

## Estimating species richness: the Michaelis-Menten model revisited

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The Michaelis-Menten model has been widely used to estimate the richness ( $S$ ) of species pools, but is largely untested. We tested whether (1) species accumulation curves follow the form predicted by the model, (2) the model gives unbiased estimates ( $\hat{S}$  and  $\hat{B}$ , respectively) of  $S$  and of the sample size,  $B$ , needed to detect  $S/2$  species, and (3) performance is robust to community structure. Performance varied with community structure. For model communities with species-abundance distributions based on MacArthur's broken-stick model with 100 or 1000 species, deviations from predicted accumulation curves were slight, and  $\hat{S}$  and  $\hat{B}$  were unbiased ( $P \geq 0.18$ ). For broken-stick communities with 10 species,  $\hat{S}$  and  $\hat{B}$  overestimated  $S$  and  $B$  by an average of 17% and 63%, respectively ( $P < 0.001$ ). For model communities with species-abundance distributions based on Tokeshi's (1990) random-fraction model with 10, 100, or 1000 species, deviations from predicted accumulation curves were large; on average,  $\hat{S}$  underestimated  $S$  by 7–37% ( $P < 0.001$ ), and (for  $S = 100$  or 1000)  $\hat{B}$  underestimated  $B$  by 67–80% ( $P < 0.001$ ). Vascular plant inventories ( $S = 42$  to 99 species) also showed large deviations from predicted curves; on average,  $\hat{S}$  underestimated  $S$  by 35% ( $P < 0.001$ ) and  $\hat{B}$  underestimated  $B$  by 72% ( $P < 0.001$ ). Because most natural communities are better described by the random-fraction than the broken-stick model, we suggest the Michaelis-Menten model will typically yield poor estimates of  $S$ . Moreover, we argue that accepted criteria for evaluating estimators of  $S$  are inadequate.

Species accumulation curves have a characteristic form, whereby the number of species observed asymptotically approaches the total richness of the species pool as sample size increases. The Michaelis-Menten equation, first developed as an enzyme kinetics model (Michaelis and Menten 1913), has been widely adapted to model species accumulation curves and, thereby, estimate the richness of the species pool (e.g., de Caprariis et al. 1976, Clench 1979, Lauga and Joachim 1987, Lamas et al. 1991, Soberón and Llorente 1993, Colwell and Coddington 1994, Denslow 1995). For such applications, the equation is commonly written as

$$S(n) = \frac{Sn}{B+n}, \quad (1)$$

where  $S(n)$  is the number of species observed after  $n$  units of sampling,  $S$  is the total number of species in the pool, and  $B$  is the sampling effort needed to detect 50% of those species. Fitting Eq. (1) to sample data yields the parameter estimates  $\hat{S}$  and  $\hat{B}$ . Equation (1) also may be written nondimensionally as

$$S^* = \frac{n^*}{1+n^*}, \quad (2)$$

where  $S^* = S(n)/S$  and  $n^* = n/B$ . Equation (2) underscores the fact that  $S$  and  $B$  are merely scaling factors, and that the basic shape of the predicted accumulation curve is rigidly determined by relative sample size.

Despite the model's popularity, it has not been shown that species accumulation curves actually conform to the shape predicted by Eq. (2) or, equivalently, that the model yields unbiased estimates of  $S$  and  $B$ . Previous studies considered the null hypothesis that  $\hat{S} = S$ , but produced conflicting results confounded by deficient study designs. For example, de Caprariis and his colleagues (de Caprariis et al. 1976, 1981, de Caprariis and Lindemann 1978, de Caprariis 1984) touted the empirical accuracy of  $\hat{S}$ , but did not measure  $S$ ; their Monte Carlo study was limited to small communities ( $S = 30$ ) whose structures were not clearly related to those expected for natural communities; and they fitted the model using the Lineweaver-Burke method, which "frequently gives grossly inaccurate estimates of the parameters" (Zivin and Waud 1982: 1410). In the only empirical test that measured the true value of  $S$ , Palmer (1990, 1991) reported that  $\hat{S}$  underestimated  $S$ , but he too fitted the model using the Lineweaver-Burke method. More rigorous tests are needed before reliable conclusions can be drawn about the accuracy of the Michaelis-Menten model in ecological applications.

Tests of methods for estimating  $S$  should consider whether performance is robust to differences in community structure (Walther et al. 1995). Because the

Michaelis-Menten model can fit curves with various initial slopes and makes no explicit assumption about species' relative abundances, it often has been regarded as nonparametric (e.g., de Caprariis et al. 1976, 1981, Clench 1979, Lamas et al. 1991). However, Soberón and Llorente (1993) and Colwell and Coddington (1994) argued that performance should vary with community structure. Support for their argument may be inferred from Eq. (2), which predicts that sampling effectiveness ( $dS^*/dn^*$ ) declines with  $n$  at a fixed relative rate. It is implausible that such a model would fit all communities equally well, since sampling effectiveness should decline at a relatively faster rate in communities with a higher proportion of rare species. However, the influence of community structure on the performance of the Michaelis-Menten model has not actually been tested.

To assess the accuracy and robustness of the Michaelis-Menten model, we tested whether (1) species accumulation curves follow the form predicted by Eq. (2), (2) the model yields unbiased estimates of  $S$  and  $B$ , and (3) performance is robust to differences in community structure. Our tests used Monte Carlo methods to simulate and sample ecologically realistic communities that varied in richness and/or evenness. Results were validated empirically using data from vascular plant inventories from Glacier National Park, Montana, USA.

## Methods

### Monte Carlo methods

We modeled two community types; each was replicated with 10, 100, and 1000 species, to give six model communities in all. We simulated communities with highly even structures using MacArthur's (1957) broken-stick model, given by

$$\pi_i = \frac{1}{S} \sum_{x=i}^S \frac{1}{x},$$

where  $\pi_i$  is the relative abundance of the  $i$ th species. The broken-stick distribution "may be thought of as the statistically realistic expression of an ideally uniform ... distribution" (May 1975: 107). We chose it to represent the most even community structure that one is likely to see in nature and, hence, the one that most nearly conforms to the uniform distribution that is implicitly assumed in the enzyme kinetics applications that the Michaelis-Menten equation was originally designed to model.

We simulated communities with moderately even structures using Tokeshi's (1990) random-fraction algorithm, which may be viewed as a stochastic analog of Preston's (1962) lognormal distribution. This distribution is characteristic of large, heterogeneous communi-

ties with many rare species (May 1975) and, hence, describes the type of community structure that Soberón and Llorente (1993) predicted the Michaelis-Menten model is best suited to. We chose the random-fraction model to simulate such communities because of its simplicity and empirical success (Tokeshi 1990, 1996, Naeem and Hawkins 1994), and because it may yield more realistic estimates of the relative abundances of rare species than does the lognormal model (Nee et al. 1991, Tokeshi 1996). We constructed the random-fraction model by setting the available "niche space" equal to one, then randomly breaking that "niche space" into two pieces. One of those pieces was then randomly selected and broken in two, to yield a total of three pieces. We repeated this process until there were  $S$  pieces, with the length of the  $i$ th piece representing the relative abundance ( $\pi_i$ ) of the  $i$ th species. The entire community structure is given by  $\pi = (\pi_1, \pi_2, \dots, \pi_S)$ . Because this is a stochastic algorithm, communities modeled in this way can differ greatly. Our analyses used the mean expectation for  $\pi$ , which we estimated by averaging the  $\pi_i$ 's over 1000 simulations for each of the three random-fraction communities we modeled. We sorted the  $\pi_i$ 's by rank after each simulation and before averaging, and corrected for subsequent rounding errors by rescaling to ensure that  $\sum_{i=1}^S \pi_i = 1$ .

We compared predicted and observed species accumulation curves for each of our six simulated communities after rescaling all curves to the nondimensional form of the model (Eq. [2]). To construct a predicted curve (Eq. [1]),  $S$  and  $B$  must be specified. In our simulations,  $S$  was known. To estimate  $B$ , we drew successive samples from each of the six model communities and calculated the number of species observed,  $S(n)$ , after each draw. We estimated  $B$  as the number of samples needed to observe exactly 50% of the species. We repeated this sampling 1000 times for each community and calculated our final estimate of  $B$  as the mean of those 1000 estimates; i.e., for each of the six communities,  $\bar{B} = \sum_{i=1}^{1000} B_i / 1000$ .

We constructed observed accumulation curves for the model communities by randomly drawing  $n = 4\bar{B}$  samples from each community and calculating the number of species observed,  $S(n)$ , after each draw. According to Eq. (2), a sample size of  $n = 4\bar{B}$  should be sufficient to observe 80% of the species. We repeated this sampling 200 times for each community and averaged the results ( $\hat{S}(n) = \sum_{i=1}^{200} S_i(n) / 200$ ) to estimate the mean observed accumulation curve for each community. We calculated 95% confidence limits as  $\hat{S}(n) \pm 1.972SE$ , where SE is the standard error of  $\hat{S}(n)$  and 1.972 is the critical value of the  $t$  distribution for  $\alpha$  (two-tailed) = 0.05 and  $df = 199$  (Zar 1984).

To test whether  $\hat{S}$  and  $\hat{B}$  were unbiased, we fitted Eq. (1) to each of the 200 sets of  $S(n)$  values generated for each model community, then used a  $t$ -test to test the null hypotheses that  $\hat{S}/S = 1$  and  $\hat{B}/B = 1$ . Several

methods exist for fitting the Michaelis-Menten model and each may yield different estimates of  $S$  and  $B$ . Selection of the most suitable method depends upon the assumptions one wishes to make concerning the error variance (Raaijmakers 1987). Recent studies (Colwell and Coddington 1994, Denslow 1995) used Raaijmakers' (1987) maximum likelihood estimator, which assumes that the variance of  $S(n)$  increases with  $S(n)$ ; i.e., that the coefficient of variation for  $S(n)$  is constant. Enzyme kinetics studies support this assumption (Zivin and Waud 1982), but we do not believe it is valid for the species-accumulation problem, where variance in  $S(n)$  should be greatest at intermediate values of  $S(n)$ , but should decline as  $S(n) \rightarrow 0$  or  $S(n) \rightarrow S$  (e.g., Colwell and Coddington 1994: Fig. 1). No existing method for fitting the Michaelis-Menten model is based upon such an assumption; however, this pattern seems most consistent with the assumption of constant variance, making least squares nonlinear regression the preferred method for fitting the Michaelis-Menten model (Raaijmakers 1987). Monte Carlo simulations comparing least squares nonlinear regression and Raaijmakers' (1987) maximum likelihood estimator supported this choice (Keating unpubl.). Thus, we used the quasi-Newton nonlinear regression algorithm in SYSTAT (Wilkinson et al. 1994) to fit the Michaelis-Menten equation to the observed accumulation curves.

### Field methods

We empirically tested the performance of the Michaelis-Menten model by applying it to inventory data for vascular plant species on 16 0.25-ha plots in the McDonald Creek Drainage of Glacier National Park, Montana, USA. Our plots were established in 1991 and 1992 as part of a study to develop protocols for species inventories and long-term ecological monitoring in US national parks. Plots were located in the western hemlock (*Tsuga heterophylla*)/queen's cup beadlily (*Clintonia uniflora*) and western hemlock/devil's club (*Oplopanax horridum*) habitat types (Pfister et al. 1977), and were stratified by stand age. In 1991, stands sampled within the western hemlock/queen's cup beadlily habitat type were 62 ( $n=4$  plots), 116–136 ( $n=3$  plots), 256 ( $n=4$  plots), and >475 ( $n=3$  plots) years of age, while the four plots in the western hemlock/devil's club habitat type were in stands >475 years old (S. W. Barrett unpubl., Glacier National Park GIS).

To inventory vascular plants, we stratified each plot into 25 10 m  $\times$  10 m cells, then randomly located a 20 cm  $\times$  50 cm quadrat within each cell during each month, June–September. Canopy coverage was estimated and recorded for all vascular plant species within each quadrat. We sampled each plot for 2–3 years. During 1994, we searched each plot during each month, June–September, to compile comprehensive, plot-specific species lists.

Because the form of species accumulation curves can vary with the order in which samples are drawn, we calculated the mean observed accumulation curve for each plot as the average of the curves produced by 20 random permutations of sampling order (Colwell and Coddington 1994). To calculate predicted accumulation curves (Eq. [1]), we estimated  $S$  as the number of species listed for the plot and interpolated the mean observed accumulation curve to estimate  $B$  as the number of quadrats required to observe exactly  $S/2$  species. We assumed species lists for the plots were complete. Although additional searches probably would have yielded more species, we believe this bias was minor and note that any such bias would foster a conservative result, as underestimating  $S$  would have caused us to underestimate differences between observed and expected values. We also assumed species compositions on the plots were essentially constant during 1991–1994. Because most species were long-lived perennials (annuals were represented by a single individual of *Poa annua*) in well-established ( $\geq 62$  year-old) communities, this assumption seemed reasonable.

For each plot, we compared observed and expected species accumulation curves after rescaling them non-dimensionally (Eq. [2]). We again used least squares nonlinear regression to fit the Michaelis-Menten equation to the mean observed species accumulation data, and a  $t$ -test to test the null hypotheses that  $\hat{S}/S = 1$  and  $\hat{B}/B = 1$ .

### Results

For the three communities structured according to the broken-stick model, comparisons revealed few differences between predicted and observed accumulation curves (Fig. 1B). For communities with 100 or 1000 species, differences between  $\hat{S}$  and  $S$  were insignificant ( $S = 100$ :  $t = 0.823$ ,  $df = 199$ ,  $P = 0.412$ ;  $S = 1000$ :  $t = 0.992$ ,  $df = 199$ ,  $P = 0.323$ ), as were differences between  $\hat{B}$  and  $B$  ( $S = 100$ :  $t = 1.34$ ,  $df = 199$ ,  $P = 0.181$ ;  $S = 1000$ :  $t = -0.280$ ,  $df = 199$ ,  $P = 0.780$ ). However, for the broken-stick community with 10 species,  $\hat{S}$  overestimated  $S$  by an average of 17% ( $t = 4.45$ ,  $df = 199$ ,  $P < 0.001$ ) and  $\hat{B}$  overestimated  $B$  by an average of 63% ( $t = 4.11$ ,  $df = 199$ ,  $P < 0.001$ ).

Comparisons for the three communities structured according to the random-fraction model revealed systematic differences between predicted and observed species accumulation curves (Fig. 1A). Sampling yielded more species than expected when  $n < B$  and fewer when  $n > B$ . As  $n$  became large, mean observed accumulation curves approached the asymptote much more slowly than predicted by the Michaelis-Menten model. Consistent with this pattern,  $\hat{S}$  underestimated  $S$  by an average of 7–37% (Fig. 2A). Discrepancies increased with  $S$

and in no case was  $\hat{S}$  unbiased ( $S=10$ :  $t = -2.03$ ,  $df = 199$ ,  $P = 0.044$ ;  $S=100$ :  $t = -119$ ,  $df = 199$ ,  $P < 0.001$ ;  $S=1000$ :  $t = -584$ ,  $df = 199$ ,  $P < 0.001$ ). Also,  $\hat{B}$  underestimated  $B$  by an average of 22–80% (Fig. 2B). Discrepancies between  $B$  and  $\hat{B}$  increased with  $S$  and were significant for communities with 100 or 1000

species ( $S=10$ :  $t = 0.015$ ,  $df = 199$ ,  $P = 0.878$ ;  $S=100$ :  $t = -120$ ,  $df = 199$ ,  $P < 0.001$ ;  $S=1000$ :  $t = -824$ ,  $df = 199$ ,  $P < 0.001$ ).

Plant inventories showed systematic differences between predicted and observed species accumulation curves that were consistent with observations for random-fraction model communities (Fig. 1C). Sampling yielded more species than expected when  $n < B$  and fewer when  $n > B$ , so that species accumulation curves approached the asymptote much more slowly than predicted. Also,  $\hat{S}$  underestimated  $S$  by an average of 35% ( $t = -20.7$ ,  $df = 15$ ,  $P < 0.001$ ) and  $\hat{B}$  underestimated  $B$  by an average of 72% ( $t = -24.2$ ,  $df = 15$ ,  $P < 0.001$ ) (Fig. 2).

## Discussion

The Michaelis-Menten model was not robust to differences in community structure. For model communities structured according to MacArthur's (1957) broken-stick model, species accumulation curves closely followed the predicted curve and the model yielded good estimates of  $S$  and  $B$  for all but the smallest ( $S=10$ ) community. However, for model communities structured according to Tokeshi's (1990) random-fraction model, species accumulation curves deviated substantially from the predicted curve, and  $S$  and  $B$  were severely underestimated. Results for plant inventories were consistent with Monte Carlo results for comparably rich random-fraction communities, suggesting that the Monte Carlo results gave a realistic measure of expected performance in heterogeneous natural communities of the kind expected to have species-abundance distributions resembling the lognormal (Preston 1962) or random-fraction (Tokeshi 1990) models. The observed relationship between accuracy and species' relative abundances suggested that the Michaelis-Menten model implicitly assumes a highly even community structure. This contradicts the view (e.g., Lamas et al. 1991) that the model is nonparametric. It also is contrary to the prediction (Soberón and Llorente 1993) that the model is most appropriate for estimating the richness of large, heterogeneous communities, since the structures of such communities typically resemble a lognormal (Preston 1962) or random-fraction (Tokeshi 1990) distribution (May 1975, Tokeshi 1996). We concluded that the Michaelis-Menten model should perform well when sampling from at least moderately large species pools where species' relative abundances conform to a broken-stick distribution. However, because most natural communities do not conform to such a distribution (May 1975), we further concluded that the Michaelis-Menten model will, typically, yield poor estimates of  $S$ . We recommend that a more reliable and robust estimator be sought.

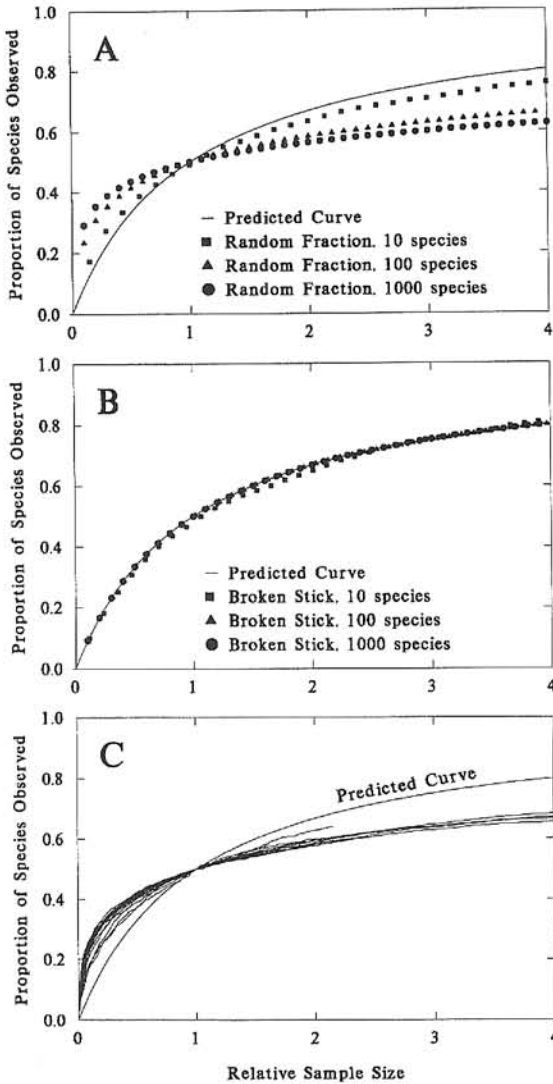
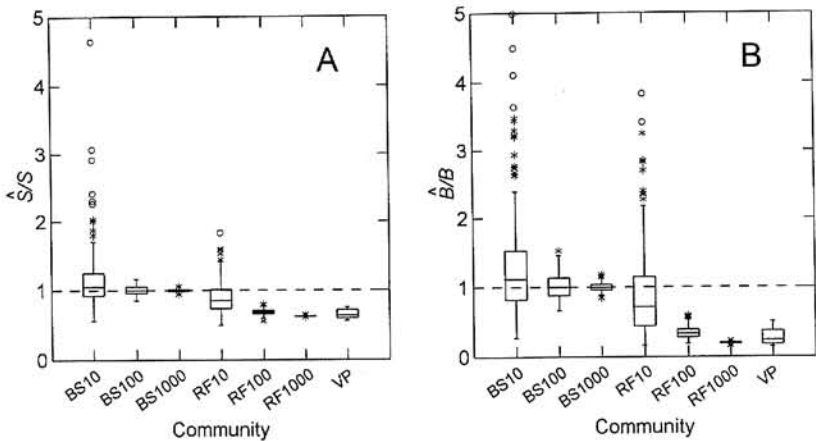


Fig. 1. Nondimensional species accumulation curve predicted by the Michaelis-Menten model versus mean observed accumulation curves for (A) three communities structured according to Tokeshi's (1990) random-fraction model, (B) three communities structured according to MacArthur's (1957) broken-stick model, and (C) vascular plant inventories on 16 0.25-ha plots in Glacier National Park, Montana, USA. In (A) and (B), 95% confidence limits were roughly equal to the width of the characters used to plot the mean curves. In (C), richness ( $S$ ) for individual plots ranged from 42 to 99 species and observed species accumulation curves were calculated as the average of 20 curves constructed from random permutations of the sampling order for each plot. In each figure, the abscissa was scaled to  $\hat{S}$  and the ordinate was scaled to the sample size needed to observe exactly 50% of the species.

Fig. 2. Box-and-whisker diagrams of the distributions of (A)  $\hat{S}/S$ , and (B)  $\hat{B}/B$ , where  $S$  is the richness of the species pool,  $B$  is the sample size needed to detect exactly  $S/2$  species, and  $\hat{S}$  and  $\hat{B}$  are fitted estimates of  $S$  and  $B$ , respectively. Distributions are for samples drawn from vascular plant communities (VP); model random-fraction communities with 10 (RF10), 100 (RF100), and 1000 (RF1000) species; and model broken-stick communities with 10 (BS10), 100 (BS100), and 1000 (BS1000) species. The center line indicates the sample median, the box marks the limits of a distribution's first and third quartiles, and the "whiskers" (solid lines) encompass values within  $1.5d$  of the box, where  $d$  is the absolute distance between the first and third quartiles. Values "outside" or "far outside" these limits are indicated by asterisks (\*) and open circles (o), respectively. The null hypothesis of an unbiased estimator predicts  $\hat{S}/S = 1$  and  $\hat{B}/B = 1$  (dashed lines). Eight extreme outliers for BS10 and RF10 were excluded by limiting the range of the graphs to  $\hat{S}/S$  and  $\hat{B}/B \leq 5$ .



When seeking alternative methods for estimating  $S$ , the criteria by which they are judged should be considered carefully. Typically, such methods have been declared successful when the species accumulation model successfully approximates the observed portions of accumulation curves, or when the estimates themselves are deemed to be "reasonable", agree with estimates calculated using other (untested) methods, or approximate known values for contrived populations. The Michaelis-Menten model has performed well against all of these criteria (de Caprariis et al. 1976, 1981, de Caprariis and Lindemann 1978, Clench 1979, Lauga and Joachim 1987, Lamas et al. 1991, Soberón and Llorente 1993, Colwell and Coddington 1994), yet failed to yield reliable estimates of  $S$  in our study. In particular, the suitability of the Michaelis-Menten model has repeatedly been inferred from the fact that its hyperbolic form is very similar to that of species accumulation curves, so that it fits the observable portions of most empirical curves quite closely (e.g., de Caprariis et al. 1976, Clench 1979, Lamas et al. 1991). We caution, however, that a good fit between a model and the observed part of a species accumulation curve

does not indicate the reliability of extrapolations made from that model. Thus, measures like  $r^2$  (e.g., Soberón and Llorente 1993) are not diagnostic of estimator performance.

Estimators of  $S$  can be critically assessed only by testing the null hypothesis that  $\hat{S}$  is unbiased when sampling from an underlying distribution that reflects the expected structure of natural communities. Dozens of alternative estimators exist (Bunge and Fitzpatrick 1993), but few have been tested against such a standard and no estimator has been shown to be robust to community structure. More rigorous tests are needed if ecologists are to generate meaningful estimates of the numbers of species occurring in particular habitats or sites.

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