

An assessment of sample-based estimators of tree species richness in two wet tropical forest compartments in Panama and India

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SUMMARY

We assessed the performance of ten incidence-based estimators of tree species richness in simulated simple random sampling with fixed-area plots. Stem diameter-limited tree species and location data came from two species-rich wet tropical forest compartments in Panama and India. Lower limits of stem diameter were 1 cm and 30 cm, respectively. Estimators varied widely in their estimates of richness and their rankings changed frequently across sites and sample designs. A gamma-Poisson estimator was overall best according to a performance score of three accuracy statistics and sample size. However, until corroborated by further studies Chao's 1981 non-parametric estimator is recommended for forest inventories with fixed-area plots.

Keywords: probability of occurrence, variance estimator, sample coverage, sample size, plot size, mixed-models.

INTRODUCTION

An important indicator of sustainable forest development is the conservation of biological diversity (McDonald and Lane 2004). The number of tree species (richness) in our forests is a key component of this diversity. Obtaining an unbiased and precise estimate of the number of forest tree species currently growing in a region, state or country poses a challenge. Species lists compiled from historic data, anecdotal evidence or tree distribution maps may not reflect current reality (Guralnick and Van Cleve 2005). It is, of course, the rare tree species that pose the challenge. A direct monitoring or survey of the status of all rare species in each area of interest would provide the needed data but this option is rarely realistic (Acharya, Bhattarai, de Gier et al. 2000, Gimaret-Carpentier, Pelissier, Pascal et al. 1998, Green 1993, Venette, Moon, and Hutchison 2002, Yatracos 1995).

Existing forest surveys would ideally provide an estimate of the number of tree species in a population of interest. A long history of research on estimation of the number of species in an area (Arrhenius 1921, Evans, Clark, and Brand 1955, Fisher, Corbet, and Williams 1943) has provided us with a plethora of estimators and estimation procedures (for examples, Chao and Bunge 2002, Chazdon, Colwell, Denslow et al. 1998, Dorazio and Royle 2003, Skov and Lawesson 2000, Tackaberry, Brokaw, Kellman et al. 1997, and Walther and Morand 1998). Each estimator rests on a set of assumptions about the population and the sampling protocol (Bunge and Fitzpatrick 1993). It is a common observation that estimates obtained from these estimators are sensitive to both the structure of the sampled population and the sample design (Brose, Martinez, and Williams 2003, Colwell, Mao, and Chang 2004, Keating, Quinn, Ivie et al. 1998). Rare species, easily missed in a survey, exert a disproportionate influence on the results (Link 2003, Mao and Colwell 2005). Samples with a poor representation of rare species cannot be expected to yield reliable estimates of richness. It is generally recognized that the estimation problem is intransigent and that estimators are biased (Bunge and Fitzpatrick 1993).

Can we expect a forest survey - designed to provide accurate estimates of the area of different forest cover-type classes, wood volume, and biomass – to provide a reliable estimate of the number of tree species in a forest? Apparently the answer will depend both on the forest and the sample strategy (sampling design and estimation). Experience with sample-based estimation of tree species richness is limited. Schreuder, Williams,

and Reich (1999) assessed 10 modifications of Chao and Lee's non-parametric estimators by sampling two large data sets with 4060 forest inventory plots from Missouri and 12260 from Minnesota, respectively. Sample sizes in the order of 500 to 700 were deemed necessary to keep bias below 15%. Sample sizes of 80 produced a (negative) bias of about 40%. Palmer (1990 and 1991) investigated eight estimators in sampling (trees, forbs, and herbs) from 30 $20\text{ m} \times 20\text{ m}$ plots in the Duke Forest (North Carolina, USA) with 40 circular 2 m^2 samples taken from each plot. The second-order jackknifed and the bootstrap (Smith and van Belle 1984) performed best in terms of accuracy and precision. Hellmann and Fowler (1999) simulated sampling with $5\text{ m} \times 5\text{ m}$ plots within five forested 0.4 ha plots in Michigan. Bias of estimates obtained with jackknifed and bootstrap estimators depended strongly on sample size with a switch from negative to positive bias as the sampled area surpassed approximately 35% of the total area. The second-order jackknifed estimator was the best for low-intensity sampling ($< 10\%$ of area sampled). Gimaret-Carpentier, Pélissier, Pascal et al. (1998) compared the behavior of Chao's and the generalized jackknifed estimators of richness in two wet tropical forests under random and systematic sampling with cluster-sizes of 1, 10, 50, and 100 trees. Chao's estimator(s) were superior to the generalized jackknifed estimator(s) and systematic sampling was more efficient than random sampling. Cluster-size effects were restricted to designs with less than a total of 400 sampled trees. Krishnamani, Kumar, and Harte (2004) reached a realistic estimate of 893 for the number of tree species in $60\,000\text{ km}^2$ of the forests in the Western Ghats (India) from just 48 (0.25 ha) plots. An index of species similarity between a pair of plots was cast as a non-linear function of inter-plot distances and used in a plug-in formula for the species-area relationship. Excellent summaries of techniques and methods for assessing species richness have been given by, for examples, Chazdon, Colwell, Denslow et al. (1998), Condit, Hubbell, Lafrankie et al. (1996) and Tackaberry, Brokaw, Kellman et al. (1997). It is well known that only an intensive survey of a population can generate an accurate estimate of richness (for example Gimaret-Carpentier, Pélissier, Pascal et al. 1998).

The objective of this study is to assess the performance (bias, precision, and accuracy) of six non-parametric and four model-based richness estimators in the context of a forest inventory. Based on the outcome of this assessment we discuss the pros and cons of attempting to estimate tree species richness from an inventory sample, and we make a recommendation for those who decide to produce an estimate of forest tree species richness from a forest inventory sample.

A forest inventory typically samples only a small fraction of a forest. Sample sizes are sufficient to estimate the mean or total of a quantitative trait with a desired accuracy and precision. It is at these low sampling intensities that estimates of richness depends most on the chosen estimator and estimators are needed the most due to a considerable negative bias in the observed richness (Walther and Moore 2005). Our assessment of the estimators is based on simulated simple random sampling with fixed-area plots in two tree species rich wet tropical forest compartments with a high frequency of rare tree species. Fixed-area plots are commonplace in forest inventories (Köhl, Magnussen, and Marchetti 2006). Simple random sampling with fixed-area plots affords unbiased estimates of stem inclusion probabilities. All information needed for an estimation of tree species richness are contained in the species incidence statistic (the number of sample plots containing a given species). Consequently only incidence-based estimators are considered (Fattorini *in press*, Hurlbert 1971). Estimators tailored towards a comparison of independent estimates of species richness (rarefaction) or temporal trends are beyond the scope of this study. We also screened out estimators that are suitable only for large sample sizes, notably estimators based on species-area and species-accumulation curves (for example, Ugland, Gray, and Ellingsen 2003, and Dorazio and Royle 2005 for a further discussion of this point).

Our final selection of incidence-based estimators of species richness has been based on a recent review (Walther and Moore 2005) and experience from a preliminary study. We anticipate that an estimator that does well on two species rich sites will also do well on sites with fewer tree species, although species richness can influence estimator performance (Walther and Morand 1998).

A good estimator is one that across a range of sample sizes and a range of populations consistently produces estimates that are closest to the actual richness (Schreuder, Williams, and Reich 1999, Walther and Morand 2005). In our assessment we take the position that an estimator should have a low risk of producing an inflated estimate of richness. This position is based on a mix of statistical and practical implications of an inflated estimate. Not only does the standard error of a richness estimate increase in proportion to the estimate of the unseen number of species, but the reliability of this estimates declines at an exponential rate (Mao and Colwell 2005). Secondly, the credibility of a forest inventory agency can be irrevocably damaged if it produces an estimate that later has to be retracted as more information becomes available.

MATERIAL AND METHODS

Data

Two stem-mapped stand-level data sets will be used for the assessment of sample-based estimators of species richness. The first is from the Kadamakal Reserve Forest (Kadagu District, Karnatiaka State, India) near the village of Uppangala in the Western Ghats mountain range (12° 30' N, 75° 39' W; 500-600 m altitude). The forest type is *Dipterocarpus indicus*-*Kingiodendron pinnatum*-*Humboldtia brunonis* (Pascal 1982). Within a 28 ha forest compartment five 20 m wide north-south oriented strips 100 m apart and 180 to 370 m long were inventoried (Pascal and Pélissier 1996). The species and the spatial location were determined for all trees with a diameter at breast height larger than 30 cm. In the inventoried area of 3.12 ha Pascal and Pélissier (1996) found 1981 such trees (635 trees per ha) with a basal area of 39.7 m² ha⁻¹. Ninety-three species belonging to 31 families were identified in the five strips. An additional 12 species were seen in the 28 ha stand but not in the five strips. Figure 1 lends an impression of the species distribution in the five strips. Here the relative number of species is plotted against the relative number of 5 m × 20 m plots in which they occur. The distribution is typical of species rich wet tropical forests. Forty-six percent of the species were found in less than 1% of the plots and 90% in less than 13%. On average a species was found in just 5% of the plots. One species was seen in 62% of the plots. Pascal and Pélissier (1996) estimated Simpson's diversity index at 0.92 (i.e. about 92 pairs of trees selected at random out of a 100 are composed of different species) and that of Shannon's at 4.56 (compare to a maximum value of 6.54). The number of different species in a 100 m² plot varied from a low of 0 in two empty plots to a high of 13 with a mean and median of 6 (Figure 2). We refer to this site as WGHAT in the results and the discussion.

[FIGURES 1 AND 2 HERE]

The second data set is from a rich old-growth stem-mapped wet tropical forest compartment dominated by *Leguminosae* and *Bomabaceae* (area 1000 m × 500 m = 50 ha) on the Barro Colorado Island in the Panama Canal (Condit, Hubbell, Lafrankie et al. 1996, He and Hubbell 2003). Data from the 1990 census are used in this study. A total of 220 000 trees (4400 ha⁻¹) of all sizes representing 301 species were identified. Further details are in He and Hubbell (2003). In Figure 3 the relative number of species is plotted against the relative number of square 156-m² plots in which they occur. The distribution is similar to that of WGHAT and also typical of species rich wet tropical forests. Thirty-six percent of the species were found in less than 1% of the plots, 50% in less than 2%,

and 90% in less than 30% of the plots. One species was found in all plots. The number of different species in a 156 m² plot varied from a low of 5 to a high of 52 with a mean and median of 30 (Figure 4). We shall refer to this site as BCI.

[FIGURES 3 AND 4 HERE]

Sampling designs and sample statistics

In WGHAT the five 20 m wide survey lines totaling 1560 m in length were subdivided into 312 100 m² rectangular (5 m × 20 m) plots. Simple random sampling with sample sizes $n = 10, 15, \dots, 30$ plots without replacement was simulated. Accordingly between 3.2% and 9.6% of the area was sampled. In BCI the 50 ha area was tessellated into 3200, 1250, and 800 square plots with side lengths of 12.5 m, 20 m, and 25 m, respectively. Simple random sampling with $n = 40, 60, \dots, 140$ plots without replacement was simulated.

Sampling followed by estimation of tree species richness (S) was repeated 2000 times for each combination of sample and plot size. Estimates of variance were corrected for finite population size by a factor $1-f_{pc}$ with f_{pc} equal to the proportion of the area sampled (Cochran, 1977).

Let S_{OBS} be the number of species encountered in n sample plots. Encountered species are labeled by an index i ($i = 1, \dots, S_{OBS}$). The sample data consist of a size $S_{OBS} \times n$ binary matrix δ with element $\delta_{ij} = 1$ if the i th species occurred in the j th plot and zero otherwise. The number of plots containing the i th species is $\delta_{i\cdot} = \sum_{j=1}^n \delta_{ij}$ and the proportion of sample plots with this species is p_i . For incidence-based estimation of richness the incidence vector $\mathbf{f} = (f_1, \dots, f_n)$ with $f_k = \#\{\delta_{i\cdot} = k\}$ contains all the needed information. We have $S_{OBS} = \sum_{k=1}^n f_k$. Simply put, \mathbf{f} is indexing the number of species encountered in 1, 2, ..., n plots (Esty 1982, Starr 1979). Species not encountered in any sampling plot are captured by f_0 , the number of ‘missed’ species. We have $S = S_{OBS} + f_0$.

The total number of times one of the observed species were encountered in the n plots is referred to as n_{catch} , in reference to the ‘total catch’, in animal capture-recapture parlance (Burnham and Overton 1978, Chao 1989). n_{catch} is a design-dependent random variable that also depends on the population structure. We have

$\hat{n}_{catch} = \sum_{i=1}^{S_{OBS}} \delta_{i\Box} = \sum_{k=1}^n k \times f_k$. The proportion of the i th species in n_{catch} is

$\hat{\pi}_i = \frac{1}{\hat{n}_{catch}} \sum_j \delta_{ij}$ with $\sum_{i=1}^{S_{OBS}} \hat{\pi}_i \equiv 1$. We shall denote π_i as the design and population

dependent ‘catch’ probability of the i th species. A design-unbiased estimator of the sampling variance of S_{OBS} is not available. The distribution of S_{OBS} has been assumed Poisson with a mean and a variance equal to S_{OBS} . We propose $S_{OBS}^2 \times n_{catch}^{-1}$ as an estimator of the sampling variance on the grounds that n_{catch} / S_{OBS} is the average number of plots per unique species in the sample.

Estimators of richness

Nine incidence-based estimators of richness are evaluated. Only a sketch of the estimators is given here. Details are found in the provided references. A software program for the estimators has been written in MATHEMATICA® (Wolfram Research 2005) and is available upon request to the senior author.

Petersen’s capture-recapture estimator (PET)

Petersen’s capture-recapture estimator (see Thompson, 1992 page 214 EQ 3) of richness is

$$(1) \quad \hat{S}_{PET} = E \left[\eta \times \frac{S_{OBS}^{(2)}}{S_{OBS}^{(1) \cap (2)}} \times S_{OBS}^{(1)} \right]$$

where $S_{OBS}^{(1)}$ denotes the number of species found only in the first-half of a random split of the sample plots, $S_{OBS}^{(2)}$ is the number of species found only in the second half of the

random split, $S_{OBS}^{(1) \cap (2)}$ is the number of species found in both halves,

$\eta = (S_{OBS}^{(1)} + S_{OBS}^{(2)}) / S_{OBS}^{(1)}$, and E stands for the expectation over random splits (here 1000).

The bootstrap estimator (BOOT)

Smith and van Belle (1984) were the first to suggest a bootstrap estimation of richness. A bootstrap sample of size n is drawn with replacement from the sample records. Let S_{BOOT}^r be the number of unique species in the r th bootstrap sample. The expected difference $E[S_{BOOT}^r - S_{OBS}]$ over all possible bootstrap samples is an estimate of the bias in the observed richness, and when added to the observed richness it yields the bootstrap estimate of richness. Smith and van Belle (1984) also detail the estimator we use for the sampling variance of the bootstrap estimate.

The generalized jackknifed estimator (JKk)

The generalized jackknifed estimator of richness is a linear combination of conventional jackknifed estimators (Sharot 1976). The order of a generalized jackknifed estimator (k) defines the linear combination of conventional jackknifed estimators that enters into the generalization. The estimator is

$$(2) \quad \hat{S}_{JKk} = \frac{1}{k!} \sum_{j=0}^k (-1)^j \binom{k}{j} (n-j)^k \hat{S}_{-j}$$

where \hat{S}_{-j} is the conventional leave j -out jackknifed estimator of richness ($\hat{S}_0 \equiv S_{OBS}$).

Burnham and Overton (1978) provided an estimator for the variance of \hat{S}_{JKk} based on the assumption of a multinomial distribution of (f_o, f_1, \dots, f_n) and application of the delta-technique (Kendall and Stuart 1969).

The CHAO1 and CHAO2 estimators

Chao (1981) and later Chao and Lee (1992) proposed the following estimator

$$(3) \quad \hat{S}_{CHAO1} = \frac{S_{OBS}}{\hat{C}_1} + \frac{f_1}{\hat{C}_1} \times \gamma^2$$

where $\hat{C}_1 = 1 - f_1 / n_{catch}$ is an estimate of the missed species, and γ is an approximation to the coefficient of variation of f_j , ($j = 1, \dots, n$). Chao and Lee (1992) also suggested the alternative in (4) as an improvement over (3)

$$(4) \quad \hat{S}_{CHAO2} = \frac{S_{obs}}{\hat{C}_2} + \frac{f_1}{\hat{C}_2} \times \gamma^2$$

where $\hat{C}_2 = 1 - f_1 - 2f_2 \times (n_{catch} - 1)^{-1} n_{catch}^{-1}$, and γ is a potentially better approximation to γ than γ .

\hat{S}_{CHAO1} and \hat{S}_{CHAO2} are both non-linear functions of f_1, K, f_n . Hence an estimator of their sampling variances can be obtained by applying the same assumptions and asymptotic approximations as for the jackknifed variance estimators. Details are in Chao and Lee (1992).

The CHAO3 estimator

Chao (1989) - in recognizing that f_1 and f_2 are the two most influential incidence frequencies for estimating richness - proposed the following estimator which we have modified slightly to make it robust against zero-valued frequencies

$$(5) \quad \begin{aligned} \hat{S}_{CHAO3} &= S_{OBS} + \frac{(f_1^*)^2}{2f_2^*} \\ f_1^* &= (S_{OBS} - f_1 - f_2) \times \frac{f_1}{f_1 + f_2} \\ f_2^* &= (S_{OBS} - f_1 - f_2) \times \left(1 - \frac{f_1}{f_1 + f_2} \right) \end{aligned}$$

A variance estimator is obtained by the same procedure as for the generalized jackknifed estimator.

The Beta-binomial estimator (BBIN)

The observed incidence vector \mathbf{f} can be viewed as a zero-censored outcome of draws from a beta-binomial distribution where the probability of success (incidence of a species) varies from plot to plot. Accordingly, Dorazio and Royle (2003) proposed a maximum likelihood estimate of $f_0 \equiv S - S_{OBS}$ under this model. By adding this estimate to the observed richness one obtains the *BBIN* estimator of richness. The estimated variance of a *BBIN* estimate of richness is obtained by the aforementioned delta-technique. Confidence intervals were derived from the profile-log-likelihood (Lloyd, 1999).

The mixed-binomial estimator (MBIN)

Mao and Colwell (2005) and Norris and Pollock (1998) viewed the vector \mathbf{f} as a zero-censored outcome of sampling from a mixture of k binomial distributions where k is an unknown parameter to be estimated. As for *BBIN*, a maximum likelihood estimate of $f_0 \equiv S - S_{OBS}$ is obtained under this model and added to the observed richness to give the *MBIN* estimate of richness. Procedures for estimating the sampling variance and confidence intervals of a *MBIN* estimate were similar to those for *BBIN*.

The gamma-mixed Poisson estimator (GPOI)

A zero-truncated gamma-mixed Poisson distribution (negative binomial) has been suggested by several as the generating distribution for \mathbf{f} (Chao and Bunge 2002, Chao and Lee 1992, Efron and Thisted 1976, Fisher, Corbet, and Williams 1943). The probability of ‘missing a species’ (P_0) is then estimated by method of maximum likelihood under this model and used to inflate the observed richness by dividing it with a factor $1 - P_0$. As for the other model-based estimators, a variance estimator for a *GPOI* estimate was obtained by application of the delta-technique. We imposed a restriction on the location parameter of the implied gamma distribution in order to avoid absurdly high estimates of richness. A robust estimation procedure proposed by Chao and Bunge (2002) was used when either the estimated richness or the estimated variance became aberrant.

The mixed-Poisson estimator (MPOI)

Here the assumption is that \mathbf{f} arises from draws from a mixture of k zero-truncated Poisson distributions otherwise the estimation process is in principle the same as for MBIN.

Finite population corrections

Our richness estimators either explicitly or implicitly assume an infinite area of the sampled population of trees. To account for the finite area of the two compartments, we reduced all estimates of richness (except the observed) in the following way:

$$(6) \quad \hat{S}'_M = S_{OBS} + (1 - f_{pc})(\hat{S}_M - S_{OBS})$$

where M stands for one of the nine richness estimators (Schreuder, Lin, and Teply 2000, Valliant, Dorfman, and Royall, 2000). This correction ensures that as $f_{pc} \rightarrow 1$ we get $\hat{S}'_M \rightarrow S_{OBS}$ as required.

Evaluating estimator performance

A main objective of our study was to assess the performance of estimators of tree species richness in the context of a forest inventory with fixed-area plots. Walther and Moore (2005) provide a recent review of performance statistics. Our assessment is derived from estimates of *i*) bias (estimated value minus the true value) *ii*) precision (standard error of an estimate), and *iii*) accuracy (overall discrepancy between an estimate and a nominal value). We use three statistics to quantify accuracy: 1) the mean absolute difference between an estimate and the true value (Mad), 2) the proportion of estimates within 10% of the true value (δ_{10}), and 3) the proportion of estimated 95% confidence intervals that includes the true value (p_{CI}). The estimator with the lowest Mad , the highest δ_{10} , and p_{CI} closest to 0.95 for a given sampling design would be our recommendation to the forest inventory community if the achieved levels of these statistics were otherwise acceptable. No absolute threshold can be given for acceptable but we surmise that an absolute error in excess of 25% and an estimate with a confidence intervals having less than 70% of the nominal coverage would probably be useless as

input to a decision making process. We use a loss function (L) in (7) to compute a performance score for each estimator (M) across all site specific sample designs:

$$(7) \quad L(M | \text{site}) = \sum_{d \in D(\text{site})} \sqrt{n_d} \times p_d \left\{ \frac{Mad}{S} + 100((1 - \delta_{10}) + |0.95 - p_{CI}|) \right\}$$

where d is a design in the set (D) of all site-specific designs, S is the true richness, p_d is the fraction of the site area sampled by design d , and the three accuracy statistics are all design specific estimates. Several variants of the above loss function was tried (not shown) with next to no consequence on the ranking of estimators. A simple average of site-specific rankings in terms of the loss computed from (7) was used as a measure of overall performance.

Plot effects

Plot size effects will depend on the spatial distribution and size of the trees of each species, the sampling design and the spatial lay-out of a plot. In practical inventory applications the important design issue is the expected effect of a change in plot size on estimates of S and whether the expected effect is statistically significant when allowing for sampling errors. We use Hotelling's multivariate T^2 test to assess the significance of plot effects across sample size (Rencher, 1995). Specifically, we tested the null hypotheses of no difference between the results obtained with 156 m² and 400 m² plots and between 400 m² and 625 m² plots. A follow-up T^2 test of plot \times sample size interactions was done for all significant plot effects.

RESULTS

Bias

Observed richness was, as expected, downward biased (Tables 1 and 2). For a given fraction of the area sampled the bias was two to three times larger in WGHAT than in BCI, a reflection of the much higher number of individual trees sampled in BCI. With 10% of the area sampled in WGHAT the bias was –56% as opposed to –20% in BCI. It will take a sampling of about 18% of the BCI compartment to bring the bias below 15%.

The choice of richness estimator is clearly important (Tables 1 and 2). The best estimator reduces the observation bias to between -1% and -15% in WGHAT and to between 1% and -11% in BCI. Even the worst estimator produced an estimate with less bias than the observed richness.

Estimates of bias varied by more than 40% between the best and the worst estimator. Least performing were MPOI, BOOT, and MBIN. The only estimates with a positive bias came from CHAO3, BBIN, and GPOI. Results for CHAO2 are not reported; they were almost indistinguishable from CHAO1 results. The jackknifed estimates were a mixture of first- (23%), second- (53%) and third- ($\sim 21\%$), and fourth-order (3%) generalized estimates.

The ranking of several estimators in terms of absolute bias varied with sample size. In WGHAT the BBIN estimator was best for $n \leq 15$ whereas CHAO3 was best for $n \geq 20$. The GPOI estimator consistently ranked second or third. The performance of CHAO1 improved with increased sample size. In BCI the estimator with the lowest average bias was CHAO3 for sample fractions below 3%, and CHAO1 when 3% to 5% of the area is sampled. At higher sample fractions GPOI or JKk were best.

[TABLES 1 AND 2 HERE]

Precision

Estimates of standard error of the richness estimates are in Tables 1 and 2. For one group of estimators (OBS, BOOT, and MPOI) the estimated error was 8% or less across all designs and sites. Richness estimates from JKk, CHAO3, and BBIN had the highest estimates of standard error. PET, CHAO1, MBIN, and GPOI produced site- and sample size dependent estimates of error.

Estimates of error should, ideally, match the actual error observed in repeated sampling. For PET the estimates of error were conservative (at least 25% too large) whereas estimates from BOOT, JKk, and GPOI appear liberal (estimated errors are at least 25% too small). Only error estimates from OBS and CHAO1 were within 25% of the empirical error observed in repeated sampling. The reliability of error estimates from CHAO3, BBIN, MBIN, and MPOI appears to depend on either site, sample size or both.

The proposed estimator of error for the observed richness appears attractive. In contrast, an error estimate based on the assumption of a Poisson distribution of the number of observed species would underestimate the empirical error by at least 70%.

Accuracy

Mean absolute differences between the estimated and the actual tree species richness (*Mad*, Tables 3 and 4) mirrored, by and large, the results on (absolute) bias. Again, the lowest values of *Mad* were obtained with GPOI and CHAO3 in WGHAT and with GPOI, CHAO1, and JKk in BCI. Least performing on both sites were OBS, BOOT and MPOI. A fluctuating performance was noted for CHAO1 in WGHAT and CHAO3 in BCI. The performance of BBIN is best described as erratic. At comparable fractions of the area sampled *Mad* in WGHAT was about two and a half to three times higher than in BCI, a difference attributed, as before, to the difference in the number of sample trees.

[TABLES 3 AND 4 HERE]

The proportion of the richness estimates that were within 10% of the true value varied among estimators, site, and sample design (Tables 3 and 4). If one wish to see 80% of the estimates within these limits, then no combination of estimator and design could meet this standard in WGHAT. In BCI, however, a combination of 156 m² plots, a sample size greater than 120, and the CHAO1 estimator would. For GPOI, PET, and JKk the sample size would need to be about three times larger in order to reach the same standard.

Estimated 95% confidence intervals failed in most cases to include the true richness (Tables 3 and 4). A coverage rate better than 75% was only reached by four estimators (CHAO1 and CHAO3 for $n \geq 25$, BBIN for $n \leq 15$, and GPOI for $n \leq 20$) in WGHAT, and by three in BCI (CHAO1 for $n = 140$ and plot-size 156 m², CHAO3 for $n < 100$, and GPOI for $n > 120$).

Overall performance ranking

By combining three statistics of accuracy, and the proportion of area sampled into a single indicator of performance we obtained the estimator ranking in Table 5. The

ranking of nine estimators was very similar across the two sites; the one exception was for BBIN. GPOI was top-ranked, while second and third place was taken by CHAO1 and JKk. Bottom ranks were given to MPOI and OBS.

[TABLE 5 HERE]

Plot effects

A larger plot contains, on average, more species than a smaller plot but the increase will be less than suggested by the ratio of areas unless the tree species are distributed completely at random throughout the study area. This plot-size effect modifies the probability of finding a species in a plot, the vector of observed incidences, and consequently, the estimate of richness. Plot effects were expected to diminish with increasing sample size. In BCI the average number of species in a 156 m² plot was 30 (± 7). A plot of 400 m² contained on average 50 (± 15) and a 625 m² plot 65 (± 10). Hence, the increase in the number of species was only 64% viz. 54% of the increase expected under complete spatial randomness of species specific tree locations. Similarly, estimates of the probability of finding a species in a 400 m² plot was as rule less than expected from a direct binomial scaling of the probabilities for a 156 m² plot (Figure 5). From the difference between the two probabilities we derived an estimate of the intra-plot species correlation (clustering) of 0.14 for the 156 m² plot. For 400 m² plots this correlation was close to zero.

[FIGURE 5 HERE]

The number of species found in just one or two plots has a disproportionate effect on most estimates of species richness. Their numbers declined, as expected, with plot-size and sample size (Figure 6). Compared to a 400 m² plot there was an addition of about seven species that would have been observed only once in sampling with 156 m² plots. The corresponding difference for 625 and 400 m² plots declined from about four at $n = 30$ to almost zero at $n = 140$. Trends in the number of species seen only in two plots were somewhat similar for $n > 30$ but otherwise less pronounced. However, when the numbers of species found in one or two plots are plotted against the fraction of area sampled (Figure 6) they appear to fall on a single line which suggests that the plot effect, if it exists, must be similar in both cases. A T^2 -test suggest that the effect is not significant at the 5% level of significance).

[FIGURE 6 HERE]

Plot effects also depend on the estimator. With BBIN and GPOI the expected reduction in bias with an increase in plot size did not materialize. A significant reduction in bias of about 10% ($P < 0.001$) could be achieved with OBS, PET, BOOT, and MPOI by increasing plot size from 156 m² to 400 m². A further increase to 625 m² had only a smaller (5%) effect (only significant for BOOT estimates). Figure 7 illustrates typical plot effects for three of the four estimators with a significant plot effect. Yet, when estimates of richness were plotted against the fraction of area sampled they appear to fall on a single line which suggests that plot effects are weak or non-existing.

[FIGURE 7 HERE]

DISCUSSION

Estimating the number of tree species in a forest community is a first step towards quantifying an important component of forest biodiversity. The statistical estimation problem and choice of estimator remains a challenge (Walther and Moore 2005). As we saw, estimators differ widely in their estimates and their differences depend on the forest community and on sample design. To paraphrase Bunge and Fitzpatrick (1993): “the problem is quite resistant to a statistical solution, essentially because no matter how many species have been observed one cannot refute the possibility of a large number of rare species”. Link (2003) states it this way: “... even with very large samples, the analysts will not be able to distinguish among reasonable models of heterogeneity, even though these yield quite distinct inferences about the number of species...”. Stark differences between estimates from related and similar models (e.g. GPOI, MPOI, BBIN, and MBIN) mirror this statement. Nayak (1996) and Starr (1979) call the problem ‘non-standard’ due to the dependency of the estimate on the unknown parameter and the data. A negative correlation between the estimate and the true value is another statistical anomaly (Starr 1979). Mao and Colwell (2005) recently demonstrated the essence of the estimation challenge: An artificial enriching of real data sets with a few individuals representing rare species significantly changed estimates of richness and their confidence intervals. O’Hara (2005) echoes these observations.

Since our study sites had many rare and just a few common tree species we cannot *a priori* expect to obtain very good estimates of tree species richness from a forest inventory. Without a universally best estimator of richness the choice must be based on

expected performance. We adopted a somewhat conservative approach to gauge the performance of richness estimators by combining three statistics of accuracy and sample size into an index of loss. These statistics are suggestive only, not ultimate judgments (Walter and Moore 2005). Our assumption that an inflated estimate of richness is harmful to credibility (Schreuder, Williams, and Reich 1999) is, of course, arguable. Both inflated and deflated estimates of tree species richness can lead to complacency in the management and protection of forest tree species diversity, albeit for very different reasons.

Palmer (1990, 1991) confirmed high rates of positive bias in JK1 (26%) and JK2 (70%) in a mixed hardwood stand in the Duke Forest in North Carolina (U.S.A.). As in our study, the bootstrap estimator did not produce any positive bias. Hellmann and Fowler (1999) assessed JK1, JK2, and BOOT in five different forest communities in Michigan. Their results are in many ways parallel to ours. While JK1 and JK2 consistently outperformed BOOT in terms of bias the high variability of their estimates and especially those of JK2 generated non-trivial rates of overestimation. Schreuder, Williams, and Reich (1999) also assessed the three CHAO estimators. No positive bias was reported for sample sizes of 20 to 700 in eleven populations representing two states (Missouri and Minnesota) and an assembly of Loblolly pine plantations in the south-eastern United States. In their study CHAO3 was at par with CHAO1 viz. CHAO2, in contrast to the large differences reported here. We surmise that differences in the ratio f_1 / f_2 and its distribution are the cause for these discrepancies. In tree species rich wet tropical forests (He and Hubbell 2003, Pascal and Pélissier 1996) the ratio f_1 / f_2 is not only much higher but also more variable than in sub-tropical and temperate forests (Liermann, Steel, Rosing et al. 2004).

We only studied incidence-based estimators in our assessment. Estimators based on extrapolation of either species-area curves or species accumulation curves have a long history in applied ecology (Engen, 1978) but have increasingly been criticized for the lack of a sample-based framework (Bunge and Fitzpatrick 1993). A species accumulation curve derived from a conventional forest inventory will, in most cases, not lend itself to extrapolation. Krishnamani, Kumar, and Harte (2004), however, obtained a surprisingly realistic estimate of 893 for the number of tree species in the Western Ghats of India from just 48 conventional inventory sample plots. A strong relationship between plot similarities (absence/presence of a species) and inter-plot distances was exploited. Cao, Larsen and White (2004) also used estimators based on plot dissimilarities for estimating bird and fish species richness in two regions of the United States of America and found

them to perform reasonably well. Condit, Hubbell, Lafrankie et al. (1996), however, found that the relationship between dissimilarity and distance to vary across a population.

Our study reiterated the importance of choosing a richness estimator and a sample design (Brose, Martinez, and Williams 2003, Bunge and Fitzpatrick 1993, Colwell, Mao, and Chang 2004, Gimaret-Carpentier, Pélissier, Pascal et al. 1998, Keating, Quinn, Ivie et al. 1998). Estimators based on a mixture of truncated distributions of the probability of species incidence do not seem to justify the added computational burden and complexity of estimation (Lindsay and Roeder 1992, Mao and Colwell 2005). At least not if the sole purpose is for an estimation of tree species richness. The promising performance of GPOI needs corroboration by additional studies since it has not previously been used for the purpose of estimating tree species richness, nor has it been widely used elsewhere. The runner-up CHAO1 (Bunge and Fitzpatrick 1993, Bunge, Fitzpatrick, and Handley 1995, Keating, Quinn, Ivie et al. 1998, Lee S.-M. and Chao 1994, Walther and Martin 2001) has a solid track record which should make it the estimator of choice until further studies corroborate our GPOI results. Petersen's estimator might be favoured by agencies opposed to any risk of an inflated estimate.

Forest inventories are generally conducted with fixed-area plots. Plot-size and shape is generally determined by considerations of cost, logistics, and statistical efficiency. It appears that for small to moderate sample sizes the sampling variation in GPOI and CHAO1 estimates of tree species richness swamps the importance of plot-size and shape (Schreuder, Williams, and Reich 1999, Schreuder, Lin, and Teply 2000). Plot-size effects are otherwise manifest due to a clustering of tree species (Condit, Hubbell, Lafrankie et al. 1996), especially if a fixed number of trees are selected at each sample location (Gimaret-Carpentier, Pélissier, Pascal et al. 1998).

CONCLUSIONS

In tree species rich forests, with many rare, a few common species, and a weak spatial clustering of tree species at small spatial scales, a conventional forest inventory with fixed-area plots can produce reasonable incidence-based estimates of tree species richness when the estimator is carefully chosen. A gamma-Poisson estimator appears most promising but until corroborated by other studies Chao's 1981 estimator is recommended.

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TABLE 1. Relative bias in estimates of tree species richness for WGHAT. Actual and average of estimated relative sampling errors are in parentheses (Actual/Estimated). Table entries are in % of the true tree species richness of 93.

	Sample size (% Area sampled)				
	10 (3.2)	15 (4.8)	20 (6.4)	25 (8.0)	30 (9.6)
OBS	-75 (4/4)	-69 (4/4)	-64 (4/4)	-60 (4/4)	-56 (4/4)
PET	-46 (4/11)	-38 (4/11)	-34 (4/10)	-29 (3/9)	-25 (3/9)
BOOT	-69 (5/3)	-62 (4/3)	-57 (4/3)	-52 (3/3)	-48 (3/3)
JKk	-49 (19/11)	-39 (20/12)	-32 (22/13)	-25 (25/14)	-20 (24/14)
CHAO1	-47 (18/17)	-36 (18/18)	-28 (17/19)	-20 (17/20)	-12 (17/21)
CHAO3	-28 (39/71)	-21 (34/70)	-15 (31/64)	-6 (35/57)	-2 (32/62)
BBIN	-2 (32/25)	10 (26/20)	20 (24/20)	34 (23/22)	45 (23/24)
MBIN	-53 (16/24)	-42 (13/36)	-40 (13/29)	-38 (13/21)	-34 (12/18)
GPOI	-10 (38/26)	-13 (23/19)	-16 (17/16)	-17 (14/14)	-18 (12/12)
MPOI	-70 (5/6)	-63 (5/6)	-57 (5/5)	-53 (5/4)	-50 (5/4)

TABLE 2. Relative bias of estimates of tree species richness for BCI. Actual and average of estimated relative sampling errors are in parentheses (Actual/Estimated). Table entries are in % of true tree species richness of 301.

	Plot area in m ²	% Area Sampled	OBS	PET	BOOT	JKk	CHAO1	CHAO3	BBIN	MBIN	GPOI	MPOI
40	156	1.2	-43 (2/2)	-27 (1/3)	-36 (3/2)	-20 (14/7)	-21 (6/6)	-4 (14/10)	87 (15/15)	-31 (14/9)	4 (19/7)	-35 (5/7)
60	156	1.9	-37 (2/1)	-23 (1/2)	-31 (2/2)	-17 (13/7)	-15 (5/6)	1 (13/9)	101 (16/16)	-31 (6/6)	10 (18/7)	-31 (5/6)
80	156	2.5	-34 (2/1)	-21 (1/2)	-28 (2/1)	-14 (16/8)	-12 (5/6)	5 (13/9)	101 (8/14)	-27 (5/7)	9 (15/6)	-28 (3/5)
100	156	3.1	-31 (1/1)	-19 (1/2)	-26 (2/1)	-15 (6/5)	-10 (4/6)	8 (12/9)	100 (9/15)	-21 (6/13)	10 (12/6)	-28 (2/5)
120	156	3.8	-29 (1/1)	-17 (1/2)	-24 (2/1)	-9 (22/9)	-8 (4/6)	12 (14/10)	107 (11/13)	-21 (5/8)	10 (10/6)	-26 (2/4)
140	156	4.4	-27 (1/1)	-16 (1/2)	-22 (2/1)	-7 (21/9)	-6 (4/6)	16 (16/10)	120 (37/34)	-12 (8/30)	11 (9/5)	-24 (2/5)
40	400	3.2	-32 (2/2)	-19 (1/3)	-26 (2/2)	-15 (10/6)	-18 (4/4)	6 (14/9)	76 (10/13)	-26 (6/3)	-11 (7/4)	-26 (4/6)
60	400	4.8	-27 (2/1)	-16 (1/2)	-22 (2/2)	-10 (18/8)	-14 (3/4)	10 (14/9)	79 (8/10)	-22 (5/4)	-9 (5/4)	-23 (3/5)
80	400	6.4	-24 (2/1)	-14 (1/2)	-19 (2/1)	-12 (6/5)	-12 (4/4)	13 (14/9)	90 (10/12)	-17 (5/8)	-7 (6/4)	-20 (2/5)
100	400	8.0	-22 (2/1)	-13 (1/2)	-18 (2/1)	-11 (6/4)	-10 (4/4)	15 (14/9)	92 (5/13)	-15 (6/6)	-6 (6/3)	-19 (2/5)
120	400	9.6	-20 (2/1)	-11 (1/2)	-16 (2/1)	-8 (13/6)	-9 (4/3)	19 (16/9)	92 (7/7)	-13 (6/5)	-5 (6/3)	-18 (2/5)
140	400	11.2	-19 (2/1)	-10 (1/2)	-15 (2/1)	-6 (8/5)	-7 (4/4)	20 (15/11)	31 (20/2)	-13 (6/9)	-3 (6/3)	-17 (2/5)
40	625	5.0	-27 (2/1)	-16 (1/2)	-22 (2/2)	-11 (13/7)	-16 (3/3)	12 (14/9)	63 (6/10)	-20 (7/5)	-13 (4/3)	-23 (3/6)
60	625	7.5	-22 (2/1)	-13 (1/2)	-18 (2/1)	-10 (6/5)	-12 (3/3)	18 (15/10)	80 (7/12)	-15 (6/4)	-9 (4/3)	-19 (2/6)
80	625	10.0	-20 (1/1)	-10 (1/2)	-16 (2/1)	-5 (13/7)	-10 (3/3)	21 (14/11)	73 (6/10)	-13 (6/6)	-7 (3/3)	-16 (3/5)
100	625	12.5	-18 (1/1)	-9 (1/2)	-14 (2/1)	-4 (11/6)	-8 (3/3)	24 (13/12)	77 (13/8)	-10 (6/6)	-5 (4/3)	-16 (2/5)
120	625	15.0	-16 (1/1)	-8 (1/1)	-12 (1/1)	-4 (5/5)	-6 (2/3)	27 (12/11)	43 (24/3)	-9 (6/11)	-3 (3/3)	-14 (2/5)
140	625	17.5	-15 (1/1)	-7 (1/1)	-11 (1/1)	-3 (7/5)	-5 (2/3)	27 (12/12)	35 (24/2)	-7 (6/13)	-2 (3/3)	-13 (2/5)

TABLE 3. Relative mean absolute error of tree species richness estimates for WGHAT. Per cent of estimates within 10% of true value (δ_{10}) and coverage rates of estimated confidence intervals (p_{CI}) are in parentheses (δ_{10} / p_{CI}).

	Sample size (% Area sampled)				
	10 (3.2)	15 (4.8)	20 (6.4)	25 (8.0)	30 (9.6)
OBS	75 (0/0)	69 (0/0)	64 (0/0)	60 (0/0)	56 (0/0)
PET	46 (2/15)	38 (3/21)	34 (3/21)	29 (5/28)	25 (8/34)
BOOT	69 (0/0)	62 (0/0)	57 (0/0)	52 (0/0)	48 (0/0)
JKk	50 (4/15)	41 (5/21)	36 (8/28)	31 (11/37)	27 (16/46)
CHAO1	47 (4/28)	37 (5/43)	29 (12/58)	22 (21/76)	17 (33/86)
CHAO3	42 (8/59)	34 (12/67)	28 (18/73)	27 (19/79)	25 (23/85)
BBIN	24 (28/78)	21 (35/79)	24 (29/63)	34 (15/36)	45 (4/13)
MBIN	56 (2/14)	53 (2/18)	47 (2/11)	41 (2/9)	37 (4/10)
GPOI	31 (23/76)	21 (28/80)	20 (26/78)	19 (27/72)	19 (24/70)
MPOI	70 (0/0)	63 (0/0)	57 (0/0)	53 (0/0)	50 (0/0)

TABLE 4. Relative mean absolute error of tree species richness estimates for BCI (in per cent of 301). Per cent of estimates within 10% of true value (δ_{10}) and coverage rates of estimated 95% confidence intervals (p_{CI}) are in parentheses (δ_{10} / p_{CI}).

n	Plot area in m ²	% Area Sampled	OBS	PET	BOOT	JKk	CHAO1	CHAO3	BBIN	MBIN	GPOI	MPOI
40	156	1.2	43 (0/0)	27 (0/0)	36 (0/0)	23 (11/19)	21 (3/12)	12 (48/76)	86 (0/0)	32 (4/4)	15 (48/60)	36 (0/0)
60	156	1.9	37 (0/0)	23 (0/0)	31 (0/0)	20 (10/16)	15 (16/32)	11 (52/84)	100 (0/0)	31 (2/0)	15 (46/56)	32 (0/0)
80	156	2.5	34 (0/0)	21 (0/0)	28 (0/0)	19 (12/20)	12 (31/47)	11 (62/84)	101 (0/0)	27 (6/6)	13 (47/60)	28 (0/0)
100	156	3.1	31 (0/0)	19 (0/0)	26 (0/0)	16 (12/18)	10 (54/66)	12 (49/88)	100 (0/0)	23 (6/6)	12 (54/58)	28 (0/0)
120	156	3.8	29 (0/0)	17 (0/0)	24 (0/0)	16 (27/27)	8 (72/74)	14 (51/74)	107 (0/0)	21 (14/12)	11 (52/57)	26 (0/0)
140	156	4.4	27 (0/0)	16 (1/0)	22 (0/0)	16 (30/41)	6 (86/90)	17 (34/66)	120 (0/0)	20 (14/12)	12 (45/50)	24 (0/1)
40	400	3.2	32 (0/0)	19 (0/0)	26 (0/0)	16 (15/24)	18 (4/3)	12 (54/81)	77 (0/0)	26 (0/2)	12 (37/32)	26 (0/0)
60	400	4.8	27 (0/0)	16 (2/0)	22 (0/0)	16 (19/27)	14 (12/3)	14 (42/72)	79 (0/0)	22 (0/0)	10 (62/34)	23 (0/0)
80	400	6.4	24 (0/0)	14 (6/0)	19 (0/0)	13 (33/33)	12 (32/19)	15 (42/64)	90 (0/0)	17 (12/12)	8 (64/46)	20 (0/0)
100	400	8.0	22 (0/0)	13 (16/0)	18 (0/0)	11 (36/34)	10 (49/20)	16 (38/62)	93 (0/0)	14 (24/24)	7 (72/49)	19 (0/0)
120	400	9.6	20 (0/0)	11 (29/1)	16 (0/0)	11 (48/50)	9 (60/38)	20 (34/48)	92 (0/0)	13 (36/36)	7 (74/57)	18 (0/0)
140	400	11.2	19 (0/0)	10 (45/1)	15 (2/0)	9 (57/51)	7 (76/50)	20 (32/46)	30 (10/0)	15 (18/18)	5 (88/64)	17 (0/0)
40	625	5.0	27 (0/0)	16 (1/0)	22 (0/0)	14 (26/35)	16 (3/1)	14 (47/73)	63 (0/0)	20 (2/2)	13 (26/16)	23 (0/0)
60	625	7.5	22 (0/0)	13 (11/0)	18 (0/0)	11 (42/40)	12 (25/4)	18 (39/57)	80 (0/0)	15 (6/6)	9 (57/32)	19 (0/0)
80	625	10.0	20 (0/0)	11 (29/0)	16 (0/0)	10 (52/48)	10 (54/14)	20 (22/55)	73 (0/0)	13 (22/22)	7 (85/44)	16 (2/2)
100	625	12.5	18 (0/0)	9 (57/0)	14 (2/0)	8 (72/62)	8 (79/33)	25 (10/42)	77 (0/0)	11 (36/38)	5 (91/60)	16 (3/3)
120	625	15.0	16 (0/0)	8 (80/2)	12 (6/0)	6 (91/72)	6 (94/52)	25 (14/32)	43 (0/0)	13 (29/29)	4 (98/82)	14 (6/6)
140	625	17.5	15 (0/0)	7 (94/4)	11 (24/0)	6 (85/63)	5 (100/67)	26 (11/30)	35 (0/0)	13 (18/28)	4 (100/84)	13 (3/4)

TABLE 5. Relative loss function scores (normalized to interval $[0;1]$) and rankings of tree species richness estimators (1 = best, 10 = worst). See EQ 7 and text for details on loss function.

	WGHAT		BCI		Overall Rank
	Rel. loss	Rank	Rel. loss	Rank	
OBS	1.00	10	0.54	9	10
PET	0.59	6	0.34	5	5
BOOT	0.95	8	0.49	7	8
JKk	0.52	5	0.13	2	4
CHAO1	0.20	3	0.14	3	2
CHAO3	0.12	2	0.25	4	3
BBIN	0.28	4	1.00	10	7
MBIN	0.78	7	0.37	6	6
GPOI	0.00	1	0.00	1	1
MPOI	0.96	9	0.50	8	9

FIGURE 1. Relative number of WGHAT tree species ($S\%$) versus relative incidence in plots of 100 m^2 .

FIGURE 2. Histogram of number of WGHAT tree species (S) in 100 m^2 plots.

FIGURE 3. Relative number of BCI tree species ($S\%$) versus relative incidence in plots of 156 m^2 .

FIGURE 4. Histogram of number of BCI tree species (S) in a 156 m^2 plot.

FIGURE 5. Left: Probability of finding a tree species in a 400 m^2 plot (p_{400}) plotted against the probability of finding it in a 156 m^2 plot (p_{156}). Estimates from data are in black and estimates obtained by a binomial scaling of results from 156 m^2 plots are in gray. Right: Corresponding estimates for the 625 m^2 versus 400 m^2 plots.

FIGURE 6. Frequencies of tree species found in only one plot (f_1) and two plots (f_2) versus sample size viz. proportion of area sampled (%Area). Plot size: 156 m^2 (black), 400 m^2 (medium gray), and 625 m^2 (light gray). The interval of plus/minus one standard error of an estimate is indicated by a vertical line.

FIGURE 7. Estimates of tree species richness versus sample size (left column) and proportion of area sampled (%Area). Plot size: 156 m^2 (black), 400 m^2 (medium gray), and 625 m^2 (light gray). The interval of plus/minus one standard error of an estimate is indicated by a vertical line.

FIGURE 1.

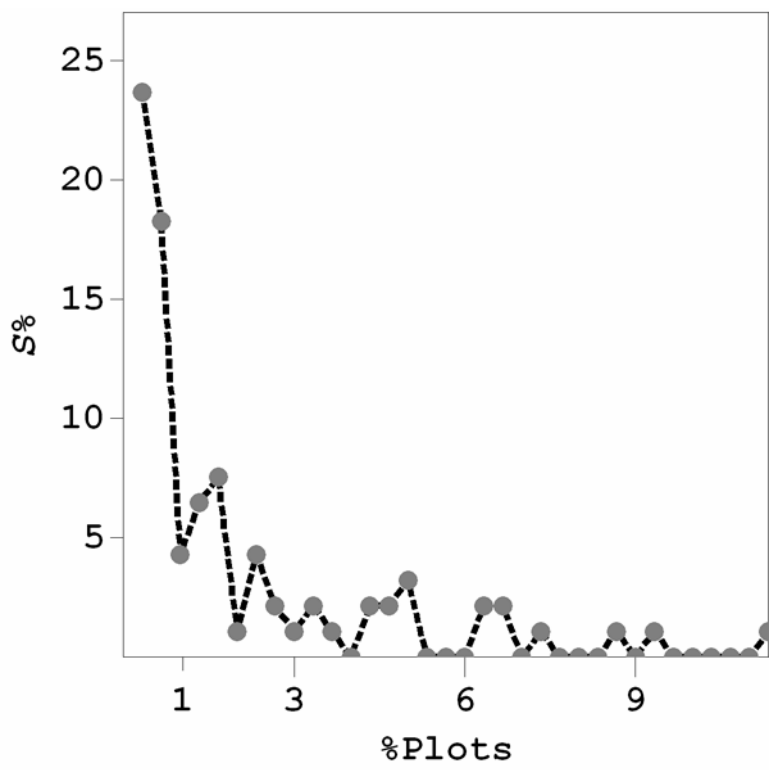


FIGURE 2.

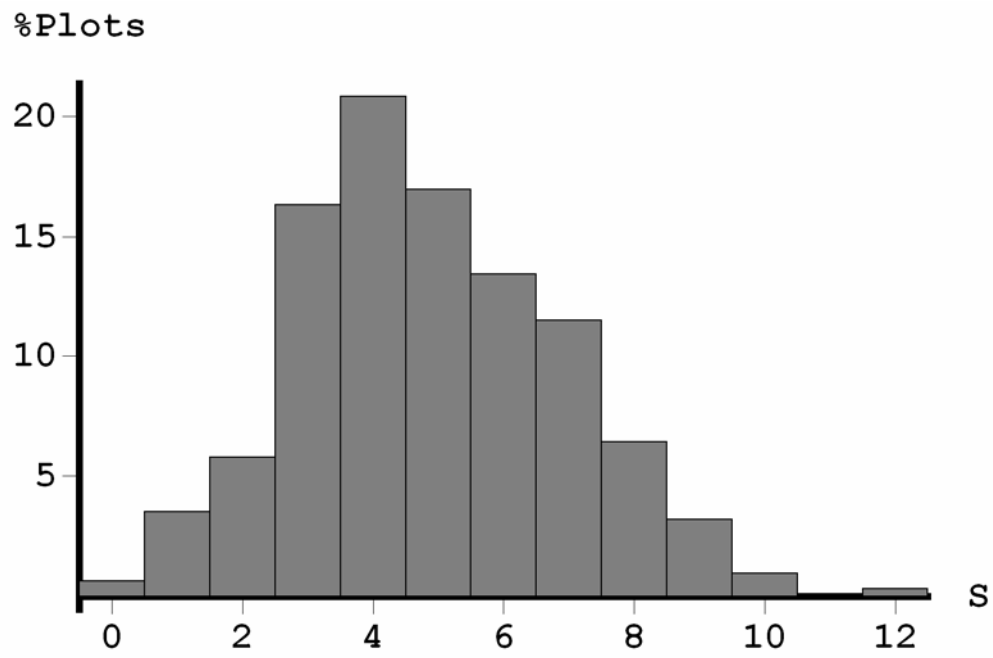


FIGURE 3.

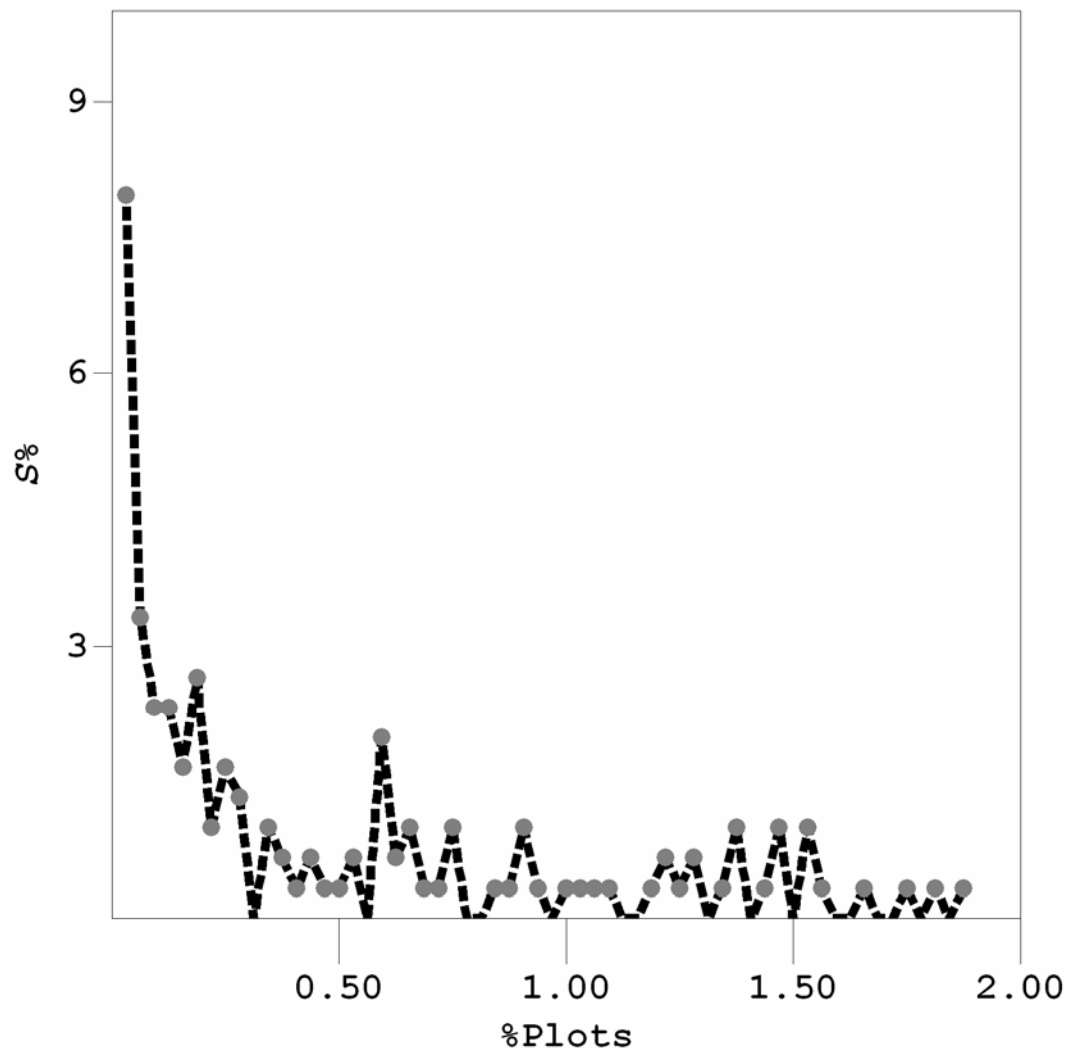


FIGURE 4.

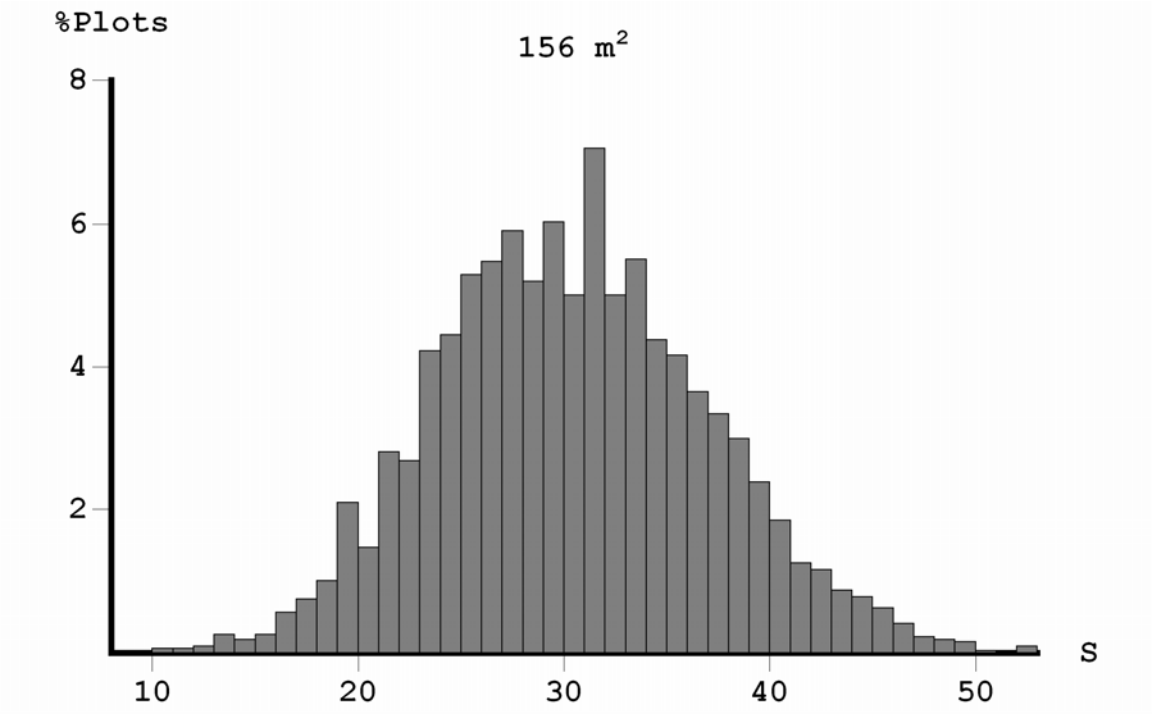


FIGURE 5

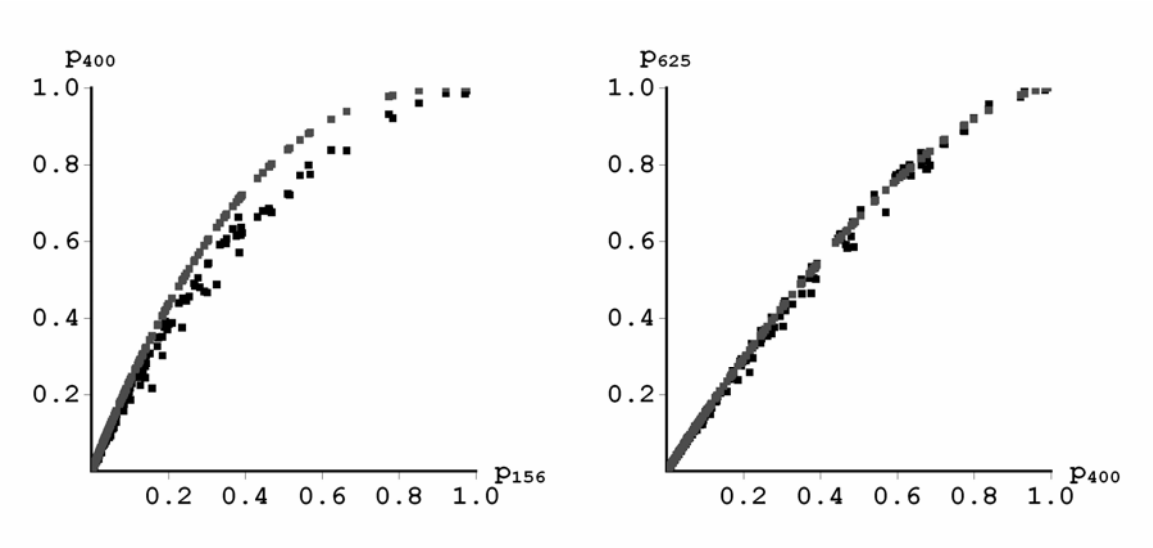


FIGURE 6.

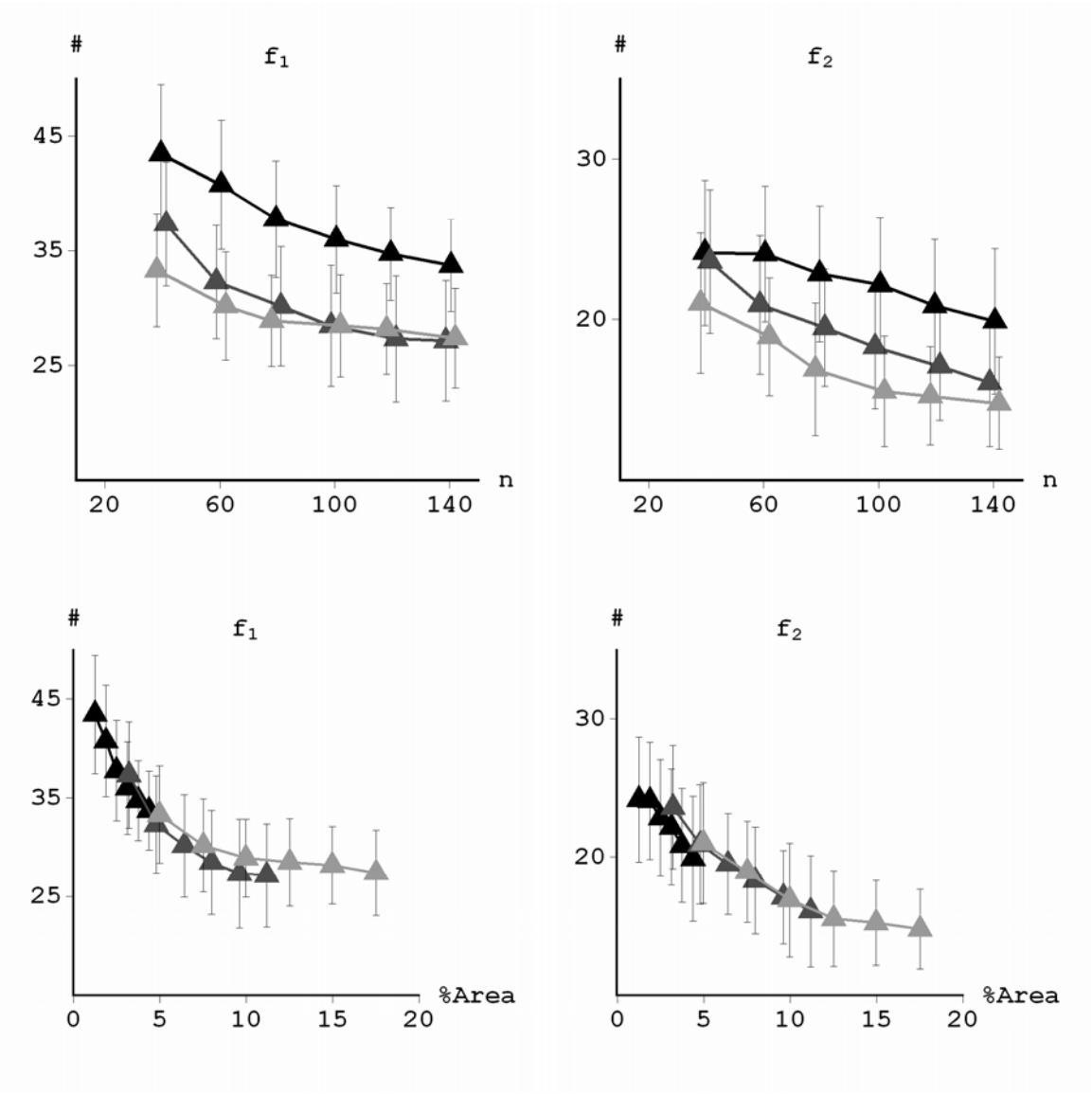


FIGURE 7.

