



A Note on the General Likelihood Measure of Overlap

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TABLE 3. "Expected" distribution of types of loop-forming omnivore links in all 40 Briand (1983) food webs. See text for derivation of expected values.

Prey trophic position	Predator trophic position					
	3	4	5	6	7	8
	No. loop-forming omnivore links					
1	82	60	25	9	7	2
2		114	37	14	9	2
3			30	15	10	2
4				6	3	1
5					4	1
6						1

spacing between trophic positions is constant along each diagonal from upper left to lower right in Tables 2 and 3.) A somewhat more refined test of the common-sense hypothesis, which takes this into account, can be done as follows.

Multiply each upper-left to lower-right diagonal in Table 3 by that factor which gives it the same total number of animal-animal links as the corresponding diagonal in Table 2. This readjusted table has a total of 219 animal-plant links, an excess of 103 over Table 2. So taking into account the overall effect on omnivory of similarity of trophic position, we are still left with a deficit of $[103/(434 + 103)] \times 100 = 19\%$ due to the larger costs of feeding on plants and animals. This still exceeds the observed 16% deficit with respect to Pimm's random models, and it should be borne in mind that any test based on Table 3 is biased against the com-

mon-sense hypothesis because of the tendency for food web data to be more coarsely categorized at lower trophic levels.

Omnivory is no more rare than one would expect on the basis of ecological common sense.

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A NOTE ON THE GENERAL LIKELIHOOD MEASURE OF OVERLAP¹

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Measures of niche overlap are commonly used in ecological studies to summarize data on resource use by two or more species. Petraitis (1979) introduced a measure of overlap which is based on the likelihood that two or more species usage vectors are samples from the same unknown vector. However, for this likelihood measure, which Petraitis termed a general measure of overlap, the lower bound, and hence, range of

possible values, is dependent upon the sample sizes and number of species considered. This distinction is important because differences in sample sizes alone may lead to deceptively large differences in values of the general likelihood measures. If a measure of overlap is to be used to compare resource use at several times, or between different groups of species at the same time, the measure should be corrected for the sample size effect.

Petraitis' general measure of overlap is estimated by

$$\hat{G} = r^E \tag{1}$$

where

r is a base

$$E = \left[\sum_{i,j} n_{ij}(\log_r \hat{c}_j - \log_r \hat{p}_{ij}) \right] / N,$$

n_{ij} is a discrete measure of the use of resource j

($j = 1, 2, \dots, R$) by species i ($i = 1, 2, \dots, s$),

TABLE 1. Sample usage data for two species i with no overlap and different sample sizes (N_i).

	Case 1			Case 2		
	Resource		N_i	Resource		N_i
	1	2		1	2	
Species 1	100	0	100	10	0	10
Species 2	0	100	100	0	190	190

$\hat{c}_j = \sum_{i=1}^s n_{ij} / \sum_{ij} n_{ij}$ is the estimated proportional use of resource j if all species were using resource j in the same proportion.

$\hat{p}_{ij} = n_{ij} / \sum_{j=1}^R n_{ij}$ is the estimated proportional use of resource j by species i , and

$N = \sum_{i=1}^s \sum_{j=1}^R n_{ij}$ is the total use of resources (i.e., the total sample size).

The above notation is Petraitis' (1979) with two exceptions. R is used for the number of resources (to distinguish the number of resources from the base r) and a $\hat{\cdot}$ is used to differentiate between an estimate (e.g., \hat{p}_{ij}) and a parameter (e.g., p_{ij}). The data vector for species i , \mathbf{n}_i , is assumed to be a sample from a multinomial distribution $M(N_i, \mathbf{p}_i)$, with $N_i = \sum_{j=1}^R n_{ij}$ denoting the sample size for species i (fixed).

To illustrate the sample-size dependence, consider the data in Table 1. In Case 1, the sample sizes are the same, while in Case 2 they are quite different. Both examples have no overlap. However, in Case 1, $\hat{G} = 0.50$ while for Case 2, $\hat{G} = 0.81$. Note that these estimates are the minimum values of \hat{G} for the given sample sizes (since there is no overlap).

The dependence on the sample sizes can then be made clearer by computing the minimum of \hat{G} for general sample sizes N_1 and N_2 . To find the minimum value of \hat{G} , we need only minimize the exponent.

$$\begin{aligned}
 E &= \sum_{i=1}^s \sum_{j=1}^R n_{ij} [\log_r(\hat{c}_j) - \log_r(\hat{p}_{ij})] / N \\
 &= (1/N) \sum_{i=1}^s \sum_{j=1}^R \left[n_{ij} \log_r \left(\sum_{i=1}^s n_{ij} \right) - n_{ij} \log_r N \right. \\
 &\quad \left. - n_{ij} \log_r n_{ij} + n_{ij} \log_r N_i \right] \\
 &= (1/N) \sum_{i=1}^s \sum_{j=1}^R \left[n_{ij} \log_r \left(\sum_{i=1}^s n_{ij} \right) \right. \\
 &\quad \left. - n_{ij} \log_r n_{ij} \right] \\
 &\quad + (1/N) \left[\sum_{i=1}^s N_i \log_r N_i - N \log_r N \right]. \tag{2}
 \end{aligned}$$

Note that the first part of the right-hand side is greater than or equal to zero and the second part is negative and fixed. Hence the minimum occurs when the first part is zero, i.e., when each resource is used by only one species.

Thus, the minimum of \hat{G} is

$$\hat{G}_{\min} = r^{1/N} \left(\sum_{i=1}^s N_i \log_r N_i - N \log_r N \right). \tag{3}$$

Since \hat{G}_{\min} depends on the N_i (which are assumed fixed), one may ask what values of N_i result in the smallest value of \hat{G}_{\min} . By recognizing the similarity of the exponent in Eq. 3 to the Shannon-Wiener diversity measure, which is minimized when all proportions are the same, the minimum is obtained when $N_i = N/s$. Then, $\hat{G}_{\min} = 1/s$. Note that if there are two species ($s = 2$), the measure is bounded as follows

$$1 \geq \hat{G} \geq \hat{G}_{\min} \geq 1/2.$$

The value of the measure should be adjusted for the minimum whenever it is used to compare resource use data.

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