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ESTIMATING THE EFFECTIVENESS OF FURTHER SAMPLING IN SPECIES INVENTORIES

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Abstract. Estimators of the number of additional species expected in the next Δn samples offer a potentially important tool for improving cost-effectiveness of species inventories but are largely untested. We used Monte Carlo methods to compare 11 such estimators, across a range of community structures and sampling regimes, and validated our results, where possible, using empirical data from vascular plant and beetle inventories from Glacier National Park, Montana, USA. We found that B. Efron and R. Thisted's 1976 negative binomial estimator was most robust to differences in community structure and that it was among the most accurate estimators when sampling was from model communities with structures resembling the large, heterogeneous communities that are the likely targets of major inventory efforts. Other estimators may be preferred under specific conditions, however. For example, when sampling was from model communities with highly even species-abundance distributions, estimates based on the Michaelis-Menten model were most accurate; when sampling was from moderately even model communities with $S = 10$ species or communities with highly uneven species-abundance distributions, estimates based on Gleason's (1922) species–area model were most accurate. We suggest that use of such methods in species inventories can help improve cost-effectiveness by providing an objective basis for redirecting sampling to more-productive sites, methods, or time periods as the expectation of detecting additional species becomes unacceptably low.

Key words: beetle inventories, Glacier National Park (USA); estimation methodologies; estimators of effectiveness; negative binomial estimation; sampling effectiveness; species-abundance distribution; species inventories, cost effectiveness; vascular plant inventories, Glacier National Park (USA).

INTRODUCTION

To protect and manage areas of biological diversity, species inventories are needed (Soulé and Kohm 1989, Stohlgren et al. 1995). Designing cost-effective inventories remains a difficult and important challenge, however, since funding is limited and the rate of species discovery declines rapidly as sampling effort or area increases. In part, sustaining an acceptable level of cost-effectiveness requires that sampling be redirected to more productive sites, methods, or time periods as the expectation of detecting additional species becomes unacceptably low. Many statistical methods exist for estimating the expected effectiveness of further sampling. For example, Efron and Thisted (1976) derived estimators of the number of additional species (Δs) expected in the next Δn samples, while Soberón and Llorente (1993) derived estimators of the sampling time needed to reduce the species-detection rate to some fraction of its initial value. Theoretically, such methods could be used to provide an objective basis for reallocating sampling efforts and thereby improving cost-effectiveness. However, such methods have not been critically evaluated or compared.

Ideally, estimates of the effectiveness of further sampling should be robust to community structure and sampling design. Evaluations of estimators should, therefore, consider how factors such as species-abundance distribution, total richness of the species pool (S), initial sample size (n), and the projected increase in sample size (Δn) influence estimator performance. We know, for example, that some species-accumulation models are sensitive to differences in species' relative abundances and the richness of the species pool (Keating and Quinn 1998), and that some estimators of future sampling effectiveness diverge as Δn increases (Efron and Thisted 1976), suggesting a relationship between Δn and accuracy. It is reasonable to suggest, too, that estimators' performances might change with n, since sample size should affect the reliability of parameter estimates.

We evaluated 11 methods for estimating the likely effectiveness of further sampling in species inventories. Using Monte Carlo methods, we tested whether (1) each estimator is unbiased, (2) all estimators are equally accurate, (3) rank accuracies of estimators vary with the richness and/or evenness of the species pool, and (4) rank accuracies of estimators vary with relative

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initial sample size (n/S) or the relative magnitude of the proposed increase in sample size ($\Delta n/n$). We validated our results, where possible, using empirical data from vascular-plant and beetle inventories from Glacier National Park, Montana, USA.

Methods

General problem

The estimators we compared address the following general problem, paraphrased largely from Bunge and Fitzpatrick (1993). Suppose that after drawing n samples from a pool of S species (where S is unknown), we observe s species. The probability of encountering the ith species is π_i, so that $\boldsymbol{\pi} = (\pi_1, \pi_2, \ldots, \pi_S)$. In our sample, species occur with frequency $\mathbf{n} = (n_1, n_2, \ldots, n_S)$ (but we do not know the identity of the $S - s$ species for which $n_i = 0$) and the number of species observed exactly j times (i.e., the number of singletons, doubletons, etc.) is $\mathbf{s} = (s_1, s_2, \ldots, s_n)$. Thus, $n = \sum_{i=1}^{S} n_i = \sum_{j=1}^{n} j s_j$, and $s = \sum_{j=1}^{n} s_j$. The problem is to estimate ($\hat{\Delta}s$) the number of additional species we would expect to see if we randomly drew Δn additional samples from the same species pool. We considered both sampling-theoretic and data-analytic (i.e., curve-fitting) methods for calculating such estimates.

Sampling-theoretic estimators

We examined three estimators derived from sampling theory. The first follows from the negative binomial (NB) model of Fisher et al. (1943) and is given as (Efron and Thisted 1976)

$$\hat{\Delta}s_{\mathrm{NB}} = -\zeta_1 \frac{\left(1 + \gamma\frac{\Delta n}{n}\right)^{-\alpha} - 1}{\gamma\alpha} \qquad (1)$$

where ζ_1 is the statistical expectation of the number of singletons occurring in a sample of size n, $\alpha > -1$ ($\alpha \neq 0$), and $0 < \gamma < 1$. The logarithmic series (LS) model (Fisher et al. 1943) follows from the special case $\alpha = 0$ and gives the estimator (Efron and Thisted 1976)

$$\hat{\Delta}s_{\mathrm{LS}} = \frac{\zeta_1}{\gamma}\log\left(1 + \gamma\frac{\Delta n}{n}\right). \qquad (2)$$

Efron and Thisted (1976) also considered nonparametric methods, like Good and Toulmin's (1956) "naive" estimator,

$$\hat{\Delta}s_{\mathrm{Naive}} = \sum_{i=1}^{n} (-1)^{i+1} s_i \left(\frac{\Delta n}{n}\right)^i.$$

Because the geometrically increasing magnitude of $(\Delta n/n)^i$ renders $\hat{\Delta}s_{\mathrm{Naive}}$ useless when $\Delta n > n$ (Efron and Thisted 1976), we did not evaluate $\hat{\Delta}s_{\mathrm{Naive}}$. However, Efron and Thisted (1976) used an Euler transformation to smooth the oscillations in $\hat{\Delta}s_{\mathrm{Naive}}$, giving the general linear estimator (GLE),

$$\hat{\Delta}s_{\mathrm{GLE}} = \sum_{i=1}^{i_0} h_i s_i \qquad (3)$$

where $h_i = (-1)^{i+1}(\Delta n/n)^i \,\mathrm{pr}(Z \geq i)$, Z is a binomially distributed random variable with index i and parameter $1/(1 + \Delta n/n)$, and i_0 is a user-selected threshold value for i. We calculated the cumulative binomial probability, $\mathrm{pr}(Z \geq i)$, using the incomplete beta function (Press et al. 1989). We fitted Eqs. 1 and 2, and chose i_0 values as follows.

To estimate γ and α in Eqs. 1 and 2, we fitted the s_i (for $i = 1, \ldots, i_0$) to the binomial model (Efron and Thisted 1976):

$$\zeta_i = \zeta_1 \frac{\Gamma(i + \alpha)}{i!\Gamma(1 + \alpha)}\gamma^{i-1} \qquad (4)$$

using s_1 as our estimate of ζ_1, and a downhill simplex (Press et al. 1989) to minimize the sum of squares. We calculated the gamma function per Press et al. (1989). To fit this distribution and calculate $\hat{\Delta}s_{\mathrm{GLE}}$ (Eq. 3), i_0 must first be specified. The parameter i_0 limits the information used in a given calculation. If $i_0 = 3$, for example, the binomial distribution would be fitted and $\hat{\Delta}s_{\mathrm{GLE}}$ calculated using only the information contained in s_1, s_2, and s_3. Efron and Thisted (1976) chose $i_0 = 40$ for calculations of $\hat{\Delta}s_{\mathrm{NB}}$ and $i_0 = 9$ for calculations of $\hat{\Delta}s_{\mathrm{GLE}}$ (they did not calculate $\hat{\Delta}s_{\mathrm{LS}}$). Although they cited species inventories as motivation for their work, Efron and Thisted actually used these values to analyze Shakespeare's vocabulary. They gave no evidence that these are good choices for ecological data. We used Monte Carlo methods to choose values of i_0 that seemed likely to maximize accuracy and precision over a variety of community structures and sampling designs, reasoning that the choice for i_0 should be robust to such factors.

We began by drawing $n = S$, $2S$, and $4S$ samples from each of three types of model communities (broken-stick, random-fraction, and geometric-series; see *Monte Carlo Study*, below), each with $S = 100$ species. After each sampling bout, we calculated the number of additional species expected ($\hat{\Delta}s$) and the number actually observed (Δs) after drawing Δn additional samples, where $\Delta n = 0.2n$, $0.5n$, n, $2n$, and $5n$ samples. Estimates of the expected number of additional species were calculated using $\hat{\Delta}s_{\mathrm{NB}}$, $\hat{\Delta}s_{\mathrm{LS}}$, and $\hat{\Delta}s_{\mathrm{GLE}}$, and were repeated for each estimator using $i_0 = 3$, 5, 10, 15, 20, 25, 30, 35, and 40. We repeated this process 25 times for each combination of estimator type, community type, n, Δn, and i_0. This gave 30 375 replicates. For each, we calculated estimator error as $\varepsilon = \hat{\Delta}s - \Delta s$ and measured the absolute deviation from the median as $D = |\hat{\Delta}s_i - \hat{\Delta}s_{\mathrm{Median}}|$, where $\hat{\Delta}s_{\mathrm{Median}}$ is the median value of $\hat{\Delta}s$ for the estimator in question. For each of the three sampling-theoretic estimators, we then used single-factor analysis of variance to test whether bias ($\bar{\varepsilon}$) or precision (D) varied with i_0. The latter is the "Lev1:median test," recommended as a robust test of equality of variances (Brown and Forsythe 1974, Conover et al. 1981). Where the null hypothesis was rejected, analysis of variance was followed by Tukey

multiple comparisons (Zar 1984). Results of those comparisons were used to select i_0 values that gave the best combination of accuracy and precision for each of the three estimators. Selected i_0 values were then used in all subsequent comparisons involving $\hat{\Delta}s_{NB}$, $\hat{\Delta}s_{LS}$, or $\hat{\Delta}s_{GLE}$.

Data-analytic estimators

Extrapolations of models of species-accumulation curves give what Bunge and Fitzpatrick (1993) termed "data-analytic" estimators. Such models assume that the number of species observed is a function of sample size; i.e., $s = f(n; \boldsymbol{\theta})$, where $\boldsymbol{\theta}$ is a parameter vector, estimated ($\hat{\boldsymbol{\theta}}$) from the data. Given $\hat{\boldsymbol{\theta}}$, estimates of $\hat{\Delta}s$ are readily calculated from such models as $\hat{\Delta}s = f(n + \Delta n; \hat{\boldsymbol{\theta}}) - s$. We examined eight such estimators.

Five of our data-analytic estimators were first derived from empirical models. The earliest of these was due to Arrhenius (1921, 1923). Reformulated to show the relationship to Δs, it is given by

$$\frac{s}{s + \Delta s} = \left(\frac{A}{A + \Delta A}\right)^{\alpha}$$

where A is the area sampled, ΔA is the increase in the area sampled, and α is a constant. This model implies that $s = \beta A^{\alpha}$, where β is a proportionality constant (Brainerd 1982), and is thus equivalent to the species–area relationship postulated by MacArthur and Wilson (1967). Substituting n for A (per Brainerd 1982), we calculated

$$\hat{\Delta}s_{Arr} = \beta(n + \Delta n)^{\alpha} - s. \quad (5)$$

Gleason (1922) proposed $s = \alpha + \ln A$. Substituting n for A gives

$$\hat{\Delta}S_{Glsn} = \alpha + \ln(n + \Delta n) - s. \quad (6)$$

Shmida (1984) suggested the more general form, $s = \alpha + \beta \ln A$, where β is the slope of the species-log(A) curve. It follows that

$$\hat{\Delta}s_{Shm} = \alpha + \beta \ln(n + \Delta n) - s. \quad (7)$$

Stohlgren et al. (1997*a*, *b*) proposed a further modification, $s = \alpha + \beta/\bar{J} \ln A$, where $\bar{J}$ is the mean value of Jaccard's index of similarity among all possible pairwise combinations of samples. We question the rationale for this model (see *Discussion* and *Conclusions*, below), but Stohlgren et al. (1997*a*, *b*) reported good success at predicting Δs when $\Delta A \approx 9A$. Substituting n for A, we calculated the estimator

$$\hat{\Delta}s_{Sto} = \alpha + \frac{\beta}{\bar{J}}\ln(n + \Delta n) - s \quad (8)$$

and Jaccard's index of similarity as (Magurran 1988)

$$J = \frac{s_c}{(s_{Sample1} + s_{Sample2} - s_c)} \quad (9)$$

where s_c is the number of species common to both samples, and $s_{Sample1}$ and $s_{Sample2}$ are the numbers of species observed in samples 1 and 2, respectively.

Developed as an enzyme-kinetics model, the Michaelis-Menten (MM) equation (Michaelis and Menten 1913) has been widely adapted to model species-accumulation curves as $s = Sn/(\alpha + n)$, where α is the number of samples needed to observe exactly $S/2$ species. This model leads to the estimator

$$\hat{\Delta}s_{MM} = \frac{S(n + \Delta n)}{\alpha + n + \Delta n} - s. \quad (10)$$

At least three other species-accumulation models have been derived by treating species accumulation as a stochastic process, whereby the probability of detecting an additional species in the next Δn samples is given by $\text{pr}(s \rightarrow s + 1)_{\Delta n} = G(s, n)\Delta n$. The Arrhenius, Gleason, and Michaelis-Menten models also can be derived in this way (Brainerd 1982, Soberón and Llorente 1993). In such models, the form of the species-accumulation curve is determined by the so-called collecting function, $G(s, n)$, the shape of which depends upon both methodological and biological factors (Soberón and Llorente 1993). By assuming that $G(s, n)$ depends minimally upon s, but declines exponentially with n, according to the relationship $G(s, n) = e^{-\alpha n}$, Brainerd (1972) derived the model $s = (1 - e^{-\alpha n})/(1 - e^{-\alpha})$, which leads to

$$\hat{\Delta}s_{Brnd} = \frac{1 - e^{-\alpha(n+\Delta n)}}{1 - e^{-\alpha}} - s. \quad (11)$$

Soberón and Llorente (1993) suggested two forms of the collecting function. In the first, they assumed $G(s, n)$ declines linearly with s (i.e., $G(s, n) = \alpha - \beta s$), which yields their exponential model, $s = S(1 - e^{-\alpha n})$. From this model, we calculated

$$\hat{\Delta}s_{Exp} = S[1 - e^{-\alpha(n+\Delta n)}] - s. \quad (12)$$

In their second model, Soberón and Llorente (1993) assumed $G(s, n)$ declines exponentially with s (i.e., $G(s, n) = \alpha e^{-\beta n}$), which leads to their logarithmic model, $s = (1/\gamma)\ln(1 + \gamma\alpha n)$, where $\gamma = 1 - e^{-\beta}$. From this model, we calculated

$$\hat{\Delta}s_{Log} = \frac{1}{\gamma}\ln[1 + \gamma\alpha(n + \Delta n)] - s. \quad (13)$$

Monte Carlo study

We used Monte Carlo methods to compare estimator accuracies over a range of community structures, initial sample sizes (n values), and proposed increases in sample sizes (Δn values). We began by modeling communities in which the evenness of the species-abundance distribution was high, medium, or low; each community type was replicated with 10, 100, and 1000 species, to give nine model communities in all.

We modeled highly even communities using MacArthur's (1957) broken-stick model

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

May (1975:107) characterized this model "as the statistically realistic expression of an ideally uniform . . . distribution." We used it to represent the most even community structure that one is likely to see in nature.

We modeled moderately even communities using Tokeshi's (1990) random-fraction model, which may be viewed as a stochastic analog of Preston's (1962) lognormal model. Empirically, such models often mimic species-abundance distributions in large, heterogeneous communities (May 1975, Tokeshi 1996), which in turn are the most likely targets of major inventory efforts. We chose the random-fraction model due to its simplicity and empirical success (Tokeshi 1990, 1996; Naeem and Hawkins 1994), and because it may yield more realistic estimates of relative abundances of rare species than does the lognormal model (Nee et al. 1991, Tokeshi 1996). We determined $\boldsymbol{\pi}$ for our random-fraction communities by setting 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 give a total of three pieces. We repeated this process until there were S pieces. The length of the ith piece represented the probability (π_i) of observing the ith species. Because this is a stochastic algorithm, communities modeled in this way can differ greatly. Our analyses used the mean expectation for $\boldsymbol{\pi}$, which we estimated by averaging the π_i's over 1000 simulations for each of the three random-fraction communities we modeled. We sorted the π_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 modeled communities with low evenness using the geometric series model (Motomura 1932, cited in May 1975):

$$\pi_i = \frac{p(1-p)^{i-1}}{1-(1-p)^S}$$

where p is the proportion of the available niche space pre-empted by each successive species. Applications of this model (Whittaker 1970, Magurran 1988, Tokeshi 1990) suggest it may be fitted best by p values of 0.4–0.6. We used $p = 0.5$.

To inventory our nine model communities, we randomly drew $n = S$, $2S$, and $4S$ samples from each, tabulated the vectors $\mathbf{n}$ and $\mathbf{s}$, then calculated $\hat{\Delta}s$ using each of the 11 estimators and assuming increases in sample size of $\Delta n = 0.2n$, $0.5n$, n, $2n$, and $5n$. We then randomly drew an additional $\Delta n = 0.2n$, $0.5n$, n, $2n$, and $5n$ samples from each community and calculated the number of additional species actually observed (Δs) for each level of additional sampling effort. We calculated $\hat{\Delta}s_{\mathrm{GLE}}$ directly per Eq. 3. We calculated the other estimators after fitting the sample data to the various underlying models, using a downhill simplex (Press et al. 1989) to minimize the sums of squares. Because the form of species-accumulation curves can vary with the order in which samples are drawn, we fitted the models underlying the data-analytic estimators to the mean observed accumulation curves produced by 20 random permutations of sampling order (Colwell and Coddington 1994). To calculate $\hat{\Delta}s_{\mathrm{Sto}}$ (Eq. 8), we estimated $\bar{J}$ as the mean of 20 J values, where each J was calculated per Eq. 9 after randomly dividing the sample into two equal-sized subsamples. We repeated these sampling/estimation procedures 25 times for each combination of community type, S, n, and Δn. After each iteration, we calculated estimator errors as $\varepsilon = \hat{\Delta}s - \Delta s$, and ranked estimators according to the absolute values of those errors. Ranks were averaged in the case of ties. Because we wished to compare magnitudes of biases (irrespective of direction), we also calculated transformed error values (ε_{T}) as follows: for estimators for which $\bar{\varepsilon} \geq 0$, $\varepsilon_{\mathrm{T}} = \varepsilon$; for estimators for which $\bar{\varepsilon} < 0$, $\varepsilon_{\mathrm{T}} = \varepsilon + 2\bar{\varepsilon}$. This transformation ensured that $\bar{\varepsilon}_{\mathrm{T}} = |\bar{\varepsilon}|$, while preserving the shapes of the distributions of ε values.

We tested two null hypotheses regarding overall estimator accuracies: (1) each estimator was unbiased (i.e., $\bar{\varepsilon}_i = 0$ for each of the $i = 11$ estimators), and (2) all estimators were equally accurate (i.e., $\bar{\varepsilon}_{\mathrm{T},1} = \bar{\varepsilon}_{\mathrm{T},2} = \ldots = \bar{\varepsilon}_{\mathrm{T},11}$). We tested null hypothesis (1) using one-sample t tests, protected for multiple comparisons using Dunn-Sidak corrections (Wilkinson et al. 1994) to adjust P values as $P_{\mathrm{adj}} = 1 - (1 - P)^j$, where j is the number of one-sample tests being made. We tested null hypothesis (2) using a Kruskal-Wallis test (Zar 1984). Because variances of ε_{T} differed greatly among estimators, subsequent multiple comparisons used two-sample separate-variance t tests, protected for multiple comparisons using Dunn-Sidak corrections.

Tests of null hypotheses 1 and 2 indicated which estimators performed best over the full range of conditions we modeled. Because we also wished to know if those same estimators were invariably preferred when sampling from particular communities, or when using particular values for n or Δn, we tested two additional null hypotheses: (3) rank accuracies of estimators did not vary with the evenness or richness of the species pool, and (4) rank accuracies of estimators did not vary with relative initial sample size (n/S) or the relative magnitude of the proposed increase in sample size ($\Delta n/n$). We tested null hypotheses 3 and 4 using multifactor analysis of variance (MANOVA) (Zar 1984).

Field studies

We empirically tested estimator accuracies using vascular-plant and beetle inventories from 31 0.25-ha plots in the North Fork Flathead River and McDonald Creek Drainages of Glacier National Park, Montana, USA. The 13 North Fork plots were among those established in 1989 to study effects of fire on beetle com-

munities. These were stratified by burn intensity (heavily burned, lightly burned, or unburned) following the 1988 Red Bench Fire, and dominant pre-burn vegetation type (meadow, lodgepole pine [*Pinus contorta*], old-growth spruce [*Picea engelmanni*], or old-growth ponderosa pine [*Pinus ponderosa*]). The 18 McDonald Creek plots were established in 1991 and 1992 as part of a study to develop protocols for species inventories and long-term ecological monitoring in U.S. national parks. These 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 the stand ages for plots within the western hemlock–queen's cup beadlily habitat type were 62 yr (n = 4 plots), 116–136 yr (n = 3 plots), 256 yr (n = 4 plots), or >475 yr (n = 3 plots), while the four plots in the western hemlock–devil's club habitat type were in stands >475 yr old (S. W. Barrett, *unpublished data*). We chose vascular plants and beetles because they are speciose taxa that are sampled in fundamentally different ways: vascular plants using presence or absence in quadrats, beetles as individuals captured in traps. Sampling details were as follows.

We used a stratified-random design to sample vascular plants on the 18 plots in western hemlock communities. Each plot was first stratified into 25 10 × 10 m cells; a 20 × 50 cm quadrat was then randomly placed within each cell during each month, June–September, and canopy coverages of vascular plant species within the quadrats were estimated and recorded. We sampled 12 plots for 3 yr (1991–1993) and the other 6 plots for 2 yr (1992–1993). We calculated $\hat{\Delta}s$ for each plot using data from the first 100 quadrats. For $\hat{\Delta}s_{\text{Sto}}$, we calculated $\bar{J}$ as the mean J value calculated for the 4950 possible pairwise comparisons among the first 100 quadrats sampled. Using n = 100 quadrats as our initial sample allowed us to compare observed and predicted sampling effectiveness for $\Delta n = n$ and $\Delta n = 2n$. Because 100 quadrats represented 1 yr of sampling, this was equivalent to estimating the number of additional species expected after either 1 or 2 yr of additional sampling.

To sample beetles, we placed five pitfall traps in each of our 31 plots; one at the plot center and four along perpendicular axes 20 m from the plot center. Traps contained propylene glycol to preserve specimens. On the 13 North Fork plots, we also used flight-intercept and Lindgren-funnel traps, but samples from these trap types were not included in these analyses because we lacked comparable data for the 18 McDonald Creek plots. We also excluded hand-collected samples from all plots because these were taken opportunistically and lacked an associated measure of sampling effort. Also, we limited analyses to samples collected during June–August because sampling outside this time period was irregular among years. On the 13 fire-effects plots, we sampled beetles for 1 wk out of every 4-wk period, yielding samples from 20 trap weeks per plot per year. On the other 18 plots, we sampled beetles continuously and collected samples monthly, yielding samples from 15 trap months per plot per year. All beetle specimens were identified and enumerated at the species level, except for Staphylinidae, which we excluded from these analyses due to taxonomic uncertainties. For the 13 fire-effects plots, we calculated $\hat{\Delta}s$ using data from the first 20 trap weeks of data, and estimated $\bar{J}$ as the mean of the J values (Eq. 9) for the 190 possible pairwise comparisons among the 20 sets of trap-week data. For the other 18 plots, we calculated $\hat{\Delta}s$ using data from the first 15 trap months, and calculated $\bar{J}$ as the mean of the J values for the 105 possible pairwise comparisons among those 15 sets of trap-month data. For all plots, we calculated $\hat{\Delta}s$ using $\Delta n = n$ and $\Delta n = 2n$. Again, this was equivalent to estimating the number of additional species we would expect to detect if sampling were continued for one or two more years, respectively.

Using the vascular plant and beetle data, we again considered whether (1) each estimator is unbiased, and (2) all estimators are equally accurate. We did not reconsider whether rank accuracies vary with the richness or evenness of the species pool, because structures of the vascular-plant and beetle communities were not fully known. We also did not reconsider whether rank accuracies of estimators vary with the relative size of the initial sample (n/S) or relative magnitude of the proposed increase in sample size ($\Delta n/n$), because we lacked meaningful, alternative choices for initial sample size (n).

Analyses strictly assumed that samples were drawn from communities whose species-abundance distributions did not vary between years. Because most plant species were long-lived perennials (annuals were represented by a single individual of *Poa annua*) in well-established (≥62-yr-old) communities, this assumption was reasonable for our plant inventories. For our beetle inventories, however, this assumption was undoubtedly violated, as species' relative abundances in such communities often vary widely between years. Nonetheless, between-year variations in species-abundance distributions are characteristic of many taxa, and a broadly applicable estimator of Δs should be robust to such variations. Our beetle inventory, thus, offers a test case replete with the untidy realities that often confound field applications.

Results

Selection of i_0 values

We estimated biases and precisions for 27 combinations of estimator type and i_0 value (Table 1). Recall: Δs = the number of additional species we would expect to see if we routinely drew Δn additional samples from the species pool; NB = negative-binomial model, LS

TABLE 1. Mean errors ($\bar{\varepsilon}$) and mean differences from median values ($\bar{D}$) of the negative binomial ($\hat{\Delta}s_{NB}$), logarithmic series ($\hat{\Delta}s_{LS}$, and general linear $\hat{\Delta}s_{GLE}$) estimators, using different threshold (i_0) values to limit the information used to estimate the number of additional species (Δs) expected after drawing Δn additional samples. Each value was based on 50 Monte Carlo replicates for each combination of community type (broken-stick, random-fraction, and geometric series), initial sample size (n = 100, 200, and 400), and increase in sample size (Δn = 0.2n, 0.5n, n, 2n, and 5n). Results are for model communities with 100 species.

	Estimator performances (in numbers of species)					
	$\hat{\Delta}s_{NB}$		$\hat{\Delta}s_{LS}$		$\hat{\Delta}s_{GLE}$	
i_0	$\bar{\varepsilon}$	$\bar{D}$	$\bar{\varepsilon}$	$\bar{D}$	$\bar{\varepsilon}$	$\bar{D}$
3	3.016	9.331	1.367	7.832	−0.404	6.393
5	2.848	9.135	1.238	7.670	0.227	7.849
10	2.629	8.851	1.064	7.434	0.929	24.877
15	2.928	9.061	1.333	7.611	−11.912	155.686
20	3.728	9.480	2.054	7.959	−184.732	1235.418
25	3.220	8.975	1.633	7.536	42.953	12 475.041
30	3.806	9.335	2.151	7.830	−12 568.578	118 450.957
35	3.647	9.290	2.008	7.798	−32 984.925	1 103 672.848
40	3.425	9.199	1.807	7.728	−883 316.344	11 933 100.000

= logarithmic-series model, and GLE = general linear estimator. For $\hat{\Delta}s_{NB}$ and $\hat{\Delta}s_{LS}$, the relationship between bias and i_0 was statistically significant ($\hat{\Delta}s_{NB}$: $F_{2,8,20241} = 7.247$, $P < 0.001$; $\hat{\Delta}s_{LS}$: $F_{2,8,20241} = 12.437$, $P < 0.001$), but trivial. In each case, i_0 (the threshold value, see Eq. 3) accounted for ≤0.5% of the observed variance in the bias. Lacking clear justification for favoring any one i_0 value, we chose $i_0 = 10$ for subsequent calculations of $\hat{\Delta}s_{NB}$ and $\hat{\Delta}s_{LS}$, simply because $i_0 = 10$ yielded the smallest observed bias and greatest precision for both estimators (Table 1).

For $\hat{\Delta}s_{GLE}$, there was no significant relationship between bias and i_0 value ($F_{2,8,20241} = 1.124$, $P = 0.343$). However, we deemed this result to be unreliable, as precisions associated with different i_0 values varied over several orders of magnitude (Table 1, $F_{2,8,20241} = 224.618$, $P < 0.001$), grossly violating the assumption of homogeneity of variances. To maximize both precision and accuracy, we chose $i_0 = 3$ for subsequent calculations of $\hat{\Delta}s_{GLE}$.

Monte Carlo study

None of the 11 estimators (see Eqs. 1–13, above) we compared was universally unbiased. When performance was averaged over the full range of conditions we modeled (Fig. 1), only $\hat{\Delta}s_{NB}$ was unbiased; $\hat{\Delta}s_{LS}$, $\hat{\Delta}s_{Arr}$, $\hat{\Delta}s_{Sto}$, $\hat{\Delta}s_{Brnd}$, and $\hat{\Delta}s_{Log}$ tended to overestimate Δs; and $\hat{\Delta}s_{GLE}$, $\hat{\Delta}s_{Glsn}$, $\hat{\Delta}s_{Shm}$, $\hat{\Delta}s_{MM}$, and $\hat{\Delta}s_{Exp}$ tended to underestimate Δs. When we evaluated estimator performances separately for each model community, $\hat{\Delta}s_{NB}$ was unbiased ($P_{adj} \geq 0.12$) except when sampling random-fraction model communities with $S = 10$ species ($\bar{\varepsilon} = 0.49$, $t = 3.187$, df = 374, $P_{adj} = 0.02$).

When performance was averaged over the full range of model conditions, accuracies of the 11 estimators varied greatly (Fig. 1; Kruskal-Wallis test statistic = 11 832.536, df = 10, $P < 0.001$). Multiple comparisons indicated that, on average, magnitudes of biases of the estimators were related as:

$$\hat{\Delta}s_{NB} < \hat{\Delta}s_{GLE} < (\hat{\Delta}s_{LS} = \hat{\Delta}s_{MM}) < (\hat{\Delta}s_{Shm} = \hat{\Delta}s_{Log}) < \hat{\Delta}s_{Exp} < (\hat{\Delta}s_{Glsn} = \hat{\Delta}s_{Brnd}) < \hat{\Delta}s_{Arr} < \hat{\Delta}s_{Sto}.$$

However, evenness and richness accounted for ~23% of the observed variation in rank accuracies (Table 2). This suggested that, although $\hat{\Delta}s_{NB}$ was the most accurate estimator overall, it may not be the "best" estimator under all conditions. Comparisons of estimators' rank accuracies for particular model communities supported this interpretation. For broken-stick model communities, $\hat{\Delta}s_{MM}$ was most accurate; for geometric-series model communities and depauperate ($S = 10$ species) random-fraction communities, $\hat{\Delta}s_{Glsn}$ was most accurate (Fig. 2). When sampling from broken-stick or geometric-series model communities, differences among rank accuracies were more pronounced as S increased, but S did not affect the choice of a "best" estimator (Fig. 2). In contrast, when sampling from random-fraction model communities, choice of a "best" estimator changed with S: for $S = 10$, $\hat{\Delta}s_{Glsn}$ was most accurate; for $S = 100$, $\hat{\Delta}s_{Log}$ was most accurate; and for $S = 1000$, $\hat{\Delta}s_{LS}$ was most accurate (Fig. 2).

Estimators' rank accuracies also varied with relative initial sample size (n/S) and the relative magnitude of the proposed increase in sample size ($\Delta n/n$) (Table 3). However, effects were minor, as these factors acccounted for only ~4% of the observed variation in estimators' rank accuracies.

Field studies

Only $\hat{\Delta}s_{Arr}$ was unbiased in field studies of both vascular plants and beetles. For the 18 vascular plant inventories, $\hat{\Delta}s_{NB}$, $\hat{\Delta}s_{LS}$, $\hat{\Delta}s_{GLE}$, and $\hat{\Delta}s_{Arr}$ yielded unbiased estimates of the numbers of additional species expected after one and two years of further sampling (Fig 1). Of the remaining estimators, $\hat{\Delta}s_{Sto}$ and $\hat{\Delta}s_{Brnd}$ tended to overestimate Δs, while $\hat{\Delta}s_{Glsn}$, $\hat{\Delta}s_{Shm}$, $\hat{\Delta}s_{MM}$, $\hat{\Delta}s_{Log}$, and $\hat{\Delta}s_{Exp}$ tended to underestimate Δs (Fig. 1). For the 31

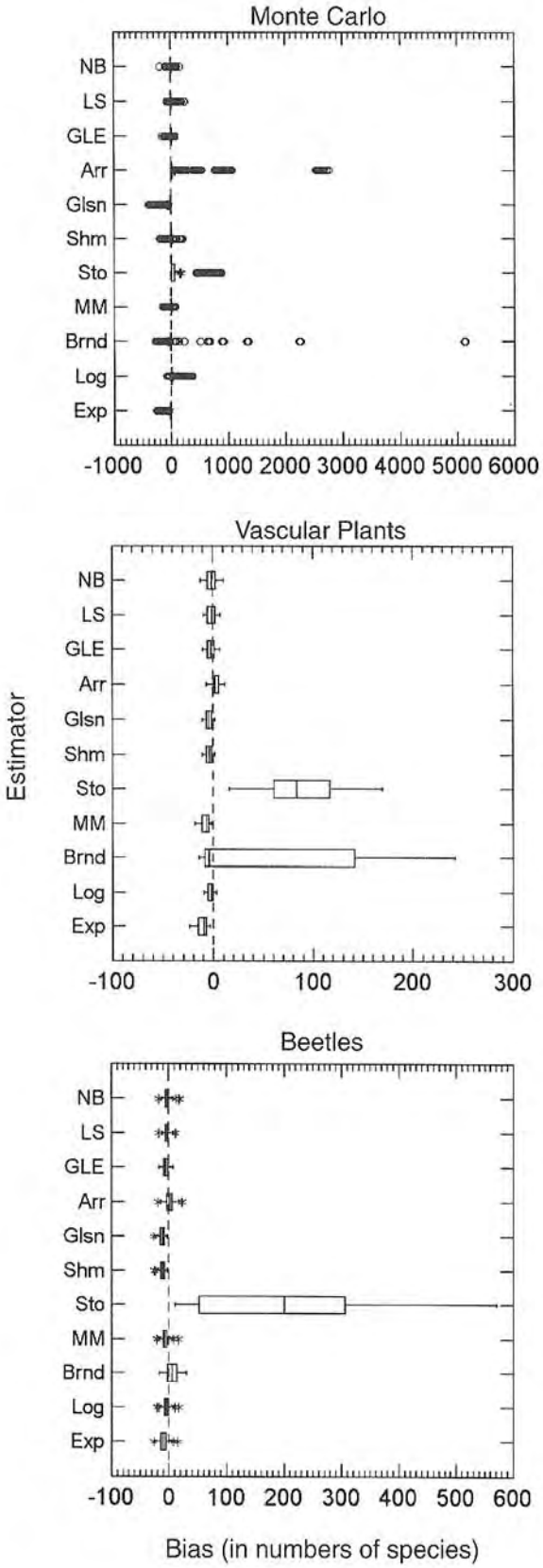

FIG. 1. Box-and-whisker diagrams of the distributions of errors for 11 estimators of the number of additional species (Δs) expected in the next Δn samples, calculated from Monte Carlo simulations of nine model communities, as well as field inventories of 16 vascular plant and 31 beetle communities. The center line indicates the sample median, the box marks the limits of a distribution's first and third quantiles, and the "whiskers" (solid lines) encompass values within $1.5d$ of the box, where d is the absolute distance between the first and third quantiles. Values "outside" or "far outside" these limits are indicated by asterisks and open circles, respectively. The null hypothesis of an unbiased estimator predicts zero bias (vertical dashed lines). Estimators included the negative binomial (NB), logarithmic series (LS), general linear estimator (GLE), Arrhenius (Arr), Gleason (Glsn), Shmida (Shm), Stohlgren (Sto), Michaelis-Menten (MM), Brainerd (Brnd), logarithmic (Log), and exponential (Exp). Note the different scales for the three data sets.

beetle inventories, only $\hat{\Delta}s_{\text{Arr}}$ was unbiased (Fig. 1); $\hat{\Delta}s_{\text{Sto}}$ and $\hat{\Delta}s_{\text{Brnd}}$ tended to overestimate Δs, while $\hat{\Delta}s_{\text{NB}}$, $\hat{\Delta}s_{\text{LS}}$, $\hat{\Delta}s_{\text{GLE}}$, $\hat{\Delta}s_{\text{Glsn}}$, $\hat{\Delta}s_{\text{Shm}}$, $\hat{\Delta}s_{\text{MM}}$, $\hat{\Delta}s_{\text{Log}}$, and $\hat{\Delta}s_{\text{Exp}}$ tended to underestimate Δs (Fig. 1).

The 11 estimators were not equally accurate when applied to data from either the 18 vascular-plant inventories (Kruskal-Wallis test statistic = 164.627, df = 10, $P < 0.001$) or the 31 beetle inventories (Kruskal-Wallis test statistic = 241.790, df = 10, $P < 0.001$). For the plant data, multiple comparisons indicated magnitudes of biases (Fig. 1) were related as

$$(\hat{\Delta}s_{\text{NB}} = \hat{\Delta}s_{\text{LS}} = \hat{\Delta}s_{\text{GLE}} = \hat{\Delta}s_{\text{Arr}} = \hat{\Delta}s_{\text{Log}} = \hat{\Delta}s_{\text{Shm}} = \hat{\Delta}s_{\text{Glsn}}) < (\hat{\Delta}s_{\text{MM}} = \hat{\Delta}s_{\text{Exp}} = \hat{\Delta}s_{\text{Brnd}}) < (\hat{\Delta}s_{\text{Brnd}} = \hat{\Delta}s_{\text{Sto}}).$$

For the beetle data (Fig. 1), multiple comparisons indicated that $\hat{\Delta}s_{\text{Arr}}$, $\hat{\Delta}s_{\text{NB}}$, $\hat{\Delta}s_{\text{LS}}$, and $\hat{\Delta}s_{\text{Log}}$ (in order of decreasing accuracy) gave the most accurate and statistically indistinguishable estimates, and that $\hat{\Delta}s_{\text{Sto}}$ was less accurate than other estimators. The remaining estimators exhibited intermediate accuracy along a gradient that lacked clear groupings.

Discussion and Conclusions

Taxonomically and geographically extensive inventories are desperately needed, but funding is scarce and species discovery rates decline rapidly with further sampling, so that truly complete inventories are not a reasonable goal. These realities underscore the importance of allocating sampling efforts in the most cost-effective manner possible. Toward this end, we believe that estimators of the expected effectiveness of further sampling can enable more informed decisions about how, where, and when to sample, and that such estimates should be calculated routinely as part of most (if not all) inventory efforts. In our inventory of beetle species, for example, estimates of Δs—the number of additional species expected after drawing Δn additional samples—calculated after the first year of sampling, would have shown that allocation of sampling effort among different trap types was suboptimal; fewer pitfall traps, and more Lindgren-funnel and flight-inter-

TABLE 2. Multifactor analysis-of-variance (MANOVA) test of the null hypothesis that rank accuracies (RANK) of 11 estimators (ESTR) of the number of additional species (Δs) expected in the next Δn samples did not vary with evenness (EVEN) or richness (S) of the species pool. The MANOVA model, specified as RANK = Constant + ESTR × EVEN + ESTR × S + ESTR × EVEN × S, accounted for $r^2 = 23\%$ of the observed variation.

Source of variation	Sum of squares	df	F	P
ESTR × EVEN	34 184.873	20	220.257	<0.001
ESTR × S	37 737.859	20	243.150	<0.001
ESTR × EVEN × S	11 620.971	40	36.438	<0.001
Error	287 469.297	37 044		

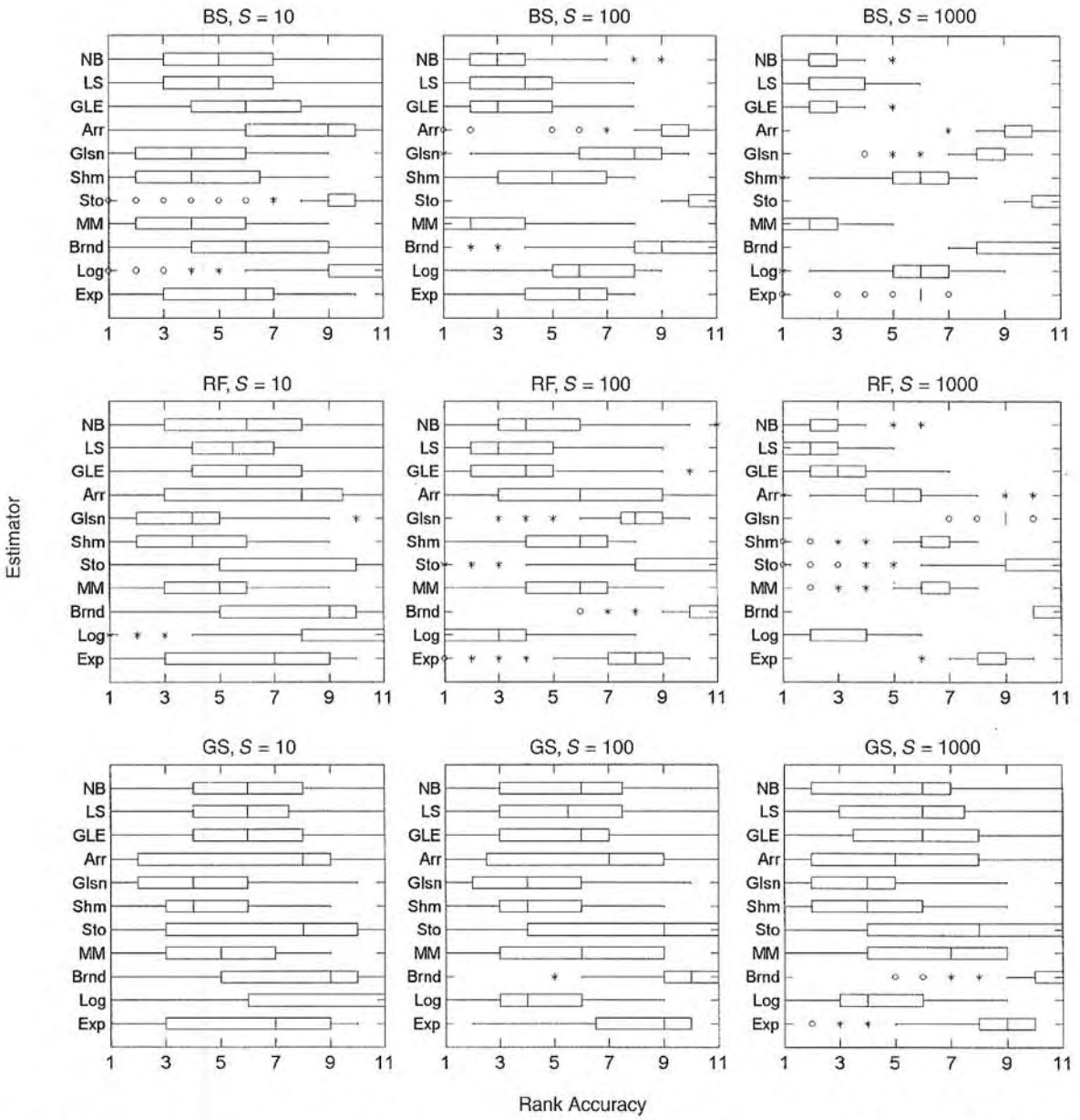

FIG. 2. Box-and-whisker diagrams of the distributions of rank accuracies for 11 estimators of the number of additional species (Δs) expected in the next Δn samples. Results are shown separately for each of nine model communities, where species' relative abundances conformed to a broken-stick (BS), random-fraction (RF), or geometric series (GS) distribution, and species richness (S) was 10, 100, or 1000. Interpretations of box-and-whisker plots and estimator abbreviations are the same as in Fig. 1.

TABLE 3. Multifactor analysis-of-variance (MANOVA) test of the null hypothesis that rank accuracies (RANK) of 11 estimators (ESTR) of the number of additional species (Δs) expected in the next Δn samples did not vary with relative initial sample size (n/S, where n is sample size and S is the richness of the species pool) or relative magnitude of the proposed increase in sample size ($\Delta n/n$). The MANOVA model, specified by RANK = Constant + ESTR × n/S + ESTR × $\Delta n/n$ + ESTR × n/S × $\Delta n/n$, accounted for $r^2 = 4\%$ of the observed variation.

Source of variation	Sum of squares	df	F	P
ESTR × n/S	3192.007	20	16.502	<0.001
ESTR × $\Delta n/n$	9230.885	40	23.862	<0.001
ESTR × n/S × $\Delta n/n$	906.410	80	1.172	0.140
Error	357 683.698	36 984		

cept traps, clearly would have yielded more species for the same cost (M. A. Ivie and L. L. Ivie, *unpublished data*).

Our provisional choice of a method for estimating Δs is the negative-binomial estimator, $\hat{\Delta}s_{\text{NB}}$. Although accuracies varied widely and no estimator was universally unbiased, $\hat{\Delta}s_{\text{NB}}$ was generally more robust to community structure and sampling design than the other estimators. Biases were observed when $\hat{\Delta}s_{\text{NB}}$ was applied to samples drawn from random-fraction model communities with $S = 10$ species, or from beetle communities; but in each case, magnitudes of biases were relatively minor (0.6 and 3.0 species, respectively).

Although $\hat{\Delta}s_{\text{NB}}$ performed best overall and $\hat{\Delta}s_{\text{Arr}}$ (Arrhenius) performed best in field studies, results suggested that other estimators may be preferred under specific conditions. For example, when sampling from communities with species-abundance distributions that conformed to MacArthur's (1957) broken-stick model, $\hat{\Delta}s_{\text{MM}}$ (Michaelis-Menten) was the most accurate estimator, and when sampling from very small species pools (on the order of $S = 10$) or those with species-abundance distributions that conformed to the geometric series model, $\hat{\Delta}s_{\text{Glsn}}$ (Gleason) was superior. We find the practical value of these estimators to be limited, however, since most communities are better described by the lognormal or random-fraction than by the broken-stick or geometric-series models (May 1975, Tokeshi 1990, 1996). Furthermore, because their performances are not robust to community structure, justifications for using $\hat{\Delta}s_{\text{MM}}$ or $\hat{\Delta}s_{\text{Glsn}}$ require a priori knowledge of the number and relative abundances of species in the species pool. In turn, such knowledge is inconsistent with the very rationale for conducting species inventories.

The estimators $\hat{\Delta}s_{\text{Brnd}}$, $\hat{\Delta}s_{\text{Exp}}$, and $\hat{\Delta}s_{\text{Sto}}$ (Brainerd, exponential, and Stohlgren, respectively) performed poorly over a broad range of conditions, suggesting that the species-accumulation models underlying these estimators are fundamentally flawed. The poor performance of $\hat{\Delta}s_{\text{Brnd}}$ was unsurprising, as Brainerd (1982) found the underlying model to be "inadequate," even for its original purpose of estimating authors' vocabularies. The fact that $\hat{\Delta}s_{\text{Exp}}$ was not robust also was unsurprising, as Soberón and Llorente (1993:486) suggested the underlying species-accumulation model may be appropriate only when sampling "small or homogeneous areas with few rare species." In our Monte Carlo study, however, $\hat{\Delta}s_{\text{Exp}}$ failed to perform well even under such conditions, which were represented by broken-stick model communities with 10 species.

We could not reconcile the poor performance of $\hat{\Delta}s_{\text{Sto}}$ with Stohlgren et al. (1997*a*, *b*), who reported that estimates of S based on the underlying species-accumulation model were >95% accurate. We attribute the poor performance of $\hat{\Delta}s_{\text{Sto}}$ to flaws in the underlying model, which is a modification of Shmida's (1984) model:

$$s = \alpha + \beta \log(A). \tag{14}$$

Stohlgren et al. (1997*a*, *b*) asserted that the negative bias observed when extrapolating Eq. 14 to larger areas was due to heterogeneity among plots, and they proposed the "correction"

$$s = \alpha + \frac{\beta}{\bar{J}}\log(A) \tag{15}$$

where $\bar{J}$ is the mean value of Jaccard's index of similarity among all possible pairwise combinations of samples. However, two lines of reasoning suggest that bias in Shmida's model was not due to heterogeneity among plots: (1) Shmida's model should account for heterogeneity via increased β values, and (2) in our Monte Carlo study, $\hat{\Delta}s_{\text{Shm}}$ was negatively biased even though the distribution of species in our model communities was strictly homogeneous. The justification for dividing β by $\bar{J}$ is, therefore, unclear. Moreover, $\bar{J}$ would be a poor choice for correcting for heterogeneity, since $\bar{J}$ is an *index* rather than a true *measure* of heterogeneity, and is likely to be negatively biased by small sample sizes (Krebs 1989). Contrary to Stohlgren et al. (1997*a*, *b*), we suggest that extrapolations of Shmida's model are negatively biased because the underlying species–log(area) relationship is nonlinear, and that Eq. 15 attempts to compensate by arbitrarily increasing the fitted slope of the linear model. We find this strategy difficult to justify.

Our results also suggest that estimates of the total richness of the species pool (S) are likely to be influenced greatly by the structure of the underlying community. Although we did not specifically evaluate estimates of S, we note that estimating S was the original

motivation for developing most of the species-accumulation models underlying the estimators we compared. Moreover, estimates of S often require extrapolations that assume Δn values much larger than we used. For example, when using species-accumulation models that are bounded by an upper asymptote (e.g., the models underlying $\hat{\Delta}s_{\text{MM}}$, $\hat{\Delta}s_{\text{Brnd}}$, or $\hat{\Delta}s_{\text{Exp}}$), S is estimated as the limiting value of $s + \Delta s$ as $n + \Delta n \rightarrow \infty$ (Bunge and Fitzpatrick 1993). Because most estimators we examined were not robust to community structure for even small values of Δn (in this study, $\Delta n \leq 5$), it seems likely that extrapolations based on even larger Δn values will often be spurious. Exceptions may occur when sampling from communities with particular species-abundance distributions. For example, $\hat{\Delta}s_{\text{MM}}$ gave good estimates of Δs when species' relative abundances conformed to a broken-stick distribution, suggesting that the Michaelis-Menten model may yield good estimates of S under these conditions (cf. Keating and Quinn 1998). Earlier studies similarly concluded that the Arrhenius, Gleason, and Michaelis-Menten models are likely to give unreliable estimates of richness (Palmer 1990, 1991, Keating and Quinn 1998). We extend these findings to include the species-log(area) models of Shmida (1984) and Stohlgren et al. (1997*a*, *b*), and the stochastic-process models of Brainerd (1982) and Soberón and Llorente (1993).

Finally, our results also have implications for mark–recapture studies of populations. The problem of estimating the number of individuals in a population is conceptually identical to that of estimating the number of species in a community (Burnham and Overton 1979). Thus, the general problem addressed by the estimators we compared can be rephrased as follows. Suppose that after drawing n samples from a population of S individuals, we observe s distinct individuals. The probability of encountering the ith individual is π_i, so that $\boldsymbol{\pi} = (\pi_1, \pi_2, \ldots, \pi_S)$. In our sample, individuals occur with frequency $\mathbf{n} = (n_1, n_2, \ldots, n_S)$ and the number of individuals observed exactly j times is $\mathbf{s} = (s_1, s_2, \ldots, s_n)$. Rephrased in this way, the methods we compared yield estimates of the number of additional individuals (Δs) we would expect to see if we randomly drew Δn additional samples from the same population. An example application is mark–recapture studies, where it may be useful to evaluate the likely costs and benefits of extending trapping periods.

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