In search of operational trophospecies in a tropical aquatic food web

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Aggregations of biological species on the basis of trophic similarity (trophospecies) are the basic units of study in food web and ecosystem research, yet little attention has been devoted to articulating objective protocols for defining such aggregations. This study formulates several possible definitions based on alternative measures of similarity and hierarchical clustering. Twenty-four alternative methods were applied to a food web consisting of 116 original trophic entities (OTEs) from a tropical floodplain, for which the relative magnitude of each trophic link was estimated based on dietary data measured as volumetric proportions. The resulting 24 trophic hierarchies were compared based on cophenetic correlation and matrices of OTE pairwise similarity, and patterns were interpreted based on additional ecological analyses for this system. Similarity measures based on topological food web (presence/absence) data yielded slightly greater cophenetic correlations than did measures based on dietary proportions (flow webs), but, overall, OTE pairwise correlations were not greater for one method relative to the other. The difference between these two approaches is driven by the treatment of weak feeding links; at least for the system considered here, distinctions among dietary generalists were obscured when weak links were weighted lightly. Additively combining the predator and resource aspects of each OTE's trophic role performed better than combining them multiplicatively. In general, there was little correspondence between OTE overlap in resource use and the extent to which predators were shared. Two measures of cluster similarity, one designed by us specifically for food webs (maximum linkage) and the other a standard method (average similarity between clusters), yielded more consistent and ecologically interpretable patterns of aggregation than other measures of cluster similarity considered. In deciding whether two trophospecies should be assigned a trophic link, the maximum linkage convention (in which a link is included if any pair of OTEs, one in each trophospecies, are linked) produced more aggregation than the minimum linkage convention (in which a link is included only if every pair of OTEs, pair members in each of the two trophospecies, is linked). The choice of similarity level for defining trophospecies remained an unresolved issue based on our analysis of this dataset. Perhaps the greatest challenge is posed by sampling bias within empirical datasets, and we ultimately conclude that it is difficult to identify trophospecies in this dataset by strictly objective criteria.

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A major goal in ecology is to comprehend patterns and processes of ecosystems in their entirety. Most recently, this objective has found expression in a purely trophic view of the ecosystem concept (see reviews in Pimm 1982, Lawton 1989, Yodzis 1989, Cohen et al. 1990,

Polis and Winemiller 1996). Within this framework, one can contemplate as a unit all the species occupying some habitat. At least two categories of trophic whole-system theories can be distinguished: static food web models and trophodynamical models (both are dis-

cussed, though not always clearly distinguished, in the reviews cited above). A topological food web is a list of which species in the system eat which others, with trophic interactions regarded simply as either present or absent for each pair of species. A dynamic food web is a model of population and predation dynamics for each species in the system. Formulation of such a model requires the specification of food web structure, but in addition to presence/absence information on feeding links, it also requires estimation of the magnitudes of those links.

A typical ecosystem contains hundreds or thousands of biological species. Even having made the simplification of adopting a purely trophic viewpoint, one is left with an impracticably complex system. Therefore, trophic studies frequently begin by grouping trophically similar species into aggregate entities that are sometimes called trophospecies (Yodzis 1988). Such aggregate entities are the fundamental units of food web research, yet, in the food web literature, trophospecies have been defined by ad hoc or subjective means rather than by objective protocols.

The first generation of whole-system trophic data contained species that were highly aggregated, and the degree of aggregation is uneven within the food web. At the base of the food web, highly aggregated trophospecies, such as algae, may contain hundreds of biological species. Other trophospecies, such as vertebrates, are resolved to the biological species level; still others, such as invertebrates, are intermediate in taxonomic resolution. Such webs introduce subjective bias into the comparative study of food web features (Paine 1988, Hall and Raffaelli 1993).

Our intent is not to denigrate the work of the compilers of such food webs, because these researchers generally were interested in the role of particular organisms within their food webs, and sometimes the structure of the food web was of secondary importance. Moreover, it may never be possible to resolve all trophic units of a food web at the level of biological species. This task would be daunting even for a large team of specialists working on a relatively species poor system. Even so, the first generation of theoretical work that was based on this flawed data base (covered in the reviews cited earlier) stimulated a second generation of empirical work that attempted to produce more highly resolved food webs (e.g., Warren 1989, Winemiller 1990, Hall and Raffaelli 1991, Martinez 1991, Polis 1991). Although uneven and subjective taxonomic aggregation remains a problem for this second generation of data, these webs tend to contain more taxa and greater taxonomic resolution than the first generation data.

Even if full resolution at the species level were possible within a food web, some degree of aggregation would be desirable. Fully resolved food webs would be too complex to work with for many purposes. For instance, population dynamical models with hundreds or thousands of species would be intractable. In addition, a tentative theoretical framework has been built up using the first generation food web data. One might wish to know how closely the first generation data approximate aggregated descriptions that have been arrived at by objective protocols rather than by ad hoc judgements (Sugihara et al. 1989, Martinez 1991, 1993). As a guide to future empirical and theoretical studies, one might want to know what kind of aggregation, and what extent of aggregation, is acceptable for a given analysis. For large complex ecosystems, studies of processes, such as nutrient cycling, probably are modelled most efficiently using aggregations of functionally similar species. For statistical comparisons of food web attributes, such as trophic link density, the rules for species inclusion and aggregation would have to be consistently applied to all webs being compared.

Conclusions drawn from trophic theories will be influenced by how trophospecies are defined. This crucial issue has only begun to be addressed up to now. In this paper, we propose, evaluate, and compare a number of different objective trophospecies definitions, using a well-documented dataset obtained from field research. The cumulative annual food web for Caño Maraca, a floodplain creek in the Venezuelan llanos (Winemiller 1990), has 88 fish species (54 common) and 62 non-fish prey taxa for a total of 150 taxa (116 common). The fishes were distinguished to the level of biological species. Non-fish taxa are more aggregated than fishes, but are relatively well resolved by earlier food web standards (e.g., invertebrate orders or families). Because the web is entirely based upon dietary data derived from estimates of feeding in the field, all feeding links involve fishes as consumers. In this food web, fishes display a diverse array of ecological niches (feeding on various forms of algae, macrophytes, detritus, protozoa, invertebrates, fishes, etc.), hence the web has considerable vertical structure. All food web datasets suffer from a variety of limitations in the inclusion and handling of basal elements, top predators, and lateral/intermediate elements. Like many datasets, the Maraca foodweb aggregates taxa such as algae and invertebrates more than vertebrates. However, this dataset has one feature that is uncommon yet essential for our analysis of trophospecies. The magnitude of each trophic link (trophic interaction strength) is estimated based on dietary volumetric data derived from large field samples for most of the consumers. This enables comparisons, as bases for the definition of trophospecies, of the coarse measures of trophic similarity based on purely topological data (trophic link presence-absence) with similarity measures based on quantitative estimates of biomass flow between prey and predator.

Methods

Trophic similarity

The central issue in defining trophospecies is how we choose to define "trophic similarity". This issue has much in common with alternative definitions of dietary similarity or resource utilization overlap, with the additional question of how to treat the simultaneous predator and resource roles of a given species within a food web. Should we combine these two aspects by regarding them as distinct dimensions of trophic activity (multiplicatively), or by regarding shared prey and shared predators as perfectly equivalent (additively)?

As well, we may use different information in defining trophic similarity, depending upon the overall trophic viewpoint adopted. We will consider similarity measures that use only the food web information of presence or absence of each species in the diet of each other species (topological similarity), and we will also consider measures that utilize quantitative information about the strengths of feeding links (flow similarity).

Original trophic entities

The ideal trophic data would be resolved to the biological species level (if not further, for instance into life stages or size classes within species), and we have been writing as if that kind of data were available. But of course, it is not. Even in the best current (and foreseeable) data, at least some of the original trophic entities (OTEs), in terms of which the data are given, are aggregates of species. We can apply all the ideas discussed thus far to such data, simply by everywhere replacing the word "species" with the acronym "OTE". We will do just that in the remainder of our discussion. In a technical sense, there is no difficulty in working with aggregate OTEs, but at this point, we do not know to what extent this might influence final outcomes of interest. Indeed, that is one question that we hope to address indirectly by investigating the influence of subsequent aggregation of OTEs.

Topological similarity

Suppose we have nothing but purely topological food web data. Probably the best known similarity measure for binary data is the similarity coefficient of Jaccard (1900), for objects that may or may not fit each of two categories:

$$S_J = \frac{a}{a+b+c}$$

where a is the number of objects that fit both categories, b is the number of objects that fit the first

category but not the second, and c is the number of objects that fit the second category but not the first.

This coefficient has been used to calculate trophic similarities in what we will call an additive way (Sugihara et al. 1989, Martinez 1991). For two species i and j, the additive Jaccard similarity is

$$S_{TA}(i,j) = \frac{a}{a+b+c} \tag{1}$$

where a is the total number of prey and predator species that species i and j have in common, b is the number of species that are prey or predators of species i but not of species j, and c is the number of species that are prey or predators of species j but not of species i. Notice that in this definition, species' roles as predators and resources are not distinguished: in each of the numbers a, b, and c, common prey and common predators are lumped indiscriminately together in the same sum.

On the other hand, if we regard the predator and resource roles as distinctly different dimensions of trophic activity, then we need to explore alternative ways in which these two aspects interact. One can imagine cases in which the composition of an animal's diet might influence the composition of its set of predators, and vice versa. For instance, different diets might require different patterns of spatial movement, which could favor success by different predators; or avoiding different predators might require different behaviors, which could influence diet. One might hope that, in general, such effects tend to be atypical, or not very strong. Then the predator and resource roles would be largely independent. Our task is analogous to calculating resource utilization overlaps in a multidimensional niche space. In that setting, independent dimensions of activity yield multiplicative overlaps (May 1975). The same reasoning applies in our case.

A multiplicative Jaccard similarity may be written

$$S_{TM}(i,j) = \frac{a_1}{a_1 + b_2 + c_3} \cdot \frac{a_2}{a_1 + b_2 + c_3} \tag{2}$$

where a_1 is the number of species that are prey of both species i and species j, b_1 is the number of species that are prey of species i but not of species j, c_1 is the number of species that are prey of species j but not of species i; and a_2 is the number of species that are predators of both species i and species j, b_2 is the number of species that are predators of species i but not of species j, c_2 is the number of species that are predators of species j but not of species i. For cases in which either of the two denominators in eq. 2 was zero, a value of zero was assigned to S_{TM}.

The multiplicative form distinguishes the roles of predator and resource for each species, and requires high similarity in both roles to achieve a high score,

unlike the additive form. For instance, two species with identical prey but completely different predators would necessarily have $S_{TM} = 0$, whereas S_{TA} could take any value in the interval $(0,1)$. We will make other comparisons below.

Flow similarity

Suppose we know, in addition to the food web topology, some measure f_{ij} of the strength of the trophic link from species i to species j, for all pairs i, j. Typically these link strengths would be quantified by some sort of interaction strength or flow through the food web. In terms of the flows f, we can define for each species i and for all other species k: the proportion p_{ki} of consumption by species i that comes from species k, and the proportion q_{ik} of consumption of species i that goes to species k. Later in this paper we will describe a method for estimating flows, hence the proportions q, from the proportions p (for instance, from stomach content data) together with data on body size.

Given the p's and the q's, we can define trophic similarities analogous to the usual dietary similarities that use only the p's; we will call them "flow similarities". Of course, we can also define topological similarities from this information (which includes the food web) if we wish. Again we will distinguish an additive form and a multiplicative form, as we did for topological similarity. We will use the additive form

$$S_{FA}(i,j) = \frac{\sum_k (p_{ki} p_{kj} + q_{ik} q_{jk})}{\sqrt{\sum_k (p_{ki}^2 + q_{ik}^2) \sum_k (p_{kj}^2 + q_{jk}^2)}} \quad (3)$$

and the multiplicative form

$$S_{FM}(i,j) = \frac{\sum_k p_{ki} p_{kj}}{\sqrt{\sum_k p_{ki}^2 \sum_k q_{ik}^2}} \cdot \frac{\sum_k q_{ik} q_{jk}}{\sqrt{\sum_k p_{kj}^2 \sum_k q_{jk}^2}} \quad (4)$$

Trophic similarity between clusters

In order to decide, at a given level of similarity, which OTEs to aggregate together into trophospecies, one must apply some sort of clustering algorithm. This requires a rule for defining similarity between arbitrary clusters (aggregates) of OTEs based on the pairwise similarities between OTEs. In many applications of cluster analysis, there is no literal functional meaning of a cluster, nor of similarity between clusters. Nevertheless, one can define "abstract" cluster similarity measures such as single linkage and complete linkage (for instance, Anderberg 1973), and use them sensibly to discover meaningful higher-level entities.

We can apply this methodology to trophic clusters, yet in doing so, we are faced with a somewhat novel situation. As a purely trophic entity, a cluster of OTEs has a literal functional meaning: it consumes, and it is consumed. Therefore, an abstract definition is not required for trophic similarity between clusters, and we can derive it from trophic similarity between OTEs. Such a derivation is, however, not entirely ambiguous. First, a convention must be adopted. In the case of topological similarities, we need a convention that tells us when there is a trophic link between two clusters; in the case of flow similarities, we need to define flows between clusters.

We will consider two alternatives, that apply both to topological and to flow similarities: maximum linkage and minimum linkage (Martinez 1991). Under the convention of maximum linkage, there is a trophic link from cluster I to cluster J if and only if there is a trophic link from some OTE in I to some OTE in J. On the other hand, minimum linkage calls for a trophic link from cluster I to cluster J if and only if there is a trophic link from every OTE in I to every OTE in J. The maximum linkage convention yields the largest number of links among clusters that one plausibly could arrive at; while minimum linkage produces the smallest number of links. The corresponding flow, when defined for OTEs, is simply the sum over all flows between OTEs in the two clusters if there is a link between the clusters; otherwise the flow is zero.

Having defined trophic linkages for clusters, we can define trophic similarities for clusters exactly the same as we did for species (or OTEs), using the additive and multiplicative Jaccard similarities STA, STM. Having defined flows for clusters, we can extend the flow similarities SFA, SFM to clusters. In both cases, when calculating the similarity between two clusters I and J, we take the sums in eqs (1–4) over all OTEs external to I and J. For each of the two contexts of topological similarity and flow similarity, this yields two similarity measures for clusters, which we will call the natural maximum linkage similarity NMAX and the natural minimum linkage similarity NMIN.

We also explored four other similarity measures taken from standard cluster analysis. In the single linkage method (SL), the similarity between two clusters is the maximum of the similarities between pairs of OTEs, one in each cluster. In the complete linkage method (CL), the similarity between two clusters is the minimum of the similarities between pairs of OTEs, one in each cluster. Following the method of average similarity within clusters (ASWC), the similarity between two clusters is the average similarity of all OTEs that would be in the new cluster formed by merging the two clusters under consideration. Following the average similarity between clusters method (ASBC), the similarity between clusters is the average similarity over all pairs of OTEs, one in each cluster.

Estimation of flows from dietary proportions

Methods used to create the Caño Maraca food web dataset are described in detail in Winemiller (1990). The fishes, which are the only consumers in the web, are resolved to species, most invertebrate taxa are resolved to order, and primary producers and detritus are separated into functional groups, such as diatoms, desmids, filamentous algae, or macro-algae (*Chara*). The trophic links in this food web are quantified as dietary volumetric proportions, p_{ij}, and not the consumption rates, or flows, f_{ij}. Generally speaking, flow data are produced less frequently than are dietary proportion data. However, we do have data on the body sizes and relative abundances of our consumers, which can be used to estimate energy flows in the food web.

The ingestion rate of individual animals within broad metabolic categories (endotherms, vertebrate ectotherms, invertebrate ectotherms) follows an allometric scaling law of the form $I = aw^b$, where I is ingestion rate, W is body weight, and a and b are constants (see data summary in Yodzis and Innes 1992). Since we only need relative ingestion rates, and all of our predators are (metabolically similar) fishes, the value of the coefficient a is irrelevant and we can simply set it equal to 1. The power b is well approximated by 0.75 for fishes (Brett 1971, Brett and Groves 1979, Gerking and Lee 1983).

Using each species' average body weight (based on all captured specimens), we obtain a crude estimate of relative ingestion per individual. Multiplying that by the relative abundance of each species produces an estimate of relative total ingestion I_j for each species j in the community. Multiplying that by the dietary proportions p_{ij} for species j converts those to estimates for the relative energy flows f_{ij}. From these numbers we can immediately obtain estimates for the proportions q_{ij}, which enables us to calculate the similarities (3,4).

Defining trophospecies

For a given food web (and possibly for an accompanying set of flows), once we have chosen a definition of trophic similarity between OTEs and a definition of trophic similarity between clusters, we can perform a hierarchical cluster analysis to get a hierarchical classification of trophospecies in that food web. Hence, for any chosen level of similarity, the clustering up to that level gives us an aggregation of OTEs into trophospecies at the given level of similarity.

We now have four alternative definitions for trophic similarity between OTEs and six alternative definitions of trophic similarity between clusters, producing 24 different hierarchies. We will denote these hierarchies by symbols of the form (S1-S2-S3), where S1 denotes the information used as a basis for similarity (S1 = T

corresponding to topological similarity, S1 = F to flow similarity), S2 indicates how the predator and resource aspects of trophic activity are combined (S2 = A corresponds to additive, S2 = M to multiplicative), and S3 gives the method used to define similarity between clusters (one of the 6 abbreviations, of 2 or 4 upper case letters, introduced for cluster methods in the above section "Trophic similarity between clusters"). Thus, for example, the clustering hierarchy (T-A-ASBC) uses topological additive similarity (eq. (1)) for OTEs, and method ASBC, average similarity between clusters, for similarity between clusters. We compared and contrasted these different classifications by means of cophenetic correlation and by an appraisal of the concordance between the resulting hierarchies for the Caño Maraca food web and the magnitudes of OTE pairwise similarities from similarity matrices based on alternative methods (T vs F, A vs M), plus any additional ecological information gathered on this system. For verbal economy, we refer to the dendrograms from hierarchical clustering as "trees".

Sokal and Rohlf (1962) proposed a method, known as cophenetic correlation, for the evaluation of hierarchical classifications. The method is based on the following idea. In a sensible hierarchical classification, one would expect that the more similar are any two OTEs, the higher should be the similarity level at which they first share membership in a cluster. Indeed, one expects that in a really good tree this should hold even in a quantitative sense: the similarity level at which any pair of OTEs first share membership in a cluster should be quite close to their original similarity as OTEs.

Sokal and Rohlf formalize this idea as follows. Given a tree, for any pair of OTEs, call their phenetic similarity the highest similarity level at which those two OTEs share membership in a cluster (that is, the similarity level at which they first become lumped together in a cluster). If we make matrices of the pairwise phenetic similarities (the phenetic matrix) and of the original similarities from which the tree was derived, then the cophenetic correlation of the tree is the product moment correlation coefficient between the elements of those two matrices. Cophenetic correlation provides an objective measure of the suitability of alternative trophospecies definitions that are based on hierarchical cluster analyses.

Results

Cophenetic correlation

Table 1 shows the cophenetic correlations of the 24 trees derived from our four OTE similarity measures ((topological vs flow web) × (additive vs multiplicative integration of consumer and resource roles)) and our six cluster similarity measures. Looking first at the OTE

Table 1. Cophenetic correlations for 24 different notions of trophic similarity, in which each OTE's role as a predator and as a resource is taken into account: 4 notions of similarity between OTEs (topological or flow, additive or multiplicative) and 6 notions of similarity between clusters of OTEs, listed in the first column.

Cluster similarity	Topological similarity		Flow similarity		Row average
	Additive	Multiplicative	Additive	Multiplicative	
NMAX	0.92	0.88	0.73	0.63	0.79
NMIN	0.59	0.53	0.72	0.65	0.62
SL	0.91	0.90	0.52	0.30	0.66
CL	0.78	0.74	0.83	0.63	0.74
ASWC	0.85	0.75	0.78	0.71	0.77
ASBC	0.95	0.96	0.86	0.78	0.89
Column average	**0.83**	**0.79**		**0.62**	

similarities, we see that, in terms of cophenetic correlation, the two topological similarity measures S_{TA} and S_{TM} tended to be superior to the two flow similarity measures S_{FA} and S_{FM}. The average similarity between clusters (ASBC), the single linkage method (SL), and the natural maximum linkage similarity (NMAX) produced the highest cophenetic correlations (average = 0.90–0.95) for topological webs. The ASBC clustering algorithm produced the highest cophenetic correlations for flow webs (average = 0.82).

Phenetic matrices also can be used to compare trees. For any two trees based on the same set of OTEs, we will call their phenetic correlation the product moment correlation coefficient of the corresponding elements of the phenetic matrices for the two trees. The more similar the two trees, at least in terms of phenetic structure, the higher the phenetic correlation. Fig. 1 is a metacluster analysis of results from our 24 cluster analyses, using phenetic correlation to measure similarity between trees, and average similarity between clusters to measure similarity between tree clusters. The major distinction seen in Fig. 1 is between topological similarities and flow similarities for OTEs. Within each of these, the additive and multiplicative similarities segregated reasonably well. The three best OTE cluster similarities (based on cophenetic correlation analysis – ASBC, SL, and NMAX) produced very similar trees for each of the two topological OTE similarities. The correlation between the ASBC-SL-NMAX clusters based on the additive versus multiplicative method for integrating consumer and resource roles in topological webs was approximately 0.4. The NMIN method produced outlier clusters among topological web-based trees, and the SL method produced an outlier cluster among flow web-based trees (Fig. 1). For the dietary proportions-based method (flow similarity), the greatest tree similarity was between the two superior clustering algorithms (ASBC and CL based on cophenetic correlation) and the additive method for integrating consumer and resource roles.

From the standpoint of cophenetic similarity, four tentative conclusions can be drawn: 1) overall, the

Jaccard-based, topological measures of similarity for OTEs tended to provide more consistent patterns than flow similarities; 2) the ASBC, SL, and NMAX clustering algorithms performed better than the other three clustering algorithms for topological webs; 3) there is little basis for choosing between the two methods of integrating consumer and resource data when using topological measures (though the additive method performed slightly better; Table 1), and between our three
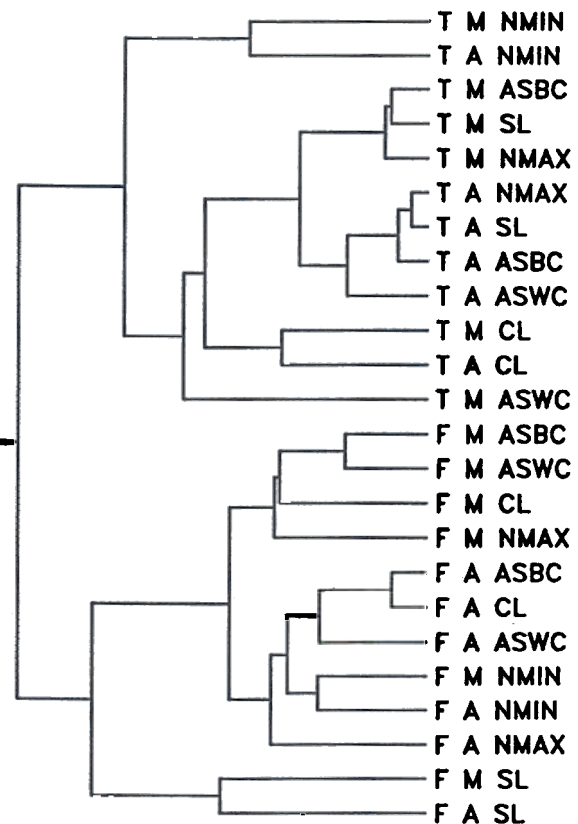

Fig. 1. Metacluster analysis of 24 alternative trophic hierarchies, based on differing trophic similarity measures, for the Caño Maraca food web. Abreviations for similarity measures are defined in the text.
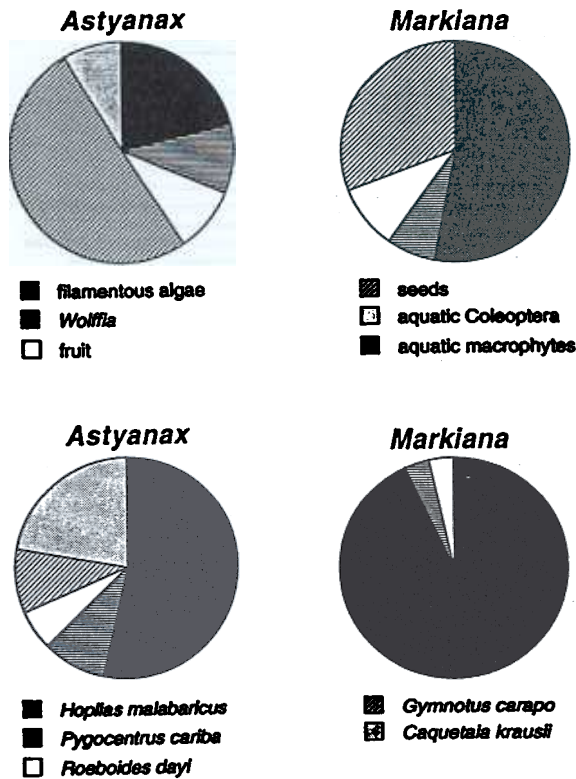
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Fig. 2. (Top) Trophic flow percentages of major diet items (volumetric $q_{ij} > 0.05$) consumed by two omnivorous characid fishes, *Astyana bimaculatus* and *Markiana geayi*, at Caño Maraca based gut contents analyses from 12 monthly samples. (Bottom) Trophic flow percentages for the major predators (volumetric $q_{ij} > 0.03$) associated with each of these omnivores during the same period.

best measures of cluster similarity using topological measures (though ASBC performed slightly better; Table 1); and 4) the ASBC and CL methods based on the additive method of consumer and resource integration performed best for flow measures of similarity.

Tree comparisons

In this section, several of the trees are compared and discussed from the standpoint of clustering patterns and the natural history of the species involved. Our objective is to see which, if any, of the trees seems to be identifying ecologically meaningful trophic aggregations. The patterns of aggregation in the trees can be interpreted in relation to the primary data on shared diet elements and shared predators. We will focus attention on two morphologically similar omnivorous characids, *Astynax bimaculatus* and *Markiana geayi*, that have a high degree of ecological overlap. Fig. 2 compares the proportional biomass flow data for each fish in terms of its dual roles as a consumer and resource. We illustrate the trees as a hierarchical set of
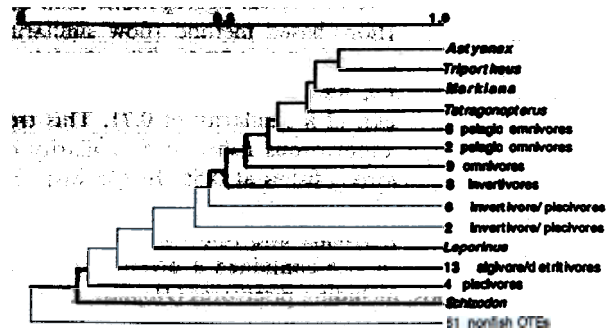

Fig. 3. Essential features of tree T-A-ASBC (cluster similarity based on topological additive similarity between OTEs and the average similarity between clusters convention) in terms of the relationship of *Astyanax fasciatus* and *Markiana geayi* with each other and with similar staxa and nodes of increasingly dissimilar taxa. Similarity varies linearly from 0 (extreme left of tree) to 1 (extreme right of tree).

branching nodes with increasing levels of aggregation in the representation of terminal nodes as one moves away from the terminal nodes *Astyanax* and *Markiana*. In this way, the size and complexity of the tree is reduced and OTE groupings within trees that were derived from alternative rules for clustering and estimating trophic similarity can be compared.

Topological vs flow similarity

Differences in the manner in which the topological (link presence/absence) and flow (dietary proportions) criteria influence hierarchical aggregation can be illustrated by comparing the positions of species in trees (T-A-ASBC, Fig. 3) and (F-A-ASBC, Fig. 4). All other factors being equal, the Jaccard-based method of computing OTE similarities (topological similarity (T))
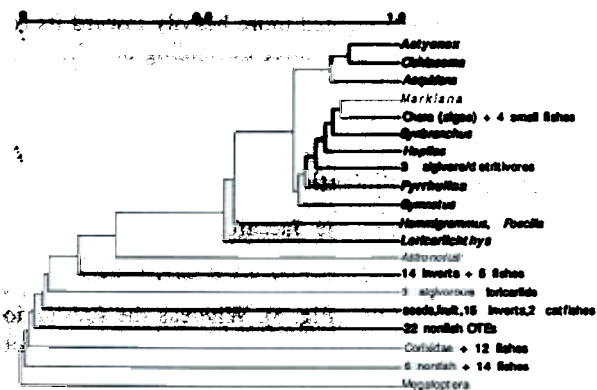

Fig. 4. Essential features of the tree F-A-ASBC (cluster similarity based on flow additive similarity between OTEs and the average similarity between clusters convention) in terms of the relationship of *Astyanax fasciatus* and *Markiana geayi* with each other and with similar staxa and nodes of increasingly dissimilar taxa.

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yielded more intuitive ecological aggregations than did the dietary proportions-based method (flow similarity (F)). For example, tree (T-A-ASBC) (Fig. 3) joined *Astyanax*, *Markiana*, and a third pelagic omnivorous characid, *Triportheus*, at a similarity of 0.71. This tree joined all pelagic omnivorous fishes at a similarity of 0.6, and all omnivorous fishes at 0.55. In contrast, the flow-based tree (F-A-ASBC) (Fig. 4) joined two larger nodes containing *Astyanax* and *Markiana* at a similarity of 0.72. These nodes contained a diverse collection of feeding guilds, including piscivores (*Hoplias*, *Gymnotus*), algivore/detritivores, invertivores, and even macroscopic algae (*Chara*). A distinguishing feature of tree (F-A-ASBC) is that it clusters some nodes based on high similarity in the role of predator, and clusters others based on high similarity in the role of resource. Tree (T-A-ASBC) performed better in grouping species with similar body sizes, microhabitats, and diets. One might assume that large similarity in body size, microhabitat utilization, and swimming behavior places species at risk of falling prey to many of the same predators, however the divergence between the trees in Figs 3 and 4 suggests that this is not a strong feature in this food web.

By using dietary proportions as weighting factors both for resource consumption and for harvest by predators, the flow web convention emphasizes resource specialization over generalization in clustering algorithms. If an animal has a broad diet (i.e., each prey contributes a small fraction to the total diet) and it is a common prey of some predator, then clustering algorithms will group that animal with the other common prey of its predator. In this case, there is greater weight assigned to the animal's role as a resource in the food web. If the animal is a resource specialist (only a few resource categories are common in the diet) and is itself a small dietary component for predators, then it will cluster with other members of a feeding guild based on its diet. So the dual roles of intermediate species in a food web will be weighted more heavily toward its role as a predator or as a resource depending on which role is more specialized.

Additive vs multiplicative similarity

Differences between the Jaccard summation (A) and Jaccard product (M) methods of calculating node similarity can be seen by comparing tree T-A-ASBC (Fig. 3) with tree T-M-ASBC (Fig. 5). Whereas the summation method joined *Astyanax* and *Markiana* (with *Triportheus*) at 0.71, the multiplicative method joined them as members of clusters at 0.2 (Fig. 5). The *Astyanax* and *Markiana* clusters in the M tree contained pelagic and benthic omnivores and invertivores, plus an invertebrate and fish-feeding cichlid (*Caquetaia*). Because the additive method produced a tree with
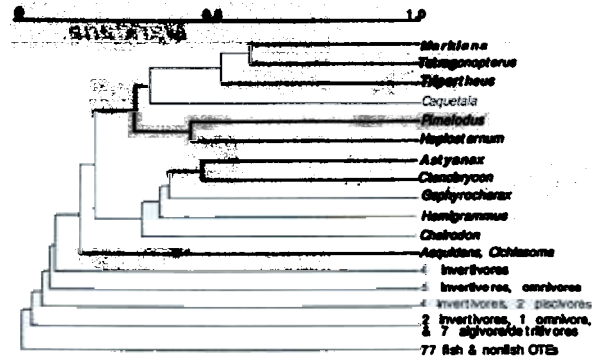

Fig. 5. Essential features of the tree T-M-ASBC (cluster similarity based on topological multiplicative similarity between OTEs and the average similarity between clusters convention) in terms of the relationship of *Astyanax fasciatus* and *Markiana geayi* with each other and with similar staxa and nodes of increasingly dissimilar taxa.

a much more hierarchical branching structure (Fig. 3) and joins ecologically and morphologically similar species at higher levels of similarity, we deem it superior to the multiplicative method. Again, patterns in tree T-M-ASBC appear to be more heavily influenced by species' roles as resources when compared with tree T-A-ASBC.

ASBC clustering vs NMAX clustering

The method of clustering had a large influence on tree structure, and two methods, ASBC (average similarity between clusters) and NMAX (natural maximum linkage), yielded superficially similar results. The structure of trees produced by the two clustering methods (in each case, using topological data and similarity based on the Jaccard summation method) is illustrated in Figs 3 and 6. In each case, the tree bifurcates into two large
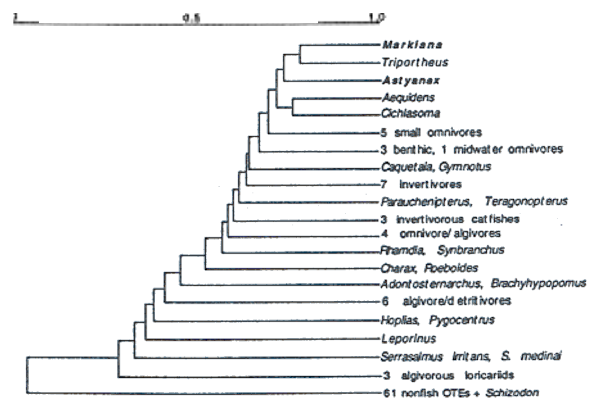

Fig. 6. Essential features of the tree T-A-NMAX (cluster similarity based on topological additive similarity between OTEs and the natural maximum linkage convention) in terms of the relationship of *Astyanax fasciatus* and *Markiana geayi* with each other and with similar staxa and nodes of increasingly dissimilar taxa.

clusters at a low similarity of about 0.05. In both trees, one cluster consists of fish OTEs (in which case, each OTE is associated with data for the role as predator and as resource) and the other cluster consisted of non-fish OTEs (nodes only associated with the role as resource). Had we quantitatively estimated diets for the non-fish nodes, the fish vs non-fish bifurcation in these two trees would likely vanish.

The ASBC and NMAX clustering methods each produced a tree with a highly hierarchical clustering structure, however the NMAX tree contained more branching nodes (Figs 3, 6). Both methods grouped *Astyanax*, *Markiana*, and *Triportheus* at high levels of similarity (ASBC at 0.71, NMAX at 0.72). In each tree, this trio of fishes was joined, at successive nodes, by clusters comprised of other omnivores, but the specific OTEs varied between the two trees. Based on species' feeding niches, ecomorphology and microhabitat use, the ASBC tree (Fig. 3) produced a more logical hierarchy of clusters than the NMAX tree (Fig. 6). For example, *Aequidens* and *Cichlasoma*, the two species that first cluster with the focal trio of pelagic omnivores in tree NMAX, are omnivorous cichlids that forage on invertebrates and seeds on or near the substrate and vegetation.

Comparisons of OTE pairwise correlations

Here we compare the magnitudes of correlations for nine selected fish OTE pairs from matrices of OTE pairwise product-moment correlations that were based on different similarity measures. This pairwise OTE analysis eliminates the choice of clustering algorithm from our evaluation of alternative rules used for estimating trophic similarity. Eight matrices were considered based on topology vs flow webs as well as treatment of resource data only, consumer data only, or additive vs multiplicative integration of resource and consumer roles. In order to have a range of possibilities for viewing OTEs' simultaneous roles as consumers and resources, we chose, more or less randomly, nine pairs of small fishes among those that feed low in the food web and are themselves preyed upon by piscivorous fishes. Similarities (product-moment correlations) between a small algivorous loricariid, *Nannoptopoma spectabilis*, and three other algivores from divergent higher taxa (*Steindachnerina argentea*, *Prochilodus mariae*, *Poecilia reticulata*) were examined. In addition, similarities between the omnivorous characid, *Ctenobrycon spilurus*, and thee other omnivores (*Astyanax bimaculatus*, *Triportheus* sp., *Aequidens pulcher*) plus an invertebrate feeder, *Hemigrammus* sp., and three other invertebrate feeders (*Aphyocharax alburnus*, *Characidium* sp., *Apistogramma hoignei*) were examined. Diets tended to have a high overlap among nine species pairs, and overlap for shared predators ranged from zero to

high, which provides a range of conditions for comparison.

We will first compare similarity measures based on dietary proportional data (i.e., flow webs). In all but one case, the additive similarity was smaller (mean = 0.42) than resource-based similarity (mean = 0.79), an indication that species with similar diets tended not to have similar predators. In the case of *Ctenobrycon* and *Astyanax*, the additive similarity was only slightly greater than the resource-based similarity (0.71 and 0.74, respectively). When additive similarities were compared with predator-based similarities, the opposite result was obtained, with all but one of the additive similarity values being larger than the predator-based similarities (mean = 0.25). Again, in the case of *Ctenobrycon* and *Astyanax* the additive similarity value was only slightly smaller than the predator-based similarity (0.74 and 0.75, respectively), indicating that these species share a large proportion of common prey and predators. In the case of the multiplicative similarities, wherever there was a zero value for one of the two similarity measures (resource-based or consumer-based) for a species pair, then the multiplicative similarity for that species pair also is zero. Consequently, the multiplicative similarities were smaller than the additive similarities in all nine cases (multiplicative mean = 0.19).

The patterns for topological webs (link presence/absence data) were very similar to those described for flow webs. In all but one case, the additive similarity was smaller (mean = 0.53) than resource-based similarity (mean = 0.60), and again, the exception was the pair *Ctenobrycon-Astyanax* with a small difference (additive similarity = 0.63, resource-based similarity = 0.60). Again, the additive similarities were larger than the consumer-based similarities, with the one exception being *Ctenobrycon-Astyanax* (consumer-based similarity = 0.86). In every case, multiplicative similarities (mean = 0.16) were smaller than additive similarities based on topological data.

If we compare the topological data vs flow data using the same basis of calculating similarity, we find that for the resource-based web, similarity values are lower in the topology web for all but one of the nine species pairs (the pair *Hemigrammus-Aphyocharax*). Using only the consumer-based web, approximately half of the species pairs had greater similarity values based on topological data and the other half had lower values. The same pattern occurred for the additive and multiplicative webs (about half were higher and half lower for topological vs flow data).

Overall, it appears that the additive method of integrating species' roles as consumers and resources in food webs is superior to the multiplicative method for aggregating species into trophospecies. The performance of topological and flow webs was similar in most comparisons, however flow data tended to yield greater similarity values than topological data when species dietary data were the sole basis for similarity.

We performed a cluster analysis of the eight similarity matrices based on the product-moment correlation coefficient of each pair of similarity matrices. The additive- and multiplicative-based similarity matrices clustered with the consumer-based similarity matrices at 0.43 and this cluster grouped with the resource-based similarity matrices at $r = 0.01$ (the flow-based and topology-based resource-based matrices clustered at $r = 0.71$), an indication that species' roles as resources for predators had a dominant influence on both the additive and multiplicative integration methods.

Discussion

Viewed at the level of biological species, even the smallest and simplest ecosystems in nature are immensely complex. There are two approaches one may take to render these systems manageable: one may consider a small subset of those species present using a fine scale of resolution, or one may aggregate species into higher order entities to consider a larger fraction of the species in the ecosystem. If aggregation is based on a trophic viewpoint, then we are conceiving trophospecies. The first approach, looking at small subsets of the species present, has been the method taken in most community studies during the past three decades or more (e.g., in viewing predator-prey interactions, guilds, mutualisms, etc.). The second approach has been under active investigation for a couple of decades, but seldom has the aggregation been performed in an objective way (Paine 1988, Polis 1991, Hall and Raffaelli 1993).

Several decisions have to be made in order to define trophospecies objectively. We will discuss each of these decisions in turn, and then we will comment on the assignment of trophic links in aggregated food webs.

Topological vs flow similarity

Our most surprising result was the superiority, in terms of cophenetic correlation, of topological similarity measures for OTEs (i.e., presence vs absence of trophic interactions) over flow similarities (i.e., the relative magnitude of trophic interactions are estimated). The evaluation of topology vs flow similarity that was based on the magnitudes of species pairwise correlations yielded equivocal results. Correlations were higher for the flow web (relative to the topology web) when based on dietary data only (i.e., the consumer role). About half of the correlations were higher and half lower for the flow webs that were based on OTE's roles as resources only. About half of the correlations were higher and half lower for the flow web based on the additive and multiplicative methods for integration of diet and predator data. One would think that flow

similarities, which take into account the relative abundances of each species' prey and predators, would form the basis for a more effective concept of trophospecies. One might expect that the more precise and accurate the information on which a model is based, the more accurate will be the outputs derived from that model. Yet, the coarser information contained in the topological presence/absence trophic data tended to yield higher cophenetic correlations than did the proportional flow data.

Do topological webs provide the most viable means for aggregating species into reasonable ecological guilds for experimental manipulations, gross food web comparisons, and so forth? If there is substantial error in the estimation of diet fractions (there will always be some), the diet proportions-based method seems to perform poorly for trophospecies estimation. But what lies behind this result? One possibility is that our flow similarities were too theory laden, in that we had to estimate the flows, then the proportions q, from allometric relationships. To test this possibility, we performed cluster analyses using OTE-similarity measures in which only the predator role, not the resource role, of each species is taken into account. This method was

$$S_{TP}(i,j) = \frac{a}{a+b+c}$$

where a is the total number of prey species only that species i and j have in common, b is the number of species that are prey of species i but not of species j, and c is the number of species that are prey of species j but not of species i; and

$$S_{FP}(i,j) = \frac{\sum_k p_{ki} p_{kj}}{\sqrt{\sum_k p_{ki}^2 \sum_k q_{kj}^2}}$$

where p_{ij} is the proportion of consumption by species j that comes from species i. Based on the resulting cophenetic correlations, topological similarity performed slightly better than flow similarity (mean correlation = 0.86 and 0.82, respectively). For the clustering method NMIN, flow similarity performed better, and flow and topology methods performed essentially the same for the method ASWC (Table 2). The two clustering methods that performed better than NMIN for the flow data (i.e., NMAX and ASBC) had cophenetic correlations that were only slightly greater when based on topological data (magnitude of the difference = 0.04 in each case).

The differences between the performance of topology- and flow-based similarities must derive from the two differing treatments of weak feeding links. Fig. 7 investigates the influence of weak links on the two additive OTE similarities (STA, SFA) using the cluster

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Table 2. Cophenetic correlations for 12 different notions of trophic similarity, in which each species' role as predator only is taken into account: 2 notions of similarity between OTEs (topological or flow) and 6 notions of similarity between clusters of OTEs, listed in the first column.

Cluster similarity	Topological similarity	Flow similarity	Row average
NMAX	0.94	0.90	0.92
NMIN	0.76	0.87	0.82
SL	0.92	0.72	0.82
CL	0.88	0.78	0.83
ASWC	0.72	0.73	0.73
ASBC	0.96	0.92	0.94
Column average	0.86	0.82	

similarity ASBC. In this figure, link threshold is allowed to vary. For each link threshold value, all feeding links are deleted in cases where the prey represents a fraction of the predator's diet less than the link threshold value. The dotted curve gives, for topological OTE similarity, the phenetic correlation of the tree incorporating the link threshold with the original tree to which no link threshold was applied. The dashed curve does the same for flow OTE similarity, whereas the solid curve is the phenetic correlation for each link threshold between the tree based on topological similarity and the tree based on flow similarity.

The flow similarity (dashed curve) is relatively insensitive to the inclusion or exclusion of rare prey, whereas the topological similarity (dotted curve) is very sensitive to rare prey (Fig. 7). As the link threshold defining "rare prey" increases, the trees produced by topological and flow similarities become more alike, but less satisfactory as expressions of the original trophic structure in our data (particularly for the topologically based trees). An almost identical figure is obtained if we compare the two multiplicative similarities STM and SFM in this way.

This suggests that, in the Caño Maraca food web, rare prey are important in ecological distinctions among trophospecies. Interestingly, these distinctions are brought out effectively by the topological, food web viewpoint, whereas they are attenuated in a more quantitative way based on dietary proportions. In such a situation, topological similarity is a better basis for defining trophospecies, provided that rare prey are carefully included (Fig. 7, dotted curve). However, one can imagine systems in which the important ecological distinctions are expressed in common prey, with rare prey a distraction that would distort topologically based trophospecies (e.g., for models of energy flow). Clearly, studies of other highly resolved systems are needed before general conclusions can be stated with confidence.

Our study raises the issue: is a trophic generalist's influence on the global properties and dynamics of a food web more diffuse, and therefore less significant, than that of a specialist that interacts strongly with only a few species? Or conversely, does the generalist, by

virtue of harvesting a greater number of species, have greater overall influence on the dynamics of the food web? The resolution of these questions would depend on a variety of theoretical issues (e.g., donor-control vs predation models) and additional empirical considerations (e.g., the relative abundances of a species' predators, prey, and competitors in the food web).

Additive vs multiplicative integration of consumer and resource roles

The additive similarity measure tended to yield higher cophenetic correlations than the multiplicative measure for integrating species' roles as consumers and resources (Table 1), and, on average, the additive method produced larger species pairwise correlations. The Jac-
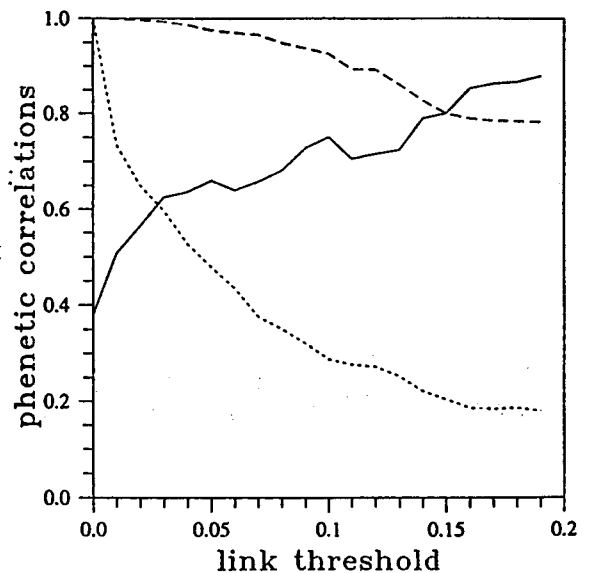

Fig. 7. Phenetic correlations vs link threshold with additive OTE similarity and ASBC cluster similarity: dotted curve, phenetic correlation between tree with and without threshold, for topological OTE similarity; dashed curve, phenetic correlation between tree with and without threshold, for flow OTE similarity; solid curve, phenetic correlation between topologically based tree and flow based tree, both with link threshold.

card summation method (e.g., tree T-A-ASBC) tended to produce aggregations more consistent with intuitive trophic guilds (see above section "Tree comparisons") than the Jaccard product method of estimating node similarity. This was especially true among the fish OTEs of the web, whereas results for the non-fish OTEs (organisms that are represented as resources but not as consumers in our dataset) are fairly comparable following the two algorithms. As indicated when we first introduced the concept, the multiplicative form of similarity rests on the assumption that each species' dual roles as consumer and resource are, to a good approximation, independent. Based on the results of cophenetic correlation and the comparison of patterns of species pairwise correlation, this assumption appears to fail, at least in the Caño Maraca food web.

Multiplicative similarity emphasizes differences between species whenever there is zero overlap based on either diet or predators (because $0 \times$ value $= 0$). In contrast, the additive measure yields a value greater than zero whenever there is at least one shared resource in species' diets or at least one shared predator. However, if one seeks a very narrow definition of trophospecies (e.g., all prey and predators are shared, sensu Pimm et al. 1991), then overlap must be unity for both diet and shared predators, a condition not observed in the Caño Maraca dataset, and one unlikely to be encountered in nature (Winemiller and Polis 1996).

Clustering algorithms

As one might expect due to its derivation from first principles, one of our "natural" cluster similarities, natural maximum linkage similarity (NMAX), performed well as a basis for defining trophospecies via hierarchical clustering. However, a standard "abstract" method, average similarity between clusters (ASBC), also performed well, and yielded trees similar to the NMAX trees. We do not perceive any clear argument why this should generally be true. In the event that results from the two methods were to conflict, we would be more confident of using the method derived from first principles, NMAX.

Yet, method ASBC offers certain advantages. For the Caño Maraca food web, it yielded somewhat better trees in terms of trophic guilds (see above section "Tree comparisons"). Furthermore, it is readily available in standard clustering software packages, while those wanting to use NMAX would need either to create their own code, or request a copy of our FORTRAN subroutine (We will provide our code to anyone who wishes to use it; however, the software provided in standard packages for ASBC will run much faster). Knowing in advance that the two methods perform similarly on our data, we took advantage of the superior execution speed of standard software

in preparing Fig. 7, which required the computation of many trees.

Choice of similarity level for trophospecies aggregation

Our discussion has revolved around the production of hierarchical classifications, but one more step is required to obtain trophospecies, namely a choice of similarity level. To some extent, this will be a subjective judgement (except in the case of Pimm et al.'s (1991) strict definition of complete overlap for diet and predators). The challenge is to find a lower limit for an acceptable similarity level for trophospecies aggregation. In other words, one must determine the maximum level of aggregation that is acceptable given the nature of the ecological problem to be addressed. One criterion might be to impose an upper limit on the range of body sizes that can be tolerated within a trophospecies (this might be desirable if one were, for instance, going to construct a population dynamical model around the trophospecies; Iwasa et al. 1987, 1989). If one were interested in some particular species or group of species (as might often be the case in management situations), one might not wish to merge the taxa of interest with other taxa into a trophospecies.

Assignment of trophic links

Having defined trophospecies, the next step in constructing an aggregated trophic theory is to define trophic links among them. This requires a nontrivial decision. If we have two trophospecies for which no pair of OTEs, one in each of the two trophospecies, is connected by a feeding link, then it is clear that the two trophospecies should not be connected by a feeding link. But how many pairs of OTEs in the two trophospecies need to be linked before we should consider the two trophospecies to be linked? The two extreme attitudes correspond precisely to the conventions labeled maximum linkage and minimum linkage by Martinez (1991), and used by us to define our cluster conventions NMAX and NMIN (refer to above section on "Trophic similarity between clusters"): maximum linkage requires just one pair of linked OTEs, while minimum linkage requires that all pairs be linked. The criterion of minimum linkage would permit us to cluster very few of the original OTEs in the Caño Maraca dataset. Our topic has been the definition of trophospecies, yet our findings have major implications for the linkage problem. The superiority of method NMAX to NMIN, at least by the criterion of cophenetic correlation in the context of topological similarity (Table 1), suggests that of the two extremes, maximum linkage allows a greater degree of aggregation.

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Conclusions

The quest for trophospecies, aggregations of species with similar roles in a food web, requires that species that consume many of the same resources also share many of the same predators. We evaluated alternative methods for aggregating the original trophic entities (mostly species) from a well-documented, aquatic food web into trophospecies, and we conclude that it would be difficult to identify trophospecies by the objective set of criteria used in this study. The greatest problem may be the limitations of the dataset: some species had no documented predators, and some consumers were not assigned resource links because these were not directly documented. In addition, there will always be a certain amount of error in estimating the magnitude of trophic links documented from field research. For example, we chose to perform this analysis on the cumulative annual food web for Caño Maraca, because it had the most complete record of resource use and predation. However, this system undergoes major seasonal changes in ambient conditions, primary productivity, and community structure which greatly influence the food web (Winemiller 1990, 1996). We performed some of the same analyses on seasonal food webs of Caño Maraca and found greater effects from bias due to incomplete data (e.g., species with no observed predators). Whereas the cumulative annual web for Caño Maraca provides one of the most extensive quantitative descriptions of a food web, it is not a complete and accurate description of this diverse, complex, and dynamic system.

The question remains, that given the error inherent in any empirical estimation of a food web, can species be aggregated into trophospecies using the best objective criteria? In terms of estimating species trophic similarity, the results of cophenetic correlation revealed a very slight advantage for a flow-based analysis, whereas patterns of species pairwise correlation yielded equivocal results. The additive method for integrating species' similarities based on their dual roles as consumers of resources and as prey of other predators was generally superior to the multiplicative method. The clustering algorithms that produced the most ecologically sensible trophic groupings were average clustering (ASBC) and maximum linkage (NMAX). The maximum linkage convention (in which a link is included if any pair of OTEs, one in each trophospecies, are linked) produced better aggregations than the minimum linkage convention (in which a link is included if every OTE pair, one in each trophospecies, are linked). The choice of similarity level for defining trophospecies was completely unresolved for this dataset, and more research of this kind using other datasets is needed to further evaluate objective criteria for aggregation into trophospecies.

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