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BIAS IN ESTIMATING NICHE OVERLAP[1]

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Abstract. Bias refers to the accuracy of a particular estimator. We evaluate bias, using analytic and simulation technics, for six measures of overlap: the likelihood ratio measure, the chi-square measure, the measure based on the Freeman-Tukey statistic, Morisita's adjusted index, Morisita's original index, and Horn's information index. We present an exact formula for a seventh, the percentage similarity measure. We consider bias due to resource sample size, total number of different resources, and evenness of resource distribution. Results indicate that of the seven measures, changes in evenness of resource distribution produce significant bias only in the percentage similarity measure and Morisita's adjusted index. All measures show increasing bias with increasing number of resources. For estimating unbiased overlap, Morisita's original measure of overlap gives the most accurate results, especially when using small sample sizes. The percentage similarity measure, one of the most commonly used measures among ecologists, is also one of the most biased and for this reason is not preferred.

Key words: bias; chi-square; Freeman-Tukey statistic; information index; likelihood ratio; Morisita's index; niche overlap; percentage similarity.

INTRODUCTION

Overlap measures have often been used by ecologists to compare resource use between pairs of species (see review in Hurlbert 1978), with limited concern for the robustness of the measures themselves. There has been recent interest concerning the statistical properties of overlap measures, including variances, confidence intervals, bias, and related attributes (Petraitis 1979, Smith et al. 1979, Ricklefs and Lau 1980, E. P. Smith and T. M. Zaret, *personal observation*).

In this paper we examine overlap measures with regard to bias, which refers to the accuracy of a particular overlap estimator. For example, suppose in a comparison of the diets of two species our actual overlap is .80 and the calculated estimate is .75 on the average, giving a bias of .05. If the standard deviation of the overlap measure is 0.1, then (assuming normality) the probability that the measure is contained within the calculated confidence interval (.75 ± .196) is .93 rather than .95. If the bias is .1, then the probability is actually .83 rather than .95. Use of an estimator with large values of bias will seriously compromise conclusions derived from overlap measures because the likelihood that the confidence interval actually spans the true overlap becomes small (Cochran 1977).

We consider bias of seven commonly used measures of overlap: (1) the likelihood ratio measure (L) suggested by Petraitis (1979): (2) the chi-square goodness-of-fit measure (CX), (3) the Freeman-Tukey measure (FT) developed by Matusita (1955) and van Belle and Ahmad (1974), (4) Morisita's (1959) index as adjusted by Horn (1966), (5) an information measure (Horn 1966), (6) the percentage similarity measure (Renkonen 1938), and (7) Morisita's (1959) original measure.

Because bias is of fundamental importance in determining which overlap measure is the most appropriate for a given data set, for each of the overlap measures we examine the relationship between bias and: (1) resource sample size, (2) total number of different resources, and (3) evenness of resource distribution. We use both analytic and computer simulation technics for our study.

METHODS

Indices

We consider two species that share a set of resources (such as prey items), with r possible resource states. Overlap indices are based on the frequencies p_{ij}, which denote the proportional use of resource j ($j = 1, 2, \ldots, r$) by species i ($i = 1, 2$). In practice the p_{ij}'s are estimated by

$$\hat{p}_{ij} = n_{ij}/N_i,$$

where n_{ij} is the amount of resource j used by species i, and $N_i = \sum_{j=1}^{r} n_{ij}$ is the total usage of resources by species i. For example, in the case of diet comparisons, n_{ij} may be the number of prey j found in the stomachs of species i, and N_i is the total number of prey items.

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We will assume, as in Petraitis (1979), that the vector of counts $\mathbf{n}_i = (n_{i1}, n_{i2}, \ldots, n_{ir})$, conditional on N_i, has a multinomial distribution: $M(N_i, p_{i1}, p_{i2}, \ldots, p_{ir})$.

In this study, we consider seven measures of overlap, three based on test statistics (Smith and Zaret, *personal observation*) and four measures commonly used in applied ecology (Hurlbert 1978).

The seven overlap measures are:

1) the measure based on the likelihood ratio test (Petraitis 1979)

$$L = \exp\left[\frac{1}{N}\sum_{i=1}^{2}\sum_{j=1}^{r} n_{ij}(\ln c_j - \ln p_{ij})\right]$$

where $c_j = (n_{1j} + n_{2j})/(N_1 + N_2)$, and $N = N_1 + N_2$,

2) the measure based on the chi-square goodness-of-fit test (van Belle and Ahmad 1974)

$$CX = 2\sum_{j=1}^{r}[p_{1j}p_{2j}/(p_{1j} + p_{2j})],$$

3) the measure based on the two-sample version of the Freeman-Tukey test (Matusita 1955, van Belle and Ahmad 1974)

$$FT = \sum_{j=1}^{r}(p_{1j}p_{2j})^{\frac{1}{2}}.$$

Although the FT measure is not frequently used in ecological studies, it has the same form as the commonly used Morisita's measure, but is based on a different distance measure. Morisita's measure may be formed as follows: the distance between the two resource usage vectors is

$$\begin{aligned} D^2 &= \sum (p_{1j} - p_{2j})^2 \\ &= \sum p_{1j}^2 - 2\sum p_{1j}p_{2j} + \sum p_{2j}^2. \end{aligned}$$

Morisita's measure is the middle term standardized by the sum of the two squared terms. The FT measure is based on the distance formula

$$\begin{aligned} M &= \sum (\sqrt{p_{1j}} - \sqrt{p_{2j}})^2 \\ &= \sum (\sqrt{p_{ij}})^2 - 2\sum \sqrt{p_{1j}}\sqrt{p_{2j}} \\ &\quad + \sum (\sqrt{p_{2j}})^2. \end{aligned}$$

If we form a measure similar to Morisita's, we get

$$\begin{aligned} C_1{}^1 &= \frac{2\sum\sqrt{p_{1j}p_{2j}}}{\sum(\sqrt{p_{1j}})^2 + \sum(\sqrt{p_{2j}})^2} \\ &= \frac{2\sum\sqrt{p_{ij}p_{2j}}}{2} = FT. \end{aligned}$$

4) Morisita's (1959) index as adjusted by Horn (1966)

$$C_1 = \frac{2\sum_{j=1}^{r} p_{1j}p_{2j}}{\sum_{j=1}^{r} p^2{}_{1j} + \sum_{j=1}^{r} p^2{}_{2j}},$$

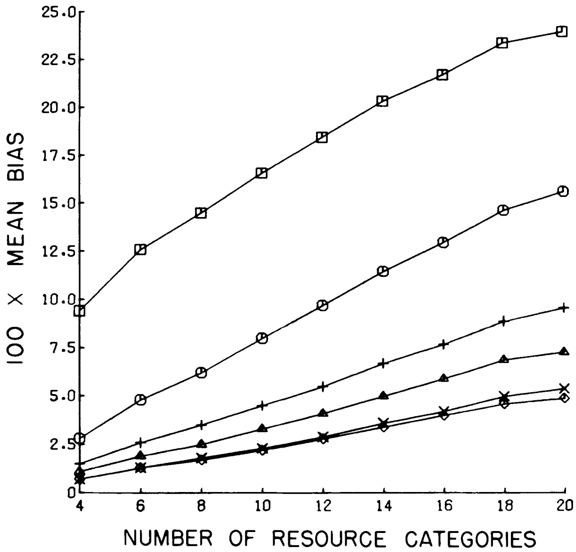

FIG. 1. The effect of changing the number of resources (r) on bias. $N_1 = N_2 = 100$, $p_{ij} = 1/r$ (i.e., $E = 1$). The mean bias values have been multiplied by 100. Key: □ percentage similarity (PS), ○ Morisita's adjusted measure (C_1), △ Horn's information measure (R_0), + chi-square measure (CX), × Freeman-Tukey measure (FT), and ◇ Petraitis' likelihood measure (L).

5) Horn's (1966) information measure

$$R_0 = \left[\sum_{j=1}^{r}(p_{1j} + p_{2j})\ln(p_{1j} + p_{2j}) - p_{1j}\ln p_{1j} - p_{2j}\ln p_{2j}\right]/2\ln 2,$$

6) the percentage similarity measure (Renkonen 1938)

$$PS = \sum_{j=1}^{r}\min(p_{1j}, p_{2j}), \quad \text{and}$$

7) Morisita's (1959) original measure

$$C_1^* = \frac{2\sum_{j=1}^{r} p_{1j}p_{2j}}{\sum_{j=1}^{r} p_{1j}\frac{n_{1j}-1}{N_1-1} + \sum_{j=1}^{r} p_{2j}\frac{n_{2j}-1}{N_2-1}},$$

where as in the above measures $\hat{p}_{ij}$ is estimated by n_{ij}/N_i.

Analytical analysis

Estimates of bias are based on a second order Taylor series expansion of the given measure which allows computation of the expected value (Benjamin and Cornell 1970:184). If we let M denote a measure of overlap, then the bias in estimating M is given by:

$$B(M) \simeq -1/2\sum_{i=1}^{2}\frac{1}{N_i}\sum_{k=1}^{r} p_{ik}(1 - p_{ik})\frac{\partial^2 M}{\partial p_{ik}{}^2} + \sum_{i=1}^{2}\frac{1}{N_i}\sum_{k<m}^{r} p_{ik}p_{im}\frac{\partial^2 M}{\partial p_{ik}\partial p_{im}}.$$

Estimates of the bias for five of the measures are:

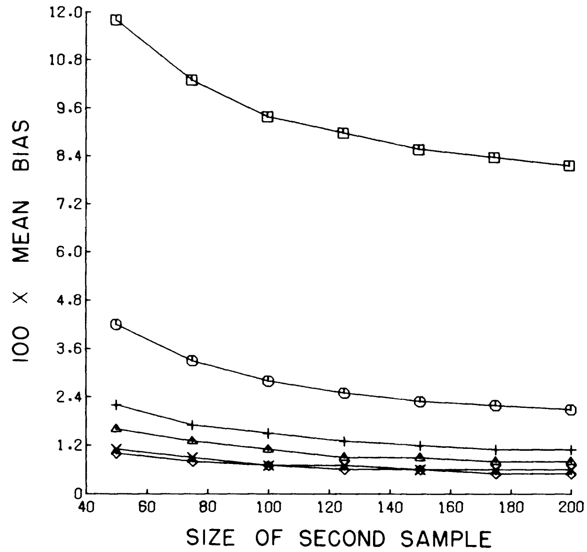

FIG. 2. The effect of the size of the second sample on bias. $N_1 = 100$, $r = 4$, and $E = 1.0$. Symbols are as in Fig. 1. The mean bias values have been multiplied by 100.

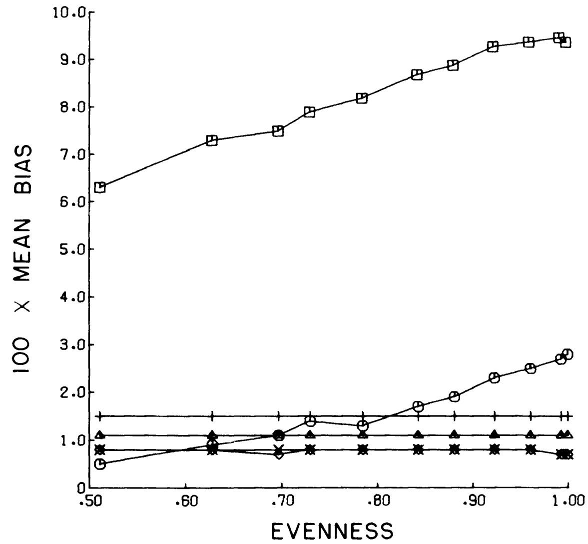

FIG. 3. The effect of evenness on bias. $N_1 = N_2 = 100$, $r = 4$. Symbols are as in Fig. 1. The mean bias values have been multiplied by 100.

$$B(L) \simeq -1/2 \sum_{i=1}^{2} \left[\frac{N_i L}{N^2} \sum_{j=1}^{r} p_{ij}(1 - p_{ij})\ln^2(p_{ij}/c_j) - \frac{N}{N_i}\left(\frac{1}{p_{ij}}\right) + \frac{1}{c_j} \right],$$

$$B(CX) \simeq \sum_{j=1}^{r} \frac{2p_{1j}p_{2j}}{(p_{1j} + p_{2j})^3} (p_{1j}/N_2 + p_{2j}/N_1 - 2p_{1j}p_{2j}/\bar{n}),$$

where $\bar{n}$ is the harmonic mean sample size $[\bar{n} = 2N_1N_2/(N_1 + N_2)]$,

$$B(FT) \simeq -1/8\left[2FT/\bar{n} - 1/N_1 \sum_{j=1}^{r} (p_{2j}/p_{1j})^{\frac{1}{2}} - 1/N_2 \sum_{j=1}^{r} (p_{1j}/p_{2j})^{\frac{1}{2}}\right],$$

$$B(R_0) \simeq -1/(4 \ln 2)\left[\sum_{j=1}^{r} 2p_{1j}p_{2j}/\bar{n}(p_{1j} + p_{2j}) - \sum_{j=1}^{r} \frac{(N_1p_{ij} + N_2p_{2j})}{N_1N_2(p_{1j} + p_{2j})}\right],$$

and $$B(C_1) \simeq -1/2 \sum_{i=1}^{2} \left[\sum_{j=1}^{r} \frac{p_{ij}(1 - p_{ij})T_{ij}}{N_i} - \sum_{j<k} \frac{p_{ij}p_{ik}S_{ijk}}{N_i} \right],$$

where
$$T_{1j} = 2/D[C_1 + (4/D)p_{1j}(p_{2j} - C_1p_{1j})],$$
$$T_{2j} = 2/D[C_1 + (4/D)p_{2j}(p_{1j} - C_1p_{2j})],$$
$$S_{1jk} = 4/D^2[p_{1j}p_{2k} + p_{2j}p_{1k} - 2C_1p_{1j}p_{1k}],$$
$$S_{2jk} = 4/D^2[p_{2j}p_{1k} + p_{1j}p_{2k} - 2C_1p_{2j}p_{2k}],$$

and $$D = \sum_{j=1}^{r} p^2_{1j} + \sum_{j=1}^{r} p^2_{2j}.$$

For the percentage similarity measure, exact values of the bias were computed using formulas from Goldstein and Wolf (1977):

$$E(\widehat{PS}) = 1/2 \sum_{j=1}^{r} \left[\sum_{z=0}^{N_2-1} \sum_{x=\left[\frac{N_1 z}{N_2}+1\right]}^{N_1} (z/N_2)b(N_1,p_{1j},x) \cdot b(N_2,p_{2j},z) + \sum_{z=0}^{N_1} \sum_{y\geq\left[\frac{N_2 z}{N_1}\right]}^{N_2} (z/N_1)b(N_1,p_{1j},z) \cdot b(N_2,p_{2j},y) \right],$$

where $b(n,p,k) = \binom{n}{k}p^k(1 - p)^{n-k}$ and the above bracketed relationship on the indices x and y denotes the greatest integer function.

Simulation technics

We used Monte Carlo analysis to evaluate the accuracy of the estimates of bias and to explore effects of the number of resource categories, sample size, and evenness on bias. The method used to generate resource use spectra followed that of Grassle and Smith (1977) and Ricklefs and Lau (1980). Random samples of size N_1 and N_2 were drawn from multinomial vectors with probabilities $\mathbf{p}_1$ and $\mathbf{p}_2$ with r resource states. Overlap measures were computed for each pair, and the bias calculated by subtracting the estimated from the actual. Samples were taken sequentially until the

TABLE 1. Examples of bias for different resource distributions (p) and various sample sizes (N). Comparisons with analytic bias estimates are included. Unless indicated, results are from simulations. Values for PS are exact values of bias calculated by formula.

Utilization	N_1	N_2	L	CX	FT	PS	R_0	C_1	C_1*
A. $\mathbf{p}_1$ = .5, .3, .1, .1									
$\mathbf{p}_2$ = .5, .1, .2, .2									
Calculated overlap measure			.957	.917	.956	.800	.937	.914	.914
Bias	100	100	.007	.012	.008	.028	.010	.016	−.000
	75	125	.007	.014	.009	.029	.011	.017	−.000
	150	50	.007	.016	.011	.033	.013	.022	−.000
B. $\mathbf{p}_1$ = .4, .1, .1, .1, .3									
$\mathbf{p}_2$ = .2, .4, .2, .1, .1									
Calculated overlap measure			.905	.867	.897	.600	.856	.666	.666
Bias	50	50	.018	.034	.025	.026	.031	.026	−.009
	50	100	.012	.027	.018	.022	.022	.020	−.006
	100	100	.009	.017	.012	.018	.015	.014	−.003
	150	200	.005	.010	.007	.013	.009	.008	−.002
	200	200	.004	.009	.006	.013	.008	.007	−.001
	300	300	.003	.006	.004	.010	.005	.005	−.001
Analytic estimate	100	100	.010	.018	.012		.015	.014	
C. $\mathbf{p}_1$ = .4, .1, .1, .1, .3									
$\mathbf{p}_2$ = .25, .2, .25, .2, .1									
Calculated overlap measure			.934	.810	.939	.650	.901	.788	.788
Bias	50	50	.019	.034	.025	.008	.031	.042	−.003
	100	100	.009	.017	.011	.001	.014	.021	−.002
	200	200	.005	.009	.006	.000	.007	.011	−.001
analytic estimate	100	100	.010	.018	.011		.015	.022	
D. $\mathbf{p}_1$ = .1, .1, .1, .1, .1, .1, .1, .1, .1, .1									
$\mathbf{p}_2$ = .4, .3, .1, .1, .05, .01, .01, .01, .01, .01									
Calculated overlap measure			.841	.667	.802	.500	.728	.536	.536
Bias	50	50	.039	.054	.091	.054	.071	.040	−.004
	100	100	.020	.027	.049	.035	.036	.019	−.003
	200	200	.010	.013	.022	.024	.018	.009	.001
	300	300	.006	.009	.013	.019	.011	.007	−.000
Analytic estimate	100	100	.020	.027	.033		.034	.020	
E. $\mathbf{p}_1$ = .2, .05, .05, .05, .10, .05, .20, .10, .10, .10									
$\mathbf{p}_2$ = .4, .3, .1, .1, .05, .01, .01, .01, .01, .01									
Calculated overlap measure			.816	.643	.779	.450	.707	.573	.573
Bias	50	50	.039	.054	.100	.017	.073	.041	−.001
	100	100	.020	.027	.052	.004	.037	.021	−.000
	200	200	.010	.013	.023	.001	.018	.011	.000
	300	300	.006	.009	.014	.000	.012	.007	−.000
Analytic estimate	100	100	.020	.026	.034		.034	.022	

largest change in any bias mean was <.001. All simulations required 500–1000 repetitions. Comparison with exact values for PS indicated accuracy on the order of .0005.

Evenness was computed using a formula from Pielou (1975):

$$E = 1/2(H_1/H_{\max_1} + H_2/H_{\max_2}),$$

where $$H_i = -\sum_{j=1}^{r} p_{ij} \ln p_{ij}.$$

This measure takes on the value of one when all resources are used evenly and a value of zero when only one resource is used. Bias was computed as the difference between the measure based on the actual probabilities and the simulated mean measure.

RESULTS

Analytic method

The equations derived from the approximate analytical method (Taylor series) are complex, and they become less accurate compared to simulations for $N < 100$. Thus, the analytical method provides few advantages over the method of simulation for computing bias. However, when $\mathbf{p}_1 = \mathbf{p}_2$, the equations are reduced considerably as below:

1) $B(L) \simeq (r - 1)/4\bar{n}$,

2) $B(CX) \simeq (r - 1)/2\bar{n}$,

3) $B(FT) \simeq (r - 1)/4\bar{n}$,

4) $B(C_1) \simeq -\left(1 - 1/\sum_{k=1}^{r} p^2_{1k}\right)/\bar{n}$,

TABLE 2. Contribution to the bias from different resource states for the *PS* measure with $N_1 = N_2 = 25$ (bias = .206).

	Resource				
	1	2	3	4	5
Proportional resource use					
$\mathbf{p}_1$	.35	.30	.20	.10	.05
$\mathbf{p}_2$	.35	.30	.20	.10	.05
Contribution to bias	.053	.051	.045	.033	.023

5) $B(R_0) \simeq (r - 1)/4\bar{n}\ln 2$.

The results for bias effects are:

A. The bias of all measures decreases as $\bar{n}$ (the harmonic mean sample size) increases.
B. The measures ordered with increasing bias will be $1 \simeq 3, <5, <2$.
C. Measure 4, Morisita's modified measure, having p in the denominator, is the only measure of the five that shows bias from resource evenness. This is not true of Morisita's unbiased index C_1^* (measure 7).

Simulation method

Results of the simulations when $\mathbf{p}_1 = \mathbf{p}_2$ are given in Figs. 1–3. In Fig. 1, the bias is shown to increase as the number of resources increases. The amount of bias may be quite large if the number of resource categories is large, even though the total sample size is large ($N = 200$). In Fig. 2, all measures show decreased bias as sample size increases. Note however, that the bias depends on both sample sizes (N_1 and N_2) and that increasing the smaller sample has a much greater effect than increasing the larger. For fixed total sample size (N), the bias is least when $N_1 = N_2$. In Fig. 3, as evenness increases, the bias increases for C_1 and *PS*, but does not affect the other measures. Exact values are given in Table 1 for *PS*.

DISCUSSION

It is important to note that the contribution to bias comes from individual resources, not from the measure itself. For instance for the percentage similarity measure in Table 2, if $p_{14} = p_{24} = .10$, and $p_{15} = p_{25} = 0$, then the contribution of bias by the fourth and fifth resource is .033. If, however, $p_{14} = p_{24} = p_{15} = p_{25} = .05$, then the total bias is .046 (.023 + .023). In both cases the total measure of overlap is the same, whereas the bias differs by .013. As another example, for the percentage similarity measure in Table 1, section B the overlap value is .600 and the bias is .026, for $N_1 = N_2 = 50$. In section C, however, the overlap is .650 and the bias is only .008. Again, it is the distributions that give rise to bias, not the value of the measures.

Figs. 1–3 are consistent with results from the analytic analysis but are more accurate values. Of the six measures graphed, only the percentage similarity (*PS*) and Morisita's adjusted measure (C_1) consistently show strong bias under changing number of resource categories, size of second sample, and resource evenness, and they should be used with caution. It is unfortunate that these are the two measures most commonly used by ecologists.

Although evenness does not produce as strong a bias as either total sample size or the number of resources, we disagree with the conclusions of Ricklefs and Lau (1980) which indicate that bias is not affected by evenness. For instance they argue that if *PS* is <.8 there is little bias, but this is not true as shown by the following example.

Let $\mathbf{p}_1 = .1, .1, .1, .1, .1, .3, .2, 0, 0, 0$, and
$\mathbf{p}_2 = .1, .1, .1, .1, .1, 0, 0, 0, .3, .2$.

If then when:

$N_1 = N_2 = 25$, $B(PS) = .165$;
$N_1 = N_2 = 50$, $B(PS) = .118$;
$N_1 = N_2 = 100$, and $B(PS) = .084$.

In this case *PS* equals .50, yet the bias, given N at values ≤ 100, would be as much as 33.0%. Bias is especially important in the percentage similarity index if $N_1 + N_2 < 100$ or if there are many resource states with equal usage. In fact, it is apparent from Ricklefs and Lau's (1980:1021) Table 1 that there is some bias due to evenness. (For example, their C_{ij} for $n = 25$ varies from $-.129$ to $-.107$ as V, their evenness measure, goes from 0 to .50.) We have been able to demonstrate greater effect of bias from evenness because we ran more evenness experiments than they did. Also our values are more exact, using from 500 to 1000 simulations, and in the case of *PS* are exact.

The effect of evenness on bias for the *PS* measure is related to the concave nature of the bias function. For an arbitrary value p_{ik}, the contribution to the bias in *PS* from p_{ik} is less than the bias contributed from any combination of sum p_{im} and p_{il} such that $p_{im} + p_{il} = p_{ik}$. For example, in Table 2, the bias contributed with the third resource state is .045 ($p_{i3} = .20$), while the contribution by the fourth is .033 ($p_{i4} = .10$). Suppose that two pairs of species have the same resource use except for two states, state 1 and state 2. Assume that for pair 1 and 2, $p_{11} = p_{21} = .20$, and $p_{12} = p_{22} = .0$ and that for species 3 and 4, $p_{31} = p_{41} = .10$, and $p_{32} = p_{42} = .10$. Then, although the estimate of *PS* is the same for both groups, the bias will be larger for the second pair (.033 + .033 > .045). Bias changes with evenness for *PS* and C_1, but evenness does not affect the other measures.

It is surprising perhaps that of the seven measures examined in our study on bias, the one most free from bias is Morisita's (1959) original measure, unmodified by Horn (1966). Although these values were not graphed in Figs. 1–3, they are presented in Table 1 and the differences are apparent, especially for small samples and for large numbers of resources. Morisita's original measure is preferred for estimating overlap.

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