Scaling of Food-Web Properties with Diversity and Complexity Across Ecosystems

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SUMMARY

Trophic scaling models describe how topological food-web properties such as the number of predator–prey links scale with species richness of the community. Early models predicted that either the link density (i.e. the number of links per species) or the connectance (i.e. the linkage probability between any pair of species) is constant across communities. More recent analyses, however, suggest that both these scaling models have to be rejected, and we discuss several hypotheses that aim to explain the scale dependence of these complexity parameters. Based on a recent, highly resolved food-web compilation, we analysed the scaling behaviour of 16 topological parameters and found significant power–law scaling relationships with diversity (i.e. species richness) and

complexity (i.e. connectance) for most of them. These results illustrate the lack of universal constants in food-web ecology as a function of diversity or complexity. Nonetheless, our power–law scaling relationships suggest that fundamental processes determine food-web topology, and subsequent analyses demonstrated that ecosystem-specific differences in these relationships were of minor importance. As such, these newly described scaling relationships provide robust and testable cornerstones for future structural food-web models.

I. INTRODUCTION

Over the last several centuries, physicists have developed a variety of scaling laws, such as Newton's law of universal gravitation, which holds that the gravitational force between two bodies is proportional to the product of their masses and the inverse of their squared distance. The change in gravitational force with distance is well described by a scaling law, where the gravitational constant and the exponent (negative square) are constant with respect to distance. Scaling laws thus indicate, but do not prove, the fundamental process that governs the relationship between variables. In search of analogues of the grand laws of physics, ecologists have been searching for ecological scaling models that can be generalized across organisms, populations and even entire ecosystems (Lange, 2005; O'Hara, 2005). Among the most promising approaches, trophic scaling models predict relationships between topological food-web properties, such as the number of predator–prey feeding interactions (links, L) and the species richness (S, hereafter: diversity) of the community (Dunne, 2006). In diversity–topology relationships, scale refers to the number of species; and ecologists have searched for universal food-web constants that equally apply to species-poor and species-rich ecosystems. Early trophic scaling models suggested that link density—the number of links per species (L/S)—is constant across food webs of varying species richness (Cohen and Briand, 1984). This 'link-species scaling law' is in agreement with the classical stability criterion of random networks, which holds that local population stability is maintained if link density remains below a critical threshold that, in turn, depends on the average interaction strength (May, 1972). Subsequent early trophic scaling models proposed constancy of additional food-web properties, including the proportions of top species (T, species consuming other species whilst they have no consumers), intermediate species (I, species that consume and are consumed by other species) and basal species (B, species without resource species below them within a food chain, e.g. plants or detritivores) (Cohen and Briand, 1984), and constant proportions of links between these trophic groups: T–I, T–B, I–I and I–B links (Cohen and Briand, 1984). Empirical tests using early food-web data rendered support to these scaling laws (Briand and Cohen, 1984; Cohen and Briand, 1984; Cole *et al.*, 2006), but the quality of the data employed has cast doubt on the validity of these findings,

largely due to poor taxonomic resolution, limited sampling effort and the presence of biological impossibilities (e.g. birds included as basal species) (Hall and Raffaelli, 1993; Ings *et al.*, 2009; Paine, 1988; Polis, 1991).

Other studies based on data of higher quality demonstrated that link density, the proportions of top, intermediate and basal species, and the proportions of *T–I*, *T–B*, *I–I* and *I–B* links are not constant across the diversity scale (Hall and Raffaelli, 1991; Martinez, 1991, 1993a; Schoener, 1989; Warren, 1989; Winemiller, 1990). Earlier findings of scale invariance were consequently ascribed to a range of methodological artefacts arising from inadequate sampling, strong species aggregation and poor data resolution (Bersier *et al.*, 1999; Goldwasser and Roughgarden, 1997; Hall and Raffaelli, 1991; Martinez, 1991, 1993b; Martinez *et al.*, 1999).

While the improved data demonstrated scale dependence of link density, an alternative hypothesis proposed that connectance (C)—the linkage probability of any pair of species in the food web ($C = L/S$)—should be constant across ecosystems of variable species richness (Martinez, 1992). Models with constant link density assume that any species can consume a fixed number of the coexisting species, whereas the constant–connectance model holds that any species can consume a fixed fraction of the coexisting species. The latter hypothesis initially received some empirical support (Martinez, 1992, 1993a, b; Spencer and Warren, 1996), but further analyses of more recent food-web data suggest that neither link density nor connectance are constant across the diversity scale (Brose and Martinez, 2004; Dunne, 2006; Montoya and Sole, 2003; Schmid-Araya *et al.*, 2002).

Much of this trophic scaling debate has focused on parameters of food-web complexity, such as the link density or connectance (Dunne, 2006). Other recent approaches that have addressed the scaling of additional topological food-web parameters have been inspired by physicists' scaling laws and introduced scale-dependent properties, but with constant scaling exponents (Camacho *et al.*, 2002a,b; Garlaschelli *et al.*, 2003). This implies that the studied food-web properties vary with the diversity of the communities, but this variance is described by universally constant exponents. For instance, they found significant scaling relationships of food-web properties such as the fractions of top, intermediate and basal species and the number of links among them (Martinez, 1994), the clustering coefficient (Camacho *et al.*, 2002a,b; Dunne *et al.*, 2002) and the average path length between any pair of species in a food web (Camacho *et al.*, 2002a,b; Williams *et al.*, 2002). However, all these studies still suffered from data limitation by either being based on older food-web collections of poor resolution or new compilations of high-quality data that included fewer than 20 food webs. Over the last decade or so, additional collections of higher quality food webs have become available (Brose *et al.*, 2006a; Brose and Martinez, 2004; Townsend *et al.*, 1998), but systematic and comprehensive analyses of scaling relationships in these data have yet to be undertaken.

In the present study, we attempt to fill this void by analysing the scaling of 19 food-web properties (see Section II for a description) with species richness (diversity) and connectance (complexity) using a collection of 65 food webs from terrestrial, lake, stream, estuarine and marine ecosystems (see Appendix for a detailed overview). Additionally, we tested for significant differences in scaling relationships among these five ecosystem types. This approach extends prior studies testing for significant deviations of marine (Dunne *et al.*, 2004) or Cambrian food-web topology (Dunne *et al.*, 2008) from those of other ecosystems. Our analyses also address whether the different ecosystem types included possess specific topologies, or whether there are consistent scaling relationships that hold across ecosystems, which would indicate the existence of general constraints upon the structure of ecological networks.

II. METHODS

A. The Food-Web Data Set

We illustrate trophic scaling relationships using a data set of 65 food webs from a variety of habitats (see Appendix for an overview of the food webs). This compilation includes 13 food webs that have been used in prior meta-studies (Cattin *et al.*, 2004; Dunne, 2006; Dunne *et al.*, 2004; Montoya and Sole, 2003; Stouffer *et al.*, 2005; Williams and Martinez, 2000) and six food webs from a meta-study on natural consumer–resource body-mass ratios (Brose *et al.*, 2006a,b). They are complemented by four further webs from the banks of Lake Neuchâtel (Cattin, 2004), nine of the largest webs from a study of 50 lakes in the Adirondack Mountains of New York State (Havens, 1992), eight stream webs from the collection of 10 New Zealand webs (Townsend *et al.*, 1998) and five terrestrial island food webs (Piechnik *et al.*, 2008). We did not consider food webs dominated by parasitoid or parasitic interactions, because the physical constraints by which they are governed differ from those that govern predator–prey interactions (Brose *et al.*, 2006a,b), thus modifying complexity patterns (Lafferty *et al.*, 2006). This choice is not meant to imply that such interactions are not of importance for the structure and function of the food webs, rather that maintaining a focus on free-living predator–prey interactions in a consistent, standardized manner helps elucidate the underlying processes. Overall, the data compilation analysed here includes food webs from 14 lakes or ponds, 25 streams or rivers, five brackish water of estuaries and salt marshes, six marine and 15 terrestrial ecosystems. The number of taxonomic species in these food webs ranges between 27 and 492, and the number of links ranges from 60 to 16,136.

B. Food-Web Topology

Nineteen food-web properties were calculated for each of the 65 taxonomic food webs studied (see Figures 1 and 3 for an overview). The properties analysed were: (1) the total number of links in the food webs, L; (2) the number of links per species, L/S; (3) connectance, C; the fractions of (4) top
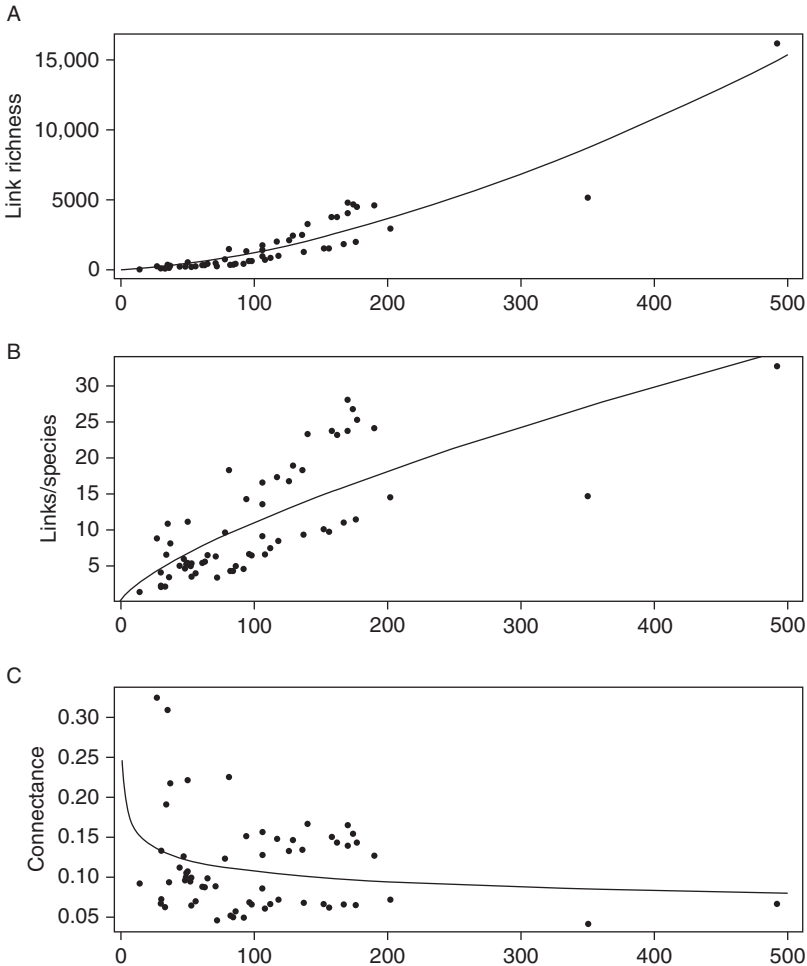

Figure 1 Diversity–complexity relationships. Scaling of (A) trophic link richness (exponent $= 1.57 \pm 0.07$, $p < 0.001$), (B) links per species (exponent $= 0.71 \pm 0.08$, $p < 0.001$) and (C) connectance (exponent $= -0.18 \pm 0.09$, $p = 0.057$) with species richness of the food webs.

species (species with resources but without consumers), (5) intermediate species (species with resources and consumers); (6) basal species (species with consumers but without resources); (7) herbivores (species that consume basal species); (8) omnivores (species consuming resources across more than one trophic level); (9) cannibals (species partially feeding on con-specifics); (10) species in loops (circular link structures originating and ending at the same species); (11 and 12) the standard deviations of the species' generality (the number of resources) and vulnerability (the number of consumers); (13) linkedness (the total number of links to resources and consumers); (14) the average short-weighted trophic level (SWTL, average of the prey-averaged trophic level and the shortest chain for each species) across all species in the food web; (15) the average shortest chain length (shortest chain of trophic links from a species to a basal species) across all species in the food web; (16) the species' mean similarity (mean of the maximum trophic similarity of each species to any other species in the same food web); (17) the characteristic path length (mean over all shortest trophic paths between any pair of species in a food web); (18) the mean clustering coefficient (probability that two inter-acting species are linked to a third species); (19) and the diet discontinuity (the proportion of triplets of taxa with an irreducible gap in feeding links over the number of possible triplets), which have also been used in prior studies (Cattin *et al.*, 2004; Dunne *et al.*, 2004).

C. Statistical Analyses

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

$$L = aS^b \tag{1a}$$

$$L/S = aS^b \tag{1b}$$

$$C = aS^b \tag{1c}$$

where a and b are constants. For the remaining 16 topological food-web properties, P, we analysed the power–law scaling with species richness, S, and connectance, C:

$$P = aS^b C^c \tag{2}$$

where a, b and c are constants. We used a non-linear least-squares regression method to fit Eqs. 1a, 1b, 1c and 2 to the data (function 'nls' within the standard package 'stats' provided by the statistical software **R** 2.9.0, R Development Core Team, 2009). Significant scaling exponents b and c were interpreted as an indication of diversity and complexity scaling, respectively.

Two prominent scaling models predict that the scaling exponent, b, of the relationship between the number of links and species richness should be one ('the link-species scaling law', Cohen and Briand, 1984) or two ('the constant connectance hypothesis', Martinez, 1992). We tested these specific predictions by calculating the normally distributed probabilities of the z scores:

$$p\left(z = \frac{b - \mu}{\sigma}\right) \tag{3}$$

where b is the estimated exponent, σ its standard error, and μ represents the expected prediction.

Subsequently, we used the residuals of the fitted power–law models (Eq. 2) to test for signatures of the five ecosystem types (lake, stream, estuarine, marine and terrestrial ecosystems) in the scaling relationships. Our first analyses addressed significant differences in the overall food-web structure between these ecosystem types by a cluster analysis based on Euclidean distances (function 'hclust' within the package 'stats' provided by the statistical software **R** 2.9.0, R Development Core Team, 2009). Prior to this analysis, the residuals were normalized to zero mean (which they already had before) and unit variance. In a second analysis, we tested for significant differences in specific topological properties among the ecosystem types. For each of the 16 food-web properties, we carried out independent ANOVAs with the residuals as dependent variables and the ecosystem type as the factorial independent variable in one-way ANOVAs. Significant ANOVAs were followed by Tukey HSD post hoc tests.

III. RESULTS

The food webs in our data collection comprise between 27 and 492 species with 60–16,136 trophic links reported, 2–32.8 links per species, and connectance values that ranged from 0.04 to 0.33 (see Appendix for an overview of the food webs). In our first analysis, we illustrate the scaling of link richness, link density (links per species) and connectance with diversity (Figure 1).

A. Complexity–Diversity Relationships

The scaling of link richness (i.e. the number of trophic links, L) with species richness (S) should follow a power law with a slope of one ($\mu = 1$, Eq. 3) according to the 'link-species scaling law' (Cohen and Briand, 1984), or a slope of two ($\mu = 2$, Eq. 3) according to the 'constant connectance hypothesis' (Martinez, 1992). The power–law model (Eqs. 1a, 1b, 1c) fitted to our data

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

	Intercept			Slope		
	Estimate	Std. error	*p*-Value	Estimate	Std. error	*p*-Value
Link richness	0.86715	0.34271	0.0139	1.57372	0.06843	<0.001
Link/species	0.4002	0.15731	0.0134	0.71976	0.07731	<0.001
Connectance	0.24588	0.09872	0.0154	−0.18032	0.094	0.0596

yielded an exponent, b, of 1.57 ± 0.07 (mean$\pm$s.e., Figure 1A, Table 1), which differed significantly from one ($z = 8.1429$, $p < 0.001$) and two ($z = -6.1429$, $p < 0.001$). Further analyses suggested that link density increased significantly ($p < 0.001$), whereas connectance tended to decrease with diversity ($p = 0.06$), (Figure 1B and C, Table 1). This implied that more diverse food webs were characterized by more links per species, but a lower connectance, than food webs of low diversity. Two of the food webs in our data set contained considerably more species than the other food webs: these were those of the Weddell Sea, with 492 species, and Lough Hyne, with 350 species. It is possible that these data points might have exerted an undue influence on our conclusions, but repeating the analyses while excluding these two data points yielded similar results.

B. Ecosystem Types and Complexity–Stability Relationships

The distribution of the data in Figure 1 suggested two groups of food webs below and above the power–law model: one group of food webs with more links, a higher link density and a higher connectance and a second group of food webs with fewer links, a lower link density and a lower connectance than predicted by the power–law regression models. This resulted in positive and negative residuals of the first and second data group, respectively. We hypothesized that these differences might be driven by characteristics of specific ecosystems, such as the higher connectance and link density that appears to generally occur in marine ecosystems (Dunne *et al.*, 2004). Hence, we employed three independent one-way ANOVAs to test for significant effects of the ecosystem type on the residuals of link richness (Figure 2A), links per species (Figure 2B) and connectance (Figure 2C). We found significant effects of the ecosystem types on link richness and links per species. Subsequent post hoc tests revealed that this pattern was driven by higher link richness ($p = 0.048$) and links per species ($p = 0.021$) in river ecosystems relative to terrestrial ecosystems (Figure 2A and B). All other differences
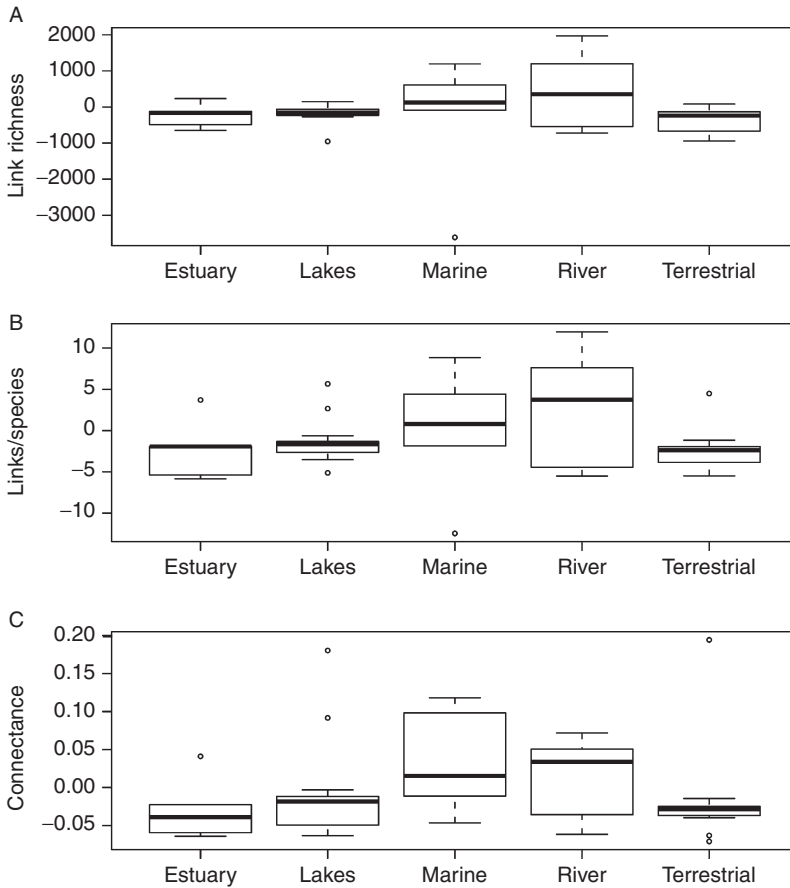
Figure 2 Ecosystem-type specific differences in diversity–complexity scaling: differences in the residuals of the diversity–complexity relationships (shown in Figure 1) for (A) trophic link richness (note that only the relationship between terrestrial and river ecosystems is significantly different; $p = 0.048$), (B) links per species (note that only the relationship between terrestrial and river ecosystems is significantly different; $p = 0.022$) and (C) connectance depending on the ecosystem types.

among pairs of ecosystem types were not significant. Interestingly, our analyses did not reveal any significant difference in connectance between the ecosystem types (Figure 2C). This also revealed that the grouping of ecosystems in types employed in our study did not explain the residual pattern apparent in Figure 1. Together, these results suggested that river ecosystems were richer in links and links per species than terrestrial ecosystems, whereas otherwise complexity was similar across ecosystem types.

C. Topology–Diversity Relationships

We subsequently analysed the scaling of 16 additional food-web properties with diversity (Figure 3) and connectance (Figure 4) by fitting the power–law regression model (Eq. 2) to the data. We found that 10 food-web properties were significantly correlated with species richness in the way predicted by a power function (Table 2): the fractions of top, intermediate, basal, omnivore and cannibalistic species, the number of species in loops, the standard

Figure 3 The diversity scaling (Eq. 2) of 16 food-web properties: fraction of (A) top, (B) intermediate, (C) basal, (D) herbivore, (K) omnivore and (M) cannibalistic species, (H) species in loops, the standard deviations of (E) generality, (F) vulnerability and (G) linkedness, (I) the mean short trophic level (SWTL), (J) the mean shortest chain length (MSC), (L) the mean similarity, (N) the characteristic path length (CPL), (O) the mean clustering coefficient (MCC) and (P) the diet discontinuity (DD). See Table 2 for fitted model parameters. For the *y*-axis, we used the normalized residuals for each food-web property and ecosystem type (see Section II for details).

Figure 4 The complexity scaling (Eq. 2) of 16 food-web properties: fraction of (A) top, (B) intermediate, (C) basal, (D) herbivore, (K) omnivore and (M) cannibalistic species, (H) species in loops, the standard deviations of (E) generality, (F) vulnerability and (G) linkedness, (I) the mean short trophic level (SWTL), (J) the mean shortest chain length (MSC), (L) the mean similarity, (N) the characteristic path length (CPL), (O) the mean clustering coefficient (MCC) and (P) the diet discontinuity (DD). See Table 2 for fitted model parameters. For the y-axis, we used the normalized residuals for each food-web property and ecosystem type (see Section II for details).

deviation of linkedness, the mean similarity, the characteristic path length and the mean clustering coefficient.

Moreover, 12 food-web properties were significantly correlated with connectance in the way predicted by the power–law model of Eq. 2 (Table 2): the fractions of top, intermediate, basal, omnivore and cannibalistic species, the number of species in loops, the standard deviatio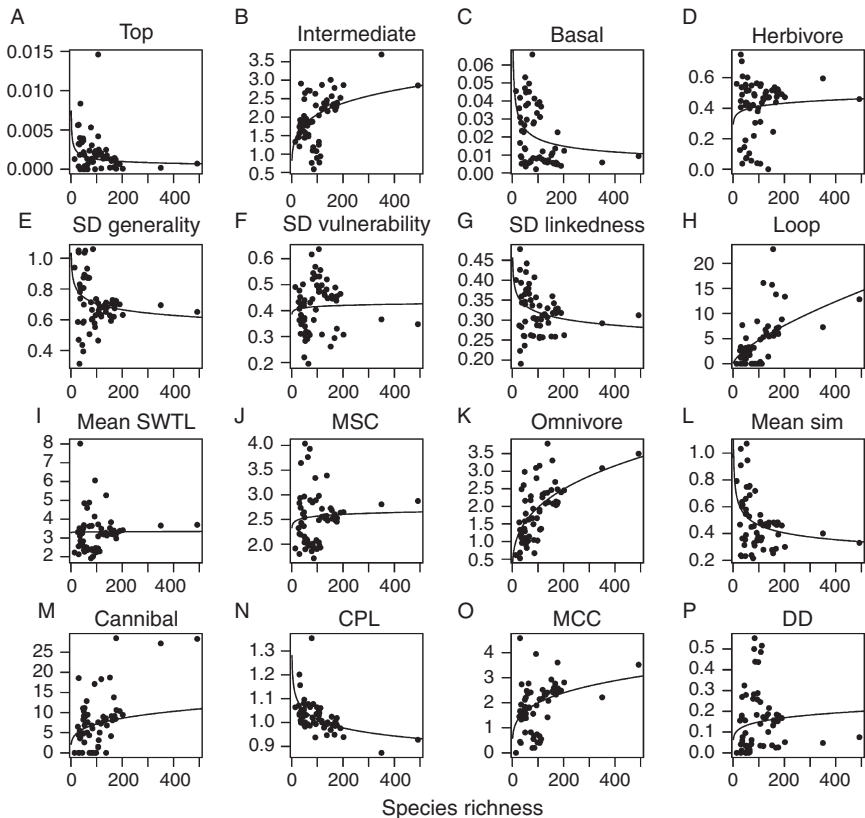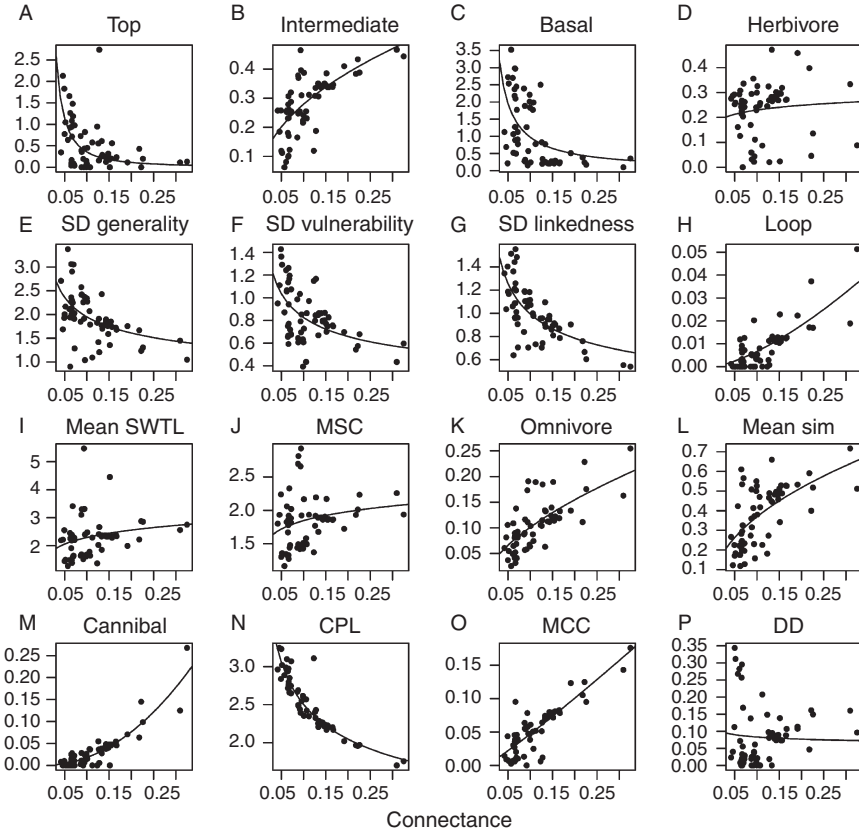ns of generality, vulnerability and linkedness, the mean similarity, the characteristic path length and the mean clustering coefficient.

Table 2 Fit of a power–law scaling model (Eq. 2) of different topological food-web properties depending on connectance and species richness

Variables	a			b (species-richness)			c (connectance)		
	Estimate	Std. deviation	p	Estimate	Std. deviation	p	Estimate	Std. deviation	p
Fraction. Top	0.007	0.008	0.368	−0.382	0.182	0.04	−1.68	0.414	<0.001
Frac. Intermediate	0.832	0.192	<0.001	0.198	0.049	<0.001	0.474	0.071	<0.001
Frac. Basal	0.097	0.072	0.187	−0.353	0.135	0.011	−1.004	0.257	<0.001
Frac. herbivore	0.298	0.132	0.028	0.071	0.09	0.438	0.112	0.13	0.392
SD generality	1.032	0.229	<0.001	−0.083	0.043	0.061	−0.276	0.066	<0.001
SD vulnerability	0.388	0.09	<0.001	0.015	0.044	0.735	−0.328	0.07	<0.001
SD linkedness	0.456	0.078	<0.001	−0.077	0.033	0.022	−0.339	0.051	<0.001
Frac. in loop	0.185	0.081	0.026	0.701	0.114	<0.001	1.445	0.192	<0.001
Mean SWTL	3.288	1.053	0.003	0.003	0.067	0.969	0.157	0.095	0.101
Mean short chain	2.335	0.458	<0.001	0.021	0.04	0.611	0.102	0.058	0.082
Frac omnivore	0.414	0.108	<0.001	0.339	0.056	<0.001	0.612	0.082	<0.001
Mean similarity	1.132	0.299	<0.001	−0.194	0.062	0.003	0.487	0.081	<0.001
Frac cannibal	2.171	0.589	<0.001	0.26	0.102	0.014	2.078	0.185	<0.001
Char path length	1.281	0.071	<0.001	−0.051	0.011	<0.001	−0.291	0.017	<0.001
Mean cluster coef.	0.588	0.147	<0.001	0.265	0.063	<0.001	1.098	0.098	<0.001
Diet discontinuity	0.064	0.064	0.317	0.183	0.192	0.344	−0.113	0.289	0.697

The food-web parameters are: fraction of top, intermediate, basal, herbivore, cannibalistic species, species in loops, the standard deviations of generality, vulnerability and linkedness, the mean short-weighted trophic level, the mean shortest chain length, the mean similarity, the characteristic path length, the mean clustering coefficient and the diet discontinuity (see Section II for details).

With increasing species richness the fractions of top and basal species decreased, whereas the fractions of intermediate and omnivorous species increased (Figure 3A–C and K). Additionally, the standard deviation of the species' linkedness and their mean trophic similarity decreased (Figure 3G and L). This implied that in the more diverse food webs the predominantly increasing number of intermediate species yielded a more similar distribution of the number of links across species but less similarity in who consumes whom. Moreover, the characteristic path length between any pair of species decreased (Figure 3N) and the mean clustering coefficient increased (Figure 3O) with increasing species richness. Thus, in more diverse food webs, the species were assembled in clusters of sub-webs and consequently, the average length of the trophic paths between pairs of species decreased.

With increasing food-web connectance, our analyses indicated that the fractions of top and basal species, the standard deviations of generality, vulnerability and linkedness, and the mean clustering coefficient decreased, whereas the fraction of intermediate, omnivore and cannibalistic species, the proportions of species in loops, the mean trophic similarity among species and the mean cluster coefficient increased with connectance (Figure 4, Table 2).

D. Ecosystem Types and Topology–Diversity Relationships

While these analyses suggested a significant fit of the general diversity and complexity scaling model for topological food-web properties (Eq. 2), we also addressed significant differences in trophic scaling among the five ecosystem types (lake, stream, estuarine, marine and terrestrial ecosystems). The cluster analysis of the normalized residuals of the fitted trophic scaling model illustrated whether the overall similarity or dissimilarity of the food-web topologies could be ascribed to the ecosystem types (Figure 5). This analysis revealed that despite some topological similarities in food webs located closely to each other, no systematic grouping of food webs according to the ecosystem types emerged. This residual analysis suggested that (1) the trophic scaling models (Figures 3 and 4) held across ecosystem types without systematic deviations, and (2) despite variance in species richness and connectance between ecosystem types, natural food webs possessed similar overall topologies.

Subsequently, we carried out more detailed analyses of variance (ANOVA) of the residuals of the 16 food-web properties among the five ecosystem types (Figures 6 and 7). We found significant signatures of the ecosystem types in the fractions of intermediate (Figure 6B), basal (Figure 6C) and herbivorous species (Figure 6D), the standard deviations
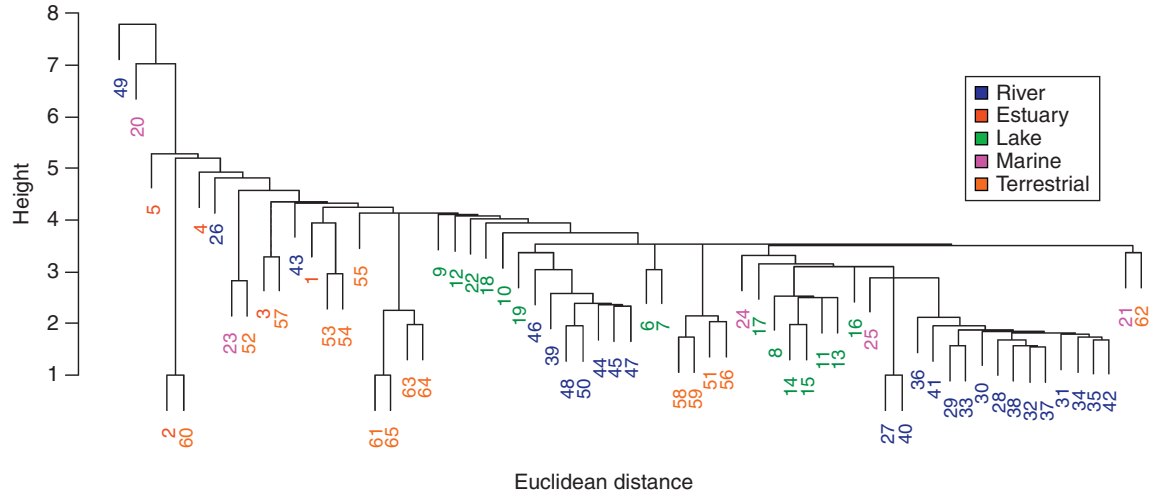
Figure 5 Clustering of food webs according to the residual variation in the 16 food-web properties (see Figures 4 and 5). Euclidian distances were calculated with species richness and connectance corrected values. Colour code for the different ecosystems: blue=rivers, red=estuaries, green=lakes, pink=marine ecosystems, orange=terrestrial ecosystems. The web numbers are given in the Appendix. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this chapter.)

Figure 6 Significant differences in topological properties (the residuals of their complexity and diversity scaling according to Eq. 2—see Figures 3 and 4) between the ecosystem types: the fractions of (A) top, (B) intermediate, (C) basal, and (D) herbivore species, the standard deviations of (E) generality, (F) vulnerability and (G) linkedness, (H) the fraction of species in loops. Significant differences between ecosystems types were calculated by Tukey HSD post hoc tests (*$p < 0.05$; ***$p < 0.001$).
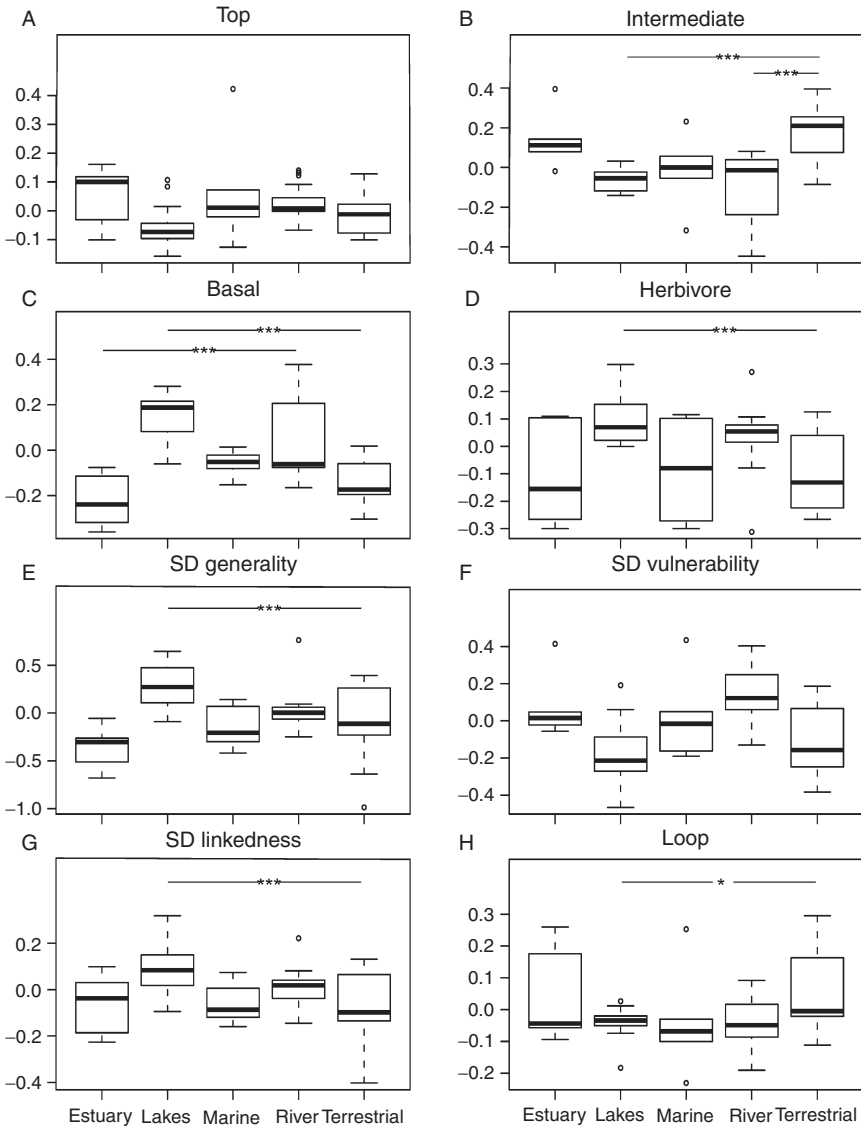
Figure 7 Significant differences in topological properties (the residuals of their complexity and diversity scaling according to Eq. 2—see Figures 3 and 4) between the ecosystem types: (A) the mean short-weighted trophic level, (B) the mean shortest chain length, (C) the fraction of omnivores, (D) the mean similarity, (E) the fraction of cannibals, (F) the characteristic path length, (G) the mean clustering coefficient and (H) the diet discontinuity. Significant differences between ecosystems types were calculated by Tukey HSD post hoc tests (*$p < 0.05$; ***$p < 0.001$).

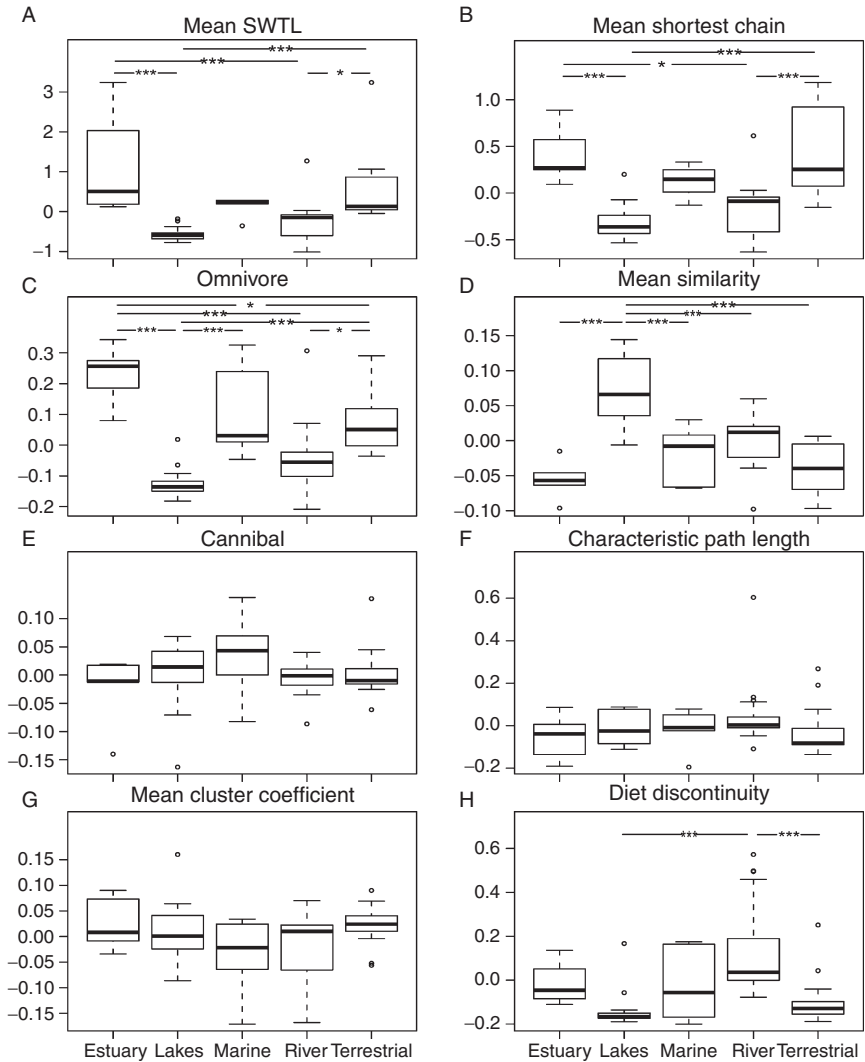of generality (Figure 6E) and linkedness (Figure 6G), the fraction of species
in trophic loops (Figure 6H), the mean short-weighted trophic levels
(Figure 7A), the mean shortest chain lengths (Figure 7B), the fraction of
omnivores (Figure 7C), the mean trophic similarity of species (Figure 7D)
and the diet discontinuity (Figure 7H). These differences were subsequently
explored in more detail using post hoc tests (Figures 6 and 7). Across the 16
food web properties, this included a total of 160 pairwise comparisons of
ecosystem types. Overall, 26% (43 out of 160 combinations) of these possible
combinations were significantly different from each other (see levels of
significance indicated in Figures 6 and 7 for details). This suggested that
the majority of topological food-web properties followed similar diversity–
complexity scaling models across ecosystems. Some systematic differences
emerged between lake and terrestrial ecosystems in terms of the fractions of
intermediate, basal, herbivorous and omnivorous species, the mean short-
weighted trophic level, the mean shortest chain length, the mean similarity
and the fraction of species in loops (Figures 6 and 7). Additionally, some
estuaries and lakes differed in the mean short-weighted trophic level, the
mean shortest chain length, the fraction of omnivores and the mean similarity.
Overall, these analyses suggest that most differences in food-web topology
occurred when comparing terrestrial and lake ecosystems, whereas terrestrial
and marine ecosystems were most similar.

IV. DISCUSSION

A. Complexity–Diversity Relationships

Over several decades, the search for universal food-web constants that
equally apply to species-poor and species-rich ecosystems has focused on
complexity–diversity relationships. While the link-species scaling law pre-
dicts constancy of the number of links per species (Cohen and Briand, 1984),
the alternative constant–connectance hypothesis holds that network connec-
tance should remain constant as species richness increases (Martinez, 1992).
Based on a new collection of novel food webs, our results suggest that both
scaling models, the link-species scaling law and the constant–connectance
hypothesis, have to be rejected. Instead, we found that link richness and the
number of links per species increase, whereas connectance decreases along
the diversity scale. Caution must be exerted, however, regarding the latter
conclusion as the result was only marginally significant, and large variation
in connectance was observed among food webs of similar species richness,
particularly at poor to intermediate richness levels. Additional food-web
data are necessary to provide a more robust evaluation of this hypothesis.
Moreover, our results suggest that there is a stronger constraint to the

maximum connectance possible for different food webs, which defines a clear upper boundary of the diversity–connectance relationship, while no lower boundary is apparent. Overall, in contrast to classic models, our results support the recent paradigm shift from the previously held perception that connectance is constant to one that it is scale dependent (Brose *et al.*, 2004; Dunne, 2006; Montoya and Sole, 2003; Schmid-Araya *et al.*, 2002).

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

B. Explanations for the Scale Dependence of Complexity

Several potential explanations for the scale dependence of links per species and connectance can be identified. First, in communities with many interacting species, the decrease of connectance with diversity might result from a methodological artefact (Paine, 1988), namely that the difficulty of identifying trophic links among a large number of species increases with species richness. This yields a potentially lower sampling intensity of links in more diverse food webs, which could account for a decrease in connectance with species richness (Bersier *et al.*, 1999; Goldwasser and Roughgarden, 1997; Ings *et al*., 2009; Martinez *et al.*, 1999). Ultimately, an adequate sampling effort can only be guaranteed if yield–effort curves demonstrate saturation in link richness with sampling effort for every food web (Ings *et al.*, 2009; Woodward and Hildrew, 2001) or if extrapolation methods suggest a high sampling coverage (Brose and Martinez, 2004; Brose *et al.*, 2003). While this is certainly desirable for future food-web compilations, the currently

available data lack this information and we cannot entirely rule out that sampling effect contributes to the decrease in connectance with species richness.

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

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

Fourth, processes that increase diversity might reduce species' ability to co-exist, which would also decrease connectance. However, the constant–connectance and link-species scaling models assume that species consume a fixed fraction or a fixed number, respectively, of the co-existing species (Cohen and Briand, 1984; Martinez, 1992). Thus, these models predict constancy in the scaling exponents only if co-existence does not change with diversity. However, potential consumer and resource species do not necessarily co-exist in meta-communities at larger spatial scales (Brose *et al.*, 2004; Olesen *et al.*, in press). If species richness across food webs increases with the spatial extent of the habitats, connectance will decrease with species richness due to a decrease in predator–prey co-occurrence. Link-area models based on this argument have successfully predicted the number of links, link density and connectance of aquatic food webs ranging in spatial scale from local habitats to landscapes (Brose *et al.*, 2004). Interestingly, the exponent of the power–law link-species model at the scale of local habitats was close to two, as predicted by the constant–connectance model, whereas it decreased to lower values when larger spatial scales were included, where species' co-existence is expected to break down (Brose *et al.*, 2004). Similarly, predator–prey co-existence may also break down with increasing habitat complexity (Keitt, 1997). Increasing habitat complexity or architectural complexity of the vegetation leads to higher species richness as many predators can specialize on specific sub-habitats, such as distinct vegetation layers (Brose, 2003; Olesen *et al.*, in press; Tews *et al.*, 2004). The localized occurrence of these predators in sub-habitats may yield reduced connectance as the predators do not co-exist with all prey species that fall within their feeding niche. Interestingly, strong support for the constant–connectance hypothesis comes from the pelagic food webs of 50 lakes (Martinez, 1993a) and aquatic microcosms (Spencer and Warren, 1996). In these relatively homogeneous habitats, increases in habitat complexity play little or no role in increasing species richness, which allows for constant connectance. In contrast, increasing species richness in stream communities was correlated with decreases in connectance, which might be partially explained by variations in habitat complexity (Schmid-Araya *et al.*, 2002).

Fifth, predator specialization might decrease connectance in the more diverse food webs. The feeding ranges of consumers are limited to specific body-size ranges of potential resource species (Brose *et al.*, 2008; Vucic-Pestic *et al.*, 2010). With increasing species richness, the likelihood of that particularly small or large species occur also increases, which should result in an increase in the body-size range with increasing species richness. If the body-size range increases with the species richness of the community, connectance will decrease with community diversity due to physical feeding constraints (i.e. upper and lower size refugia from predation). Moreover, the possibility to select from multiple prey species increases for any predator with increasing species richness. Therefore, predators in more diverse communities may

specialize on a subset of their potential feeding niche that includes prey species that are easier to exploit or are less defended. In addition, uneven abundances of potential prey within the feeding range may induce predator switching behaviour that creates temporally unexploited prey of low abundances. This hypothesis suggests that the prey abundance of the unrealized links should be lower than that for the realized links (e.g. Olesen *et al.*, in press). In concordance with these arguments, Beckerman *et al.* (2006) offer a mechanistic explanation for how patterns in connectance arise within food webs. Based on foraging theory, they assume that predators feed preferentially on the energetically most rewarding prey. Their 'diet breadth model' relates food-web complexity to the species' foraging biology and does well in predicting the scaling of connectance with species richness (Beckerman *et al.*, 2006). The optimization constraints regarding the species' foraging behaviour thus determine the complexity of their predicted food webs. Interestingly, recent extensions of this optimal foraging approach in the allometric diet breadth model also provide successful predictions of the topology of complex food webs: that is not simply how many links are expressed, but also where they are located within the feeding matrix (Petchey *et al.*, 2008). Together, these models stress the key role of the natural body-mass structure in determining food-web topology, which also supports the hypothesis that connectance may decrease with increasing species richness, as a result of extended body-mass ranges within the community size spectrum.

Each of the aforementioned hypotheses may offer only a partial explanation of the variance of connectance with species richness, and they are not mutually exclusive. Most likely, the mechanisms underlying the observed patterns are multi-causal and vary with the spatial scale. The 'sampling hypothesis' suggests that mere sampling artefacts are responsible for the decrease in connectance with species richness, whereas all other hypotheses invoke ecological processes as the drivers behind this pattern. In addition to the empirical patterns, these biological hypotheses support the conclusion that connectance decreases with diversity and lend weight to the emerging paradigm that connectance is scale dependent in community food webs.

C. Topology–Diversity Relationships

Analyses of topological scaling relationships in our new data collection revealed significant diversity scaling of 10 food-web properties and complexity scaling for 12 out of the 16 properties. Our results support the conclusion of prior studies that the fractions of top and basal species decrease with diversity and that the fraction of intermediate species increases (Hall and Raffaelli, 1991; Martinez, 1991, 1993a; Schoener, 1989; Warren, 1989; Winemiller, 1990), thus supporting the classic scaling relationships. They

also indicate that species-rich food webs exhibit greater variability in species' linkedness (i.e. the overall number of links) than do species-poor webs. This finding is consistent with an earlier study (Montoya and Sole, 2003) that suggests that species-rich food webs have a more uneven distribution of links among species, a feature that may increase population stability. Moreover, we found that the mean clustering coefficient (the likelihood that two species that are linked to the same species are also linked to each other) increases with diversity. Surprisingly, this empirical result contradicts a prior analytical result based on niche-model food webs (Camacho *et al.*, 2002b). It does, however, lend support to another analytical finding that the mean shortest path length between species decreases with diversity (Williams *et al.*, 2002). Together, these findings suggest that species-rich food webs are more compartmentalized and have shorter average path length between pairs of species than species-poor ones, which suggests that food webs of high diversity are organized by combining sub-web compartments, within which species are closely linked to each other.

D. Ecosystem Types and Trophic Scaling Relationships

While our analyses indicated robust scaling models of topological food-web properties with diversity and complexity, substantial residual variation around these trends remained. In line with earlier approaches for marine (Dunne *et al.*, 2004) and Cambrian food-web topology (Dunne *et al.*, 2008), we aimed to examine significant signatures of ecosystem types in this residual variation. However, in contrast to these previous studies, we did not employ the niche model (Williams and Martinez, 2000) as the null model to remove the dominant effects of species richness and connectance on food-web topology. Analyses based on the niche model share its assumptions whilst ignoring those of alternative topological models and their predictions (Allesina *et al.*, 2008; Cattin *et al.*, 2004; Stouffer *et al.*, 2005; Williams and Martinez, 2008). To avoid such pre-assumptions of the analyses, we used power–law scaling models of food-web topology against species richness and connectance to test for effects of ecosystem type on the residuals of the scaling relationships. These residuals were thus independent of the effects of diversity and complexity on food-web topology.

As in the studies of Dunne *et al.* (2004, 2008), we did not find strong effects of ecosystem types on food-web topology. While our cluster analysis indicated that food-web topologies were not generally grouped according to their ecosystem type, the more detailed analyses of variance for individual food-web properties suggested the presence of more specific differences, as revealed by pairwise comparisons. Our comparison of 160 pairwise combinations in post hoc tests could be criticized for multiple comparisons, since,

on average, chance events should result in significant differences ($p < 0.05$) for at least 5% of the combinations. Family-wise corrections of Type I error probability for such a large number of comparisons (Peres-Neto, 1999) render the power of the tests uninformatively low (García, 2004; Moran, 2003). From a 'false-rejection-rate' perspective (García, 2004), however, our analyses identified significant differences among pairs for 26% (43 out of 160) of the combinations, which shows that differences among ecosystem types were more than just random events. To avoid over-interpreting potential statistical artefacts, however, we refrain from a detailed interpretation of individual pairwise combinations of food-web topologies from different ecosystems, although there were indications of some systematic differences between lake and terrestrial ecosystems (eight significant differences in topological properties), and between estuaries and lakes (four significant differences in topological properties). A cautious interpretation of these differences suggests that pelagic ecosystems such as lakes might possess a somewhat different network topology than terrestrial and estuarine (mainly benthic) ecosystems (cf. Yvon-Durocher *et al.*, 2010). Interestingly, this is consistent with differences in the body-mass structure between these ecosystems, which may be related to systematic effects of hard surfaces employed by predators while consuming carcasses (Brose *et al.*, 2006a,b). Overall, however, our analyses indicated that the majority of topological food-web properties followed similar diversity–complexity scaling rules across ecosystems. These robust scaling models are certainly suggestive of the presence of general building rules for ecological networks, even across seemingly very different ecosystem types.

V. CONCLUSIONS

As in some previous studies (Brose *et al.*, 2004; Dunne, 2006; Montoya and Sole, 2003; Schmid-Araya *et al.*, 2002), our results suggest that neither links per species nor connectance are scale-invariant constants across communities of varying species richness. In the same vein, our results also illustrated that most food-web properties scaled with the diversity and complexity of the communities. After several decades of debate surrounding trophic scaling theories, it now seems unlikely that there are universal scale-independent constants in natural food webs that hold true for all communities, from those that are relatively depauperate to those that are species rich. Nevertheless, recent works support trophic scaling models that predict relationships between parameters of food-web topology and diversity with constant scaling exponents (Camacho *et al.*, 2002a; Garlaschelli *et al.*, 2003). While these scaling relationships are certainly not as easy to explain as may be desired, they provide a means of understanding the inevitable interrelation of the

different parameters within complex food webs. A mechanistic understanding of why complex food webs appear to share a fundamental network structure mediated by species richness and connectance is yet to be achieved—perhaps we share this aspect with physicists, who are still lacking a mechanistic explanation with rigorous empirical support for the gravitational force several centuries after Newton phrased the universal law of gravitation.

Despite this lack of universal constants in food-web ecology, many theoretical aspects of food-web ecology have been clarified and substantially refined in the last decade. Recent structural food-web models (Allesina *et al.*, 2008; Cattin *et al.*, 2004; Stouffer *et al.*, 2005; Williams and Martinez, 2000) include dependence of network topology on species richness and connectance, and predict food-web properties depending on contiguous feeding ranges within an ordered set of species' niches (Williams and Martinez, 2000), phylogenetic constraints on feeding interactions (Cattin *et al.*, 2004) and exponential degree distributions (Stouffer *et al.*, 2005). The integration of such research with core concepts from other research areas, such as the role of body-size constraints on predator–prey interactions (Beckerman *et al.*, 2006; Brose, 2010; Brose *et al.*, 2006a,b, 2008; Layer *et al.*, 2010; McLaughlin *et al.*, in press; Petchey *et al.*, 2008; Vucic-Pestic *et al.*, 2010; Woodward *et al.*, 2005a,b, 2010;Wootton and Emmerson, 2005), offers a potentially promising way in which to start to develop a more mechanistic basis for explaining the trophic patterns we see in nature.

APPENDIX

Table A1 Overview of all food webs sources used in this study, with references of predation matrix, number of interactions, number of links, proportion of links/species, connectance and the general habitat

Webnr.	Common web name	Taxonomic species	Links	Links/species	conn*	Predation matrix source
	Estuary/Saltmarsh					
1	Carpinteria	72	238	3.31	0.05	Lafferty *et al.* (2006)
2	Chesapeake Bay	36	121	3.36	0.09	Baird and Ulanowicz (1989)
3	St. Mark's	48	220	4.58	0.1	Christian and Luczkovich (1999)
4	Ythan2010	92	416	4.52	0.05	Cohen *et al.* (2009)
5	Mangrove Estuary wet season	94	1339	14.24	0.15	Heymans *et al.* (2002)
	Lakes					
6	Alford Lake	56	219	3.91	0.07	Havens (1992)
7	Balsam Lake	53	182	3.43	0.06	Havens (1992)
8	Beaver Lake	61	327	5.36	0.09	Havens (1992)
9	Big Hope Lake	30	120	4	0.13	Havens (1992)
10	Bridge Brook Lake	75	552	7.36	0.1	Havens (1992)
11	Chub Pond	65	417	6.42	0.1	Havens (1992)
12	Connery Lake	30	60	2	0.07	Havens (1992)
13	Hoel Lake	49	254	5.18	0.11	Havens (1992)
14	Long Lake	65	416	6.4	0.1	Havens (1992)
15	Stink Lake	53	280	5.28	0.1	Havens (1992)
16	Little Rock Lake	176	2009	11.41	0.06	Havens (1992)
17	Sierra Lakes	37	298	8.05	0.22	Harper-Smith *et al.* (2005)
18	Skipwith Pond	35	379	10.83	0.31	Warren (1989)

Table A1   (*continued*)

Webnr.	Common web name	Taxonomic species	Links	Links/species	conn*	Predation matrix source
19	Tuesday Lake 1984	50	268	5.36	0.11	Jonsson *et al.* (2005)
	Marine					
20	Chile Food web	106	1436	13.55	0.13	Navarette and Wieters (unpublished data)
21	Lough Hyne	350	5131	14.66	0.04	Jacob (unpublished data)
22	Mondego Zostera Meadows	47	278	5.91	0.13	Patricio and Marques (2006)
23	Caribbean Reef, small	50	555	11.1	0.22	Opitz (1996)
24	NE US Shelf	81	1482	18.3	0.23	Link (2002)
25	Weddell Sea	492	16136	32.8	0.07	Brose *et al.* (2006a,b) and Jacob (2005)
	River/streams					
26	Bere Stream	137	1276	9.31	0.07	Woodward *et al.* (2008)
27	Broadstone Stream	34	221	6.5	0.19	Woodward *et al.* (2005b)
28	Alamitos Creek	162	3756	23.19	0.14	Harrison (2003)
29	Caldero Creek	126	2109	16.74	0.13	Harrison (2003)
30	Corde Matre Creek	106	1757	16.58	0.16	Harrison (2003)
31	Coyote	190	4583	24.12	0.13	Harrison (2003)
32	Guadeloupe Creek	174	4662	26.79	0.15	Harrison (2003)
33	Guadeloupe River	136	2487	18.29	0.13	Harrison (2003)
34	Los Gatos Creek	177	4480	25.31	0.14	Harrison (2003)
35	Los Trancos Creek	129	2440	18.91	0.15	Harrison (2003)
36	San Francisquito Creek	140	3266	23.33	0.17	Harrison (2003)

37	Saratoga Creek,	158	3754	23.76	0.15	Harrison (2003)
38	Steverson Creek	170	4776	28.09	0.17	Harrison (2003)
39	Blackrock	82	348	4.24	0.05	Harrison (2003)
40	Broad	34	221	6.5	0.19	Townsend *et al.* (1998)
41	Ross	117	2024	17.3	0.15	Townsend *et al.* (1998)
42	Penetetia creek	170	4037	23.75	0.14	Harrison (2003)
43	Sutton	86	422	4.91	0.06	Townsend *et al.* (1998)
44	Canton	108	707	6.55	0.06	Townsend *et al.* (1998)
45	Dempster	106	965	9.1	0.09	Townsend *et al.* (1998)
46	German	84	352	4.19	0.05	Townsend *et al.* (1998)
47	Healy	96	633	6.59	0.07	Townsend *et al.* (1998)
48	Kyeburn	98	628	6.41	0.07	Townsend *et al.* (1998)
49	Little Kyeburn	78	749	9.6	0.12	Townsend *et al.* (1998)
50	Stony	112	831	7.42	0.07	Townsend *et al.* (1998)
	Terrestrial					
51	Grand Caricaie Cl C1	118	997	8.45	0.07	Cattin Blandenier (2004)
52	Coachella	27	237	8.78	0.33	Polis (1991)
53	EcoWeb 59	30	65	2.17	0.07	Cohen (1989)
54	EcoWeb 60	33	68	2.06	0.06	Cohen (1989)
55	El Verde	156	1509	9.67	0.06	Waide and Reagan (1996)
56	Grand Caricaie Sn C2	152	1525	10.03	0.07	Cattin Blandenier (2004)
57	St. Martin	44	217	4.93	0.11	Goldwasser and Roughgarden (1993)
58	Grand Caricaie Cm C1	202	2930	14.5	0.07	Cattin Blandenier (2004)
59	Grand Caricaie Cm M2	167	1830	10.96	0.07	Cattin Blandenier (2004)
60	Simberloff_E1	36	121	3.36	0.09	Simberloff and Abele (1975)
61	Simberloff_E2	63	347	5.51	0.09	Simberloff and Abele (1975)
62	Simberloff_E3	49	242	4.94	0.1	Simberloff and Abele (1975)
63	Simberloff_E7	52	255	4.9	0.09	Simberloff and Abele (1975)
64	Simberloff_E9	71	446	6.28	0.09	Simberloff and Abele (1975)
65	Simberloff_ST2	63	347	5.51	0.09	Simberloff and Abele (1975)

*conn = connectance.

Binary link structures of these 65 food webs are available upon request by 'Ulrich Brose'.

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