

Effects of taxonomic and trophic aggregation on food web properties

George Sugihara · Louis-Félix Bersier · Kenneth Schoenly

Abstract Historically, ecologists have been more interested in organisms feeding at the tops of food chains than in organisms feeding at or near the bottom. The problem of taxonomic and trophic inconsistency within and among described food webs is central to criticisms of contemporary food web research. To study the effects of taxonomic and trophic aggregation on food web properties, 38 published food webs, each containing a large fraction of investigator-defined biological species, were systematically aggregated by taxonomy and trophic (functional) group similarity. During each step of taxonomic and trophic aggregation, eight food web properties (MIN, MAX, mean chain lengths; the fractions of basal, intermediate and top species; the ratio of all links by the total number of species, L/S ; and rigid circuits) were calculated and their departures from the original, unaggregated version were recorded. We found only two properties showing wide systematic departure from initial values after both taxonomic and trophic group aggregation: the fraction of basal species and L/S . One reason for the relative 'constancy' of the six other properties was due in part to large numbers of trophically equivalent species (species with identical sets of prey and predators) found in these and other published webs. In the 38 webs, the average number of trophically

equivalent species was 45% and ranged from a low of 13% in aquatic webs to a high of 71% in certain terrestrial systems (i.e., carrion webs). Six of the eight properties (MIN, MAX and mean chain lengths, the fractions of top and basal species, and the L/S ratio) were found to be more sensitive to taxonomic than to trophic aggregation. The relatively smaller variations observed in trophically lumped versions suggest that food web properties more aptly reflect functional, rather than taxonomic, attributes of real food webs. These findings parallel earlier trophic-based results, and bolster the conclusion that uneven lumping of taxonomic and trophic groups in published food web reports do not modify markedly the scaling behaviour of most of their descriptive properties.

Key words Food web scaling laws · Data resolution · Scale-invariance · Community structure

Introduction

Historically, ecologists have been more interested in organisms feeding at the tops of food chains than in organisms feeding at or near the bottom (e.g., Pimm 1982). The problem of trophic and taxonomic inconsistency within and among described food webs is central to criticisms of contemporary food web research (Cohen 1978, pp. 118–125; Pimm 1982, p. 168; Paine 1988; Lawton 1989, pp. 67–68; Cohen et al. 1990, pp. 20–22; Winemiller 1990; Pimm et al. 1991; Martinez 1991; Cohen et al. 1993; Hall and Raffaelli 1993; Polis and Winemiller 1996). Called into question is whether various measures of food web structure, such as network connectance or food chain length, are constrained by natural forces or more simply by the resolution of published data. Consequently, distinguishing food web properties that are robust to data resolution from those that are more sensitive and understanding the basis of their robustness and sensitivity are natural next steps in food web research.

Following initial work on the sensitivity of certain food web properties (Sugihara 1982, 1983; Auerbach 1984; Briand and Cohen 1984; Paine 1988), Sugihara

G. Sugihara · L.-F. Bersier (✉)¹
Scripps Institution of Oceanography,
University of California at San Diego,
La Jolla, CA 92093-0202, USA

K. Schoenly
Entomology and Plant Pathology Division,
International Rice Research Institute,
P.O. Box 933, 1099 Manila, Philippines

Present address:

¹ Zoological Institute,
Rue Emile-Argand 11,
CH-2007 Neuchâtel, Switzerland

et al. (1989) tested the robustness of several properties by varying the resolution of food web data through systematic aggregation of trophic (functional) groups. Using the Schoenly-Beaver collection of 60 community-type food webs as a database (in Cohen 1989), they found quite unexpectedly that six of eight commonly used food web properties (food chain lengths, predator-to-prey ratio, fractions of top and intermediate species, rigid circuits) were invariant over a wide range of data resolution after individual webs were aggregated to approximately one-half their original size. Two of the eight properties, the fraction of basal species and SC (the product of species richness S and web connectance C , see below), showed large systematic departures from initial conditions following increased trophic aggregation. These results suggested that most so-called scaling laws were generally valid, despite concerns about uneven resolution of trophic groups in the published data. It was concluded that these properties may be useful in cross-system comparisons, at least in published studies whose resolution of trophic groups vary within a factor of two. This analysis, however, left open the possibility that food web properties in individual webs may still be sensitive to aggregation based on differences in taxonomic resolution.

Consequently, in this study, we compare the effects of taxonomic and trophic aggregation on eight food web properties using webs from the same collection as in our earlier analysis. Specifically, we ask whether the differences we observe after lumping of taxonomic groups are as small as those found in our earlier trophic aggregation study. Because different steps of taxonomic aggregation (e.g. lumping congeneric species to produce a smaller genus-level web) can produce a variable number of different-sized versions of the original web, only trophically lumped webs of the same size and number as taxon-lumped versions were used in each comparison. We continue this work using edited webs from the Schoenly-Beaver collection because the original authors provided taxonomic refinement at the level of individual species in most cases and because higher taxonomic relations for most species in this collection have been analysed previously (Schoenly 1990). The criteria used for web selection and potential sources of taxonomic and sampling bias revealed by sensitivity analyses of species and links in this collection can be found in Schoenly et al. (1991, Appendix A, pp. 623–626).

Food web properties

We analysed eight properties that are customarily used to describe food webs.

(a–c) *Food chain length.* We calculated food chain length in three ways depending on whether chain length is determined as the length of the longest minimal path (MIN) in a web linking a top predator to a basal species (Sugihara et al. 1989; Cohen and Luczak 1992), the

length of the longest maximal path (MAX) connecting a top and basal species (Yodzis 1981; Briand 1983; Schoenly et al. 1991; Cohen and Luczak 1992), or the mean length of all maximal paths (μ ; Cohen 1978; Martinez 1991; Schoenly and Cohen 1991; Cohen and Luczak 1992). In the 38 original webs listed in Appendix 1, the range of MIN links is 1–3, the range of MAX links is 1–7, and μ ranges from 1.0 to 4.56.

(d) *Link density.* We calculated the link density, L/S , as the number of food web links L observed in the web divided by the total number of species S . This property is equivalent to the product SC in Sugihara et al. (1989), since the connectance C was measured as L divided by S^2 . The range of L/S values in the 38 unaggregated webs is 1.12–4.38 with a mean of 2.30 (Appendix 1).

(e–g) *Species fractions.* The fraction of top predators % T (species not reported as prey to any other species in the web), basal species % B (pure autotrophs or detritus), and intermediate species % I (species with predators and prey) in the 38 webs are approximately 0.47, 0.10 and 0.43, respectively (Appendix 1). Note that % T , % I and % B are not independent properties since their sum equals one. These properties show a wide scatter across webs of different sizes, and it has been suggested that this extreme variability is the sole reason for their scale-invariance (Hall and Raffaelli 1991). However, this high variability is not seen in all collections of food webs (e.g. Winemiller 1990; Havens 1992; Deb 1995), and these properties continue to provide meaningful information to food web researchers.

(h) *Rigid circuit.* Species trophic niches tend to be packed tightly together in that most predator overlap graphs are rigid circuit graphs (e.g. Sugihara 1982, 1983, 1984; Yodzis 1989; Pimm et al. 1991). From a graph theoretic perspective, a rigid circuit graph is one in which all circuitous paths through more than three points are shortened by a chord (Sugihara 1984). Sugihara et al. (1989) found that the rigid circuit property was present in all but three of the predator overlap graphs from the 60 community-type food webs of the Schoenly-Beaver collection.

These properties have been formerly analysed using large collections of published food webs (Cohen 1977, 1978, 1989; Pimm 1982; Sugihara 1982; Briand 1983; Briand and Cohen 1984; Cohen and Briand 1984; Sugihara et al. 1989; Schoenly et al. 1991; Havens 1992; Martinez 1993, 1994). A number of intriguing empirical generalisations have emerged from these analyses, of which several are regarded by some authors as scale-invariant: they stay roughly constant across a variety of webs spanning a wide range in the number of species they contain. However, together with criticisms of the data sets used to demonstrate these properties (e.g. Paine 1988; Polis 1991), recently compiled food webs cast some doubt on the validity of some of the scale-invariant laws

(e.g. Winemiller 1989; Warren 1990; Hall and Raffaelli 1991; Martinez 1991; Polis 1991; Havens 1992; Deb 1995). The least robust property appears to be the link density metric, the behaviour of which may depend on the prevalence of indiscriminate feeders in the system under investigation (Havens 1992, 1993; Bersier and Sugihara 1997). These findings led Martinez (1991, 1992, 1993, 1994), and Martinez and Lawton (1995) to put forward the hypothesis that most food web properties (all properties analysed here except rigid circuit) vary with the number of species in a web.

Whether the behaviour of the food web properties is scale-invariant or scale-dependent is peripheral to our study. The robustness of these properties to trophic and taxonomic aggregation is an important feature that any investigator should be aware of, whatever the scaling behaviour of the properties. Nevertheless, the results of our study may be useful in assessing the validity, or lack thereof, of the scale-invariant hypothesis.

Methods of aggregation

To study aggregation and the resulting loss of resolution in food web data, different methods were used to distinguish between the effects of taxonomic aggregation from trophic aggregation. Both aggregation methods were applied to each of the 38 food webs listed in Appendix 1.

Taxonomic aggregation was performed at each of four taxonomic 'steps' along the hierarchy: genus–family–order–class. Since aggregating a web beyond the rank of class effectively strips it of most taxonomic as well as trophic detail, lumping ceased when the reduced web contained the greater of either 10 aggregated species or class-level resolution. However, since aggregating at the class level was possible for 3 webs only, the results of these will generally not be considered here. The use of finer taxonomic subdivisions, such as superclass, infra-class and suborder, was avoided because these categories are typically reserved for large and taxonomically diverse groups (e.g. fishes and insects; Hickman et al. 1984). In the first step of taxonomic aggregation, each set of congeneric species (if any) were lumped into single clusters, producing a smaller genus-level web; in the second step, all confamilial genera (if any) were lumped to form a smaller family-level web; and so on. Web categories with no obvious taxonomic affiliation (e.g. detritus, older organic debris) were left in their originally reported state. Family, order and class affiliations for most species are usually available from the original food web reports; in remaining instances we consulted various taxonomic authorities (Cloudsley-Thompson 1958; Jordan 1963; Borrer et al. 1976; Pennak 1978; Clements 1981; Anderson and Knox Jones 1984).

Trophic aggregation was performed one species at a time, using the clustering algorithm of Sugihara et al. (1989) based on increasing trophic similarity (see Martinez 1991 for an alternative and more extensive set of

algorithms for trophic aggregation). Trophic similarity for each species pair was calculated as the number of predators and prey shared in common, divided by the total number of predators and prey in their union. Like other measures of faunal similarity, this statistic is taken over the interval (0,1). Thus, each step of the trophic aggregation procedure involved lumping the two species with the most similar sets of predators and prey. The path for trophically aggregating a web is unambiguous if similarities computed from the species pairs are unique. However, if computed similarities for two or more species pairs are identical, which is the case for trophically equivalent taxa, the number of paths for trophically aggregating a web increases. To resolve this problem, species pairs belonging to the same similarity threshold were aggregated at random, one pair at a time, until the last pair from that threshold was aggregated.

In both algorithms, taxonomic and trophic aggregates were defined as the union of their constituent species, and clusters of species were formed if two or more species shared a link in the original food web graph. During each step of both aggregations, the eight food web properties defined above were recalculated and their departures from the original, unaggregated version were recorded. To distinguish between the effects of taxonomic and trophic aggregation for a given food web property, we compared the two lumped versions of the same size, S (genus, family and order levels were contrasted with trophically based levels 1, 2 and 3, respectively). The lumping procedure ceased when each web contained fewer than 10 aggregated species. We adopted this '10 species stopping rule' to avoid artificial biases that appear in species-poor webs (Sugihara 1982; Sugihara et al. 1989; Bersier and Sugihara 1997).

Results

We first examined how the taxonomic and trophic aggregation processes affected the distribution of taxa in each trophic level. Basal species were assigned a trophic level of 1, other species were assigned a trophic level equal to the maximal path to a basal species plus one (Yodzis 1989). Figure 1 compares the original distribution with that obtained after each consecutive step of trophic and taxonomic aggregation. First, it is striking to see that taxonomic and trophic aggregation produced similar distributions in the three steps of aggregation (Fig. 1A–C). The first step of aggregation produced an excess of taxa at the second trophic level and a loss at the first, third and fourth levels (Fig. 1A). This indicates that basal species (trophic level 1), and predators in trophic levels 3 and 4 were lumped together in disproportionately higher proportions than herbivores and detritivores (trophic level 2). These disproportionalities held at the following step of aggregation (Fig. 1B). Continuing aggregation at the order stage and trophic step 3 strongly decreased the number of taxa in trophic level 2 (Fig. 1C), showing that lumping here affected

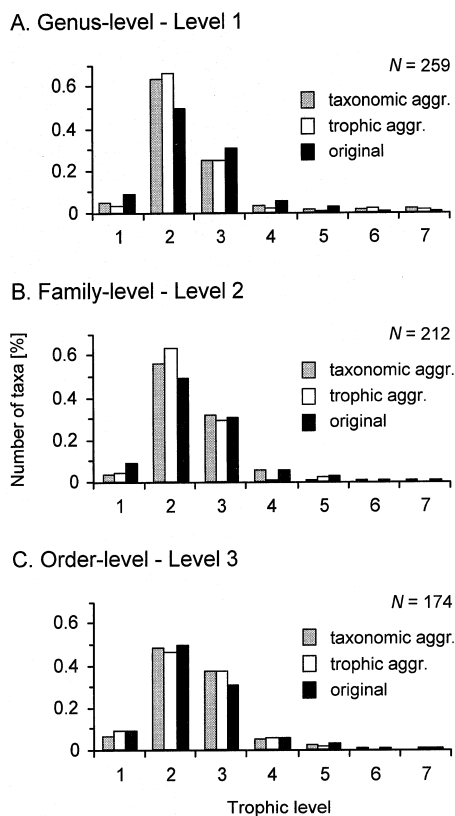


Fig. 1A–C Distributions of the relative number of taxa in each trophic level after each step of trophic and taxonomic aggregation. The original distribution is given for comparison. The number of taxa (N) used to compute the distributions for the aggregated webs is given in each panel

predominantly herbivores and detritivores. Taken together these test results demonstrate the ability of our aggregation algorithms to mimic the uneven lumping bias seen in published food web reports.

Aggregation results for eight properties are presented in Appendix 1 and Fig. 2. Webs were reduced from 9% (cases 4.2b and 35 in Appendix 1) to as low as 89% (case 18b) of their original size without violating the 10 species stopping rule. Most webs of Appendix 1 could not be aggregated above the degree of family (or step 2 trophic aggregation; order-level or step 3 trophic aggregation was possible in 11 of the 38 webs). Thus, sample sizes decreased at higher stages of aggregation and summary statistics became correspondingly less meaningful.

Figure 2 shows the distributions of fractional errors for each property after webs were reduced by three steps of taxonomic and trophic aggregation. The fractional error for each property was calculated as the difference between the aggregated and original value, divided by the original value. For each property we summarised variability in these aggregations using the sum of the ranges, over the first three stages of aggregation, of the fractional errors in each distribution. In taxonomically lumped webs, the sums of the three ranges for five of the eight properties were as follows: mean chain length

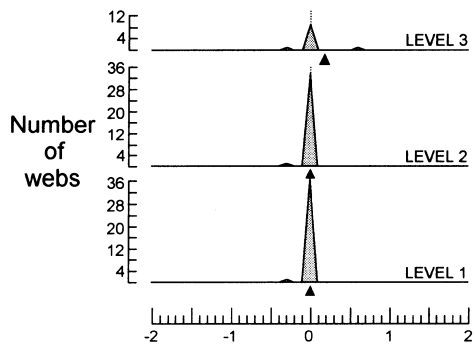
(2.620), L/S (1.899), intermediate species (3.924), top species (3.811) and basal species (12.851). In trophically aggregated webs, smaller sums were noted in five of these properties: mean chain length (1.177), L/S (1.679), intermediate species (4.204), top species (3.122) and basal species (8.046).

Inspection of the means of the distributions of fractional errors (the triangles in Fig. 2) confirmed that the basal species fraction displayed wide systematic departures from initial conditions, tending to rise markedly following increased aggregation (Fig. 2G). The average deviations were much smaller for the link density metric and for the fractions of top and intermediate species, and even smaller for the three measures of chain length. The differences found in the means of fractional errors for the same properties generally widened at higher stages of aggregation. Except for the MIN property, taxonomic and trophic aggregation produced average deviations that went in similar directions, and generally to a comparable extent. In sum, food web properties were slightly more sensitive following taxonomic aggregation than trophic aggregation and larger differences were found in both sets of aggregations as webs were lumped at ever-coarser stages of data resolution.

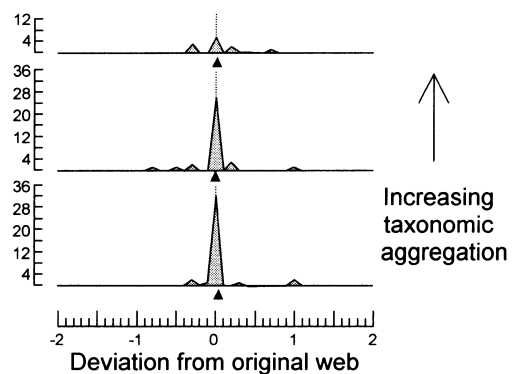
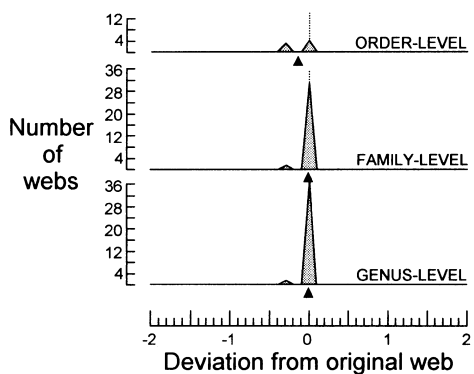
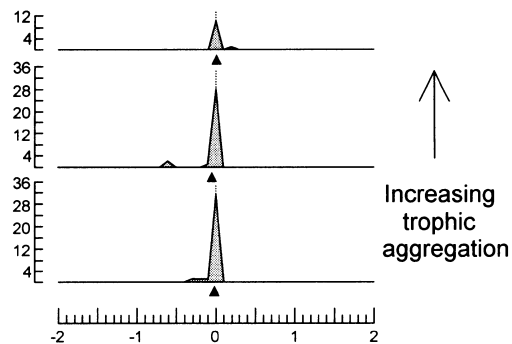
As reported earlier (Sugihara et al. 1989), one of the surprises of this analysis was the relative constancy of food chain lengths. Chain length based on the MIN criterion was once again more robust to variation in data resolution than the MAX statistic used by some researchers (Yodzis 1981; Briand 1983, Schoenly et al. 1991). MIN chain lengths remained constant throughout taxonomic and trophic aggregation in 82% and 84% of the cases, respectively (Appendix 1). By comparison, MAX chain lengths remained invariant in only 53% and 71% of the webs following taxonomic and trophic aggregation, respectively (Appendix 1). Of these two integer measures, MIN chain length was the more robust chain statistic in both taxonomically and trophically lumped webs; however, like most of the other properties discussed above, the variability of MIN and MAX chains were slightly larger after taxonomic aggregation.

Sugihara et al. (1989) also reported that much of the apparent scale-invariance in food web properties was attributable to the presence of trophically equivalent species, i.e. species that have identical diets and predators. In the present analysis, when webs were reduced from their original size down to their last trophically equivalent species, the median fractional errors for seven of these properties, taken from taxonomically and trophically lumped webs, were as follows: MIN length = 0, 0; MAX length = 0, 0; μ length = 0.010, 0.006; top = -0.017, -0.024; basal = 0.062, 0.100; intermediate = 0.061, 0.046; L/S = -0.004, -0.033, respectively. If we then compare these values to the same aggregations taken beyond the degree of trophic equivalence down to 10 species or class-stage aggregation, median errors for all but the first two properties became noticeably larger: MIN length = 0, 0; MAX length = 0, 0; μ length = -0.020, 0.046; top = -0.077,

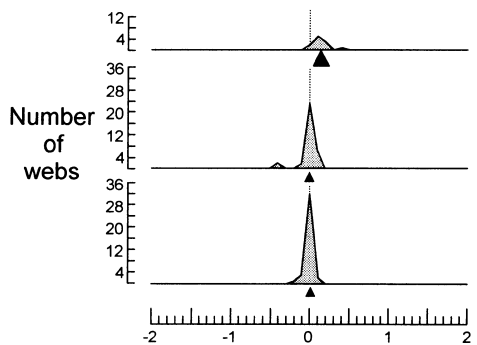
A. MIN chain length



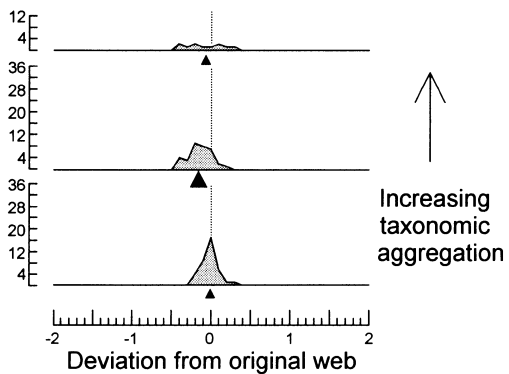
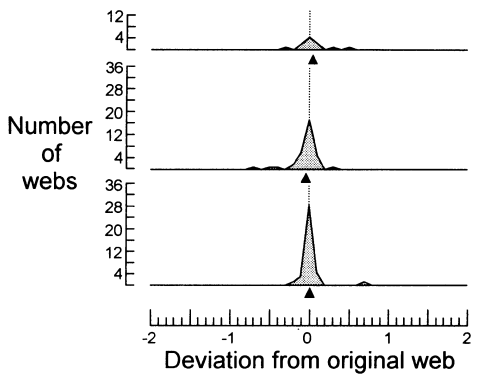
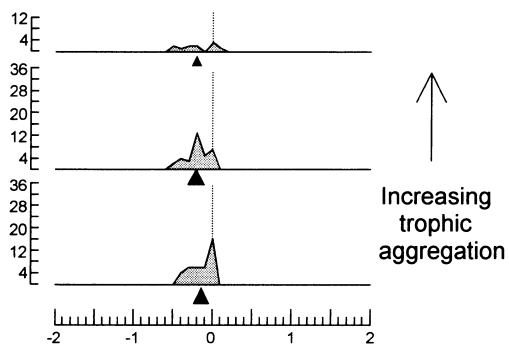
B. MAX chain length



C. Mean chain length



D. Link density



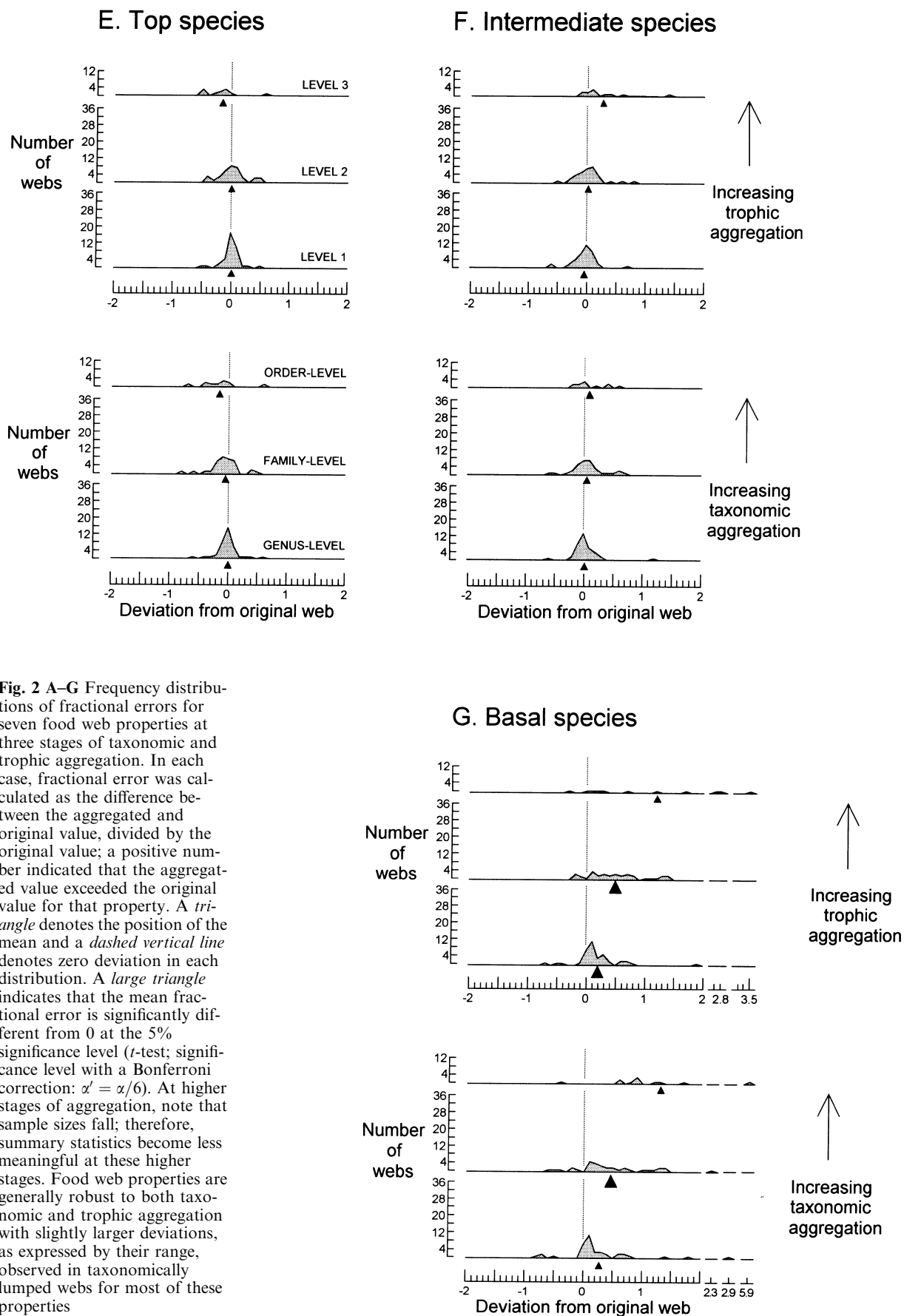


Fig. 2 A–G Frequency distributions of fractional errors for seven food web properties at three stages of taxonomic and trophic aggregation. In each case, fractional error was calculated as the difference between the aggregated and original value, divided by the original value; a positive number indicated that the aggregated value exceeded the original value for that property. A *triangle* denotes the position of the mean and a *dashed vertical line* denotes zero deviation in each distribution. A *large triangle* indicates that the mean fractional error is significantly different from 0 at the 5% significance level (*t*-test; significance level with a Bonferroni correction: $\alpha' = \alpha/6$). At higher stages of aggregation, note that sample sizes fall; therefore, summary statistics become less meaningful at these higher stages. Food web properties are generally robust to both taxonomic and trophic aggregation with slightly larger deviations, as expressed by their range, observed in taxonomically lumped webs for most of these properties

-0.108; basal = 0.800, 0.304; intermediate = -0.024, 0.059; L/S = -0.119, -0.206. Thus, once webs were aggregated beyond the degree of trophic equivalence, most of these seven properties became slightly more sensitive to coarser degrees of data resolution. Nonetheless, even as webs were collapsed beyond trophic equivalence and/or one-half their original size, fractional errors for most of these statistics remained very small.

In trophically aggregated versions, the sequence to which the three trophic position properties were lumped beyond trophic equivalence generally followed the trend: intermediate, top, basal species. In cross-habitat comparisons, however, aquatic systems appeared to be an outlier to this trend, with 3 of 6 webs (cases 33a, 34, 36 in Appendix 1) following a different sequence (basal, intermediate, top). Basal species appeared to be lumped sooner in aquatic webs because different phytoplankton species were more alike trophically (i.e. they have no prey and tend to have similar sets of predators) than other species in the web. This feature would be masked, however, in webs with coarsely resolved basal species.

The rigid circuit property is present in 57 out of the 60 webs of the Schoenly-Beaver collection and present in almost every web of the Briand-Cohen catalogue of 113 webs (Sugihara et al. 1989). The last column of Appendix 1 shows that the rigid circuit property is present in 34 out of the 38 webs before aggregation commenced. We also reported that if a web was initially rigid, it remained rigid for every step of the trophic aggregation procedure. This finding was confirmed in the 34 webs in both taxonomically and trophically lumped versions (Appendix 1): Of the 4 webs not initially rigid (cases 31, 34, 37, 39), 2 remained non-rigid throughout trophic aggregation (cases 31, 37) but all 4 became rigid after taxonomic aggregation. Unlike the other seven properties, the robustness of the rigid circuit property remained fixed after webs were aggregated beyond the degree of trophic equivalence.

Discussion

Most of the eight food web properties included in this analysis appeared relatively insensitive to the degree of data resolution in taxonomically and trophically lumped versions even after webs were reduced to greater than 50% of their original size. Not surprisingly, after a few webs had been aggregated to 70–89% of their original size, even the sturdiest food web properties became sensitive to these coarser degrees of data resolution. For example, food chain lengths in some webs became shorter at higher stages of aggregation (cases 15l, 18b in Appendix 1, Fig. 2A–C). Compared to trophic aggregation, all but two of the eight properties (intermediate species, rigid circuits, Fig. 2F, Appendix 1) were more sensitive to taxonomic aggregation. One reason for these largely scale-independent results is, in part, the presence of large numbers of trophically equivalent taxa reported

in published food webs. These results are in general agreement with our earlier trophic-based findings (Sugihara et al. 1989) and appear to bolster the conclusion that uneven reporting of taxonomic and trophic groups in published food webs does not modify markedly the scaling behaviour of most properties.

The basal species fraction displayed wide systematic departures from initial conditions following both taxonomic and trophic aggregation (Fig. 3G). In the majority of terrestrial webs, basal species remained largely intact throughout the aggregation process because this fraction generally contains more coarsely resolved (e.g. live insects) or taxonomically ambiguous (e.g. dead organic matter) categories compared to intermediate and top species fractions. On the other hand, basal species in 3 out of 6 aquatic webs were lumped sooner and with other basal species because they appear to be more similar trophically (e.g. phytoplankton species) than other aquatic denizens. These features contributed to the wide-ranging and systematic departures of basal species in the 38 webs analysed in this study. The extent to which this aquatic-terrestrial distinction is a product of nature or an artefact reflecting cultural differences in established methodologies, however, still remains unresolved.

In these 38 webs, the mean number of trophically equivalent species is 45% and ranges from a low of 13% in freshwater systems (cases 30–39, Table 1) to a high of 71% in carrion webs (cases 21.1a–24b). Variation in the number of trophic species in different systems is due in part to how the original authors counted basal species. For example, in carrion webs, trophically equivalent species tend to be concentrated at the first consumer level (detritus feeders) because carcass tissues are typically depicted as a single basal resource (e.g. Cornaby 1974; Jiron and Cartin 1981). On the other hand, aquatic ecologists tend to split basal species into one or more grazer-based and one or more detritus-based components in their studies. The result is a smaller fraction of trophically equivalent species in aquatic webs, especially at the primary consumer level. Although gall-forming tissue is also customarily treated as a single basal resource in gall-parasitoid webs (Askew 1971; Hawkins and Goeden 1984), the community of arthropod predators, parasitoids, hyperparasitoids and inquilines in these webs are more polyphagous, on average, than species found in other arthropod-rich systems (Schoenly et al. 1991). Consequently, most gall-associated species tend to have different sets of prey and predators, leaving correspondingly fewer numbers of trophically equivalent species.

Another study explored the effects of taxonomic aggregation on the food web properties in one large food web (Hall and Raffaelli 1991). The robustness of four properties analysed here was also examined (L/S , the fractions of top, intermediate and basal species), and the results were similar to ours: these properties were insensitive to the aggregation process. The fraction of basal species increased slightly, which parallels our result

(Fig. 2G). In contrast, they found that chain length was much affected by the taxonomic aggregation process that was used (Fig. 5, p. 831 in Hall and Raffaelli 1991), such that MIN chain length remained constant, but MAX chain length and the mean chain length decreased markedly. This discrepancy may be due to average food chain length being longer and degree of omnivory being higher in their web than in the webs analysed here. Aggregating omnivores at different trophic levels could tend to decrease the complexity of the pathways in a web, which would mainly affect MAX chain length, and to a lesser extent mean chain length.

Other methods of comparing the effects of taxonomic and trophic aggregation are conceivable. For example, one could imagine using an alternative criterion such as the number of discontinuities (or thresholds) encountered during trophic aggregation as the quantity for making trophic/taxonomic comparisons (J. Rice, personal communication). However, this method would add a second clustering algorithm to the trophic aggregation procedure and would increase the number of arbitrary decisions forced on the observer. We believe the *S*-based method is the most direct and the most sensible choice given that food web properties are customarily analysed against web size.

If one can imagine different ways of defining clusters of trophically similar taxa, one can also use different criteria to assign a trophic link between newly formed clusters. Here, we drew a link between two clusters if at least one species in one cluster was linked to at least one species in the other cluster. This procedure has been called the “maximum-linkage criteria” (Martinez 1991), and its validity has been questioned (Martinez 1993). Martinez gave preference to the “intermediate-linkage criteria”, where a link is drawn between two clusters if the number of pre-existent links is at least half the product of the number of species in each cluster. We did not use this method for two reasons. First, the aim of the aggregation algorithm is to mimic what researchers are prone to do when they assemble a food web. For example, if a trophic link is observed between two species each belonging to different aggregated taxa, the practice is to report it, not to ignore it until an arbitrary threshold is met. Second, the intermediate-linkage method has the undesirable tendency to generate disconnected webs, where clusters which do not meet the criteria for a drawn link can be separated from the original web (Martinez 1991). Again, we believe this does not mirror the way ecologists assemble webs. Because of these limitations, the intermediate-linkage method is not suited to analyses of the sensitivity of food web properties to aggregation.

In the present study, the differences found between trophically and taxonomically lumped webs have at least three important implications. (1) The relatively smaller variations observed in trophically lumped versions pro- pound the hypothesis that the scaling behaviour of the eight food web properties more aptly reflects functional, rather than taxonomic, attributes of real food webs. (2) As webs were lumped at ever-coarser degrees of resolution, differences between trophically and taxonomically lumped versions widened for most properties. Thus, this analysis is consistent with the empirical intuitions of field ecologists and systematists that trophically similar species do not split cleanly along taxonomic lines; that is, members of one taxon may frequently occupy different trophic roles in the same ecosystem (for population-based examples and a review, see Polis 1984). (3) Food web properties were more fragile after aggregating higher taxa (e.g. classes) than lower taxa (e.g. genera). Clearly, greater involvement of taxonomic specialists is needed in food web studies to ensure that the same degree of taxonomic refinement traditionally afforded to the large, rare and conspicuous organisms of a food web is also given to smaller, more common and less conspicuous organisms.

Finally, the generally small fractional errors found in both sets of aggregation suggest that food webs exhibit some degree of self-similarity when viewed across a wide range of trophic and taxonomic resolution. That is, as in the ideal snowflake, these properties persist at both fine and coarse scales of observation (Sugihara and May 1990). The degree to which these findings are a product of natural forces and/or human perception will likely remain unresolved for some time. However, as investigators turn their attention to more dynamic attributes of food web structure, such as temporal (e.g. Kitching 1987; Warren 1989; Winemiller 1990; Schoenly and Cohen 1991; Closs and Lake 1994; Deb 1995), spatial (e.g. Beaver 1985; Kitching 1987; Warren 1989; Winemiller 1990; Closs and Lake 1994) and ontogenetic (Pimm and Rice 1987) influences, new and larger sources of variability in their component properties will emerge. Explaining this variability is likely to be one of the next major challenges in food web research.

Acknowledgements We are grateful to Paul Dixon, Harold Hastings, Robert Paine, Stuart Pimm, Jake Rice, Dave Raffaelli and the anonymous reviewers for their comments on this and earlier versions of the manuscript. We also thank Roger Beaver for his earlier assistance in the compilation and editing of some of the food webs used in this study. G.S. was supported by NSF grant BSR 88-07404, ONR grants N00014-92-J-4068 and N00014-95-1-0034, and by endowment income from the John Dove Issacs Chair in Natural Philosophy, L.-F.B. by the Swiss National Science Foundation, and by the Ciba-Geigy Jubilee Foundation.

Appendix 1 Properties of 38 food webs aggregated by taxonomy and trophic similarity. Community-type food webs from the Schoenly-Beaver collection with 11 or more taxa were used. Aggregation stopped in each case when the lumped web had fewer than 10 taxa (see text for details). Case numbers follow the coding system in Schoenly (1990) and Schoenly et al. (1991). Predation matrices, species lists and bibliographical information for the 38 original webs are available in Cohen (1989). For each web, the first row gives eight properties of the original, unaggregated version; pairs of values in subsequent rows reveal the effects of trophic (*T*) and taxonomic aggregation on food web properties as the web is reduced in size (*G* genus-stage, *F* family-stage, *O* order-stage, *C* class-stage taxonomic aggregations). *S* is the number of taxa in the original or aggregated web. The sum of top, basal and middle fractions of species exceeds 1 in some webs due to rounding error

Case no.	Description of food web	Comparison or lumped size (<i>S</i>)	Food web property				Fraction of top species	Fraction of basal species	Fraction of intermediate species	Link density <i>L/S</i>	Rigid circuit
			MIN chain length	MAX chain length	Mean chain length (μ)	Fraction of species					
1a	Pitchers (<i>Nepenthes albobmarginata</i>) West Malaysia	Original	3	4	2.5	0.368	0.158	0.474	1.84	Yes	
		Tr1/G Tr2/F	3/3 2/2	4/4 4/4	2.57/2.40 2.55/2.33	0.353/0.412 0.385/0.385	0.177/0.177 0.231/0.231	0.471/0.412 0.385/0.385	1.77/1.65 1.46/1.54	Yes/yes Yes/yes	
1b	Pitchers (<i>Nepenthes ampullaria</i>) West Malaysia	Original	2	4	3	0.222	0.167	0.611	2.33	Yes	
		Tr1/G Tr2/F	2/2 2/2	4/4 4/4	3.08/2.77 3.02/2.65	0.231/0.308 0.300/0.300	0.231/0.231 0.300/0.300	0.539/0.462 0.400/0.400	2.00/1.85 1.50/1.50	Yes/yes Yes/yes	
4.2a	Tree holes (<i>Tristania conferta</i> , <i>Ficus</i> sp.) Australia	Original	2	7	4.56	0.083	0.25	0.667	2	Yes	
		Tr1/G Tr2/F	2/2 2/2	6/5 6/5	4.00/3.45 4.00/3.45	0.091/0.091 0.091/0.091	0.273/0.273 0.273/0.273	0.636/0.636 0.636/0.636	1.64/1.64 1.64/1.64	Yes/yes Yes/yes	
4.2b	Tree holes (<i>Tristania conferta</i> , <i>Ficus</i> sp.) Australia	Original	2	3	2.33	0.182	0.364	0.455	1.36	Yes	
		Tr1/G Tr2/F	2/2 2/2	3/3 3/3	2.33/2.25 2.33/2.25	0.200/0.200 0.200/0.200	0.400/0.400 0.400/0.400	0.400/0.400 0.400/0.400	1.10/1.10 1.10/1.10	Yes/yes Yes/yes	
8b	Oak-birch-pine canopy Central Europe	Original	2	2	2	0.52	0.08	0.4	1.12	Yes	
		Tr1/G	2/2	2/2	2.00/2.00	0.421/0.421	0.105/0.105	0.474/0.474	1.11/1.21	Yes/yes	
11	Young pines Oxshott Heath, UK	Original	3	4	3.57	0.174	0.087	0.739	2.09	Yes	
		Tr1/G Tr2/F	3/3 3/3	4/4 4/4	3.57/3.78 3.57/3.77	0.182/0.182 0.267/0.200	0.091/0.046 0.133/0.067	0.727/0.773 0.600/0.733	2.05/2.18 1.60/2.00	Yes/yes Yes/yes	
12	Mistletoe fauna South Texas, USA	Original	3	4	2.55	0.696	0.044	0.261	1.13	Yes	
		Tr1/G Tr2/F	3/3 3/3	4/4 4/4	2.55/2.55 2.61/2.61	0.696/0.696 0.667/0.667	0.044/0.044 0.048/0.048	0.261/0.261 0.286/0.286	1.13/1.13 1.14/1.14	Yes/yes Yes/yes	
15l	Oak gall system Wytham Wood, UK	Original	3	7	4.28	0.371	0.016	0.613	2.98	Yes	
		Tr1/G	2/2	5/6	3.43/3.89	0.546/0.364	0.046/0.045	0.409/0.591	1.96/2.55	Yes/yes	
15m	Oak gall system Wytham Wood, UK ^a	Original	3	6	3.72	0.441	0.17	0.542	2.39	Yes	
		Tr1/G	3/3	5/6	3.46/4.03	0.455/0.409	0.046/0.045	0.500/0.546	1.73/2.32	Yes/yes	
16a	<i>Atriplex canescens</i> galls South California, USA ^b	Original	2	5	3.25	0.389	0.028	0.583	2.14	Yes	
		Tr1/G Tr2/F	2/2 2/2	5/5 2/6	3.44/3.18 1.83/3.67	0.381/0.333 0.333/0.333	0.048/0.048 0.067/0.067	0.571/0.619 0.600/0.600	1.71/1.91 1.53/2.00	Yes/yes Yes/yes	
16b	<i>Atriplex polycarpa</i> galls South California, USA ^b	Original	2	5	3.25	0.351	0.027	0.622	2	Yes	
		Tr1/G Tr2/F	2/2 2/2	5/5 2/6	3.38/3.19 2.00/3.68	0.296/0.370 0.263/0.263	0.037/0.037 0.053/0.053	0.667/0.593 0.684/0.684	2.04/2.00 1.63/2.21	Yes/yes Yes/yes	
18a	Oak logs (1st year) North Carolina, USA ^b	Original	3	4	2.63	0.553	0.043	0.404	1.36	Yes	
		Tr1/G Tr2/F Tr3/O	3/3 3/3 3/2	4/4 4/4 4/5	2.63/2.63 2.79/2.71 3.12/2.88	0.578/0.556 0.467/0.467 0.250/0.417	0.044/0.044 0.067/0.033 0.167/0.083	0.378/0.400 0.467/0.500 0.583/0.500	1.33/1.36 1.40/1.43 1.33/1.83	Yes/yes Yes/yes Yes/yes	

18b	Oak logs (> 3 years) North Carolina, USA ^b	Original Tr1/G Tr2/F Tr3/O Tr4/C	87 82 52 19 10	3 3/3 3/3 3/2 2/2	4 4/4 4/4 4/3 2/4	2.04 2.04/2.06 2.20/2.20 2.84/1.88 2.00/2.00	0.782 0.817/0.768 0.750/0.635 0.421/0.526 0.400/0.400	0.023 0.024/0.024 0.038/0.038 0.105/0.158 0.100/0.300	0.195 0.159/0.207 0.212/0.327 0.474/0.316 0.500/0.300	1.32 1.24/1.32 1.21/1.58 1.32/1.47 1.20/1.40	Yes Yes/yes Yes/yes Yes/yes Yes/yes
18c	Pine logs (1st year) North Carolina, USA ^b	Original Tr1/G Tr2/F Tr3/O	90 81 52 16	3 3/3 3/3 3/2	3 3/3 3/3 3/5	2.32 2.29/2.35 2.39/2.41 2.65/3.00	0.589 0.568/0.605 0.481/0.577 0.500/0.563	0.033 0.037/0.037 0.058/0.019 0.125/0.063	0.378 0.395/0.358 0.462/0.404 0.375/0.375	1.69 1.72/1.56 1.44/1.42 1.25/1.56	Yes Yes/yes Yes/yes Yes/yes
18d	Pine logs (> 3 years) North Carolina, USA ^b	Original Tr1/G Tr2/F Tr3/O	36 34 27 16	3 3/3 3/3 3/2	3 3/3 3/3 3/3	1.9 1.90/1.84 1.93/1.90 2.32/1.86	0.667 0.647/0.706 0.593/0.667 0.438/0.625	0.028 0.029/0.029 0.037/0.037 0.063/0.063	0.306 0.324/0.265 0.370/0.296 0.500/0.313	1.36 1.38/1.27 1.37/1.33 1.50/1.31	Yes Yes/yes Yes/yes Yes/yes
21.1a	Toad carrion Guauna-caste, Costa Rica	Original Tr1/G Tr2/F	26 17 11	1 1/1 1/1	1 1/2 1/2	1.00/1.67 1.00/1.30	0.808 0.882/0.706 0.818/0.636	0.192 0.118/0.059 0.182/0.091	0 0.000/0.235 0.000/0.273	1.89 1.24/2.35 0.91/1.18	Yes Yes/yes Yes/yes
21.2a	Toad carrion de Osa, Costa Rica	Original Tr1/G Tr2/F	50 31 18	2 2/2 2/2	2 2/2 2/2	1.68 1.63/1.86 1.69/1.71	0.26 0.290/0.419 0.389/0.389	0.14 0.065/0.032 0.111/0.056	0.6 0.645/0.548 0.500/0.556	2.62 1.65/2.36 1.39/1.50	Yes Yes/yes Yes/yes
22	Dog carcass Central Valley, Costa Rica	Original Tr1/G Tr2/F Tr3/O	27 24 20 10	2 2/2 2/2 2/2	2 2/2 2/2 2/2	1.68 1.70/1.73 1.77/1.42 1.91/1.60	0.852 0.917/0.833 0.900/0.900 0.800/0.800	0.037 0.042/0.042 0.050/0.050 0.100/0.100	0.111 0.042/0.125 0.050/0.050 0.100/0.100	1.74 1.00/1.83 1.00/1.00 1.00/1.10	Yes Yes/yes Yes/yes Yes/yes
23.1a	Carrion Aden Crater (day 2), New Mexico, USA	Original Tr1/G Tr2/F	18 15 11	2 2/2 2/2	2 2/2 2/2	1.36 1.39/1.33 1.30/1.20	0.889 0.867/0.867 0.818/0.818	0.056 0.067/0.067 0.091/0.091	0.056 0.067/0.067 0.091/0.091	1.28 1.27/1.27 1.00/1.00	Yes Yes/yes Yes/yes
23.2a	Carrion Hueco Mountains (day 9), Texas, USA	Original Tr1/G Tr2/F	27 21 18	2 2/2 2/2	4 4/3 4/5	2.55 2.65/2.21 2.65/2.77	0.185 0.095/0.191 0.111/0.167	0.037 0.048/0.143 0.056/0.056	0.778 0.857/0.667 0.833/0.778	2.67 2.29/2.05 2.11/2.22	Yes Yes/yes Yes/yes
23.3a	Carrion White Sands (day 8), New Mexico, USA	Original Tr1/G Tr2/F	21 16 12	2 2/2 2/2	2 2/2 2/2	1.61 1.48/1.64 1.59/1.46	0.762 0.813/0.750 0.750/0.750	0.048 0.063/0.063 0.083/0.083	0.191 0.125/0.188 0.167/0.167	1.91 1.06/1.94 1.08/1.25	Yes Yes/yes Yes/yes
24a	Carrion Franklin Mountains (day 4), Texas, USA	Original Tr1/G Tr2/F	25 21 15	2 2/2 2/2	3 3/4 3/3	1.87 1.87/2.14 2.00/1.96	0.52 0.524/0.524 0.333/0.400	0.04 0.048/0.095 0.067/0.133	0.44 0.429/0.381 0.600/0.467	2.6 1.86/2.76 1.73/2.13	Yes Yes/yes Yes/yes
24b	Carrion Franklin Mountains (day 14), Texas, USA	Original Tr1/G	14 11	2 2/2	2 2/2	1.67 1.65/1.75	0.714 0.818/0.636	0.071 0.091/0.091	0.214 0.091/0.273	2.14 1.27/2.46	Yes Yes/yes
25a	Dung (all links) Illinois, USA	Original Tr1/G Tr2/F	17 16 14	2 2/2 2/2	2 2/2 2/2	2 2.00/2.00 2.00/2.00	0.471 0.438/0.438 0.429/0.429	0.059 0.063/0.063 0.071/0.071	0.471 0.500/0.500 0.500/0.500	2.06 2.06/2.13 1.64/1.71	Yes Yes/yes Yes/yes
25b	Dung (common links) Illinois, USA	Original Tr1/G Tr2/F	16 15 13	2 2/2 2/2	2 2/2 2/2	2 2.00/2.00 2.00/2.00	0.438 0.400/0.400 0.462/0.385	0.063 0.067/0.067 0.077/0.077	0.5 0.533/0.533 0.462/0.539	1.94 1.60/2.20 1.46/1.77	Yes Yes/yes Yes/yes
26	Bovine, equine dung West Texas, USA	Original Tr1/G Tr2/F	28 22 13	2 2/2 2/2	2 2/2 2/2	1.48 1.48/1.42 1.43/1.36	0.75 0.773/0.864 0.769/0.846	0.036 0.046/0.045 0.077/0.077	0.214 0.182/0.091 0.154/0.077	1.32 1.05/1.18 0.92/0.92	Yes Yes/yes Yes/yes

Appendix 1 (continued)

Case no.	Description of food web	Comparison or lumped size (S)	Food web property			Fraction of basal species	Fraction of intermediate species	Link density L/S	Rigid circuit
			MIN chain length	MAX chain length	Mean chain length (μ)				
28.1a	Dung (day 1, all links) New York, USA	Original	1	4	3	0.039	0.5	2.69	Yes
		Tr1/G	1/1	4/4	3.13/3.25	0.067/0.067	0.533/0.667	2.40/3.00	Yes/yes
		Tr2/F	1/1	4/1	3.18/1.00	0.091/0.091	0.546/0.818	2.36/2.82	Yes/yes
28.1b	Dung (day 1, established links only) New York, USA	Original	1	2	1.68	0.038	0.308	2.35	Yes
		Tr1/G	1/1	2/4	1.77/1.71	0.067/0.067	0.533/0.667	2.40/3.00	Yes/yes
		Tr2/F	1/1	2/2	1.83/1.57	0.091/0.091	0.546/0.364	2.36/2.00	Yes/yes
28.2a	Dung (day 5, all links) New York, USA	Original	2	4	3.06	0.029	0.486	4.17	Yes
		Tr1/G	2/2	4/4	3.11/3.13	0.046/0.046	0.409/0.591	3.27/4.18	Yes/yes
		Tr2/F	2/2	4/2	3.14/1.60	0.067/0.067	0.467/0.733	3.27/3.00	Yes/yes
28.2b	Dung (day 5, established links only) New York, USA	Original	2	3	2.49	0.03	0.485	3.67	Yes
		Tr1/G	2/2	3/3	2.53/2.55	0.048/0.048	0.381/0.571	2.48/3.62	Yes/yes
		Tr2/F	2/2	3/2	2.58/1.50	0.067/0.067	0.467/0.667	2.80/2.80	Yes/yes
30	Thermal spring, Yellowstone National Park, USA	Original	2	2	2	0.067	0.6	2.87	Yes
		Tr1/G	2/2	2/2	2.00/2.00	0.083/0.083	0.500/0.500	2.08/3.00	Yes/yes
		Tr2/F	2/2	2/2	2.00/2.00	0.091/0.091	0.455/0.455	1.73/2.73	Yes/yes
31	Crocodile Creek, Lake Nyasa, Africa ^a	Original	3	4	1.84	0.152	0.303	1.64	No
		Tr1/G	3/3	4/4	1.89/1.87	0.167/0.167	0.333/0.333	1.70/1.70	No/no
		Tr2/F	3/3	4/4	2.09/1.90	0.192/0.192	0.308/0.385	1.58/1.69	No/yes
33a	River Clydach, South Wales, UK ^b	Tr3/O	2/3	4/4	2.03/1.97	0.191/0.238	0.381/0.429	1.62/1.91	No/yes
		Original	2	3	2.19	0.241	0.483	3.62	Yes
		Tr1/G	2/2	3/3	2.19/2.21	0.259/0.259	0.444/0.482	3.26/3.59	Yes/yes
34	Deep Creek, Idaho-Utah, USA ^b	Tr2/F	2/2	3/3	2.21/2.22	0.250/0.292	0.458/0.458	2.75/3.29	Yes/yes
		Tr3/O	3/2	3/2	2.47/2.00	0.273/0.091	0.455/0.364	1.64/2.82	Yes/yes
		Original	3	3	2.16	0.531	0.281	4.38	No
35	Doe Run, Kentucky (station 1), USA	Tr1/G	3/3	3/3	2.16/2.16	0.531/0.531	0.281/0.281	4.38/4.38	No/no
		Tr2/F	3/3	3/3	2.16/2.22	0.462/0.462	0.308/0.346	3.73/3.92	No/yes
		Tr3/O	3/2	3/2	2.26/1.60	0.385/0.308	0.308/0.385	2.15/2.54	Yes/yes
36	Morgan Creek, Kentucky, USA	Original	2	4	2.83	0.182	0.636	2.73	Yes
		Tr1/G	2/2	4/4	2.79/2.78	0.200/0.200	0.600/0.600	2.60/2.50	Yes/yes
		Tr2/F	2/2	4/4	2.79/2.78	0.200/0.200	0.600/0.600	2.60/2.50	Yes/yes
36	Morgan Creek, Kentucky, USA	Original	2	6	3.73	0.125	0.625	3.92	Yes
		Tr1/G	2/2	6/6	3.73/3.69	0.130/0.130	0.609/0.609	3.65/3.78	Yes/yes
		Tr2/F	2/2	6/6	3.73/3.73	0.100/0.150	0.600/0.600	3.10/3.45	Yes/yes
36		Tr3/O	2/2	7/6	4.40/3.88	0.154/0.231	0.615/0.539	2.85/2.92	Yes/yes

37	Streambeds Aire, Nidd and Wharfe Rivers, Yorkshire, UK	Original Tr1/G Tr2/F Tr3/O Tr4/C	60 55 46 31 20	3 3/3 3/3 3/3 3/3	4 4/4 4/4 4/4 5/5	3.34 3.36/3.20 2.95/3.18 3.49/3.23 3.65/3.10	0.317 0.309/0.327 0.283/0.283 0.161/0.323 0.150/0.300	0.117 0.127/0.127 0.152/0.152 0.194/0.226 0.250/0.350	0.567 0.564/0.546 0.565/0.565 0.645/0.452 0.600/0.350	3.08 2.98/2.87 2.85/2.87 2.42/2.45 2.45/1.90	No No/no No/no No/yes No/yes
39	Dee River, Wales UK	Original Tr1/G Tr2/F Tr3/O Tr4/C	34 33 32 19 11	3 3/3 3/3 3/3 2/2	4 4/4 4/4 4/5 2/3	2.04 2.04/2.06 2.04/2.09 2.34/3.02 1.80/1.97	0.412 0.424/0.394 0.438/0.375 0.368/0.263 0.273/0.273	0.265 0.242/0.273 0.219/0.281 0.263/0.421 0.182/0.546	0.324 0.333/0.333 0.344/0.344 0.368/0.316 0.546/0.182	3.12 3.15/3.18 3.19/3.16 2.53/3.37 2.27/2.00	No No/no No/no Yes/yes Yes/yes

^a Added since Sugihara et al. (1989)

^b Revised since Sugihara et al. (1989)

References

- Anderson S, Knox Jones J Jr (eds) (1984) Orders and families of recent mammals of the world. Wiley, New York
- Askew RR (1971) Parasitic insects. Elsevier, New York
- Auerbach MJ (1984) Stability, probability, and the topology of food webs. In: Strong DR, Simberloff D, Abele LG, Thistle AB (eds) Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, NJ, pp 413–436
- Beaver RA (1985) Geographical variation in food web structure in *Nepenthes* pitcher plants. *Ecol Entomol* 10:241–248
- Bersier LF, Sugihara G (1997) Scaling regions for food web properties. *Proc Natl Acad Sci USA*, 94:1247–1251
- Borner DJ, Delong DM, Triplehorn CA (1976) An introduction to the study of insects. Holt, Reinhart and Winston, New York
- Briand F (1983) Environmental control of food web structure. *Ecology* 64:253–263
- Briand F, Cohen JE (1984) Community food webs have scale-invariant structure. *Nature* 307:264–266
- Clements J (1981) Birds of the world: A checklist. Facts on File, New York
- Closs GP, Lake PS (1994) Spatial and temporal variation in the structure of an intermittent-stream food web. *Ecol Monogr* 64:1–25
- Cloudsley-Thompson JL (1958) Spiders, scorpions, centipedes and mites. Pergamon, London
- Cohen JE (1977) Ratio of prey to predators in community food webs. *Nature* 270:165–167
- Cohen JE (1978) Food webs and niche space. *Monogr Popul Biol* 11. Princeton University Press, Princeton, NJ
- Cohen JE (1989) Ecologists' co-operative web bank (ECOWeB) version 1.0. Machine-readable data base of food webs. Rockefeller University, New York
- Cohen JE, Briand F (1984) Trophic links of community food web. *Proc Natl Acad Sci USA* 81:4105–4109
- Cohen JE, Luczak T (1992) Trophic levels in community food webs. *Evol Ecol* 6:73–89
- Cohen JE, Briand F, Newman CM (1990) Community food webs: data and theory. Springer, Berlin Heidelberg, New York
- Cohen JE, Beaver RA, Cousins SH, DeAngelis DL, Goldwasser L, Heong KL, Holt R, Kohn AJ, Lawton JH, Martinez N, Omalley R, Page LM, Patten BC, Pimm SL, Polis GA, Rejmanek M, Schoener TW, Schoenly K, Sprules WG, Teal JM, Ulanowicz RE, Warren PH, Wilbur HM, Yodzis P (1993) Improving food webs. *Ecology* 74:252–258
- Cornaby BW (1974) Carrion reduction by animals in contrasting tropical habitats. *Biotropica* 6:51–63
- Deb D (1995) Scale-dependence of food web structures: tropical ponds as paradigm. *Oikos* 72:245–262
- Hall SJ, Raffaelli DG (1991) Food-web patterns: lessons from a species-rich web. *J Anim Ecol* 60:823–842
- Hall SJ, Raffaelli DG (1993) Food webs: theory and reality. *Adv Ecol Res* 24:187–239
- Havens KE (1992) Scale and structure in natural food webs. *Science* 257:1107–1109
- Havens KE (1993) Predator-prey relationships in natural community food webs. *Oikos* 68:117–124
- Hawkins BA, Goeden RD (1984) Organization of a parasitoid community associated with a complex of galls on *Atriplex* spp. in southern California. *Ecol Entomol* 9:271–292
- Hickman CP Jr, Roberts LS, Hickman FM (1984) Integrated principles of zoology. Times Mirror/Mosby, St Louis
- Jiron LF, Cartin VM (1981) Insect succession in the decomposition of a mammal in Costa Rica. *J NY Entomol Soc* 89:158–165
- Jordan DS (1963) The genera of fishes and a classification of fishes. Stanford University Press, Stanford, Calif
- Kitching RL (1987) Spatial and temporal variation in food webs in water-filled treeholes. *Oikos* 48:280–288
- Lawton JH (1989) Food webs. In: Cherrett JM (ed) Ecological concepts. Blackwell, Oxford, pp 43–78

- Martinez ND (1991) Artifacts or attributes? Effects of resolution on food-web patterns in Little Rock Lake, Wisconsin. *Ecol Monogr* 61:367–392
- Martinez ND (1992) Constant connectance in community food webs. *Am Nat* 139:1208–1218
- Martinez ND (1993) Effects of resolution on food web structure. *Oikos* 66:403–412
- Martinez ND (1994) Scale-dependent constraints on food-web structure. *Am Nat* 144:935–953
- Martinez ND, Lawton JH (1995) Scale and food-web structure – from local to global. *Oikos* 73:148–154
- Paine RT (1988) Food webs: road maps of interactions or grist for theoretical development. *Ecology* 69:1648–1654
- Pennak RW (1978) Freshwater invertebrates of the United States. Wiley, New York
- Pimm SL (1982) Food webs. Chapman and Hall, New York
- Pimm SL, Rice JC (1987) The dynamics of multispecies, multi-life-stage models of aquatic food webs. *Theor Popul Biol* 32:303–325
- Pimm SL, Lawton JH, Cohen JE (1991) Food web patterns and their consequences. *Nature* 350:669–674
- Polis GA (1984) Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? *Am Nat* 123:541–564
- Polis GA (1991) Complex trophic interactions in deserts: an empirical critique of food-web theory. *Am Nat* 138:123–155
- Polis GA, Winemiller K (eds) (1996) Food webs: integration of patterns and dynamics. Chapman and Hall, New York
- Schoenly K (1990) The predators of insects. *Ecol Entomol* 15:333–345
- Schoenly K, Cohen JE (1991) Temporal variation in food web structure: 16 empirical cases. *Ecol Monogr* 61:267–298
- Schoenly K, Beaver RA, Heumier TA (1991) On the trophic relations of insects: a food web approach. *Am Nat* 137:597–638
- Sugihara G (1982) Niche hierarchy: structure, organization and assembly in natural communities. PhD thesis, Princeton University, NJ
- Sugihara G (1983) Holes in niche space: a derived assembly rule and its relation to intervality. In: DeAngelis DL, Post WM, Sugihara G (eds) Current trends in food web theory. Report on a food web workshop. Oak Ridge National Laboratory, National Technical Information Service, no 5983. US Department of Commerce, Springfield, Va, pp 25–35
- Sugihara G (1984) Graph theory, homology and food webs. In: Levin SA (ed) Population biology. Proc Symp Appl Math vol 30. American Mathematical Society, Providence, RI pp 83–101
- Sugihara G, May RM (1990) Applications of fractals in ecology. *Trends Ecol Evol* 5:79–86
- Sugihara G, Schoenly K, Trombla A (1989) Scale invariance in food web properties. *Science* 245:48–52
- Warren PH (1989) Spatial and temporal variation in the structure of a freshwater food web. *Oikos* 55:299–311
- Warren PH (1990) Variation in food-web structure: the determinants of connectance. *Am Nat* 136:689–700
- Winemiller K (1989) Must connectance decrease with species richness? *Am Nat* 134:960–968
- Winemiller K (1990) Spatial and temporal variation in tropical fish trophic networks. *Ecol Monogr* 60:331–367
- Yodzis P (1981) The structure of assembled communities. *J Theor Biol* 92:103–117
- Yodzis P (1989) Introduction to theoretical ecology. Harper & Row, New York