Complexity in quantitative food webs

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Abstract. Food webs depict who eats whom in communities. Ecologists have examined statistical metrics and other properties of food webs, but mainly due to the uneven quality of the data, the results have proved controversial. The qualitative data on which those efforts rested treat trophic interactions as present or absent and disregard potentially huge variation in their magnitude, an approach similar to analyzing traffic without differentiating between highways and side roads. More appropriate data are now available and were used here to analyze the relationship between trophic complexity and diversity in 59 quantitative food webs from seven studies (14–202 species) based on recently developed quantitative descriptors. Our results shed new light on food-web structure. First, webs are much simpler when considered quantitatively, and link density exhibits scale invariance or weak dependence on food-web size. Second, the "constant connectance" hypothesis is not supported: connectance decreases with web size in both qualitative and quantitative data. Complexity has occupied a central role in the discussion of food-web stability, and we explore the implications for this debate. Our findings indicate that larger webs are more richly endowed with the weak trophic interactions that recent theories show to be responsible for food-web stability.

Key words: connectance; diversity; ecological network; food-web stability; scaling; stability; trophic complexity and species diversity.

Introduction

Up until the early 1970s, "conventional wisdom" among ecologists held that complexity begets stability in natural systems. Communities comprising many species and interactions were assumed to be more stable than simpler ones. The verbal rationale was that the presence of more links and species increased the number of routes by which energy could flow through the system, and that this multiplicity of pathways would buffer fluctuations (Odum 1953, MacArthur 1955). This conviction was challenged by May (1974) on the basis of mathematical models (McCann 2000): randomly assembled systems will remain stable if the product of average interaction strength, α, and the square root of $S \times C$, remains smaller than 1, where S is the number of species in a food web, and C is the connectance. Connectance is a measure of network complexity and represents the probability that any pair of species interacts (see Warren [1994] for definitions). According to this theory, if α and C remain approximately constant, any system with sufficiently large S is unstable. Interestingly, initial analyses of simple empirical food webs found the link density, LD, ($LD = L/S \propto S \times C$, where L is the total number of links) to be scale-invariant, i.e., it remained more or less constant in food-web data sets spanning a wide range in species richness (Cohen and Briand 1984, Sugihara et al. 1989). Great importance was attached to this invariance since, assuming constant α, even high species diversity would not induce instability (May 1983, Sugihara et al. 1989, McCann 2000). Following criticism of the quality of the early data sets (May 1983, Paine 1988, Polis 1991), a reappraisal came from analyses of more highly resolved food webs that comprised a greater number of species. The link density LD was now found

to increase with scale (Winemiller 1990, Havens 1992, Deb 1995) and it was argued instead that directed connectance ($C_d = L/S^2$) was constant (Martinez 1992). These contrasting patterns (constant LD or C_d, with species linked to a constant number or to a constant fraction of other species, respectively) have very different implications for community assembly and the way in which complexity scales with increasing species number (Warren 1994). As a consequence, the scale dependence of LD raised the stability question for large systems anew, and fostered a large body of research (e.g., McCann 2000, de Ruiter et al. 2005, Pascual and Dunne 2006).

To date, however, food-web analysis has rarely been based on quantitative data. The debate about linkage complexity was therefore derived from topological (i.e., qualitative) food webs that take only the presence or absence of species and links into consideration—a situation somewhat similar to analyzing traffic without distinguishing between highways and side roads. Moreover, C_d and LD have been found to be highly sensitive to sampling effort (Goldwasser and Roughgarden 1997, Martinez et al. 1999), and intrinsically scale-dependent systems have been shown to appear scale invariant when sampled with low intensity (Bersier et al. 1999). In more highly resolved food webs, which include trophic links with huge differences in magnitude (Appendix A: Fig. A1), the number of "weak" links is strongly affected by variation in sampling effort. These problems stress the need for quantitative estimates of food-web structure (May 1983, Montoya et al. 2006), and new descriptors that account for variation in link magnitude have recently been devised (Bersier et al. 2002).

Here, we are interested in assessing the behavior of the new quantitative versions of link density with respect to scale, measured by species richness. Such an undertaking is fundamental to understand how the complexity of trophic interactions varies with species diversity in natural food webs (see Plate 1). In an attempt to link these static patterns of ecological networks to their dynamics, we then explore how the observed levels of complexity translate in terms of stability based on May's (1974) approach.

MATERIALS AND METHODS

Data set

We compiled seven collections of food webs suited for quantitative analysis. These include: (a) seven detritus-based soil webs from natural and agricultural areas in Georgia and Colorado (USA), The Netherlands, and Sweden (de Ruiter et al. 1995, 1998); (b) eight invertebrate-dominated meadow webs sampled during two seasons in Switzerland (Cattin 2004); (c) eight seasonal webs from the Everglades of south Florida (USA) (Ulanowicz et al. 1997, 1998, 1999, 2000); (d) 10 seasonal webs of Little Rock Lake, Wisconsin (USA) (Merz 2003); (e) nine seasonal webs from four lowland

streams in Costa Rica and Venezuela (Winemiller 1990); (f) the 10 largest time-specific parasitoid–cynipid gall-wasp webs compiled by Schönrogge and Crawley (2000) in Quercus forests from across Britain; and (g) seven time-specific detritus-based webs from the macroinvertebrate riffle community of Duffin Creek, Ontario, Canada (Tavares-Cromar and Williams 1996).

The data sets can be divided into two groups according to their scope: collections a–e were designed to give a complete picture of the communities, whereas f and g represent only fractions of food webs based on interactions associated with a particular functional group. Furthermore, collections a, b, and f encompass terrestrial systems, whereas d, e, and g are aquatic, and c covers the aquatic–terrestrial interface. Further information on methods, and the strengths and weaknesses of the collections, are supplied in Appendix B. Different methodologies and degrees of sampling effort can affect the perceived structure of food webs (Cohen et al. 1993, Bersier et al. 1999), particularly when comparing systems described by different investigators (Winemiller et al. 2001). We therefore performed regression analyses for each study separately before pooling the community webs (collections a–e), and employed quantitative descriptors, which are much more robust against sampling variation than topological ones (Banašek-Richter et al. 2004) and consequently more reliable for between-web comparisons. Notwithstanding the caution still advised with regard to the results of such meta-analyses, we think that methodological artifacts are unlikely when the patterns seen within and among collections are consistent. For our analyses, we chose only webs with species richness $S \geq 14$ to avoid bias due to small web size (Bersier and Sugihara 1997). Note that we extend the word "species" to also represent higher taxonomic levels, depending on the taxonomic resolution of the data sets.

Quantitative measures of link density

The derivation of a quantitative counterpart for link density is based on Shannon's entropy (Ulanowicz 1986, Ulanowicz and Wolff 1991, Bersier et al. 2002). For each species, the "effective" number of prey is computed by first applying Shannon's formula to the quantitative diet (the inflows, measured as the amount of biomass obtained from each prey per unit time and space, or by other quantitative estimates), and second by computing the exponential of this value. The result corresponds to the number of prey species eaten in equal quantities that would yield the same Shannon's index as the observed diet. While topological link density can be computed by averaging the number of prey species over all consumers, analogously, a quantitative measure of link density is the average of the effective number of prey. So far, however, this only accounts for the role of species as consumers. To consider their role as prey, the effective number of predators is computed in analogy to the procedure

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above, but based on outflows (amount of biomass going to consumers). The average of the effective number of predators and of prey is termed the "quantitative unweighted link density" (LD_q'), because each species is given the same weight. Weighting the averages by each species' total in- and outflows accounts for the energetic importance of each species in a community and yields the "quantitative weighted link density" (LD_q).

The equations of these food-web metrics are the following. Given an S-by-S quantitative food-web matrix $\mathbf{b} = [b_{ij}]$, with b_{ij} the amount of biomass passing from taxon i to taxon j per unit surface area and time (or other measures of importance for trophic interactions), $b_{i\cdot}$ the sum of row i, $b_{\cdot j}$ the sum of column j, and $b_{\cdot\cdot}$ the total sum, the taxon-specific Shannon indices of inflows and outflows are

$$H_j = -\sum_{i=1}^{s} \frac{b_{ij}}{b_{\cdot j}} \cdot \ln\frac{b_{ij}}{b_{\cdot j}}$$

$$H_i = -\sum_{j=1}^{s} \frac{b_{ij}}{b_{i\cdot}} \cdot \ln\frac{b_{ij}}{b_{i\cdot}}.$$

respectively; the effective number of prey and of predators are $N_j^* = \exp(H_j)$ and $N_i^* = \exp(H_i)$, respectively; the quantitative unweighted link density is

$$LD_q' = \frac{1}{2S}\left(\sum_{i=1}^{s} N_i^* + \sum_{j=1}^{s} N_j^*\right) \qquad (1)$$

and the quantitative weighted link density is

$$LD_q = \frac{1}{2b_{\cdot\cdot}}\left(\sum_{i=1}^{s} b_{i\cdot}N_i^* + \sum_{j=1}^{s} b_{\cdot j}N_j^*\right).$$

The quantitative unweighted and weighted connectance are simply obtained by dividing LD_q' and LD_q by S, respectively. Multiplying the number of species by the quantitative unweighted link density gives the total number of quantitative links, L_q ($L_q = S \times LD_q'$); note that the distinction between weighted and unweighted measures does not apply here. More information on quantitative and qualitative measures of complexity in food webs can be found in Warren (1994) and Bersier et al. (2002).

LD_q' is always smaller than or equal to LD, and the difference between the two descriptors can be interpreted as the degree to which the magnitudes of trophic links in the webs depart from a uniform distribution. Since LD_q further weights the species by their total in- and outflows, the difference between LD_q' and LD_q is attributable to the partitioning among species of the total biomass flowing through the community (Appendix A: Fig. A2). LD_q can be smaller or larger than LD_q'. The latter occurs when species connected to the greatest numbers of prey and predators also contribute the highest biomass flows.

Average interaction strength

To estimate average interaction strength from quantitative data, we follow Ulanowicz (2002) in assuming that unweighted quantitative link density LD_q' can be broken down into contributions from both the topological link density LD and the average interaction strength α: for a given food web, α is defined as the constant value that, when multiplied with each b_{ij} in the equation of LD_q' (Eq. 1), yields $LD_q' = LD$. When all b_{ij} are equal, $\alpha = 1$; the more inequitable the distribution of b_{ij}, the smaller the value of α ($0 < \alpha \le 1$). It is thus possible to express α in terms of LD and LD_q', and to reveal which food webs are stable and which are unstable according to May's (1974) stability criterion. There is a common misunderstanding about average interaction strength and the quantity used in May's criterion. May (1974:64) indicated that α (called "s" in the original formulation) "may be thought of as expressing the average interaction strength." In fact, it is not strictly this average, but the standard deviation of the normal distribution from which interaction strengths were randomly drawn. This distribution has a mean of 0. The relationship between the standard deviation s and the average of the absolute values α (i.e., the average interaction strength) of a normal distribution is $\alpha = 2 \cdot s/(2\pi)^{0.5}$. Consequently, when measuring average interaction strength from data, one should multiply α by $(2\pi)^{0.5}/2$ before applying May's criterion. The estimates of the criterion (after applying the above correction) for each of the 59 webs are given in Appendix C. The average interaction strength thus obtained is admittedly a crude estimate, but even if the values differ from the real values by a factor of 2, the division into stable and unstable food webs would render the same results in most cases.

RESULTS AND DISCUSSION

The results of analyzing the seven collections of food webs separately are given in Fig. 1. Striking at first sight is that LD_q' (the quantitative unweighted link density) and LD_q (the quantitative weighted link density) are typically only one third to half as large as the link density, LD. Although LD_q' is necessarily smaller than or equal to LD, such large discrepancies indicate that structure based on flow is much less complex than topological structure, so food webs actually appear simpler when viewed quantitatively. Since complexity is central to arguments about stability in food webs, the consequences of this feature are explored below. In accordance with highly resolved topological webs (Winemiller 1990, Havens 1992, Deb 1995), topological link density (LD) is scale dependent (Table 1 and Fig. 1). The relationship is, however, weak in the collections of subsystems (f and g), with slopes not significantly different from 0. Scale dependence is weaker for LD_q' than for LD: slopes are always shallower for LD_q' than for LD. The quantitative weighted link density (LD_q), which takes total in- and outflows into account, is
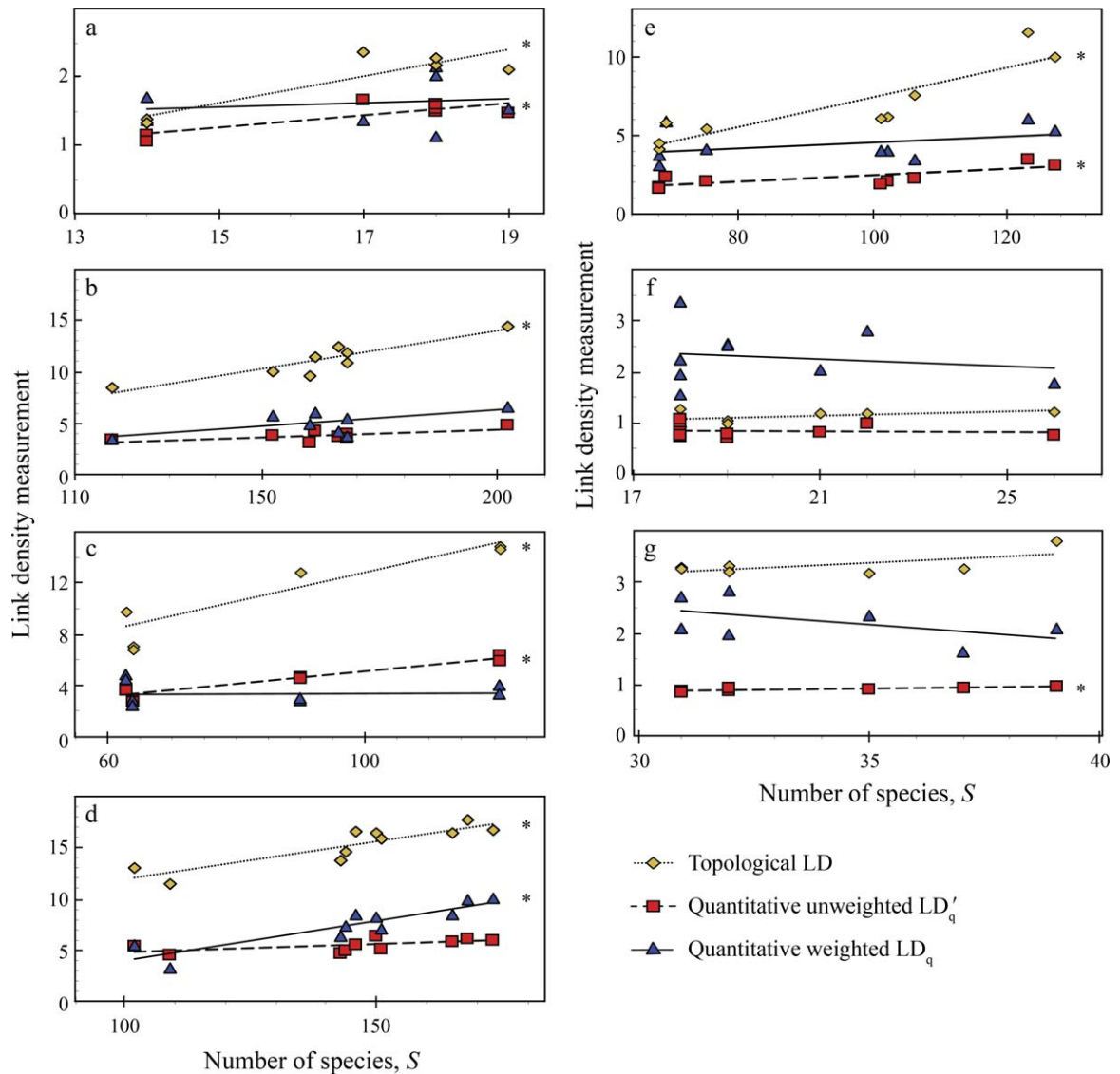
FIG. 1. Data and least-squares regressions (lines) of topological (diamonds), quantitative unweighted (squares), and quantitative weighted (triangles) link density for seven collections of food webs (data sets a–g; see *Materials and methods: Data sets*). A star to the right of the regression line indicates significance at $P < 0.05$ (see Table 1 for parameter estimates). These graphs show how complexity of trophic interactions varies with species richness in food webs (note different x-axis scales). When considered quantitatively, complexity is most often lower and less dependent on scale.

TABLE 1. Parameters of the Fig. 1 linear regression analyses of link density (LD) for the seven collections of food webs.

| Food-web collection data set	Topological link density, LD			Quantitative unweighted link density, LD'_q			Quantitative weighted link density, LD_q		
	Slope	r	P	Slope	r	P	Slope	r	P
a	0.192	0.803	0.006	0.090	0.706	0.018	0.031	0.029	0.715
b	0.074	0.823	0.002	0.016	0.447	0.070	0.032	0.414	0.085
c	0.114	0.827	0.002	0.049	0.919	<0.001	0.002	0.002	0.917
d	0.075	0.788	0.001	0.015	0.353	0.070	0.079	0.814	<0.001
e	0.093	0.797	0.001	0.020	0.600	0.014	0.018	0.161	0.285
f	0.018	0.218	0.174	−0.003	0.004	0.866	−0.033	0.025	0.662
g	0.042	0.414	0.119	0.010	0.633	0.032	−0.066	0.251	0.252

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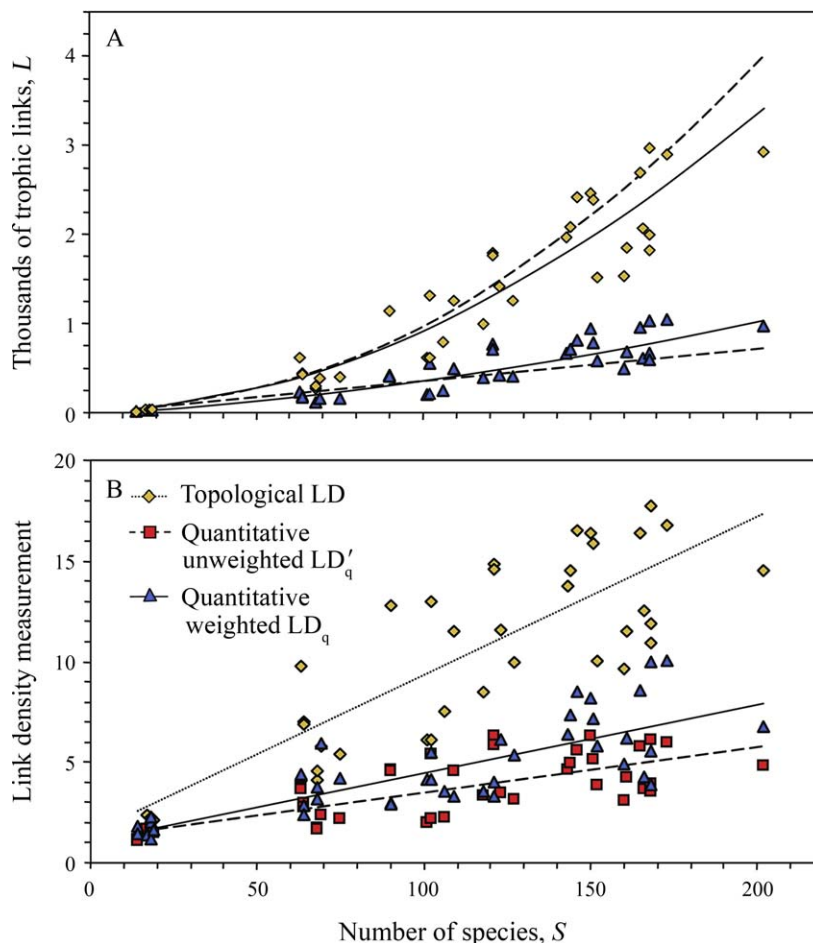
FIG. 2. (A) Topological and quantitative number of trophic links and (B) link density with respect to species richness for all ecosystem food webs (collections a–e, the same collections as in Fig. 1 and Table 1). In (A) the topological number of links, L (diamonds), scales with S as $L = 0.58S^{1.62}$ ($r^2 = 0.88$, $P < 0.001$), and quantitative number of links (triangles) as $L_q = 0.44S^{1.47}$ ($r^2 = 0.83$, $P < 0.001$); the upper dashed line represents constant connectance (exponent equal to 2), while the lower dashed line represents constant link density (linear relationship between L and S). In (B), symbols correspond to those in Fig. 1 with (top line) $LD = 1.46 + 0.079S$ ($r^2 = 0.72$), (middle line) $LD_q = 1.07 + 0.034S$ ($r^2 = 0.62$), and (bottom line) $LD'_q = 1.26 + 0.022S$ ($r^2 = 0.55$); $P < 0.001$ for all equations.

statistically scale invariant for all data sets except the Little Rock Lake webs (d).

Scale-dependent link density for topological webs is believed to stem from the adaptation of species to specific resources that fall within a more-or-less-restricted range of features in terms of size, morphology, behavior, or habitat use. With increasing species richness, the number of resources that fall within this range is likely to increase and consequently be exploited (Warren 1990). An increase in available resources allows predators to widen their diet breadth, and, similarly, prey have more potential predators in species-rich environments.

In all community webs, LD increases more rapidly with species number than LD'_q does (Table 1). This increasing discrepancy between LD'_q and LD indicates that the partitioning of biomass in- and outflows becomes more skewed (i.e., few strong and many weak

flows, yielding a long-tailed distribution) with increasing species richness. The effect is most pronounced in collections b and d, where LD'_q is independent of scale while LD increases with web size. The fact that this discrepancy is still present but not as strong in collections a, c, and e, suggesting more even (i.e., short-tailed) distributions of dietary items, can be accounted for by two possible explanations. First, communities in dynamic habitats such as running water (e) contain many generalist species (gatherers and collectors), which are able to consume a broad range of food materials. Second, greater spatial heterogeneity in terrestrial and mixed habitats (a and c), may limit access to potential prey in the system as well as reducing the probability of encountering rare prey species.

Weighted quantitative link density LD_q appears scale invariant for all data sets except the Little Rock Lake food webs (Fig. 1d). In lentic aquatic systems,

PLATE 1. The simplest building block of complex food webs: a trophic interaction, here between the European Bee-eater (*Merops apiaster*) and a carpenter bee (*Xylocopa* sp.). Photo credit: Olivier Seydoux.

indiscriminate feeders (zooplankton) have the opportunity to eat a large number of different prey, as well as accounting for a large portion of total in- and outflows. In systems that comprise a large number of such consumers, scale-dependent LD_q is expected. While this trophic structure is a common feature of many lentic systems, consumers at lower trophic levels in terrestrial habitats (i.e., herbivores) are known to be more specialized (Havens 1997), thus leading to scale-invariant LD_q. LD_q also departs from the general trend for the collection of gallwasp webs (Fig. 1f): it is much larger than LD irrespective of web size. Contrary to the situation in the other collections, species with the highest numbers of effective prey and predators also account for the highest total flows of biomass in these subsystems.

In summary, we found that (1) the complexity of trophic interactions is much lower when considered quantitatively (with the exception of collection f), and (2) scale dependence is observed for topological link density while both quantitative measures appear scale invariant or weakly scale dependent within each set of community webs. Do these trends for LD_q and LD_q' persist when considering the full range of species richness spanned by the food webs of our data sets? To answer this question, we pooled all ecosystem data sets (a–e), and examined the relationship between species richness and the number of trophic links (Fig. 2A). The number of topological links increases at a rate lower than that predicted by the constant connectance hypothesis (Martinez 1992), corresponding instead to a linear decrease of connectance with species richness (C_d
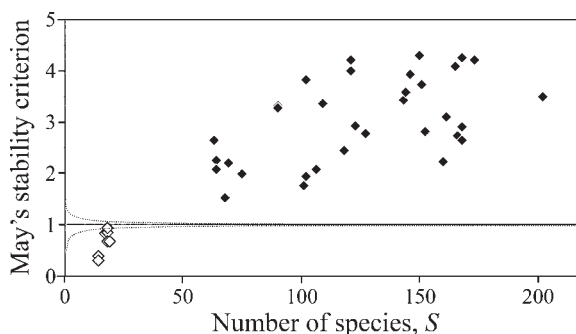

FIG. 3. Estimated stability of observed community food webs in relation to species richness. Stability is assessed following May's (1974) stability criterion, $\alpha(S \times C)^{1/2}$, where α is the average interaction strength, S is the number of species in the food web, and C is the connectance. The horizontal line separates food webs predicted to be stable (open diamonds) from those predicted to be unstable (solid diamonds); the dotted lines indicate the transition region within which webs may or may not be stable according to May's plausibility argument (May 1974).

[directed connectance] $= 0.12 - 0.00021S$; $r^2 = 0.17$, $P = 0.006$). The number of quantitative links increases at an even lower rate. However, the slope is not low enough to be consistent with constant link density, but rather appears to be adequately described by a power law (see Fig. 2A legend for statistics). Accordingly, both quantitative versions of link density increase with species richness (Fig. 2B). We are aware that merging studies with different methodologies may yield artifactual results (Winemiller et al. 2001), and that some food webs are not independent within their data set (see Appendix B). However, the regression slopes of LD'_q and LD_q within each study are always positive and are significant in three cases and one case, respectively, alluding to a consistent tendency across data sets. By and large, scale dependence of quantitative measures of link density is a reasonable hypothesis, but this relationship is likely to be very weak. This subject is of great importance, since the way the complexity of trophic interactions scales with diversity is central to the stability–diversity debate (Cohen et al. 1990, Pimm et al. 1991).

Given that complexity in food webs is much lower when considered quantitatively, it is possible that communities never enter the unstable region of parameter space according to May's (1974) framework. It may thus not be necessary to invoke a positive complexity–stability relationship to understand why large systems are stable. To shed further light on this question we now explore how the observed levels of complexity may translate in terms of the dynamical behavior of these systems.

Following the approach of Ulanowicz (2002) to estimate the average interaction strength for quantitative food webs, all of the analyzed webs with more than 60 species are predicted to be highly unstable (Fig. 3), and should thus collapse according to May's classical criterion. Yet these food webs exist. We cannot rule out that this mismatch between prediction and observations is due to unrealistic estimates of interaction strengths, or to the inadequacy of local stability analyses (e.g., Hall and Raffaelli 1993, Winemiller and Layman 2005, Winemiller 2007). A plausible explanation for their existence, however, is that real ecosystems must possess special features—as compared to random graphs—that allow them to persist in nature (de Ruiter et al. 1995, McCann et al. 1998, McCann 2000, Neutel et al. 2002, Kondoh 2003, Otto et al. 2007). The comparison of qualitative and quantitative measures of LD may be instructive in this regard, since it suggests an increasing skew in the distribution of interaction strengths with increasing species richness. It has been argued that the presence of weak interactions and their placement in long trophic loops confers community stability due to the role they play in dampening population oscillation (McCann et al. 1998, Neutel et al. 2002, 2007). Our analysis shows that larger food webs are more richly endowed with such interactions, which may be the key to their stability.

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APPENDIX A

Schematic depictions of (1) the Chesapeake Bay (USA) food web and (2) three hypothetical food webs illustrating various measures of link density (LD) (*Ecological Archives* E090-099-A1).

APPENDIX B

Information on the seven food-web data sets (*Ecological Archives* E090-099-A2).

APPENDIX C

A table with the values of link density for the 59 food webs analyzed (*Ecological Archives* E090-099-A3).

Reports