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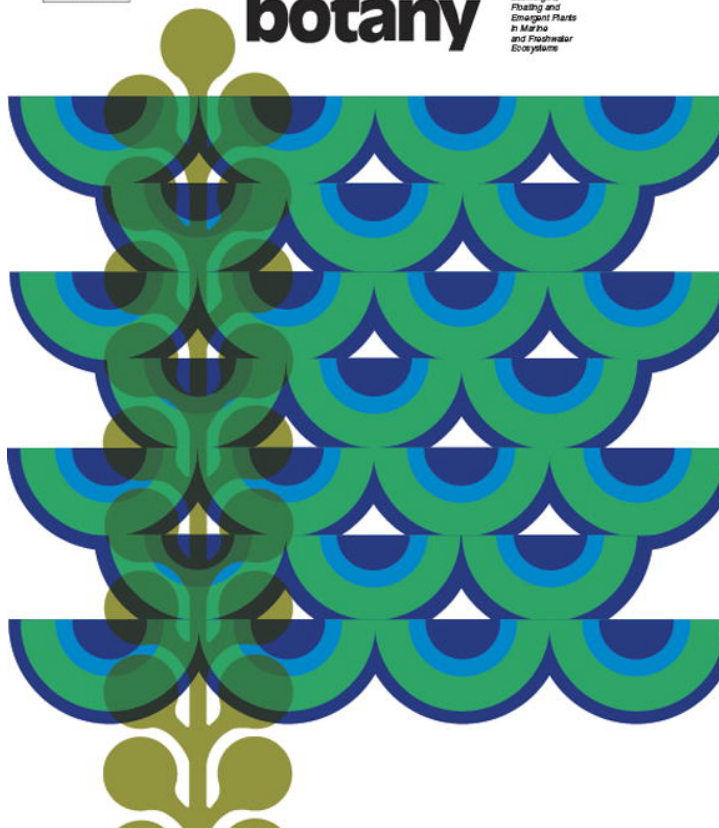


Volume 86, issue 4, May 2007

ISSN 0304-3770

Aquatic botany

An International
Scientific Journal
dealing with
Applied and
Fundamental
Research on
Submerged
Floating and
Emergent Plants
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Assessment of methods to estimate aquatic macrophyte species richness in extrapolated sample sizes

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Received 11 September 2006; received in revised form 18 December 2006; accepted 15 January 2007

Abstract

We evaluated six methods to estimate species richness in extrapolated sample size using presence–absence data for aquatic macrophyte assemblages. Methods suitable for assemblages involving terrestrial and non-clonal (unitary) organisms may not be valid for aquatic macrophytes. The extrapolation of a species accumulation curve using a logarithmic function or using a linear model on the log of accumulated sampling units consistently overestimated species richness. The newly proposed Total-Species method gave similar results. The Negative Binomial and Logarithmic Series methods and the recently proposed Binomial Mixture Model were unbiased and accurate. We conclude that current extrapolation techniques are valid for estimation of species richness in macrophyte assemblages, and recommend the Logarithmic Series, Binomial Negative or Binomial Mixture Model methods.

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Keywords: Diversity; Ecological method; Species inventory; Community ecology

1. Introduction

The ecological importance of aquatic macrophytes has been widely recognized (Wetzel, 2001; Duarte et al., 1994). In recent decades, ecological studies have focused mainly on the physical and chemical variables that allow prediction of abundance and biomass of several species, and on tests of hypotheses regarding mechanisms that cause variations in these attributes (e.g., Nilsson and Keddy, 1988; Rørslett, 1991; Bini et al., 1999; Lacoul and Freedman, 2006; Rolon and Maltchik, 2006). Additionally, the recognition by ecologists and society in general of the importance of biodiversity has stimulated assessments of species richness and, in particular, the factors that determine aquatic plant diversity (Murphy et al., 2003; Edvardsen and Økland, 2006).

Several recent investigations have studied the association of aquatic organisms with aquatic plant beds in tropical and subtropical (natural or man-made) aquatic ecosystems. The important role of macrophytes in maintaining aquatic

biodiversity has been shown for micro- and macro-invertebrates (Lansac-Tôha et al., 2003; Takeda et al., 2003), fish (Araújo-Lima et al., 1986; Delariva et al., 1994; Agostinho et al., in press) and large terrestrial vertebrates (Pott and Pott, 2000). For instance, Agostinho et al. (2003) found a significant positive relationship between fish diversity and aquatic plant diversity in subtropical Brazilian reservoirs. This finding emphasizes the important role that aquatic plant diversity may have in these geologically new, artificial ecosystems, where management practices should aim to increase biodiversity.

The number of species is the most frequently and widely applied measure of biodiversity (Magurran, 2004). This simple metric captures much of the biodiversity essence, is a measurable parameter, its meaning is widely understood, and much data on species richness already exists (Gaston, 1996). Nevertheless, it is widely recognized that this apparently simple attribute is nearly always underestimated in inventories because of its strong dependency on sample effort. In other words, observed species richness is a negatively biased estimator of the true richness in the sampled community (Chazdon et al., 1998). Because richness increases in direct relation to the number of individuals, area, and variety of habitats sampled, differences in sampling methods may introduce statistical and ecological bias

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into comparisons of diversity among different localities (Schluter and Ricklefs, 1993).

To overcome these problems, several methods to estimate species richness in communities have been developed and popularized in the last decade (Colwell and Coddington, 1994; Chazdon et al., 1998; Bini et al., 2001; Melo and Froehlich, 2001), despite criticisms of their performance in real situations (Chiarucci et al., 2003; Melo, 2004). An old and related problem faced by ecologists is to estimate species richness not in the community, but at an extrapolated sample size (Evans et al., 1955; Keating et al., 1998; Melo et al., 2003). Estimation of species richness in extrapolated sample sizes is useful during survey optimization, when the following question is constantly asked by ecologists and conservationists: how many unseen species would be found in an additional sampling effort? Thus, when comparing species richness among assemblages, researchers may opt to standardize sample size by extrapolating species accumulation curves of the less-sampled assemblages to the sample size of the best-sampled assemblage.

Despite the interest of some early researchers in estimates of species richness in extrapolated sample sizes (Evans et al., 1955), the topic received little attention from ecologists for decades. Recently, evaluations and reviews of current methods (Keating et al., 1998; Melo et al., 2003), together with the development of new methods (Ugland et al., 2003; Colwell et al., 2004) have again attracted the attention of ecologists.

In this paper, we investigate whether current methods available to estimate species richness in extrapolated sample sizes are suitable for modular organisms, such as aquatic macrophytes, for which only incidence data are available. We also evaluate the performance of some recently developed methods that still remain largely untested, using data from macrophytes.

2. Materials and methods

2.1. Study area

The Itaipu Reservoir is located on the Rio Paraná, on the border of Brazil and Paraguay. The reservoir was filled in 1982, extends 170 km upstream, has an average width of 7 km and occupies an area of 1350 km². The sites studied were located in eight arms of the eastern side of the reservoir, formed by the rivers Arroio Guaçu, São Francisco Verdadeiro, São Francisco Falso, São João, São Vicente, Ocoi, Pinto and Passo Cuê (Fig. 1).

2.2. Field survey

The survey was carried out during April 1999, at 30 sampling sites in each arm, except for the Arroio Guaçu and Pinto arms, where 26 and 29 sites, respectively, were surveyed. A total of 235 sampling sites (stations) were thus obtained. The sampling sites were distributed along the arms, from their uppermost part down to the reservoir main body. Detailed information about sampling methods was given by Bini and Thomaz (2005).

Surveys were carried out by two persons in a boat moving at constant, low speed during approximately 10–15 min in a strip ca. 100 m along the bank. Sampling for periods longer than 10 min did not increase the number of species found at a given site (data not shown). Submerged species were collected with forks to a depth of 3.5 m, the limit of colonization for most species in Itaipu (Bini and Thomaz, 2005). Sampling effort was similar at each site.

The plants collected were identified according to Hoehne (1979), Moore (1986), Lorenzi (1991) and Cook (1990). Most samples were deposited at the Universidade Estadual de Maringá Herbarium (HUM).

2.3. Data analysis

The approach adopted in the study was the estimation of species richness in the full sample (235 sampling sites distributed in eight arms), using different subsample sizes. A good method should be able to accurately estimate total species richness (i.e., the richness recorded in 235 sampling sites) using a small subsample size. In addition, a good method should be precise (similar results obtained with different subsamples of a given size). In order to evaluate precision, 50 random samples of each subsample size were obtained and used to extrapolate species richness. We used the standard deviation of estimates produced by these 50 subsamples as a measure of precision. Estimates from each method described below were compared to the total species richness observed in the full sample (235 sampling sites). In order to best evaluate differences among estimates and observed species richness, we computed the confidence interval for total observed species richness using the method developed by Colwell et al. (2004).

Six methods to extrapolate species richness were evaluated. Three of these methods were chosen after their good performance with data regarding stream macro-invertebrates and a range of terrestrial assemblages (Keating et al., 1998; Melo et al., 2003). The first method is the extrapolation of a species accumulation curve using a Logarithmic function (hereafter Log; Soberón and Llorente, 1993; Melo et al., 2003). The second and third methods, Negative Binomial (NB hereafter) and Logarithmic Series (LS), are derived from relative abundance models (Efron and Thisted, 1976; Keating et al., 1998). Detailed descriptions and formulae for these methods are available in Melo et al. (2003).

Colwell et al. (2004) proposed a general Binomial Mixture Model (BMM) for the species accumulation function based on incidence data. The function is an analytical solution for the species accumulation curve, and can be used to estimate species richness either in interpolated or extrapolated sample sizes. Except for the data sets used in the original publication (birds, seeds, ants and trees), we are not aware of any evaluation of this new method.

Ugland et al. (2003) proposed an estimator of species richness in extrapolated sample sizes that takes into account the spatial heterogeneity among sampling units. The method, termed Total-Species (hereafter T-S), explicitly uses data from sampling units collected in different locations (in our study,

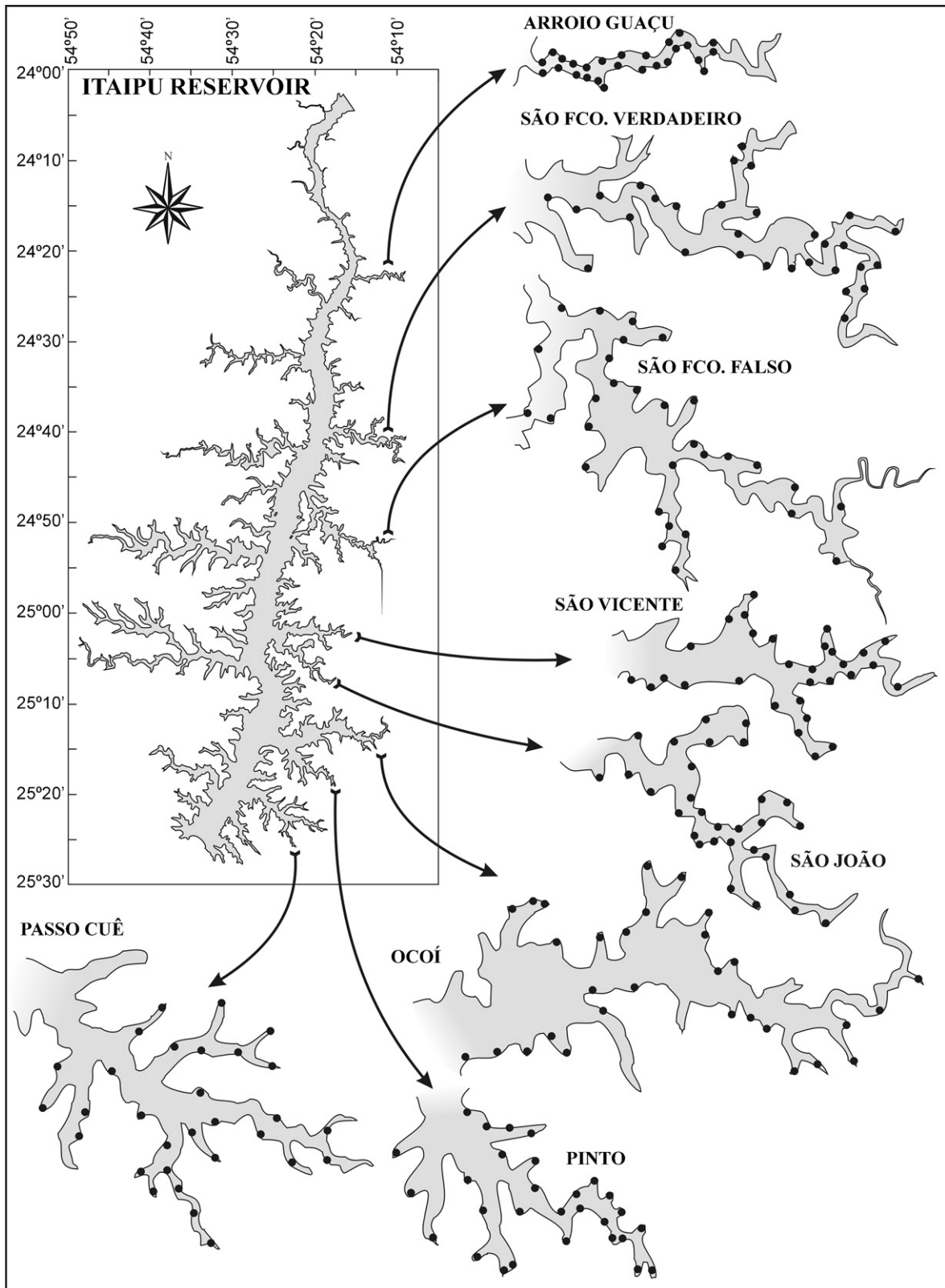


Fig. 1. Map of the Itaipu Reservoir and the eight arms studied. Dots indicate sampling sites.

arms). Species accumulation curves are constructed for each location and the mean curve obtained (Fig. 2). Locations are then combined in all possible pairs and a mean species accumulation curve is obtained. The same procedure is

repeated, but now using combinations of three locations. The procedure ends when all locations are combined and a single curve is obtained (the traditional species accumulation curve) (Fig. 2). Given the general observation that sampling units from

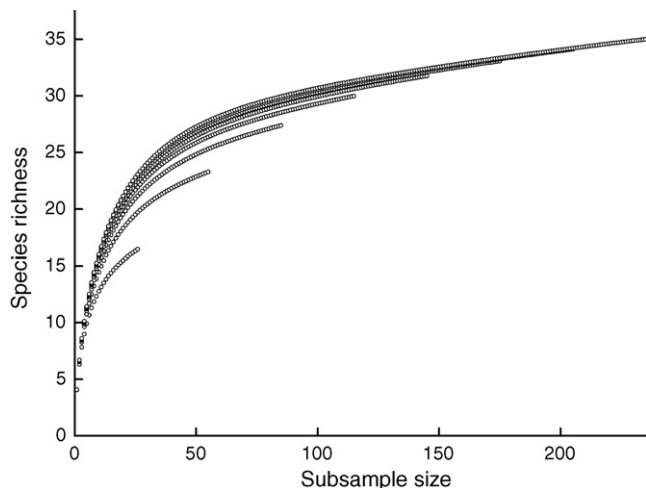


Fig. 2. Illustration of the Total-Species (T-S) method to estimate species richness in extrapolated sample sizes. The shortest curve indicates the mean of species accumulation curves obtained in each arm. The second shortest curve indicates the mean of species accumulation curves obtained by all combinations of two arms. The remaining curves were obtained successively by combining additional arms up to the number of arms available (eight, the longest curve). For the example above, all sampling units of each arm were used. The species richness observed at the terminal point of each curve is regressed on the log of the number of accumulated sampling units. The T-S method is the extrapolation of the fitted straight line.

the same location are usually more similar in species composition to each other than to sampling units from different locations, the mean species accumulation curve has a lower slope than the curve constructed using sampling units obtained from all locations pooled (the traditional species accumulation curve). On the other hand, if locations have the same species composition, the mean accumulation curve and the species accumulation curve will be nearly identical. The species richness observed at the terminal point of all curves is used to construct the T-S curve. Estimates of species richness are obtained by extrapolating the T-S curve. If locations have different numbers of sampling units, the T-S curve is obtained not by the terminal points of the mean curves, but by the mean richness in the subsample size of the smallest curve. We followed the extrapolation procedure of Uglund et al. (2003) and used a simple linear regression to fit T-S values against the log of the number of sampling units. Our data are well suited to this method, because the surveys were carried out in eight distinct locations (arms) that differ considerably according to

their limnology and morphology (Bini and Thomaz, 2005). Thus, differently from other methods, in which data from different locations were pooled, the T-S method also took the benefit of the spatial variation (among arms) in species composition (beta diversity) to estimate “total” species richness from a small sample size. O’Dea et al. (2006) evaluated the method using data for birds in Ecuador.

The last method evaluated was simply the linear extrapolation of the species accumulation curve regressed on the log of sample size (LogLin). The method is one of the simplest and oldest available in the literature, and originated from the species-area debate of early ecologists (Magurran, 2004). LogLin is equivalent to the T-S method, without taking into account heterogeneity among locations. Whereas accumulation curves for the T-S method are constructed using *all* sampling units from a particular location(s), curves for LogLin are constructed using sampling units randomly selected from all locations, i.e., the traditional species accumulation curve (Colwell and Coddington, 1994).

A set of 50 subsamples for each subsample size was used for methods Log, NB, LS, BMM and LogLin. Subsample sizes for these methods were 5, 10, 15, ..., 230 sampling units. The T-S method requires stratified sampling according to locations, and thus the method was computed using a different set of 50 subsamples for each subsample size. For the T-S method, subsample sizes were 16, 24, 32, ..., 208, 215, 222, 229 and corresponds to 2, 3, 4, etc. sampling units of each location (arm). The last three subsample sizes are not multiples of 8, because one arm (Arroio Guaçu) contained only 26 sampling sites.

All calculations were done using the R software (R Development Core Team, 2005). Species accumulation curves were calculated using the function available in the package ‘vegan’ (Oksanen et al., 2005). The method BMM was computed using R functions written by C.X. Mao (University of California, Riverside, USA). Specific functions were written to obtain subsamples and calculate the remaining methods.

3. Results

Thirty-five species were identified in the eight arms. The most frequent species, considering all 235 sampling sites, were the emergent *Urochloa plantaginea* (Link) Welster (63%), *Ludwigia suffruticosa* (L.) Hara (61%), *Eleocharis filiculmis* Kunth. (53%), the submerged *Egeria najas* Planch. (38%) and

Table 1
Main attributes of the aquatic macrophyte assemblage surveyed

Arm	Mean <i>S</i> per stand (S.D.)	Observed richness	Number of uniques	Number of duplicates
AG	3.3 (1.6)	13	4	5
SFV	2.6 (1.4)	13	6	7
SFF	4.3 (2.2)	25	1	6
SV	3.5 (1.6)	14	3	5
SJ	4.4 (1.5)	13	1	3
Ocoi	5.2 (2.6)	21	1	3
Pinto	4.2 (2.1)	20	2	1
PC	4.9 (1.9)	16	0	2

S, species richness; S.D., standard deviation; uniques, number of species collected in only one stand; duplicates, number of species collected in only two stands; AG, Arroio Guaçu; SFV, São Francisco Verdadeiro; SFF, São Francisco Falso; SV, São Vicente; SJ, São João; PC, Passo Cuê.

the rooted with floating leaves *Nymphaea amazonum* Mart. et Zucc. (25%). Six species occurred at only one sampling site, the emergents *Echinodorus grandiflorus* Mitch., *Hydrocotyle ranunculoides* L., *Polygonum stelligerum* Cham., *Pontederia cordata* L., *Typha domingensis* Pers, and the free-floating *Pistia stratiotes* L.

The arms showed considerable differences regarding species richness per stand (site) and total species richness. On average, the poorest stands were found in the São Francisco Verdadeiro arm (2.6 species), and the richest ones in the Ocoi arm (5.2

species) (Table 1). The arms also differed in total species richness, which ranged from 13 species (Arroio Guaçu, São Francisco Verdadeiro and São João arms) to 25 species (São Francisco Falso arm) (Table 1). The number of uniques and duplicates in each arm ranged from 0 to 6 and 1 to 7, respectively (Table 1).

The methods Log, LogLin and T-S were relatively robust (i.e., precise) for different subsamples for a given sample size (Fig. 3). In contrast to the other methods, the high precision of Log, LogLin and T-S methods was evident even at very small

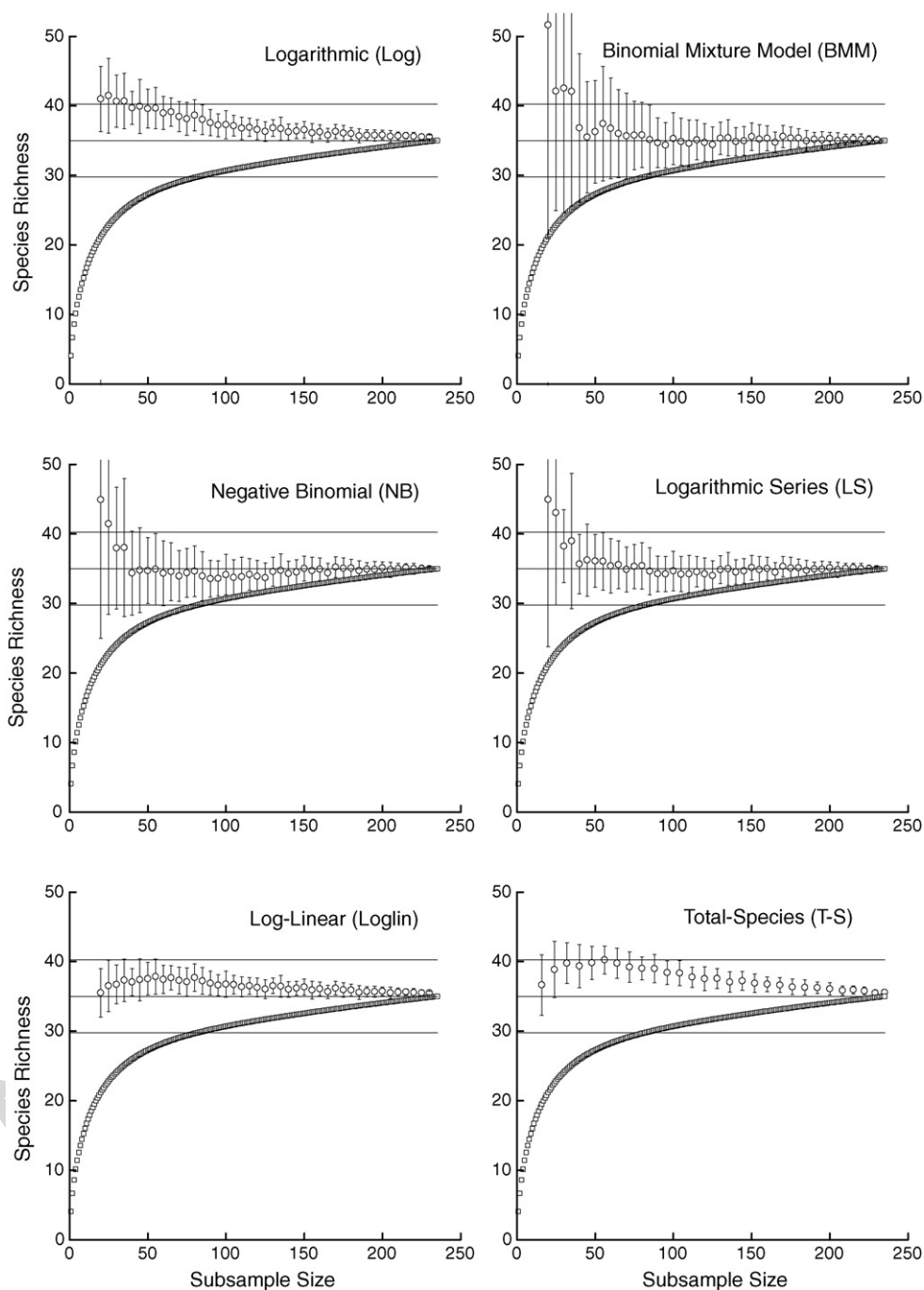


Fig. 3. Species accumulation curve of aquatic macrophytes in 235 sampling units obtained in eight arms of the Itaipu Reservoir, and estimates of species richness in the total sample using subsamples. Horizontal lines indicate the total species richness in 235 sampling units and its confidence interval. Dots indicate the mean estimates of species richness in 235 sampling units, using 50 subsamples of different sizes. Error bars indicate 1S.D. of estimates obtained by 50 subsamples.

subsample sizes (<50 sampling sites). Despite their high precision, Log, LogLin and T-S methods were biased and consistently overestimated observed species richness in the full sample. For instance, the lower ends of the standard deviation error bars for most of the subsample sizes exceeded the observed species richness in the full sample. This overestimation was more severe for Log and T-S.

The methods BMM, NB and LS were affected by different subsamples, and accordingly produced high standard deviations of estimates (Fig. 3). This level of imprecision was particularly high for the BMM method at small subsample sizes. The NB and LS methods tended to be more precise for subsamples larger than 40 sampling sites, whereas the BMM attained reasonable precision only after accumulation of 75–100 sampling sites. The BMM, NB and LS methods overestimated total species richness in very small sample sizes, but attained excellent accuracy with subsample sizes larger than 35 sampling sites (i.e., 15% of the full sample). All mean estimates from the BMM, NB and LS methods using sample sizes larger than 35 sampling sites were within the confidence interval for the observed species richness in the full sample.

4. Discussion

Our results show that the three extrapolation methods suggested by Melo et al. (2003) for non-clonal organisms (Log, NB and LS) performed differently for data on aquatic macrophytes. In particular, the NB and LS methods were very accurate (estimated values close to the observed richness), unbiased (low predominance of higher and lower values compared to the observed richness), and showed good precision (short error bars) after 35 sampling units (i.e., 15% of the total samples) had been accumulated. On the other hand, despite its high precision, the Log method showed consistent positive bias. The recently proposed BMM method was as accurate as the NB and LS methods, but was less precise in small subsample sizes. The performance of the T-S method was similar to the Log method in terms of bias and precision. However, different from the Log method, the T-S method was unusual in showing a curved trend in accuracy (low, high and then low again). Similarly to the Log and T-S, the LogLin method showed good precision but high bias. The LogLin method differed from Log and T-S methods, however, in giving better accuracy.

The unbiased and accurate estimates produced by the NB and LS methods confirm previous findings using data from terrestrial organisms, aquatic macro-invertebrates and simulated assemblages (Keating et al., 1998; Melo et al., 2003). Melo et al. (2003) recommended that extrapolations should be made up to 1.8–2.0 times the current sample size. In the present study, the NB and LS methods were good at estimating species richness in 235 sampling units, using as few as 50 sampling units, an extrapolation of 4.7 times the current subsample size. In other words, for this subsample size, the mean estimates were very similar to the observed species richness. Perhaps more importantly, most of the individual estimates (1S.D.) were within the confidence interval of the observed species richness.

The NB and LS methods are derived from the Log-Series distribution of abundances (Fisher et al., 1943). Accordingly, one can expect that these methods are valid only for data sets following the Log-Series distribution. Keating et al. (1998) evaluated these two methods in a range of simulated communities obtained from broken-stick, random-fraction and geometric series species abundance distributions. They found that, among the 11 estimators evaluated, NB was the best in most of the simulated data sets. Additionally, Keating et al. (1998) observed that the NB was robust to different empirical data sets. Similarly, Melo et al. (2003) used six contrasting field data sets and concluded that NB and LS were the best methods evaluated. The results of the present study and of those of Keating et al. (1998) and Melo et al. (2003) indicate that good performances of NB and LS are mostly independent of specific species abundance distributions. Further simulated studies are needed to determine the range of species abundance distributions for which NB and LS produce reliable estimates.

We observed that the BMM method, based on sophisticated statistical reasoning (Colwell et al., 2004; Mao et al., 2005), was not robust for differences among subsamples until around 100 sampling units had been accumulated. This means that despite the overall accuracy of this method, users can have low confidence in the single estimate obtained in their studies when extrapolating to very large sample sizes. The largest magnitude of extrapolation for the BMM method obtained in this study and which still produced precise estimates was around 2.75. However, this is within the range of 2–3 recommended by Colwell et al. (2004) and even superior to the range 1.8–2 recommended by Melo et al. (2003).

The Log, T-S and LogLin methods were all positively biased. The biased behavior of the Log method contrasts with its excellent performance in a previous study carried out with datasets of stream macro-invertebrates and a range of terrestrial organisms (Melo et al., 2003). The positive bias of LogLin observed in the present study confirms the results of Melo et al. (2003). The recently proposed T-S method was evaluated by O'Dea et al. (2006), using data from bird assemblages in Ecuador. Similarly to our results, they found that the method usually overestimated species richness in extrapolated sample size. O'Dea et al. (2006) also contrasted the results of the T-S method against those obtained using the LogLin method, and concluded that the latter is more accurate. Our results are very similar to their conclusions, despite the marked difference in assemblage structure of forest birds and aquatic macrophytes. Accordingly, O'Dea et al. (2006) discussed the suggestion of Ugland et al. (2003) to incorporate spatial heterogeneity in extrapolations of species accumulation curves (T-S is basically the LogLin method incorporating spatial heterogeneity).

Our results suggest that methods developed to estimate species richness in extrapolated sample sizes of terrestrial and non-clonal organisms are equally valid for data from subtropical macrophyte assemblages. In particular, the NB, LS and BMM methods were unbiased, accurate and precise and very reliable to extrapolations in the range 2–3 times the current sample size.

Acknowledgements

We acknowledge with appreciation Maria do Carmo Roberto and Raul Ribeiro (Universidade Estadual de Maringá) and Sandro Alves Heil (Itaipu Binacional) for field assistance. Débora Cristina de Souza (CEFET-Campo Mourão) was helpful in the field and identification of plant species. Two anonymous referees and Jan Vermaat suggested improvements to the manuscript. Janet Reid reviewed the English. Funds for this research were provided by Itaipu Binacional (to SMT) and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (proc. 476256/2004-6 to ASM, and proc. 302707-2004-2 and 4725372004-0 to LMB). Dr. Chang X. Mao provided the R functions to calculate the BMM estimator.

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