



Must Connectance Decrease with Species Richness?

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NOTES AND COMMENTS

MUST CONNECTANCE DECREASE WITH SPECIES RICHNESS?

Over the past decade, considerable discussion has revolved around May's (1972) hypothesis that increased community complexity, in the form of greater numbers of pair-wise species interactions, reduces local (Lyapunov) stability in the absence of compensatory reductions in the average strength of ecological interactions (reviews in May 1975; Pimm 1982, 1984; Auerbach 1984; Kikkawa 1986). Central to the argument is May's formula defining stable regions of parameter space for randomly constructed systems,

$$s(Cm)^{-1/2} < 1,$$

where s is the average interaction strength, C is food-web connectance, and m is species richness. *Connectance* is the number of observed pair-wise interactions expressed as a fraction of the total number of interactions possible in an $m \times m$ matrix. Connectance can be defined as

$$C = k/(m - 1),$$

where k is the average number of observed interactions per species, and intraspecific effects are not considered. A number of authors challenged May's result as a general phenomenon of questionable relevance to natural communities, given their nonrandom structure (DeAngelis 1975; Gilpin 1978; Lawlor 1978; McNaughton 1978; Auerbach 1979; Tregonning and Roberts 1979; Yodzis 1981) and difficulties of relating stability in the mathematical sense to alternative definitions of community stability, such as resilience and persistence (Pimm 1979, 1984). Some randomly constructed community matrices actually exhibit positive relations between C and m when biologically feasible constraints are imposed (DeAngelis 1975; Lawlor 1978).

Although issues of community complexity and stability are in their infancy and far from resolved, theory tenacity and confirmation bias (Loehle 1987) appear to have already taken hold. Several tests of May's hypothesis have been performed using published real food webs as the data base. In all cases, an inverse relation between C and m was consistent with May's basic model (Rejmánek and Stary 1979; Yodzis 1980; Pimm 1982; Briand 1983; Auerbach 1984; Cohen et al. 1985). Lawlor (1978) showed that if the product Cm is held constant, the probability of encountering a locally stable community from a universe of randomly constructed

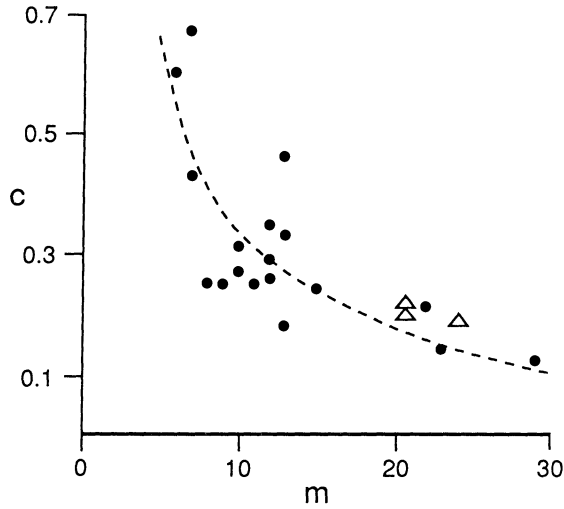


FIG. 1.—Three qualitative food webs (*triangles*, tropical fish and desert lizards) plotted on Pimm's (1982) distribution of connectance (C) by species richness (m) for real food webs (*dots*).

systems increases. Rejmánek and Stary (1979) found that plant-aphid-parasitoid communities exhibit a hyperbolic relation corresponding to $Cm = 3$, and Pimm (1982) obtained $Cm = 3.1$ for published food webs (fig. 1). Briand (1983) and Auerbach (1984) argued that $Cm = 2$ represents the limit for minimally connected food webs. May's hypothesized inverse relation between food-web connectance and species richness (i.e., for unchanging average interaction strength) and empirical support for the hypothesis of Cm constancy have gained considerable popularity in general treatments of community ecology (e.g., Begon et al. 1986; Kikkawa 1986).

General acceptance of the notion of Cm constancy has occurred despite virtual absence of critical evaluations of the empirical data, which, in all instances, were gleaned from diverse ecological literature. Paine (1980, 1983, 1988) expressed skepticism that connectance values based on food-web graphs taken from the literature could have any ecological meaning. His objections were based on the highly subjective nature of published food-web drawings, resulting from differences in (1) criteria for the inclusion of species owing to differential commonness or apparency, (2) levels used for defining food-web units (e.g., biological species, higher taxa, or "trophospecies"), (3) temporal and spatial scales of communities studied, and (4) personal idiosyncracies in editing food webs. Paine (1988) also recognized a common practice (referred to as "artistic convenience") of drawing a greater fraction of the estimated or observed links in species-poor webs relative to species-rich webs. Paine noted that this practice alone might yield constancy in the product Cm , as well as the constant predator-prey ratio (4:3) noted by Cohen (1978) and Briand and Cohen (1984). Moreover, a constant value of Cm assumes a constant threshold for average strength of pair-wise species interactions for sta-

bility according to May's model. Yet, how does one test for it? Estimates of the magnitude of all interspecific interactions would be exceedingly difficult to achieve for any natural assemblage of organisms. In addition, Pimm (1982) discussed the common practice of defining smaller species positioned near the base of food webs at higher taxonomic levels than larger species positioned near the top. Given the subjective, highly qualitative nature of empirical support for the stability model, ought we proceed in further elaboration of this line of theoretical reasoning without more-critical empirical testing of the assumption of Cm constancy (Paine 1983, 1988; Auerbach 1984)?

I examined food-web properties of tropical aquatic communities at four sites over the course of an annual cycle (Winemiller 1987). Two of the sites are located in the western llanos in the state of Portuguesa, Venezuela. The region receives approximately 2.0 m of rainfall annually, most of which falls during four consecutive months. Eighty-three fish species were collected at Caño Maraca, a swamp/creek of the Río Apure–Río Orinoco drainage. The other Venezuelan site, Caño Volcán, is a small stream of the low Andean piedmont located on the fringe of the llanos. Twenty fish species were collected at Caño Volcán during the course of the study. Two other sites are located in Parque Nacional Tortuguero in the Limón province of Costa Rica's Atlantic lowlands. This region receives between 3.5 and 5.0 m of rainfall annually, with two brief dry seasons during March–May and September–October in most years. Fifty-six species were collected at Caño Agua Fría Viejo, a shallow, broad creek that flows through swamp/rain forest. Twenty-three fish species were collected from Quebrada, a small forest creek flowing into the Laguna Tortuguero.

Stomach-content analyses were performed on large numbers of fish specimens at each locality (total $N = 9950, 4222, 3040, 2078$). The volumetric fraction of each prey category in a consumer's diet (p_{ij}) was employed as an estimate of relative strength of the predator-prey interaction. Whenever possible, fish prey were identified to species and invertebrates to order (usually) or family (rarely). Unidentified fishes were not included in food webs; unidentified insects were grouped into either of two categories, miscellaneous aquatic and terrestrial insects. Operational taxonomic units at the base of food webs were defined as diatoms, desmids, filamentous algae, *Chara* species (algae), aquatic macrophytes, terrestrial plants (nonreproductive tissues), fruits and associated seeds, flowers, independent seeds, plant spores, silty detritus, coarse mixed detritus, and vegetative detritus. Although accuracy and objectivity are compromised by limited ability to identify all prey at the species level and to estimate feeding rates in any attempt at food-web quantification, data from each of these tropical systems were collected and handled in an identical manner. This uniformity of methods and criteria employed by a single investigator should result in less biased between-web comparisons relative to comparisons based on diverse literature sources.

By defining the universe of the food web in different ways, diet data taken over the course of a year could be used to produce several legitimate food webs from the same study site. First, each system was divided into seasonal (wet, dry) and combined-annual food webs. Second, the community occurring at a site was de-

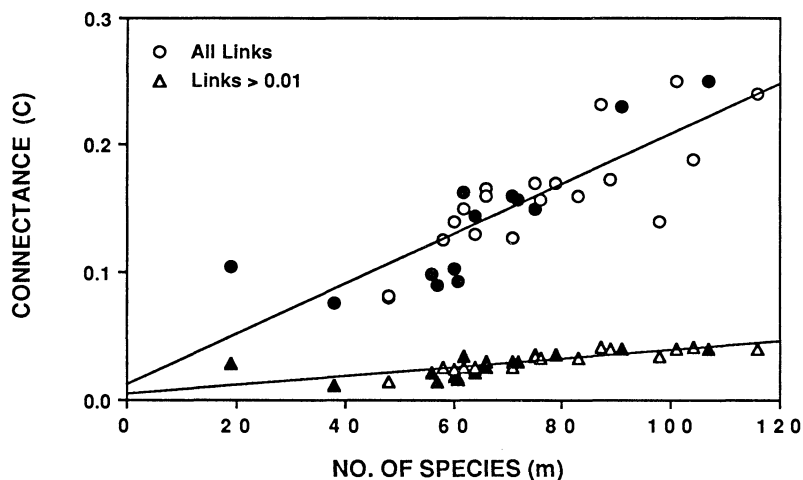


FIG. 2.—Relation between food-web connectance and species richness for 34 food webs derived from four tropical fish study systems. *Solid symbols*, Top-predator sink webs. Regression equations and statistics are given in the text.

finned as either the “total” (all species except rare ones with a sample size of one or two) or “common community” (only the most common species contributing to 95% of the total number of individual fishes collected during the sampling period). Food webs were assembled as either the complete web or the top-predator sink web, the former defined by the assemblage of fishes collected at a site, and the latter defined as an assemblage consisting of the top predator, all of its prey, all of the prey’s prey, and so on. Finally, connectance was calculated using all observed trophic links or excluding all weak trophic links represented by $p_{ij} < 0.01$.

Food-web connectance is *positively* associated with species richness for food webs containing all trophic links (fig. 2; $C = 0.002m + 0.011$; $r = 0.83$; $F = 72.3$; $df = 1, 32$; $P < 0.0001$). A similar but less pronounced trend was obtained for webs containing only strong interactions ($C = 0.0003m + 0.004$; $r = 0.79$; $F = 52.1$; $df = 1, 32$; $P < 0.0001$). Both regression slopes differ significantly from zero ($t = 8.5, 7.2$; $df = 33$; $P < 0.0001$) and from one another (ANCOVA $F = 395.9$; $df = 1, 64$; $P < 0.0001$). Several factors appear to account for this result, which contrasts with previous findings for real food webs. First, all of my tropical aquatic connectance values were comparatively low. Connectance in all cases fell below 0.3, whereas a number of published food webs greatly exceeded 0.3 (most of the latter occur at $m < 20$). Low connectance in my webs was due primarily to the use of only fishes as consumers. As species richness of food webs increased, the ratio of fish nodes to interactive non-fish prey also increased to some extent. Differential grouping of species into higher taxonomic categories probably affects these ratios in my webs just as those reported by others previously. When connectance was recalculated using $k = 3$ as a crude estimate of average diet breadth for non-fish consumer nodes, C increased by an average of 0.055 (range

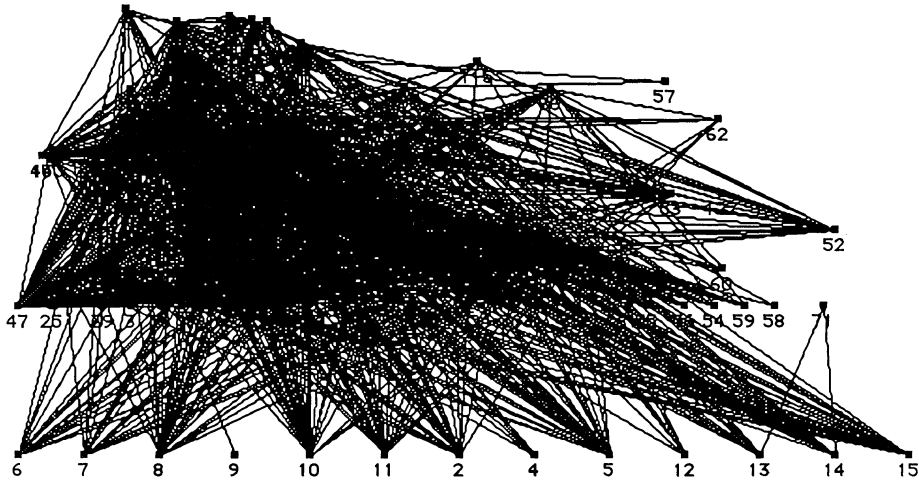


FIG. 3.—Computer-generated food-web digraph for Caño Maraca, Venezuela, based on the total-community, wet-season resource matrix (72 predators \times 113 prey). Numbers identify individual operational taxonomic units. Consumers were assigned vertical positions by trophic level calculated from the trophic-continuum algorithm of Adams et al. (1983). Nodes 2 through 15 are primary producers and detritus. Consumer horizontal positions were also calculated hierarchically from bottom to top based on the fraction of aquatic (*left*) versus terrestrial (*right*) sources of primary production in diets (consumed either directly or indirectly via heterotrophic prey). Trophic links are represented as undirected lines between predator and prey. Lines were drawn with a uniform width for all nonzero links (i.e., all $p_{ij} \neq 0$ drawn as if equal).

of new C values = 0.16–0.28). These webs also yielded a positive regression of C with m , but with more scatter ($C = 0.001m + 0.145$; $r = 0.52$; $F = 12.2$; $df = 1, 32$; $P = 0.001$).

Second, trophic interactions were quantified for diverse tropical aquatic assemblages without regard for visual traceability of links between units in their corresponding food-web digraphs. Computer-generated digraphs for the most diverse tropical systems appear far more complex than previously published digraphs with large numbers of species used in earlier comparative analyses (fig. 3; Winemiller 1987). Several authors have argued that C must logically decrease in assemblages that are more species-rich because of guild structure and functional limits on consumer diet breadth (Rejmánek and Stary 1979; Yodzis 1980; Pimm 1982; Briand 1983). My study systems contrast with this line of reasoning in that connectance was already comparatively low in relatively species-poor systems. Trophic guild structure was observed in all four of the tropical fish assemblages (Winemiller 1987). On the average, consumers in species-poor systems did not feed on a greater variety of prey. Yet, a larger fraction of items consumed by fishes in species-rich systems were estimated to be of lesser importance, as evidenced by the lower slope for C versus m based on food webs excluding weak links relative to the all-inclusive webs (fig. 2). Apparently, weak interactions are responsible for most of the increase in connectance as the number of species

increases. As a consequence, diet specializations were still apparent in a large number of consumers from more-diverse systems. Fishes consuming large proportions of small numbers of prey and trace amounts of large numbers of less important prey had small values for diet breadth (Winemiller 1987). Ontogenetic dietary shifts, well-known features of fish ecology (Werner and Gilliam 1984; Lowe-McConnell 1987), may also have contributed to higher connectance in more-diverse aquatic food webs, since no functional distinction was made between size classes when defining operational taxonomic units. Potential sources of confounding variation in earlier patterns of food-web connectance include the use of (1) webs based on small sample sizes or studies of short duration and (2) diverse methods for assessing trophic links (sometimes subjectively estimated as all or none; see arguments in Paine 1980, 1983).

The generally reported inverse, hyperbolic relation between C and m may be a consequence of the practical difficulty of representing all trophic links in food-web digraphs composed of many elements (Paine 1988). Obviously, a system containing only a handful of species lends itself to pictorial representation more easily than a system containing 50 or 100 units. As illustrated earlier, visual traceability of web digraphs was not a significant concern in my analysis of food-web connectance (fig. 3; Winemiller 1987). As a test of Paine's hypothesis, I calculated food-web connectance for three food webs not yet used in comparative analyses of web connectance. Two were drawn to represent trophic interactions within fish communities of Costa Rica's Osa Peninsula (Winemiller 1983). These webs were published with the intention of representing the basic community trophic network in a traceable, holistic fashion, as opposed to the previously discussed tropical aquatic systems that were constructed for quantitative food-web analyses. Although similar collection and diet-assessment techniques were used in both studies, my earlier Osa Peninsula aquatic food webs were based on much smaller samples and much shorter time intervals. A third food web based on large samples and long time intervals (Australian desert lizards) was published by Pianka (1988) with similar intentions (Pianka, pers. comm.). Connectance and richness values for these three food webs yielded very good fits with the earlier regressions of C and m (fig. 1; Yodzis 1980; Pimm 1982; Briand 1983; Auerbach 1984) but not with distributions based on the current analysis. This admittedly anecdotal analysis clearly supports Paine's hypothesis nonetheless.

Several authors have shown either a horizontal (Rejmánek and Stary 1979; Auerbach 1984) or negative (Yodzis 1980) slope when $(Cm)^{-1/2}$ was plotted against species richness. Given the paucity of data for estimating magnitude of interaction strengths by direct means (Paine 1980), $(Cm)^{-1/2}$ was interpreted as a rough estimate for an upper threshold of average interaction strength (s) according to May's formula. Following May's theoretical finding, one line of reasoning asserts that a reduction in average interaction strength could facilitate local stability at higher levels of diversity and complexity (May 1975). Despite the current result, which opposes the earlier inverse relation between C and m , $(Cm)^{-1/2}$ declined with m in my data as it did in previous tests that were based on webs taken from the literature (fig. 4). However, inferences concerning the full significance of this seemingly valid pattern would be risky in light of the species-aggregation problem

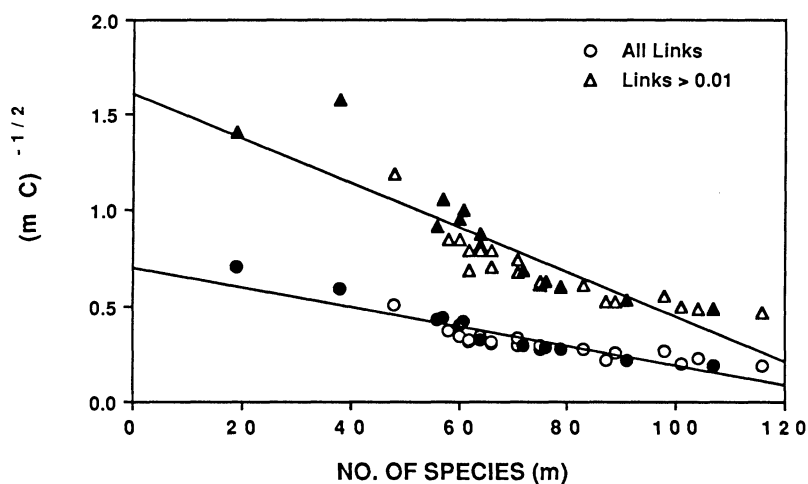


FIG. 4.—May's (1972) approximation for the threshold of average interaction strength (s) against species richness for the same food webs used in figure 1. The regression equation for webs including all links is $y = -0.005x + 0.69$ ($r = 0.91$; $F = 152.8$; $df = 1, 32$; $P < 0.0001$). The regression equation for webs including only links represented by $p_{ij} > 0.01$ is $y = -0.012x + 1.61$ ($r = 0.89$; $F = 124.1$; $df = 1, 32$; $P < 0.0001$). The two slopes are different ($F = 157.4$; $df = 1, 64$; $P < 0.0001$).

in the definition of food-web units, among other factors. Since the dependent variable $(Cm)^{-1/2}$ contains the independent variable m , an inverse relation between the two might be expected.

In conclusion, I caution against premature acceptance and overzealous interpretation of patterns based on culled sets of published *real* food webs. These food webs actually are not real; rather, all are abstractions adjusted to the varying intentions of the original field investigators. On the basis of an extensive empirical data set and attempts to reduce between-system variation in methods, I obtained a positive association between C and m , especially when very weak interactions were included. Until greater objectivity is attained and more data are available, we must exercise caution against confirmation bias for models based on random structure not observed in natural communities. As Rejmánek and Stary (1979) suggested, premature application of corollaries of May's theory is potentially dangerous for a planet marked by damaged, stressed, and partially exterminated natural ecosystems. The issues of complexity and stability are central to community ecology, and progress in the field is vital to our ability to analyze and solve problems in the future. Unfortunately, we are racing the clock in our pursuit of information from intact natural ecosystems.

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