

NICHE BREADTH, RESOURCE AVAILABILITY, AND INFERENCE¹

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Abstract. Measures of niche breadth are discussed in relation to the distance between the resource use distribution and the resource availability distribution. Methods are developed for comparing breadth measures, testing a breadth measure equal to a given value, and for estimating confidence intervals. A new breadth measure is presented which has good statistical properties and is related to some commonly used niche overlap measures.

Key words: chi-square tests; confidence intervals; delta method; niche breadth; niche width; resource availability.

INTRODUCTION

Hutchinson (1957) formalized the niche as an n -dimensional hypervolume whose axes are critical physical and environmental factors determining the existence of a species. This concept of the niche as a function of measurable factors has provided a foundation for many theoretical and field studies. Much recent theoretical speculation including competitive coexistence, species packing, and limiting similarity is described in terms of this geometric model, often through a geometric descriptor, such as niche breadth and niche overlap (Cody 1974, May 1974, Pianka 1974a). In testing hypotheses generated from theoretical studies, an ecologist often measures these descriptors in the field and compares observed and theoretical patterns (Cody 1974, Pianka 1974b).

One important niche descriptor is niche breadth, which is defined as the "distance through" the niche along some line in niche space. Niche breadth is primarily used as an inverse measure of ecological specialization (Colwell and Futuyma 1971). Measures of niche breadth have been used to test hypotheses, for example, that smaller animals exhibit greater diet specialization than do larger animals (Emlen 1973, Rotenberry 1980) or that wide-niched species are better adapted to uncertain environments (Levins 1968, Slobodkin and Sanders 1969, Rotenberry and Wiens 1980).

Recent interest has focused on the measurement and analysis of niche breadth. Two approaches may be considered, depending on whether the niche space is continuous or discrete. Continuous data typically occur when the niche refers to habitat variables, for example with bivalve molluscs, physical variables such as depth and mean sediment particle size (Green 1971). With continuous data, multivariate statistical methods are typically applied to reduce a possibly large set of correlated variables into a smaller set of independent factors. When one is interested in determining and

characterizing factors that separate species, discriminant analysis is useful (Green 1971, 1974, Dueser and Shugart 1978, 1979). On the other hand, when maximized differences are not important, a principal-components analysis is better (Johnson 1977, Rotenberry and Wiens 1980). Estimates of niche breadth are then based on the reduced set of variables from the multivariate analysis. For example, Dueser and Shugart (1979) suggest using the variability of the distances of the sample points from the origin of the discriminant space as a measure, while M'Closkey (1976) suggests the standard deviation of the discriminant scores as a useful measure of breadth. Rotenberry and Wiens (1980) estimate breadth as diversity along a principal-components axis.

When the data are discrete, the data set is typically not reduced (but see Colwell and Futuyma 1971, Inger and Colwell 1977), and axes (usually a small number) are considered independently. In estimating breadth, data are collected on the use of a set of resources, and measures are then computed based on p_i , the proportion of resource state i used by a given species (Colwell and Futuyma 1971, Petraitis 1979). A resource state represents an ecological category important to a species, such as food type or habitat type.

The two most commonly used measures of niche breadth are due to Levins (1968):

$$H = -\sum_{i=1}^R p_i \ln(p_i), \quad (1)$$

and

$$B = 1/\sum_{i=1}^R p_i^2, \quad (2)$$

where p_i is the proportion of resource i used, and R is the total number of resource states.

Although these measures are criticized for many reasons (see for example Colwell and Futuyma 1971), the objection that has received the most attention is that the measures do not take into account resource availability (Hurlbert 1978, Petraitis 1979, Feinsinger et al. 1981). With most measures, the use of rare resources is given the same weight as the use of common

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ones. Three basic approaches have been suggested to deal with this problem. Hurlbert (1978) suggests that measures of niche breadth be weighted by resource availability and recommends using a weighted version of Levins' measure:

$$B' = 1 / \sum_{i=1}^R (p_i^2 / q_i), \quad (3)$$

where q_i is the proportion of resource i available for use. Petraitis (1979) develops a statistical approach for measuring niche breadth based on the likelihood that the observed proportional usages are the same as the proportions available and suggests the measure:

$$W_1 = (\lambda)^{1/N} \quad (4)$$

where

$$\ln \lambda = \sum_{i=1}^R n_i \ln(q_i) - \sum_{i=1}^R n_i \ln(p_i), \quad (5)$$

n_i is the amount of resource i used (or the number of individuals using resource i),

and

$$N = \sum_{i=1}^R n_i.$$

Feinsinger et al. (1981) propose using the percentage similarity measure:

$$PS = \sum_{i=1}^R \min(p_i, q_i) = 1 - \frac{1}{2} \sum_{i=1}^R |p_i - q_i|, \quad (6)$$

as it measures the area in common between the use and availability distributions.

The primary purpose of this paper is to discuss and derive methods for comparing measures of niche breadth that involve resource availability. These include comparisons of the observed use with what is available, testing breadth equal to a given value, comparing breadth measures between two areas, and calculating confidence intervals for breadth measures. In addition, the relationship among the above approaches to measuring niche breadth is discussed. In particular, I argue that the above methods are similar in that all are based on the distance between use and availability. Finally, a new measure which is related to some commonly used overlap measures and has good statistical properties is presented.

STATISTICAL ASSUMPTIONS

The assumptions for the statistical methods in this paper follow Petraitis (1979) and Feinsinger et al. (1981). I assume that a species samples randomly from an inexhaustible pool of available resources whose relative proportions (q_i) are assumed to be known. The species' use distribution, conditioned on the total number of items used (N), is then multinomial.

VARIANCE ESTIMATES

Variance estimates of the above measures are important because they lead to confidence intervals and hence tests of hypotheses about the measures. Exact variance estimates and confidence intervals for the above measures are difficult to obtain in tractable forms. For example, the exact variance for the PS measure is derived in the Appendix. Note that this variance estimate is not the same as given in Feinsinger et al. (1981). Also note (Table A1) that the estimate of PS is biased (contra Feinsinger et al. 1981). The formulas, however, were verified by simulation (see Appendix). The variance estimate will require a large amount of computer time except for small sample sizes and in practice would not be exact, as the p_i 's would be estimated. Hence simpler estimates of the variance are considered.

A method using simulation to estimate variance was given in Ricklefs and Lau (1980). Although intended for niche overlap measures, the method could be used to estimate variances for niche breadth measures, by keeping the resource availability distribution constant. One would sample repeatedly (with replacement) from the resource use distribution (the p_i 's), compute the measure of breadth, and then estimate the variance. An alternate method is to approximate the measure with a Taylor series and compute the variance of the approximation, ignoring higher-order terms. This method is known as the "delta" method, and examples and a discussion of its use are given in Seber (1973:7). Using this method, the following formulas result:

$$V_A(\hat{W}_1) = W_1^2 \left\{ \sum_{i=1}^R p_i [\ln(q_i/p_i) - 1]^2 - \left(\left[\sum_{i=1}^R p_i \ln(q_i/p_i) \right] - 1 \right)^2 \right\} / N \quad (7)$$

$$V_A(\hat{B}') = 4B'^4 \left[\sum_{i=1}^R p_i^3 / q_i^2 - (1/B')^2 \right] / N \quad (8)$$

$$V_A(\hat{PS}) = \left[1 - \left(\sum_{i=1}^R p_i I_i \right)^2 - \sum_{i=1}^R p_i J_i \right] / N, \quad (9)$$

$$\text{where } I_i = \begin{cases} -1 & \text{if } p_i > q_i \\ 0 & \text{if } p_i = q_i \\ 1 & \text{if } p_i < q_i \end{cases}$$

$$\text{and } J_i = \begin{cases} 1 & \text{if } p_i = q_i \\ 0 & \text{else.} \end{cases}$$

In all cases, one would use the maximum-likelihood estimates for p_i , i.e., $p_i = n_i/N$ in evaluating the variance formulas and estimating the measures. Estimates are denoted using a $\hat{\cdot}$. Note that the variance estimates depend on the observed uses in all three cases. This dependence implies that the variance may change with changing uses even if the measure does not change.

A NEW BREADTH MEASURE

As an alternative to the above measures, I suggest

$$FT = \sum_{i=1}^R (p_i q_i)^{\frac{1}{2}} \quad (10)$$

This measure was originally suggested as a measure of affinity between two distributions (Matusita 1955, 1967) and has many nice properties. The measure takes on values between zero and one (zero if no overlap, one if completely overlapping) and is interpretable as a function of the distance measure:

$$M = \sum_{i=1}^R (\sqrt{p_i} - \sqrt{q_i})^2 \quad (11)$$

Analogous to Petraitis' (1979) likelihood measure, the *FT* measure may be extended to measure overlap between a pair of species or among a group of species (Matusita 1967). In addition, the measure is interpretable in terms of angular components (as in Petraitis 1981). The angular distance between two vectors is given by

$$A = \cos^{-1}(FT) \quad (12)$$

(Balakrishnan and Sanghvi 1968). Furthermore, the measure is related to both Pianka's measure of overlap and the Horn-Morisita measure since the measure is the ratio of the middle term standardized by the square terms in the expansion of Eq. 11 (May 1975). The difference is, however, that the square root of the proportions is used (rather than the actual proportions) so the standardizing terms have the value 1. For example, Pianka's form would be:

$$PA = \frac{\sum (p_i q_i)^{\frac{1}{2}}}{[\sum (p_i)^{\frac{1}{2}} \cdot \sum (q_i)^{\frac{1}{2}}]^{\frac{1}{2}}} = \sum (p_i q_i)^{\frac{1}{2}} \quad (13)$$

The asymptotic variance of the *FT* measure is:

$$V_A(\hat{FT}) = (1 - FT^2)/(4N). \quad (14)$$

As can be seen in the above formula, the asymptotic variance is only a function of the measure. A variance stabilizing formula is available to remove the dependence on the measure and is

$$G(FT) = 2 \arcsin(FT). \quad (15)$$

Of what import is the above transformation for ecological studies? If one is using niche breadth measures as part of a larger experimental design, then when using the *FT* measure, one can treat the transformed measures as normal random variables with variance 1. Hence if the measures are used in an analysis of variance or regression design, the assumption of constant variance will be satisfied only if the transformed *FT* measure is used.

COMPARISON OF VARIANCE ESTIMATES

The approximate variance estimates are compared with simulated variances in Table 1. For a sample size of 50, the "delta method" gives quite accurate estimates. As most experimental studies have sample sizes at least as large as those in Table 1, the "delta method" should provide a reasonable method of obtaining variance estimates. Ricklefs and Lau's (1980) suggestion to use simulation to estimate the variance in niche overlap measures could be applied by holding the resource availability distribution as fixed; however, the simulations will require more time but will not improve accuracy unless sample sizes are small (≈ 20).

For reasonable sample sizes, the above measures may be treated approximately as normal random variables (Seber 1973:7). Hence confidence intervals and tests follow the usual procedures, using normal random variables. For example, an approximate 95% confidence interval for the *FT* measure based on Eq. 15 is

$$\sin[\arcsin(\hat{FT}) \pm 1.96/(2\sqrt{N})]. \quad (16)$$

For the data in Table 2, an approximate 95% confidence interval for *FT* is (.872, .957). Note that the resulting confidence interval is not symmetric, reflecting the skewness in the distribution. As another example, to test the hypothesis $H_0: PS = .5$, one would use:

$$Z = (\hat{PS} - .5)/[\hat{V}_A(\hat{PS})]^{\frac{1}{2}}, \quad (17)$$

and treat *Z* as a standard normal random variable. For the data in Table 2, $Z = (.7 - .5)/(.0012) = 5.7$. Hence the null hypothesis would be rejected. Note that the above methods apply for single tests. Since data and comparisons are often for a group of species, simultaneous methods may be more appropriate (Miller 1966), although the variance estimators will not change.

To compare two estimates of breadth, say at time 1 and time 2, one would use:

$$Z = (\hat{y}_1 - \hat{y}_2)/[\hat{V}_A(\hat{y}_1) + \hat{V}_A(\hat{y}_2)]^{\frac{1}{2}}, \quad (18)$$

where y_1 and y_2 are the respective measures. The resulting statistic would be treated as a normal statistic.

TESTING BREADTH = 1

The above methods are useful if the measures are not equal to one. In particular, if *y* represents one of the measures, one has that under the hypothesis $H_0: y \neq 1$

$$\mathcal{L}(\hat{y} - y) \rightarrow N[0, V_A(y)], \quad (19)$$

where $V_A(y)$ is the asymptotic variance of the measure *y*. However, under the hypothesis $H_0: y = 1$, we do not get asymptotic normality. Rather, one has that under H_0' ,

$$\chi^2_L = -2N \ln(\hat{W}_1), \quad (20)$$

$$\chi^2_{R'} = N(1/\hat{B}' - 1), \quad (21)$$

TABLE 1. Comparison of simulated variance vs. variance estimated using the delta method. In both cases $N = 50$.

Resource use and availability		Measure			
		W_1	B'	FT	PS
p: .2 .1 .2 .4 .1	Breadth	.548	.405	.847	.500
q: .1 .2 .1 .1 .5	Simulated variance	.0050	.0037	.0017	.0029
	Approximate variance	.0054	.0032	.0015	.0032
p: .2 .1 .1 .3 .1 .2	Breadth	.731	.574	.923	.650
q: .1 .3 .2 .1 .05 .25	Simulated variance	.0062	.0075	.0011	.0040
	Approximate variance	.0063	.0071	.0009	.0048

and

$$\chi^2_{FT} = 8N(1 - \widehat{FT}) \quad (22)$$

are all asymptotically distributed as χ^2_{r-1} random variables. (The formulas for $\chi^2_{B'}$ and χ^2_{FT} follow from Petraitis [1979, 1981], and the formula for χ^2_{FT} follows from Bishop et al. [1978:513].) Note that Eq. 20 is the likelihood ratio test statistic. Eq. 21 is the chi-square goodness of fit statistic, and Eq. 22 is the goodness of fit statistic for the Freeman-Tukey residuals test.

I have not found an expression based on the PS measure to use as a test statistic for H_0' . However, one could use Monte Carlo methods to test the above hypothesis, by drawing samples from the known vector of resources (the q 's), compute the measure PS for each Monte Carlo sample, and count the number of times the observed value of PS is larger than the simulated value. One then has a "P-value" for the test. This P-value is, however, only approximate.

Table 2 illustrates the above methods on data from Root (1967). The measures W_1 and FT are not numerically close but yield quite similar test statistics. The measure B' is much smaller than the other two measures and yields a much larger test statistic. Much of the contribution to this statistic comes from the first resource state and reflects the strong selectivity for membracid insects. The other measures do not give as much weight to this rare resource, and hence Hurlbert's measure may be more indicative of selectivity than the other measures.

Note that the test of $H_0': y = 1$ is the natural "randomness" test (sensu Caswell 1976). That is, one is testing whether the observed breadth differs from what would be observed if the species was using the resources randomly. Deviations then suggest that there is selection (or avoidance) of some resources over others. In testing the hypothesis $H_0': y = 1$, the test statistics are often significant (i.e., nonrandom use). When sample sizes are large, minor violations of the underlying assumptions will be inflated and give a significant result. Hence some caution should be applied in using the test statistics.

The test statistics may also be used to compare the measures. Under H_0' , the three statistics all have the same asymptotic distribution and the same moments (for H_0 , the distributions are normal, but the moments are different). The statistics should be reasonably close to each other if H_0' is true, even though the actual measures (W_1 , B' , and FT) need not be close. This relationship facilitates comparisons of the measures, and differences between measures are more apparent.

CONCLUSIONS AND REMARKS

The measures of niche breadth which adjust for resource availability appear to be quite different but are in fact quite similar. Of the four measures considered in this paper, three are related as functions of the distance between the resource availability distribution and the resource use distribution (recall that the PS measure is a function of the Manhattan measure of distance). The fourth measure, the likelihood measure of Petraitis (1979), although not a distance measure or

TABLE 2. Example of methods (B) for testing breadth = 1, using data (A) from Root (1967). The significance value for PS is the proportion of times a simulated value is smaller than .70, using 1000 trials. In each trial a sample p is taken from a multinomial distribution with parameters $N = 81$ and q (the resource vector), and compared with q .

A.	Resource or use				
	Membracid	Cicadellidae	Miridae	Lepidopterous larvae	Other
Deciduous oaks (q)	.046	.160	.046	.015	.733
Gnatcatchers (p)	.307	.136	.049	.049	.459
B. Measure	Estimated breadth	Test statistic	P		
W_1	.70	57.78	<.001		
FT	.92	51.25	<.001		
B'	.37	134.79	<.001		
PS	.70	...	=.000		

function of a distance measure is related distributionally to two of the other measures (B' and FT). In addition it can be shown, by taking a Taylor's series expansion, that the likelihood test is approximately equivalent to the chi-square goodness of fit test (Bishop et al. 1978:514).

What makes the measures different is the way that the rare and dominant resources are treated in the measures. The measure suggested by Hurlbert (1978), B' , is sensitive to selectivity of rare resources, and hence these are given much larger weight in determining the value of the breadth measure. The measures of Matusita (FT) and Petraitis (W_i) are much less sensitive to selectivity. At the other extreme, the Percentage Similarity measure gives greater weight to dominant resources and is more indicative of avoidance than selectivity.

Feinsinger et al. (1981) have argued that the PS measure is the easiest to interpret, as it directly measures the area in common between the availability and use distributions. On the basis of this study, the relationship with the chi-square goodness of fit test makes the measure of Hurlbert (1978) just as easy to interpret, and the sensitivity of the measure to selectivity indicates the usefulness of the measure. In addition, if the data are to be used in a statistical model, the FT measure has advantages over the other proposed measures.

The approach taken in this paper assumes that the resource use vector is multinomial, and the resource availabilities are fixed and known. In actual studies, the availabilities are often estimated and change in response to use (hence are not fixed). Hence, the variance formulas presented represent lower bounds on the actual variances. To account for resource variability, the variances could be estimated, using the simulation approach of Ricklefs and Lau (1980). On the other hand, the delta method could be used, assuming that both availability and use are multinomial vectors. When the data consist of measurements on individuals (e.g., individual diet vectors), an approach using the nonparametric jackknife method is useful (see Zahl 1977 for a related example).

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not use any of the remaining resources, the delta method estimates the variance as zero. This result occurs because the value of PS is entirely determined by the values of the q 's, i.e.,

$$PS = \sum_{(i: p_i > 0)} q_i. \quad (A3)$$

Since the q 's are fixed, the partial derivatives are zero; hence the p 's do not contribute to the variance, and the delta es-

timate is zero. When this situation occurs in the data, the simulation method is the best alternative, as the computing time is much smaller than for the exact method. Case E represents a situation that is much more likely to occur in applications since use is mixed, with some use greater than availability, some less than availability, and some resources not used. As the estimates are close, in most cases, the delta method represents the simplest method of the three for estimating variance.