

Trophic links of community food webs

(scale invariance/predators/prey/directed graphs/constant and fluctuating environments)

JOEL E. COHEN* AND FRÉDÉRIC BRIAND†

*Rockefeller University, 1230 York Avenue, New York, NY 10021; and †Department of Biology, University of Ottawa, Ottawa, Ontario K1N 6N5, Canada

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ABSTRACT This report describes and explains regularities in the numbers and kinds of trophic links in community food webs. To a first approximation, the mean number of trophic links in a community food web is proportional to the total number of trophic species. The mean number of trophic links between any two categories of trophic species (basal, intermediate, and top) is proportional to the geometric mean number of species in the categories joined. These linear relationships, and scale-invariance in the proportions of basal, intermediate, and top species, make it possible to predict with remarkable precision the proportions of each kind of trophic link among all community food webs. The differences between food webs in constant and in fluctuating environments reflect apparently greater constraints on the trophic organization of food webs in fluctuating environments.

PROBLEM AND HYPOTHESES

How does the total number L of links in a web vary as the number S of species increases? At least three hypotheses are plausible. First, the number of potential links increases as S^2 because the maximal number of edges in a directed graph on S nodes is $S(S-1)$. If there were a constant probability that any potential link were a real link, the mean $E(L)$ of L would be proportional to S^2 . Second, if each species could eat or serve as food for only a finite number of other species, regardless of how many species were present in the community, the mean $E(L)$ would be proportional to S . Third, both of the preceding hypotheses might apply over different ranges of values of S . When the number of species in a community is small, L may be constrained only by the availability of potential links and hence vary as S^2 . When the number of species in a community is large, L may be limited by the potential for interaction of each species and hence vary as S . The same relation between L and S might also arise because field ecologists might be more thorough in recording links when the total number of species in the community is small, but proportionally more prone to omission when the number of species is large.

According to these three hypotheses, plots against S , on the abscissa, of (a) the square root of L , (b) L , or (c) some power of L between $1/2$ and 1 , on the ordinate, should be approximately linear.

DEFINITIONS AND DATA

A community food web (henceforth abbreviated to “web”) includes the feeding relations among all organisms found in a well-defined habitat by the original investigator. Organisms with identical sets of prey and identical sets of predators have been combined into a single “lumped” species (1). Throughout this paper, “species” means trophic species, not necessarily a single biological species. A “top” species is a predator that has no predator. An “intermediate species” is a

species that is both a predator and a prey. A “basal” species is a prey that has no prey. The number of basal, intermediate, top, and all species in a web will be denoted by B , I , T , and S .

A “trophic link” (hereafter, “link”) is any reported feeding or trophic relation between two species in a web. Observers use various criteria to decide how much feeding justifies the reporting of a link and how much failure to observe feeding justifies reporting the absence of a link.

Webs are classified as arising in “fluctuating” or “constant” environments. The environment is considered to be fluctuating if the original report indicates temporal variations of substantial magnitude in temperature, salinity, water availability, or any other major physical parameter. This fluctuation may result from a pronounced seasonality, as in temperate terrestrial systems, from daily oscillation, as in intertidal systems, or from irregular perturbations, such as hurricanes. The magnitude, and not the predictability, of the fluctuations is the criterion of classification. Only 19 of 62 environments in our sample qualify as constant, including the deep sea and most, but not all, tropical systems. Since the classification of an environment as constant or fluctuating is to some extent subjective, we point out that this task was carried out before we had analyzed the data and uncovered any pattern.

The 62 webs analyzed here are drawn from published studies. Details not yet presented by Briand (2) or Cohen (3) will be published elsewhere (unpublished data).

RESULTS

Fig. 1 shows, plotted against S , $L^{1/2}$ (a), L (b), and $L^{3/4}$ (c). The slopes of the straight lines plotted through the origin are computed on the assumption that the variance of the (transformed) ordinates is proportional to the abscissa. Visual inspection of Fig. 1a rejects the first hypothesis: the trend of the data points is distinctly concave compared to the fitted straight line. When the square roots of links vs. species are plotted separately (not shown here) for constant and fluctuating webs, both graphs show a concave trend like that of Fig. 1a. Visual comparison of Fig. 1b and c is less decisive. Plotting the $3/4$ power of L (Fig. 1c) brings the points closer to the fitted line at low values of S but, at high values of S , lets most of the points fall below the line.

We accept $E(L)$ as proportional to S . This approximation does no obvious violence to the data and simplifies further analysis.

If $E(L) = cS$ and the variance in L is proportional to S , then the estimate $c = 1.8559$ is the ratio of the total number of links, 1919, to the total number of species, 1034, in our 62 webs. The standard deviation of c is 0.0740.

The number L of links is the sum of the numbers L_{BI} , L_{BT} , L_{II} , and L_{IT} of links from basal to intermediate, from basal to top, from intermediate to intermediate, and from intermediate to top species, respectively. Fig. 2 shows, plotted against S , the proportions of links in each category L_{BI}/L (a), L_{BT}/L (b), L_{II}/L (c), and L_{IT}/L (d). No increasing or decreasing trends are evident. Thus, the mean proportions of links of each kind are roughly invariant with respect to the total num-

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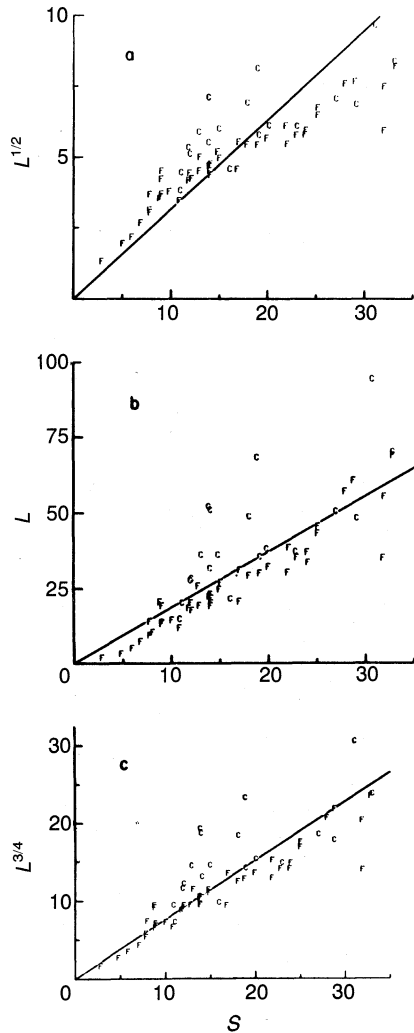


FIG. 1. Number of links (L) as a function of the number of trophic species (S) in 62 webs. Plotted against S are $L^{1/2}$ (a), L (b), and $L^{3/4}$ (c). C = constant environment; F = fluctuating environment. The symbols F and C have been perturbed from their exact locations by a small random amount to indicate when several food webs have exactly the same coordinate. In the straight lines through the origin plotted here and in Fig. 3, the slopes are computed assuming that the variance of the ordinates (as transformed, in a and c) is proportional to the abscissa. In a, the trend of the data points is concave compared to the fitted straight line. In c, the points lie closer to the fitted line at low values of S but, at high values of S , most of the points fall below the line.

ber of species in the web, though variability around the mean is evident. It follows that the average numbers of links of each kind, in addition to the average total number of links, increase in proportion to the total number of species, again with variability.

Table 1 shows the numbers L_{BI} , L_{BT} , L_{II} , and L_{IT} and proportions of links in each of the four categories, summed for constant, fluctuating, and all webs. The proportions of each category of links are highly variable among webs, compared to the variation among webs that would be expected from multinomial sampling with proportions that are the same for all webs. If the counts of links are arranged in a 4×62 contingency table with one row for each type of link and one column for each web, a homogeneity test yields a χ^2 of 794.2 with 183 degrees of freedom (df). If the summed link counts of the constant webs are compared to the summed link counts of the fluctuating webs in a 4×2 contingency table (the counts are shown in Table 1), a homogeneity test yields a χ^2 of 33.0 with 3 df. A homogeneity test of the link counts

for the 19 constant webs alone yields a χ^2 of 510.3 with 54 df, while the same test for the 43 fluctuating webs alone yields a χ^2 of 284.0 with 126 df. Under the assumption, which is open to doubt, that the observations of different webs are mutually independent, the astronomically low significance level of each of these values of χ^2 rejects the null hypothesis that the variation among webs in the proportions of links of each category is due to random sampling.

We now display the relation between number of links and number of species at a level of resolution finer than that of Figs. 1 and 2. Our previous analysis of community webs (1) established that there are fixed positive constants r , p , and q such that, within multinomial sampling error, for each web, $E(B) = rS$, $E(I) = qS$, and $E(T) = pS$. These equations mean that the average number of basal species is proportional to the total number of species and similarly for intermediate and top species. For all webs, $r = 0.190$, $q = 0.525$, and $p = 0.285$ (Table 1). The differences between constant and fluctuating webs are within multinomial sampling error (1). As a consequence of this simple proportionality, the geometric mean of any two of B , I , and T should be roughly proportional to S . Since, as Fig. 2 implies, the number of links of each kind is also proportional to S (with substantial variability, in light of the above inhomogeneity), L_{BI} should be roughly proportional to $(BI)^{1/2}$, with variability.

Fig. 3a plots L_{BI} against $(BI)^{1/2}$. The remaining panels of Fig. 3 give similar plots for basal-top links (b), intermediate-intermediate links (c), and intermediate-top links (d). The linear model in Fig. 3b is least satisfactory because for many webs, both constant and fluctuating, there are no links from basal to top species.

The linearity or near-linearity in Fig. 3 is not materially changed when the links of constant and fluctuating webs are plotted separately on the same axes or when the links of constant and fluctuating webs are plotted separately against the product of the corresponding species numbers—e.g., L_{BI} against BI rather than against $(BI)^{1/2}$ (not shown). For fluctuating webs, the apparent convexity of L_{BT} against $(BT)^{1/2}$ is somewhat diminished in the plot against BT .

Table 2 gives the regression coefficients, and their standard deviations, of the number of each kind of link against the geometric mean number of species in the source and sink class, for all webs (corresponding to the slopes of the lines plotted in Fig. 3 a-d) and for constant and fluctuating webs separately. Regressions (not reported here) that assume a line through the origin with the standard deviation of the residuals proportional to the abscissa give, in every case, a larger mean square residual and a visually poorer fit.

The regression coefficients in Table 2 and the values of r , q , and p in Table 1 can, in some cases, be combined to predict accurately the proportion of each kind of link shown in Table 1. For example, suppose that the proportion of basal-intermediate links is given by

$$p_{BI} = L_{BI}/L,$$

that the regression in Fig. 3a is summarized by

$$L_{BI} = a_{BI}(BI)^{1/2},$$

and that B , I , and T are all proportional to S . Then

$$p_{BI} = a_{BI}(BI)^{1/2} / [a_{BI}(BI)^{1/2} + a_{BT}(BT)^{1/2} + a_{II}(II)^{1/2} + a_{IT}(IT)^{1/2}] = a_{BI}(rq)^{1/2} / [a_{BI}(rq)^{1/2} + a_{BT}(rp)^{1/2} + a_{II}q + a_{IT}(qp)^{1/2}].$$

Table 3 shows the predicted proportions of links of each category, based on the regression coefficients a_{ij} from Table 2,

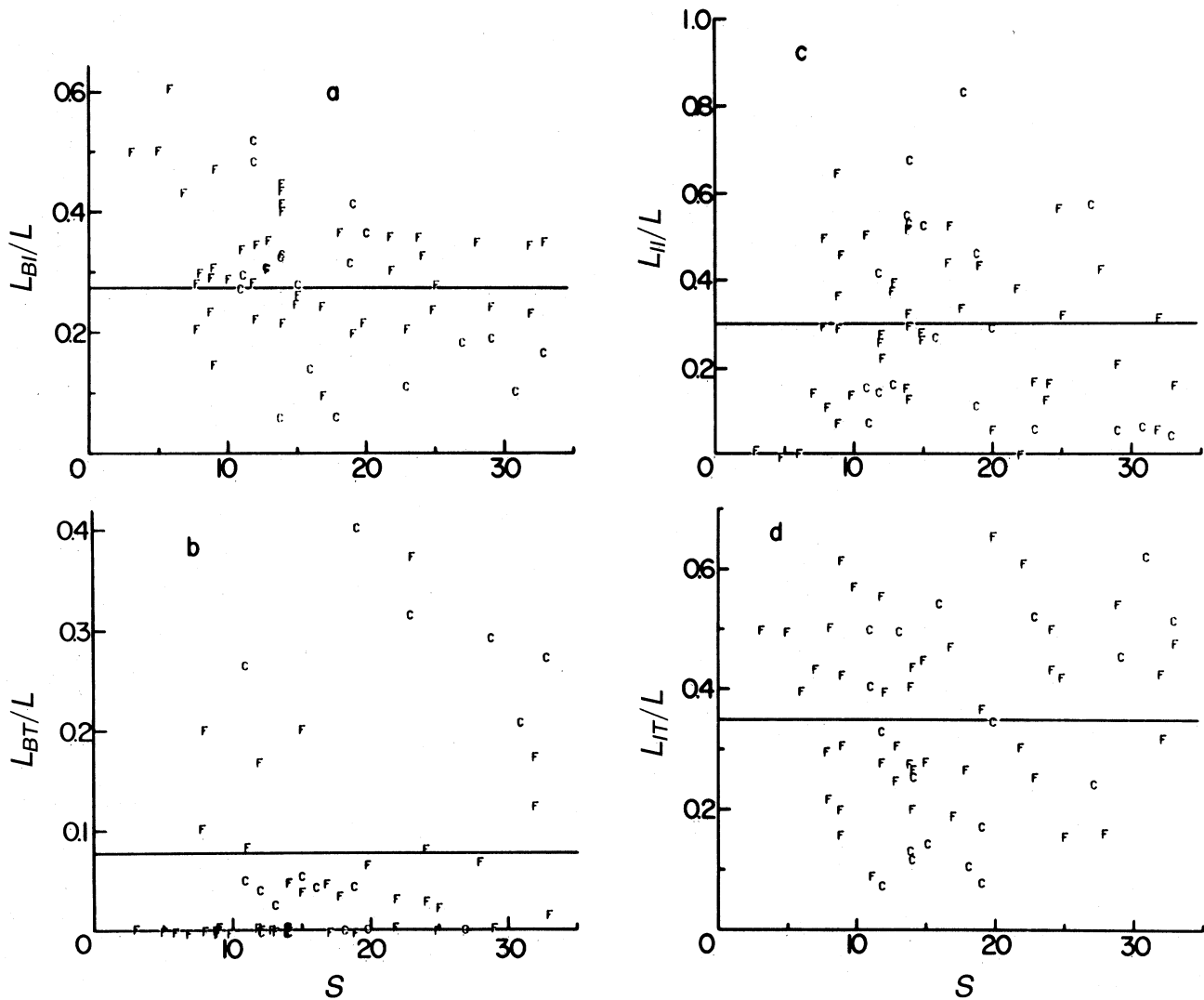


FIG. 2. The proportions of links in each category as a function of species. Plotted against S are L_{BI}/L (a), L_{BT}/L (b), L_{II}/L (c), and L_{IT}/L (d), where L_{BI} , L_{BT} , L_{II} , and L_{IT} are the numbers of links from basal to intermediate, from basal to top, from intermediate to intermediate, and from intermediate to top species, respectively. No increasing or decreasing trends are evident in the data. The points in the upper left corner of a are based on very few links. The heights of the fitted horizontal lines are the ratio of the links in the given category, summed over all webs, to the total links, summed over all webs.

the values of p , q , and r from Table 1, and a goodness-of-fit χ^2 (with 3 df) when the predicted proportions are compared with the observed proportions of links of each category. For all webs combined, the predicted proportions agree remark-

Table 1. Summary statistics of the numbers of species and links in 62 webs, by type of web, type of species, and category of link

Type of unit	Webs					
	Constant		Fluctuating		All	
	No.	Fraction	No.	Fraction	No.	Fraction
Webs	19		43		62	
All species	351	1.000	683	1.000	1034	1.000
B	66	0.188	130	0.190	196	0.190
I	177	0.504	366	0.536	543	0.525
T	108	0.308	187	0.274	295	0.285
All links	811	1.000	1108	1.000	1919	1.000
B-I	198	0.244	327	0.295	525	0.274
B-T	92	0.113	56	0.051	148	0.077
I-I	260	0.321	318	0.287	578	0.301
I-T	261	0.322	407	0.367	668	0.348

B, basal; I, intermediate; T, top.

ably well with the observed; the discrepancy could be attributed entirely to sampling fluctuation.

However, this good agreement is not a strong confirmation that the number of links of each category scales according to the geometric mean rather than, say, according to the product. If, for example, in the above equations the regression coefficient of L_{BI} against BI is used and $(BI)^{1/2}$ is replaced by BI , and similarly for BT , II , and IT , then the predicted proportions also agree remarkably well, though not as well, with the observed ($\chi^2 = 3.95$). The excellent agreement between observed and predicted proportions of links of each category is rather robust with respect to the exact way in which the numbers of links scale with an increasing number of species.

For constant and fluctuating webs considered separately, the quantitative discrepancies between the observed and predicted proportions of each category of link are not large, but the χ^2 statistic indicates that the fit would be rejected at any conventional level of significance, under the assumption of independence among webs. Among constant webs, fewer basal-intermediate links and more basal-top links are observed than predicted. Among fluctuating webs, more basal-intermediate and fewer basal-top links are observed than

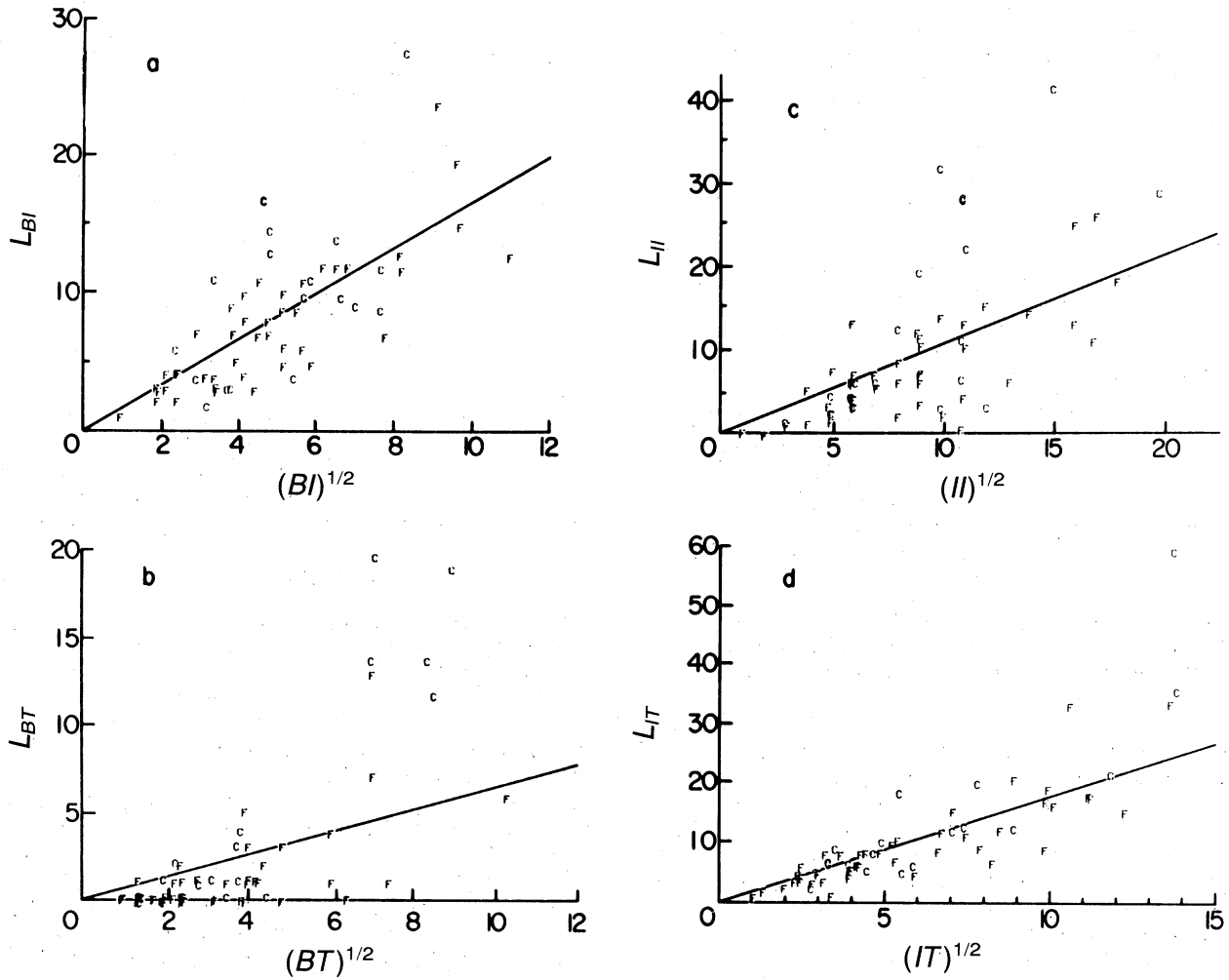


FIG. 3. (a) Plot of the number L_{BI} of basal–intermediate links against the geometric mean $(BI)^{1/2}$ of basal and intermediate species and analogous plots for basal–top links (b), intermediate–intermediate links (c), and intermediate–top links (d). A straight line through the origin is most plausible as a description of the data in a and d, less so for c, and least so for b. In b, many webs, both constant and fluctuating, lack links from basal to top species.

predicted. These discrepancies precisely cancel when all webs are considered together. [When constant webs are compared with fluctuating webs, rather than each with the predictions of a model, the ratio of basal–intermediate links to total species is higher in constant webs ($198/351 = 0.564$) than in fluctuating webs ($327/683 = 0.479$), contrary to the comparison with the model. The ratio of basal–top links to total species is higher in constant webs ($92/351 = 0.262$) than in fluctuating webs ($56/683 = 0.082$), in parallel with the model comparison.]

When a web has intermediate species (as do all those in

Table 2. Regression coefficients of the number (y) of links in a specified category against the geometric mean number (x) of the corresponding types of species

Type of link	Webs					
	Constant		Fluctuating		All	
	Slope	SD	Slope	SD	Slope	SD
B–I	1.3824	0.0989	1.5817	0.1038	1.6802	0.0908
B–T	0.4437	0.1530	0.8317	0.1265	0.6580	0.0976
I–I	0.8258	0.0877	1.0907	0.1092	1.0645	0.0906
I–T	1.5464	0.0938	1.8053	0.1206	1.7891	0.0983

All regressions assume that the variance in the ordinate y is proportional to the abscissa x. SD = standard deviation of the estimated slope coefficient. B, basal; I, intermediate; T, top.

our sample), the presence of basal–top links gives the top species collectively a more flexible trophic strategy, in that some top predators prey on intermediate species and some (possibly the same) top predators prey on basal species. The deficit of basal–top links in fluctuating webs and the excess of basal–top links in constant webs, relative to the proportions expected from our simple model of scaling, suggests that fluctuating webs are trophically more constrained than constant webs.

Table 3. Predicted fractions of links of each category, for constant and fluctuating webs separately and for all webs

Type of link	Webs		
	Constant	Fluctuating	All
B–I	0.2732	0.2561	0.2740
B–T	0.0685	0.0963	0.0791
I–I	0.2672	0.2966	0.2889
I–T	0.3911	0.3510	0.3579
χ^2	44.6144	31.2953	1.6049

The χ^2 statistic to measure goodness of fit between the observed fractions (given in Table 1) and the predicted fractions given here has 3 df. When computing the predictions for the constant webs, both the regression coefficients and the proportions of species of each type were derived from the constant webs only and similarly for the fluctuating webs. B, basal; I, intermediate; T, top.

Further evidence that fluctuating webs may be more severely constrained than constant webs is provided by comparing the standard deviations of characteristics of fluctuating and constant webs. Since the number of species in our sample of constant webs ranges from 11 to 33, while the number of species in our sample of fluctuating webs ranges from 3 to 33, we have, for the purposes of this comparison, removed from the sample of fluctuating webs those 13 webs with fewer than 11 species. Compared to the 19 constant webs, the remaining 30 fluctuating webs have smaller standard deviations of the number of: basal-intermediate links, basal-top links, intermediate-intermediate links, intermediate-top links, total number of links, basal species, intermediate species, top species, total species, predator species ($T + I$); and smaller standard deviations of the ratios: links per species, basal links ($L_{BI} + L_{BT}$) per basal species, intermediate links ($L_{BI} + L_{II} + L_{IT}$) per intermediate species, and top links ($L_{BT} + L_{IT}$) per top species. The 30 fluctuating webs were slightly more variable than the 19 constant webs only in the number of prey species ($B + I$).

DISCUSSION

According to our newly assembled data, the mean number of links L in a web is approximately proportional to the total number of species S . The coefficient of proportionality is ≈ 1.8559 with a standard deviation of 0.0740.

The hypothesis that the mean of L is proportional to S may be derived from empirical observations that the connectance C varies approximately inversely as S . The observation was first made by Rejmánek and Starý (4) in a collection of 31 plant-aphid-parasitoid webs and confirmed by Pimm (5, 6) in a sample of 18 miscellaneous webs, including those assembled by Cohen (3). Since C is approximately proportional to LS^{-2} , if C varies approximately as $1/S$ then L/S is approximately independent of S , or L is approximately proportional to S . (Conversely, if L is proportional to S , then C varies as $1/S$.) Pimm (ref. 5; ref. 6, p. 89) interpreted his empirical generalization as a consequence of a behavioral supposition: "Suppose each species in a community feeds on a number of species of prey that is independent of the total number of species in the community."

The alternative hypothesis, that some power of L between $1/2$ and 1 is proportional to S , may be new and is also not ruled out by the data.

The only prior explicit examination of the relation between L and S appears to be Briand's (ref. 2, p. 256, and his figure 2a) empirical finding, based on 40 "unlumped" webs, that $L = S^{1.1}$. He observed that this relation was "nearly linear."

Without presuming to discriminate between a power law exponent of 1.1 and one of 1.0, we find that Fig. 1, which is based on 62 lumped webs, confirms the approximate correctness of Briand's finding and is consistent with the hypothesis of Pimm, at least within the range of S , 3-33, covered.

That the mean of L is approximately proportional to S indicates that the trend of SC or L/S is roughly independent of variation in S . This may appear to contradict Briand's (ref. 7, p. 37) finding, based on a principal components analysis, that the product of species S times "upper connectance" is a major discriminator of variation among webs. However, upper connectance counts both links and "potential competitive links," and the latter increases as a nearly quadratic function of S (ref. 2, p. 256, and his figure 2b). Therefore S times upper connectance is much more variable among webs than is SC , since connectance C , as used here and in refs. 4-6, counts only links.

Links are more subject to errors of omission than are species, because a feeding interaction between a predator and

prey must be observed or inferred for a link to be recorded, whereas no special behavior need be observed for a species to be recorded. Consequently, future webs collected with more systematic attention to recording all links may yield larger estimates of c than that based on present data.

The likelihood of recording a link may vary more among observers than the likelihood of recording a species. Variability among observers in the probability of recording a link may explain why the above homogeneity tests for links, under the assumption of independence, reject the null hypothesis of multinomial sampling fluctuations with constant proportions.

The approximately linear relation in Fig. 3 between the expected number of links of each category and the geometric mean number of species in the source and sink categories appears to be new.

Earlier observations have suggested that fluctuating webs are more severely constrained in trophic structure than constant webs (1, 2). The finding here that fluctuating webs have significantly fewer basal-top links, and constant webs have significantly more basal-top links, than expected from a simple model based on pooled proportions, may be interpreted to be consistent with the earlier observations. Similarly, the standard deviations of many characteristics of constant webs exceed those of fluctuating webs.

CONCLUSION

Together, this paper and ref. 1 show that the main features of the structure of food webs—namely, the numbers of top, intermediate, and basal species and the numbers of links from each kind of predator to each kind of prey—all behave in quantitatively simple, interpretable ways as the number of species in webs ranges from 3 to 33. The data on which our quantitative generalizations are based are the most extensive and most carefully edited presently available. Nevertheless, because of variations among observers in field practices and definitions of concepts, the present generalizations will have to stand the test of more consistent and thorough field work in the future.

Our findings open at least three lines of further inquiry. First, how can these ecological generalizations be explained in terms of the behavior, genetics, and population dynamics of species, individually and in interaction? Second, do these ecological generalizations suffice to explain other significant features of food webs (3, 8, 9)? Third, what characteristics of individual communities account for their deviations from the overall trends?

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