Sampling tropical spiders: Estimating the biodiversity of the orbweaving families Araneidae, Nephilidae and Tetragnathidae in natural and disturbed habitats in Trinidad, West Indies

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Abstract: Detailed ecological knowledge and information on efficient sampling is lacking for many diverse tropical groups such as spiders. In this study sampling efficiency, in terms of the comparison of observed and estimated species richness, was evaluated at 64 sites in both natural and disturbed habitats in Trinidad. Sampling efficiency was 56-57 % in both natural and disturbed habitats after five 3-hour samples per site, each of 1 h sweeping and 2 h visual search. The performance of nine species richness estimators was evaluated based on bias and precision. It was found that the bootstrap and Michaelis-Menten estimators performed poorly, while the coverage estimators performed the best. The median of the nine was, however, preferred to any single estimator as a robust measure of total species richness.

Resumen: Se carece de conocimiento ecológico detallado y de información sobre el muestreo eficiente de muchos grupos tropicales diversos como las arañas. En este estudio la eficacia del muestreo, medida en términos de la comparación de las riquezas de especies observada y la estimada, fue evaluada en 64 sitios en Trinidad, incluyendo tanto hábitats naturales como perturbados. La eficacia del muestreo fue 56-57 % tanto en los hábitats naturales como en los perturbados después de cinco muestreos de 3 horas por sitio, cada uno con 1 h de barrido y 2 h de inspección visual. El desempeño de nueve estimadores de la riqueza de especies fue evaluado de acuerdo con el sesgo y la precisión. Se encontró que los estimadores 'bootstrap' y de Michaelis-Menten tuvieron un desempeño pobre, mientras que el mejor desempeño correspondió a los estimadores basados en la cobertura. No obstante, para tener una medida robusta de la riqueza total de especies se prefirió usar la mediana de los nueve estimadores en lugar de usar un solo estimador.

Resumo: Oconhecimento ecológico detalhado e informações sobre a eficiência da amostragem está faltando para muitos e diversos grupos tropicais, como as aranhas. Neste estudo, a eficiência de amostragem, em termos de comparação dos dados observados e da riqueza específica estimada, foi avaliada em 64 locais quer em habitats naturais e quer em perturbados na Trindade. A eficiência da amostragem foi de 56-57 % em ambos os habitats naturais e perturbados depois de cinco de amostras de 3 hora por local: 1 h de varrimento e 2 h de busca visual. O desempenho de nove estimadores de riqueza específica foi avaliada com base em desvios e precisão. Verificou-se que os estimadores de reamostragem, "bootstrap" e Michaelis Menten, mostraram um desempenho fraco, enquanto os estimadores de cobertura tiveram o melhor desempenho. No entanto, a mediana dos nove foi preferida a qualquer estimador singular como uma medida robusta da riqueza específica total.

Key words: Bias, Neotropics, precision, sampling efficiency, species richness, spiders.

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Introduction

Currently there are just over 43,000 described species of spiders (Platnick 2012), a number which is believed to represent only about one-fifth of the actual world total (Coddington & Levi 1991). Tropical regions have long been associated with high species richness (e.g. Clarke & Downie 2004; DeVries et al. 1997), but their spider faunas are little known compared to those of temperate regions (Coddington & Levi 1991; Chen & Tso 2004). Faunal surveys are usually limited by duration and resources and so tend to favour vertebrates (Green et al. 2009) and plants, resulting in only the most well-known but least diverse groups being adequately sampled (Scharff et al. 2003). There is, therefore, a lack of information on groups such as arthropods (Longino 1994), considered the most diverse organisms in terrestrial ecosystems. Sampling arthropods is a challenge because of traits such as small size, diversity, population fluctuations, and strict environment requirements (microhabitats) (Scharff et al. 2003). However, it is these same traits that make them ideal for use in mapping environmental diversity and tracking environmental changes rapidly and precisely.

Species richness is one of the oldest and most fundamental measures in community ecology (Peet 1974), important as it acts as a "surrogate for the more complex concept of biological diversity" (Hellmann & Fowler 1999). Species richness has many features that make it ideal for biodiversity assessment, such as the ease with which it can be attained from samples; its generality as a comparative value across communities; and the ease with which it is understood by persons from a variety of educational backgrounds. All of these features also make species richness an important factor when developing conservation plans (Hellmann & Fowler 1999). The observed species richness is simply determined by counting the species obtained at each locality. However, many factors make it impossible to collect all of the species present in a locality or habitat. Species richness estimators have, therefore, been developed to estimate the total number of species present from incomplete samples (Colwell & Coddington 1994). In this study nine species richness estimators were applied; they are derived from several different underlying models and methods so that they have their own individual strengths and weaknesses (Petersen & Meier 2003). This study thus had two aims: first, to define the sampling effort needed to obtain reliable estimates of the

species richness of a guild of spiders in neotropical habitats. Second, to compare the performance of different estimators of species richness on this tropical arthropod fauna.

Members of the orb-weaving spider families Araneidae, Nephilidae and Tetragnathidae were selected for study because they lead a uniform lifestyle, forming a recognisable ecological guild, and because their webs increase the ease of detection. Two general methods were used for sampling habitats; visual search and sweepnetting. The number of sampling methods was kept to a minimum in order to reduce complication of the sampling protocol as suggested by Coddington et al. (1991). Marrett & Snazell (1983) and Churchill (1993) conclude that the use of different specialized collection methods can lead to misrepresentation of certain components of spider assemblages, rather than producing a thorough sample of the area under investigation.

Materials and methods

Study areas

This study took place on the island of Trinidad in the West Indies (11° 00'N 61° 00'W) which has an area of 512,800 ha and a maximum elevation of 940 m. The Gulf of Paria, which is 14 km wide at the narrowest point, separates the island from South America; Trinidad is a continental island with a neotropical fauna.

Sample sites including all of the main natural and disturbed vegetation types were selected based on the vegetation classification of Beard (1946). A total of 46 sites were sampled from 16 different natural habitat types, which include rainforests, savanna, swamp, mangrove woodland, littoral woodland and riparian vegetation, and 18 sites from three disturbed habitats (secondary forests, cocoa fields, and farmland) (Sewlal 2012). The areas of secondary forest were originally primary forest habitat cleared for agriculture, firewood or timber extraction within the past 50 years, but since undisturbed. Cocoa fields included areas used for the cultivation of cocoa (*Theobroma cacao*), and included trees such as immortelle (Erythrina poeppigiana) which are used to shade the cocoa trees and banana trees (Musa spp.). The areas sampled were actively cultivated, except for the Centeno Research Centre, where cocoa was grown for research purposes. Farmland refers to land currently in use for agriculture of short term crops such as tomatoes, string beans, pumpkins, ochroes,

corn and sweet peppers in a mixed-cropping system. Areas had not been sprayed with pesticides within 2 - 6 weeks before sampling. When present, the vegetation between the crops, consisting of grass or weeds, was also included in the sampling.

Sampling

The topography of some sites made it difficult to establish plots so time-based collection methodsvisual search and sweep-netting were used. For visual search the collector walked around and collected the spiders seen by hand. The surface of plants, tree stems and logs were searched to above head height, but not leaf litter or under logs and stones. Sweep-netting was carried out by sweeping the vegetation to a height of about 2.5 m with a tough canvas insect net. For farmland sites the vegetation between the rows of crops in addition to the crops were sampled using visual search, however, sweep-netting was primarily concentrated in the between-row vegetation and carried out lightly on the crops so that the vegetables would not be damaged. After each round of sweeping, large pieces of vegetation such as leaves and twigs were shaken in the net to dislodge any spiders and then discarded. All spiders seen were removed from the net by hand and placed in glass vials filled with 70 % alcohol. The transfer of specimens to the vials was carried out entirely within the confines of the net to prevent the loss of material. Sweeping was not carried out in the mangrove woodland and herbaceous swamp habitats, which lack an understory vegetation stratum. Both methods were carried out with the presence of an assistant, who did not participate in collection or contribute to the total search time. The sampling session was timed using a stop watch, which was paused during data collection and recording.

Sampling methods were tested during preliminary surveys at two sites of evergreen seasonal forest and one of deciduous seasonal forest. Species accumulation curves for each site levelled off after five 3-hour sampling days. In this study each site was, therefore, sampled for 15 hours, consisting of five samples each of 1 hour sweep-netting and 2 hours visual search. Each sample was in a separate area of the same habitat; where possible this was contiguous with the others at that site, but in any case with a maximum total spread of 1 km between the samples at a site. Sampling was carried out intermittently, based on weather conditions and the availability of field guides, and occurred on 190 days and in 27 months in the period March 2006 to May 2009. Each site was located at least 6 km from any other site, and was sampled within a space of two weeks to reduce the chances of species richness being inflated by a succession of different transient species.

Analysis

Spiders have soft bodies, especially abdomens, so they cannot be pinned and dried like insects; the loss of the abdomen is detrimental as it results in the loss of diagnostic features such as spinnerets and the epigynum of females. For identification to family, all specimens were transferred from numbered plastic snap cap vials to 70 % alcohol in small Petri dishes, and manipulated with Bioquip soft tweezers and probes under an X40 Olympus SZ-ST dissecting microscope. Specimens belonging to the three families under study were then identified to species level and subsequently stored in 15×45 mm glass vials with a plastic plug.

It is the typical practice in spider biodiversity studies (for instance Toti *et al.* 2000 and Sørensen *et al.* 2002) to discard juveniles because certain diagnostic features, such as the genitalia, are not fully developed, making identification to species level ambiguous, difficult and time-consuming. However, in order to obtain a reliable estimate of species richness their presence was included as many araneid species have distinguishing body shapes and colour patterns making accurate identification of juveniles possible, as used in some previous studies such as Jiménez-Valverde & Lobo (2007).

Voucher specimens from this study were deposited in the Land Arthropod Collection of The University of the West Indies, St. Augustine; in the National Museum of Trinidad and Tobago; and in a personal collection (Sewlal 2010).

Species accumulation curves were constructed for each site sampled. Nine species richness estimators were calculated, using the program Estimates 8.0 (Colwell 2006): abundance-based coverage estimator ACE (Chao *et al.* 1993; Chazdon *et al.* 1998), incidence-based coverage estimator ICE (Chazdon *et al.* 1998; Lee & Chao 1994), Chao's estimators Chao 1 (Chao 1984) and Chao 2 (Chao 1987), first and second order jackknife estimators Jack 1 and Jack 2 (Burnham & Overton 1978, 1979; Heltshe & Forrester 1983), the repeated subsampling bootstrap (Smith & van Belle 1984), and two based on species accumulation curves, Michaelis-Menten Means and Michaelis-Menten Runs (Raaijmakers 1987). Subsequent statistical analysis used Minitab.

Results

Estimated species richness

Estimates of species richness for the nine separate estimators across the 64 sites (i.e. n = 576) were strongly right skewed, with values ranging up to 83 species (Fig. 1). The median was, therefore, more appropriate than the mean as a measure of central tendency to summarise each site. The individual estimates are given in Sewlal (2012).

The nine estimators were all significantly correlated with each other, and with their median value (Table 1, all P << 0.001). Parametric (Pearson) correlation coefficients were in general lower than nonparametric (Spearman) rank correlations, but showed the same trends. The two Michaelis-Menten estimators showed the lowest correlations with the other estimators (mean correlation coefficient against the other eight estimators) and with the median, followed by Bootstrap and ICE (Fig. 2). The remaining estimators showed no consistent pattern, and were strongly correlated with each other and with the median. In general, related estimators showed the strongest correlations (Table 1), such as between ACE and ICE (0.994 - 0.995), Chao 1 and Chao 2 (0.996 - 0.999), and Jack 1 and Jack 2 (0.984 -0.985).

All nine estimators provided the best fit to the median for at least one site (Table 2), though there was substantial variation in their effectiveness in this respect. ACE was the best fit to the median at 15 sites, including eight sites at which it was joint first (counted as half); at seven sites it was joint with ICE and at one site with Chao 1. ICE also performed well as it was the best fit to the median at 10.5 sites, including seven jointly with ACE. Chao 1 and Chao 2 were joint first at three sites. The poorest performing estimator in this respect was the bootstrap, which was the best fit to the median at only one site. Seven sites were best fitted by multiple (range 4 - 9) estimators, and were not considered in Table 2. The efficiency of the estimators according to "best fit" follows the order ACE > ICE > Jack 1 = Jack 2 > Chao 1 > Chao 2 > MM Runs > MM Means > Bootstrap.

A third way of assessing the performance of

the individual species richness estimators is to compare the estimates they produced with the observed species richness as this sets a lower limit on the number of species that must be present, i.e. an extreme measure of bias. Using this criterion, Jack 2 and both Michaelis-Menten estimators performed poorly, producing estimates lower than the observed in two or three sites each (Table 2). Another measure of bias is whether the estimate was significantly more often greater than the median (positive bias) compared to lower than the median. Three estimators (ICE, Jack 2 and Michaelis-Menten Runs) showed significant positive bias, another three (Chao 1, Chao 2 and Bootstrap) showed significant negative bias, and the other three (ACE, Jack 1 and Michaelis-Menten Means) were not significantly biased (Table 2).

A fourth criterion is precision, the average unsigned deviation of the estimate from the median, which varied significantly among the estimators ($F_{8,567} = 12.0$, P < 0.001). ACE and the two Chao and Jack estimators performed well in this respect, with average precision within 2.0 of the median (Table 2). The bootstrap and the two Michaelis-Menten estimators had low precision. Another measure of precision is the number of sites at which an estimator gave the highest value, as the individual estimates were right skewed (Fig. 1) and the maxima were well above the medians in all cases. Michaelis-Menten Runs was particularly poor in this respect, giving the highest value at 39 of the 64 sites (Table 2).

There was, therefore, substantial variation in the effectiveness of the nine separate estimators, with ACE, ICE, and the two Chao and Jack estimators being most consistent. Nevertheless all the separate estimators, with perhaps the exception of ACE, gave poor results at a proportion of sites. ACE was highly correlated with the median of all nine estimators, and the median was, therefore, used as the estimated species richness for each site when calculating sampling efficiency.

Sampling efficiency

There was a significant relationship between median estimated species richness (S_{est}) and observed species richness (S_{obs}) among the 46 sites with natural habitats (Fig. 3). The regression equation was:

$$S_{est} = 1.773 S_{obs} - 1.73$$
(1)

 $(F_{1,44} = 124.8; P < 0.001, r^2 = 0.73)$. The constant of -1.73 was not significantly different from zero (S.E. = 1.24, t = -1.40, P = 0.17). The estimated

Table 1. Similarity matrix using Spearman's rank correlation (r_s , top half) and Pearson's correlation (r, lower half) values between the nine species richness estimators and with their median value, for 64 sites of natural and disturbed habitats. All values are significant at P << 0.001.

	ACE	ICE	Chao 1	Chao 2	Jack 1	Jack 2	Bootstrap	MMR	MMM	Median
ACE	-	0.994	0.970	0.966	0.934	0.962	0.898	0.805	0.926	0.976
ICE	0.995	-	0.963	0.957	0.918	0.952	0.878	0.782	0.918	0.967
Chao 1	0.927	0.899	-	0.999	0.958	0.974	0.932	0.805	0.865	0.988
Chao 2	0.918	0.887	0.996	-	0.961	0.973	0.937	0.809	0.861	0.987
Jack 1	0.838	0.790	0.861	0.863	-	0.984	0.993	0.860	0.896	0.975
Jack 2	0.892	0.853	0.911	0.907	0.985	-	0.962	0.851	0.899	0.987
Bootstrap	0.778	0.723	0.808	0.813	0.991	0.956	-	0.863	0.879	0.952
MMR	0.680	0.644	0.704	0.683	0.755	0.766	0.729	-	0.845	0.850
MMM	0.881	0.883	0.703	0.691	0.773	0.794	0.734	0.636	-	0.909
Median	0.942	0.909	0.969	0.968	0.924	0.957	0.880	0.770	0.781	-



Fig. 1. Frequency distribution of estimated species richness of orb-weaving spiders for 64 sites of natural and disturbed habitats in Trinidad, for separate values of nine estimators (n = 576).

species richness was thus simply 1.773 times the observed species richness, and the sampling efficiency was 1/1.773 or 56 %. An ANCOVA of S_{est} by habitat type among the natural habitats, with S_{obs} as covariate, was not significant ($F_{15,29} = 0.49$; P = 0.93). There was, therefore, no significant variation of sampling efficiency with habitat type among the natural habitats.

There was also a significant relationship between estimated and observed species richness among the 18 sites of disturbed habitats (Fig. 3), following the regression equation:

$$S_{est} = 1.742 S_{obs} + 0.93$$
 (2)

 $(F_{1,16} = 37.5; P < 0.001, r^2 = 0.68)$. An ANCOVA comparing the disturbed and natural habitats showed a significant effect of the covariate ($F_{1,61} = 164.03, P < 0.001$) and a significant effect of distur-



Fig. 2. The mean correlation coefficient between each estimator and the other eight estimators, versus the correlation with the median of all nine estimators, across the 64 sites. Pearson (• and solid line) and Spearman (O and broken line) correlations are shown separately. Each point is a single estimator, as labelled, with regression fits to the two data sets.

bance ($F_{1,61} = 5.12$; P = 0.027). The mean difference between disturbed and natural habitats was 2.5 species (S.E. = 1.1, t = 2.26, P = 0.027, Tukey simultaneous test). A comparison of full and reduced model ANCOVAs showed no significant difference between the slopes for disturbed and natural habitats ($F_{1,60} = 0.001$, P > 0.50). The sampling efficiency in disturbed habitats was thus similar to that in natural habitats (1/1.742 = 57 %, compared to 56 %), with an additional mean of 2.5 extra estimated species at disturbed sites across all values of S_{obs} (Fig. 3). An ANCOVA of the disturbed habitats showed no significant effect of

Table 2. Performance of the separate species richness estimators on 64 sites of natural and disturbed habitats. Best fits is the number of sites at which each estimator was closest to the median, either alone (first) or equal with one other estimator (joint, contributing 0.5 each to the total of best fits). < S_{obs} and -/+ are the number of sites at which each estimator was below the observed species richness, and below/above the median, respectively; Highest is the number of sites at which it was the highest of all nine estimators. The *P* value is for the null hypothesis of no bias, i.e. below and above the median at an equal number of sites (χ^2 test, 1 df); ns = *P* > 0.05. Precision is the mean unsigned difference between the estimator and the median.

Estimator	Best fit	First/Joint	$< S_{\rm obs}$	-/+	P	Highest	Precision
ACE	15	11/8	0	18 / 20	ns	0	1.1
ICE	10.5	7/7	0	1 / 42	< 0.001	7	2.2
Chao 1	4	2 / 4	0	39 / 12	< 0.001	2	1.4
Chao 2	3.5	2/3	0	42 / 10	< 0.001	0	1.4
Jack 1	9	9 / 0	0	28 / 22	ns	0	1.8
Jack 2	9	9 / 0	2	17 / 35	< 0.05	6	1.2
Bootstrap	1	1/0	0	56 / 4	< 0.001	0	3.0
MMRuns	3	3 / 0	2	5 / 53	< 0.001	39	7.9
MMMeans	2	2 / 0	3	22 / 36	ns	6	3.4

habitat type ($F_{2,14} = 2.09$; P = 0.16), indicating that sampling efficiency did not differ among them.

Discussion

Comparison of estimators

Determining the effectiveness of species richness estimation is needed as species diversity is the "starting point" of research in community ecology (Hellmann & Fowler 1999). Two important properties of an estimator are bias and precision. The bias of an estimator is the presence of a consistent over- or under-estimation of the parameter (Hellmann & Fowler 1999; Walther & Morand 1998). Consistent overestimation of species richness is taken as "positive bias", whereas a consistent underestimation is regarded as "negative bias" (Hellmann & Fowler 1999). Precision is defined as "a measure of the overall closeness of the estimate to the parameter without measuring bias", i.e. the average unsigned difference between estimate and parameter (Walther & Morand 1998; Zar 1996). The performance of these species richness estimators can be evaluated based on their bias and precision, assuming that the median estimate is close to the true species richness. In this study three species richness estimators provided estimates lower than the observed and, therefore, exhibited extreme negative bias (see Table 2). The poor performance of some of these estimators, for example Jack 2, may be due to sensitivity to sample sizes (Magurran 2004).

When the estimators were compared with respect to "best fit" to the median estimated species richness (precision), the coverage estimators were best, in particular ACE. The estimates produced by the coverage estimators (ACE and ICE) are based on species found in less than or equal to ten sampling units (Magurran 2004), as in the sampling design used here (five samples). A disadvantage of these estimators is that they assume homogeneity amongst samples (Magurran 2004). These estimators, therefore, function poorly when estimating across sites where there are large differences in species composition, for example along ecological gradients (Magurran 2004). The ecology of tropical forests is poorly understood (Singh & Sharma 2009); the high performance of the coverage estimators in this study indicates that there is little heterogeneity over the scale (within 1 km) sampled.

Sampling efficiency

The large number of arthropods makes it challenging to sample and fully assess their species richness (Cardoso *et al.* 2007), especially in the tropics. The best method suggested to sample spider faunas is semi-quantitative sampling (Cardoso 2009), that is, an approximation of the number of species in each sample. This method of sampling has been used in a variety of studies (Coddington *et al.* 1991; Coddington *et al.* 2009; Scharff *et al.* 2003; Sørensen *et al.* 2002; Toti *et al.* 2000), as in the present investigation.



Fig. 3. The relationship between median estimated species richness S_{est} and observed species richness S_{obs} for natural (• and solid line) and disturbed habitats (O and broken line), with regression fits (equations 1 and 2 in text).

Sampling efficiency was similar across habitats for both natural (56 %) and disturbed (57 %) habitats. The difference in intercepts of the regression lines in Fig. 3 is due to an extra 2 - 3 "unsampleable" species in disturbed habitats. One possible reason for this difference could be the presence of more transient species in disturbed habitats, coming from neighbouring natural areas. Transient species are less likely in natural habitats, which occur over broader areas and are more likely to have reached equilibrium of species composition. Transient species which are not permanent members of the community cause the species richness to be high as they act as rare species (Coddington et al. 1996); because rare species are present in such low numbers they can be missed by sampling (Mallis & Hurd 2005).

Preliminary sampling showed seasonality to have little influence on the species composition of the samples so it was not pursued further. It is possible that the general sampling methods used under-represented some species, such as the genera Alpaida and Pronous which live near the ground and in leaf litter. Nevertheless, sampling was carried out at a range of vegetation heights, and species of both Alpaida and Pronous were recorded at several sites during this survey (records for particular species and sites are given in Sewlal 2010). Other specialized sampling methods could be used to avoid artificial rarity (Hsieh & Linsenmair 2011; Longino et al. 2002) which can drive up species richness estimates. For example, examination of nests of mud-dauber wasps



Fig. 4. Observed accumulation curves (• and solid lines) and randomisation curves (O and broken lines) for the sites at (a) Lalaja Road, the high outlier in Fig. 3, $S_{obs} = 13$, $S_{est} = 38$, (b) Caura River, a typical site, $S_{obs} = 11$, $S_{est} = 15$.

that are provisioned with orb-weaving spiders has proved a useful supplementary collection method for this group (Krombein 1967). There is a balance to be struck between completeness and distortion of the sample when deciding on the number of sampling methods to be used; the use of a small number of general methods was found to be effective in this study, and has the advantages of simplicity and repeatability.

This study has shown that a good estimate of species richness of tropical orb-weaving spiders can be made from five 3-hour samples in both natural and disturbed habitats, with almost 60 % of the species present being captured and permitting an estimate of the total species richness. Further sampling would be needed where the species composition was the primary focus, and where sampling failed to approach a plateau after five samples. The accumulation curve for the high outlier in Fig. 3 is shown in Fig. 4a, compared with a typical curve which approaches a plateau (Fig. 4b). The accumulation curve for the outlier was still rising steeply after five samples, and the median estimated species richness was 38. Individual estimators gave values of S_{est} ranging from 16 - 47 species for this site (where, $S_{obs} = 13$). In such cases it would be advisable to collect further samples until the accumulation curve began to level off clearly, to give a more reliable estimate of total richness.

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