model. The webs were constructed using the rules of the niche model (Williams and Martinez, 2000). This model arranges the trophic links (L) in the food web using its species richness (S) and connectance ($C = L/S^2$) as parameters. It has been successfully tested against empirical data (Williams and Martinez, 2000). For each web the initial species number and initial connectance were randomly drawn from truncated normal distributions. The mean species number was 40 species, with a standard deviation of 10 species and an upper and lower boundary of 20 and 60 species, respectively. The initial connectance was chosen with a mean of 0.15, a standard deviation of 0.05 and a lower and upper boundary of 0.05 and 0.25, respectively. These values fall within the range found in natural communities (Digel *et al.*, 2011) and ensure a variety of naturally plausible webs to explore and understand.

Following the dynamic model, the rate of change in the biomass through time ($\dot{B}$) of the primary producers (eq. 2.1) and consumers (eq. 2.2) in the system are given by:

$$\dot{B}_i = r_i G_i B_i - \sum_j \frac{x_j y_j B_j F_{ji}}{e_{ji}} \tag{2.1}$$

$$\dot{B}_i = -x_i B_i + \sum_k x_i y_i B_i F_{ik} - \sum_j \frac{x_j y_j B_j F_{ji}}{e_{ji}} \tag{2.2}$$

$B_{i,j}$ denotes the biomass density of the populations i and j, respectively, r_i i's mass-specific intrinsic growth rate, G_i is the logistic growth rate, $x_{i,j}$ denotes the mass-specific metabolic rate of the populations i and j, $y_{i,j}$ the consumer's maximum consumption rate relative to its metabolic rate and e_{ji} is j's assimilation efficiency when it consumes species i. The suffix k describes the resources of i and the suffix j its consumers.

The logistic-growth model assumes that the growth of each basal species is dependent on the carrying capacity (K) of the population. The term of the logistic growth is

$$G_i = (1 - \frac{B_i}{K_i}) \tag{2.3}$$

where G_i describes the deviation of the population i from K_i. To keep the energy content of the food webs constant and the webs comparable we used a system wide carrying capacity ($K_{sys} = 5$), calculating each primary producer's share by dividing K_{sys} by the number of plant species in the food web. Rall *et al.* (2008) studied the effects of enrichment on consumer-resource models and complex food webs by varying the carrying capacity in the system. They found starvation of high trophic level consumers for low K and extinctions due to dynamic instability at high values of K (Rall *et al.*, 2008). A K_{sys} of 5 is somewhere in the middle of these extremes while still maintaining a variety of cases to explore.

F_{ji}, the functional response, describes the resource density dependent feeding of a consumer j on a resource i influenced by all other j's resources k:

$$F_{ji} = \frac{\omega_{ji} B_i^h}{B_0^h + cB_j + \omega_{ji} B_i^h + \sum_k \omega_{jk} B_k^h} \tag{2.4}$$

The functional response is described by ω_{ji}, a dimensionless positive weight factor (set to 0.5, see Koen-Alonso (2007) for more details), B_0, the half-saturation density (i.e. the population density at which half the maximum consumption of the species is reached), the predator interference term, c, and the Hill exponent, h, that regulates the shape of the function. An increasing Hill exponent renders the shape of the curve more sigmoidal, which is interpreted as a refuge effect for prey species at low prey densities (see Williams and Martinez (2004*b*) and Rall *et al.* (2008) for more details).

Metabolic theory suggests that the biological rates of production (R), metabolism (X) and maximum consumption (Y) scale with the species' body mass with a negative-quarter power law (Enquist *et al.*, 1999; Brown *et al.*, 2004). We used this established scaling coefficient in our simulation, but it should be kept in mind that recently a lower scaling coefficient was found (Ehnes *et al.*, 2011). However, this should not detract from the applicability of our results.

$$R_P = \alpha_r M_P^{-0.25} \tag{2.5}$$

$$X_{C,P} = \alpha_x M_{C,P}^{-0.25} \tag{2.6}$$

$$Y_C = \alpha_y M_{C,P}^{-0.25} \tag{2.7}$$

where the suffixes C and P indicate consumer and producer parameters, respectively, α_r, α_x and α_y are allometric constants. In our model, these biological rates are normalized by the mass-specific intrinsic growth rate of the smallest basal species j, (R_j). This results in different growth rates for j and all other basal species, i, and defines the time scale of the system:

$$r_j = \frac{R_j}{R_j} = 1 \tag{2.8}$$

$$r_i = \frac{R_i}{R_j} = \left(\frac{M_i}{M_j}\right)^{-0.25} \tag{2.9}$$

Accordingly, the mass-specific metabolic rates (eq. 2.6) are normalized by the production and thus the time scale (eq. 2.5), leading to:

$$x_i = \frac{X_{C,P}}{R_P} = \frac{\alpha_x}{\alpha_r}\left(\frac{M_{C,P}}{M_P}\right)^{-0.25} \tag{2.10}$$

The maximum consumption (eq. 2.7) is normalized by the metabolic rates (eq. 2.6):

$$y_i = \frac{Y_C}{X_C} = \frac{\alpha_y}{\alpha_x} \tag{2.11}$$

Inserting equations (2.9), (2.10) and (2.11) into equations (2.1) and (2.2) results in a population dynamic model with parameters that are allometrically scaled.

We used the following assimilation efficiencies: $e_{ij} = 0.85$ for carnivore links, $e_{ij} = 0.45$ for herbivore links. The maximum consumption rate of the species was kept at ($y = 8$). The normalized metabolic rate (α_x/α_r) was set to 0.314 (Brose *et al.*, 2006*b*). The predator interference term was randomly chosen from a truncated normal distribution with a mean of 0.1 and a lower boundary of zero, the hill exponent from one with the mean of 1.1 and lower boundary of 1. Both had a standard deviation of 0.05 and an upper boundary of 2. Again, these values fall well within the range of natural communities while providing a range of parameter combinations to screen (Yodzis and Innes, 1992; Brose *et al.*, 2006*b*; Vucic-Pestic *et al.*, 2010). The initial abundances of the species were randomly chosen between 0.1 and 1.

The body masses of the species increase with the species' trophic level, modified by a factor sampled from a normal distribution with a mean of 10 and a standard deviation of 10. This stochastic factor yields variation in body masses within trophic levels while preserving the increase in mass with trophic level that can be found in natural systems (Riede *et al.*, 2011). Trophic level and body mass are thus highly correlated variables but can influence a species' extinction risk and time-to-extinction independently.

All food webs were assembled and simulated for 100,000 time steps. A species was considered extinct if its biomass fell below 10^{-30}. Contrary to other studies we did not force any extinctions but only registered the ones occurring "naturally" in the food webs.

Throughout the simulation we recorded several variables at time step zero to test for their influence on the species' susceptibility to extinction.

As food-web variables, we recorded the initial species number and connectance of the web. To characterize the species and its relations to the other species in the web we recorded the prey-averaged trophic level of the species (Williams and Martinez, 2004*a*), the Hill exponent, predator interference term, body mass and initial biomass as well as the average body-size ratio of the species to its prey, the standard deviation of this ratio, the average body-size ratio to its predators and the standard deviation thereof.

Also recorded for each species were the generality (number of prey species), the vulnerability (number of predators) and linkedness (number of links). We then calculated for each of these variables the mean and maximum the species shares with all other species in the web. We furthermore calculated the mean and maximum number of "var" each species shares with other species with which it shares at least one "var" where "var" is prey species, predator species or links. We also calculated the number of species each species shares prey species, predator species, or links with.

Additionally, we calculated the similarity of the species to each of the other species in the web as follows: $I = C/(A + B + C)$ where I is the similarity, A the prey, predators or links unique to the species, B the prey, predators or links unique to the other species in the web and C the prey, predators or links that both species share. We recorded the species' maximum and mean prey, predator and link similarity to all other species in the web and its mean prey, predator and link similarity to the species it is sharing at least one prey species or one predator species or one link with.

As dependent variables we recorded whether the species went extinct (1) or not (0) and the extinct species' time-to-extinction.

Statistics

Step 1: To determine which parameters have the largest influence in determining if a species goes extinct or not we performed a classification tree analysis (Ripley, 2010) with all recorded variables plus the log-transformed values of the species' body mass and biomass. This is used for exploratory data analysis and investigates the relative importance of variables in explaining the variance of a dependent variable, in this case the binary variable stating if the species went extinct during the simulation (1) or survived (0). To obtain a more quantitative understanding, the significant explanatory variables of the regression tree analysis were entered in a generalized linear model (R Development Core Team, 2009) to see how they influence the extinction probability of the species. We performed this analysis once with all species in the web and once without the basal species. The trends in

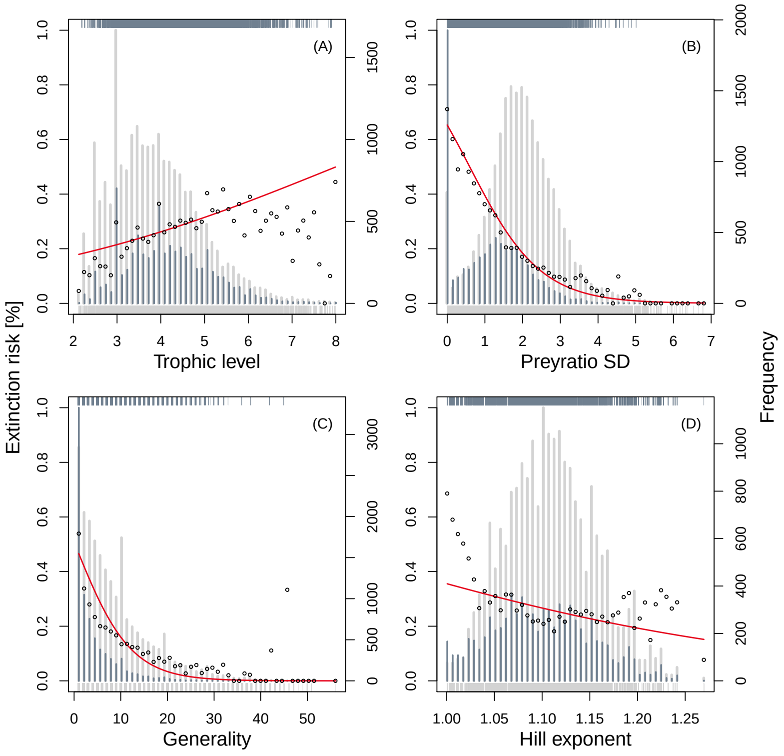

Figure 2.1 – The variables influencing a species' susceptibility to extinction. Plotted is the binary extinction variable on the first y-axis (dark-gray lines above y=1 correspond to extinct species, light-gray lines below y=0 to species being alive at the end of the simulation) and the frequency of observation on the second y-axis (the dark-gray histogram corresponds to dead species, the light-gray histogram to species being alive at the end of the simulation) over the explanatory variable. The red solid line illustrates the extinction probability calculated by the general linear model based on the the observed values. The circles denote the fraction of extinctions from the overall data points at that x value. The plots are based on data excluding basal species to make the trends clearer. The explanatory variables are (A) the species' trophic level, (B) the standard deviation of the species' body-mass ratio to its prey items, (C) the species' generality (number of prey) and (D) the species' hill exponent, shaping its feeding interactions.

both cases were the same, but more pronounced when focusing on the consumer species and in this paper we present the results obtained with the basal species excluded.

Step 2: We examined the species that had died out during the simulation. To analyze which parameters influence the time to extinction of these species we ran a generalized additive model (Wood, 2006) on the data set and all recorded variables. This model uses a back-fitting smoothing algorithm to link the explanatory variables to the time-to-extinction. The smoothers are calculated with respect to the best representation of the relationship of the explaining variable and the partial residuals are calculated by removing the effect of all other predictor variables on the dependent variable.

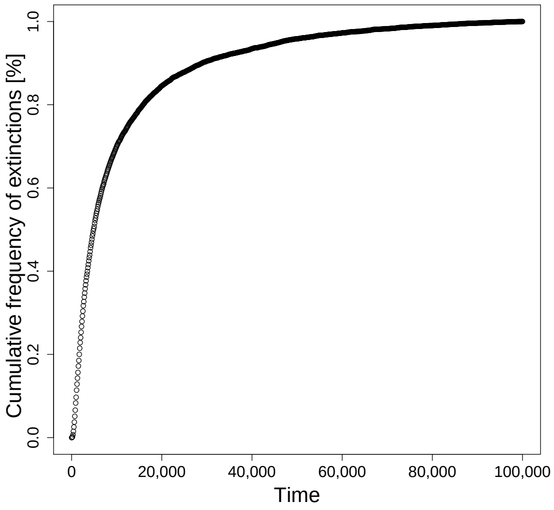

Figure 2.2 – Cumulative percentage of extinctions over time. The slope of the tangent of the plotted curve gives the extinction rate at that point in time. As the simulation time (x-axis) progresses the extinction rate levels off, indicating that the number of extinctions decreases over time with almost no extinctions at the end of the simulation.

Results

Step 1: *Species with a high trophic level, low variation in prey size, low generality and low Hill exponent are most susceptible to extinction.*

The regression tree analysis identified four out of 35 tested variables as having a significant influence ($R^2 < 0.001$) on a species' extinction risk. Their trends, as calculated by the generalized linear model, are depicted in Fig. 2.1. The higher the trophic level of the species the greater the chances of that species going extinct during the simulation (Fig. 2.1A). A trophic level of two is associated with an extinction probability of less than 20% while a trophic level of eight increases the extinction probability to 50% (solid line in Fig. 2.1A). The proportion of extinct species at the higher trophic levels deviates from the expected extinction risk as calculated by the generalized linear model (the circles below the solid line). This pattern suggests that the generalized linear model might overestimate the frequency of extinctions at the highest trophic levels. However, focussing on the frequency distribution of the data points (histograms in the background of the plot) reveals that the model might be oriented to fit the area with a high density of data points (and therefore high informative value) and extrapolates its curve on that basis.

Fig. 2.1B shows the influence of the variation in body size of the prey utilized by the focal species, given as the standard deviation of the body-mass ratio between the species and its prey: the more differently sized prey items a species feeds on the lower its extinction risk (Fig. 2.1B). The extinction risk of a species decreases with increasing generality (number of prey), with almost no extinctions of species with more than 30 prey items (Fig. 2.1C). The higher the Hill exponent the lower the extinction risk of the species. Interestingly, using natural food web structures and simulating their dynamic behavior for an equivalent of 30 years yields the same results as the simulations using the niche model webs (data not shown).

Fig. 2.2 shows the cumulative percentage of extinctions over time. As the simulation progresses the extinction rate, as indicated by the slope of the tangent of the plotted curve, decreases and approaches zero at the end of the time-series. Over 80% of all extinctions occur in the first fifth of the time-series and almost none by the end indicating that the vast majority of extinctions that will take place in the food webs we created are within our observed time frame. This clearly separates the data into surviving species and those that went extinct. For the latter, we also addressed the question of which parameters affect the time until extinction.

Step 2: *Species with low body mass, large prey and large predators are the first to go extinct.*

We identified six parameters that influence a species' time to extinction. All six influencing parameters together explain 61.1% of the variation in the data set. We cannot assess each individual parameters' contribution to the model, but the visualization of the influences of the parameters on the time to extinction (Fig. 2.3) clearly shows a major influence of the body mass of the species. The higher the body mass of the species the longer it takes that species to go extinct (Fig. 2.3A). A higher mean body-mass ratio of the species' predators to the species (i.e. having predators that are much larger than itself) decreases the time to extinction (Fig. 2.3B). A higher mean body-mass ratio of the species to its prey (i.e. having small prey in comparison to its own body size) increases the time to extinction (Fig. 2.3C). Predator interference, a measure of how much time the species spends competing with con-specifics (Fig. 2.3D), the maximum number of species the species is sharing prey items with (max preyshared, Fig. 2.3E) and the generality (number of prey) of the species (Fig. 2.3F) also contribute to the species' time to extinction, but their individual influence is not great (Fig. 2.3).

Discussion

In this study, we focused on two questions concerning a species' extinction risk. Step 1 investigated the species' vulnerability to extinction and parameters influencing it. In a second step we explored which parameters affect the time to extinction of the species dying out. Our study shows that a combination of a few factors influence a species' susceptibility to extinction: accessibility of energy, availability of energy pathways and population dynamics. Interestingly, a species' body mass influences its time-to-extinction, but not its extinction risk.

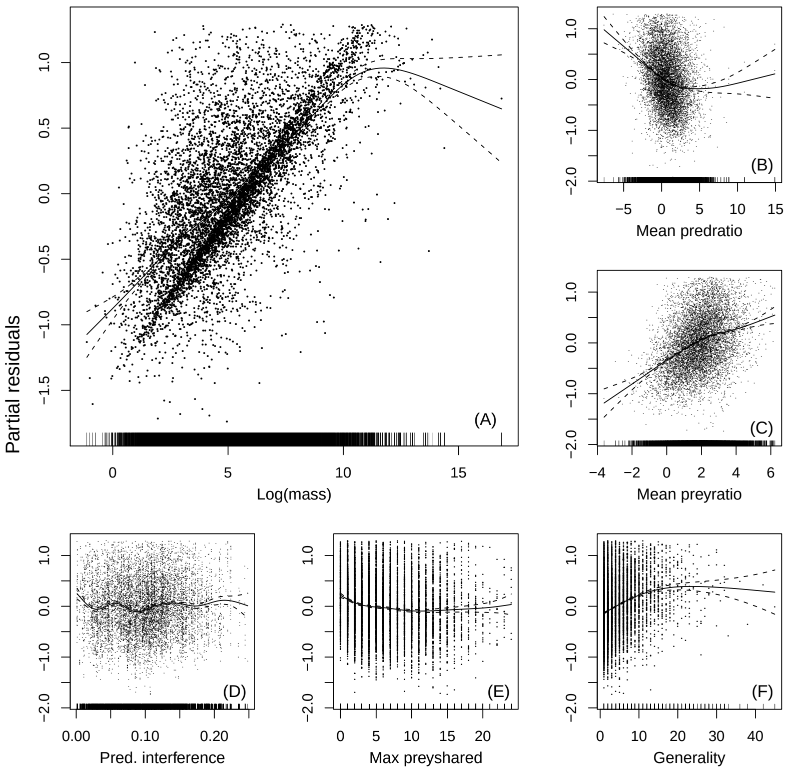

Figure 2.3 – Variables influencing the species' time-to-extinction. Plotted are the partial residuals of the model against the explanatory variable. The continuous line is the local regression smoother, the dotted lines the corresponding 95% point-wise confidence bands. The dashes on the x-axis give the distribution of observed values. The influencing variables are: (A) the log body mass of the species (log(mass)), (B) the average body-mass ratio of the predators to the species (mean predratio), (C) the average body-mass ratio of the species to its prey (mean preyratio), (D) the predator interference term, (E) the maximum number of prey shared with other species in the web (max preyshared) and (F) the generality (number of prey) of the species.

Step 1: *A species' ability and flexibility to gain energy through the web is crucial to determine its susceptibility to extinction.*

The trophic position can be seen as a measure of how much the species is separated from the food web's source of energy at the base, such as phytoplankton in marine ecosystems, primary decomposers in soil food webs or vascular plants in terrestrial systems. Each trophic level receives less energy in comparison to the lower levels: the higher the species' trophic level the less energy is available to balance its metabolic needs. This explains the higher extinction risk of high trophic level species. The species' community does not provide enough energy for the species to survive. Already Hutchinson argued that energy transfer limits the length of food chains in food webs (Hutchinson, 1959) which found empirical support in microbial systems (Kaunzinger and Morin, 1998). Pimm and Lawton disturbed food chains and found that the more trophic levels in the chain the longer it took the system to get back into equilibrium. The population dynamics of the system lead to a higher probability of extinction and therefore decreases stability (Pimm and Lawton, 1977). Later studies emphasized the importance of ecosystem size to the number of feasible trophic levels in a system (Post *et al.*, 2000; Post, 2002). Unfortunately our model does not incorporate effects of spatial patterns. Also, species at higher trophic levels might suffer the cumulative effects of disturbance and oscillatory dynamics of the species situated lower in the web, leaving them more vulnerable to extinction (Purvis *et al.*, 2000). This wide variety of reasons can cause the higher risk of extinction we found for species with higher trophic levels.

Here we find that the trophic level and not the body mass of the species determines the species' risk of extinction. In empirical studies body mass is often identified as a major driving factor of extinction risk (Cardillo *et al.*, 2005). However, empirical studies usually do not measure a species' trophic level because it is more complicated to measure compared to the species' body mass. Our results indicate that even if correlated, trophic level and body mass are not equivalent in predicting a species' extinction risk and time-to-extinction. This introduces the possibility that trophic level might be more important to the risk of extinction of a species in natural systems than hitherto imagined and important to take into account as a separate parameter in models of food web and extinction dynamics.

The size variability of the prey items of a species (here expressed as the standard deviation of its size-ratio) is a measure of the species' specialization on specific size classes, and consequently a measure of the flexibility of the species to obtain energy from different prey. Species with a broader prey size spectrum can subsist on other prey to obtain energy from and escape extinction more easily. At the same time, variation in prey sizes means that the species is gaining energy through different pathways with different dynamics. In the case of a perturbation these energy channels act complementary and thus save the species from extinction. This is in line with findings from (Rooney *et al.*, 2006) who stated that a predator preying on differently sized prey links multiple asymmetric energy channels with fast (small prey) and slow (large prey) dynamics, which ultimately enhances stability in the chains and the food web. While space constraints prevent own analyses of these population dynamics, they are well documented in prior publications (Yodzis and Innes, 1992; Brose *et al.*, 2006*b*).

The generality of a species characterizes its ability to modify its energetic income and is linked to its vulnerability to bottom-up extinctions. A species with only a few prey items is more at risk when loosing prey than one with more prey. Generality and variation in prey size are highly correlated in our data set but emphasize different aspects of a species energy availability. Generality is a safeguard against loss of energy channels and a species trait pertaining to the structure of the food web. Variability in prey size relates to the dynamics between species because it influences the availability of energy for the feeding species throughout time. Our model analyses are thus in line with classic food-web analyses stating that specialization lowers food web stability and increases species efficiency (MacArthur, 1955). Our results suggest that a high rate of specialization of a species does not only decrease the food web's stability but also decreases that very same species' ability to survive.

A high Hill exponent causes effective top-down control to low equilibrium densities. This dampens the biomass oscillation of consumer and resource and increases dynamic stability, thus reducing a species extinction risk. Interestingly, our results are thus entirely consistent with prior studies demonstrating the importance of type-III functional responses (high Hill coefficients) for food-web stability (Williams and Martinez, 2004*b*; Rall *et al.*, 2008). Dynamic stability in a food web is influenced by species traits such as the Hill exponent as well as food-web properties such as the dynamic of energy channels.

Overall our results suggest that it is most important for a species to be able to obtain enough energy to be able to survive, whereas other factors play only a minor role. Certainly, this is an expected result in a purely trophic network and future extensions of our approach should also include other interaction types. The data suggests that there are a few key concepts that minimize a species' extinction risk. (1) A high energy supply through the food web. In our scenario this translates into a low trophic level and thus less energy loss through trophic levels that separate the species from the energy supply at the base. (2) Security against the loss of energy pathways. A species with a high generality, feeding on many species, is less likely to lose all sources of energy than a species preying on only a few species. (3) Dynamic stability. A higher Hill exponent stabilizes a species' population dynamic and thus decreases its extinction risk. The same is true for species with a high variation in prey sizes that couple different energy pathways.

Step 2: *A species' metabolism (energy need) determines its time-to-extinction.*

Metabolic theory links the metabolism of a species to its body mass, indicating that with increasing mass the species' metabolism is increasing with a power-law exponent of 0.75 (Enquist *et al.*, 1999) or slightly lower (Ehnes *et al.*, 2011). This implies that with increasing body mass a species' metabolism becomes more efficient, resulting in a lower per-unit body mass metabolism for larger species in comparison to smaller ones. In our simulated scenario this explains the huge influence of the species' body mass to its time-to-extinction: a smaller species needs proportionally more energy per unit biomass to stay alive than a larger species resulting in a shorter time-to-extinction in the case of an energy cut-off. As the same rules apply to natural ecosystems this implies that even if only small-species extinctions can be observed quickly after a perturbation there might be larger species already doomed to extinction but still present in the system. In our simulations these "living dead" are high trophic level and therefore high body mass species. It is these that depress the observed extinction rate below that predicted by the model (Fig. 2.1A). We expect those species to constitute the few extinctions that would take place if the time-series would be prolonged.

Conclusions

Our data set suggests three fundamental processes that minimize a species' extinction risk: high energy accessibility, availability of energy pathways and stable population dynamics. A species' body mass does not influence its extinction risk, but its time-to-extinction. This shows that extinction events in natural systems are not random. Instead we see that specialists (species with low generality and little variation in prey size) with a high trophic level are most vulnerable to extinction. Studies dealing with consequences of extinctions should consider these scenarios as the most likely (Curtsdotter *et al.*, 2011). Basic individual species' traits and simple measures of interaction between species provide good estimates of its susceptibility to extinction. Our model furnishes researchers in the field with simple predictors, giving them easy-to-use indicators (such as body mass and trophic level of a species) to assess a species' risk of extinction and helping them to focus their conservation attention. Simulating natural food web structures with the same dynamics yielded the same results, indicating a congruency of our model with reality. At the same time it should be kept in mind that our model does not provide information about any individual system, but takes a wider approach, trying to assess a species intrinsic extinction risk that is independent from specific ecosystems and the basis on which disturbance experiments should be evaluated.

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Chapter 3.

Predator body mass determines the strength of positive and negative trophic cascades in complex food webs

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Abstract

Trophic cascades, their occurrence and strength, have been the subject of many studies for decades. However, it is very complicated to manipulate entire food webs and so many of these studies were restricted to isolated food chains. Here, we used a dynamic, bioenergetic population model to investigate whether the results from isolated food chains capture the behaviour of trophic cascades in complex food webs with their intricate system of species interactions. Based on food web simulations we developed statistical models explaining the sign and strength of trophic cascades for food chains embedded in complex food webs. In the isolated food chain, trophic cascades were always positive and their strength was determined by the body mass of the intermediate and the abundance of the top species. In the simulated food webs, trophic cascades could be positive and negative and their strength was determined by the body mass and abundance of the top species of the embedded chain as well as those of its basal species. Our simulations therefore indicate that trophic cascades in food webs are fundamentally different from those in isolated food chains. Thus results derived from isolated food chains are not informative regarding trophic cascades in food chains that are embedded in food webs. However, the drivers of cascade strength in food webs are all population parameters that are easy to measure. This may offer an easy tool for conservationists to investigate trophic cascades in their field.

Keywords | allometry, network motif

Introduction

Trophic cascades are a well known example of how the interplay of direct and indirect interactions determines the distribution of species biomasses (Polis, 1994; Schmitz *et al.*, 2004). Classically, trophic cascades occur when carnivores exert an indirect, positive effect on plants by reducing the biomass of herbivores (Hairston *et al.*, 1960; Sommer, 2008). However, trophic cascades are not restricted to specific trophic levels (Paine, 1980). Once described, they were found in a variety of ecosystems (Strong, 1992; Pace *et al.*, 1999; Persson, 1999; Shurin *et al.*, 2002) even though their extent (Polis, 1999; Polis *et al.*, 2000) and strength (Strong, 1992; Chase, 2000; Halaj and Wise, 2001) were discussed intensively. In a meta study Borer *et al.* (2005) suggested that the strength of trophic cascades was independent of the ecosystem type (i.e. aquatic, terrestrial), but dependent on biological characteristics of the species such as metabolic rate and metabolic type (invertebrate, vertebrate ectotherm, endotherm), thus shedding new light on a longstanding debate.

Simultaneously, Shurin and Seabloom (2005) approached trophic cascades theoretically. To determine factors influencing the strength of trophic cascades they used the tri-trophic food-chain model presented by McCann and Yodzis (1994) which is based on the predator-prey model by Yodzis and Innes (1992) and calculated equilibrium densities for the species in the chain. Their analytical study emphasized the importance of the intermediate species body mass and system productivity for the strength of 'per biomass' trophic cascades. With their study they followed a long standing tradition in food web ecology to break down the enormous complexity of food webs (Pimm *et al.*, 1991; Polis and Strong, 1996) into "community modules" (Holt, 1997) or "network motifs" (Milo *et al.*, 2002; Stouffer and Bascompte, 2010), smaller trophic networks consisting of three to four species.

These modules and motifs are easier to study than entire food webs and are often seen as simple representations of food webs (McCann and Yodzis, 1994; Bascompte and Melián, 2005; Otto *et al.*, 2007; Stouffer and Bascompte, 2010). Using results from isolated modules, such as food chains, to draw conclusions about the behaviour of complex food webs can be problematic however, since the web context can crucially change the dynamics within the module. New, emergent patterns cannot be predicted from modules alone (Cohen *et al.*, 2009) and embedding modules in larger food webs is necessary to test for the importance of extra-modular interactions (Polis, 1994; Fox and Olsen, 2000; Brose *et al.*, 2005; Kondoh, 2008).

We therefore investigated whether the results from isolated food chains capture the behaviour of trophic cascades in complex food webs. To do so, we first followed the approach of Shurin and Seabloom (2005) and derived an analytical solution for the isolated food chain. This represents the information that can be derived from analyses of isolated food chains. Complex food webs are unfortunately not analytically solvable. Consequently, we used a numerical dynamic population model first to simulate the behaviour of isolated food chains and then to simulate the behaviour of food chains embedded in food webs. Simulation of isolated chains reproduced the results of the analytical model. Radically different results were produced, however, by simulations of isolated and embedded chains. Based on the outcome of both the isolated chain and the food web simulations we developed statistical models and compared the occurrence, sign and strength of trophic cascades in the isolated food chain and in complex food webs. In the isolated chain the top species always exerts a substantial positive *per capita* effect on the basal species, mainly through its abundance. In food webs the majority of the cascades are very weak but display wide variance and can be highly positive or negative. Their strength is explained by a combination of the body mass and abundance of the top species and the abundance of the basal species. Thus, the combination of factors influencing the strength of trophic cascades in simulated complex food webs can be surprisingly simple.

Methods

To ensure mathematical tractability the analytical solution for trophic cascades has to follow certain assumptions (Shurin and Seabloom, 2005): (i) the biomasses of the species must be in an equilibrium state ($dB/dt = 0$), (ii) the feeding interactions follow a type II functional response, and (iii) the three species food chain has to be isolated with no other species present. Also, the basal species is assumed to have a trophic level of one. These assumptions do not necessarily hold in natural communities and the bioenergetic model can easily handle deviations from them. In this study, we show results for isolated food chains (food chain simulation) that closely follow the assumptions required by the analytical solution and for chains embedded in complex webs (food web simulation) that did not follow these restrictive assumptions. This enables us to present solutions for trophic cascades that can be applied to natural food webs. All trophic cascades in this paper describe the *per capita* effect of the top on the basal species of a food chain.

Network structure

The network structure for the analytical solution and the food chain simulation was a simple three trophic food-chain: a basal species was fed on by an intermediate species which in turn was consumed by a top species. The networks for the food web simulations were generated with the niche model (Williams and Martinez, 2000). This model distributes the links (L) in the network on the basis of species richness (S) and connectance ($C = L/S^2$) and generates food webs that closely resemble natural food webs (Williams and Martinez, 2000). For each of the 2000 webs simulated the species richness and connectance were randomly and independently drawn from uniform distributions ($10 \leq S \leq 30$ and $0.1 \leq C \leq 0.2$).

Population dynamics

The population dynamics were simulated according to the consumer-resource model developed by Yodzis and Innes (1992) which was extended to multi species systems (Williams and Martinez, 2004*b*) and updated with allometric coefficients (Brown *et al.*, 2004). The differential equations of the model describe how species biomasses (B) change over time, depending on their feeding links (for details please refer to Brose *et al.* (2006*b*) and Binzer *et al.* (2011)) :

$$\dot{B}_i = r_i G_i B_i + \sum_{s=prey} x_i y_i B_i F_{is} - \sum_{j=predators} \frac{x_j y_j B_j F_{ji}}{e_{ji}} - x_i B_i \tag{3.1}$$

Species gain biomass by feeding on prey items, s, or by growth (mass specific maximum growth rate $r_i \geq 0$ for primary producers, $r_i = 0$ for all other species and population logistic growth rate, $G_i = 1 - (B_i/K_i)$, where K_i is the carrying capacity for species i). Species lose biomass to predation by predators, j, or due to metabolism (mass-specific metabolic rate, $x_i = 0$ for primary producers, $x_i \geq 0$ for all other species, all assumed to be invertebrates, normalization constant set to 0.314 (details in (Brose *et al.*, 2006*b*))). Changes in biomass due to feeding interactions are determined by the mass-specific metabolic rate of the consumer, x, its maximum consumption rate relative to its metabolic rate, $y = 12$, its biomass B, the assimilation efficiency ($e = 0.85$ for carnivore species and $e = 0.45$ for herbivore species), and the functional response F, describing the resource density dependent feeding of a consumer on its prey, while accounting for its other prey species. F is influenced by the Hill exponent, h, which describes the shape of the function, and the half saturation density, $R_0 = 0.5$, the preys population density at which half the predators maximum consumption is reached. The analytical solution and the food chain simulations are restricted to a type II functional response (Hill exponent = 1). In the food web simulations, however, for each web the Hill exponent and a term, c, defining the degree of interference between predators was randomly and independently drawn from normal distributions ($1 \leq h \leq 2$, mean: 1.5, standard deviation: 0.25, $0 \leq c \leq 1$, mean: 0.5, standard deviation: 0.25). These values include those required by the functional response in the analytical solution while also allowing for more natural, varied feeding interactions. In the model, the body mass of the species determines the biological rates of the species. The metabolic rate, the growth term and the maximum consumption scale with the species body mass according to a negative quarter power law (Enquist *et al.*, 1999; Brown *et al.*, 2004). The body mass ratios of the species in the analytical solution and the food chain simulations varied systematically between 10^0 and 10^6. For the food web simulations the body-mass of a species increases with its trophic level with a mean of 10 and a standard deviation of 10 (Riede *et al.*, 2011).

The indirect per capita effect of the top species on the biomass of the basal species, $pcIS_b$, is the base 10 logarithm of the ratio B_3/B_2 divided by the abundance of the top species, A_t. Here, B_3 is the biomass of the basal species when the top species is present and B_2 its biomass when the top species is absent (Borer *et al.*, 2005).

$$pcIS_b = \frac{\log 10(B_3/B_2)}{A_t} \tag{3.2}$$

When the presence of the top species increases the biomass of the basal species $pcIS_b$ is positive and it is negative when the presence of the top species reduces the biomass of the basal species.

Numerical simulations

Each simulation was run once with all species present and once after removing the top species of each food chain as identified after the initial simulation (food chain: one additional run if all three species were alive, food web: one additional run for each embedded food chain, defined as a living species fed on by another living species which is consumed by yet another living species). It is important to note that in the food chain simulations the basal species of the chain always had a trophic level of one, whereas in the food webs the basal species could have a higher trophic level. Whilst this does not change the effect of embedding the food chain into a food web (Binzer, 2009), allowing for more varied trophic positions enables predictions for more general trophic cascades. A species was considered extinct if its biomass fell below 10^{-30} at any time during the simulation. At the end of each simulation run (food chain: 200,000 time steps, food web: 5000 time steps) the biomasses of the basal (B), intermediate (I) and top species (T) of the modules were averaged over the last half (food chain) or three quarters (food web) of the time series. This yielded the time averaged biomasses of the species for the full three species module (B_3, I_3 and T_3) and when the top species was absent (B_2, I_2). The time averaged abundances, A, of all three species were calculated accordingly. Species biomasses were assumed to be in equilibrium if their time averaged biomass equaled the final biomass. To match the assumptions of the analytical solution, all food chain simulations with non-equilibrium dynamics were discarded. Discarding the first part of the time series ensured that possible transient dynamics were not included in the analyses. Averaging the biomasses and abundances safeguarded against analyzing extreme biomasses and abundances that are atypical of the time series.

In the food chain simulations the averaged biomasses, averaged abundances and the masses of the species were recorded. In the food web simulations other parameters were additionally recorded characterizing the species in the module (such as their trophic level, body mass and Hill exponent), their immediate surroundings in the web (such as their number of predators and prey) and the food web in general (such as the number of species and the connectance). This yielded 71 recorded parameters (see supplement) that we tested for their ability to explain the sign and the strength of trophic cascades in food webs.

Statistics

For the numerical simulations “classification and regression tree“ (CART, R-package “tree“ (Ripley, 2010)) analysis was used to model the sign of $pcIS_b$, the magnitude of its absolute value and to select the explanatory variables for linear regression models (R-package ”lm” (R Development Core Team, 2009)). The complex food web data set was randomly split into two groups of 1000 webs each. The statistical models explaining the sign and strength of trophic cascades in the simulated food webs were developed on one group of the food webs (training data) and with fixed parameters tested on the other half (test data).

Results

Analytical solution

Setting the dynamic equations of the species in the food chain to zero and solving them for the biomass of the basal species yields the following equations for the biomass of the basal species in the two-species (B_2) and the three-species chain (B_3):

$$B_2 = \frac{R_0}{(y-1)} \tag{3.3}$$

$$B_3 = \frac{E}{(2ey-2e)} \tag{3.4}$$

with

$$\begin{aligned} E = &\sqrt{(-4R_0eKx_i + e^2K^2 + 2R_0e^2K + R_0^2e^2)y^2 + e^2K^2 + 2R_0e^2K + R_0^2e^2} \\ &\overline{+(4R_0eKx_i - 2e^2K^2 - 4R_0e^2K - 2R_0^2e^2)y} + (eK - R_0e)y - eK + R_0e, \end{aligned} \tag{3.5}$$

where x_i is the mass-specific metabolic rate of the intermediate species:

$$x_i = 0.314(M_i)^{-0.25}, \tag{3.6}$$

and e the assimilation efficiency of the intermediate species ($e = 0.45$).

Inserted into the equation 3.2 this yields the strength of trophic cascades in the isolated food chain.

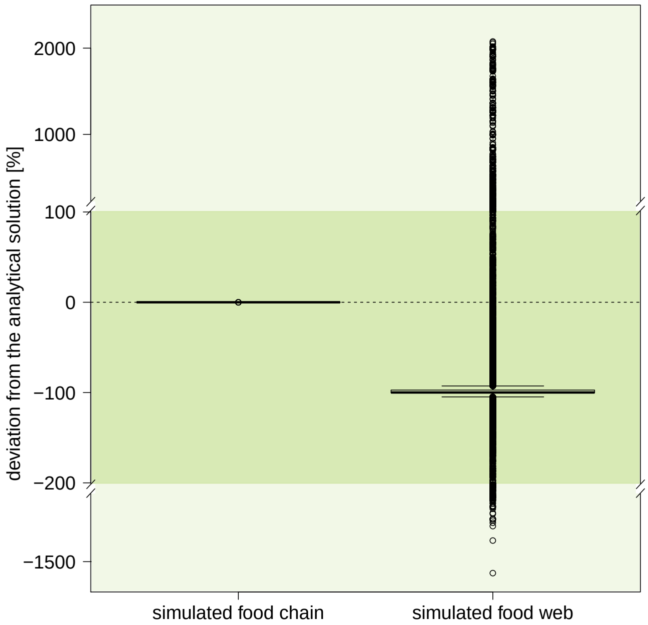

Figure 3.1 – Deviation of the numerical simulations from the analytical solution in percent. The horizontal dashed line marks the prediction of the analytical solution. The food chain simulations (left side) are congruent with the analytical solution's assumptions, the food web simulations (right side) allow for more flexible and natural dynamics.

The intermediate species metabolic rate, x_i and therefore its body mass, M_i, influences the biomass of the basal species when the functional response parameters and the carrying capacity of the system remain constant (see eq. 3.6). This is perfectly in line with Shurin and Seabloom (2005). The *per capita* effect of the top species is calculated by dividing this 'per biomass' interaction strength by the abundance of the top species. Consequently, the abundance of the top species influences the effect on the biomass of the basal species species strongly. It is a surprise that other biological parameters of the basal, intermediate and, especially so, of the top species play no role. In the analytical model, the presence of the top species always exerts a positive influence on basal species biomass.

Numerical simulations

In the food chain simulations the strength of the trophic cascade coincided perfectly with that of the analytical solution. The strength of trophic cascades in embedded food chains, in contrast, deviated substantially with a mean deviance of -85% (figure 3.1). The analytical solution generally overestimated the strength of trophic cascades in the food web simulation and the majority of cascades were weak. However, cascades in food webs were highly variable and could deviate in both directions, positively and negatively, up to 20-fold from

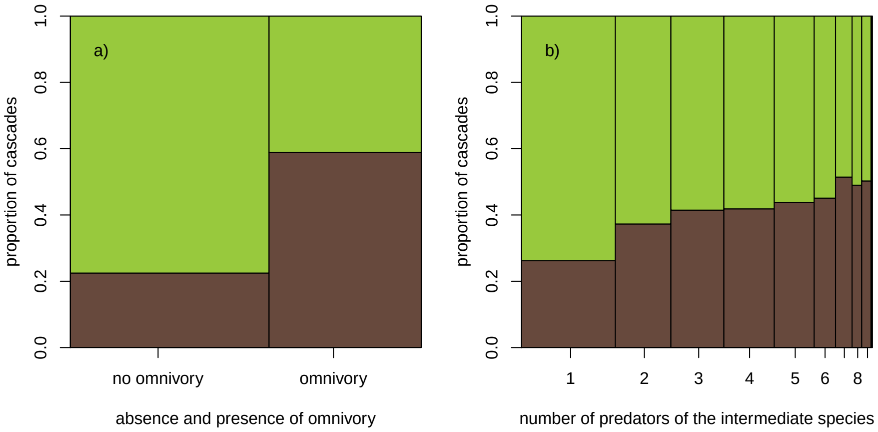

Figure 3.2 – The parameters influencing the sign of trophic cascades. The proportion of positive and negative trophic cascades in each category (y-axis, positive cascades in green, negative cascades in brown) as a function of the presence and absence of omnivory in the module (panel a) and the number of species preying on the module's intermediate species (panel b). The widths of the bins indicate the proportion of data points in the test data that belong to that category.

the analytical solution (figure 3.1).

Of particular interest is that there was an exclusively positive effect of the top species on the biomass of a species two feeding links lower in the isolated food chain. It could be positive (in 61% of the cases) and negative (in 39% of the cases), however, for embedded chains (figure 3.1). CART analyses revealed that the presence of an omnivorous link (a feeding interaction linking the top and basal species of the food chain directly) and the number of predators of the intermediate species contributed to the occurrence of negative cascades (figure 3.2). The cascade was more likely to be negative when the top species fed directly on the basal species (figure 3.2a) and when the intermediate species had many other predators (figure 3.2b).

In the simulated isolated food chains the abundance of the top and the body mass of the intermediate species explained the strength of the trophic cascades. This was entirely consistent with the analytical solution. However, the analytical solution did not predict the strength of trophic cascades occurring in the simulated food webs (figure 3.3a). In that case, the strength of the cascades was explained by a linear model using a combination of only three of the 71 parameters tested. These were the body mass (m_t) and abundance (A_t) of the top species and the abundance of the basal species, A_b:

$$log10(|pcIS_b|) = -1.29 + 0.39log10(m_t) - 0.31log10(A_t) - 0.21log10(A_b) \tag{3.7}$$

This statistical model explained 72% of the variance in the strength of the cascade in the

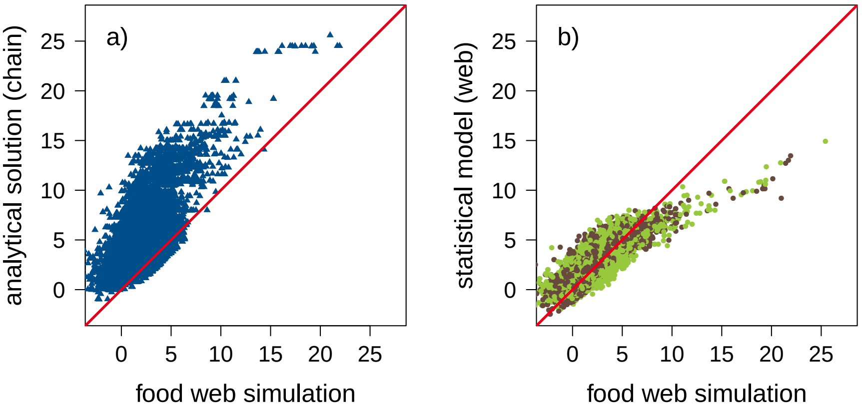

Figure 3.3 – The per capita strength of the trophic cascades, $log10(|pcIS_b|)$, observed in the simulated food webs (test data, x-axes) against a) the predictions of the analytical solution (equations 3.3 to 3.6) and b) the predictions of the statistical model developed on the simulated food webs of the training data (equation 3.7, green dots for positive cascades, brown dots for negative cascades) on the y-axes. For points lying on the red diagonals the cascade strengths in the test data match the respective prediction.

training data and 68% in the test data (figure 3.3b). This model is very simple compared to the complexity of food webs. Notice that it explained the strength of the cascades in the simulated food webs regardless of their sign - the clouds of the positive (green) and negative cascades (brown) overlap (figure 3.3b).

The body mass of the top species has a positive effect on cascade strength. The greater its body mass, the stronger its effect on the basal species (figure 3.4a). The opposite is true for top species abundance. The more individuals of the top species there are in the system, the weaker their *per capita* influence on basal species biomass (figure 3.4b). Similarly, the abundance of the basal species has a negative effect. The effect of the top species is stronger the fewer individuals of the basal species there are in the web (figure 3.4c).

Discussion

Trophic cascades in food chains embedded in food webs are fundamentally different than in isolated food chains. The web structure, which offers many direct and indirect pathways along which effects can travel, drastically changes the dynamics within the chains. It is clear therefore that the complex structure of food webs must be considered in order to understand trophic cascades. In complex species communities the cascading effect of one species on the prey of its prey can be positive and negative. The strength of both these positive and negative trophic cascades can be predicted by a simple model consisting of three easily measured population traits. These are the body mass and abundance of the embedded food chains top species and the basal species abundance. The *per capita* strength

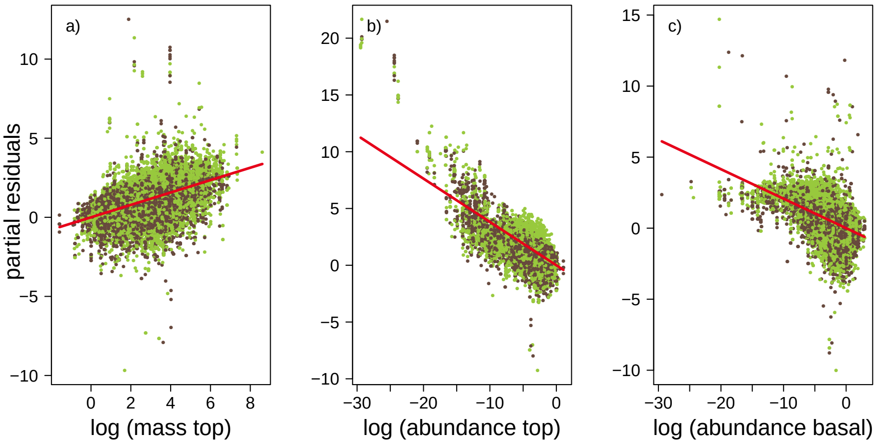

Figure 3.4 – The three parameters constituting the model predicting the strength of the trophic cascade, $log10(|pcIS_b|)$, in food webs, with regression lines in red. The mass (panel a) and abundance (panel b) of the modules' top species influence the cascades strength as well as the abundance of the modules' basal species (panel c). Positive cascades are plotted in green, negative cascades in brown.

of the trophic cascade in isolated food chains is explained by the abundance of the top species and the body mass of the intermediate species which has no influence in the food web at all.

Match of analytical solution and simulated food chains:

The perfect match of the analytical solution and that of the numerical simulation of the isolated food chain is no coincidence but a result of the basic assumptions and their restrictions. In the food chain there are just two direct feeding links and the only way the top species can influence the biomass of the basal species is via its feeding link to the intermediate species. So this simple system must produce a trophic cascade. Whenever a top species is present, its feeding will have a negative impact on the intermediate species. This then releases the basal species from feeding pressure and positively affects its biomass. These results are inevitable in analyses based on the assumptions of the isolated food chain.

Differences and mismatch between simulated food chains and food webs:

There are substantially different results for simulations of food chains embedded in webs. Whilst this difference could be an artifact of the model, we think it a result of the more natural dynamics that the deviations from the assumptions allow. In the simulated food webs, apart from embedding the food chains into a food web context, we also allowed variation in the functional responses and non-equilibrium dynamics. Just like our simulated webs, natural food webs are reticulate and consist of many species (Pimm *et al.*, 1991; Polis and Strong, 1996), display non-equilibrium dynamics (Fox and Olsen, 2000) and a wide variety of functional responses (Sarnelle and Wilson, 2008; Kratina *et al.*, 2009; Vucic-Pestic *et al.*, 2010; Rall *et al.*, 2011). All of these deviations are accounted for in the food web simulations and can change species interactions. In multi-species food webs, for example, the effect of the top species can travel many different pathways. Depending on whether their net effect is neutral, positive or negative, they attenuate, magnify or reverse the effect of the top species.

The mismatch in the simulations between the food chains and food webs is largely due to food web structure. Simulated food webs with strict type II functional responses deviate just as much from the analytical solution as the simulated food webs with varying functional responses (see appendix, figure 3.5). Previous simulations in which the assumptions of the analytical solution were successively discarded also showed that the biggest mismatch between the analytical solution and the numerical simulations results from embedding the chain in a web and not from changing the functional response from that in the isolated food chain (Binzer, 2009).

Additional complexities of natural ecosystems include habitat structure (Kalinkat *et al.*, 2012), non-trophic interactions (Kéfi *et al.*, 2012) and phenological mismatch (Otto *et al.*, 2008) all of which enormously alter the functional responses of interactions. Changes in behavior, for example, have been shown to weaken or strengthen species interactions and therefore trophic cascades (Beckerman *et al.*, 1997; Schmitz, 1998; Utsumi *et al.*, 2010). While our model can easily be extended to include such natural complexities we present the unmodified nature of cascades as triggered by feeding interactions alone. This can be a baseline for future studies on trophic cascades in specific ecosystems.

Differences of cascades in the isolated and embedded module:
The strength of cascades declines strongly with increasing network complexity. Many strong cascades are found in simple networks such as freshwater and marine mesocosm experiments, fewer in lake experiments and very few in marine field studies (Sommer, 2008). Likewise, in terrestrial systems, community diversity and cascade strength are negatively correlated (Schmitz *et al.*, 2000; Halaj and Wise, 2001). In nature, food web complexity, the tight network of species interactions, limits the strength and occurrence of cascades (Polis, 1994; Strong, 1992; Fox and Olsen, 2000; Halaj and Wise, 2001). Our food chain simulations represent the low end of this complexity gradient and our food web simulations the upper end. In small scale studies, as illustrated by our food chain simulations, the effect of the top species is not obscured by any additional interactions. Its effect thus reaches the basal species undiluted. In food webs, as illustrated by our web simulations, the effect of the top species dissipates in the network and the majority of cascades are therefore very weak and undetectable in an experimental setting. Complexity is thus an important buffer of natural communities against disturbance.

Even though the mean strength of the cascade is weak in the simulated food webs, the variance in strength increases drastically between the food chain and food web simulations. This reflects a growing variance in the net effect within the embedded food chain. This can render cascades both very strongly positive or negative. This high variability of trophic cascades in complex systems could imply that they are less predictable. However, we show that the strength of trophic cascades in food webs can be explained by a relatively simple model. The complexity of the result does not increase to the same degree as the complexity of the system (Berlow *et al.*, 2009).

Factors determining the sign of the cascades:
Trophic cascades are positive when the net effect of the top species on the basal species is positive. They are negative when the sum of its direct and indirect effects is negative. Trophic cascades reported in the literature are overwhelmingly positive. However, negative trophic cascades have been found (Schmitz *et al.*, 2004; Bruno and O'Connor, 2005; Finke and Denno, 2005; Schneider *et al.*, 2012) and our results highlight the high probability of their occurrence.

Even if none of the 71 tested parameters, alone or in any combination, explain more than 15% of the sign of the cascade, there are two factors that favor the prevalence of negative effects in food webs. These are the presence of an omnivorous feeding link and large numbers of predators of the intermediate species. Omnivory establishes a direct negative effect of the top species on the basal species. This increases the likelihood of negative cascades because it can tip the net effect of the top species to being negative. Omnivory is prevalent in food webs (Polis, 1994) and is known to damp or prevent trophic cascades (Persson, 1999; Pace *et al.*, 1999; Bascompte *et al.*, 2005). Here, we propose that omnivory can also cause negative cascades, a negative indirect effect of the top species on the basal species. This has been shown in terrestrial microcosm experiments (Schneider *et al.*, 2012; Schneider and Brose, 2013) but we expect negative cascades not to be restricted to terrestrial systems.

Empirical studies indicate that increasing predator diversity, at the level of the top species, can have negative effects on plant biomass (Bruno and O'Connor, 2005; Finke and Denno, 2004). Finke and Denno (2004) argue that increased intraguild predation amongst predators reduces their impact on the herbivores and basal resources (Finke and Denno, 2004, 2005). Our simulations, however, suggest that the likelihood of negative trophic cascades increases with the number of predators of the intermediate species. We did not account for the trophic level of these predators, so increased intraguild predation amongst omnivorous intermediate species could account for this effect. Additionally, we think that with an increasing number of predators, the effect of each predator on the intermediate species is diminished. The top species of the embedded food chain is less and less able to control the biomass of the intermediate species. Instead of a positive cascade caused by the top species we then expect an almost neutral effect on the basal species biomass. Consequently, other, negative effects can dominate and turn the cascade negative. This increases the probability of negative trophic cascades.

Factors determining the strength of the cascades:
Interestingly, the strength of both the positive and the negative cascades are explained by the same set of parameters, the body mass and abundance of the top species as well as the abundance of the basal species. All of them are population parameters of the embedded motif and not the network surrounding the module. This implies that the network structure changes the dynamics within the module and is important for developing a model explaining the strength of cascades in food webs. However, similar to what was shown in other studies (Brose *et al.*, 2005; Berlow *et al.*, 2009), an explicit knowledge of the network structure is not needed to predict the effect of the top species on the basal species. Strong *per capita* cascades occur when few large bodied individuals of the top species co-occur with a basal species of low abundance. These traits are relatively easy to measure in any given system, which makes the model interesting for conservationists wanting to estimate the effect a species might have on other species or the community.

Body size determines species metabolism, growth and feeding rates (Peters, 1983; Brown *et al.*, 2004; Ehnes *et al.*, 2011). The larger a species the stronger its interaction strength, its impact on the basal species and therefore the trophic cascades it triggers. In contrast to the results of the isolated food chain in food webs, it is the body mass of the top species and not that of the intermediate species that affects the strength of trophic cascades. The importance of large top predators for inducing cascading effects in natural systems has recently gained much attention (Wood *et al.*, 2010; Estes *et al.*, 2011; Ripple and Beschta, 2012). After the re-introduction of wolves into the Yellowstone National Park evidence for top down cascading effects were detected again (Ripple and Beschta, 2012) and Estes *et al.* show impressively how large apex predators change their environment through trophic cascades (Estes *et al.*, 2011). Our results for the embedded food chain thus reconcile lingering disjunctions between food-chain theory and empirical studies of trophic cascades.

Predators with higher abundances can control their prey more effectively and thus have a greater per population impact on the prey of their prey. With increasing population abundance the single effect of each top species individual contributes less to the overall effect on the basal species. The *per capita* effect of the top species therefore decreases. Similarly, a basal species with only a few individuals is more easily affected by direct and indirect effects than a basal species with a higher abundance. Removing an individual from a low abundance population has a bigger effect on the population than removing an individual from a high abundance population. This could easily be examined in laboratory communities or, less easily but more realistically, in the field.

Conclusions

Our dynamic population model uses allometrically scaled biological parameters and provides a mechanistic insight into trophic cascades and their drivers. It integrates top-down and bottom-up effects and generates a basic understanding of dynamics in food webs based on biological parameters and feeding interactions. It is, however, flexible enough to incorporate additional aspects of natural ecosystems such as habitat structure, behavioral changes and other non-trophic interactions. Our simulations suggest that the strength of trophic cascades in food webs is determined by a combination of body mass and abundance of the top species and the abundance of the basal species in the constituent food chains. These parameters are relatively easy to measure in natural communities and can give conservationists a useful starting point for investigating trophic cascades in their system. In food webs the effect of the top species on the basal species is generally diluted by the multitude of direct and indirect pathways through which this effect can travel. However, under certain circumstances, the different effects can add up, resulting in strong positive or negative cascades which are not predicted by solutions based on the isolated cascade module. We have shown, using the example of trophic cascades, that predictions based on isolated food web motifs do not necessarily hold in more natural multi-species food webs. This indicates that findings derived from isolated network motifs cannot simply be transferred to entire food webs. The network structure changes the net effect of direct and indirect effects and has to be considered in developing predictive models for trophic cascades in the field.

Acknowledgement

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Appendix

Table 3.1 – Parameters screened for their influence on the sign and the strength of trophic cascades. Unless indicated differently, each parameter was either valid over the entire simulation, or saved when the top species was present. The terms "top species", "intermediate species" and "basal species" refer to the respective species position in the examined food chain. "Upper species" refers to species in the food web that are not predated on, "lower species" to species in the food web that do not feed on other species and have a trophic level of one and "middle species" to species that have prey they feed on and predators that feed on them.

no.	parameter name	parameter description
		food web parameters and parameters constant for all species in the web
1	S	number of species in the food web
2	connectance	connectance of the food web, number of links divided by the number of species squared
3	plants	number of species without prey and with a positive growth rate in the web
4	mean trophic level	mean prey averaged trophic level of all species in the web
5	c	predator interference term
6	Hill	the Hill exponent, shaping the feeding interaction
7	y	the maximum feeding rate of the species in the web
8	metabolic type	metabolic type of the species in the web – they are invertebrates
9	size ratio	mean body mass ratio between a predator and a prey in the web
10	half saturation density	prey density at which the predator reaches half its maximum consumption rate
11	carrying capacity	the maximum biomass the system can sustain
12	specialized middle species	number of species in the food web that feed solely on the lower species
13	cannibals	number of species in the web that feed on themselves
14	fraction upper	fraction of upper species in the food web
15	fraction middle	fraction of middle species in the food web
16	fraction lower	fraction of lower species in the food web
17	fraction specialized middle	fraction of middle species that solely feed on the lower species
18	fraction cannibals	fraction of species that feed on themselves
19	links upper to middle	number of links connecting upper and middle species in the food web
20	links middle to middle	number of links amongst the middle species in the food web

21	links upper to lower	number of links connecting upper and lower species in the food web
22	links middle to lower	number of links connecting the middle and lower species in the food web
23	links per species	average number of links every species in the food web has
24	links	number of links in the food web
25	SD generality	standard deviation of the number of prey species of the species in the web
26	SD vulnerability	standard deviation of the number of predatprs of the species in the web
27	mean trophic level	mean prey averaged trophic level of the species in the food web
28	SD trophic level	standard deviation of the prey averaged trophic level of the species in the food web
29	maximum trophic level	maximum prey averaged trophic level of the species in the food web
30	mean amplitude	amplitude of biomass oscillation in the food web, averaged over the second half the time series for all species in the web
31	mean biomass	biomass averaged over the second half the time series and all species in the food web
32	SD biomass	standard deviation of the mean biomass
33	mean variance	averaged variance of biomasses within the second half of the time series
34	mean coefficient of variation	averaged coefficient of variation of the of the biomasses of all species within the second half of the time series
	network vicinity	
35	vulnerability of the basal species	number of predators of the modules basal species with the top species present
36	generality of the basal species	number of prey of the modules basal species
37	vulnerability of the predators of the basal species	average number of predators of the predators of the modules basal species
38	generality of the predators of the basal species	average number of prey species of the predators of the modules basal species

39	vulnerability of the prey species of the basal species	average number of predators of the prey species of the modules basal species
40	generality of the prey species of the basal species	average number of prey species of the prey species of the modules basal species
41	vulnerability of the intermediate species	number of predators of the modules intermediate species with the top species present
42	generality of the intermediate species	number of prey of the modules intermediate species
43	vulnerability of the predators of the intermediate species	average number of predators of the predators of the modules intermediate species
44	generality of the predators of the intermediate species	average number of prey species of the predators of the modules intermediate species
45	vulnerability of the prey species of the intermediate species	average number of predators of the prey species of the modules intermediate species
46	generality of the prey species of the intermediate species	average number of prey species of the prey species of the modules intermediate species
47	vulnerability of the basal species	number of predators of the modules basal species with the top species present
48	generality of the basal species	number of prey of the modules basal species
49	vulnerability of the predators of the top species	average number of predators of the predators of the modules top species
50	generality of the predators of the top species	average number of prey species of the predators of the modules top species
51	vulnerability of the prey species of the top species	average number of predators of the prey species of the modules top species

52	generality of the prey species of the top species	average number of prey species of the prey species of the modules top species
	population parameters	
53	omnivory	One if the top species of the module feeds directly on the basal species
54	trophic level basal species	prey averaged trophic level of the modules basal species
55	trophic level intermediate species	prey averaged trophic level of the modules intermediate species
56	trophic level top species	prey averaged trophic level of the modules top species
57	identity top	identification number of the top species
58	identity intermediate	identification number of the intermediate species
59	identity basal	identification number of the basal species
60	log_{10} basal mass	decadic logarithm of the basal species body mass
61	log_{10} intermediate mass	decadic logarithm of the intermediate species body mass
62	log_{10} top species	decadic logarithm of the top species body mass
63	log_{10} basal biomass	decadic logarithm of the basal species biomass
64	log_{10} intermediate biomass	decadic logarithm of the intermediate species biomass
65	log_{10} top species biomass	decadic logarithm of the top species biomass
66	log_{10} basal abundance	decadic logarithm of the basal species abundance
67	log_{10} intermediate abundance	decadic logarithm of the intermediate species abundance
68	log_{10} top abundance	decadic logarithm of the top species abundance
69	log_{10} massratio top to intermediate	decadic logarithm of the ratio of top species body mass to intermediate species body mass
70	log_{10} massratio top to basal	decadic logarithm of the ratio of the top species body mass to basal species body mass
71	log_{10} massratio intermediate to basal	decadic logarithm of the ratio of the intermediate species body mass to basal species body mass

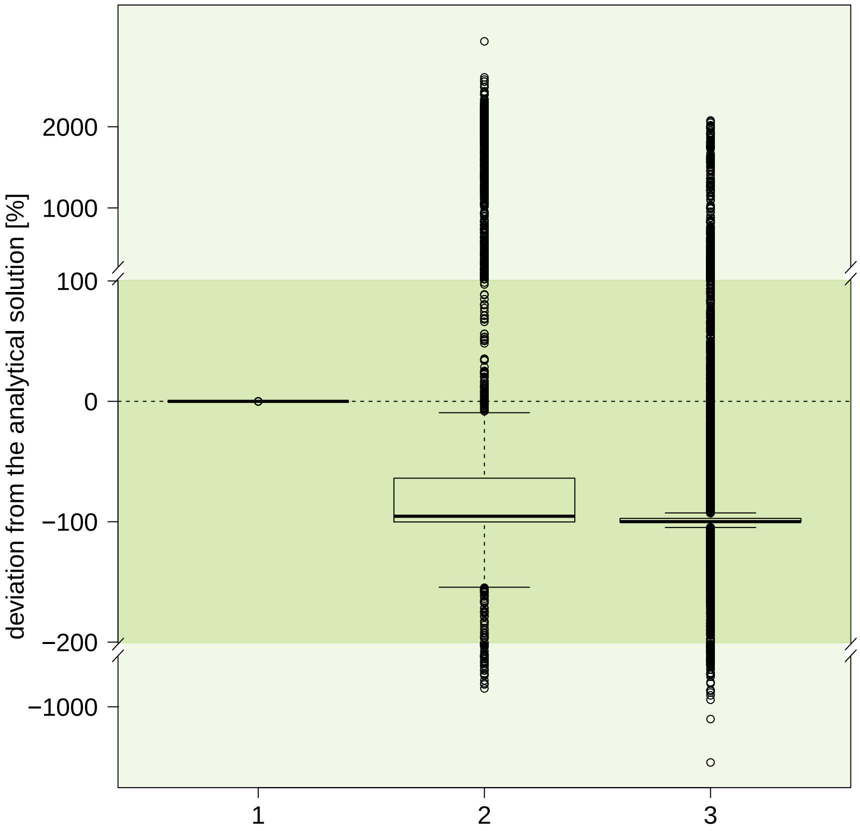

Figure 3.5 – The deviation from the analytical solution (dashed line) of 1) the simulated food chains with strict type II functional responses, 2) simulated food webs with a strict type II functional response and 3) the simulated food webs with varying functional responses.

Chapter 4.

The dynamics of food chains under climate change and nutrient enrichment

Amrei Binzer, Christian Guill, Ulrich Brose, Björn C. Rall

Abstract

Warming has profound effects on biological rates such as metabolism, growth, feeding and death of organisms, eventually affecting their ability to survive. Using a nonlinear bioenergetic population-dynamic model that accounts for temperature and body-mass dependencies of biological rates, we analysed the individual and interactive effects of increasing temperature and nutrient enrichment on the dynamics of a three-species food chain. At low temperatures, warming counteracts the destabilizing effects of enrichment by both bottom-up (via the carrying capacity) and top-down (via biological rates) mechanisms. Together with increasing consumer body masses, warming increases the system tolerance to fertilization. Simultaneously, warming increases the risk of starvation for large species in low-fertility systems. This effect can be counteracted by increased fertilization. In combination, therefore, two main drivers of global change and biodiversity loss can have positive and negative effects on food chain stability. Our model incorporates the most recent empirical data and may thus be used as the basis for more complex forecasting models incorporating food-web structure.

Keywords | global warming, metabolism, paradox of enrichment, fertilization, biodiversity loss, temperature

Introduction

Current changes in our planet's ecosystems have the potential to cause species extinctions (Barnosky *et al.*, 2011). The changes in nutrient availability (enrichment) and temperature (climate warming) were identified by the Millennium Ecosystem Assessment as two major direct drivers of biodiversity loss (Nelson, 2005). They predict the impact of both these drivers to increase very rapidly in all biomes (Millennium Ecosystem Assessment (2005) p.9). To predict accurately the community effects of enrichment and warming, it is important to understand their interactive impact on biological rates. This helps in developing community protection measures and in conserving important ecosystem functions.

Both enrichment and warming have wide-ranging implications for food-web and ecosystem structure, many of which are mediated by changes in population dynamics (Tylianakis, 2008; Vasseur and McCann, 2005; Rosenzweig, 1971; Yvon-Durocher *et al.*, 2010; Petchey *et al.*, 1999; Parmesan, 2006; Brose, 2008; Rall *et al.*, 2008). Rosenzweig (1971) analytically investigated the effect of increased energy input on the dynamics of a predator-prey system and coined the term "paradox of enrichment": enrichment drives a predator-prey system from stable equilibria into oscillations and finally into extinction when population minima hit extinction boundaries (Rosenzweig, 1971). This has recently been generalized as the principle of energy flux: any process increasing energy fluxes relative to consumer loss rate will destabilize systems by shifting biomass up the trophic levels (Rip and McCann, 2011). This moves the isoclines of the species towards unstable equilibria. Interestingly, when consumer mass systematically increases with trophic levels (Riede *et al.*, 2011), the destabilizing effects of enrichment are ameliorated (Rall *et al.*, 2008).

Warming has profound effects on biological rates such as organism metabolism (Hansen *et al.*, 1997; Gillooly *et al.*, 2001; Ehnes *et al.*, 2011), growth (Savage *et al.*, 2004), feeding (Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2011) and death (Brown *et al.*, 2004). However, the interplay of these physiological effects at the population level is not yet entirely clear, and there are several possibilities. Warming might simply accelerate population dynamics. In a seminal study of population dynamics, Vasseur and McCann (2005) found that increasing temperature destabilizes systems and increases the amplitudes of oscillations. These findings are based on assumptions such as temperature invariance of the system carrying capacity (the maximum biomass the system can support) and the consumer's half saturation density. While the former is certainly not supported by empirical data (Meehan, 2006), the latter characterizes the consumer's efficiency at attacking resources and more recent studies showed that it is likely to change with temperature (Vucic-Pestic *et al.*, 2011; Englund *et al.*, 2011; Lang *et al.*, 2012). Additionally, Vasseur and McCann (2005) assumed that in most natural communities the species ingestion increases more with warming than does their metabolism. However, feeding interactions among terrestrial and marine invertebrates indicate the opposite (Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2011; Twomey *et al.*, 2012). These studies found that warming increases species metabolism more strongly than ingestion rates. The decreasing energetic efficiencies (the ratio of ingestion rate to metabolism) lead to increasing energetic restrictions for predators and decreasing predator biomasses. This stabilizes the system dynamics and reduces biomass oscillations. These studies emphasize the possibility of predator starvation at high temperatures when metabolism exceeds ingestion rates (Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2011). However, dynamic model analyses of these empirical patterns are still lacking.

Here, we fill this void by developing a nonlinear bioenergetic population-dynamic model that includes empirical body-mass and temperature dependencies for the major biological rates affecting population dynamics such as carrying capacity (Meehan, 2006), production (Savage *et al.*, 2004), metabolism (Ehnes *et al.*, 2011), and functional response parameters (Rall *et al.*, 2012). With this model, we numerically investigated the solitary and interactive effects of two major drivers of global change, enrichment and warming, on the population dynamics of a three-species food chain. We were particularly interested in the following questions: i) What are the individual effects of enrichment and warming on the dynamics of the food chain? ii) What are the combined effects of enrichment and warming on these dynamics? and iii) Does the community size structure with systematically increasing body mass ratios influence these effects?

Methods

The bioenergetic dynamic model used is based on Yodzis and Innes' consumer-resource model (Yodzis and Innes, 1992) and is updated with allometric coefficients and temperature dependencies of the biological rates. In the three-species food chain, the basal species (B) is fed on by the intermediate species (I) which in turn is consumed by the top species (T). The biomass changes of the species ($\dot{B_B}, \dot{B_I}$ and $\dot{B_T}$, respectively) are described by the following differential equations:

$$\dot{B_B} = r_B G_B B_B - B_I f_{IB} \tag{4.1}$$

$$\dot{B_I} = e_{IB}(B_I f_{IB}) - B_T f_{TI} - x_I B_I \tag{4.2}$$

$$\dot{B_T} = e_{TI}(B_T f_{TI}) - x_T B_T \tag{4.3}$$

Here, r_B is the basal species' mass and temperature-specific maximum growth rate, G_B, the basal species' logistic growth term, B_B is its population biomass density. The functional responses f_{IB} and f_{TI} describe the feeding dynamics of the feeding links in the food chain. The assimilation efficiencies (efficiency of conversion of prey biomass into predator biomass), e_{IB}, and e_{TI}, are both set to 0.85 because both species are carnivores

(Yodzis and Innes, 1992). The metabolism of the intermediate and top species, x_I and x_T also depend on their masses and the temperature of the system.

We used a logistic growth term where the potential growth of the population depends on its current population biomass and its body-mass and temperature-dependent carrying capacity, K_B:

$$G_B = (1 - \frac{B_B}{K_B}). \tag{4.4}$$

The functional response, f_{ji}, describes the feeding dynamics between consumer j and its prey i. It depends on the consumer's maximum consumption rate when feeding on species i, y_{ji}, which depends on the body-masses of both species j and i and the temperature, the Hill exponent, h, which determines the shape of the function and the half saturation density B_0. B_0 gives the prey population density at which half the maximum consumption of the consuming species is reached and depends on the body-masses of species j and i and the temperature of the system.

$$f_{ji} = \frac{y_i B_i^h}{B_{0_{ji}}^h + B_i^h} \tag{4.5}$$

The mass and temperature dependencies of the the maximum growth rate of the basal species r_B $[s^{-1}]$ is calculated as follows:

$$r_B = e^{I_r} m_B^{s_{rB}} e^{Ea_r \frac{T_0 - T}{kTT_0}}. \tag{4.6}$$

Here, e^{I_r} is the rate specific constant, calculated for a species' body mass of $1g$ and a temperature of $20°C$ ($= 293.15\ K$). Its value is modified by the second term, the body-mass dependency, expressed by the mass of the species m and a rate specific scaling coefficient, s. The term of the temperature dependency is an extended notation of the Arrhenius equation, where Ea is the activation energy, T_0 the normalization temperature, T the temperature of the system and k $[eVK^{-1}]$ the Boltzmann constant.

The mass and temperature dependent metabolism of the intermediate and top speciesx_i $[1/s]$ and the carrying capacity of the basal species K_B $[g/m^2]$ are calculated accordingly:

$$x_i = e^{I_x} m_i^{s_{xi}} e^{Ea_x \frac{T_0 - T}{kTT_0}} \quad \text{and} \tag{4.7}$$

$$K_B = e^{I_K} m_B^{s_{KB}} e^{Ea_K \frac{T_0 - T}{kTT_0}}. \tag{4.8}$$

Both terms of the functional response, the maximum ingestion, y_{ji}, and the half saturation density, $B_{0_{ji}}$, depend not only on the temperature of the system and the body mass of species i, but also on the body mass of its predator j:

$$y_{ji} = e^{I_y} m_j^{s_{yj}} m_i^{s_{yi}} e^{Ea_y \frac{T_0 - T}{kTT_0}} \quad \text{and} \tag{4.9}$$

$$B_{0_{ji}} = e^{I_{B_0}} m_j^{s_{B_{0j}}} m_i^{s_{B_{0i}}} e^{Ea_{B_0} \frac{T_0 - T}{kTT_0}}. \tag{4.10}$$

Analyses of extensive databases (Rall *et al.*, 2012) revealed additional dependencies of the parameters of the functional response. To understand these it is best to refer to the traditional Holling type II functional response model (Holling, 1965):

$$f_{ji} = \frac{\alpha_{ji} B_i^h}{1 + \alpha_{ji} th_{ji} B_i^h}. \tag{4.11}$$

Instead of using the maximum ingestion and half saturation density of the other notation (eqn. 4.5) this uses α_{ji}, the attack rate of the consumer when it feeds on i, and the handling time, $t_{h_{ji}}$, the time the consumer needs to process one prey item before it can start looking for another one. The attack rate and the handling time both show a hump-shaped relationship with the body-mass ratio of the consumer and its prey. The exponential equations for these dependencies follow the same principle as already introduced (see equations 4.6 to 4.10):

$$\alpha_{mji} = e^{I_{am} + s1_{ai} \ln \frac{m_j}{m_i} + s2_{ai} (\ln \frac{m_j}{m_i})^2} \quad \text{and} \tag{4.12}$$

$$th_{mji} = e^{I_{thm} + s1_{thi} \ln \frac{m_j}{m_i} + s2_{thi} (\ln \frac{m_j}{m_i})^2}. \tag{4.13}$$

Here, I_m is the intercept, and the consumer-prey mass ratio has a twofold influence on the feeding parameters: the slope $s1$ is the ratio's scaling coefficient in its simple form, whereas $s2$ is the scaling coefficient for its quadratic form.

The handling time also displays a hump shape with temperature:

$$th_{Tji} = e^{I_{thT} + s1_{thTi} T + s1_{thTi} T^2}. \tag{4.14}$$

These additional scaling relationships of the functional response parameters can be incorporated into the equations for the maximum consumption and half saturation density by using the interrelation of the parameters of the two different notations of the functional response:

$$B_0 = \frac{1}{\alpha t_h} \quad \text{and} \tag{4.15}$$

$$y = \frac{1}{t_h}. \tag{4.16}$$

Table 4.1 – The parameter values of the model's mass and temperature dependencies of the carrying capacity (K in $[gm^{-2}]$, from Meehan (2006)), growth (r in $[s^{-1}]$, from Savage *et al.* (2004)), maximum ingestion (y in $[s^{-1}]$, from Rall *et al.* (2012)), half saturation density (B_0 in $[gm^{-2}]$, from Rall *et al.* (2012)) and metabolism (x in $[s^{-1}]$, from Ehnes *et al.* (2011)). Generally, the parameters scale with the body mass of the resource species (i) of the considered species pair, only the feeding parameters scale additionally with the body mass of the consumer species (j). The conversion factor used to transform the metabolism of the species from Joule per hour to s^{-1} was taken from Peters (1983).

	K_i	r_i	y_{ji}	$B_{0_{ji}}$	x_i
intercept (I)		-15.68	-9.66	3.44	-16.54
slope resource species i (s_i)	0.28	-0.25	0.45	0.2	-0.31
slope consumer species j (s_j)			-0.47	0.33	
activation energy (Ea)	0.71	-0.84	-0.26	0.12	-0.69

Table 4.2 – The parameter values for the body-mass ratio and temperature-dependent hump shape of the functional response parameters, attack rate and handling time. The mass ratio and temperature dependencies of the attack rate (in m^2s^{-1}, mass dependency a_m) and handling time (in s, mass dependency th_m, temperature dependency th_T).

	a_m	th_m	th_T
intercept (I)	-1.81	1.92	0.5
slope term 1 ($s1$)	0.39	-0.48	-0.055
slope term 2 ($s2$)	-0.017	0.0256	0.0013

This yields the following equations to express the body-mass and temperature scaling of the functional response parameters:

$$y_{ji} = e^{I_y} m_j^{s_{yj}} m_i^{s_{yi}} e^{Ea_y \frac{T_0 - T}{kTT_0}} \frac{1}{th_{mji}} \frac{1}{th_{Tji}} \tag{4.17}$$

$$B_{0_{ji}} = e^{I_{B_0}} m_j^{B_{0yj}} m_i^{B_{0yi}} e^{Ea_{B_0} \frac{T_0 - T}{kTT_0}} \frac{1}{\alpha_{mji} th_{mji}} \frac{1}{1 th_{Tji}} \tag{4.18}$$

Inserting all equations accounting for the allometric and temperature scaling of the biological rates (equations. 4.6, 4.7, 4.8, 4.17 and 4.18) into the differential equations 4.1, 4.2 and 4.3 yields a nonlinear bioenergetic population-dynamic model of a three-species food chain.

In this study, we modelled a food chain parameterized solely for invertebrates. Whenever possible, we incorporated values extracted from extensive empirical databases. These parameters represent a wide range of different species and ecosystem types. The scaling relationships for the biological rates and their sources are summarized in tables 4.1 and 4.2. Using these relationships yields a model with five free parameters: (i) the body mass of the basal species, (ii) the body-mass structure of the species in the food chain, (iii) the temperature of the system, (iv) the Hill coefficient shaping the functional response, and (v) the intercept of the carrying capacity (basic fertilization level). We used constants for the

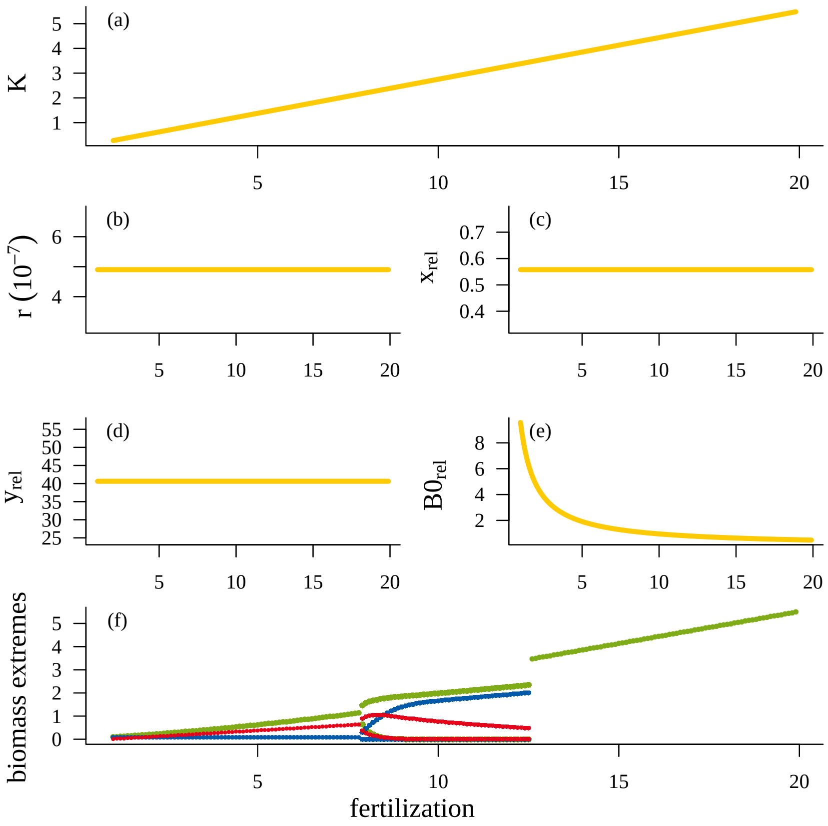

Figure 4.1 – The mass- and temperature-dependent parameters of the model and a bifurcation diagram on a fertilization gradient. All parameter values are calculated for species with a body mass of $0.01g$ at a temperature of 20° Celsius. Shown are a) the carrying capacity of the basal species (K $[gm^{-2}]$), b) the growth rate of the basal species (r,$[s^{-1}]$), c) the metabolism of a consumer relative to the basal species' growth rate ($x_{rel} = xr^{-1}$, dimensionless), d) the maximum consumption of the species relative to their metabolism ($y_{rel} = yx^{-1}$), e) the species' half-saturation density relative to the carrying capacity ($B0_{rel} = B_0K^{-1}$) and f) the biomass extremes of the three species (basal species: green; intermediate species: blue, top species: red, $[gm^{-2}]$) on a fertilization gradient.

basal body mass ($0.01g$) and the Hill coefficient (1, yielding type-II functional responses). A species was considered extinct and removed from the system when its biomass fell below $10^{-12}gm^{-2}$. To investigate the individual and combined effects of enrichment and warming, we systematically varied the intercept of the carrying capacity (fertilization gradient, range from 1 to 20), temperature (range from 0°C to 40°C) and the size structure of the community in three levels: (i) all species equally sized (no size structure), or consumers (intermediate or top) are (ii) 10 times larger, or (iii) 100 times larger than their resources. Every species started with a biomass density $[gm^{-2}]$ equal to half the carrying capacity of the system with that particular enrichment and temperature combination. All simulations ran for 100 000 years and we recorded species biomasses and survival.

Results

(a) Single effects of enrichment and warming:

Increasing system fertility at a constant temperature increases the carrying capacity linearly (see figure 4.1a for an example at 20°C). The growth rate, the relative metabolism of the species and its ingestion efficiency are not affected (figure 4.1b-d). However, there is an inverse proportional decrease in the half saturation density relative to the carrying capacity (figure 4.1e). This implies that fertilization increases the efficiency of consumers in attacking resources. The bifurcation diagram shows the classical pattern of the ”paradox of enrichment“. At low fertility, all species coexist in an equilibrium at low densities; the equilibrium biomasses increase as fertility increases until the biomasses start cycling (figure 4.1f). The amplitude of these cycles increases until both the top and the intermediate species are driven into extinction and only the basal species survives, growing up to its carrying capacity. Increasing the fertility thus destabilizes the system. Both increasing bottom-up supply (figure 4.1a) and increasing top-down pressure (figure 4.1e) contribute to this progressive instability of the system.

Increasing the temperature of the system at a constant fertilization level decreases the carrying capacity exponentially (see figure 4.2a for an example at a fertilization value of 3). At the same time, the growth rate of the basal species increases (figure 4.2b). The metabolism of the species increases with temperature at a slower rate, resulting in a decrease in the relative metabolism (metabolism relative to basal production) of the species (figure 4.2c). The ingestion efficiency (ratio of ingestion and metabolism of a species) decreases with temperature: a species' metabolism increases more strongly with temperature than its ingestion (figure 4.2d). At the same time, the relative half saturation density of the species increases (figure 4.2e). This results in a reduced flux of energy from the base to the top of the food chain. Warming has a marked effect on species biomasses (figure 4.2e). At low temperatures, only the basal species survives, growing up to its carrying capacity. At higher temperatures the biomasses of the species oscillate with decreasing amplitudes along the temperature gradient. Finally, the system crosses over an inverse Hopf bifurcation and reaches equilibrium dynamics. A further temperature increase pushes the top species beyond the point where its ingestion cannot keep up with its metabolism and it dies as a result of to a poor ingestion efficiency. At even higher temperatures, the same happens to the intermediate species and it also dies of starvation. Warming up the system thus stabilizes population dynamics, with a pattern of a reversed enrichment gradient, but very high temperatures can lead to the extinction of species.

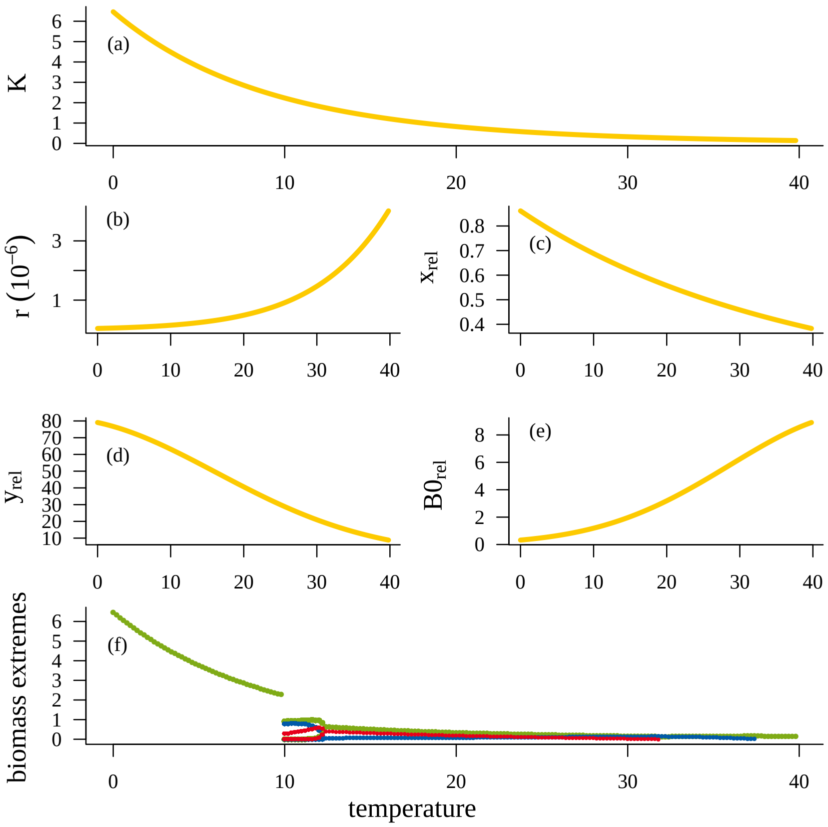

Figure 4.2 – The mass- and temperature-dependent parameters of the model and a bifurcation diagram on a temperature gradient. All parameter values are calculated for species with a body mass of $0.01g$ at an artificial fertilization level of 3. Shown are a) the carrying capacity of the basal species (K $[gm^{-2}]$), b) the growth rate of the basal species (r,$[s^{-1}]$), c) the metabolism of a consumer relative to the basal species' growth rate ($x_{rel} = xr^{-1}$, dimensionless), d) the maximum consumption of the species relative to their metabolism ($y_{rel} = yx^{-1}$), e) the species' half-saturation density relative to the carrying capacity ($B_{0_{rel}} = B_0K^{-1}$) and f) the biomass extremes of the three species (basal species: green; intermediate species: blue, top species: red, $[gm^{-2}]$) on a temperature gradient.

(b) Interactive effect of enrichment and warming:

The carrying capacity increases with fertilization and decreases with warming. This leads to the highest carrying capacities at combinations of high fertilization and low temperature and the lowest carrying capacities at combinations of low fertilization and high temperature (figure 4.3a). The number of species extant after 10 000 years across all combinations of fertilization and temperature is shown in the remaining panels of figure 4.3. In the scenario without body-mass structure, increasing fertility at low temperatures leads to species extinctions (figure 4.3b). Warming counteracts these detrimental effects of enrichment: the higher the temperature, the more the system can be fertilized before it loses species. The exceptions are high temperature, low fertility systems (upper left corner, same panel) where warming decreases the relative ingestion and increases the relative half saturation density of

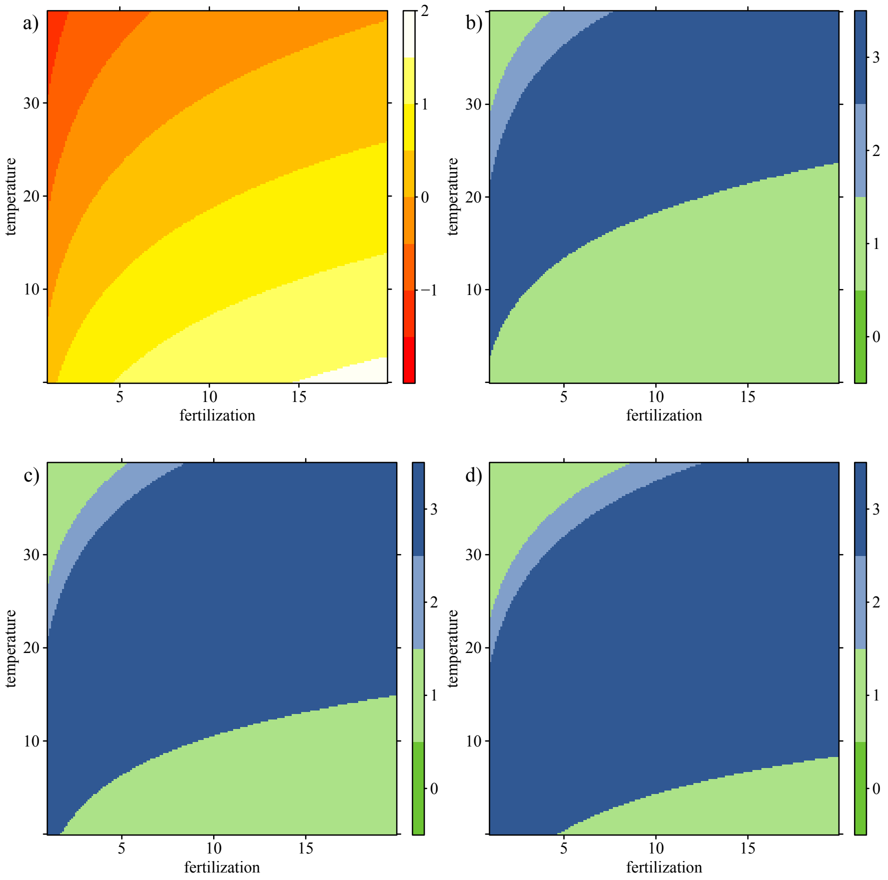

Figure 4.3 – The log_{10} of the carrying capacity of the three-species system (panel (a), colour-coded, see colour-key) and the number of species surviving after 10 000 years (panel (b): no body-mass structure, panel (c): consumer 10 times larger than its prey, panel (d): consumer 100 times larger than its prey, colour-coded, see colour-key) on a combined gradient of fertilization (x-axis) and temperature (y-axis, [°C]).

the consumer, reducing its efficiency. Consequently, first the top and then the intermediate species cannot ingest as much energy as they need to survive and become extinct. These extinctions at high temperatures are prevented by higher levels of fertilization. The lower two panels show the surviving species in a scenario with size structure (figure 4.3c, consumer 10 times larger than its prey; basal species: $0.01g$, intermediate species: $0.1g$, top species: $1g$; figure 4.3d, consumer 100 times larger than its prey; basal species: $0.01g$, intermediate species: $1g$, top species: $100g$). A three-species food chain with a structured body-size distribution, as is likely in nature (Brose *et al.*, 2006*a*; Riede *et al.*, 2011), is generally less susceptible to the paradox of enrichment, and at low temperatures the extinctions are postponed to higher fertilization levels. The rescuing effect of warming that prevents extinctions caused by unstable oscillations is more pronounced in size-structured food chains, but the top and intermediate species are more vulnerable to starvation and in, the

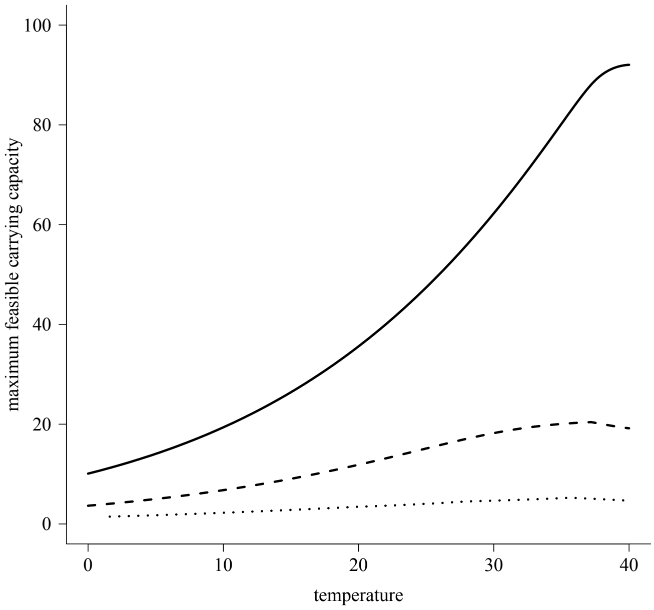

Figure 4.4 – The maximum feasible carrying capacity able to sustain all three species in the system (y-axis), depending on the temperature (x-axis, [°C]) for the approach without body-mass structure (dotted line), with the respective consumer 10 times larger than its prey (dashed line) and with the respective consumer 100 times larger (solid line).

low fertility region, extinctions occur at lower temperatures. At high temperatures, it takes more fertilization to rescue the consumers from starvation due to lower ingestion efficiencies. Warming thus counteracts the paradox of enrichment at low temperatures but increases the starvation risk of species with higher trophic levels in high temperature, low fertility systems. At high temperatures, increasing fertility prevents consumer extinctions. The stabilizing and destabilizing effects of warming are more pronounced the larger consumers are.

Increasing enrichment increases the carrying capacity and destabilizes the biomass dynamics of the species. Extinctions occur when the carrying capacity exceeds a certain threshold. Warming, in contrast, reduces the carrying capacity and stabilizes species biomass dynamics. No further extinctions occur when the carrying capacity falls below a certain threshold. If both enrichment and warming would act entirely through the carrying capacity (i.e. via bottom-up effects) these thresholds would be the same across all temperature and fertilization combinations. A carrying capacity value above this threshold would lead to extinctions, whereas none would occur at lower carrying capacities. We refer to this threshold as the maximum feasible carrying capacity: it is the maximum carrying capacity the system can be subjected to without losing species. However, instead of being constant, the maximum feasible carrying capacity follows a nonlinear curve with temperature, with a maximum at approximately 38°C (figure 4.4, all curves). This indicates a "top-down" component in the impact temperature has on the dynamics of the system.

Additionally, applying a body-mass structure to the food-chain increases the maximum feasible carrying capacity (no structure: 1.47-5.24, consumers ten times larger: 3.65-20.42, consumers 100 times larger: 10.09-92.04). Warming operates via both bottom-up and top-down effects. This increases the maximum carrying capacity that the system can tolerate without losing species. Again, the effect of temperature is more pronounced in size-structured food chains.

Discussion

Using a nonlinear bioenergetic population-dynamic model for a three-species food chain parameterized with the latest body-mass and temperature dependencies for biological rates, we investigated the individual and combined effects of two main drivers of biodiversity loss, nutrient enrichment and warming, in food chains with different body size structures. Consistent with expectations (Rosenzweig, 1971; Fussmann *et al.*, 2000), enrichment destabilizes the system and ultimately leads to extinctions. Warming stabilizes the system by reducing the carrying capacity and the ingestion efficiency and increasing the relative half saturation density of the species. When the ratio between maximum ingestion and metabolism of a species falls below a critical threshold, it becomes extinct as a result of starvation. Thus, high temperature surprisingly counteracts the destabilizing effects of enrichment. High temperatures, however, also increase the risk of consumers starving in oligotrophic and low fertility systems. Higher levels of fertilization, in turn, counteract these detrimental effects of warming. Larger consumer body masses enhance the stabilizing as well as the destabilizing effect of warming and postpone the effects of fertilization. Additionally, warming increases the maximum carrying capacity at which the system retains all its species, and again, increasing consumer body masses enhance this effect drastically. This implies novel interactions between two drivers of global change: nutrient enrichment and warming. Moreover, we found striking effects of the community size structure amplifying the impacts of warming.

(a) Single effects of enrichment and warming:

The carrying capacity of the three-species food chain increases with enrichment. This decreases the ratio of half saturation density to carrying capacity and consequently increases the energy flux from the basal to the top species (Yodzis and Innes, 1992; Vasseur and McCann, 2005). This direct conversion of bottom-up supply into top-down pressure destabilizes the system along the fertilization gradient and results in the biomass patterns of the “paradox of enrichment” (Rosenzweig, 1971). Consistent with prior studies (Rall *et al.*, 2008), simulations with differently sized consumers and prey display a reduced severity of this effect (figure 4.3b-d). Inedible, invulnerable or unpalatable prey and inducible defenses can alleviate the paradox of enrichment in natural and laboratory environments (Abrams and Walters, 1996; Genkai-Kato and Yamamura, 1999; Vos *et al.*, 2004; Roy and Chattopadhyay, 2007; Van Donk *et al.*, 2011). These are not accounted for in our model.

Warming stabilizes the biomass oscillations within the food chain, leading to a pattern of an inverse "paradox of enrichment". This corroborates recent feeding studies of terrestrial arthropods (Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2011) and is contrary to the predictions of Vasseur and McCann (2005). This discrepancy is explained by differences in the temperature dependencies of the biological rates. We assumed that the carrying capacity of the system decreases with temperature. Simultaneously, the half saturation density of the species relative to the carrying capacity increases with warming, decreasing the flux of energy to the top of the chain and stabilizing the dynamics. Vasseur and McCann (2005) assumed the carrying capacity, the half saturation density and therefore also their ratio to be temperature independent. The parameter values of our system suggest that the growth rate of the basal species increases faster with warming than the consumers' metabolism. The increase in production outpaces the increasing metabolic demands of the consumers, enhancing the system's ability to keep energy at the lower trophic levels (Vasseur and McCann, 2005). This reduces biomass oscillations. Also, the temperature dependencies of ingestion and metabolism (Ehnes *et al.*, 2011; Rall *et al.*, 2012) suggest that a species metabolism increases faster with warming than its maximum ingestion, reducing its ingestion efficiency and thus biomass oscillations. Vasseur and McCann (2005) discussed all possibilities but then assumed that warming induces faster increases in species metabolism than in basal species growth rate and the increase of ingestion to outpace the increase of metabolism. Together, this leads to the destabilization of the system they found. The parameterization of our study is well supported by empirical data (Meehan, 2006; Savage *et al.*, 2004; Rall *et al.*, 2012; Ehnes *et al.*, 2011), suggesting a broad generality of the results presented here. There are, however, cases where warming destabilizes population dynamics. Warming increased population oscillations of the rotifer *Brachionus calyciflorus* (Halbach, Udo, 1970) and also induced the development of defensive spines (Halbach, 1970). Inducible defences thus might attenuate not only the detrimental effects of enrichment (Vos *et al.*, 2004; Van Donk *et al.*, 2011) but also the effects of temperature we found. Similarly, warming can disrupt species interactions (Harley, 2011) and thus dynamics in many ways, for example via changing developmental schedules (Tuda and Shimada, 1995) or dissimilar range shifts (Voigt *et al.*, 2003). Our model is based solely on energetig considerations and does not account for other effects that can modify a system's response to warming.

At high temperatures, the metabolism of the consumers exceed their ingestion rates; so their metabolic demands are higher than the energy gained by ingestion. In consequence, they can be surrounded by prey but starve to death. This phenomenon was observed in terrestrial (Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2011) and aquatic (Petchey *et al.*,

1999) microcosm experiments, where high trophic level species were found to be at risk of starvation at high temperatures. A three-species laboratory system involving plankton was destabilized at a high temperature (Beisner *et al.*, 1996, 1997). The data indicate no oscillations though, and temperature-induced changes of population rates are likely to have led to consumer starvation (Beisner *et al.*, 1997). Moreover, increased risk of starvation might help to explain the warming-induced shift towards smaller species in aquatic systems (Daufresne *et al.*, 2009; Yvon-Durocher *et al.*, 2011). Through changing size distributions, warming can indirectly have profound effects on species communities and ecosystem functioning (see Brose *et al.* (2012) and citations within).

(b) Interactive effect of enrichment and warming:

Fertilization and warming together have interactive effects on the dynamics of the food chain. At low temperatures, warming counteracts the degrading effects of enrichment: both the onset of the oscillations and the occurrence of extinctions connected to increasing fertilization are delayed. Kratina *et al.* (2012) corroborate our findings and showed for pond mesocosms that fertilization destabilized chlorophyll biomass dynamics at ambient temperature but not under three degrees of warming. Interestingly, this stabilizing effect of a small amount of warming was observed in a temperate seasonal environment with an annual range of about $20°C$ in daily average temperature. Moreover,Shurin *et al.* (2012) found a negative interaction between nutrient content and warming in the experimental ponds: warming reduced the effects of eutrophication. A study of a host-parasitoid community, however, showed no interactive effect of temperature and nitrogen levels (de Sassi *et al.*, 2012). This might be due to the different nature of host-parasitoid feeding relationships and its different body-size structure. We found that the rescuing effect of temperature was more pronounced when the consumers were larger than their prey. Larger species are more susceptible to the effect of temperature on their biological rates. A fundamental difference between terrestrial (without interactive effect) and aquatic (with interactive effect) systems ist not supported by our data since the parameterization of the model incorporates data of different ecosystems.

At high temperatures, higher fertility counteracts the detrimental effects of warming. Fertilization increases the attack efficiency of the consumers and can thus save species from warming-induced starvation. In size-structured communities, this rescuing effect is delayed to higher fertilization levels. The biological rates of large species react more strongly to warming and so need more fertilization to antagonize its effect. Laboratory studies could test this model prediction, but it should be kept in mind that at different temperatures varying resource quality affects small species differently than larger species (Ott *et al.*, 2012).

The increasing maximum feasible carrying capacity with warming is a sign for a top-down component in the effect of warming. Warming has been shown to strengthen top-down control in food webs (O'Connor *et al.*, 2009; Hoekman, 2010; Kratina *et al.*, 2012), explaining the increase in the maximum carrying capacity. Also, warming has stronger effects on larger species. This increases the maximum feasible carrying capacity in size-structured food chains. Its slight decrease at high temperatures is caused by the curve of the maximum ingestion (maximum around 30°C). The decreasing maximum consumption at higher temperatures accelerates the decrease of the species' ingestion efficiency and decreases the maximum feasible carrying capacity after its maximum.

Conclusions

In this study, we show that it is important to understand the interactive effects of drivers of global change. On the basis of our simulations, we expect climate change to have different effects on nutrient-poor and nutrient-rich communities, and nutrient enrichment to act differently in different climates. Warming in both nutrient-poor and nutrient-rich communities generally decreases biomass oscillations and stabilizes population dynamics, with nutrient-poor communities being more stable at low temperatures than their nutrient-rich counterparts. At high temperatures, however, consumers in nutrient-poor communities run a risk of starvation because of an unfavourable ratio of ingestion to metabolism. This does not happen in nutrient-rich communities within the temperature range we simulated. Both the stabilizing and the destabilizing effect of increasing temperatures are more pronounced when the consumers are larger than their prey. Consequently, nutrient-poor biomes are fragile and especially large consumers are at risk of starvation when temperatures increase. Nutrient-rich systems are stabilized by increasing temperatures. Enrichment has different effects on communities in cold and warm environments. In cold climates, nutrient enrichment has the detrimental effects described by the 'paradox of enrichment'. This harmful impact of nutrient loading is attenuated by an increasing body-size structure in the food chain. Hence, large top consumers of cold climates are less prone to extinction by nutrient enrichment than small consumers. In warm environments, increasing nutrient levels save the consumer species from starvation and we observe a beneficial effect of nutrient enrichment. Increasing consumer body masses delay the onset of this rescuing effect of enrichment. Therefore, a small body size is advantageous for consumers at high temperatures, but this advantage is lost with increasing enrichment.

With our simulations, we have taken an important step to disentangle the effects of two main direct drivers of global change. We have shown that the combined effects of warming and nutrient enrichment are far from trivial and can, depending on the situation, be supportive or detrimental for the stability of food chains. Increasing body-mass ratios generally accentuate the effects of changing temperatures. This knowledge will help to develop conservation measures that are tailored to the specific conditions of the species environment.

Acknowledgement

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Chapter 5.

How temperature, energy availability and predator prey body mass ratios help shape complex food webs

Amrei Binzer, Christian Guill, Björn C. Rall, Ulrich Brose

Abstract

Understanding the drivers of biodiversity loss is crucial to understand the future of our ecosystems. However, past investigations showed that warming and enrichment, (i.e., ecosystem fertility), two important drivers of species loss, are likely to interact with each other and with predator-prey body masses. Here, we use a dynamic population model to assess the effect of temperature, fertility and predator-prey body mass ratios on species persistence and link distribution in complex food webs, as well as final food web connectance. The biological parameters of our model are parameterized with empirical body mass and temperature scaling relationships. We found that body-mass ratios, temperature and fertility interactively affect food web connectance, species persistence and link distributions. Body-mass ratio influences the effects of temperature on persistence and determines the interactive effects of temperature and fertility. In food webs with small body-mass ratios, in which predator and prey species are roughly of equal size, warming increases species persistence and enrichment reduces it. In food webs with large body mass ratios, in which predators are substantially larger than their prey, warming generally reduces persistence, whereas enrichment can reduce or increase it. Moreover, increasing body mass ratios reduce the final food web connectance. This effect is independent of final species number but driven by a selective extinction risk. At high body mass ratios, specialist consumers with only few feeding links are more likely to survive. Body-mass ratios are thus not only a major determinant of the effect of both temperature and food web fertility but also influence the relative extinction risk of generalists and specialists. Because of the multifarious interactions of temperature, fertility and body mass ratios, responses in the real world are extremely varied and divergent. Models like the one we present here can help disentangling these complex effects of climate change and build theory that can then be tested in the field.

Keywords | global warming, metabolism, paradox of enrichment, fertilization, biodiversity loss, temperature

Introduction

Global change, and with it decreasing biodiversity, is a major threat to the worlds ecosystems as we know them. But even though the main drivers of biodiversity loss are identified (Millennium Ecosystem Assessment, 2005), their exact impact and possible interactions remain poorly understood (Peñuelas *et al.*, 2013). The impact of two direct drivers, climate warming and nutrient enrichment, is predicted to become more and more important in the future (Millennium Ecosystem Assessment, 2005). While the independent effects of these drivers have been addressed by several studies (Parmesan, 1996; Petchey *et al.*, 1999; Rall *et al.*, 2008, 2010; Davis *et al.*, 2010), the question whether their effects are independent or interactive remained unresolved. In a recent theoretical study on a three species food chain, we found that warming and enrichment interactively affect population dynamics and ultimately the survival of species (Binzer *et al.*, 2012). In the isolated food chain, increasing enrichment led to species extinctions which did not occur at warmer temperatures. The classic paradox of enrichment (Rosenzweig, 1971; Rall *et al.*, 2008) was thus restricted to colder temperature regimes. At very high temperatures, however, consumers could not meet their metabolic demands anymore and starved, thus supporting prior hypotheses of empirical studies (Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2011). This in turn did not occur at higher fertilization levels, where the higher system productivity prevented starvation. Surprisingly, these results suggest that warming and enrichment effects on species' persistence may at least partially cancel each other out (Binzer *et al.*, 2012). Because prior model studies indicated the major importance of the body-mass structure of the food webs (Brose *et al.*, 2006*b*; Heckmann *et al.*, 2012), warming and enrichment effects were anticipated to be modified by the community size structure (Brose *et al.*, 2012). Consistent with these expectations, increasing the body mass ratio between predator and prey strengthened the effect of warming on food-chain persistence (Binzer *et al.*, 2012). These theoretical predictions how warming, enrichment and the community size structure should interact found support in recent empirical studies (Shurin *et al.*, 2012; de Sassi *et al.*, 2012). Together, these studies illustrate the importance to analyze the consequences of the global change drivers in relation to the community size structure.

Natural communities, however, comprise a diversity of species connected by a multitude of interactions (Pimm *et al.*, 1991; Polis and Strong, 1996). This intricate network of interactions can substantially alter community responses to environmental changes such as warming (Davis *et al.*, 1998; Jiang and Morin, 2004). The behaviour of the three species chain therefore does not necessarily reflect the behaviour of a more complex species community (Kondoh, 2008; Cohen *et al.*, 2009). Considering these complex interactions is necessary to understand impacts of global change on species communities (Harmon *et al.*, 2009; Nomdedeu *et al.*, 2012). In this vein, ecosystem fertility interacts with food-web complexity and the community body-mass structure in determining species' persistence (Rall *et al.*, 2008), but similar analyses of warming effects or their interactions with fertility in complex food webs have not been studied yet.

Here, we expand our previous model and investigate the effects of temperature, fertilization and body mass structure on species persistence (fraction of surviving species) in models of complex food webs. Additionally, we analyzed the effect of different temperatures on food web connectance (the ratio of realized links to all possible links between species) and species link distributions (number of predators and number of prey) in food webs of different body size structures. To do so we ran dynamic food-web simulations (i) at different temperature-fertilization combinations, replicated for four different body mass structures (varying mean predator-prey body mass ratios) and (ii) at different at different temperature-body mass ratio combinations, replicated for three different fertilization levels. The numerical model includes empirical body-mass and temperature dependencies for the major biological rates such as production (Savage *et al.*, 2004), metabolism (Ehnes *et al.*, 2011), carrying capacity (Meehan, 2006), and feeding parameters (Rall *et al.*, 2012).

We found that temperature, fertilization and body mass structure interactively influenced species persistence. In food webs, warming increased species persistence when predator and prey were similarly sized or in high fertility food webs in which predators were up to 10 times larger than their prey. When predators were 100 or more times larger than their prey species persistence declined with warming. Enrichment reduced species persistence when predator and prey were similarly sized or, by a little, at low temperatures. At high temperatures, increasing system fertility led to higher species persistence. Increasing mean body mass ratios between a predator and its prey increased species persistence a low temperatures. At high temperatures species richness first increased with increasing predator size but then showed a depression with another maximum at the highest body mass ratios. Final food web connectance and species link distributions generally decreased with mean predator-prey body mass ratio and temperature.

Our model suggests that, to understand the effect of climate change in complex food webs, investigations of warming temperatures alone are not sufficient. Varying predator-prey body mass ratios considerably change the interactive effect of temperature and fertility and also influence the relative extinction risk of specialists and generalists. This has far-reaching implications for food web structure. We show that the interactions of temperature with fertility and especially predator-prey body mass ratios help shape food webs as we see them.

Methods

Food web structure

The food webs we analyzed were built according to the niche model (Williams and Martinez, 2000). It has successfully been tested against empirical data (Williams and Martinez, 2000). This model determines the distribution of feeding links, L, between the species of the food web. Its two input parameters are the initial species number, S, and connectance, C, the fraction of possible feeding interactions that are realized, $C = L/S^2$. Every simulation had an initial species number of 30 and initial connectance of 0.1.

Dynamic model

The differential equations we used to track each species biomass during the simulations are based on the consumer-resource model by Yodzis and Innes (1992) which was expanded to accommodate multiple species (Williams and Martinez, 2004*b*; Brose *et al.*, 2006*b*) as well as allometrically (Brown *et al.*, 2004) and temperature (Binzer *et al.*, 2012) scaled coefficients. The change of biomass, $\dot{B}$, of species i is then:

$$\dot{B}_i = r_i(1 - \frac{B_i}{K_i})B_i - \sum_m F_{mi}B_m \tag{5.1}$$

$$\dot{B}_i = \sum_s e_s F_{is} B_i - \sum_m F_{mi}B_m - x_i B_i. \tag{5.2}$$

In this model, basal species (eqn. 5.1) gain biomass by growing logistically. This growth was calculated using the basal species maximum growth rate, r_i, its biomass B_i, and its carrying capacity K_i. Both the maximum growth rate and the carrying capacity scale with the species body mass and the ambient temperature (see section allometric and temperature scaling). Basal species lose biomass because predators feed on them (second term in equation 5.1). The predators gain biomass by feeding on prey species, s, (first term in equation 5.2; $e_s = 0.85$ is the efficiency with which the prey can be assimilated by the predator) and lose biomass to other predators and through metabolism, which is also body mass and temperature dependent (second and third term of equation 5.2). Biomass changes caused by feeding interactions depend on predator biomass and functional response F_{ij}:

$$F_{ij} = \frac{a_{ij}B_j^h}{1 + \sum\limits_k Th_{ik}a_{ik}B_k^h} \tag{5.3}$$

The functional response describes the density-dependent feeding rate of a predator i on prey species j. This rate depends on the feeding-interaction specific attack rate, a, of i on j and its other prey species k, the biomass of j, the time the predator needs to handle j and k (Th_{ij} and Th_{ik}) and their biomasses. Both the attack rate and the handling time depend on the ambient temperature and the body masses of the predator and prey. The shape of this relationship is described by the Hill exponent, h. A Hill exponent of 1 indicates a typeII functional response, where the prey biomass consumed increases with the its biomass density and saturates at $1/Th$.

In this study, we used a Hill exponent of 1.2, which introduces a slight hyperbolic curve at low prey densities. This relieves the prey from feeding pressure at low densities and thus stabilizes prey populations. We ran all food web simulations for an equivalent of 1000 years. This excludes transient dynamics and any major effects are likely to be revealed within that time. We defined a species as extinct and removed it from the network when its biomass fell below 10^{-12} or if it had no prey species left.

Allometric and temperature scaling

The biological parameters of the model scale with the species body mass and the system temperature. Thus metabolism, growth and attack rate, handling time as well as the carrying capacity are functions of temperature and body mass.

The mass and temperature dependencies of the species maximum growth rate r_B $[1/s]$ are implemented as follows:

$$r_i = e^{I_r} m_i^{s_{ri}} e^{Ea_r \frac{T_0 - T}{kTT_0}}. \tag{5.4}$$

Where, e^{I_r} is the growth rate specific constant, calculated for a species' body mass of $1g$ and a temperature of $20°C$ $(= 293.15\ K)$. The body mass, m, of the species influences the growth rate via its rate specific scaling coefficient, s. The temperature dependency term is an extended form of the Arrhenius equation, where Ea is the activation energy, $T_0 = 293.15$ the normalization temperature, T the temperature of the system and k $[eVK^{-1}]$ the Boltzmann constant.

The mass and temperature dependent metabolism for predators x_i $[1/s]$ and the carrying capacity of species at the base of the food web K_i $[g/m^2]$ are calculated accordingly:

$$x_i = e^{I_x} m_i^{s_{xi}} e^{Ea_x \frac{T_0 - T}{kTT_0}} \quad \text{and} \tag{5.5}$$

$$K_i = e^{I_K} m_i^{s_{Ki}} e^{Ea_K \frac{T_0 - T}{kTT_0}}. \tag{5.6}$$

The attack rate, a in $[m^2/s]$, and the handling time, Th, in $[s]$, of the functional response are specific to the predator prey interaction they represent. They accordingly scale with the temperature and the body masses of both the predator, j, and its prey i:

$$a_{ji} = e^{I_a} m_j^{s_{aj}} m_i^{s_{ai}} e^{Ea_a \frac{T_0 - T}{kTT_0}} \quad \text{and} \tag{5.7}$$

$$Th_{ji} = e^{I_{Th}} m_j^{s_{Thj}} m_i^{s_{Thi}} e^{Ea_{Th} \frac{T_0 - T}{kTT_0}}. \tag{5.8}$$

We parameterized the model with empirically derived scaling coefficients. They have already been used in a previous study (Binzer *et al.*, 2012) and represent many different species and ecosystems (Rall *et al.*, 2012). Hereby, the data for invertebrate species are most comprehensive and therefore most reliable. To avoid biased results due to inadequate data we assumed all species in the presented food webs to be invertebrates. The scaling parameters were chosen accordingly (table 5.1).

The body masses of the species in the food web scale according to their prey averaged trophic level (mean trophic level of their prey plus one, determined by the food web structure). The slope of this relationship is determined by the mean body mass ratio applied. Thus, in food webs with a mean log_{10} body mass ratio of zero the predators where on average the same size of their prey. In food webs with a higher log_{10} body mass ratio they were accordingly larger and in food webs with a negative log_{10} body mass ratio correspondingly smaller. Changing the mean body mass ratio enabled us to test the persistence of species in food webs of different body size structures. To avoid that all species of a trophic level (e.g. herbivores of trophic level two) are equally sized, we added random deviations from these strict scaling relationships by sampling residuals from a log-normal distribution with a mean of 0.01 and a standard deviation of 1. These residuals were sampled for each species independently and added to the value predicted by the scaling relationship between body-masses and trophic levels.

We set the initial biomasses of the basal species to their respective carrying capacity and the initial predator biomasses to one eighth of the mean carrying capacity of those basal species. This made sure that basal species did not go extinct immediately because of too strong top down pressure. Changing the reference body mass within ecological plausible boundaries or the initial biomasses does not qualitatively change our results, as long as the starting biomasses of the basal species are high enough to survive initial predator attacks.

Simulation sequence and analyses

Interactive effects of temperature and fertilization:

To study the effects of temperature and different fertility levels on species persistence we systematically varied the temperature of the system between 0°C and 40°C in steps of 1°C, and the intercept of the carrying capacity (representing the fertility of the ecosystem), and thereby the basic energy content of the food web, between 1 and 20 in steps of 1. We

Table 5.1 – Model mass and temperature scaling parameters: carrying capacity (K in $[g/m^2]$ (Meehan, 2006)), growth (r in $[1/s]$, (Savage *et al.*, 2004)), metabolism (x in $[1/s]$, (Ehnes *et al.*, 2011)) attack rate (a in $[m^2/s]$) and handling time (Th in $[s]$, both calculated from Rall *et al.* (2012)). The parameters scale with the body mass of the resource species (j) of the species pair considered , attack rate and handling time scale additionally with the body mass of the consumer species (i). We calculated the species metabolism using the conversion factor from Peters (1983). Inserting the values below into equations 5.4 to 5.8 yields the body mass and temperature scaled model we worked with.

	K_i	r_i	a_{ji}	Th_{ji}	x_i
intercept (I)		-15.68	-13.1	9.66	-16.54
body mass scaling species i (s_i)	0.28	-0.25	0.25	-0.45	-0.31
body mass scaling predator j (s_j)			-0.8	0.47	
temperature scaling activation energy (Ea)	0.71	-0.84	-0.38	0.26	-0.69

repeated this for 100 food webs on four different body mass structures by setting the log_{10} mean predator prey body mass ratio to 0, 1, 2 and 3.

Interactive effects of temperature and mass structure:

To closer study the effect of temperature and different body size structures on species persistence we systematically varied the temperature as above and the log_{10} mean body mass ratio between -1 (the predators are 0.1 the size of their prey) and 4 (the predators are on average 10^4 times larger than their prey) for 100 webs at low, intermediate and high fertilization levels (intercept of the carrying capacity $= 1, 10$ and 20) each.

For both of the temperature and fertilization and the temperature and body mass structure simulation regimes we constructed 100 food webs which each were subjected to all temperature and fertilization or temperature and body mass ratio combinations. To assess species persistence under different scenarios we averaged the percentage of surviving species of these 100 food webs. The interactive effects of enrichment and body mass ratios have already been investigated in an earlier study (Rall *et al.*, 2008) and are therefore not included here.

Effects on connectance and species link distributions:

To assess the influence of temperature and body mass structure on food web connectance we averaged the deviation of the final connectance from the initial connectance over all 100 webs at the same temperature-fertility-mass structure combination.

To assess the temperature and body mass structure influence on the species link distribution we calculated the deviance of the mean log_{10} generality and vulnerability of the food webs above from the mean log_{10} generality and vulnerability of 10 000 reference niche-model food webs of the same species number, but initial connectance. These reference food webs represent our expectation that temperature, fertility and body mass ratio does not influence the species link distribution. To plot them we expressed this deviance from the expectation in the standard deviation of the generality and vulnerability distribution of the reference webs.

Results

Interactive effects of temperature and fertilization

The effect of temperature and fertilization on the persistence of species depends strongly on the body mass structure of the network (figure 5.1). Generally, species persistence increased with increasing body mass structure, but fertilization and temperature interact differently depending on the body mass structure (figure 5.1a-d).

In food webs with no body mass structure (log_{10} body mass ratio $= 0$) food webs higher along the fertility gradient always exhibited lower species persistence than webs at lower fertilization levels (figure 5.1a). Networks at high temperatures generally retained more species than their low temperature counterparts of the same fertilization. The exception here were food webs on very low levels of fertilization (intercept of carrying capacity < 2.5) and at very high temperatures ($T > 35°$ C). In these webs species persistence was slightly lower than in corresponding food webs at lower temperatures (figure 5.1a, upper left corner). Nevertheless, the general pattern indicates that enrichment decreases species persistence, whereas warming has positive effects in these communities without a size structure.

This pattern changed in communities with size structure when the predators were larger than their prey (figure 5.1b-d). When they were on average 10 times larger than their prey (log_{10} body mass ratio $= 1$), higher fertility webs showed reduced species persistence only at low to medium temperatures (figure 5.1b). At high temperatures this relationship was reversed and low fertility communities displayed lower species persistence than webs of higher fertilization levels (figure 5.1b, upper left corner). Also, species persistence was reduced along the temperature gradient at low fertility levels, but increased along the temperature gradient at high fertility levels (figure 5.1b).

In food webs with predators on average 100 times larger than their prey (log_{10} body mass ratio $= 2$) species persistence generally declined along the temperature gradient, regardless of the fertilization level (figure 5.1c). The ambient temperature of the food web determines the effect of different fertility levels: at low temperatures species persistence was higher in low fertility food webs than in high fertility food webs. At high temperatures on the other hand, species persistence was lower in low fertility food webs and higher in high fertility food webs.

Quantitatively the same pattern was produced when the predators were 1000 times larger than their prey (log_{10} body mass ratio $= 3$, figure 5.1c): again, species persistence

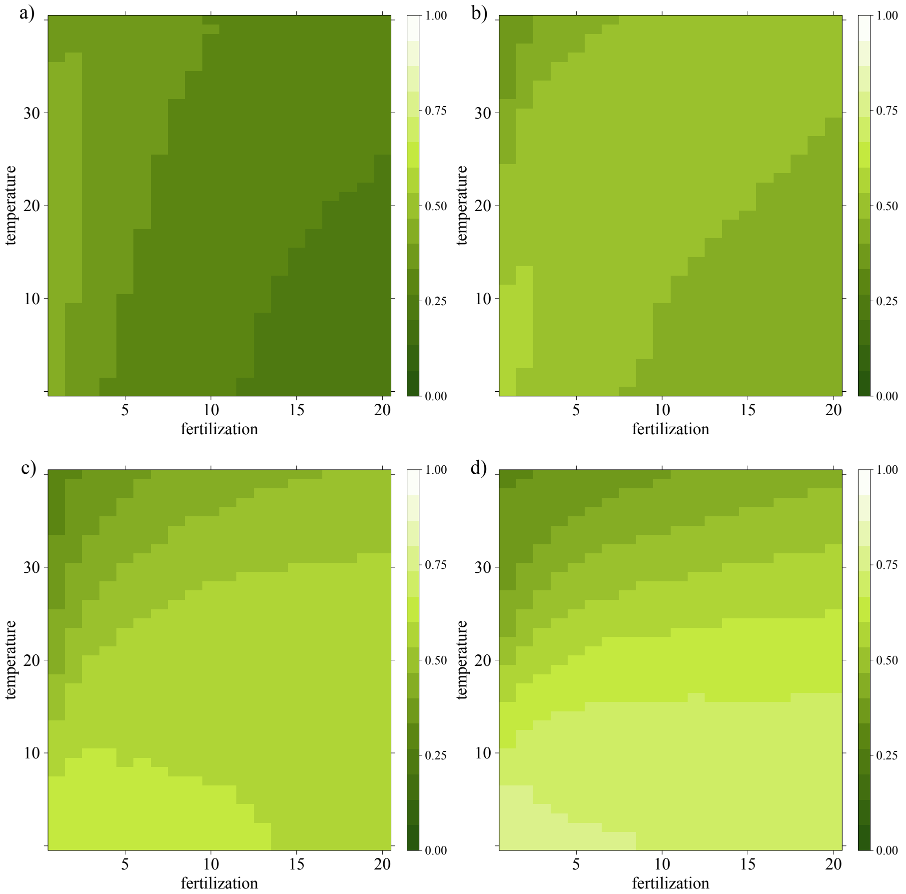

Figure 5.1 – The influence of temperature (y-axes) and fertilization (x-axes) on the persistence of species (averaged over 100 food webs; in %, color coded, see color key) in food webs of different size structures: a) predators on average of the same age as their prey (log_{10} body mass ratio = 0), b) predators on average 10 times larger than their prey (log_{10} body mass ratio = 1), c) predators on average 100 times larger than their prey (log_{10} body mass ratio = 2) and d) predators on average 1000 times larger than their prey (log_{10} body mass ratio = 3).

is reduced along the temperature gradient and increases along the fertilization gradient. Only at low temperatures did low fertility food webs retain more species than their higher fertility counterparts (figure 5.1c, lower left corner).

Overall, greater body mass structure in food webs modified the influence of temperature and fertilization on species persistence. Whereas warming increased species persistence in low fertility networks with equally sized species (figure 5.1a) and high fertility food webs when predators were 10 times larger than their prey (figure 5.1b), it reduced persistence in food webs with even larger predators (figure 5.1c, d). Fertilization destabilized food webs with equally sized species at all temperatures (figure 5.1a) and low-fertility, low-temperature food webs with predators larger than their prey but increased species persistence in mass structured food webs at high to medium temperatures (figure 5.1b-d).

Interactive effects of temperature and mass structure

Temperature and body mass structure synergistically influenced species persistence. This interactive effect was altered depending on the fertilization level of the web, especially at high temperatures and in food webs where predators were larger than their prey.

At low fertilization, species persistence was lowest in food webs in which the predators were on average smaller than their prey (figure 5.2a). Increasing fertility enlarged this low persistence region towards communities in which the predators were slightly larger than their prey (figure 5.2b,c). Regardless of web fertilization, species persistence was slightly larger at higher temperatures in these low body mass structure, low persistence food webs (figure 5.2a-c, lower part of each panel). Higher temperatures generally reduced species persistence in food webs with a positive predator prey body mass ratio (figure 5.2a-c, upper part of each panel).

Along the the body mass ratio gradient species persistence increased dramatically when temperatures were low (figure 5.2a-c, left side of each panel). Increasing network fertility expanded this stabilizing region towards higher temperatures (figure 5.2a-c). At medium to high temperatures species persistence did not increase linearly along the body mass ratio gradient but displayed a two-maximapattern. In low fertility webs, species persistence was highest when predators were only slightly larger than their prey (log_{10} body mass ratio $= 0.5$, figure 5.2a) as well as when they were much larger than their prey items (log_{10} body mass ratio $= 4$). Species persistence was lowest

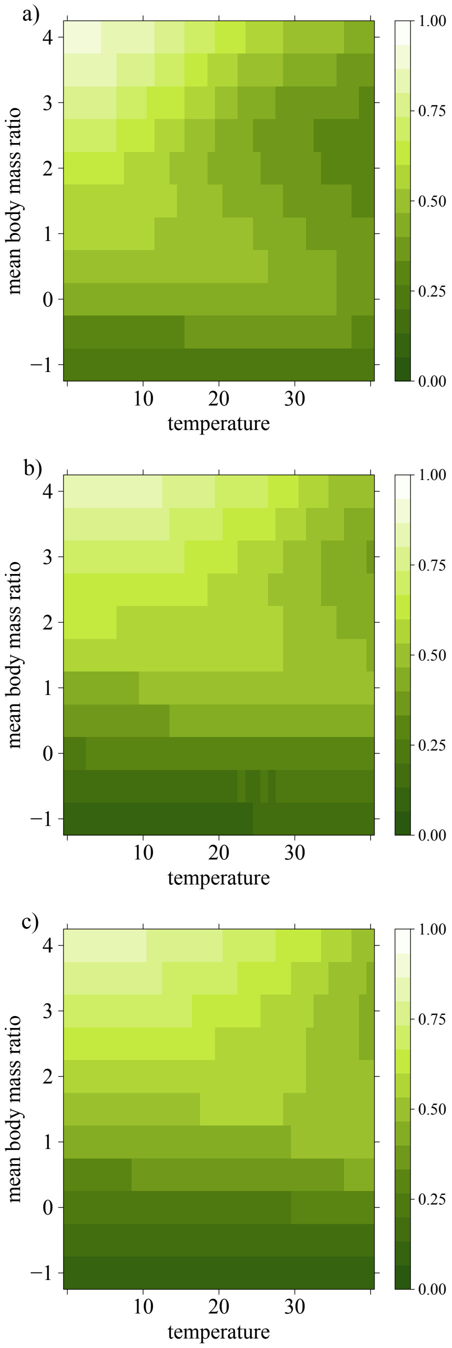

Figure 5.2 – The influence of temperature (x-axes) and body mass structure (y-axes) on the persistence of species (averaged over 100 food webs; in %, color coded, see color key) in food webs of a) low fertility, b) intermediate fertility and c) high fertility.

when predators were smaller than their prey (log_{10} body mass ratio = -1) and displayed another minimum at intermediate body-mass ratios (log_{10} body mass ratio = 2.5). The bifurcation became more pronounced at higher temperatures (figure 5.2a, right side). The interactive effects of temperature and body mass ratio resulted in a persistence hump the ridge of which ran from a log_{10} body mass ratio of 2 at low temperatures to 0 at high temperatures (figure 5.2a).

Increasing web fertility shifted the persistence bifurcation point towards higher temperatures (figure 5.2a-c). At low fertility, persistence bifurcated at around 15°C (figure 5.2a). At intermediate fertilization this point was at around 27°C (figure 5.2b) and at high fertility at around 37°C (figure 5.2c).

Increasing system fertility did not change the persistence minimum at log_{10} body mass ratio = -1, or the maximum at log_{10} body mass ratio = 4. But it shifted the second maximum up the body mass gradient to around 10^1 at intermediate fertilization levels and to $10^{1.5}$ at high fertilization levels (figure 5.2b,c). The second minimum shifted to $10^{2.5}$ and 10^3, respectively (figure 5.2a-c). This shift in temperature and body mass effects resulted in a shift of the ridge of the species-persistence hump towards higher body mass ratios (figure 5.2a-c).

Effects on connectance and link distributions

Effects on food web connectance:

Final connectance of the food webs differed depending on body mass structure and ambient temperature (figure 5.3). Interestingly, this effect is disconnected from the final species number but dominated by the body mass structure of the food webs. Generally, connectance decreased in food webs in which predators are much larger than their prey (figure 5.3, upper half) and increased in food webs with a smaller body mass ratio (figure 5.3, lower half). The exception were webs with predators on average 10 times smaller than their prey (log_{10} body mass ratio = -1). These food webs lost so many of their species that their connectance decreased. Overall, the gain or loss of connectance also depended on temperature: food webs at low temperatures were generally more connected than their high-temperature counterparts (figure 5.3, from left to right). The exceptions were again food webs with predators smaller than their prey. In these increasing temperatures increased food web connectance (figure 5.3, two lowest rows).

Effects on species vulnerability:

Final vulnerability of the species in the webs also changed depending on temperature and body mass structure (figure 5.4a). The mean vulnerability was higher than expected in food webs in which predators were moderately larger than their prey (log_{10} body mass

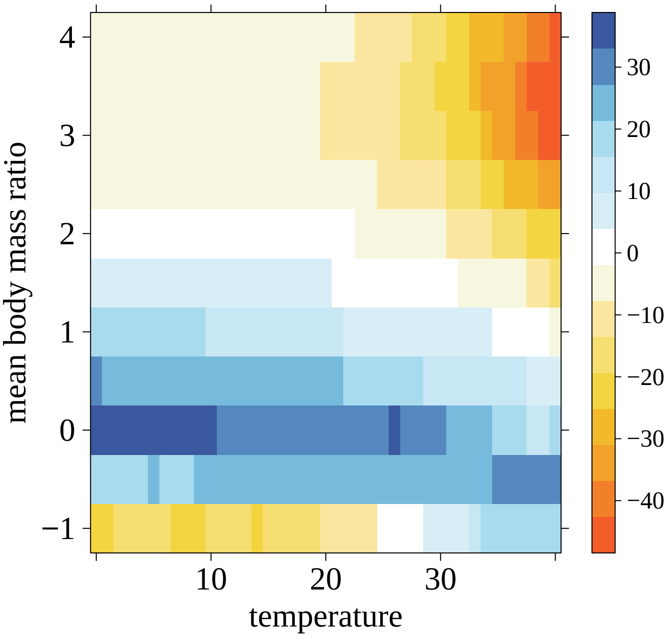

Figure 5.3 – Influence of temperature (x-axis) and body mass structure (y-axis) on the deviation of final to initial connectance ($C = 0.1$), in percent (color coded, see color key) and averaged for 100 food webs at intermediate fertilization.

ratio ≤ 1.5, figure 5.4, lower half). It was lower than expected in webs with much larger predators (log_{10} body mass ratio ≥ 2, figure 5.4, upper half). With the exception of webs with smaller predators, species mean vulnerability was reduced along the predator prey body mass ratio gradient and also along the temperature gradient. This leads to highest species vulnerabilities in low temperature, low body mass ratio food webs and lowest species vulnerabilities in high temperature, high body mass ratio food webs.

Effects on species generality:

Interestingly, mean generality does only negatively deviate from the expectation: on average, species have either the same number or fewer prey species than expected (figure 5.4b). With the exception of very low and very high body mass ratios (log_{10} body mass ratio = -1 and 4) the mean generality of the species was reduced along the body mass ratio and the temperature gradient. The mean generality is thus highest in low temperature, low body mass ratio food webs and lowest in high temperature, high body mass ratio webs.

Discussion

Temperature, fertility and predator-prey body mass ratios interact and shape complex food webs via changes of interaction strengths, energy demand and energy availability.

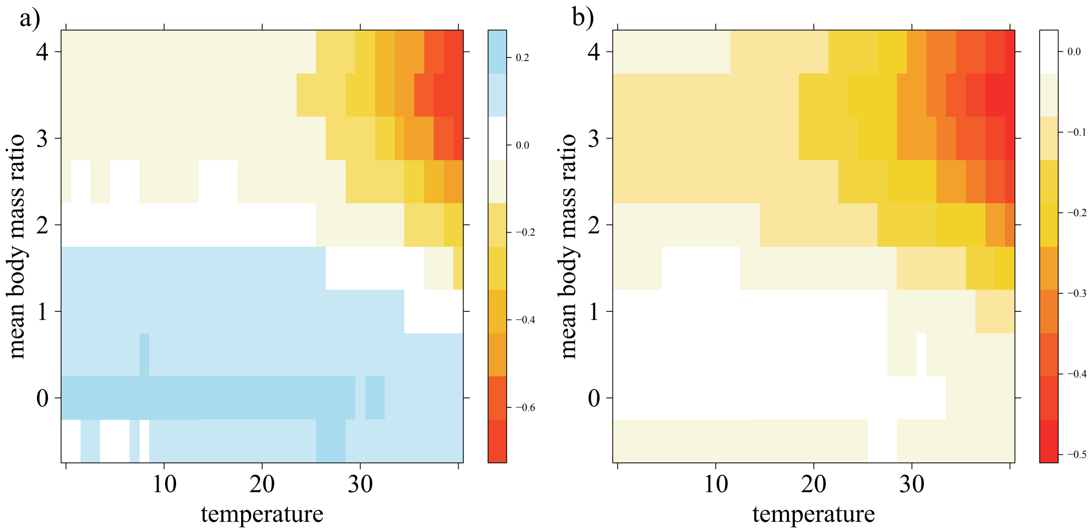

Figure 5.4 – Influence of temperature (x-axis) and body mass structure (y-axis) on the deviation of the mean food web vulnerability (panel a) and generality (panel b) from the expected mean values derived from 10 000 food webs of the same species number but initial connectance (see Methods for further details), expressed in standard deviations of the expected link distributions.

Increasing fertility increases the energy input into the food web and therefore the biomass flux to upper trophic levels. Increasing temperatures reduce the feeding efficiency of predators, lowering the top-down pressure. Due to a mismatch in the temperature response of consumption and metabolism, warming also increases the risk of starvation, especially for predators. If these mechanisms reduce or increase species persistence depends on the body mass ratio of the food web. When the ratio is low, warming increases and enrichment reduces species persistence. With higher ratios, the response is not so clear cut. When a predator and its prey are similarly sized the interaction strength between them is strong. Larger predators have relatively lower consumption and respiration rates. This reduces the interaction strength. Thus, at low body mass ratios, increasing temperatures decrease the strong interaction strength and increase persistence. At high body mass ratios, warming induced starvation sets in earlier because the rapidly increasing respiration rates outpace the already low consumption rates at lower temperatures. At high body-mass ratios, generalist predators are more likely to go extinct than specialist predators. This is because generalist predators have many, weak feeding interactions. With increasing temperatures and respiration rates those weak links do not yield enough energy to survive. This leads to decreased final food web connectances at high body mass ratios and especially at high temperatures. At low body-mass ratios, species with only few predators can accumulate more biomass than species with more predators. This increases oscillations and their extinction risk. It also increases the relative vulnerability of the surviving species and the final food web connectance.

Interactive effects of temperature and fertilization

There is an interactive effect of temperature and fertilization on the species persistence of the complex food webs that were analyzed. The decreasing persistence along the fertilization gradient is caused by the classical "paradox of enrichment" (Rosenzweig, 1971). This can be seen in food webs with similarly sized species. Enrichment increases the energy input into the food web and therefore increases consumer biomasses. This shifts biomass up to higher trophic levels and the isoclines of species towards unstable equilibria (Rip and McCann, 2011). Consequently, populations become dynamically unstable and extinctions can occur. Increasing temperatures counteracted this destabilizing effect of enrichment in food webs in which all species were similarly sized. Warming reduces the feeding efficiency of consumers (Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2011) and therefore reduces the flux of energy towards higher trophic levels. The resulting lower population-level top-down pressure stabilizes population dynamics (Binzer *et al.*, 2012). Consistent with these theory predictions, increasing temperatures counteracting the destabilizing effects of enrichment have been found in freshwater mesocosm experiments (Kratina *et al.*, 2012; Shurin *et al.*, 2012).

Increasing predator-prey body mass ratios increases species persistence. They reduce the predators relative rates of consumption and metabolism (Yodzis and Innes, 1992). These lower per biomass consumption rates translate into reduced interaction strengths, lower the top-down pressure in predator-prey interactions, and thus increase species persistence (Brose *et al.*, 2005, 2006*b*; Kartascheff *et al.*, 2009). For our simulations, it follows that food webs with a higher predator prey body mass ratio have on average lower interaction strengths. These lower average interaction strengths alter the effect of enrichment and temperature on species persistence in the food web. Under this lower interaction strength regime in the food-webs with high body-mass ratios increasing temperatures reduce species persistence. Although warming generally increases each species consumption and metabolism, the increase in metabolism thereby outpaces the increase in consumption rates (Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2011) (see scaling coefficients, table 5.1). Warming thus continuously decreases the ratio between energy gain of the population by consumption and energy loss to metabolism. At some threshold temperature, the species cannot meet its metabolic demand anymore and starves to death (Binzer *et al.*, 2012; Glazier, 2012; Lemoine and Burkepile, 2012). In the communities with high body-mass ratios, the lower average interaction strengths cause low energy supply for the predators and the mismatch in the warming effects on consumption and metabolism thus becomes detrimental for species persistence. The low average interaction strengths that are responsible for the high persistence of these food webs with high body-mass ratios as a consequence of low top-down control, thus come at the cost of susceptibility to extinction under warming due to starvation by subcritical bottom-up energy supply. However, enrichment of these food webs with high body-mass ratios increases the bottom-up energy supply for consumers, which counteracts the warming effects. Thus our simulations suggest that in food webs in which predators are larger than their prey, as commonly found in nature (Brose *et al.*, 2006*a*) the paradox of enrichment can be resolved. This has been found in another theoretical study (Rall *et al.*, 2008) and is in line with empirical studies that found that food web complexity and environmental factors determine the effect of enrichment (Trzcinski *et al.*, 2005; Artigas *et al.*, 2013).

However, not all empirical studies report this pattern. Warming reduced total biomass in a marine system but only with enrichment (O'Connor *et al.*, 2009). At low fertility there was no change because of the restricted resources. Warming and fertility also interacted to increase biomass in an aquatic mesocosm (Lefébure *et al.*, 2013). Neither of these studies reported loss of species, likely because their warming and enrichment were not as high as in our simulations. They therefore did not reach the metabolic limits that our simulations revealed. The effects of temperature and enrichment on species persistence in food webs depend strongly on the mean body mass structure of the food web. Persistence might even depend on the predator-prey mass ratio of every single interaction (Otto *et al.*, 2007). The effect of body mass structure likely lies behind the varied responses to enrichment in empirical studies (O'Connor *et al.*, 2009; Lefébure *et al.*, 2013; Artigas *et al.*, 2013). Two studies reporting species diversity in natural sea grass communities along a nutrient gradient, for example, documented reduced diversity and thus smaller numbers of species (Tewfik *et al.*, 2007; Coll *et al.*, 2011). This situation likely results from the approximately 1:1 body mass ratios in this system. They therefore resemble communities with equally sized species in our simulations of temperature and fertilization (figure 5.1a). Streams experiencing different temperatures also responded differently to enrichment (Lefébure *et al.*, 2013). Differences in body-mass ratios, judging from the species involved, may have contributed to these differences. Their impact is difficult to disentangle from the many other factors operating in these natural streams (Lefébure *et al.*, 2013).

The effects of body mass ratios on the interaction between warming and enrichment are intriguing. A wider variety of body sizes within trophic levels is easily incorporated into our model and their effect would be very interesting to test, not only theoretically but also empirically. Of course, the effect found in our study depended strongly on the values of the models scaling coefficients. Especially different scaling relationships for metabolism and feeding rates could change the behaviour of the model (Vasseur and McCann, 2005). However, our parameterization for these rates is securely based on the largest and most comprehensive empirical databases compiled so far (Ehnes *et al.*, 2011; Rall *et al.*, 2012). So even if in specific cases scaling relationships might deviate from the ones we used here, our results represent the general response of biological parameters to temperature and fertility thus providing a general signature how natural ecosystems may respond to these interactive global change drivers.

Interactive effects of temperature and mass structure

There is a clear interaction of the effects of temperature and mass structure on complex food webs. Consistent with results of prior model studies (Brose *et al.*, 2006*b*; Rall *et al.*, 2008; Heckmann *et al.*, 2012), species persistence is positively affected by increasing body mass ratios. Larger ratios lead to lower consumption and metabolic rates. This decreases top down pressure and leads to lower interaction strengths and higher persistence (see section 5). Increasing temperature has two effects on species persistence. First, it reduces the consumers feeding efficiency thus lowering top-down control. Second, it simultaneously reduces the bottom-up energy supply for the consumers, which can cause extinctions due to starvation (see section 5). Which of these two consequences takes effect along the temperature gradient depends on the body mass ratio and therefore on the interaction strengths within the food web. At very high interactions strengths (low log_{10} body mass ratios) persistence is generally low and warming has no effect. Increasing the consumer body size slightly reduces the interaction strength to levels that are high, but susceptible to the effect of warming. Then warming first increases species persistence by reducing consumer feeding efficiencies, but continued warming leads to starvation at high temperatures. Further reducing the interaction strengths by increasing body mass ratios shifts these effects of warming towards lower temperatures. Species persistence is higher at lower temperatures than in webs with smaller body size ratios, but at the same time starvation sets in at lower temperatures as well. In consequence, food webs with larger body mass ratios are more susceptible to warming induced starvation. This is how the balance between body mass ratio induced interaction strength and warming induced feeding efficiency and starvation creates the persistence hump in figure 5.2. The apparent high persistence at very high body mass ratios and medium temperatures is due to the longer generation time of larger predators (Gillooly, 2000). If simulations where run for a longer time, these larger bodied species would also go extinct (Binzer *et al.*, 2011).

Consistent with these results, microcosm experiments demonstrated that warming increased biomass of bacteria and their consumers, but led to extinction of larger predators (Petchey *et al.*, 1999). Experiments with terrestrial arthropods indicate not only that warming induced extinctions also occur in terrestrial systems, but also that predators which are much larger than their prey (high body mass ratio) are especially likely to starve (Rall *et al.*, 2010). However, in Icelandic geothermal streams, ranging from 5°C to 45°C, the mean individual size and abundance of the largest top predators (brown trout) increased with increasing temperatures (Woodward *et al.*, 2010*b*). The coldest stream in which brown trout occurred was 10°C (Woodward *et al.*, 2010*a*). Warming increased food web productivity, which was then able to sustain higher populations of brown trout. A meta study of spring ecosystems showed that species numbers gradually decline with increasing temperature until around 50°C, where species numbers drop sharply (Glazier, 2012).

Increasing fertility levels increase the predators bottom-up energy supply (see section 5). In the light of our simulations, this means that the food webs at higher fertility levels have a higher "backround" energy supply that is then altered by the body mass ratio and the temperature. These increased "backround" energy supply shifts the hump of maximum persistence towards higher body mass ratios and higher temperatures.

Even though there is a growing body of work reporting the twofold influence of temperature and the mismatch of metabolism and consumption (Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2011; Lemoine and Burkepile, 2012), few studies tested it in a food web context (but see (Petchey *et al.*, 1999; O'Connor *et al.*, 2009; Woodward *et al.*, 2010*b*; Glazier, 2012)). Here, we present a systematic screen of how predator-prey body mass ratios alter the effect of temperature, regardless of any ecosystem type or species identity. Our results again indicate that, to understand the effects of warming on food webs, the individual predator-prey body mass ratio is crucial. We propose that, with increasing temperatures, species involved in feeding interactions in which consumers are about 100 times larger than their prey are amongst the first to be negatively affected. However, empirical studies explicitly setting out to test this relationship are needed to elucidate the importance of body mass ratios in natural food webs.

Effects on connectance and link distributions

Final food web connectance decreases with increasing body mass ratios and increasing temperatures. In our simulations, all 100 food webs were subjected to every body mass ratio-temperature combination. Consequently, the starting conditions for every combination were the same. The clear pattern in final connectance therefore is caused by a systematic effect of body mass ratios and temperature on the extinction risk of generalists and specialists. Higher body mass ratios and especially high temperatures disproportionately increase the extinction risk of generalist species (species feeding on relatively many prey species). Accordingly, there is a prevalence of specialist species (species with few prey species) at high temperatures and high body mass ratios, which can be explained by differences in their energy supply. In the notation of the multi-prey functional response (see equation 5.3), each additional feeding link diminishes the strength of each individual link by increasing the value of the denominator. As a result, specialists have few, strong feeding links, whereas generalists have many, weak links to prey. Increasing body mass ratios decrease the species consumption and metabolism, reducing the average interaction strength (see section 5). At these low average interaction strengths, increasing temperatures have different effects on generalists and specialists. With warming consumption increases, but metabolism increases faster. This mismatch ultimately causes species extinctions (see section 5). Consequently, at the verge of starvation the strengths of existent feeding links of the species become crucially important. At this point, the specialists with their few but strong feeding interactions have an advantage over the generalists whose higher number of links cannot save them from starvation because those links are too weak to sustain them. So, at high body mass ratios and high temperatures generalists die due to the lower energy supply through their weaker interactions and specialists survive, being supported by the higher energy supply of their stronger interactions.

Unfortunately, data that relates body size ratios and temperature to species degree of generalism are rare or absent. However, species richness increases from the poles to the tropics and increasing species specialization has been suggested to account for it (MacArthur, 1972; Janzen, 1973). Subsequent studies, however, have given mixed results (Beaver, 1979; Hawkins, 1990; Ollerton and Cranmer, 2002). Some of these indicate specialism at low latitudes although others are dubious or suggest generalism. Some mutualistic networks have more specialized species in the tropics (Dalsgaard *et al.*, 2011). However, a major recent study showed that generalism is common for these networks too (Schleuning *et al.*, 2012). Mutualistic networks probably function differently from trophic networks, however, and our model does not address them. The amount of generalism or specialism in mutualistic networks can therefore not be used to test our findings, but, a major meta-analysis of food webs from very different ecosystems found also only ambiguous evidence on the temperature and geographical distribution of specialism (Newth, 2008). Unfortunately the body size structure of these species interactions is not reported. Our model simulations suggest that not all food webs per se should display increased specialism, but primarily the ones with very high predator prey body mass ratios. The degree of specialism might even vary systematically depending on each individual predator-prey interaction and the body mass ratio between the predator and its prey. These natural communities likely contain a wider range, and therefore greater variety, of body mass ratios than our simulated food webs. Unfortunately this is not reported. Comparing the overall species specialization is therefore likely to miss the pattern that our simulations suggest.

The low species vulnerability at high temperatures and body mass ratios is caused by the loss of generalists in the webs. Every generalist that dies at high temperatures releases its prey from feeding pressure and decreases its number of predators. Low mean generality and low mean vulnerability thus go hand in hand. The increased connectance in webs with low body mass ratios, however, is due to the increased vulnerability of the species in those webs. These food webs at low temperatures combine high interaction strengths with low respiration rates. Consequently, species gain much energy from feeding, but little of it is metabolized. The remaining energy supports growth and biomass accumulates, which results in higher biomass densities. These higher consumer biomass densities lead to biomass oscillations that are particularly strong for species with only few predators. This increases the probability of extinction for species with few consumers. With increasing temperatures the respiration rate of the species increases and more energy is metabolized. The biomass oscillations decrease and slightly fewer species go extinct. This pattern is reflected in the final connectance of the food webs. At low body mass ratios connectance increases because species with few predators are lost preferentially. At high body mass ratios, and especially high temperatures, connectance decreases because generalist species die.

Conclusions

It is evident that temperature interacting with enrichment and body size ratios strongly affects species persistence. Our dynamics population biomass model is parameterized with empirically derived temperature and body mass scaling relationships. It therefore can offer information about how changes in feeding rates or metabolism scale up to affect species persistence and food web structure. It provides a mechanistic explanation about how temperature, inherent body size structure and system fertility help structure food webs. It shows that taking predator-prey body mass ratios into account can help disentangle the complex effects of climate change. These mass ratios not only are a major determinant of the effect of both temperature and food web fertility but also influence the relative extinction risk of generalists and specialists. Increasing body mass ratios can resolve the “paradox of enrichment” up to the point where increasing system fertility increases species persistence by saving species from warming induced starvation. Our model suggests furthermore that the susceptibility to warming induced starvation also depends strongly on the mean body mass ratio in the food web. With warming, food webs with intermediate body mass ratios showed the lowest species persistence. We therefore conclude that with increasing temperatures species interactions are driven into two different directions: to either involve predators that are a little larger than their prey, or to involve predators that are much larger than their prey. High body mass ratios have also been shown to favor the extinction of generalists. Therefore, the feeding interactions involving very large predators we expect to involve a larger proportion of specialists than if the predators are only a little larger than their prey. Considering temperature alone is clearly insufficient. In the real world, the one we have to predict and manage, responses are multivariate and divergent. Temperature, body mass ratio and fertility interact and help shape complex food webs.

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Part III.

General discussion

Chapter 6.

Drivers and consequences of biodiversity loss

The research chapters of this thesis elucidate different aspects of why and how extinctions might occur in food webs. To be able to assess extinctions in food webs in changing environments it is important to know what constitutes the basic extinction risk of species. Chapter 2 shows that the extinction risk within food webs is not homogeneously distributed. Instead, the risk of extinction in food webs is determined by a few general key concepts such as accessibility of energy, availability of energy pathways and population dynamics. More specifically, this means that extinction risk is highest for species on high trophic levels (thus far away from the source of energy in the web (Golley, 1960)) that consume few species (and are more likely to be negatively affected by the loss of a prey) of similar body size (thereby relying on species with similar population dynamics) with a type II functional response (which renders the population dynamics more unstable). The time to extinction of species is mainly governed by their body mass. Large species take longer to become extinct than smaller species because their lower per-unit body-mass metabolic rate. While some of these findings, such as an increased extinction risk for high trophic level species, have already been reported for specific species groups (Purvis *et al.*, 2000; Cardillo *et al.*, 2004), chapter 2 provides a general, mechanistic understanding of extinctions in food webs. This framework can be applied to a multitude of species and species communities. The theory and results I presented in chapter 2 increase the understanding how disturbances change extinction risk and might even provide a vantage point to evaluate the effects of non-trophic interactions, which have been shown to affect energy fluxes through species networks (Hacker and Gaines, 1997; Holland *et al.*, 2002; Cardinale *et al.*, 2002; Kéfi *et al.*, 2012).

Due to the multitude of interactions in food webs, the loss of one species effects the biomass of other species (Berlow *et al.*, 2009) and subsequently their extinction risk (Sole and Manrubia, 1996; Ingram and Steel, 2010). Trophic cascades are an example of how a species can directly or indirectly affect other species in a food web via feeding interactions. In chapter 3 I show that the effects of a consumer on a species two feeding links down are fundamentally different in an isolated food chain compared to those in a complex food web. In isolated three-species food chains the impact of the top on the basal species was always positive. Whereas, when embedded in a food web, the top species impact was much more variable and could be both positive and negative. Its strength was determined by the body mass and abundance of both the top species and the basal species. The high number of direct and indirect routes an effect can take in food webs frequently dilutes the impact of a consumer on a species two feeding links down. Sometimes though, these pathways amplify the effect of the consumer and it can be very strongly positive or negative. Neither the dilution, nor the amplification of effect strength can take place in the isolated food chain. For extinction studies this indicates that the complexity of species interactions should be taken into account (Harley, 2011), even if exploring the behaviour of food web modules is important and provides useful insights into how complex communities function. However, this study only looks at trophic cascades and how their direct and indirect effects are changed by embedding them into a food web. Other, future studies could test if the same also applies to other food web motifs, even if there is evidence that it will (Cohen *et al.*, 2009).

Warming and enrichment will affect extinctions in food webs in various ways (Steiner *et al.*, 2005; Durant *et al.*, 2007; Glazier, 2012; Davis *et al.*, 2013). Warming directly alters species biological rates, such as growth (Savage *et al.*, 2004), metabolism (Gillooly *et al.*, 2001; Brown *et al.*, 2004; Ehnes *et al.*, 2011) and feeding rates (Vucic-Pestic *et al.*, 2011; Lang *et al.*, 2012; Rall *et al.*, 2012). Enrichment increases the available energy and affects population dynamics (Rosenzweig, 1971; Rall *et al.*, 2008). Thus, both factors, which are major drivers of biodiversity loss (Millennium Ecosystem Assessment, 2005), can change species feeding interactions and population dynamics. However, the effects of temperature and its interplay with enrichment effects was not clear yet (Vasseur and McCann, 2005). In chapter 4, dynamic simulations of three species food chains, parameterized with empirically derived body-mass and temperature scaling relationships (Ehnes *et al.*, 2011; Rall *et al.*, 2012), show that increasing temperatures stabilize population dynamics and can counteract the destabilizing effect of enrichment. But increasing temperatures can also lead to starvation, because the increase in metabolic rates are higher than the increases in consumption. Increasing energy availability saves species from starvation. These findings are supported by empirical data (Petchey *et al.*, 1999; Kratina *et al.*, 2012; Shurin *et al.*, 2012) and are an important step to disentangle the effects of warming and enrichment. But, even if this study indicate interactive effects on population dynamics in a three species food chain, it is important to test this in a food web setting.

Subsequently, in chapter 5, I combined complex food web structures (Williams and Martinez, 2000) and the dynamic population model (Yodzis and Innes, 1992; Binzer *et al.*, 2012) with empirically derived temperature and body-mass scaling relationships for biological rates (Binzer *et al.*, 2012; Rall *et al.*, 2012). Whilst the general patterns of warming and enrichment effects seen in chapter 4 are also valid in food webs, I could show in chapter 5 that predator-prey body mass ratios influence the effect of temperature on species persistence crucially. As in the food chain, warming increases species consumption rates and their metabolic demands. More precisely, metabolism increases stronger than consumption. At low body mass ratios, the consumption rates are high and species can take higher temperatures before their metabolism outpaces their consumption. At high body mass ratios, the overall consumption rates are lower. Thus, species starvation can be observed at lower temperatures. The body mass ratios also determine the interactive effects of warming and enrichment. At low body mass ratios, the energy that enrichment adds to the system increases biomass oscillations and decreases species persistence. This is conceptually comparable to the paradox of enrichment (Rosenzweig, 1971). Warming induced higher consumption rates decrease these oscillations at low body mass ratios and thus increase persistence. At high body mass ratios, added energy increases persistence, but warming induced sharp increase in metabolism reduces it. Interestingly, the body-mass ratio even influences the relative extinction risk of specialist and generalist consumers (species with few or many prey). At high temperatures and in food webs with high body-mass ratios, specialist consumers can meet their metabolic demand due to few, but relatively strong feeding interactions. Surprisingly, generalist consumers die because none of their many, relatively weak feeding interactions yield enough energy for their survival. These effects reverberate into the final food web connectance. At low body-mass ratios and temperatures the food webs gain connectance, whereas connectance decreases at high body mass ratios and temperatures.

This study strongly suggests that body masses and species interactions (Jiang and Morin, 2004) play a major role in determining the effects of warming and enrichment and can help disentangle the complex effects of climate change. It thereby reiterates the immense importance of species body masses in food webs (Yodzis and Innes, 1992; Brown *et al.*, 2004; Brose *et al.*, 2006*a*,*b*; Otto *et al.*, 2007; Vucic-Pestic *et al.*, 2010). However, chapter 5 looks at overall species persistence, ignoring differences between species in the food web. As seen in chapter 2, these can lead to an inhomogeneous extinction risk within the food web. Further studies should therefore look at species specific extinction risks. Other studies, such as the comparison of a food web held at a constant temperature, and a food web warmed up to the same temperature would further elucidate the effect of warming on food webs. Combined with different starting connectances and species numbers, as well as varying functional responses such a study could test how food web complexity affects the effects of climate change. The food web model presented here is flexible enough to address these and many other questions in the future.

One of the basic assumptions of the model used in this thesis is that the biological parameters used to model the energy flow between species scale with the species body size (Yodzis and Innes, 1992; Brose *et al.*, 2006*b*). This assumption is based on ample evidence (Kleiber, 1932; Gillooly *et al.*, 2001; Brown *et al.*, 2004; Lang *et al.*, 2012; Ehnes *et al.*, 2011). However, there is mounting evidence that physiological rates might not only depend on the species body mass, but might actually affect it (Ohlberger, 2013). Decreasing mean body sizes with warming have been reported for many species (Sheridan and Bickford, 2011) and increases in mean annual temperatures are said to select for small body sizes (Gardner *et al.*, 2011). This as such is not implemented in the model as it is, but this trend can be explained by the model as it is. In chapter 5 it became apparent that, at higher temperatures, species in food webs with larger predator-prey body mass ratios are less persistent. The predators in these food webs have a larger body size. This decreases the interaction strength (Brose *et al.*, 2006*b*) and makes them more vulnerable to warming induced extinction (chapter 5). Smaller body sizes would therefore decrease the risk of warming induced starvation. However, this argument is not valid if, with warming, the body masses of all species decrease at the same rate, thus preserving the original body mass ratios. However, there is evidence of a heterogeneity in the temperature response of body-mass (Sheridan and Bickford, 2011). This observation is very interesting and could be helpful to understand the response of species to climate change. A mixture of empirical and theoretical studies can help elucidate it further.

Interestingly, even though the effects of the physiological parameters cascade up organizational levels and can have a huge impact on species dynamics and survival (chapters 2, 4 and 5), they can be much different, depending on the number of interacting species. In this thesis, I present two cases where the same effect was simulated once in a three species food chain and another time in a complex food web (chapter 3 and chapters 4 and 5). Both times, the isolated food chain did not represent the full behaviour of the complex food web. However, there was a difference in the magnitude of change between studies. In chapter 3, I looked at trophic cascades both in isolated chains and in food webs. Embedded in the food web, the trophic cascades were radically different than in the isolated chain, the effect of the top species sometimes even reverted and was negative instead of positive. In the other case, I first simulated the effects of warming and enrichment on species in an isolated food chain (chapter 4) and then on species in complex food webs (chapter 5). Here, the patterns found in the food chain were echoed in the food web, but where determined by the body-mass ratio. One critical difference between those two studies is that trophic cascades, by their very nature, depend on the indirect, feeding induced effect of the top species on the species two feeding links down. In the food web context this effect is easily obfuscated by the direct and indirect effects of additional feeding links (Persson *et al.*, 2001). The effects of warming and enrichment do not rely on indirect feeding effects. This might be why they are not radically changed in a food web context. This suggests that studies on indirect effects should take food web context into account, not doing so could seriously impair the broad applicability of their results.

In a theoretical study on keystone effects, the community context determined whether the keystone species could realize its potential of preventing competitive exclusion through consumption of dominant prey species (Brose *et al.*, 2005). This points towards a larger applicability of the results found in this thesis.

This thesis emphasizes the importance of energy availability and dynamic stability as factors determining the extinction risk of species. These energy fluxes are modeled based on ecological meaningful biological parameters and thus are likely to reflect the reality of natural food webs. Thus, models like the one used throughout this thesis are capable of identifying complex effects and provide possible mechanistic explanations of extinctions in recent food webs, as well as ones affected by climate change. Therefore, they can provide explanations and hypotheses for experimental testing and can help understanding and protecting the awe-inspiringly complexity of global diversity.

Part IV.

Appendix

References

Abrams, P. A. and Walters, C. J. (1996). Invulnerable prey and the paradox of enrichment. *Ecology* 77:1125–1133.

Artigas, J., García-Berthou, E., Bauer, D. E., Castro, M. I., Cochero, J., Colautti, D. C., Cortelezzi, A., Donato, J. C., Elosegi, A., Feijoó, C., Giorgi, A., Gómez, N., Leggieri, L., Muñoz, I., Rodrigues-Capítulo, A., Romaní, A. M., and Sabater, S. (2013). Global pressures, specific responses: effects of nutrient enrichment in streams from different biomes. *Environmental Research Letters* 8:014002.

Barnosky, A. D., (2009). *Heatstroke: Nature in an Age of Global Warming.* Island Press. ISBN 9781597265294.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., and Ferrer, E. A. (2011). Has the earth's sixth mass extinction already arrived? *Nature* 471:51–57.

Bascompte, J. and Melián, C. J. (2005). Simple trophic modules for complex food webs. *Ecology* 86:2868–2873.

Bascompte, J., Melián, C. J., and Sala, E. (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.

Beaver, R. A. (1979). Host specificity of temperate and tropical animals. *Nature* 281:139–141.

Beckerman, A. P., Uriarte, M., and Schmitz, O. J. (1997). Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Academy of Sciences of the United States of America* 94:10735–10738.

Beisner, B., Mccauley, E., and Wrona, F. (1996). Temperature-mediated dynamics of planktonic food chains: the effect of an invertebrate carnivore. *Freshwater Biology* 35:219–232.

Beisner, B., McCauley, E., and Wrona, F. (1997). The influence of temperature and food chain length on plankton predator-prey dynamics. *Canadian Journal of Fisheries and Aquatic Sciences* 54:586–595.

Berlow, E. L., Dunne, J. A., Martinez, N. D., Stark, P. B., Williams, R. J., and Brose, U. (2009). Simple prediction of interaction strengths in complex food webs. *Proceedings of the National Academy of Sciences* 106:187–191.

Berlow, E. L., Neutel, A., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen, V. A. A., Jones, J. I., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., and Petchey, O. (2004). Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology* 73:585–598.

Binzer, A., (2009). The strength of trophic cascades in model communities.

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

Binzer, A., Guill, C., Brose, U., and Rall, B. C. (2012). The dynamics of food chains under climate change and nutrient enrichment. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367:2935–2944.

Borer, E. T., Seabloom, E. W., Shurin, J. B., Anderson, K. E., Blanchette, C. A., Broitman, B., Cooper, S. D., and Halpern, B. S. (2005). What determines the strength of a trophic cascade? *Ecology* 86:528–537.

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., Berlow, E. L., and Martinez, N. D. (2005). Scaling up keystone effects from simple to complex ecological networks. *Ecology Letters* 8:1317–1325.

Brose, U., Dunne, J. A., Montoya, J. M., Petchey, O. L., Schneider, F. D., and Jacob, U. (2012). Climate change in size-structured ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367:2903–2912.

Brose, U., Jonsson, T., Berlow, E. L., Warren, P., Banasek-Richter, C., Bersier, L., Blanchard, J. L., Brey, T., Carpenter, S. R., Blandenier, M. C., Cushing, L., Dawah, H. A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M. E., Martinez, N. D., Memmott, J., Mintenbeck, K., Pinnegar, J. K., Rall, B. C., Rayner, T. S., Reuman, D. C., Ruess, L., Ulrich, W., Williams, R. J., Woodward, G., and Cohen, J. E. (2006*a*). Consumer-resource body-size relationships in natural food webs. *Ecology* 87:2411–2417.

Brose, U., Williams, R. J., and Martinez, N. D. (2006*b*). Allometric scaling enhances stability in complex food webs. *Ecology Letters* 9:1228–1236.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., and West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.

Bruno, J. and O'Connor, M. (2005). Cascading effects of predator diversity and omnivory in a marine food web. *Ecology Letters* 8:1048–1056.

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., Orme, C. D. L., and Purvis, A. (2005). Multiple causes of high extinction risk in large mammal species. *Science* 309:1239–1241.

Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J., and Mace, G. M. (2004). Human population density and extinction risk in the world's carnivores. *PLoS Biol* 2:e197.

Cardinale, B. J., Palmer, M. A., and Collins, S. L. (2002). Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* 415:426–429.

Chase, J. M. (2000). Are there real differences among aquatic and terrestrial food webs? *Trends in Ecology & Evolution* 15:408–412.

Chitty, H. (1948). The snowshoe rabbit enquiry, 1943-46. *The Journal of Animal Ecology* 17:39.

Clarke, A. (2006). Temperature and the metabolic theory of ecology. *Functional Ecology* 20:405–412.

Cohen, J. E. and Newman, C. M. (1985). A stochastic theory of community food webs: I. models and aggregated data. *Proceedings of the Royal Society of London. Series B. Biological Sciences* 224:421–448.

Cohen, J. E., Schittler, D. N., Raffaelli, D. G., and Reuman, D. C. (2009). Food webs are more than the sum of their tritrophic parts. *Proceedings of the National Academy of Sciences* 106:22335–22340.

Coll, M., Schmidt, A., Romanuk, T., and Lotze, H. K. (2011). Food-web structure of seagrass communities across different spatial scales and human impacts. *PLoS ONE* 6.

Curtsdotter, A., Binzer, A., Brose, U., de Castro, F., Ebenman, B., Eklöf, A., Riede, J. O., Thierry, A., and Rall, B. C. (2011). Robustness to secondary extinctions:

Comparing trait-based sequential deletions in static and dynamic food web. *Basic and Applied Ecology* 12:571–580.

Dalsgaard, B., Magård, E., Fjeldså, J., Martín González, A. M., Rahbek, C., Olesen, J. M., Ollerton, J., Alarcón, R., Cardoso Araujo, A., Cotton, P. A., Lara, C., Machado, C. G., Sazima, I., Sazima, M., Timmermann, A., Watts, S., Sandel, B., Sutherland, W. J., and Svenning, J.-C. (2011). Specialization in plant-hummingbird networks is associated with species richness, contemporary precipitation and quaternary climate-change velocity. *PLoS ONE* 6:e25891.

Darwin, C., (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London.

Daufresne, M., Lengfellner, K., and Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences* .

Davis, A. J., Jenkinson, L. S., Lawton, J. H., Shorrocks, B., and Wood, S. (1998). Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391:783–786.

Davis, J. M., Baxter, C. V., Minshall, G. W., Olson, N. F., Tang, C., and Crosby, B. T. (2013). Climate-induced shift in hydrological regime alters basal resource dynamics in a wilderness river ecosystem. *Freshwater Biology* 58:306–319.

Davis, J. M., Rosemond, A. D., Eggert, S. L., Cross, W. F., and Wallace, J. B. (2010). Long-term nutrient enrichment decouples predator and prey production. *Proceedings of the National Academy of Sciences* 107:121–126.

de Sassi, C., Staniczenko, P. P. A., and Tylianakis, J. M. (2012). Warming and nitrogen affect size structuring and density dependence in a host–parasitoid food web. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367:3033–3041.

Digel, C., Riede, J. O., and Brose, U. (2011). Body sizes, cumulative and allometric degree distributions across natural food webs. *Oikos* 120:503–509.

Dunne, J. A. and Williams, R. J. (2009). Cascading extinctions and community collapse in model food webs. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:1711–1723.

Dunne, J. A., Williams, R. J., and Martinez, N. D. (2004). Network structure and robustness of marine food webs. *Marine Ecology Progress Series* 273:291–302.

Durant, J. M., Hjermann, D., Ottersen, G., and Stenseth, N. C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* 33:271–283.

Ebenman, B., Law, R., and Borrvall, C. (2004). Community viability analysis: the response of ecological communities to species loss. *Ecology* 85:2591–2600.

Ehnes, R. B., Rall, B. C., and Brose, U. (2011). Phylogenetic grouping, curvature and metabolic scaling in terrestrial invertebrates. *Ecology Letters* 14:993–1000.

Eitzinger, B. and Traugott, M. (2011). Which prey sustains cold-adapted invertebrate generalist predators in arable land? examining prey choices by molecular gut-content analysis. *Journal of Applied Ecology* 48:591–599.

Eklöf, A. and Ebenman, B. (2006). Species loss and secondary extinctions in simple and complex model communities. *Journal of Animal Ecology* 75:239–246.

Elmhagen, B. and Rushton, S. P. (2007). Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecology Letters* 10:197–206.

Elton, C. and Nicholson, M. (1942). The ten-year cycle in numbers of the lynx in canada. *The Journal of Animal Ecology* 11:215.

Elton, C. S., (1927). *Animal ecology.* Sidgwick and Jackson, London.

Englund, G., Öhlund, G., Hein, C. L., and Diehl, S. (2011). Temperature dependence of the functional response. *Ecology Letters* 14:914–921.

Enquist, B., West, G., Charnov, E., and Brown, J. (1999). Allometric scaling of production and life-history in vascular plants. *Nature* 401:907–911.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., Shurin, J. B., Sinclair, A. R. E., Soulé, M. E., Virtanen, R., and Wardle, D. A. (2011). Trophic downgrading of planet earth. *Science* 333:301–306.

Finke, D. L. and Denno, R. F. (2004). Predator diversity dampens trophic cascades. *Nature* 429:407–410.

Finke, D. L. and Denno, R. F. (2005). Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters* 8:1299–1306.

Fox, J. W. and Olsen, E. (2000). Food web structure and the strength of transient indirect effects. *Oikos* 90:219–226.

Fussmann, G. F., Ellner, S. P., Shertzer, K. W., and Hairston Jr, N. G. (2000). Crossing the hopf bifurcation in a live predator-prey system. *Science* 290:1358–1360.

Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., and Heinsohn, R. (2011). Declining body size: a third universal response to warming? *Trends in Ecology & Evolution* 26:285–291.

Genkai-Kato, M. and Yamamura, N. (1999). Unpalatable prey resolves the paradox of enrichment. *Proceedings of the Royal Society B: Biological Sciences* 266:1215–1209.

Gillooly, J. F. (2000). Effect of body size and temperature on generation time in zooplankton. *Journal of Plankton Research* 22:241–251.

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., and Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science* 293:2248–2251.

Glazier, D. S. (2012). Temperature affects food-chain length and macroinvertebrate species richness in spring ecosystems. *Freshwater Science* 31:575–585.

Golley, F. B. (1960). Energy dynamics of a food chain of an old-field community. *Ecological Monographs* 30:187–206.

Hacker, S. D. and Gaines, S. D. (1997). Some implications of direct positive interactions for community species diversity. *Ecology* 78:1990–2003.

Hairston, N. G., Smith, F. E., and Slobodkin, L. B. (1960). Community structure, population control, and competition. *The American Naturalist* 94:421.

Halaj, J. and Wise, D. H. (2001). Terrestrial trophic cascades: How much do they trickle? *The American Naturalist* 157:262–281.

Halbach, U. (1970). Die ursachen der temporalvariation von *Brachionus calyciflorus* pallas (Rotatoria). *Oecologia* 4:262–318.

Halbach, Udo. (1970). Einfluss der temperatur auf die populationsdynamik des planktischen raedertieres *Brachionus calyciflorus* pallas (Influence of temperature on the population dynamics of the rotifer brachionus calyciflorus pallas). *Oecologia* 4:176–207.

Hansen, P., Bjornsen, P., and Hansen, B. (1997). Zooplankton grazing and growth: Scaling within the 2-2,000-mu m body size range. *Limnology and Oceanography* 42:687–704.

Harley, C. D. G. (2011). Climate change, keystone predation, and biodiversity loss. *Science* 334:1124–1127.

Harmon, J. P., Moran, N. A., and Ives, A. R. (2009). Species response to environmental change: Impacts of food web interactions and evolution. *Science* 323:1347–1350.

Hawkins, B. A. (1990). Global patterns of parasitoid assemblage size. *The Journal of Animal Ecology* 59:57.

Heckmann, L., Drossel, B., Brose, U., and Guill, C. (2012). Interactive effects of body-size structure and adaptive foraging on food-web stability. *Ecology letters* 15:243–250.

Hoekman, D. (2010). Turning up the heat: temperature influences the relative importance of top-down and bottom-up effects. *Ecology* 91:2819–2825.

Holland, J. N., DeAngelis, D. L., and Bronstein, J. L. (2002). Population dynamics and mutualism: Functional responses of benefits and costs. *The American Naturalist* 159:231–244.

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.

Holling, C. S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada* 45:1–60.

Holt, R. D., (1997). Community modules. Pages 333–349 *in* Multitrophic Interactions in Terrestrial Ecosystems. Blackwell Science, Oxford.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., and Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.

Hutchinson, G. E. (1959). Homage to santa rosalia or why are there so many kinds of animals? *The American Naturalist* 93:145–159.

Ingram, T. and Steel, M. (2010). Modelling the unpredictability of future biodiversity in ecological networks. *Journal of Theoretical Biology* 264:1047–1056.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J., and Warner, R. R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–637.

Janzen, D., (1973). Comments on host-specificity of tropical herbivores and its relevance to species richness. Pages 201–211 *in* Taxonomy and ecology, volume 5. Academic Press, London.

Jiang, L. and Morin, P. J. (2004). Temperature-dependent interactions explain unexpected responses to environmental warming in communities of competitors. *Journal of Animal Ecology* 73:569–576.

Kalinkat, G., Brose, U., and Rall, B. C. (2012). Habitat structure alters top-down control in litter communities. *Oecologia* .

Kartascheff, B., Guill, C., and Drossel, B. (2009). Positive complexity-stability relations in food web models without foraging adaptation. *Journal of theoretical biology* 259:12–23.

Kaunzinger, C. M. K. and Morin, P. J. (1998). Productivity controls food-chain properties in microbial communities. *Nature* 395:495–497.

Kéfi, S., Berlow, E. L., Wieters, E. A., Navarrete, S. A., Petchey, O. L., Wood, S. A., Boit, A., Joppa, L. N., Lafferty, K. D., Williams, R. J., Martinez, N. D., Menge, B. A., Blanchette, C. A., Iles, A. C., and Brose, U. (2012). More than a meal... integrating non-feeding interactions into food webs. *Ecology Letters* 15:291–300.

Kleiber, M. (1932). Body size and metabolism. *Hilgardia* 6:315–353.

Koen-Alonso, (2007). A process-oriented approach to the multispecies functional response *in* From energetics to ecosystems: the dynamics and structure of ecological systems. Springer.

Kondoh, M. (2008). Building trophic modules into a persistent food web. *Proceedings of the National Academy of Sciences* 105:16631–16635.

Kratina, P., Greig, H., Thompson, P. L., Carvalho-Pereira, T. S. A., and Shurin, J. B. (2012). Warming modifies trophic cascades and eutrophication in experimental freshwater communities. *Ecology* .

Kratina, P., Vos, M., Bateman, A., and Anholt, B. (2009). Functional responses modified by predator density. *Oecologia* 159:425–433.

Lang, B., Rall, B. C., and Brose, U. (2012). Warming effects on consumption and intraspecific interference competition depend on predator metabolism. *Journal of Animal Ecology* .

Lefébure, R., Degerman, R., Andersson, A., Larsson, S., Eriksson, L.-O., Båmstedt, U., and Byström, P. (2013). Impacts of elevated terrestrial nutrient loads and temperature on pelagic food-web efficiency and fish production. *Global change biology* .

Lemoine, N. P. and Burkepile, D. E. (2012). Temperature-induced mismatches between consumption and metabolism reduce consumer fitness. *Ecology* 93:2483–2489.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., Tilman, D., and Wardle, D. A. (2001). Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294:804–808.

Lotka, A., (1925). *Elements of physical biology.* Williams & Wilkins, Baltimore.

MacArthur, R. (1955). Fluctuations of animal populations and a measure of community stability. *Ecology* 36:533.

MacArthur, R. H., (1972). *Geographical ecology: patterns in the distribution of species.* Princeton University Press. ISBN 9780691023823.

MacArthur, R. H. and Rosenzweig, M. L. (1963). Graphical representation and stability conditions of predator-prey interactions. *American Naturalist* 97:209–223.

May, R. M. (1972). Will a large complex system be stable? *Nature* 238:413–414.

McCann, K. and Yodzis, P. (1994). Biological conditions for chaos in a three-species food chain. *Ecology* 75:561–564.

McKinney, M. L. (1997). Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics* 28:495–516.

Meehan, T. D. (2006). Energy use and animal abundance in litter and soil communities. *Ecology* 87:1650–1658.

Millennium Ecosystem Assessment, (2005). *Millennium Ecosystem Assessment, Ecosystems and Human Well-being: Biodiversity Synthesis.* World Resources Institute, Washington, DC.

Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., and Alon, U. (2002). Network motifs: Simple building blocks of complex networks. *Science* 298:824–827.

Nee, S. and May, R. M. (1997). Extinction and the loss of evolutionary history. *Science* 278:692–694.

Nelson, G. C., (2005). *Millenium Ecosystem Assessment: Drivers of ecosystem change: summary chapter.* World Resources Institute, Washington, DC.

Newth, D. (2008). Food web complexity: latitudinal trends, topological properties and stability. *Complexity international* 12.

Nomdedeu, M. M., Willen, C., Schieffer, A., and Arndt, H. (2012). Temperature-dependent ranges of coexistence in a model of a two-prey-one-predator microbial food web. *Marine Biology* 159:2423–2430.

O'Connor, M. I., Piehler, M. F., Leech, D. M., Anton, A., and Bruno, J. F. (2009). Warming and resource availability shift food web structure and metabolism. *PLoS Biol* 7:e1000178.

Ohlberger, J. (2013). Climate warming and ectotherm body size – from individual physiology to community ecology. *Functional Ecology* Pages 1–11.

Ollerton, J. and Cranmer, L. (2002). Latitudinal trends in plant-pollinator interactions: are tropical plants more specialised? *Oikos* 98:340–350.

Ott, D., Rall, B. C., and Brose, U. (2012). Climate change effects on macrofaunal litter decomposition: the interplay of temperature, body masses and stoichiometry. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367:3025–3032.

Otto, S. B., Berlow, E. L., Rank, N. E., Smiley, J., and Brose, U. (2008). Predator diversity and identity drive interaction strength and trophic cascades in a food web. *Ecology* 89:134–144.

Otto, S. B., Rall, B. C., and Brose, U. (2007). Allometric degree distributions facilitate food-web stability. *Nature* 450:1226–1229.

Pace, M. L., Cole, J. J., Carpenter, S. R., and Kitchell, J. F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution* 14:483–488.

Paine, R. T. (1966). Food web complexity and species diversity. *The American Naturalist* 100:65–75.

Paine, R. T. (1980). Food webs: Linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* 49:667–685.

Parmesan, C. (1996). Climate and species' range. *Nature* 382:765–766.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* 37:637–669.

Pascual, M. and Dunne, J. A., (2005). *Ecological Networks: Linking Structure to Dynamics in Food Webs*. Oxford University Press. ISBN 9780199884919.

Peñuelas, J., Sardans, J., Estiarte, M., Ogaya, R., Carnicer, J., Coll, M., Barbeta, A., Rivas-Ubach, A., Llusià, J., Garbulsky, M., Filella, I., and Jump, A. S. (2013). Evidence of current impact of climate change on life: a walk from genes to the biosphere. *Global change biology* .

Persson, A., Hansson, L. A., Brönmark, C., Lundberg, P., Pettersson, L. B., Greenberg, L., Nilsson, P. A., Nyström, P., Romare, P., and Tranvik, L. (2001). Effects of enrichment on simple aquatic food webs. *The American naturalist* 157:654–669.

Persson, L. (1999). Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. *Oikos* 85:385–397.

Petchey, O. L., Beckerman, A. P., Riede, J. O., and Warren, P. H. (2008). Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences* 105:4191–4196.

Petchey, O. L., McPhearson, P. T., Casey, T. M., and Morin, P. J. (1999). Environmental warming alters food-web structure and ecosystem function. *Nature* 402:69–72.

Peters, R. H., (1983). *The ecological implications of body size*. Cambridge University Press. ISBN 9780521288866.

Pimm, S. L. (1980). Food web design and the effect of species deletion. *Oikos* 35:139–149.

Pimm, S. L. and Lawton, J. H. (1977). Number of trophic levels in ecological communities. *Nature* 268:329–331.

Pimm, S. L., Lawton, J. H., and Cohen, J. E. (1991). Food web patterns and their consequences. *Nature* 350:669–674.

Pimm, S. L., Russell, G. J., Gittleman, J. L., and Brooks, T. M. (1995). The future of biodiversity. *Science* 269:347–350.

Polis, G. (1999). Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* 86:3 –15.

Polis, G. A. (1994). Food webs, trophic cascades and community structure. *Australian Journal of Ecology* 19:121–136.

Polis, G. A., Sears, A. L. W., Huxel, G. R., Strong, D. R., and Maron, J. (2000). When is a trophic cascade a trophic cascade? *Trends in Ecology & Evolution* 15:473–475.

Polis, G. A. and Strong, D. R. (1996). Food web complexity and community dynamics. *The American Naturalist* 147:813–846.

Post, D. M. (2002). The long and short of food-chain length. *Trends in Ecology & Evolution* 17:269–277.

Post, D. M., Pace, M. L., and Hairston, N. G. (2000). Ecosystem size determines food-chain length in lakes. *Nature* 405:1047–1049.

Purvis, A., Gittleman, J. L., Cowlishaw, G., and Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences* 267:1947–1952.

R Development Core Team, (2009). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL `http://www.R-project.org`, ISBN 3-900051-07-0.

Rall, B. C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O., and Petchey, O. L. (2012). Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences* 367:2923–2934.

Rall, B. C., Guill, C., and Brose, U. (2008). Food-web connectance and predator interference dampen the paradox of enrichment. *Oikos* 117:202–213.

Rall, B. C., Kalinkat, G., Ott, D., Vucic-Pestic, O., and Brose, U. (2011). Taxonomic versus allometric constraints on non-linear interaction strengths. *Oikos* 120:483–492.

Rall, B. C., Vucic-Pestic, O., Ehnes, R. B., Emmerson, M., and Brose, U. (2010). Temperature, predator-prey interaction strength and population stability. *Global Change Biology* 16:2145–2157.

Raup, D. M., (1992). Extinction: Bad genes or bad luck? Pages 563–564 in *J. C. Barry, ed. American Journal of Physical Anthropology*. New York: W. W. Norton.

Real, L. A. (1977). The kinetics of functional response. *The American Naturalist* 111:289–300.

Regan, H. M., Lupia, R., Drinnan, A. N., and Burgman, M. A. (2001). The currency and tempo of extinction. *The American Naturalist* 157:1–10.

Riede, J. O., Brose, U., Ebenman, B., Jacob, U., Thompson, R., Townsend, C. R., and Jonsson, T. (2011). Stepping in elton's footprints: a general scaling model for body masses and trophic levels across ecosystems. *Ecology Letters* 14:169–178.

Rip, J. M. K. and McCann, K. S. (2011). Cross-ecosystem differences in stability and the principle of energy flux. *Ecology Letters* 14:733–740.

Ripley, B., (2010). *tree: Classification and regression trees*. URL `http://CRAN.R-project.org/package=tree`, r package version 1.0-28.

Ripple, W. J. and Beschta, R. L. (2012). Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation* 145:205–213.

Rooney, N., McCann, K., Gellner, G., and Moore, J. C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature* 442:265–269.

Rosenzweig, M. L. (1971). Paradox of enrichment: Destabilization of exploitation ecosystems in ecological time. *Science* 171:385–387.

Roy, S. and Chattopadhyay, J. (2007). The stability of ecosystems: a brief overview of the paradox of enrichment. *Journal of Biosciences* 32:421–428.

Sarnelle, O. and Wilson, A. E. (2008). Type III functional response in daphnia. *Ecology* 89:1723–1732.

Savage, V. M., Gillooly, J. F., Brown, J. H., West, G. B., and Charnov, E. (2004). Effects of body size and temperature on population growth. *The American Naturalist* 163:429–441.

Schleuning, M., Fründ, J., Klein, A.-M., Abrahamczyk, S., Alarcón, R., Albrecht, M., Andersson, G. K. S., Bazarian, S., Böhning-Gaese, K., Bommarco, R., Dalsgaard, B., Dehling, D. M., Gotlieb, A., Hagen, M., Hickler, T., Holzschuh, A., Kaiser-Bunbury, C. N., Kreft, H., Morris, R. J., Sandel, B., Sutherland, W. J., Svenning, J.-C., Tscharntke, T., Watts, S., Weiner, C. N., Werner, M., Williams, N. M., Winqvist, C., Dormann, C. F., and Blüthgen, N. (2012). Specialization of mutualistic interaction networks decreases toward tropical latitudes. *Current biology: CB* 22:1925–1931.

Schmitz, Hambäck, and Beckerman. (2000). Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. *The American Naturalist* 155:141–153.

Schmitz, O. J. (1998). Direct and indirect effects of predation and predation risk in Old-Field interaction webs. *The American Naturalist* 151:327–342.

Schmitz, O. J., Krivan, V., and Ovadia, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* 7:153–163.

Schneider, F. D. and Brose, U. (2013). Beyond diversity: how nested predator effects control ecosystem functions. *Journal of Animal Ecology* 82:64–71.

Schneider, F. D., Scheu, S., and Brose, U. (2012). Body mass constraints on feeding rates determine the consequences of predator loss. *Ecology Letters* 15:436–443.

Sheridan, J. A. and Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change* 1:401–406.

Shurin, J. B., Borer, E. T., Seabloom, E. W., Anderson, K., Blanchette, C. A., Broitman, B., Cooper, S. D., and Halpern, B. S. (2002). A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* 5:785–791.

Shurin, J. B., Clasen, J. L., Greig, H. S., Kratina, P., and Thompson, P. L. (2012). Warming shifts top-down and bottom-up control of pond food web structure and function. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367:3008–3017.

Shurin, J. B. and Seabloom, E. W. (2005). The strength of trophic cascades across ecosystems: predictions from allometry and energetics. *Journal of Animal Ecology* 74:1029–1038.

Simberloff, D., (1998). Small and delining populations. Pages 116–134 in *W. J. Sutherland, ed. Conservation science and action.* Oxford, UK: Blackwell Science.

Solan, M., Cardinale, B. J., Downing, A. L., Engelhardt, K. A. M., Ruesink, J. L., and Srivastava, D. S. (2004). Extinction and ecosystem function in the marine benthos. *Science* 306:1177–1180.

Sole, R. V. and Manrubia, S. C. (1996). Extinction and self-organized criticality in a model of large-scale evolution. *Physical Review E* 54:R42–R45.

Solow, A. R. (1996). On the goodness of fit of the cascade model. *Ecology* 77:1294.

Sommer, U. (2008). Trophic cascades in marine and freshwater plankton. *International Review of Hydrobiology* 93:506–516.

Steiner, C. F., Long, Z. T., Krumins, J. A., and Morin, P. J. (2005). Temporal stability of aquatic food webs: partitioning the effects of species diversity, species composition and enrichment. *Ecology Letters* 8:819–828.

Stouffer, D. B. and Bascompte, J. (2010). Understanding food-web persistence from local to global scales. *Ecology Letters* 13:154–161.

Strong, D. R. (1992). Are trophic cascades all wet? Differentiation and Donor-Control in speciose ecosystems. *Ecology* 73:747–754.

Summerhayes, V. S. and Elton, C. S. (1923). Introduction. *The Journal of Ecology* 11:214.

Tewfik, A., Rasmussen, J. B., and McCann, K. S. (2007). Simplification of seagrass food webs across a gradient of nutrient enrichment.(report). *Canadian Journal of Fisheries and Aquatic Sciences* 64:956–967.

Trzcinski, M. K., Walde, S. J., and Taylor, P. D. (2005). Stability of pitcher-plant microfaunal populations depends on food web structure. *Oikos* 110:146–154.

Tuda, M. and Shimada, M. (1995). Developmental schedules and persistence of experimental host-parasitoid systems at two different temperatures. *Oecologia* 103:283–291.

Twomey, M., Brodte, E., Jacob, U., Brose, U., Crowe, T. P., and Emmerson, M. C. (2012). Idiosyncratic species effects confound size-based predictions of responses to climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367:2971–2978.

Tylianakis, J. M. (2008). Understanding the web of life: The birds, the bees, and sex with aliens. *PLoS Biol* 6:e47.

Utsumi, S., Kishida, O., and Ohgushi, T. (2010). Trait-mediated indirect interactions in ecological communities. *Population Ecology* 52:457–459.

Van Donk, E., Ianora, A., and Vos, M. (2011). Induced defences in marine and freshwater phytoplankton: a review. *Hydrobiologia* 668:3–19.

Vasseur, D. A. and McCann, K. S. (2005). A mechanistic approach for modeling temperature-dependent consumer-resource dynamics. *The American Naturalist* 166:184–198.

Voigt, W., Perner, J., Davis, A., Eggers, T., Schumacher, J., Bährmann, R., Fabian, B., Heinrich, W., Köhler, G., Lichter, D., Marstaller, R., and Sander, F. (2003). Trophic levels are differentially sensitive to climate. *Ecology* 84:2444–2453.

Volterra, V. (1926). Fluctuations in the abundance of a species considered mathematically. *Nature* 118:558–560.

Vos, M., Kooi, B. W., DeAngelis, D. L., and Mooij, W. M. (2004). Inducible defences and the paradox of enrichment. *Oikos* 105:471–480.

Vucic-Pestic, O., Ehnes, R., Rall, B. C., and Brose, U. (2011). Warming up the system: higher predator feeding rates but lower energetic efficiencies. *Global Change Biology* 17:1301–1310.

Vucic-Pestic, O., Rall, B. C., Kalinkat, G., and Brose, U. (2010). Allometric functional response model: body masses constrain interaction strengths. *Journal of Animal Ecology* 79:249–256.

Wagler, R. (2011). The anthropocene mass extinction: An emerging curriculum theme for science educators. *The American Biology Teacher* 73:78–83.

Wake, D. B. and Vredenburg, V. T. (2008). Colloquium paper: Are we in the midst of the sixth mass extinction? a view from the world of amphibians. *Proceedings of the National Academy of Sciences* 105:11466–11473.

West, G. B., Brown, J. H., and Enquist, B. J. (1997). A general model for the origin of allometric scaling laws in biology. *Science* 276:122–126.

Williams, R. J. and Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature* 404:180–183.

Williams, R. J. and Martinez, N. D. (2004*a*). Limits to trophic levels and omnivory in complex food webs: theory and data. *The American Naturalist* 163:458–468.

Williams, R. J. and Martinez, N. D. (2004*b*). Stabilization of chaotic and non-permanent food-web dynamics. *The European Physical Journal B - Condensed Matter* 38:297–303.

Williams, R. J. and Martinez, N. D. (2008). Success and its limits among structural models of complex food webs. *Journal of Animal Ecology* 77:512–519.

Wood, S., (2006). *Generalized Additive Models: An Introduction with R.* Chapman and Hall/CRC.

Wood, S. A., Lilley, S. A., Schiel, D. R., and Shurin, J. B. (2010). Organismal traits are more important than environment for species interactions in the intertidal zone. *Ecology Letters* 13:1160–1171.

Woodward, G., Dybkjær, J. B., Ólafsson, J. S., Gíslason, G. M., Hannesdóttir, E. R., and Friberg, N. (2010*a*). Sentinel systems on the razor's edge: effects of warming on arctic geothermal stream ecosystems. *Global Change Biology* 16:1979–1991.

Woodward, G. and Hildrew, A. G. (2001). Invasion of a stream food web by a new top predator. *Journal of Animal Ecology* 70:273–288.

Woodward, G., Perkins, D. M., and Brown, L. E. (2010*b*). Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2093–2106.

Yodzis, P. and Innes, S. (1992). Body size and Consumer-Resource dynamics. *The American Naturalist* 139:1151–1175.

Yvon-Durocher, G., Jones, J. I., Trimmer, M., Woodward, G., and Montoya, J. M. (2010). Warming alters the metabolic balance of ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2117–2126.

Yvon-Durocher, G., Montoya, J. M., Trimmer, M., and Woodward, G. (2011). Warming alters the size spectrum and shifts the distribution of biomass in freshwater ecosystems. *Global Change Biology* 17:1681–1694.

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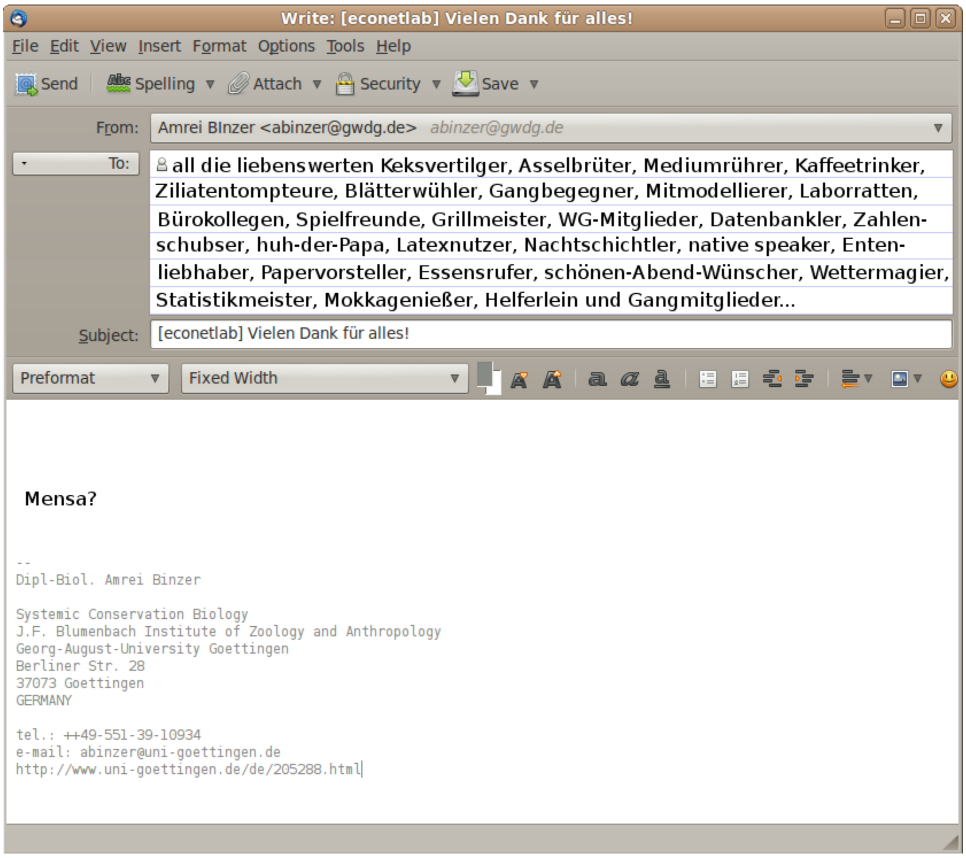

From: Amrei BInzer <abinzer@gwdg.de> abinzer@gwdg.de

To: all die liebenswerten Keksvertilger, Asselbrüter, Mediumrührer, Kaffeetrinker, Ziliatentompteure, Blätterwühler, Gangbegegner, Mitmodellierer, Laborratten, Bürokollegen, Spielfreunde, Grillmeister, WG-Mitglieder, Datenbankler, Zahlenschubser, huh-der-Papa, Latexnutzer, Nachtschichtler, native speaker, Entenliebhaber, Papervorsteller, Essensrufer, schönen-Abend-Wünscher, Wettermagier, Statistikmeister, Mokkagenießer, Helferlein und Gangmitglieder...

Subject: [econetlab] Vielen Dank für alles!

Mensa?

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Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Arbeit selbstständig angefertigt, keine unerlaubten Hilfsmittel verwendet und bisher noch keinen Promotionsversuch unternommen habe.

Amrei Binzer
Göttingen,