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Topology and stability of complex food webs

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ZUSAMMENFASSUNG

Bereits im frühen zwanzigsten Jahrhundert wurden diverse Gesetze entwickelt, um Stabilität von natürlichen Nahrungsnetzen zu erklärn. Bis heute konnten aber keine allgemein gültigen Abhängigkeiten gefunden werden. Das Hauptziel der Ökologie ist es, den "Zugrundlegenden Mechanismus" zu verstehen, der Dynamiken in Nahrungsnetzen beschreibt, um dem globalen Artensterben entgegenzuwirken. Die hier präsentierten Studien, untersuchen die generelle Skalierung von Nahrungsnetz- (z.B. Diversität, Grad der biologischen Verknüpftheit der Arten [nachstehend: connectance]) und Arten Eigenschaften (z.B. Körpergröße, Trophische Ebene) und wie diese Eigenschaften Sekundäres Aussterben in Nahrungsnetzen beeinflussen. Das Rückgrat dieser Arbeit bildet dabei eine Nahrungsnetz Datenbank, welche Informationen über Art Interaktionen, Metabolische Typen und Art Körpermassen enthält.

In der Vergangenheit wurde der Zusammenhang zwischen Diversität und Topologie stark diskutiert. Spezielle die Hypothese, dass eine konstante Anzahl von Arten Pro Link zu einer Abnahme der connectance bei einer ansteigenden Artenzahl führt. Die Alternative zu dieser Hypothese ist die 'constant connectance' Hypothese. Dabei ist die connectance gleichbleibend mit steigender Artenzahl.

Im Rahmen meiner Doktorarbeit, (Kapitel 2) analysierte ich den Zusammenhang von Topologischen Eigenschaften in der von mir zusammengestellten Datenbank. Dabei fand ich heraus, dass connectance mit zunehmender Artenzahl abnimmt. Darüber hinaus wurden allgemeine Parameter der Biokomplexität (z.B. Fraktion der Top, Intermediären und Basal Arten oder der mittlere Trophische Level) hinsichtlich ihrer Skalierung gegen connectance und Diversität untersucht. Interessanterweise unterscheidet sich in machen fällen die Steigung zwischen verschieden Ökosystem Typen.

Viele Arteigenschaften sind abhängig von der Körpermasse (z.B. Räuber-Beute Interaktionen, Stoffwechsel, Mobilität). Dies macht Körpermasse zu einem der wichtigsten Arten Attribute. Kapitel 3 beschäftigt sich mit der Verteilung von mittleren Populationskörpermassen in Artgemeinschaften verschiedener Ökosysteme. Körpermasse ist dabei meist log–normal (Terrestrische und Fluss Nahrungsnetze) oder multimodal (See und Marine Nahrungsnetze) verteilt, zudem zeigen die meisten Netzwerke eine exponentielle kumulative Gradverteilung (die Gradverteilung beschreibt die durchschnittliche Anzahl der Links pro Art in einem Netzwerk). Eine Ausnahme bilden dabei die Flussnahrungsnetze, welche oft eine einheitliche Gradverteilung zeigen. Zudem steigt mit der Körpergröße die Verwundbarkeit (Anteil Räuber pro Art) in 70% der untersuchten Netze ab, und die in 80% der Nahrungsnetze nimmt die Generalität (Anteil

Beuten pro Art) zu.

Elton's Paradigmen zuwendend, analysierte ich die Beziehung von Prädatoren Masse zu Beute Masse und trophischer Position, sowie die Beziehung des Verhältnisses von Prädatoren–Beuten Masse [nachstehend: Massenverhältnis] zur trophischen Position des Prädatoren (Kapitel 4). Im Jahr 1927 fand Elton herraus, dass (i) die mittlere Beute Masse sich mit der Prädatoren Masse erhöht , (ii) die Prädatorenmasse zunehmender trophischer Ebene ansteigt, und (iii) das Massenverhältnis konstant über trophische Ebenen ist. Durch die Analyse meiner Datenbank, konnte ich die Paradigmen (i) und (ii) bestätigen. Allerdings, im Einklang mit theoretischen Vorhersagen, fand ich eine systematische Abnahme der Massenverhältnisse mit der trophischen Ebene des Prädatores. Dieses Ergebnis zeigt, dass im Durchschnitt Prädatoren an der Spitze der Nahrungskette bezüglich ihrer Größe ihren Beuten ähnlicher als Arten näher an der Basis sind.
Nahrungsnetze Stabilität hängt entscheidend vom Artenverlust ab. In zwei Projekten (Kapitel 5, 6), benutzte ich einen bioenergetischen Modell-Ansatz, um Artenverlust in 1000 Nischenmodell Nahrungsnetzen (Kapitel 5) und in 30 zufällig ausgewählten empirischen Nahrungsnetzen (Kapitel 6) zu simulieren. In der ersten Studie untersuchte ich den Einfluss topologischer– , Körpergröße correllierter– und dynamischer Eigenschaften, auf die Stabilität von Modell Nahrungsnetzen. Die Ergebnisse zeigen, dass Nahrungsnetz Robustheit durch Faktoren aus allen drei Gruppen beeinflusst wird. Der stärkste Effekt geht dabei vom Verhältnis von Körpergröße zur Abundanz aus, sowohl die Steigung als auch der Achsenabschnitt stabilisiert im Modell die Robustheit der Netzwerke.

In der zweiten Studie untersuchte ich in empirischen Nahrungsnetzen sowohl netzwerkspezifische Eigenschaften (z.B. Diversität, connectance) als auch artspezifische Eigenschaften (z.B. Körpermasse, trophischer Level). Interessanterweise reagieren alle untersuchten Ökosystem Typen (See, Fluss, Meer und Terrestrische Ökosysteme) auf die gleiche Weise auf Artensterben. Allgemein sind Nahrungsnetze mit einer hohen Arten Vielfalt und einer geringen Standardabweichung der Vulnerabilität weniger stark von sekundärem Aussterben betroffen. Auf der Artenebene fand ich, dass der Verlust von großen Prädatoren auf hohen trophischen Ebenen das Aussterberisiko für alle anderen Arten im Ökosystem erhöht. Die hier vorgestellte Arbeit trägt zum Verständnis der zugrunde liegenden Mechanismen und Dynamiken zwischen interagierenden Arten in
Ökosysteme bei. Sie zeigt Unterschiede zwischen den Ökosystem Typen auf. Insgesamt trägt diese Arbeit dazu bei zu verstehen, wie Energieflüsse zur Stabilität von Nahrungsnetzen beitragen, topologische Eigenschaften die Interaktionen zwischen Art Populationen beeinflussen und wie komplexe Artgemeinschaften auf den Verlust von Arten reagieren.

SUMMARY

Since the early twentieth century, different general laws have been investigated to understand mechanisms driving stability in natural ecosystems, but until today the mechanisms are still generally unexplored. The main goal for ecology is to understand mechanisms driving food web dynamics, to counteract the hazard of global species loss. The studies presented in this thesis investigate the general scaling of different strucural food web (e.g. diversity, connectance, vulnerabilty) and species properties (e.g. body mass, trophic level), and how these properties influence secondary extinctions in food webs. The backbone of this thesis is a database of food webs , including information about predator–prey interactions, the metabolic type, and the species' body mass. The relationship between diversity and topology is widely discussed, especially the hypothesis that a constant number of species per link leads to a decreasing connectance with increasing number of species. The alternative to this idea has been the 'constant connectance hypothesis', where connectance is constant with increasing number of species. As part of my thesis (Chapter 2), I analysed the scaling of topological properties based on my compiled database and found power–law scaling relationships with diversity and complexity for most properties. Also, connectance tends to decrease with increasing number of species. The results illustrate the lack of universal constants in food web ecology as a function of diversity and complexity. Furthermore, common measures of bio–complexity (e.g. the fractions of top, intermediate and basal species, and the average trophic level) have been reinvestigated, as scale–dependent on diversity and connectance to. Interestingly, the scale dependence is partly significantly different between ecosystem types. A lot of species' characteristics depend on body mass (eg. predator–prey interactions, metabolism, mobility) thus nominating body mass as the most important species attribute. Chapter 3 illustrates the distribution of mean population body masses in communities for different ecosystem types. The body masses are often roughly log–normally (terrestrial and stream ecosystems) or multi–modally (lake and marine ecosystems) distributed, and most networks exhibit exponential cumulative degree distributions. An exception are stream networks which most often possess uniform degree distributions. Furthermore, with increasing body mass vulnerability decreases in 70% of the food webs and generality increases in 80% of the food webs.

Facing paradigms developed by Elton, I analysed the relationship of predator mass to prey mass and trophic level and the relationship between predator–prey body–mass ratio (hereafter: mass ratio) and trophic level (Chaper 4). In 1927, Elton suggested that (i) the mean prey mass increases with predator mass, (ii) the predators become larger in size with increasing trophic level,

and (iii) the mass ratio is constant across trophic levels. After analysing the data base, the result supports the paradigms (i) and (ii). However, consistant with theoretical derivations, I found a systematic decrease in mass ratios with the trophic level of the predator. This result indicates the general pattern that on average predators at the top of the food webs are more similar in size to their prey than those closer to the base.

Food–web stability is critically dependent on species loss. In two subsequent projects (Chapter 5, 6), I applied a bioenergetic model approach to simulate species loss in a set of (Chapter 5) 1000 model food webs and (Chapter 6) 30 empirical food webs randomly chosen from the food web data base . I analysed the stability of model food webs in respect of effects of topological, size–based, and dynamical properties. Stabiltiy has been messured as the number of secondary extinctions after removing one species from the network. The results show that food–web robustness is affected by factors from all three groups. However, the most striking effect was related to the body mass–abundance relationship which points to the importance of body mass relationships for food web stability.
Additionally to the network–related properties (e.g. diversity, connectance), I analysed species related properties (e.g. body mass, trophic level). Overall, ecosystem-types (lake, stream, marine, and terrestrial ecosystems) react in the same way to species loss. I found food webs with high diversity and a low standard deviation of vulnerability were less affected by secondary extinctions. At the species level, consistent with classical conservation biology findings, I found that the loss of large–bodied top predators increases the extinction–risk for all others species in the ecosystem.

The work presented here contributes to the understanding of underlying mechanisms and dynamics between interacting species in ecosystems. It illustrates differences between ecosystem types, where ”streams tend to be different than other ecosystems”. Overall, the studies show how energy fluxes can contribute to the stability of natural communities, how topological properties influence the interplay between animal populations and how complex communities react to species loss.

Contents

1 INTRODUCTION

"Most of the fundamental ideas of science are essentially simple, and may, as a rule, be expressed in a language comprehensible to everyone."

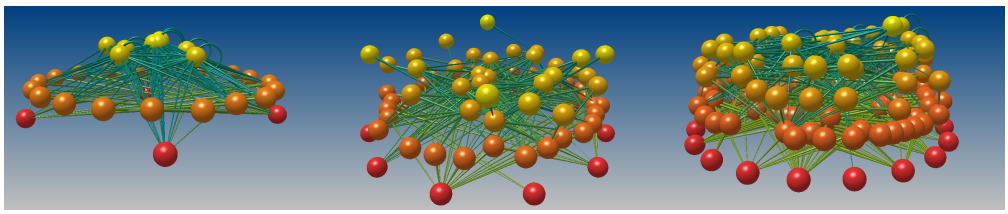
(Albert Einstein)

1.1 Aim and Scope

My motivation of this work is to understand the influence of species and food webs properties on the stability of complex food webs. Because of the complex interrelationship between species the loss of one species in a complex food web can lead to a cascade of further species extinctions. To understand the consequences of a single species loss it is important to understand the general mechanisms influencing dynamics in food webs.
To adress questions about mechanisms and stability, I compiled a large database consisting of highly resolved food webs and species' body masses. Body masses are important for species–species interactions, energy flow, and metabolism in food webs. In this thesis I raised the question how species–species interactions are organised in food webs (Chapter 2 - 4), focusing mainly on body–mass. Additionally to these studies, I used computer simulations and multivariate statistic methods to study the impact of species loss in theoretical (Chapter 5) and empirical food webs (Chapter 6).

1.2 From graphs to food webs

If we talk about food webs, we should consider that the term is a combination of different ideas merged into one expression. Even nowadays the term "food web" can be stretched in different directions. In 'Oxford dictionaries' the definition of a food web sounds simple: "Food web, a system of interlocking and interdependent chains". However, in nature food webs are more difficult to describe. In general, food webs consist of interrelationships between species that coexist in an ecosystem, such as pollination of plants by insects, interactions between parasites and hosts or interactions between a consumer and his resource (Ings et al., 2009), just to name the most prominent. In this thesis the focus is on interactions between consumers and resources, mainly predator–prey interactions.
Going back in time mathematicians have formulated some comparable problems. The first who mentioned the problem about connections between different locations was Leonhard Euler when he solved the seven bridges problem in Königsberg (Euler, 1735). However, the expression 'graph' was used first by James Joseph Sylvester when refering to chemical structures (Sylvester,



(a) Broadstone Stream (b) Carpinteria (c) Littlerock Lake

Figure 1.1: Images of three food webs a) Broadstone Stream (stream), b) Carpinteria (salt marsh) and c) Littlerock Lake (lake) compiled with Network3D *www.peacelab.org*.

1878). Graphs are mathematical objects consisting of nodes and edges (connections between nodes) (Harary, 1969; Dale and Fortin, 2010). Several rules apply to graphs, for example, edges must exist between two nodes, a node can have only one edge. Nodes can be linked by edges according to several rules (e.g. mutually nearest neighbours, nearest neighbours (Dale, 2005) or possibility of feeding interactions in a beta distribution around one species (Williams and Martinez, 2000)). The number of nodes and edges affect the degree of connectivity. The edges in a graph may be directed (asymmetric) or undirected (symmetric). One node can be connected with more than one other node by edges (multi graph).

Food webs are directed graphs, where species (or species populations) are nodes and interactions between species are edges. More simple, interactions in graphs are bitrophic interactions of one consumer species consuming one resource. Adding one species to this consumer resource pair leads to a couple of possible configurations or motifs. The most simple food web motif being a food chain. Other combinations are two consumers feeding on one resource, leading to interspecific competition, because both consumer species competing for one resource, or one consumer consumig two resources. A more complex possibility is omnivory, at which the top consumer in a chain consumes both the intermediate species and the resource species. A food web is a complex graph build of motifs as basal units. In ecology the network type earning most interrest is the predator–prey food web. Important for predator–prey webs are body–masses, consumers being usually bigger than their resources (Cohen et al., 1993; Brose et al., 2006b; Riede et al., 2011b). Even if food webs can be seen as graphs and can be examined with its mathematical tools, the hisristorical interrest in food webs pre–dates graph theroy.

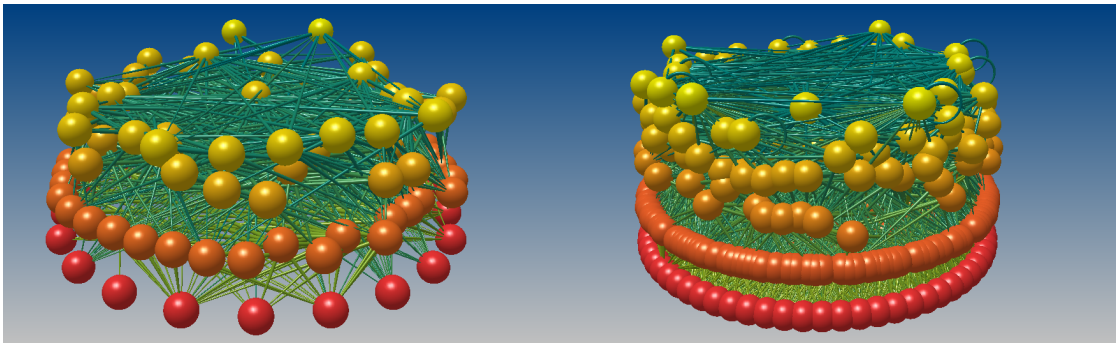
1.3 Forming the food web concept

"All animals, in short, can not exist without food,
neither can the hunting animal escape being hunted in his turn."
(Al-Jahiz $\sim 816AD$)

Early descriptions of feeding interactions between consumer and resource species were observations in nature. Al-Jahiz wrote a book with the title "Kitab al-Hayawan" (Book of Animals), where he philosophised about the interactions between species and their environment. This is the first published source of animal interactions. In the late 1600s Maria Sibylla Merian started to describe interactions between plants and the metamorphosis of butterflies, when she engraved intercations between species on copperplate. The observation and description of feeding interactions between species became more scientific with the descriptions by Carl Linnaeus in "The Economy of Nature" (1775) and Darwin on his voyage with the MSS Beagle 1839 when he passed the island of St. Paul:

"By the side of many of these nests a small flying-fish was placed; which, I suppose, had been brought by the male bird for its partner quickly a large and active crab (Craspus), which inhabits the crevices of the rock, stole the fish from the side of the nest, as soon as we had disturbed the birds. Not a single plant, not even a lichen, grows on this island; yet it is inhabited by several insects and spiders. The following list completes, I believe, the terrestrial fauna: a species of Feronia and an acarus, which must have come here as parasites on the birds; a small brown moth, belonging to a genus that feeds on feathers; a staphylinus (Quedius) and a woodlouse from beneath the dung; and lastly, numerous spiders, which I suppose prey on these small attendants on, scavengers of the waterfowl."
(Charles Darwin, *The origin of species, 1859*)

At the end of the 19th century, Stephen Alfred Forbes published an entire lake food web (Forbes, 1887). The first visualisation of a food web, probably was published by Lorenzo Camerano in 1880. In the earlier 1900s the concept of food webs became more popular, in this period the food webs was driven by economical interests like the network of predators and parasites on cotton-feeding weevils (Pierce et al., 1912), or the "useful animal" food web of the Kattegat (Petersen, 1915). Other authors described interactions between species in a more hypothetical animal–oriented perspective (Shelford, 1913). When in the 1920s Elton raised the more conceptional idea of food webs (Summerhayes and Elton., 1923), the idea of energetic fluxes between species in cycles was born, which we now call food webs. The next advance in food web ecology started in the 1978 when Cohen published the first collection of food webs (Cohen, 1978).



(a) Grande Caricaie CLC2 (b) Weddell Sea

Figure 1.2: Images of two food webs a) Grande Caricaie CLC2 (terrestrial) and b) Weddell Sea (marine) compiled with Network3D *www.peacelab.org*.

He compiled a set of 30 food webs from literature with binary links. In the early 1990 a debate about the quality of food webs started when several scientists published food webs with higher taxonomical resolution (Martinez, 1991; Polis, 1991; Winemiller, 1990). More recently food webs with binary links have been improved by measuring or estimating the population body mass (Brose et al., 2006b).

To give a more general picture of the current data it is important to track the flaws of the data. Food webs often are compiled to answer a particular question, (e.g. productivity of a system, fishing rate) and the emphasis is often on one particular taxonomical group, like invertebrates or fish. The debate of resolution is an unsolved problem in food web ecology, the literature contains many examples of low resolved food webs. Often the aggregation of species makes it difficult to find general patterns. Former studies discussed this resultion problem (Martinez, 1993a; Pimm, 1980; Cohen, 1989; Hodkinson and Coulson, 2004), and assumed poorly resolved webs could be misleading with respect to biodiversity, general network properties like connectance or body–mass correlated properties. The quality of food webs has improved in the last decade, current published food webs have more taxonomic species (Bersier et al., 1999). The currently best resolved food web is the Weddell Sea food web (Jacob et al., 2011) with 492 species and around 16,000 feeding interactions. Currently, the resolution of food webs profits from modern techniques, like gut content analysis or the molecular gut content analysis (King et al., 2008; Eitzinger and Traugott, 2011).

1.4 Food–web structure

A challenge of the work with food webs is to understand the underlying mechanisms. Former studies adressed this challenge, using different approaches (e.g. topological models and dynamic–population models). As one part of this thesis, I used a topological approach to find general structural trends in complex food webs (Chapter 2-4). The consequences of extinctions have been explored by using a dynamic allometric populations model (Chapter 5-6).
Adopting terms of graph–theorie, food–webs can be characterised by the number nodes (species richness S) and the number of interactions or links (L). Species are energy pools and the links are energetic pathways between the pools. The energy flows from the bottom to the top, while each species dissipates energy. Topological models have often been used to understand energy pathways through the food web. To explore the underlying mechanism in food webs, characterisation of general topological food–web properties is essential. Properties used for structural analysis are often simple, like the number of species in a food-web (species richness/ diversity) or the number of links. However, propotion of food web properties are better, if comparing food webs with a variable number of species. Established are the proportions of links to species: links/species (L/S) (Cohen and Newman, 1985), or the proportion of links to possible links called connectance ($C = (L/S^2)$)(Martinez, 1991). Connectance has often been used to explain food web stability. The importance of connectance to food-web stability is a long time controversly debated topic. In 1973, Robert May published his stability criteria (May, 1973),

$$a(SC)^2 < 1$$

where a is the intermediate interaction strength, S the species richness and C the connectance (interaction strength gernerally gives an impression about the quantity of interactions between species, in May's approach interaction was drawn out of a normal distribution between 0 and 1). This theoretical prediction was inconsistent with empirical observations, as the prediction implicates that the product of connectance and species number are constant. Complexity is often found in natural ecosystems, many studies have shown that in diverse food webs species are often highly connected with each other (Polis, 1991; Williams and Martinez, 2000; Ings et al., 2009).

The discrepancy between theoretical predictions and empirical studies triggered a heated debate about how real systems could be stable. Theoretical results have been picked up by an early study using empirical data. They calculated the connectance of 64 food webs with low species richness (Cohen and Newman, 1985), and found that the connectance decreases exponentially with increasing species richness (Cohen and Newman, 1985; Briand and Cohen, 1984)(link–scaling hypothesis). In contrasts to the link scaling law, another theory has been developed by

Martinez (1992), when he analysed a set of highly divers food–webs. He supposed that the connectance is constant regardless of the species richness (constant connectance hypotheses). All three hypothesis triggered a heated debate (so called, ”Food Web War”) about how complex food webs can be stable in nature.

In chapter 2 of this thesis I revisit these hypotheses using a dataset of 65 food webs to analyse the scaling behaviour of sixteen topological parameters. I found significant power-law scaling relationships with species richness (i.e. diversity) and connectance (i.e. complexity) for most of the food webs. Many more food web properties have been used to study food web stability in topological food webs, for example the average and maximum chain length within food webs (Williams et al., 2002), or loops in food webs (Neutel et al., 2002) and generality (in–degree of one node, prey species) and vulnerability (out–degree, of one node being consumed by predator species) of species, their connectedness or link distribution (Montoya and Sole, 2003). Furthermore, this chapter investigates 16 topological food-web properties. The results illustrate the lack of universal constants in food webs.

1.5 Body mass

”Size has a remarkably great influence on the organisation of animal communities”
(*Charles Elton 1927*)

Body size is a fundamental ecological characteristic of organisms (Brown et al., 2004) and physiological traits like metabolic rate are related to mass (Peters and Wassenberg, 1983; Ehnes et al., 2011). Moreover, the parameters defining ecological interactions, such as ingestion rates, interaction strength with other species, the ability to handle prey and the risk of being attacked by predators are correlated to body mass (Brose, 2008; Brose et al., 2006b; Emmerson and Raffaelli, 2004; O’Gorman and Emmerson, 2009; Vucic-Pestic et al., 2010). Furthermore, the distribution of body mass influences the structure of communities (Elton, 1927; Cohen et al., 1993; Jonsson et al., 2005; Brose et al., 2006a; Rall et al., 2008). Prior studies focused on empirical data found that body masses are log normally distributed (Jonsson et al., 2005; Woodward et al., 2005a). However, both studies used aquatic freshwater food webs and they identified pattern could be different across other ecosystems. A combination of body mass and topological traits has been used to explain complex natural food–webs, like degree (degree distribution = the number of connections or links the species has to other species) or allometric degree distributions (Woodward et al., 2005a; Montoya et al., 2006; Otto et al., 2007; Berlow et al., 2009). The general scalig of body–mass in food webs has been used to develop allometric scaling models that successfully predict the binary link structure of food webs (Petchey et al., 2008) or the interaction

strengths between species across complex natural food webs (Brose, 2008; Berlow et al., 2009; Vucic-Pestic et al., 2010).

In chapter 3 of this thesis I analysed 94 natural food webs across four different ecosystem types, in respect to body mass distribution, cumulative degree distribution (vulnerability, generality and linkedness) and allometric degree distribution(eg., generality–body mass relationships). Besides the distribution of body-size the ratio between predator size and the average size of their prey have an important role in explaining regularities of food–web structure (Warren and Lawton, 1987; Cohen et al., 2003; Brose et al., 2006b; Petchey et al., 2008). The dynamics and stability of food–webs can be essentially influenced by the predator–prey body–mass ratio (Jonsson and Ebenman, 1998; Emmerson and Raffaelli, 2004; Weitz and Levin, 2006; Otto et al., 2007; Berlow et al., 2009). Consequently, predicting the distribution and variation in body–mass ratios, is an important jigsaw piece to understand food–web structure, dynamics and stability. Since the seminal work of Charles Elton (1927), several questions were raised. In his work he formulated serveral rules about body mass in food webs, as predator mass increases when the prey mass increases as well, predators become larger with increasing feeding level and the predator–prey body–mass ratio do not vary along food chains. His rules are based on a field trip to ”Spitzbergen”, focusing on one food web. However, food webs can be significantly different in structure, and the size composition of species as well as the body-mass ratios are different between ecosystems (Brose et al., 2006b).
The fundamental rules by Elton are picked up in chapter 4 of this thesis. I analysed 35 high resolved food–webs to find evidence for Elton rules about body size in food webs. To account for the possibility of differences between ecosystems, I separated my dataset into different ecosystem types (marine, streams, lakes and terrestrial) and three different metabolic predator types (invertebrates, endotherm–, and ectotherm vertebrates).

1.6 Food–web dynamics

By consider into the dimnesion ”time” in topological species interactions—food webs become dynamic. First observations of dynamics betweens species have been used to describe the abundance of one population in dependence on another in time. The most prominent expample of developing a dynamic model out of empirical data is population dynamics of lynx and snowshoe hare in Canada. This dataset has been compiled in the 19th century by the Hudson’s Bay Company, when they registered the amount of lynx furs for 90 years. Elton and Nicholson (1942) used it, to compile a time series of the lynx population (Elton and Nicholson, 1942). Besides the description in fluctuation of population abundance, scientists developed mathematical-physical models. These dynamical models help to understand how the perturbation of one species trig-

gers cascading effects to other species.
The most prominent model is the Lotka–Volterra model developed by Alfred Lotka and Vivo Volterra (Lotka, 1925; Volterra, 1926). The Lotka–Volterra equation describes the interactions between two species with two non–linear differential equations of first–order. Simple assumptions of this model are that prey abundance increase with an exponential equation, and that the functional response is linear. The original model has often been improved by replacing the linear functional term with a non-linear term, representing the effect of a limited per capita consumption of prey (Holling, 1959; Jeschke, 2002). Similarly the intrinsic growth rate for resources is often replaced with logistic growth (Rosenzweig and MacArthur, 1963). Later, considering biological rates, and population body masses the model was generalised to explore natural populations (Yodzis and Innes, 1992). In this bioenergetic population model each species has a characteristic body mass, and allometric scaling of metabolism is used to express maximum per capita energy intake rates and losses (Brose et al., 2006a).
Both the models by Rosenzweig–MacArthur and Yodzis–Innes, account for energetic effects from basal species to top species (bottom–up effects), as the Lotka–Volterra model as well, but these models additionally consider effects in the opposite direction (top–down).

Both of these effects, the top-down pressure and bottom-up force, are important to understand the dynamical energy flow in food webs (Hairston et al., 1960). Hairson and co-workers introduced the concept of a ”green world”, is which based on the assumption that the resource limitation depends on the species' trophic position in the food-chain. Conceptually, the energetic pathway goes from the basal species up to the top species, the top species are controlled by energy gain via consuming the intermediate species. This releases the basal species form pressure of the intermediate. These concepts are essential to understand dynamic stability in complex food webs.

1.7 Stability

In earth history five periods of mass extinctions are known from fossil data. A mass extinction is characterised as a time when three quarters of all global species go extinct. Biologists speculate about a current sixth mass extinction wave, assumedly having started in the last century (Pimm et al., 1995; Sala et al., 2000; Barnosky et al., 2011). Problems to define a mass extinction wave are based on the normal duration of the event [1]. The expression ”stability” has gained importance in the context of species loss. However, stability is not clearly defined in literature, as there are serveral expressions for stability like persistence, resilience, resistance, and robustness (see

[1] The last mass extinction wave ended $\sim$ 65 million years ago, the duration was 2.5 million years, where 40% genera were lost, approximatively 76% species

(McCann, 2000) for a detailed definition).
Chapter 5 and 6 focus on persistence, defined as the number of secondary extinctions caused by primary extinctions. Going beyond persistence many topological parameters have been assumed to be important for persistence in food web. The first parameter discussed in this context has been species diversity (Elton, 1933; Odum, 1953; MacArthur, 1955). With increasing species diversity the possibility of redundancy of ”energetic pathways” (compensatory capacity of the food webs in case of species loss) increases as well. In this vein, MacArthur postulated that an increase in diversity and complexity increase the stability of food webs (MacArthur, 1955). While this paradigm has been favoured by empirical ecologists observing food webs it has been challenged by early theoretical studies (Gardner and Ashby, 1970; May, 1972, 1973).

When mathematical models emerged in food–web ecology, the analytical results suggested that higher complexity leads to less stable systems (May, 1972). The antagonism between theory and empiricism led to a controversial scientific debate about stability, which is still ongoing in ecology (McCann, 2000; Montoya et al., 2006). The debate started with arguments of the lack of reasonable biological assumptions in early models as random interaction models. To improve the model, one attempt was to adjust the assimilation effciencies. This leads to more stability in complex food webs (DeAngelis et al., 1975). Moreover, recent studies have shown that stability increases with species diversity, when system are pertubed by removing single species from the network (Borrvall et al., 2000; Ebenman et al., 2004).

Beside this dynamical studies, many studies ignored dynamics and focused on persistence in topological food webs (Dunne et al., 2002; Solè and Montoya, 2001). In topological food webs, a species is extinct when it looses all its prey links. Considering graph theorie, different network properties have been investigate to explain stablity in food webs. Important for this topological approach is the ”Small World” concept. This concept describes the phenomenon in a network, that not all nodes are neighbours to each other, but most of them can be reached by a small number of steps. This can be described mathematically as $L \propto \log(N)$, where L is the distance between two randomly chosen nodes and (N) is number of nodes in the network. The small world phenomenon has been found in different real networks such as social-, scientific-, gene networks, or the connectivity of the internet and food webs (Watts and Strogatz, 1998). In ”small world” networks perturbation effects emerge rapidly through the network, because of the short path length between all nodes and the high degree of connectance. In food webs species are typically separated by less than three links (Dunne et al., 2002; Montoya and Sole, 2002; Montoya et al., 2006). Adopting this concept into the context of food web stability, connectance has been identified as important for food webs stabilty, as increasing connectance decreases the number of secondary extinctions in natural food webs (Dunne et al., 2002; Staniczenko et al.,

2010; Gravel et al., 2011).

Current studies combined dynamic food web models with topological approaches. A common method is to create a food web structure with a statistical method and use this structure as input web for the dynamic model (Kondoh, 2003; Williams and Martinez, 2004b; Brose et al., 2006a). This model has been used for studies presented in Chapters 5 and 6. Chapter 5 of this thesis focuses on the identification of food web and species properties influencing food web stability (persistence). The topological structure is generated by the niche model. As input for the niche model a range of empirically defined parameters are used. Species characteristics have been drawn from a range of empirical realistic properties. Contrasting this approach in Chapter 6, empirical food webs have been used to evaluate the consequences of secondary extinctions. Furthermore I used empirically measured species body masses as input for the dynamical food web–model.

Table 1.1: Food web informations table with all in this thesis used food webs. Food webs used in chapter 2, 3, 4, 6 have been marked with an ”x”. The informations includes webname, number of species, connectance, source for predations matrix and body masses.

No	Common web name	Spec*	conn**	Predation matrix source	Body size source	Chapter 2	3	4	6
	Estuary/ Saltmarsh								
1	Carpinteria	72	0.05	(Lafferty et al., 2006)	(Petchey et al., 2008)	x	x	x	x
2	Chesapeake Bay	36	0.09	(Baird and Ulanowicz, 1989)	NA	x			
3	St. Mark’s	48	0.10	(Christian, 1999)	Riede unpublished	x		x	
4	Ythan	92	0.05	(Cohen et al., 2009)	(Cohen et al., 2009)	x	x	x	x
5	Mangrove Estuary wet season	94	0.15	(Heymans et al., 2002)	NA	x			
	Lakes								
6	Alford Lake	56	0.07	(Havens, 1992)	Riede unpublished	x	x	x	x
7	Balsam Lake	50	0.10	(Havens, 1992)	Riede unpublished	x	x		
8	Burntbridge Lake	53	0.07	(Havens, 1992)	Riede unpublished		x		
9	Beaver Lake	56	0.09	(Havens, 1992)	Riede unpublished	x	x	x	
10	Big Hope Lake	61	0.09	(Havens, 1992)	Riede unpublished		x		
11	Brandy Lake	30	0.13	(Havens, 1992)	Riede unpublished		x		
12	Bridge Brook Lake	75	0.10	(Havens, 1992)	Riede unpublished	x	x	x	x
13	Brook Trout Lake	15	0.08	(Havens, 1992)	Riede unpublished		x		
14	Buck Pond	41	0.09	(Havens, 1992)	Riede unpublished		x		
15	Cascade Lake	35	0.10	(Havens, 1992)	Riede unpublished		x		
16	Chub Lake	36	0.06	(Havens, 1992)	Riede unpublished	x	x		x
17	Chub Pond	54	0.14	(Havens, 1992)	Riede unpublished		x	x	
18	Connery Lake	65	0.10	(Havens, 1992)	Riede unpublished	x	x	x	x
19	Constable Lake	32	0.06	(Havens, 1992)	Riede unpublished		x		
20	Deep Lake	19	0.08	(Havens, 1992)	Riede unpublished		x		
21	Emerald Lake	22	0.12	(Havens, 1992)	Riede unpublished		x		
22	Falls Lake	39	0.10	(Havens, 1992)	Riede unpublished		x		
23	Fawn Lake	32	0.12	(Havens, 1992)	Riede unpublished		x		
24	Federation Lake	22	0.12	(Havens, 1992)	Riede unpublished		x		
25	Goose Lake	40	0.06	(Havens, 1992)	Riede unpublished		x		
26	Grass Lake	44	0.09	(Havens, 1992)	Riede unpublished		x		
27	Gull Lake	45	0.10	(Havens, 1992)	Riede unpublished		x		
28	Gull Lake North	16	0.10	(Havens, 1992)	Riede unpublished		x		
29	Helldiver Pond	41	0.10	(Havens, 1992)	Riede unpublished		x		
30	High Pond	24	0.15	(Havens, 1992)	Riede unpublished		x		
31	Hoel Lake	72	0.11	(Havens, 1992)	Riede unpublished	x	x		
32	Horseshoe Lake	49	0.11	(Havens, 1992)	Riede unpublished		x		
33	Indian Lake	35	0.08	(Havens, 1992)	Riede unpublished		x		
34	Long Lake	65	0.10	(Havens, 1992)	Riede unpublished	x	x		
35	Loon Lake	35	0.10	(Havens, 1992)	Riede unpublished		x		
36	Lost Lake	31	0.15	(Havens, 1992)	Riede unpublished		x		
37	Lost Lake East	41	0.08	(Havens, 1992)	Riede unpublished		x		
38	Little Rainbow Lake	52	0.09	(Havens, 1992)	Riede unpublished		x		
39	Lower Sister Lake	37	0.12	(Havens, 1992)	Riede unpublished		x		
40	Oswego Lake	33	0.13	(Havens, 1992)	Riede unpublished		x		
41	Owl Lake	30	0.08	(Havens, 1992)	Riede unpublished		x		
42	Rat Lake	50	0.11	(Havens, 1992)	Riede unpublished		x		
43	Razorback Lake	42	0.10	(Havens, 1992)	Riede unpublished		x		
44	Rock Lake	22	0.09	(Havens, 1992)	Riede unpublished		x		
45	Russian Lake	24	0.11	(Havens, 1992)	Riede unpublished		x		
46	Safford Lake	44	0.12	(Havens, 1992)	Riede unpublished		x		
47	Sand Lake	29	0.10	(Havens, 1992)	Riede unpublished		x		
48	South Lake	22	0.07	(Havens, 1992)	Riede unpublished		x		
49	Squaw Lake	41	0.10	(Havens, 1992)	Riede unpublished		x		
50	Stink Lake	53	0.10	(Havens, 1992)	Riede unpublished	x	x	x	
51	Twin Lake East	13	0.10	(Havens, 1992)	Riede unpublished		x		
52	Twin Lake West	26	0.09	(Havens, 1992)	Riede unpublished		x		
53	Twelfth Tee Lake	31	0.09	(Havens, 1992)	Riede unpublished		x		
54	Whipple Lake	32	0.13	(Havens, 1992)	Riede unpublished		x		
55	Wolf Lake	27	0.06	(Havens, 1992)	Riede unpublished		x		
56	Sierra Lakes	37	0.22	(Harper-Smith et al., 2006)	(Brose et al., 2006b)	x	x	x	x
57	Skipwith Pond	35	0.31	(Warren, 1989)	(Brose et al., 2006b)	x	x	x	x
58	Tuesday Lake 1984	50	0.11	(Jonsson et al., 2005)	(Brose et al., 2006b)	x	x	x	

Continued

Table 1.1: Food web informations table with all in this thesis used food webs. Food webs used in chapter 2, 3, 4, 6 have been marked with an ”x”. The informations includes webname, number of species, connectance, source for predations matrix and body masses.

No	Common web name	Spec*	conn**	Predation matrix source	Body size source	Chapter 2	3	4	6
59	Littlerock Lake	181	0.07	(Martinez, 1991)	Riede unpublished	x	x	x	x
	Marine								
60	Chile Food web	106	0.13	Navarette and Wieters unpublished	Navarette and Wieters unpublished	x			
61	Lough Hyne	350	0.04	(Yvon-Durocher et al., 2008)	(Jacob et al. in prep)	x			x
62	Mondego Zostera Medows	47	0.13	(Patricio and Marques, 2006)	(Baeta et al., 2009)	x	x	x	
63	Mondego bare sediment	43	0.13	(Patricio and Marques, 2006)	(Baeta et al., 2009)				x
64	Carribean Reef, small	50	0.22	(Opitz, 1996)	Riede unpublished	x	x	x	
65	NE US Shelf	81	0.23	(Link, 2002)	NA	x			
66	Weddell Sea	492	0.07	(Brose et al., 2006b)	(Jacob2011)	x	x	x	
67	Benguela	25	0.28	(Yodzis, 1989)	(Yodzis, 1989)		x		
	River/Streams								x
68	Berestream	137	0.07	(Woodward et al., 2008)	(Riede et al., 2011b)	x	x	x	x
69	Broadstone	34	0.19	(Woodward et al., 2005b)	(Woodward et al., 2005b)	x	x	x	x
70	Alamitos creek	162	0.14	(Harrison, 2003)	Riede unpublished	x	x	x	x
71	Caldero Creek	126	0.13	(Harrison, 2003)	Riede unpublished	x	x	x	
72	Corde Matre Creek	106	0.16	(Harrison, 2003)	Riede unpublished	x	x	x	
73	Coyote Creek	190	0.13	(Harrison, 2003)	Riede unpublished	x	x	x	x
74	Guadeloupe Creek	174	0.15	(Harrison, 2003)	Riede unpublished	x	x		
75	Guadeloupe River	136	0.13	(Harrison, 2003)	Riede unpublished	x	x		
76	Los Gatos Creek	177	0.14	(Harrison, 2003)	Riede unpublished	x	x		x
77	Los Trancos Creek	129	0.15	(Harrison, 2003)	Riede unpublished	x	x		
78	San Francisquito Creek	140	0.17	(Harrison, 2003)	Riede unpublished	x	x		x
79	Saratoga Creek,	158	0.15	(Harrison, 2003)	Riede unpublished	x	x		
80	Steverson Creek	170	0.17	(Harrison, 2003)	Riede unpublished	x	x		
81	Penetetia creek	170	0.14	(Harrison, 2003)	Riede unpublished	x	x		x
82	Blackrock	82	0.05	(Townsend et al., 1998)	(Riede et al., 2011b)	x	x		
83	Sutton	86	0.06	(Townsend et al., 1998)	(Riede et al., 2011b)	x	x		
84	Canton	108	0.06	(Townsend et al., 1998)	(Towers et al., 1994)	x	x	x	
85	Dempster	106	0.09	(Townsend et al., 1998)	(Towers et al., 1994)	x	x		
86	German	84	0.05	(Townsend et al., 1998)	(Towers et al., 1994)	x	x	x	
87	Healy	96	0.07	(Townsend et al., 1998)	(Towers et al., 1994)	x	x		
88	Kyeburn	98	0.07	(Townsend et al., 1998)	(Towers et al., 1994)	x	x		
89	Little Kyeburn	78	0.12	(Townsend et al., 1998)	(Towers et al., 1994)	x	x	x	
90	Stony	112	0.07	(Townsend et al., 1998)	(Towers et al., 1994)	x	x	x	
91	Broad	34	0.19	(Townsend et al., 1998)	(Towers et al., 1994)	x	x	x	
92	Ross	117	0.15	(Townsend et al., 1998)	(Towers et al., 1994)				
93	BEA***	30	0.21	(Layer et al., 2010)	(Layer et al., 2010)				
94	BRO***	25	0.28	(Layer et al., 2010)	(Layer et al., 2010)				
95	COI***	22	0.19	(Layer et al., 2010)	(Layer et al., 2010)				
96	CON***	22	0.12	(Layer et al., 2010)	(Layer et al., 2010)				
97	D1***	35	0.23	(Layer et al., 2010)	(Layer et al., 2010)				
98	D2***	44	0.20	(Layer et al., 2010)	(Layer et al., 2010)				
99	D3***	21	0.24	(Layer et al., 2010)	(Layer et al., 2010)				
100	D4***	19	0.20	(Layer et al., 2010)	(Layer et al., 2010)				
101	D5***	29	0.23	(Layer et al., 2010)	(Layer et al., 2010)				
102	D6***	20	0.29	(Layer et al., 2010)	(Layer et al., 2010)				
103	DAR***	21	0.22	(Layer et al., 2010)	(Layer et al., 2010)				
104	ETH***	44	0.22	(Layer et al., 2010)	(Layer et al., 2010)				
105	GWY***	24	0.23	(Layer et al., 2010)	(Layer et al., 2010)				
106	HAF***	25	0.22	(Layer et al., 2010)	(Layer et al., 2010)				
107	MHA***	40	0.21	(Layer et al., 2010)	(Layer et al., 2010)				
108	Millstream	87	0.22	(Layer et al., 2010)	(Layer et al., 2010)				
109	NAR***	61	0.20	(Layer et al., 2010)	(Layer et al., 2010)				
110	OAK***	24	0.28	(Layer et al., 2010)	(Layer et al., 2010)				
111	OLD***	23	0.26	(Layer et al., 2010)	(Layer et al., 2010)		x		
112	Ln***	41	0.21	(Layer et al., 2010)	(Layer et al., 2010)				
	Terrestrial								
113	Grande Caricaie ClC1	146	0.10	(Cattin et al., 2004)	(Brose et al., 2006b)	x	x		
114	Grande Caricaie CLC2	102	0.10	(Cattin et al., 2004)	(Brose et al., 2006b)		x	x	x

Continued

Table 1.1: Food web informations table with all in this thesis used food webs. Food webs used in chapter 2, 3, 4, 6 have been marked with an ”x”. The informations includes webname, number of species, connectance, source for predations matrix and body masses.

No	Common web name	Spec*	conn**	Predation matrix source	Body size source	Chapter 2	3	4	6
115	Grande Caricaie SCM1	202	0.07	(Cattin et al., 2004)	(Brose et al., 2006b)		x		
116	Grande Caricaie SCM2	167	0.06	(Cattin et al., 2004)	(Brose et al., 2006b)		x		
117	Grande Caricaie SCC1	159	0.06	(Cattin et al., 2004)	(Brose et al., 2006b)		x		
118	Grande Caricaie SCC2	152	0.07	(Cattin et al., 2004)	(Brose et al., 2006b)	x	x	x	x
119	Grande Caricaie CLM1	168	0.07	(Cattin et al., 2004)	(Brose et al., 2006b)	x	x		
120	Grande Caricaie CLM2	161	0.07	(Cattin et al., 2004)	(Brose et al., 2006b)	x	x		
121	St.Martin	44	0.11	(Goldwasser and Roughgarden, 1993)	Riede unpublished	x			
122	Simberlofff_E1	36	0.09	(Simberloff and Abele, 1976)	Riede & Grischkat	x	x	x	x
123	Simberlofff_E2	63	0.09	(Simberloff and Abele, 1976)	Riede & Grischkat	x	x	x	x
124	Simberlofff_E3	49	0.10	(Simberloff and Abele, 1976)	Riede & Grischkat	x	x	x	x
125	Simberlofff_E7	52	0.09	(Simberloff and Abele, 1976)	Riede & Grischkat	x	x	x	
126	Simberlofff_E9	71	0.09	(Simberloff and Abele, 1976)	Riede & Grischkat	x	x	x	x
127	Simberlofff_ST2	63	0.09	(Simberloff and Abele, 1976)	Riede & Grischkat	x	x	x	x
128	Hainich	89	0.11	(Digel unpublished)	(Digel unpublished)			x	
129	Coachella	27	0.33	(Polis, 1991)	(Petchey et al., 2008)		x		x
130	Montane Forest, Arizona	30	0.07	(Cohen, 1989)	(Jonsson and Ebenman, 1998)	x		x	x
131	Trelease Woods, Illinois	33	0.06	(Cohen, 1989)	(Jonsson and Ebenman, 1998)	x		x	x
132	El Verde	156	0.06	(Reagan, 1996)	NA	x			
133	Broom Source	52	0.04	(Memmott et al., 2000)	(Brose et al., 2006b)	x	x		

*= species, **=connectance, ***=(Allt a’Mharcaidh (MHA, N.E. Scotland), Allt na Coire nan Con (COI, N.W Scotland) and Dargall Lane (DAR, S.W. Scotland); Old Lodge (OLD), Broadstone Stream (BRO) and Lone Oak (OAK)(S.E. England); Duddon Pike Beck (D1), Hardknott Gill (D2), Mosedale Beck (D3), Duddon (D4), Wrynose Beck (D5), Duddon Beck a (D6) and River Etherow (ETH)(N.W. England); Mill Stream (MIL) and Narrator Brook (NAR)(S.W. England); Afon Hafren (HAF) and Afon Gwy (GWY)(mid-Wales); and Beagh’s Burn (BEA) and Coneyglen Burn (CON)(N. Ireland). Note that 10 of these sites (Allt a’Mharcaidh, Allt na Coire nan Con, Afon Hafren, Afon Gwy, Narrator Brook, River Etherow, Old Lodge, Dargall Lane, Beagh’s Burn, Coneyglen Burn) are part of the U.K. Acid Waters Monitoring Network (http://www.ukawmn.ucl.ac.uk).)

1.8 Contributions to publications

Chapter 2; Scaling of food-web properties with diverstiy and complexity across ecosystems

Authors: **Jens O. Riede**, Björn C. Rall, Carolin Banasek-Richter,
Sergio A. Navarete, Evie A. Wieters, Mark C. Emmerson, Ute Jacob And Ulrich Brose
Published in: *Advances in Ecological Research* (2010), Volume 42, Issue 10, Pages 139–170
Contributions: Idea by U.B., J.O.R. & B.C.R., empirical data from: C.B.R., S.A.N., E.A.W., M.C.E. & J.O.R., analysis performed by J.O.R., text was mainly by JOR, BCR & UB

Chapter 3; Stepping in Eltonś footprints: a general scaling model for body masses and trophic levels across ecosystems

Authors: **Jens O. Riede**, Ulrich Brose, Bo Ebenman, Ute Jacob, Ross Thompson, Colin R. Townsend, Tomas Jonsson
Published in: *Ecology Letters* (2011) Volume 14, Issue 2, pages 169–178
Contributions: Idea by J.O.R., T.J. & U.B., empirical data from: U.J., R.T., C.R.T & J.O.R., analysis performed by J.O.R., error propagation by: T.J.; text was written by JOR & UB

Chapter 4; Body sizes, cumulative and allometric degree distributions across natural food webs

Authors: Christoph Digel, **Jens O. Riede** and Ulrich Brose
Published in: *Oikos* (2011) Volume 120, Issue 4, pages 503–509
Contributions: Idea by C.D. & U.B. , empirical data from: J.O.R., analysis performed by C.D. & J.O.R., text was written by C.D. & UB with minor contributions of J.O.R.

Chapter 5; Size–based food web characteristics govern the response to species extinctions

Author: **Jens O. Riede**, Amrei Binzer, Ulrich Brose, Alva Curtsdotter, Björn C. Rall, Francisco de Castro , Anna Eklöf
Published in: *Basic and Applied Ecology* (2011) 12(7): 581-589
Idea by all authors, analysis by F.C, A.E & J.O.R, text was by A.E & J.O.R

Chapter 6; Loss of large top predators in species–poor food webs yields the highest secondary extinction risk

Author: **Jens O. Riede**, Sonja Otto, Neo Martinez, Ulrich Brose

in preparation

Idea by all authors, analysis by J.O.R, text was by J.O.R & U.B.

2 SCALING OF FOOD–WEB PROPERTIES WITH DIVERSTIY AND COMPLEXITY ACROSS ECOSYSTEMS

2.1 Abstract

Trophic scaling models describe how topological food web properties such as the number of predator-prey links scale with species richness of the community. Early models predicted that either the link density (i.e., the number of links per species) or the connectance (i.e. the linkage probability between any pair of species) is constant across communities. More recent analyses, however, suggest that both of these scaling models have to be rejected, and we discuss several hypotheses that aim to explain the scale-dependence of these complexity parameters. Based on a recent, highly resolved food web compilation, we analysed the scaling behaviour of sixteen topological parameters and found significant power-law scaling relationships with diversity (i.e., species richness) and complexity (i.e., connectance) for most of them. These results illustrate the lack of universal constants in food web ecology as a function of diversity or complexity. Nonetheless, our power-law scaling relationships suggest that fundamental processes determine food web topology, and subsequent analyses demonstrated that ecosystem-specific differences in these relationships were of minor importance. As such,, these newly-described scaling relationships provide robust and testable cornerstones for future structural food web models.

2.2 Introduction

Over the last several centuries, physicists have developed a variety of scaling laws, such as NewtonS law of universal gravitation, which holds that the gravitational force between two bodies is proportional to the product of their masses and the inverse of their squared distance. The change in gravitational force with distance is well described by a scaling law, where the gravitational constant and the exponent (negative square) are constant with respect to distance. Scaling laws thus indicate, but do not prove, the fundamental process that governs the relationship between variables. In search of analogues of the grand laws of physics, ecologists have been searching for ecological scaling models that can be generalized across organisms, populations, and even entire ecosystems (Lange, 2005; O'Hara, 2005). Among the most promissing approaches, trophic scaling models predict relationships between topological food web properties, such as the number of predator-prey feeding interactions (links, L) and the species richness (S, hereafter : diversity) of the community (Dunne, 2006). In diversity-topology relationships, scale refers to the number of species, and ecologists have searched for universal food web constants that equally apply to species-poor and species-rich ecosystems. Early trophic scaling models suggested that link density—the number of links per species (LS)—is constant across food webs of varying species richness (Cohen and Newman, 1985). This " link-species scaling law" is in agreement with the classical stability criterion of random networks, which holds that local population stability is maintained if link density remains below a critical threshold that, in turn, depends on the average interaction strength (May, 1972). Subsequent early trophic scaling models proposed constancy of additional food web properties, including the proportions of top species (T, species consuming other species whilst they have no consumers), intermediate species (I, species that consume and are consumed by other species) and basal species (B, species without resource species below them within a food chain, e.g. plants or detritivores) (Cohen and Newman, 1985), and constant proportions of links between these trophic groups:*T-I*, *T-B*, *I-I* and *I-B* links (Cohen and Newman, 1985). Empirical tests using early food web data rendered support to these scaling laws (Briand and Cohen, 1984; Cohen and Newman, 1985; Cole et al., 2006), but the quality of the data employed has cast doubt on the validity of these findings, largely due to poor taxonomic resolution, limited sampling effort, and the presence of biological impossibilities (e.g., birds included as basal species) (Paine, 1988; Polis, 1991; Hall and Raffaelli, 1993; Ings et al., 2009). Other studies based on data of higher quality demonstrated that link density, the proportions of top, intermediate and basal species, and the proportions of *T-I, T-B, I-I* and *I-B* links are not constant across the diversity scale (Schoener, 1989; Warren, 1989; Winemiller, 1990; Hall and Raffaelli, 1991; Martinez, 1991, 1993b). Earlier findings of scale-invariance were consequently ascribed to a range of methodological artefacts arising from inadequate sampling, strong species aggregation and poor data resolution (Hall and Raffaelli, 1991; Martinez,

1991, 1993b; Goldwasser and Roughgarden, 1997; Bersier et al., 1999; Martinez et al., 1999). While the improved data demonstrated scale dependence of link density, an alternative hypothesis proposed that connectance (C)—the linkage probability of any pair of species in the food web (C = L/S^2)—should be constant across ecosystems of variable species richness (Martinez, 1992). Models with constant link density assume that any species can consume a fixed number of the coexisting species, whereas the constant-connectance model holds that any species can consume a fixed fraction of the coexisting species. The later hypothesis initially received some empirical support (Martinez, 1992, 1993b; Spencer and Warren, 1996), but further analyses of more recent food web data suggest that neither link density nor connectance are constant across the diversity scale (Schmid-Araya et al., 2002; Montoya and Sole, 2003; Brose and Martinez, 2004; Dunne, 2006). Much of this trophic scaling debate has focused on parameters of food web complexity, such as the link density or connectance dunne2006. Other recent approaches that have addressed the scaling of additional topological food web parameters have been inspired by physicists' scaling laws and introduced scale-dependent properties, but with constant scaling exponents (Camacho et al., 2002a,b; Garlaschelli et al., 2003). This implies that the food-web properties studied vary with the diversity of the communities, but this variance is described by universally constant exponents. For instance, they found significant scaling relationships of food web properties such as the fractions of top, intermediate and basal species and the number of links among them (Martinez, 1994), the clustering coefficient (Camacho et al., 2002a,b; Dunne et al., 2002), and the average path length between any pair of species in a food web (Camacho et al., 2002a,b), (Williams et al., 2002). However, all of these studies still suffered from data limitation by either being based on older food web collections of poor resolution, or new compilations of high quality data that included fewer than 20 food webs. Over the last decade or so, additional collections of higher quality food webs have become available (Brose and Martinez, 2004; Townsend et al., 1998; Brose et al., 2006b), but systematic and comprehensive analyses of scaling relationships in these data have yet to be undertaken. In the present study, we attempt to fill this void by analysing the scaling of 19 food web properties (see Methods for a description) with species richness (diversity) and connectance (complexity) using a collection of 65 food webs from terrestrial, lake, stream, estuarine and marine ecosystems (see table1.1 for a detailed overview). Additionally, we tested for significant differences in scaling relationships among these five ecosystem types. This approach extends prior studies testing for significant deviations of marine (Dunne et al., 2004) or Cambrian food web topology (Dunne et al., 2008) from those of other ecosystems. Our analyses also address whether the different ecosystem types included possess specific topologies, or whether there are consistent scaling relationships that hold across ecosystems, which would indicate the existence of general constraints upon the structure of ecological networks.

2.3 Methods

2.3.1 The food web data set

We illustrate trophic scaling relationships using a data set of 65 food webs from a variety of habitats (see table 1.1 for an overview of the food webs). This compilation includes 13 food webs that have been used in prior meta–studies (Williams and Martinez, 2000; Montoya and Sole, 2003; Cattin, 2004; Dunne et al., 2004; Stouffer et al., 2005; Dunne, 2006) and six food webs from a meta-study on natural consumer–resource body–mass ratios (Brose et al., 2006b). They are complemented by four further webs from the banks of Lake Neuchatel (Cattin, 2004), nine of the largest webs from a study of fifty lakes in the Adirondack Mountains of New York State (Havens 1992), eight stream webs from the collection of ten New Zealand webs (Townsend et al., 1998), and five terrestrial island food webs (Piechnik et al., 2008). We did not consider food webs dominated by parasitoid or parasitic interactions, because the physical constraints by which they are governed differ from those that govern predator–prey interactions (Brose et al., 2006b), thus modifying complexity patterns (Lafferty et al., 2006). This choice is not meant to imply that such interactions are not of importance for the structure and function of the food webs, rather that maintaining a focus on free–living predator–prey interactions in a consistent, standardised manner helps elucidate the underlying processes. Overall, the data compilation analyzed here includes food webs from fourteen lakes or ponds, twenty–five streams or rivers, five brackish water of estuaries and salt marshes, six marine and fifteen terrestrial ecosystems. The number of taxonomic species in these food webs ranges between 27 and 492, and the number of links ranges from 60 to 16,136.

2.3.2 Food web topology

Nineteen food web properties were calculated for each of the 65 taxonomic food webs studied (see Fig. 2.1 and 2.3 for an overview). The properties analysed were: (1) the total number of links in the food webs, L; (2) the number of links per species, LS; (3) connectance, C; the fractions of (4) top species (species with resources but without consumers), (5) intermediate species (species with resources and consumers), (6) basal species (species with consumers but without resources); (7) herbivores (species that consume basal species); (8) omnivores (species consuming resources across more than one trophic level); (9) cannibals (species partially feeding on con-specifics); (10) species in loops (circular link structures originating and ending at the same species); (11 12) the standard deviations of the species' generality (the number of resources) and vulnerability (the number of consumers); (13) linkedness (the total number of links to resources and consumers); (14) the average short-weighted trophic level (SWTL, average of the

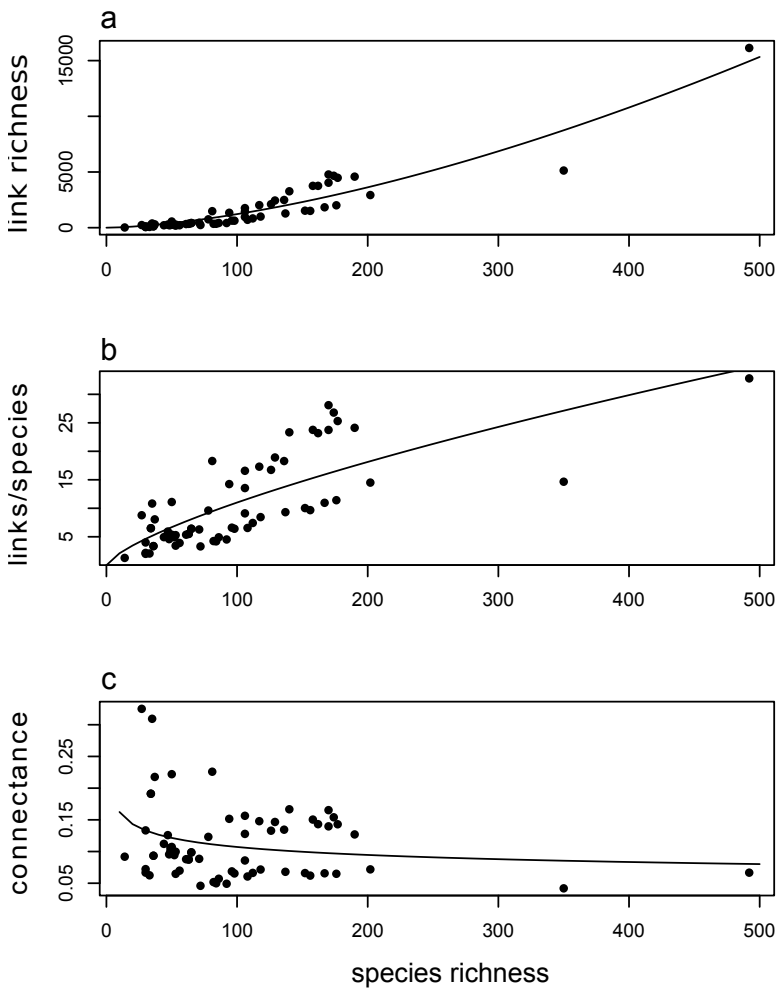


Figure 2.1: Diversity–complexity relationships. Scaling of (A) trophic link richness ($exponent = 1.57 \pm 0.07, p < 0.001$),(B) links per species (exponent=0.71±0.08, p<0.001) and (C) connectance (exponent= $-0.18 \pm 0.09, p = 0.057$) with species richness of the foodwebs.

prey-averaged trophic level and the shortest chain for each species) across all species in the food web; (15) the average shortest chain length (shortest chain of trophic links from a species to a basal species) across all species in the food web; (16) the species' mean similarity (mean of the maximum trophic similarity of each species to any other species in the same food web); (17) the characteristic path length (mean over all shortest trophic paths between any pair of species in a food web); (18) the mean clustering coefficient (probability that two interacting species are both linked to a third species); (19) and the diet discontinuity (the proportion of triplets of taxa with an irreducible gap in feeding links over the number of possible triplets), which have also been used in prior studies (Dunne et al., 2004) (Cattin, 2004).

2.3.3 Statistical analyses

First, we analysed the power-law scaling of the complexity parameters (1-3, as listed above): L, $L/\S$, and C, as a function of species richness, S:

$$L = aS^b \tag{2.1}$$

$$L/\ S = aS^b \tag{2.2}$$

$$C = aS^b \tag{2.3}$$

where a and b are constants. For the remaining sixteen topological food web properties, P, we analyzed the power-law scaling with species richness, S, and connectance, C:

$$P = aS^bC^c \tag{2.4}$$

where a, b, and c are constants. These power-law scaling models (equ. 1 and 2) were fitted by non-linear least-squares regressions (function nls in R, R -Project 2.8.1, free statistic software) to estimate the constants. Significant scaling exponents b and c were interpreted as indication of diversity and complexity scaling, respectively. Two prominent scaling models predict that the scaling exponent, b, of the relationship between the number of links and species richness should be one ("the link-species scaling law", (Cohen and Newman, 1985) or two (" the constant connectance hypothesis ", (Martinez, 1992)). We tested these specific predictions by calculating the normally distributed probabilities of the z scores:

$$p\left(z = \frac{b-\mu}{\sigma}\right) \tag{2.5}$$

where b is the estimated exponent, σ its standard error, and μ represents the expected prediction. Subsequently, we used the residuals of the fitted power-law models (equ. 2) to test for signatures of the ecosystem types (lake, stream, estuarine, marine and terrestrial ecosystems) in the scaling relationships. Our first analyses addressed significant differences in the overall food-web structure between these ecosystem types by a cluster analysis based on euclidian distances

(function 'hclust' within the package 'stats' provided by the statisticalsoftware R 2.9.0, (Team, 2011)). Prior to this analysis, the residuals were normalized to zero mean and unit variance. In a second analysis, we tested for significant differences in specific topological properties between the ecosystem types. For each of the sixteen food-web properties, we carried out independent ANOVAs with the residuals as dependent variables and the ecosystem type as the factorial independent variable. Significant ANOVAs were followed by Tukey HSD posthoc tests.

2.4 Results

The food webs of our data collection comprise between 27 and 592 species with 60 to 16136 trophic links, 2 to 32.8 links per species, and a connectance between 0.04 and 0.33 (Tab1.1). In our first analysis, we illustrate the scaling of links, link density (links per species) and connectance with diversity (Fig. 2.1).

2.4.1 Complexity–Diversity Relationships

The scaling of link richness (i.e. the number of trophic links, L) with species richness (S) should follow a power law with a slope of one (μ = 1 , Eq. 3) according to the 'link-species scaling law' (Cohen and Newman, 1985), or a slope of two (μ = 2, Eq. 3) according to the 'constant connectance hypothesis' (Martinez, 1992). The power–law model (Eqs. 1a, 1b, 1c) fitted to our data data yielded an exponent, b, of 1.57 $\pm$ 0.07 (mean $\pm$ s.e., Fig. 2.1a, Tab.1), which differs significantly from two (z = -6.14, p ¡ 0.001) and one (z = 8.14, p ¡ 0.001). Further analyses suggested that link density increases significantly (p $<$ 0.001), whereas connectance tend to decrease with diversity (p = 0.06), (Fig. 2.1b and c, Tab 2.1). This implies that more diverse food

Table 2.1: Fit of power law scaling models (Eqs. 1a, 1b, 1c) for link richness, links / species and connectance depending on species richness

	slope			intercept		
	Estimate	std. error	p-value	estimate	std. error	p-value
Link richness	0.86715	0.34271	0.0139	1.57372	0.06843	$\leq$ 0.001
Link/species	0.4002	0.15731	0.0134	0.71976	0.07731	$\leq$ 0.001
Connectance	0.24588	0.09872	0.0154	0.18032	0.094	0.0596

webs are characterized by a higher number of links per species but a lower connectance than food webs of low diversity. Two of the food webs in our data set comprise more species than the

other food webs: these food webs are those of the Weddell Sea with 492 species and the Lough Hyne with 350 species. Certainly, these data points might drive our conclusion, but repeating the analyses while excluding these two data points yielded similar results.

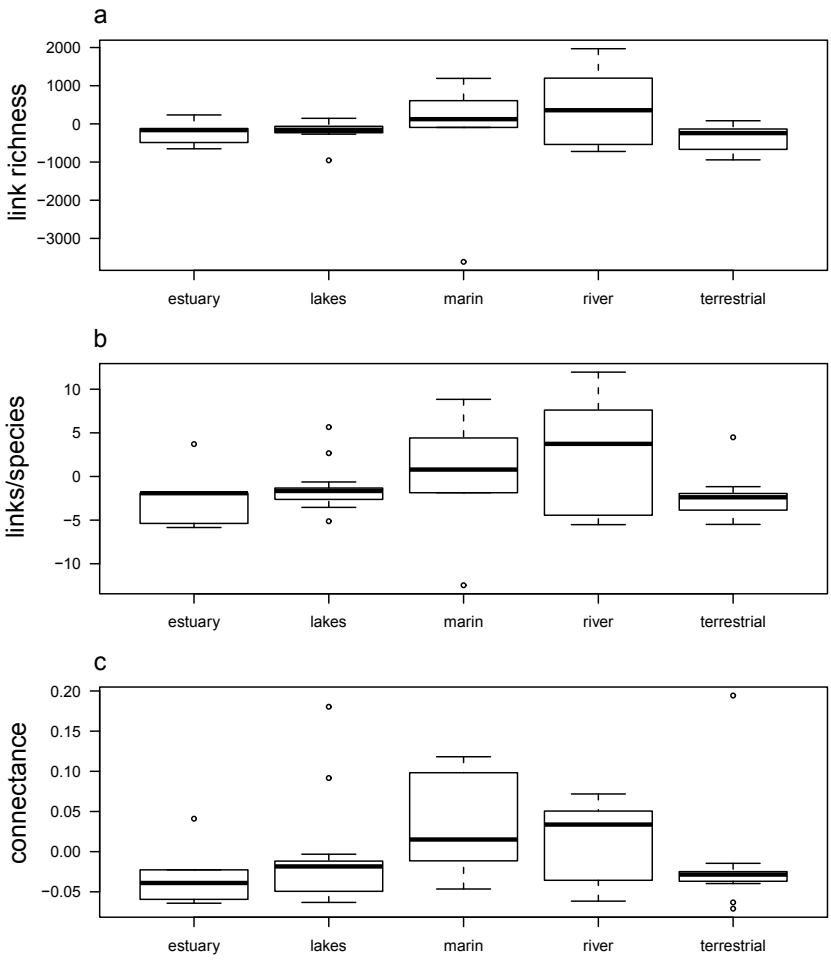


Figure 2.2: Ecosystem–type specific differences in diversity–complexity scaling: differences in the residuals of the diversity–complexity relationships (shown in Figure 2.1) for(A) trophic link richness (note that only the relationship between terrestrial and river ecosystems is significantly different; p=0.048), (B) links per species (note that only the relationship between terrestrial and river ecosystems is significantly different; p=0.022) and (C) connectance depending on the ecosystem types.

2.4.2 Ecosystem Types and Complexity–Stability Relationships

The distribution of the data in Fig. 2.1 suggests two groups of food webs below and above the power-law model: one group of food webs with more links, a higher link density and a higher connectance and a second group of food webs with less links, a lower link density and a lower connectance than predicted by the power–law regression model. This results in positive and negative residuals of the first and second group, respectively. We hypothesized that these differences might be driven by characteristics of specific ecosystems such as the higher connectance and link density that appears to generally occur in marine ecosystems (Dunne et al., 2004). Hence, we employed three independent ANOVAs to test for significant effects of the ecosystem type on the residuals of link richness (Fig. 2.2a), links per species (Fig. 2.2b), and connectance (Fig. 2.2c). We found significant effects of the ecosystem types on link richness and links per species. Subsequent post-hoc tests revealed that this pattern is driven by higher link richness ($p = 0.048$) and and links per species ($p = 0.021$) in river than in terrestrial ecosystems (Fig. 2.2a, b). All other differences among pairs of ecosystem types were not significant. Interestingly, our analyses did not reveal any significant difference in connectance between the ecosystem types (Fig. 2.2c). This also reveals that the grouping of ecosystems in types employed in our study does not explain the residual pattern apparent in Fig. 2.1. Together, these results suggest that river ecosystems are richer in links and links per species than terrestrial ecosystems, whereas otherwise complexity is similar across ecosystem types.

2.4.3 Topology–Diversity Relationships

We further analyzed the scaling of 16 additional food-web properties with diversity (Fig. 2.3) and connectance (Fig. 2.4) by fitting the power-law regression model (equ. 2) to the data. We found that ten food-web properties are significantly correlated with species richness (Tab. 2): fraction of top, intermediat, basal, cannibalistic species, species in loop, the standard deviations of linkedness, mean similarity, characteristic path length and the mean clustering coefficient. Moreover, twelve food-web properties are significantly correlated with connectance (Tab. 2): fraction of top, intermediat, basal, cannibalistic species, species in loop, the standard deviations of generality, vulnerability and linkedness, mean similarity, characteristic path length, and the mean clustering coefficient. With increasing species richness of the food webs the fractions of top and basal species decrease, whereas the fractions of intermediate and omnivorous species increase (Fig. 2.3a, b, c, k). Additionally, the standard deviation of the species' linkedness

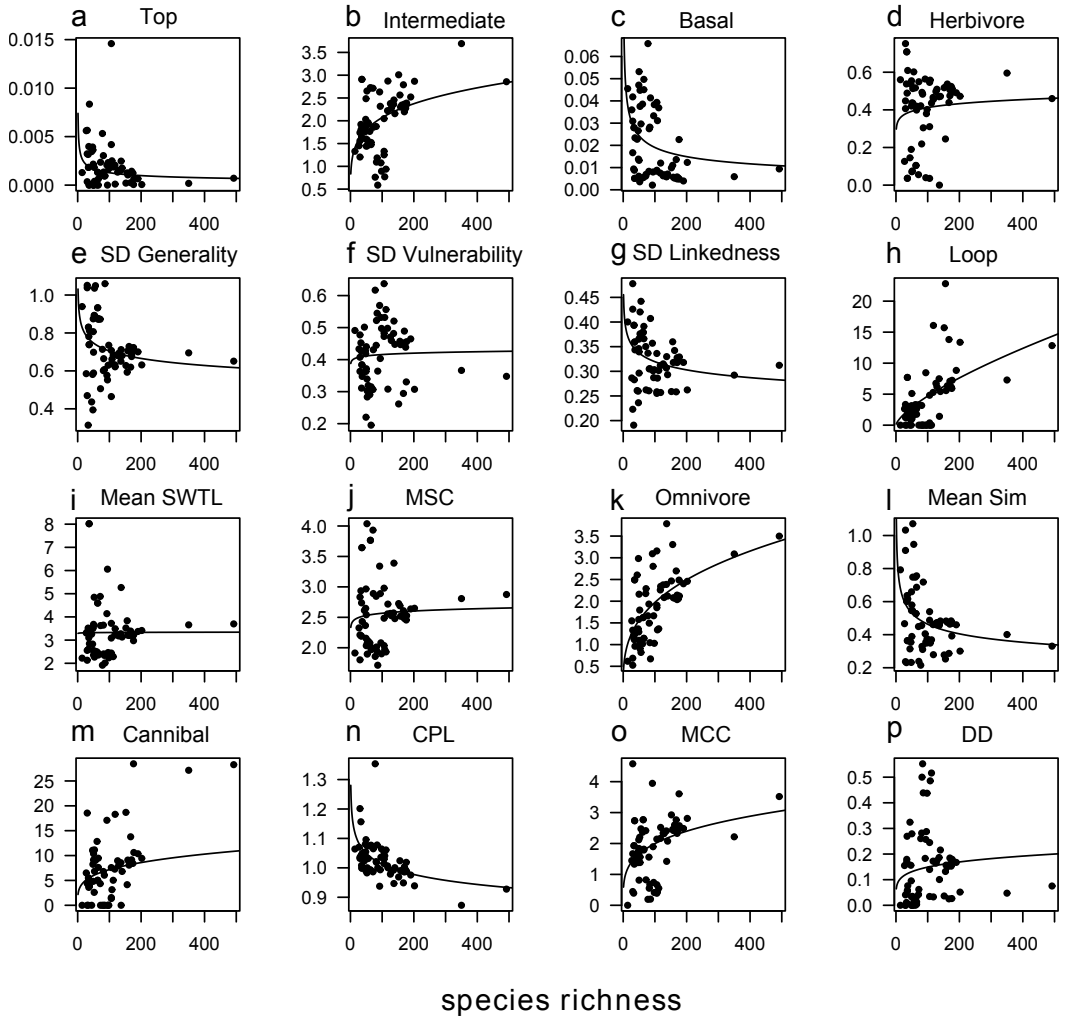


Figure 2.3: The diversity scaling (Eq. 2) of 16 food–web properties: fraction of (A) top, (B) intermediate, (C) basal, (D) herbivore, (K) omnivore and (M) cannibalistic species, (H) species in loops, the standard deviations of (E) generality, (F) vulnerability and (G) linkedness, (I) the mean short trophic level (SWTL), (J) the mean shortest chain length (MSC), (L) the mean similarity, (N) the characteristic path length (CPL), (O) the mean clustering coefficient (MCC) and (P) the diet discontinuity (DD). See Table 2 for fitted model parameters. For the y–axis, we used the normalized residuals for each food–web property and ecosystem type (*see Section II for details*).

and their mean trophic similarity decrease (Fig. 2.3g, l). This implies that in the more diverse food webs the predominantly increasing number of intermediate species yields a more similar distribution of the number of links across species but less similarity in who consumes whom.

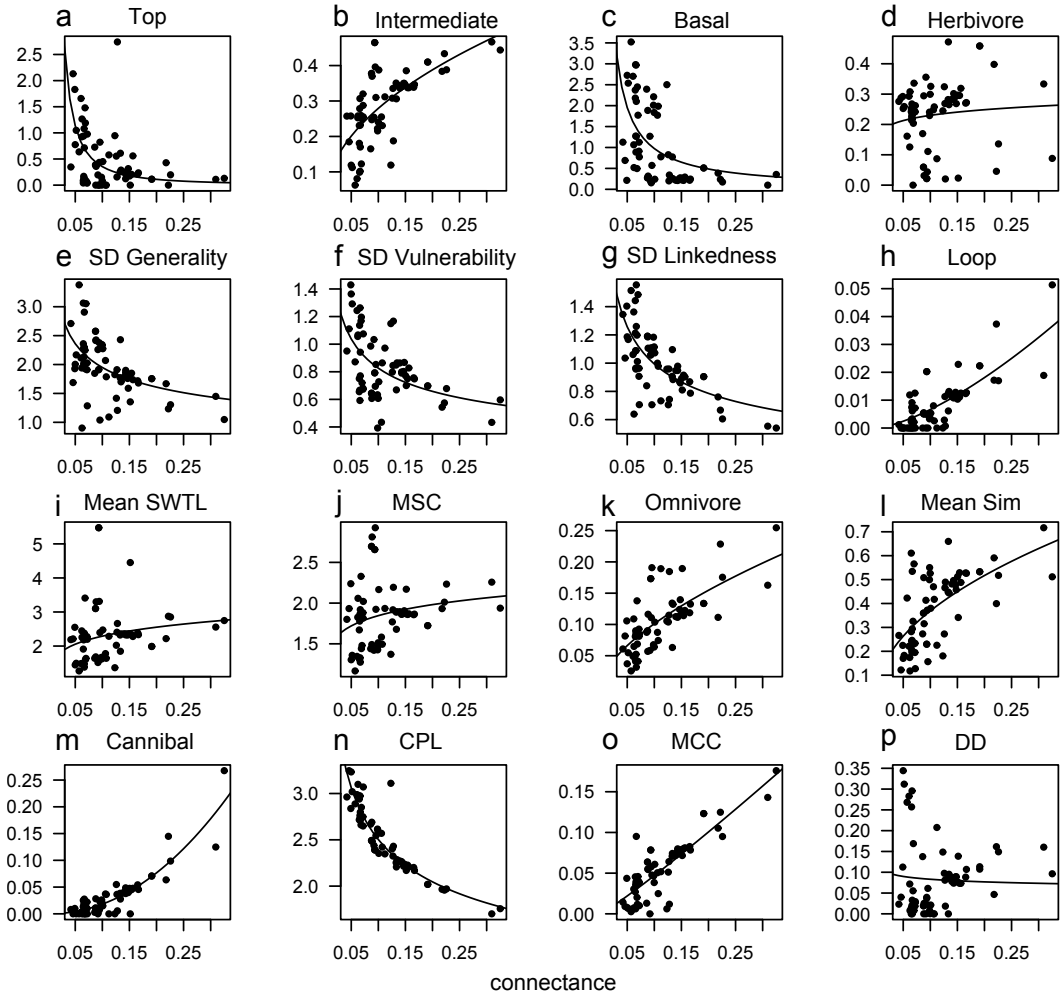


Figure 2.4: The complexity scaling (Eq. 2) of 16 food–web properties: fraction of (A) top, (B) intermediate, (C) basal, (D) herbivore, (K) omnivore and (M) cannibalistic species, (H) species in loops, the standard deviations of (E) generality, (F) vulnerability and (G) linkedness, (I) the mean short trophic level (SWTL), (J) the mean shortest chain length (MSC), (L) the mean similarity, (N) the characteristic path length (CPL), (O) the mean clustering coefficient (MCC) and (P) the diet discontinuity (DD). See Table 2 for fitted model parameters. For the y–axis, we used the normalized residuals for each food–web property and ecosystem type (*see Section II for details*).

Moreover, the characteristic path length between any pair of species increases (Fig. 2.3n) and the clustering coefficient decreases (Fig. 2.3o) with increasing species richness. Thus, in more diverse food webs, the species are assembled in clusters of sub-webs and consequently, the average length of the trophic paths between species increases.

Table 2.2: Fit of a power-law scaling model (equ. 2) of different topological food web properties depending on connectance and species richness. The food web parameters are: fraction of top, intermediate, basal, herbivore, cannibalistic species, species in loops, the standard deviations of generality, vulnerability and linkedness, the mean short-weighted trophic level, the mean shortest chain length, the mean similarity, the characteristic path length, the mean clustering coefficient and the diet discontinuity (see Methods for details).

variables	a			b (species-richness)			c (connectance)		
	estimate	std. deviation	p-value	estimate	std. deviation	p-value	estimate	std. deviation	p-value
Fraction. Top	0.007	0.008	0.368	-0.382	0.182	0.04	-1.68	0.414	< 0.001
Frac. Intermediate	0.832	0.192	< 0.001	0.198	0.049	< 0.001	0.474	0.071	< 0.001
Frac. Basal	0.097	0.072	0.187	-0.353	0.135	0.011	-1.004	0.257	< 0.001
Frac. Herbivore	0.298	0.132	0.028	0.071	0.09	0.438	0.112	0.13	0.392
SD Generality	1.032	0.229	< 0.001	-0.083	0.043	0.061	-0.276	0.066	< 0.001
SD Vunerability	0.388	0.09	< 0.001	0.015	0.044	0.735	-0.328	0.07	< 0.001
SD Linkedness	0.456	0.078	< 0.001	-0.077	0.033	0.022	-0.339	0.051	< 0.001
Frac. in Loop	0.185	0.081	0.026	0.701	0.114	< 0.001	1.445	0.192	< 0.001
Mean SWTL	3.288	1.053	0.003	0.003	0.067	0.969	0.157	0.095	0.101
Mean Short Chain	2.335	0.458	< 0.001	0.021	0.04	0.611	0.102	0.058	0.082
Frac Omnivore	0.414	0.108	< 0.001	0.339	0.056	< 0.001	0.612	0.082	< 0.001
Mean Similarity	1.132	0.299	< 0.001	-0.194	0.062	0.003	0.487	0.081	< 0.001
Frac Cannibal	2.171	0.589	< 0.001	0.26	0.102	0.014	2.078	0.185	< 0.001
Char Path Length	1.281	0.071	< 0.001	-0.051	0.011	< 0.001	-0.291	0.017	< 0.001
Mean Cluster Coef.	0.588	0.147	< 0.001	0.265	0.063	< 0.001	1.098	0.098	< 0.001
Diet Discontinuity	0.064	0.064	0.317	0.183	0.192	0.344	-0.113	0.289	0.697

2.4.4 Ecosystem Types and Topology–Diversity Relationships

While these analyses suggested a significant fit of the general diversity and complexity scaling model for topological food–web properties (Eq. 2), we also addressed significant differences in trophic scaling among the five ecosystem types (lake, stream, estuarine, marine and terrestrial ecosystems). The cluster analysis of the normalized residuals of the fitted trophic scaling model illustrated whether the overall similarity or dissimilarity of the food–web topologies could be ascribed to the ecosystem types (Figure 2.5). This analysis revealed that despite some topological similarities in food webs located closely to each other, no systematic grouping of food webs according to the ecosystem types emerged. This residual analysis suggested that (1) the trophic scaling models (Figures 2.3 and 2.4) held across ecosystem types without systematic deviations, and (2) despite variance in species richness and connectance between ecosystem types, natural food webs possessed similar overall topologies.

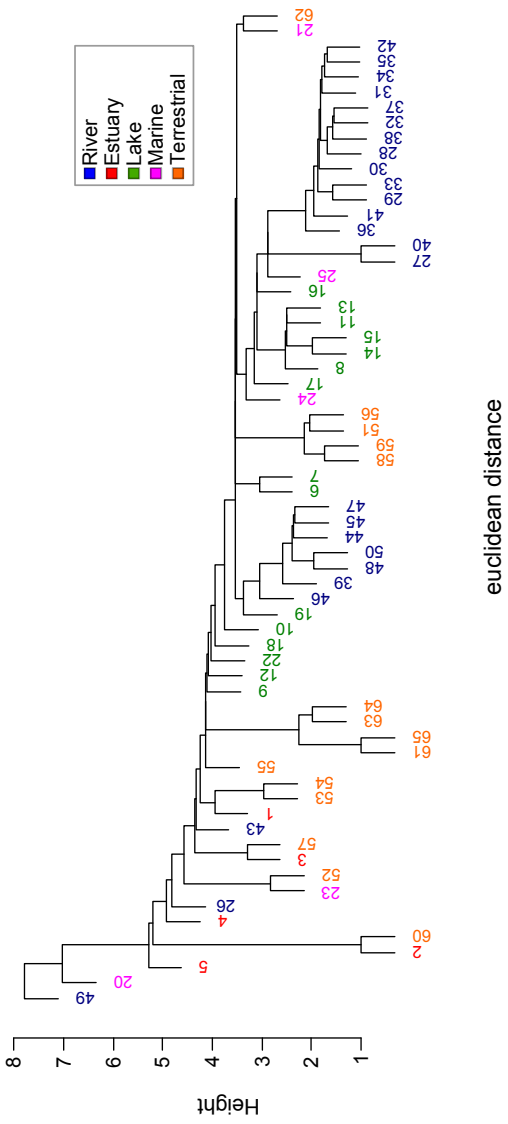


Figure 2.5: Clustering of food webs according to the residual variation in the 16 food–web properties (see Figures 2.4 and 2.5). Euclidian distances were calculated with species richness and connectance corrected values. Colour code for the different ecosystems: blue=rivers, red=estuaries, green=lakes, pink=marine ecosystems, orange=terrestrial ecosystems. The web numbers are given in table 1.1. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this chapter.).

Subsequently, we carried out more detailed analyses of variance (ANOVA) of the residuals of the 16 food-web properties among the five ecosystem types (Figures 2.6 and 2.7). We found significant signatures of the ecosystem types in the fractions of intermediate (Figure 2.6B), basal (Figure 2.6C) and herbivorous species (Figure 2.6D), the standard deviations of generality (Figure 2.6E) and linkedness (Figure 2.6G), the fraction of species in trophic loops (Figure 2.6H), the mean short–weighted trophic levels (Figure 2.7A), the mean shortest chain lengths (Figure 2.7B), the fraction of omnivores (Figure 2.7C), the mean trophic similarity of species (Figure 2.7D) and the diet discontinuity (Figure 2.7H). These differences were subsequently explored in more detail using post hoc tests (Figures 2.6 and 2.7). Across the 16 food web properties, this included a total of 160 pairwise comparisons of ecosystem types. Overall, 26% (43 out of 160 combinations) of these possible combinations were significantly different from each other (see levels of significance indicated in Figures 2.6 and 2.7 for details). This suggested that the majority of topological food–web properties followed similar diversity–complexity scaling models across ecosystems. Some systematic differences emerged between lake and terrestrial ecosystems in terms of the fractions of intermediate, basal, herbivorous and omnivorous species, the mean shortweighted trophic level, the mean shortest chain length, the mean similarity and the fraction of species in loops (Figures 2.6 and 2.7). Additionally, some estuaries and lakes differed in the mean short-weighted trophic level, the mean shortest chain length, the fraction of omnivores and the mean similarity. Overall, these analyses suggest that most differences in food–web topology occurred when comparing terrestrial and lake ecosystems, whereas terrestrial and marine ecosystems were most similar.

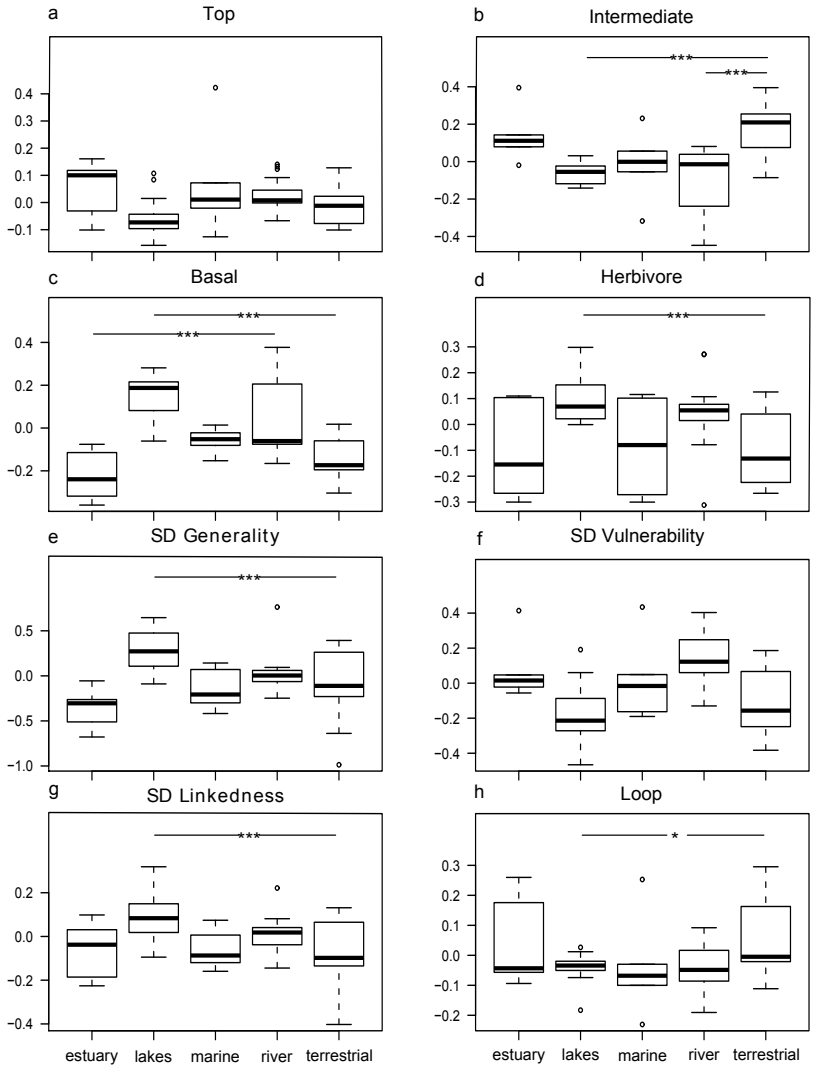


Figure 2.6: Significant differences in topological properties (the residuals of their complexity and diversity scaling according to Eq. 2–see Figures 2.3 and 2.4) between the ecosystem types: the fractions of (A) top, (B) intermediate, (C) basal, and (D) herbivore species, the standard deviations of (E) generality, (F) vulnerability and (G) linkedness, (H) the fraction of species in loops. Significant differences between ecosystems types were calculated by Tukey HSD post hoc tests ($*p < 0.05; * * *p < 0.001$).

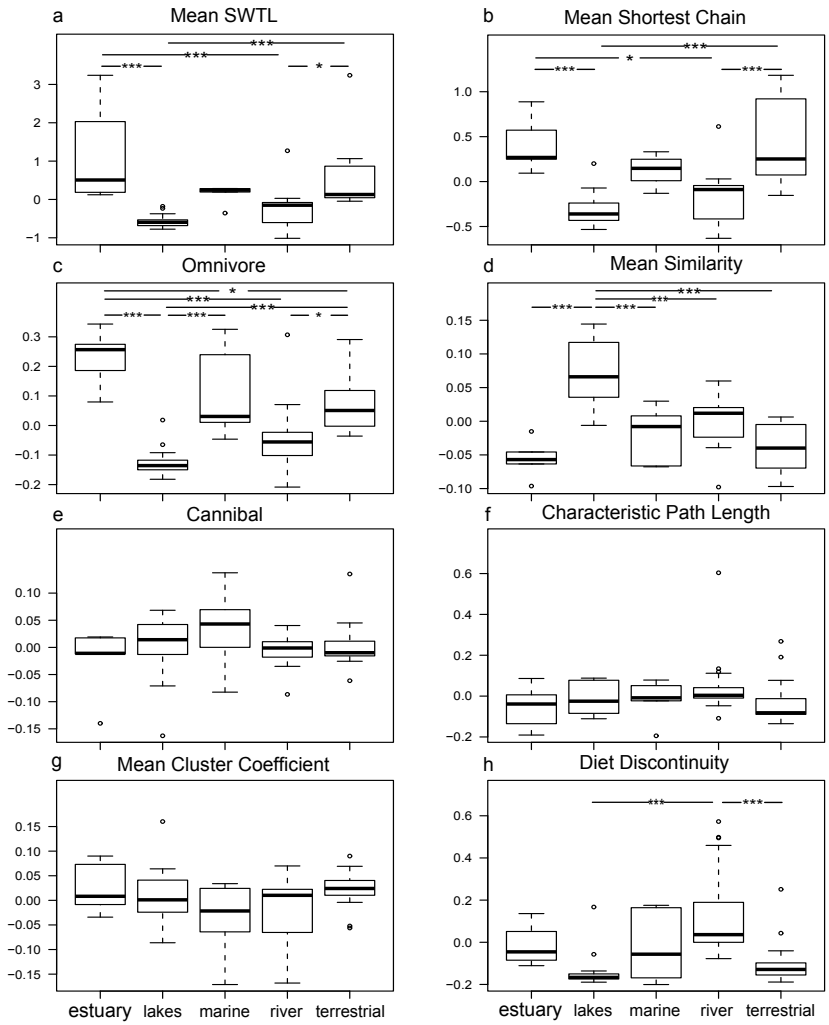


Figure 2.7: Significant differences in topological properties (the residuals of their complexity and diversity scaling according to Eq. 2–see Figures 2.3 and 2.4) between the ecosystem types: the fractions of (A) top, (B) intermediate, (C) basal, and (D) herbivore species, the standard deviations of (E) generality, (F) vulnerability and (G) linkedness, (H) the fraction of species in loops. Significant differences between ecosystems types were calculated by Tukey HSD post hoc tests ($*p < 0.05; * * *p < 0.001$).

2.5 Discussion

2.5.1 Complexity–diversity relationships

Over several decades, the search for universal food–web constants that equally apply to species–poor and species–rich ecosystems has focused on complexity–stability relationships. While the link–species scaling law predicts constancy of the number of links per species (Cohen and Newman, 1985), the alternative constant connectance hypothesis holds that food–web connectance should be constant (Martinez, 1992). Based on a new collection of novel food webs, our results suggest that both scaling models, the link–species scaling law and the constant–connectance hypothesis, have to be rejected. Instead, we found that link richness and the number of links per species increase, whereas connectance decreases along the diversity scale. Instead of the classic models, our results support a recent change in paradigm from constant to scale–dependent connectance (Schmid-Araya et al., 2002; Montoya and Sole, 2003; Brose and Martinez, 2004; Dunne, 2006).

Interestingly, the link–species scaling law is in agreement with the classical stability criterion of random networks holding that local population stability is maintained if link density falls below a critical threshold which in turn depends on the average interaction strength (May, 1972). The lack of constancy in the number of links per species in our and other recent empirical analyses indicates that this topological stability criterion should not be responsible for the stability of complex natural food webs. Instead, recent work has demonstrated that the specific body–mass structure of natural food webs may provide the critically important dynamic stability of the trophic networks (Otto et al., 2007; Brose, 2010a). In particular, negative diversity–stability relationships in complex food webs without body–mass structure are converted into neutral to slightly positive relationships if the natural body–mass structure is accounted for (Brose et al., 2006a) (Brose, 2010a). Moreover, implementing natural body-mass distributions in models of complex food webs also yields positive relationships between complexity and stability (Rall et al., 2008). Together, these dynamic model analyses provide a potential explanation for the stability of highly diverse food webs, despite the high number of links per species.

2.5.2 Explanations for the scale-dependence of complexity

Several potential explanations for the scale-dependence of links per species and connectance can be identified. First, in communities with many interacting species, the decrease of connectance with diversity may result from a methodological artefact (Paine, 1988), namely that the difficulty of identifying trophic links among a large number of species increases with species richness. This yields a potentially lower sampling intensity of links in more diverse food webs, which would account for a decrease in connectance with species richness (Goldwasser and Roughgarden, 1997; Bersier et al., 1999; Martinez et al., 1999). Ultimately, an adequate sampling

effort can only be guaranteed if yield-effort curves demonstrate saturation in link richness with sampling effort for every food web (Woodward and Hildrew, 2001) (Ings et al., 2009) or if extrapolation methods suggest a high sampling coverage (Brose, 2003a; Brose and Martinez, 2004). While this is certainly desirable for future food-web compilations, the currently available data lack this information and we cannot entirely rule out that sampling effect contributes to the decrease in connectance with species richness.

Second, the increase in links per species with species richness could be primarily driven by an increasing number of weak links (i.e. links with a low energy flux), whereas the number of strong links per species might be constant. Empirical studies have indeed found interaction strengths to be highly skewed towards many weak and a few strong links (Paine, 1992; Goldwasser and Roughgarden, 1993; Fagan and Hurd, 1994; Wootton, 1997; Woodward et al., 2005b; O'Gorman et al., 2010). Taking the variability in energy flux between links into consideration, initial tests found the overall number of links per species to increase with species richness, whereas quantitative versions of link density, weighing the links according to their energy flux, remain scale invariant (Banasek-Richter et al., 2005). Thus, the distribution of energy fluxes becomes more unequal as systems accrue in species number, possibly due to the increase in weak links. This implies that species can have strong interactions with only a fixed number of the coexisting species, while the number of weak interactions continuously increases with species richness. While the former "sampling effect" suggests that the number of sampled links is too low in more diverse food webs, the approach of using quantitative food-web data along with their corresponding descriptors (Bersier et al., 2002; Banasek-Richter, 2004) implies that most of the links in diverse food webs are weak and may even be unimportant for calculating connectance or link density. However, this implication needs to be reconciled with recent theoretical work stressing the importance of weak links for the organisation of natural food webs (McCann et al., 1998; Berlow, 1999; Navarrete and Berlow, 2006; O'Gorman and Emmerson, 2009).

Third, food-web stability might require that during community assembly diversity is negatively correlated to complexity. This argument is based on the finding that species-poor communities exhibit Poissonian degree distributions (i.e., the frequency of species with links), whereas species-rich communities have more skewed distributions (Montoya and Sole, 2003). Thus, increasing diversity primarily leads to an increase in species with few links, which decreases connectance. Classic stability analyses have shown that population stability decreases with both, diversity and connectance (May, 1972). When natural food webs assemble, the destabilizing effect of increasing diversity needs to be balanced by a resulting decrease in connectance to avoid instability (Montoya and Sole, 2003). This stability argument mechanistically links variation in species diversity and community complexity.

Fourth, processes that increase diversity may reduce species' co-existence, which decreases connectance. However, the constant-connectance and link-species scaling models assume that

species may consume a fixed fraction or a fixed number, respectively, of the co-existing species (Cohen and Newman, 1985; Martinez, 1992). Thus, these models predict constancy in the scaling exponents only if co-existence does not change with diversity. However, potential consumer and resource species do not necessarily co-exist in meta-communities at larger spatial scales (Brose and Martinez, 2004; Olesen et al., 2010). If species richness across food webs increases with the spatial extent of the habitats, connectance will decrease with species richness due to a decrease in predator-prey co-occurrence. Link-area models based on this argument have successfully predicted the number of links, links density and connectance of aquatic food webs ranging in spatial scale from local habitats to landscapes (Brose and Martinez, 2004). Interestingly, the exponent of the power-law link-species model at the scale of local habitats was close to two as predicted by the constant-connectance model, whereas it decreases to lower values when larger spatial scales are included, where species' co-existence breaks down (Brose and Martinez, 2004). Similarly, predator-prey co-existence may also break-down with increasing habitat complexity (Keitt, 1997). Increasing habitat complexity or architectural complexity of the vegetation leads to higher species richness as many predators are specialized on specific sub-habitats such as distinct vegetation layers (Brose, 2003b; Tews et al., 2004; Olesen et al., 2010). The localized occurrence of these predators in sub-habitats may yield reduced connectance as the predators do not co-exist with all prey species that fall within their feeding niche. Interestingly, strong support for the constant connectance hypothesis comes from the pelagic food webs of 50 lakes (Martinez, 1993a) and aquatic microcosms (Spencer and Warren, 1996) . In these very homogeneous habitats, increases in habitat complexity play no role in increasing species richness - a constellation which sets the frame for constant connectance. In contrast, increasing species richness in stream communities was correlated with decreases in connectance, which may be explained by variation in habitat complexity (Schmid-Araya et al., 2002).

Fifth, predator specialisation may decrease connectance in the more diverse food webs. The feeding ranges of consumers are limited to specific body-size ranges of potential resource species (Brose et al., 2008; Vucic-Pestic et al., 2010). If the body-size range increases with the species richness of the community, connectance will decrease with community diversity due to physical feeding constraints. Moreover, the possibility to decide upon multiple prey species increases for any predator with increasing species richness. Therefore, predators in more diverse communities may specialize on a subset of their potential feeding niche that includes prey species that are easier to exploit or less defended. Additionally, uneven abundances of potential prey within the feeding range may induce a predator switching behaviour that creates temporally unexploited prey of low abundances. This hypothesis suggests that the prey abundance of the unrealized links should be lower than the prey abundance of the realized links. In compliance with these arguments, (Beckerman et al., 2006) offer a mechanistic explanation for connectance. Based on optimal foraging theory, they assume that predators preferentially feed on the energetically most

rewarding prey. Their "diet breadth model" relates food-web complexity to the species' foraging biology and does well in predicting the scaling of connectance with species richness (Beckerman et al., 2006). The optimization constraints regarding the species' foraging behaviour thus entail the complexity of their food web. Interestingly, recent extensions of this optimal foraging approach in the allometric diet breadth model provide successful predictions of the topology of complex food webs (Petchey et al., 2008). Together, these models stress the outstanding importance of the natural body-mass structure for constraining food-web topology, which supports the hypothesis that connectance may decrease with increasing species richness due extended body-mass ranges in the community.

Each of the aforementioned hypotheses may be partial in explaining the variance of connectance with species richness, and they are not mutually exclusive. Most likely, the mechanisms underlying the observed patterns are multi-causal and vary with the spatial scale. The "sampling hypothesis" suggests that mere sampling artefacts are responsible for the decrease in connectance with species richness, whereas all other hypotheses presume ecological processes behind this pattern. In addition to the empirical pattern, these biological hypotheses substantiate the conclusion that connectance is not constant but decreases with diversity. This supports a change in paradigm from constant to scale-dependent connectance in community food webs.

2.5.3 Topological scaling relationships

Analyses of topological scaling relationships in our new food-web data collection revealed significant diversity scaling of ten out of the sixteen food-web properties and complexity scaling for twelve out of the sixteen food-web properties. Our results support the conclusion of prior studies the fractions of top and basal species decrease with diversity, while the fraction of intermediate species increases with scale (Schoener, 1989; Warren, 1989; Winemiller, 1990; Hall and Raffaelli, 1991; Martinez, 1991, 1993b) thus supporting the classic scaling relationships. Our analyses also indicate that species-rich food webs exhibit a higher variability in species' linkedness (i.e. the overall number of links) than species-poor webs. Consistent with a prior study (Montoya and Sole, 2003), this suggests that species-rich food webs have a more uneven distribution of links among species, a feature which may effect an increase in population stability. Moreover, we found that the clustering coefficient (the likelihood that two species that are linked to the same species are also linked to each other) increases with diversity. Surprisingly, this empirical result contradicts a prior analytical result based on niche-model food webs (Camacho et al., 2002a,b). In contrast, our results support another analytical finding that the mean shortest path length between species decreases with diversity (Williams et al., 2002). Together, these findings suggest that species-rich food webs are more compartmentalized and have shorter average path length between pairs of species than species-poor ones, which suggests that food

webs of high diversity are organized by combining sub-web compartments in which species are closely linked to each other.

2.5.4 Ecosystem types

While our prior analyses indicated robust scaling models of topological food-web properties with diversity and complexity substantial residual variation around these trends remained. Consistent with prior approaches for marine (Dunne et al., 2004) or Cambrian food-web topology (Dunne et al., 2008), we addressed significant signatures of ecosystem types in this residual variation. However, in contrast to these prior studies, we did not employ the niche model (Williams and Martinez, 2000) as the null model to remove the dominant effects of species richness and connectance on food-web topology. Analyses based on the niche model share the niche models assumptions while ignoring assumptions and predictions of alternative topological models (Cattin, 2004; Stouffer et al., 2005; Allesina et al., 2008; Williams and Martinez, 2008). To avoid such pre-assumptions of the analyses, we used power-law scaling models of food-web topology against species richness and connectance to subsequently test effects of the ecosystem types on the residuals of the scaling relationships. These residuals are independent of the effects of diversity and complexity on food-web topology. Consistent with prior studies (Dunne et al., 2004, 2008), we did not find dominant effects of ecosystem types on food-web topology. While our cluster analysis indicated that food-web topologies cannot be grouped according to their ecosystem type, the more detailed analyses of variance for individual food-web properties suggested some differences. Certainly, our comparison of 160 pairwise combinations in posthoc tests could be criticized. On average, chance events should result in significant differences ($p<0.05$) for at least 5% of the combinations. Family–wise corrections of Type I errorprobability for such a large number of comparisons (Peres-Neto, 1999)render the power of the tests uninformatively low (Garcia, 2004; Moran, 2003). From a 'false–rejection–rate perspective (Garcia, 2004), however, our analyses identified significant differences among pairs for 26% (43 out of 160) of the combinations, which shows that differences among ecosystem types were more than just random events. To avoid statistical criticism, however, we refrain from interpreting individual pairwise combinations of food-web topologies from different ecosystems. Instead, we suggest the interpretation of our results that some systematic differences emerged between lake and terrestrial ecosystems (eight significant differences in topological properties), and between estuaries and lakes (four significant differences in topological properties). A cautious interpretation of these differences suggests that pelagic ecosystems such as lakes might possess a somewhat different network topology than terrestrial and estuarine (mainly benthic) ecosystems (Yvon-Durocher et al., 2011). Interestingly, this is consistent with differences in the body–mass structure between these ecosystems, which was explained by systematic effects of hard surfaces employed by predators while consumer carcasses (Brose et al., 2006b). Neverthe-

less, our analyses also suggest that for the majority of topological food-web properties follows the same diversity-complexity scaling models across ecosystems. These robust scaling models should indicate general building rules of ecological networks across different ecosystem types.

2.6 Conclusion

Consistent with previous studies (Schmid-Araya et al., 2002; Montoya and Sole, 2003; Brose and Martinez, 2004; Dunne, 2006), our results suggest that neither links per species nor connectance are scale-invariant constants. In the same vein, our results also illustrate that most food-web properties scale significantly with the diversity and complexity of the communities. After several decades of debate in the trophic scaling theory it remains thus unlikely that there are universal scale-independent constants in natural food webs that hold for all communities, from those that are low in diversity to those that are species rich. Nevertheless, recent work supports trophic scaling models predicting relationships between parameters of food-web topology and diversity with constant scaling exponents (Camacho et al., 2002a) (Garlaschelli et al., 2003). While these scaling relationships are certainly not as simple as often desired, they enable an understanding of the interrelation of the many parameters of complex food webs. A mechanistic understanding of why complex food webs appear to share a fundamental network structure mediated by species richness and connectance is yet to be gained - just as physicists are still lacking a mechanistic explanation of the gravitational force several centuries after Newton phrased the universal law of gravitation. Despite this lack of universal constants in food-web ecology, theoretical aspects of food-web ecology have made substantial progress in the last decade. Recent structural food-web models (Williams and Martinez, 2000; Cattin, 2004; Stouffer et al., 2005; Allesina et al., 2008) implement dependence of network topology on species richness and connectance and predict food-web properties depending on contiguous feeding ranges within an ordered set of species' niches (Williams and Martinez, 2000), phylogenetic constraints on feeding interactions (Cattin et al., 2004) and exponential degree distributions (Stouffer et al., 2005). The integration of such research with core concepts from other research areas, such as the body-size constraints on predator-prey interactions (Wootton and Emmerson, 2005; Beckerman et al., 2006; Brose et al., 2006a, 2008; Brose, 2010a; Petchey et al., 2008; Vucic-Pestic et al., 2010; Layer et al., 2010; McLaughlin et al., 2010; Woodward et al., 2005a,b, 2010), is a very promising way to start to develop a mechanistic basis for observed trophic patterns.

2.7 Acknowledgments

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3 Body sizes, cumulative and allometric degree distributions across natural food webs

3.1 Abstract

The distributions of body masses and degrees (i.e., the number of trophic links) across species are key determinants of food-web structure and dynamics. In particular, allometric degree distributions combining both aspects in the relationship between degrees and body masses are of critical importance for the stability of these complex ecological networks. They describe decreases in vulnerability (i.e., the number of predators) and increases in generality (i.e., the number of prey) with increasing species' body masses. We used an entirely new global body-mass database containing 94 food webs from four different ecosystem types (17 terrestrial, 7 marine, 54 lake, 16 stream ecosystems) to analyze (1) body mass distributions, (2) cumulative degree distributions (vulnerability, generality, linkedness), and (3) allometric degree distributions (e.g., generality– body mass relationships) for significant differences among ecosystem types. Our results demonstrate some general patterns across ecosystems: (1) the body masses are often roughly log-normally (terrestrial and stream ecosystems) or multi-modally (lake and marine ecosystems) distributed, and (2) most networks exhibit exponential cumulative degree distributions except stream networks that most often possess uniform degree distributions. Additionally, with increasing species body masses we found significant decreases in vulnerability in 70% of the food webs and significant increases in generality in 80% of the food webs. Surprisingly, the slopes of these allometric degree distributions were roughly three times steeper in streams than in the other ecosystem types, which implies that streams exhibit a more pronounced body mass structure. Overall, our analyses documented some striking generalities in the body-mass (allometric degree distributions of generality and vulnerability) and degree structure (exponential degree distributions) across ecosystem types as well as surprising exceptions (uniform degree distributions in stream ecosystems). This suggests general constraints of body masses on the link structure of natural food webs irrespective of ecosystem characteristics.

3.2 Introduction

Complexfood webs depict energy flows from producer (e.g. photoautotroph) and other basal-species to higher trophic levels. They provide an integrated understanding of the diversity, organization and functioning of natural communities. Challenged by the ecological complexity of natural ecosystems, recent theoretical advances in our understanding of food-web structure and their dynamic stability have documented the importance of body mass, degree and allometric degree distributions (Berlow et al., 2008; Montoya et al., 2006; Otto et al., 2007; Woodward et al., 2005b) These new approaches offer possibilities of reducible complexity via allometric scaling relationships as a proxy of structural and dynamic aspects of complex food webs that unravel regularities across ecosystem types. Body mass is among the most fundamental traits of organisms with strong implications for most of their other physiological and ecological characteristics

including metabolic rates, ingestion rates, interaction strength with other species, the ability to handle prey and the risk of being attacked by predators (Brose et al., 2008, 2006a; Brown et al., 2004; Emmerson and Raffaelli, 2004; O'Gorman and Emmerson, 2009; Peters and Wassenberg, 1983; Rall et al., 2009; Vucic-Pestic et al., 2010). In consequence, a species body mass determines its trophic position in the food web (Cohen et al., 2003; Jennings et al., 2001; Woodward and Hildrew, 2002; Woodward et al., 2005b). Recently, interest in classic body-mass patterns of natural food webs (Elton, 1927) has been invigorated by allometric scaling models that successfully predict the binary link structure and the interaction strengths between species across complex natural food webs (Berlow et al., 2009; Brose, 2008; Petchey et al., 2008; Vucic-Pestic et al., 2010). To allow detecting generalities across ecosystems, these theoretical advancements trigger an urgent need for comprehensive quantitative descriptions of natural body-mass distributions. Pioneering studies documented that the body mass distributions of natural food webs can be approximated by log normal distributions (Jonsson et al., 2005; Woodward et al., 2005b), but generalizations of these findings across ecosystem types are lacking.

In complex natural food webs, the energy, produced by plants and other basal species is distributed across the species by trophic interactions (Allesina and Bodini, 2004). The links and their distribution across the food web describe the generalities in energy fluxes. These generalities across food webs are conceptualized in degree distributions for linkedness (total number of links of a species), generality (number of links to prey), and vulnerability (number of links to predators). Degree distributions describe the frequency $(f(l))$ of one of these linkedness variables (l)across all populations in the network, whereas the more often employed cumulative degree distributions characterize the cumulative frequency of all populations with a linkedness variables higher than a threshold $(f(l > k))$. While most biological networks exhibit scale–free power–law cumulative degree distributions (i.e., cumulative frequency decreases linearly with an increasing number of links on a log–log scale) (Albert and Barabási, 2002), food webs are best characterized by exponential (i.e., cumulative frequency decreases linearly with an increasing number of links on a lin–log scale) or uni form (i.e.cumulative frequency is constant across the number of links) degree distributions (Camacho et al., 2002a; Dunne et al., 2002). Power-law cumulative degree distributions have been documented only in small food webs with unusually low connectance (Dunne, 2006; Dunne et al., 2002). Mathematically, however, a specific cumulative degree distribution does not necessarily imply that the non–cumulative distribution follows the same form (Tomas Jonnson, personal communication). Interestingly, the predictive success of recent topological food-web models (Allesina et al., 2008; Cattin et al., 2004; Williams and Martinez, 2000) is closely related to their built–in assumption of approximately exponential degree distributions (Stouffer et al., 2005).
While studies addressing the distributions of body masses and degrees across food webs have a long tradition in ecology (Schoener, 1989), interest in their relationship as conceptualized in

allometric degree distributions has emerged recently (Jonsson et al., 2005; Otto et al., 2007). Allometric degree distributions describe how linkedness, generality and vulnerability scale with species' body masses irrespective of their taxonomy or other traits. In this context, we employ the term " allometric " in a broad sense to refer to the scaling of a degree property with the population–averaged body mass, whereas this does not imply a power-law scaling. Across five natural food webs, the vulnerability increased and generality decreased with increasing body mass (Otto et al., 2007). Interestingly, these specific allometric degree distributions are crucially important for the stability of complex food webs (Otto et al., 2007), but empirical analyses of their generality across ecosystems are lacking. //

In this study, we present novel findings that generalize the work of previous studies on the distributions of body masses, cumulative degrees and allometric degrees across a much larger data set of 94 natural food webs. Our analyses address systematic differences in these relationships between marine, lake, stream and terrestrial ecosystems.

3.3 Material and Methods

We gathered a data set comprising 94 natural food webs from different ecosystems. Each of these food webs contains information on (1) the consumer–resource links (who is eating whom), and (2) the body masses of all species. The consumer–resource link were published in the original sources, and the body masses were taken from a data base (Brose et al., 2005) and other published sources (**Tabel 1**). Food webs were grouped by four ecosystem types: marine, stream, lake and terrestrial (**Table A1**). For our analyses, we removed some taxa representing trophic species that aggregate taxonomic species of different body masses (e.g., Gastropoda).

For each taxon, we used the food–web matrices to calculate (1) the vulnerability as the number of its consumer taxa (2) the generality as the number of its resource taxa and (3) the linkedness as the total number of links (equal to the sum of vulnerability and generality).

To analyze the body–mass distributions across the four ecosystem types, we used the pooled species list for each ecosystem type and calculated histograms with a class width of 1 on a log_{10} body mass [g] scale. Subsequently, we calculated the cumulative degree distributions as the fraction of species $P(k)$ that have k or more trophic links. Independent cumulative degree distributions were calculated for vulnerability, generality and linkedness for each of the ecosystem types. After log_{10} transformation of the cumulative degrees, the data was fitted with linear least square regressions in R 2.11 (Team, 2011). While linear relationships in this semi–log plot indicate exponential cumulative distributions, uniform and power–law cumulative distributions exhibit downward (i.e., linear on lin–lin scale) and upward curves (i.e., linear on a log–log scale), respectively. This first graphical impression was subsequently tested by fitting linear models to lin–lin, lin–log and log–log data. Additionally the cumulative degree distributions were calcu-

lated for each single food web. The goodness of fit (i.e., the coefficient of determination, r^2 of linear least square regressions to log–log plots (power–law relationships), semi–log plots (exponential distributions) and untransformed plots (uniform distributions) was calculated and used to compare the effects of species richness and connectance on the goodness of fit of the different distributions. This was tested by linear least squares regressions of the ratios of goodness of fits of (1) exponential to power law (r^2_{exp}/r^2_{pl}) and (2) exponential to uniform (r^2_{exp}/r^2_{univ}) against species richness and connectance.

To study allometric degree distributions we calculated the linear least square regressions of the number of predators (vulnerability), the number of prey (generality) and the number of links (linkedness) per species (y) on the log_{10} body mass (x) of the species for each of the 94 food webs independently. Subsequently, we tested for significant differences in the slopes of the allometric degree distributions between the ecosystem types by employing a linear mixed effect model with body mass (continuous explanatory variable) and ecosystem type (categorical explanatory variable) as fixed effects and the food webs as a random factor.

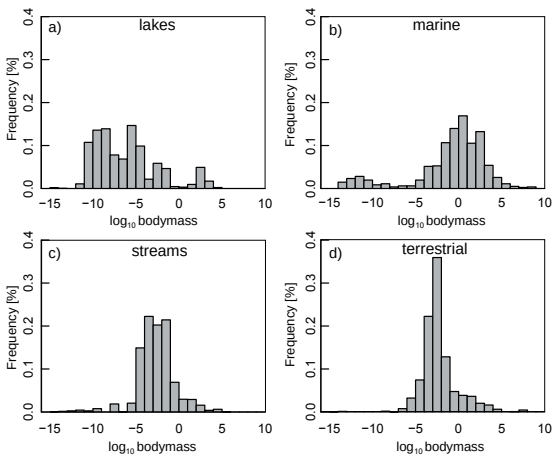

Figure 3.1: The body-mass structure of natural food webs: histograms of body masses for lake, marine, stream and terrestrial ecosystems.

3.4 Results

Body masses were approximately log–normally distributed in stream and terrestrial ecosystems, whereas they were multi–modal for lake and marine ecosystems (Fig. 3.1). Body masses from stream and terrestrial ecosystems had the highest frequency in the category between 10^-3 and 10^-2 gram. Terrestrial ecosystems were dominated by invertebrate species with the addition of some birds and vertebrates (e.g. coyotes, foxes, and birds). The largest individuals were coyotes

(4550g) of the sand community food web from Coachella Valley, and the smallest species were soil microbes (10^-8g) of the Coachella food web. Stream ecosystems were also dominated by invertebrate species, whereas also few fish species occurred. The size range of the stream food webs spanned from algae (10^-15g) to trouts (12,000g).

In contrast to the terrestrial and stream ecosystems, the body–mass distributions of lakes and marine ecosystems clearly exhibited multiple peaks (Fig. 3.1). For lake ecosystems, we found a high frequency of body masses in the category between 10^-10 and 10^-8g, which corresponds to the body–mass range of phytoplankton. The second peak occurred in the category between 10^-6 and 10^-4g representing zooplankton species. A third smaller peak occurred in the category between 10^2 and 10^3 g corresponding to the largest trouts. We found the largest range in body masses in the marine food webs. Here the smallest individuals are diatoms with a mass of 10^-13g and the largest individuals in the food webs are baleen whales with a body mass of 80 tonnes. Marine systems exhibited the inverse pattern to lake systems with the highest frequency of body masses in the category between 10 and 10^3g representing small birds (preying on fish in marine ecosystems), fishes and invertebrates such as sponges, sea urchins and starfishes, and a second smaller peak in the body–mass category between 10^-12 and 10^-10g corresponding to phytoplankton and zooplankton (e.g. algae and foraminiferans).

Analyses at the meta–community level lumping all data for each of the ecosystem types indicate that food webs of lakes, marine and terrestrial ecosystems should have exponential cumulative degree distributions for vulnerability, generality and linkedness (indicated by roughly linear relationships in Fig. 3.2), whereas stream food webs exhibited downward curved relationships for generality and linkedness indicative of more uniform degree distributions (Fig. 3.2). Statistical tests of these relationships are carried out for each of the food webs independently (see below). Additionally, the food webs of the four ecosystems differed in the maximum linkedness for a single species: 45 for lakes, 300 for marine, 138 for stream and 201 for terrestrial ecosystems.

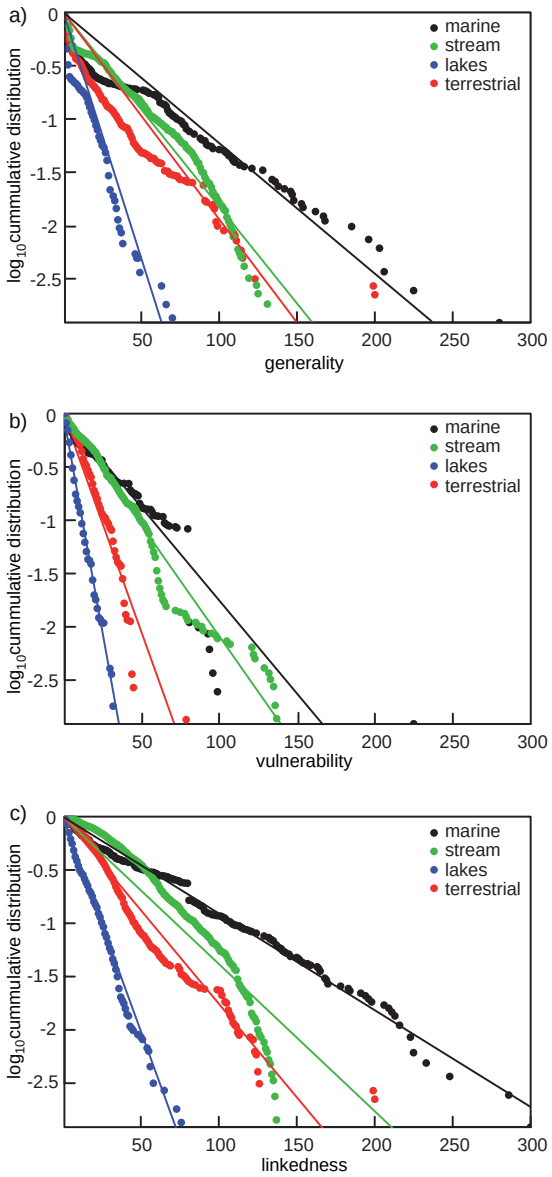

Figure 3.2: Linear-log plots of cumulative degree distributions in the different ecosystems of the number of predator links per species (generality; p<0.001, r^2=0.97 for lake; p<0.001, r^2=0.97 for marine; p<0.001, r^2=0.98 for stream and p<0.001, r^2=0.94 for terrestrial ecosystems);**b)** the number of prey links per species (vulnerability; p<0.001, r^2=0.99 for lake; p=<0.001, r^2=0.94 for marine;p<0.001, r^2=0.99 for stream and p<0.001, r^2=0.98 for terrestrial ecosystems); **c)**the total number of links per species (linkedness; p<0.001, r^2=0.99 for lake; p<0.001, r^2>0.99 for marine; p<0.001, r^2=0.95 for stream and p<0.001, r^2=0.98 for terrestrial ecosystems)

Subsequent analyses at the local–community level with individual data sets for each of the 94 food webs studied generally confirmed these findings. In 54 % of the individual food webs cumulative degree distributions were best characterized by exponential regressions using the r^2 as an estimate of goodness of fit , whereas a better goodness of fit of uniform and power–law cumulative distributions occurred in 45% and 1% of the webs, respectively (Table 1.1). Some differences in the relative frequency of the different distributions (indicated by the highest r^2 of the regressions) between the ecosystem types were detected: lake food webs exhibited exponential cumulative degree distributions in 57% (30 of 53) of the food webs, uniform cumulative degree distributions in 43% (23 of 53) and one food web with a power law cumulative degree distribution; in marine food webs we found 57 % (4 of 7) uniform cumulative distributions and 43% (3 of 7) exponential cumulative distributions; stream food webs exhibited uniform cumulative distributions in 87.5% (14 of 16) of the food webs and exponential cumulative distributions in 12.5% (2 of 16) of the food webs; terrestrial food webs exhibited exponential cumulative distributions in 94% (16 of 17) of the food webs, and uniform cumulative distributions in only one (6%) of the 17 terrestrial food webs.

Across all ecosystem types, the goodness of fit plots demonstrate that power law cumulative degree distributions occurred only in very few food webs with low species richness and low connectance (Fig. 3.3a, b, data points with goodness of fit ratio exponential to power law lower than one). Generally, the fit of exponential cumulative degree distributions improved over that of power–law cumulative degree distributions with increasing species richness and connectance. In contrast, uniform cumulative degree distributions occurred in the food webs with the highest connectance (Fig. 3.3d, data points with goodness of fit ratio exponential to uniform lower than one), whereas species richness did not affect the probability of encountering uniform cumulative degree distributions (Fig 3.3c).

Our analyses suggest that allometric degree distributions are wide spread across all ecosystem types. For instance, in the food web of the Mondego Estuary Zostera seagrass bed we found a significant decrease in vulnerability and a significant increase in generality with the log_{10}body masses of the species (Fig. 3.4 a, b). In contrast, the linkedness (the total number of links equal to the sum of vulnerability and generality) did not vary significantly with the log_{10}body masses of the species (Fig. 3.4 c). Consistent with this pattern, we found a significant decrease in vulnerability in 70% (66 food webs) and a significant increase in generality in 80% (75

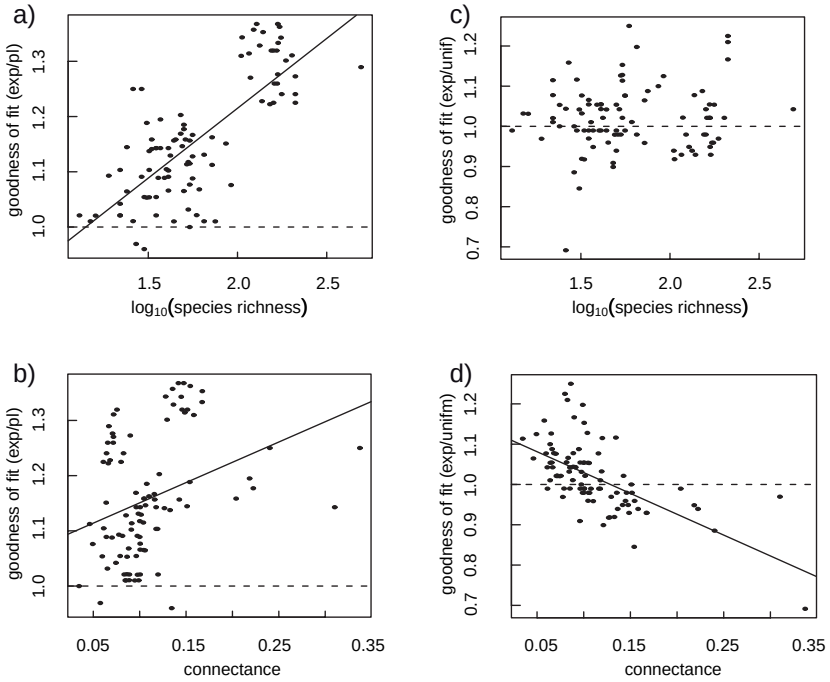

Figure 3.3: Goodness of fit ratio plots with r^2 values of exponential degree distributions (exp) over r^2 values of power-law (pl; a, c) or uniform degree distributions (unif; b, d) depending on log_{10} species richness (a, b) and food-web connectance (c, d). Points under the dashed lines indicate a better fit of uniform or power-law distributions, whereas points above the dashed line suggest a better fit of exponential degree distributions. Linear least square regressions: (a) p<0.001, r^2=0.58; (b) p<0.001, r^2=0.11; (c) not significant; (d) p<0.001, r^2=0.38.

food webs) of the 94 food webs analyzed (significant increases or decreases indicated by linear least squares regressions with slopes significantly different from zero, p<0.05, see appendix for data). Furthermore, we found a slightly significant effect (negative or positive) of body masses on linkedness in 40% (38 of 94) of the food webs (see appendix).

The slopes of the allometric degree distributions quantify the strength of the decrease and increase in vulnerability and generality, respectively, with the log_{10}body masses. These slopes differed significantly between the ecosystem types (Fig. 3.5). Linear mixed effects models indicated significant differences between the four ecosystems. The vulnerability slopes of stream ecosystems were the steepest, whereas the slopes of terrestrial systems were the shallowest. The slopes of marine and lake systems ranged between these two groups (Fig. 3.5a, Table A1 in appendix). Linear mixed effects models indicated the same pattern for generality, with the steepest slopes in stream food webs, the shallowest slopes in terrestrial food webs and intermediate slopes in marine and lake ecosystems (Fig. 3.4b, Table A1 in appendix). The steeper slopes in

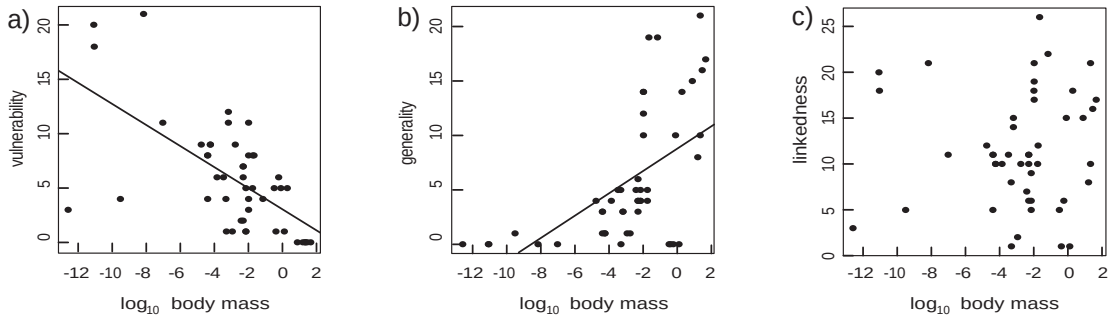

Figure 3.4: Allometric degree distributions of the food web of the Mondego Estuary Zostera seagrass bed: vulnerability (i.e., number of predators) depending on log_{10} body mass (p $<$0.001, r^2=0.39); generality (i.e., number of prey) depending on log_{10} body mass (p $<$0.001, r^2=0.32); linkedness (i.e.,total number of links) depending on log_{10} body mass (p=0.78).

stream food webs indicate a stronger relationships between the body mass and the number of predator or prey links. Thus, in stream ecosystems individuals with higher body mass have on average less predators and more prey than large species in other ecosystems. The shallow slopes of terrestrial food webs indicate a weak relationship between body mass and degree suggesting that the influence of body masses on the vulnerability or generality is weaker than in the other ecosystems. The slopes of linkedness were shallower ranging around zero and exhibited only little differences among ecosystems (Fig. 3.5c).

3.5 Discussion

In this study, we analyzed a new allometric food–web data base containing data from 94 natural communities across four ecosystem types. Despite substantial variation in ecosystem and species characteristics, some regularities across ecosystem types were identified: exponential degree distributions dominated the food–web topologies across all ecosystem types except for streams, and allometric degree distributions of vulnerability and generality occurred in most food webs studied. Our novel results generalize previous findings (Camacho et al., 2002a; Dunne et al., 2002; Otto et al., 2007) to cover marine, freshwater and terrestrial food webs using a new extensive global data base of 94 food webs.

Our analyses documented some systematic differences in the body–mass distributions between ecosystem types. We found approximately log–normally distributed body masses in stream and terrestrial food webs, whereas the body–mass distributions of lakes and marine ecosystems ex-

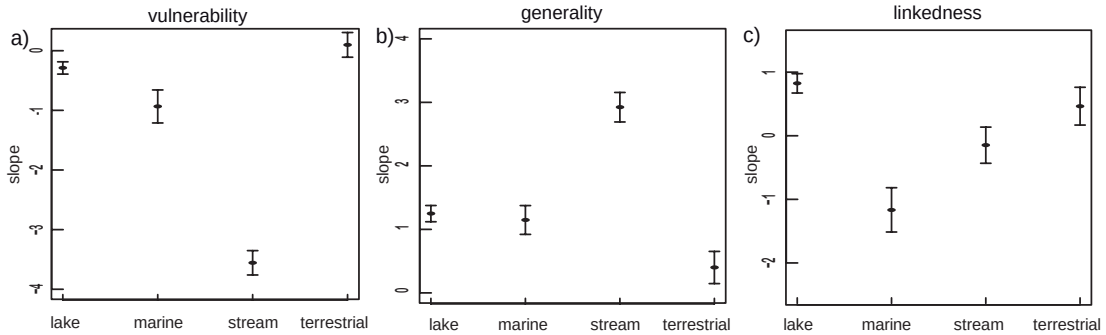

Figure 3.5: Slopes of the linear mixed effect models of the allometric degree distributions in the different ecosystems: vulnerability slopes, with $F_{1.7345}$ = 114.30 and p<0.001 for log_{10}(bodymass), $F_{3.90}$= 25.22 and p<0.001 for ecosystem type and $F_{1.7345}$= 97.71 and p<0.001 for log_{10}(bodymass) ecosystem type; generality slopes, with $F_{1.7345}$ = 329.35 and p<0.001 for log_{10}(body mass), $F_{3.90}$ = 22.19 and p<0.001 for ecosystem type and $F_{1.7345}$ = 28.60 and p<0.001 for log_{10}(body mass ecosystem type; linkedness slopes, with $F_{1.7345}$ = 19.76 and p<0.001 for log_{10}(body mass), $F_{3.90}$ = 38.84 and p<0.001 for ecosystem type and $F_{1.7345}$ = 12.52 and p<0.001 for log_{10}(body mass) ecosystem type.

hibited multiple peaks. This corresponds to the occurrence of multiple dominant species groups in these ecosystems: phytoplankton, zooplankton and fish species in lakes and phytoplankton, zooplankton and birds, fishes and large invertebrates in marine ecosystems.

Consistent with prior studies (Dunne et al., 2002), our analyses indicate that in contrast to other biological networks, food webs rarely exhibit power–law degree distributions. While the topology of most biological networks is well predicted by preferential attachment algorithms (Barabasi and Albert, 1999), food–web structure follows more complex models (Allesina et al., 2008; Cattin et al., 2004; Williams and Martinez, 2000). These food–web models have two common features: (1) the species are hierarchically ordered according to a set of arbitrary niche values, and (2) each species has a specific exponentially decaying

probability of preying on a given fraction of the species with lower niche values (Stouffer et al., 2005). Our analyses support the interpretation that body masses can serve as a proxy for the ordered set of niche values, and they suggest that exponential degree distributions are a generality across lake, marine and terrestrial food webs. Surprisingly, stream food webs exhibited more uniform degree distributions suggesting that taxa with an average linkedness are more frequent than in food webs of the other ecosystem types. Consistent with this pattern, the generality of the stream consumers was higher than in the other ecosystem types. One biological interpretation of this pattern is that the strong drift of stream ecosystems prevents the occurrence of highly

specialized consumers, because consumer–resource interactions are more driven by random encounters than by specific search (Hildrew, 2009). Interestingly, the lack of an exponential degree distribution for stream food webs suggests that their topology might be less well predicted by the current structural models than food webs of other ecosystem types (Allesina et al., 2008; Cattin et al., 2004; Williams and Martinez, 2000). However, this suggestion remains a hypothesis to be tested. Consistent with previous findings (Dunne et al., 2002), we found that power law degree distributions only occurred in food webs with very low species richness and with low connectance (<0.1). In contrast, uniform degree distributions occurred in few food webs with a high connectance, but high species richness had no influence on the occurrence of uniform distributions. In the present data set, most of the high connectance food webs with uniform degree distributions are streams, and it is difficult to determine whether the high connectance or the ecosystem type stream are responsible for this result. Until more terrestrial, lake and marine food webs of higher connectance are sampled, our analyses generally confirm the conclusion that exponential degree distributions best characterize most natural food webs except for stream ecosystems.

Our analyses demonstrate that allometric degree distributions occur in the majority of the food webs studied. These allometric degree distributions hold that generality (the number of links to resources) increases and vulnerability (the number of links to consumers) decreases with a species' population–averaged body mass. Interestingly, under the assumption that body masses are a proxy of the topological models' niche values (Allesina et al., 2008; Cattin et al., 2004; Williams and Martinez, 2000), the hierarchical ordering of species predominantly preying on lower ranked species (i.e., those of smaller body masses) in these models would imply similar allometric degree distributions. Empirically, these relationships were first documented for the food webs of Tuesday Lake (Jonsson et al., 2005). A subsequent study (Otto et al., 2007) has identified these allometric degree distributions as a characteristic of natural food webs that is crucially important for their stability. While food webs with allometric degree distributions as documented in the present study constrain their food chains in a domain of parameter combinations that yields species persistence, topological randomizations only reduce persistence if allometric degree distributions are disrupted (Otto et al., 2007). The results of the present study now demonstrate the generality of these allometric degree distributions across a much larger data set of 94 natural food webs suggesting that based on theoretical arguments stability might be a more general property of complex food webs than previously anticipated.

Together, our results document the body–mass and link structure of natural food webs across ecosystem types as well as surprising deviations such as the occurrence of uniform degree distributions in stream food webs. This stresses the need for more detailed topological analyses of stream food webs to provide a better understanding whether and why they deviate from other ecosystems'food webs. Moreover, the present data set is lacking data of terrestrial soil food

webs, and data for marine pelagic communities is scarce. Urgently, future empirical studies should fill these gaps. Nevertheless, the regularities documented here suggest that allometric scaling models may provide a useful tool for building abstract ecosystem models. Generally, these models should employ exponential degree distributions and allometric degree distributions for generality and vulnerability. These abstract models will certainly not allow mimicking quantitative dynamics or exact topologies of natural food webs, but they will enable a deepened understanding of the general physical and biological principles that govern natural ecosystems.

3.5.1 Acknowledgements

We are particularly grateful to Julia Blancard and the members of the sizemic steering committee for organizing the sizemic meetings and promote this special issue. We thank Tomas Jonnson and Mark Emmerson for providing very helpful reviews. Tomas Jonnson has provided derivations that the form of cumulative and non-cumulative degree distributions cannot necessarily be inferred from each other. We thank Ute Jacob, Denise Piechnik, Kateri Harrison and Neo Martinez for providing data. Franziska Grischkat has been a tremendous help in unearthing body-mass data. Helpful suggestions have been provided by Jennifer Dunne and Neo Martinez. Financial support for this study is provided by funds to C.D., J.R. and U.B. by the German Research Foundation (BR 2315/ 4-1, 9-1).

3.5.2 appendix

Ninty-four natural food webs

The table contains the common food–web names used in this article. For each food web, the predation matrices and the species' body sizes were compiled from a variety of sources. These natural food webs contain producers, herbivores, carnivores, parasites, and parasitoids. The organisms display a range of feeding interactions including predation, herbivory, bacterivory, parasitism, and parasitoidism. The orginal sources of publications of the predation matrices and the body masses are documented in table 1.1 .

Table 3.1: Overview of all food webs sources used in this study, with references of predation matrix, references of the body-masses, the statistics of the allometic degree distributions with a) vulnerability, b) generality and c) linkedness including regression slopes, p-values and r-square values. Furthermore the statistic for the different cumulative degree distributions: uniform, exponential and power law.

		allometric degree distributions									cumulative degree distributions					
		vulnerability			generality			linkedness			uniform		exponential		power law	
food web	**type**	**slope**	**p**	r^2	**slope**	**p**	r^2	**slope**	**p**	r^2	r^2	**p**	r^2	**p**	r^2	**p**
Alford Lake	lake	-0.13	0.28	0.02	1.21	<0.001	0.21	1.06	<0.01	0.16	0.92	<0.001	0.99	<0.001	0.91	<0.001
Balsam Lake	lake	-0.43	<0.001	0.26	1.65	<0.001	0.38	1.21	<0.001	0.25	0.93	<0.001	0.98	<0.001	0.92	<0.001
Burntbridge Lake	lake	-0.32	<0.01	0.19	0.93	<0.01	0.16	0.58	0.06	0.07	0.87	<0.001	0.98	<0.001	0.95	<0.001
Beaver Lake	lake	-0.15	0.09	0.05	1.08	<0.001	0.31	0.91	<0.001	0.21	0.98	<0.001	0.97	<0.001	0.86	<0.001
Big Hope Lake	lake	-0.27	0.02	0.09	1.11	<0.001	0.23	0.81	0.01	0.12	0.93	<0.001	0.94	<0.001	0.88	<0.001
Brandy Lake	lake	-0.58	<0.001	0.49	1.03	0.01	0.23	0.46	0.22	0.05	0.86	0.01	0.96	<0.001	1	<0.001
Bridge Brook Lake	lake	-0.5	<0.001	0.23	1.88	<0.001	0.35	1.36	0	0.2	0.91	<0.001	0.99	<0.001	0.98	<0.001
Brook Trout Lake	lake	-0.29	0.08	0.22	0.5	0.11	0.19	0.21	0.51	0.03	0.94	<0.001	0.97	<0.001	0.96	<0.001
Buck Pond	lake	-0.82	<0.001	0.4	1.06	0.01	0.18	0.23	0.53	0.01	0.93	<0.001	0.97	<0.001	0.88	<0.001
Cascade Lake	lake	-0.24	<0.001	0.29	0.57	0.01	0.19	0.31	0.14	0.06	0.97	<0.001	0.96	<0.001	0.84	<0.001
Chub Lake	lake	-0.04	0.67	0.01	0.64	0.01	0.17	0.55	0.05	0.11	0.97	<0.001	0.98	<0.001	0.9	<0.001
Chub Pond	lake	-0.64	<0.001	0.23	1.59	<0.001	0.41	0.95	<0.01	0.15	0.94	<0.001	0.96	<0.001	0.83	<0.001
Connery Lake	lake	-0.33	<0.001	0.29	1.27	<0.001	0.27	0.92	<0.01	0.15	0.81	<0.001	0.97	<0.001	0.96	<0.001
Constable Lake	lake	-0.22	0.09	0.09	0.54	0.06	0.11	0.3	0.33	0.03	0.91	<0.001	0.98	<0.001	0.93	<0.001
Deep Lake	lake	-0.18	0.14	0.12	0.55	0.03	0.24	0.35	0.17	0.11	0.97	<0.001	0.94	<0.001	0.86	<0.001
Emerald Lake	lake	-0.02	0.92	0	1.03	0	0.37	0.92	0.02	0.25	0.87	<0.001	0.97	<0.001	0.95	<0.001
Falls Lake	lake	-0.57	<0.001	0.38	0.82	0.01	0.18	0.23	0.45	0.02	0.93	<0.001	0.98	<0.001	0.9	<0.001
Fawn Lake	lake	-0.32	<0.01	0.25	0.78	<0.01	0.27	0.43	0.1	0.09	0.93	<0.001	0.96	<0.001	0.87	<0.001
Federation Lake	lake	-0.42	<0.01	0.41	0.41	0.09	0.14	-0.05	0.83	0	0.95	<0.001	0.96	<0.001	0.87	<0.001
Goose Lake	lake	-0.06	0.42	0.02	0.65	<0.01	0.21	0.57	0.02	0.14	0.96	<0.001	0.95	<0.001	0.86	<0.001
Grass Lake	lake	-0.23	0.06	0.08	0.78	<0.01	0.18	0.53	0.06	0.08	0.95	0.01	0.99	<0.001	0.98	0.0014
Gull Lake	lake	-0.36	0.06	0.08	1.6	<0.001	0.52	1.23	<0.001	0.27	0.99	<0.001	0.95	<0.001	0.82	<0.001
Gull Lake North	lake	-0.2	0.16	0.27	0.57	0.02	0.34	0.29	0.25	0.09	0.96	<0.001	0.99	<0.001	0.97	<0.001
Helldiver Pond	lake	-0.44	<0.001	0.25	0.94	<0.001	0.29	0.5	0.07	0.08	0.97	<0.001	0.96	<0.001	0.84	<0.001
High Pond	lake	-0.54	<0.001	0.45	0.42	0.2	0.07	-0.17	0.62	0.01	0.95	<0.001	0.95	<0.001	0.83	<0.001
Hoel Lake	lake	-0.32	0.01	0.1	1.6	<0.001	0.4	1.27	<0.001	0.24	0.97	<0.001	0.93	<0.001	0.8	<0.001
Horseshoe Lake	lake	-0.19	0.01	0.12	1.02	<0.001	0.33	0.8	<0.001	0.21	0.96	<0.001	0.94	<0.001	0.82	<0.001
Indian Lake	lake	-0.7	<0.01	0.24	1.4	<0.001	0.35	0.65	0.1	0.08	0.91	<0.001	0.97	<0.001	0.95	<0.001
Long Lake	lake	-0.24	0.05	0.06	1.46	<0.001	0.35	1.22	<0.001	0.23	0.97	<0.001	0.95	<0.001	0.84	<0.001
Loon Lake	lake	-0.21	0.11	0.08	0.76	0.01	0.2	0.53	0.08	0.09	0.92	<0.001	0.97	<0.001	0.92	<0.001
Lost Lake	lake	-0.59	<0.001	0.66	0.87	<0.001	0.39	0.25	0.24	0.05	0.97	<0.001	0.82	<0.001	0.69	<0.001
Lost Lake East	lake	-0.38	<0.01	0.2	0.96	<0.01	0.24	0.55	0.06	0.09	0.91	<0.001	0.96	<0.001	0.88	<0.001
Little Rainbow Lake	lake	-0.65	0.63	0.17	1.63	<0.001	0.37	0.98	0.01	0.13	0.94	<0.001	0.98	<0.001	0.88	<0.001
Lower Sister Lake	lake	-0.41	<0.01	0.23	1.16	<0.001	0.36	0.74	0.01	0.17	0.97	<0.001	0.96	<0.001	0.84	<0.001
Oswego Lake	lake	-0.59	<0.001	0.46	0.8	0.01	0.19	0.16	0.6	0.01	0.97	<0.001	0.89	<0.001	0.78	<0.001

Continued

Table 3.1: Overview of all food webs sources used in this study, with references of predation matrix, references of the body-masses, the statistics of the allometic degree distributions with a) vulnerability, b) generality and c) linkedness including regression slopes, p-values and r-square values. Furthermore the statistic for the different cumulative degree distributions: uniform, exponential and power law.

		allometric degree distributions									cumulative degree distributions					
		vulnerability			generality			linkedness			uniform		exponential		power law	
food web	**type**	**slope**	**p**	r^2	**slope**	**p**	r^2	**slope**	**p**	r^2	r^2	**p**	r^2	**p**	r^2	**p**
Owl Lake	lake	-0.51	<0.001	0.38	0.69	0.02	0.17	0.17	0.57	0.01	0.98	<0.001	0.97	<0.001	0.92	<0.001
Rat Lake	lake	-0.27	0.01	0.13	1.12	<0.001	0.32	0.82	<0.01	0.16	0.97	<0.001	0.95	<0.001	0.82	<0.001
Razorback Lake	lake	-0.41	<0.001	0.27	0.86	<0.01	0.2	0.45	0.12	0.06	0.94	<0.001	0.96	<0.001	0.85	<0.001
Rock Lake	lake	-0.81	<0.01	0.35	0.58	0.06	0.16	-0.25	0.5	0.02	0.9	<0.001	0.97	<0.001	0.95	<0.001
Russian Lake	lake	-0.35	0.05	0.16	0.87	<0.001	0.47	0.51	0.07	0.15	0.94	<0.001	0.99	<0.001	0.93	<0.001
Safford Lake	lake	-0.41	<0.001	0.26	0.99	<0.001	0.31	0.57	0.04	0.1	0.97	<0.001	0.96	<0.001	0.83	<0.001
Sand Lake	lake	-0.17	0.02	0.19	0.46	0.01	0.2	0.27	0.17	0.07	0.96	<0.001	0.96	<0.001	0.88	<0.001
South Lake	lake	-0.7	<0.01	0.33	0.75	<0.001	0.44	0.06	0.86	0	0.97	<0.001	0.99	<0.001	0.95	<0.001
Squaw Lake	lake	-0.36	<0.001	0.47	1	<0.001	0.26	0.62	0.03	0.12	0.92	<0.001	0.97	<0.001	0.91	<0.001
Stink Lake	lake	-0.39	<0.01	0.18	1.38	<0.001	0.31	0.96	0	0.16	0.97	<0.001	0.95	<0.001	0.85	<0.001
Twin Lake East	lake	-0.27	0.05	0.3	0.42	0.01	0.48	0.1	0.57	0.03	0.98	<0.001	0.97	<0.001	0.95	<0.001
Twin Lake West	lake	-0.67	<0.001	0.42	0.82	<0.01	0.3	0.12	0.65	0.01	0.91	<0.001	0.95	<0.001	0.94	<0.001
Twelfth Tee Lake	lake	-0.23	0.01	0.22	0.5	0.02	0.18	0.24	0.26	0.04	0.95	<0.001	0.99	<0.001	0.94	<0.001
Whipple Lake	lake	-0.23	0.09	0.09	0.84	<0.001	0.36	0.61	0.01	0.19	0.99	<0.001	0.91	<0.001	0.8	<0.001
Wolf Lake	lake	-0.2	0.16	0.08	0.87	0.01	0.27	0.65	0.05	0.15	0.82	0.01	0.95	<0.001	0.98	<0.001
Littlerock Lake	lake	-0.32	0.02	0.03	0.55	<0.001	0.26	0.22	0.15	0.01	0.93	<0.001	0.98	<0.001	0.79	<0.001
Sierra Lakes	lake	-0.66	<0.001	0.27	1.81	<0.001	0.43	1.14	0	0.21	0.97	<0.001	0.92	<0.001	0.77	<0.001
Skipwith Pond	lake	-1.77	0.01	0.18	5.11	<0.01	0.27	3.21	0.01	0.2	0.99	<0.001	0.96	<0.001	0.84	<0.001
Tuesday Lake 1984	lake	-0.86	<0.01	0.19	2	<0.001	0.52	1.09	0.01	0.13	0.97	<0.001	0.96	<0.001	0.81	<0.001
Benguela	marine	-0.37	0.23	0.05	1.16	<0.001	0.35	0.77	0.02	0.18	0.96	<0.001	0.85	<0.001	0.68	<0.001
Carpinteria	marine	-1.16	<0.001	0.31	0.77	<0.001	0.19	-0.39	0.15	0.03	0.93	<0.001	0.99	<0.001	0.89	<0.001
St. Marks	marine	-0.59	0	0.31	0.41	0	0.25	-0.16	0.4	0.02	0.99	<0.001	0.9	<0.001	0.77	<0.001
Mondego Esturay Zostera	marine	-0.97	<0.001	0.4	1.06	<0.001	0.32	0.08	0.78	0	0.99	<0.001	0.89	<0.001	0.74	<0.001
Small Reef	marine	-1.08	<0.001	0.3	1.13	0.01	0.15	0.01	0.98	0	0.99	<0.001	0.93	<0.001	0.79	<0.001
Weddel See	marine	-3.74	<0.001	0.4	0	<0.001	0.08	-1.02	0.04	0.01	0.94	<0.001	0.98	<0.001	0.76	<0.001
Ythan Estuary	marine	-1.04	<0.001	0.15	1.02	<0.001	0.19	-0.03	0.94	0	0.88	<0.001	0.99	<0.001	0.92	<0.001
Alamitos Creek	stream	-3.54	<0.001	0.12	3.46	<0.01	0.05	-0.1	0.94	0	0.97	<0.001	0.95	<0.001	0.72	<0.001
Bere Stream	stream	-2.46	<0.001	0.4	1.76	<0.01	0.29	-0.7	0.06	0.03	0.9	<0.001	0.97	<0.001	0.79	<0.001
Broadstone Stream	stream	-0.33	0.35	0.03	1.13	0.07	0.1	0.77	0.23	0.05	0.96	<0.001	0.95	<0.001	0.82	<0.001
Calero Creek	stream	-2.78	<0.001	0.14	2.72	<0.01	0.08	-0.04	0.93	0	0.97	<0.001	0.95	<0.001	0.7	<0.001
Corte Madera Creek	stream	-2.83	<0.001	0.11	3.38	<0.01	0.09	0.54	0.64	0	0.99	<0.001	0.93	<0.001	0.71	<0.001
Coyote Creek	stream	-4.77	<0.001	0.22	4.7	<0.001	0.12	-0.09	0.93	0	0.98	<0.001	0.95	<0.001	0.73	<0.001
Guadelupe Creek	stream	-4.51	<0.001	0.14	5.82	<0.001	0.1	1.3	0.36	0	0.98	<0.001	0.94	<0.001	0.69	<0.001
Guadelupe River	stream	-3.41	<0.001	0.2	2.02	0.01	0.05	-1.41	0.1	0.02	0.99	<0.001	0.93	<0.001	0.7	<0.001
Los Gatos Creek	stream	-4.63	<0.001	0.16	4.43	<0.001	0.07	-0.22	0.86	0	0.98	<0.001	0.94	<0.001	0.7	<0.001

Continued

Table 3.1: Overview of all food webs sources used in this study, with references of predation matrix, references of the body-masses, the statistics of the allometic degree distributions with a) vulnerability, b) generality and c) linkedness including regression slopes, p-values and r-square values. Furthermore the statistic for the different cumulative degree distributions: uniform, exponential and power law.

		allometric degree distributions									cumulative degree distributions					
		vulnerability			generality			linkedness			uniform		exponential		power law	
food web	**type**	**slope**	**p**	r^2	**slope**	**p**	r^2	**slope**	**p**	r^2	r^2	**p**	r^2	**p**	r^2	**p**
Los Trancos Creek	stream	-3.23	<0.001	0.15	3.71	<0.001	0.11	0.2	0.65	0	0.98	<0.001	0.93	<0.001	0.68	<0.001
Mill Stream	stream	-1.34	<0.001	0.5	0.79	<0.001	0.47	-0.55	<0.01	0.1	0.9	<0.001	0.99	<0.001	0.86	<0.001
Penninterra Creek	stream	-5.01	<0.001	0.2	2.74	0.01	0.04	-2.27	0.05	0.02	0.98	<0.001	0.93	<0.001	0.68	<0.001
Ross Creek	stream	-3.53	<0.001	0.18	3.37	<0.001	0.13	-0.17	0.87	0	0.99	<0.001	0.92	<0.001	0.7	<0.001
San Francisquito Creek	stream	-4.03	<0.001	0.17	4.35	<0.001	0.1	0.3	0.78	0	0.99	<0.001	0.92	<0.001	0.68	<0.001
Sarratoga Creek	stream	-4.44	<0.001	0.16	4.77	<0.001	0.09	0.33	0.8	0	0.97	<0.001	0.95	<0.001	0.72	<0.001
Stevens Creek	stream	-5.36	<0.001	0.17	5.02	<0.001	0.08	-0.36	0.8	0	0.99	<0.001	0.92	<0.001	0.69	<0.001
Broom Source	terrestrial	0	0.98	0	0.1	0.18	0.03	0.1	0.5	0.01	0.88	<0.001	0.98	<0.001	0.98	<0.001
Coachella	terrestrial	-0.46	0.17	0.08	1.27	<0.01	0.33	0.81	0.04	0.16	0.94	<0.001	0.65	<0.001	0.52	<0.001
Florida Islands E1	terrestrial	0.29	0.15	0.01	0.15	0.05	0.02	1.44	0.01	0.03	0.8	<0.001	0.98	<0.001	0.8	<0.001
Florida Islands E2	terrestrial	1.41	0.01	0.03	-0.32	0.18	0.1	1.09	0.05	0.07	0.76	<0.001	0.95	<0.001	0.93	<0.001
Florida Islands E3	terrestrial	0.3	0.15	0.01	1.14	0.05	0.02	1.44	0.01	0.03	0.81	<0.001	0.98	<0.001	0.79	<0.001
Florida Islands E7	terrestrial	1.56	0.01	0.04	-0.39	0.14	0.11	1.17	0.05	0.07	0.86	<0.001	0.97	<0.001	0.87	<0.001
Florida Islands E9	terrestrial	1.49	0.03	0.04	-0.42	0.14	0.09	1.07	0.09	0.05	0.91	<0.001	0.98	<0.001	0.84	<0.001
Florida Islands Metaweb	terrestrial	0.83	0.1	0.01	2.82	0.04	0.02	3.64	<0.01	0.04	0.84	<0.001	0.98	<0.001	0.77	<0.001
Florida Islands ST2	terrestrial	-0.49	0.05	0.07	1.66	0.01	0.13	1.17	0.05	0.07	0.85	<0.001	0.98	<0.001	0.91	<0.001
Grande Caricaie CLControl	terrestrial	0.34	0.44	0	-0.09	0.9	0	0.27	0.68	0	0.93	<0.001	0.95	<0.001	0.72	<0.001
Grande Caricaie CLControl2	terrestrial	-0.25	0.39	0.01	0.1	0.84	0	-0.13	0.79	0	0.92	<0.001	0.94	<0.001	0.74	<0.001
Grande Caricaie CLMown1	terrestrial	0.38	0.32	0	-1.11	0.1	0.01	-0.73	0.27	0.01	0.95	<0.001	0.97	<0.001	0.74	<0.001
Grande Caricaie CLMown2	terrestrial	0.24	0.4	0	-0.31	0.55	0	-0.06	0.9	0	0.92	<0.001	0.97	<0.001	0.77	<0.001
Grande Caricaie SC_Control1	terrestrial	-0.67	0.01	0.04	-0.44	0.33	0.01	-1.1	0.02	0.04	0.94	<0.001	0.98	<0.001	0.8	<0.001
Grande Caricaie SC_Control2	terrestrial	-0.6	0.01	0.04	-0.08	0.88	0	-0.67	0.16	0	0.91	<0.001	0.99	<0.001	0.81	<0.001
Grande Caricaie SCMown1	terrestrial	-0.33	0.45	0	-0.09	0.72	0	-0.42	0.33	0.01	0.95	<0.001	0.97	<0.001	0.76	<0.001
Grande Caricaie SCMown2	terrestrial	-0.71	0.14	0	0.04	0.86	0.01	-0.67	0.15	0.01	0.95	<0.001	0.97	<0.001	0.77	<0.001

4 STEPPING IN ELTON'S FOOTPRINTS: A GENERAL SCALING MODEL FOR BODY MASSES AND TROPHIC LEVELS ACROSS ECOSYSTEMS

4.1 Abstract

Despite growing awareness of the significance of body–size and predator–prey body–mass ratios for the stability of ecological networks, our understanding of their distribution within ecosystems is incomplete. Here, we study the relationships between predator and prey size, body–mass ratios and predator trophic levels using body–mass estimates of 1313 predators (invertebrates, ectotherm and endotherm vertebrates) from 35 food–webs (marine, stream, lake and terrestrial). Across all ecosystem and predator types, except for streams (which appear to have a different size structure in their predator–prey interactions), we find that (1) geometric mean prey mass increases with predator mass with a power–law exponent greater than unity and (2) predator size increases with trophic level. Consistent with our theoretical derivations, we show that the quantitative nature of these relationships implies systematic decreases in predator–prey body–mass ratios with the trophic level of the predator. Thus, predators are, on an average, more similar in size to their prey at the top of food–webs than that closer to the base. These findings contradict the traditional Eltonian paradigm and have implications for our understanding of body–mass constraints on food–web topology, community dynamics and stability

4.2 Introduction

Since Charles Elton's seminal work (Elton 1927), an enduring and recently rejuvenated debate on the structure of natural communities has focused on whether and how interactions between predators and their prey are driven by the species' body masses (see (Ings et al., 2009; Brose, 2010a) for reviews). Body–size is an important ecological characteristic of organisms (Brown et al., 2004) and the distribution of body–sizes in communities influences their structure and functioning (Cohen et al., 1993; Neubert et al., 2000; Loeuille and Loreau, 2004; Jonsson et al., 2005; Brose et al., 2006a; Rall et al., 2008). In particular, ratios between predator size and the average size of their prey (hereafter: body–mass ratios) have an important role in explaining regularities in food–web structure (Warren and Lawton, 1987; Cohen et al., 2003; Brose et al., 2006a; Petchey et al., 2008), influencing patterns in interaction strength (Emmerson and Raffaelli, 2004; Vucic-Pestic et al., 2010) and, consequently, the dynamics and stability of food–webs (Jonsson and Ebenman, 1998; Emmerson and Raffaelli, 2004; Weitz and Levin, 2006; Otto et al., 2007; Berlow et al., 2009). Hence, predicting how body–mass ratios vary among consumers (or resources) and among and within ecological communities will be important for a better understanding of community structure, dynamics and stability. Predator–prey body–mass ratios are systematically higher in lake habitats than in marine, stream or terrestrial habitats and vertebrate predators have, on an average, higher body–mass ratios to their prey than invertebrate predators (Brose et al., 2006a; Bersier and Kehrli, 2008). However, an unresolved issue is whether predator–prey body–mass ratios systematically change with the mass or trophic level of the predator. Thus,despite growing awareness of the significance of body–mass ratios in ecological networks Ings et al. (2009); Brose (2010a) our understanding of how they are distributedwithin natural food–webs is incomplete. Traditional concepts that have been accepted as a paradigm (Elton, 1927) are: (a) predator and mean prey mass are positively correlated, (b) predator masses increase with trophic level and (c) predator–prey body–mass ratios do not vary consistently across trophic levels (i.e., along food chains). Although these concepts are widely believed to be general features of ecosystems, it is important to remember that (1) the scatter in the relationships among prey mass, predator mass and trophic level can be substantial (e.g.,(Vander Zanden et al., 2000)), (2) a few studies have reported different relationships (see below) and (3) concept (c) has not (to our knowledge) been explicitly analysed, neither within nor across ecosystems. Furthermore, in contrast to the accepted wisdom, recent theoretical models of food–web structure, such as the cascade model, the niche model or the allometric diet breadth model (Cohen and Newman, 1985; Williams and Martinez, 2000; Petchey et al., 2008), suggest various and differing scaling relationships among prey mass, predator mass and trophic level. Differences between these opposing concepts are yet to be reconciled. Here, we use a data set of 35 natural food–webs across four ecosystem types (marine, stream, lake, ter-

restrial) to address the scaling relationships between predator and prey masses, predator trophic levels and predator–prey body–mass ratios (see points a, b, c above). While the first two scaling relationships are more easily and often studied, the dynamically important scaling of body–mass ratios with predator trophic level has been largely ignored. Subsequently, we derive theoretical predictions about the third relationship from the first two relationships, provide empirical tests of these relationships and discuss the implications for community structure, dynamics and stability.

4.2.1 Theortical predictions

Predators normally consume prey of smaller body–mass, which differentiates them from parasitic or parasitoid interactions (Brose et al., 2006a). Here we thus assume that predator body-mass, M_P and mean prey body-mass, $\overline{M_R}$, are allometrically related:

$$\overline{M_R} = bM_P^a \tag{4.1}$$

where *a* and *b* are constants (Cohen et al., 1993; Brose et al., 2006b; Bersier and Kehrli, 2008). Using eqn 1, the expected predator–prey body–mass ratio, ρ, can be expressed as a function of predator body–mass:

$$\rho = \frac{M_P}{\overline{M_R}} = b^{-1}M_P^{1-a} \tag{4.2}$$

In the early 20th century, Elton (Elton, 1927) suggested that predator body–mass increases along food chains. In complex food–webs, predator mass should thus increase with the trophic level, *T*, as expressed by exponential relationships reported in some studies:

$$\log_{10} M_P = d + cT \tag{4.3}$$

with constants *d* and *c* (Woodward and Hildrew, 2002; Cohen et al., 2003), whereas a few studies have found negative (Burness et al., 2001) or no relationships (Layman et al., 2005). To consider the relationship between predator–prey body–mass ratios and predator trophic levels, we inserted eqn 3 in eqn 2, which yields:

$$\log_{10}(\rho) = -\log_{10}(b) + d(1-a) + c(1-a)T = f + cT \tag{4.4}$$

where f describes the intercept and e the slope constant for T (trophic level). Elton (1927) suggested that predator–prey body–mass ratios do not vary consistently within communities and thus are independent of trophic level. This implies that the term $e = c(1-a)$ in eqn 4 equals zero, which results if *c* = 0 or *a* = 1. This may occur if predator masses do not vary across trophic levels (c = 0 in eqn 3) or if the mean prey mass increases linearly with predator mass on a log–log scale with a slope of unity (*a* = 1 in eqn 1). However, assuming a positive relationship between predator mass and trophic level ($c > 0$ in eqn 3), the body-mass ratio is expected to decrease with trophic level if $a > 1$ (eqn 1), but should increase with trophic level if

$a < 1$ (eqn 1). Together, these relationships (eqns 1–4) characterize important aspects of trophic interactions in natural food–webs. In this study, we gathered data from 35 empirical food–webs and analysed the relationships between (1) predator masses and average prey masses (eqn 1), (2) predator masses and trophic levels (eqn 3) and (3) body–mass ratios and trophic levels (eqn 4). Separate analyses are carried out for four habitat types (marine, stream, lake and terrestrial) and three predator types (invertebrates, ectotherm and endotherm vertebrates).

4.3 Methods

We analysed the trophic structure and species' body masses of 35 empirical food webs: 5 marine, 12 stream, 10 lake, and 8 terrestrial food webs (**SUPPLEMENTARY INFORMATION (SI)**). The food–web data were collected from three sources. First, seven food webs are derived from a large global food–web database: Grand Cariçaie cl control 2, Grand Cariçaie sc control 2, Sierra Lakes, Skipwith Pond, Tuesday Lake 1984, Weddell Sea and Broadstone Stream. Second, two food webs are taken from the Ecoweb database: Trelease Woods Illinois and Montane Forest Arizona. Third, for twenty–six additional food–webs (Carpinteria, Coachella, Small Reef, Little Rock Lake, Alford Lake, Beaver Lake, Bridge Brook Lake, Chub Pond, Connery Lake, Stink Lake, Mondego Estuary, St. Marks, Bere Stream, Calero Creek, Corde, Madre Creek, Coyote Creek, Guadalupe Creek, Alamitos Creek, German, Little Kye Burn, Stony, Broad, Hainich HEW1, Ythan Estuary, Florida Islands), we obtained the trophic structure and species' body masses (mainly) from published sources (see Table 4.1.1 for an overview of the food webs studied and the primary references for food–web structure and body masses). We studied only the predator–prey interactions of the food webs while excluding herbivore–plant, parasite–host and parasitoid–host interactions, which are characterized by different body–mass ratios than predator–prey interactions (Brose et al., 2006a). For each predator, we calculated the mean prey mass ($\overline{M_R}$) as the geometric mean of the body masses of all prey species of the predator, the predator–prey body–mass ratio (hereafter: ρ) as the ratio between predator mass M_P and mean prey mass, and predator trophic level (T) as the prey–averaged trophic level (one plus the average trophic level of all prey of the consumer) (Williams and Martinez, 2004b). These prey–averaged trophic levels were calculated using a matrix algebra method Levine (1980) that sums an infinite geometric series including the contributions from all loops. ρ is calculated using predator–prey interactions between species where the predator species has a trophic level higher than two (thus excluding herbivore and detritivore feeding interactions). After log_{10} transformation, we normalized all food–web parameters (mean prey masses, predator masses, predator–prey body–mass ratios and trophic levels) independently, to a mean of zero and a standard deviation of unity. This normalisation allows lumping food webs that differ in parameter space (e.g., food webs with different ranges in body masses). We grouped the 35 food webs

into four different ecosystem types: marine, stream, lake and terrestrial food webs. Furthermore, we grouped the predators into three different metabolic types (invertebrates, ectotherm and endotherm vertebrates). These group follow prior analyses (Brose et al., 2006a; Bersier and Kehrli, 2008) suggesting that predator–prey body–mass ratios differ among these categories. First, Pearson correlation analyses were used to assess whether there were statistically significant associations between $log_{10}(M_R)$ and $log_{10}(M_P)$, between $log_{10}(M_P)$ and *T*, and between ρ and T. Next, regression analyses were used to estimate the quantitative nature of the scaling between these variables (i.e., estimating constants a, b, c, d, e and f in the allometric and exponential relationships in equ. 1, 3 & 4). When the causal relationship between two variables is not clear or both variables are subject to measurement error, model I regression (ordinary least squares regression: OLS) is not appropriate. Instead, several type II regression methods have been proposed (see (Isobe et al., 1990; Warton et al., 2006) for reviews). These include ordinary least squares bisector (BIS) and reduced major axis (RMA) regressions. RMA regression has been suggested as the preferred method for line fitting when the independent variable is subject to measurement error and the primary aim of the analysis is estimating the slope of the line that best describes the bivariate scatter in the dependent and independent variables (Sokal, 1995; Warton et al., 2006), but see (Schmid et al., 2000). In our study, the results from RMA and BIS regressions were consistent (see supporting informations for details), and the results presented below are focused on RMA regressions while BIS results can be found in the Supplementary Information. The significance of the regression parameters was assessed through error estimates (95% confidence intervals) that were calculated by bootstrapping over 10,000 replicates. We calculated the predicted slope, epredicted, of the relationship between the predator–prey body–mass ratio and trophic level (see eq. 4) for each combination of metabolic predator type and ecosystem type independently and compared these values with the observed values, $e_{observed}$, from our regressions. Although our theoretical predictions above (eq 4) suggests that $log(\rho)$ should be proportional to $c(1-a)T$, this is for relationships without any error or uncertainties. However, our relationships will include considerable parameter uncertainty and thus, we do not expect the estimated values of the slopes of $log(\rho)$ as a function of T (i.e. $e_{observed}$) to be equal to $c_{observed}(1-a_{observed})$ (where $a_{observed}$ and $c_{observed}$ are regression estimates of a and c in eq 1 & 3). Instead, we expect the observed value of the slope of $log(\rho)$ as a function of T, based on RMA regressions, to be

$$e_{RMA} = c_{RMA}\sqrt{1 + a_{RMA}^2 - 2r_{logM_P,logM_R a_{RMA}}}, \tag{4.5}$$

where $r_{X,Y}$ is the Pearson product moment correlation coefficient between variables X and Y. See **SUPPORTING INFORMATION** for a derivation of this relationship. The significance of the correlation between $e_{predicted}$ from equation (5) with $e_{observed}$ from regressions was evaluated with a Pearson correlation analysis

4.4 Results

Generally, a lack of data hindered analyses of the relationships for endotherm vertebrates in lakes and streams. Moreover, data for terrestrial ectotherm and endotherm vertebrates were scarce. First, we analysed the relationship between predator mass and mean prey mass. After log–log transformation of the data, the slope of the linear relationship equals the exponent, a, of the power–law relationship in equ. (1). We found significant, positive relationships with slopes larger than unity across most ecosystems and predator groups (Table 4.1, Fig. 4.1, see below for exceptions to this pattern). This indicates that prey become disproportionately larger for larger predators, and that larger predators should be more similarly sized to their prey than small predators. Subsequently, we studied the relationship between log_{10} predator mass and predator trophic level to obtain estimates of the slope c in equ. (3). We found significant, positive relationships (Table 4.1, Fig. 4.2) across all ecosystem types and predator metabolic types, except for terrestrial and stream vertebrates, which exhibited a lack of significance (Table 4.1).

Table 4.1: Slopes and intercepts for the RMA regressions(BIS) of log_{10} mean prey mass (MPM) vs. log_{10} predator mass (PM), log_{10} predator mass (PM) vs. trophic level (TL) and predator-prey body-mass ratio (ρ) vs. trophic level (TL). Significance is indicated by Pearson correlation analyses for the relationships and by the upper and lower confidence interval(CI) for each slope and intercept. The number of species for each combination is indicated by n. Upper and lower confidence intervals for the intercepts and slopes were obtained by bootstrapping over $10,0000$ cases.

		marine food webs			stream food webs			lake food webs			terrestrial food webs		
		MPM vs. PM	PM vs. TL	ρ vs. TL	MPM vs. PM	PM vs. TL	ρ vs. TL	MPM vs. PM	PM vs. TL	ρ vs. TL	MPM vs. PM	PM vs. TL	ρ vs. TL
Invertebrates	r	0.49	0.34	-0.24	0.21	0.22	-0.02	0.65	0.49	-0.17	0.75	0.25	-0.29
	p-value	<0.001	<0.001	<0.001	<0.001	<0.001	0.63	<0.001	<0.001	0.03	<0.001	<0.001	<0.001
	intercept	0.01	0.35	-0.31	0.16	-0.35	-0.75	0.43	-0.68	-0.58	0.37	-0.85	-0.35
	upper/lower CI	1.54/-0.18/	0.46/0.26	0.29	0.61/0.09	-0.67	0.14	1.2/0.2	-0.78	0.55	1.08/0.27	0.81	0.63
	slopes	1.76	0.53	-0.82	0.71	0.81	-1.04	1.40	0.82	-0.89	1.20	0.6	-0.52
	upper/lower CI	1.54	0.61/0.46	3.02/-0.97	0.83/0.61	0.91/0.71	1.12/-1.18	1.61/1.2	0.93/0.72	0.59	1.33/1.08	0.69/0.53	0.69
	n		234			388			156			179	
Ectotherm vertebrates	r	0.68	0.46	-0.57	0.23	0.19	-0.25	0.39	0.32	-0.69	0.65	0.3	-0.68
	p-value	<0.001	<0.001	<0.001	0.11	0.19	0.08	<0.001	0.01	<0.001	0.04	0.4	0.03
	intercept	-1.35	0.77	01.02.11	-1.03	1.06	1.60	-2.77	1.02	1.98	-1.52	0.78	0.83
	upper/lower CI	1.7/-1.75	0.85/0.68	1.14/0.89	0.56/-1.31	1.2/0.91	1.81/1.44	1.61/-1.31	1.2/0.85	2.19/1.75	1.28/-1.86	1.31/0.6	1.07/0.59
	slopes	1.98	0.41	-0.58	0.79	0.63	-0.83	2.13	0.76	-1.48	2.33	0.21	-0.36
	upper/lower CI	2.32/1.7	0.47/0.36	0.7	1.07/0.56	0.94/-0.6	0.48	2.85/1.61	0.97/0.58	0.01	3.79/1.28	0.34/-0.25	0.48
	n		117			50			68			16	
Endotherm vertebrates	r	0.62	0.61	-0.27	NA	NA	NA	NA	NA	NA	0.72	0.15	0.28
	p-value	<0.001	<0.001	0.01	NA	NA	NA	NA	NA	NA	<0.001	0.38	0.09
	intercept	-1.04	1.20	01.09.11	NA	NA	NA	NA	NA	NA	-1.5	1.20	0.48
	upper/lower CI	1.2/-1.72	1.29/1.11	1.27/0.92	NA	NA	NA	NA	NA	NA	1.8/1.86	1.45/1.06	0.51/0.07
	slopes	1.50	0.42	-0.49	NA	NA	NA	NA	NA	NA	2.17	0.34	0.51
	upper/lower CI	1.99/1.2	0.51/0.31	0.69	NA	NA	NA	NA	NA	NA	2.46/1.8	0.45/-0.45	0.74/0.35
	n		84			NA			NA			37	

In all other cases, these analyses demonstrate systematic increases in predator mass with predator trophic level across all ecosystem and predator types. Finally, we analysed the relationship between the log_{10} predator–prey body–mass ratio and trophic level to obtain empirical estimates of the slope of this relationship that could be compared with the theoretical prediction $c(1--a)$ in equ. (4) and epredicted in equ. (5). We found significant, negative relationships (Table 4.1, Fig 4.3) across most combinations of ecosystem and predator types (with a few exceptions, see below). This suggests that the relative size difference (log_{10} body–mass ratio) between a predator and its prey decreases with trophic level of the predator. Looking in more detail at the results, there are interesting exceptions to the general trends outlined above. First, there is one group of marine invertebrates feeding on small resources despite intermediate to high body mass of these consumers (data points at the bottom of Fig. 4.1a). These outliers of the scaling relationship are mainly benthic suspension feeders and scavengers, which stresses that the scaling relationships presented here best characterize predatory interactions. Second, our analyses also demonstrates that stream communities systematically follow a different scaling pattern to other systems, with slopes smaller than unity (stream invertebrates: slope = 0.71, stream ectotherm vertebrates: slope = 0.79, Table 4.1, Fig. 4.1). Third, the negative relationship between the log_{10} predator–prey body–mass ratio and trophic level was non–significant for stream ectotherm vertebrates (p=0.08) and stream invertebrates (p = 0.63, Table 4.1). Fourth, there was only one exception to the general trend of decreasing size difference between a predator and its prey with increasing predator trophic level: we found a non–significant positive relationship for terrestrial endotherm vertebrates (p= 0.09). The correlation between observed values from regressions, eobserved, and predicted values for epredicted from equation (5) that accounts for error propagation is very high (Pearson correlation coefficient = 0.99, Table 4.2). Consistently, the more simple prediction of the slope not accounting for error propagation (i.e. $c(1--a)$ in equation (4)) yielded only slightly weaker correlations (r=0.89, p=0.007, based on the seven significant slopes, Table 4.2).

4.5 Discussion

Our analyses of the relationships between predator and prey mass, body–mass ratios and trophic levels have shown that across different types of ecosystems and predators some generalities hold: (a) the log_{10} of average prey mass increases with the log_{10} of predator mass with a slope larger than unity, (ii) the log_{10} of predator mass increases with predator trophic level, and (iii) the log_{10} of the predator–prey body–mass ratio (i.e., the ratio of predator mass to average prey mass) decreases with predator trophic level. Our theoretical derivations show that the third relationship is the consequence of the first two relationships, which is supported by our empirical data. Exceptions to these patterns were identified for stream ecosystems and for endotherm

Table 4.2: Observed and predicted predator-prey body-mass ratios. Predicted slopes, without error propagation based on equ. 4 and with error propagation are based on equ. 5) for each combination of metabolic predator type and ecosystem type.

		observed slopes empirical	predicted slopes with equ. 4	predicted slopes with equ. 5
marine	invertebrates	-0.82	-0.4	-0.82
stream		-1.04	0.23	-0.89
lake		-0.89	-0.32	-87
terrestrial		-0.52	-0.12	-0.49
marine	ectotherm	-0.58	-0.4	-0.62
stream	vertebrates	-0.83	0.13	-0.71
lake		-1.48	-0.86	-1.5
terrestrial		-0.36	-0.28	-0.39
marine	endotherm	-0.49	-0.21	-0.49
terrestrial	vertebrates	0.51	-0.4	0.56

consumers in terrestrial ecosystems, and potential reasons for these deviations are discussed below.

Our analyses are based on the largest allometric food–web data base (including information on trophic links between consumers and resources and the species' body masses) compiled so far. Despite this wealth of data, some combinations of ecosystem type and metabolic group were under–represented. While endotherm vertebrates in streams and lakes are naturally rare, the scarcity of data for terrestrial vertebrates will most likely be removed by future food–web compilations. Consistent with former studies (Cohen et al., 1993; Brose et al., 2006a; Bersier and Kehrli, 2008), we found that predator and prey masses are positively correlated. Our study generalizes this finding across combinations of ecosystem types (marine, lake, terrestrial) and predator types (invertebrate, ectotherm and endotherm vertebrate). The relationship had a slope larger than unity across all of these combinations of metabolic types and ecosystems except for streams. Some notable outliers of this relationship were characterized as marine benthic omnivorous suspension feeders (sponges, bryozoans, hydrozoans, and ascidians) and scavengers (e.g. polychaetes, gastropods, echinoderms and amphipods) that consume small resources despite their large body mass. These outliers highlight that the scaling relationship presented here is particularly suited to describe interactions among predators and their prey, whereas other consumer types may follow different scaling relationships. In stream ecosystems invertebrate and piscivorous predator species consumed a larger range of prey body masses than predators in other ecosystems. This causes a shallower slope (smaller than unity) for the relationship between predator body–mass and average prey body–mass in stream ecosystems. While previous analyses of this relationship for data pooled for ecosystem and predator types suggested

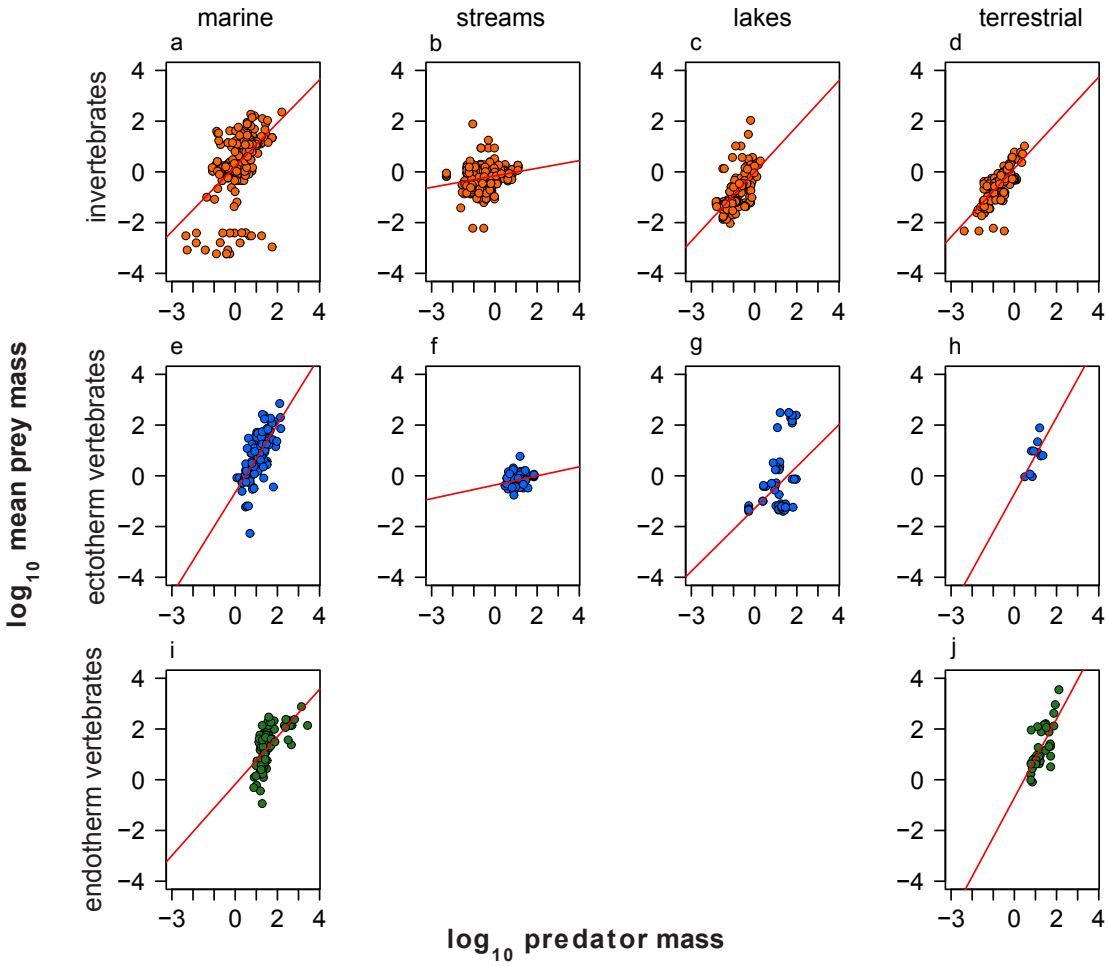

Figure 4.1: The relationship between log_{10} mean prey mass [gram] and log_{10} predator mass [gram]. The panels show different metabolic predator types - invertebrates (top), ectotherm vertebrates (middle) and endotherm vertebrates (low panels) - and different ecosystems types - marine (left), stream (second), lake (third) and terrestrial ecosystems (right panels). The solid lines represent the RMA regressions (see Table 4.1 for details). Prior to analyses, data were normalized for each web independently.

exponents smaller than unity (Brose et al., 2006a), recent analyses accounting for differences amongst predator types found exponents larger than unity (Bersier and Kehrli, 2008). Note that these prior studies (Brose et al., 2006a; Bersier and Kehrli, 2008) addressed the relationship between predator mass and average prey mass, whereas the present study has reversed the axes of this relationship to allow a closer match between theoretical derivations and empirical tests. Our analyses, based on a much larger set of natural food webs, support the conclusion that the

exponents are prevalently larger than unity (Bersier and Kehrli, 2008; Costa, 2009). This indicates a regularity in community structure that holds across ecosystems except for streams: prey become disproportionately larger with increasing predator mass, and larger predators tend to be more similarly sized to their prey than small predators.

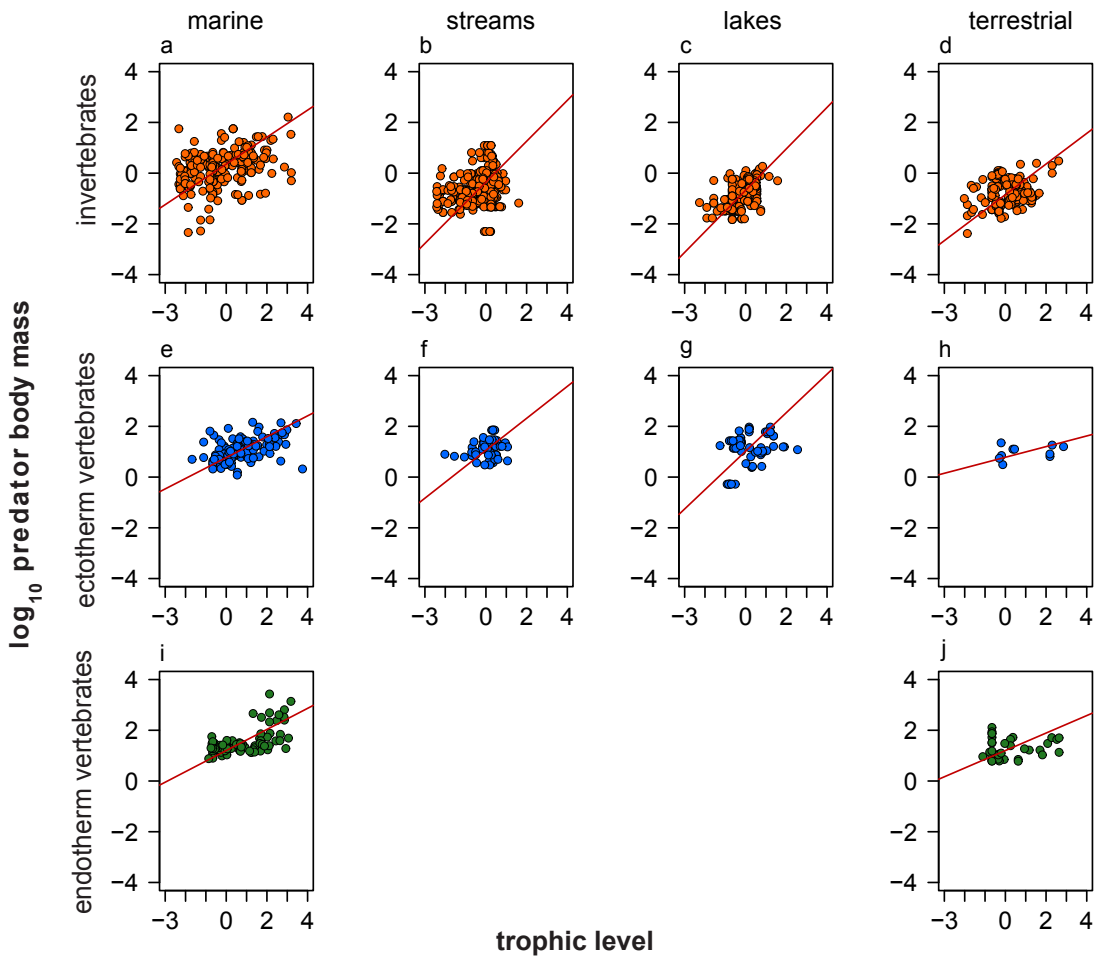

Figure 4.2: The relationship between log_{10} predator masses [gram] and predator trophic level. The panels show different predator metabolic types - invertebrates (top), ectotherm vertebrates (middle) and endotherm vertebrates (low panels) - and different ecosystems types - marine (left), stream (second), lake (third) and terrestrial ecosystems (right panels). The solid lines represent the RMA regressions (see Table 4.1 for details). Prior to analyses, data were normalized for each web independently.

Across all ecosystem and predator types we found positive relationships between predator mass and trophic level. This correlation was not significant for vertebrates in stream and terrestrial

ecosystems. This lack of a significant relationship for stream vertebrates is consistent with prior studies (Layman et al., 2005), indicating a potential general difference between stream and other ecosystems. The broader feeding niches of opportunistic, omnivorous predatory fishes in streams (Winemiller, 1990) could be responsible for this systematic difference. In contrast, we anticipate that the lack of significant correlations for terrestrial vertebrates may be explained by the limited amount of data available. Interestingly, our results contrast with a prior study documenting the lack of a relationship between predator mass and trophic level in a marine food web (Jennings et al., 2001). The highly significant relationships documented here across communities suggest that marine food webs might be less different from other ecosystems than previously anticipated. Overall, and except for stream and terrestrial vertebrates, our analyses have provided support for the classic paradigm (Elton, 1927) that predators in food chains become progressively larger in size. On the assumption that the size increase of predators and their prey per trophic level is constant and similar, this classic paradigm also suggests that the mean predator–prey body–mass ratio should be invariant with respect to predator trophic level (Elton, 1927). In contrast, our analyses demonstrate that the correlation between trophic level and body–mass ratio is negative for all combinations of ecosystem and predator types except for terrestrial endotherm vertebrates. We anticipate that this exception is caused by data scarcity in this group. In contrast, the lack of significance in this correlation for stream invertebrates suggests a systematic difference in the body–mass structures. We can only speculate as to the mechanisms (or lack of mechanisms) that may result in this pattern. Forces generated by flowing water and hydrologic disturbance are known to constrain body size in stream invertebrates, (e.g. (Townsend, 1989; Townsend and Scarsbrook, 1997; Snook and Milner, 2002), as does size of stream substrates (Bourassa and Morin, 1995). Streams differ from the other systems reviewed in that the community is predominantly comprised of larval stages of flying adults. If selective pressure for size is mainly exerted on adult stages, this could explain the lack of a pattern for larvae. Finally, there is the potential for omnivory to alter body size relationships. Omnivory is a recurrent feature of food webs, but is rare in stream systems (Thompson et al., 2007). This reflects the relatively short food chains in streams, which may reduce the potential for large size disparities between predators and prey. Other mechanisms are certainly possible, and more detailed study of the constraints on size ratios in streams is warranted.

Our theoretical derivations relate the general decrease in predator–prey body–mass ratios with trophic level to the combination of increases in predator mass with trophic level and increases in mean prey mass with predator mass with an exponent larger than unity. Because equation (4) is a function of equations (1)–(3) we should expect error propagation in the regression parameters. That is, the uncertainties in estimates of parameters e and f will actually be a function of uncertainties in parameters a, b, c and d. Because of this we should not be surprised by the considerable scatter in Fig. 4.3. More specifically, it can be shown (see Supporting Information)

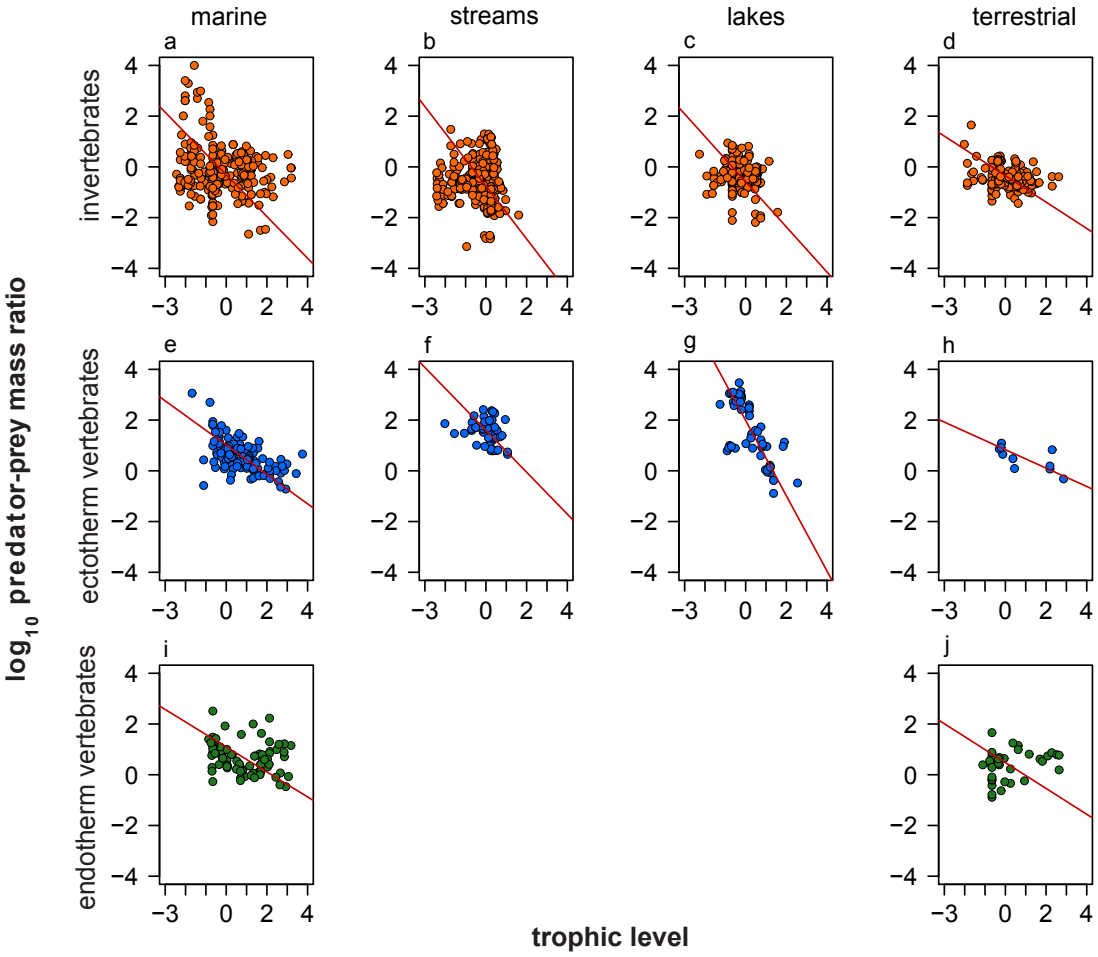

Figure 4.3: The relationship between log10 predator-prey body-mass ratio and predator trophic level. The panels show different predator metabolic types - invertebrates (top), ectotherm vertebrates (middle) and endotherm vertebrates (low panels) - and different ecosystems types - marine (left), stream (second), lake (third) and terrestrial ecosystems (right panels). The solid lines represent the RMA regressions (see Table 4.1 for details). Prior to analyses, data were normalized for each web independently.

that the error estimates of the slopes in Figs. 4.1–3 are expected to propagate in a multiplicative fashion from Figs. 4.1 and 4.2 to Fig. 4.3. Accordingly, our results should be interpreted as qualitative scaling models, whereas quantitative predictions of body–mass ratios remain less accurate. Together, our theoretical derivations and empirical tests demonstrate the broad generality of decreasing body–mass ratios with increasing trophic level. Thus, species with high trophic levels such as top predators are more equal in size to their average prey than predators with low

trophic levels. This finding generalizes across ecosystem and predator types (with the possible exception of terrestrial endotherms and stream invertebrates) with profound implications for our understanding of food–web structure, the distribution of predator–prey interaction strengths and community stability, as discussed below. It is interesting to note that the positive correlation between prey and predator mass across all species and systems (ignoring streams) is compatible with theoretical models of food–web topology such as the cascade model (Cohen and Newman, 1985), whereas the more specific results presented here deviate from patterns produced by these models. Under the cascade model, species are arranged in a trophic cascade on a hypothetical niche axis (e.g. according to body size) (Cohen and Newman, 1985), and trophic links are distributed at random between a species and every other species with lower rank (smaller body size). In consequence, small predators can feed only on a few prey, whereas larger predators can feed on a much larger range of prey (including the smaller prey of small predators). Hence, large predators should have a larger variance in the size of their prey than small consumers (see(Wilson, 1975)), and they should be more dissimilar in size to their average prey (mean log size) than small predators. Indeed, this is what previous studies (Cohen et al., 1993; Brose et al., 2006a) on the relationship between prey and predator size found while lumping predator types. Consistent with another recent study (Bersier and Kehrli, 2008), however, we found the opposite relationship when accounting for different predator and ecosystem groups. This supports a prior finding that the cascade model is unable to reproduce the empirical relationship between mean predator–prey body–mass ratio and predator trophic level (Jonsson and Ebenman, 1998). Potential explanations for this disparity include: (a) the trophic hierarchy of natural food webs is independent of body masses, and (b) trophic links are not distributed as assumed by the cascade model (i.e. randomly among every species smaller than a particular consumer species). The positive relationship between predator body mass and trophic level in our study contrasts with the first explanation, whereas the second explanation is consistent with prior conclusions that the equal predation probability assumption of the cascade model does not generally hold across food webs (Neubert et al., 2000). More recent models of trophic structure, namely the niche (Williams and Martinez, 2000), nested–hierarchy (Cattin et al., 2004), generalized cascade model (Stouffer et al., 2005), and minimum potential niche model (Allesina et al., 2008), incorporate additional restrictions on the distribution of trophic links, but our results indicate that even the assumptions of these models may have to be modified. Under these models, the consumers feed on prey that fall within a feeding range on the niche axis. As the center of this feeding range, also representing the average body mass of the prey, is randomly chosen within a range between zero and the niche value of the consumer, these models produce a pattern that the ratio between a predator's niche value and the average niche value of the prey (i.e., the center of the feeding range) increases with the predator's niche value. Assuming similarity among niche values and body masses, this suggests that predator–prey body–mass ratios and predator

body masses should be positively correlated, which is opposed by our empirical results. While there is thus only limited concordance between our empirical results on the body–mass structure of natural food webs and some emergent patterns of static food–web models, their consistency with a more recent allometric diet breadth model using body mass data to predict feeding links (Petchey et al., 2008) remains to be explored. Recent theoretical and empirical approaches in food–web ecology have related predator–prey body–mass ratios to their interaction strengths and energy fluxes through the feeding links. Some studies based on metabolic theory have proposed power–law increases in interaction strengths with body–mass ratios (Emmerson and Raffaelli, 2004), see (O'Gorman et al., 2010) for a recent study of the correlation between theoretical predictions based on metabolic theory and empirical estimates of interaction strengths). In combination with the results of the present study this suggests that the strongest interactions should be found between small species at the lowest trophic levels of food webs, whereas weak interactions should characterize the links between large species at higher trophic levels. However, studies of foraging ecology have reported hump–shaped relationships with the strongest interactions at intermediate body–mass ratios (Wilson, 1975; Persson et al., 1998; Vucic-Pestic et al., 2010). Based on the results of the present study, we suppose that the strongest interactions should be located at intermediate trophic levels. While these lingering gaps between metabolic and foraging ecology need to be reconciled, the results of the present study will allow systematic predictions on the distribution of interaction strengths across food webs. Furthermore, general differences concerning size structure between stream ecosystems and other food webs need to be addressed in subsequent studies.

4.6 Conclusion and Caveats

Charles Elton (1927) laid the foundation for what today is called "food–web ecology" by introducing the concept of food chains and food cycles as well as suggesting the importance of body size in animal community organization. As pointed out by Warren (2005), the conventional wisdom in ecology accepts Elton′s observations and suggestions that animal predators are in general both larger and less abundant than their prey. However, these ideas were not pursued in great detail until recently when body size has come into focus in many food web studies (Cohen et al., 1993; Brose et al., 2006b; Otto et al., 2007). The central question of the present study was thus whether Elton's paradigm is an adequate description of natural communities. Based on our analyses of 35 natural food webs, we agree with Elton that (a) predator body mass and mean prey mass are positively correlated, and (b) predator body mass increases with trophic level. However, we disagree with Elton's claim that predator–prey body–mass ratios are invariant with trophic level (i.e. along food chains). Instead, based on the first two points, our theoretical derivations demonstrated that this is unlikely, and our data support systematic

decreases in body–mass ratios with trophic level. Herbivorous and detritivorous interactions were ignored in this study. Herbivores and detritivores rarely consume their entire resource, but rather parts of its biomass. Our choice not to focus on these groups was motivated by systematic differences in interactions among ecosystem types: in contrast to their aquatic counterparts, terrestrial herbivores and detritivores are often much smaller than their resources. Prior studies have shown that the consumer–resource body–mass ratio of aquatic consumers on plants or on detritus is several magnitudes higher than the predator–prey body–mass ratios in the same system (Brose et al., 2006a). These higher body–mass ratios at the food–web base would strengthen the trend of decreasing body–mass ratios with trophic level in aquatic ecosystems, whereas the lower ratios might blur the relationship in terrestrial ecosystems. Rather than focusing on these well–known differences between terrestrial and aquatic ecosystems, we decided in this study to document surprising regularities in the predator–prey body–mass structure of natural food webs that hold across terrestrial and aquatic ecosystems. In contrast to Elton's paradigm, we conclude that predator and prey species become more similarly sized with increasing body mass and trophic level of the predator. Is this difference important? Based on correlations between body–mass ratios and interaction strengths (Persson et al., 1998; Emmerson and Raffaelli, 2004; Vucic-Pestic et al., 2010), our results suggest a systematic distribution of interaction strengths across food webs. Ultimately, these interaction strength distributions will be crucially important for understanding constraints on food–web stability (Brose et al., 2006b; Neutel et al., 2007; Otto et al., 2007; Rall et al., 2008). Modifying Elton's paradigm of the body–size structure of natural communities may thus allow us to gain a better understanding of community structure, dynamics and stability.

4.7 Supporting Informations

4.7.1 Dataset of Thirty-five real food webs

The food webs used in this paper are describted in tabel 1.1 containing the original sources of publication of the predation matrices and food-web common names used in this article. For each food web, the predation matrices and the species' body sizes were compiled from a variety of sources. These real food webs contain producers, herbivores, carnivores, parasites, and parasitoids. The organisms display a range of feeding interactions including predation, herbivory, bacterivory, parasitism, and parasitoidism. In this study, only predator-prey interactions were analysed.

4.7.2 Comparison between Reduced major axis regression and Ordinary least squares bisector regression

We analyzed all combinations of metabolic predator type and ecosystem type and all relationships in the paper (e.g. predator mass vs. mean prey mass) with the reduced major axis regression (RMA) as well as with the Ordinary least squares bisector regression (OLS-bis) method. Both methods are used, in previous publications, to calculate the slope between variables with indefinable errors in the data (Warton2006, Schmid2000). The estimated regression coefficients based on the RMA method are shown in table 4.1 in the main text, the estimated regression coefficients based on the BIS method are shown in table S2. To visually compare the results of the two methods see figures S1-S3. We plotted the relationships between log_{10} mean prey mass against log_{10} predator mass (Fig S1) and used the calculated slops of the two regression methods (RMA and BIS). We used the same methods for the relationship between log_{10} predator mass against trophic level (Fig. S2) and the relationship between log_{10} predator-prey body-mass ratio agains trophic level (Fig. S4). In most case the results of the two regression technique are very similar, except for terrestrial endotherm vertebrates. Further studies should focus on this phenomen. To visually compare the results of the two methods see figures S1–S3. We plotted the relationships between log_10 mean prey mass against log_10 predator mass (Fig S1) and used the calculated slops of the two regression methods (RMA and BIS). We used the same methods for the relationship between log_10 predator mass against trophic level (Fig. S2) and the relationship between log_10 predator–prey body–mass ratio agains trophic level (Fig. S4). In most case the results of the two regression technique are very similar, except for terrestrial endotherm vertebrates. Further studies should focus on this phenomen.

Table 4.3: Slopes and intercepts for the ordinary least squares bisector regressions (BIS) of log_{10} mean prey mass (MPM) vs. log_{10} predator mass (PM), log_{10} predator mass (PM) vs. trophic level (TL) and predator-prey body-mass ratio (ρ) vs. trophic level (TL). Significance is indicated by Pearson correlation analyses for the relationships and by the upper and lower confidence interval (CI) for each slope and intercept. The number of species for each combination is indicated by n. Upper and lower confidence intervals for the intercepts and slopes were obtained by bootstrapping over $10,0000$ cases.

		marine food webs			stream food webs			lake food webs			terrestrial food webs		
		MPM vs. PM	PM vs. TL	ρ vs. TL	MPM vs. PM	PM vs. TL	ρ vs. TL	MPM vs. PM	PM vs. TL	ρ vs. TL	MPM vs. PM	PM vs. TL	ρ vs. TL
		marine food webs			stream food webs			lake food webs			terrestrial food webs		
		MPM vs. PM	PM vs. TL	ρ vs. TL	MPM vs. PM	PM vs. TL	ρ vs. TL	MPM vs. PM	PM vs. TL	ρ vs. TL	MPM vs. PM	PM vs. TL	ρ vs. TL
Invertebrates	Pearson corr.	0.49	0.34	-0.24	0.21	0.22	-0.02	0.65	0.49	-0.17	0.75	0.25	-0.29
	p-value	<0.001	<0.001	<0.001	<0.001	<0.001	0.63	<0.001	<0.001	0.03	<0.001	<0.001	<0.001
	intercept	0.05	0.39	-0.34	0.25	-0.33	-0.74	0.39	-0.67	-0.6	0.36	-0.87	-0.32
	upper/	1.76/	0.76/	-0.16/	0.94/	0.97/	-1.03/	1.55/	0.95/	-0.84/	1.31/	0.93/	-0.60/
	lower CI intercept	0.22	0.51	-0.52	0.33	-0.26	-0.83	0.62	-0.58	-0.41	0.46	-0.77	-0.23
	slopes	1.57	0.67	-0.92	0.87	0.91	-1	1.36	0.85	-0.96	1.19	0.78	-0.69
	upper/	1.39/	0.59/	-0.86/	0.79/	0.85/	1.01/	1.19/	0.77/	-1.02/	1.08/	0.67/	-0.83/
	lower CI slope	-0.11	0.28	-0.98	0.17	-0.40	-0.12	0.18	-0.75	-0.73	0.26	-0.98	-0.41
Ectotherm vertebrates	Pearson corr.	0.68	0.46	-0.57	0.23	0.19	-0.25	0.39	0.32	-0.69	0.65	0.3	-0.68
	p-value	<0.001	<0.001	<0.001	0.11	0.19	0.08	<0.001	0.01	<0.001	0.04	0.4	0.03
	intercept	-1.26	0.71	1.05	-1.15	1.04	1.6	-2.29	1.01	1.98	-1.38	0.65	0.85
	upper/	2.20/	0.63/	1.16/	0.69/	0.99/	-0.72/	2.19/	0.98/	-1.25/	3.61/	0.89/	-0.28/
	lower CI intercept	-0.94	0.81	0.93	-1.30	1.21	1.79	-1.91	1.19	2.19	-0.31	1.79	1.27
	slopes	1.9	0.49	-0.62	0.9	0.84	-0.91	1.71	0.85	-1.45	2.19	0.35	-0.38
	upper/	1.64/	0.42/	-0.54/	1.02/	-0.95/	-1.10/	1.32/	0.76/	-1.69/	1.14/	-0.86/	-0.73/
	lower CI slope	-1.62	0.57	-0.72	-0.93	0.88	1.43	-2.89	0.83	1.75	-2.70	0.13	0.60
Endotherm vertebrates	Pearson corr.	0.62	0.61	-0.27	NA	NA	NA	NA	NA	NA	0.72	0.15	0.28
	p-value	<0.001	<0.001	0.01	NA	NA	NA	NA	NA	NA	<0.001	0.38	0.09
	intercept	-0.95	1.17	1.24	NA	NA	NA	NA	NA	NA	-1.4	1.13	0.24
	upper/	1.84/	0.54/	1.53/	NA	NA	NA	NA	NA	NA	2.41/	0.97/	0.94/
	lower CI intercept	-0.52	1.27	1.0	NA	NA	NA	NA	NA	NA	-0.86	1.59	0.52
	slopes	1.44	0.45	-0.68	NA	NA	NA	NA	NA	NA	2.09	0.7	0.69
	upper/	1.18/	0.36/	-0.53/	NA	NA	NA	NA	NA	NA	1.63/	-0.96/	0.47/
	lower CI slope	-1.52	1.06	-0.9	NA	NA	NA	NA	NA	NA	-1.80	0.92	0.01

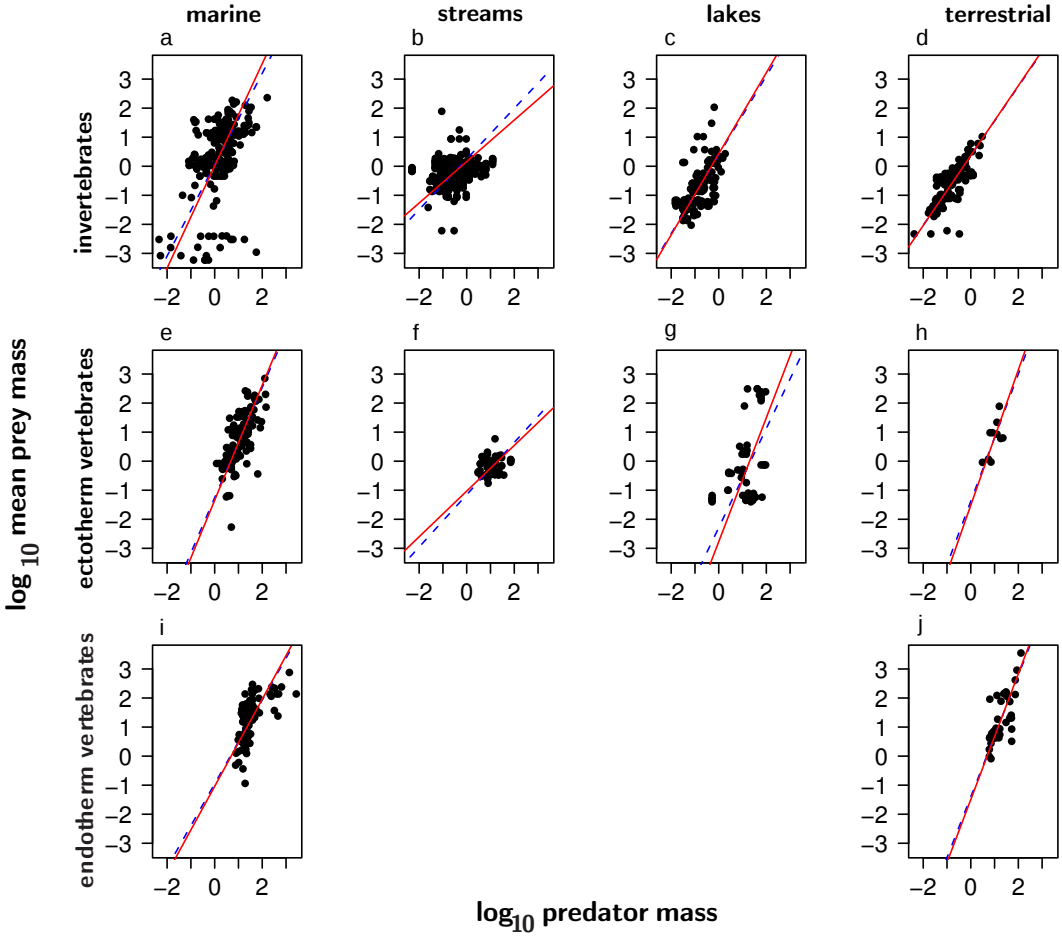

Figure 4.4: The relationship between log_{10} mean prey mass and log_{10} predator mass. The red solid line represents the slope obtained from RMA regression, the blue dashed line represents the slope obtained from BIS regression

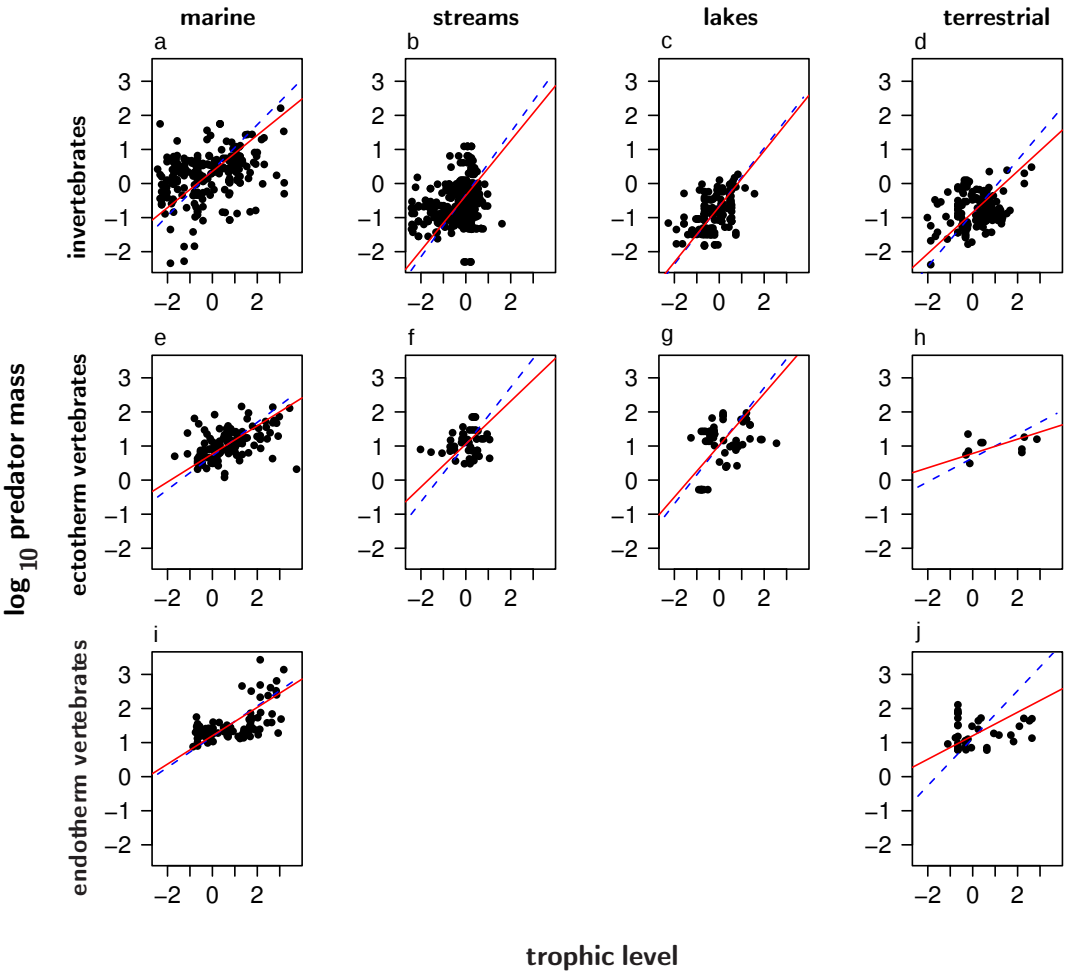

Figure 4.5: The relationship between log_{10} predator mass and trophic level. The red solid line represents the slope obtained from RMA regression, the blue dashed line represents the slope obtained fromBIS regression.

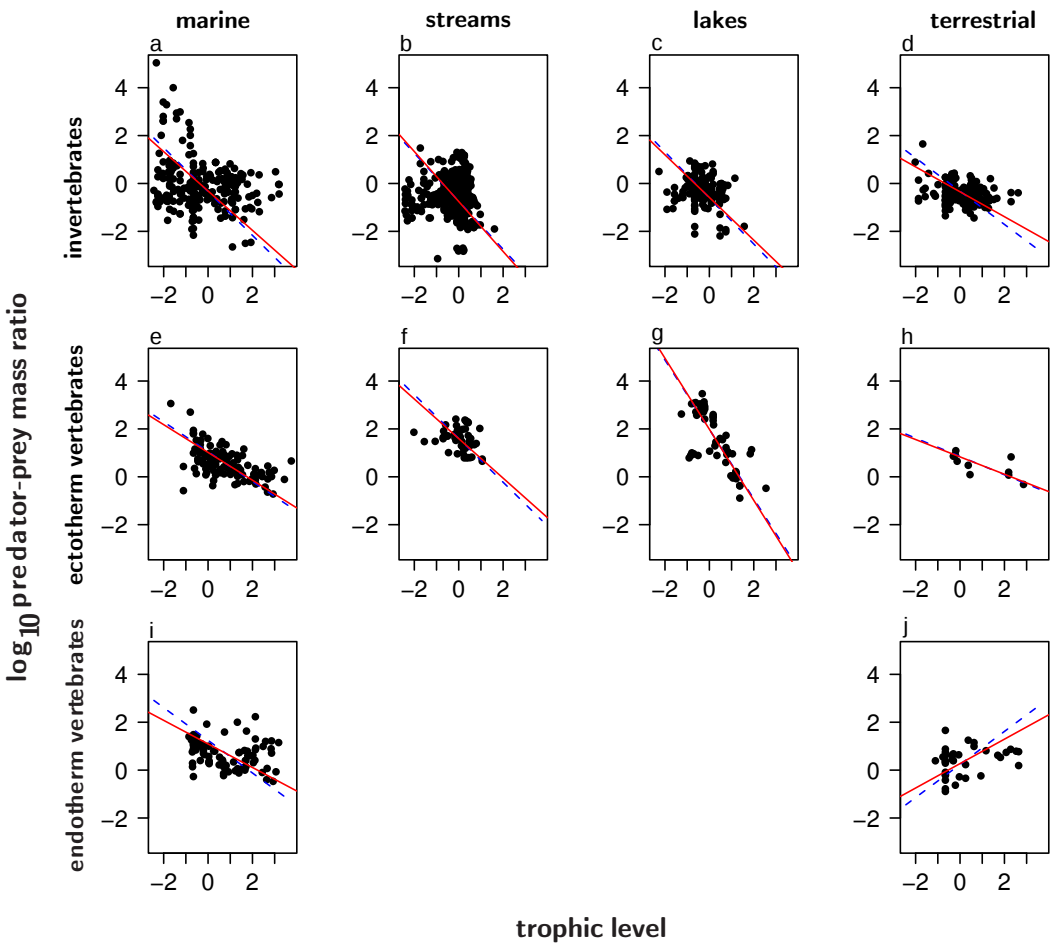

Figure 4.6: The relationsip between log_{10} predator-prey body-mass ratio and trophic level. The red solid line represents the slope obtained from RMA regression, the blue dashed line represents the slope obtained from BIS regression.

4.7.3 The regression slopes of dependent functions

Here we will show that although our theoretical predictions (eq 4 in the main text) suggest that $log(\rho)$ should be proportional to $e = c(1-a)T$, we should not expect $e_{observed} = c_{observed}(1 - a_{observed})$ (where $a_{observed}, c_{observed}$, and $e_{observed}$ are the slopes of the relationships between $log(MP)$ and, between T and $log(MP)$, and between T and $log(\rho)$). This is because a, c, and e are the "true" values for relationships without any error or uncertainties, while $a_{observed}, c_{observed}$, and $e_{observed}$ are regression estimates of these values from the available data.
We have

$$\begin{aligned}
(1): &\quad \log(\overline{M}_R) = b + a\log(M_P) \\
(2): &\quad \log(M_P) = d + cT \\
(3): &\quad \log_\rho = log(M_P) - \log(\overline{M}_R) = f + eT
\end{aligned}$$

from which follows that $e = c(1-a)$.
What relationship should we expect among $a_{observed}$, $c_{observed}$, and $e_{observed}$ if these are estimated from data using RMA regression?
First, we note that the reduced major axis (RMA) regression slope is

$$\beta_{RMA} = sign(cov(X,Y)) \cdot \sqrt{\frac{var(Y)}{var(X)}},$$

and the ordinary least squares (OLS) regression slope

$$\beta_{OLS} = \frac{cov(X,Y)}{var(X)}$$

for the relationship between two variables X and Y (where $var(X)$is the variance in X, and $cov(X,Y)$ is the covariance between X and Y). Furthermore,

$$\beta_{OLS} = r_{X,Y} \cdot \beta_{RMA}$$

where $r_{X,Y}$ is the Pearson product moment correlation coefficient between variables X and Y. This means that

$$\begin{aligned}
s^2_\beta(T, log\rho) &= s^2_e \propto \tfrac{var(log\rho)}{var(T)} - \tfrac{cov^2(T,log\rho)}{var^2(T)} &&= e^2_{RMA} - e^2_{OLS} \\
s^2_\beta(T, logM_P) &= s^2_c \propto \tfrac{var(logM_P)}{var(T)} - \tfrac{cov^2(T,M_P)}{var^2(T)} &&= c^2_{RMA} - c^2_{OLS} \\
s^2_\beta(logM_P, logM_R) &= s^2_a \propto \tfrac{var(log\overline{M}_R)}{var(M_P)} - \tfrac{cov^2(M_P,log\overline{M}_R)}{var^2(logM_P)} &&= a^2_{RMA} - a^2_{OLS}
\end{aligned}$$

Now, if $e = c(1-a)$ is true also for our estimated regression slopes this would mean that

$$\begin{aligned}
e^2_{RMA} &= c^2_{RMA}(1 - a_{RMA})^2 &&= c^2_{RMA}(1 - 2a_{RMA} + a^2_{RMA}) \\
e^2_{OLS} &= c^2_{OLS}(1 - a_{OLS})^2 &&= c^2_{OLS}(1 - 2a_{OLS} + a^2_{OLS})
\end{aligned}$$

Starting with the reduced major axis regression, we get:

$$\begin{aligned}
e^2_{RMA} &= \frac{var(log\rho)}{var(T)} = \frac{var(logM_P - log\overline{M}_R)}{var(T)} \\
&= \frac{var(logM_P) + var(log\overline{M}_R) - 2cov(logM_P, log\overline{M}_R)}{var(T)} \\
&= \frac{var(logM_P)}{var(T)}\left(1 + \frac{var(log\overline{M}_R)}{var(logM_P)} - \frac{2cov(logM_P, log\overline{M}_R)}{var(log(M_P)}\right) \\
&= c^2_{RMA}\left(1 + a^2_{RMA} - \frac{2cov(logM_P, log\overline{M}_R}{)} var(logM_P)\right) \\
&= c^2_{RMA}\left(c^2_{RMA} - 2a_{OLS}\right) \\
&= c^2_{RMA}\left(1 + a^2_{RMA} - 2r_{logM_P, log\overline{M}_R} a_{RMA}\right)
\end{aligned}$$

Unless $r_{logM_P, log\overline{M}_R} = 1$ this means that

$$\begin{aligned}
e^2_{RMA} &= c^2_{RMA}(1 + a^2_{RMA} - 2r_{logM_P, log\overline{M}_R} a_{RMA}) \\
&\neq c^2_{RMA}(1 + a^2_{RMA} - 2a_{RMA}) \\
&= c^2_{RMA}(1 - a_{RMA})^2
\end{aligned}$$

Thus, the estimate of e based on reduced major axis regression analyses is expected to be:

$$e_{RMA} = c_{RMA}\sqrt{1 + a^2_{RMA} - 2r_{logM_P, log\overline{M_R}} a_{RMA}} \tag{4.4}$$

Similarly, for an ordinary least squares regression:

$$\begin{aligned}
e^2_{OLS} &= r^2_{T, logM_P} \cdot e^2_{RMA} \\
&= r^2_{T, logM_P} \cdot c^2_{RMA} \cdot (1 + a^2_{RMA} - 2r_{logM_P, log\overline{M_R}} a_{RMA}) \\
&= r^2_{T, logM_P} \frac{c^2_{OLS}}{r^2_{T, logM_P}} \left(1 + \frac{a^2_{OLS}}{r^2_{logM_P, log\overline{M_R}}} - 2r_{logM_P, log\overline{M_R}} \frac{a_{OLS}}{r_{logM_P, log\overline{M_R}}}\right) \\
&= c^2_{OLS}\left(1 + \frac{a^2_{OLS}}{r^2_{logM_P, log\overline{M_R}}} - 2a_{OLS}\right) \neq c^2_{OLS}\left(1 + a^2_{OLS} - 2a_{OLS}\right)
\end{aligned}$$

Thus, the estimate of e based on ordinary least squares regression analyses is expected to be:

$$e_{OLS} = c_{OLS}\sqrt{1 + \frac{a^2_{OLS}}{r^2_{logM_P, log\overline{M_R}}}} \tag{4.5}$$

To summarize, we should not expect that the estimated value of e, based on a regression analysis of log(ρ) as a function of T (i.e. $e_{observed}$), should equal $c_{observed}(1 - a_{observed})$ (where $a_{observed}$ and $c_{observed}$ are regression estimates of a and c in eq 1 & 3). Instead, we expect the observed value of e from a reduced major axis regression to be given by equation 4 (and equation 5 for an ordinary least squares regression).

4.7.4 Error propagation as measured by the standard errors of the regression slopes of dependent functions

According to Sokal & Rohlf (1995), the standard error of the RMA slope can be approximated by the standard error of the OLS slope. We will use this approximation here to show how the standard error of $e_{observed}$ (the slope of the relationship between T and $log(\rho)$) will be a function of the standard errors of $a_{observed}$ (the slope of the relationship between $log(M_P)$ and $\overline{M_P}$) and $c_{observed}$ (the slope of the relationship between T and $log(M_P)$).

The standard error of an ordinary least squares regression slope $(s\beta)$: $s\beta = \sqrt{\frac{MS_{res}}{SS_x}}$, where MS_{res} is the mean squared error, or residual mean square, and $SS_x = \sum (X_i - \overline{X})^2 = (n-1) \cdot var(X)$ is the sum of squares of x. By noting that $MS_res = \frac{1}{n-2}(SS_{tot} - SS_{reg})$; where $SS_{tot} = \sum Y_i - \overline{Y}^2 = (n-1) \cdot var(Y)$ is the total sum of squares, and $SS_{reg} = \frac{(\sum (X_i - \overline{X})(Y_i - \overline{Y})^2}{\sum (X_i - \overline{X})} = \frac{(n-1)^2 cov^2(X,Y)}{(n-1)var(X)}$ is the regression sum of squares, it can be shown that

$$s_\beta^2 = \frac{1}{n-2}\left(\frac{var(Y)}{var(X)} - \frac{cov^2(X,Y)}{var^2(X)}\right) \Rightarrow s_\beta^2 \propto \frac{var(Y)}{var(X)} - \frac{cov^2(X,Y)}{var^2(X)}.$$

Now, since the reduced major axis (RMA) regression slope

$$\beta_{RMA} = \pm\sqrt{\frac{var(Y)}{var(X)}}, \text{it turns out that} s_\beta^2 \propto \frac{var(Y)}{var(X)} - \frac{cov^2(X,Y)}{var^2(X)} = \beta_{RMA}^2 - \beta_{OLS}^2,$$

or the standard error of a regression slope $s_\beta \propto \sqrt{\beta_{RMA}^2 - \beta_{OLS}^2}$.

This means that:

$$\begin{array}{lclcl}
s_\beta^2(T, log\rho) & = & s_e^2 & \propto & \frac{var(log\rho)}{var(T)} - \frac{cov^2(T,log\rho)}{var^2(T)} & = & e_{RMA}^2 - e_{OLS}^2 \\
s_\beta^2(T, logM_P) & = & s_c^2 & \propto & \frac{var(logM_P)}{var(T)} - \frac{cov^2(T,M_P)}{var^2(T)} & = & c_{RMA}^2 - c_{OLS}^2 \\
s_\beta^2(logM_P, logM_R) & = & s_a^2 & \propto & \frac{var(log\overline{M}_R)}{var(M_P)} - \frac{cov^2(M_P,log\overline{M}_R)}{var^2(logM_P)} & = & a_{RMA}^2 - a_{OLS}^2
\end{array}$$

$$\Rightarrow s_e^2 \propto e_{RMA}^2 - e_{OLS}^2$$

$$= c_{RMA}^2(1 + a_{RMA}^2 - 2r_{logM_P,logM_R}a_{RMA}) - c_{OLS}^2\left(1 + \frac{a_{OLS}^2}{r_{logM_P,logM_R}^2} - 2a_{OLS}\right)$$
$$= c_{RMA}^2 - c_{OLS}^2 + c_{RMA}^2(a_{RMA}^2 - 2r_{logM_P,logM_P}a_{RMA}) - c_{OLS}^2\left(\frac{a_{OLS}^2}{r_{logM_P,logM_R}^2} - 2a_{OLS}\right)$$
$$= s_c^2 + c_{RMA}^2(a_{RMA}^2 - 2a_{OLS}) - c_{OLS}^2(a_{RMA}^2 - 2a_{OLS})$$
$$= s_c^2 + (c_{RMA}^2 - c_{OLS}^2)(a_{RMA}^2 - 2a_{OLS})$$

Thus:

$$= s_c^2(1 + a_{RMA}^2 - 2a_{OLS})$$
$$= s_c^2(1 + a_{RMA}^2 - a_{OLS}^2 + a_{OLS}^2 - 2a_{OLS}$$
$$= s_c^2(s_a^2 + (a_{OLS} - 1)^2) = s_c^2\left(s_a^2 + \left(\frac{cov(logM_P,log\overline{M}_R)}{var(logM_P)}\right)^2\right)$$

$$s_e \propto s_c \cdot \sqrt{s_a^2 + \left(\frac{cov(logM_P,log\overline{M}_R)}{var(logM_P)-1}\right)^2} \geq s_c \cdot s_a$$

To summarize, the uncertainty (standard errors) in the regression slopes for relationships (1) and (2) will propagate in a multiplicative fashion so that the uncertainty in the regression slope for relationship (3) is greater than (or equal to) the product of the standard errors in the regression slopes for relationships (1) and (2)

4.7.5 Predicted slopes versus observed slopes

To test our model prediction, we plotted $e_{observed}$ (i.e.,the observed slopes of the RMA regression between predator–prey body–mass ratio and trophic level against the predicted slope($e_{predicted}$) (i) without taking error propagation into account (4) (i.e., $e_{predicted} = c_{observed}(1 - a_{observed})$) and (ii) by taking inot account (i.e.,
$e_{predicted} = sign(cov(T, log\rho)) \cdot c_{observed}\sqrt{1 + a_{observed}^2 - 2r_{logM_P,log\overline{M_R}}a_{observed}})$.
The correlation between $e_{observed}$ and $e_{predicted}$ is poor (non-significant) based on all ecosystem types and predator metabolic types if $e_{predicted}$ is based on eq 4 (Fig S4a). Using only those combinations of ecosystem type and predator metabolic type that yielded a significant correlation for $e_{observed}$ (see Table 1), the correlation between $e_{observed}$ and $e_{predicted}$ (based on eq S13) increases (Fig S4b). If instead $e_{predicted}$ is based on eq S16, the correlation between $e_{observed}$ and $e_{predicted}$ is very strong (Fig S4c–d), based on all ecosystem types and predator metabolic types as well as using only those ecosystem types and predator metabolic types that yielded a significant correlation for $e_{observed}$ (see Table 1).

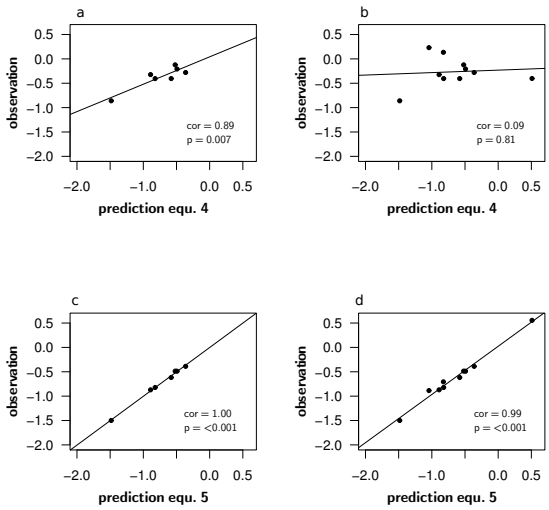

Figure 4.7: Predicted slopes for the relationship between predatro-prey body-mass ratio against observed values. (Tab. 2). In panel a) and b) the prediction is calculated with equ. 4 $(c(1-a))$, in panel c) and d) the prediction is calculated with equ. 5. Furterhmore in b) and d) are all posible combinations out of ecosystem and metabolic predator types considered, in a) and c) only significant observed slopes. All relatinoships are statistical proofed with the pearson correlation (see the results in each panel)

5 SIZE-BASED FOOD WEB CHARACTERISTICS GOVERN THE RESPONSE TO SPECIES EXTINCTIONS

5.1 abstract

How ecological communities react to species extinctions is a long-standing yet current question in ecology. The species constituting the basic units of ecosystems interact with each other forming complex networks of trophic relationships and the characteristics of these networks are highly important for the consequences of species extinction. Here we take a more general approach and analyze a broad range of network characteristics and their role in determining food web susceptibility to secondary extinctions. We extend previous studies, that have focused on the consequences of topological and dynamical food web parameters for food web robustness, by also defining network-wide characteristics depending on the relationships between the distribution of species body masses and other species characteristics. We use a bioenergetic dynamical model to simulate realistically structured model food webs that differ in their structural and dynamical properties as well as their size structure. In order to measure food web robustness we calculated the proportion of species going secondarily extinct. A multiple regression analysis was then used to fit a general model relating the proportion of species going secondarily extinct to the measured food web properties. Our results show that there are multiple factors from all three groups of food web characteristics that affect food web robustness. However, we find the most striking effect was related to the body mass-abundance relationship which points to the importance of body mass relationships for food web stability.

5.2 Introduction

Loss of biodiversity is one of the most severe threats to the earth's ecosystems today. A long-standing challenge for ecologists has been to characterize systems particulary fragile for which a reduction in diversity is likely to give rise to additional losses through cascading effects. The species forming the basic units in the ecosystems are not isolated, but interact with each other forming intricate networks of trophic interactions. The effects of a single extinction event could therefore vary considerably depending on the nature of the network the target species is involved in. Several studies looking solely at the topology of food webs have suggested several properties potentially having large effects on the response of the web to species loss. Characteristics such as number of species, fractions of species on different trophic levels and the connectedness between species, have all been analyzed for their implications for food web robustness (Dunne et al., 2002; Montoya and Sole, 2002; Allesina et al., 2009). However, studies based exclusively on topology do not take the magnitude of species interactions into account and therefore ignore population dynamics and its consequences (Ebenman and Jonsson, 2005). Including this can extensively change the outcome, for exmaple additional cascading extinctions can occur due to density dependent indirect effects. Thus, including population dynamics has been shown to

sometimes drastically change the number of secondary extinctions following an initial species removal (Curtsdotter et al., 2011; Eklöf and Ebenman, 2006).

Recently, in trying to improve their realism, models of food webs have begun to incorporate specific species traits relevant to the presence or absence and strength of interactions. Body mass is one of the most fundamental properties of an organism and a trait frequently suggested to be important in determining species interactions (for reviews see Woodward et al., 2005a; White et al., 2007; Brose, 2010b). Body mass relationships between consumers and resources strongly determine foraging possibilities and diet breath and therefore the topology of the network (Brose, 2010b; Petchey et al., 2008). Recent theories have also found predator-prey body mass relationships to be crucial for food web persistance and stability (Emmerson and Raffaelli, 2004; Loeuille and Loreau, 2005; Brose et al., 2006b; Otto et al., 2007). Body mass is also recognized as one trait often associated with the susceptibility of a species to extinction (McKinney, 1997; Cardillo, 2005; Pauly et al., 1998), for example, larger species often have smaller population sizes and are dependent on multiple trophic levels for their survival. These findings lead to the hypothesis that relationships between species' body masses and food web structure are likely to be important for the ability of a food web to cope with extinctions.

Food webs from different types of ecosystems show differences in their patterns considering the distribution of body size dependent interactions (Riede et al., 2011b). In this study we construct size-structured model food webs using the niche model (Williams and Martinez, 2000). There the assumption is that larger animals on average consume smaller organisms, even if exceptions are allowed. This is the predator prey relationship characterizing size structured systems. Other feeding interactions like parasite-host and herbivore-plant could be better described by other body size relationships between resource and consumer (Riede et al., 2011b).

The aim of this paper is to take a more general approach on food web robustness to secondary extinctions. In particular, we analyze the effects of size-based properties within the context of traditional topological and dynamical analyzes. In order to investigate these relationships we consider several measurements of the size-structure of an ecological network. The goal is to analyze which of this suite of food web characteristics affect a food web's susceptibility to secondary extinctions, thereby easing the identification of food webs especially robust or vulnerable to biodiversity loss.

5.3 Methods

Food webs

We constructed 1000 model food webs of different structures using the niche model (Williams and Martinez, 2000). The niche model uses species richness, S, and food web connectance (i.e., the total number of links present in the food web divided by the maximum possible number of

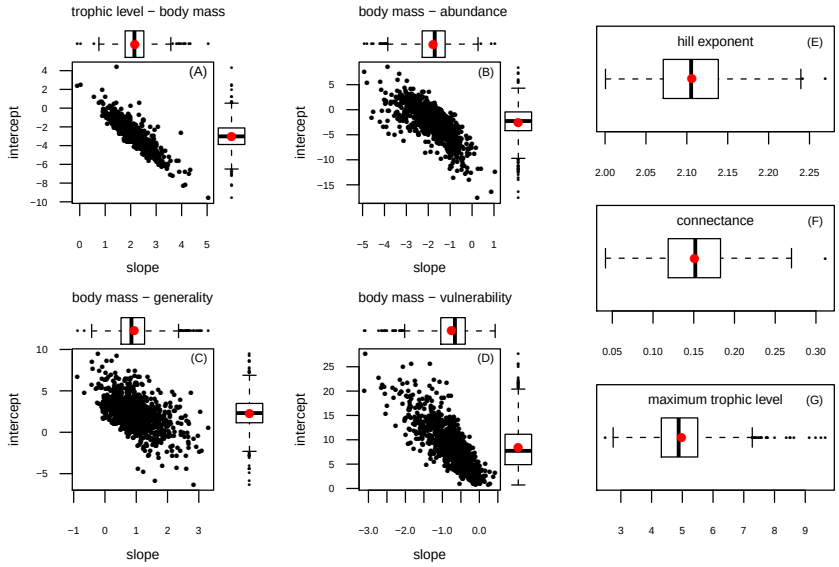

Figure 5.1: Calculated network descriptors after 5000 time steps, before the species removals. Each point represents a single food web. Panels A-D shows the relationship for body mass and trophic level, abundance, generality and vulnerability, respectively. The side bars shows the distribution of the values, where the red point is the average. Panels E and F show the distribution for the Hill exponent, connectance and maximum trophic level respectivly. The red point is the average of the distribution. All descriptors are normally distributed.

links), C, as input parameters and arranges the trophic links, L, based on this information. S and C were sampled from uniform distributions (Table 5.1; Fig. 5.1). Species body-masses were distributed according to a mass-trophic level relationship, such that body masses increase with trophic level by a factor sampled from a log-normal distribution with a mean of 10 and a standard deviation of 100. This correlation between trophic level and body mass is consistent with empirical data across ecosystem types (Table 5.1 Riede et al., 2011b) . This factor is sampled independently for each of the species in a food web consistent with Berlow et al. (2009).

5.3.1 Dynamical simulation

The population dynamics of the food webs were simulated using an allometric consumer-resource model (Williams and Martinez, 2004a; Yodzis and Innes, 1992) in order to describe the changes in biomass over time for all species (for a detailed description of the model see Binzer et al., 2011). The initial biomasses where drawn from a uniform distribution [0.1; 1].

Table 5.1: Comparison of the range of parameter values used for the dynamical simulations. Values shown both before (initial webs) and after the system settled down (webs after 5000 time steps) and fo 94 empirical food webs (empirical webs) (Digel et al., 2011). The measurements are given as the interval between the minimum and maximum value of the parameter.

Parameter	Initial webs	Webs after 5000 ts	Empirical webs
Number of species	10 - 60	9 - 59	27 - 492
Connectance	0.04 - 0.33	0.04 - 0.31	0.04 - 0.31
Maximum trophic level	2.5 -9.5	2.5 - 9.7	2.75 - 5.4
%mean generality	0 -20	0 - 20	0 - 135
%mean vulnerability0 - 20		0 - 20	0 - 138
Slope trophic level vs. bodymass	1.0 - 3.0	(-0.09) - 5.04	0.15 - 8.14

Species body masses were used to parameterize the dynamical model; the metabolic rate and the maximum rate of consumption of the consumers scale with a three quarter power function with their body masses. The basal species are competing for a fixed amount of nutrients and have a logistic growth rate. The consumers have a non-linear functional response whose shape is defined by the predator interference and the Hill exponent, sampled from uniform distributions in the range [0 ; 1] and [1 ; 1.3] respectively. The Hill exponent yields functional responses from Holling type II (Hill exponent = 1) to increasingly sigmoid, Holling type III-like curves with increasing values of the exponent (see Rall et al., 2008, for a detailed description).

Each food web was simulated initially for 5000 time steps in order to give the system time to settle and remove initial transient dynamics. The potentially reduced food webs produced after this initial simulation then were used for species removal experiments. The constructed food webs had parameter values close to parameter values for empirical food webs (Table 5.1).

The removal experiments were preformed for each of the 1000 constructed food webs as follows. One species was removed by reducing its biomass to zero. The system was then simulated for 10.000 time steps. This procedure was repeated for each species independently and after each simulation (species removal) the number of secondary extinction was recorded. A species was considered extinct if its biomass density fell below 10^{-30}.

5.3.2 Food web descriptors

After the initial 5000 time steps a number of descriptors of food web topology and body mass structure for each web were recorded. In order to acquire measurements of the size structure in each of the food webs, we analyzed five body mass-dependent relationships: the body mass

of each species versus its abundance, trophic level (prey-averaged trophic level as described in Williams and Martinez, 2004b, 2008), linkedness (the sum of all prey and all predators per species), vulnerability (the number of consumers) and generality (the number of resources). We analyzed the abundance-mass relationships on a log-log scale (e.g., Peters and Wassenberg, 1983) whereas the relationships between body mass and trophic level and the link variables were analyzed on a log-linear scale. All descriptors were normally distributed (Fig. 5.1). In order to account for the difference in diversity and connectance of the food webs, we normalized the explanatory variables so that the species with the largest value of a specific explanatory variable were set to unity and the values of that variable for all other species were expressed relative to this number.

All relationships were analyzed with independent ordinary least squares regressions and slopes and intercepts were recorded for statistical analysis, regardless of their p-value or r^2-value. This simplification enabled comparisons across all food webs.

This gave us a total of 15 food web descriptors, which can be divided into three different groups: topological descriptors (species richness, maximum trophic level, connectance), dynamical descriptors (Hill exponent, predator interference) and body mass dependent descriptors (intercept and slope of body mass versus linkedness, generality, vulnerability, abundance, trophic level). The slopes and intercepts of these relationships varied between the analyzed food webs (Fig. 5.1).

5.3.3 Statistical analysis

The dataset analyzed here clearly suggested that multiple factors influenced the risk of secondary extinctions and that no single factor had a dominant effect over the others. We used multiple linear regression to assess the effects of the different food web characteristics on the proportion of species going secondarily extinct. This proprtion was calculated as the average number of secondary extinct species taken over all species removals, normalized by the number of species in the food web minus one (due to the forced primary extinction). As predictors we used all the food web descriptors (see section Food web descriptors). The set of 1000 produced food webs was split into two equal groups of 500; one was used to fit the model (training set) while the other was used to test the predictions (test set). The proportion of species going secondarily extinct varied from 0 to 0.45 with an average of 0.06 after removal of one species (Fig. 5.2). Eight of the 1000 analyzed food webs did not experience any secondary extinctions. These webs were included in the statistical analyses, but did not affect our general conclusions.

We started with a full model including all 15 food web descriptors, and their quadratic forms to account for potential non-linear effects. Additionally, we added the cubic form for the Hill

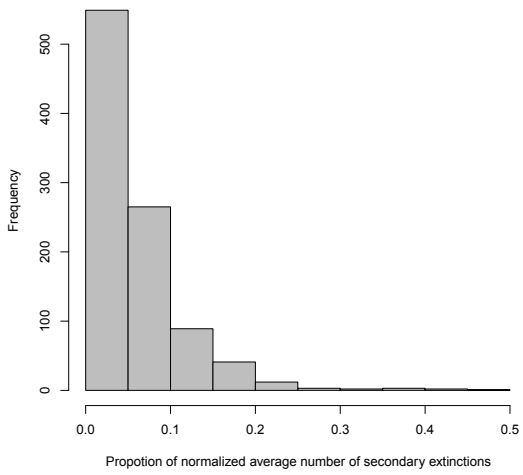

Figure 5.2: The frequency of the proportion of species going secondary extinct averaged over all species removals. Data shown for all 1000 analyzed food webs.

exponent which gave us a total of 31 parameters. After fitting the model using linear modelling procedure (R version 2.11.1) we performed a backward stepwise multiple regression. We removed the parameter with the highest, non-significant p-value and repeated the analysis. The quadratic forms of the parameters were removed first, in order to reduce the complexity of the final model as much as possible. This procedure was repeated until only significant ($p < 0.05$) factors remained and these comprised our final model (Table 5.2). Partial residuals for each parameter were computed by removing the effects of all other parameters. The partial residuals indicate the unique effects of the dependent variables in the overall model on the proportion of species going secondarily extinct.

Results

13 of the 31 starting parameters ended up as significant as a result from the regression analysis, of which 10 were significant and had a p-value less than 0.001. These parameters explained 43 percent of the variation in the proportion of species going secondarily extinct in 500 of the simulated training networks and 39 percent of the variance in the remaining 500 test networks (Table 5.2).

The significant parameters were the species richness, the maximum trophic level, the Hill exponent, the intercept of the linkedness, the slope and intercept of the body mass-generality relationship, intercept of the body mass-vulnerability relationship and slope and intercept of the body mass-abundance relationship (Table 5.1). Several parameters remained with significant linear

Table 5.2: The significant parameters in the stepwise multiple regression model using the proportion of species going secondarily extinct as dependent variable. All parameters are sorted by category (top = topological, dyn = dynamical and size = size based). The estimates are the coefficients of the variable. Standard errors and p-values were calculated within the multiple regression model.

Parameter	Category	Estimate	Std. error	p-value
Number of species	top	0.21	0.05	< 0.001
Maximum trophic level	top	0.22	0.05	< 0.001
(Maximum trophic level)^2	top	-0.09	0.02	< 0.001
(Hill exponent)^2	dyn	0.24	0.03	< 0.001
(Hill exponent)^3	dyn	-0.07	0.01	< 0.001
(Intercept linkedness)^2	size	0.10	0.04	0.010
Slope generality	size	-0.28	0.06	< 0.010
(Slope generality)^2	size	-0.05	0.02	0.020
Intercept generality	size	-0.19	0.06	< 0.001
(Intercept generality)^2	size	-0.05	0.02	0.020
(Intercept vulnerability)^2	size	-0.14	0.04	< 0.001
Intercept abundance	size	-0.60	0.05	< 0.001
Slope abundance	size	-0.72	0.05	< 0.001

and quadratic terms in the final model. This suggests that those parameters are related to food web robustness in a non-linear way (Fig. 5.3).

Regarding the topological descriptors, number of species and the maximum trophic level (the latter with both linear and quadratic terms) were significant in the final model (Table2, Fig. 5.3A,B).

The starting model used the dynamical properties of interference and the Hill exponent, which are both related to the functional response of the species in the web. The final model predicted that the squared and cubed Hill exponent were significant (Fig. 5.3C). Low Hill exponents increase the normalized secondary extinctions, while an increasing Hill exponent decreases the average normalized secondary extinct species.

Of the body-mass correlated predictors, the slope of the body mass-abundance relationship was found to be the parameter with the clearest relationship to robustness, displaying a clear negative trend (Fig. 5.3I). The intercept for the same relationship also shows the same trend (Fig. 5.3H). Parameters such as the intercepts of vulnerability, generality and linkedness, slope generality and

the maximum trophic level can be considered to have weaker, though still significant, effects. The quadraic terms of these variables remained in the final model (Table 5.2, Fig. 5.3).
Of interest are also parameters excluded from the model for being non-significant. Variables that in other studies have been demonstrated to be of importance for food web robustness, such as connectance, did not end up in the final model. Nor did the slope for linkedness-body mass relationship, the slope for the vulnerability-body mass relationship, the slope and intercept for the trophic level-body mass relationship and the strength of interference competition.

5.4 Discussion

The aim of this study was to evaluate the impact of different food web characteristics, in particular properties based on the size structure, on food web response to species loss. The purpose has been to come closer to an understanding of what kinds of food webs are more or less robust to secondary extinctions. The parameters describing the food web characteristics can be roughly divided into three different groups: parameters describing i) food web topology, ii) population dynamics and iii) body size structure.
The effect of the network topology on a food web's robustness has, to date, been the of research most investigated (Dunne, 2006). This is a logical consequence of that the topology is the simplest way to describe species' interactions and the topological approach points out the minimum damage species removals can cause. The first topological parameter we here found to have a significant effect on food web robustness was species richness. A positive trend was observed so that increasing the number of species increased the proportion of species going secondarily extinct. This shows that there is an apparent contrast to neutral diversity-stability relationships in complex food webs with a size structure (Brose et al., 2006b; Brose, 2008; Rall et al., 2008) similar to the food webs modeled here. This result suggests that species' extinctions are a severe perturbation with consequences that cannot be predicted by solely analysing local stability. We propose the following explanation for our results. As the total energy available by primary production was set by system-level carrying capacity (see Binzer et al., 2011), increasing species richness implies distribution of energy across more populations. Ultimately, this results in lower biomass densities and a higher risk of secondary extinctions. Future extensions of our approach should address whether additive or interactive resource uptake by basal species (e.g., Brose, 2008) will affect the results concerning the effects of species richness on food-web vulnerability to species loss.
Connectance is a food web characteristic that in many studies has been shown to have large effects on food web robustness, both in pure topological analyses (Dunne et al., 2004, 2002) and studies incorporating population dynamics (Eklöf and Ebenman, 2006; Petchey et al., 2008).

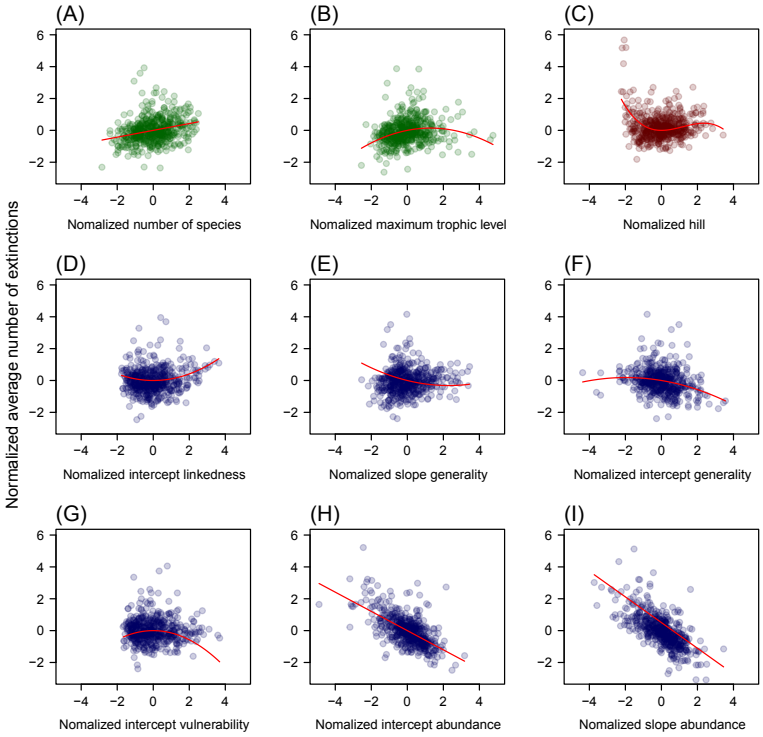

Figure 5.3: Partial residual plots of the effects of each significant descriptor on the proportion of species going secondarily extint. Red lines show the from of the model fitted values. The effects of the topological descriptors are shown in the first two panels and represented by green points; the number of species (A) and the maximum trophic level (B). The effect of the dynamical descriptor is represented by red points; the Hill exponent (C). The effect of the body mass-related descriptors are represented by blue points; the intercept linkedness (D), slope generality (E), intercept generality (F), intercept abundance (H) and slope abundance (G).

One possible explanation for the lack of importance of connectance here could be that additional dynamical parameters are included, i.e., a different kind of functional response. There are also examples of other studies showing that including population dynamics can suppress the positive effect of an increased number of connections when additional parameters, such as an explicit spatial structure, are included (Eklöf, 2009). This is most likely due to the fact that when population dynamics are included and the connectance is high there are multiple pathways for a disturbance to branch out in the network, for example, oscillations in species densities could be distributed more widely. The negative relationship is in strong contrast to the pattern observed in purely topological analyses, which suggests the effect would be positive due to extra links providing insurance to species against the loss of prey (Dunne et al., 2004, 2002; Thierry et al., 2011). It appears that in the present study the two effects (both positive and negative) balance each other.

We show here that the higher the maximum trophic level in a food web is the less robust it is to secondary extinctions. An increase in the maximum trophic level implies that, on average, more species are at higher trophic levels and these species are the ones having the highest extinction risks (Binzer et al., 2011).

Of the two parameters describing the population dynamics, the Hill exponent and the interference, only the Hill exponent remained in the final model. This parameter is important for the interactions between predator and prey and describes the type of functional response. A Hill exponent of 1 describes a type II functional response and an increase in the Hill exponent makes the functional response more sigmoidal (type III). In agreement with unforced extinction results (Binzer et al., 2011; Eklöf and Ebenman, 2006; Petchey et al., 2008) and results from sequential species removals (Curtsdotter et al., 2011) we found that an increase in the Hill exponent decreases the proportion of species going secondary extinct. Previous studies have shown that a type III functional response decreases the oscillations of the system (Rall et al., 2008; Williams and Martinez, 2004a) and should thereby dampen the extinction risk of each species and increases the stability of food webs.

Of all the parameters examined we found the strongest relationship between food web robustness and the slope of the body mass-abundance relationship. This relationship has been shown to have a narrow range of slope around -3/4 (on a log-log scale) in both empirical (Jennings and Mackinson, 2003) and theoretical (Damuth, 2007) analyses (but see Reuman et al., 2009, for exceptions). This value is approximately the inverse of the metabolic rate-body mass relationship of 3/4 (Brown et al., 2004). These relationships sum to energetic equivalence (Damuth, 1987; Nee et al., 1991) which states that there is an approximate independence of energy use and body mass in local populations. A positive or even much less negative slope would therefore be unrealistic for ecological systems. Surprisingly, we found a strong negative relationship, indicating that relationships with smaller slopes make food webs more robust. However, in

the food webs before species removals this relationship varies within a wide range, where the supposed relationship of 3/4 is underrepresented (Fig. 5.1). In the food webs analyzed here a steeper body mass-abundance slope is caused by the larger species being less abundant. Large-bodied species are usually species at higher trophic levels and they are more prone to extinction (Binzer et al., 2011). For example they have lower growth rates and depend - for their energy intake - on species from multiple lower trophic levels. In summary, this would strongly suggest that food webs with steep negative slope are suceptible to secondary extinctions. On the other hand, when the slope is more positive (compared to -3/4) the small-bodied species have relatively low abundance and, accordingly, could be more likely to go extinct. However, in our model the smallest species are often basal species which due to, for example, their high growth rates and lack of dependence on other trophic levels for energy, are initially not prone to go extinct.

We also found that several other of the size dependent relationships are important and these are all coupled to the number of feeding interactions a species possesses. This points out the importance of the distribution of interactions and body masses for food web stability and robustness, which has been shown for tri-trophic food chains (Otto et al., 2007). The combination of size-structure and topological features stands out as a determining factor for the stability of food webs to cope with disturbances both in smaller motifs as well as larger networks.

5.4.1 Caveats and Future Directions

In this statistical approach we used descriptors which might be correlated, for example the slope and intercept of body-mass versus vulnerability, generality and linkedness in the same model. While the linkedness is the sum of all prey and all predators per species, we could assume that these values are collinear in the model. We repeated the analysis without linkedness and found the r^2-value was not strongly affected by removal of this descriptor. In the training data set, the three descriptors are no longer significant if we ignore linkedness within the multiple model. However, repeating this with the test data set shows that vulnerability and generality were still significant with linkedness ignored. This suggests that our results are robust and not affected by co-linearity.

In this analysis we adopted a more general perspective taking the characteristics of the whole network into account. This means that each data point analyzed represents a single web and the parameters are averages over all the species in the web. However, it would also be interesting to adopt a reductionist viewpoint and follow the extinction sequence to analyze how the characteristics of the species initially removed and the characteristics of the species going secondary extinct are related.

One could also argue that the forced species removals preformed here are unrealistic since a natural extinction event is most often a gradual process where the target species abundance decreases with time. This might change the dynamics and the cascading extinctions might take

other paths throughout the food web, especially if species are also allowed to adjust their feeding behavior (Thierry et al., 2011; Kondoh, 2003). The disturbance we here implement is also severe and irreversible. It would be interesting to see if the results presented here also would hold for smaller disturbances and species gradually decreasing to extinction.
As in all modeling excercises several assumptions are made putting constraints on the systems. Future developments should for example additionally focus on different distributions of body sizes. It is reasonable to assume that species body size distributions will play a different role in systems where a different size structure applies, such as terrestrial plant-herbivore interactions and systems where parasitic trophic interactions are common. Also, additional species traits and ecosystem characteristics, such as their spatial distribution, would be relevant to include in future analyses. Body size is certainly an important trait shaping species interactions but does not suffice to describe all trophic interactions (Zook et al., 2010) and additional relationships are therefore likely to have effect on food web dynamics and thereby food web robustness.

5.4.2 Conclusions

Here we have taken a further step towards a more detailed understanding of which food web characteristics are of huge importance for food web robustness. Our approach has allowed us to investigate a broad range of food web characteristics including, for the first time, its size-structure in order to asses their individual role for food web robustness. The results highlight the importance of incorporating realistic food web characteristics such as population dynamics and body mass-dependent relationships. The striking effect of the body mass - abundance relationship shows that the ongoing efforts of both empiricists and theoreticians to understand the role that species body mass distributions play for food web stability and robustness is an important path for future ecological research.

5.5 Acknowledgment

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6 Loss of large top predators in species–poor food webs yields the highest secondary extinction risk

6.1 Abstract

The current wave of species extinctions triggered a debate how primary loss of species may further accelerate indirect losses of biodiversity in natural complex ecosystems. We explore such interdependence by simulating the nonlinear population dynamics resulting from eliminating consumer species within thirty complex natural food webs. We find that the risk of ”secondary” species extinctions following ”primary” species loss depends on characteristics of the species initially lost and the food webs within which they interact. While all ecosystem-types (freshwater, marine, terrestrial) respond similarly to species loss, we found that food webs with high diversity and a low standard deviation of vulnerability are less effected by secondary extinctions. At the species level, we found that the loss of large-bodied top predators increases the extinction-risk for all others species in the ecosystem. Together, these findings offer new opportunities for understanding and predicting the sensitivity of ecosystems and their services to species loss.

6.2 Introduction

Accelerated recent extinction rates have triggered a debate on the sixth mass extinction wave (Barnosky et al., 2011). Currently, the world's ecosystems are experiencingone of the largest and fastest waves of extinctions since life established on earth and also the local loss of species' populations at rates orders of magnitude higher than current extinction rates (Hughes et al., 1997). Such primary species losses can trigger avalanches of further species loss (Paine, 1966; Power et al., 1996; Srinivasan et al., 2007) and greatly alter the stability and functioning of ecosystems (Luck et al., 2003). Currently, the biggest challenge for ecologists is to analyse the key factors supporting or avoiding the progressing species loss that undermines the biodiversity of natural ecosystems (de Ruiter, 2005; Montoya et al., 2006). Studies find that properties of food webs (i.e. networks of species linked by feeding interactions) and characteristics of species initially lost help elucidate this crucial question (Pimm, 1980; Borrvall et al., 2000; Solè and Montoya, 2001; Dunne et al., 2002; Ebenman et al., 2004; Thebault et al., 2007; Allesina et al., 2009; de Visser et al., 2011). However, the low number of species, minimal complexity, or linear dynamics of the systems explored in studies limits the degree to which answers may apply to naturally diverse and complex ecosystems with their non-linear dynamics.

Early linear stability analyses of small food-web modules (Pimm, 1980) suggest that food-web extinction risk (percentage of species going secondarily extinct; hereafter extinction risk) increases with increasing food-web diversity (i.e., the number of species; hereafter: diversity). This is expected based on negative diversity-stability relationships found in similar analyses of random interaction networks (May, 1972). In contrast, recent extensions of such analyses suggest that extinction risk decreases with increasing species diversity within functional groups

and increasing trophic position of the species primarily lost (Borrvall et al., 2000; Ebenman et al., 2004). These discrepancies are thought to be due to the presence (Borrvall et al., 2000) or absence (Pimm, 1980) of intraspecific competition in these studies (Thebault et al., 2007). While such dynamical analyses focus on small food-web modules with few species, several structural analyses ignored population dynamics and top-down effects but focused on bottom-up effects in whole natural food webs of high diversity (Solè and Montoya, 2001; Dunne et al., 2002). By analyzing secondary extinctions that occur only when a species looses all of its prey, these analysis find that extinction-risk is independent of diversity (Dunne et al., 2002), increases with the number of links to the species removed (Solè and Montoya, 2001; Dunne et al., 2002; Gravel et al., 2011) and decreases with connectance (Dunne et al., 2002; Staniczenko et al., 2010; Gravel et al., 2011). Clearly, the substantial contradictions and limitations of these studies leave a promising scientific space to combine and enhance their approaches. Recent advances integrated the structure of large complex food webs with allometrically parametrized models of population dynamics and found that high predator-prey body-mass ratios are critical for food-web stability (Emmerson and Raffaelli, 2004; Loeuille and Loreau, 2005; Brose et al., 2006b; Otto et al., 2007). Here, we extend these approaches and integrate structural and dynamical methods to analyze secondary extinctions following removal of consumer species from models of thirty natural food webs parametrized with the empirical feeding relationships and body masses of the species found in those food webs. We test several hypotheses including whether or not the removed species' body mass (Brose et al., 2006b; Otto et al., 2007; Berlow et al., 2008), trophic level (Borrvall et al., 2000), see also (Ebenman et al., 2004; Thebault et al., 2007) or connectedness (Sole2001, Dunne2002, Gravel2011) affect secondary extinction risk in natural food-webs. For the first time, we combine population dynamic models, applied to smaller food-web modules in prior studies, with complex natural food-web topologies. This approach allows addressing bottom-up (as prior topological studies) and top-down effects (as prior module studies) on secondary extinction risks. Specifically, we tackle the key questions: (1) which ecosystems are most sensitive to extinction avalanches and, (2) which species extinctions are most likely to cause secondary extinctions.

6.3 Methods

6.3.1 modeling

We explored food-web robustness by simulating species loss within thirty empirical food webs. We removed one species ('species removed', hereafter SR) at the first time step of each simulation and repeated this independently for each species in each food web (removal runs). After species removal, other populations of species went extinct if their biomass densities fell below a critical extinction threshold $(Bi < 10^{-}30)$. We normalized the extinction-risk across food webs

by performing the dynamics first without removing any species for each food web (non-removal run). Subsequently, we calculated the food-web extinction-risk (ER) for each removal run independently depending on the ratio between the number of persistent species in the removal run $(Sp, \text{excluding} SR)$ and those in the non-removal run (Si). The final number of species after the non-removal run was used to normalize the number of secondary species after the second run with removing all species one by one. This lead to the food-web extinction-risk (ER) as the fraction of initial species that persist after species removal: $ER = 1 - (Sp/Si)$: Population dynamics. We use a bioenergetic consumer–resource (Yodzis and Innes, 1992; Williams and Martinez, 2004b) to describe the change of biomass over time, B_i, of autotroph producer species (eq. 1a) and heterotroph consumer species (eq. 1b) in an n-species system:

$$B_i' = r_i(M_i)G_iB_i - \sum_{j=consumers} \frac{x_j(M)_j y_j B_j F_{ij}(B)}{e_{ji} f_{ji}} \tag{6.1a}$$

$$B_i' = -x_i(M)_i B_i + \sum_{j=resources} x_i(M)_i y_i B_i F_{ij}(B) - \sum_{j=consumers}^{n} \frac{x_j(M)_j y_j B_j F_{ji}(B)}{e_{ji}} \tag{6.1b}$$

For each species $i, B_i$is its biomass, r_i is its mass-specific maximum growth rate, M_i is its average body mass, G_i is its logistic net growth $(G_i = 1 - B_i/K)$ with a carrying capacity K, x_i is its mass-specific metabolic rate, y_i is its maximum consumption rate relative to its metabolic rate, and e_{ji} is the assimilation efficiency of population j consuming population $i.F_{ij}$ describes the fraction of y_i that is realized when consuming j:

$$F_{ij} = \frac{\Omega_{ij} B_j}{B_0 + cB_i \sum_{k=resoures} \Omega_{ik} B_k} \tag{6.2}$$

where B_0 is the density of prey at which species i attains half its maximum consumption rate; Ω_{ij} is the proportion of y_i targeted to consuming j, and c quantifies predator interference (Beddington, 1975; DeAngelis et al., 1975). The predator–interference term in the denominator quantifies the degree to which individuals within population i interfere with one another's consumption activities, which reduces i's per capita consumption if $c > 0$. We used uniform relative consumption rates for consumers with n resources $\Omega_{ij} = 1/n$ — that is, consumers do not have an active resource preference, but rather feed according to the relative biomasses of their resource species. The biological rates of production, W, metabolism, X, and maximum consumption, Y, follow negative–quarter power–law relationships with the species' body masses (Enquist et al., 1999; Brown et al., 2004):

$$W_P = a_r M_P^{-0.25}, \tag{6.3a}$$
$$X_C = a_x M_C^{-0.25}, \tag{6.3b}$$
$$Y_C = a_y M_C^{-0.25}, \tag{6.3c}$$

where a_r, a_x and a_y are allometric constants and C and P indicate consumer and producer parameters respectively, (Yodzis and Innes, 1992) The time scale of the system is defined by normalizing the biological rates by the mass-specific growth rate of the smallest producer species $P*$. Then, the maximum consumption rates, Y_C, are normalized by the metabolic rates X_C:

$$r_i = \frac{W_P}{W_{P*}} = \frac{M_P^{-0.25}}{M_{P*}} \tag{6.4a}$$
$$x_i = \frac{X_C}{W_{P*}} = \frac{a_x}{a_r}\left(\frac{M_C}{M_{P*}}\right)^{-0.25} \tag{6.4b}$$
$$y_i = \frac{Y_C}{X_C} = \frac{a_y}{a_x} \tag{6.4c}$$

Substituting equations 4a-c into equations 1a-b yields a population dynamic model with allometrically-scaled and normalized parameters. We used constant values for the following model parameters: predator interference $c = 1$, maximum ingestion rate $y_i = 8$ assimilation efficiency $e_{ij} = 0.85$ for carnivores and $e_{ij} = 0.45$ for herbivores; carrying capacity $K = 1$, half saturation density of the functional response $B_0 = 0.5$; allometric constants $a_x/a_r = 0.314$ for invertebrates and $a_x/a_r = 0.88$ for ectotherm vertebrates. Independent simulations of each food web started with uniformly random initial biomass densities $(0.05 < B_i < 1)$, and they run for 30 years as calculated by inserting $MP*$ in (3a) and taking the inverse of $W_P * [1/years]$. Structural and metabolic parameters were set using thirty natural food webs (four marine, nine lake, seven stream, and ten terrestrial food webs) of high taxonomic resolution for which body-mass data were available (Table 1).

6.3.2 Statistics

We performed a ANOVA to evalute differences in extinction–risk between ecosystem-types (stream, lake, marine and terrestrial ecosystems).To address susceptibility to extinction avalanches at the community level, we analysed the effects of twelve food-web parameters (diversity, connectance, fraction basal species, fraction omnivore species, fraction cannibalistic species, average trophic level, mean similarity, mean cluster coefficient, diet discontinuity and the standard deviations of vulnerability, generality and linkedness) on the food-webs average secondary extinction risk (mean extinction-risk of all removed species) with a linear generalized least squares

fit model with maximum likelihood estimates (hereafter gls, using the packages nlme and MASS provided by the statistical software (Team, 2011)).
We employed a stepwise, backward multiple glm model removing variables with collinearity in the output correlation matrix of the lme function (R package nlme). Variables were removed according to their covarianz higher than 0.7 to other variables (Crawley, 2007) until the remaining variables did not exhibit collinearity. Subsequently, the backward selection process was continued by eliminating all non significant variables according to the highest $p - value$s as long as this reduced the model's AIC.

Subsequently, we addressed which species extinctions are most likely to cause secondary extinctions. To discount the block effect of food-web identity from these analyses at the species level, we used a linear mixed effect model with maximum likelihood estimates. While we used the food-web identity as a random effect, all other independent variables were treated as fixed effects. These independent variables were the $log_{10}SR$ body mass and six characteristics of the local network environment of the SR — its trophic level (TL), vulnerability (number of predators), generality (number of prey), mean path length (the average path length between any pair of species in a food web, predator generality (the number of prey items for each predator species) and prey vulnerability (proportion of predators consuming the same prey items). In a stepwise procedure, independent variables were removed from the full model following the same strategy as described above for the stepwise gls model.

6.4 Results

We explored which variables were responsible for secondary extinctions in dynamical food web models of 30 empirical food webs (see Table 1). We focused on the food-web and species level drivers of secondary extinction risk (proportion of relative secondary extinctions). The normalized extinction risk for each web varied between zero to 0.42 (equivalent to 42% secondary extinct species), while the mean risk of secondary extinction across all food webs was around 0.03 (equivalent to 3% secondary extinct species). At the food-web level, only two predictors out of twelve initial food web parameters exhibited significant effects on the food-web averaged secondary extinction risks. The risk of secondary extinctions decreased with increasing species diversity ($p - value$ = 0.04; Fig. 1a) and increased with an increasing standard deviation of vulnerability ($p - value$ <0.001; Fig. 1b). The final model did not include any significant differences in extinction risk between the four ecosystem types (stream, lake, marine and terrestrial ecosystems; Fig. 1c; $p - value$ = 0.8). These results suggest that communities of low diversity with a high standard deviation of vulnerability are most sensitive to primary extinctions.

At the species level, the stepwise linear mixed effect model demonstrated a strongly increasing secondary extinction risk with an increasing body mass of the species that went primarily extinct (Fig. 2a, $p-value$ <0.001). Moreover, the secondary extinction risk increased with the trophic level of the primary extinct species (Fig. 2b, $p-value$ = -0.011) and the average vulnerability of its prey (Fig. 2c, $p-value$ <0.001). Together, these results suggest that the risk of secondary extinctions is highest following the loss of large, high trophic level species whose prey has many additional consumers.

Table 6.1: Studied food webs with: n = species richness, C = connectance, number of basal species, mean SWTL = average short–weighted trophic level of all species, habitat = ecosystem type. References for consumer resource interactions and body mass data are describted in table 1.1 in the general introduction. Only consumer–resource interactions, parasitic interactions are excluded.

Food web	n	C	No. basal	mean SWTL	habitat
Alamitos Creek	159	0.15	6	2.35	stream
Alford Lake	56	0.07	24	1.65	lake
Bere Stream	137	0.07	31	1.92	stream
Blackrock River	82	0.05	44	1.51	lake
Bridge Brook Lake	75	0.1	39	1.58	lake
Broadstone Stream	34	0.19	5	2.01	stream
Caldero Creek	123	0.14	6	2.34	stream
Carpinteria Saltmarsh	72	0.05	10	2.36	marine
Chub Pond	65	0.1	33	1.64	lake
Grand Cariçaie, clc2	118	0.07	21	2.26	terrestrial
Grand Cariçaie, scs2	152	0.07	22	2.3	terrestrial
Coachella Valley	26	0.34	3	2.84	terrestrial
Connery Lake	30	0.07	19	1.39	lake
Florida Islande E1	48	0.1	4	2.35	terrestrial
Florida Islande E2	62	0.09	5	2.37	terrestrial
Florida Islande E3	49	0.1	4	2.29	terrestrial
Florida Islande E9	70	0.09	7	2.46	terrestrial
Florida Islande St1	53	0.11	3	2.52	terrestrial
Mountain Forest	33	0.06	5	2.28	terrestrial
Guadeloupe Creek	172	0.15	6	2.35	stream
Littlerock Lake	177	0.06	63	1.94	lake
Los Trancos Creek	128	0.15	6	2.35	stream
Mondego Estuary	48	0.12	10	2.04	marine
Saratoga Creek	155	0.15	6	2.37	stream
Sierra Lake	37	0.22	3	2.24	lake
Small Reef	50	0.22	3	2.9	marine
Skipwith Pond	34	0.31	15	1.7	lake
Stink Lake	53	0.1	24	1.68	lake
Trelasea Wood	30	0.07	6	2.22	terrestrial
Ythan Estuary	92	0.05	4	2.58	marine

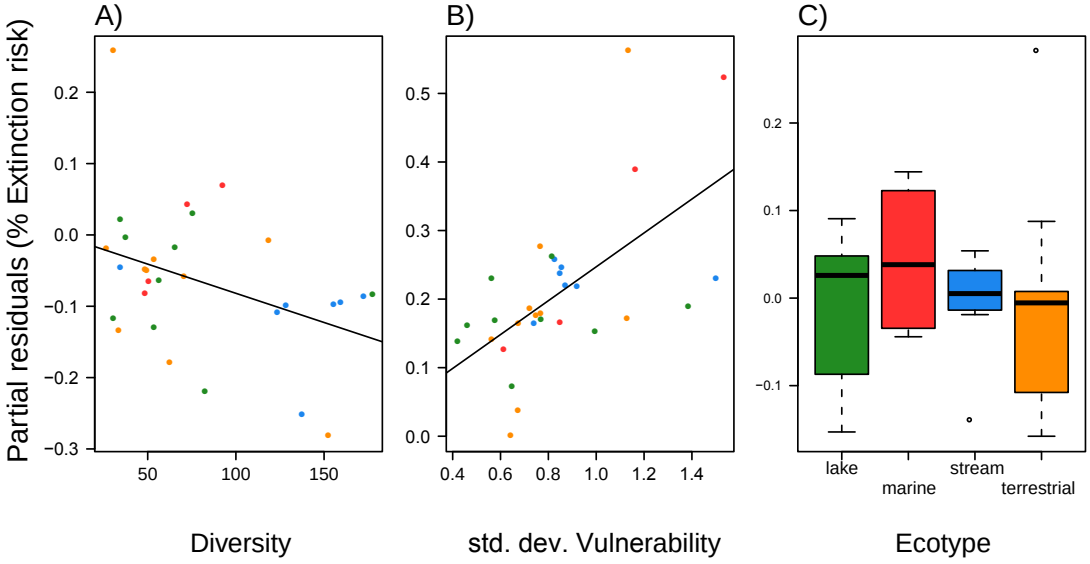

Figure 6.1: Variables explaining extinction risk on food web level calculated with a backward-stepwise gls. The variables are standardized extinction-risk depending on (A) diversity, slope $= -0.001, p-value = 0.04$; (B) and SE standard deviation vulnerability, slope $= 0.252, p - value =< 0.001$. Panel (C) give an impression about the risk of secondary extinctions across different ecosystem types (ANOVA: $p-value = 0.31$).

6.5 Discussion

We addressed the risk of secondary extinctions following single primary extinctions in 30 well-resolved, complex natural food webs. While prior studies studied extinctions in theoretical network models (Riede et al., 2011a; Curtsdotter et al., 2011) or structural models of natural food webs (Dunne et al., 2002; Srinivasan et al., 2007; Allesina et al., 2009), our approach is novel in applying dynamic modelling to natural food-webs. Dynamic modelling allows detecting top-down effects of primary extinctions such as trophic cascades that are missed by structural models (Curtsdotter et al., 2011). Dovetailing this dynamic modelling into empirical food-web topologies accounts for the complexities and specificities of natural ecosystems, which enables more realistic forecasting of extinction risks.

One important generality emerging from our results is that there are no significant differences in extinction risks between marine, freshwater and terrestrial ecosystems. Across all 2420 simulated extinctions, the mean extinction risk for each food web was prone to lose in average 4% species secondarily after a single primary extinction Addressing food-web level differences in sensitivity to secondary extinctions, we found that extinction-risk decreased with species diversity and increased with the standard deviation of vulnerability, whereas none of the other network parameters tested imposed a significant effect.

Our results thus generalize prior conclusions for small modules (Thebault et al., 2007) to the level of complex natural food webs. Assuming that intraspecific competition is common in natural populations

(Skalski and Gilliam, 2000; Kratina et al., 2008; Lang et al., ress), they suggest that communities of high diversity are less sensitive to secondary extinctions than those of lower diversity. Importantly, they also document that decreasing diversity may increase secondary extinction risks thus potentially accelerating extinction avalanches.

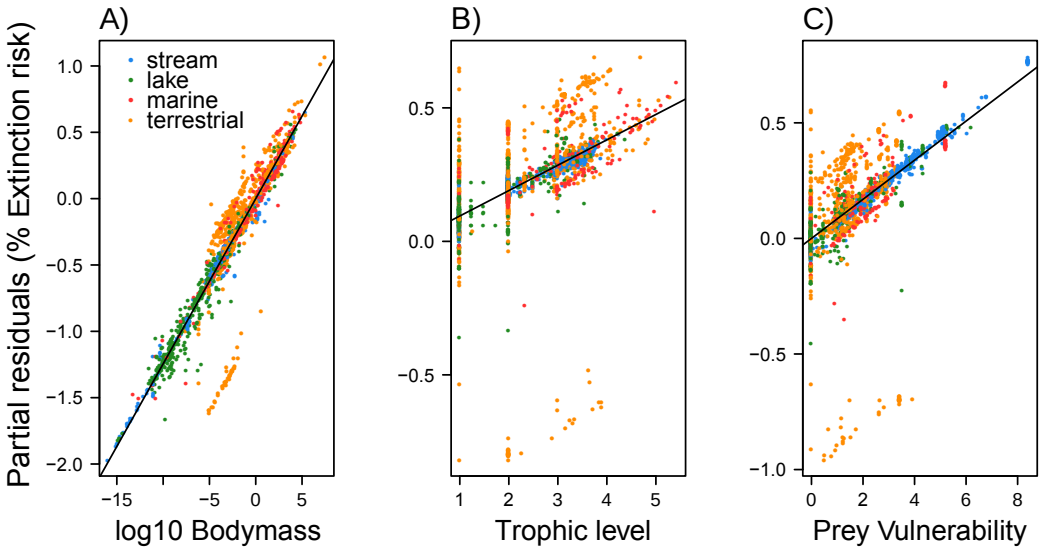

Figure 6.2: The plots give an impression about the impact of the species characteristics on risk of secondary extinctions: (A) log_{10}SE body mass, $slope = 0.006, p - value =< 0.001; (C) SEtrophiclevel, slope = -0.011, p - value = 0.009; (C) SEpreyvulnerability, slope = -0.014, p - value =< 0.001$. We performed a stepwise LME-model of standardized extinction–risk to identify significant effects.

Surprisingly, our model predicts that extinction risk increases with an increasing standard deviation of vulnerability. The standard deviation of vulnerability indicates the variability in the number of links from resource populations to consumers thus expressing differences in predation risks. Interestingly, our results indicate that food webs where the predation risk is equally distributed across species are more robust than those where the risk of predation is very variable among species. We interpret this as an indicator of redundancy of species: the more variable the predation risk the lower the consumer redundancy. In consequence, our results suggest that consumer redundancy as indicated by low standard deviations of vulnerability may provide an insurance against top-down mediated secondary extinction cascades.
Surprisingly and in contrast to topological studies (Dunne et al., 2002; Gravel et al., 2011), food-web connectance did not influence the extinction risk. . Interestingly, our results support a recent study employing dynamic niche model food webs Riede et al. (2011a). Hence, prior topological approaches may have overemphasized the dominant role of connectance in driving food-web sensitivity to secondary

extinctions. Instead, our results suggest that diversity may be far more important when top-down and other indirect effects mediated by dynamics are accounted for.

At the species level, we found that primary extinctions of larger species are more likely to trigger a cascade of secondary extinctions than primary extinctions of smaller species. This is consistent with recent analyses, showing that high predator-prey body-mass ratios provide food-web stability (Brose et al., 2006b; Otto et al., 2007) and large species have the strongest interaction strengths in complex food webs (Berlow et al., 2009). Corroborating prior analyses of small modules (Borrvall et al., 2000; Ebenman et al., 2004), we found that the extinction risk is highest following primary extinction of high trophic level species. This supports . earlier findings that losses of large top predators trigger secondary extinctions via trophic cascades in theoretical (Bascompte, 2005) and empirical studies (Borer et al., 2005). In natural ecosystems, the loss of large top predators can severely modify the structure, composition, and functioning of basal plant communities (Beschta and Ripple, 2009). Our result contrasts prior purely topological studies emphasizing the detrimental effects of extinctions at low trophic positions that cut off other species from their energy source at the base of the food web Dunne et al. (2002); Srinivasan et al. (2007); Allesina et al. (2009) . However, strong effects of top species extinctions can only emerge in dynamic models such as ours that can yield trophic cascades and indirect effects. Critically, large species are particularly prone to extinction due to human induced chances in their environment (e.g. (Jackson et al., 2001; Cardillo, 2005; Sergio et al., 2008; de Visser et al., 2011)). Our results suggest that preventing avalanches of secondary extinctions requires protecting these large top predators.

Interestingly, our results suggest that the extinction risk increases with increasing variability of prey vulnerability. Again, this stresses the importance of top-down cascades in driving secondary extinctions. The strength of these trophic cascades is diminished with increasing vulnerability of the prey, because other consumers exert compensating effects (Polis and Strong, 1996).

6.6 Conclusions

Our study has stressed the importance of top-down cascades and indirect effects in causing secondary extinctions. Ultimately, these effects may further propagate through food-web networks and lead to severe effects on ecosystem processes such as primary production. The potential for such effects make it a continuing research challenge to integrate knowledge of complex food-web structures (Dunne, 2006), allometric population dynamics (Yodzis and Innes, 1992) and risks of primary extinctions (Petchey, 2004) to produce a general framework for predicting the consequences of species loss in multitrophic systems on ecosystem functioning (Thebault et al., 2007). Contrasting earlier studies, our approach goes beyond well-known limitations of both dynamic models of small food-web modules (Pimm, 1980; Borrvall et al., 2000; Ebenman et al., 2004; Thebault et al., 2007) and structural models of complex food webs (Solè and Montoya, 2001; Dunne et al., 2002; Allesina et al., 2009) that lack dynamics. Our results suggest that global food-web parameters as well as individual species traits affect the risk of secondary extinctions after species loss. Overall, our analyses suggest that food webs with low diversity and large differences in the distribution of predation risk across resource species are most sensitive to be affected by primary extinctions. Hence, lower diversity levels caused by extinctions may reduce food-web robustness against secondary extinctions, which implies that extinction may become a self-accelerating process when natural communities drop below critical diversity levels. Moreover, the losses of large-bodied consumer at high

trophic levels are much more likely to cause secondary extinctions than loss of small-bodied consumers at low trophic levels. Conservation priorities should be put on protecting these large top predators that may balance the complex interaction networks of natural ecosystems.

6.7 Acknowledgements

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7 GENERAL DISCUSSION

7.1 Topology

This thesis addresses the questions how species and network characteristics are distributed in food webs and how they influence the stability of complex food webs. The innovation of this thesis is the combination of topological and dynamic approaches to identify traits contributing to the structure and stability The entirely new dataset used includes 133 highly resolved empirical food webs including 9467 species (Table 1.1) across 5 ecosystem-types (marine,estuary, stream, lake, terrestrial) with information about feeding interactions and body masses. This dataset allows to detect general patterns of food web characteristics and species traits on a global scale and to identify differences between ecosystem-types. Pioneers in ecology used simple food webs to find generalities in structure, species interactions (Elton, 1927; MacArthur, 1955), and energy transfer (Lindeman, 1942). In this thesis I revisited some ecological concepts to explore topological generalities across food webs and to investigate the impact of topological characteristics on secondary extinctions. In general, this thesis can be divided into two sections. The first section is about topological relationships (Chapter 2–4) and in the second section the focus is on secondary extinctions in food webs using a bioenergetic–dynamical population–model (Chapter 5–6). One challenge in ecology is to understand mechanisms driving species interactions and the stability of food webs. Early studies often used data with low resolution (Ings et al., 2009), the novelty of this thesis is the use of a large dataset of high resolved food webs with this dataset I investigate structural differences between ecosystems (marine, estuary, stream, lake, terrestrial)

In his seminal work, May showed that the stability of food webs decreases with an increase in diversity (number of species) (May, 1972). This theoretical prediction was inconsistent with empirical observations, as the prediction implicates that the product of connectance and species number are constant. Complexity is often found in natural ecosystems, many studies have shown that in diverse food webs species are often highly connected with each other (Polis, 1991; Williams and Martinez, 2000; Ings et al., 2009). While the link–species scaling law predicts constancy of the number of links per species (Cohen and Newman, 1985), the alternative constant connectance hypothesis holds that food–web connectance should be constant (Martinez, 1992).To evaluate the scaling of species versus connectance to hypotheses have been developed the ”link–scaling law” (Cohen and Newman, 1985; Briand and Cohen, 1984) where the connectance decreases exponentially with increasing species richness, as result of constancy of the number of links per species. In contrast to the ”link–scaling law” is the ”constant–connectance hypothesis” (Martinez, 1992) supposed that connectance is constant with increasing species richness.

In chapter 2 of this thesis, I tested the relationship between diversity and connectance in a large dataset. I found power–law scaling relationships with diversity and complexity (connectance) for most of the food webs. I observed that link richness and the number of links per species increase with increasing diversity, which is in contrast to the ”constant connectance hypothesis” and to the ”link–scaling law”. Furthermore, I found some interesting differences in the scaling of topological properties with diversity and connectance across different ecosystem-types (e.g. omnivory, mean short weighted trophic level). These results illustrate the lack of universal scale–independent constants in natural food webs.

Many food web traits (e.g. connectance, degree distributions, body mass) have been used to predict

(a) Marine (b) Stream (c) Lake (d) Terrestrial

Figure 7.1: Pictures of four ecosystem types a) Tasman Sea (Paparoa-Nationalpark, New Zealand), b)Rainbach (Wildgerlostal, Austria), c) mountain pond in upper Engadin (Switzerland) d) Laurel forest (Tenerife).

the structure of food webs. In contrast to other biological networks, which are well predictable by preferential-attachment algorithms (Barabasi and Albert, 1999), food web structure follows more complex models (Allesina et al., 2008; Williams and Martinez, 2000). Several topological parameters such as connectance (Williams and Martinez, 2000), phylogenetic constraints on feeding interactions (Cattin et al., 2004) and exponential degree distributions (Stouffer et al., 2005) have been used to predict food web structure. However, all these models used stochastic methods to predict the structure while ignoring parameters correlated with species identity such as body mass or predator interference term. Other research areas used species correlated parameters to investigate interactions between species. Body mass has often been used to explain feeding interaction between species (Beckerman et al., 2006; Brose, 2010a; Brose et al., 2006a; Woodward et al., 2005a; Vucic-Pestic et al., 2010). Some novel models employ body masses to predict food web structure in a deterministic way (Petchey et al., 2008; Allesina, 2011).

The need for integrating body mass into topological scaling is getting obvious when investigating general structural properties in food webs. This interrelationship is described by allometric degree distributions, that describe the distribution number of species' predators (vulnerability) and/or the number of prey (generality) with increasing body mass. Some general trends in ecosystems are identified in Chapter 3: body mass is roughly log-normally distributed, cumulative degree distributions are mainly exponential and increasing body masses are negative correlated with vulnerability and positive correlated with generality. The results generalize previous findings (Camacho et al., 2002a; Dunne et al., 2002; Otto et al., 2007) across all ecosystems investigated here. Consistent with prior studies (Dunne et al., 2002), my results show the differences between food webs and other biological networks. All current food web models share some common features: (1) species are hierarchically ordered according to a set of arbitrary niche values (Cattin et al., 2004) (2) each species has a specifc exponentially decaying probability of preying on a given fraction of the species with lower niche values (Stouffer et al., 2005). My results suggest that body mass might be a good proxy for an ordered set of niche values. Allometric degree distributions are crucially important for the stability of food webs, as shown in a prior study where topological randomizations only reduced persistence if allometric degree distributions are disrupted (Otto et al., 2007). Comparing this theoretical observation of food-web stability with my results shows that stability might

be a more general property in natural food webs.

The distribution of body masses across trophic levels in food webs has been identified as being important for stability (Brose et al., 2006a; Otto et al., 2007). Early ecologists have developed some paradigms in respect to the distribution of body masses. In his work, Elton (1927) formulated some fundamental concepts of interactions between species. He suggested that: (i) predators are in general larger than their prey, (ii) predator body mass increases along a food chain, and (iii) the body mass ratio between consumer and resource is invariant with trophic level of the consumer. Later studies have found a general scaling between predator and prey mass as predator mass and prey mass are positively correlated (Cohen et al., 1993; Brose, 2003a; Bersier and Kehrli, 2008) and predator mass increases with trophic level (Layman et al., 2005), (but see (Jennings et al., 2001) for a contrasting relationship). In chapter 4 of this thesis, I address Elton's concepts. In accordance with Elton, I found that predator mass is positively correlated with prey mass and that predator mass increases with trophic level. However, I found for most of the metabolic predator types (invertebrates, ecotherm- and endotherm vertebrates) and across ecosystems (marine, streams, lakes and terrestrial) a decreasing predator–prey body–mass ratio with increasing trophic level. This result seems to be contradictory to Elton, but can be justified by our usage of a large food web data set, whereas Elton's idea was based on only one food web.
In the first part of this thesis, I found some generalities in food webs: using the novel dataset I found that diversity and connectance increase with a power law relationship. Furthermore, I found the allometric cumulative degree distributions are mainly exponential with increasing body mass. On the scaling of body masses related traits with trophic level I found that predator body mass increases with trophic level while the ratio decreases with trophic level. All these results suggest a clear pattern in the structure of complex food webs. However, some outliers indicate the challenge of identifying generalities in complex food webs. One example for the are streams, which show in all studies interesting deviations form the global pattern. One reason for this could be physical effects generated by flowing water and hydro logic disturbance, these forces influence the size structure of stream communities (Townsend, 1989; Townsend and Scarsbrook, 1997; Snook and Milner, 2002). One topological trait that has been identified as different in stream food webs in comparison to other ecosystems is omnivory. Omnivory is a recurrent feature of food webs, but it is rare in stream systems (Thompson et al., 2007). However, further studies should address the mechanisms which cause these topological differences in ecosystems. Interestingly, streams show the same response to the loss of species as other ecosystems (chapter 6).
The dataset I used would benefit on more data of highly resolved marine, terrestrial and soil food webs, to increase the general evidence. Further work could fill this gap and increase the impact of novel food web models.

7.1.1 Stability

In the second part of this thesis (Chapter 5–6), I focused on the stability of complex food webs. Today, regarding human impact to ecosystems and species extinctions world wide, stability of complex food webs becomes very important. Global warming, changing atmospheric conditions, habitat fragmentation, pollution, overfishing, over-hunting, invasive species, pathogens, and deforestation are anthropogenic ef-

fects (Barnosky et al., 2011; Pereira et al., 2010). Especially, large species are particularly threatened with extinctions due to human induced changes in their environment (Petchey et al., 1999; Jackson et al., 2001; Duffy, 2002; Petchey, 2004; Sergio et al., 2008; de Visser et al., 2011).
Due to the complexity of a food web the exploration of mechanisms in food webs is a very difficult process. In a food web of intermediate size with 100 species and 5000 interactions amongst them it is impossible to study the consequences of a single species loss for other species in the food web with empirical methods. To solve this problem theoretical modelling became the most important tool in food web ecology. This is aided by the improvements of computational power of modern data processors. Modern computational models use empirically measured parameters to simulate natural conditions. The probably most important recent advantage in theoretical ecology was the consideration of species body masses in dynamic food web models (Yodzis and Innes, 1992; Brose et al., 2006a; Neutel et al., 2007; Otto et al., 2007).

In a more general approach, using a bioenergetic model (Yodzis and Innes, 1992), I tested the impact of several global food web properties, on the stability of 1000 niche model food webs (Chapter 5).The aim of this was to identify the impact of different parameters on food-web stability considering prior studies which have focused on the effect of the network topology on a food web's robustness (Dunne et al., 2002; Gravel et al., 2011).
In this study, I found nine effects to be significantly correlated with robustness: two topological traits (diversity and maximum trophic level), the hill coefficient as a dynamic property and six body mass correlated relationships (the intercept of the linkedness–body mass relationship, the slope and intercept of the generality–body mass relationship, intercept of the vulnerability– body mass relationship and slope and intercept of the abundance– body mass relationship). Within this set, three parameters contribute most to stability: the relationship between abundance and mean population body mass, the Hill exponent and the number of species. I found that the Hill coefficient is increasing the robustness of food webs, which corroborated prior studies that have shown that a small increases of the Hill coefficient stabilizes population dynamics (Williams and Martinez, 2004b; Rall et al., 2008) yielding to a lower species extinction risk.
In empirical food webs (Chapter 6), I identified species diversity and the standard deviation of vulnerability as significantly correlated with food web robustness. Furthermore, I have found that robustness increases with increasing species diversity and decreases with an increasing standard deviation of vulnerability at the food-web level. Beside the results on general topology, I identified the impact of species traits on robustness. I found that the extinctions of large top predators causes most secondary extinctions in food webs. The tragedy of this is that in empirical studies large-bodied species of high trophic level often have the highest extinction risk (McKinney, 1997; Pauly et al., 1998; Purvis and Hector, 2000) By reviewing the impact of food web and species traits to secondary extinctions in the chapter 5 and 6 I found some interesting similarities of simulations with empirical networks to simulations with niche model networks. In both studies, robustness is related to diversity, trophic level and body mass. This underpins the importance of body mass for the stability of complex food webs as found in prior studies (Otto et al., 2007; Brose et al., 2006b; Emmerson and Raffaelli, 2004). Surprisingly, the impact of connectance has not been identified to be important for food web robustness in both studies. This result stands in contrast to prior observations (Dunne et al., 2002; Gravel et al., 2011), but can be explained by the application

of different methods, while prior studies have used topological approaches for their predictions (Borrvall et al., 2000; Dunne et al., 2002; Gravel et al., 2011) I used a combination of a dynamical bioenergetic model (Yodzis and Innes, 1992; Brose et al., 2006b) niche model food webs (Williams and Martinez, 2000) or empirical food web structures to explore the consequences of species extinctions. Instead of connectance I identified other structural properties related to the link structure as significant important for stability such as the slope of the generality–body mass relationship (Chapter 5) or the standard deviation of vulnerability (Chapter 6).

"Few problems are less recognized, but more important than, the accelerating disappearance of the earth's biological resources. In pushing other species to extinction, humanity is busy sawing off the limb on which it is perched."

(Paul Ehrlich)

7.1.2 Conclusion and perspective

Overall, this thesis shows how complex food webs are structured and how network and species characteristics contribute to the stability of complex food webs. I found some interesting generalities such as the power law relationship between diversity and connectance or the exponential allometric degree distribution. These generalities of food web properties can be used to develop new of food web models that predict structure or dynamics (Hartvig, 2011).
In particular, this includes the scaling of trophic position with predator mass or predator prey body mass ratio, because as shown in the simulation section of this thesis species body masses play an important role in stabilising the dynamics of complex food webs. Body mass has been used in former studies to predict the topological structure of food webs (Petchey et al., 2008; Allesina, 2011), with the results of this thesis these models can be modified to increase the prediction rate of deterministic models. One application of this kind model models could be the estimation of possible feeding interactions in complex ecosystems.
Important differences between streams and other ecosystems have been identified, which includes deviations in topology and species body size relationships. One jigsaw piece to understand the nature of biodiversity would be the investigation of interactions between different ecosystems, such as energy flow, shared resources or seasonal changes in species composition. One important example for interactions between streams and terrestrial ecosystems is the importance of terrestrial invertebrates in the gut content of predatory fish (up to 80% (*personal communication Katrin Layer)*) . Consideration of species and network interactions between ecosystems would lead to a better understanding of natural systems and with this a better understanding of how species loss will affected global biodiversity.

Bibliography

Albert, R. and Barabási, A.-L. (2002). Statistical mechanics of complex networks. *Reviews of Modern Physics*, 74:47–97.

Allesina, S. (2011). Predicting trophic relations in ecological networks: a test of the allometric diet breadth model. *Journal of Theoretical Biology*, 279:161–168.

Allesina, S., Alonso, D., and Pascual, M. (2008). A general model for food web structure. *Science*, 320(5876):658–661.

Allesina, S. and Bodini, A. (2004). Who dominates whom in the ecosystem? energy flow bottlenecks and cascading extinctions. *Journal Of Theoretical Biolology*, 230:351–358.

Allesina, S., Bodini, A., and Pascual, M. (2009). Functional links and robustness in food webs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1524):1701.

Baeta, A., Valiela, I., Rossi, F., Pinto, R., Richard, P., Niquil, N., and Marques, J. C. (2009). Eutrophication and trophic structure in response to the presence of the eelgrass zostera noltii. *Marine Biology*, 156:2107–2120.

Baird, D. and Ulanowicz, R. E. (1989). The seasonal dynamics of the chesapeake bay ecosystem. *Ecological Monographs*, 59(4):329–329.

Banasek-Richter, C. (2004). Sampling effects and the robustness of quantitative and qualitative food-web descriptors. *Journal of Theoretical Biology*, 226(1):23–32.

Banasek-Richter, C., Cattin Blandenier, M.-F., and Bersier, L. F. (2005). Food web structure: from scale invariance to scale dependence, and back again? In *Dynamic Food Webs*, pages 48–55. Academic Press, Burlington, USA.

Barabasi, A. and Albert, R. (1999). Emergence of scaling in random networks. *Science*, 286:509–512.

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(7336):51–57.

Bascompte, J. (2005). Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences*, 102(15):5443–5447.

Beckerman, A. P., Petchey, O. L., and Warren, P. H. (2006). Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences*, 103(37):13745–13749.

Beddington, J. R. (1975). Mutual interference between parasites or predators and its effect on searching efficiency. *The Journal of Animal Ecology*, 44(1):331–331.

Berlow, E., Brose, U., and Martinez, M. D. (2008). The goldilock factor in food webs. *Proceedings Of The American Society*, 105:4191–4196.

Berlow, E. L. (1999). Strong effects of weak interactions in ecological communities. *Nature*, 398(6725):330–334.

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(1):187–191.

Bersier, L. and Kehrli, P. (2008). The signature of phylogenetic constraints on food-web structure. *Ecological Complexity*, 5:132–139.

Bersier, L.-F., Banasek-Richter, C., and Cattin, M.-F. (2002). Quantitative descriptors of food-web matrices. *Ecology*, 83(9):2394–2407.

Bersier, L.-F., Dixon, P., and Sugihara, G. (1999). Scale-invariant of scale-dependent behaviour of the link density propery in food webs: A matter of sampling effort? *American Naturalist*, 153(6):676–682.

Beschta, R. L. and Ripple, W. J. (2009). Large predators and trophic cascades in terrestrial ecosystems of the western united states. *Biological Conservation*, 142(11):2401–2414.

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(7):590 – 599.

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 strenght of a trophic cascade? *Ecology*, 86(2):528–537.

Borrvall, C., Ebenman, B., and Tomas Jonsson, T. J. (2000). Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters*, 3(2):131–136.

Bourassa, N. and Morin, A. (1995). Relationships between size structure of invertebrate assemblages and trophy and substrate composition in streams. *Journal of the North American Benthological Society*, 14:393–403.

Briand, F. and Cohen, J. E. (1984). Community food webs have scale-invariant structure. *Nature*, 307(5948):264–267.

Brose, U. (2003a). Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? *Oecologia*, 135(3):407–413. Times Cited: 2 Article English Cited References Count: 26 684gx.

Brose, U. (2003b). Regional diversity of temporary wetland carabid beetle communities: a matter of landscape features or cultivation intensity? *Agriculture Ecosystems & Environment*, 98(1-3):163–167. Times Cited: 4 Article English Cited References Count: 13 726ce.

Brose, U. (2008). Complex food webs prevent competitive exclusion among producer species. *Proceedings of the Royal Society B: Biological Sciences*, 275(1650):2507.

Brose, U. (2010a). Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Functional Ecology*, 24(1):28–34.

Brose, U. (2010b). Improving nature conservancy strategies by ecological network theory. *Basic and Applied Ecology*, 11(1):1–5.

Brose, U., Cushing, L., Berlow, E. L., Jonsson, T., Banasek-Richter, C., Bersier, L. F., Blanchard, J. L., Brey, T., Carpenter, S. R., Cattin Blandenier, M.-F., Cohen, J. E., Dawah, H. A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Knapp, R. A., Ledger, M. E., Memmott, J., Mintenbeck, K., Pinnegar, J. K., Rall, B. C., Rayner, T., Ruess, L., Ulrich, W., Warren, P., Williams, R. J., Woodward, G., Yodzis, P., and Martinez, N. D. (2005). Body sizes of consumers and their resources. *Ecology*, 86(9):2545.

Brose, U., Ehnes, R., Rall, B., Vucic-Pestic, O., Berlow, E., and Scheu, S. (2008). Foraging theory predicts predator–prey energy fluxes. *Journal of Animal Ecology*, 77(5):1072–1078.

Brose, U., Jonsson, T., Berlow, E. L., Warren, P., Banasek-Richter, C., Bersier, L. F., Blanchard, J. L., Brey, T., Carpenter, S. R., Cattin Blandenier, M.-F., 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., Reuman, D. C., Ruess, L., Ulrich, W., Williams, R. J., Woodward, G., and Cohen, J. E. (2006a). Consumer-resource body-size relationships in natural food webs. *Ecology*, 87(10):2411–2417.

Brose, U. and Martinez, N. D. (2004). Estimating the richness of species with variable mobility. *Oikos*, 105(2):292–300. Times Cited: 0 Article English Cited References Count: 27 805rj.

Brose, U., Williams, R. J., and Martinez, N. D. (2006b). 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(7):1771–1789.

Burness, G. P., Diamond, J., and Flannery, T. (2001). Dinosaurs, dragons, and dwarfs: the evolution of maximal body size. *Proc Natl Acad Sci U S A*, 98(25):14518–14523.

Camacho, J., Guimerà, R., and Amaral, L. A. N. (2002a). Analytical solution of a model for complex food webs. *Phys Rev E Stat Nonlin Soft Matter Phys*, 65(3 Pt 1):030901.

Camacho, J., GuimerÃ , R., and Nunes Amaral, L. (2002b). Robust patterns in food web structure. *Phys. Rev. Lett.*, 88(22):–.

Cardillo, M. (2005). Multiple causes of high extinction risk in large mammal species. *Science*, 309(5738):1239–1241.

Cattin, B. M.-F. (2004). *Food web ecology: models and applications to conservation.* PhD thesis, University of Neuchatel (Switzerland).

Cattin, M.-F., Bersier, L.-F., Banasek-Richter, C., Baltensperger, R., and Gabriel, J.-P. (2004). Phylogenetic constraints and adaptation explain food-web structure. *Nature*, 427(6977):835–839.

Christian, R & Luczkovic, J. (1999). Organizing and understanding a winter's seagrass food web network through effective trophic levels. *Ecological Modelling*, 117(1):99–124.

Cohen, J. (1978). *Food Webs and Niche Space*. Princeton University Press.

Cohen, J. (1989). *Ecologists Co–operative Web Bank (ECOWebTM).*

Cohen, J., Jonsson, T., and Carpenter, S. (2003). Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences*, 100(4):1781.

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 B: Biological Sciences*, 224:421–448.

Cohen, J. E., Pimm, S. L., Yodzis, P., and Saldaña, J. (1993). Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology*, 62(1):pp. 67–78.

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(52):22335–22340.

Cole, J. J., Carpenter, S. R., Pace, M. L., Van de Bogert, M. C., Kitchell, J. L., and Hodgson, J. R. (2006). Differential support of lake food webs by three types of terrestrial organic carbon. *Ecol Letters*, 9(5):558–568.

Costa, G. C. (2009). Predator size, prey size, and dietary niche breadth relationships in marine predators. *Ecology*, 90(7):2014–2019.

Crawley, M. J. (2007). *The R Book.* John Wiley & Sons, Ltd, Chichester, UK.

Curtsdotter, A., Binzer, A., Brose, U., Eklöf, A., Riede, J., de Castro, F., Ebenman, B., Thierry, A., and Rall, B. (2011). Species traits affecting robustness to secondary extinctions: sequential deletions in static and dynamic food webs. *Basic and Applied Ecology*, 12:571–580.

Dale, M. (2005). *Spatial analysis: a guide for ecologists*. Cambridge University Press.

Dale, M. and Fortin, M. (2010). From graphs to spatial graphs. *Annual Review of Ecology, Evolution, and Systematics*, 41:21–38.

Damuth, J. (1987). Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. *Biological Journal of the Linnean Society*, 31(3):193–246.

Damuth, J. (2007). A macroevolutionary explanation for energy equivalence in the scaling of body size and population density. *The American naturalist*, 169(5):621.

de Ruiter, P. C. (2005). Food web ecology: Playing jenga and beyond. *Science*, 309(5731):68–71.

de Visser, S. N., Freymann, B. P., and Olff, H. (2011). The serengeti food web: empirical quantification and analysis of topological changes under increasing human impact. *Journal of Animal Ecology*, 80(2):484–494.

DeAngelis, D. L., Goldstein, R. A., and O'Neill, R. V. (1975). A model for trophic interaction. *Ecology*, 56(4):881–881.

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

Duffy, J. E. (2002). Biodiversity and ecosystem function: the consumer connection. *Oikos*, 99(2):201–219.

Dunne, J. (2006). *Ecological Networks: Linking Structure to Dynamics in Food Webs*. Oxford University Press.

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

Dunne, J. A., Williams, R. J., and Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol Letters*, 5(4):558–567.

Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., and Erwin, D. H. (2008). Compilation and network analyses of cambrian food webs. *Plos Biology*, 6(4):e102.

Ebenman, B. and Jonsson, T. (2005). Using community viability analysis to identify fragile systems and keystone species. *Trends in Ecology & Evolution*, 20(10):568–575.

Ebenman, B., Law, R., and Borrvall, C. (2004). Community viability analysis: The response of ecological communities to species loss. *Ecology*, 85(9):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. (2009). *Species extinctions in food webs: local and regional processes*. Department of Physics, Chemistry and Biology, Linköping University.

Eklöf, A. and Ebenman, B. (2006). Species loss and secondary extinctions in simple and complex model communities. *Journal of animal ecology*, 75(1):239–246.

Elton, C. (1933). *Exploring the animal world*. G. Allen & Unwin, London.

Elton, C. and Nicholson, M. (1942). The ten-year cycle in numbers of lynx in canada. *Journal of Animal Ecology*, 11:215–244.

Elton, C. S. (1927). *Animal ecology*. University of Chicago Press, Chicago.

Emmerson, M. and Raffaelli, D. (2004). Predator–prey body size, interaction strength and the stability of a real food web. *Journal of Animal Ecology*, 73(3):399–409.

Enquist, B. J., West, G. B., Charnov, E. L., and Brown, J. H. (1999). Allometric scaling of production and life-history variation in vascular plants. *Nature*, 401(6813):907–911.

Euler, L. (1735). Solvtio promblematis ad geometriam sitvs. *Commentarii academiae scientiarum Petropolitanae 8*, pages 128–140.

Fagan, W. F. and Hurd, L. E. (1994). Hatch density variation of a generalist arthropod predator - population consequences and community impact. *Ecology*, 75(7):2022–2032.

Forbes, S. (1887). The lake as a microcosm. *Bulletin of the Illinois State Labroratory of Natural History*, 1:1–17.

Garcia, L. V. (2004). Escaping the bonferroni iron claw in ecological studies. *Oikos*, 105(3):657–663.

Gardner, M. and Ashby, W. (1970). Connectance of large dynamic (cybernetic) systems: critical values for stability. *Nature*, 288:784.

Garlaschelli, D., Caldarelli, G., and Pietronero, L. (2003). Universal scaling relations in food webs. *Nature*, 423(6936):165–168.

Goldwasser, L. and Roughgarden, J. (1993). Construction and analysis of a large caribbean food web. *Ecology*, 74(4):1216–1233.

Goldwasser, L. and Roughgarden, J. (1997). Sampling effects and the estimation of food-web properties. *Ecology*, 78(1):41–54.

Gravel, D., Canard, E., Guichard, F., and Mouquet, N. (2011). Persistence increases with diversity and connectance in trophic metacommunities. *PLoS ONE*, 6(5):e19374–e19374.

Hairston, N., Smith, F. E., and Slobodkin, L. B. (1960). Community structure, population control, and competition. *The American Naturalist*, 879:421–425.

Hall, S. and Raffaelli, D. (1991). Food-web patterns: Lessons from a species-rich web. *Journal of Animal Ecology*, 60(3):823–841.

Hall, S. J. and Raffaelli, D. (1993). Food webs - theory and reality. *Advances In Ecological Research, Vol 24*, 24:187–239.

Harary, F. (1969). *Graph Theory*. Reading, MA: Addison-Wesley.

Harper-Smith, S., Berlow, E., Knapp, R., Williams, R., and Martinez, N. (2006). Communicating ecology through food websVisualizing and quantifying the effects of stocking alpine lakes with trout. In *Dynamic Food Webs*, pages 407–423. Elsevier.

Harrison, K. (2003). *Effects of land use and dams on stream food web ecology in Santa Clara Valleyhall*. PhD thesis, San Francisco State University.

Hartvig, M. (2011). *2011*. PhD thesis, Department of Biology Lund University.

Havens, K. (1992). Scale and structure in natural food webs. *Science*, 257(5073):1107–1109.

Heymans, J. J., Ulanowicz, R. E., and Bondavalli, C. (2002). Network analysis of the south florida everglades graminoid marshes and comparison with nearby cypress ecosystems. *Ecological Modelling*, 149(1-2):5–23.

Hildrew, A. G. (2009). Chapter 4 sustained research on stream CommunitiesA model system and the comparative approach. In *Advances in Ecological Research*, volume 41, pages 175–312. Elsevier.

Hodkinson, I. D. and Coulson, S. J. (2004). Are high arctic terrestrial food chains really that simple? the bear island food web revisited. *Oikos*, 106(2):427–431.

Holling, C. (1959). Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, 91:385–398.

Hughes, J. B., Daily, G. C., and Ehrlich, P. R. (1997). Population diversity: it's extent and extinction. *Science*, 278:689–692.

Ings, T. C., Montoya, J. M., Bascompte, J., Bluethgen, N., Brown, L., Dormann, C. F., Edwards, F., Figueroa, D., Jacob, U., Jones, J. I., Lauridsen, R. B., Ledger, M. E., Lewis, H. M., Olesen, J. M., van Veen, F. J. F., Warren, P. H., and Woodward, G. (2009). Ecological networks - beyond food webs. *Journal of Animal Ecology*, 78(1):253–269.

Isobe, T., Feigelson, E. D., Akritas, M. G., and Babu, G. J. (1990). Linear regression in astronomy. *The Astrophysical Journal*, 364:104.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradshaw, 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*, 293:629–638.

Jacob, U., Thierry, A., Brose, U., Arntz, W. E., Berg, S., Brey, T., Fetzer, I., Jonsson, T., Mintenbeck, K., Möllmann, C., Petchey, O. L., Riede, J. O., and Dunne, J. A. (2011). The role of body size in complex food webs. In *Advances in Ecological Research*, volume 45, pages 181–223. Elsevier.

Jennings, S. and Mackinson, S. (2003). Abundance–body mass relationships in size-structured food webs. *Ecology Letters*, 6(11):971–974.

Jennings, S., Pinnegar, J. K., Polunin, N. V. C., and Boon, T. W. (2001). Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology*, 70(6):934–944.

Jeschke, J.M. and Kopp, M. R. (2002). Predator functional responses: discriminating between handling and digesting prey. *Ecological Monographs*, 72:95112.

Jonsson and Ebenman (1998). Effects of predator-prey body size ratios on the stability of food chains. *Journal Of Theoretical Biolology*, 193(3):407–417.

Jonsson, T., Cohen, J. E., and Carpenter, S. R. (2005). Food webs, body size, and species abundance in ecological community description. In Caswell, H., editor, *Food Webs: From Connectivity to Energetics*, volume 36 of *Advances in Ecological Research*, pages 1 – 84. Academic Press.

Keitt, T. H. (1997). Stability and complexity on a lattice: coexistence of species in an individual-based food web model. *Ecological Modelling*, 102(2-3):243–258.

King, R. A., Read, D. S., Traugott, M., and Symondson, W. O. C. (2008). Molecular analysis of predation: a review of best practice for dna-based approaches. *Molecular Ecology*, 17(4):947–963.

Kondoh, M. (2003). Foraging adaptation and the relationship between food-web complexity and stability. *Science*, 299(5611):1388.

Kratina, P., Vos, M., Bateman, A., and Anholt, B. R. (2008). Functional responses modified by predator density. *Oecologia*, 159(2):425–433.

Lafferty, K. D., Dobson, A. P., and Kuris, A. M. (2006). Parasites dominate food web links. *Proceedings of the National Academy of Sciences of the United States of America*, 103(30):11211–11216.

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

Lange, M. (2005). Ecological laws: what would they be and why would they matter? *Oikos*, 110(2):394–403.

Layer, K., Riede, J. O., Hildrew, A. G., and Woodward, G. (2010). Food web structure and stability in 20 streams across a wide ph gradient. *Advances In Ecological Research: Ecological Networks*, 42:265–299.

Layman, C. A., Winemiller, K. O., Arrington, D. A., and Jepsen, D. B. (2005). Body size and trophic position in a divers tropical food web. *Ecology*, 86:2530–2535.

Levine, S. (1980). Several measures of trophic structure applicable to complex food webs. *Journal of Theoretical Biology*, 83:195–207.

Lindeman, R. (1942). The trophic-dynamic aspects of ecology. *Ecology*, 23:399–418.

Link, J. (2002). Does food web theory work for marine ecosystems? *Marine Ecology–progress Series*, 230:1–9.

Loeuille, N. and Loreau, M. (2004). Nutrient enrichment and food chains: can evolution buffer top-down control? *Theor Popul Biol*, 65(3):285–298.

Loeuille, N. and Loreau, M. (2005). Evolutionary emergence of size-structured food webs. *Proceedings of the National Academy of Sciences of the United States of America*, 102(16):5761.

Lotka, L. (1925). *Elements of physical biology*. Willams & Wilkins, Baltimor.

Luck, G. W., Daily, G. C., and Ehrlich, P. R. (2003). Population diversity and ecosystem services. *Trends in Ecology & Evolution*, 18(7):331–336.

MacArthur, R. H. (1955). Fluctuations of animal populations, and a measure of community stability. *Ecology*, 36:533–536.

Martinez, M. D. (1994). Scale-dependent constraints on food-web structure. *The American Naturalist*, 144:935–953.

Martinez, N. D. (1991). Artifacts or attributes - effects of resolution on the littlerock lake food web. *Ecological Monographs*, 61(4):367–392.

Martinez, N. D. (1992). Constant connectance in community food webs. *American Naturalist*, 139(6):1208–1218.

Martinez, N. D. (1993a). Effect of scale on food web structure. *Science*, 260:242–243.

Martinez, N. D. (1993b). Effects of resolution on food web structure. *Oikos*, 66(3):403–412.

Martinez, N. D., Hawkins, B. A., Dawah, H. A., and Feifarek, B. P. (1999). Effects of sampling effort on characterization of food-web structure. *Ecology*, 80(3):1044–1055.

May, R. (1973). *Stability and complexity in model ecosystems*. Princeton University Press.

May, R. M. (1972). Will a large complex system be stable? *Nature*, 238(5364):413–414.

McCann, K., Hastings, A., and Huxel, G. R. (1998). Weak trophic interactions and the balance of nature. *Nature*, 395(6704):794–798.

McCann, K. S. (2000). The diversity–stability debate. *Nature*, 405:228–233.

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

McLaughlin, O. B., Jonsson, T., and Emmerson, M. C. (2010). Temporal variability in predator-prey relationships of a forest floor food web. *Advances In Ecological Research: Ecological Networks, Vol 42*, pages 171–264.

Memmott, J., Martinez, N., and Cohen, J. (2000). Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. *Journal of Animal Ecology*, 69:1–15.

Montoya, J. M., Pimm, S. L., and Sole, R. V. (2006). Ecological networks and their fragility. *Nature*, 442(7100):259–264.

Montoya, J. M. and Sole, R. V. (2002). Small world patterns in food webs. *Journal of Theoretical Biology*, 214:405–412.

Montoya, J. M. and Sole, R. V. (2003). Topological properties of food webs: from real data to community assembly models. *Oikos*, 102(3):614–622.

Moran, M. D. (2003). Arguments for rejecting the sequential bonferroni in ecological studies. *Oikos*, 100(2):403–405.

Navarrete, S. A. and Berlow, E. L. (2006). Variable interaction strengths stabilize marine community pattern. *Ecol Lett*, 9(5):526–536.

Nee, S., Read, A., Greenwood, J., and Harvey, P. (1991). The relationship between abundance and body size in british birds. *nature*, pages 312–313.

Neubert, M. G., Blumenshine, S. C., Duplisea, D. E., Jonsson, T., and Rashleigh, B. (2000). Body size and food web structure: Testing the equiprobability assumption of the cascade model. *Oecologia*, 123:241–251.

Neutel, A.-M., Heesterbeek, J. A. P., and Ruiter, P. C. D. (2002). Stability in real food webs: weak links in long loops. *Science*, 296(5570):1120–1123.

Neutel, A.-M., Heesterbeek, J. A. P., van de Koppel, J., Hoenderboom, G., Vos, A., Kaldeway, C., Berendse, F., and de Ruiter, P. C. (2007). Reconciling complexity with stability in naturally assembling food webs. *Nature*, 449(7162):599–602.

Odum, E. (1953). *Fundamental of ecology*. Philadelphia: Saunders.

O'Gorman, E. J. and Emmerson, M. C. (2009). Perturbations to trophic interactions and the stability of complex food webs. *Proceedings of the National Academy of Sciences*, 106(32):13393–13398.

O'Gorman, E. J., Jacob, U., Jonsson, T., and Emmerson, M. C. (2010). Interaction strength, food web topology and the relative importance of species in food webs. *Journal Of Animal Ecology*, 79(3):682–692.

O'Hara, R. B. (2005). The anarchist's guide to ecological theory. or, we don't need no stinkin' laws. *Oikos*, 110(2):390–393.

Olesen, J. M., Dupont, Y. L., O'Gorman, E., Ings, T. C., Layer, K., Melián, C. J., Trøjelsgaard, K., Pichler, D. E., Rasmussen, C., and Woodward, G. (2010). From broadstone to zackenberg: Space, time and hierarchies in ecological networks. In Woodward, G., editor, *Ecological Networks*, volume 42 of *Advances in Ecological Research*, pages 1 – 69. Academic Press.

Opitz, S. (1996). Trophic interactions in caribbean coral reefs. Technical report, ICLARM.

Otto, S. B., Rall, B. C., and Brose, U. (2007). Allometric degree distributions facilitate food-web stability. *Nature*, 450(7173):1226–1229.

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

Paine, R. T. (1988). Food webs - road maps of interactions or grist for theoretical development. *Ecology*, 69(6):1648–1654. DEC ECOLOGY.

Paine, R. T. (1992). Food-web analysis through field measurement of per capita interaction strength. *Nature*, 355:73–75. Analysis of the intercation strength in guild of intertidal herbivores on Tatoosh Island. Presents index to express interaction strength on a per capita basis.; file-author; file-thesis,.

Patricio, J. and Marques, J. C. (2006). Mass balanced models of the food web in three areas along a gradient of eutrophication symptoms in the south arm of the mondego estuary (portugal). *Ecological Modelling*, 197:21–34.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. (1998). Fishing down marine food webs. *Science*, 279(5352):860.

Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P. W., Fernandez-Manjarrés, J. F., Araújo, M. B., Balvanera, P., Biggs, R., Cheung, W. W. L., Chini, L., Cooper, H. D., Gilman, E. L., Guénette, S., Hurtt, G. C., Huntington, H. P., Mace, G. M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R. J., Sumaila, U. R., and Walpole, M. (2010). Scenarios for global biodiversity in the 21st century. *Science*, 330(6010):1496–1501.

Peres-Neto, P. (1999). How many statistical tests are too many? the problem of conducting multiple ecological inferences revisited. *Marine Ecology Progress Series*, 176:303–306.

Persson, L., Leonardsson, K., de Roos, A. M., Gyllenberg, M., and Christensen, B. (1998). Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. *Theor Popul Biol*, 54(3):270–293.

Petchey, O., Beckerman, A., Riede, J., and Warren, P. (2008). Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences*, 105(11):4191–4196.

Petchey, O. L. (2004). On the statistical significance of functional diversity effects. *Functional Ecology*, 18(3):297–303.

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(6757):69–72.

Peters, R. and Wassenberg, K. (1983). The effect of body size on animal abundance. *Oecologia*, 60(1):89–96.

Petersen, C. G. J. (1915). A preliminary result of the investigations on the valuation of the sea. *Report of the Danish Biological Station*, 23:29–33.

Piechnik, D. A., Lawler, S. P., and Martinez, N. D. (2008). Food-web assembly during a classic biogeographic study: species' "trophic breadth" corresponds to colonization order. *Oikos*, 117(5):665–674.

Pierce, W., Cushman, R., and C.E., H. (1912). The insect enemies of the cotton boll weevil. *U.S. Department of Agriculture, Bureau of Entomology Bulletin*, 100:1–99.

Pimm, S., Russel, G., Gittelman, J., and Brooks, T. (1995). The future of biodiversity. *Science*, 269:347–350.

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

Polis, G. A. (1991). Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist*, 138:123–155.

Polis, G. A. and Strong, D. R. (1996). Food web complexity and community dynamics. *American Naturalist*, 147(5):813–846.

Power, M. E., Tilman, D., Estes, J., Menge, B. A., Bond, W. J., Mills, L. S., Daily, G., Castilla, J. C., Lubchenco, J., and Paine, R. T. (1996). Challenges in the quest for keystones. *BioScience*, 46:609–620.

Purvis, A. and Hector, A. (2000). Getting the measure of biodiversity. *Nature*, 405(6783):212–219.

Rall, B. C., Guill, C., and Brose, U. (2008). Food-web connectance and predator interference dampen the paradox of enrichment. *Oikos*, 117(2):202–213.

Rall, B. C., Vucic-Pestic, O., Ehnes, R. B., Emmerson, M. C., and Brose, U. (2009). Temperature, predator–prey interaction strength and population stability. *Glob Chan Biol*, 9999(9999):–.

Reagan, D. (1996). *The food web of a tropical rain forest*. University of Chicago Press, Chicago.

Reuman, D. C., Mulder, C., (true graphic)]Richter, C. B., (true graphic)]France Cattin Blandenier, M., Breure, A. M., Hollander, H. D., Kneitel, J. M., Raffaelli, D., Woodward, G., and Cohen, J. E. (2009). Chapter 1 allometry of body size and abundance in 166 food webs. In Caswell, H., editor, *Advances of Ecological Research*, volume 41 of *Advances in Ecological Research*, pages 1 – 44. Academic Press.

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

Riede, J. O., Brose, U., Ebenman, B., Jacob, U., Thompson, R., Townsend, C. R., and Jonsson, T. (2011b). Stepping in eltons footprints: a general scaling model for body masses and trophic levels across ecosystems. *Ecology Letters*, 14(2):169–178.

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

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., and Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287:1771–1774.

Schmid, P. E., Tokeshi, M., and Schmid-Araya, J. M. (2000). Relation between population density and body size in stream communities. *Science*, 289(5484):1557–1560.

Schmid-Araya, J. M., Schmid, P. E., Robertson, A., Winterbottom, J., Gjerløv, C., and Hildrew, A. (2002). Connectance in stream food webs. *Journal of Animal Ecology*, 71:1056–1062. pdf.

Schoener, T. W. (1989). Food webs from the small to the large. *Ecology*, 70(6):1559–1589.

Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., McHugh, K., and Hiraldo, F. (2008). Top predators as conservation tools: Ecological rationale, assumptions, and efficacy. *Annu. Rev. Ecol. Evol. Syst.*, 39(1):1–19.

Shelford, V. E. (1913). *Animal communities in temperate America as illustrated in the Chicago region.* University of Chicago Press, Chicago, Illinois, USA.

Simberloff, D. S. and Abele, L. G. (1976). Island biogeography theory and conservation practice. *Science*, 191(4224):285–286.

Skalski, G. T. and Gilliam, J. F. (2000). Modeling diffusive spread in a heterogeneous population: A movement study with stream fish. *Ecology*, 82:1685–1700.

Snook, D. and Milner, A. (2002). Biological traits of macroinvertebrates and hydraulic conditions in a glacier-fed catchment (french pyrénées). *Archiv für Hydrobiology*, 153:245–271.

Sokal, R. (1995). *Biometry : the principles and practice of statistics in biological research.* W.H. Freeman, New York, 3rd ed. edition.

Solè, R. V. and Montoya, J. M. (2001). Complexity and fragility in ecological networks. *Proceedings of the Royal Society B: Biological Sciences*, 268(1480):2039–2045.

Spencer, M. and Warren, P. H. (1996). The effects of habitat size and productivity on food web structure in small aquatic microcosms. *Oikos*, 75(3):419–430. Times Cited: 12 Article English Cited References Count: 48 Ux389.

Srinivasan, U. T., Dunne, J. A., Harte, J., and Martinez, N. D. (2007). Response of complex food webs to realistic extinction sequences. *Ecology*, 88(3):671–682.

Staniczenko, P. P. A., Lewis, O. T., Jones, N. S., and Reed-Tsochas, F. (2010). Structural dynamics and robustness of food webs. *Ecology Letters*, 13(7):891–899.

Stouffer, D. B., Camacho, J., Guimera, R., Ng, C. A., and Amaral, L. A. N. (2005). Quantitative patterns in the structure of model and empirical food webs. *Ecology*, 86(5):1301–1311. Article.

Summerhayes, S. V. and Elton., C. S. (1923). Contribution to the ecology of spitsbergen and bear island. *Journal of Ecology*, 11:214–268.

Sylvester, J. J. (1878). Chemistry and algebra. *Nature*, 17:284–284.

Team, R. D. C. (2011). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M. C., Schwager, M., and Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, 31(1):79–92. Times Cited: 0 Review English Cited References Count: 130 757fh.

Thebault, E., Huber, V., and Loreau, M. (2007). Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure. *Oikos*, 116(1):163–173.

Thierry, A., Beckerman, A. P., Warren, P. H., Williams, R. J., Cole, A. J., and Petchey, O. L. (2011). Adaptive foraging and the rewiring of size-structured food webs following extinctions. *Basic and Applied Ecology*, 12(7):562 – 570.

Thompson, R., Hemberg, M., B.M., S., and J.B., S. (2007). Trophic levels and trophic tangles: The prevalence of omnivory in real food webs. *Ecology*, 88:612–617.

Towers, D. J., Henderson, I. M., and Veltman, C. J. (1994). Predicting dry-weight of new-zealand aquatic macroinvertebrates from linear dimensions. *New Zealand Journal of Marine and Freshwater Research*, 28(2):159–166.

Townsend, C. R. (1989). The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society*, 8:36–50.

Townsend, C. R. and Scarsbrook, M. R. (1997). The intermediate disturbance hypothesis, refugia and biodiversity in streams. *Limnology and Oceanography*, 42:938–949.

Townsend, C. R., Thompson, R. M., McIntosh, A. R., Kilroy, C., Edwards, E., and Scarsbrook, M. R. (1998). Disturbance, resource supply, and food-web architecture in streams. *Ecology Letters*, 1(3):200–209.

Vander Zanden, M. J., Shuter, B. J., Lester, N. P., and Rasmussen, J. B. (2000). Within- and among-population variation in the trophic position of a pelagic predator, lake trout (salvelinus namaycush). *Canadian Journal of Fisherie and Aquatic Science*, 57:752–731.

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

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(1):249–256.

Warren, P. H. (1989). Spatial and temporal variation in the structure of a fresh-water food web. *Oikos*, 55(3):299–311.

Warren, P. H. and Lawton, J. H. (1987). Invertebrate predator-prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure? *Oecologia*, 74:231–235.

Warton, D. I., Wright, I. J., Falster, D. S., and Westoby, M. (2006). Bivariate line-fitting methods for allometry. *Biol Rev Camb Philos Soc*, 81(2):259–291.

Watts, D. J. and Strogatz, S. H. (1998). Collective dynamics of 'small-world' networks. *Nature*, 393(6684):440–442. PMID: 9623998.

Weitz, J. S. and Levin, S. A. (2006). Size and scaling of predator-prey dynamics. *Ecol Lett*, 9(5):548–557.

White, E., Ernest, S., Kerkhoff, A., and Enquist, B. (2007). Relationships between body size and abundance in ecology. *Trends in Ecology & Evolution*, 22(6):323–330.

Williams, R. and Martinez, N. (2004a). Stabilization of chaotic and non-permanent food-web dynamics. *The European Physical Journal B-Condensed Matter and Complex Systems*, 38(2):297–303.

Williams, R., Martinez, N. D., Berlow, E. L., Dunne, J. A., and Barabàsi, A.-L. (2002). Two degrees of separation in complex food webs. *Proceedings of the National Academy of Science*, 99:12913–12916.

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. (2004b). 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. (2008). Success and its limits among structural models of complex food webs. *Journal of Animal Ecology*, 77(3):pp. 512–519.

Wilson, D. (1975). Adequacy of body size as a niche difference. *American Naturalist*, 109:769–784.

Winemiller, K. O. (1990). Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs*, 60(3):331–367.

Woodward, G., Benstead, J. P., Beveridge, O. S., Blanchard, J., Brey, T., Brown, L. E., Cross, W. F., Friberg, N., Ings, T. C., and Jacob, U. (2010). Ecological networks in a changing climate. In *Advances in Ecological Research*, volume 42, pages 71–138. Elsevier.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J., Valido, A., and Warren, P. (2005a). Body size in ecological networks. *Trends in Ecology & Evolution*, 20(7):402–409.

Woodward, G. and Hildrew, A. (2001). Invasion of a stream food web by a new top predator. *Journal of Animal Ecology*, 70(2):273–288.

Woodward, G. and Hildrew, A. G. (2002). Body-size determinants of niche overlap and intraguild predation within a complex food web. *Journal of Animal Ecology*, 71(6):1063–1074.

Woodward, G., Papantoniou, G., Edwards, F., and Lauridsen, R. B. (2008). Trophic trickles and cascades in a complex food web: impacts of a keystone predator on stream community structure and ecosystem processes. *Oikos*, 117(5):683–692.

Woodward, G., Speirs, D. C., and Hildrew, A. G. (2005b). Quantification and resolution of a complex, size-structured food web. In *Advances in Ecological Research*, volume 36, pages 85–135. Elsevier.

Wootton, J. T. (1997). Estimates and tests of per-capita interaction strength: diet, abundance, and impact of intertidally-foraging birds. *Ecological Monographs*, 67:45–64.

Wootton, J. T. and Emmerson, M. (2005). Measurement of interaction strength in nature. *Annual Reviews Ecol. Evol. Systems*, 36:419–444.

Yodzis, P. (1989). Patterns in food webs. *Trends Ecology and Evolultion*, 4(2):49–50.

Yodzis, P. and Innes, S. (1992). Body size and consumer-resource dynamics. *American Naturalist*, 139(6):1151–1175.

Yvon-Durocher, G., Montoya, J. M., Emmerson, M. C., and Woodward, G. (2008). Macroecological patterns and niche structure in a new marine food web. *Central European Journal of Biology*, 3(1):91–103.

Yvon-Durocher, G., Reiss, J., Blanchard, J., Ebenman, B., Perkins, D. M., Reuman, D. C., Thierry, A., Woodward, G., and Petchey, O. L. (2011). Across ecosystem comparisons of size structure: methods, approaches and prospects. *Oikos*, 120(4):550–563.

Zook, A., Eklöf, A., Jacob, U., and Allesina, S. (2010). Food webs: Ordering species according to body size yields high degree of intervality. *Journal of Theoretical Biology*, pages –.

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Scientific publications

2011

Curtsdotter, A., Rall, BC., Binzer A., Brose, U., de Castro, F.,Ebenman, B., Eklöf, A., **Riede, JO.**, Thierry A., Rall, BC. (2011): Robustness to secondary extinctions: Comparing deletions in static and dynamic food webs. *Basic and Applied Ecology (accepted).*

Riede, J.O., Binzer, A., Brose, U., de Castro, F., Curtsdotter, A., Rall, B.C., Eklöf, A. (accepted): Size-based food web characteristics govern the response to species extinctions. *Basic and Applied Ecology (accepted).*

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

Jacob, U.,Thierry, A., Brose, U., Arntz, WE., Berg, S., Thomas, B., Fetzer, I., Jonsson,T., Mintenbeck, K., Möllmann, C., Petchey, OL., **Riede, JO.** and Dunne, JA.: The role of body size in complex food webs: A cold case. *Advances in Ecological Research, 45: 181-223*

Layer, K., Hildrew, A.G., Jenkins, G.B., **Riede, J.O**., Rossiter, S.J., Townsend, C.R., Woodward, G.: Long-term dynamics of a well-characterised food web: Four decades of acidification and recovery in the broadstone stream model system. *Advances in Ecological Research, 44: 69 - 117*

Riede J.O., Brose, U., Ebenman, B., Jacob, U., Thompson, R., Townsend, C.R., Jonsson, T.: Stepping in Elton's footprints: a general scaling model for body masses and trophic levels across ecosystems, *Ecology Letters, 14(2):169-178*

Digel, C., **Riede, J.O.**,Brose, U.: Allometric degree distributions across natural food webs, *Oikos,* 120 (4): 503-509.

Petchey O.L., Beckerman A.P., **Riede J.O.**, Warren P.H.: Fit, efficiency, and biology: some thoughts on judging food web models, *Journal of Theoretical Biology,* 279 (1): 169-171.

2010

Riede J.O., Rall, B.C., Banasek-Richter,C., Navarrete, S.A., Wieters, E.A., Emmerson, M.C., Jacob, U., Brose, U.: Scaling of food web properties with diversity and complexity across ecosystems, *Advances in Ecological Research 42: 139 - 170*

Layer, K., **Riede J.O.**, Hildrew, A.G., Woodward, G.: Food web structure and stability in 20 streams across a wide ph-gradient, *Advances in Ecological Research 42: 265-299*

2008

Petchey, O.L., Beckerman, A.P., **Riede J.O.**, Warren, P.: Size, foraging and food web structure, *Procedings of the national academy of sciences of the United States of America (105) : 4191-4196*

Reviewer of the journals

Journal of Animal Ecology; Journal of Freshwater Ecology ;
Ecological Complexity

Presentations and talks

Riede, J.O, Brose, U. (2011): Stepping in Elton's footprints: a general scaling model for body masses and trophic levels across ecosystems, *Oral presentation at the 96th ESA Annual Meeting in Austin(TX)*

Riede, J.O. (2011): Dawn of death: species and food web extinction risk, *Poster presentation at the International Scientific Conference: Functions and Services of Biodiversity, University of Göttingen*

Riede, J.O., Brose, U. (2010): Allometric scaling relationships across food webs in different ecosystems, *Oral presentation at the British Ecological Society Annual Meeting, Leeds University*

Riede, J.O., Brose, U. (2010): Body mass and network structure drive food-web robustness against species loss, *Oral presentation at the GfÖ Annual Meeting, Gießen University*

Riede, J.O., Jonsson, T., Jacob, U., Brose, U. (2008): Trophic level scaling of predator-prey body-mass relationships, *Poster presentation at the British Ecological Society Annual Meeting , Imperial College London*

Practical experience

7/2009: DAAD fellowship (three Months) at Queen-Mary University

London, 3-month working visit to the working group of Dr. Woodward.

Between 2008 – 2010 several working visits to Sweden (Linköping University), England (University of Sheffield) and Spain (Institut de Ciències del Mar, Barcelona) via the ESF founded scientific network SIZEMIC in total six weeks.

Accreditations

Youth (development) officer at auxiliary firefighters Pfungstadt between 2002 and 2009

Communal youth (development) officer at auxiliary firefighters Pfungstadt since 2009

Computer Skills

Operating systems	Windows, Linux
Software Expertise	ArcGIS, C++, R, Jump-in, Statistica, Microsoft Office Package, Endnote, Sigma Plot, LATEX and more

EIDESSTATTLICHE ERKLÄRUNG

Hiermit erkläre ich, dass diese Arbeit weder in gleicher noch in ähnlicher Form bereits anderen Prüfungsbehörden vorgelegen hat.

Weiterhin erkläre ich, dass ich mich an keiner anderen Hochschule um einen Doktorgrad beworben habe.

Göttingen, den 23.01.2012

Jens Olaf Riede

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Hiermit erkläre ich eidesstattlich, dass diese Dissertation selbständig und ohne unerlaubte Hilfe angefertigt wurde.

Göttingen, den 23.01.2012

Jens Olaf Riede

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