

## Scale-Invariant or Scale-Dependent Behavior of the Link Density Property in Food Webs: A Matter of Sampling Effort?

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Studies of initial compilations of food webs resulted in the intriguing generalization that the link density property,  $L/S$  (the number of trophic links  $L$  divided by the total number of species  $S$  in a web), may be scale invariant; that is, this ratio may remain constant across webs of varying size (Rejmánek and Stary 1979; Yodzis 1980; Cohen and Briand 1984; Sugihara et al. 1989). However, along with increasing recognition of the weakness of the existing data (e.g., Paine 1988; Polis 1991) came a proposal that scale-dependent power laws might provide a more accurate fit for collections of food webs (Schoener 1989; Cohen et al. 1990; Pimm et al. 1991). Indeed, recently compiled collections of food webs do not support scale invariance for this property (Warren 1989, 1990; Winemiller 1989, 1990; Havens 1992; Martinez 1992; Deb 1995). Martinez (1992) proposed that the directed connectance (the number of links divided by the total number of possible links in a system:  $L/S^2$ ) should be scale invariant across food webs. Using empirical data, he found that  $L/S^2 = 0.11$ , which corresponds to the link density depending linearly on scale:  $L/S = 0.11 \times S$ . Constant connectance implies that predators eat, on average, a constant proportion of the prey species available across webs of different sizes, while they eat a fixed number of prey species in the case of constant link density.

The link density and the various measures of connectance (see Warren 1994 for a list of definitions) are of central importance to food web ecology for several reasons. First, as a direct measure of complexity, connectance lies at the heart of the complexity-stability debate (e.g., Pimm 1984). Second, the number of links per species is the key parameter of the cascade model (Cohen and Newman 1985; Cohen et al. 1990), a stochastic model accounting

for some of the patterns seen in food web structure. Finally, elucidating the mechanisms responsible for determining the number of trophic links in communities remains a primary aim of food web ecology (Lawton 1989; Warren 1994; Bengtsson and Martinez 1996).

Recent interest in this issue stems not only from recent improvements in the available data but also from the fact that it illustrates general principles about sampling effects that may apply to many other analyses of ecological communities. Goldwasser and Roughgarden (1997) show that food web properties, link density included, are influenced by the degree of sampling effort. We extend this line of evidence in this note and explore how differing sampling effort used to document collections of food webs affects the scaling behavior of the link density property. Using two models, we show that low sampling effort tends to produce the appearance of scale invariance in intrinsically scale-dependent systems. Empirical data support this finding. This result resolves the apparently conflicting findings of earlier studies and helps to reconcile the opposed views about the scale dependence versus invariance of the link density property.

### Sampling Effort

The natural way to assess the effect of increasing sampling effort on the link density is to compute this property for a collection of webs after increasing hours of observation using, for example, yield-effort curves (Cohen et al. 1993). Unfortunately, we lack such information for large collections of webs. Instead, we will rely on information about

the biomass transferred by individual links, assuming that links that transfer large amount of biomass are more likely to be sampled first. Note that link strength as considered here does not equal interaction strength (e.g., Paine 1992; Polis 1994). Following this assumption, one can mimic decreasing sampling effort by retaining in the analyses stronger and stronger links (Cohen and Newman 1988; Kenny and Loehle 1991). At the lowest sampling effort, only the strongest links in the diet of the predator species are taken into account. This method, based on increasing threshold values, can be applied directly to data sets for which quantitative estimates of the importance of links are provided. This method is also implemented in the first model below. For the second model, we will mimic increasing sampling effort with a process where the probability of a trophic link to be sampled is proportional to its size. This process is biologically more realistic because it allows the occasional sampling of weak links (Goldwasser and Roughgarden 1997). Goldwasser and Roughgarden (1997) provide an extensive discussion on procedures for simulating sampling effort in food web studies.

### Models of Sampling Bias

As a first step to understanding the effect of variable sampling effort on the observed link density of real food webs, it is useful to consider this effect on model food webs. Such models contain two basic parts: a method for the generation of imaginary food webs and a method for the sampling of those webs. A model that specifically investigates the effect of sampling is the random web/link sample bias (RW/LSB) model (Kenny and Loehle 1991). It treats food webs as randomly constructed undirected connected graphs. The model basically consists of four steps: For a number  $n$  of vertices (=species), construct all possible connected graphs; for a particular graph, assign to each link an importance value according to a geometric series distribution; scale the importance values so that their sums are equal for all graphs (so that all graphs represent webs with the same transferred biomass); compute the average link density for all possible webs with  $n$  vertices, first keeping all the original links (this is the link density one would expect if webs were random graphs), then removing all the links smaller than a certain threshold value, and so on, with increasing threshold values. Repeat all steps of the procedure for different values of  $n$ .

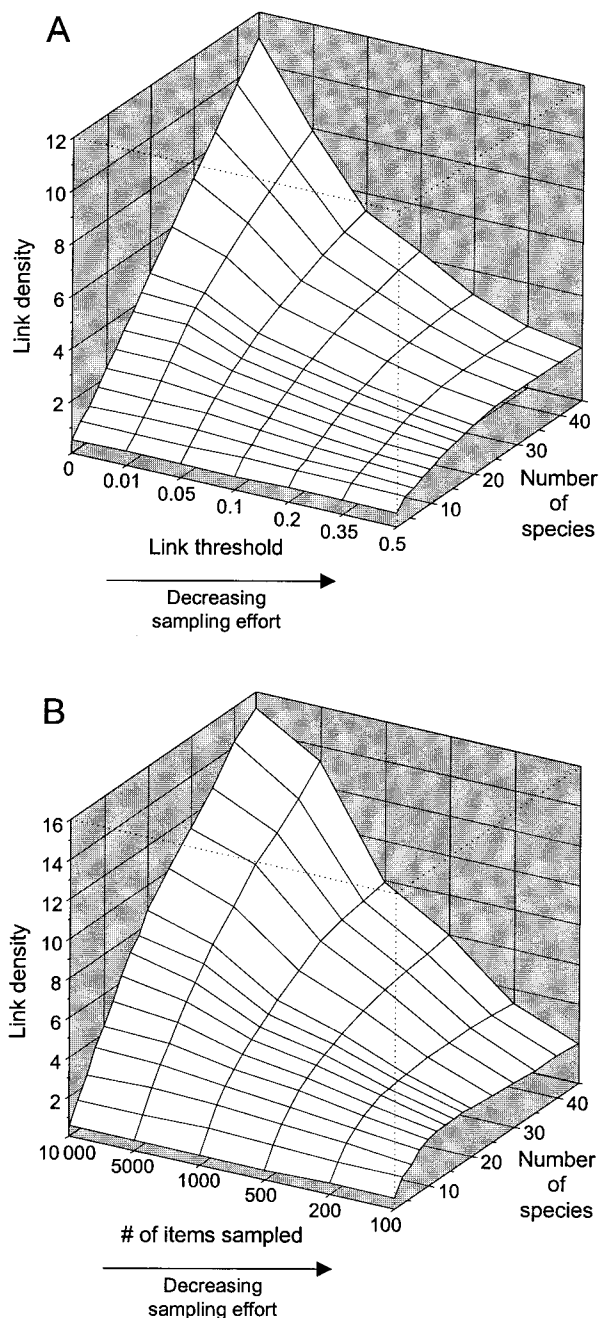
The full description of the RW/LSB model involves more intermediate steps, which can be found in the original paper (Kenny and Loehle 1991). The choice of the geometric series distribution in the second step of the procedure arises from observations of the magnitudes of trophic transfers in real ecosystems (Kenny and Loehle

1991; Ulanowicz and Wolff 1991). However, the suitability of this particular distribution has been questioned (Pahl-Wostl 1992; Ulanowicz and Wolff 1992), and a log-normal distribution has been reported to fit the empirical distribution of link frequencies for the St. Martin Island food web (Goldwasser and Roughgarden 1993). Here, we continue to use the geometric series both for simplicity and because other decreasing distributions (e.g., log normal) lead to qualitatively the same results.

Figure 1A presents the results of the RW/LSB model for the link density property. At low sampling effort (all links  $<0.5$  are discarded), the link density is statistically invariant for webs  $>15$  species but is scale dependent for smaller webs. As sampling effort increases, link density becomes increasingly sensitive to scale. When all the links are taken into account (0 threshold value), the link density rapidly approaches a linear asymptote described by  $L/S = -0.25 + 0.25S$  (this corresponds to a constant connectance value of 0.5).

The RW/LSB model involves random graphs, whereas the topology of real food webs has been shown to possess characteristic regularities, such as intervality, rigid circuit, and a lack of topological holes (Cohen 1978; Sugihara 1982, 1984; Auerbach 1984; Pimm 1991; Huxham et al. 1996). A biologically more satisfactory model of food web structure is the cascade model of Cohen and Newman (1985). This stochastic model postulates a simple ordering among species in a community such that a species can potentially prey only on species of a lower ranking. The total number of trophic interactions is a parameter of the model set by the investigator. To incorporate sampling effort in this model, we applied the following procedure: Links were weighted to follow a geometric series distribution and scaled so that the sum of the weights is constant for all webs (as in the RW/LSB model). We then set the total number of links in a web to its maximum,  $S(S-1)/2$ ; that is, we imposed strong scale dependence on our model. In contrast to the RW/LSB model, we then sampled randomly within this distribution, with the probability of a link to be sampled being proportional to its size. We randomly picked 100, 200, 500, 1,000, 5,000, and 10,000 items (an item can be thought of as an observed trophic interaction belonging to any trophic link) in webs composed of two to 45 species and computed the link density at these different levels of sampling effort. We performed 100 simulations of this model.

The results of sampling the cascade model with increasing effort, shown in figure 1B, are very similar to those for the RW/LSB model: with up to 200 items sampled, the link density is statistically scale invariant for webs with  $>12$  species, and smaller webs are scale dependent. With increasing sampling effort, the link density is scale dependent over the whole range of species.



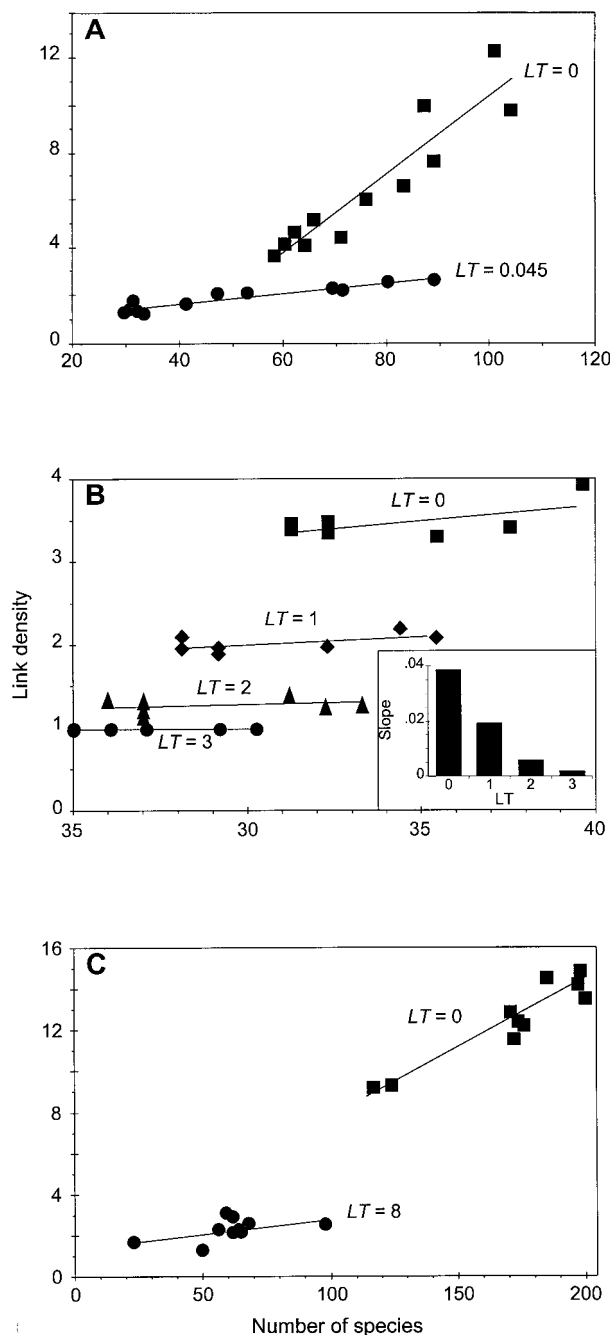
**Figure 1:** The effect of variable sampling effort on the scaling behavior of the link density property: results from (A) random web/link sample bias model (Kenny and Loehle 1991) and (B) the cascade model (Cohen et al. 1990). Limited sampling effort is simulated by discarding all links smaller (in term of biomass transferred) than a link threshold value in A and by sampling different numbers of items in a hypothetical distribution of link importance in B. Scale dependence is built in both models and is recovered with a high sampling effort. The relationship between link density and web size becomes weaker as sampling effort decreases. With low sampling effort, the link density increases smoothly up to about 15 species and then levels off, becoming scale invariant.

It is important to be aware that scale dependence is built into both models, which means that, with high sampling effort, one is guaranteed to find scale dependence. What these models demonstrate is that with a low sampling effort, one can obtain scale invariance in systems that are intrinsically scale dependent. Despite their differences (topology of the webs, simulation of sampling effort) both models give similar results, which suggests that these sampling effects may apply to real systems as well. It is interesting to note that, with low sampling effort, both models predict scale dependence of small webs and scale invariance of large webs, a feature of the Sugihara et al.'s (1989) data set of 60 food webs, where a break point was found at 13 species (Bersier and Sugihara 1997).

### Empirical Evidence

In a study on food webs dominated by tropical fishes, Winemiller (1990) assessed the relative importance of trophic links in terms of biomass transferred by analyzing the gut contents of fishes. He was able to analyze the various web statistics at differing thresholds of link magnitude (from a link threshold [LT] of 0.0, thus retaining all links, to an LT of 0.045, retaining only links that account for more than 4.5% of the diet of the fish species). His analysis of the link density property (fig. 2A) fits extremely well with the results of the RW/LSB model. When all links are included (LT = 0; i.e., high sampling effort), the link density increases markedly with scale (linear regression:  $L/S = 0.162S - 5.897$ ). However, with only the strongest links included (LT = 0.045; i.e., low sampling effort), the slope of the regression line falls to a value of 0.02.

In a recent study, Tavares-Cromar and Williams (1996) analyzed seven seasonal food webs for the macroinvertebrates in a detritus-based stream. Dietary information was obtained from gut content analyses, and the relative importance of the trophic links was quantified. They defined four importance classes (very strong, strong, moderate, and weak) that we use here to assess the effect of sampling effort (fig. 2B). Retaining all links (high sampling effort), the link density increases with the number of species in the webs. However, the slope of a linear regression is 0.04, which is not statistically significantly different from 0 ( $P = .145$ ,  $t$ -test). This indicates that, in these small systems, the dependence of the link density on the number of species is weak. Despite this weak scale dependence, we note that sequentially eliminating the weak, the moderate, and finally the strong links to simulate decreasing levels of sampling effort further reduces the slope of the regression. This monotonic decline of the slope parameter (see inset in fig. 2B) is consistent with the results of both models and has a probability of occurrence of 1 divided



**Figure 2:** Scaling behavior of the link density property for three collections of food webs at different link threshold values (LT). A, Tropical fish communities (adapted with permission from Winemiller 1990). B, Seasonal macroinvertebrate communities of a detritus-based stream (Tavares-Cromar and Williams 1996). C, Seasonal webs of Little Rock Lake, Wisconsin. All trophic links are taken into account when  $LT = 0$  (see the text for the units). In all cases, increasing  $LT$ , thus simulating a decrease in sampling effort, leads to a weaker dependence of the link density to scale. Lines are the result of linear regressions; in B, the inset gives the slope estimates.

by 24 ( $P = .042$ ). This result shows that, rather than creating the appearance of scale dependence in systems that are intrinsically close to scale invariance, low levels of sampling reduce the weak dependence of link density even further.

The 10 Little Rock Lake seasonal webs provide an additional data set able to address the question of sampling effect (see Martinez 1991 for a qualitative version of the annual food web for this lake). The body of Little Rock Lake (Wisconsin) consists of two basins that were separated in 1984 by a polyvinyl curtain to carry out a 6-yr acidification program (Watras and Frost 1989; Webster et al. 1992; Brezonik et al. 1993). Five seasonal webs (winter, early spring, late spring, summer, and fall) for each basin were documented, ranging from a minimum of 133 taxa to a maximum of 205. The biomass or abundance of all aquatic organisms except endoparasites and microorganisms was assessed (only presence-absence data is at our disposal for the macrophytes and for some transient species), and the trophic relationships were determined directly for the fishes by gut content analyses and indirectly from knowledge of prey-size selectivity, morphology, and seasonal prey availability for the other species. Since information on the flow of biomass involved in the trophic links is available only for the fish species, we will use information on the biomass or abundance to flesh out the bare bones of the binary links. The procedure we adopted to weight the links was as follows: for each predator species, each trophic link was assigned a weight class between 0 (no trophic interaction) and 10 (strong trophic interaction). Class boundaries were defined to follow a  $\log_2$  progression between the abundances of these least (class 1) and most important species. This assignment in importance classes was performed for each major group but not for all prey species pooled, since units used to report the abundances and biomass of the major groups were not easily comparable. Our assignment in importance classes is obviously a very crude estimate of the true biomass distribution of the trophic links. However, for the purpose of simulating sampling effort, our procedure makes sense since trophic links involving rare prey species are likely to be more difficult to discover than those involving abundant prey.

The result for the 10 Little Rock Lake webs is shown in figure 2C. Again, using all available information on trophic interactions (high sampling effort), the behavior of the link density property is strongly dependent on the number of species in the webs ( $L/S = 1.347 + 0.065S$ ;  $P < .001$ ,  $t$ -test). In contrast, when only the most important links are taken into account, the relationship between the link density property and scale becomes flatter. The slope of the regression is no longer significantly different from zero when only the links from the classes 8, 9, and 10

alone are taken into account ( $L/S = 1.409 + 0.014S$ ;  $P = .162$ ,  $t$ -test).

### Discussion

The sensitivity of link density to sampling effort affects the scaling behavior of this property in a specific fashion: low sampling effort results in a tendency toward scale invariance in intrinsically scale-dependent collections of food webs. This simple explanation accounts for the discrepancies found in the literature regarding the scaling behavior of link density. The food webs used in earlier studies (Cohen and Briand 1984; Sugihara et al. 1989; Cohen et al. 1990) were gathered from the literature, and these webs were not intended to reflect the full complexity of the fluxes of biomass in these systems (e.g., May 1983; Paine 1988) but instead are limited to the most conspicuous links and those of particular interest to the investigator. These collections of webs can be thought of as having been sampled with low effort, and they show scale invariance or weak scale dependence. In recent compilations of food webs, much effort has been devoted to obtaining relatively complete lists of species and links in the communities. These collections can be broadly classified in two groups according to the methods used to assess the presence of trophic links between predator and prey species: those for which the trophic links were determined directly, by analysis of stomach-gut contents (Winemiller 1990; fish species of the seasonal Little Rock Lake webs); and those for which the links were inferred indirectly, by consulting experts or published diets in the literature (Havens 1992; Deb 1995; most species other than fishes of the seasonal Little Rock Lake webs). Both groups of webs show scale dependence. Other collections of food webs, spanning a smaller range of species, fall in this framework (Warren 1989; Carney et al. 1997).

Other nonexclusive hypotheses can account for the discrepancies found in the scaling behavior of the link density. Collections showing strong scale dependence come from aquatic environments (Winemiller 1990; Havens 1992; Deb 1995; Little Rock Lake), while scale-invariant collections (Sugihara et al. 1989; Cohen et al. 1990) combine webs from various habitats. After factoring out the effect of web size, Bengtsson (1994) found a similar difference between aquatic and terrestrial webs in the Schoenly et al. (1991) data set, which is an extended version of the Sugihara et al. (1989) collection. Havens (1997) proposed that this environmental difference in the scaling behavior of the link density in pelagic communities was due to the predominance of filter-feeding predators and to the very high diversity of small autotrophic prey species.

Apart from such biological effects, other methodological

problems influence the number of trophic links found in a web. For example, the number of trophic links observed will depend on the criteria chosen to establish a trophic link, and stricter criteria will lower the observed value of the link density (Martinez 1993). In the same vein, Hawkins et al. (1997) showed that reducing the number of basal species in food webs tended to decrease the value of  $L/S$ . This result is in accordance with the second hypothesis of Havens (1997) above and speaks to the inadequacy of source webs (sensu Cohen 1978) to represent complete communities. Concerned specifically with the effect of sampling effort, Goldwasser and Roughgarden (1997) analyzed 21 food web properties, using as their standard a single, large, and highly resolved food web (St. Martin Island food web; Goldwasser and Roughgarden 1993). They found that most properties, the link density included, were sensitive to sampling effort and that a high level of sampling was necessary to reach the original values of the properties. The main difference with our analysis is that, by dealing with collections of food webs instead of a single one, we are able to assess the effect of sampling on the scaling behavior of the link density property.

The high sensitivity of the link density to sampling effort raises questions about the usefulness of this property. First, the estimation of the parameters of models describing the relationship of the link density to scale (e.g., the slope of a linear regression) will depend on the choice of sampling procedures and the amount of effort expended in carrying them out. Second, putting together food webs from various sources to explore the scaling behavior of the link density may provide only approximate results, since this sensitivity is likely to be the source of undesirable variability (Cohen and Briand 1984; Sugihara et al. 1989; Schoenly et al. 1991; Martinez 1992). Third, in cross-system comparisons, it will be difficult to disentangle effects due to differences in sampling effort from those due to biological differences. For example, differences in sampling effort are likely to account for part of the variation found by Havens (1997) in comparing the scaling behavior of the link density property of pelagic versus other, mostly terrestrial communities.

The distribution of link importance in highly resolved webs is likely to be highly uneven (e.g., log normal as in Goldwasser and Roughgarden 1993). Giving the same weight to all links distorts the picture of the structure of the food webs and blurs our perception of this structure (Kenny and Loehle 1991). This points to desiderata expressed in earlier studies highlighting the need for quantitative data to allow a more sensible approach to food web structure (e.g., May 1983; Kenny and Loehle 1991; Pimm et al. 1991; Cohen et al. 1993). Consequently, we have to think of alternative ways of expressing the link density property that take into account the disequity of the distribution of link importance; the effective con-

nectance of Ulanowicz and Wolff (1991) is a promising solution. An additional difficulty lies in the choice of a currency for the measure of link importance. Measures based on biomass (e.g., flow of carbon: Baird and Ulanowicz 1989; feeding rate: de Ruiter 1995; volume: Wine-miller 1990; index of relative importance: Tavares-Cromar and Williams 1996) or on the frequency of trophic interactions (Goldwasser and Roughgarden 1993) are adequate.

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