

EFFECTS OF SAMPLING EFFORT ON CHARACTERIZATION OF FOOD-WEB STRUCTURE

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Abstract. A critical and poorly understood aspect of food-web theory concerns the possibility that variable observation effort, such as widely different sampling intensities among investigators, confounds structural food-web patterns. We evaluated this possibility by simulating the effects of variable observation effort on the structure of a food web including 77 insect species found inside the stems of 10 species of grasses. A highly detailed description of the trophic structure of this community was provided by an exhaustive sampling program involving dissection of 164 215 grass stems over 12 yr. Most significantly, the data describe the frequency at which each of the consumers and their 126 different trophic links were observed. During the simulated increase in sampling, consistent trends were observed among trophic-species webs as the species richness of these webs increased to a maximum of 73 trophic species. Connectance remained surprisingly constant, while the fractions of top and basal species decreased, and the fraction of intermediate species increased. These trends were much less consistent among taxonomic-species webs. This suggests that comparative analyses of connectance among trophic-species webs constructed with varying degrees of moderate observation effort are generally robust. In contrast, the fractions of species appear to require corrections for variable sample sizes for such analyses. These corrections may be easier to develop for trophic-species webs because of their relatively simple changes with sampling effort.

Key words: *food webs; observation effort; quantitative food-web patterns; sampling effort; scale; scale dependence; scale invariance; trophic species.*

INTRODUCTION

How much sampling effort is necessary to characterize food-web structure? The answer to this question would greatly enrich food-web theory, whose empirical base is limited by the magnitude and scope of sampling that biases specification of trophic relationships (May 1983, Lawton 1989, Schoener 1989, Winemiller 1990, Pimm et al. 1991, Cohen et al. 1993, Goldwasser and Roughgarden 1997, Holt et al., *in press*). Faced with a similar problem, biogeographers developed a rich literature addressing the effects of observation effort on species-diversity theory (see Magurran 1988, Colwell and Coddington 1994, Rosenzweig 1995, and Gaston 1996). Analogous contributions to the food-web literature are still in their infancy. One of the earliest of these contributions concerned the relatively low rate of increase of trophic links with species richness among food webs, previously referred to as the “link-species scaling law” (Cohen et al. 1990). The contribution as-

serted that the low rate was a result of inadequate effort spent documenting the structure of larger webs (Paine 1988). Researchers corroborated this critique by expending more effort to estimate trophic links in larger, more species-rich webs (Warren 1989, 1990, Winemiller 1989, 1990, Martinez 1991). This work led to the description of a higher rate of increase, referred to as the “constant connectance hypothesis,” that accurately predicts the variation of trophic links with species richness (Martinez 1992, 1993a, 1995, Warren 1994, 1995).

If biases resulting from variable observation effort continue to be corrected (Pimm et al. 1991, Goldwasser and Roughgarden 1993, Martinez 1993b, Bengtsson 1994), then food-web theory may efficiently develop as a general theory that quantitatively predicts relationships between structural (i.e., species richness) and functional (i.e., trophic interactions) aspects of biodiversity in terrestrial and aquatic systems (Martinez 1995, 1996). Finding precise patterns of interactions among all species within these habitats may lead to discovery of general mechanisms responsible for the structure and function of ecological

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systems (Martinez 1994, Lawton 1995). Without such corrections, large amounts of observational effort may be needed to go beyond the limitations imposed by poorly sampled webs that misrepresent the trophic structure of ecological systems (May 1983, Paine 1988, Lawton 1989, Winemiller 1990, Martinez 1991, Polis 1991, Cohen et al. 1993, Goldwasser and Roughgarden 1993, 1997).

To address these issues, we examined the sensitivity of food-web properties to sampling effort using an exceptionally complete composite web compiled in the United Kingdom between 1980 and 1992 (Dawah et al. 1995). This completeness was made possible though an extraordinary effort directed towards a taxonomically narrow group of 77 metazoan species found within the highly restricted endophytic environment of the stems of 10 co-occurring species of grasses. The food-web properties examined include the relationship between the number of species and the number of trophic links, along with the fractions of top, intermediate, and basal species. A trophic interaction or "link" occurs between species when a member of one species consumes and respire the biomass of (i.e., eats) a member of another or the same (cannibalistic) species. Top species have prey but no predators, intermediate species have predators and prey, and basal species have predators but no prey (Briand and Cohen 1984).

We analyzed two versions of food webs based on two types of species. Taxonomic species are morphologically and otherwise classified groups of organisms that taxonomists determine to belong to a specific group (Gaston 1996). Trophic species are functional groups that contain organisms that appear to eat and be eaten by the exact same species within a food web (Cohen and Briand 1984). A trophic species and a taxonomic species are identical when the trophic species contains only one taxon. Magnitudes of the trophic links of taxa aggregated into trophic species can vary substantially. Use of trophic species is a widely practiced (e.g., Cohen et al. 1990, Pimm et al. 1991, Martinez 1993b) and sometimes criticized (Paine 1988, Polis 1991) convention in food-web analysis. Such use reduces both taxonomic biases of investigators (Cohen 1989) and variation not explainable by current theory (Martinez 1993b, 1994).

Observational effort has played an important role in the development of food-web theory. Prominent early theories asserted that the ratio of links per species and the fractions of top, intermediate, and basal species are "scale invariant," or roughly constant among webs with widely varying species richness (e.g., Cohen et al. 1990, Pimm et al. 1991, Havens 1992, Bersier and Sugihara 1997). Critique of the low and variable amount of observational effort involved in early food-web data (Warren 1989, Winemiller 1990, Hall and Raffaelli 1991, Martinez 1991, Polis 1991, Goldwasser and Roughgarden 1993) led to rejection of the scale-invariant patterns, referred to as "food-web laws," in

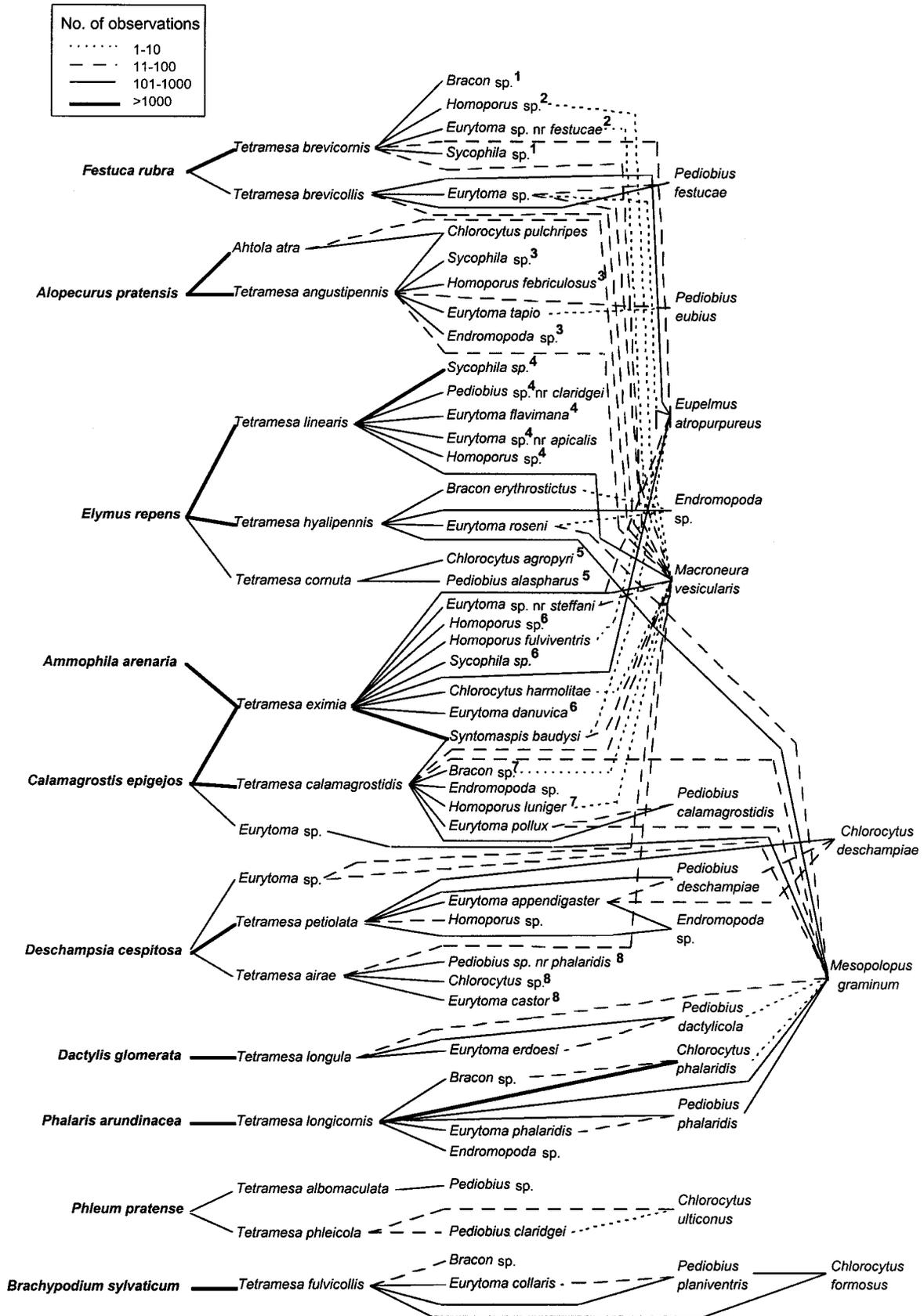
favor of "scale-dependent" patterns (Lawton 1995). The scale-dependent patterns assert that the fractions of top and basal species decrease with increasing species richness while the link-per-species ratio and the fraction of intermediate species increase (Martinez 1991, 1993a, b, 1994, Murtaugh 1994, Deb 1995, Martinez and Lawton 1995). Here, we briefly discuss the degree to which variable observational effort can inform this debate. More importantly, we also address variation in taxonomic focus and spatiotemporal boundaries of food webs (Yodzis 1993, Martinez 1995) by comparing our results to similar studies that focus on different taxa within different boundaries.

DATA AND METHODS

We analyzed the food web illustrated in Fig. 1. The web includes all vascular plants within the sampled quadrats plus all insects and trophic interactions found inside stems of plants. All plant stems within 2–7 m² quadrats containing only grasses were collected annually from 1980 to 1992 from 24 sites distributed within England and Wales. All of the 164 215 collected stems were dissected to identify the taxa and feeding relationships (see empirical details in Dawah et al. 1995). Whenever an insect was observed within a host or in close proximity to the remains of a host, a trophic link between the host and the consuming insect was observed. This is because larval and pupal development of stem-boring and parasitoid insects takes place within or on the host species. All such observed links were substantiated by observations of parasitoid oviposition and adult emergence. Identification of species was based on morphological characteristics supported by biological and behavioral observations and crossing experiments (Claridge 1959a, b, 1961, Graham et al. 1965, Dawah, 1987, 1988a, b, 1989, Henneicke et al. 1992, Claridge and Dawah 1994).

The food web contains 77 species of endophytic consumers within 10 species of grasses (Fig. 1). A total of 62 781 observed feeding events revealed 126 different trophic links averaging 546 (1 SD = 1 284) observations per feeding link. The number of times each species of consumer was observed is distributed log-normally between the rarest species (*Pediobius eubius*), observed 29 times, and the most frequent species (*Tetramesa linearis*), observed 11 036 times (Fig. 2a). Trophic links are similarly distributed between the rarest link (*Homoporus luniger-Macroneura vesicularis*), observed twice, and the most frequent link (*Elymus repens-Tetramesa linearis*), observed 11 036 times (Fig. 2b). Consistent with a large group of trophic ecologists' recommendations (Cohen et al. 1993), explicit and exhaustive construction methods conferred an unprecedented degree of taxonomic and trophic resolution on the web.

Samples from the widely dispersed quadrats appear to reflect a more contiguous community. This is shown by "beta diversity" analyses that measure differences



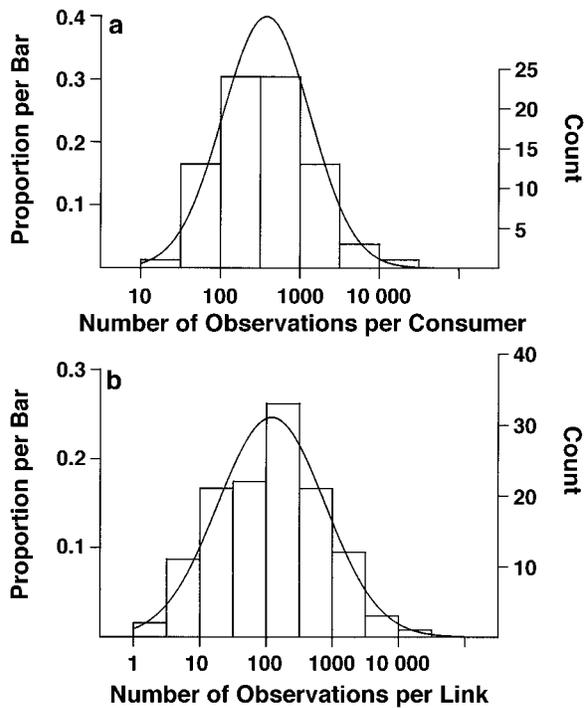


FIG. 2. Distribution of the number of species (a) and links (b) in Fig. 1 among classes describing the number of times each species and link was observed. The curves fitted to the distributions illustrate the close approximation of the distribution to the lognormal distribution.

between local species diversity at the quadrat level and regional species diversity of Great Britain. Only a few of the grasses, and hence their specialized herbivores, occur in isolated habitats. Most of the herbivores and all of the parasitoid species associated with each herbivore species accounting for 107 of the 126 observed links occur throughout Great Britain. Analyses of the parasitoid communities conducted by Dawah et al. (1995) demonstrated that beta diversity among quadrats is statistically indistinguishable from zero. Thus, the vast majority of links identified in the current web represent potential interactions among species that occur in all local communities. Analysis of this composite web's structure may be reasonably assumed to be similar to analysis of more contiguously defined community webs (Cohen 1978).

We designed a simulation to generate less sampled versions of our highly sampled web. To do this, the total number of dissected stems was divided by the number of times each trophic link was observed to

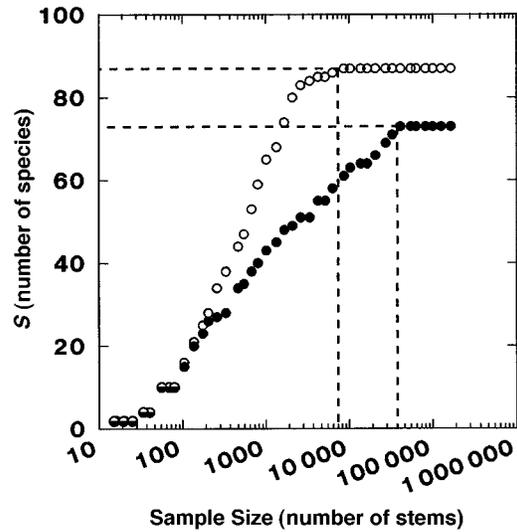


FIG. 3. Effects of mean sample size on number of taxonomic and trophic species (S) in taxonomic webs (empty circles) and trophic webs (filled circles). Half-filled circles are coincident taxonomic and trophic webs. Dashed lines denote the asymptotes discussed in the text.

estimate "mean sample size," or the mean number of randomly selected stems that would have to be dissected in order to observe each link for the first time. Sequences of "taxonomic webs," based on taxonomic species, and "trophic webs," based on trophic species, were constructed by sequentially including the most frequently observed links (i.e., links with the lowest mean sample size) and associated species until all observed links and species were present in the webs. This procedure creates a series of progressively lower frequency thresholds that links and species must attain in order to be included in the webs. After each addition, the resulting webs were analyzed for the number of taxonomic and trophic species (both referred to as S), the number of trophic links (L), and the fractions of top (T), intermediate (I), and basal (B) species. From this sequence, the 34 unique (i.e., non-identical) taxonomic webs based on mean sample sizes corresponding to every 0.1 increment of log mean sample size from 1.1 to 5.2 and their associated 34 trophic webs were analyzed further. Note that S in trophic webs depends on which links happen to be "sampled" and not on the full complement of links in the complete web (Fig. 1). Web properties were analyzed against S because S strongly correlates with observational effort (Fig. 3, Rosenzweig 1995), and because food-web the-

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FIG. 1. Food-web diagram of grass-feeding insects and their parasitoid consumers. Line thickness represents the total number of times each trophic link was observed. Grasses are in the left column in bold type. Herbivores are in the next column to the right, while parasitoids and hyper-parasitoids are in the three columns furthest on the right. Superscripts signify the taxa grouped into eight different trophic species in the fully sampled web. Contra Polis and Strong (1996), most species (82%) can be unambiguously assigned to discrete trophic levels.

ory focuses on properties as a function of S (e.g., MacArthur 1965, May 1974). This focus on S is currently referred to as an issue of "scale" (e.g., Briand and Cohen 1984, Havens 1992, Martinez 1994, Martinez and Dunne 1998).

Webs constructed in this manner represent the most likely sequence of webs to be observed as the ecological system is increasingly sampled. Therefore, the sequence provides plausible data describing specific webs that could result from increasing observational effort. Still, it is highly unlikely that each link would be observed in precisely the same sequence as indicated by mean sample sizes. Instead, one expects variations, with links being observed in samples smaller and larger than the links' mean sample size. We employed a Monte Carlo method to simulate this variation. The simulation assigned each link to an interval between zero and one proportional to the fraction of the 62 781 observed feeding events that the link constituted. Random numbers drawn from a uniform distribution between zero and one were used to randomly sample links according to the probabilities represented by the size of each link's interval. Simulated sample sizes were selected from 10 to 50 000 at increments of 0.075 log sample size. Sampling at each size was repeated 2000 times to generate 95% confidence intervals for the mean of each food-web property observed.

RESULTS AND DISCUSSION

The number of taxonomic and trophic species in the 34 webs increases as a function of mean sampling effort (Fig. 3). Taxonomic species and trophic species reach asymptotes near 87 and 73 at mean sample sizes of roughly 8000 and 40 000 stems, respectively. The trophic-species asymptote is attained after five times more sampling than the taxonomic-species asymptote, even though all taxa are present at less sampling. Apparently, further sampling results in the observation of trophic links that functionally distinguish taxa that appear trophically equivalent (Cohen 1989) under less intense sampling.

T , I , B , and L/S are strongly dependent on observational effort across the full range of sampling intensities among both taxonomic and trophic webs (Fig. 4). Properties of the webs including only abundant species and links are on the left sides of the graphs in Fig. 4, while the properties of webs that also include rarer species and links are on the right sides of the graphs. In taxonomic webs, T , I , and L/S show complex, non-linear relationships with S . Most dramatically, T increases from 0.5 to almost 0.7 and then plummets to 0.4 at the highest sampling intensities. After initial increases, I remains relatively flat at roughly 0.2 among webs with 23 to 83 species, and then rapidly increases at the highest sampling intensities. Variation of T and I among trophic webs is much simpler and relatively linear, while B is curvilinear. Regressions explain an average of 92% of the variance of T , I , and B with S

among trophic webs (Table 1). The natural log of B was regressed because B illustrated easily linearized curvilinearity and appears to be approaching the asymptote hypothesized by Martinez and Lawton (1995).

The weighted links in Fig. 1 depict two important points: (1) links at lower trophic levels are generally more frequent than those at higher levels, and (2) intermediate species typically consume more frequently than they are consumed. This explains the hump-shaped pattern of T among taxonomic webs. That is, less sampling ($S < 80$, Fig. 4; stems < 2000, Fig. 3) causes many of these intermediate species to appear as top species that dramatically reappear as intermediate species upon more sampling ($S > 80$, stems > 2000). Aggregation into trophic species limits the proliferation of apparent top species so that both T and I behave more regularly. B behaves similarly among both taxonomic and trophic webs. These webs attain their maximum complement of 10 taxonomic and trophic species at the basal level only in webs with $S > 43$ and 33, respectively.

We graphed the 95% confidence intervals from the Monte Carlo simulation (Fig. 4) by converting simulated sample size to species number using the average number of species observed at each sample size. The properties of the 34-web sequences generally coincide within the intervals, suggesting that the sequences successfully mimic a more stochastic sampling process. Still, deviations from the intervals are more frequent and extreme for taxonomic webs than for trophic webs, especially in taxonomic webs with roughly 80 species. Apparently, at least a few of the rare links that drastically lower T while also raising I and L/S among taxonomic webs are very likely to be observed before their mean sample size during a stochastic sampling procedure. This comparison of the 34 webs with Monte Carlo results makes the important point that systematic exclusion of rare links and species may result in some unusual webs having properties that fall outside the 95% confidence intervals of a stochastic sampling process. Alternatively, one could assert that stochastic sampling results in webs that contain unusually rare species and links. In both cases, trophic webs appear much less prone to these discrepancies.

L/S varies irregularly among both taxonomic- and trophic-species webs in Fig. 4d. This suggests that researchers should look for other relationships between L and S that may simplify observation of complexity. Connectance (C), a measure of complexity equal to the fraction of all possible links that are realized, has been hypothesized to be approximately independent of food-web size (Warren 1990, Martinez 1991). More formally, this "constant connectance hypothesis" referred to in the introduction asserts that directed connectance ($C = L/S^2$, Martinez 1991) is roughly constant among webs with variable S (Martinez 1992). Many recent data corroborate this hypothesis (Martinez 1993a, 1995, Warren 1994, 1995, Deb 1995), suggesting that

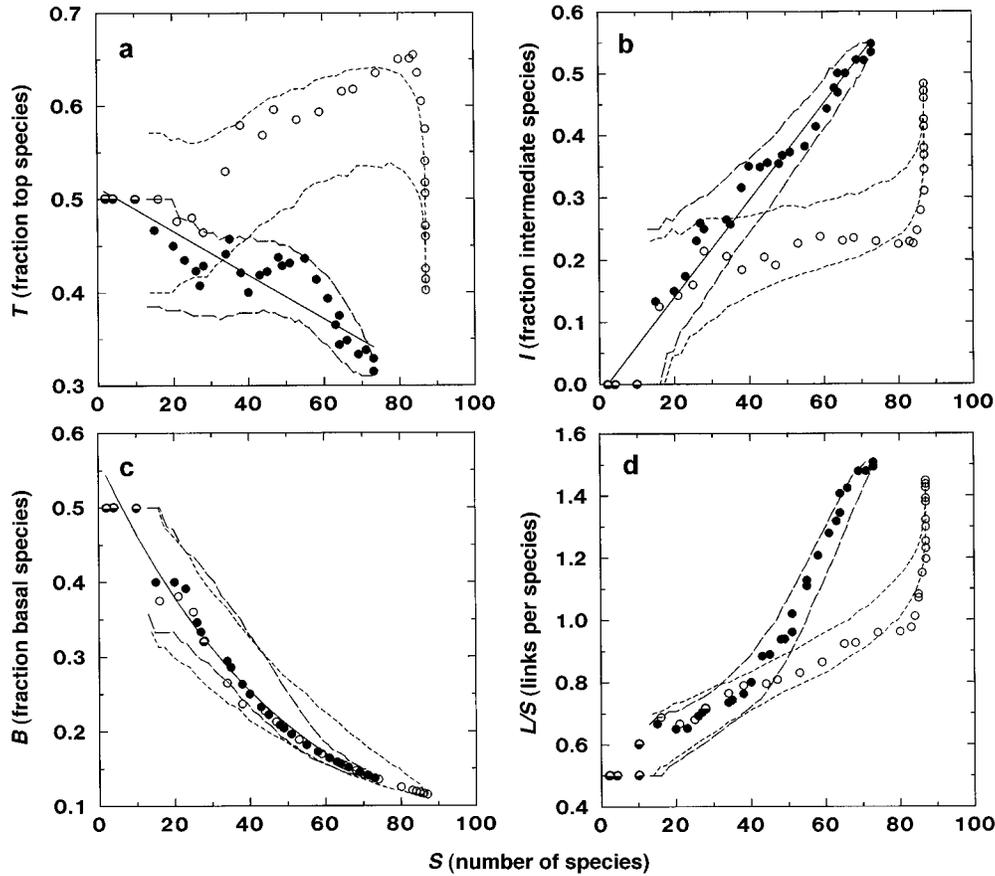


FIG. 4. Relationships between food-web properties and S among taxonomic webs (empty circles) and trophic webs (filled circles). Half-filled circles indicate coincident taxonomic and trophic webs. Dashed lines delimit the 95% confidence intervals for the mean of the properties observed during the Monte Carlo simulation described in the text. Statistics for the illustrated simple least-squares regressions of the food-web properties vs. S are presented in Table 1. In the most highly sampled taxonomic web, $T = 0.402$, $I = 0.483$, $B = 0.115$, and $L/S = 1.44$. In the most highly sampled trophic web, $T = 0.315$, $I = 0.548$, $B = 0.137$, and $L/S = 1.51$.

C is useful for comparing linkage complexity among food webs.

In minimally sampled webs, C varies substantially in both taxonomic and trophic webs (Fig. 5). However, among trophic webs, the estimate stabilizes at 0.02 for almost 3 orders of magnitude difference in sampling effort, beginning with mean sample sizes as low as 400 stems ($S = 32$) and ending with 126 215 stems ($S = 73$). C among taxonomic webs, in contrast, is much more variable and sensitive to sample size, even in the

most highly sampled webs (Fig. 5). Thus, while the data indicate that 0.021 is a robust and readily achieved estimate of C in trophic webs, C of the most complete taxonomic web (0.017) may be much more difficult to estimate.

Directed connectance of 0.02 is much less than the range of 0.1–0.2 usually observed in other food webs (Warren 1990, 1994, 1995, Martinez 1991, 1992, 1995, Locke and Sprules 1994, Deb 1995, Reagan et al. 1996, Tavares-Cromar and Williams 1996), including vertebrate-dominated webs (Winemiller 1990, Hall and Raffaelli 1991, Goldwasser and Roughgarden 1993, Martinez 1993a). This difference corroborates Warren’s (1990) assertion that some webs, such as this one, have more trophically specialized species than other webs. However, this difference contradicts Pimm’s (1984: 324) assertion that “stability should permit insect-parasitoid systems to be substantially more connected than vertebrate dominated systems.” Virtually all links in this web represent energy flows from larger to smaller

TABLE 1. Statistical summary of regressions illustrated in Fig. 4. The curvilinearity of B (Fig. 4c) was linearized using the natural log of B .

Property	Trophic-species regressions				
	Slope	SE _{slope}	Constant	R ²	P
T	-0.00224	0.00020	0.511	0.791	<0.001
I	0.00763	0.00023	-0.007	0.972	<0.001
ln B	-0.01997	0.00033	-0.570	0.991	<0.001

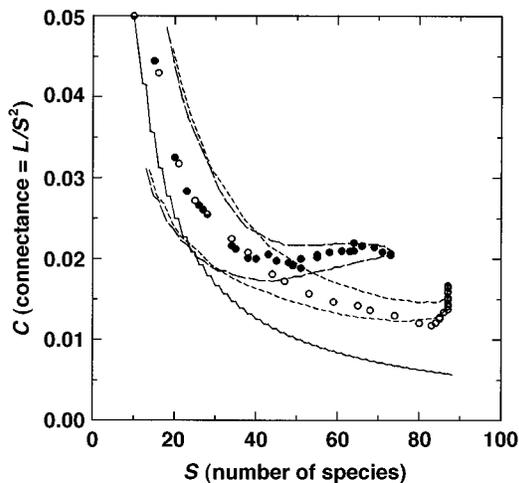


FIG. 5. Relationship between directed connectance (L/S^2) and S among taxonomic webs (empty circles) and trophic webs (filled circles). Half-filled circles indicate coincident taxonomic and trophic webs. The lower limit of connectance (solid line) was calculated using L equal to the largest integer $<(S/2) + 1$. This limit is imposed by the methodological constraint of observing a new trophic link every time a species is added to the web. This limit is lower than the more widely used limit ($L = S - 1$; Martinez 1992, Warren 1994) among webs with $S > 3$ because, while all species are usually required to be linked to the same web, our methods allow every two species to exist in separate webs.

organisms. The vast majority of links in other webs represent flows from smaller to larger organisms (see Warren and Lawton 1987). The correspondence of specialization and the direction of flow is consistent with Cousins' (1991:192) conjecture "that the passage of energy from large to small organisms involves problems so great that the parasite has to specialize on a single species or single family of species." We note that all of the consumers in this web consume, live, and develop within or on their hosts. The addition of host-as-habitat interactions to more typical consumer-resource interactions may be responsible for many of the problems to which Cousins (1991) refers. Overall, we expect webs with both large and small organisms eating each other to have connectance intermediate between 0.02 and 0.1 as recently found in a trophic species web that includes predators, parasites, and pathogens (Memmott et al., *in press*).

Comparisons of sampling effects on scale-dependent properties among studies

The biology of the trophic interactions in our web appears unusual in that each time an individual consumer is observed, a prey and a trophic link associated with that consumer are also observed. Also, the taxonomic composition and habitat boundary of the web are quite narrow, while the spatiotemporal boundaries are quite wide. We address these issues by comparing our results to other studies of sampling effects on food

webs. These other studies focus on different taxa, habitats, and spatiotemporal boundaries (Fig. 6). Fig. 6 shows that the effects of increasing observational effort among our parasitoid-dominated trophic webs are very similar to previously demonstrated effects of systematically including rarer species and links in four tropical fish-dominated webs (Winemiller 1990). This similarity of scale dependence (i.e., both increasing sampling effort and including rarer species consistently increases S and I and decreases T and B) also applies to Goldwasser and Roughgarden's (1997) study, which simulates the effects of increasing sampling effort on an *Anolis*-centered terrestrial food web from the island of St. Martin. This overall similarity suggests that the identified trends in T , I , and B are robust to large differences in biological details, spatiotemporal boundaries, and taxonomic focus.

Surprisingly, the compatibility between Winemiller's and our results transcends large methodological differences between our studies. Winemiller constructed the food webs by examining the prey of aquatic vertebrate consumers, whereas our food web was constructed by examining the consumers of terrestrial plant and invertebrate hosts. The generally consistent results among our studies suggest that differences between measuring sampling effort in terms of the number of stems examined and in terms of the fraction of gut contents (Winemiller 1990) are effectively normalized by using species number as a surrogate for sampling effort.

The St. Martin analysis would seem more methodologically similar to ours in that both analyses in Fig. 6 describe the effects of variably sampling trophic-species webs. However, the St. Martin analysis starts with abundant links and both abundant and rare taxa and then adds primarily rare links and a few rare prey taxa. This makes the attendant increase of connectance in the St. Martin web methodologically suspect. Winemiller's and our analyses start with abundant links and taxa, and then add rarer links *and* taxa. Increasing sampling effort by a factor of over 30 among the St. Martin webs results only in a 20% increase in S , compared to a roughly 200% increase in S resulting from a 30-fold increase of sampling effort among our webs (Fig. 3). Even the relatively small 20-fold increase in sampling effort among Winemiller's four webs increases S by an average of 70%. Thus, the comparatively drastic scale dependence of T and I within the St. Martin web (Fig. 6) reflects an unusually low sensitivity of S to sample size. Larger differences in S between the least and most sampled St. Martin webs could reduce the steep slopes of T and I and make these slopes more similar to others in Fig. 6.

While the trends among studies are similar, the particular values of T and I in our webs appear unusually high and low, respectively (Fig. 6). This may reflect our study's restrictive spatial boundaries. If we included organisms outside the grass stems, such as spiders that generally prey upon insects, many of the appar-

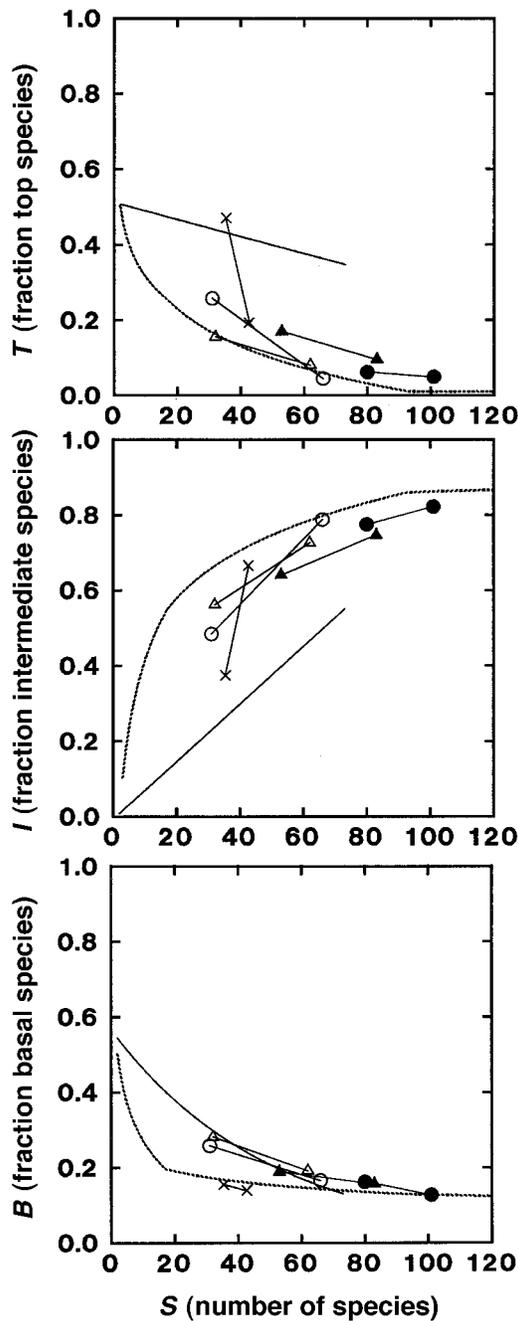


FIG. 6. Comparison between the trophic-web results obtained here and the results obtained by Goldwasser and Roughgarden (1997) and Winemiller (1990). The long solid lines are the regressions for trophic webs shown in Fig. 4. Dotted lines describe previously predicted and observed scale-dependent patterns among webs (Martinez and Lawton 1995). The \times 's denote the least and most sampled (from prey direction) St. Martin trophic-webs analyzed by Goldwasser and Roughgarden. The four remaining short lines connect data depicting two variably sampled versions of Winemiller's four cumulative "annual" tropical stream webs. Filled circles denote stream webs from the Caño Maraca site. Empty circles denote webs from the Caño Volcán site. Filled triangles denote webs from the Caño Aqua Fría site, and empty triangles denote webs from the Quebrada site. The less

ently top species would become intermediate species. This could ease the discrepancies by decreasing T and increasing I in our webs.

The effects of increasing observational effort on food-web structure closely parallel both previously observed scale-dependent effects of increasing S among webs (Martinez 1993a, 1994, Murtaugh 1994, Deb 1995, Martinez and Lawton 1995) and also increasing trophic resolution within webs (Martinez 1991, 1993b). Each of these three factors consistently increases I and L/S , decreases T and B , and leaves connectance relatively unaffected in all but the smallest webs. This parallel may result partly from the high degree of correlation among observational effort, resolution, and S .

Our findings extend scale dependence (Martinez 1993a, 1994) as applicable to variably sampled trophic-species versions of the same web. We also refine scale dependence by suggesting that the methodological process of sampling is a partial explanation for differences of S , T , I , and B among webs. With regard to scale invariance (Cohen et al. 1990, Pimm et al 1991, Havens 1992, Bersier and Sugihara 1997), our results demonstrate an additional case where approximate constancy of T , I , B , and L/S as a function of S should be rejected.

Comparisons among food webs

Our results have important implications for comparing food webs. Quantitatively predictable sampling effects allow ecologists more efficiently to test comparative theories. For example, theories predicting particular values of connectance may be tested simply and directly with trophic webs based on samples that include the abundant half of the species and their trophic interactions within an ecological system (Martinez 1991, 1993b). A recent intensive study of a stream food web also found relative constancy of connectance between webs, based on short sampling periods requiring less effort and the cumulative web requiring much more effort (Tavares-Cromar and Williams 1996). The robustness of connectance suggests that comparisons of connectance among ecological systems, based on moderately and variably sized samples, are methodologically acceptable.

Our results suggest that a more complex procedure that corrects for variable sampling effort is required

← species-rich and less intensely sampled webs include the common fish species (i.e., those fishes that contribute 95% of the individuals collected) and also the diet items that made up 5% or more by volume of the sampled gut contents of the fishes. The more species-rich and more intensely sampled webs include all diet items observed for the same common fish species. Winemiller's webs are not as taxonomically resolved as is our web, and they appear to be more comparable with our trophic webs than taxonomic webs. Furthermore, Winemiller's cumulative annual webs, as opposed to the seasonal webs, are most comparable to our cumulative webs.

for comparing scale-dependent properties such as T , I , and B among webs. The relatively consistent behavior of T , I , and B among trophic-species webs, along with the log-normal distributions in Fig. 2, indicates that it may be possible to develop sample-size corrected characterizations of these properties analogous to Fisher's α (Fisher et al. 1943) and Simpson's index of concentration for species richness (Magurran 1988, Rosenzweig 1995). Without such characterizations, it may be erroneous to compare T , I , or B of one web to that of another web if sampling intensities differ. While this conclusion would tend to undermine food-web theory based on these properties (e.g., Pimm et al. 1991, Martinez and Lawton 1995), correcting for S among webs constructed with variable sampling effort (Goldwasser and Roughgarden 1993, Bengtsson 1994) may already inadvertently correct for variable sampling effort. This is because observational effort and S correlate strongly (Magurran 1988, Rosenzweig 1995), and T , I , and B consistently depend on S . This suggestion of inadvertent correction is corroborated by the fact that the connectance and scale-dependent patterns described here are similar to patterns among webs constructed with consistent methods, including consistent amounts of sampling effort (Martinez 1993a, Murtaugh 1994, Deb 1995). Indeed, such methodological consistency may be the conceptually simplest way to address sampling concerns. While conceptually simple, such consistency requires significant efforts in the field. We suggest that corrections for sampling effort may more likely refine rather than undermine recent food-web theory.

Implications of results concerning trophic species

One of the most challenging questions left by this and other studies is why trophic-species webs behave more consistently than taxonomic-species webs. A similar result of employing trophic aggregation was reported in a reanalysis of the classic biogeography experiments conducted by Simberloff and Wilson (1969, 1970, Simberloff 1969, Wilson and Simberloff 1969). Heatwole and Levins' (1972) reanalysis asserts that community structure described in terms of trophically defined functional groups is more tightly constrained than the taxonomic composition of the islands during the increase of species richness that accompanies island recolonization (but see Simberloff 1979). Still, this assertion of structural constraint based on functional trophic groups foreshadowed our result instead of answering our question.

Trophic species were originally developed (Cohen and Briand 1984, Cohen 1989) to ameliorate the variable taxonomic biases of different investigators (e.g., resolving vertebrates to species level, while small organisms and lower trophic levels are grouped into much grosser taxa). More recent research indicates that the behavior of food webs is also much more consistent among trophic versions of webs whose species are much more evenly resolved (Martinez 1991, 1993b,

1994). This improvement means that the variation in trophic structure of ecological systems described in terms of trophic species is generally less, or easier to explain, than the same structure described in terms of taxonomic species. Martinez (1994) explains this improvement as a result of the greater methodological consistency in using trophic criteria to define both groups of organisms as well as their interactions. Mixing trophic and taxonomic criteria to define taxonomic webs results in less consistent patterns (Martinez 1993b).

Another methodological explanation is that some of the consistency of sampling results may result from only one taxonomic member of a trophic species needing to be identified for the trophic species to be recognized. No structural changes of trophic webs accompany discovery of additional taxonomic members of a trophic species. However, this somewhat "artifactual" consistency may be undermined by the very high levels of sampling required to recognize other trophic species (Fig. 2). In other words, trophic species are not necessarily easier to detect, as suggested from their definition as aggregates of trophically similar taxa.

A more biological answer hypothesizes that regularities in niche space (Warren 1994) are more easily detected by employing trophic species. Taxonomic distinctions resulting from unusually fine discrimination among certain taxa (e.g., birds) or evolutionary processes such as convergence may obscure such regularities. A recent study corroborated taxonomically obscured regularities in niche space by showing that *Anolis* lizards evolved into many different taxa that consistently filled a much smaller set of ecological niches (Losos et al. 1998). This happened on four islands despite different evolutionary origins. The use of trophic species may help to delineate such regularities elsewhere.

On link thresholds

It has been suggested that link thresholds should be employed to prevent inclusion in food webs of links that are, from a population dynamic perspective, trivial (e.g., Paine 1988, Lawton 1992, McCann et al. 1998). To do this, one must first make choices, such as whether energetic, interaction strength, or stability criteria should define the threshold. This is difficult, because these criteria do not correlate well (de Ruiter et al. 1995). Even after a criterion is chosen, difficult choices remain. Should energetic thresholds be absolute or relative to the resource or consumer? Should interaction strength be measured on a per capita basis (Paine 1992) or a per population basis (Power et al. 1996)? Should stability be based on mathematical equilibria (May 1974, Haydon 1994) or permanence (Law and Morton 1996)? Finally, all of these choices could be wrong if evolution (Martinez 1994) or some process besides population dynamics drives food-web structure (Paine 1988).

To all these difficulties concerning link thresholds, our results add another. Sampling needs to be extensive enough confidently to assign values around a chosen threshold. If sampling is insufficient, links below the threshold that happen to be highly sampled will be included, while links above the threshold that happen to be lowly sampled will be excluded. The effects of this discrepancy are most prominent among our taxonomic webs with $S \approx 80$. Points depicting webs that exclude species and links below a threshold fall outside the confidence intervals depicting webs that are most likely to be sampled (Figs. 4 and 5). Our trophic webs avoid this discrepancy. The properties of trophic webs likely to be observed at a given sampling level are very similar to the properties of trophic webs that exclude links rarer than that implied by the sampling level. Still, incongruous results may occur even among trophic webs when a threshold is applied to links but not to species, as in the St. Martin web (see *Comparisons of sampling effects on scale-dependent properties among studies*).

CONCLUSION

Our analyses indicate that the trophic complexity of the highly sampled grassland web could be accurately characterized with two orders of magnitude less observational effort by using trophic species as a basic unit of analysis and connectance as the relevant measure of complexity. We generalize these results by suggesting that connectance of trophic webs may be adequately characterized with relatively small sample sizes. Such efficiency may become true for T , I , and B if sample-size corrected indices of these properties are developed. Our trophic-species results suggest that such indices are attainable in a manner similar to the way increases of species richness with observational effort lead to sample-size corrected measures of species richness (Colwell and Coddington 1994). Although developing indices may be relatively straightforward for trophic webs, similar indices using taxonomic webs appear more problematic. Comparisons of the most and least sampled taxonomic webs express overall trends in previously predicted and observed directions (Martinez 1994, Murtaugh 1994, Deb 1995, Martinez and Lawton 1995). However, estimation of whether a taxonomic web has more or less T , I , B , or L/S than another web is confounded by more complex sensitivity of taxonomic webs to observational effort. Connectance among taxonomic webs is less sensitive than T , I , and B , but is still not as robust as among trophic webs. We anticipate that these findings will enhance the precision and tractability of food-web research, while assisting ecologists to observe and predict the organization of ecological interactions.

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