SCALE-DEPENDENT CONSTRAINTS ON FOOD-WEB STRUCTURE

NEO D. MARTINEZ*

Bodega Marine Laboratory, University of California, Davis, Bodega Bay, California 94923-0247

Submitted January 4, 1993; Revised November 5, 1993; Accepted December 27, 1993

Abstract.—For over a decade, ecologists have repeatedly asserted that community food webs possess fundamental properties that are roughly constant among webs with widely varying numbers of species. This assertion of "scale invariance" is reevaluated here among 60 food webs originally published in its support. This analysis contradicts the conventional view of scale invariance by demonstrating highly significant trends in six of eight properties investigated. As the size of food webs increases to 54 trophic species, the fraction of intermediate species, the links/species ratio, and the fraction of links between intermediate species also increase. Concurrently, the fractions of top species, basal species, and links between top and basal species decrease. Only one of these properties, the links/species ratio, is widely thought not to be scale invariant. These trends corroborate hypotheses of scale-dependent food-web structure that successfully predict properties of new, high-quality food webs containing many more than 54 species. This success suggests that general, quantitative, and successfully predictive constraints in fundamental aspects of ecological organization have been discovered. Such discoveries are particularly important, because the lack of general prediction among all terrestrial and aquatic systems seriously impedes the maturation of ecology as a scientific discipline.

The food web, or who eats whom in nature, is one of the earliest and most central concepts of ecological organization (Elton 1927; Lindeman 1942). Whereas ecology has become increasingly specialized into rather separate subdisciplines, food webs are still considered fundamental to most ecological subdisciplines from community ecology (see, e.g., Elton 1927; Paine 1980) to ecosystem studies (see, e.g., Lindeman 1942; Odum 1971). Food webs are also considered fundamental to microbial (Margulis et al. 1986), invertebrate (Schoenly et al. 1991), and vertebrate (Schoener 1989) ecologists. This pervasive centrality allows food webs to unify the insights of many specialists into taxonomically comprehensive trophic portraits of ecological organization (Martinez 1991a). These synthetic and comprehensive traits enable food webs to illuminate commonality among our increasingly disparate subdisciplines (Cohen 1991; Martinez, in press). Despite the rich history and central nature of food webs, quantitative analysis of the structure of food webs has begun only recently (Cohen 1977, 1978). The most celebrated finding of such studies is that food webs contain scale-invariant properties that are roughly constant among food webs with widely varying numbers of species (Cohen 1977, 1978, 1989; Pimm 1982; Briand and Cohen 1984; Cohen and Briand 1984; May 1986, 1988; Lawton 1989; Schoener 1989; Sugihara

* E-mail: ndmartinez@ucdavis.edu.

Scale generally refers to the extent and resolution of data (Allen and Starr 1982; O’Neill et al. 1986). Extent refers to the spatial, temporal, or statistical domain of the data. Resolution refers to how finely this domain is subdivided by the data. Within early food-web studies, scale refers to extent in terms of the number of species in food webs (Cohen 1977, 1978; Briand and Cohen 1984; Cohen and Briand 1984). More recent food-web studies have systematically examined the role of resolution by investigating the effects of aggregation on food-web structure (Martinez 1988, 1991a, 1991b, 1993b; Sugihara et al. 1989; Hall and Raffaelli 1991). Also, investigation of extent and resolution has diversified recently through the examination of spatial and temporal variation in food-web structure (Warren 1989; Winemiller 1990; Cohen and Newman 1991; Schoenly and Cohen 1991). This study emphasizes scale in the early sense of Cohen and Briand: the extent of the numbers of species in food webs. However, since food-web data have so few widely accepted standards, the numbers of species in food webs may also reflect the resolution or the spatial and temporal extent of the data (Martinez 1991a).

The highly variable quantity or “importance” of trophic exchanges represented by links in structural food webs is usually not estimated. Instead, these links are designated as present or absent. These binary designations avoid problems of describing the large and uncertain variability of trophic exchanges, as well as of defining highly variable material-, individual-, and population-based notions of importance. The relatively simple designations of both trophic links and species as either present or absent also allow structural food webs to explicitly embrace a much larger fraction of biodiversity (Winemiller 1990; Hall and Raffaelli 1991; Martinez 1991a; Schoenly et al. 1991; Havens 1992) than do other approaches that emphasize detailed analysis of trophic links (see, e.g., Paine 1980; Baird and Ulanowicz 1989). Structural food webs lend themselves to generalization and encourage formalization and testing of a wide array of hypotheses regarding the trophic structure of ecological systems (N. D. Martinez and J. A. Dunne, unpublished manuscript). Early hypotheses about food-web structure have been tested, rejected, and modified so that they accurately predict robust relationships between trophic interactions and species diversity among a wide variety of terrestrial and aquatic systems (Martinez 1993a). This type of successful and general quantitative prediction appears to be what ecology needs most to continue to grow beyond its roots in natural history and join the ranks of more mature sciences (Peters 1991).

DEFINITIONS AND DATA

Community food webs, hereafter called “webs,” are structural food webs that delineate binary feeding links between prey and their reported predators in a
particular habitat (Cohen 1978). Here, "predator" broadly includes parasitism, cannibalism, and any form of trophic resource consumption of an organism's biomass by another organism. "Top species" have prey but no predators (Briand and Cohen 1984). "Basal species" have predators but no prey (Briand and Cohen 1984). "Intermediate species" have both predators and prey (Briand and Cohen 1984). "Original species" are simply the taxa designated by the original author of a food web. "Trophic species" are aggregations of original species that share the same set of predators and prey within a specific food web (Cohen and Briand 1984). Food-web "properties" describe fractions, ratios, and arrangements of these links and species.

This analysis focuses on eight properties commonly used to describe web structure. These include the fractions of all species in a web (S) that are top species (%Top), intermediate species (%Intermediate), and basal species (%Basal; Briand and Cohen 1984), as well as the number of all links in a web (L) divided by the number of species (L/S; Cohen and Briand 1984). Additionally, the fractions of links between top and intermediate species (%Top-Intermediate), top and basal species (%Top-Basal), intermediate species (%Intermediate-Intermediate), and intermediate and basal species (%Intermediate-Basal) are examined (Cohen and Briand 1984).

Current convention holds that the different fractions of species (%Top, %Intermediate, %Basal) and links (%Top-Intermediate, %Top-Basal, %Intermediate-Intermediate, %Intermediate-Basal) are, on average, invariant among webs with widely differing numbers of species (Briand and Cohen 1984; Cohen and Briand 1984; Sugihara et al. 1989; Cohen et al. 1990; Pimm et al. 1991; Havens 1992). (For the rest of this article, "scale invariance" will refer to the constancy of food-web properties with S as advocated by these references.) The ratio L/S is generally thought to be scale invariant in webs with few species but may increase with the number of species in large webs (Sugihara et al. 1989; Cohen et al. 1990; Pimm et al. 1991). This latter assertion is the most controversial (Hildrew et al. 1985; Martinez 1988, 1991a; Paine 1988; Strong 1988; Schoener 1989; Winemiller 1989; Warren 1990; Polis 1991; Havens 1992; Hall and Raffaelli 1993), with several refutations based on the poor quality of the data (Martinez 1988, 1991a; Paine 1988) and the absence of empirical support (Schoener 1989; Havens 1992; Martinez 1992, 1993a). However, studies that address limitations in the data are thought to have confirmed the scale-invariant patterns (Pimm et al. 1991; Havens 1992). The purportedly constant nature of these properties in webs has prompted characterization of the scale-invariant fractions as food-web "laws" (Cohen et al. 1990).

A prominent analysis concluded that this constancy or lawlike behavior of several properties, which includes L/S, also applies to a relatively new collection of 60 webs from a variety of aquatic and terrestrial environments (Sugihara et al. 1989). These 60 invertebrate-dominated webs, also analyzed here, represent an important improvement over previous collections (Cohen 1978; Briand and Cohen 1984, 1987; Cohen et al. 1990), because the 60 webs contain a wider range of S (between two and 54 trophic species) and a relatively even and high degree of taxonomic resolution (Sugihara et al. 1989; Schoenly et al. 1991).
Fig. 1.—Data and least-squares regressions (solid lines) of the fractions of top, intermediate, and basal species and $L/S$ among 60 trophic-species webs. Data points have been randomly displaced a small distance to illuminate coincident points. Solid points represent the trophic-species versions of the 41 webs with 10 or more original species for which Sugihara et al. (1989) performed a regression. The vertical dashed lines at $S = 7$ are drawn to facilitate comparison with table 2. The horizontal dashed lines represent scale-invariant mean values for Briand and Cohen’s trophic-species webs (Cohen et al. 1990). The statistics for these and other regressions are summarized in table 1. Curvilinear relationships similar to those suggested by the plots of %Intermediate, %Basal, and %Top-Basal have been illustrated elsewhere (Cohen et al. 1990; Martínez 1991a; Martínez and Lawton, in press).

ANALYSES

Following convention (Cohen 1978, 1989; Briand 1983; Briand and Cohen 1984; Cohen and Briand 1984; Sugihara et al. 1989; Winemiller 1989; Cohen et al. 1990; Havens 1992), simple, linear, least-squares regressions are used to analyze the relationship between the eight properties and $S$ among the 60 webs. Two versions of the 60 webs were analyzed. In the conventional version, species distinguished in the original documentation of the webs were lumped into trophic species if the original species shared the same predators and prey (Briand and Cohen 1984, 1987; Cohen and Briand 1984; Briand 1985; Schoener 1989; Cohen and Palka 1990; Cohen et al. 1990; Martínez 1991a, 1992, 1993b; Pimm et al. 1991). This
Fig. 2.—Data and least-squares regressions (solid lines) of the fractions of links between top, intermediate, and basal species among 60 trophic-species webs. Solid and empty data points as well as solid and dashed lines are similar to those in fig. 1. The statistics for these and other regressions are summarized in table 1. Curvilinear relationships similar to those suggested by the plots of %Top-Basal have been illustrated elsewhere (Cohen et al. 1990; Martinez 1991a).

Lumping appears to ameliorate the disparate taxonomic biases of authors’ depictions of food-web data (Briand and Cohen 1984; Cohen and Briand 1984; Briand 1985; Cohen 1989; Schoener 1989; Cohen et al. 1990; Martinez 1992, 1993b). In the less conventional version, the highly variable original species’ designations (e.g., “live insects,” “T. tenax,” and “bacteria/protozoa” exist in one web [Schoenly et al. 1991]) were maintained (Sugihara et al. 1989; Schoenly et al. 1991). These two versions are called trophic-species webs and original-species webs, respectively. The 60 webs contain between two and 54 trophic species (mean, 12.3) and between two and 87 original species (mean, 21.7).

If the assumptions of simple linear least-squares regressions are accepted for these data, figures 1 and 2 and table 1 demonstrate that six of the eight properties vary in a highly significant manner ($P \leq .001$) with $S$ among the 60 trophic-species webs. The properties $L/S$, %Intermediate, and %Intermediate-Intermediate increase with $S$, whereas %Top, %Basal, and %Top-Basal decrease with $S$. The
TABLE 1

<table>
<thead>
<tr>
<th>Property</th>
<th>Type of Species</th>
<th>Regression Slope</th>
<th>SE_{slope}</th>
<th>P</th>
<th>R^2</th>
</tr>
</thead>
<tbody>
<tr>
<td>%Top</td>
<td>Trophic species</td>
<td>-.492*</td>
<td>.137</td>
<td>.001</td>
<td>.18</td>
</tr>
<tr>
<td></td>
<td>Original species</td>
<td>.031</td>
<td>.159</td>
<td>.847</td>
<td>.00</td>
</tr>
<tr>
<td>%Intermediate</td>
<td>Trophic species</td>
<td>1.230*</td>
<td>.223</td>
<td>&lt;.001</td>
<td>.34</td>
</tr>
<tr>
<td></td>
<td>Original species</td>
<td>.393*</td>
<td>.173</td>
<td>.028</td>
<td>.08</td>
</tr>
<tr>
<td>%Basal</td>
<td>Trophic species</td>
<td>-.738*</td>
<td>.161</td>
<td>&lt;.001</td>
<td>.27</td>
</tr>
<tr>
<td></td>
<td>Original species</td>
<td>-.424*</td>
<td>.091</td>
<td>&lt;.001</td>
<td>.27</td>
</tr>
<tr>
<td>L/S</td>
<td>Trophic species</td>
<td>.058*</td>
<td>.006</td>
<td>&lt;.001</td>
<td>.60</td>
</tr>
<tr>
<td></td>
<td>Original species</td>
<td>.023*</td>
<td>.006</td>
<td>&lt;.001</td>
<td>.19</td>
</tr>
<tr>
<td>%Top-Intermediate</td>
<td>Trophic species</td>
<td>.350</td>
<td>.239</td>
<td>.148</td>
<td>.04</td>
</tr>
<tr>
<td></td>
<td>Original species</td>
<td>.395*</td>
<td>.168</td>
<td>.022</td>
<td>.09</td>
</tr>
<tr>
<td>%Top-Basal</td>
<td>Trophic species</td>
<td>-1.653*</td>
<td>.399</td>
<td>&lt;.001</td>
<td>.23</td>
</tr>
<tr>
<td></td>
<td>Original species</td>
<td>-.743*</td>
<td>.258</td>
<td>.006</td>
<td>.13</td>
</tr>
<tr>
<td>%Intermediate-Basal</td>
<td>Trophic species</td>
<td>.915*</td>
<td>.181</td>
<td>&lt;.001</td>
<td>.31</td>
</tr>
<tr>
<td></td>
<td>Original species</td>
<td>.308*</td>
<td>.134</td>
<td>.025</td>
<td>.08</td>
</tr>
<tr>
<td>%Intermediate-Intermediate</td>
<td>Trophic species</td>
<td>.388*</td>
<td>.179</td>
<td>.034</td>
<td>.08</td>
</tr>
<tr>
<td></td>
<td>Original species</td>
<td>.040</td>
<td>.113</td>
<td>.724</td>
<td>.00</td>
</tr>
</tbody>
</table>

Note.—P values represent two-tailed tests of the scale-invariance hypotheses (Cohen et al. 1990) that the regression slopes are equal to zero.

* P < .05.

two remaining properties, %Top-Intermediate and %Intermediate-Basal, vary much less significantly (P ≥ .034), which is probably because these links are between species whose fractions vary in opposite directions (%Top and %Basal decrease with S, whereas %Intermediate increases with S).

Most of the original claims of scale-invariant food-web structure were based on a set of 62 webs with between three and 33 trophic species (Briand and Cohen 1984; Cohen and Briand 1984). Briand and Cohen’s collection has grown to include 113 trophic-species webs with between two and 48 trophic species (Briand and Cohen 1987; Cohen et al. 1990). I combined the 113 webs with Schoenly et al.’s (1991) 60 webs and found that the highly significant trends among the 60 webs also exist in regressions of all 173 trophic-species webs at P ≤ .001—except for the negative %Top trend, where P = .073 (Martinez 1991b). The less significant %Top trend may be due to the widely criticized tendency for authors of food-web data to differentiate more species at higher trophic levels (Pimm 1982; May 1983; Moore et al. 1989; Cohen et al. 1990; Hall and Raffaelli 1991, 1993; Paine 1988; Martinez 1991a, 1991b, 1993b; Pimm et al. 1991; Schoenly et al. 1991; Havens 1992), a phenomenon that appears even more pronounced in Briand and Cohen’s larger webs (Martinez 1991b). Schoenly et al.’s 60 webs are much more evenly resolved across trophic levels (Sugihara et al. 1989; Schoenly et al. 1991) and therefore are less affected by this bias. For example, fewer than 50% of the taxa in an influential subset (Briand 1983) of 40 of Briand and Cohen’s 62 webs (Briand and Cohen 1984; Cohen and Briand 1984) are resolved to taxonomic species, whereas 83% are resolved to taxonomic species in Schoenly et al.’s (1991) webs. For this reason, Schoenly et al.’s webs are emphasized here.
These regression analyses may be criticized because the data violate assumptions of simple linear regressions. Linear trends of proportions may not continue beyond 0% or 100%. Instead, the trends must be curvilinear or discontinuous (Martinez 1993a; Martinez and Lawton, in press). Also, the outlying cluster of small webs with no intermediate species (figs. 1 and 2) indicates that the data are not bivariate normally distributed. Because of these problems, linear regressions appear inappropriate for these analyses. Instead, we may use correlations to test hypotheses regarding relationships between $S$ and the fractions of species and links (Schoener 1989). The common criticism that such regressions and correlations of variables with common terms (e.g., $L/S$ vs. $S$) are statistically invalid or “spurious” is currently recognized as mistaken (Prairie and Bird 1989). Given the limitations of the data, nonparametric (rank) correlation appears more valid and is more conservative in favor of accepting the traditional scale-invariance hypotheses than are parametric tests. This is because nonparametric tests are more susceptible to Type II errors of accepting the null hypotheses when they are false than are their parametric counterparts. In exchange for the lowered statistical power, nonparametric correlation tests do not assume linearity or bivariate normality.

Another important statistical consideration is the specification of alternative hypotheses to the null hypothesis ($H_0$). Here, $H_0$ denotes the widely accepted scale-invariance hypotheses. As an alternative ($H_1$), I have argued that the fractions of top, intermediate, and basal species, and the fractions of links between these species, are scale-dependent (Martinez 1991a, 1991b, 1993a, 1993b). Specifically, $\%\text{Intermediate}$ and $\%\text{Intermediate-Intermediate}$ are hypothesized to increase with $S$, whereas $\%\text{Top}$, $\%\text{Basal}$, and $\%\text{Top-Basal}$ decrease with $S$. These scale dependencies may be because webs with small $S$ possess high $\%\text{Top}$ and $\%\text{Basal}$ due to aggregation (Martinez 1991a, 1993b; Havens 1992) and incompleteness of data (Winemiller 1990; Martinez 1991a; Polis 1991). These are the reasons hypothesized for the difference between a large and highly resolved food web, that of Little Rock Lake, Wisconsin, and the purportedly scale-invariant fractions of earlier catalogues of webs (Martinez 1991a). The 93 trophic species web of Little Rock Lake has $\%\text{Top}$, $\%\text{Basal}$, and $\%\text{Top-Basal}$ lower than and $\%\text{Intermediate}$ and $\%\text{Intermediate-Intermediate}$ higher than the mean fractions in the earlier webs.

Relatively large $\%\text{Top}$ and $\%\text{Basal}$ in small webs may also result from restricting observation of food webs to small temporal and spatial scales where only few species and links are observed. At the extreme, severely restricted scales may result in the observation of only two species, one of which eats the other (Sugihara et al. 1989; Martinez 1992). This results in small webs with $\%\text{Top} = 50$, $\%\text{Basal} = 50$, and $\%\text{Top-Basal} = 100$, whereas $\%\text{Intermediate} = 0$ and $\%\text{Intermediate-Intermediate} = 0$. At the other limit, it appears that the vast majority of species on the planet are animals, mostly insects (May 1988), all of which have prey and few if any are known to be free of consumers, which include parasites and cannibals (Winemiller 1990). If global species estimates are used to evaluate the theoretical limit of the largest-scaled food web (Martinez and Lawton, in press), this “global” food web may be estimated to have $\%\text{Inte-
mediate \gg 50, \%Intermediate-Intermediate > 0, \%Top \ll 50, \%Basal < 50, and \%Top-Basal \ll 100. The differences between the smallest and largest scales suggest that \%Intermediate and \%Intermediate-Intermediate increase with increasing scale, whereas \%Top, \%Basal, and \%Top-Basal decrease with increasing scale. Another article (Martínez and Lawton, in press) describes several details of these hypothesized scale dependencies, which include the functional forms and the existence of asymptotes. Here, I only consider whether these fractions do or do not systematically depend on scale in a statistically significant manner and, if so, in which direction (negative or positive).

In light of specific scale-dependence hypotheses and the observed scatter in the data, the scale-invariance hypotheses (H₀) that food-web properties are not significantly correlated with S are tested against the scale-dependence hypotheses (Hₙ) that \%Top, \%Basal, and \%Top-Basal are negatively correlated with S, and that \%Intermediate and \%Intermediate-Intermediate are positively correlated with S (Martínez 1993b), by means of one-tailed P values (in which P is the probability that the observed trend suggested by the scale-dependence hypothesis would be observed by chance, if the data represent a random sample from a population with scale-invariant properties or a correlation equal to zero). Kendall’s coefficient of rank correlation (‘τ-test’) shows that these five scale-invariance hypotheses should be rejected in favor of the scale-dependence hypotheses (table 2) at \( P = .000001 \) for these data. The two-tailed test, which tests the two scale-invariance hypotheses that have no specific alternative scale-dependence hypotheses, rejects scale-invariant \%Top-Intermediate and \%Intermediate-Basal at \( P = .01 \) (table 2). These results strongly corroborate the scale-dependence hypotheses and reject the scale-invariance hypotheses. If two-tailed probabilities are used to test scale invariance of the other five fractions without considering specific scale-dependence hypotheses, τ-tests still reject scale invariance at \( P = .01 \) for each fraction.

There are several possible reasons for the discrepancy between the trends described here and the scale invariance reported elsewhere. One possibility is that the discrepancies are primarily due to inclusion of an outlying cluster of 13 small webs with no intermediate species (\%Intermediate = 0) and, therefore, with only top-basal links (\%Top-Basal = 100, \%Intermediate-Intermediate = 0). Although this cluster of webs does emphasize the scale dependencies described here, even when these webs are eliminated from the analysis, τ-tests still reject scale invariance in favor of scale dependence at \( P = .004 \), with the exception of \%Top-Basal, whose negative trend is significant at \( P = .055 \) (table 2). Another possible statistical flaw is that the regressions are “artificially” biased by the large number of small webs. This possibility is discounted by τ-tests of the 36 trophic-species webs with \( S \geq 7 \) that reveal statistically significant correlations (\( P < .04 \)) in the scale-dependent directions (table 2). The laws of scale invariance are asserted to be valid for webs of as few as three to five species (Cohen et al. 1990).

Even τ-tests of the 30 webs with \( S \geq 9 \) display correlations in the same directions suggested by the scale-dependence hypotheses (excepting only the negative trend of \%Top-Basal), although only the \%Basal trend is significantly different
<table>
<thead>
<tr>
<th>Type and Number of Webs Analyzed</th>
<th>Statistic</th>
<th>%Top</th>
<th>%Intermediate</th>
<th>%Basal</th>
<th>%Top-Intermediate</th>
<th>%Top-Basal</th>
<th>%Intermediate-Basal</th>
<th>%Intermediate-Basal</th>
</tr>
</thead>
<tbody>
<tr>
<td>$H_0$ hypotheses</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$H_1$ hypotheses</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trophic species ($n = 60$)</td>
<td>$\tau$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$\tau$</td>
<td>negative</td>
<td>positive</td>
<td>negative</td>
<td>unspecified</td>
<td>negative</td>
<td>unspecified</td>
<td>unspecified</td>
</tr>
<tr>
<td></td>
<td>$P$</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>.007</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Original species ($n = 60$)</td>
<td>$\tau$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$\tau$</td>
<td>negative</td>
<td>positive</td>
<td>negative</td>
<td>unspecified</td>
<td>negative</td>
<td>unspecified</td>
<td>unspecified</td>
</tr>
<tr>
<td></td>
<td>$P$</td>
<td>.350</td>
<td>.001</td>
<td>&lt;.001</td>
<td>.005</td>
<td>.015</td>
<td>&lt;.001</td>
<td>.101</td>
</tr>
<tr>
<td>Trophic species %Intermediate $&gt; 0$ ($n = 47$)</td>
<td>$\tau$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$\tau$</td>
<td>negative</td>
<td>positive</td>
<td>negative</td>
<td>unspecified</td>
<td>negative</td>
<td>unspecified</td>
<td>unspecified</td>
</tr>
<tr>
<td></td>
<td>$P$</td>
<td>.004</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>.007</td>
<td>.055</td>
<td>&lt;.001</td>
<td>.109</td>
</tr>
<tr>
<td>Trophic species $S \geq 7$ ($n = 36$)</td>
<td>$\tau$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$\tau$</td>
<td>negative</td>
<td>positive</td>
<td>negative</td>
<td>unspecified</td>
<td>negative</td>
<td>unspecified</td>
<td>unspecified</td>
</tr>
<tr>
<td></td>
<td>$P$</td>
<td>.020</td>
<td>.003</td>
<td>.002</td>
<td>.832</td>
<td>.031</td>
<td>.037</td>
<td>.651</td>
</tr>
<tr>
<td>Trophic species $S \geq 9$ ($n = 30$)</td>
<td>$\tau$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$\tau$</td>
<td>negative</td>
<td>positive</td>
<td>negative</td>
<td>unspecified</td>
<td>negative</td>
<td>unspecified</td>
<td>unspecified</td>
</tr>
<tr>
<td></td>
<td>$P$</td>
<td>.470</td>
<td>.054</td>
<td>.021</td>
<td>.112</td>
<td>.433</td>
<td>.179</td>
<td>.824</td>
</tr>
</tbody>
</table>

Note.—$P$ values represent one-tailed tests of the null hypotheses ($H_0$ is scale invariance, or $\tau = 0$) versus the scale-dependence hypotheses in the second row excepting %Top-Intermediate and %Intermediate-Basal, where $P$ values are two-tailed tests of $H_0$ alone. All significant correlations with properties that $H_1$ asserts are scale-dependent corroborate $H_1$. $S$, species number.

* $P = .05$. 
from 0 at \( P = .05 \) (table 2). Such a reduction of statistical significance among highly variable data is to be expected when the difference in scale is reduced from a factor of 26 to a factor of six and the quantity of data is reduced by a factor of two. Still, how likely are such correlations in the scale-dependent directions? To answer this question, I assigned random fractions of species to 1,000 sets of 30 webs with the same number of species as the 30 webs with \( S \geq 9 \). This randomization tests the probability of observing correlations by chance alone with scale invariance assumed. Three random fractions between zero and one were chosen for each web. Each fraction of species was set equal to one of the random fractions divided by the sum of all three random fractions. Only three of the 1,000 sets of three correlations observed were as strong or stronger than those observed in the scale-dependent directions among the actual 30 webs. Thirty-three of the 1,000 correlation sets were in the same direction as the scale-dependence hypotheses and had a mean absolute value of the correlations greater than or equal to the mean observed in the actual webs (0.152). This suggests that the probability of all three correlations of "scale-invariant" \( (H_0) \) fractions of species corroborating the scale-dependence hypotheses \( (H_1) \) at the observed magnitudes is .033 or less.

In summary, these analyses demonstrate that the scale-dependence hypotheses are robust to varying statistical tests and to the employment of directional and nondirectional alternate hypotheses. The analyses range from parametric tests to nonparametric tests that use complete data sets, data sets with various groups of small webs excluded, and data sets that exclude an influential outlying cluster of webs.

**DISCUSSION**

*Explanation and Prediction of Scale Dependence*

The demonstrated significant trends in the fractions of top, intermediate, and basal species and the links between them clearly contradict the scale-invariance view of community food webs. Also contrary to convention (Pimm et al. 1991), no tendency toward constant \( L/S \) in small webs is suggested by the trophic-species webs shown in figures 1 and 2 (Martinez 1992).

The significant trends in \%Top, \%Intermediate, \%Top-Basal, and \%Intermediate-Intermediate have not been observed previously in collections of trophic-species webs (except in Martinez 1991b). The properties \%Top-Basal and \%Intermediate-Intermediate have not been previously examined in Schoenly et al.'s webs. The significant trends in \( L/S \) and \%Basal have been observed in other data (Martinez 1988, 1992, 1993a; Schoener 1989; Warren 1989, 1990; Winemiller 1990; Hall and Raffaelli 1991; Havens 1992), but only the significant decrease of \%Basal had been recognized in the webs analyzed here (Sugihara et al. 1989; Schoenly et al. 1991). Constant \( L/S \) with \( S \) has been considered an ecological law relatively recently (Cohen et al. 1990) even though \( L/S \) was recognized to increase with \( S \) over a decade ago (Cohen and Briand 1984; Cohen et al. 1986). Apparently,
the appealing simplicity of scale-invariant $L/S$ is difficult to resist (Pimm et al. 1991).

The trends in $\%\text{Top}$, $\%\text{Intermediate}$, and $L/S$ were not observed in the previous 60-web analysis (Sugihara et al. 1989), because regressions in that analysis involved properties among only the 41 original-species webs with $S \geq 10$ and ignored the trophic-species convention. The highly significant trends in $L/S$, $\%\text{Top}$, $\%\text{Intermediate}$, $\%\text{Basal}$, $\%\text{Top-Basal}$, and $\%\text{Intermediate-Intermediate}$ are clearly evident in regressions of properties versus $S$ among trophic-species versions of the same 41 webs ($P \leq .027$, results not shown; see solid data points in figs. 1 and 2) and among all 60 original-species webs ($P \leq .028$, except $\%\text{Top}$, where $P > .05$; table 1). Schoenly et al. (1991) found that the positive slope of the regression of $\%\text{Intermediate}$ versus $S$ was not significantly different from zero ($P > .1$) because of a discrepancy between the treatment of two webs. These two webs were originally considered separate 15- and 75-original-species webs, because there were no trophic links between them (felled pine logs, 1 yr, webs 1 and 2, Sugihara et al. 1989, ref. 48). Schoenly et al. (1991) treated these two webs as a single 90-original-species web. In the 15-original-species web (which collapses down to a two-trophic-species web), $\%\text{Top} = 93$, $\%\text{Intermediate} = 0$, and $\%\text{Basal} = 7$ (Sugihara et al. 1989). Combining the two separate webs causes the 90-original-species web to contain relatively low $\%\text{Intermediate}$ and to have an unnecessarily large effect on the regression.

Recent analyses (Martínez 1991a, 1993b) predict that webs with large $S$ have higher $L/S$, $\%\text{Intermediate}$, and $\%\text{Intermediate-Intermediate}$ and lower $\%\text{Top}$, $\%\text{Basal}$, and $\%\text{Top-Basal}$ than webs with small $S$ because of the effects of variable resolution (variable level of detail) on food-web properties. These analyses demonstrate that, as the resolution of food webs is reduced by the aggregation of trophic species into fewer trophically similar species, $L/S$, $\%\text{Intermediate}$, and $\%\text{Intermediate-Intermediate}$ decrease, whereas $\%\text{Top}$, $\%\text{Basal}$, and $\%\text{Top-Basal}$ increase. These results were interpreted as suggesting that these properties are scale-dependent, and that the properties have been mistakenly considered scale invariant because the early unevenly aggregated and poorer-quality data obscured the scale dependencies. Pimm et al. (1991, p. 670) counter these suggestions by stating, “Possible artefacts ought not to apply equally to webs from special microhabitats described in detail and to those more aggregated webs summarizing interactions throughout larger communities.” However, studies (Martínez 1988, 1993a, 1993b)—including this one—demonstrate that the scale dependencies predicted from the aggregation studies also apply to food webs of different sizes. Contrary to Pimm et al., this correspondence suggests that the pattern of high $\%\text{Top}$, $\%\text{Basal}$, and $\%\text{Top-Basal}$ and low $\%\text{Intermediate}$, $\%\text{Intermediate-Intermediate}$, and $L/S$ in webs with small $S$ applies both to highly aggregated webs from large-scaled habitats and to detailed small webs from small-scaled habitats.

Beyond explaining the variance of web properties with $S$ among the food-web collections, the scale-dependence hypotheses predict that other webs with large $S$ also have higher $L/S$, $\%\text{Intermediate}$, and $\%\text{Intermediate-Intermediate}$, and lower $\%\text{Top}$, $\%\text{Basal}$, and $\%\text{Top-Basal}$ than webs with small $S$ (table 3). The
### TABLE 3
**Comparison of Recently Observed Food-Web Properties with Purportedly Scale-invariant Properties Observed Earlier (Cohen et al. 1990)**

<table>
<thead>
<tr>
<th>Reference</th>
<th>S</th>
<th>%Top</th>
<th>%Intermediate</th>
<th>%Basal</th>
<th>L/S</th>
<th>%Top-Intermediate</th>
<th>%Top-Basal</th>
<th>%Intermediate-Basal</th>
<th>%Intermediate-Basal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cohen et al. 1990</td>
<td>16.7</td>
<td>29</td>
<td>53</td>
<td>19</td>
<td>1.9</td>
<td>35</td>
<td>8</td>
<td>27</td>
<td>30</td>
</tr>
<tr>
<td>Warren 1989:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open water</td>
<td>17.2</td>
<td>13</td>
<td>80</td>
<td>7</td>
<td>4.0</td>
<td>30</td>
<td>2</td>
<td>51</td>
<td>18</td>
</tr>
<tr>
<td>Margin</td>
<td>26.4</td>
<td>10</td>
<td>85</td>
<td>5</td>
<td>6.0</td>
<td>20</td>
<td>1</td>
<td>70</td>
<td>9</td>
</tr>
<tr>
<td>Hall and Raffaelli 1991</td>
<td>92</td>
<td>28</td>
<td>68</td>
<td>4</td>
<td>4.4</td>
<td>30</td>
<td>.5</td>
<td>60</td>
<td>10</td>
</tr>
<tr>
<td>Martinez 1991a</td>
<td>93</td>
<td>1</td>
<td>86</td>
<td>13</td>
<td>11</td>
<td>0</td>
<td>0</td>
<td>91</td>
<td>9</td>
</tr>
<tr>
<td>Goldwasser and Roughgarden 1993</td>
<td>44</td>
<td>18</td>
<td>68</td>
<td>14</td>
<td>5.0</td>
<td>23</td>
<td>3.2</td>
<td>55</td>
<td>18</td>
</tr>
<tr>
<td>Winemiller 1990</td>
<td>75</td>
<td>11</td>
<td>73</td>
<td>16</td>
<td>6.3</td>
<td>N.R.</td>
<td>N.R.</td>
<td>N.R.</td>
<td>N.R.</td>
</tr>
<tr>
<td>Polis 1991</td>
<td>30</td>
<td>0</td>
<td>90</td>
<td>10</td>
<td>9.6</td>
<td>N.R.</td>
<td>N.R.</td>
<td>N.R.</td>
<td>N.R.</td>
</tr>
</tbody>
</table>

**Note.**—All the recent observations are consistent with the scale-dependent ($H_i$) hypotheses. That is, recently observed values of $S$, %Intermediate, L/S, and %Intermediate-Intermediate are higher than those reported by Briand and Cohen (1984) and Cohen and Briand (1984), whereas %Top, %Basal, and %Top-Basal are lower. The properties of Warren’s (1989) and Winemiller’s (1990) webs represent the mean estimates reported by these authors. “N.R.” stands for values not reported by the author.
93-trophic-species web of Little Rock Lake, Wisconsin (Martinez 1988, 1991a), confirms each of these predictions, as do those constructed by Warren (1989), Hall and Raffaelli (1991), and Goldwasser and Roughgarden (1993). Winemiller’s (1990) and Polis’s (1991) webs also confirm each scale-dependence prediction with the possible exception of the fractions of links, which were not reported.

Whereas the new data in table 3 are anomalous to the scale-invariance paradigm, the data are uniformly consistent with the scale-dependence hypotheses. Few if any of the results of recent studies of data collected for the purpose of structural food-web analysis contradict the scale dependencies asserted here (Martinez 1993a). Perhaps the success of scale-dependence food-web theory will foster what Lightman and Gingerich (1992) call “retrorecognition” of the anomalies in table 3 to the scale-invariant convention. Retrorecognition refers to the fact that exceptions to conventional wisdom are often only recognized as anomalies after a competing theory is advanced that explains the “anomalies” more accurately than the conventional theory. For example, the large %Intermediate and small %Basal in Hall and Raffaelli’s web is considered to be within the range of variation of previous data as opposed to an anomaly (Hall and Raffaelli 1991).

It should be noted that %Top in Hall and Raffaelli’s 92-species web, which is only slightly below the previously reported scale-invariant mean (Briand and Cohen 1984), is overestimated. This is because the three basal species (detritus, phytoplankton, and macroalgae) in Hall and Raffaelli’s web are resolved much more coarsely than is usual in a large food web. More consistent resolution of the basal species would lower %Top (Hall and Raffaelli 1991), raise %Basal from its lowest value in table 3, and result in a better fit to the scale-dependence hypotheses.

Although difficult to compare quantitatively, the scale-dependent predictions that larger webs will have properties larger or smaller than the previously identified means (table 3) are more precise than the assertion that these properties “are roughly constant with high variance” (Pimm et al. 1991). This is because the large standard deviations about the mean of Briand and Cohen’s (1984; Cohen and Briand 1984) 62 webs make the 95% confidence intervals of the scale-invariant predictions larger than the scale-dependence predictions. For each property, this scale-invariant interval (SD multiplied by four) compared to the scale-dependent interval (table 3) is 52 compared to 28 for %Top, 52 compared to 47 for %Intermediate, 32 compared to 18 for %Basal, 36 compared to 7 for %Top-Basal, and 76 compared to 73 for %Intermediate-Intermediate. The observed intervals of the new data are typically much smaller than the intervals suggested by the scale-dependence hypotheses. Further research that more precisely specifies the functional forms of scale dependence (Martinez and Lawton, in press) could reduce the predicted intervals further. For example, further analyses have estimated that \(L/S\) increases as 0.1\(S\) and that \(L/S^2\) equals 0.1, with standard deviations equal to 0.03 (Martinez 1992) and 0.02 (Martinez 1993a). This hypothesis of constant connectance is much more precise than the mere assertion that \(L/S\) increases with \(S\) and also successfully explains 90% of the variance of \(L\) with \(S\) among Havens’s 50 webs (Martinez 1993a, in press).
Unexplained Variation and Observation Biases

Among the six scale-dependent properties, aggregation of original species into trophic species dramatically increases the proportion of variance of the properties accounted for by $S$ (increases $R^2$ of the regressions from a mean of 0.13 to 0.32 and increases strength of the correlation from a mean of 0.26 to 0.44) and also dramatically increases the probability that the regression coefficient is not zero (decreases $P$ from a mean of .151 to .001). These increases are consistent with the assertion that aggregation into trophic species reduces the scatter in the data by reducing arbitrary and inconsistent biases (Briand 1985; Cohen 1989; Moore et al. 1989; Schoener 1989; Cohen et al. 1990; Martinez 1991a, 1993b; Pimm et al. 1991).

Such biases appear to come from original authors of the data inconsistently employing taxonomic and trophic specificity among organisms (Briand 1985; Cohen 1989; Schoener 1989; Cohen et al. 1990; Martinez 1991a, 1992, 1993b). Use of trophic species reduces such biases by means of the consistent application of trophic criteria to define both the web's components (i.e., species) and the relations between components (i.e., links). In original-species webs, distinctions between components are less consistently made with either taxonomic or trophic criteria. Taxonomic distinctions between species are based on morphological and phylogenetic criteria. Trophic distinctions between species emphasize functional criteria for specifying when members of species consume and respire the biomass of members of another or even the same species. My results show that mixing of these criteria, as in original-species webs, adds unexplained variability to the regressions and weakens the correlations.

Such mixed criteria may explain why scale dependence is relatively weak among Havens's (1992) 50 webs (Martinez 1993a). Most of the 10–74 (mean, 38) taxa in Havens's webs describing the pelagic portions of 50 Adirondack lakes are resolved to taxonomic species and are not aggregated into trophic species. The scale dependencies in this study also apply, albeit weakly, to Havens's data (Martinez 1993a). One could test this explanation for relatively weak scale dependence by aggregating Havens's webs into trophic-species webs. Employing the trophic-species definition should reduce the proportion of variation unaccounted for by the regressions and increase the regression and correlation coefficients, which thus enables a more accurate prediction.

In addition to employing the trophic species definition, the effects of human bias may be reduced by describing "ecosystem food webs," which are webs based on explicit and consistent trophic and taxonomic criteria that include all organisms, regardless of their taxonomy and trophic function, within explicit spatial and temporal boundaries (Martinez 1991a, in press). As the discussion of Hall and Raffaelli's web suggests, the lack of consistency and the presence of different taxonomic and trophic biases may explain much of the remaining variability among the webs in table 3 not explained by scale dependence. Still, the presence of statistically significant and successfully predictive patterns suggests that variability of biases among investigators as to what constitutes a trophic link or membership in a community is highly constrained. If such biases were not
constrained, unlimited variability in observation biases would make strong patterns in trophic structure difficult to discover.

*Pattern and Process of Structural Dynamics*

The success of the scale-dependence hypotheses suggests that general and accurate quantitative constraints in ecological organization have been discovered. These constraints successfully predict properties in the highest quality data available for a wide range of organisms (microbes to vertebrates) in a wide variety of aquatic and terrestrial systems (tables 2 and 3). Such generality suggests that the processes responsible for the patterns are also general (Foster 1991). Evolutionary (Matsuda and Namba 1991), autecological (Schoener 1989; Havens 1993), and community assembly (Yodzis 1984; Cohen and Newman 1988; Drake 1991) processes are strong candidates. Compared to qualitative constraints, quantitative constraints are particularly powerful, because their precision allows for more rigorous and decisive tests of processes hypothesized to be generally responsible for the structure of ecological organization (Peters 1991). Such tests will also be improved by increasing our understanding of the relationship between methodology and web properties (MacDonald 1979; Paine 1988; Warren 1989; Winemiller 1990; Martinez 1991a, in press; N. D. Martinez and J. A. Dunne, unpublished manuscript). Beyond these ecological and methodological processes, new or previously ignored processes may be discovered that have the power to enforce the observed conformity on ecological organization.

Since $S$ typically increases and decreases as communities assemble and disassemble, scale-dependent web structure appears related to the dynamics of community assembly. The similarity between aggregated large webs and more highly resolved small webs may be due to correspondence between community disassembly (Mikkelson 1993) and trophic aggregation (Martinez 1991a, 1993b) or, conversely, initial community assembly (Jenkins and Kitching 1990) and trophic disaggregation. That is, both pairs of processes appear to affect the structural appearance of the community in a consistent, scale-dependent manner with the assumption that $S$ and community assembly are related (but see Mikkelson 1993). The dynamics of community assembly (and disassembly) may be investigated for structural webs to examine how trophic niche space is created (and lost) and partitioned between species. If the process of trophic aggregation could be specified in a manner that permits the process to be reversed (trophic disaggregation), the structural dynamics of community assembly would be able to be predicted. Independent of aggregation, community structure may be predicted to develop in the scale-dependent directions as time progresses and $S$ increases. Whether these predictions are accurate and, if so, whether the accuracy is a coincidence or indicative of powerful general ecological processes are important questions for future research.

**CONCLUSION**

Using the highest quality and most extensive data available, scale dependence characterizes six web properties conventionally thought to be scale invariant. As
the number of species increases, so do \(L/S\), \(\%\text{Intermediate}\), and \(\%\text{Intermediate-Intermediate}\). Concurrently, \(\%\text{Top}\), \(\%\text{Basal}\), and \(\%\text{Top-Basal}\) decrease. These robust scale dependencies are demonstrated in each of several statistical techniques for several sets of data. The scale-dependence hypotheses successfully predict the differences between large, high-quality webs recently constructed for the purpose of structural food-web analyses (table 3) and earlier webs with fewer species (Cohen et al. 1990). Still, new properties or reformulations of conventional properties may be discovered that are more scale invariant (e.g., \(L/S^2\) is much more scale invariant than \(L/S\); Martinez 1992, 1993a, 1993b).

The similarity between aggregated webs from large communities and disaggregated webs from small communities poses important theoretical and empirical opportunities and problems (see Pattern and Process of Structural Dynamics). Theoretically, we need to clarify why these similarities exist. Empirically, we need to document the scale of food-web data by explicitly stating the extent of time and space that the data encompass and standardizing the taxonomic and trophic resolution employed (Martinez 1988, 1991a, in press; Lawton 1989; Warren 1989; Winemiller 1990; Hall and Raffaelli 1991; Pimm et al. 1991; Cohen et al. 1993).

It is unwise to ignore robust constraints on web structure just because biological explanation of these patterns is not immediately apparent. Similar rejections of broad geological similarities between continents delayed the discovery and acceptance of the powerful mechanism of plate tectonics. One hopes that ecologists can learn from this type of mistake rather than repeat it. A more immediate contribution of general structural constraints is that the generality of the predictions arising from the constraints goes far beyond the characteristically local predictions of natural history. Without such general predictions, ecology would be an immature and largely descriptive field with relatively little scientific credibility (Peters 1991).

Scale dependence suggests that among-web comparisons of scale-dependent properties need to be corrected for differences in \(S\) (Martinez 1991a; Goldwasser and Roughgarden 1993; Bengtsson 1994). The currently unknown functional forms of the scale dependencies are critical to such comparisons and, thus, need further study. The functional forms will also provide more precise benchmarks to the testing of models that attempt to explain community structure (Yodzis 1984; Cohen and Newman 1988; Schoener 1989; Cohen et al. 1990; Drake 1991; Hairston and Hairston 1993). Investigating food-web structure is crucial to the advancement of ecology, because it improves our ability to predict and to investigate fundamental processes responsible for the structure of all ecological systems containing consumers and their trophic resources.

ACKNOWLEDGMENTS

and J. Bengtsson are appreciated for their comments, ideas, and constructive criticisms. Special thanks go to J. A. Dunne for extensive editorial assistance. This research partially fulfilled the requirements for a Ph.D. in energy and resources at the University of California at Berkeley. Support was provided by the U.S. National Institute of Environmental Health Sciences (U.S. Public Health Service grant P42 ES 04705), the National Science Foundation (grants BIR-9207426 and DEB-9208122), and the Ford Foundation.

LITERATURE CITED


The American Naturalist

952


Associate Editor: Peter Chesson