2.3 | FOOD WEB STRUCTURE: FROM SCALE INVARIANCE TO SCALE DEPENDENCE, AND BACK AGAIN?

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Food webs are complex and variable, and a general understanding of their structure and functioning must rely on a careful examination of their regularities. The search for scale-invariant features is of special interest in this respect (Briand and Cohen, 1984), since scale-invariance may represent basic structural constraints valuable for the discovery of underlying processes. An illuminating example of such a scale-invariant property drawn from astronomy and physics is Kepler's third law of planetary motion, which relates the revolution time t of a planet to its average distance from the sun d: t^2/d^3 is a constant value; the finding of this invariant property was a decisive step in the discovery of the underlying process, the law of universal gravitation. Most natural ecosystems are orders of magnitude more complicated and more variable than planetary motion. Their elements—species or sets of species—are themselves complex objects: they are composed of heterogeneous individuals, each involved in a wealth of interactions between themselves and their biotic and abiotic environment, and each able to adapt and to evolve. Many details have to be discarded to tackle the study of such intricate systems. Hence, food web ecologists concentrate on just one type of interaction depicting a vital aspect of

ecosystems: trophic interactions describe feeding relations between species.

The burst of interest in the study of trophic interactions within communities stems from the stability-complexity debate; the finding that local stability in random systems is not a mathematical consequence of complexity (Gardner and Ashby, 1970; May, 1973; Cohen and Newman, 1984) bolstered the study of natural systems. In this framework, complexity was expressed as the product of the number of species in the community (S) and connectance (C), calculated as the quotient of the number of effective interactions (L) and the number of possible interactions (S^2). The so defined measure of complexity equals link density ($LD = L/S$). Studies of initial compilations of food webs resulted in the intriguing generalization that LD is scale invariant, meaning that this property remains constant across webs of varying size (Rejmánek and Stary, 1979; Yodzis, 1980; Cohen and Briand, 1984; Sugihara et al., 1989). This finding is in agreement with May's stability criterion (May, 1983) and was perceived as a fundamental structural constraint of food webs. However, together with criticism of the data used to assess the scaling behaviour of the link density property (Paine, 1988; Polis, 1991), a scale-dependent power law was soon proposed to provide a more accurate fit of link density to variable food web collections (Schoener, 1989; Cohen et al., 1990a; Pimm et al., 1991). Indeed, subsequently compiled collections of food webs did not uphold scale invariance for this property (Warren, 1989, 1990; Winemiller, 1990; Havens, 1992; Deb, 1995).

Link density's scaling behavior is illustrated in Figure 1 for six food web compilations on which this debate is based. Collections a and b were compiled from early literature data and appear scale-invariant. More recently assembled collections on the other hand (c – f), are clearly scale-dependent. One hypothesis to explain this discrepancy is that link density's scaling behavior is system dependent: all collections showing strong scale-dependence come from aquatic environments (Winemiller, 1990; Havens, 1992; Deb, 1995; Martimez, 1991), while the other two combine webs from various habitats (Sugihara et al., 1989; Cohen et al., 1990a). In the same vein, after factoring out the effect of web size, Bengtsson (1994a) found a similar difference between aquatic and terrestrial webs in a data set extended from collection **a** (Schoenly et al., 1991). Havens (1997) proposed biological features to explain the scaling behavior of link density in pelagic communities, namely (1) the predominance of filter-feeding predators and (2) the very high diversity of small autotrophic prey species. Most terrestrial systems however, may also be much more complex than those reported in data sets **a** and **b** (Polis and Hurd, 1996; Reagan and Waide, 1996). We studied terrestrial
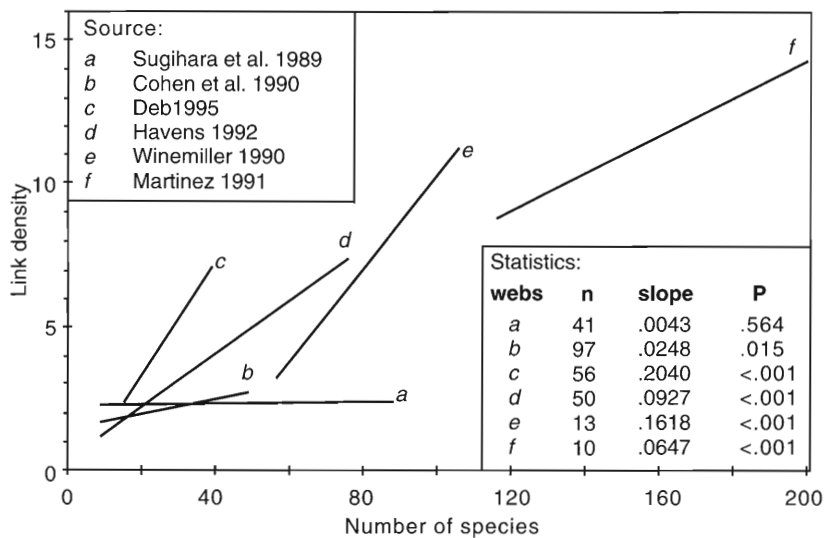
FIGURE 1 | Relationship between the link density property and web size for six collections of food webs. Lines are the results of linear regressions over the individual data points, which are omitted from the representation. Early collections of food webs drawn from literature studies not intended to represent the whole complexity of the systems (a, b) appear (approximately) scale invariant. More recent collections of webs characterized by high sampling effort (c, d, e, f) show strong scale dependence. Number of webs in each collection (n), estimates of the slope from linear regression, and P-values from a t-test are given in the inset. For collections a and b, webs with 10 species or less were omitted following Bersier and Sugihara (1997).

food webs in wet meadows, which exhibit scale-dependence for the link density property (see later discussion). Thus, intrinsic differences between systems are likely, but they cannot explain the opposing results of Figure 1 unanimously.

Another hypothesis relates these discrepancies to differences in sampling procedures and variable effort exerted toward the description of the data. Concerned specifically with the problem of sampling effort, Goldwasser and Roughgarden (1997) analyzed 21 web properties for a large, highly resolved food web (Goldwasser and Roughgarden, 1993). These authors employed different procedures to mimic increasing sampling effort, and found most properties, link density included, to be sensitive to sampling effort with high levels of sampling necessary to reach the properties' original values. A similar conclusion was reached by Martinez et al. (1999) who analyzed sampling effects in a highly resolved food web consisting of grasses and stem-borer insects. However, both former studies did not tackle the effect of sampling effort on the scaling behavior of

LD in collections of food webs. Using two models and three data sets, Bersier et al. (1999) showed that low sampling effort tends to produce the appearance of scale invariance in intrinsically scale dependent systems. This is a simple explanation reconciling the studies in Figure 1, since early collections of food webs taken from the literature (Cohen and Briand, 1984; Sugihara et al., 1989; Cohen et al., 1990a) were most often not intended to reflect the full complexity of the trophic interactions.

These sampling effects highlight the following problem inherent to the qualitative approach. The distribution of link importance in highly resolved food webs is likely to be exceedingly uneven (Goldwasser and Roughgarden, 1993). By giving the same weight to all links, binary food webs distort the true picture of their structure (Kenny and Loehle, 1991). Thus, quantitative data, which allows a more sensible approach to food web structure, is needed (May, 1983; Kenny and Loehle, 1991; Pimm et al., 1991; Cohen et al., 1993b; Bersier et al., 1999). Consequently, we must think of alternative ways of defining food web properties that take the disequitability in the distribution of link importance into account.

QUANTITATIVE LINK DENSITY

The process of formulating a quantitative counterpart for traditionally defined qualitative properties will be demonstrated in detail on the example of the link density property. The qualitative version, *LD*, is defined as the number of links (L) per species in the web ($LD = L/S$). For the quantitative version we base our calculations on information theory, namely the diversity index of Shannon (1948), H. For a system comprising x events, maximum diversity is attained when all events occur in equal proportion ($H_{max} = \log x$), while minimum diversity is a function of the number of cases that each event consists of. In our context, an event refers to a species and a case to a flux of biomass to or from a species (Ulanowicz and Wolff, 1991). The application of Shannon's equation to a quantitative food web matrix is visualized step by step in Figure 2: (1) In a food web matrix, species in their function as predators are conventionally listed column-wise (j), while the same species are arranged row-wise (i) in their function as prey. A matrix element b_{ij} thus expresses the amount of biomass passing from species i to species j (j eats i) per unit time and space. The total biomass output of species k to all its predators in the web consequently equals the sum of row k (b_k). (2) The outflows from species k to each predator in the food web can be visualized. (3) Applying the Shannon index results in the diversity of species k's biomass outflows (H_{Pk}). (4) For our purposes, the "reciprocal" of H_{Pk} is more interesting—it is understood as
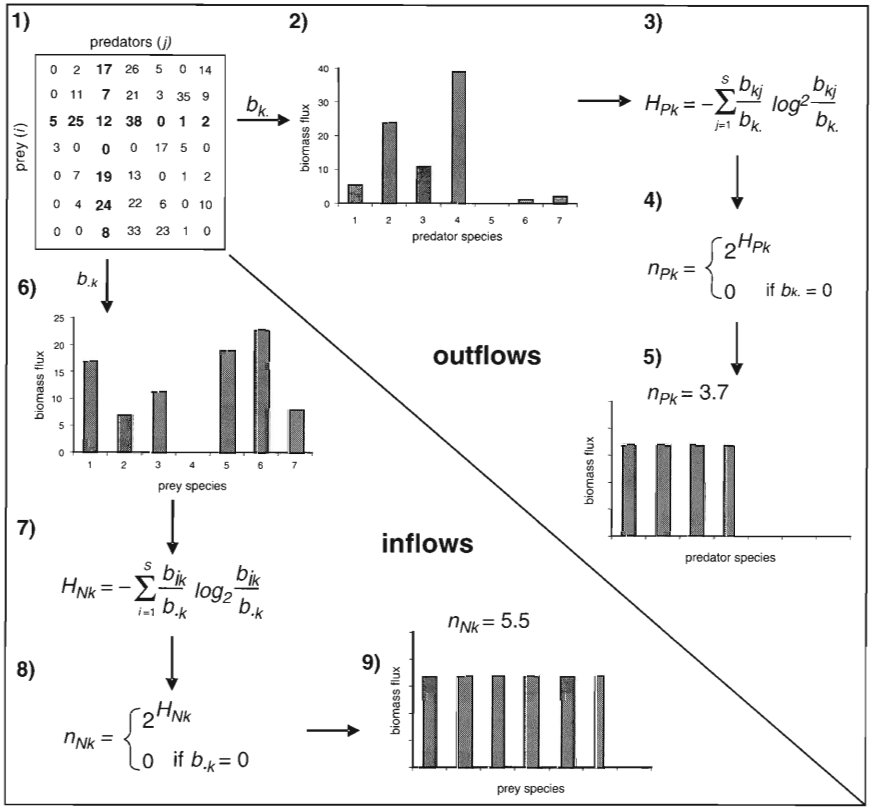
FIGURE 2 | Process of finding a quantitative definition of link density. Biomass inflow and outflow for species k are considered separately in the lower left and the upper right half of the figure, respectively. (1) Arbitrarily assembled quantitative food web matrix, highlighting the feeding interactions of species k. (2) Distribution of species k's biomass outflows; $b_{k.}$ = total biomass output from species k. (3) Shannon formula applied to species k's biomass outflows; H_{Pk} = diversity of species k's biomass outflows. (4) Reciprocal of H_{Pk}; n_{Pk} is the equivalent number of predators for species k. (5) Distribution of n_{Pk} outflows equal in magnitude, which yield the same value of H_{Pk}. (6-9) Analogous to (1) to (5), for biomass inflows to species k. $b_{.k}$ = total biomass input to species k, H_{Nk} = diversity of k's biomass inflows, n_{Nk} = equivalent number of prey for species k.

the number of predators feeding on species k in equal proportion that would generate the same diversity as H_{Pk}, and is termed the "effective number of predators" (n_{Pk}). The reciprocal of H has the desirable feature of recovering the original units, namely the number of species, but is now a real number; and (5) for the given example, n_{Pk} takes on a value of 3.7, rendering a distribution with 3.7 predators that display an equal intensity of consumption with respect to k. Thus, the diversity generated by this

distribution is equivalent to that of species k's biomass output. The same approach is followed with regard to species k's biomass inflows in steps (6) to (9), yielding the effective number of prey (n_{Nk}).

A quantitative version of link density can be formulated on the basis of the previously defined indices n_{Pk} and n_{Nk}. For easier comprehension it is important to note that qualitative link density LD can be calculated either as the average number of prey computed over all species (the total number of prey divided by S), or as the average number of predators (the total number of predators divided by S). In analogy, one could formulate a quantitative link density either by averaging over all n_{Pk} values, or by averaging over all n_{Nk} values. Since it seems implausible to only consider either biomass in- or outflows, we average over both means to obtain a quantitative version of link density LD_q':

$$LD_q' = \frac{1}{2}\left(\sum_{i=1}^{s}\frac{1}{S}\cdot n_{Pi} + \sum_{j=1}^{s}\frac{1}{S}\cdot n_{Nj}\right) \tag{1}$$

This approach does not account for the fact that species vary in the amount of biomass transferred by them, and we thus refer to LD_q' as the "unweighted" quantitative link density. To include varying amounts of biomass transfer, $1/S$ in equation (1) is substituted by the quotient of each species' biomass output and total outflow over all species ($b_{i.}/b_{..}$). In other words, the effective number of predators for species i is weighted by i's contribution to total outflow. The same is done for inflow and the "weighted" quantitative link density LD_q is obtained by averaging over both equations:

$$LD_q = \frac{1}{2}\left(\sum_{i=1}^{s}\frac{b_{i.}}{b_{..}}\cdot n_{Pi} + \sum_{j=1}^{s}\frac{b_{.j}}{b_{..}}\cdot n_{Nj}\right). \tag{2}$$

For any given food web, LD_q' will always be smaller or equal to LD. This difference is an expression of the degree to which biomass flow in the system departs from a uniform distribution. The difference between LD_q' and LD_q in turn is attributable to the variation between species with respect to the partitioning of total biomass flowing in the system as expressed in unequal row and column sums for the quantitative matrix ($b_{k.}$ and $b_{.k}$ in Figure 2).

Species at high trophic levels are typically characterized by low biomass and consequently little in- and outflow, while greater biomass and more extensive biomass flux is generally a feature of species at low trophic levels. Therefore, trophodynamical constraints (Lindeman, 1942) have a determining influence on the value of LD_q.

We examined the effect of increasing sampling effort on qualitative, unweighted quantitative, and weighted quantitative link density for 10 extensively documented quantitative webs (Banašek-Richter et al., 2004). Both quantitative versions were found to be much more robust against variable sampling effort than their qualitative counterpart. This increase in accuracy is accomplished at the cost of a slight decrease in precision as compared to the qualitative link density. Conversely, the quantitative versions also proved less sensitive to differences in evenness with respect to the distribution of link magnitude. In sum, quantitative properties are not only useful as bearer of ecological information, they also represent a much more robust description of weighted matrices.

SCALING BEHAVIOR OF LINK DENSITY—RESULTS AND DISCUSSION

The scaling behavior of the conventional qualitative link density and its newly defined quantitative counterparts is compared for a collection of eight seasonal food webs from the southern shore of Lake Neuchâtel near the village of Chabrey in Switzerland (Cattin et al., 2003). These arthropod-dominated webs were collected in early summer and early fall of 2001. For each season there are two webs from a *Schoenus nigricans* dominated and two from a *Cladium mariscus* dominated vegetation zone. Of these, one web is from an area with mowing treatment, one from a control area without mowing. Species richness spans a range of 118–202 species.

The relation between link density and scale for the Chabrey collection is depicted in Figure 3. Qualitative link density (LD) is scale dependent in the sense that it experiences a significant increase with scale. Concurrently, the linear regression slopes for the two versions of quantitative link density (LD_q' and LD_q) are not significantly different from zero, thus indicating (moderate) scale-invariance for both properties. These results lead us to infer on the one hand that in a species-rich environment, consumers feed on a wider range of prey than in an environment with more limited resources (as expressed by increasing LD). On the other hand, scale-invariant LD_q' and LD_q imply that the diversity in link magnitude does not change with species richness for the food webs of the Chabrey collection. Thus, the diet of consumers (and the preys' predator list) must be more diverse only with respect to species number but not with respect to the partitioning of biomass consumed (or allocated) in large ecosystems. In fact, as systems accrue in species number, the distribution of in- and outflows must become progressively more inequitable to counteract the increase in qualitative link density.
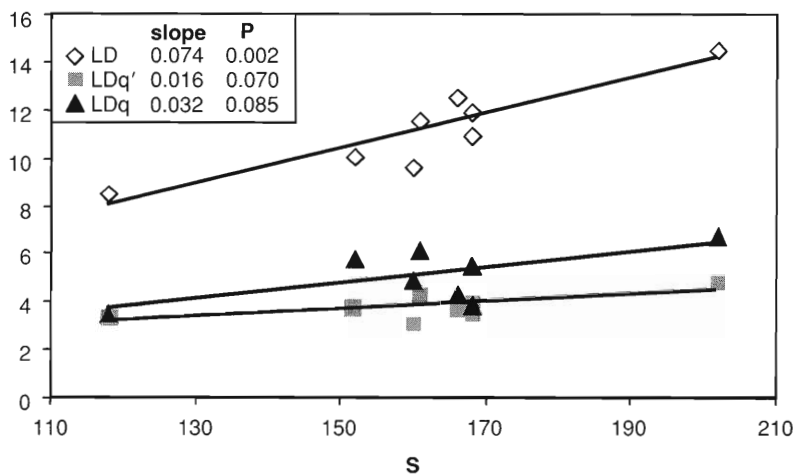
FIGURE 3 | Data and least-squares regressions (solid lines) of qualitative link density ($\Diamond$), unweighted quantitative link density (■), and weighted quantitative link density (▲) for eight seasonal food webs from wet meadows on the southern shore of Lake Neuchâtel (Switzerland).

These findings raise the question if the food web collection analyzed here is structurally constrained with respect to the diversity of link magnitude and if so, what mechanisms give rise to such limitations. With regard to the search for regularities in food web structure, the result of scale-invariant (quantitative) link density would certainly be of extreme relevance with profound implications for the issue of stability and complexity.

Requisite to the derivation of new food web regularities based on the approach pursued here however is the collection and analyses of more high-quality quantitative food web data (Banasek-Richter et al., unpublished manuscript). This could serve to substantiate and supplement the obtained results, as well as to ascertain patterns in food-web structure pertaining to biomass flux which sensibly complement the results of qualitative analyses.

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