CONSTANT CONNECTANCE IN COMMUNITY FOOD WEBS

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Abstract.—The constant connectance hypothesis states that among community food webs, trophic links increase approximately as the square of the number of functionally distinct or "trophic" species. This hypothesis is corroborated by the following analysis of 175 community food webs (2–93 trophic species), which shows that the exponent of the link-species relationship is approximately two. This scaling contradicts the widely accepted link-species scaling law, which asserts that links increase linearly with the number of species and that the link-species exponent is one. My results combined with related findings regarding food chain lengths indicate that large food webs have many more links and much longer food chains than previously suggested.

Quantitative food web analysis is an active and controversial area of theoretical ecology (May 1983; Strong 1988; Lawton 1989; Cohen et al. 1990). One of the most basic and frequently cited quantitative food web patterns is the variation of the number of trophic links with the number of species in a web (May 1983; Strong 1988). Although it is clear that links increase with species (Cohen and Briand 1984), the rate of this increase is not clear (Martinez 1988, 1991a; Paine 1988; Schoener 1989; Pimm et al. 1991). Furthermore, some ecologists (e.g., Paine 1983, 1988) state that such patterns do not even warrant interpretation due to the poor-quality data used, whereas other ecologists have elevated a hypothesis regarding the variation of links with species to the status of an ecological "law" (Cohen et al. 1990).

A primary goal of quantitative food web research is to find universal quantitative patterns in food webs. Such patterns may lead to the discovery of fundamental principles of ecology (May 1983, 1988; Cohen 1989). This article describes a pattern that is a universal description of an intermediate state of trophic complexity in food webs. This state exists between two theoretically possible extremes rarely if ever seen in nature. One extreme is a community of only pervasive, voracious, and cannibalistic predators in which each species eats every species in a community. The other extreme is a community in which each species consumes no species (e.g., a community of only nonpredacious plants). The balance between these extremes appears to affect basic patterns in ecosystems including the length of food chains (Newman and Cohen 1986; Briand and Cohen 1987) and the reported scale invariance of quantitative food web patterns (Briand and Cohen 1984; Cohen and Briand 1984; Sugihara et al. 1989). The following definitions have been useful in examining this balance.

A trophic species web, from now on called "web," refers to a community food web...
web (Cohen 1978) that describes the trophic links among trophic species in a certain location. Trophic species, or “species,” are groups of organisms that appear to have identical sets of predators and prey (Briand and Cohen 1984) in a food web. Trophic links, or “links,” are feeding interactions directed from prey to their identified predators within a defined location. The constant connectance hypothesis states that among community food webs, the number of links in a web increases approximately as the square of functionally distinct or “trophic” species (Martínez 1988, 1991a).

The link-species scaling law (Cohen and Newman 1985), originally based on 62 webs with 3–33 species (Cohen and Briand 1984), states that on the average the number of links \( L \) per species \( S \) in a web is constant and scale invariant at roughly two (i.e., \( L/S = 2 \) or \( L = 2S \); fig. 1) (Cohen and Newman 1988; Cohen et al. 1990). In other words, this convention maintains that species are linked to
a constant number of species independent of how many species are in the community (Pimm 1982; Cohen and Briand 1984; Pimm et al. 1991).

Yet, the alternative advanced here may be more plausible. Consider a species of insectivorous birds that occupies two communities, A and B. Assume that A has twice the number of insect species as B. One might expect that the birds of this species in A would eat twice the number of species as those birds in B. Generalizing this situation to whole communities, one might expect that the average number of each predator’s prey increases roughly in proportion to the number of species in the community. This expectation may be called the constant connectance hypothesis. It states that on the average species are linked to a roughly fixed fraction of the species in webs (i.e., \( L/S \approx kS \) or \( L/S^2 = k \), where \( k = \) a constant; fig. 1) (Martinez 1988, 1991a).

Connectance is the proportion of all possible interactions within a system that are realized (Gardner and Ashby 1970). Directed connectance \( (L/S^2) \) (Martinez 1988, 1991a) is the proportion of observed links to all possible links, including cannibalism and mutual predation (Polis 1991), within a food web. If webs display constant directed connectance, then on the average a fixed fraction of all possible links in a web is realized independent of the number of species in the community.

QUANTITY AND QUALITY OF THE DATA

I evaluated the link-species scaling law and the constant connectance hypothesis using 175 webs with 2–93 trophic species. This set includes 113 webs gathered by Briand and Cohen (Cohen et al. 1990), 60 webs gathered by Schoenly et al. (1991; Sugihara et al. 1989), and two additional webs. The set of 113 webs includes the 62 webs on which the link-species scaling law was originally based (Cohen and Briand 1984; Cohen and Newman 1985). This is the largest set of community food webs to date, both in number of webs and in the range of \( S \), employed to address the relationship between \( L \) and \( S \). Briand and Cohen gathered 113 of the webs with 3–48 species (\( \bar{X} = 17 \)) from published and unpublished reports describing trophic relations in a wide range of aquatic and terrestrial ecosystems (Cohen 1978; Briand 1983; Cohen and Briand 1984; Briand and Cohen 1987). Schoenly et al. (1991; Sugihara et al. 1989) collected the 60 invertebrate-dominated webs that contain 2–54 trophic species (\( \bar{X} = 12 \)) from similar sources. Since the taxa in these 60 webs were not yet aggregated into trophic species, it was necessary to aggregate the 60 webs into trophic species webs for this analysis. Typically, the original sources of these data are reports describing trophic relations among a small group of unevenly aggregated organisms within an ecosystem (May 1983, 1988; Martinez 1988, 1991a; Paine 1988; Lawton 1989; Cohen et al. 1990). The objectives of these investigations rarely included quantitative food web analysis (Paine 1988).

One of the two additional webs is a large 42-species web that integrates many years of fieldwork on the Caribbean island of St. Martin for the purpose of examining quantitative food web patterns (Roughgarden, in press; L. Goldwasser and J. Roughgarden, personal communication). The other is the largest and possibly the most complete and evenly resolved web to date. This web of Little Rock
Lake, Wisconsin (Martinez 1988, 1991a), was originally documented to accurately portray the relatively complete trophic structure of a natural ecosystem. It was constructed from descriptions of the trophic habits of 182 taxa provided by nine field ecologists who specialize in and study organisms within the Little Rock Lake ecosystem. The Little Rock Lake web, with 93 trophic species from all trophic groups (producer, consumer, and decomposer), is relatively evenly aggregated among trophic groups. The web describes the lake's trophic structure before experimental acidification (Watras and Frost 1989).

Several problems with these data have been reported (May 1983, 1988; Paine 1983, 1988; Strong 1988). Aggregation of taxa in the original reports is highly variable (May 1983; Paine 1988). Even after aggregation of taxa into trophic species, much of this variability remains. Fortunately for this analysis, connectance appears to be one of the food web statistics least affected by varying the degree of aggregation within a web except in the smallest webs where aggregation tends to increase connectance (Martinez 1988, 1991a). Several authors of the 175 webs contend that \( L \) is generally underrepresented in webs with large \( S \) because only the most important links are included in large webs (Cohen and Briand 1984; Cohen and Newman 1988; Martinez 1988, 1991a; Paine 1988). In webs with small \( S \), it is convenient to more accurately and completely document \( L \) (Cohen and Newman 1988; Paine 1988). When food webs with high \( S \) are constructed explicitly avoiding this bias, relatively high \( L \) is consistently observed (Hildrew et al. 1985; Martinez 1988, 1991a; Warren 1989; Winemiller 1989; Polis 1991; Roughgarden, in press).

**ANALYSES**

Assuming a simple relationship (Cohen and Briand 1984) in the form of \( L = \alpha S^\beta \) (where \( \alpha \) and \( \beta \) are constants), we can see in figure 1 that if \( L = \alpha S^\beta \) is valid for very large \( S \), the true \( \beta \) must lie within the range of one (link-species scaling law) and two (constant connectance hypothesis). The artifact of small \( L \) in webs with large \( S \) artificially reduces the observed \( \beta \) of the link-species relationship (fig. 1). A log-log regression of the 175 webs estimates \( \beta = 1.54 \) (SE\(_{\text{Slope}} = 0.03, R^2 = 0.93; \) all regressions are simple least-squares regressions). Despite the bias toward low \( \beta \), 1.54 is significantly higher \((P = .001)\) than the exponent asserted by the link-species scaling law (Martinez 1988; Schoener 1989). Consistent with the bias, 1.54 is significantly lower \((P = .001)\) than the exponent asserted by the constant connectance hypothesis. Additionally, the link-species scaling law predicts only 82 of the 206 links in the St. Martin web and 173 of the 1,036 links in the Little Rock Lake web, whereas the constant connectance hypothesis much more accurately predicts \( L \) in these two webs (fig. 1). The constant connectance hypothesis also fits the observed \( L \) in small webs \((S < 8)\) by accurately predicting \( L \) to within three-quarters of a link \((0.76)\) of that observed (fig. 1). In contrast, the link-species scaling law consistently overestimates \( L \) in these webs by predicting 2.8–3.7 more links than observed (fig. 1).

An analysis of 12 of the 175 webs containing the full range of 2–93 trophic
species ($\bar{X} = 18$) supports the constant connectance hypothesis over the link-species scaling law (fig. 2). This set of 12 webs includes the St. Martin and Little Rock Lake webs plus five food webs in pitcher plants in Malaysia, Sri Lanka, Madagascar, and Seychelles (Beaver 1985), four food webs from tree holes in Alabama and Germany (Kitching and Pimm 1985), and a tree-canopy food web in western Europe (Rejmánek and Starý 1979). These mostly invertebrate-dominated webs are objectively distinguished by the enumeration of $L$ in the original reports describing these webs. This distinction appears to be a substantial improvement over the inclusion of webs described by reports in which $L$ is so peripheral that it is not enumerated in the report. Therefore, these 12 webs appear to be more suitable for this analysis than the full set of 175 webs. The log-log
regression of these 12 webs estimates $\beta = 1.73$ (SE$_{\text{slope}} = 0.09$, $R^2 = 0.98$). Two of the 12 webs contain only two species and one link and therefore may be considered too trivial for inclusion in the analysis. If these two webs are excluded from the regression, one can estimate that $\beta = 1.78$ (SE$_{\text{slope}} = 0.12$, $R^2 = 0.96$).

A similar regression analysis by Sugihara et al. (1989) recently excluded all food webs with 10 or fewer taxa to "avoid obvious artificial biases that must occur in very small webs" (Sugihara et al. 1989, p. 50). Such biases have been previously demonstrated in one of Sugihara et al.'s references (Martinez 1988), especially with regards to connectance. When webs with less than 10 species are excluded from this 12-web subset, the log-log regression of the remaining five webs estimates $\beta = 2.04$ (SE$_{\text{slope}} = 0.26$, $R^2 = 0.95$).

Recently, an additional set of 12 community food webs has been described (Hildrew et al. 1985; Warren 1989; Polis 1991) that contain 12–32 taxa ($\bar{X} = 25$) that are not yet aggregated into trophic species. I did not aggregate these webs because they were not available in a standardized form capable of being machine-readable. Both hypotheses examined here attempt to explain the relation between links and species only in trophic species webs. Therefore, interpretation of these new data should be tempered because these data are not within the strict domain of these hypotheses. Still, this recent set of 12 community webs is of high quality and was originally constructed from field experience and field data to examine quantitative food web patterns. The log-log regression of these 12 webs estimates $\beta = 2.18$ (SE$_{\text{slope}} = 0.21$, $R^2 = 0.92$). Winemiller (1989) and Warren (1990) have also noted tendencies toward constant connectance among nontrophic species webs.

**DISCUSSION**

These regressions of the sets of 12 trophic species webs and the other 12 community food webs corroborate both the constant connectance hypothesis and the reported bias (Paine 1988) of the 163 generally less germane webs. The regression of the 12 "unlumped" community webs also suggests that the constant connectance hypothesis may apply to community food webs other than trophic species webs.

These results require rejection of the link-species scaling law, which should now be termed a hypothesis rather than a law. The reported bias in the data and the above analyses suggest that the true exponent is well above 1.54 but may not be above 2 over a large range of S. New high-quality webs with large S and containing only trophic species are needed to distinguish between exponents in this range. Pending such data, the constant connectance hypothesis may be accepted because it is consistent with the bulk of the webs, the reported bias of the webs, and especially the most credible of the 12 more pertinent food webs. The variation (fig. 1) and problems in the data—for example, limited range of S (Paine 1988; Lawton 1989)—plus the sensitivity of $\beta$ to the choice of data sets suggest that specification of $\beta$ to two significant digits is unwarranted. Therefore, my primary argument is that the true exponent ($\beta$) is much closer to two than to one.

If $\beta$ is assumed to equal two, then $\alpha (\alpha = k)$ can be very roughly estimated to
be the mean directed connectance of the 175 webs \( \pm 1 \text{ SD} \) (0.14 \( \pm 0.06 \) or 0.08–0.20). The mean directed connectance of the 12-web subset is similar at 0.16 (SD = 0.06). Given the bias toward high connectance in small webs (Martinez 1988, 1991a), the most defensible estimate may be the mean directed connectance of the five directly constructed webs with more than 10 species (\( \bar{X} = 0.11, \text{ SD} = 0.03 \)).

The log-log regression of 163 webs, excluding the 12-web subset (fig. 2), estimates \( \beta = 1.49 \) (SE_{slope} = 0.04, \( R^2 = 0.91 \)). The difference between \( L \) predicted by the regression of 163 webs (0.46\( S^{1.5} \)) and the constant connectance hypothesis (0.14\( S^2 \); fig. 1) may be attributed to investigators’ missing a proportion of links in webs with \( S > 10 \) roughly equal to \( 1 - 3.35^{-0.5} \). In other words, if the probability of recording a link declines among the 163 webs with \( S = 20, 30, 40, \) and 50 by factors of 0.74, 0.61, 0.53, and 0.47, respectively, then the true \( L \) in these webs closely fits the constant connectance hypothesis. Cohen and Newman (1988) propose that dynamic links are similarly but more severely underestimated as a decreasing function of \( S \). They hypothesize that this bias, estimated to be a factor of 0.1 in webs with \( S = 50 \), is due to incomplete observation of links in webs with large \( S \). Additionally, the difference between \( L \) suggested by the 163 webs and the constant connectance hypothesis is consistent with Paine’s (1988) “artistic convenience” hypothesis that \( L \) in large webs is underestimated due to the difficulty of graphically recording \( L \) in large webs. Use of predation matrices avoids many of the problems of artistic convenience (Cohen et al. 1990). A predation matrix contains a nonzero element wherever a predator, represented by a matrix column, consumes a prey represented by a matrix row. Such a representation of a food web requires much less effort to document links in large webs than do verbal and graphic food web representations. Yet, predation matrices are rarely used by original investigators to describe food webs. Also, accurate observation and documentation of \( L \) are usually not priorities of original food web studies (Paine 1988). The effort of both investigating and either graphically or verbally documenting \( L \) thus decreases the probability of recording a link in large webs much more than in small webs. The hypothesis that \( \beta \approx 2 \) is consistent with the number of links being underestimated in large indirectly constructed webs. Also, \( \beta \approx 2 \) suggests that the number of links in webs more directly constructed for the purpose of quantitative food web study (e.g., the subset of 12 trophic-species webs) is estimated relatively accurately.

Webs may have constant \( L/S^2 \) due to a balance of species-level and community-level constraints (O’Neill et al. 1986, 1989) on trophic niches. Species-level constraints are determined by how physiology (e.g., mouth parts, digestive capabilities) and behavior (e.g., mobility, temporal activity) affect which organisms a species can eat or be eaten by. Community-level constraints are determined by the distribution of capabilities to capture prey and avoid predators (Schoener 1989) among species in the community. The balance of these constraints may plausibly determine \( L \).

If species on the average eat a fixed fraction of everything in the range they can eat and the number of species falling within this range is proportional to the

Eventually, the extent of data will expand (O’Neill et al. 1986, 1989) to include several habitats such as lakes, streams, and forests in one web. In such data, we may find that environmental heterogeneity constrains trophic relationships in the web (Pimm and Lawton 1980) to some threshold below $L/S^2 \approx 0.08-0.20$ but well above two links per species. This raises the possibility that instead of being constants, $\alpha$ or $\beta$ may be functions of observation variables such as spatial and temporal scale (O’Neill et al. 1986, 1989; Paine 1988; Warren 1989) and ecological variables such as habitat heterogeneity (Pimm and Lawton 1980), environmental disturbance (Briand 1983), productive space (Schoener 1989), community type (Briand 1985; Schoener 1988; Lawton 1989), and even $S$.

Despite these possibilities, roughly constant connectance within relatively homogeneous environments, where the vast majority of species within a community can travel, is difficult to reject. Constant connectance is intuitively more consistent than the link-species scaling hypothesis with field observations of predators consuming over 100 species of prey in species-rich communities (Polis 1991). This consistency occurs because $L/S^2 \approx 0.08-0.20$ forces food webs with $S > 30$ toward much higher $L/S$ than if $L/S = 2$ (fig. 1). It should be emphasized that hypotheses of link-species scaling are field testable via diet comparisons of species that occupy different communities with a wide range of species richness (R. Dial, personal communication). The variations of a species’ diet breadth with community species richness may further illuminate the relationship between $L$ and $S$.

Warren (1990) also argues a hypothesis similar to $\beta = 2$. However, I suggest that webs are more tightly constrained toward a lower value of connectance than Warren suggests. Data collected by Winemiller (1990) suggest that the constant connectance hypothesis is still valid when links accounting for less than 5% of a predator’s diet are excluded. Therefore, constant connectance does not appear to be an artifact of including rarer links as webs get larger.

If $\beta \approx 2$ or even just 1.5, then $L/S$ increases as a fixed proportion of $S$ or $S^{0.5}$,
respectively. Such increases in $L/S$ have important ramifications regarding the length of food chains. This is demonstrated by the following analysis of mean chain length or the mean number of links in every possible chain connecting prey without prey to predators without predators, among the 175 webs. When mean chain length ($y$) is regressed as a function of $L/S$ ($x$) among the 175 webs, the result is $y = 0.68x + 1.4$ (SE$_{\text{slope}} = 0.06$, $R^2 = 0.47$, $P < .001$). A similar analysis of the 12-web subset yields $y = 0.70x + 1.0$ (SE$_{\text{slope}} = 0.04$, $R^2 = 0.97$, $P < .001$). Though these increases are significant, they are less than half the rate of $2 \cdot L/S$ suggested by the cascade model (Newman and Cohen 1986). Of course, the logical extension of these results is that mean chain length significantly increases with $S$. The highly significant positive slopes of the regressions of the 175-web set ($y = 0.048S + 1.9$; SE$_{\text{slope}} = 0.006$, $R^2 = 0.25$, $P < .001$) and 12-web subset against $S$ ($y = 0.084S + 1.1$; SE$_{\text{slope}} = 0.004$, $R^2 = 0.98$, $P < .001$) confirm this extension.

Contrary to convention (Pimm 1982; Briand and Cohen 1987; Sugihara et al. 1989), these findings demonstrate a significant positive relationship between mean chain length and $S$. These findings also suggest that large food webs have much longer food chains (Martinez 1988, 1991a, 1991b) than currently appreciated (Pimm 1982; Newman and Cohen 1986; Lawton 1989). In fact, constant connectance and the above regression coefficients of mean chain length as functions of $L/S$ and $S$ suggest that food webs with 200 species have $L/S \approx 20–30$ and mean chain lengths of 10–20. Such long food chains are important because they may increase the susceptibility of communities to bioaccumulation of toxic pollution (Martinez 1988, 1991a).

CONCLUSION

The widely accepted link-species scaling hypothesis (Gardner and Ashby 1970; Pimm 1982; May 1983, 1988; Cohen and Newman 1988; Sugihara et al. 1989; Cohen et al. 1990; Pimm et al. 1991) and scale-invariant, limited chain length pattern are shown to be false and may be merely inaccurate abstractions from low resolution data (Martinez 1988, 1991a, 1991b; Paine 1988; Lawton 1989). A sensitivity analysis of the effects of resolution on these patterns in the Little Rock Lake web (Martinez 1988, 1991a) and in 11 of Schoenly et al.'s (1991) largest webs supports this interpretation (Martinez 1991b). Invalidation of the link-species scaling hypothesis equivalently invalidates the hyperbolic connectance pattern (Rejmánek and Stary 1979; Cohen and Newman 1988) and a basic assumption of the cascade model (Cohen and Newman 1985, 1988), which predicts the numbers and distributions of links, species, and chain lengths in webs.

Before developing more food web models, we should critically reexamine quantitative food web patterns by directly constructing relatively complete and evenly resolved food webs from the field rather than from the literature (Hildrew et al. 1985; Martinez 1988, 1991a; Warren 1989; Winemiller 1989; Polis 1991; Roughgarden, in press). Then we could decide more clearly that certain patterns are ecological attributes worth modeling and other patterns are artifacts to be avoided (Martinez 1988, 1991a, 1991b; Lawton 1989).
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LITERATURE CITED


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