Trophic links of community food webs
(scale invariance/predators/prey/directed graphs/constant and fluctuating environments)

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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 $L^{1/4}$ (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 $L_{Bj}$, $L_{Bt}$, $L_{It}$, and $L_{Tj}$ 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 $L_{Bj}/L$, $L_{Bt}/L$, $L_{It}/L$, and $L_{Tj}/L$. 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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for the 19 constant webs alone yields a $\chi^2$ of 510.3 with 54 df, while the same test for the 43 fluctuating webs alone yields a $\chi^2$ 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 $\chi^2$ 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 number of species at a level of resolution finer than that of Table 1. For example, suppose that the proportion of 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 $L_{BI}$ 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 vary, 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

$$p_{BI} = a_{BI}(BI)^{1/2}/[a_{BI}(BI)^{1/2} + a_{BT}(BT)^{1/2} + a_{IT}(IT)^{1/2} + a_{IT}(IT)^{1/2} + a_{IT}(IT)^{1/2} + a_{IT}(IT)^{1/2}].$$

Table 3 shows the predicted proportions of links of each category, based on the regression coefficients $a_{BI}$ 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 $\chi^2$ (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-
ably well with the observed; the discrepancy could be attrib­
uted entirely to sampling fluctuation.

However, this good agreement is not a strong confirma­
tion that the number of links of each category scales accord­
ing to the geometric mean rather than, say, according to the product. If, for example, in the above equations the regres­
sion coefficient of $L_{BI}$ against $BI$ is used and $(BI)^{1/2}$ is re­
placed by $BI$, and similarly for $BT$, $II$, and $IT$, then the pre­
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 $\chi^2$ 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 ob-
served than predicted. Among fluctuating webs, more basal–
intermediate and fewer basal–top links are observed than

<table>
<thead>
<tr>
<th>Type of unit</th>
<th>Constants</th>
<th>Fluctuating</th>
<th>All</th>
</tr>
</thead>
<tbody>
<tr>
<td>Webs</td>
<td>19</td>
<td>43</td>
<td>62</td>
</tr>
<tr>
<td>All species</td>
<td>351</td>
<td>683</td>
<td>1034</td>
</tr>
<tr>
<td>B</td>
<td>66</td>
<td>130</td>
<td>196</td>
</tr>
<tr>
<td>I</td>
<td>177</td>
<td>366</td>
<td>543</td>
</tr>
<tr>
<td>T</td>
<td>108</td>
<td>187</td>
<td>295</td>
</tr>
<tr>
<td>All links</td>
<td>811</td>
<td>1108</td>
<td>1919</td>
</tr>
<tr>
<td>B–I</td>
<td>198</td>
<td>327</td>
<td>525</td>
</tr>
<tr>
<td>B–T</td>
<td>92</td>
<td>56</td>
<td>148</td>
</tr>
<tr>
<td>I–I</td>
<td>260</td>
<td>318</td>
<td>578</td>
</tr>
<tr>
<td>I–T</td>
<td>261</td>
<td>407</td>
<td>668</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Type of Webs</th>
<th>Constant</th>
<th>Fluctuating</th>
<th>All</th>
</tr>
</thead>
<tbody>
<tr>
<td>B–I</td>
<td>0.2732</td>
<td>0.2561</td>
<td>0.2740</td>
</tr>
<tr>
<td>B–T</td>
<td>0.0685</td>
<td>0.0963</td>
<td>0.0791</td>
</tr>
<tr>
<td>I–I</td>
<td>0.2672</td>
<td>0.2966</td>
<td>0.2889</td>
</tr>
<tr>
<td>I–T</td>
<td>0.3911</td>
<td>0.3510</td>
<td>0.3579</td>
</tr>
</tbody>
</table>

The $x^2$ 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 species, basal-intermediate links, intermediate-top links, and top links. 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 $\approx 1.8559$ 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-insect-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, 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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