Community food webs have scale-invariant structure

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We have analysed 62 community food webs drawn from published studies and have found a remarkable regularity in ecosystem structure: in biological communities, the proportions of top, intermediate and basal species are, on average, independent of the total number of species. Hence, there is a direct proportionality between the numbers of prey and predators.

The finding[1] that, in community food webs, the ratio of prey to predators is 3:4 may be challenged on two grounds: first, it is based on a relatively small set of 14 webs, and second it may indicate that taxonomists have exercised greater taxonomic refinement in classifying organisms at higher than at lower trophic levels[2].

A community food web involves the feeding, that is, trophic, relations among all organisms found in a well-defined habitat by the original investigator. Organisms are separated into 'trophic species', which may be a single biological species, or a size class or stage in the life cycle of a single biological species, or a collection of functionally or taxonomically related biological species, according to the original report. Throughout this paper a 'species' refers to a 'trophic species', not necessarily to 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 community food webs analysed include 40 webs assembled and described by Briand[3]; of these, 13 are corrected and drawn from the 14 originally used by Cohen[1]. Details of the food webs not yet presented by Cohen[4] or Briand[3] will be published elsewhere (F.B., in preparation). We find that the number of prey is roughly proportional to the number of predators with a slope less than 1 (Fig. 1a). This is also true for webs from constant and fluctuating environments, although they are quite different in overall structure[3]. On the far right of Fig. 1a, four outliers emerge from the general relationship: a cluster of three constant food webs (C), all from Fryer's study[5] of littoral communities of Lake Nyasa, and one fluctuating food web (F) representing a salt meadow from New Zealand[6].

There can be no direct test of Pimm's conjecture[2] of why the slope is less than 1, without repeating the original field studies with a uniform attention to taxonomic detail. As an indirect test, we examined the ratio of prey to predators in the 62 food webs, after we had 'lumped' trophically identical species. That is, in each food web, whenever two or more species are preyed on by exactly the same set of predators, and prey upon exactly the same set of prey, we treated them as one. This procedure, which we call 'lumping', removes possible differences in the propensity to split, both among observers and among trophic levels.

Lumping moves the outliers into or much closer to the bulk of the remaining data points, for both fluctuating and constant webs (Fig. 1b). The correlation coefficient between numbers of predators and prey among the 43 fluctuating webs increases from 0.83 before lumping to 0.92 after, and from 0.58 to 0.64 among the 19 constant webs. In other words, eliminating predators or prey that are trophically identical tightens the relation between numbers of predators and prey.

Because individual observers tend to influence prey–predator ratios, we shall deal only with the lumped version of the webs. Because some observers contributed more than one food web to our collection, the assumption of independence that is required to justify attaching probability values to significance tests using the unlumped data is open to challenge. Though the assumption of independence is probably more acceptable with the lumped version of the webs, we shall base our statistical analysis primarily on descriptive statistics. Fortunately the patterns in the data are clear.

If a straight line, either with arbitrary intercept or through the origin, is fitted to a scatter plot of the 62 community food webs, the squared residuals increase with the number of predators. This reveals that the usual least-squares procedure, which assumes the variance of residuals constant regardless of the abscissa, is not appropriate to these data.
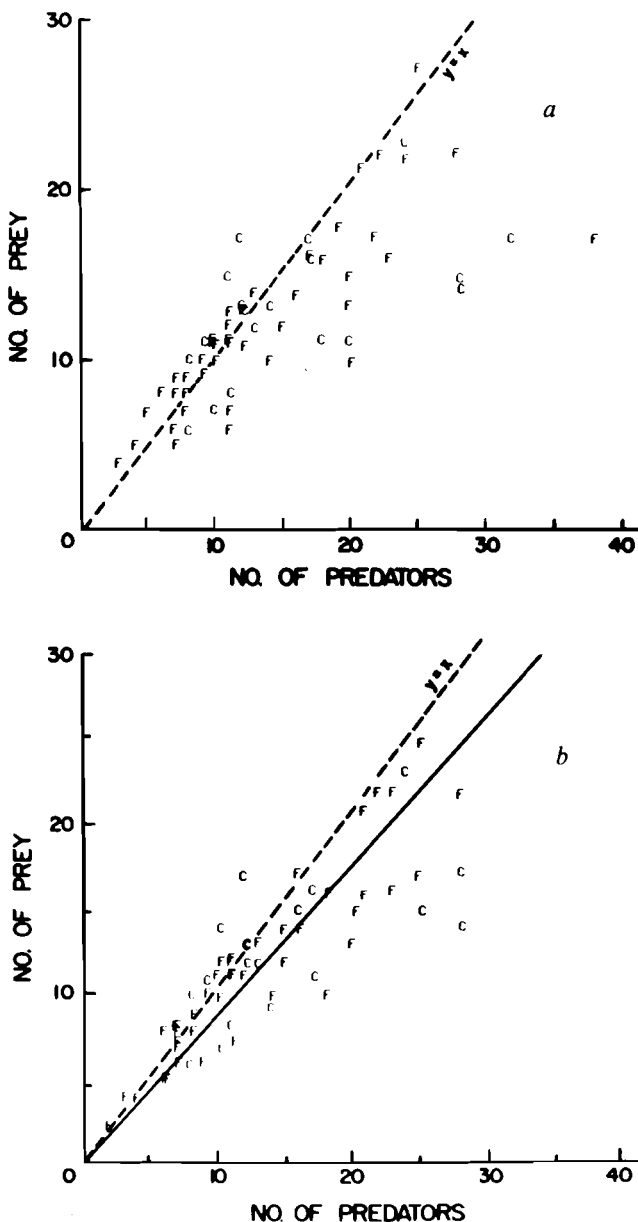

Fig. 1 Number of prey species as a function of number of predator species in 62 community food webs. F, fluctuating environment. C, constant environment. An environment is classified as 'fluctuating' if the original report indicates temporal variations of substantial magnitude in temperature, salinity, water availability, or any other major physical parameter. The magnitude, and not the predictability, of the fluctuations is the criterion of classification. The symbols F and C have been shifted from their exact locations by a small random amount to indicate when several food webs have exactly the same coordinates. *a*, Original data; *b*, after lumping. The solid line through the origin is fitted on the assumption that the variance of the residuals is proportional to the number of predators. The slope is 0.8819.
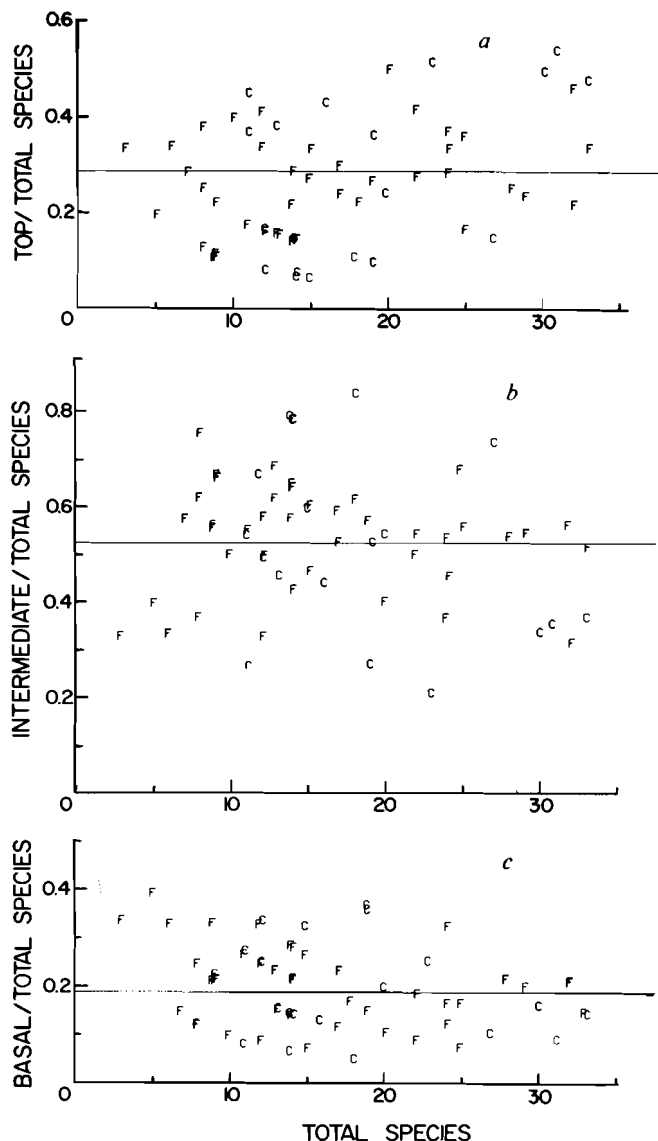
Fig. 2 Three ratios plotted as a function of the number of species. The fitted lines are constrained to be horizontal (slope = 0). *a*, Top species/total species. The height of the line is 0.2853. *b*, Intermediate species/total species. The height of the line is 0.5251. *c*, Basal species/total species. The height of the line is 0.1896.

If a regression line is fitted through the origin on the assumption that the variance of the residuals is proportional to the number of predators, then the estimator of the slope is simply the ratio of the mean number of prey divided by the mean number of predators. Under this assumption, a straight line through the origin fitted to all 62 food webs has slope 0.8819 or approximately 0.9.

This slope is higher than the slope near 0.75 found by Cohen[1], so there appears to be some merit in Pimm's suggestion[2] that ecologists have exercised greater taxonomic refinement at high trophic levels than at low. This suggestion, however, is not quantitatively sufficient to account for the excess, that remains after lumping, in the number of predators over the number of prey.

Classical ecological theory views predators as generally limited by resources, and the diversity of predators in particular as being limited by the diversity of prey. From this perspective it would seem more natural to treat the number of prey as an independent variable and the number of predators as a dependent variable. However, when the number of predators is regressed against the number of prey, using a straight line

through the origin with variance of residuals proportional to the abscissa, the standard error of estimate (with 61 degrees of freedom) increases from 3.1 to 3.5.

This observation means that the number of predators is a better predictor of the number of prey than the reverse. This raises the intriguing possibility that, in both constant and fluctuating environments, the number of predators is causally more important in controlling the number of prey than vice versa. Evidence and theory in favour of this suggestion have been independently reviewed by Jeffries and Lawton[7].

That we find a linear relationship between number of prey and number of predators is not too surprising, since the *x*- and *y*-axes share a similar quantity, namely the intermediate species, which are both prey and predators. What is surprising is the tightness of the fit, considering the size and heterogeneity of the sample examined. This suggests two possibilities: either the redundant variable, that is, the number of intermediate species, is very large compared with the number of basal and top species in most communities, or the proportions of all species in a food web that fall into each of these three categories are, overall, independent of the total number of species.

Figure 2 illustrates the reality of the second alternative: in the 62 webs examined, the fractions of top, intermediate and basal species are, on average, independent of the total number of species, although there is a slight tendency for the fraction of top species to increase and for the fraction of basal species to decrease as the total number of species increases. To obtain a global estimate of the proportions of species in each of the three categories (top, intermediate, basal), we summed over all food webs the observed numbers in each category, and divided by the sum total of species over all food webs. The global proportions of top, intermediate and basal species correspond to the heights of the horizontal lines in Fig. 2*a-c*.

The scatter of points about the horizontal lines in Fig. 2, when constant and fluctuating food webs are considered together, agrees with the hypothesis that in each food web the top, intermediate and basal species are multinomially sampled from the total species in proportions that are constant for all webs. If the species counts are arranged in a 3×62 contingency table with rows for top, intermediate and basal species and one column for each web, a homogeneity test yields a χ^2 of 138.9 with 122 d.f., which is not significant at the 0.1 level.

There is no evidence for a difference between constant and fluctuating food webs in the mean proportions of top, intermediate and basal species. A homogeneity test of a 3×2 contingency table with rows for top, intermediate and basal species and columns for constant and fluctuating food webs, and the summed species counts as cell entries, gives a χ^2 statistic of 1.4 with 2 d.f., which is not significant at the 0.1 level.

However, the proportions of top, intermediate and basal species in constant food webs, considered separately, are significantly more variable, and the proportions in fluctuating food webs, considered separately, are significantly less variable, than expected from multinomial sampling (using a 0.02 significance level). Separate homogeneity tests of the constant webs (in a 3×19 contingency table) and of the fluctuating webs (in a 3×43 contingency table) yield χ^2 of 82.8 with 36 d.f. and 56 with 84 d.f., respectively. The visual counterpart of this statistical result is the appearance in each panel of Fig. 2 of fluctuating food webs near the horizontal line and of constant food webs scattered above and below the band of fluctating webs. Food web structure appears more constrained in fluctuating than in constant environments, as previously noted[3,8].

We now show that the empirical regularities in Fig. 1*b* can be derived from the approximate scale-invariance shown in Fig. 2.

Let S be the total number of species in a single community food web, T the expected number of top species in that web, I the expected number of intermediate species, B the expected number of basal species, R the expected number of predators and Y the expected number of prey. By definition

$$S = T + I + B \qquad (1)$$

$$R = T + I \qquad (2)$$

$$Y = I + B \qquad (3)$$

By observation

$$T/S = p \quad \text{or} \quad T = pS, \qquad \hat{p} = 0.2853 \text{ (Fig. 2a)} \qquad (4)$$

$$I/S = q \quad \text{or} \quad I = qS, \qquad \hat{q} = 0.5251 \text{ (Fig. 2b)} \qquad (5)$$

$$B/S = r \quad \text{or} \quad B = rS, \qquad \hat{r} = 0.1896 \text{ (Fig. 2c)} \qquad (6)$$

Adding equations (5) and (6) and dividing by the sum of equations (4) and (5), we recover the observed regularity (Fig. 1b)

$$Y/R = a \quad \text{or} \quad Y = aR, \qquad a = (q+r)/(q+p) \qquad (7)$$

The predicted value $(\hat{q}+\hat{r})/(\hat{q}+\hat{p}) = 0.8819$ is identical to the observed $\hat{a} = 0.8819$ because of the formulas we used to estimate the slope a and the proportions p, q and r. However, the observation in Fig. 1b that the average number of prey is a linear function of the number of predators is not a tautologous consequence of the estimation formulas. The proportionality of prey to predators follows from the scale-invariance we have discovered here. Were data available, it would be interesting to examine whether the distribution of biomass into top, intermediate and basal species is also scale-invariant.

We conclude that the values of any two of the three parameters p, q and r summarize succinctly a substantial amount of information about the empirical regularities found in community food webs and provide a factually grounded benchmark against which the deviations of particular food webs may be measured. Why these proportions take the values they do and why the proportions are scale-invariant remain open questions.

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