

Effect of Scale on Food Web Structure

Karl Havens (1) infers that 50 highly and evenly resolved food webs confirm the convention (2) that seven food web properties are "scale-invariant" or roughly constant among food webs with widely varying numbers of species. Also in line with the convention, an eighth food web property, connectance, is inferred to be scale-dependent and to decrease as the number of species increases (2). I have reanalyzed the 50 food webs and found that the conventional patterns should be rejected in favor of the competing hypotheses (3–5) that six of the seven properties are scale-dependent and that the eighth, connectance, is scale-invariant (4).

Havens (1) analyzes 50 lake food webs with from 10 to 74 (mean = 38) species. The fractions of top (T), intermediate (I), and basal (B) species as well as the fractions of all trophic links (L) between top and intermediate species (TI), top and basal species (TB), intermediate and intermediate species (II), and intermediate and basal species (IB) are analyzed as a function of the total number of species (S) in the webs. [Top species have prey but no predators; intermediate species have both prey and predators; and basal species have predators but no prey (6).] Havens asserts that none of these fractions varies in a statistically significant manner with S and that the variation of L with S matches the previously suggested (2) function $L = S^{1.4}$. This forces directed connectance [L/S^2 , (4)] to decrease with S.

Alternative hypotheses assert that fractions of species and links are scale-dependent (3, 5). Significant fractions of T, TI, and TB may occur only in webs with small S, in which predators of top species are often missed or excluded. Food webs with large S contain mostly I and II and relatively small B. The theoretical and empirical support (3, 5) for these alternative hypotheses suggests that T, B, TI, and TB decrease with S while I and II increase. The scale-dependence hypotheses and the scale-invariance convention lead to different predictions that can be tested with one-tailed P tests, using the data in the report by Havens.

If one assumes that simple linear regressions are valid, significant decreases in T and B, and the significant increase in I with S ($P < 0.05$), corroborate the scale-dependence hypothesis (Fig. 1). (We assume that the simple linear regressions in the report by Havens are valid.) The results of decreases in TI and TB and an increase in II corroborate the scale-dependence hypothesis (7). At $P = 0.064$, the decrease in TB is only slightly above the conventionally accepted level of statistical significance of $P = 0.05$. Because no specific alternatives to the scale-invariance

hypothesis for IB have been proposed, a two-tailed test is applied that rejects the scale-invariance hypothesis at $P = 0.014$.

These statistical tests may be criticized because the data may violate assumptions of simple linear regressions. Decreasing and increasing linear trends of proportions can-

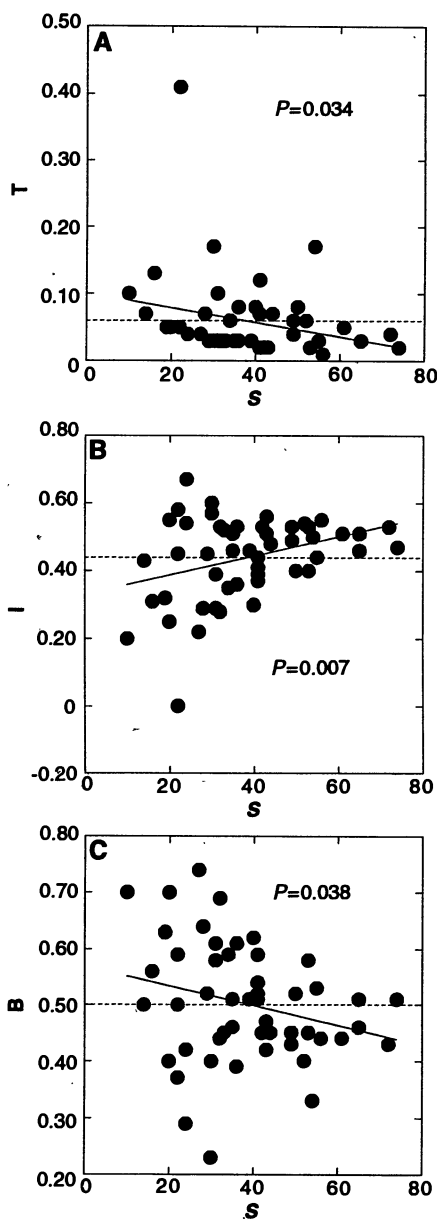


Fig. 1. Fraction of species in (A) top, (B) intermediate, and (C) basal categories as a function of S. Horizontal dashed lines represent scale-invariant estimates from (1). The simple least squares regressions, shown as solid lines, suggest that (fractions converted to percentages) $T = -0.107S + 10$ ($SE_{\text{slope}} = 0.057$, $R^2 = 0.07$), $I = 0.284S + 33$ ($SE_{\text{slope}} = 0.110$, $R^2 = 0.12$), and $B = -0.177S + 57$ ($SE_{\text{slope}} = 0.098$, $R^2 = 0.06$).

not continue beyond 0 or 100%. Instead, the trends must be curvilinear or discontinuous (3, 5) among webs with a large range of species numbers. Also, the data do not appear to be homoscedastic or bivariate normally distributed (for example, the variance above the T regression exceeds that below). Nonparametric correlations (Kendall's rank correlation or "τ-test") were used to test the sensitivity of the regression results to these assumptions of simple linear regressions (8). Such tests are typically less powerful and therefore more conservative in favor of the null (scale-invariant) hypothesis as compared with parametric tests.

I have tested the null hypotheses that the properties are not significantly correlated with S (2) against alternative hypotheses that T, B, TB, and TI are negatively correlated with S while I and II are positively correlated with S (3, 5). The τ-tests consistently reject the scale-invariant hypotheses in favor of the scale-dependent hypotheses at even lower P levels [$P < 0.04$ (8)] than do the regressions. The two-tailed test rejects scale-invariant IB (8). If two-tailed probabilities are used to test scale-invariance without consideration of specific scale-dependent hypotheses (1), τ-tests reject scale-invariance at $P = 0.04$ for each fraction except B and TI.

Havens used a log-log regression of L and S to estimate $L = S^{1.4}$, forcing a log-log regression through the zero intercept (Fig. 2). When one allows the data to determine the intercept, an exponent of 1.9 is obtained [$\log L = 1.87 (\log S) - 0.81$, $SE_{\text{slope}} = 0.081$; $P < 0.001$, $R^2 = 0.92$]. Because the antilog of zero (1.0) is almost an order of magnitude greater than the intercept (0.16) that is suggested by the unforced log-log regression, the estimate by Havens is forced above the value for food webs with small S. The unforced result is

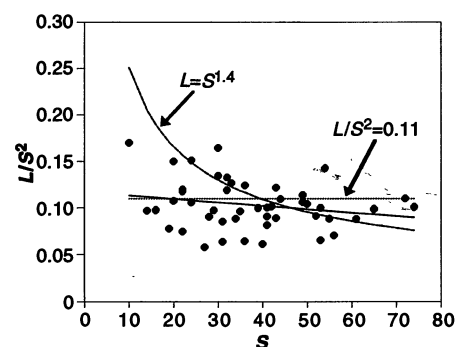


Fig. 2. Variation of directed connectance [L/S^2 , (4)] with S. The simple least squares regression [Havens' estimate (1)], shown as a solid line ($L/S^2 = -0.00037S + 0.117$, $SE_{\text{slope}} = 0.00024$, $R^2 = 0.05$), is not significantly different from the constant connectance hypothesis [$L/S^2 = 0.11$ (4)] at $P = 0.129$. Havens estimated (1) that $L = S^{1.4}$.

statistically indistinguishable ($P = 0.13$) from an exponent of roughly 2, as predicted by the constant connectance hypothesis (4). Furthermore, L/S^2 among the food webs studied by Havens (mean = 0.10, SD = 0.04) corroborates a previously estimated mean of 0.11 (SD = 0.03) that was based on other data [figure 2 in (4)]. A one-tailed τ -test confirms that L/S^2 is not significantly correlated with S (8).

After inferring that new improved data support conventionally accepted patterns, Havens concludes (1), "Ecologists must now turn to the more interesting question of what causes those patterns." Such statements (1, 2) are premature (3–5). Reanalysis rejects the conventional patterns in favor of constant connectance (4) and scale-dependent fractions of species and links (3, 5). Although selective exclusion of food webs least consistent with scale-invariance would weaken the observed scale dependencies, hypotheses that successfully explain more data should be preferred over those that explain less. For example, scale-dependence (3, 5) successfully predicts that new food webs with large S have higher I and II and lower T, B, TI, and TB (3, 5, 9–12) than food webs with smaller S (13). Such observations are anomalies to the theory of scale invariance. These findings suggest that attempts to account for scale-invariance, such as the cascade model (13), may explain patterns that do not exist in nature (3–5, 14). In contrast, explanations of roughly constant connectance may elucidate a robust attribute of ecological organization (3–5).

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7. My simple least squares regressions, calculated on fractions converted to percentages, suggest that $TI = -0.183S + 17$ ($SE_{\text{slope}} = 0.104$, $R^2 = 0.06$, $P = 0.042$), $TB = -0.216S + 13$ ($SE_{\text{slope}} = 0.139$, $R^2 = 0.05$, $P = 0.064$), $II = 0.813S + 1.2$ ($SE_{\text{slope}} = 0.163$, $R^2 = 0.34$, $P < 0.001$), and $IB = -0.414S + 69$ ($SE_{\text{slope}} = 0.162$, $R^2 = 0.12$, $P = 0.014$).
8. Results of τ -tests: T , $\tau = -0.301$, $P = 0.0010$; I , $\tau = +0.205$, $P = 0.0192$; B , $\tau = -0.187$, $P = 0.0311$; TI , $\tau = -0.164$, $P = 0.0381$; TB , $\tau = -0.253$, $P = 0.0046$; II , $\tau = +0.405$, $P = 0.0001$; IB , $\tau = -0.310$, $P = 0.0015$; L/S^2 , $\tau = -0.093$, $P = 0.1701$.
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15. I thank D. Strong, J. Harte, and J. Cronin for helpful comments; J. Kollar and A. Adhikari for statistical assistance; and the Ford Foundation and NSF grants DEB-9208122 and BIR-9207426 for support.

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Response: With regard to links and species in natural webs, I stated in my report that in the smallest webs "there is evidence of a reduced fraction of intermediate species and an increased fraction of basal species. These trends are not statistically significant. . . ." I also stated that in the smallest webs, "the fraction of top-basal links is increased while the fraction of intermediate-intermediate links is reduced to zero. The trends are not statistically significant. . . ." Martinez states that the relations between S and the various species and link fractions are significant. He uses a nonparametric test (Kendall's τ), noting that the use of rank correlation appears to be a more valid approach, given the limitations of the data. A nonparametric approach was not called for. In the bivariate analyses in my report, one variable (S) is normally distributed (Shapiro-Wilk test, $W > 0.97$), and in three of the analyses both variables approximate normality (1). When the null hypothesis (H_0) of no correlation is tested, R may be used provided that at least one variable is normal (2). Therefore, a parametric approach was valid. Martinez is correct that for two comparisons, S plotted against I and S plotted against IB, the P values associated with the test (H_0 : no relation) are marginally significant; for the relation S plotted against II, P is less than 0.01. The correlation coefficients calculated by Martinez are small, which reflects a great scatter in the data. Hence, the predictive power of the regression equations used by Martinez is questionable.

The conclusion drawn by Martinez raises an important question: Are trends in species and link fractions consistent across the entire range of S ? They are not. In the Adirondack lakes from which the data originated, there is great variation in water chemistry and pH. The relations that I mentioned but did not include in my report, and which Martinez argues were significant, are driven by 11 small, simplified food webs composed only of zooplankton and algae. These webs occur in acidified lakes, where vertebrate predators have become extinct. Links between intermediate species are absent, and one web has no intermediates. Others (3, 4) have excluded such small "biased" webs from quantitative analyses. When I excluded the aberrant webs and reexamined the relations between S and the species and link fractions, seven of the resulting R values were nonsignificant and one, associated with the relation S plotted

against II, was marginal (5). In several cases, the data suggest a relation between S and the species and link fractions that neither Martinez nor I mentioned: an increase in the amount of variability in smaller webs. The structure of smaller webs may be less predictable.

I conclude that species and link fractions in these natural food webs are scale-invariant, as predicted by scaling laws (6–8). An exception is that, in a subset of simplified webs, there is a reduced fraction of intermediate species and links and an increased fraction of top and basal species and links.

Martinez also comments on the relation between L/S and S in the 50-web data set, saying that it fits the equation $L = kS^\beta$, where k is a constant (0.1) equal to the mean directed connectance of the webs and β is 2. He is correct; constant connectance (4) is a property of these natural webs. Yet, the finding that β is closer to 2 than 1.4 seems less important than the discovery that the relation between L and S is a power function. Food web researchers have suggested (7) that the relation between S and L might be nonlinear, and Pimm *et al.* (9) recently said that the power function was a "viable description" of that relation. The data in my report support the proposition that such a relation exists in natural, non-aggregated webs. In natural communities, food web complexity increases with S . This relates directly to, for example, community stability and biomagnification. Both properties may depend on food web complexity and, therefore, on the more easily measured parameter S .

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1. The Shapiro-Wilk test statistics (W) associated with the variables were TF (0.60), IF (0.95), BF (0.98), LTI/L (0.80), LTI/L (0.35), LII/L (0.88), and LII/L (0.98). Values of 0.95 and greater indicate distributions that are not significantly different from normal.
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10. I thank R. Carlson for this comments on an earlier version of this response.

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