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Source food webs as estimators of community web structure

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Abstract

Taxonomically restricted "source webs" are commonly used to represent the community food webs of which they are part. This raises a methodological problem if source webs provide biased estimates of food web structure. We use four high quality, extensive food webs containing multiple source species to measure the sensitivity of food web metrics to the number of source species used to generate a web. The total number of species (*S*), linkage density (*L/S*), directed connectance (L/S^2), and the fractions of basal (*B*), intermediate (*I*), and top (*T*) species are all sensitive to the number of source species. Further, the pattern of variation for the latter fractions is inconsistent and web dependent, indicating that source webs are inappropriate for characterizing these properties. Linkage densities increase with the numbers of source species in all four cases, with webs based on single or few sources severely underestimating values obtained for the full webs.

Connectance shows more constrained decreases with increasing numbers of sources, suggesting that multiple-source webs may provide reasonable estimates of connectance for community webs.

Keywords: Food webs, source webs, community webs, scale dependence, estimating food web parameters.

Résumé

Des « réseaux source » taxonomiquement restreints sont communément utilisés pour représenter les réseaux trophiques des communautés dont ils font partie. Ceci soulève un problème méthodologique si les réseaux source fournissent des estimations biaisées sur la structure des réseaux trophiques. Nous avons pris quatre réseaux trophiques complets et de très bonne qualité, contenant de multiples espèces source, pour mesurer la sensibilité des paramètres du réseau trophique au nombre d'espèces source utilisées pour générer un réseau. Le nombre total d'espèces (*S*), l'intensité de liaison (*L/S*), la connectance dirigée (L/S^2) et les fractions d'espèces de base (*B*), intermédiaires (*I*) et de sommet de chaîne (*T*) sont tous sensibles au nombre d'espèces source. De plus, le patron de variation pour les dernières fractions est contradictoire et dépendant du réseau, ce qui indique que les réseaux source ne sont pas appropriés pour caractériser ces propriétés. L'intensité de liaison augmente avec le nombre d'espèces source dans les quatre cas, les réseaux reposant sur une source unique ou un petit nombre de sources sous-estimant sévèrement les valeurs obtenues pour les réseaux entiers. La connectance présente des diminutions plus contraintes avec une augmentation du nombre des sources, ce qui suggère que des réseaux à sources multiples fournissent des estimations de connectance raisonnables pour les réseaux de communautés.

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INTRODUCTION

The analysis of topological food webs has generated a growing literature over the past 20 years, a major goal of which has been to identify general patterns in food web structure (reviewed by LAWTON, 1989; PIMM *et al.*, 1991; HALL & RAFFAELLI, 1993; WINEMILLER & POLIS, 1996). On the other hand, there has been widely publicized concern that such patterns may partially or entirely reflect artifacts arising from the highly variable quality of published food webs (*e.g.* PAINE, 1988; POLIS, 1991; MARTINEZ, 1991; COHEN *et al.*, 1993). In its extreme form, this concern had lead to calls to abandon the analysis of topological food webs in favor of the experimental manipulation of communities needed to generate "interactive" webs (PAINE, 1983, 1988). However, a more moderate position is to curtail using data bases generated by trawling the literature and to focus on newer webs that deal explicitly with at least some of methodological and conceptual problems that may frustrate the search for general patterns in food web structure (PIMM & KITCHING, 1988; HALL & RAFFAELLI, 1993; WARREN, 1994). Methodological issues that have been addressed to date include effects of resolution of taxa (HALL & RAFFAELLI, 1991; MARTINEZ, 1991, 1993*a*), temporal and spatial variation in web structure (KITCHING, 1987; WARREN, 1989; WINEMILLER, 1990, 1996; SCHOENLY & COHEN, 1991; CLOSS & LAKE, 1994; TAVARES-CROMAR & WILLIAMS, 1996), and scale effects including web size (MARTINEZ, 1993*b*, 1994; BENGTSSON, 1994), link thresholds (WINEMILLER, 1990), and sampling intensity (GOLDWASSER & ROUGHGARDEN, 1997; N. D. MARTINEZ, B. A. HAWKINS, H. A. DAWAH & B. P. FEIFAREK, unpubl. data). WINEMILLER & POLIS (1996) and BENGTSSON & MARTINEZ (1996) provide up-to-date reviews of the state of the field.

A fundamental aspect of constructing and analyzing food webs is their inclusiveness. The ideal topological web is a complete community web that describes all of the trophic relationships for all species that occur in a delimited habitat (MARTINEZ, 1995). However, for the vast majority of terrestrial habitats, the diversity of the entire biota precludes this approach (POLIS, 1991). Less laborious alternatives include restricting observation to "sink" and "source" webs (COHEN, 1978). Sink webs only include one or more consumers, the consumers' resources, the resources' resources, and so on to the "base" of the web. Source webs are based on one or more basal species (prey without prey), their consumers, their consumers' consumers and so on to the "top" of the web. Such webs provide a systematic way to restrict food webs to more manageable numbers of species. Source webs in particular have played an important role by being a substantial fraction of some influential collections of food webs (COHEN, 1978; SUGIHARA *et al.*, 1989). For example, over half of a set of 60 "community" food webs (SUGIHARA *et al.*, 1989; SCHOENLY *et al.*, 1991; MARTINEZ, 1994) have only one basal species and may be more appropriately called source webs. In general, food webs may be placed on a source-to-community web "inclusivity" spectrum that indicates the fraction of basal species within a habitat that are included within a web describing that habitat. In the rare case when a habitat has only one basal or producer species, the source and community webs may be identical. However, in the vast majority of habitats, the spectrum is expanded and the presence of a single source species indicates a highly restricted source web that is much less inclusive than a community web. For all but the most narrowly defined habitats (*e.g.* treeholes or pitcher plants), source webs will be relatively easier to generate and will probably remain a common type of web produced by community ecologists.

A priori, source webs would be expected to produce a biased picture of food web structure, particularly in the metrics that are typically calculated from topological webs (Pimm *et al.*, 1991). For example, the proportion of basal species in a community would be severely underestimated in the extreme case of a source web based on a single basal species supporting many polyphagous intermediate species (species with both consumers and resources) and top species (species with no consumers). Linkage density (the number of links per species) would also be underestimated if intermediate and top species are polyphagous and feed on many prey that are not directly linked to the source species selected. Thus, using source webs to estimate community web structure represents a potentially important methodological problem in the interpretation of food webs independently of, and in addition to, the other sources of variation that have been identified.

In this paper, we explore the relationship between source webs and the larger community webs from which they are drawn. Unlike previous analyses of the characteristics of source webs, in which the properties of a highly variable collection of single-source webs were compared with those from an equally variable collection of more extensive webs (Cohen, 1978), we use four high quality "community" webs containing many basal species. We then sequentially deconstruct the webs into source webs containing fewer and fewer basal species to determine if, and how, web parameters change with the number of source species. If webs based on single to few sources do not generate biased estimates of web parameters, or at least if the biases are consistent and predictable, then source webs can be used as substitutes for community webs to estimate topological parameters. On the other hand, if source webs provide unpredictable or highly variable estimates of such parameters, then source webs will be of extremely limited value, and further attempts to identify meaningful patterns in web structure will be hampered until a number of highly resolved, complete community webs have been worked out.

METHODS

The analysis is based on four food webs selected because of their quality and the degree of resolution achieved by the original workers. The webs are: (1) Little Rock Lake (Martinez, 1991), (2) Caño Maraca stream during the transition season (Winemiller, 1990), (3) the Ythan Estuary (Hall & Raffaelli, 1991), and (4) the parasitoids of grass-feeding Hymenoptera (Dawah *et al.*, 1995). The Little Rock Lake and Ythan Estuary webs represent reasonably complete community webs; the Caño Maraca web is a multiple-sink web based on stream fishes, and the grass web is a multiple-source web based on 10 grass species and their hymenopteran consumers. The latter webs were selected because, although taxonomically restricted, they were well sampled, highly resolved, and contain numerous source species. The Little Rock Lake and grass webs were taken directly from publications; the Caño Maraca and Ythan webs were provided by K. O. Winemiller and S. J. Hall, respectively.

Analysis initially comprised calculating parameter values for each complete web. Then one of n basal species was removed and parameters were recalculated for all possible webs based on n-1 basal species. A second basal species was then removed (producing webs of n-2 basal species), and the process repeated until only a single source remained. Parameters were calculated for all possible combinations for each number of basal species, except when the number of possible combinations of webs exceeded 2000, in which case a random sample of 2000 combinations was selected. For all but the complete webs, means and standard deviations were calculated for all web parameters. Parameters selected for analysis included S (the number of species), the fractions of top (T), intermediate (I), and basal (*B*) species, linkage density (*L/S*), and directed connectance (L/S^2). Two versions of each web were analyzed. "Taxonomic webs" were based on the taxa distinguished in the investigators' original descriptions of the webs, and "trophic webs" were based on trophic species. Trophic species represent functional groups that contain all taxa within a web that share the same predators and prey (Briand & Cohen, 1984).

RESULTS

All parameters show sensitivity to the number of source species on which the webs are based either in terms of mean values or in terms of variability (figs 1-4). The strongest and most consistent relationship is with the total number of species in the web (figs 1*a*, 2*a*, 3*a*, 4*a*), which increases both because the inclusion of additional basal species necessarily increases the total numbers of species in the web, and because relatively specialized species will on average be absent from more restricted subwebs. The variation in *S*, on the other hand, decreases with increasing species richness, since variation in richness is more constrained as larger portions of the total web are included. Both taxonomic and trophic webs show qualitatively similar patterns for both the means and standard deviations, although the numbers of trophic species increase at lower rates than do taxonomic species. It should be recognized that the increases in species richness are not asymptotic since the inclusion of additional source species always increases the total number of species represented in the webs.

Similar to *S*, the number of links per species (*L/S*) increases as webs are based on more source species (figs 1*b*, 2*b*, 3*b*, 4*b*). In the Little Rock Lake and grass webs, linkage density also asymptotes, whereas it continuously increases in the Caño Maraca and Ythan webs. In contrast, webs containing fewer sources overestimate connectance in all four cases (figs 1*c*, 2*c*, 3*c*, 4*c*). This pattern is the simple consequence of species richness increasing at a faster rate than linkage density. One of the most consistent link-species patterns among all webs is that linkage density approaches the community value from below whereas connectance approaches it from above.

The relationships between the fractions of top (*T*), intermediate (*I*), and basal (*B*) species and the numbers of source species are inconsistent among the webs. In the relatively densely linked Little Rock Lake and Caño Maraca webs (figs 1*b*, 2*b*), webs based on few source species underestimate the fractions of basal species (figs 1*f*, 2*f*) and overestimate the fractions of intermediate species (figs 1*e*, 2*e*). The mean fractions of top species vary only slightly (figs 1*d*, 2*d*), although as with most other parameters, estimates based on fewer sources are more variable. In the less tightly linked Ythan Estuary web, webs based on few sources overestimate the fraction of top species and underestimate the fraction of intermediate species (fig. 3*d*, *e*). In the highly specialized grass web, on the other hand, the fractions change little with increasing numbers of source species (fig. 4*d*, *e*, *f*).

DISCUSSION

As expected, web metrics generated from source webs differ substantially from those generated from more broadly based webs (Cohen, 1978). These patterns are best explained by the underlying relationships between web size and web properties. It has recently become apparent that almost all of the frequently discussed food web properties are scale-dependent (Winemiller, 1990; Hall & Raffaelli, 1991; Martinez,

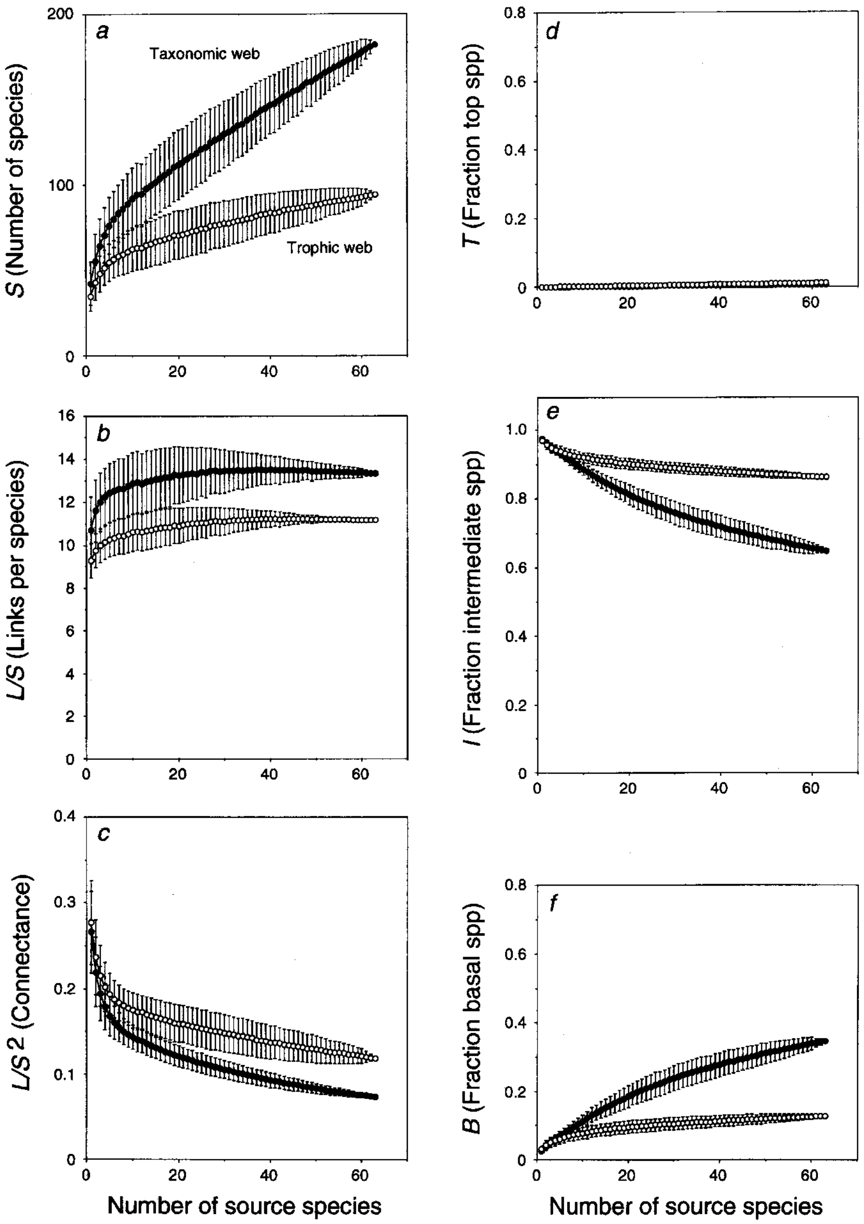

FIG. 1. – Mean (± 1 SD) parameter values for the Little Rock Lake food web, based on the number of source species included in the web. Filled circles represent taxonomic webs, and open circles represent trophic webs. (*a*) Number of species, (*b*) linkage density, (*c*) connectance, (*d*) the proportion of top species, (*e*) the proportion of intermediate species, and (*f*) the proportion of basal species.

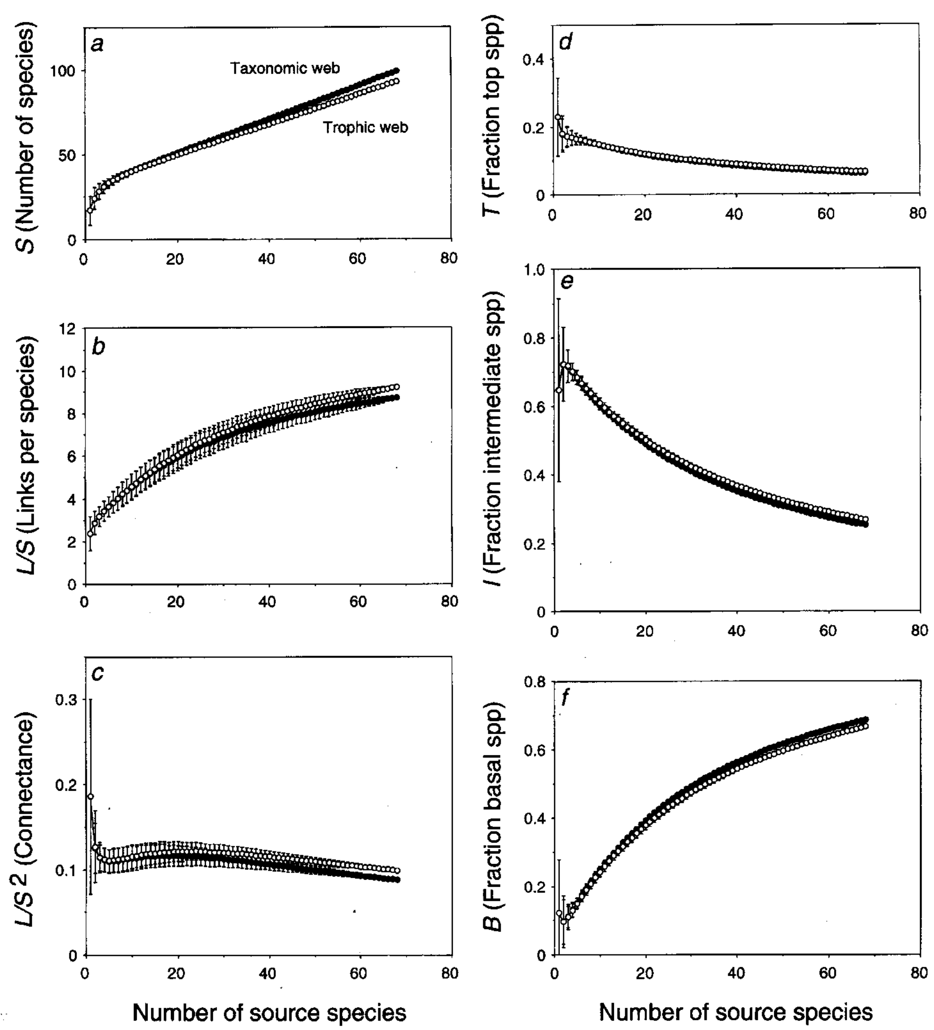

Fig. 2. – Mean (± 1 SD) parameter values for the Caño Maraca food web, based on the number of source species included in the web. Filled circles represent taxonomic webs, and open circles represent trophic webs. (*a*) Number of species, (*b*) linkage density, (*c*) connectance, (*d*) the proportion of top species, (*e*) the proportion of intermediate species, and (*f*) the proportion of basal species.

1991, 1993*b*; Havens, 1993; Bengtsson, 1994; Martinez & Lawton, 1995; Deb, 1995; Martinez *et al.*, unpubl. data). A partial exception may be connectance, which is also scale-dependent in small webs but appears to be scale-invariant in moderate to large webs (Martinez, 1993*b*, 1995; Murtaugh, 1994). Thus, any methodology that causes variation in the number of species represented in the web will potentially influence quantitative estimates of web structure. Because increasing the number of source

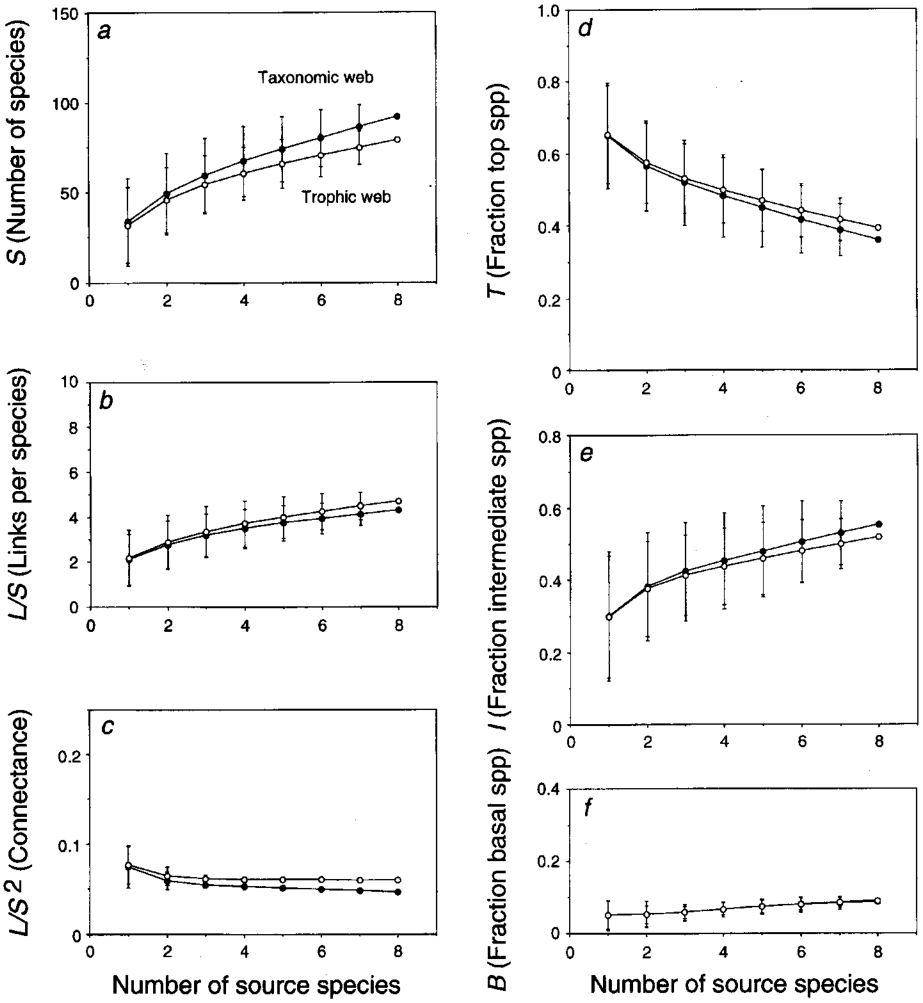

FIG. 3. – Mean (± 1 SD) parameter values for the Ythan Estuary food web, based on the number of source species included in the web. Filled circles represent taxonomic webs, and open circles represent trophic webs. (*a*) Number of species, (*b*) linkage density, (*c*) connectance, (*d*) the proportion of top species, (*e*) the proportion of intermediate species, and (*f*) the proportion of basal species.

species sampled in a community, however taxonomically or trophically defined, also increases the total number of species, quantitative estimates of food web structure will vary.

The observed pattern of variation in linkage density is consistent with other studies that have investigated the effects of scale in web structure; *L/S* increases with increasing *S* (SCHOENER, 1989; HALL & RAFFAELLI, 1991; MARTINEZ, 1992, 1994;

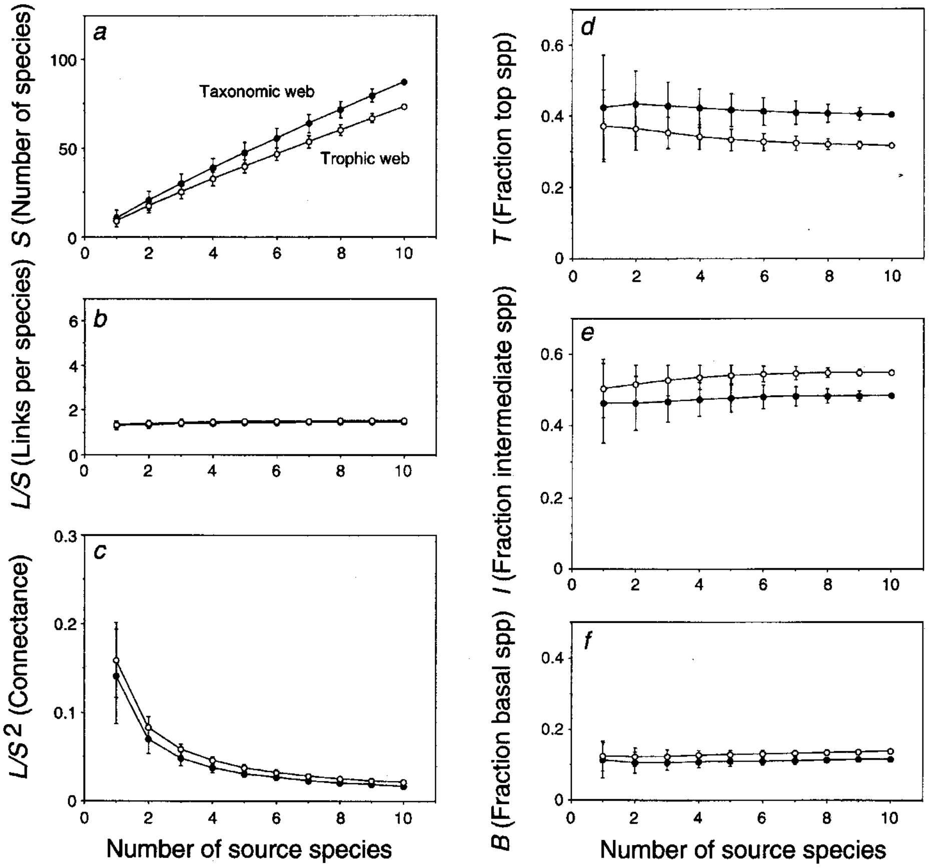

FIG. 4. – Mean (± 1 SD) parameter values for the grass-Hymenoptera food web, based on the number of source species included in the web. Filled circles represent taxonomic webs, and open circles represent trophic webs. (*a*) Number of species, (*b*) linkage density, (*c*) connectance, (*d*) the proportion of top species, (*e*) the proportion of intermediate species, and (*f*) the proportion of basal species.

HAVENS, 1993; DEB, 1995; GOLDWASSER & ROUGHGARDEN, 1997). Since source webs will usually have lower S than the community webs from which they are extracted, they will generally appear to contain more trophically specialized species and will have lower linkage densities than community webs in all but the most specialized communities. Among our sample of webs, the grass web is by far the most specialized ($L/S = 1.43$, $L/S^2 = 0.02$) and is the only web insensitive to the number of sources. Thus, for linkage density to be scale invariant, a web has to be heavily compartmentalized, which rarely occurs within habitats (LAWTON, 1989; PIMM *et al.*, 1991).

We also find in all four webs that L/S^2 decreases as the number of (source) species increases. This relationship has been observed many times (REJMÁNEK & STARY, 1979; YODZIS, 1980; PIMM, 1982; LAWTON, 1989), although it has been suggested that this may be an artifact, resulting from (1) increased difficulty of graphically illustrating all of the feeding relationships in larger webs (PAINE, 1988; WARREN, 1994), and (2) the lower limit of L/S^2 rapidly increasing as small webs ($S < 15$) get even smaller ($S < 10$) (MARTINEZ, 1992, 1993*b*). For example, minimum connectance in a 2-species web is 0.25, whereas the minimum in a 10-species web is 0.09. The first artifact cannot explain the variation we find here, since all links in the source webs are also present in the complete webs. The second artifact may contribute to the rapid decrease in connectance as the number of source species increases beyond one, but it appears to be unable to account for the variation among larger webs.

We note that in seven of the eight sets of calculations, L/S^2 does not stabilize fully with increasing numbers of source species; the trophic Ythan web being the exception (*see* fig. 3*c*). On the other hand, in all cases connectance values for the complete webs are within one or two standard deviations of the estimates based on half of the full numbers of source species. Thus, although source webs are likely to overestimate connectance to some extent at virtually all scales, it may only be a serious methodological problem when webs are based on only a few sources.

Variation in connectance in the Caño Maraca web varies slightly from other webs in that over part of the range of values for the number of source species (5-22), average connectance increases slightly with increasing numbers of sources (*see* fig. 2*c*). WINEMILLER (1989) found when using a large number of different versions of this and three other fish-dominated webs that connectance was positively associated with web size. There may be some special characteristics of these webs that produce an atypical relationship between S and L/S^2, but that does not negate our general result that the lowest estimates of connectance are found in the most complete webs.

The fractions of species occupying basal, intermediate, and top positions in food webs have been observed to change systematically as the scale of the web increases (MARTINEZ, 1994; DEB, 1995; MARTINEZ & LAWTON, 1995; MARTINEZ *et al.*, unpubl. data). Theories of "scale dependence" specifically predict that the fraction of intermediate species will increase, whereas the fractions of top and basal species will decrease with increasing S. However, none of our webs follow these trends. In the Little Rock Lake and Caño Maraca webs, I decreases and B increases with increasing numbers of sources (*see* figs 1, 2). In the Ythan web, I increases and T decreases with more sources, as expected, but B varies little (*see* fig. 3). In the grass web, on the other hand, all fractions are insensitive to the number of sources (*see* fig. 4). The latter result is particularly notable since randomly resampling the grass web has been shown to drastically alter these fractions in the predicted directions (MARTINEZ *et al.*, unpubl. data).

The nonconformity of these fractions to predicted patterns provides the clearest evidence for unique patterns of variation among different sized webs based on variable numbers of source species. Previous analyzes of the effects of scale (*i.e.*, S) on the fractions of basal, intermediate, and top species have modified S by varying the minimal threshold for the inclusion of links (*e.g.* WINEMILLER, 1990; GOLDWASSER & ROUGHGARDEN, 1997), taxonomic resolution (*e.g.*, HALL & RAFFAELLI, 1991; MARTINEZ, 1991), or sampling intensity (GOLDWASSER & ROUGHGARDEN, 1997; MARTINEZ *et al.*, unpubl. data). Trophically higher organisms (*e.g.* carnivores) are typically paid more taxonomic and trophic attention than lower species. This disparity results in more information being available on the taxonomic diversity and trophic activity of higher species. Therefore, the sources of variation examined in earlier studies should influence relationships near the tops of webs more than near sources. In contrast, varying the number of source species, by definition, influences the size of the basal species pool most directly. This adds basal species to webs at a faster rate than it does intermediate and top species, causing the fraction of basal species to increase. As a consequence, fractions of either (or both) intermediate or top species must fall with increasing S, except when webs are overwhelming composed of very specialized species, such as in the grass web. Because of the few linkages across sources in this web, adding a new source species also adds new intermediate and top species, maintaining the relative fractions. Thus, highly specialized webs, such as those represented by parasitoids or parasites, should be the most robust to the bias introduced by basing webs on few sources. But other parameters from such webs remain sensitive to the number of sources (*see* fig. 4).

In sum, our analysis identifies an additional source of variation in topological food web metrics. But it should be noted that the patterns we describe here operate at the fundamental level of web "inclusivity", somewhat independent of taxonomic restrictions or how intensely trophic relationships are sampled. Our own sample of webs includes this potential problem. Although the Little Rock Lake and Ythan Estuary webs reflect less biased "community" webs, both the Caño Maraca and grass webs are more taxonomically and trophically restricted. We use these webs to illustrate the sensitivity of food web properties to how webs are delimited and sampled, as did the original compilers (Winemiller, 1990; Martinez *et al.*, unpubl. data), but we uniquely focus on source species. This leads to inconsistent results regarding the fractions of species in different trophic positions, suggesting that source webs are inappropriate for characterizing these fractions. To a lesser extent, L/S is also sensitive to how inclusive the web is, complicating attempts to characterize linkage densities for across-web comparisons. Finally, L/S^2 varies much more consistently and in a more constrained manner, suggesting that source webs may be a pragmatic method for estimating connectance in community webs.

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