

Species richness estimation of bird communities: how to control for sampling effort?

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Since estimates of total species richness increase with sampling effort, methods to control for this sampling effect need to be tested and used. We present seven non-parametric and 12 accumulation curve methods that have been used recently in the ecological literature. To test their performance, we used data from bird communities in the Queen Charlotte Islands, Canada. The performance of each method was evaluated by calculating the bias and precision of its estimates against the known total species richness. For our data set, the two Chao estimators were the overall least biased and most precise estimation methods, followed by the two jackknife estimators, thus supporting results of previous studies. Non-parametric estimators tended to perform better than accumulation curve models. Most estimation methods had the problem that they tended to underestimate species richness for early samples, but slightly overestimated it for late samples. We briefly discuss the practical use of these methods which may greatly increase our ability to answer ecological questions and to guide conservation decisions, especially for species-rich tropical bird communities.

To test ecological questions or to make informed conservation decisions, it is often necessary to determine the total species richness of a bird community (Colwell & Coddington 1994, Gaston 1996). For example, one may want to rank sites according to their total species richness to decide which sites should be protected (Elphick 1997). However, species richness estimates increase with sampling effort (Woolhouse 1983, Walther *et al.* 1995, Neave *et al.* 1997) thereby confounding comparisons. One solution may be to standardize sampling effort across all sites (Elphick 1997). Although sites could thus be reliably ranked, total species richness would still not be known (unless sampling was exhaustive). More important, however, is that equal sampling effort remains an elusive goal in most real situations. Even worse, sampling effort is often not even used to correct species richness estimates. For example, bird species richness and sampling effort were reported for 18 South American sites (Remsen 1997). However, none of these studies tried to correct for the influence of sampling effort, thus making comparisons of species richness between sites

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difficult if not impossible (Remsen 1994, Rahbek 1995). Therefore, it has become paramount to develop, test and use methods to correct for the influence of sampling effort on estimates of total species richness. To alleviate the sampling effort problem, Harrison and Martinez (1995) suggested the use of a modified Shannon diversity index, whereas Elphick (1997) proposed a regression model. We believe the proposed approaches are problematic for the following reasons. The use of diversity indices remains controversial for methodological reasons (Hurlbert 1971, Magurran 1988, Simberloff & Moore 1997). Some diversity indices (e.g. the Shannon index) emphasize species richness over evenness, whereas others assign low weights to rare species. Therefore, rare species may contribute little to the magnitude of a diversity measure, even though they may be the most important ones to conserve (Elphick 1997). Most importantly, however, the Shannon index used by Harrison and Martinez (1995) is unstable as it decreases with sampling effort (their Fig. 4). To avoid mathematically weighting species, Elphick (1997) proposed a curve model (which was never defined) to fit a relationship between sampling effort and species richness. This relationship can be used to calculate deviations from the expected species richness

ness, which can then be used to rank sites. However, Elphick did not explain the mathematical reasoning of this approach. Furthermore, this method uses just one datum for each site. We therefore present species richness estimation methods that have a solid basis in mathematical sampling theory, use all the data collected at each site, and yield relatively unbiased and precise estimates of the total species richness of each site.

The total number of estimation methods is truly staggering, as is evident from recent reviews (Bunge & Fitzpatrick 1993, Colwell & Coddington 1994, Flather 1996, Nichols & Conroy 1996, Boulinier *et al.* 1998b, Chazdon *et al.* 1998, Keating *et al.* 1998). In ecological contexts, however, two approaches appear to be the most promising: accumulation curve models and non-parametric estimators, whereas a third approach, the fitting of species abundance distributions, remains problematic (Colwell & Coddington 1994). Details of these methods are published elsewhere (see reviews). However, the general ideas are as follows. When sampling bird communities, new species initially

accumulate quickly, but at lower and lower rates later on. If one plots a measure of sampling effort against observed species richness, the resulting curve is similar to a logarithmic growth curve, which should, however, approach an asymptote equal to the total species richness (Fig. 1). Accumulation curve models fit a mathematical model to the data using standard statistical methods (e.g. Flather 1996, Keating & Quinn 1998). The asymptotic value of the resulting model is then defined as the estimated species richness. Non-parametric estimators, on the other hand, use the abundance or incidence of rare species to estimate the number of yet undiscovered species which is added to the number of already discovered species (Colwell & Coddington 1994). The purpose of this paper is to present a concise review of most of the methods used in ecological contexts, to provide an example by testing them on one exceptionally well-sampled bird community, and thus, hopefully, to encourage more researchers to test and use these methods. We do not consider this paper a definitive test of these methods (see Discussion).

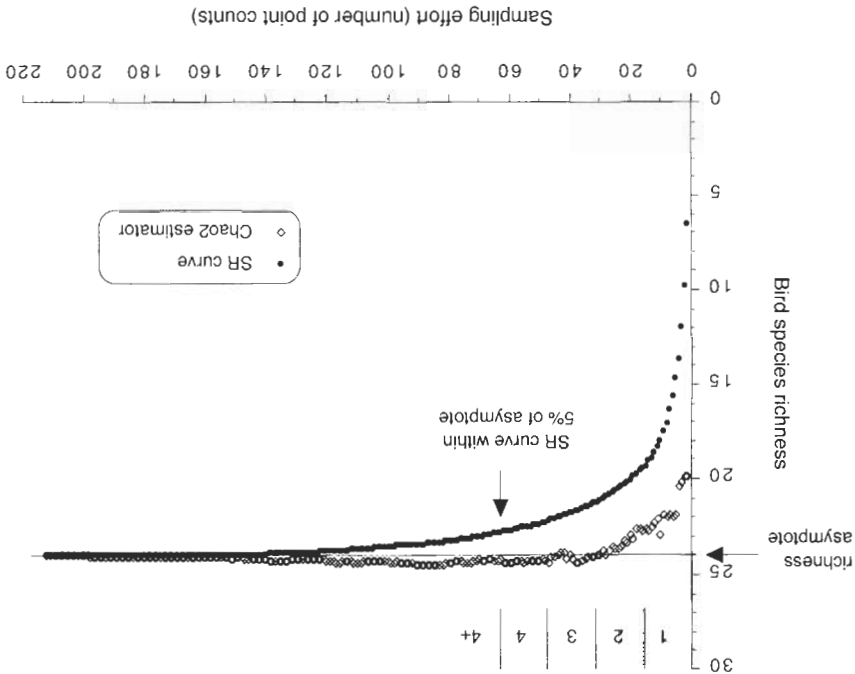


Figure 1. Plot of sampling effort ($n = 212$ point counts) against bird species richness (total species richness = 24) of the archipelago of the Queen Charlotte Islands (Martin *et al.* 1995). The species richness curve (SR curve) initially rises quickly, but later merges with the total species richness asymptote. The SR curve was generated by repeatedly reshuffling the entire pool of samples, i.e. using different random orders of samples, also called runs (in this case, 1000 runs; see Colwell and Coddington 1994 for details). The 1000 resulting curves were then averaged to generate the SR curve. The Chao2 estimator uses extrapolation techniques to estimate the total species richness long before the SR curve reaches the asymptote. To evaluate the performance of different estimation methods, we arbitrarily divided the sampling effort axis into five segments: quarters 1–4 evenly divide sampling effort prior to the SR curve reaching within 5% of the asymptote while the segment 4+ and includes all subsequent samples (see Walther & Moran 1998). Thus we can evaluate the performance of estimation methods for early and late samples (see Table 1).

curve comes within 5% of the asymptote was used as an arbitrary cut-off point to divide prior sampling effort into four equal quarters (Fig. 1). During the first quarter, sampling effort is still so low that the values of both the species richness curve and estimation methods are very inaccurate and should not be used for performance evaluation. In the second and third quarters, the species richness curve is still far from the asymptote. However, estimation methods may already yield reliable estimates for these 'early samples'. During 'late samples' (quarter 4 and all subsequent samples), estimation methods should remain close to the total species richness asymptote.

To quantify the performance of each estimation method, we calculated the bias and precision of each method's estimates against the total species richness. Bias measures whether an estimate consistently underestimates or overestimates total species richness; precision measures the overall closeness of the estimate to the total species richness without measuring bias (Zar 1996). Good estimators should thus have bias values close to zero and small precision values. We calculated:

$$\text{Bias} = \sum [(E_j - A_j) / [A_j n]]$$

$$\text{precision} = \sum [(E_j - A_j)^2 / [A_j^2 n]]$$

with $j = 1$ to $j = n$ (see Walther & Moran 1998 for details). n is the number of sampling units, E_j is the species richness as extrapolated by the respective estimation method and A_j is the asymptote of total species richness (assumed to be known as 24 species for the Queen Charlotte Islands data set; see above). Data were entered into a table with species in rows and units of equal sampling effort in columns and analysed with the programs *EstMates* (available from Robert K. Colwell, Dept. of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-3042, USA) and *MacCuneFit* (available from Kevin Raner Software, 77 Therese Avenue, Mt. Waverley, Victoria 3149, Australia).

RESULTS

The two Chao estimators were the overall least biased and most precise estimation methods (Table 1). The modified power function model and first- and second-order jackknifes also performed well for early samples, but were rather imprecise for late samples. The hyperbolic curve model performed best under the least-squares method, supporting Keating and Quinn's (1998) results. Non-parametric estimators tended to

To illustrate and test several of these methods, we used the exceptionally well-sampled bird communities of the Queen Charlotte Islands (c. 53°N 132°W) on the west coast of Canada, which were sampled by means of 20-min point counts with fixed radius (Martin *et al.* 1995). During each point count, the number of individuals of each species was recorded. Point counts were distributed over the archipelago in such a way that (1) larger islands received more point counts in proportion to their area and (2) enough smaller islands were sampled to balance sampling across island size classes (for details, see Martin *et al.* 1995). All 24 observed bird species were recorded at least three times. This lack of single or double observations indicates that the entire bird community was recorded (Colwell & Coddington 1994). Furthermore, a plot of sampling effort (in this case, point counts) versus species richness shows that sampling effort was probably adequate to determine the total species richness asymptote of this bird community (Fig. 1).

METHODS

We extrapolated the total species richness of this community with each of the following 19 estimation methods at increasing levels of sampling effort: the non-parametric estimators based on the abundance- and incidence-based species richness estimators Chao1 and Chao2, the abundance- and incidence-based coverage estimators ACE and ICE, and the estimators based on the first- and second-order jackknife and the bootstrap methods (Colwell & Coddington 1994, Chazdon *et al.* 1998); and the accumulation curves based on the rational function, modified negative exponential, beta-P, Weibull (Flather 1996), collector's curve (Pielou 1975), modified power function (Bateman 1992), finite-area (Buys *et al.* 1994), modified logarithmic (Soberon & Lorente 1993), negative exponential and hyperbolic curve model (Soberon & Lorente 1993, Colwell & Coddington 1994). The last model is based on the Michaelis-Menten equation of enzyme kinetics and was used in three ways: species richness was estimated for each run (cf. Fig. 1) using Raaijmakers' maximum likelihood estimator (Colwell & Coddington 1994), then all runs were averaged (MM-Runs); the averaged species richness curve was used to estimate species richness just once using Raaijmakers' estimator (MM-Mean), or non-linear least square regression methods were used (MM-least-squares, Keating & Quinn 1998).

To evaluate the performance of these methods, we divided sampling effort into two categories: early and late samples. The point when the species richness

Table 1. Performance of 19 estimation methods for the Queen Charlotte Islands data set (Martin *et al.* 1995). The species richness accumulation curve (SR curve) was averaged over 1000 randomized runs (see Fig. 1). Data are presented separately for early samples 16–47 (quarters 2 and 3), late samples 48–212 (quarters 4 and 4+) and all samples = (early samples + late samples)/2, thus giving more weight to early samples (see Fig. 1 and Walther & Morand 1998 for details). For clarity, the SR curve is underlined and accumulation curves are set in *italics*. Estimation methods are ranked according to their precision with the top method being the most precise. The boldy printed values indicate the overall least biased and most precise method within each category.

Early samples			Late samples			All samples		
Estimation method	Bias	Precision	Estimation method	Bias	Precision	Estimation method	Bias	Precision
Chao2 estimator	-0.01012	0.00054	Chao1 estimator	0.00683	0.00007	Chao2 estimator	-0.00099	0.00032
Modified power function	-0.02362	0.00066	Chao2 Estimator	0.00814	0.00010	Chao1 estimator	-0.00528	0.00053
Chao1 estimator	-0.01388	0.00099	Bootstrap	0.00712	0.00015	2-order jackknife	0.01046	0.00081
2-order jackknife	0.01598	0.00099	ICE estimator	0.00604	0.00015	1-order jackknife	-0.00110	0.00082
1-order jackknife	-0.02128	0.00113	ACE estimator	0.00615	0.00016	Rational function	-0.01384	0.00089
Rational function	-0.03824	0.00150	<i>MM-least-squares</i>	0.00055	0.00017	<i>MM-least-squares</i>	-0.02311	0.00120
<i>MM-least-squares</i>	-0.04877	0.00224	<i>MM-Runs</i>	-0.00916	0.00025	<i>Modified Power function</i>	0.00898	0.00128
<i>MM-Runs</i>	-0.04819	0.00234	<i>MM-Mean</i>	-0.00908	0.00026	<i>MM-Runs</i>	-0.02866	0.00129
<i>MM-Mean</i>	-0.05425	0.00299	<i>Rational function</i>	0.01057	0.00028	<i>MM-Mean</i>	-0.03167	0.00162
ICE estimator	-0.05788	0.00367	Weibull	0.00588	0.00030	ICE estimator	-0.02592	0.00191
Beta-P	-0.03627	0.00408	1-order Jackknife	0.01908	0.00051	ACE estimator	-0.03082	0.00263
ACE estimator	-0.06779	0.00509	SR curve	-0.01579	0.00063	Bootstrap	-0.03260	0.00309
Bootstrap	-0.07332	0.00603	2-order Jackknife	0.00495	0.00064	Weibull	-0.04375	0.00487
Weibull	-0.09338	0.00944	<i>Modified logarithmic</i>	-0.01904	0.00074	Beta-P	0.03449	0.00783
SR curve	-0.12131	0.01580	<i>Modified negative exponential</i>	-0.02785	0.00129	SR curve	-0.06855	0.00822
<i>Modified negative exponential</i>	-0.12630	0.01646	<i>Modified power function</i>	0.04158	0.00191	<i>Modified negative exponential</i>	-0.07707	0.00888
Finite-area	-0.13960	0.02002	Finite-area	-0.04045	0.00223	Finite-area	-0.09003	0.01112
Negative exponential	-0.15987	0.02619	Negative exponential	-0.05872	0.00410	Negative exponential	-0.10929	0.01514
Modified logarithmic	-0.13267	0.03700	Beta-P	0.10525	0.01158	Modified logarithmic	-0.07586	0.01887
Collector's curve	459	481893	Collector's curve	0.07450	0.01301	Collector's curve	230	240947

Chazdon *et al.* 1998). Jackknife estimators, on the other hand, performed well in several other comparative tests (Palmer 1990, 1991, Boulinier *et al.* 1998b and references therein). Therefore, we currently recommend the use of these estimators. Nevertheless, we hope to encourage further tests of these methods using bird data sets, as we cannot draw firm conclusions from testing just a single data set (Colwell & Coddington 1994). Ideally, such comparative performance tests should be done using a combination of real and simulated data sets, consider a wide variety of model communities and test a large number of estimation methods (Palmer 1990, 1991, Colwell & Coddington 1994, Flather 1996, Boulinier *et al.* 1998b, Chazdon *et al.* 1998, Keating *et al.* 1998, Walther & Morand 1998). Recent tests using just a few estimation methods (range 2–4, mean 2.75) must therefore remain relatively inconclusive (Baltanas 1992, Samu & Lövei 1995, Winkler *et al.* 1997, Natuhara *et al.* 1998, 1999, Zelman & Esch 1999). In this study, non-parametric methods tended to perform better than accumulation curve models. Curve models may, however, perform better when fitted to

perform better than an accumulation curve models; e.g. all estimation methods (but one) that were even less precise than the species richness curve were accumulation curve models. Most estimation methods had the problem that they tended to underestimate species richness for early samples, but slightly overestimated it for late samples (with the exception of the second-order jackknife and the collector's curve model which overestimated species richness even for early samples).

DISCUSSION

Using bias and precision as criteria, the two Chao estimators had the best overall performance, followed by the two jackknife estimators. Other studies support the all-round performance of the Chao and jackknife estimators. For example, the Chao2 and the first-order jackknife estimators had the best performance in a comprehensive test using parasitic data sets (Walther & Morand 1998). The Chao estimators were also recommended based on the analysis of seed bank and tree seedling data sets, with the Chao2 estimator being much less sensitive to clumped data sets than the Chao1 estimator (Colwell & Coddington 1994,

Thirdly, the performance of these methods depends, of course, on the quality of the underlying data. Good statistical methods do not make bad data better. Without dabbling too far, we would like to point out that species richness needs to be defined in terms of the species, habitats, areas and time periods selected (Remsen 1994), that the influence of sampling methods should be considered (Coddington *et al.* 1991, Dawson *et al.* 1995, Remsen & Good 1996, Neave *et al.* 1997, Helbig & Flade 1999) and that differential observer abilities may have an influence on estimates of species richness (Boulinier *et al.* 1998b).

We suggest that using species richness estimation methods can greatly increase our ability to answer ecological questions and to guide conservation decisions. Of course, species richness alone should not be used to guide conservation decisions. Other factors such as endemism (Stattersfield *et al.* 1998), rarity (Gaston 1994), habitat specialization (Remsen 1994, Harrison & Martinez 1995), species sensitivity (Fornasari *et al.* 1999), complementarity of sites (Colwell & Coddington 1994) and biological organization (Maddock & du Plessis 1999) also need to be taken into account. Nevertheless, if species richness is used as one of the criteria, it should be properly determined. Especially for species-rich tropical bird communities, species richness estimation methods may prove to be the only useful rapid-assessment tools, as reliable estimates of abundance are much more difficult to obtain for tropical than for temperate species (Remsen & Good 1996), thus ruling out the use of diversity measures. Unlike diversity measures, species richness avoids judgements on the relative 'weight' or 'value' given to any species. Therefore, species richness still is the simplest and intuitively most satisfying measure of diversity' (Harrison & Martinez 1995).

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the real sampling curve, which often has a different shape from the randomly reshuffled accumulation curve (see Fig. 1). Furthermore, accumulation curve models may have some advantages. First, they allow a practical graphical depiction of the relationship between species richness and sampling effort. Secondly, these models are based on continuous and differentiable functions and can thus be used to predict the sampling effort needed to observe a set proportion of all species and the rate at which previously unobserved species will accumulate (Soberton & Llorente 1993). However, some non-parametric estimators have also been developed to deal with these problems (Keating *et al.* 1998, Solow & Polasky 1999).

These methods may prove useful not just for estimating bird species richness (e.g. Thiollay 1995), but may also be used to extrapolate the unknown size of a population (Sutherland 1996) or a song repertoire (Kroodsma 1982) or to estimate spatial and temporal variation of bird communities (Boulinier *et al.* 1998a, Nichols *et al.* 1998a, 1998b). For the practical use of these methods, three points should be kept in mind. First, an estimate of species richness without some associated measure of error, e.g. variance, is not very useful. Many species richness estimation methods have such variance estimators, but their performance also needs to be evaluated (for discussion of this problem, see e.g. Soberton & Llorente 1993, Colwell & Coddington 1994, Nichols *et al.* 1998a). A related problem is the minimum sample size needed to obtain a reliable species richness estimate (e.g. de Caprariis *et al.* 1981, Schleier & van Berem 1998). For example, one could sample a community until the variance estimate falls below a certain threshold. Alternatively, one could comprehensively sample a representative community, determine the sample size needed to attain a predetermined accuracy, and then use this sample size to sample other similar communities (Chazdon *et al.* 1998, see also Tackaberry *et al.* 1997).

Secondly, one needs to establish an appropriate unit of sampling effort. Such units may be equal time intervals, equal areas covered or equal numbers of individuals or species encountered (Bibby *et al.* 1992). Whatever sampling unit is used, producing two-dimensional tables (with species and sampling units in rows and columns) instead of one-dimensional species lists greatly increases the amount of information available. Besides enabling us to extrapolate species richness, such tables may be used to calculate abundance and diversity measures, detect seasonal population fluctuations, species co-occurrences and

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