

Food webs and the dimensionality of trophic niche space

(interval graphs/predator-prey models/niche overlap/applied combinatorics)

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ABSTRACT If the trophic niche of a kind of organism is a connected region in niche space, then it is possible for trophic niche overlaps to be described in a one-dimensional niche space if and only if the trophic niche overlap graph is an interval graph. An analysis of 30 food webs, using the combinatorial theory of interval graphs, suggests that a niche space of dimension 1 suffices, with unexpectedly high frequency and perhaps always, to describe the trophic niche overlaps implied by real food webs in single habitats. Consequently, real food webs fall in a small subset of the set of mathematically possible food webs. That real food webs are compatible with one-dimensional trophic niche spaces, more often than can be explained by chance alone, has not been noticed previously.

Ecological studies of where the organisms in communities are and what the organisms do (especially what they eat) frequently use the concept of niche space, the set of the environmental (including biotic) factors acting on an organism (1-5). Studies of what organisms eat frequently also use the concept of a food web (6, 7).

Here is presented a new technique for using food webs to gain information about the minimum number of dimensions of a niche space necessary to represent, in a specific sense, the overlaps among observed trophic niches. Based on the application of this technique to data, it is inferred that, within habitats of limited physical and temporal heterogeneity, the overlaps among niches along their trophic (feeding) dimensions can be represented in a one-dimensional space far more often than expected by chance alone.

MATERIALS AND METHODS

Classification and Selection of Food Webs. Prior to analysis, published or privately communicated food webs were characterized as describing a single habitat or as describing a composite of several habitats. Food webs were also characterized as attempting to describe all the kinds of organisms (possibly restricted to some location, size, or taxa) in a habitat, without reference to the eating relationships among them ("community food webs"); or as attempting to describe all the prey taken by a set of one or more predators, plus all the prey taken by the prey of those predators, and so on ("sink food webs"); or as attempting to describe all the predators on a set of one or more prey organisms, plus all the predators on those predators, and so on ("source food webs"). Source food webs were excluded from further study because they are uninformative about whether the community food webs of which they form a part are interval. Hypothetical or schematic constructions and avowedly incomplete, partial, or tentative food webs were also excluded. Fourteen community food webs and 16 sink food webs from 21 different papers were thus selected.

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Units of Description. These food webs describe the diets or predators not of individual organisms but of kinds of organisms. A "kind of organism" may be a stage in the life cycle or a size class within a single species, or it may be a collection of functionally or taxonomically related species, according to the practice of the original report. This analysis assumes that a group of organisms qualifies as one "kind" of organism in a food web only if its niche, viewed as a region or set of points in niche space, is connected along the trophic dimensions—that is, only if it is possible to pass from any one point in the niche to any other without leaving the niche. For example, if two stages in the life cycle of a single species of insect were so different that the region in niche space corresponding to one stage were unconnected to the region corresponding to another, it is assumed that the two stages would have feeding habits sufficiently different that the stages would be distinguished as different "kinds" in a food web.

Machine Representation of Food Webs. Each food web selected for study was stored in a computer as a matrix with m rows and n columns. Each column corresponds to a predator or other kind of organism that consumes at least one of the kinds of organisms in the food web. Each row corresponds to a prey or other kind of organism eaten by at least one of the kinds of organisms in the food web. Some kinds of organisms are both predators and prey. Let w_{ij} be the entry in the i th row and j th column of a given food web matrix. Then $w_{ij} = 1$ if predator j eats prey i and $w_{ij} = 0$ if predator j does not eat prey i . Version A of a food web includes only eating relationships that could be unambiguously established from the original report; version B includes any additional eating relationships that were uncertain or probable.

The Overlap Matrix and the Number of Niche Overlaps. If two kinds of predators both eat some kind of prey, then along some trophic dimensions the niches of those two predators logically must overlap. The n by n overlap matrix which describes the overlaps among the trophic niches of the predators has 1 wherever the predator corresponding to the row and the predator corresponding to the column both eat some kind of prey in common, and 0 elsewhere. The overlap matrix is symmetric with respect to its main diagonal, which contains all 1s. The number of niche overlaps E is defined as the number of 1s above the main diagonal. Overlap matrices were constructed corresponding to version A and version B of each food web.

The Overlap Matrix and the Dimension of Trophic Niche Space. We say that a food web is interval, and that the trophic niche overlaps that it describes can be represented in a one-dimensional niche space, when its overlap matrix is the adjacency matrix of an interval graph (8). An interval graph is the intersection graph of a set of intervals of the real line. More explicitly, a food web is interval if and only if, for each kind of predator i in the food web, there exists an interval i' of the real line such that for any two predators i and j , $\sum_{k=1}^n w_{ki}w_{kj} > 0$ when and only when the corresponding intervals i' and j'

Table 1. Numbers of interval and noninterval food webs

Habitats	Community food webs		Sink food webs	
	Interval	Noninterval	Interval	Noninterval
Single	7	2	13	1
Composite	1½*	3½*	1	1

* One food web was interval in version A and noninterval in version B. There were no other discrepancies between versions A and B.

overlap. Not every food web with four or more predators is interval.

To test whether a food web is interval, a computer program implementing the algorithm of Fulkerson and Gross (9) was written by Thomas Mueller. The performance of this algorithm was verified by hand for several hundred examples, and the same algorithm was used for both observed and artificially generated food webs (see below).

Monte Carlo Estimation of the Probability of an Interval Food Web. In order to compare the observed frequency of interval food webs with the frequency that would be expected if the food webs or niche overlaps were drawn by chance, it is necessary to estimate the frequency of interval food webs in a universe of possible food webs from which the observed food webs may be drawn. Two possible universes, or models of a random food web, are described here; the results of five other models are consistent with these.

Model 6 assumes that every predator in a given food web has a constant and independent probability p of preying on each prey. The probability p is estimated separately for each food web as $A/(mn)$ in which A is the sum of all elements in the food web matrix (that is, the observed number of feeding relationships) and mn is the maximum possible number of relationships in the food web. For each food web, 100 artificial food webs are generated by distributing a 1 with probability p and a 0 with probability $1 - p$ into each element of an m by n matrix, independently for each element.

Model 7 assumes that the number E of niche overlaps in a given food web is fixed but that the pairs of predators that have overlapping trophic niches are randomly determined. For each food web with E overlaps, 100 artificial overlap matrices are generated by distributing E 1s at random among the elements above the main diagonal.

Let f_{ij} be the proportion of the 100 artificial food webs that are interval according to model j using the parameter values (A, E, m, n) of food web i . For a set S of food webs (e.g., the set

of version A community food webs), the mean μ and variance σ^2 of the number of interval food webs expected according to model j are $\mu = \sum_{i \in S} f_{ij}$ and $\sigma^2 = \sum_{i \in S} f_{ij}(1 - f_{ij})$, respectively. The probability of a discrepancy between an observed number of interval food webs in a set S and the expected μ is assessed by treating $z = (\text{observed number of interval food webs} - \mu)/\sigma$ as a standardized normal random variable. Assuming the validity of the normal approximation, the probability that z exceeds 3.1 by chance alone is less than 0.001 (one-tailed test).

RESULTS

Most food webs based on single habitats are interval (Table 1). The one sink food web and the two community food webs that are not interval are reviewed below. A higher proportion of food webs based on composite communities are noninterval. This finding does not conflict with the hypothesis that most or all single-habitat food webs are interval (see *Discussion*).

Because the distinction between single and composite habitats is less clear-cut, both conceptually and in ecological reports, than that between community and sink food webs, the comparison between the observed number of interval food webs and the number expected by chance from two model universes of food webs retains only the distinction between community and sink food webs (Table 2). Community food webs are interval significantly more frequently than expected by chance, assuming either random eating relationships (model 6) or random niche overlaps (model 7). Sink food webs are interval significantly more frequently than expected by chance, assuming random niche overlaps (model 7) but not assuming random eating relationships (model 6), considering either version A (definite information only) or version B (additional uncertain information) food webs only. The significant excess of sink interval food webs when all versions are considered together ($z = 4.01$) is an artifact of the lack of independence between different versions of the same food web.

Individual Cases. One food web (10) reports prey organisms consumed by vermivorous species of the gastropod genus *Conus* in Hawaii at subtidal reef stations and at marine bench and deep water habitats. It is thus a sink food web describing a composite habitat, and it is not interval. The numbers of specimens examined of each predator range from 4 to 342. It seems plausible that, when only a few specimens of a predator are examined, some kinds of prey eaten on occasion might not be seen. The resulting omission of some trophic niche overlaps may cause a true underlying one-dimensional trophic niche space to appear to be more than one-dimensional. When only predators represented by more than 20 specimens (a threshold deter-

Table 2. Comparison of observed frequencies of interval food webs with expectations assuming random predatory relations (model 6) or random niche overlap (model 7)

Set of food web versions	Versions in set, no.	Observed no. interval	Model 6			Model 7		
			Mean, μ	SD, σ	Normal deviate, z	Mean, μ	SD, σ	Normal deviate, z
All versions*								
Community food webs	24	14	4.83	1.13	8.11	2.95	1.26	8.73
Sink food webs	20	18	14.47	0.88	4.01	13.42	0.66	6.96
Version A								
Community food webs	14	9	3.27	0.93	6.16	2.19	0.96	7.09
Sink food webs	16	14	12.48	0.87	1.74	11.42	0.66	3.92
Version B								
Community food webs	14	8	2.89	0.82	6.21	1.82	0.86	7.19
Sink food webs	16	14	11.65	0.79	2.99	10.42	0.66	5.44

* Food webs for which versions A and B are identical are counted only once here.

mined in advance) are included in a reanalysis, the food web is still not interval.

From this food web, the specimens taken at subtidal reef stations were selected to create the only sink, single-habitat food web which turned out to be noninterval (Table 1). However, if predators represented by 20 or fewer specimens taken at the subtidal reef stations are excluded, the resulting food web is interval. In this case, restricting attention to the adequately sampled predators is not enough to make the food web based on composite habitats interval but does yield an interval food web for a single habitat. Because the food webs of the single habitat and the composite community are reported by the same observer, the difference between them cannot be attributed to different definitions of "kind of organism."

The two single-habitat community food webs that are noninterval describe the sandy shore and Crocodile Creek of Lake Nyasa (11); a third food web describing the rocky shore is interval. The coded forms of these food webs incorporate extensive additions, based on the text, to the ambiguous food web graphs. The number of specimens of each predator examined is not reported, so it is impossible to exclude predators that were lightly sampled.

DISCUSSION

Community Food Webs. The number of community food webs that are interval greatly (and significantly) exceeds the number expected assuming either random eating relations (model 6) or random trophic niche overlaps (model 7). The quantitative adequacy of two noninterval community food webs based on single habitats cannot be assessed. The finding that several composite-habitat community food webs are noninterval is consistent with the hypothesis that every niche space within a single habitat is one-dimensional. It is likely that the features that differentiate one habitat from another are multidimensional (12, 13) and different from the dimension of variation within a habitat.

Sink Food Webs. The only single-habitat sink food web that is noninterval becomes interval if lightly sampled predators are excluded. All single-habitat sink food webs based on sufficient sampling are interval. The number of sink food webs that are interval greatly (and significantly) exceeds the number expected, assuming random trophic niche overlaps. The parameters of the sink food webs evidently specify a region of the model universe 6, which assumes random eating relationships, in which the frequencies of interval food webs are nearly as high as those observed.

Because all of the adequately sampled sink food webs are consistent with a one-dimensional niche space in single habitats, the failure of the observed frequency of interval sink food webs to be significantly larger than expected from some models in no way weakens the conclusion that all or nearly all single-habitat community or sink food webs are interval.

Nonuniqueness of the One Dimension. If a one-dimensional niche space can represent trophic niche overlaps in a single habitat, the single dimension identified in one community may differ from that in another. In a single habitat, the one dimension may be chosen from a manifold of monotonically related dimensions such as predator size and prey size (14).

What Is the One Dimension? A few food web studies provide enough information on feeding and distribution to suggest what the one dimension may be. For example, among Hawaiian snails (10), *Conus sponsalis*, *C. abbreviatus*, *C. ebraeus*, and *C. chaldaeus* have all possible pairwise overlaps of diet on marine benches and, in all four species, individuals between 27 and 28 mm long were found on the marine bench at station

5. If the dietary overlaps found from the pooled marine bench samples are faithfully reflected at station 5, the length of the snails is then a candidate for the single dimension of a space in which trophic niche overlaps can be represented. On the other hand, on reef platforms, the food web is again interval. There the diets of *C. ebraeus* and *C. sponsalis* overlap, but neither diet overlaps with that of *C. flavidus* or *C. lividus*, which do overlap with each other. Because all four species are found between 0 and 30% of the distance from the shore to the outer edge of the reef platforms at stations 3, 7, and 9, that distance measure can be excluded in this case as the one dimension along which trophic niche overlaps can be represented.

Operational Definitions of "Dimension." Different kinds of studies of niche space, such as those of resource partitioning (12, 13) or those based on competition experiments, use different operational definitions of "dimension." Niche overlap inferred from food webs is a necessary but not a sufficient condition for exploitation competition when one common limited resource is food. Niche overlap is neither necessary nor sufficient for interference competition (5). Therefore, a low level of exploitation competition may be inferred when a low level of niche overlap is observed in food webs; but a high level of niche overlap implies only the possibility of a high level exploitation competition. A concordance among the results of the different kinds of studies of "dimensionality" would represent a major empirical discovery. If a concordance among the different operational definitions of "dimension" is taken for granted but turns out to be contrary to fact, the word will become a conceptual trap for the unwary.

Why One Dimension? Several interpretations are possible of why the trophic niche space of single habitats appears to be representable in one dimension. If the finding were a tautology because we say that communities describe composite habitats when their niche spaces turn out not to be one-dimensional, then we would not have the embarrassment of the two single-habitat community food webs that are not interval. This interpretation cannot explain the excess frequency of interval food webs observed in comparison with expectations from random models. We dismiss the accusation of tautology.

It is plausible to expect a predator that can take prey at two different values of any natural continuous variable (such as prey size, seed hardness, altitude, or humidity) to be able to take prey at all intermediate values of the same variable. This argument implies only that a trophic niche should be convex, and hence (8) that three independent dimensions are always sufficient to represent trophic niche overlap. The argument does not explain why *one* dimension suffices.

It may be shown that there is no necessary connection between the one dimensionality of a community's niche space and the qualitative stability (15) of the dynamical system implied by its food web. The possibility of a statistical association between qualitatively stable and interval food webs remains uninvestigated.

The finding that single-habitat food webs are interval while trophic niches are commonly described in multidimensional terms may reflect the difference between community ecology and physiological ecology. Organisms may have more degrees of freedom in their physiological capacities to exist under varied circumstances than the biotic, especially trophic, interactions with other kinds of organisms in their community permit them to enjoy.

Extensions. When food webs are not interval, a combinatorial approach can reveal whether the niche overlaps could be represented by the overlaps of regions in a higher dimensional space (16), but it is necessary to have quantitative information

about the actual shape of niches before applying this theory. When a food web is not interval, it may also be worth examining how far it is from being interval (17).

Shortcomings of This Approach. These results suffer from at least four major shortcomings. First, the concepts in terms of which the data are reported and the results are framed are ambiguous (e.g., what constitutes a "single habitat"?). Second, statistical features of the data used, especially the sampling design and reporting, leave much to be desired. Third, even if the concepts were clear and the statistics of the data impeccable, the claimed results do not attempt to answer important quantitative questions. In particular, most available food webs record feeding relationships as either present or absent. It is impossible to determine whether the high frequency of interval food webs depends in some special way on replacing underlying continuous variables that describe the frequency of predation by a dichotomous representation. Finally, a derivation of the claimed results from a more fundamental dynamic theory is lacking. Each of these shortcomings opens opportunities for further empirical and theoretical investigation.

A review of these results, including examples of the technique of analysis, the complete food web data, a discussion of each food web, a fuller analysis of the consequences, interpretation, and limitations, and recommendations for further research, as well as a synthesis with related results, will appear elsewhere (18).

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