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Allometric structure and topology of food webs:

Energetic constraints conserve food-web structure across ecosystems and space

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Summary

Natural ecosystems comprise an innumerable amount of different organisms. These organisms are not separated, they interact and depend on each other. Today's ecosystems are facing an enormous decline in biodiversity due to human impacts with thus far unknown consequences. One key objective of ecological research is to understand the mechanisms generating and maintaining this incredible amount of diversity. However, comprehensive analyses of natural ecosystems are impeded by their complexity and diversity. Food webs, therefore, provide an excellent tool to analyze the complexity of ecosystems. They depict the system‘s diversity and species interactions in a condensed form. Furthermore, food-web structure can help to predict the interaction strengths between species and the energy pathways through the system. In my thesis, I use food web structure to analyze structural properties which separate food webs from other network types and furthermore I investigate generalities and differences of food-web structure across different ecosystems.

One of the most important ecosystems is the soil ecosystem, as it provides the base for aboveground productivity. However, detailed soil food webs are scarce. In chapter 2, I assembled the complex food webs of 48 forest soil communities and analyzed if soil food webs differ in their topological parameters from those of other ecosystems. I found that soil food webs are characterized by a higher number of omnivorous and cannibalistic species. Moreover, they comprise more trophic chains and intraguild-predation motifs than food webs from other ecosystems. Finally, soil food webs showed high average and maximum trophic levels. These differences in network structure to other ecosystem types may be a result of ecosystem-specific constraints on hunting and feeding characteristics of the species that emerge as network parameters at the food-web level. Despite these differences, soil food webs showed the same scaling of their properties with connectance and size. In a second analysis of land-use effects, I found significant but only small differences of soil food web structure between different beech and coniferous forest types, which may be explained by generally strong selection effects of the soil that are independent of human land use. This study has unravelled systematic structures of soil food-webs, extending our mechanistic understanding how their environmental characteristics determine patterns at the community level. Additionally, I have shown that the general scaling laws also apply for soil food webs.

In addition to purely topological properties, I analyzed another important aspect of food webs. The distributions of body masses and degrees across species are key determinants of food-web structure and dynamics. In chapter 3, I analyzed body masses of species and their systematic distributions across food-web structure. In particular, allometric degree distributions combine both aspects in the relationship between degrees and body masses. They are of critical importance for the stability of complex ecological networks. I used an

entirely novel global body-mass database including food-web structures of four different ecosystem types to analyze body-mass distributions, cumulative degree distributions, and allometric degree distributions regarding differences among ecosystem types. My results demonstrate some general patterns across ecosystems: the body masses are either roughly log-normally (terrestrial and stream ecosystems) or multimodally (lake and marine ecosystems) distributed, and 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. Overall, these analyses document striking generalities in the body-mass and degree structure 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.

While I revealed general patterns of food-web topology in chapter 2 and 3, I investigated the drivers of these general patterns in chapter 4. Therefore, I analyzed the influence of different external factors on community (beta diversity) and food-web structure. Two main theoretical bodies explain β-diversity, the niche theory and neutral theory. However, neutral theory predicts only distributions for trophically identical species, whereas influences of local niches or neutral effects on food-web structure as a crucial part of the multitrophic structure of ecosystems are not taken into account. In chapter 4, I therefore analyzed the effects of spatial distance and environmental dissimilarity on the species dissimilarity (beta diversity) and food web dissimilarity (structural dissimilarity) of multitrophic forest communities. I showed that the mechanisms proposed by neutral theory can adequately predict the beta diversity of multitrophic species communities. Furthermore, food-web structure was robust and affected neither by spatial distance (random dispersal, neutral theory) nor by environmental filtering (niche theory). I additionally analyzed model food webs (random and niche topology) and compared their dissimilarities to empirical food webs. The highest dissimilarity was reached by random food webs whereas niche model food webs were in between and the lowest distances were expressed by empirical food webs. Further, random food webs displayed the highest mean trophic level (115), while niche model food webs showed lower (5) and empirical food webs the lowest (4) mean trophic level values. Hence, food-web structure appears to be energetically optimized with local species adapted to energetic niches within the food web while species identity within these niches remains random. This suggests that different species could be adapted to the same energetic niches and, while following random drift, still assemble into similar food web structures.

Altogether, the results of this thesis demonstrate the practicality of food-web structure in unravelling generalities across different ecosystems. Furthermore, food-web structure explains species distributions across the environment and provides additional important information on the ecosystem.

The observed generalities indicate constraints on food-web structure. The allometric degree distributions demonsrate such constraints on food-web structure by distributing the links in dependence of the species body masses. Finally, my results from chapter 4 indicate that, additionally to global topological constraints, local communities have to meet certain energetic constraints to explain the similarity found across food webs.

Contributions to the chapters of this thesis

Chapter 2: Unravelling the complex structure of forest soil food webs: higher omnivory and more trophic levels

Christoph Digel, Alva Curtsdotter, Jens O. Riede, Bernhard Klarner, Ulrich Brose

C.D. and U.B. designed the study, the database was assembled by C.D. and B.K. Data were analyzed by C.D., A.C. and J.O.R. The text was written by C.D., A.C. and U.B.

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

Christoph Digel, Jens O. Riede, Ulrich Brose

All authors designed the study. The database was assembled by J.O.R. Data were analyzed by C.D. and J.O.R. The text was written by C.D. and U.B. with inputs from J.O.R.

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Chapter 4: Neutral species distributions yield non-random food-webs

Christoph Digel, David Ott, Franziska Grischkat, Ulrich Brose

C.D., F.G. and U.B. designed the study. The database was assembled by C.D., D.O. and F.G. Data were analyzed by C.D. The text was written by C.D. and U.B. with inputs from D.O. © 2014 the Authors

Part I
General introduction

Chapter 1: Introduction

1.1. Aims and scope of this thesis

Life on earth comprises an innumerable amount of different organisms. These organisms are not separated; they coexist, interact and evolve. One of the key objectives in ecology is to unravel the mechanisms which create and maintain the extraordinary biodiversity on our planet. In the early 20th century, ecological consensus was that the key to stability is complexity (MacArthur 1955; Elton 1958; McCann 2000). Many empirical studies found that diverse ecosystems are more stable than systems with a low diversity. In 1972 Robert May challenged this paradigm with his theoretical work on stability and complexity in model ecosystems (May 1973; McCann 2000). Robert May showed that complexity and species richness is not a guarantee for stability but that more diverse systems are mathematically unstable. May's work stimulated the diversity stability debate in ecology which resulted in a large number of new theoretical models explaining the coexistence of species (Yodzis 1981; Pimm 1982; Tilman 1999; McCann 2000).

May's and many other theoretical models analyzing stability and diversity using the framework of food webs (May 1973; Yodzis 1981; McCann 2000). Food webs depict the species diversity, their interactions in an ecosystem and display the pathways along which the energy is distributed through the system (Dunne 2009). These aspects of species coexistence all affect the stability of the community by influencing the energy distributions and interaction strengths between the species (McCann 2000). Consequently, food web structures are a promising subject in the search for drivers of biodiversity and stability. Comparative studies revealed that food webs differ from other known networks (e.g. protein networks, power networks, etc.) (Dunne et al. 2002; Albert & Barabasi 2002). Interestingly, food webs show only few differences to other networks in their structural parameters (e.g. connectance, clustering, and degree) but differ consistently in their degree distributions (Dunne et al. 2002). This results in large topological differences in network architecture. Another interesting aspect of food webs is that the topological properties show unique scaling relationships with connectance and species richness. These scaling relationships can be found across different ecosystems and are suggested to be a general feature of food webs (Riede et al. 2010).

To develop a more detailed analysis of food web topology and to gain more ecologically relevant information, newer studies add ecological parameters to the purely mathematically approach of graph theory (Otto et al. 2007). Especially the inclusion of the species body mass into topological parameters is a promising approach to analyze interactions of species in an ecosystem. Furthermore, the distribution of body mass across the food web topology is an important factor explaining stability. Degree distributions (the numbers of predators and prey of a species) scale with body mass and model networks have revealed the strong beneficial effect on stability of these allometric degree distributions (Otto et al. 2007). These topological parameters including ecological information demonstrate that food web structure can be used to gain mechanistic understanding of ecological processes. Furthermore, the inclusion of body mass as an ecological property incorporated into food web models provides an ecological resolution for the mathematical problem of stability. (Otto et al. 2007).

These studies revealed promising insights into topological and scaling properties of food webs. Further, they clearly demonstrated how food web structural parameters can be applied to answer ecological questions. In my thesis I addressed several different aspects of food web structure. I analyzed a large number of different food webs to investigate if the previously revealed similarities in topology and scaling could be a generalized to be a universal feature over all food webs, separating them from other network types. Furthermore, food-web structure revealed some consistencies which and I analyzed the ecological implications and drivers of these similarities. The three research chapters of this thesis are divided into three areas:

(I) Food web topological parameters and their scaling:

Highly resolved soil food web structures are notoriously scarce, although soil ecosystems are highly important as the base of the aboveground productivity. I filled this gap and assembled 48 soil food webs. I analyzed these soil food webs in detail to a) investigate if the generalities in scaling proposed by previous research could be extended to hold across a very large database including the new soil food webs, b) to analyze the differences in topology of soil food webs compared to other food webs and c) to analyze the influences of land use intensity on soil food web topology.

(II) Body mass scaling of degrees (allometric degree distributions):

Previous studies suggested that allometric degree distributions stabilize food webs and that natural food webs also show this body mass scaling of degrees (Otto et al. 2007). In consequence, I analyzed the generality of allometric degree distributions across a large number of natural food webs from different ecosystems. Therfore I used a database including 96 food webs and the body masses of all species to analyze differences in body mass distributions, the degree distributions and the allometric degree distributions between ecosystems.

(III) What are the drivers of the structural robustness of food webs?

Food webs have distinct topological features separating them from other network types (Dunne et al. 2002; Albert & Barabasi 2002). (I) and (II) revealed that food web structural properties are conserved across different ecosystems. Also the food web parameters scaled similarly with complexity and size (Chapter 2, Riede et al. 2010). This suggests that food web structure is constrained. I analyzed possible ecological and evolutionary drivers conserving the food web structure by applying the theoretical body of neutral or niche theory to unravel the influence of spatial and environmental factors on the community structure and food web topology.

In the following paragraphs I will provide deeper background information on the area of food webs and diversity. Therefore, I start on the scale of single species which are the nodes of in food web and give some information about their traits as they are important regulators of the interactions strengths. Second I scale up to different species on different trophic levels which share feeding interactions which are the links in food webs. Further I give a short definition of diversity and conclude my introduction with the conceptual framework of food web topology and its application.

1.2. From individual species to diversity

1.2.1. The concept of species

Ecosystems comprise different organisms which produce organic compounds, reproduce and interact with other organisms. All organisms can be separated into two major groups: autotrophs and heterotrophs. Autotrophic organisms (producers) produce their energy in the form of complex organic compounds using abiotic sources such as light energy (photosynthesis) or chemical energy gained from the use of inorganic substrates (chemosynthesis) (Reece 2014). In contrast, heterotrophic organisms (consumers) are not able to produce organic compounds, but they rather need to consume other organisms to obtain the base compounds they need.

Organisms can be classified into different species. Species are the basic unit of biological taxonomy. A species comprises the organisms which share the same traits and which are capable of reproducing (Ax 1995; Westheide 2013). This definition works well for multicellular organisms but is only of limited use regarding unicellular prokaryotes (Fraser et al. 2009). In this thesis I concentrate on multicellular organisms and will therefore go with the above basic definition of species. For the analysis of diversity and food web structure the classification into species is vital as they are the key element of food webs.

Today's species have a long evolutionary history. They have evolved from the first unicellular organisms in the primordial soup into the tremendously diverse and complex life forms of the present (Ridley 2004; Storch et al. 2013). At first, the changing abiotic environment of the species put selective pressure on them. They adapted and evolved traits that helped them thrive in their environment. As species started interacting, new selective pressures arose through these biotic interactions (Benton 2009). Hereby, species have undergone co-evolutionary processes evolving new traits, arms and defenses (Ridley 2004; Storch et al. 2013).

Species can be characterized by their traits (morphological and ecological). These traits have important effects on the interactions between different species. The primary research topic of this thesis is food webs and one of the most important species traits influencing the feeding interactions and dynamic stability of the food web is body mass (Otto et al. 2007; Kalinkat, Schneider, et al. 2013). Body mass affects many physiological and ecological properties of the species. Nearly all of these properties (e.g. metabolic rates, moving speed and interactions strengths with other species) scale with body masses following a power law relationship (Peters 1983; Brown et al. 2004; Brose, Williams, et al. 2006; Brose 2010; Vucic-Pestic, Rall, et al. 2010). Additionally, ecosystem relevant properties (e.g., species abundances) scale with body mass (higher abundances of small species vs. low abundances of large species)(Jennings & Mackinson 2003; Ehnes et al. 2014). Body mass provides an easily measurable parameter and simultaneously explains many ecologically important species traits.

1.2.2. Diversity

Diversity is often used synonymously with species richness but has a much broader range of meanings. It can describe the genetic diversity within a single species as well as, on the other end of the scale, describing the variation in habitats (e.g. meadows, stages of woodland succession, deserts or others) (Begon et al. 2006). In my thesis I will follow the classification of diversity devised by Whittaker (1960). He differentiates three different scales of biodiversity (Figure 1):

(I) Alpha diversity describes the local diversity i.e. species richness of a habitat or a sampling site. Species richness hereby is influenced by the abiotic and biotic characteristics of the habitat.

(II) Beta diversity describes the diversity between communities and is usually measured using presence-absence data. If two communities are very different in their species composition (i.e. they have very few species in common) then they have high beta diversity. A common unit of beta diversity is the Jaccard similarity index, where J is the number of species common in both samples divided by the total number of species in both samples (Jaccard 1912). The beta diversity is mainly influenced by species distribution patterns along a spatial or environmental gradient.

(III) Gamma diversity describes diversity on a landscape scale. It includes all alpha diversities in the considered geographical area. It could, for example, also comprise the alpha diversities of different climatic regions. The gamma diversity is influenced by the total species richness of a region (described by the intersection of the different alpha diversities).

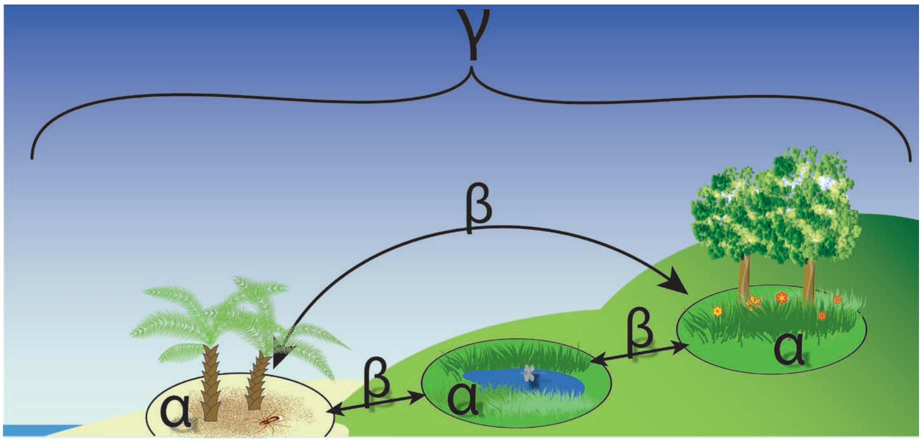

Figure 1: The three different diversities and their relation to each other.

In my thesis I analyzed data based on the alpha diversity level (species richness) to assemble and compare food web structures between forests and other ecosystems. Furthermore, I used data on the beta diversity level to compare the influences of spatial and environmental gradients on species dissimilarity and food web structure. I will now give a more detailed background on the theoretical body of beta diversity as it is an integral part of my fourth research chapter.

Beta diversity is mainly influenced by species distributions across the environment. These species distributions arise through the dispersal restrictions of species (Thompson & Townsend 2006). Successful dispersal of a species into another area can be divided into three crucial steps: (a) Departure: the species needs to leave its habitat. (b) Transfer: the species needs to traverse a spatial distance. (c) Settlement: the species needs to successfully invade a habitat (Bonte et al. 2012; Clobert et al. 2009). Dispersal restrictions can arise from species traits and preadaptation to the abiotic and biotic environment (Hutchinson 1959; Soberón 2007). Niche theory assumes that abiotic conditions or biotic interactions determine the distribution of species which are consequently well adapted to their local environments (Graham & Fine 2008). A niche is defined by the abiotic (e.g. space and light availability, temperature, pH value, minerals) as well as by the biotic conditions (e.g. resource availability, predators, parasites and competing species) (Leibold 1995). According to niche theory, all species can be everywhere (no dispersal limitation) but the local species are filtered through the availability of suitable niches (Graham & Fine 2008; Hutchinson 1959). Consequently, the local community is affected only by abiotic and biotic properties of the habitat and not by spatial distance.

In contrast to niche theory, neutral theory proposes a strikingly simple mechanism for predicting species distributions, similar to distributions found in nature (Hubbell 1997; Hubbell 2001). Hereby, it makes three assumptions: (I) The local community is saturated (grows until it exhausts all available biotic and abiotic resources), (II) new species can be recruited by dispersal of surrounding species or by randomly evolving new species and (III) new species can only invade the local community if, due to random demographic effects, a species dies out and biotic as well as abiotic resources become available again (Hubbell 1997). Neutral theory is often viewed as a null hypothesis of diversity and dispersal because the species' environment and the biotic interactions have no effect on species dispersal and are therefore considered neutral (Gravel et al. in press). According to neutral theory, spatial distance (dispersal) is the only parameter shaping the species composition of local communities.

1.3. From biotic interactions to food webs

1.3.1. Interactions

In natural ecosystems, species are not separated but interact in many different ways. Interactions between organisms are important research topics in ecology and influence species in many different ways (Cardinale et al. 2002; Begon et al. 2006; Krebs 2009; Ings et al. 2009). They range across competition, mating, mutualism (e.g. pollination), predation, facilitation and hyper parasitism and can occur within species (intra specific) or between species (inter specific) (Kéfi et al. 2012; Begon et al. 2006). Of the different types of species interactions, I focus on feeding interactions as they are the major component of food webs. Feeding transfers the energy from the producer to the consumer species and further up through the different trophic levels of the ecosystem (Box 2). It is the only process through which heterotrophic organisms can assimilate energy. At every step along a food chain a part of the energy is lost from resource to consumer due to metabolism and assimilation inefficiencies (Peters 1983; Brown et al. 2004).

The strength of feeding interactions depends on the traits and abundance of the prey and predator but also on the structure of the habitat. Refuges, for example, can decrease the predation pressure on a prey species (Vucic-Pestic, Birkhofer, et al. 2010; Kalinkat, Brose, et al. 2013; Toscano & Griffen 2013; Kalinkat, Schneider, et al. 2013). The interaction itself can also differ in strength as, for example, generalist predators with many different prey organisms usually have a lower influence on a specific prey species. Predators can forage on varying numbers of prey species (generality), depending on the grade of specialization. Prey species can have varying numbers of predators (vulnerability) depending on defensive traits or specialization. However, species are generally constrained by many tradeoffs between specialization and generalization. The strengths of the interactions and their topology in a food web influence the dynamic stability of the system (Vucic-Pestic, Rall, et al. 2010; Kalinkat, Schneider, et al. 2013).

1.3.2. Food webs

Communities of species and their interactions can be mapped as food webs. They describe the ecosystem with its species diversity and associated trophic interactions in a very condensed way. In addition, food webs depict the energy distribution pathways of the ecosystem and its structural organization. Food webs have a long history in ecology. Simple food chains were already described in the late 1800s (Dunne 2009) and the first food webs with higher complexity were already published by 1912 (Pierce et al. 1912). Charles Elton was the first to published larger food webs in 1927 (Elton 1927). During the 20th century, the amount of food web descriptions increased constantly (Dunne 2006; Dunne 2009) but the resolution of food webs remained low (Dunne 2009). In 1977 the first comparative study of 30 different food webs was analyzed and published (Cohen 1977). In this work, for the first time food web structure was converted into a machine-readable matrix form (Cohen 1977). In 1991

Box 1: Food web glossary

Species, node or vertex: The representation of a species population in a food web.

Link or edge: The representation of a feeding interaction between two species.

Links per species: The average number of links per species (l/s).

Connectance: Complexity measure of a network. It gives the fraction of links established of all possible links (l/s^2).

Clustering coefficient: The probability that two species which are both linked to another species are also linked.

Degree/ linkedness: Parameter of a species node, describing its number of links (outgoing and ingoing).

Indegree/ Generality: Parameter of a species node, describing its number of prey species.

Outdegree/ Vulnerability: Parameter of a species node, describing its number of predator species.

SD generality: normalized standard deviation of generality (number of resources per species).

SD vulnerability: normalized standard deviation of vulnerability (number of consumers per species).

Degree correlation: Correlation coefficient between degrees of species in a food web. If positive, highly connected species tend to be connected to other highly connected species and sparsely connected to sparsely ones, if negative, then highly and sparsely connected species tend to interact.

Small world: special case of network topology, every node could reach every other node by passing only few links. Food webs are usually also small world networks.

the first highly resolved and large scale food webs were published (Polis 1991; Martinez 1991) and critique on the previous small and low-resolved food webs became more prevalent (Polis 1991). This increased the efforts to assemble larger and more highly resolved food webs that became available from 2000 onwards. For the analyses in my thesis I used a database which comprised these new large-scale and highly resolved food webs (Riede et al. 2010). It contains food webs from different aquatic ecosystems (marine, lakes and streams) as well as from terrestrial ecosystems. To this collection I added 48 soil food webs from different forest stands across Germany.

The food webs I analyzed in my thesis belong to the group of binary interaction food webs which contain information for feeding (1) or no feeding (0). These food webs are mathematical representations (network graphs) describing the community. Graphs are part of a larger field of network sciences. A graph describes the interaction network with nodes or vertices (i.e. species in food webs) which are connected by edges (i.e. feeding links in food webs). In network sciences many different types of networks are analyzed such as communication networks, the internet, social interaction networks, food webs, protein networks and gene expression networks (Albert & Barabasi 2002).

Graph theory goes back to Euler in 1736. Euler was the first to construct a graph that solves the "Königsberg bridge problem" by using nodes as a representation of the islands and edges for the connecting bridges (Euler 1758). This was the foundation for early analyses of mostly small-scale graphs. Graph theory became increasingly popular in the late 1990's favored by the increasing number of large-scale networks (e.g. Internet, complex communication networks and gene expression networks) (Barabási 2009). Graph theory provided an excellent tool to analyze and compare networks. In biology, graph theory was increasingly applied to protein or gene expression networks but also to food webs (Albert & Barabasi 2002; Dunne 2009). There is an increasing number of mathematical parameters which can be calculated from graphs (Box 1). Beside the graph theoretical parameters, ecologists developed ecologically reasonable parameters and also higher-order parameters to characterize the interactions between species (Box 2)(Dunne 2009).

1.3.3. General differences between food webs and other networks

With the increasing popularity of network science and graph theory, combined with better computational possibilities, many different networks were analyzed and underlying structural generalities were revealed (Watts & Strogatz 1998; Albert et al. 1999; Albert et al. 2000; Strogatz 2001; Albert & Barabási 2002; Barabási et al. 2002). Most of the social networks and also biological networks (e.g. protein networks or gene expression networks) share the same small-world topology with power-law degree distributions, high clustering but small path lengths (Watts & Strogatz 1998; Albert & Barabási 2002). Food webs display similar path lengths but lower clustering. They are also distinctly different in their degree distributions. Other networks have mostly power-law or scale-free degree distributions which results from a high number of nodes with a low degree and a low number of nodes with a very high degree (hubs). In contrast, food webs have exponential or even uniform degree distributions, i.e. the links are more evenly distributed through the network (Dunne et al. 2002) (Chapter 3).

1.3.4. Recent research topics using food web structure

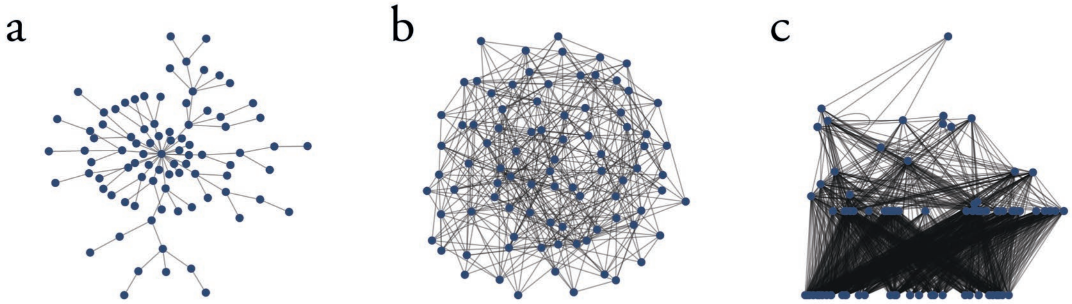

Figure 3: Network graphs with different topological characteristics. The nodes (blue balls) are connected by links. a) a graph generated using preferental attachment, many technical networks share these topologies. b) a random graph generated using the Erdös-Reny algorithm. c) a food web graph from the Schorfheide Biodiversity Exploratories dataset.

Despite the differences separating food webs from other networks, there is also interest in analyzing topological characteristics of food webs (Dunne et al. 2004; Dunne et al. 2008; Riede et al. 2010). Ecosystems differ widely in their abiotic and biotic properties. Environmental differences between ecosystems can be extreme, for example if a freshwater lake is compared to a desert. Besides these large-scale differences between distinct ecosystem types, conditions can also differ within an ecosystem type. Aquatic lakes, for example, could be further divided depending on their nutrient contents into eutrophic and oligotrophic lakes which are indeed very different systems. Furthermore, conditions differ strongly across climatic zones. These abiotic environmental characteristics of ecosystems influence the biotic communities, the interactions between the species (Hutchinson 1959; Begon et al. 2006) and therefore should affect food web structure. Mapped into food webs, topological properties enable the comparative analysis of completely different systems rather than just comparing species richness and identity (e.g. Riede et al. 2010). This can help to reveal some topological generalities and provide insight into the ecological processes structuring the community in dependence of the properties of the habitat.

Box 2: Ecological food web parameters

Trophic level: Position of the species in the food web. The trophic level of the basal resource is 1; the trophic level of the species feeding on the basal resource is 2. If a species feeds on the basal resource and on the species of level two the trophic level would be 1.5.

Fraction of cannibals: The fraction of species which have a link to themselves.

Fraction of herbivores: Species which feed on the basal species.

Fraction of omnivores: Species that feed on species of different trophic levels.

Food web motifs: Food web structure can be divided into small 3 species symbols. The four most frequent motifs are **MIGP, MTC, MAC, MEC**.

MIGP: The fraction of intra guild predation motifs in a food web.

MTC: The fraction of the trophic chain motifs in a food web.

MAC: The fraction of the apparent competition motifs in a food web.

MEC: The fraction of the exploitative competition motifs in a food web.

SD generality: normalized standard deviation of generality (number of resources per species).

SD vulnerability: normalized standard deviation of vulnerability (number of consumers per species).

Allometric degree distribution: the relationship of the species body mass to its links. Large species tend to have a higher generality than small species, further large species tend to have a lower vulnerability compared to small species.

Comparing different ecosystems revealed only small differences in the structural properties of food webs (Dunne et al. 2004; Dunne et al. 2008; Riede et al. 2010). This implies that food web structure is relatively conservative and follows scaling laws independent of ecosystem differences. Most of the food web properties show scaling relationships with connectance and size (species richness) which is also consistent over different ecosystem types (Dunne et al. 2002; Dunne 2006; Riede et al. 2010). Many important properties of food webs are further correlated with species body sizes. Food web structure follows allometric scaling laws which correlate with the distribution of the body masses in the food web (Brose, Jonsson, et al. 2006; Otto et al. 2007; Brose 2010). The concept of degree distributions extended to allometric degree distributions describes the relationship of indegree (generality) or outdegree (vulnerability) in dependence of the species body mass (Otto et al. 2007). Large predators tend to have more prey species than small predators. Small prey species have more predators than large prey species. These allometric degree distributions stabilize the community dynamic and prevent extinctions in food webs (Otto et al. 2007).Therefore, allometric degree distributions are a promising research topic explaining diversity and stability.

1.4. Conclusion

Life on earth comprises an innumerable number of different species and complex interactions. The mechanisms driving and maintaining this species richness and complexity are important research topics of ecology. However, this sheer amount of complexity and interactions between species makes the analysis difficult. Food webs, therefore, provide a promising approach dealing with such complexity. Extended by ecologically reasonable topological parameters, the analysis of food webs can help to shed light on different ecological processes relating complexity and stability.

1.5. Outline of this thesis

The research chapters included in this thesis address different aspects of food web topology. In chapter 2, I compare topological parameters of soil ecosystems with other ecosystems and analyze the influence of land use intensity on food web structure of the soil ecosystem. Further I investigate the scaling relationships of the topological parameters across soil food webs and other ecosystems. In chapter 3, I analyze the generality of allometric degree distributions across different ecosystems. In chapter 4, I analyze the influence of neutral and niche effects on food web structure and beta diversity.

Soil communities are often overlooked in their importance for aboveground processes although, the soil community fulfills important ecosystem functions for plant communities (Wall et al. 2012). Highly resolved large-scale soil food webs are scarce to date. In chapter 2, I fill this void with 48 new food webs from different forest soil communities. I compare their structural properties to food webs from other ecosystems. Furthermore, I analyze the scaling relationships of different food web properties in dependence on the size (species richness) or complexity (connectance) of the food webs. I finalize the analysis of the 48 soil communities by comparing the influences of different land-use intensities (expressed as different forest types) on soil food web structure.

One of the most important traits of species is their body mass. Allometric degree distributions integrate species body mass into food web structure. Further allometric degree distributions are important for food web stability and were shown for some food webs (Otto et al. 2007). If allometric degree distributions are a general feature of natural ecosystems this could help to understand the stability of natural systems. In chapter 3, I generalize these previous findings by applying a large food web database including 96 food webs from different ecosystems. I analyze the body mass distributions and the cumulative degree distributions of different ecosystems and moreover the allometric degree distributions across different ecosystems.

While I reveal general patterns of food web topology in chapter 2 and 3, I investigate the drivers of these general patterns in chapter 4. Therefore, I analyze the influence of different external factors on food web structure. Firstly, I analyze if the mechanisms used by neutral and niche theory could predict species distributions in multitrophic communities. Secondly I analyze if these mechanisms could also explain dissimilarities in food web structure. I conclude this chapter with the analysis of hypothetical food webs generated using the mechanisms proposed by niche and neutral theory and compare these to real world food webs.

Part II
Research chapters

Chapter 2: Unravelling the complex structure of forest soil food webs: higher omnivory and more trophic levels

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Food web topologies depict the community structure as distributions of feeding interactions across populations. Although the soil ecosystem provides important functions for aboveground ecosystems, data on complex soil food webs is notoriously scarce, most likely due to the difficulty of sampling and characterizing the system. To fill this gap we assembled the complex food webs of 48 forest soil communities. The food webs comprise 89 to 168 taxa and 729 to 3344 feeding interactions. The feeding links were established by combining several molecular methods (stable isotope, fatty acid and molecular gut content analyses) with feeding trials and literature data. First, we addressed whether soil food webs (n = 48) differ significantly from those of other ecosystem types (aquatic and terrestrial aboveground, n = 77) by comparing 22 food web parameters. We found that our soil food webs are characterized by many omnivorous and cannibalistic species, more trophic chains and intraguild-predation motifs than other food webs and high average and maximum trophic levels. Despite this, we also found that soil food webs have a similar connectance as other ecosystems, but interestingly a higher link density and clustering coefficient. These differences in network structure to other ecosystem types may be a result of ecosystem specific constraints on hunting and feeding characteristics of the species that emerge as network parameters at the food-web level. In a second analysis of land-use effects, we found significant but only small differences of soil food web structure between different beech and coniferous forest types, which may be explained by generally strong selection effects of the soil that are independent of human land use. Overall, our study has unravelled some systematic structures of soil food-webs, which extends our mechanistic understanding how environmental characteristics of the soil ecosystem determine patterns at the community level.

Introduction

Food webs depict how feeding links are distributed across populations constraining the flow of energy through a community from the basal level (autotrophs) to the top predators (Pimm et al. 1991, Thompson et al. 2012). These directed binary networks comprise species as nodes that are connected by their feeding interactions as links or directed edges (Fig. 1). The structure of food webs is described by network parameters ranging from general graph theory metrics such as connectance, clustering coefficient, characteristic path length or degree correlation (Erdös and Rényi 1960) to typical ecological-community variables including the maximum trophic level, the fraction of omnivores or the fraction of intra-guild predation motifs (Dunne et al. 2002b, 2004, Riede et al. 2010). These network parameters allow characterisations and comparisons of communities irrespective of species' identities (Williams and Martinez 2000, Dunne et al. 2002b, Dunne 2006, Riede et al. 2010, Digel et al. 2011, Stouffer et al. 2007, 2012). In addition, model analyses have shown their importance for community stability, resilience and functionality (Dunne et al. 2002a, Williams et al. 2002, Montoya et al. 2006, Otto et al. 2007, Tylianakis et al. 2010, Stouffer and Bascompte 2010) and robustness against secondary extinctions (Dunne et al. 2002a, Staniczenko et al. 2010, Gravel et al. 2011, Curtsdotter et al. 2011, Riede et al. 2011). Thus, these network parameters allow not only comparison of ecological community structure across different ecosystems, but they also enable predictions of their sensitivity to disturbances.

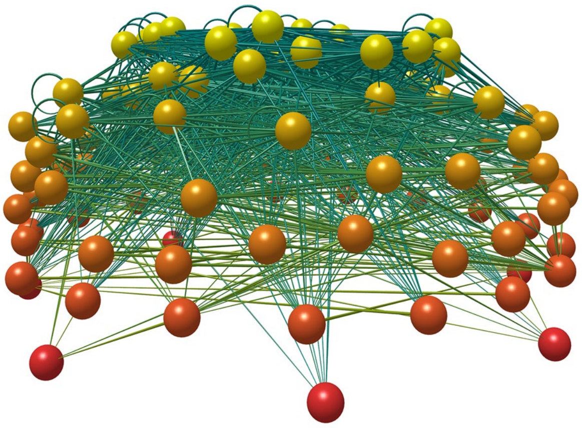

Figure 1. Food web structure of a natural beech forest with 1896 links among 118 species. Image produced with Network3D, written by R. J. Williams.

Former studies used food web parameters to analyze the differences between ecosystems (Dunne et al. 2002a, Riede et al. 2010). However, these studies are lacking highly resolved food-web data of soil ecosystems, which may deviate even more from other ecosystems (Scheu 2002). Stable isotope data of soil species are widely available (Scheu and Falca 2000, Scheu 2002), but taxonomically highlyresolved descriptions of their complex network structures that allow comparison of food web parameters with other ecosystems are lacking. In this study, we filled this gap and assembled the complex food-web structures of 48 forest soil communities to compare the forest soil food web structure with the structural parameters of other ecosystems.

The soil ecosystem has some striking differences to other habitat types, such as the aboveground compartments of terrestrial ecosystems or aquatic systems, as it has a strongly structured space composed of the litter layer and the pores of the soil (Coleman et al. 2004). The porous structure provides refuges for small prey species, which can strongly affect predator–prey interactions (Vucic-Pestic et al. 2010b, Kalinkat et al. 2013b) and exerts evolutionary pressure to limit predator body diameter so they can access prey refuges (Scheu and Setälä 2002). Hence, soil ecosystems comprise many predators with a small body diameter but a large body mass such as centipedes (Chilopoda or Geophilidae). In consequence, the soil community is also strongly size structured including small basal microfauna (nematodes and protists), mesofauna (microarthropods and enchitraeids) and macrofauna (beetles, millipedes, and earthworms). This strong compartmentalisation into size classes has profound effects for species interactions (Vucic-Pestic et al. 2010a, Rall et al. 2011, 2012), which can cascade up to determine network parameters (Brose 2010). For instance, studies of other ecosystem types have shown a strong relationship between the average body mass and the trophic level of a population (Riede et al. 2011) or between the average body mass and the level of generality (i.e. number of prey species) or vulnerability (number of predator species) of a species (Digel et al. 2011). Concerning these network parameters, soil communities, which are strongly structured by size, may thus differ from other ecosystem types.

The strong habitat heterogeneity causes that soils in temperate regions support unexpectedly high species diversities ("poor man's rain forest", Giller 1996). Many predators of the soil use a non-selective or sit-and-wait foraging strategy. For instance, spiders use tactile organs to detect possible prey organisms and rely on vibratory cues for prey detection (Uetz 1992). Predatory mites use a similar sensory apparatus (Krantz and Walter 2009), and their foraging behavior is likely to be determined by similar constraints. Moreover, centipedes are known to be sit and wait predators that benefit from the high abundance of soil mesofauna species (Poser 1988, Ferlian et al. 2012). In addition, random encounters are more important for soil predators compared to aboveground or aquatic systems, where predators are able to actively search their prey and other foraging modes are dominant. Speculatively, this combination of non-selective, sit-and-wait foraging strategies and random encounters should lead to a higher amount of omnivorous, generalist intra-guild predators and less specialists in the soil food webs.

In addition to its function as a habitat, the soil is also a resource for many species. The soil ecosystem includes not only the mineral soil itself but also an organic humus and litter layer. This organic litter layer can be of different depth depending on the decomposition rates and the amount of deposition, which has important implications for the biomass densities of all species (Ott et al. 2014). Detritus (i.e. leaf litter, POM, DOM) as the main basal resource differs strongly from basal resources of other ecosystems that are often based on plants and other living organisms. Since detritus is a dead resource, there is no evolutionary pressure on detritus to avoid consumption (Scheu and Setälä 2002). Also, detritus is very poor in nutritional value compared to other resources such as plant tissue or animal prey, which leads to low consumption efficiencies (Ott et al. 2012). In consequence, most detritivores cannot digest litter material directly, because they lack the necessary enzymes and instead rely on the microorganisms and fungi (Scheu and Setälä 2002). As an exception, some primary decomposers (e.g. Glomerida) can feed directly on litter material, which is evident from their stable isotope signatures (Pollierer et al. 2007, Klarner et al. 2014). Nevertheless, most species feeding on detritus (leaf litter) digest mainly the microorganisms that are growing on the litter or a mixture of "pre-digested" litter and microorganisms (Cummins 1974). This should lead to an increased number of trophic levels in soil ecosystems compared to ecosystems with basal resources such as plants that are directly consumed by herbivores.

In this study, we analysed the soil ecosystem of deciduous and coniferous forests. The land use intensities in forest systems should be a magnitude lower compared to intensive farmlands (Mulder and Elser 2009), but the forest soil should also be influenced by the use of pesticides, differences in tree ages, tree composition varying the stoichiometric quality of the litter (Ott et al. 2014) and soil compression by harvesting machines. These effects of land use intensity should translate into differences in the food-web structure of the communities. To account for effects of land use intensity, we analysed forest soil food webs across four different land use types: 1) coniferous forests, 2) managed young beech forests, 3) managed old beech forests and 4) unmanaged beech forests. We used food web structural parameters to address the following questions. First, is the food-web structure of soil ecosystems different from those of other ecosystems? We expected that the striking differences of the soil ecosystem as a habitat compared to aboveground and aquatic ecosystems should yield differences in food web structural parameters such as higher trophic levels. Moreover, the behavioural and morphological adaptations to the soil ecosystem should also influence food web structural parameters. Due to the dominance of non-selective and sit-and-wait foraging strategies in soil ecosystems, we expected to find higher amounts of omnivorous and generalist intra-guild predators in the soil food webs. Second, we also addressed the question: does the land-use type have an influence on the structure of soil food webs? We hypothesized that different land-use types represented by different beech age classes and coniferous forests should modify food-web structures by 1) different tree species and litter types determining the quality and quantity of the basal resource input, and 2) disturbances caused by harvesting and transportation of the trees.

Methods

Study site

Our study was conducted in beech and coniferous forest sites of the Biodiversity Exploratories that provide a long-term research platform to analyse the effects of varying land use intensities on functional biodiversity (Fischer et al. 2010). The exploratories are situated in three geographical areas in southern, central and northern Germany. In each exploratory, different land use types are realized. The southern Biodiversity Exploratories project is located in the Swabian Alb, an approx. 200 km long low mountain range in south Germany near the city of Ulm with limestone as bedrock. It has a mean annual precipitation of 700–800 mm and a mean annual temperature of 6–7 °C. The central exploratory is located in the area of the Hainich a forest hill chain near the city Eisenach in Thuringia. It has a mean annual precipitation of 500–800 mm and a mean annual temperature of 6.5–8 °C. The northern exploratory is located in the Schorfheide a nature reserve in Brandenburg near the city Chorin north of Berlin. The mean precipitation ranges from 500–600 mm and the mean annual temperature is 8–8.5 °C (Fischer et al. 2010). The forests in each of the three exploratories range from intensively managed coniferous monocultures to natural unmanaged beech forests with trees more than 100 years old.

Sampling

In total, we sampled 48 different forest plots divided in16 forest sites in each exploratory (Schorfheide, Hainichand Alb). Within each exploratory, we chose 16 sites representing different land use intensities: 1) high intensity: monoculture coniferous forests, 2) intermediate intensity: young beech forests, 3) low intensity: old managed beech forests and 4) nearly natural: unmanaged beech forests with four replicates for each land use type.

For sampling of the soil fauna, we used four different methods to achieve a comprehensive overview of the different animal groups: 1) small soil cores, 2) large soil cores, 3) mustard extraction, and 4) litter sieving. We used a small soil corer (Ø 5 cm, two samples per plot) to sample the small mesofauna and a large soil corer (Ø 20 cm, two samples per plot) to sample the soil macro fauna. Animals were extracted from these soil cores by heat (Kempson et al.1963). We extracted earthworms from the soil by pouring a mustard solution on the ground (100 g ground mustard seed in 10 l water) (Eisenhauer et al. 2008). To run the mustard extraction, we fenced an area of 0.25 m^2 and removed the litter covering the soil. Then, we applied five litre mustard solutions twice with 15 min between applications. Earthworms escape the mustard solution by leaving the soil pores and going aboveground. These earthworm individuals were manually collected. To sample the mobile macro fauna living within and on the litter layer we sieved 1 m^2 of litter material. This was done in four fenced 0.25m^2 subplots that were chosen randomly within a plot to account for microclimatic variations. We removed the litter layer of the subplots and used metal sieves with a mesh size of one centimetre. Animals and fine litter falling through the sieves were collected in a plastic bin. We collected all individuals out of the bins and controlled the plots for 20 min to collect individuals that escaped the sampling.

Earthworms and individuals collected with the sieves were preserved for further analyses. The soil cores were transferred to the laboratory and the soil fauna was extracted from the soil cores using a high gradient heat extractor method (Macfadyen 1961).

Species identification

Species were identified to the species level. In cases where identification to the species level was not possible (e.g. juveniles), individuals were identified to the lowest possible level. Additionally, the length or the weight of each individual was measured for later food web construction, and lengths were converted into masses by specific mass-length regressions. We used regressions ranging from phylogenetic class level to family specific regressions when available to provide the most accurate level of body masses for the species (Ehnes et al. 2011). We divided the species into size classes if the masses of individuals within one species differed by more than one order of magnitude, because we expected size-dependent feeding interactions for some of the generalist predators (Rall et al. 2011, 2012). For subsequent analyses and the construction of the food webs, we calculated the mean weights across all individuals of the population(either species or size class of a species).

Food web construction

We constructed 48 forest soil food webs following several steps. 1) We started with a species list including all species of all plots. 2) The feeding classes of species were based on available data from stable isotopes analyses of soil animals. Concentrations of the naturally occurring heavy isotope of nitrogen (^{15}N) increase from food sources to consumers (Peterson and Fry 1987, Scheu 2002). The enrichment in ^{15}N content of detritivores has been shown to below, ranging around 0.5 ‰ relative to the detritus resource (Vanderklift and Ponsard 2003). The average enrichment in ^{15}N content for predators is suggested to be 3.4 ‰ above

Table 1. F-table of the general linear model ($\log_{10}$ food web parameter ~ food web type × ($\log_{10}$ connectance + $\log_{10}$ species richness)) of different topological food-web parameters depending on food web type and connectance and species richness and the interactions of food web type with connectance and species richness.

	Intercept 'other'			Intercept 'soil'			Slope species richness			Slope connectance			Foodw. type x sp. rich.			Foodw. type x conn.		
Variable	Estimate	F	p	Estimate	F	p	Estimate	F	p	Estimate	F	p	Estimate	F	p	Estimate	F	p
Cluster coeff. (Clust)	0.196	758.6	<0.001	0.167	758.6	<0.001	0.083	121.1	<0.001	0.249	305.3	<0.001	−0.069	2.3	n.s.	−0.040	0.9	n.s.
Basal (Bot)	0.197	138.7	<0.001	1.337	138.7	<0.001	−2.775	159.0	<0.001	−3.804	31.2	<0.001	0.742	0.1	n.s.	3.932	3.6	0.049
Intermediate (Int)	0.002	129.5	<0.001	−2.785	129.5	<0.001	2.581	188.2	<0.001	3.965	54.6	<0.001	1.334	0.9	n.s.	−0.535	0.1	n.s.
Top (Top)	−1.270	4.4	0.039	3.167	4.4	0.039	−1.047	12.3	0.001	−0.079	1.5	n.s.	−5.411	5.8	0.018	−8.782	15.1	<0.001
Herbivores (Herbiv)	−0.354	305.1	<0.001	−2.212	305.1	<0.001	0.220	2.8	n.s.	0.645	3.4	n.s.	−0.309	0.1	n.s.	−1.853	4.1	0.044
Omnivores (Omniv)	−1.692	332.9	<0.001	0.012	332.9	<0.001	1.759	122.3	<0.001	2.411	25.7	<0.001	−0.263	0.1	n.s.	−1.722	3.2	n.s.
Cannibals (Cannib)	0.020	863.6	<0.001	0.496	863.6	<0.001	0.816	31.0	<0.001	4.054	223.4	<0.001	−0.281	0.3	n.s.	−1.424	6.3	0.012
Std. dev. Generality (GenSD)	0.283	83.1	<0.001	−0.447	83.1	<0.001	−0.056	12.3	0.001	−0.212	59.7	<0.001	0.220	6.4	0.008	0.054	0.7	n.s.
Std. dev. Vulnerability (VulSD)	0.125	13.7	<0.001	0.024	13.7	<0.001	0.016	0.9	n.s.	−0.097	19.5	<0.001	−0.077	0.8	n.s.	−0.121	1.9	n.s.
Max. similarity (MxSim)	2.262	5.6	0.019	−2.476	5.6	0.019	−0.370	2.2	n.s.	−0.295	0.2	n.s.	1.368	1.0	n.s.	0.559	0.2	n.s.
Mean trophic level (mean.TL)	0.459	288.3	<0.001	0.372	288.3	<0.001	0.145	53.7	<0.001	0.227	31.7	<0.001	−0.144	1.5	n.s.	−0.034	0.2	n.s.
Max. trophic level (Max.TL)	0.592	237.7	<0.001	0.485	237.7	<0.001	0.076	18.1	<0.001	0.039	0.9	n.s.	−0.136	1.6	n.s.	0.076	18.1	n.s.
Char. path length (CPL)	0.363	16.4	<0.001	0.041	16.4	<0.001	−0.038	112.4	<0.001	−0.186	773.6	<0.001	−0.004	0.0	n.s.	0.021	0.7	n.s.
Motive appar. compet. (MAC)	−0.532	187.7	<0.001	−7.552	187.7	<0.001	−0.406	4.8	0.031	−1.326	21.6	<0.001	2.319	5.2	0.024	−1.948	2.2	n.s.
Motive trophic chain (MTC)	−1.485	187.3	<0.001	3.695	187.3	<0.001	−0.676	30.5	<0.001	−0.978	11.0	0.001	−0.589	0.6	n.s.	1.501	2.8	n.s.
Mot. exploitat. compet. (MEC)	−2.216	109.2	<0.001	1.798	109.2	<0.001	0.331	1.7	n.s.	−0.210	3.4	n.s.	−2.879	7.2	0.008	−3.535	10.7	0.001
Motive intra guild pred. (MIGP)	−1.499	469.6	<0.001	4.908	469.6	<0.001	1.368	88.1	<0.001	3.497	158.3	<0.001	−2.188	6.9	0.010	−0.583	0.8	n.s.
Degree correlation (DC)	−0.084	81.1	<0.001	0.424	81.1	<0.001	0.132	15.2	<0.001	0.271	17.5	<0.001	−0.117	0.3	n.s.	0.095	0.1	n.s.
Rel. modularity (relMod)	−0.448	160.8	<0.001	0.434	160.8	<0.001	0.402	201.0	<0.001	0.074	0.0	n.s.	−0.066	0.1	n.s.	0.271	1.8	n.s.

their prey (Oelbermann and Scheu 2002, Post 2002).We used available data on ^{15}N content to group the species along a trophic level axis and to separate the basal species from the higher trophic levels (Oelbermann and Scheu 2002, Schneider et al. 2004, Chahartaghi et al. 2005, Klarner et al. 2013, 2014). We pre-grouped all species into feeding classes (depending on their stable isotope enrichment and literature data): detritivores (leaf and root litter), secondary decomposers (litter, microorganisms and fungi), microbivores (bacteria, protozoa), herbivores (algae, living roots), fungivores and predators (different trophic levels). 3) We assigned feeding links from detritivores, secondary detritivores, microbivores, herbivores and fungivores to their resources using literature (Bardgett 2005, Dunger 2008) and stable isotope data. For omnivores and predator species we evaluated every possible predator–prey feeding interaction. For centipedes, nematode feeding oribatid mites and collembolans we used data from molecular gut content analyses to determine feeding interactions with possible prey species (Eitzinger and Traugott 2011, Eitzinger et al. 2013, Günther et al. 2014, Heidemann et al. 2014). 4) Further, we used data from own laboratory feeding trials with pairwise combinations of as many species as possible in small arenas with a single leaf as habitat structure to test feeding interactions. 5) For some species we had no molecular or stable isotope data and no feeding trials. For these species, we searched the literature e.g. monographs, identification keys and articles. We also used related species, families or communities present at our sampling sites and information about their feeding interactions to verify our suggested links and to get an overview of the ecology and feeding preferences (cannibalistic feeding, intra guild predation, etc.) of these species (Christiansen 1964, Moulder and Reichle 1972, Walter and Ikonen 1989, Karg 1999, Dunger 2008). We excluded several feeding interactions, for example oribatid mites are strongly sclerotized and therefore most adult oribatid mites can only be fed on by specialist predators (Peschel et al. 2006). We also considered behavioural characteristics regarding the probability of a feeding interaction, e.g. web building spiders do not encounter soil living collembolans. Further, we chose a body mass range based on several studies from 1 to 1/100 of the predators body size to define a size window within which feeding interactions are possible (Moulder and Reichle 1972, Brose et al. 2006, 2008, Rall et al. 2011).We allowed exceptions from this body mass range for spiders and centipedes (10 to 1/100) and for specialists (no size limitations) such as Scydmaenidae which are specialist oribatid mite predators (Peschel et al. 2006). If the literature data and molecular data about the feeding interactions disagreed, we used the molecular or feeding trial data to assign a link and not the data from the literature. We reviewed the resulting interactions with expert knowledge to account for specialists' species and exceptions to our assumptions (Scheu et al. pers. comm.). Together, these five steps yielded binary food web matrices including links estimated by different methods, which is comparable to the food webs of other ecosystem types to which they are compared.

Statistical analysis

We analysed a total of 125 food webs, 77 of which were from aquatic and terrestrial ecosystems, obtained from a food-web database (Riede et al. 2010), and 48 of which were

Table 2. F-table of the linear mixed effect model ($\log_{10}$ food web parameter ~ land use type × ($\log_{10}$ connectance + $\log_{10}$ species richness)) of different topological food-web parameters depending on food web type and connectance and species richness with the random factor exploratory area (AEW, HEW and SEW). Interactions of food web type with connectance or species richness were all non-significant and are not included in the table.

	Managed coniferous			Managed young beech			Managed beech old			Unmanaged beech			Slope connectance			Slope spec. rich.		
Variable	Estimate	F	p	Estimate	F	p	Estimate	F	p	Estimate	F	p	Estimate	F	p	Estimate	F	p
Cluster coeff. (Clust)	0.350	2606	< 0.001	0.352	2606	< 0.001	0.305	2606	< 0.001	0.347	2606	< 0.001	0.194	110	< 0.001	0.034	0.89	n.s.
Basal (Bot)	0.127	2368	< 0.001	0.156	2368	< 0.001	0.100	2368	< 0.001	0.129	2368	< 0.001	0.005	2.09	n.s.	−0.034	125	< 0.001
Intermediate (Int)	0.324	5821	< 0.001	0.170	5821	< 0.001	0.129	5821	< 0.001	0.260	5821	< 0.001	0.068	34.7	< 0.001	0.103	10.7	0.002
Top (Top)	−0.163	13.6	< 0.001	0.111	13.6	< 0.001	0.224	13.6	< 0.001	−0.036	13.6	< 0.001	−0.127	28.4	< 0.001	−0.156	5.14	0.030
Herbivores (Herbiv)	−0.156	439	< 0.001	−0.060	439	< 0.001	0.090	439	< 0.001	0.031	439	< 0.001	−0.026	7.49	0.010	−0.023	0.05	n.s.
Omnivores (Omniv)	0.197	12546	< 0.001	0.108	12546	< 0.001	0.029	12546	< 0.001	0.106	12546	< 0.001	0.008	12.6	0.001	0.099	23.2	0.001
Cannibals (Cannib)	0.138	423	< 0.001	0.203	423	< 0.001	0.226	423	< 0.001	0.208	423	< 0.001	0.200	83.5	< 0.001	0.037	3.43	n.s.
Std. dev. Generality (GenSD)	−0.374	2071	< 0.001	−0.099	2071	< 0.001	−0.103	2071	< 0.001	−0.061	2071	< 0.001	−0.141	13.8	0.001	0.144	23.5	< 0.001
Std. dev. Vulnerability (VulSD)	0.314	1340	< 0.001	0.044	1340	< 0.001	0.022	1340	< 0.001	0.071	1340	< 0.001	−0.222	73.8	< 0.001	−0.003	1.16	n.s.
Max. similarity (MxSim)	0.297	21907	< 0.001	0.123	21907	< 0.001	0.192	21907	< 0.001	0.211	21907	< 0.001	0.021	3.06	n.s.	0.043	11.4	0.002
Mean trophic level (mean.TL)	0.978	7920	< 0.001	0.950	7920	< 0.001	0.681	7920	< 0.001	0.704	7920	< 0.001	0.121	39.0	< 0.001	0.039	0.13	n.s.
Max. trophic level (Max.TL)	1.394	17746	< 0.001	1.323	17746	< 0.001	1.062	17746	< 0.001	0.888	17746	< 0.001	0.139	10.5	0.003	−0.059	2.10	n.s.
Char. path length (CPL)	0.317	57486	< 0.001	0.398	57486	< 0.001	0.450	57486	< 0.001	0.364	57486	< 0.001	−0.164	124.7	< 0.001	−0.063	6.75	0.014
Motive appar. compet. (MAC)	−0.300	31.3	< 0.001	−0.271	31.3	< 0.001	0.131	31.3	< 0.001	0.019	31.3	< 0.001	−0.078	5.66	0.023	−0.045	0.39	n.s.
Motive trophic chain (MTC)	0.419	2388	< 0.001	0.264	2388	< 0.001	0.376	2388	< 0.001	0.279	2388	< 0.001	0.049	1.59	n.s.	−0.107	24.8	< 0.001
Mot. exploitat. compet. (MEC)	0.208	13.3	< 0.001	0.192	13.3	< 0.001	−0.161	13.3	< 0.001	−0.015	13.3	< 0.001	−0.215	7.79	0.009	0.000	0.82	n.s.
Motive intra guild pred. (MIGP)	0.367	125	< 0.001	0.246	125	< 0.001	0.258	125	< 0.001	0.282	125	< 0.001	0.154	48.0	< 0.001	−0.006	0.01	n.s.
Degree correlation (DC)	−0.378	16.3	< 0.001	0.143	16.3	< 0.001	0.254	16.3	< 0.001	0.443	16.3	< 0.001	0.262	15.6	< 0.001	0.014	0.26	n.s.
Rel. modularity (relMod)	0.649	1500	< 0.001	−0.179	1500	< 0.001	−0.152	1500	< 0.001	−0.033	1500	< 0.001	0.260	26.7	< 0.001	0.362	18.1	< 0.001

soil food webs that we constructed. The number of species in these food webs ranged from 22 to 492 and the number of links from 42 to 16 136 links. In total, the food webs of our analyses included 45 lake food webs, six marine food webs, two estuary food webs, 14 stream food webs, 10 terrestrial aboveground food webs and the 48 new forest soil food webs.

We analysed 22 food web parameters for each of the 125 food webs and we assigned ecosystem types to every food web to enable comparison of the food web parameters for each different ecosystem type. The 22 food web properties we analysed were: 1) the total number of species in the food webs; 2) the average number of links per species; 3) connectance (connection probability: ratio between number of links realized divided by number of links possible); 4) the clustering coefficient (the probability that two nodes which are both linked to a third node are also linked); the fractions of 5) basal species (species without resources); 6) intermediate species (species with resources and predators); 7) top species (species with resources but without predators); 8) herbivores (species that consume basal species); 9) omnivores (species consuming resources across more than one trophic level); 10) cannibals (species partially feeding on con-specifics); 11) the standard deviations of the species' generality (the number of resources) and 12) vulnerability (the number of predators); 13) the maximum similarity (mean across taxa of the maximum trophic similarity in the link pattern of each taxon to other taxa); 14) the mean trophic level (mean of the short weighted trophic level), 15) the maximum trophic level (maximum short weighted trophic level); 16) the characteristic path length (mean over all shortest trophic paths between any pair of species in a food web); the fractions of food web motifs: 17) apparent competition, 18) trophic chain, 19) exploitative competition and 20) intra guild predation; 21) the degree correlation (correlation of degree between species pairs with interaction); 22) the modularity (Cattin et al. 2004, Dunne et al. 2004, Guimerà and Amaral 2005a, b, Dunne 2009, Riede et al. 2010).

Many food web parameters are correlated with connectance and species richness (Dunne et al. 2002a, Riede et al. 2010), and these relationships have been used to develop different food web models such as the niche model (Williams and Martinez 2000). Therefore, a direct comparison of the food web parameters needs to be disentangled from differences in connectance and diversity between the communities compared. To cope with this problem, we followed prior work (Riede et al. 2010) and included the power-law scaling of the food-web parameters in the statistical models testing for differences between food web types.

In our first analysis, we addressed if the diversity or complexity of the soil food webs differs from those of other ecosystem types. We used ANOVAs to analyse the differences between the factorial independent variable food-web type (soil food web or other food web type) using the logarithm of the food web parameters species richness, average number of links per species and connectance as dependent variables.

Second, we analysed the scaling relationships of the remaining 19 topological food web parameters (Table 1) with connectance and species richness and whether the topological food web parameters differed between our soil food webs and food webs of other ecosystems. We used a general linear model to analyse the scaling relationships the food web parameters as dependent variable and food web type (soil, others) as factorial independent variable and the interactions with connectance and species richness (parameter ~ food web type X ($\log_{10}$(connectance) X $\log_{10}$(species richness)). For food web parameters that are proportions (e.g. fraction of top, intermediate, basal species and fractions of food web motives) we used a general linear model with a binomial distribution. Continuous food web parameters were log10 transformed. Significant slopes were interpreted as an indication of a scaling relationship with species richness or connectance. Significant interactions were interpreted as a difference in the scaling relationships between food web types. Differences in the intercepts were interpreted as a difference in the topological parameter between the ecosystem types. To address which of the 'other food webs' were responsible for our results, we also analysed the connectance and species richness corrected residual variation of the previous scaling relationships of the19 food web parameters. We used ANOVAs to analyse the differences between the food web types soil, terrestrial aboveground, stream, lake and marine. We used the residual variation of the food web parameters as the independent variable and the ecosystem types (soil, terrestrial aboveground, stream, lake, marine) as factorial dependent variables. The means of the food web parameters on different ecosystem types were compared by Tukey HSD posthoc tests with Bonferroni corrections (Tukey's honestly significant difference test; (Sokal and Rohlf 1995).

Third, to analyse the effects of land use intensity on forest soil food web structural parameters, we used linear mixed effects models. We employed the logarithm of the food web parameters as dependent variables. As independent variables we included the factorial

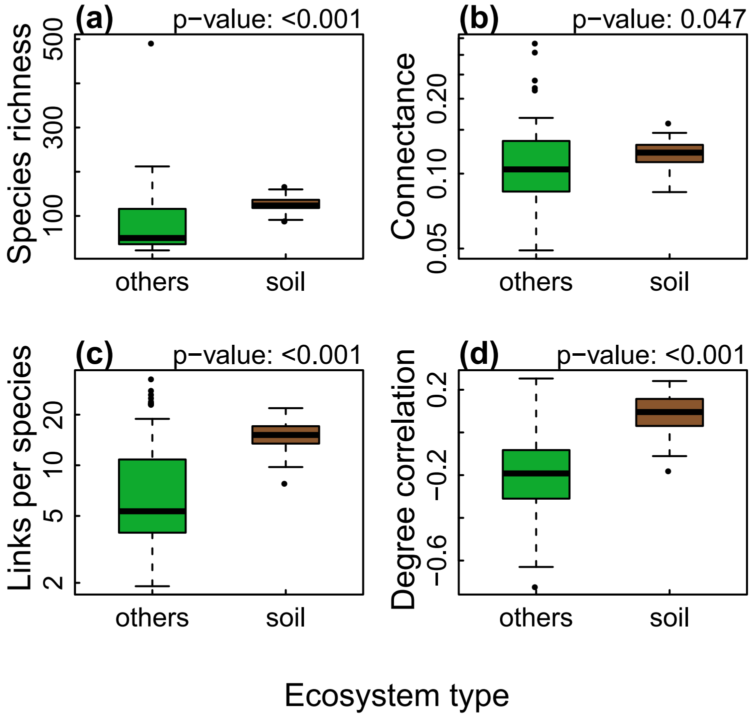

Figure 2. Boxplots with boxes representing the 95% quantiles and the mean of (a) connectance (b) the number of species (c) the number of links per species and (d) the degree correlations.

variable land use (coniferous, beech young, beech intermediate, beech old)and the logarithm of connectance and species richness and the interaction between the logarithm of connectance and species richness (Table 2). We included exploratory site (Schorfheide, Hainich, Alb) as a random factor to account for the effects of large-scale landscape characteristics on food web structure. The means of the topological food web parameters at the different forest types were then tested using a post hoc Tukey HSD test with Bonferroni corrections (Tukey's honestly significant difference test; (Sokaland Rohlf 1995).

All statistical analyses were carried out using the statistical software R 3.0.1. Linear mixed effects models were carried out using the R package nlme (Pinheiro et al. 2013). The post hoc tests were carried out using the R package multcomp (Hothorn et al. 2008).

Results

Food web structure

We assembled 48 forest soil food webs ranging from 89 to168 species with 729 to 3344 trophic links. The soil food webs had connectance values ranging from 0.084 to 0.16.We compared the forest soil food webs to a food web set comprising lake, stream, marine, estuary and terrestrial aboveground ecosystems (Riede et al. 2010). The species number in this data set ranged from 22 to 492 species with 42 to 16 136 links and connectance values ranging from 0.04 to 0.33.

In our first analysis, the ANOVA indicated that connectance of soil food webs was only slightly different when compared to the other ecosystem types (Fig. 2b). In contrast, the species number was higher in soil food webs (Fig. 2a) and consequently the number of links per species was also higher in soil food webs (Fig. 2c). Thus, while soil food webs have a comparable degree of connectance as other ecosystems, they comprise more species that are more densely linked.

Scaling of food web parameters with connectance and species richness

In our second analysis, we comprehensively analysed how the food web parameters for the soil food webs and the other food web types scaled with species richness and connectance (Riede et al. 2010). The range in connectance and species richness (x-axis) of the soil food webs was smaller compared to the other ecosystem types (Fig. 3, 4; brown dots). For 11 of the 19 food web parameters, the scaling of soil food webs with connectance and species richness in soil food webs was similar to that in other ecosystems, i.e. they had the same slope (Fig. 3, 4, Table 1).Five of the food web parameters exhibited significant interactions between the food web type and connectance and five with species richness, i.e. the scaling relationship of soil food webs differed from the scaling of the other food web types. In detail, we found an interaction of food web type with connectance for the food web parameters fraction of basal species, fraction of top species, fraction of herbivores, fraction of cannibalistic species and for

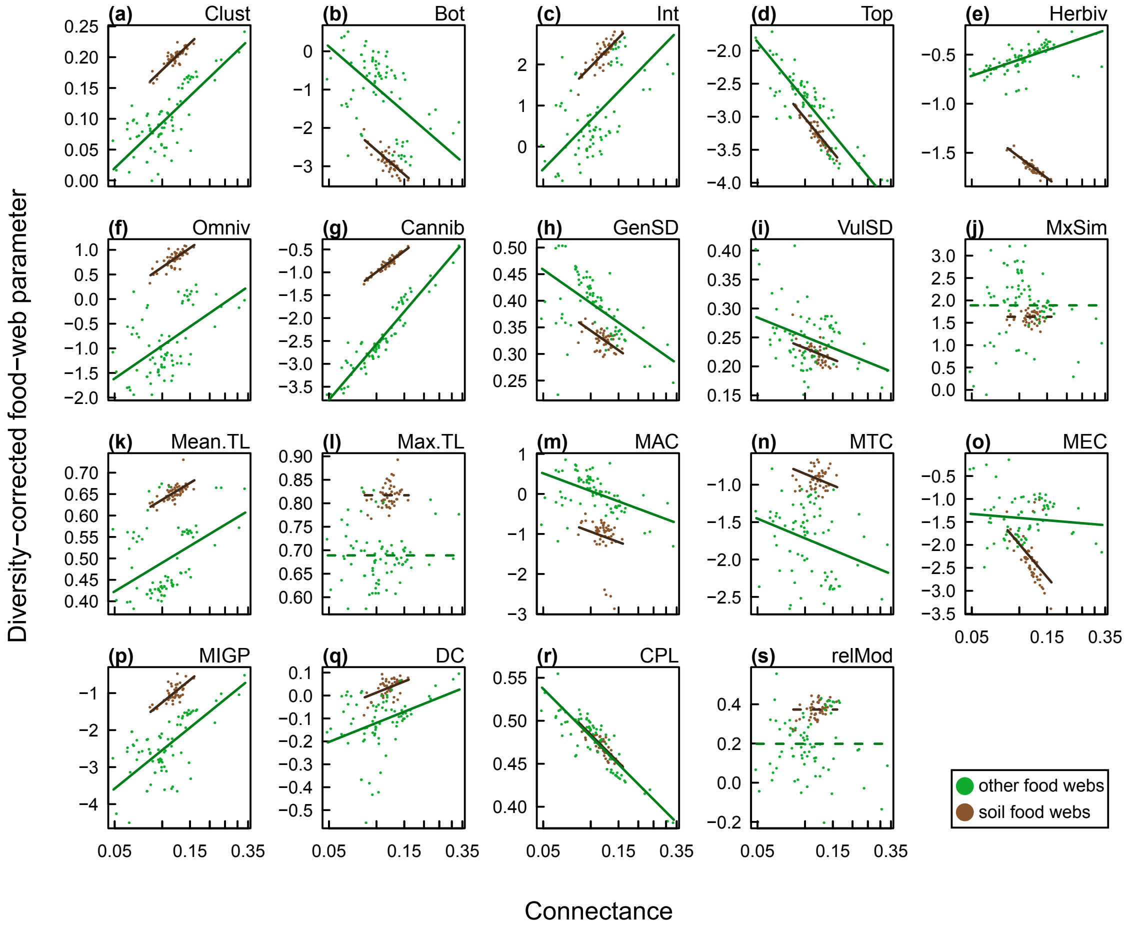

Figure 3. Complexity scaling of 19 species-richness corrected food web properties (partial residuals of the $\log_{10}$ or logit transformed food web parameters of the scaling relationships with species richness, Fig. 4) for each food web property (a-s) and ecosystem type. Soil food webs are plotted in brown, other food webs in green. Dashed lines indicate a non-significant slope of the scaling relationship. For abbreviations of food-web structural parameter see Table 1 or Fig. 5.

the fraction of the motif exploitative competition (Fig. 3d–e, g, o, Table 1), and we found a significant interaction of food web type and species richness for the food web parameters fraction of top predators, standard deviation of generality fraction of motive apparent competition, fraction of motive exploitative competition and for the fraction of the motif intra guild predation (Fig. 3d, h, m, o–p, Table 1). Fraction of herbivores, fraction of the motive exploitative competition and maximum similarity were the only food web parameters that showed no significant scaling relationship with connectance and species richness (Fig. 3, 4, Table 1). The standard deviation of vulnerability showed only a significant scaling with connectance but not with species richness. The fraction of top predators, the maximum trophic level and the relative modularity showed only a significant scaling relationship with species richness but not with connectance. Overall, we found a significant scaling of 13 food web parameters with connectance(Fig. 3, Table 1), and 15 food web parameters scaled significantly with species richness (Fig. 3, Table 1).We found eight food web parameters which scaled differently in soil food webs compared to other food webs(significant interactions)(Fig. 3, 4, Table 1). As in other ecosystems, the network structure of the soil food webs varies with connectance and species richness, and the large majority of the food-web parameters exhibit a similar scaling behaviour across ecosystem types.

Differences between soil food webs and other ecosystems

We further compared the topology between soil and other ecosystems as expressed by the differences in the intercept of the scaling relationships. We found a higher amount of omnivory in soil food webs (Fig. 3f, 4f), which is mainly an effect of stream, and lake food webs that have much lower levels of omnivory (Fig. 5f). Also, the fraction of cannibalistic species was higher in soil food webs compared to the other ecosystems (Fig. 3g, 4g, Table 1), which was consistent across all other food web types (Fig. 5g). This suggests that soil food webs are characterized by a higher level of generalist feeding and a higher number of species feed on different trophic levels. Moreover, the intercept of the standard deviation of generality was lower in soil food webs compared to other ecosystems (Fig. 3h, 4h, Table 1).This indicates that the omnivorous predators in soil food webs have a more equal number of prey species (i.e. the same generality) in contrast to a higher variation in prey species number in other ecosystems (i.e. different values of generality). This difference is most pronounced concerning lake and stream food webs (Fig. 5h). Additionally, we found a higher amount of intra-guild predation motifs in soil food webs compared to other ecosystems (Fig. 3p, 4p, Table 1),which is consistent across all other ecosystem types (Fig. 5p). This suggests that in soil food webs there are more species that prey not only on species of a lower trophic level but also consume other predators. The intercept of the clustering coefficient was higher in soil food webs compared to other food webs (Fig. 3a, 4a, Table 1), which is also consistent across all other ecosystem types (Fig. 5a). This is in line with our finding of a higher amount of intra guild predation motifs, because the clustering coefficient describes the probability that two species that are both connected to a third species are therefore also connected. Regarding these feeding related food web properties (the larger fraction of omnivores, the higher intercept of intra guild predation motifs as well as the higher amount of cannibalism) soil food webs overall have a structure that is more based upon opportunistic feeding. The predators have a higher amount of links (higher number of links per species in soil food webs) as they feed on more trophic levels of the food web. The intercepts of mean trophic levels as well as the maximum trophic levels were higher in soil food webs compared to food webs of other ecosystems (Fig. 3k–l, 4k–l, Table 1), which is most pronounced for stream and lake ecosystems (Fig. 5k–l). Similarly, the intercept of the frequency of the tri-trophic chain motif was also higher in soil food webs compared to other food webs (Fig. 3n, 4n, Table 1), which is consistent across all other food-web types (Fig. 5n). Hence, these results suggest that the soil food webs are composed of more chains. In addition, we also found that the characteristic path lengths, expressing the average number of links between any pair of species in the food web, is longer in soil food webs (Fig. 4r, 5r, Table 1), which could be also a result of longer chains.

Soil food webs have a positive degree correlation coefficient (Fig. 2d), which indicates that species with a similar number of feeding interactions tend to interact with each other (high degree species with high degree species; low degree species with low degree species). In contrast, the degree correlation of food webs from other ecosystems is negative indicating reciprocal specialisation of species with a high number of feeding interactions on species

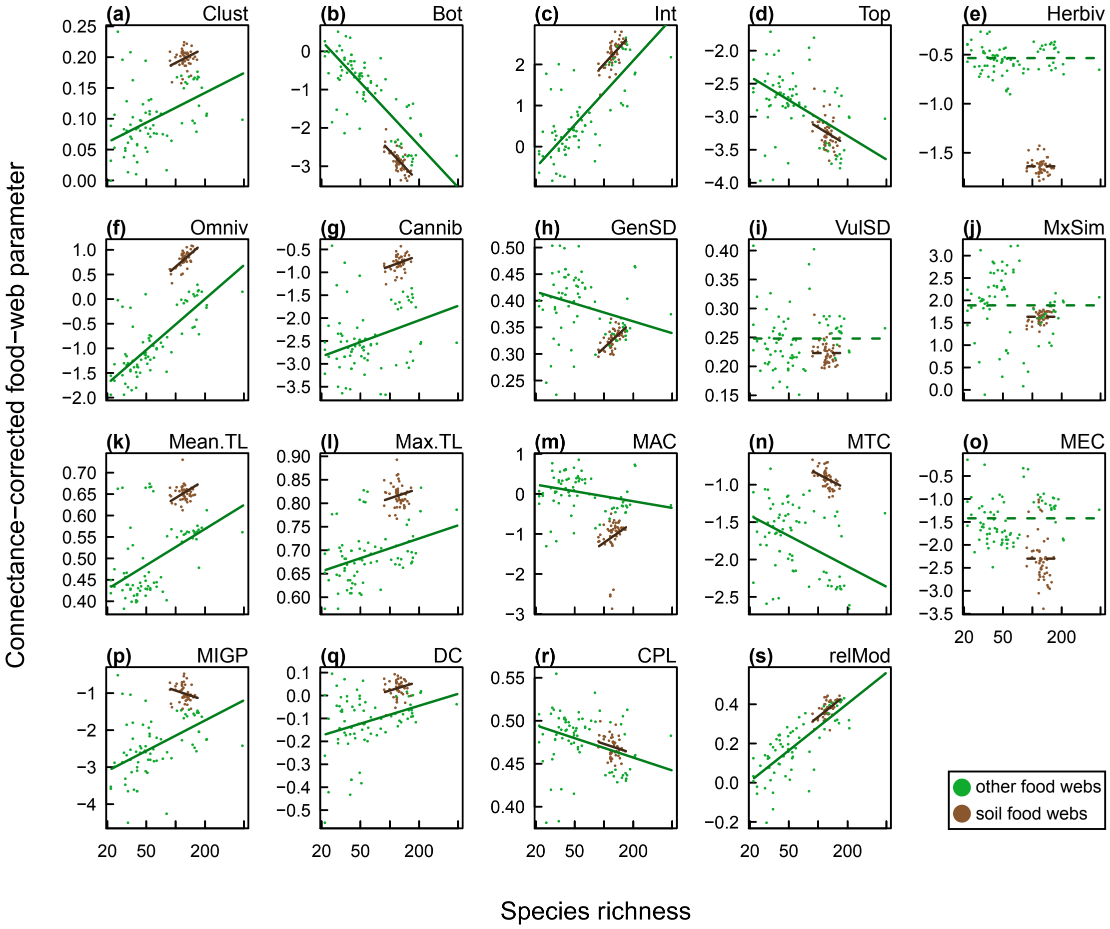

Figure 4. Diversity scaling of 19 connectance-corrected food web properties (partial residuals of the $\log_{10}$ or logit transformed food web parameters of the scaling relationships with connectance, Fig. 3) for each food web property (a-s) and ecosystem type. Soil food webs are plotted in brown, other food webs in green. Dashed lines indicate a non-significant slope of the scaling relationship. For abbreviations of food-web structural parameter see Table 1 or Fig. 5.

with a low number of feeding interactions. These differences in the degree correlations could explain that soil food webs showed a more interwoven and opportunistic architecture indicated by the high amount of omnivory, intra guild predation and cannibalism (Fig. 3f–g, p, 4f–g, p, Table 1), but at the same time also more chain like structures indicated by the high amount of trophic chain motives and a higher characteristic path length. Together, these two characteristics balance each other to yield similar connectance levels as other food web types (Fig. 2b).

We found smaller fractions of the apparent competition and exploitative competition motifs in soil food webs compared to food webs of other ecosystems (Fig. 3m, o, 4m, o, Table 1), which is consistent across all other food-web types except for marine food webs which have an equal fraction of apparent competition motives (Fig. 5m, o). However, we found higher fractions of the intra-guild predation and tri-trophic chain motifs. In soil food webs, competition between predators for a prey species and competition of two prey species resulting through a shared predator were less frequent.

Effects of land use type on food web structure

Interestingly, the forest type did not influence the species richness (p = 0.52), connectance (p = 0.3) or the number of links per species (p = 0.52) of our food webs. Moreover, the effect of land use intensity on food web structure was generally very weak as we found significant effects on only 7 of the 22 parameters (fraction intermediate species, fraction of top species, fraction of cannibals, standard deviation of vulnerability, mean trophic level, maximum trophic level and the fraction of intra-guild predation motifs) and differences between the forest types were low (Fig. 6, Table 2). In six cases, we found significant differences between coniferous and deciduous forests types. The fraction of top and intermediate species was higher in coniferous forests than in the forest types of young managed beech forests (Fig. 6a–b, Table 2), whereas the fraction of cannibalistic species was lower in coniferous forest as in young managed beech forests (Fig. 6c, Table 2). We found also differences in the standard deviation of vulnerability between coniferous and old beech forests (Fig. 6d, Table 2). This pattern could be driven by the higher fraction of top predator species which have a vulnerability of zero and therefore increase the variation in vulnerability. The maximum trophic level was higher in coniferous forests than in unmanaged beech forests, and we found a higher amount of the motif intra guild predation in coniferous forests than in all of the beech forest land-use types (Fig. 6e–f, Table 2). Additionally to the effects of coniferous forests, we found differences within the beech forests land use types. The mean trophic levels were higher in young managed beech forests compared to the unmanaged beech forests (Fig. 6g, Table 2). Interestingly, the effects of land use type within the beech land use types were mainly effects of the land use type young managed beech forest which differed from the other beech forests but not from the coniferous forest types. We found no significant effects of land-use intensity on the other 15 structural food web properties. Overall, our results suggest that – despite some differences between coniferous and deciduous forests and very few within the deciduous forest – the structure of soil food webs seems to be relatively robust to changes in land use intensity expressed by the different forest types.

Discussion

We found strong differences in the structural properties of soil food webs compared to those of other ecosystems. Despite this, soil food webs had a similar complexity (i.e. connectance) as other ecosystems, but interestingly they also had a higher link density and clustering coefficient. Additionally, we found soil food webs to be more opportunistic in their organisation, which is illustrated by the high number of omnivore and cannibalistic species. Also, the number of trophic levels in soil food webs is higher and the feeding interactions are more organized in chains and with more intra guild predation motifs compared to the other ecosystems. This is in line with our initial hypothesis and could be a result of the characteristics of the soil ecosystem as discussed below. In addition, the differences between the forest types were only marginal, which indicates that the structure of soil food web seems to be relatively robust to the differences in the analysed land-use intensity. Our structural analyses illustrate the influence of habitat properties on food web structure and could help to

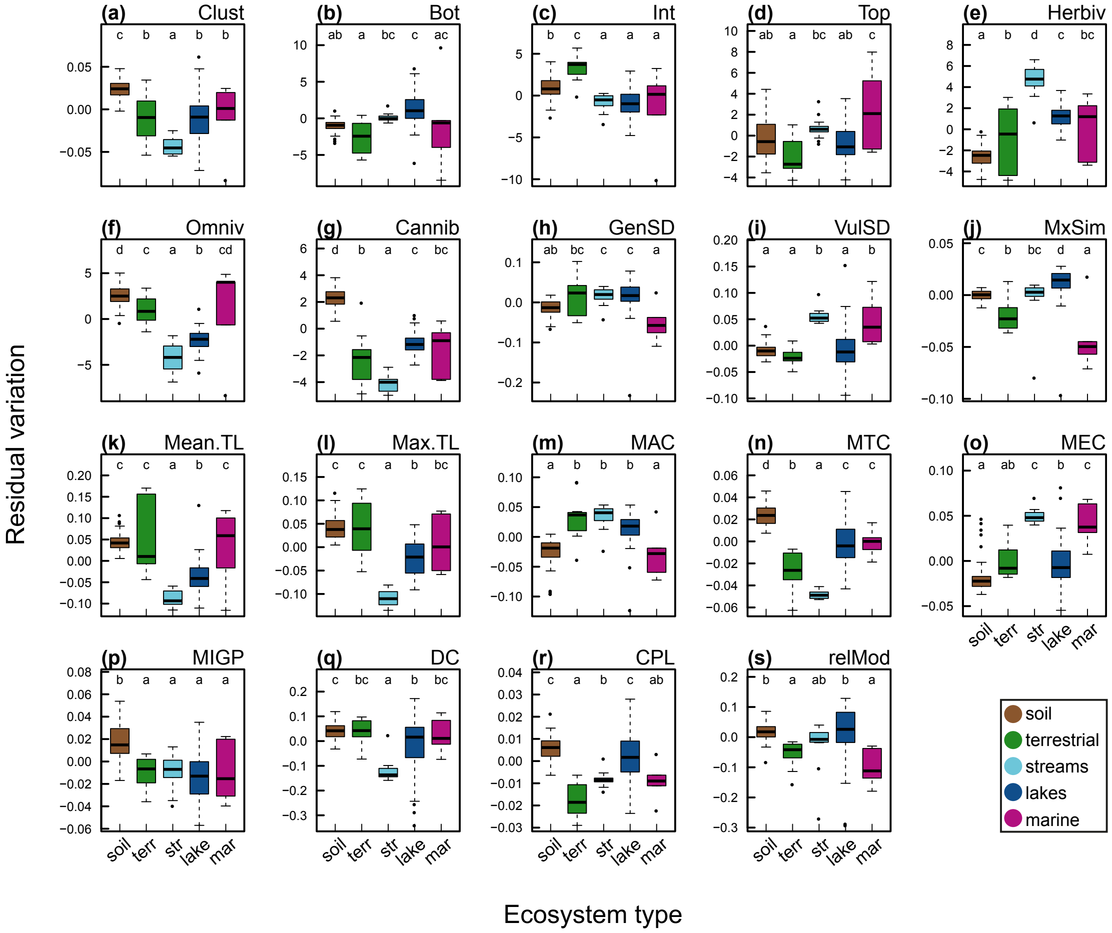

Figure 5. Boxplots with boxes representing the 95% quantiles and the mean of the connectance and species richness corrected residual variation (see methods for details) of (a) the clustering coefficient (Clust), (b) the fraction of basal species (Bot), (c) the fraction of intermediate species (Int), (d) the fraction of top predators (Top), (e) the fraction of herbivore species (Herbiv), (f) the fraction of omnivore species (Omniv), (g) the fraction of cannibalistic species (Cannib), (h) the standard deviation of generality (GenSD), (i) the standard deviation of vulnerability (VulSD), (j) the maximum similarity (MxSim), (k) the mean trophic level (Mean.TL), (l) the maximum trophic level (Max.TL), (m) the frequency of the motive apparent competition (MAC), (n) the frequency of the motive tri trophic chain (MTC), (o) the frequency of the motive exploitative competition (MEC), (p) the frequency of the motive intra guild predation (MIGP), (q) the degree correlation (DC), (r) the characteristic path length (CPL), and (s) the relative modularity (relMod) of food webs from different ecosystem types. Different letters indicate significant differences between means ($p < 0.05$, Tukey's HSD).

extend our mechanistic understanding of the forces that structure the soil communities and influence their functioning.

Differences in diversity and complexity

Soil food webs have a similar connectance as food webs from other ecosystems supporting prior conclusions that food web connectance may be independent of habitat type (Martinez 1992). In contrast, the soil food webs have a higher diversity, which is consistent with their classic description as the "poor man's rainforest" (Giller 1996). However, the high species richness of these soil networks may also be caused by the fact that most individuals were identified to the species level. Consequently, the analysed soil food webs are very highly resolved with fewer nodes that comprise organisms only identified to the family or genus level. The higher species richness in combination with an equal connectance leads to a higher amount of links per species, which indicates that soil food webs are more densely linked than the food webs of other ecosystems. However the differences in food web structure might also be a result of methodical differences in food web constructions (e.g. higher taxonomic resolution, different methods to establish links). While we have used standard protocols for building food webs, these methodological effects cannot be ruled out entirely. In future studies, molecular gut content analyses (Eitzinger et al. 2013, 2014) might help to assemble food webs in different ecosystems that are constructed using the same methods. Currently, however, such data sets are not available, and the use of high quality food-web data from different studies as in our approach is providing the most reasonable and ecologically realistic insight in structural differences of natural communities.

As in a previous study, scaling of different food web parameters with connectance and species richness was found (Riede et al. 2010). We extended this analysis and included new data for 48 forest soil food webs. We found a comparable scaling of food web properties with connectance and species richness in the new combined data set compared to the scaling of the previous study. Interestingly we found ten significant interactions, where soil food webs scaled differently compared to other food webs. Most of the interactions had a weak effect on the slope of the scaling relationships (Fig. 3, 4). We found a significant interaction of the food web type and the motif apparent competition, which scaled strongly positively with species richness in soil food webs whereas it scaled negatively with species richness in other ecosystems. The slope of the fraction of the motif exploitative competition with connectance was steeper in soil systems compared to other ecosystems. This could be a direct effect of the higher connectance, because the possibility of an intra-guild predation motif rises with a higher amount of links present in a food web. Interestingly, we found no interaction with connectance and the fraction of the motif apparent competition, which should also be influenced by a higher connectance. Further the standard deviation of generality in soil food webs scaled less strongly with species richness than in other ecosystems. This reflects that the generality is more evenly distributed in soil food webs. Interestingly the high values in the standard deviation of generality were reached in food webs with low species richness, whereas the standard deviation of generality was lowest in species rich food webs. Despite the ten interactions of the structural properties with soil food webs and those of other ecosystems, these scaling relationships seem to hold across different ecosystem types (see Riede et al. 2010 for a detailed discussion of the scaling relationships, which is beyond the scope of the present study).

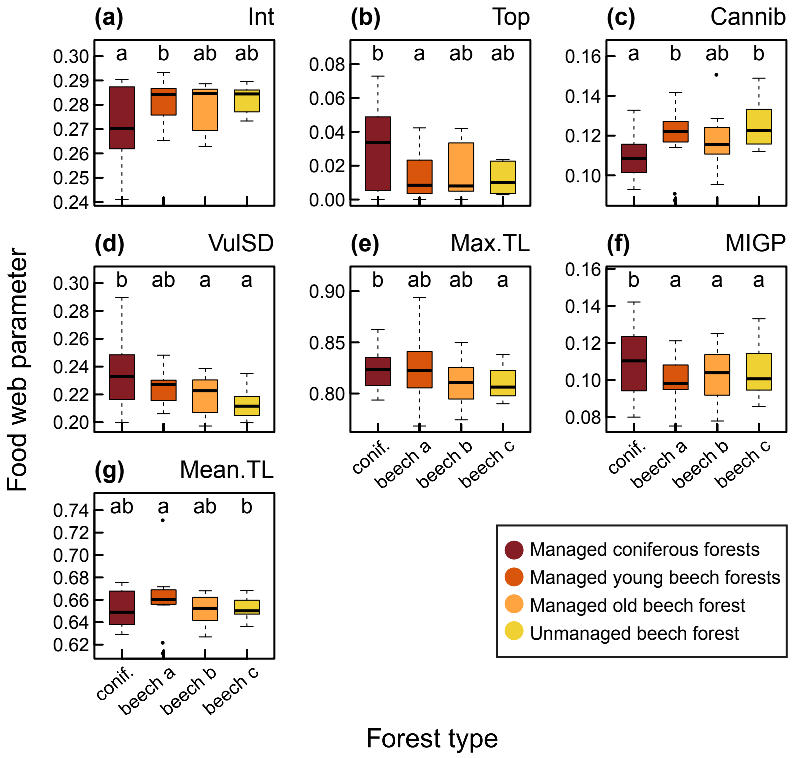

Figure 6. Boxplots of the food web parameters that are significantly affected by different land use intensities: conif (managed coniferous forests), beech a (young managed beech forests), beech b (old managed beech forests) and beech c (unmanaged beech forests). Different letters indicate significant differences between means ($p < 0.05$, Tukey's HSD). For abbreviations of food-web structural parameters see Table 1.

Opportunistic soil food webs

The soil ecosystem is very different in its habitat properties compared to other ecosystems, which is reflected in the structural parameters of the soil food webs. The structure of the soil leads to an evolutionary pressure on the soil living organisms to adapt to the soil habitat (Lavelle 1997, Scheu and Setälä 2002), either in morphological or behavioural ways.

Morphological adaptations of the soil organisms to the porous structure of their habitat are widespread. Many soil arthropods share reduced body appendages. For instance, soil living collembola have a reduced furca and a prolonged body shape (e.g. Tullbergidae, Onychuridae, some Isotomidae), but interestingly collembola living on the litter layer have a furca (e.g. Entomobryidae) (Hopkin 2007). Moreover, centipedes (e.g. Chilopoda or Geophilomorpha) are also morphologically well adapted to the porous structure of the soil. They have a reduced body diameter but still have a large body size due to elongation of their body. Centipedes are well adapted to forage in the porous structure of the soil and share two other characteristic adaptations of soil living predators: the use of poison to kill prey and extra intestinal digestion (Lewis 2007). This provides an adaptive advantage that allows predators to subdue and kill their prey without being much bigger in size (i.e. diameter) and also be able to digest their prey externally in the soil pores. Many morphological adaptations to soils as habitats are also visible in strategies to avoid predation. Oribatid mites, for example, have a strongly sclerotized cuticle and can only be feed on by specialized beetles (Peschel et al. 2006) and therefore avoid predation by the generalist predators in the soil. Overall, our study illustrates for the first time that these differences in habitat properties that cause evolutionary pressures on species may cause visible characteristics at the network level, though this interpretation of our results remains speculative.

In contrast, behavioural adaptations to the soil habitat such as special foraging strategies (e.g. sit and wait predation or omnivory) (Eckschmitt et al. 1997, Scheu and Setälä 2002) are not easily detected, but they should also translate into changes of food web structure. At the food web level, we found these adaptations were expressed as higher amounts of omnivore and cannibalistic species and a larger fraction of intra guild predation motifs. We also found that the standard deviation of generality is lower, which indicates that the higher generality of the species is not driven by few extreme generalists. Instead, this result indicates that generalism as a feeding strategy is widespread across the consumers of the soil ecosystems.

The dominance of intra guild and generalist predation strategies may be a consequence of on the dominance of random encounters among individuals and unselective prey choice by predators. Further, the high intra guild predation and clustering coefficient explains the lower amount of competition motifs (i.e. apparent and exploitative competition) we found in soil food webs: if two predators share a prey species or two prey species are consumed by the same predator the probability of a link between the two predators is higher (high fraction of intraguild predation motifs), consequently the probability of the two prey species being connected is also higher in soil food webs (higher clustering coefficient).

We also found an increased amount of trophic chain motifs and a higher characteristic path length, which is surprising in combination with the high intra guild predation and clustering of the networks. This could be a result of the correlation of the degree of species which are connected that is described by the degree correlation. Soil food webs had a positive degree correlation coefficient, which indicates that species with high degree (i.e. number of interactions) are more often connected to other high degree species, whereas species with a low degree tend to interact also more with low degree species. This yields a network structure in which compartments with mainly generalist consumers resulting in high omnivory, intra guild predation and cannibalism is separated from others with more specialized feeders causing a higher amount of chains and a high characteristic path length. This structure represents a highly significant signature of soil communities.

Higher trophic levels in soil food webs

Nearly 90 % of the primary production is returned to the soil ecosystem by dead organic matter (Coleman 2013). For the soil ecosystem, this detritus is one of the most important energy resources. Because detritus is dead organic matter there are some interesting implications for the feeding relationships, as there is no evolutionary pressure on the resource to avoid predation (Scheu and Setälä 2002). Indirectly though the quality of the detritus is under evolutionary pressure as it is advantageous for the plants, that contribute most to of the detritus pool by their leaf and root litter, to absorb as much of the nutrients from their leaves as possible before leaf abscission (Berg and McClaugherty 2003, Hättenschwiler et al. 2005). Consequently, leaf litter is a very poor resource compared to living tissue or animals leading to low consumption efficiencies (Ott et al. 2012). Therefore, detritus is mostly consumed by bacteria or fungi that have the necessary enzymes to digest cellulose (Cummins 1974, Lavelle 1997). Previous studies have shown that only few animal species are capable of directly digesting detritus or leaf litter. However there are some detritivore species that can digest litter directly e.g. some earthworm species, mites or termites (Swift et al. 1979, Pollierer et al. 2007), but the majority of the soil fauna rely on the bacteria and fungi growing on the litter to decompose the detritus. Thus, we find an additional trophic level in the soil ecosystem above the 'real detritivores', which comprises the secondary decomposer animals feeding on litter material and the associated bacteria and fungi (Swift et al. 1979, Scheu and Setälä 2002, Pollierer et al. 2007). This leads to a higher number of trophic levels in the structure of soil food webs and to a higher fraction of tri-trophic chain motifs (in particular food chains from detritus to microbes to microbivores). In this vein, the energy is channelled through the bacteria and fungi to the mesofauna. The species constituting the mesofauna are not only microbivores but also higher level predators feeding on other mesofauna species. For these mesofauna predators, intra guild predation and cannibalism is supposed to be common (Karg 1999). Further, the predators in the mesofauna are an important resource for macrofauna predators such as centipedes or staphylinid beetles. These long chains of trophic interactions increase the trophic height of the soil food webs even more. Therefore, the differences in the habitat structure and basal resource of the soil system translate to alter the structure of the entire food web.

Effects of land use type on soil food web structure

We found only very weak effects of land use intensity on soil food-web structure and the effects we found could be explained according to the dominant tree species of the community. The four different forest types we analysed comprised coniferous forests compared to three different age classes of deciduous beech forests. We found for six of the food web parameters differences in the food web structure of the coniferous forests compared to the deciduous forest types. The higher fraction of top predators, intra guild predation motifs, the higher maximum trophic levels and the smaller fraction of intermediate species in coniferous forests could be mainly driven by the diverse mesofauna community which dominates the coniferous forest types. The fewer macrofauna predators in the coniferous forests leads to a higher number of top predators in the mesofauna, because the species that are intermediate predators in the beech forests have no predators in the coniferous forests and thus become top predators. In addition, many mesofauna predators are omnivores and potential intra-guild predators, e.g. the dietary spectrum of mesostigmatid mites likely includes predatory Collembola and Nematoda, which may explain the higher amount of intra-guild predation motives we found in coniferous forest types.

Overall, we found only few effects of the land-use types on food-web topology. Most of these effects could readily be assigned to the dominant tree species that cause different litter types (needles vs leaf litter) and habitat structures (Ferlian and Scheu 2014, Günther et al. 2014). This suggests that the structure of soil food webs is relatively robust against variation in forest types. We caution, however, that the differences in land-use intensity across our plots were not very strong.

Consequences

In this study, we assembled a new highly resolved food web data set and showed that soil food webs had a similar connectance as other food webs and also showed a similar scaling of their topological parameters with connectance and diversity. These results corroborate prior suggestions of general structural principles across food webs (Martinez 1992, Brose et al. 2004, Riede et al. 2011) that may be caused by general body-size constraints on feeding interactions (Petchey et al. 2008, Brose 2010, Brose et al. 2008, Kalinkat et al. 2013a).

Despite these universal characteristics, soil food webs clearly differed in their structural parameters from other ecosystem types. These differences in structure might be a result of selection on the soil living animals to adapt to the distinctive habitat structure of the soil system that prevents long-range detection of resources thus making generalism the most profitable feeding strategy. In consequence, soil food webs exhibited a higher link density and clustering, and more intra-guild predation. Moreover, the basal resources of low stoichiometric quality lead to an extra, pre-digesting trophic level of bacteria and fungi, which results in a greater trophic height of the soil food webs. Together, these characteristics of the soil food webs may reduce the top– down control of the predatory compartments on lower trophic levels (Lang et al. 2014, Schneider et al. 2012), which may buffer the functionality of the systems against environmental disturbances. This buffering, however, requires high predator diversity (Schneider and Brose 2013) as documented here for the natural forest communities. The network structures documented in our study may thus explain the apparent contradiction between high predator diversity and limited top–down pressure on the basal levels that carry out decomposition as the ecosystem function.

Across the forest sites of our study, we found only weak effects of land use intensity on soil food web structure indicating that the network structure of the soil communities is relatively robust against changes in land use intensity. Interestingly, this specific and robust structure of the soil food webs including high generality, omnivory and a strongly size-structured architecture across trophic levels should provide a high intrinsic stability (Brose et al. 2006, 2008, Heckmann et al. 2012) as well as buffer against extinction waves (Dunne et al. 2002a, Curtsdotter et al. 2011, Riede et al. 2011) and climate change (Binzer et al. 2012, Brose et al. 2012). In addition to unravelling some consistent specialities of soil food web structures, our results thus help to understand how soil communities might be impacted by global change.

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

Christoph Digel, Jens O. Riede and Ulrich Brose

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 multimodally (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.

Introduction

Complex food 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 (Woodward et al. 2005, Montoya et al. 2006, Otto et al. 2007, Berlow et al. 2008). 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 (Peters 1983, Brown et al. 2004, Emmerson and Raffaelli 2004, Brose et al. 2006, 2008, O'Gorman and Emmerson 2009, Rall et al. 2010, Vucic-Pestic et al. 2010). In consequence, a species body mass determines its trophic position in the food web (Jennings et al. 2001, Woodward and Hildrew 2002, Cohen et al. 2003, Woodward et al. 2005). 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 (Brose et al. 2008, Petchey et al. 2008, Berlow et al. 2009, 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 lognormal distributions (Jonsson et al. 2005, Woodward et al. 2005), 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 Barabasi 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 uniform (i.e. cumulative frequency is constant across the number of links) degree distributions (Camacho et al. 2002, 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 Jonsson pers. comm.). Interestingly, the predictive success of recent topological food-web models (Williams and Martinez 2000, Cattin et al. 2004, Allesina et al. 2008) 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.

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. 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 2.9 (R Development Core Team 2009). 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 calculated 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

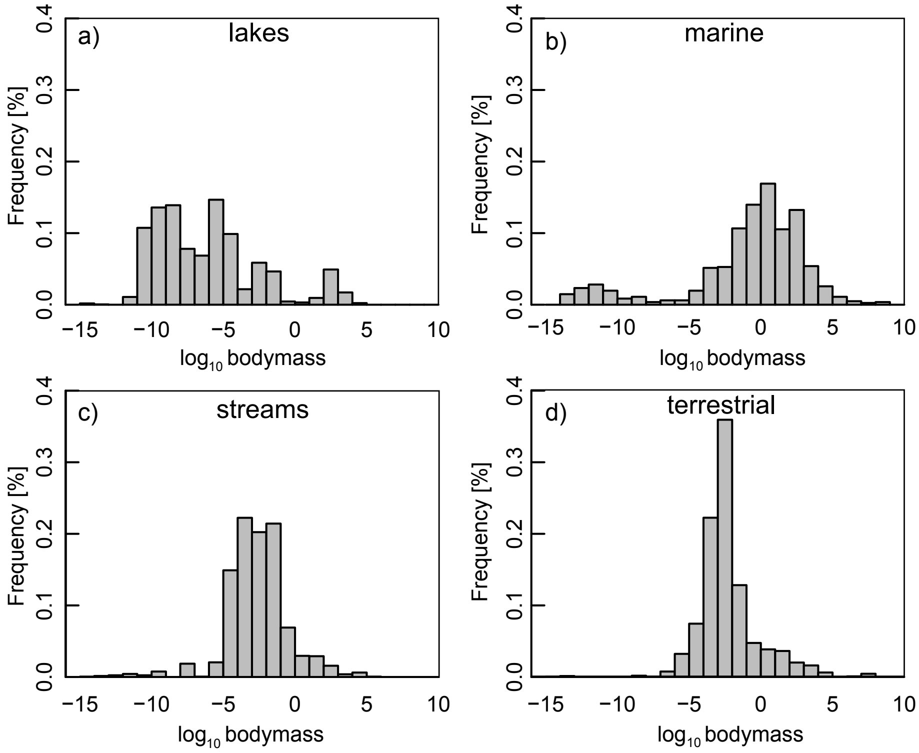

Figure 1. The body-mass structure of natural food webs: histograms of body masses for (a) lake, (b) marine, (c) stream and (d) terrestrial ecosystems.

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.

Results

Body masses were approximately log-normally distributed in stream and terrestrial ecosystems, whereas they were multi-modal for lake and marine ecosystems (Fig. 1). Body masses from stream and terrestrial ecosystems had the highest frequency in the category between 10^{-3} and 10^{-2} g. 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 (4550 g) of the sand community food web from Coachella Valley, and the smallest species were soil microbes (10^{-8} g) 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^{-15} g) to trouts (12 000 g).

In contrast to the terrestrial and stream ecosystems, the body-mass distributions of lakes and marine ecosystems clearly exhibited multiple peaks (Fig. 1). For lake ecosystems, we found a high frequency of body masses in the category between 10^{-10} and 10^{-8} g, which corresponds to the body-mass range of phytoplankton. The second peak occurred in the category between 10^{-6} and 10^{-4} g 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

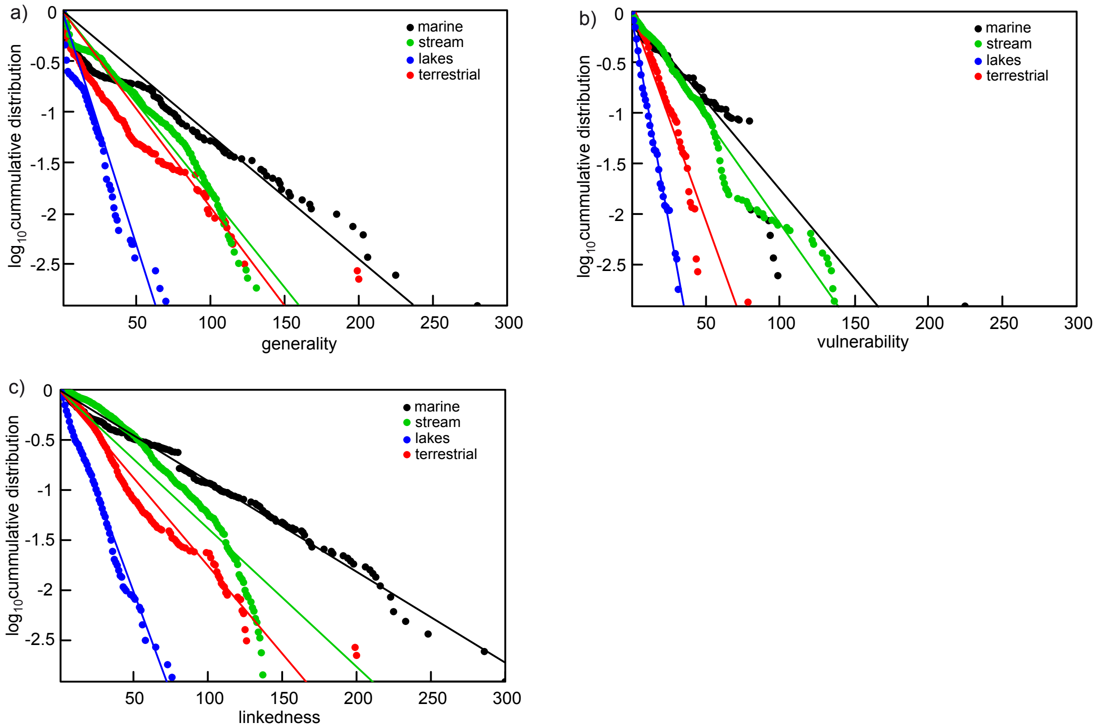

Figure 2. (a) Linear-log plots of cumulative degree distributions in the different ecosystems of the number of predator links per species (generality; $p < 0.001$, $r^2=0.97$ for lake; $p < 0.001$, $r^2=0.97$ for marine; $p < 0.001$, $r^2=0.98$ for stream and $p < 0.001$, $r^2=0.94$ for terrestrial ecosystems); (b) the number of prey links per species (vulnerability; $p < 0.001$, $r^2=0.99$ for lake; p <ä0.001, $r^2=0.94$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).

diatoms with a mass of 10^{-13} g 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 10^3 g 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^{-10} g 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. 2), whereas stream food webs exhibited downward curved relationships for generality and linkedness indicative of more uniform degree distributions (Fig. 2). Statistical tests of these relationships are carried out for each of the food webs independently. 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.

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

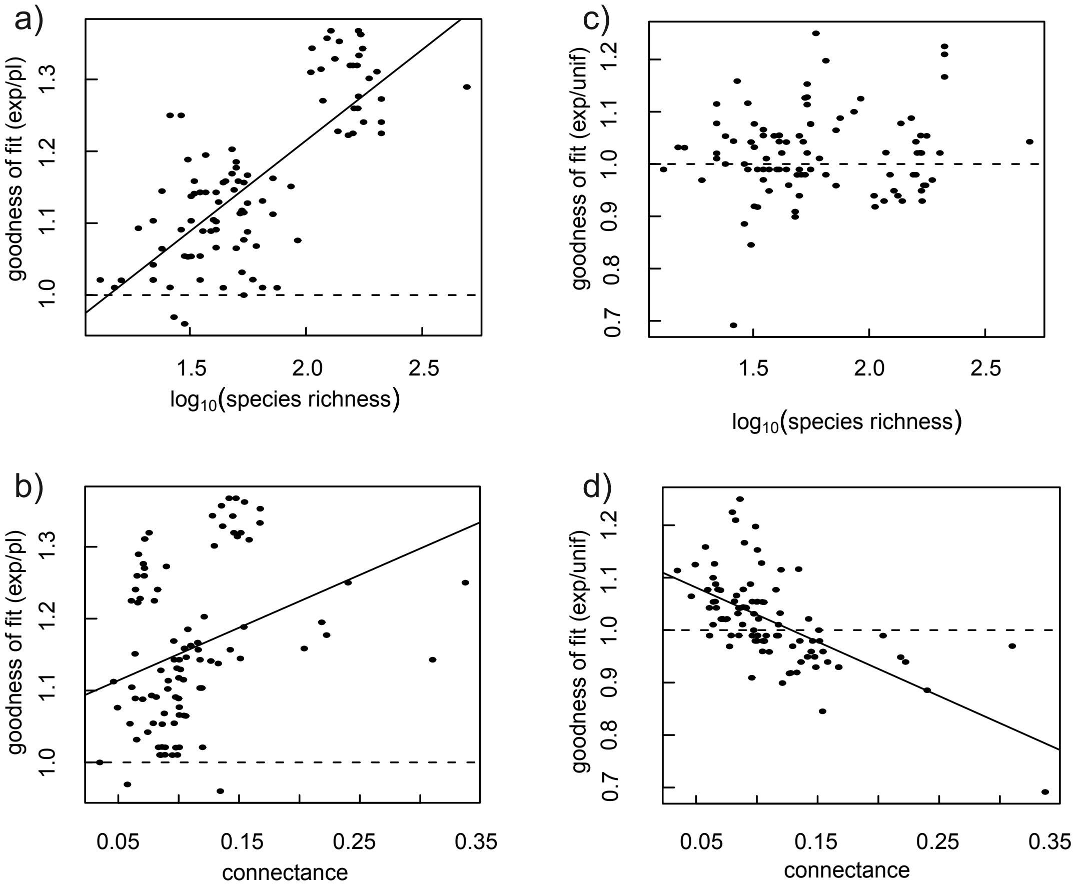

Figure 3. Goodness of fit ratio plots with r^2 values of exponential degree distributions (exp) over r^2 values of power-law (pl; a, c) or uniform degree distributions (unif; b, d) depending on $\log_{10}$ species richness (a, b) and food-web connectance (c, d). Points under the dashed lines indicate 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) $p < 0.001$, $r^2=0.38$.

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 (Supplementary material Appendix 1, Table A1). 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

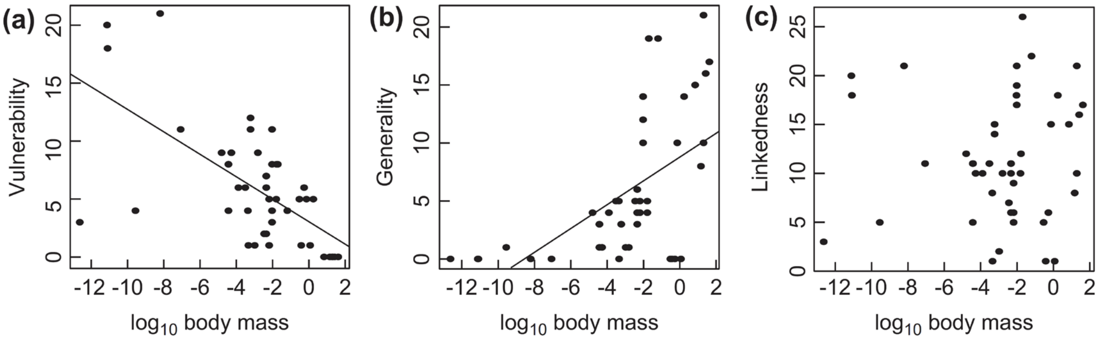

Figure 4. Allometric degree distributions of the food web of the Mondego Estuary Zostera seagrass bed: (a) vulnerability (i.e. number of predators) depending on $\log_{10}$ body mass ($p<0.001$, $r^2=0.39$); (b) generality (i.e. number of prey) depending on $\log_{10}$ body mass ($p<0.001$, $r^2=0.32$); (c) linkedness (i.e. total number of links) depending on $\log_{10}$ body mass ($p=0.78$).

degree distributions occurred only in very few food webs with low species richness and low connectance (Fig. 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. 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 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. 4a, 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. 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 food webs) of the 94 food webs analyzed (significant increases or decreases indicated by linear least squares regressions with slopes significantly different from zero, $p < 0.05$, data in Supplementary material Appendix). Furthermore, we found a slightly significant effect (negative or positive) of body masses on linkedness in 40% (38 of 94) of the food webs (Supplementary material Appendix 1).

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. 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. 5a, Supplementary material Appendix 1, Table A1). 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. 4b, Supplementary

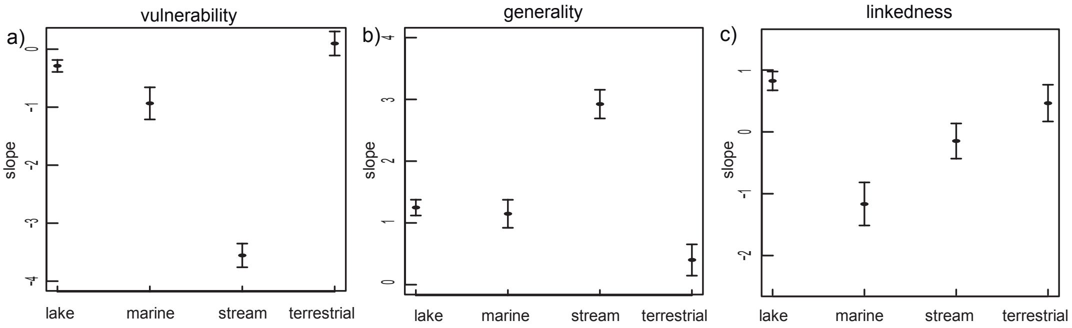

Figure 5. Slopes of the linear mixed effect models of the allometric degree distributions in the different ecosystems: (a) vulnerability slopes, with $F_{1,7345}$=114.30 and $p<0.001$ for $\log_{10}$ (body mass), $F_{3,90}$=25.22 and $p<0.001$ for ecosystem type and $F_{1,7345}$=97.71 and $p<0.001$ for $\log_{10}$ (body mass) ecosystem type; (b) 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; (c) 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.

material Appendix 1, Table A1). The steeper slopes in stream food webs indicate a stronger relationship 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. 5c).

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. 2002, 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 exhibited 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 (Williams and Martinez 2000, Cattin et al. 2004, Allesina et al. 2008). 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 (Williams and Martinez 2000, Cattin et al. 2004, Allesina et al. 2008). 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 (Williams and Martinez 2000, Cattin et al. 2004, Allesina et al. 2008), 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.

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Chapter 4: Neutral species distributions yield non-random food-webs

Christoph Digel, David Ott, Björn C. Rall, Franziska Grischkat and Ulrich Brose

Current biodiversity is the result of the evolutionary history of different ecosystems. Species distributions and their adaptations to the environment have been one of the most important subjects of ecological research. In particular, understanding the factors driving β-diversity (variation in community composition) provides precious insights into the conservation of biodiversity on the planet. Two main theoretical bodies explaining β-diversity emerged during the last two decades. According to niche theory environmental characteristics filter the species pool yielding the local community of species adapted to the local niche (Elton 1927, Hutchinson 1959, Soberón 2007). In contrast, the neutral theory claims that only random dispersal and random speciation determine the local diversity and species turnover (Hubbell 1997, 2001), which predicts many patterns of beta diversity quite accurately. However, neutral theory predicts only distributions for trophically identical species, whereas influences of local niches or neutral effects on food web structure as a crucial part of the multitrophic structure of ecosystems have not yet been analyzed. Therefore we analyzed 48 multitrophic forest soil communities. We analyzed the effects of spatial distance and environmental dissimilarity on the species dissimilarity (beta diversity) and food web dissimilarity. In this study, we show that the mechanisms proposed by neutral theory can predict the beta diversity of multitrophic species communities quite well as the effects of spatial distance on the beta diversity are much stronger than effect of environmental dissimilarity. Furthermore, food-web structure is robust and affected neither by spatial distance (random dispersal, neutral theory) nor by environmental filtering (niche theory). We additionally analyzed model food webs (random and niche topology) and compared their dissimilarities to our dataset of soil food webs. The highest dissimilarity between food web pairs was reached in random food webs were as the niche model food webs were in between and the lowest distances were expressed by the empirical food webs. The major difference between the three food web types arises through their trophic levels. Random food webs had highest mean trophic level (115), niche model had lower (5) and empirical food webs showed the lowest mean trophic levels (4). Hence, food-web structure appears to be energetically optimized with local species adapted to energetic niches within the food web while species identity within these niches remains random. This suggests that different species could be adapted to the same energetic niches, and therefore following random drift, still yield similar food web structures.

Introduction

Neutral & Niche Theory

For several decades, the patterns in biodiversity, composition and structure of natural communities have been explained by two important theoretical bodies: neutral and niche theories (Hutchinson 1959, Hubbell 1997, Leibold et al. 2004, Tilman 2004, Soberón 2007, Chase and Myers 2011). Niche theories hold that abiotic conditions or biotic interactions determine the distribution of species that are well adapted to their local environments (Hutchinson 1959) comprising environmental and biotic niches (Graham and Fine 2008). While environmental niches depend on the abiotic habitat conditions, biotic niches are constrained by species interactions. Most importantly, feeding interactions describe the energy supply pathways among species that compose complex food webs with multiple trophic levels (Thompson et al. 2012). Food-web studies demonstrated that the successful establishment as well as the extinction probability of species in these communities depend on the combination of species traits and surrounding network structures (Romanuk et al. 2009, Binzer et al. 2011). This interactive selection of locally persistent species yields food-web structures that are surprisingly consistent across ecosystem types (Digel et al. in press) and spatial scales (Brose et al. 2004). In this vein, classic niche theory assumes an omnipresent species pool that is locally filtered by the availability of abiotic environmental or biotic niches (Hutchinson 1959). While traditional biodiversity studies were restricted to abiotic filtering of single-trophic-level communities, food-web analyses provide novel means to include biotic filtering in multi-trophic communities, which remained unexplored so far.

Alternatively, neutral theory assumes that only random speciation and random drift of the species across the landscape determine patterns of species distribution, whereas local filtering by abiotic or biotic conditions should be unimportant (Hubbell 1997, 2001, Bell 2001). Despite its simplicity, the mechanisms of the neutral theory predict patterns in local diversity and abundance as well as species turnover rates (i.e., beta diversity) surprisingly well (Hubbell 2001, Tuomisto et al. 2003, Chase 2010). While the neutral theory originally assumed that all species within the community are in the same trophic group (Hubbell 1997), natural communities comprise more than a single trophic group (Thompson et al. 2007) with various different biological interactions and knock-on effects for evolutionary processes (Graham and Fine 2008). Although the neutral processes of random drift and random speciation could also be applied to complex communities, neutral theory has not yet been tested for multitrophic communities.

Using a comprehensive data set of 48 forest soil communities, we analyzed predictions by the niche and neutral theory for multitrophic communities comprising detritivores, herbivores and several trophic levels of predators. This new dataset contains species lists, environmental parameters, food web structures and geographic coordinates (for additional information see supplementary information). The total species pool included 909 species, whereas the species richness of the local communities ranged from 89 to 168 species. These species were connected by 729 to 3344 trophic links (feeding interactions) composing complex food webs whose mean trophic levels ranged from 3.1 to 4.5 (maximum trophic levels between 4.9 and 6.9). For each pair of these communities, we calculated (1) the beta diversity as the dissimilarity between the species compositions (Jaccard dissimilarity), (2) the spatial distance, (3) the environmental dissimilarity based on Euclidian distances in the abiotic parameter space of nine variables affecting species biomass densities (for details see methods supplement). First, we tested if species dissimilarity among forest sites (i.e. beta-diversity) depends on (i) environmental dissimilarity indicating variation in available niches or (ii) spatial distances as a consequence of neutral processes. Subsequently, we addressed if this species turnover directly yields a similar turnover in the energetic organization of the communities as described by network parameters of their complex food webs. For the first time, we also analyzed whether the processes of random drift and random speciation underlying the neutral theory correctly predict turnover in food-web structures between habitats.

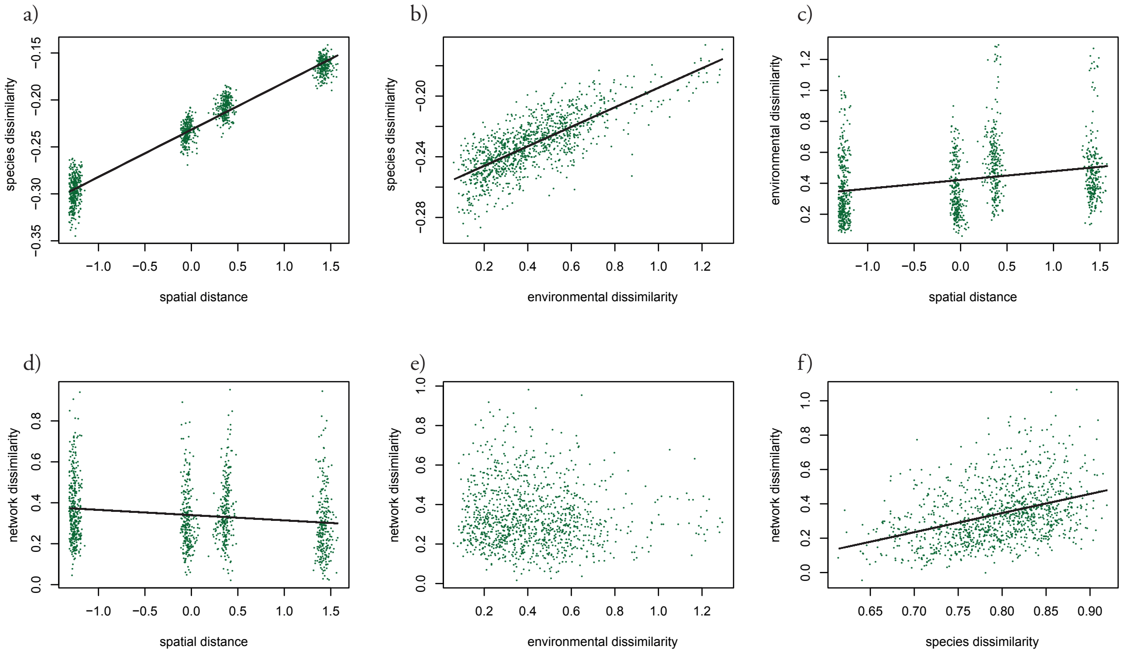


Figure 1. Species dissimilarity depends on a) spatial distance (intercept = -0.259, slope = 0.050, p<0.001) and b) environmental dissimilarity (intercept = -0.259, slope = 0.064, p <0.001) c) Environmental dissimilarity spatial distance relationship (intercept = 0.422, slope = 0.056, p <0.001). Dissimilarity in network structure dependence on d) spatial distance (intercept = -0.526, slope = -0.026, p<0,001), e) environmental dissimilarity (intercept = -0.526, slope = -0.045, p=0.051) and (f) species dissimilarity (intercept = -0.526, slope = 1.114, <0.001).

Results & Discussion

Beta diversity & community dissimilarities

Interestingly, we found that the species dissimilarity (Jaccard dissimilarity) increased with increasing spatial distance (Fig. 1a) and also with increasing environmental dissimilarity (Fig 1b). However, our analyses also exhibited a significant positive but weak correlation between environmental dissimilarity and spatial distance (Pearson's ρ=0.26, p<0.001, fig 1c). To assess the importance of these multiple effects we employed model simplification based on the Akaike information criterion (AIC) starting with the most complex model including spatial distance, environmental dissimilarity and their interaction. The most adequate model (lowest AIC) included only the simple effects of spatial distance and environmental dissimilarity (Supplementary table 1). Additionally, species dissimilarity was strongly correlated with spatial distance (Pearson's ρ=0.73, p<0.001), whereas the correlation with environmental dissimilarity was weak (ρ=0.37, p<0.001).

Consistent with prior studies of single-trophic level communities (Tuomisto et al. 2003, Soininen et al. 2007, Keil et al. 2012, McClain et al. 2012), our results suggest that the mechanisms of random dispersal and random speciation proposed by the neutral theory are more important than environmental filtering by abiotic niches for constraining the local species communities. However, none of those prior studies could address whether these processes also lead to realistic multitrophic community structures of complex food webs that define the biotic niche of the species.

Clearly, the processes of random speciation and random drift should lead to local communities comprising random species combinations and random network structures with a spatial turnover similar to that of the species. To explore this hypothesis we created (1) 50 metawebs with a random food-web topology mimicking the consequences of random speciation and (2) 50 niche model metawebs (Williams and Martinez 2000) representing energetically optimized networks and thus non-random speciation. Then, we randomly drew 200 local communities from each metaweb mimicking the species turnover of the empirical food webs. We calculated the food web dissimilarities based on Euclidian distances in the food web parameter space of eleven food web parameters between each pair of the empirical communities and compared them to pairs of food webs with similar species dissimilarity randomly drawn from (1) random metawebs and (2) niche-model metawebs (for details see method supplement). These random draws represent the consequences of random species drift. We compared the resulting food-web dissimilarities of the random and niche metawebs to those of the empirical communities. In consequence, we tested three different scenarios: (i) The local food-web structure is completely random and determined by random speciation (i.e., random metawebs) and random drift (example web in Fig. 2a). (ii) Food web structure is restricted to follow energetic constraints and scaling laws; we thus assumed non-random speciation (i.e. niche model metawebs) but random drift (Fig 2b). (iii) Natural food webs underlie non-random speciation and energetic filtering of the species pool by the availability of biotic niches suggesting conservative food-web structures that are preserved despite species turnover (example web in Fig 2c).

First, we analyzed the dependence of the empirical food-web dissimilarity on spatial distance, environmental dissimilarity and species dissimilarity starting with the most complex model including all these variables and their interactions. Model simplification suggested that the model including all explanatory variables but not their interactions described the relationship best (lowest AIC, Supplementary Table 1). Interestingly, if species dissimilarity is included in the model, the dissimilarity of food web structures decreases with spatial distance (Fig. 1d). This would imply that food webs become more similar in their structures the further away they are from each other. This surprising pattern is a result of the correlation between species dissimilarity and food web dissimilarity (Pearson's ρ=0.26, $p<0.001$). This pattern disappears in models without species dissimilarity, in which food-web dissimilarity increases with increasing spatial distance (Supplementary Table 2, Supplementary Fig. 1). Furthermore, food-web dissimilarity was not influenced by environmental dissimilarity in the models with (Fig. 1e) and without species dissimilarity. This result implies that the food-web structures are highly similar across the strong gradients in abiotic variables in our data (Supplementary Table 3).

In addition, Pearson correlation coefficients indicated no correlation of food web dissimilarity with environmental dissimilarity (Pearson's ρ = -0.04237706, p = 0.12.) and weak correlations with spatial distance (Pearson's ρ = 0.12, $p<0.001$) and species dissimilarity (ρ=0.26, p<0.001). Hence, while food web dissimilarity increased slightly with species dissimilarity (fig 1f), the network structures of the food webs were surprisingly consistent across gradients in abiotic variables, spatial distances and species turnover. This indicates that spatial distances and the associated strong species turnover are not dominant drivers of food web structures.

Food web dissimilarity vs. community dissimilarity

In our comparisons of empirical and model food webs, we found the highest increase of food web dissimilarity with increasing species dissimilarity between the local communities

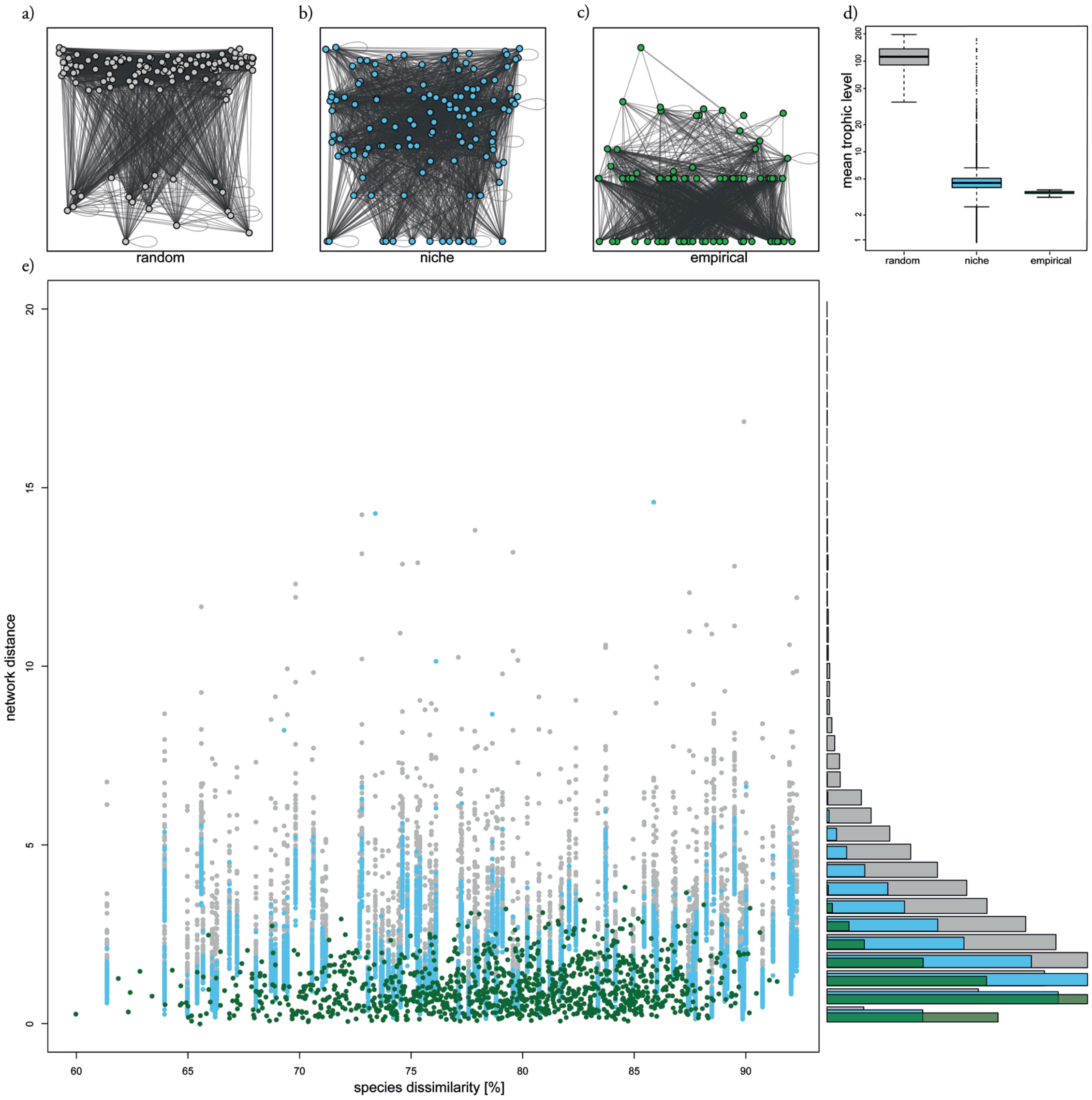


Figure 2. Example network graphs of a) random networks with 91 species and 1414 links, b) a niche model network with 91 species and 1414 links and c) an empirical food web with 140 species and 3335 links. d) Box-whisker plots of the mean trophic levels of random (grey), niche (blue) and empirical (green) food webs, e) network distance scaling with species dissimilarity. Grey dots representing random food webs, grey bars show the distribution of dissimilarities in random food webs. Blue dots show the dissimilarities of food webs derived from niche model food webs. Blue bars show the frequency of the dissimilarities. Green dots show the distances derived from the empirical food webs. Green bars show the distribution of the distances.

in models employing random metawebs (Fig. 2a, 2e grey dots and bars). In addition, the communities sampled from niche model metawebs showed a shallower increase in food web dissimilarity with species dissimilarity (fig. 2b, 2e blue dots and bars), but the dissimilarity between natural food webs was still far lower (fig. 2c, 2e green dots and bars). The most severe difference between the three food-web types occurred between the trophic levels (Fig. 2d). Random food webs showed the highest mean trophic levels (average across webs of 115), the mean trophic levels of niche food webs (average of 5) were close to empirical food webs which had the lowest trophic levels (average of 4, Fig. 2d). Together, these results suggest that the processes of random speciation (random metawebs, grey dots in Fig. 2e) and random local species assembly (niche-model metawebs, blue dots in Fig. 2e) cannot explain the conservation of natural food-web structures (green dots in Fig. 2e) despite strong turnover in species composition. While the processes proposed by neutral theory thus provide predictions that are highly consistent with natural patterns of species distributions (Fig. 1), our results clearly demonstrate that they are not able to predict multitrophic community patterns (Fig. 2). Together, our species distribution and food-web structure results indicate local communities should be assembled by a combination of random species drift across large-scale spatial gradients as predicted by neutral theory, but also local filtering of these drifting species by the energetic niches of complex food webs. In particular, the neutral processes lead to networks with trophic levels that are significantly higher than those of natural food webs, where assimilation losses of energy limit the number of high-trophic level species. Hence, the neutral processes of random speciation and random drift yield energetically unrealistic food-web structures.

Food-web studies have shown that topological parameters follow systematic scaling laws (Dunne et al. 2002, Riede et al. 2010, Digel et al. 2011) constraining energy flows into stable community configurations (Otto et al. 2007, Kalinkat et al. 2013). Our finding that these network topologies are independent of abiotic conditions is consistent with prior studies demonstrating their consistency across different ecosystem types (Dunne et al. 2004, 2008, Digel et al. 2011, Riede et al. 2011). This is providing strong evidence that food-webs are energetically forced into stable configurations, which also explains the local filtering of the species pool in our analyses. Despite these conservative network structures we also found a strong species turnover, which indicates that the analyzed meta-communities apparently comprise a high amount of energetically redundant species. The occurrence of these species in local communities could be influenced by random drift, but the trophic niches and the energy availability in the local food webs determine the success of their establishment. For instance, the random establishment of a species in a local community may prevent subsequent colonization by species that are redundant concerning their biotic niche in the food web. Synthesizing neutral and food-web theory, our analyses suggest that a mixture of neutral (random species drift) and biotic niche (energetic filtering of the randomly drifting species) constraints interactively drive the composition and structure of species communities.

Methods summary

Sites and data

We used a dataset of 48 forest soil communities from sites of three regions in Germany within the Biodiversity Exploratory project (Fischer et al. 2010). The dataset comprises species lists, environmental properties, food webs and geographic coordinates of 48 forest sites. The forest sites comprise 12 coniferous and 36 deciduous forests of different age classes.

Computer generated data

We established 100 different 1000 species metawebs, 50 with a random network topology and 50 with a niche model topology (Williams and Martinez 2000). 200 local communities were drawn from each of the metawebs. The network structural properties were calculated and normalized to a mean of zero and a variance of unity over the population of all 20000 model communities and the 48 empirical food webs. Then, we calculated Euclidean distances in network structures based on the structural properties between the 200 communities for each of the 50 niche and 50 random metawebs separately and compared these distances to the empirical food webs.

Statistics

We applied a linear model using species dissimilarity and network dissimilarity as dependent variables. Both models included environmental dissimilarity and spatial dissimilarity as well as their interaction term as dependent variables

We applied a generalized linear model to analyze the dependence of the species dissimilarity (i) on the environmental dissimilarity (ii) and on the spatial distance (iii) and the interaction between the explanatory variables (ii * iii). Further we applied a linear model to analyze the dependence of the network dissimilarity on (iv) the environmental dissimilarity (ii), the spatial distance (iii), the species dissimilarity (i) and the interactions of the explanatory variables (ii * iii * i). We used an automatic stepwise procedure to obtain the most parsimonious model by using Akaike's information criterion. Pearson Correlation Coefficients were calculated for all of the analyzed relationships.

Supplementary information

Detailed methods

Sites and data

We compiled a dataset of 48 forest soil communities of three regions in Germany within the Biodiversity Exploratory project (Fischer et al. 2010). The sampling was conducted in coniferous and deciduous forests. The dataset contains species lists of the 48 different

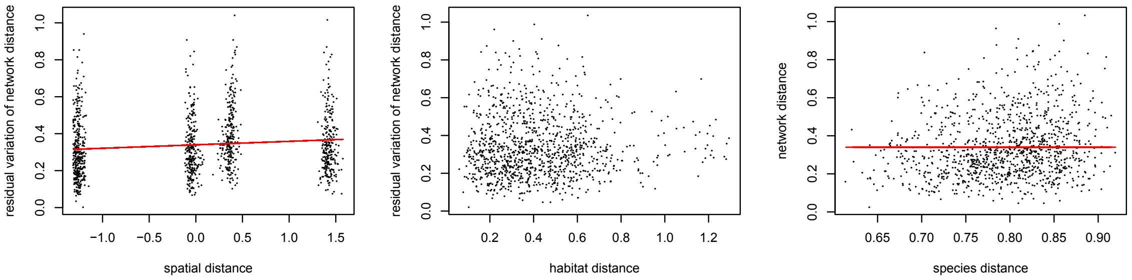


Figure A1: Dissimilarity in network structure dependent on a) spatial distance and b) environmental dissimilarity, the species dissimilarity was excluded from the model for this plot (see table 3).

forest sites, the GPS coordinates and the environmental properties of each site i.e. the pH value, the quality of the basal litter resource indicated by the elemental contents of calcium (Ca), copper (Cu), iron (Fe), manganese (Mn) and zinc (Zn) (Ott et al. in prep). Feeding interactions between soil invertebrates were established using data of stable isotope analyses, fatty acid analyses and molecular gut contents and the body masses of the species (Digel et al. in press). From the single interactions we established feeding matrices of soil communities on the 48 forest sites (Digel et al. in press). For these food webs we calculated the food web parameters connectance, links per species, mean trophic level, maximum trophic level, standard deviation of trophic levels, cluster coefficient, characteristic path length, standard deviation of generality and vulnerability, closeness and betweenness.

We used the whole dataset of soil communities, geographical and environmental information to calculate four different distances between all possible plot pair combinations (1128 plot pairs). We calculated (I) the Jaccard distance (species dissimilarities) between the local communities as: d_j (A,B)= $(|A \cup B|-|A \cap B|)/(|A \cup B|)$ where A and B denote two given samples, this a pair of forest sites in our case (Jaccard 1912). (II) The continuous environmental properties were $\log_{10}$ transformed to improve normality and homoscedasticity. Further, all environmental variables were normalized to a mean of zero and a variance of unity. We then calculated the environmental dissimilarity as the Euclidean distance in environmental properties and (III) the spatial distances using GPS coordinates of the sampling sites. Lastly, we calculated (IV) the food-web dissimilarity as the Euclidean distance between the food web structural properties of every plot pair.

Computer generated data

We generated 100 meta food webs with 1000 species each, 50 with a random topology (uniform link distributions) and 50 with a niche model topology (Williams and Martinez 2000). We used these 100 meta food webs as a pool to draw local communities using the following approach.

Species Vectors

To analyze the effect of random dispersal on food web topology we generated a set of 200 random species lists ranging in species dissimilarity from 8% to 100% species turnover. We

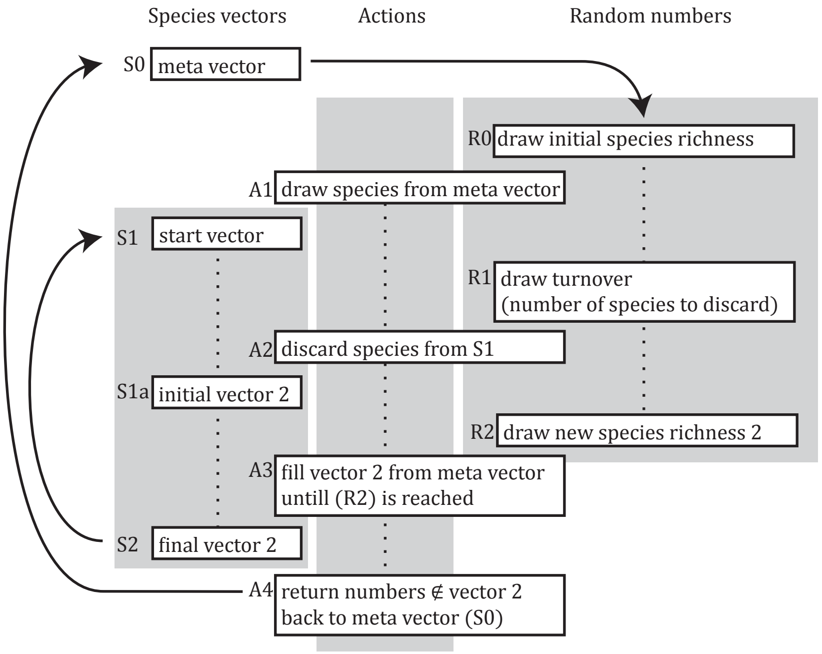


Figure A2. Scheme of the random generation of local species communities.

restricted each species list to a range from 89 to 169 species (minimum and maximum of the empirical dataset). The set of 200 species lists was generated using the following steps: (I) We determined the species number by randomly chose a diversity within our range (Figure 2, R0). (II) Then we used this diversity to draw randomly species out of the 1000 species pool without replacing (Figure A2, A1). (III) Third we draw another random number (R1) representing the fraction of species which should be discharged (A2)(min=0, max=length of S1)(Figure 2, R1, A2, S1a). After determining the species numbers (R2) for a new second species list (S2), new species were drawn from the 1000 species vector (A3) until the deleted species from the start list were replaced and the new target species number (R2) was reached (Figure 2, R2, A3, S2). For the following species list the second list (S2) becomes the start template (S0). The species which were deleted and are not element of the second species list (S2) are replaced back to the 1000 species pool (A4)(Figure 2, A4). This approach was repeated until 200 species lists were generated. By choosing the amount of species which are deleted we achieved a uniform distribution of different species dissimilarities ranging from 12% to 100%. We used the same set of 200 species lists to draw the local webs from each of the different meta food webs.

Network dissimilarities

We draw 200 local food webs from each of the 100 meta food webs which resulted in 10,000 local food webs drawn from random topology meta webs and 10,000 local food webs drawn from niche model topology meta webs. For each meta web we analyzed the effect of local species dissimilarity on the local food web dissimilarity. Therefor we calculated the structural properties of the local food webs. To enable comparison of dissimilarities between the local food webs of the different meta food webs and the empirical food webs, the resulting network structural properties were normalized to a mean of zero and a variance of unity over all 20,000 local communities and the 48 empirical food webs. Then we calculated the Euclidean distance between each of the 200 local food webs for each meta matrix separately. Since the species turnover was chosen stepwise from local food web to local food web we used only the corresponding 200 distances. The resulting network dissimilarities were plotted in figure 2 .

Statistics

We analyzed the dependence of the species dissimilarity (i) on the environmental dissimilarity (ii) and on the spatial distance (iii) and the interaction between the explanatory variables (ii * iii) using a generalized linear model with a binomial distribution for the species dissimilarity. We further analyzed the dependence of the network dissimilarity on (iv) the environmental dissimilarity (ii), the spatial distance (iii), the species dissimilarity (i) and the interactions of the explanatory variables (ii * iii * i). We used generalized linear models with binomial distributions for the species dissimilarities and Gaussian distributions for the network dissimilarities. We used an automatic stepwise procedure to delete explanatory variables one by one in order to obtain the most parsimonious model by using Akaike's information criterion (AICs see table 2, 4).

We further calculated the Pearsson Correlation Coefficient to analyze the correlations of species dissimilarity and food web dissimilarity with habitat distance and spatial distance. We further analyzed the correlations of habitat dissimilarity and spatial distance as well as the correlation of species dissimilarity and distance in food web structure (correlation coefficients see table 5).

All data were analyzed using the statistical program R, version 3.0.1 (R Core Team 2013) with the additional packages igraph (Csardi and Nepusz 2006) for calculation of food web properties, vegan (Oksanen et al. 2013) for calculation of the Jaccard dissimilarities and fossil to calculate the spatial distances from the gps data(Vavrek 2011).

Supplementary tables:

Table 1: T- table of the generalized linear models, the full model was: species dissimilarity ~ spatial distance * environmental dissimilarity

Model	Intercept			Slope spatial distance			Slope env. dissimilarity			Sp. diss X env. diss		
	Estimate	Std. err.	p	Estimate	Std. err.	p	Estimate	Std. Error	p	Estimate	Std. err.	p
full model	-0.259	0.007	<0.001	0.052	0.007	<0.001	0.065	0.016	<0.001	-0.005	0.016	0.737
no interactions	-0.259	0.007	<0.001	0.050	0.003	<0.001	0.064	0.015	<0.001	NA	NA	NA
spec. diss. ~ sp. dist.	-0.232	0.003	<0.001	0.054	0.003	<0.001	NA	NA	NA	NA	NA	NA
spec. diss. ~ env. diss	-0.281	0.007	<0.001	NA	NA	NA	0.120	0.015	<0.001	NA	NA	NA
env. diss ~ sp. dist	0.422	0.006	<0.001	0.056	0.006	<0.001	NA	NA	NA	NA	NA	NA

Table 2: AIC values from the different GLM models of the species dissimilarity relationships

Model	df	AIC	Delta AIC
species dissimilarity ~ spatial distance * environmental dissimilarity	4	7242	2
species dissimilarity ~ spatial distance + environmental dissimilarity	3	7240	0
species dissimilarity ~ spatial distance	2	7255	15
species dissimilarity ~ environmental dissimilarity	2	7447	207

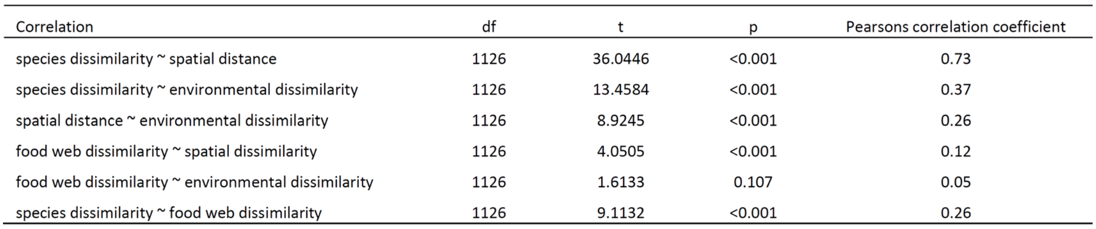
Table 3: T - table of the generalized linear model, the full model was: network dissimilarity ~ spatial distance*environmental dissimilarity*species dissimilarity. All Interactions of the full model were not significant and are therefore not shown

Model	Intercept			Slope spatial distance			Slope env. dissimilarity			Slope species dissimilarity		
	Estimate	Std. Error	p value	Estimate	Std. Error	p value	Estimate	Std. Error	p value	Estimate	Std. Error	p value
full model	-0.625	0.232	0.007	-0.073	0.179	0.682	0.177	0.478	0.712	1.235	0.287	<0.001
without interact.	-0.526	0.095	<0.001	-0.026	0.007	<0.001	-0.045	0.023	0.050	1.114	0.122	<0.001
~ sp. dist. + env. dis.	0.334	0.011	<0.001	0.019	0.005	<0.001	0.014	0.023	0.547	NA	NA	NA
~ sp. dist. + spec. diss	-0.492	0.093	<0.001	-0.025	0.007	<0.001	NA	NA	NA	1.047	0.117	<0.001
~ env. diss + spec. diss	-0.270	0.066	<0.001	NA	NA	NA	-0.043	0.023	0.063	0.791	0.086	<0.001
~ sp. dist	0.340	0.005	<0.001	0.020	0.005	<0.001	NA	NA	NA	NA	NA	NA
~ env. diss	0.325	0.010	<0.001	NA	NA	NA	0.036	0.022	0.107	NA	NA	NA
~ spec. dist	-0.241	0.064	<0.001	NA	NA	NA	NA	NA	NA	0.731	0.080	<0.001

Table 4: AIC values from the different GLM models of the network dissimilarity relationships

Model	df	AIC	Delta AIC
food web dissimilarity ~ spatial distance * environmental dissimilarity * species dissimilarity	9	-973	8
food web dissimilarity ~ spatial distance + environmental dissimilarity + species dissimilarity	5	-981	0
food web dissimilarity ~ spatial distance + environmental dissimilarity	4	-902	79
food web dissimilarity ~ spatial distance + species dissimilarity	4	-979	2
food web dissimilarity ~ environmental dissimilarity + species dissimilarity	4	-969	12
food web dissimilarity ~ spatial distance	3	-904	77
food web dissimilarity ~ environmental dissimilarity	3	-890	91
food web dissimilarity ~ species dissimilarity	3	-968	13

Table 5: Pearsons correlation coefficients of the different distance parameters



Correlation	df	t	p	Pearsons correlation coefficient
species dissimilarity ~ spatial distance	1126	36.0446	<0.001	0.73
species dissimilarity ~ environmental dissimilarity	1126	13.4584	<0.001	0.37
spatial distance ~ environmental dissimilarity	1126	8.9245	<0.001	0.26
food web dissimilarity ~ spatial dissimilarity	1126	4.0505	<0.001	0.12
food web dissimilarity ~ environmental dissimilarity	1126	1.6133	0.107	0.05
species dissimilarity ~ food web dissimilarity	1126	9.1132	<0.001	0.26

Part III
General discussion

Chapter 5: General discussion

Natural ecosystems are constantly changing. Species and their interactions have adapted to environmental changes but have also faced several mass extinction events, followed by evolution and speciation. Taken together, these processes have resulted in today's biodiversity (Storch et al. 2013, Westheide 2013). However, biodiversity is decreasing drastically due to the increase of the human population, resource exploitation and habitat destruction (Millennium Ecosystem Assessment 2006, IPCC 2007). Today we are facing a massive decline in biodiversity over nearly all ecosystems (Barnosky et al. 2011), with thus far unknown consequences. Therefore, a mechanistic understanding of the drivers of diversity and ecosystem functioning is crucial for understanding and preparing for potential future scenarios of global biodiversity and ecosystem functioning. This thesis aims to provide and extend this mechanistic understanding of the complexity and the maintenance of diversity in ecosystems and herein addresses the distinctive features of food webs. Food web structures provide an excellent toolset to analyze and compare complex ecosystems in their diversity and complexity. I used 30 different food web parameters to analyze generalities of food web structure across different ecosystems and at different scales. I showed that food web structure is quite conservative across land-use and environmental gradients and further follows general scaling laws across ecosystems (chapter 2, 4). I further showed that body mass is an important factor relating to these scaling laws, as allometric degree distributions are also a general feature of food web structure (chapter 3). The major finding of my thesis is that food web structure is possibly the result of energetic constraints on communities. These energetic constraints arise through the body size and their distributions across the food web structure. The presented studies extend previous knowledge on the mechanisms structuring the earths' ecosystems, which will hopefully support further ecological research.

Matching food web theory with empirical research, I compiled 48 new highly resolved food webs of soil communities. These soil food webs enriched my large database on food webs of different ecosystems. In chapter 2 I present results on the differences of soil food web structure compared to other ecosystems. I showed that environmental differences in the physical structure of the soil translate into food web structure by affecting the traits of the soil species. Many of the differences in topology of soil food webs could be explained by ecological traits of the species (i.e. body size, extra intestinal digestion, small diameter but elongated body shape)(Scheu and Setälä 2002, Bardgett 2005, Wall et al. 2012). The feeding type and the high generalism of soil predators results in a high number of omnivores and intra guild predation motives. Furthermore, detritus as a basal resource increased the number of trophic levels because of the inability of most of the arthropod species to directly consume litter (Scheu and Setälä 2002, Dunger 2008). Therefore, an additional layer of primary decomposers (i.e. bacteria, fungi) is needed to make the resources available to other species (Scheu and Setälä 2002). Previous studies found similar topological parameters across ecosystems (Dunne et al. 2002, 2008, Stouffer et al. 2005, Riede et al. 2010). Here I demonstrate that soil food webs differ in their ecological food web parameters from these other ecosystems and that environmental properties can influence food web structure by influencing traits of the soil species. Interestingly, soil food webs had the same complexity (connectance) and comparable size (species richness) compared to other systems. Moreover, despite their topological differences, soil food webs showed a similar scaling of most of their topological parameters with connectance and species richness. These results confirm previous suggestions on general scaling laws in food web structure and hold across different ecosystems (Martinez 1992, Brose et al. 2004, Riede et al. 2010). Furthermore, in the analyzed soil food webs, the structure was only weakly affected by land-use intensity.

In consequence, food web structure is robust to external influence (i.e. land use intensity) and common concepts, like the general scaling laws, are more important drivers of food web structure. A million years ago in the Cambrian, food webs already had shown similar structural properties and scaling relationships compared to recent food webs. The general food web architecture has been preserved, indicating that topological parameters of food webs are even similar across geological time scales (Dunne et al. 2008). A major player for this pattern might be thermodynamic, dynamic stability or evolutionary constraints on food web structure (Dunne et al. 2008). This leads to the question of how these physical parameters can be projected on the species level i.e. the species body mass.

In chapter 3 I investigated the degree distributions and especially the allometric degree distributions in 94 food webs across four ecosystem types. Allometric degree distributions map the relationship of body masses with the species' linkedness, vulnerability and generality. Thus they include species body mass-dependent feeding constraints into food web structure. I showed that the analyzed food webs expressed exponential degree distributions and, more importantly, I showed that allometric degree distributions are a general feature of food webs across ecosystems. This allometric scaling has important implications for energy distribution across the food webs and, additionally, for the stability of the system (Brose et al. 2006, Otto et al. 2007) as it influences the interaction strengths between the species. Interaction strengths are conceptualized as functional responses which describe the feeding relationship of a predator on a prey dependent on its density (Holling 1959). An extension of this concept utilizes body masses to predict the feeding rate in relationship to the density and the body mass of the prey (Vucic-Pestic et al. 2010, Kalinkat et al. 2013). In combination, the allometric degree distributions and the allometric functional responses strongly stabilize food webs (Otto et al. 2007, Kalinkat et al. 2013). This underpins the importance of body mass and its indications for energy distribution. Body mass therefore is an auspicious suspect as a driving force constraining food web structure.

In chapter 2 and 3, I revealed and extended generalities of food web topology and scaling. Food web structure is unique in its topological properties and clearly separates them from other network types. These consistencies of food web structure were already present in Cambrian communities (Dunne et al. 2008). This points towards important processes constraining food web topology. To analyze these constraints, I investigated food web structure using a different approach. I applied the theoretical body of neutral and niche theories to disentangle the influence of biotic and abiotic factors in addition to stochastic processes on the local community and food web structure. Neutral theory predicts local community compositions surprisingly well (Hubbell 1997, Tuomisto et al. 2003). It uses the mechanisms of random drift and evolution to predict dissimilarities between communities (beta diversity)(Hubbell 1997, 2001). According to neutral theory, species therefore are only influenced by the spatial distances between the communities (Hubbell 1997, 2001). In contrast, niche theory uses the mechanism of environmental filtering of species to predict the dissimilarities between communities. According to niche theory, species are not limited in their dispersal (i.e. could be everywhere) but preadaptation to different environmental niches influence the local species composition and the successful settlement (Hutchinson 1959). Neutral theory has only been used to analyze communities of single trophic levels (e.g. plant communities, marine grazer communities) whereas niche theory is applied to multitrophic questions and food web theory. I found that I) the mechanisms of neutral theory described the communities of a multitrophic soil community well, II) comparing species dissimilarities, there is a very high turnover between soil communities, III) the topology of food webs is weakly influenced by spatial distance and species dissimilarity but not by environmental dissimilarity. Here, I want to emphasize that the species compositions at the different local communities comprise a high number of different species but the food webs were topologically similar. Furthermore, food web structures were not influenced by environmental differences. Again, this demonstrates that food web structure has to be constrained following scaling laws that are independent of environmental factors.

I analyzed the influence of energetic constraints on food web structure applied at the global and local scale. Therefore, I compared local model food webs constructed using two different methods: first, random meta webs (neutral) and, second, niche meta webs (energetically constrained) to local food webs from the "Biodiversity Exploratories". This analysis revealed a high topological dissimilarity between local webs from random food webs, a lower dissimilarity between local webs from niche food webs and the lowest dissimilarity among the empirical food webs. In combination with the previous findings (weak influence of environmental differences on the local community but high species turnover and topologically similar food webs), these results have two important implications: (I) globally, the meta web follows energetic constraints but (II) locally the community is constrained into a topology by an additional energetic filtering. The local energetic filtering of the community paired with a high species turnover but conserved topology indicates that different species can have the same function within the food webs (expressed as topological position). This is analogous to studies of model food webs which use energetically reasonable structural scaling to produce reproductively stable systems (Brose et al. 2006, Otto et al. 2007, Petchey et al. 2008). From the perspective of species traits and interactions, different species fulfill the same energetic function in food webs. This energetic function in a food web arises through species body masses and the number of feeding interactions a particular species has with predators or prey.

Many food web related analyses of species interactions point towards energetic niches in food webs (Brose et al. 2006, Kalinkat et al. 2013). Body mass still remains one of the most important traits determining the energetic position of a species in a food web. To conclude, I found evidence that the local community structure is influenced by energetic niches which constrain the local species composition. Species distributions, therefore, are determined by dispersal (spatial distance), weakly by environmental properties and, more importantly, by the availability of local energetic niches. This mechanistic approach provides insights into the possible drivers of food-web structure. I demonstrated that food web structure is not random (which could also be the case for independence from environmental gradients). Furthermore, a possible global energetic constraint on food web structure (niche web topology) needs to be accomplished by additional local energetic filtering of the community to produce the high topological similarity found in natural food webs.

Overall, in my thesis I used food web structure as a tool to compare ecosystems. The topological food web parameters provided superior insight into the mechanisms of community structure and species interactions. One benefit of using food web structural parameters is the independence from species taxonomic identities. Topological parameters visualize the architecture of the energy pathways through the different levels of the ecosystem. My thesis demonstrates that food web properties can help to examine mechanistic and energetic drivers that structure different ecosystems. It further enables the comparison of completely different ecosystems on their structural level, such as marine andecosystems with terrestrial. Food web structure enables the analysis of the architecture of species interactions across different ecosystems and environmental gradients.

One groundbreaking result of this work is that structural generalities of natural food webs are robust across ecosystems, land-use gradients and spatial scales. This work comprises analyses across ecosystems and over a very large number of food webs. Therefore, I compiled a dataset, containing information on the ecosystem type, the species body masses and the food-web structures. I firstly integrated highly resolved soil food webs into comparative studies on food-web topology. A highly important factor constraining food web structure is the species' body mass influencing the degree distributions and interaction strengths. This supports earlier studies (Peters 1983, Brose et al. 2008) describing body mass as one of the most fundamental traits of a species. Body mass multiplies its importance and effects on species within the interaction network of food webs. In food webs, it influences the energy which channels through the system and, additionally, is critical for its stability (Otto et al. 2007, Vucic-Pestic et al. 2010, Kalinkat et al. 2013).

I also found indications that local communities are energetically filtered to match the scaling and structural properties of food webs. This might be reasoned in dynamical stability criteria which need scaling mechanisms to distribute the available energy with a minimum of loss and additionally dampen oscillating predator-prey densities. In ecological terms, this suggests that a community needs a balanced exploitation of resources over the different trophic levels. A new species needs the right energetic traits (i.e. body mass, vulnerability, generality) to successfully establish in a community. Therefore, energetic niches have important implications for the conservation of diversity because energetic filtering adds an additional layer to environmental adaptations of species to be considered.

I showed that food-web structure can be utilized for finding generalities across ecosystems. Furthermore, food-web structure explains species distributions across the environment and provides additional important information on the ecosystem. Therefore, this work contributes to the ecological research on the mechanisms generating and maintaining diversity.

Part IV
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Part V
Appendix

Supplementary information - Chapter 2:

Unravelling the complex structure of forest soil food webs: higher omnivory and more trophic levels

Table II.A1:

Food web properties of 48 forest soil food webs calculated from the binary feeding structure

food web					structural food web parameter							
plotname	species richness	links	connectance	links / species	clustering coeff.	bottom	intermediate	top	herbivores	omnivores	cannibalistic	gen. SD
AEW01	121	1840	0.1257	15.2066	0.6037	0.0496	0.9174	0.0331	0.1653	0.7025	0.2893	0.0095
AEW02	153	3344	0.1429	21.8562	0.6038	0.0458	0.9477	0.0065	0.1634	0.6993	0.3464	0.0076
AEW03	122	1844	0.1239	15.1148	0.5988	0.0492	0.9344	0.0164	0.1885	0.6803	0.2787	0.0092
AEW04	125	1837	0.1176	14.6960	0.5914	0.0640	0.8640	0.0720	0.1280	0.7200	0.3200	0.0091
AEW05	126	1875	0.1181	14.8810	0.5384	0.0556	0.9286	0.0159	0.1746	0.6667	0.2937	0.0098
AEW06	120	1744	0.1211	14.5333	0.5663	0.0583	0.9333	0.0083	0.1917	0.6583	0.3000	0.0097
AEW07	129	1957	0.1176	15.1705	0.5387	0.0543	0.8915	0.0543	0.1860	0.6744	0.2946	0.0095
AEW08	136	2304	0.1246	16.9412	0.6076	0.0515	0.9265	0.0221	0.1397	0.7279	0.3235	0.0082
AEW09	134	2373	0.1322	17.7090	0.6133	0.0522	0.9328	0.0149	0.1791	0.7164	0.3433	0.0087
AEW11	120	1864	0.1294	15.5333	0.5479	0.0500	0.9417	0.0083	0.1333	0.7417	0.2667	0.0094
AEW17	145	2863	0.1362	19.7448	0.6201	0.0552	0.9034	0.0414	0.1655	0.7034	0.3172	0.0080
AEW18	111	1608	0.1305	14.4865	0.5442	0.0631	0.9369	0.0000	0.1351	0.7027	0.3063	0.0100
AEW25	123	1853	0.1225	15.0650	0.5636	0.0569	0.9350	0.0081	0.1382	0.7236	0.3252	0.0088
AEW27	120	1345	0.0934	11.2083	0.4615	0.0583	0.9417	0.0000	0.2667	0.6000	0.2333	0.0111
AEW30	114	1422	0.1094	12.4737	0.5915	0.0614	0.8772	0.0614	0.1579	0.6842	0.2456	0.0100
AEW49	154	2882	0.1215	18.7143	0.5786	0.0455	0.9481	0.0065	0.1883	0.6948	0.3182	0.0077
HEW01	134	1572	0.0875	11.7313	0.5066	0.0448	0.8284	0.1269	0.2015	0.6866	0.2388	0.0097
HEW02	126	1778	0.1120	14.1111	0.5642	0.0556	0.8810	0.0635	0.1825	0.6984	0.3016	0.0090
HEW03	123	1667	0.1102	13.5528	0.6153	0.0569	0.8455	0.0976	0.1707	0.6992	0.3089	0.0083
HEW04	116	1195	0.0888	10.3017	0.4402	0.0603	0.8707	0.0690	0.2069	0.6379	0.2241	0.0104
HEW05	168	3137	0.1111	18.6726	0.5730	0.0357	0.9643	0.0000	0.1131	0.7798	0.3274	0.0071
HEW06	142	2345	0.1163	16.5141	0.5921	0.0493	0.9437	0.0070	0.1549	0.7324	0.3028	0.0084
HEW10	91	888	0.1072	9.7582	0.5379	0.0659	0.8791	0.0549	0.1538	0.6484	0.3077	0.0112
HEW11	132	1930	0.1108	14.6212	0.5755	0.0530	0.8939	0.0530	0.1818	0.6591	0.2955	0.0092
HEW12	143	2515	0.1230	17.5874	0.5877	0.0490	0.9441	0.0070	0.1748	0.6993	0.3287	0.0085
HEW13	144	2153	0.1038	14.9514	0.5482	0.0486	0.8403	0.1111	0.1944	0.6806	0.2708	0.0089
HEW16	132	2274	0.1305	17.2273	0.6057	0.0455	0.9318	0.0227	0.1742	0.7045	0.3636	0.0088
HEW17	139	2109	0.1092	15.1727	0.5521	0.0504	0.9353	0.0144	0.1511	0.7338	0.3237	0.0085
HEW21	146	1998	0.0937	13.6849	0.4816	0.0479	0.9110	0.0411	0.1507	0.7329	0.2808	0.0085
HEW22	137	2137	0.1139	15.5985	0.5720	0.0511	0.9343	0.0146	0.1606	0.7080	0.3358	0.0081
HEW36	160	3250	0.1270	20.3125	0.5906	0.0438	0.9313	0.0250	0.1750	0.7000	0.3625	0.0072
HEW47	148	3072	0.1402	20.7568	0.6559	0.0473	0.9324	0.0203	0.1419	0.7432	0.3446	0.0076
SEW01	104	1244	0.1150	11.9615	0.6007	0.0673	0.8269	0.1058	0.1442	0.6827	0.2596	0.0098
SEW02	93	729	0.0843	7.8387	0.4465	0.0753	0.7419	0.1828	0.1720	0.6237	0.2473	0.0118
SEW03	123	2191	0.1448	17.8130	0.6574	0.0488	0.9512	0.0000	0.0976	0.7805	0.3577	0.0080
SEW04	120	1603	0.1113	13.3583	0.5559	0.0667	0.9167	0.0167	0.1250	0.7000	0.3000	0.0091
SEW05	101	1238	0.1214	12.2574	0.5531	0.0594	0.8416	0.0990	0.2376	0.6238	0.2871	0.0113
SEW06	127	2044	0.1267	16.0945	0.6063	0.0551	0.8425	0.1024	0.0551	0.7244	0.3937	0.0076
SEW07	132	2786	0.1599	21.1061	0.6696	0.0606	0.9318	0.0076	0.1667	0.6742	0.4091	0.0079
SEW08	118	1896	0.1362	16.0678	0.6128	0.0678	0.9237	0.0085	0.1525	0.7034	0.3898	0.0090
SEW09	89	1038	0.1310	11.6629	0.6208	0.0674	0.8764	0.0562	0.1910	0.6180	0.3034	0.0116
SEW18	124	1938	0.1260	15.6290	0.6791	0.0565	0.8145	0.1290	0.1290	0.7016	0.2903	0.0088
SEW35	101	1183	0.1160	11.7129	0.5871	0.0594	0.8416	0.0990	0.1683	0.6634	0.3069	0.0102
SEW36	89	959	0.1211	10.7753	0.5662	0.0674	0.8315	0.1011	0.1236	0.6742	0.3258	0.0109

food web	structural food web parameter											
plotname	vuln. SD	max. similarity	mean trophic level	max trophic level	trophic level SD	char. path length	MAC	MTC	MEC	MIGP	degree correlation	modularity
AEW01	0.0059	0.8556	3.4496	5.3891	1.2048	1.8451	0.2835	0.2676	0.0884	0.3067	0.0575	0.2453
AEW02	0.0038	0.8678	3.5960	5.6944	1.2980	1.8085	0.3031	0.2691	0.0501	0.2787	0.0258	0.2315
AEW03	0.0053	0.8385	3.4630	5.6005	1.2975	1.8902	0.2802	0.3011	0.0637	0.2999	0.0684	0.2636
AEW04	0.0055	0.8391	3.5818	6.1231	1.3654	1.9788	0.2590	0.2931	0.0763	0.2508	0.0937	0.2645
AEW05	0.0049	0.8327	3.4121	5.4923	1.2437	1.9375	0.3297	0.2710	0.0746	0.2154	0.0426	0.2450
AEW06	0.0050	0.8375	3.3539	5.2059	1.2076	1.9076	0.3138	0.2790	0.0698	0.2470	0.1468	0.2506
AEW07	0.0047	0.8436	3.3254	5.2021	1.1661	1.9557	0.3426	0.2604	0.0797	0.2336	0.1093	0.2598
AEW08	0.0048	0.8530	3.5544	5.8898	1.2901	1.9029	0.2609	0.2917	0.0680	0.2769	0.1000	0.2836
AEW09	0.0048	0.8450	3.4912	5.6281	1.2833	1.8742	0.2862	0.2627	0.0601	0.2580	0.1472	0.2484
AEW11	0.0052	0.8496	3.6663	6.2607	1.3422	1.8260	0.2897	0.3078	0.0837	0.2507	-0.0629	0.2544
AEW17	0.0043	0.8531	3.5369	5.4461	1.2858	1.9126	0.2923	0.2548	0.0534	0.2630	0.1759	0.2327
AEW18	0.0052	0.8518	3.5445	5.8519	1.2883	1.8146	0.2937	0.2923	0.0855	0.2241	-0.0127	0.2874
AEW25	0.0049	0.8527	3.5800	5.7921	1.2586	1.9010	0.2909	0.2936	0.0885	0.2543	0.0644	0.3273
AEW27	0.0057	0.8290	3.1021	4.8647	1.1123	2.0079	0.3803	0.2654	0.1069	0.1951	-0.0616	0.2974
AEW30	0.0064	0.8342	3.3468	5.1880	1.1743	1.9848	0.2867	0.2657	0.1079	0.2836	0.2408	0.2803
AEW49	0.0041	0.8522	3.4477	5.3819	1.2112	1.9279	0.3028	0.2829	0.0657	0.2495	0.0825	0.2638
HEW01	0.0060	0.8109	3.2882	5.4207	1.1764	2.1162	0.3310	0.2535	0.1286	0.2143	0.0349	0.2578
HEW02	0.0052	0.8213	3.3801	5.4304	1.2268	1.9689	0.2955	0.2853	0.0904	0.2607	0.1221	0.3017
HEW03	0.0060	0.8109	3.4333	5.6619	1.2931	2.0315	0.2223	0.3319	0.0922	0.3343	0.1914	0.2862
HEW04	0.0066	0.8454	3.1883	4.9639	1.1018	2.0575	0.3368	0.2827	0.1609	0.1890	-0.1108	0.3192
HEW05	0.0043	0.8567	3.6920	5.8233	1.2436	1.9052	0.2935	0.2589	0.0948	0.2481	0.0006	0.2934
HEW06	0.0048	0.8175	3.4414	5.2583	1.2178	1.9329	0.3017	0.2587	0.0769	0.2572	0.1831	0.2504
HEW10	0.0079	0.8242	3.4303	5.6732	1.2928	2.0227	0.2363	0.3079	0.1412	0.2182	0.1254	0.3281
HEW11	0.0053	0.8288	3.3586	5.3231	1.2215	1.9713	0.3031	0.2579	0.0857	0.2372	0.1384	0.2718
HEW12	0.0044	0.8406	3.4738	5.1654	1.2064	1.8686	0.3291	0.2406	0.0694	0.2613	0.0852	0.2743
HEW13	0.0049	0.8545	3.3069	5.2175	1.1495	2.0292	0.3355	0.2535	0.0897	0.2337	0.0796	0.2815
HEW16	0.0046	0.8289	3.5668	5.3743	1.2635	1.8953	0.3144	0.2385	0.0638	0.2532	0.2013	0.2667
HEW17	0.0049	0.8336	3.5671	5.4056	1.2436	1.9440	0.3049	0.2767	0.0941	0.2402	0.0168	0.2898
HEW21	0.0050	0.8335	3.4263	5.4435	1.1812	1.9955	0.3418	0.2549	0.1351	0.1964	-0.0664	0.3333
HEW22	0.0048	0.8477	3.5545	5.4266	1.2494	1.9325	0.2840	0.2832	0.0914	0.2481	0.1057	0.3124
HEW36	0.0037	0.8509	3.4635	5.3140	1.2100	1.9124	0.3024	0.2787	0.0573	0.2603	0.1296	0.2655
HEW47	0.0044	0.8543	3.6375	5.6140	1.2828	1.8515	0.2700	0.2544	0.0516	0.3170	0.1602	0.2230
SEW01	0.0073	0.8619	3.6412	5.9721	1.4076	2.0155	0.2226	0.3305	0.1077	0.3228	0.0250	0.3034
SEW02	0.0102	0.8290	3.2569	5.6548	1.2274	2.1390	0.2673	0.2948	0.2194	0.2023	-0.1783	0.3290
SEW03	0.0053	0.8203	3.8711	5.8996	1.3942	1.8188	0.2239	0.3123	0.0635	0.3686	0.2214	0.2551
SEW04	0.0058	0.8408	3.5227	5.6021	1.2800	1.9033	0.2797	0.3075	0.1053	0.2715	-0.0192	0.3154
SEW05	0.0067	0.8220	3.2354	4.9467	1.1429	1.9922	0.3178	0.2940	0.0949	0.2886	0.0682	0.2548
SEW06	0.0056	0.8315	3.8325	6.1385	1.3636	1.8940	0.2138	0.3232	0.1100	0.3118	0.0034	0.3071
SEW07	0.0044	0.8583	3.5922	5.4218	1.3300	1.7932	0.2461	0.2961	0.0328	0.3584	0.1986	0.2196
SEW08	0.0050	0.8229	3.6612	5.6592	1.3833	1.8769	0.2592	0.3037	0.0598	0.2905	0.1539	0.2460
SEW09	0.0073	0.8087	3.4492	5.2393	1.2725	1.9260	0.2557	0.3033	0.0791	0.3309	0.1879	0.2851
SEW18	0.0063	0.8414	3.7283	6.2853	1.3849	2.0112	0.2168	0.2837	0.0744	0.3871	0.1862	0.2311
SEW35	0.0071	0.8062	3.5547	5.6218	1.3228	2.0174	0.2462	0.3217	0.1064	0.3089	0.1611	0.2790
SEW36	0.0077	0.7956	3.6363	6.0734	1.3858	1.9763	0.2348	0.3411	0.1133	0.2895	0.0662	0.2823

Supplementary information

Supplementary information - Chapter 3:

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

Table III.A1: Ninty-four natural food webs

Original sources of publication of the predation matrices and food-web common names used in chapter 3. 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. Overview of 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						Sources	
		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	Predation matrix source	Body size source
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	(Havens 1992)	Riede unpubl.
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	(Havens 1992)	Riede unpubl.
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	(Havens 1992)	Riede unpubl.
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	(Havens 1992)	Riede unpubl.
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	(Havens 1992)	Riede unpubl.
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	1.00	<0.001	(Havens 1992)	Riede unpubl.
Bridge Brook Lake	lake	–0.50	<0.001	0.23	1.88	<0.001	0.35	1.36	0.00	0.20	0.91	<0.001	0.99	<0.001	0.98	<0.001	(Havens 1992)	Riede unpubl.
Brook Trout Lake	lake	–0.29	0.08	0.22	0.50	0.11	0.19	0.21	0.51	0.03	0.94	<0.001	0.97	<0.001	0.96	<0.001	(Havens 1992)	Riede unpubl.
Buck Pond	lake	–0.82	<0.001	0.40	1.06	0.01	0.18	0.23	0.53	0.01	0.93	<0.001	0.97	<0.001	0.88	<0.001	(Havens 1992)	Riede unpubl.
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	(Havens 1992)	Riede unpubl.
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	0.90	<0.001	(Havens 1992)	Riede unpubl.
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	(Havens 1992)	Riede unpubl.
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	(Havens 1992)	Riede unpubl.
Constable Lake	lake	–0.22	0.09	0.09	0.54	0.06	0.11	0.30	0.33	0.03	0.91	<0.001	0.98	<0.001	0.93	<0.001	(Havens 1992)	Riede unpubl.
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	(Havens 1992)	Riede unpubl.
Emerald Lake	lake	–0.02	0.92	0.00	1.03	0.00	0.37	0.92	0.02	0.25	0.87	<0.001	0.97	<0.001	0.95	<0.001	(Havens 1992)	Riede unpubl.

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	0.90	<0.001	(Havens 1992)	Riede unpubl.
Fawn Lake	lake	–0.32	<0.01	0.25	0.78	<0.01	0.27	0.43	0.10	0.09	0.93	<0.001	0.96	<0.001	0.87	<0.001	(Havens 1992)	Riede unpubl.
Federation Lake	lake	–0.42	<0.01	0.41	0.41	0.09	0.14	–0.05	0.83	0.00	0.95	<0.001	0.96	<0.001	0.87	<0.001	(Havens 1992)	Riede unpubl.
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	(Havens 1992)	Riede unpubl.
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	(Havens 1992)	Riede unpubl.
Gull Lake	lake	–0.36	0.06	0.08	1.60	<0.001	0.52	1.23	<0.001	0.27	0.99	<0.001	0.95	<0.001	0.82	<0.001	(Havens 1992)	Riede unpubl.
Gull Lake North	lake	–0.20	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	(Havens 1992)	Riede unpubl.
Helldiver Pond	lake	–0.44	<0.001	0.25	0.94	<0.001	0.29	0.50	0.07	0.08	0.97	<0.001	0.96	<0.001	0.84	<0.001	(Havens 1992)	Riede unpubl.
High Pond	lake	–0.54	<0.001	0.45	0.42	0.20	0.07	–0.17	0.62	0.01	0.95	<0.001	0.95	<0.001	0.83	<0.001	(Havens 1992)	Riede unpubl.
Hoel Lake	lake	–0.32	0.01	0.10	1.60	<0.001	0.40	1.27	<0.001	0.24	0.97	<0.001	0.93	<0.001	0.80	<0.001	(Havens 1992)	Riede unpubl.
Horseshoe Lake	lake	–0.19	0.01	0.12	1.02	<0.001	0.33	0.80	<0.001	0.21	0.96	<0.001	0.94	<0.001	0.82	<0.001	(Havens 1992)	Riede unpubl.
Indian Lake	lake	–0.70	<0.01	0.24	1.40	<0.001	0.35	0.65	0.10	0.08	0.91	<0.001	0.97	<0.001	0.95	<0.001	(Havens 1992)	Riede unpubl.
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	(Havens 1992)	Riede unpubl.
Loon Lake	lake	–0.21	0.11	0.08	0.76	0.01	0.20	0.53	0.08	0.09	0.92	<0.001	0.97	<0.001	0.92	<0.001	(Havens 1992)	Riede unpubl.
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	(Havens 1992)	Riede unpubl.
Lost Lake East	lake	–0.38	<0.01	0.20	0.96	<0.01	0.24	0.55	0.06	0.09	0.91	<0.001	0.96	<0.001	0.88	<0.001	(Havens 1992)	Riede unpubl.
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	(Havens 1992)	Riede unpubl.
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	(Havens 1992)	Riede unpubl.
Oswego Lake	lake	–0.59	<0.001	0.46	0.80	0.01	0.19	0.16	0.60	0.01	0.97	<0.001	0.89	<0.001	0.78	<0.001	(Havens 1992)	Riede unpubl.
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	(Havens 1992)	Riede unpubl.

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	(Havens 1992)	Riede unpubl.
Razorback Lake	lake	–0.41	<0.001	0.27	0.86	<0.01	0.20	0.45	0.12	0.06	0.94	<0.001	0.96	<0.001	0.85	<0.001	(Havens 1992)	Riede unpubl.
Rock Lake	lake	–0.81	<0.01	0.35	0.58	0.06	0.16	–0.25	0.50	0.02	0.90	<0.001	0.97	<0.001	0.95	<0.001	(Havens 1992)	Riede unpubl.
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	(Havens 1992)	Riede unpubl.
Safford Lake	lake	–0.41	<0.001	0.26	0.99	<0.001	0.31	0.57	0.04	0.10	0.97	<0.001	0.96	<0.001	0.83	<0.001	(Havens 1992)	Riede unpubl.
Sand Lake	lake	–0.17	0.02	0.19	0.46	0.01	0.20	0.27	0.17	0.07	0.96	<0.001	0.96	<0.001	0.88	<0.001	(Havens 1992)	Riede unpubl.
South Lake	lake	–0.70	<0.01	0.33	0.75	<0.001	0.44	0.06	0.86	0.00	0.97	<0.001	0.99	<0.001	0.95	<0.001	(Havens 1992)	Riede unpubl.
Squaw Lake	lake	–0.36	<0.001	0.47	1.00	<0.001	0.26	0.62	0.03	0.12	0.92	<0.001	0.97	<0.001	0.91	<0.001	(Havens 1992)	Riede unpubl.
Stink Lake	lake	–0.39	<0.01	0.18	1.38	<0.001	0.31	0.96	0.00	0.16	0.97	<0.001	0.95	<0.001	0.85	<0.001	(Havens 1992)	Riede unpubl.
Twin Lake East	lake	–0.27	0.05	0.30	0.42	0.01	0.48	0.10	0.57	0.03	0.98	<0.001	0.97	<0.001	0.95	<0.001	(Havens 1992)	Riede unpubl.
Twin Lake West	lake	–0.67	<0.001	0.42	0.82	<0.01	0.30	0.12	0.65	0.01	0.91	<0.001	0.95	<0.001	0.94	<0.001	(Havens 1992)	Riede unpubl.
Twelfth Tee Lake	lake	–0.23	0.01	0.22	0.50	0.02	0.18	0.24	0.26	0.04	0.95	<0.001	0.99	<0.001	0.94	<0.001	(Havens 1992)	Riede unpubl.
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	0.80	<0.001	(Havens 1992)	Riede unpubl.
Wolf Lake	lake	–0.20	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	(Havens 1992)	Riede unpubl.
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	(Martinez 1991)	Riede unpubl.
Sierra Lakes	lake	–0.66	<0.001	0.27	1.81	<0.001	0.43	1.14	0.00	0.21	0.97	<0.001	0.92	<0.001	0.77	<0.001	(Brose et al. 2006)	(Brose et al. 2006)
Skipwith Pond	lake	–1.77	0.01	0.18	5.11	<0.01	0.27	3.21	0.01	0.20	0.99	<0.001	0.96	<0.001	0.84	<0.001	(Warren 1989)	(Brose et al. 2006)
Tuesday Lake 1984	lake	–0.86	<0.01	0.19	2.00	<0.001	0.52	1.09	0.01	0.13	0.97	<0.001	0.96	<0.001	0.81	<0.001	(Jonsson et al. 2005)	(Brose et al. 2006)
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	(Yodzis 1998)	(Yodzis 1998)
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	(Lafferty et al. 2006)	Riede unpubl.

St. Marks	marine	–0.59	0.00	0.31	0.41	0.00	0.25	–0.16	0.40	0.02	0.99	<0.001	0.90	<0.001	0.77	<0.001	(Christian and Luczkovich 1999)	Riede unpubl.
Mondego Esturay Zostera	marine	–0.97	<0.001	0.40	1.06	<0.001	0.32	0.08	0.78	0.00	0.99	<0.001	0.89	<0.001	0.74	<0.001	(Patricio and Marques 2006)	Jacob unpubl.
Small Reef	marine	–1.08	<0.001	0.30	1.13	0.01	0.15	0.01	0.98	0.00	0.99	<0.001	0.93	<0.001	0.79	<0.001	(Opitz 1996)	Riede unpubl.
Weddel See	marine	–3.74	<0.001	0.40	0.00	<0.001	0.08	–1.02	0.04	0.01	0.94	<0.001	0.98	<0.001	0.76	<0.001	(Brose et al. 2006)	(Brose et al. 2006)
Ythan Estuary	marine	–1.04	<0.001	0.15	1.02	<0.001	0.19	–0.03	0.94	0.00	0.88	<0.001	0.99	<0.001	0.92	<0.001	(Cohen et al. 2009)	(Cohen et al. 2009)
Alamitos Creek	stream	–3.54	<0.001	0.12	3.46	<0.01	0.05	–0.10	0.94	0.00	0.97	<0.001	0.95	<0.001	0.72	<0.001	(Harrison 2003)	Riede unpubl.
Bere Stream	stream	–2.46	<0.001	0.40	1.76	<0.01	0.29	–0.70	0.06	0.03	0.90	<0.001	0.97	<0.001	0.79	<0.001	(Woodward et al.2008)	Riede unpubl.
Broadstone Stream	stream	–0.33	0.35	0.03	1.13	0.07	0.10	0.77	0.23	0.05	0.96	<0.001	0.95	<0.001	0.82	<0.001	(Woodward and Hildrew 2001)	(Harrison 2003)
Calero Creek	stream	–2.78	<0.001	0.14	2.72	<0.01	0.08	–0.04	0.93	0.00	0.97	<0.001	0.95	<0.001	0.70	<0.001	(Harrison 2003)	Riede unpubl.
Corte Madera Creek	stream	–2.83	<0.001	0.11	3.38	<0.01	0.09	0.54	0.64	0.00	0.99	<0.001	0.93	<0.001	0.71	<0.001	(Harrison 2003)	Riede unpubl.
Coyote Creek	stream	–4.77	<0.001	0.22	4.70	<0.001	0.12	–0.09	0.93	0.00	0.98	<0.001	0.95	<0.001	0.73	<0.001	(Harrison 2003)	Riede unpubl.
Guadelupe Creek	stream	–4.51	<0.001	0.14	5.82	<0.001	0.10	1.30	0.36	0.00	0.98	<0.001	0.94	<0.001	0.69	<0.001	(Harrison 2003)	Riede unpubl.
Guadelupe River	stream	–3.41	<0.001	0.20	2.02	0.01	0.05	–1.41	0.10	0.02	0.99	<0.001	0.93	<0.001	0.70	<0.001	(Harrison 2003)	Riede unpubl.
Los Gatos Creek	stream	–4.63	<0.001	0.16	4.43	<0.001	0.07	–0.22	0.86	0.00	0.98	<0.001	0.94	<0.001	0.70	<0.001	(Harrison 2003)	Riede unpubl.
Los Trancos Creek	stream	–3.23	<0.001	0.15	3.71	<0.001	0.11	0.20	0.65	0.00	0.98	<0.001	0.93	<0.001	0.68	<0.001	(Harrison 2003)	Riede unpubl.
Mill Stream	stream	–1.34	<0.001	0.50	0.79	<0.001	0.47	–0.55	<0.01	0.10	0.90	<0.001	0.99	<0.001	0.86	<0.001	(Brose et. al. 2006)	(Brose et. al. 2006)
Penninterra Creek	stream	–5.01	<0.001	0.20	2.74	0.01	0.04	–2.27	0.05	0.02	0.98	<0.001	0.93	<0.001	0.68	<0.001	(Harrison 2003)	Riede unpubl.
Ross Creek	stream	–3.53	<0.001	0.18	3.37	<0.001	0.13	–0.17	0.87	0.00	0.99	<0.001	0.92	<0.001	0.70	<0.001	(Harrison 2003)	Riede unpubl.
San Francisquito Creek	stream	–4.03	<0.001	0.17	4.35	<0.001	0.10	0.30	0.78	0.00	0.99	<0.001	0.92	<0.001	0.68	<0.001	(Harrison 2003)	Riede unpubl.
Sarratoga Creek	stream	–4.44	<0.001	0.16	4.77	<0.001	0.09	0.33	0.80	0.00	0.97	<0.001	0.95	<0.001	0.72	<0.001	(Harrison 2003)	Riede unpubl.

Stevens Creek	stream	–5.36	<0.001	0.17	5.02	<0.001	0.08	–0.36	0.80	0.00	0.99	<0.001	0.92	<0.001	0.69	<0.001	(Harrison 2003)	Riede unpubl.
Broom Source	terrestrial	0.00	0.98	0.00	0.10	0.18	0.03	0.10	0.50	0.01	0.88	<0.001	0.98	<0.001	0.98	<0.001	(Memmott et al. 2000)	(Brose et al. 2006)
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	(Polis 1991)	Riede unpubl.
Florida Islands E1	terrestrial	0.29	0.15	0.01	0.15	0.05	0.02	1.44	0.01	0.03	0.80	<0.001	0.98	<0.001	0.80	<0.001	(Simberloff and Abele 1975)	Riede and Grischkat
Florida Islands E2	terrestrial	1.41	0.01	0.03	–0.32	0.18	0.10	1.09	0.05	0.07	0.76	<0.001	0.95	<0.001	0.93	<0.001	(Simberloff and Abele 1975)	Riede and Grischkat
Florida Islands E3	terrestrial	0.30	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	(Simberloff and Abele 1975)	Riede and Grischkat
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	(Simberloff and Abele 1975)	Riede and Grischkat
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	(Simberloff and Abele 1975)	Riede and Grischkat
Florida Islands Metaweb	terrestrial	0.83	0.10	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	(Simberloff and Abele 1975)	Riede and Grischkat
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	(Simberloff and Abele 1975)	Riede and Grischkat
Grande Caricaie CLControl	terrestrial	0.34	0.44	0.00	–0.09	0.90	0.00	0.27	0.68	0.00	0.93	<0.001	0.95	<0.001	0.72	<0.001	(Cattin et al. 2004)	(Brose et al. 2006)
Grande Caricaie CLControl2	terrestrial	–0.25	0.39	0.01	0.10	0.84	0.00	–0.13	0.79	0.00	0.92	<0.001	0.94	<0.001	0.74	<0.001	(Cattin et al. 2004)	(Brose et al. 2006)
Grande Caricaie CLMown1	terrestrial	0.38	0.32	0.00	–1.11	0.10	0.01	–0.73	0.27	0.01	0.95	<0.001	0.97	<0.001	0.74	<0.001	(Cattin et al. 2004)	(Brose et al. 2006)
Grande Caricaie CLMown2	terrestrial	0.24	0.40	0.00	–0.31	0.55	0.00	–0.06	0.90	0.00	0.92	<0.001	0.97	<0.001	0.77	<0.001	(Cattin et al. 2004)	(Brose et al. 2006)
Grande Caricaie SC_Control1	terrestrial	–0.67	0.01	0.04	–0.44	0.33	0.01	–1.10	0.02	0.04	0.94	<0.001	0.98	<0.001	0.80	<0.001	(Cattin et al. 2004)	(Brose et al. 2006)
Grande Caricaie SC_Control2	terrestrial	–0.60	0.01	0.04	–0.08	0.88	0.00	–0.67	0.16	0.00	0.91	<0.001	0.99	<0.001	0.81	<0.001	(Cattin et al. 2004)	(Brose et al. 2006)
Grande Caricaie SCMown1	terrestrial	–0.33	0.45	0.00	–0.09	0.72	0.00	–0.42	0.33	0.01	0.95	<0.001	0.97	<0.001	0.76	<0.001	(Cattin et al. 2004)	(Brose et al. 2006)
Grande Caricaie SCMown2	terrestrial	–0.71	0.14	0.00	0.04	0.86	0.01	–0.67	0.15	0.01	0.95	<0.001	0.97	<0.001	0.77	<0.001	(Cattin et al. 2004)	(Brose et al. 2006)

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Eidesstattliche Erklärung

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

Christoph Digel

Göttingen,

List of Publications, conference contributions and seminars

Publications in peer-reviewed journals

Digel, C., Ott, D., Grischkat, F., Brose, U.:Neutral species distributions yield non-random food-webs. (in prep.);

Ott, D., **Digel, C.**, Rall, B.C., Maraun, M., Scheu, S., Brose, U.: Unifying elemental stoichiometry and metabolic theory in predicting species abundances. *Ecology Letters* (in press), doi: 10.1111/ele.12330;

Ott, D., **Digel, C.**, Klarner, B., Maraun, M., Pollierer, M., Rall, B.C., Scheu, S., Seelig, G., Brose, U.: Litter elemental stoichiometry and biomass densities of forest soil invertebrates. *Oikos* (in press), doi: 10.1111/oik.01670;

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Digel, C., Grischkat, F., Brose, U. :Beta diversity and species area relationships of forest soil food webs (oral presentation), BES Annual Meeting 2012, 17-20 Dezember , University of Birmingham, UK

Digel, C., Riede J. O., Brose U.: Forest soil food webs (oral presentation), Tagung der Deutschen Bodenkundlichen Gesellschaft Kommission III Bodenbiologie und Ökologie, 20-21 September 2012 Universität Hohenheim

Digel, C., Riede J. O., Brose U.: Structure of forest soil food webs on a land-use gradient (poster), Functions and Services of Biodiversity 2011, 20-22 Juni, Universität Göttingen

Digel C, Riede J. O. and Brose U: Allometric degree distributions across natural food webs (poster), BES Annual Meeting 2010, 7-9 September, University of Leeds, UK