

ESTIMATING SPECIES RICHNESS: SENSITIVITY TO SAMPLE COVERAGE AND INSENSITIVITY TO SPATIAL PATTERNS

ULRICH BROSE,¹ NEO D. MARTINEZ, AND RICHARD J. WILLIAMS

Romberg Tiburon Center, Department of Biology, San Francisco State University, 3152 Paradise Drive, Tiburon, California 94920 USA

Abstract. The number of species in an area is critical to the development of evolutionary and ecological theory from mass extinctions to island biogeography. Still, the factors influencing the accuracy of estimators of species richness are poorly understood. We explored these factors by simulating landscapes that varied in species richness, relative abundances, and the spatial distribution. We compared the extrapolations of nine nonparametric estimators and two species accumulation curves under three sampling intensities. Community evenness of species' abundances, sampling intensity, and the level of true species richness significantly influenced bias, precision, and accuracy of the estimations. Perhaps most surprisingly, the effects of gradient strength and spatial autocorrelation type were generally insignificant. The nonparametric estimators were substantially less biased and more precise than the species accumulation curves. Observed species richness was most biased. Community evenness, sampling intensity, and the level of true species richness influenced the performance of the nonparametric estimators indirectly via the fraction of all species found in a sample or "sample coverage." For each particular level of sample coverage, a single estimator was most accurate. Choice of estimator is confounded by a priori uncertainty about the sample coverage. Accordingly, researchers can extrapolate species richness by various estimators and base the estimator choice on the mean estimated sample coverage. Alternatively, the most reliable estimator with respect to community evenness can be chosen. These predictions from our simulations are confirmed in two field studies.

Key words: biodiversity; estimations; extrapolations; gradients; jackknife estimators; nonparametric estimators; relative abundance distribution; sample coverage; spatial autocorrelation; species accumulation curves.

INTRODUCTION

Studies of biodiversity initiated the study of evolution and have continued to become more centrally important to ecology (Gaston 1996). However, the measurement of biodiversity has been surrounded by a considerable debate (Peet 1974, May 1975, Pielou 1975, Magurran 1988, Colwell and Coddington 1994, Gaston 1996, Gotelli and Colwell 2001, Petchey and Gaston 2002). Historically, diversity has been measured by a bewildering range of diversity indices that often consist of two components: the number of species and the relative evenness of their abundances (Magurran 1988). Both the compound character and the variety of different indices make comparisons across studies difficult. More recently, both components have generally been measured separately, and much emphasis has been put on species richness (Colwell and Coddington 1994, Gaston 1996), which continues to be the most frequent measure of biodiversity. Earlier, Whittaker (1972) proposed α diversity to be within-habitat species richness, β diversity between-habitats species turnover, and γ

diversity landscape species richness. Measurements of β diversity or "complementarity" have subsequently been treated separately from species richness (Magurran 1988, Colwell and Coddington 1994, Colwell 1997, Harte et al. 1999). In contrast to this, the separation of α and γ diversity has been modified into a concept of species richness on a continuous scale from local to global (e.g., Ricklefs and Schluter 1993), and the methodology of measuring local or global species richness is not considered to be qualitatively different (Colwell and Coddington 1994, Gaston 1996). This concept of species richness is currently the most basic and often used parameter, not only in biodiversity studies but also in community and trophic ecology (Gaston 1996, Martinez et al. 1999, Williams and Martinez 2000). Despite the centrality of species richness, many difficulties regarding its measurement are not well understood nor agreed upon. In most empirical studies, the observed number of species, S_{obs} , is used as a surrogate for the true number of species, S_{true} . Still, S_{obs} typically excludes many rare species and seriously underestimates S_{true} (Palmer 1990, Baltanás 1992, Colwell and Coddington 1994, Martinez et al. 1999). This bias increases with increasing S_{true} and decreases with mean species detectability, which frequently invalidates hypothesis testing (Palmer 1990, Boulinier et al. 1998). A large

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¹ E-mail: brose@sfsu.edu

number of extrapolation methods have been developed to reduce this bias (reviews in Bunge and Fitzpatrick 1993, Soberón and Llorente 1993, Colwell and Coddington 1994, Colwell 1997), but their performance has been compared in only few studies (Palmer 1990, 1991, Baltanás 1992, Colwell and Coddington 1994, Walther and Morand 1998, Longino et al. 2002). Most of these methods can be classified as either species accumulation curves or nonparametric estimators. Although generally less biased, the nonparametric estimators are seldom used in biodiversity studies, where species accumulation curves are preferred (e.g., Chazdon et al. 1999).

Species accumulation curves extrapolate species richness vs. sample size data to an asymptote of total richness (Soberón and Llorente 1993, Colwell and Coddington 1994). The most often used species accumulation curves are the exponential equation (Holdridge et al. 1971) and the Michaelis-Menten model (Michaelis and Menten 1913). Their performance varies with the underlying relative abundance distributions (Keating and Quinn 1998), spatial aggregation of species (Baltanás 1992) and habitat heterogeneity (Colwell and Coddington 1994, Lande et al. 2000).

Nonparametric estimators are sampling theoretic extrapolation methods that only require the number of samples in which each species is found rather than any parametric information about their abundance. They were originally developed to estimate population sizes with capture–recapture data in closed populations (Otis et al. 1978, Burnham and Overton 1979). The technique can be adapted to estimate species richness by substituting recaptures of species in different samples for recaptures of individuals of the same species in time between mark and recapture. The underlying models assume species-specific detection probabilities that follow an arbitrary distribution (e.g., model M_h , Otis et al. 1978), which relaxes the implicit assumption of equal detection probabilities made when using S_{obs} (Boulinier et al. 1998). However, the distribution of capture probabilities among individuals in a species' population is likely to be more even than the distribution of detection probabilities among species with strong variations in their abundances. This could restrict legitimate use of the estimators to communities with highly even relative abundance distributions. Furthermore, the estimators that are based on model M_h have a second assumption: that the species-specific detection probabilities are constant for all sampling units, which assumes spatially homogeneous species distributions. This assumption is violated in almost every type of community due to environmental gradients and spatial autocorrelation (Legendre 1993).

In this study, we examine the sensitivity of different estimators' bias and accuracy to abundance distributions, strength of environmental gradients, spatial autocorrelation, the level of S_{true} and sampling intensity

in simulated landscapes. The predictions of the sensitivity analyses are tested in two field studies.

METHODS

Simulations

Rectangular communities were simulated using lattices of 100 by 50 cells (x, y), each representing 1 m². S_{true} is the number of species present in these simulated landscapes and S_{obs} is the number of species found in samples taken from these landscapes. The landscapes contained communities that systematically differed due to S_{true} , relative abundance, spatial gradients, and spatial autocorrelation. The combination of seven levels of S_{true} (25, 50, 100, 150, 200, 250, and 500 species), three relative abundance models, three gradient strengths, and three types of spatial autocorrelation resulted in a total of 189 different types of communities. Monte Carlo simulations with 100 replicates for each community type were repeated for three sampling intensities, yielding a total of 56 700 simulated landscapes.

In each landscape, the abundance of each species, which also equals the number of cells occupied, was derived from relative abundance distributions possessing an average of 200 individuals per species. We then independently assigned each species i a probability of occurrence $p_i(x, y)$ in every cell (x, y) of the lattice. These $p_i(x, y)$ depend on the respective species-specific probability functions of the gradients and the spatial autocorrelation: $p_i(x, y) = p_{i,grad}(x) + p_{i,auto}(x, y)$ such that all individuals of a species are subjected to the same spatial distribution of probabilities but the distribution may be different for each species. For each species the individuals were placed on the lattice according to $p_i(x, y)$. First, the cells were ranked according to their p_i . Second, a number was sampled from a normal distribution with a mean of zero, and a standard deviation equal to the number of empty cells divided by two, and the chosen number was converted to a rank equal to the absolute value of the number. Third, an individual was assigned to the cell with the chosen rank and that cell was no longer available for occupation by an individual of the same species. The second and third steps were repeated until the number of cells occupied equalled the species' abundance. This procedure was repeated for all remaining species.

We estimated species richness under three intensities of sampling from the 5000-cell communities: low (25 cells), intermediate (200 cells), and high intensity (500 cells). We applied 12 estimators of species richness to each sample: nine nonparametric estimators, two species accumulation curves, and S_{obs} . The performance of these estimators was compared concerning bias, precision, and accuracy.

Relative abundance distributions

We used three stochastic relative abundance models: the broken-stick, random-fraction, and random assort-

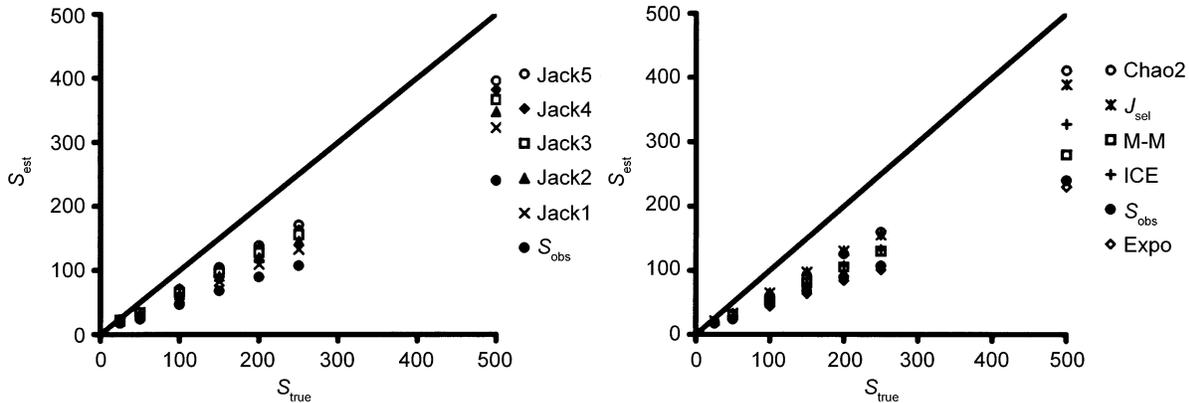


FIG. 1. Mean estimated species richness, S_{est} , plotted against S_{true} . The solid line indicates an idealized unbiased estimator with $S_{\text{est}} = S_{\text{true}}$. Regression details are given in Table 1. Key to abbreviations: $J_{\text{sel}} = \text{Jack}_{\text{sel}}$; M-M = Michaelis-Menten model; Expo = Exponential equation.

ment models. Stochastic models generate much more variable individual communities than deterministic models do. We chose the stochastic models because they represent more accurately natural communities that are simultaneously influenced by various factors, and they estimate the relative abundances of rare species more precisely. This allows stochastic models to encompass a broad range of community types (Nee et al. 1991, Tokeshi 1993, Naeem and Hawkins 1994).

The broken-stick model represents a rarely observed, extremely even community with low sequential dominance and few rare species. The relative abundance of S_{true} species is determined by placing $S_{\text{true}} - 1$ points randomly on a line of unit length. Breaking the line at those points yields S_{true} segments whose lengths represent the relative abundances of S_{true} species (MacArthur 1957). Broken-stick abundance distributions characterize some of the most even natural communities observed (Tokeshi 1993). The random-fraction model yields comparatively uneven communities with abundance distributions similar to Preston's (1948) deterministic lognormal model (see Tokeshi 1993: Fig. 1). Randomly breaking a line of unit length into two parts, and then repeating the process on randomly chosen parts until S_{true} segments are produced, generates a random-fraction community (Tokeshi 1993). The random-assortment model yields more highly uneven communities that are analogous to those described by geometric series (Tokeshi 1993). The random-assortment model assigns a random fraction of the line to the first species, a random fraction of the remaining part of the line to the second species, and so on until S_{true} segments are produced.

For comparative purposes, we calculated community evenness by the ratio of observed diversity to maximum diversity (Magurran 1988):

$$\text{evenness} = \frac{-\sum p_i \ln p_i}{\ln S}$$

where p_i is the proportion of individuals of species i and S is the number of species.

Gradients

Gradients such as flooding regimes on shorelines can be expressed as functions of the geographic coordinates x and y (Legendre 1993). We simulated landscapes with strong and weak gradients along the x coordinate as well as landscapes with no gradient. Gradient strength was expressed as the turnover distance d_{turn} at which on average all species were exchanged once (Jongmann et al. 1995). A strong gradient was characterized by one full turnover along the x coordinate of the lattice ($d_{\text{turn}} = 100$ cells), a weak gradient by a quarter turnover along the lattice ($d_{\text{turn}} = 400$ cells).

The individuals of a species i on a gradient are typically normally distributed with an optimum o_i (the mean) and an amplitude a_i (standard deviation) (Jongmann et al. 1995). For every species i and every cell, we simulated these probabilities as

$$p_{i,\text{grad}}(x) = \exp[-0.5(x - o_i)^2/a_i^2].$$

For every species i , we randomly derived the optimum o_i from a uniform distribution with $0 < o_i \leq 100$. Given that one species turnover equals approximately four standard deviations, the amplitude a_i of every species i was randomly sampled from a normal distribution (mean = $d_{\text{turn}}/4$, standard deviation = $d_{\text{turn}}/8$).

Spatial autocorrelation

Our simulations of spatial autocorrelation (Legendre 1993) vary the occurrence probabilities associated with each cell based on variably located autocorrelation sources. These probabilities were independently applied for every species i by locating between 1 and 10 autocorrelation sources on the lattice in the same way as individuals, that is, either in a uniformly random manner or according to $p_{i,\text{grad}}$. The probabilities at the source and in neighboring cells were established by parameterizing a sill, range, and nugget. The sill is the asymptotic occurrence probability at a certain range from the nugget. The nugget indicates the maximum

deviation from the sill at the autocorrelation source and therefore determines the strength of autocorrelation. Probabilities between the nugget and the sill are linear functions of commonality dependent on the distance to the autocorrelation source. We simulated communities with biologically reasonable values (Mistral et al. 2000; J. B. Wilson, *personal communication*) of long-range autocorrelation (sill = 0.27, nugget = 0.72, and range = 5 m) and short-range autocorrelation (sill = 0.27, nugget = 0.62, and range = 2 m). Species-specific functions were derived to determine $p_{i_{\text{auto}}}(x, y)$, the autocorrelation probabilities of occurrence for every cell (x, y) :

$$p_{i_{\text{auto}}}(x, y) = \begin{cases} \frac{0.033 - 0.33d(x, y)}{\text{range}_i - 0.1} + c & 0 \leq d \leq \text{range}_i \\ 0 & d > \text{range}_i \end{cases}$$

where $d(x, y)$ is the distance to the autocorrelation source, range_i is a species-specific range of autocorrelation, and c is the autocorrelation strength that equals 0.35 for short-range and 0.45 for long-range autocorrelation. The values of range_i were randomly sampled from normal distributions (short-range autocorrelation: mean = 2, $\text{LSD} = 1$; long-range autocorrelation: mean = 5, $\text{LSD} = 2.5$). In the model without autocorrelation we defined for all species i : $p_{i_{\text{auto}}} = 0$.

The spatial autocorrelation patterns were independently created for every species i by (1) choosing 1–10 autocorrelation sources from a uniform random distribution, (2) placing the sources on the landscape according to the $p_{i_{\text{grad}}}$ in the same way as individuals (see *spatial autocorrelation*), and (3) calculating a new landscape of probabilities of occurrence as $p_i(x, y) = p_{i_{\text{grad}}}(x) + p_{i_{\text{auto}}}(x, y)$.

Extrapolation of species richness

We compared estimations of two species accumulation curves and nine nonparametric estimators (Appendix). This includes the two most frequently used species accumulation curves, the exponential equation (Holdridge et al. 1971) and the Michaelis-Menten model (Michaelis and Menten 1913). To minimize arbitrary effects, cell sample order for accumulation curves was randomized 100 times in each sample. The mean species numbers $S(n)$ were calculated for each value of n cells sampled. Following Keating and Quinn (1998), we used least squares nonlinear regressions with the quasi-Newton algorithm to fit the Michaelis-Menten model and the exponential equation to the mean $S(n)$ data. The often-discussed difference between number of individuals and number of samples as measurements of sampling intensity (Chazdon et al. 1999, Gotelli and Colwell 2001) is minimal in our simulations, because when averaged across all species the individuals are evenly distributed across the lattice.

The nine nonparametric estimators used include the first- to fifth-order jackknife estimators (Jack1–Jack5, Burnham and Overton 1979), a selected and an interpolated jackknife estimator (Jack_{sel}, Jack_{int}, Burnham and Overton 1979), the incidence-based estimator (Chao2, Chao 1987), and the incidence-based coverage estimator (ICE, Lee and Chao 1994). Since the original formulations of Chao2 and ICE are undefined for zero duplicates and when all infrequent species are uniques, respectively, we used a corrected version of Chao2 (Colwell 1997; also see the Appendix) and replaced ICE estimates by Chao2 estimates in the undefined cases. To calculate Jack_{sel}, the jackknife estimates are sequentially compared to the estimates of the next higher order until the first estimate is reached that does not significantly differ from the next (see Burnham and Overton 1979 for the exact test statistics). Jack_{int} is an interpolated estimator between Jack_{sel} and the preceding estimator.

Estimator evaluation

We based our estimator evaluation on bias, precision, and accuracy. Positive and negative bias indicates overestimation and underestimation, respectively. Precision is the closeness of repeated measurements of the same quantity to each other (Sokal and Rohlf 1995). Accuracy is the closeness of a measured or computed value to its true value (Sokal and Rohlf 1995). Overall bias and precision were calculated for each estimator in all simulations across all community types using linear least-squares regressions of estimated species richness, S_{est} , as a function of true species richness, S_{true} , forced through an intercept of zero (method suggested by N. Gotelli, *personal communication*). All data points fall on a straight line with a slope of one for an unbiased and perfectly precise estimator. We measured bias as the difference between the observed slope of the regression and the expected slope of one: $\text{Bias} = \text{observed slope} - 1$. Precision was measured by the r^2 values of the regressions.

We also calculated bias and inaccuracy for single samples. In this case, bias was defined as the proportional deviation of S_{est} from S_{true} :

$$\text{bias} = \frac{S_{\text{est}} - S_{\text{true}}}{S_{\text{true}}}$$

We measured inaccuracy using the square proportional deviation of S_{est} from S_{true} :

$$\text{inaccuracy} = \left(\frac{S_{\text{est}} - S_{\text{true}}}{S_{\text{true}}} \right)^2$$

For groups of data sets, we calculated mean bias and mean inaccuracy, and imprecision was measured using the standard deviation of the bias. Bias, imprecision and inaccuracy were measured as percentage of S_{true} .

RESULTS

Overall, no single estimator consistently performed better than all others in each situation, but the non-

TABLE 1. General bias and precision of the estimators determined by linear regressions of S_{est} on S_{true} and correlation of the independent variables with the residuals.

Estimator	Bias	Precision	Rad [†]	Grad [‡]	Auto [‡]	Sampling [†]
S_{obs}	-0.558	0.679	-0.80	0.00	-0.02	0.39
Chao2	-0.372	0.762	-0.64	-0.02	-0.02	0.50
Jack1	-0.457	0.733	-0.83	0.00	-0.02	0.33
Jack2	-0.404	0.765	-0.82	-0.01	-0.02	0.31
Jack3	-0.366	0.784	-0.80	-0.01	-0.02	0.32
Jack4	-0.336	0.788	-0.74	-0.02	-0.02	0.34
Jack5	-0.309	0.764	-0.62	-0.02	-0.01	0.35
Jack _{sel}	-0.363	0.785	-0.72	-0.02	-0.02	0.43
Jack _{int}	-0.366	0.784	-0.72	-0.02	-0.02	0.44
ICE	-0.466	0.735	-0.75	-0.01	-0.02	0.42
M-M	-0.474	0.664	-0.87	0.01	0.00	0.17
Expo	-0.588	0.677	-0.85	0.01	-0.01	0.25

Notes: Bias = slope - 1; Precision = r^2 . $P < 0.001$ for all regressions. Standard errors of all biases are 0.002. Spearman rank correlation coefficients are given in the last four columns. Key to abbreviations: ICE = incidence-based coverage estimator, M-M = Michaelis-Menten model, Expo = exponential equation, Rad = relative abundance distribution, Grad = gradient strength, Auto = autocorrelation type.

[†] All values, $P < 0.001$.

[‡] All values not significant.

parametric estimators as a group did generally outperform the other estimators with respect to both bias and precision. In contrast, several estimators consistently performed poorly, most notably the most popular measure of biodiversity, S_{obs} . We first present the general performance of the estimators followed by the effects of abundance distribution and sample coverage on this performance. Finally, we compare results from our simulated landscapes with results of similar analyses of empirical data collected from field studies.

General performance of the estimators

We evaluated the general performance of the estimators using linear regressions of S_{est} as a function of S_{true} . All estimators were much more variable in the 25-species simulations and comparatively less biased in the 500-species simulations. Furthermore, Chao2 showed an extraordinary high variance in these high-richness simulations. Therefore, we avoided heteroscedasticity and nonlinearity in evaluations of bias and precision by excluding results from landscapes with $S_{\text{true}} = 25$ and $S_{\text{true}} = 500$. We also excluded the $S_{\text{true}} = 50$ samples from the analyses of Jack4 and Jack5 due to high variances. All estimators were negatively biased, but only the exponential equation provided more biased results than S_{obs} (Fig. 1). The Michaelis-Menten model and ICE were the most biased of the remaining estimators. The regression details are given in Table 1. All estimators except the Michaelis-Menten model and the exponential equation yielded more precise estimates than S_{obs} . Due to their poor general performance, the Michaelis-Menten model and the exponential equation were excluded from further analyses. Bias decreased with increasing order of the jackknife estimators, resulting in Jack4 and Jack5 being least biased while Jack4 and Jack_{sel} were most precise (Table 1). Surprisingly, Jack_{int} was more biased and imprecise

than Jack_{sel}, and was also excluded from further analyses. Chao2 performed intermediately with respect to both bias and precision.

Regression residuals were significantly correlated with relative abundance distributions and sampling intensity, indicating that these two factors had a substantial additional impact on estimator performance (Table 1). For most estimators, relative abundance distributions were twice as highly correlated with the residuals as were sampling intensities. Surprisingly, gradient strength and autocorrelation type were not correlated with the residuals in any of the situations analyzed. Therefore, we further analyzed the impact of the relative abundance distributions on estimator performance in more detail.

Relative abundance distributions

The bias of all estimators was influenced by the relative abundance distributions as well as by sampling intensity and S_{true} (Fig. 2). At each level of sampling intensity and S_{true} , the differences in mean bias between the three relative abundance distributions groups were highly significant for all estimators (Kruskal-Wallis $P < 0.001$). S_{obs} was reasonably unbiased only in very even (broken-stick) communities under intermediate or high sampling intensity, but S_{obs} was never the least biased. In all uneven communities, all estimators were substantially less biased than S_{obs} (Fig. 2). In general, the estimators were up to 50-fold more biased in the uneven (random-fraction) communities than in the even (broken-stick) communities (Fig. 2). The estimates in the highly uneven (random-assortment) communities were generally extremely biased, with mean estimates usually well below 50% of S_{true} . This increase in bias coincided with a decrease in evenness from broken-stick (mean = 0.92, range 0.86–0.95) to random frac-

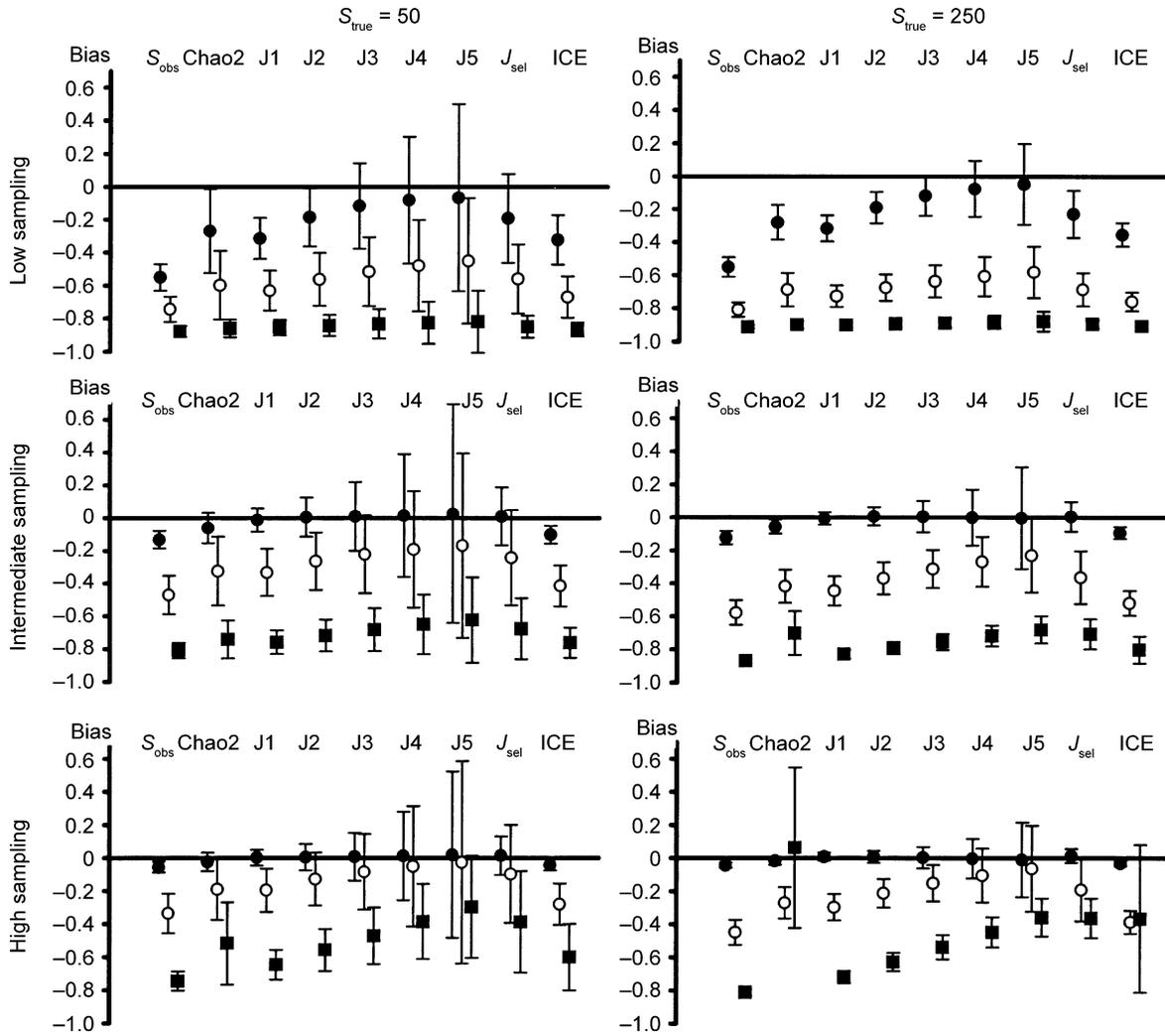


FIG. 2. Influence of the relative abundance distributions on estimator bias (mean) and imprecision (standard deviations) at different levels of S_{true} and sampling intensity. Results are depicted for broken-stick (solid circles), random fraction (open circles), and random assortment (solid squares) communities. $J_{sel} = Jack_{sel}$.

tion (mean = 0.62, range 0.25–0.87) and random assortment communities (mean = 0.47, range 0.22–0.60).

Jack4 and Jack5 were generally the least biased estimators, but they were also the least precise, as indicated by the large standard deviations of their mean biases (Fig. 2). Chao2 and ICE were markedly imprecise in some data sets (e.g., Fig. 2, random assortment communities with $S_{true} = 250$ under high sampling). Jack1 and Jack2 were more biased, yet substantially more precise, than Jack4 and Jack5. Jack3 and Jack_{sel} performed intermediately with respect to bias and precision. Jack1 and Jack2 performed best with respect to accuracy in highly even communities, and Jack2, Jack3, and Jack4 performed best with respect to accuracy in the uneven and highly uneven communities. However, estimator ranking also depended on sampling intensity.

Sample coverage

S_{true} , sampling intensity (i.e., the number of samples per community), and the community evenness mediated by the relative abundance distributions influence S_{obs} , and therefore the sample coverage, i.e., the proportion of species present in the sample. Among all simulations, the sample coverage was strongly correlated with sampling intensity (Spearman rank correlation, $r = 0.456$) and community evenness ($r = 0.836$), but correlations with S_{true} ($r = 0.144$) were surprisingly weak ($P < 0.001$ for all three Spearman rank correlations). There were no significant correlations with spatial autocorrelation type and gradient strength. Estimator bias was significantly correlated with all independent variables (Table 2). With respect to the correlation coefficients, sample coverage was the most im-

TABLE 2. Simple Spearman rank and partial correlations among estimator bias and the explanatory variables: S_{true} , sampling intensity, community evenness, and sample coverage.

Estimator	Simple correlations				Partial correlations		
	S_{true}	Sampling intensity	Evenness	Sample coverage	S_{true}	Sampling intensity	Evenness
Chao2	-0.033	0.524	0.664	0.843	0.137	0.276	-0.031
Jack1	-0.144	0.394	0.862	0.985	-0.065	-0.243	0.280
Jack2	-0.139	0.361	0.848	0.950	-0.047	-0.136	0.226
Jack3	-0.122	0.345	0.796	0.891	-0.032	-0.047	0.163
Jack4	-0.090	0.341	0.703	0.800	-0.020	0.015	0.101
Jack5	-0.048	0.324	0.562	0.660	-0.011	0.045	0.053
Jack _{sel}	-0.094	0.452	0.739	0.885	0.019	0.147	0.045
ICE	-0.110	0.474	0.785	0.930	0.048	0.162	0.043

Notes: $P < 0.001$ for all correlations; in partial correlations the effect of sample coverage was removed prior to further correlation analyses.

portant independent variable and S_{true} the least important. After the effect of sample coverage on estimator bias had been removed in partial correlation analyses, the other independent variables only had a minor direct impact on the remaining variance of estimator bias despite strong simple correlations (Table 2). Overall, community evenness and sampling intensity controlled sample coverage, which substantially influenced the bias of the nonparametric estimators.

We analyzed the relationship between sample coverage and estimator performance in more detail by plotting estimator bias, imprecision, and inaccuracy in 1% steps against sample coverage (Fig. 3). While bias and inaccuracy decreased with increasing sample coverage, imprecision was highest at intermediate levels of sample coverage. All estimators reduced the bias substantially in comparison to S_{obs} , which, however, was most precise (Fig. 3c–d). The least biased estimators, Jack3, Jack4, and Jack5 (Fig. 3a–b), were markedly less precise than the other estimators (Fig. 3c–d), whereas more precise estimators like Jack1, Jack2, and ICE reduced bias less than the other estimators did except S_{obs} (Fig. 3a–b). Chao2 was particularly imprecise under low sample coverage, but was among the most precise estimators under high sample coverage (Fig. 3d). Chao2 reduced bias less under high sample coverage than the jackknife estimators. At sample coverage >95%, all jackknife estimators had a positive bias. With respect to accuracy, the estimators showed a more complex response to sample coverage: the estimators' curves intersected, and for different levels of sample coverage, different estimators were most accurate (Fig. 3e–f). These intersections indicated that the most accurate estimators were Jack5 up to a sample coverage of 26%, Jack4 up to 38%, Jack3 up to 50%, Jack2 up to 74%, Jack1 up to 96%, and $S_{\text{obs}} > 96\%$ (Fig. 3e–f, intersections are accurate $\pm 1\%$).

Field studies

To test the predictions of our simulations, we analyzed data from two field studies on plant communities that provided independent information about plant in-

ventories within plots and S_{true} of the entire habitats. The first study was carried out on 12 temporary wetlands in East German farmland with a mean habitat area of 1078 m² (Brose 2001). Systematic transect searches (five times) were used to quantify S_{true} , and nine 0.25-m² plots per study site were installed in a stratified random design. The plant communities were characterized by a mean S_{true} of 30 species (range: 19–44 species) and a mean evenness of 0.92 (range: 0.91–0.93), which is comparable to the 50-species broken-stick communities. The mean sample coverage was 75%, which is between the mean values of the simulated broken-stick communities sampled with low (45%) and intermediate intensity (90%). The results are very consistent with the simulations predicting that (1) in broken-stick communities of 50 species, under low to intermediate sampling intensity, the jackknife estimators are the least biased (Figs. 2 and 4a), (2) imprecision increases with increasing order of the jackknife estimators (Figs. 2, 3c–d, and 4a), and (3) under a sample coverage of 75% Jack1 and Jack2 are the most accurate estimators (Figs. 3e and 4a).

The second field study was carried out on five dry grasslands on mountain slopes in the area of Pécselyi, ~20 kilometers north of the Balaton in central Hungary. The mean habitat area was ~1 km². The vegetation was surveyed three times in 1999 and ranged from subalpine communities to dry grasslands. On each of the five grasslands, 40 1-m² plots stratified with respect to altitude and soil depth were installed. S_{true} was obtained by combining observed species lists with a multiyear survey (Bauer 2000). S_{true} (mean: 133 species, range: 83–177 species) was bracketed by our simulated S_{true} values of 100 and 150 species. Their extreme unevenness (mean = 0.27; range: 0.26–0.27) is comparable to our random-fraction and random-assortment communities. Sample coverage (mean 73%) is higher than in any of the simulated uneven communities. Randomly selecting 8 plots per grassland generated a less sampled version of this data set. Species richness was estimated in 20 replications and the mean estimates were calculated for each estimator. Sample coverage

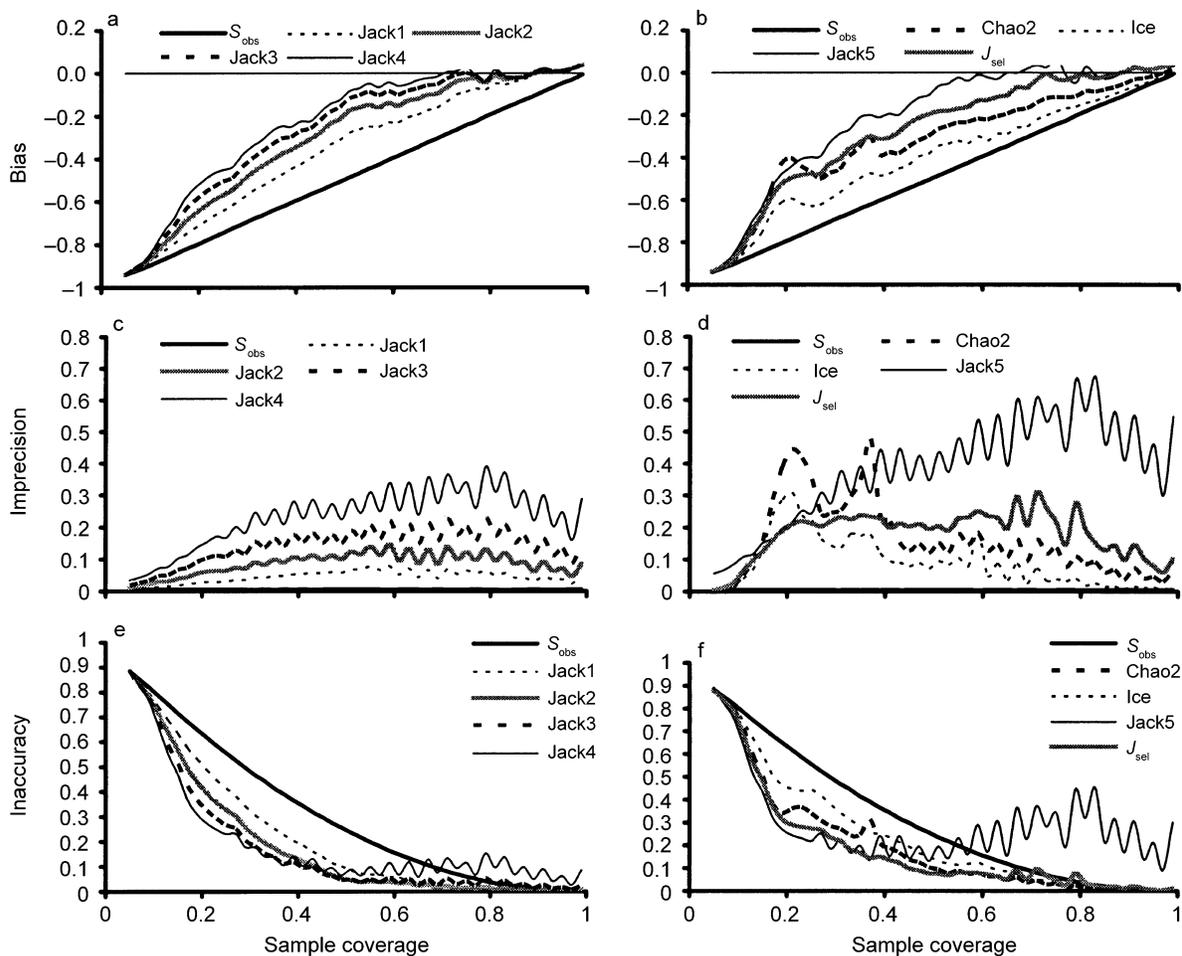


FIG. 3. Bias, imprecision, and inaccuracy of the nonparametric estimators as functions of sample coverage. All values were determined for 1% ranges. $J_{sel} = Jack_{sel}$.

(mean 50%) was comparable to intermediate sampling of our random-fraction simulations (53%, 50 species; 43%, 250 species). In accordance with our simulations, the jackknife estimators were less biased than the other estimators except Jack1, which was more biased than Chao2 under intermediate sampling intensity with 8 samples (Figs. 1 and 4b–c). Most results are consistent with our simulations predicting that (1) bias and precision decreased with increasing jackknife order (Figs. 1, 2, and 4b–c), (2) under a sample coverage of 50% Jack3 is among the most accurate estimators (Figs. 2 and 4b), and (3) under 73% sample coverage Jack2 performs most accurately (Figs. 3e and 4c). However, Jack4 and Jack5 under intermediate sampling and Jack3 under high sampling performed more accurately than in our simulations.

DISCUSSION

Our general results have shown that most estimators perform significantly better than S_{obs} , and that the nonparametric estimators are substantially less biased and

more precise than the extrapolations of species accumulation curves. This is consistent with previous studies (Palmer 1990, Baltanás 1992, Colwell and Coddington 1994, and with some exceptions Walther and Morand 1998 and Longino et al. 2002). In our study, it was shown that these results hold for a large range of communities with differences in evenness and spatial patterns. In contrast to field studies, these parameters are not only exactly known in the simulated landscapes used in the present study, they were also systematically controlled as independent variables. Based on this approach, it was shown that species richness estimation depends on the relative abundance distribution, S_{true} , and sampling intensity, but not on spatial patterns.

Bias, precision and accuracy

Our results indicate that choosing estimators depends on whether bias-reduction or precision is more important. While Jack5 was the least biased and least precise estimator, S_{obs} was most precise and most biased (see

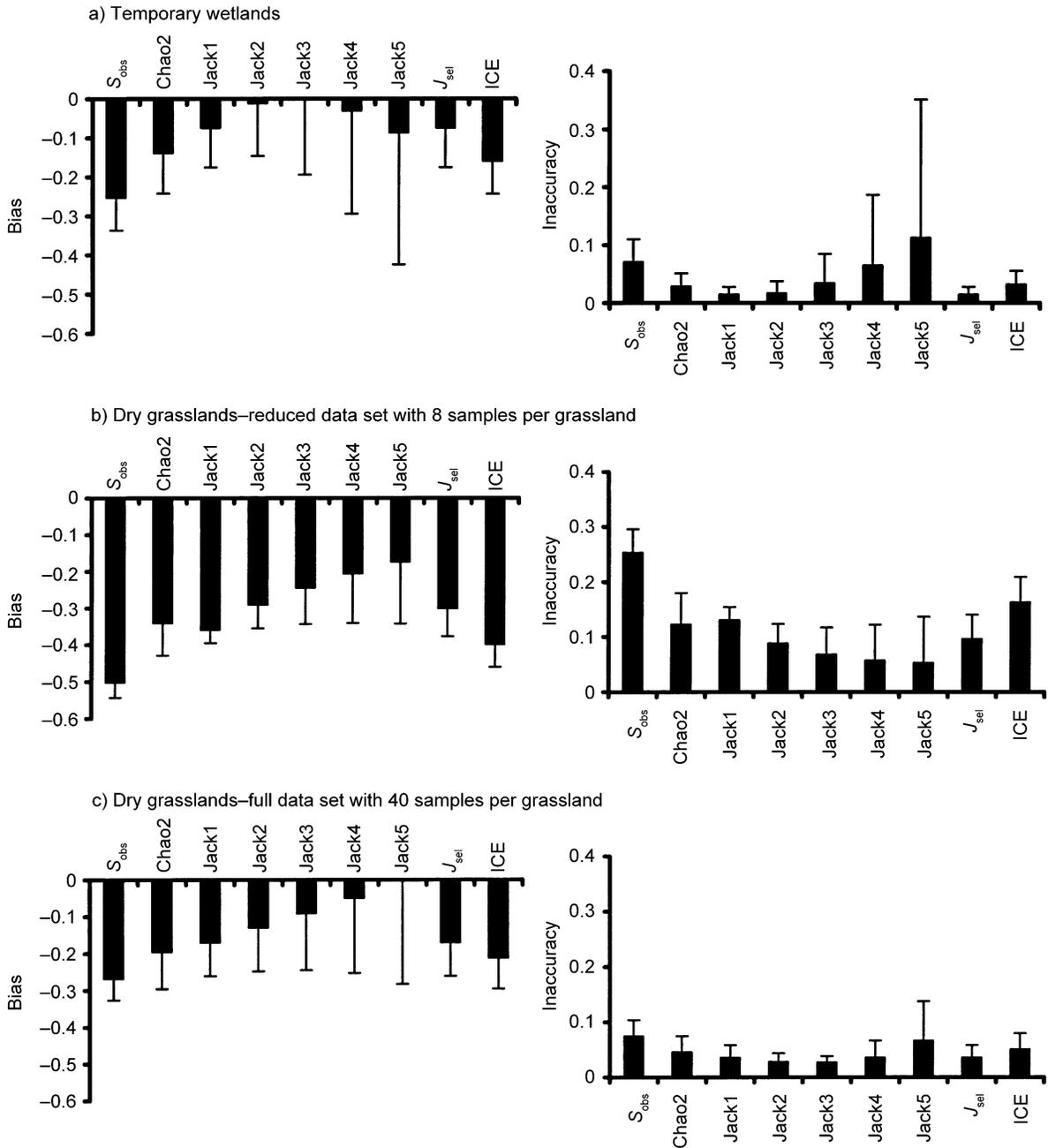


FIG. 4. Bias (mean), imprecision (standard deviation of bias), and inaccuracy (mean + 1 SD) of the estimators on (a) temporary wetlands, and dry grasslands in (b) a reduced data set with eight samples per grassland, and (c) the full data set with 40 samples per grassland. $J_{sel} = Jack_{sel}$.

Fig. 3). In our simulations as well as in the field studies, both estimators would have yielded problematic results. Bias indicates systematic over- or underestimation of the mean estimation when several independent estimates are taken into account (Sokal and Rohlf 1995). Precision measures the similarity of independent estimates, and therefore, it indicates the repeatability of an estimate, whether or not it is biased. Biodiversity

studies typically prevent systematic evaluation of bias and precision by restricting evaluation to one data set rather than several independent estimates as in our study. Accordingly, estimators used in such biodiversity studies not only need to be as unbiased as possible, they also need to be reliable in terms of precision in order to reduce arbitrary variation while conducting similar surveys or experiments. Accordingly, choosing

the least biased estimator may be appropriate for studies in which several independent data sets are available to yield one mean estimate. This might be typical when the concern is to estimate global biodiversity or the species richness of an entire biome. In contrast to this, field studies at smaller spatial scales are typically based on single data sets, which makes precision critically important. Our results indicate that there is a trade-off between bias-reduction and precision of the estimators. Following Sokal and Rohlf (1995), we feel that evaluations should be based on accuracy defined as a combination of bias and precision. Similar to bias, accuracy measures the deviation of the estimate from S_{true} , but without the sign, which prevents underestimates from averaging with overestimates to yield a very low mean bias.

Fig. 5 illustrates this critical issue in terms of three hypothetical estimators: Estimator1 is unbiased, imprecise and inaccurate (bias = 0, imprecision = 0.5, inaccuracy = 0.23), Estimator2 is biased, precise, and inaccurate (bias = -0.4, imprecision = 0.1, inaccuracy = 0.17), Estimator3 is slightly more biased than Estimator1, slightly less precise than Estimator2, and most accurate of the three estimators (bias = -0.05, imprecision = 0.15, inaccuracy = 0.02). Although Estimator1 is unbiased on average, its individual estimates are usually highly biased and over- or underestimate S_{true} substantially (Fig. 5a). In contrast to this, Estimator2 consistently underestimates S_{true} . Only the accurate Estimator3 consistently provides unbiased estimates. To see the consequences of using biased, imprecise, or accurate estimators, we then applied these three estimators to a hypothetical study gathering data that follows a relationship of $y = x$ (Fig. 5b-d). The imprecise Estimator1 yielded a correct regression slope, but a comparatively low coefficient of determination and a lower significance level than the other estimators (Fig. 5b). The biased Estimator2 provided a higher r^2 value, but markedly underestimated the regression slope (Fig. 5c). Only the accurate Estimator3 yielded the approximately correct regression slope and the highest r^2 value (Fig. 5d). In actual field studies that include additional sources of variation, these effects are most likely even stronger. This example demonstrates that basing estimator choice only on bias or precision is potentially misleading, while accuracy shows that the estimates are constantly close to the true value. Our results indicate that accuracy benefits from bias-reduction under low sample coverage when all estimators have a substantial negative bias, and precision under high sample coverage when all estimators are less biased.

Impact of the relative abundance distributions and spatial patterns

Our results strongly corroborate the hypothesis that uneven detection probabilities affect estimator performance: the relative abundance distribution was the

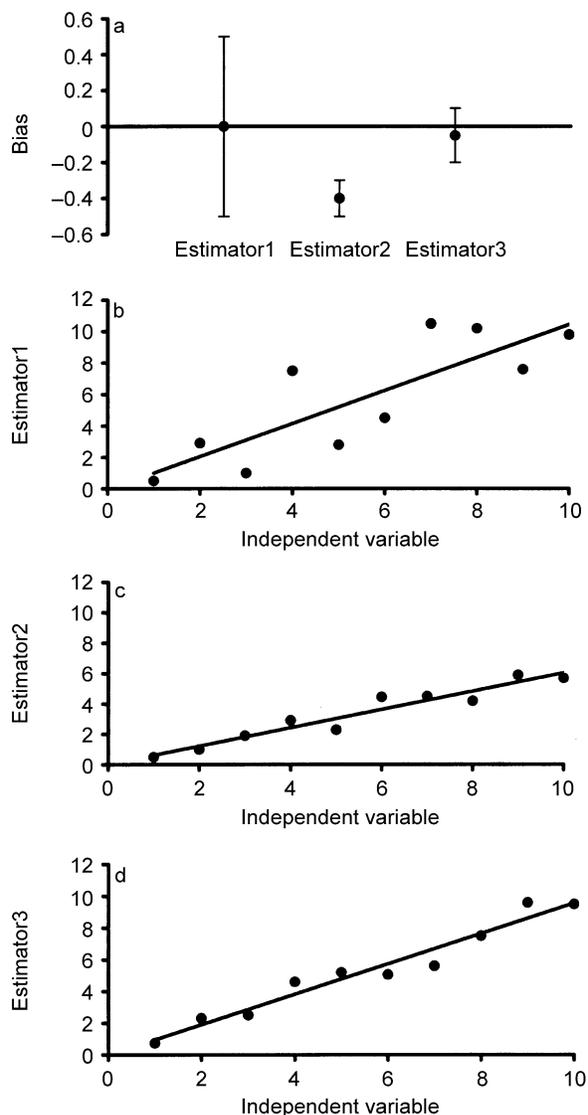


FIG. 5. (a) Bias (mean) and precision (standard deviation) of three hypothetical estimators. In panels (b)–(d) these three estimators were used for regression analyses representing a hypothetical relationship $y = x$: (b) Estimator1 (regression: $y = x$, $r^2 = 0.68$, $P < 0.01$); (c) Estimator2 ($y = 0.6x$, $r^2 = 0.93$, $P < 0.001$); (d) Estimator3 ($y = 0.95x$, $r^2 = 0.95$, $P < 0.001$).

most important factor influencing estimator bias. This is consistent with Boulinier et al. (1998) who concluded that the capture–recapture model M_h (Otis et al. 1978), which assumes heterogeneous detection probabilities of the species, is generally the most appropriate for the estimation of species richness. Accordingly, the nonparametric estimators based on model M_h are best suited to deal with heterogeneous detection probabilities but, as our results indicate, these estimators are still substantially biased. This bias is most likely caused by the fact that the nonparametric estimators have originally been developed to estimate population size in

closed capture–recapture studies. However, detection probabilities among different species are likely to be more uneven than the detection probabilities of different individuals of one species. Our results are also consistent with Heltshe and Forrester (1983) and Baltanás (1992), who found that the dispersion of the log-normal distribution in communities affects the bias of the first-order jackknife estimator. Our study has expanded this finding to (1) all other estimators studied, (2) communities with high species richness, (3) communities of a broader evenness range, and (4) communities with strong spatial gradients and autocorrelation. Therefore, heterogeneous detection probabilities caused by uneven relative abundance distributions pose a major challenge for the extrapolation of species richness. Even for the nonparametric estimators based on model M_{hr} , a more complex extrapolation procedure that corrects for heterogeneous detection probabilities is required for comparing species richness and derived measures (e.g., connectance, Martinez et al. 1999) between communities that vary in evenness. Until evenness-corrected estimators are developed, our findings assist the choice of appropriate estimators based on the evenness in the sample. We found that the most accurate estimators are Jack1 and Jack2 in highly even brokenstick and Jack2, Jack3, and Jack4 in the uneven random-fracture or random-assortment communities. Jack2 appears to be the best overall estimator with respect to accuracy.

To allow a detailed impact analysis of spatial patterns, we distinguished spatial autocorrelation from gradients. Gradients restrict the distribution of species below the variation permissible in random and autocorrelation communities. Therefore, the commonality of two sampling plots on a gradient will be generally lower than in plots lacking a gradient. Furthermore, we differentiated the effects of the strengths of autocorrelation and its range. However, our results suggest that spatially heterogeneous species distributions mediated by spatial autocorrelation and gradients do not affect estimator bias. This is in contrast to previous studies in which spatial autocorrelation strength had a small but significant effect on estimator bias (Baltanás 1992, Chazdon et al. 1998) or diversity indices (Fager 1972). The estimator studies, however, varied autocorrelation strength more than the present study, and testing the effects of observed, randomized or moderately patchy species distributions resulted mainly in nonsignificant differences (Chazdon et al. 1998). Furthermore, Chazdon et al. (1998) have shown that abundance-based estimators are more susceptible to be affected by patchy distributions than the incidence-based estimators used in the present study. Our results suggest that various different spatial aggregation patterns in a realistic parameter space are not likely to have a substantial impact on estimator performance. This is consistent with an empirical study that concluded that capture–recapture models assuming spatial heterogeneity are rarely ap-

propriate for the estimation of species richness (Boulinier et al. 1998). Accordingly, violating the assumption of spatially homogeneous species distributions does not seriously challenge the extrapolation of species richness.

Sample coverage

In our study, no single estimator performed best across the different levels of community evenness, S_{true} , and sampling intensity, and these variables should be addressed simultaneously while evaluating estimators. Our results suggest that community evenness, S_{true} , and sampling intensity indirectly influence the nonparametric estimators through effects of sample coverage. Surprisingly, there was only a minor influence of S_{true} , which indicates that the nonparametric estimators are well suited to estimate species richness in communities with substantially different levels of S_{true} . Accordingly, sample coverage mainly combines the effects of sampling intensity and community evenness on the estimators. With respect to sample coverage, studying a more even community has the same effect as studying an uneven community with higher sampling intensity. Therefore, our results concerning sample coverage are independent of the specific levels of community evenness and sampling intensity chosen, and represent the full range of theoretically possible data sets. Knowing the exact sample coverage in a case study would make the decision for a specific estimator straightforward, but, of course, unnecessary. However, when sample coverage is approximately known, our results indicate which estimators are most accurate (Fig. 6). Although the bias of each estimator was consistent for each level of sample coverage, bias-correction based on sample coverage is not reliable, as it would add the error of sample coverage estimation to the error of the species richness estimates.

S_{obs} is usually not the best choice to measure species richness, and in most data sets, ICE and Chao2 were less accurate than the jackknife estimators. The low accuracy of Chao2 was caused by a low precision under low sample coverage and high bias under high sample coverage. Surprisingly, Chao2, Jack3, Jack4, and Jack5 performed much more precisely in our general evaluation (Table 1) than in the more detailed evaluations (Figs. 2 and 3). This is caused by the fact that the data sets with their most imprecise performances were excluded from the regression analyses in the general evaluation to avoid heteroscedasticity. Therefore, the general precision values in Table 1 provide a relatively flattering image of their precision, and the detailed results shown in Figs. 2 and 3 are more meaningful.

In empirical studies, there has been some disagreement about the relative performance of the nonparametric estimators: while Palmer (1990) concluded that Jack1 is the least biased estimator, Colwell and Coddington (1994) argued in favour of Chao2 and Jack2 and Walther and Morand (1998) preferred Chao2 and

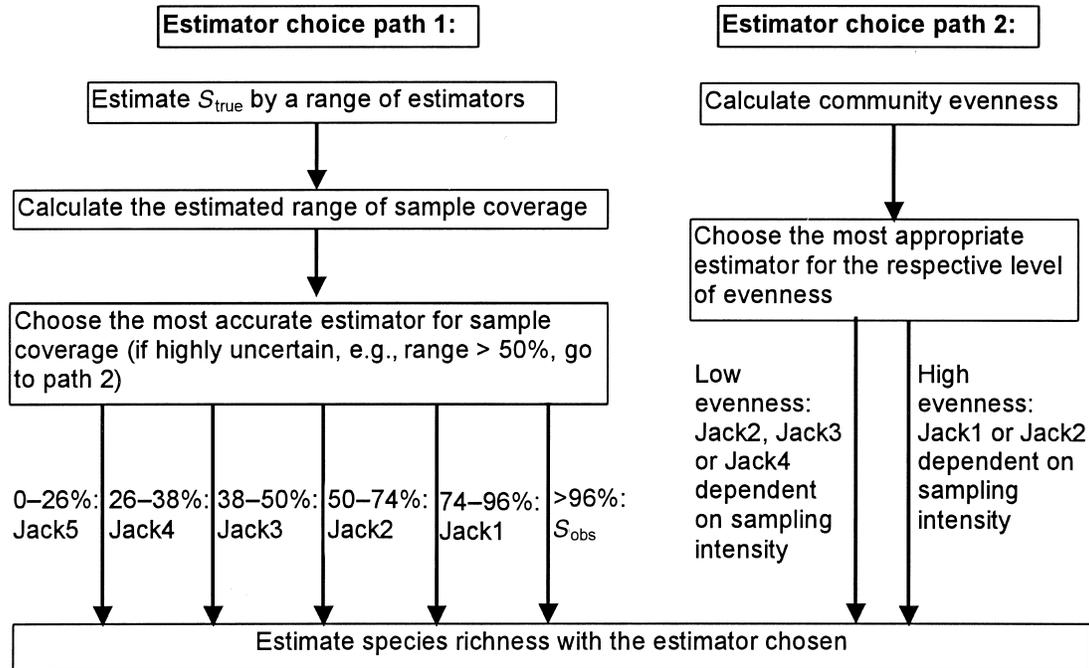


FIG. 6. Two alternative ways to choose the most appropriate estimator based on either an estimated range of sample coverage or the community evenness. S_{obs} = observed species richness. Thresholds are accurate within $\pm 1\%$.

Jack1. Our results indicate that this might stem from the differences in their sample coverage. The field data sets in the present study give an example that evaluations under different sampling intensity, community evenness, and consequently different sample coverage yield different results concerning estimator ranking. In contrast to this, in simulated landscapes, S_{true} , sampling intensity, and community evenness are not only unquestionably known, they are also controlled as independent variables. This has led to the new estimator performance model based on sample coverage in the present study.

All jackknife estimators were positively biased above 95% sample coverage. This has previously been reported in field studies by Heltshe and Forrester (1983), Colwell and Coddington (1994), and Hellmann and Fowler (1999), but with different magnitudes. In contrast to this, the jackknife estimators did not overestimate in the studies of Palmer (1990, 1991) and Baltanás (1992). Potential explanations include the following. First, differences in the sample coverage between the studies might be responsible. Second, particularly in field studies, the determination of S_{true} is prone to underestimation. Such lower S_{true} may account for some of the jackknife estimator's overestimations. In our simulations, however, the first- and second-order jackknife estimators were less positively biased under high sample coverage than previously reported (e.g., Hellmann and Fowler 1999).

Estimator choice

We will subsequently present a framework for the choice of the most appropriate nonparametric estimator depending on sample coverage (see Fig. 6). However, unless the sample contains the entire community, one can only guess about the sample coverage, which makes the estimator choice more problematic. An estimator evaluation based on sampling intensity, i.e., the percentage of total quadrats sampled (Hellmann and Fowler 1999), only provides an incomplete framework, since sampling intensity is only one of the factors influencing sample coverage. This framework remains specific for the respective levels of community evenness, S_{true} and habitat area. As independent reliable information about S_{true} is scarcely obtainable in field studies, the most promising procedure to choose the appropriate estimator is iterative (Fig. 6, path 1). First, a range of S_{true} needs to be calculated by various estimators. Then, the most accurate estimator can be chosen based on the resulting mean estimated sample coverage. Applying this procedure to the field data sets yields mean inaccuracies of 1.5% of S_{true} for the temporary wetlands and 3.5% of S_{true} and 9.6% of S_{true} for the dry grasslands in the full and reduced data set, respectively. While these estimates are the most accurate for the temporary wetlands, they are only slightly outperformed by Jack2 and Jack3 on the dry grasslands. Compared to a decision based on community evenness (Fig. 6, path 2), the decision path based on estimated sample coverage (Fig. 6, path 1) is more

elaborate. For every level of sample coverage just one estimator is most accurate. However, uncertainty of sample coverage might force researchers to rely on path 2 if the estimated range of sample coverage is large. In contrast to this, estimates of evenness are highly accurate even when based on very few samples. For example, under low sampling intensity evenness was calculated with a mean absolute proportional deviation of 9.8% in our simulated landscapes. Although the decision based on evenness is more reliable, it does not offer conclusive advice, as estimator choice still depends on sampling intensity. In conclusion, we recommend that researchers examine both alternatives and rely primarily on path 1. Although this procedure surely does not satisfy the desire for a single generally applicable estimator, we do provide a method for choosing estimators that should generally increase accuracy beyond current methods and certainly beyond the widespread measurement of species richness by S_{obs} . Beyond choosing among available estimators, our *in silico* methods could be used to evaluate and design new estimators to be more highly accurate and also avoid problems such as consistent negative bias at low sample coverage.

CONCLUSIONS

Our analyses demonstrate that in most community types the nonparametric estimators perform substantially more accurately than S_{obs} or the species accumulation curves. As specific spatial patterns and S_{true} were of minor importance, our results appear spatially scale invariant, making no differences between α and γ diversity. Irrespective of scale, our results suggest that species richness may be calculated accurately under intermediate or high sampling intensity if the most appropriate estimator is chosen. Community evenness and sampling intensity, however, have a strong influence on estimator accuracy. With respect to these factors, there was not a single generally most accurate estimator, and an optimal decision has to be based on knowledge about the sample coverage that can only be estimated from the samples. There are two possibilities to deal with this dilemma (Fig. 6). First, species richness can be extrapolated by various estimators to base the decision about the most appropriate estimator on the estimated ranges for the sample coverage. Second, the least sensitive estimator with respect to community evenness can be chosen. Our study indicates a need for nonnegatively biased estimators for low sample coverage and a more complex extrapolation procedure that corrects for the very heterogeneous detection probabilities of species in natural communities. Until such estimators are developed, we anticipate that our findings will enhance the precision and accuracy of species richness estimations, while assisting researchers to choose the appropriate estimator for a particular community structure or sample coverage.

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APPENDIX

A comparison of formulas for the estimators of species richness is available in ESA's Electronic Data Archive: *Ecological Archives* E084-057-A1.