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Undersampling bias: the null hypothesis for singleton species in tropical arthropod surveys

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Summary

1. Frequency of singletons – species represented by single individuals – is anomalously high in most large tropical arthropod surveys (average, 32%).

2. We sampled 5965 adult spiders of 352 species (29% singletons) from 1 ha of lowland tropical moist forest in Guyana.

3. Four common hypotheses (small body size, male-biased sex ratio, cryptic habits, clumped distributions) failed to explain singleton frequency. Singletons are larger than other species, not gender-biased, share no particular lifestyle, and are not clumped at 0·25–1 ha scales.

4. Monte Carlo simulation of the best-fit lognormal community shows that the observed data fit a random sample from a community of ~700 species and 1–2 million individuals, implying approximately 4% true singleton frequency.

5. Undersampling causes systematic negative bias of species richness, and should be the default null hypothesis for singleton frequencies.

6. Drastically greater sampling intensity in tropical arthropod inventory studies is required to yield realistic species richness estimates.

7. The lognormal distribution deserves greater consideration as a richness estimator when under-sampling bias is severe.

Key-words: Araneae, Guyana, neutral theory, sampling intensity, species richness estimation, spiders

Null models in biology perform the useful function of explaining many data in often infuriatingly simple ways (Gotelli & Graves 1996; Colwell & Lees 2000; Harte *et al.* 2001; Hubbell 2001; Green & Ostling 2003). Often they counterbalance ad hoc explanations of the pattern at hand. In this paper, we propose that the high frequency of 'singleton' species (those represented by single individuals) in tropical arthropod inventories or surveys is simply explained as undersampling, and use a large but incomplete survey of spiders in Guyana to make the point. Species richness estimation continues to play an increasingly important role in conservation and biological inventory assessment in multiple contexts (Cardoso *et al.* 2008; de Thoisy, Brosse, & Dubois 2008; Shen & He 2008; Schoeman, Nel, & Soares, 2008).

Table 1 gives the results of a keyword search of *Biological Abstracts* (through 2007) for the largest and most ambitious tropical arthropod surveys that provide data on singletons. As these studies clearly show, high singleton frequencies characterize typical tropical arthropod surveys, averaging 32% of species from the 71 studies. Why are there so many singletons in those surveys? Clearly, community-level singletons (and the species they represent) would have no chance to reproduce and could play no significant ecological role. Although the tropics are said to harbour many rare species, presumably most are not so rare as to lack at least a few conspecific neighbours with whom successfully to mate. Hence, singletons in biological surveys are anomalies, and as such have attracted much attention. To explain them, an array of ad hoc hypotheses have been proposed. However, we propose that, particularly when singleton frequencies are high, undersampling as a null hypothesis should precede more biological ad hoc explanations (McGill 2003).

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Table 1. Summary of tropical arthropod surveys. Arthropod surveys from tropical forest sites reporting total abundance (abun., or species presence per sample for ants, Agosti *et al.* 2000), species richness (spp.), and singletons (reported, calculated from figures given, or approximated as Fisher's α, noted in source column). Intensity is abun./spp. A search of Biological Abstracts (1986–2007) on the terms (species richness) and (Arthropoda) and (Oriental region or Australasian region or Neotropical region or Ethiopian region) produced 514 results, many of which did not provide the required inventory statistics or were not from wet tropical sites. Those meeting our criteria, in addition to those known to us personally, are listed below. References for this table are listed in the Appendix

Taxon	Study site	Abun.	Spp.	Singletons	Intensity	Percentage of Singletons	Source
Arthropods	Australia	20 507	759	271	27	36	Basset & Kitching 1991
Insecta	Costa Rica (Area 1)	488	142	91	3	64	Janzen & Schoener 1968
Insecta	Costa Rica (Area 2)	1362	262	165	5	63	' '
Insecta	Costa Rica (Area 3)	4857	404	254	12	63	' '
Insecta	Costa Rica (Area 4)	1339	545	390	2	72	' '
Insecta (leaf-chewing+ sap-sucking)	New Guinea	80 062	1050	278	76	26	Novotný & Basset 2000
Insecta	Guyana	27 735	604	229·5	46	38	Basset *et al.* 2001 (singletons calculated)
Blattaria	Panama (BCI)	3224	79	15	41	19	Wolda 1983 (Fisher's α)
Coleoptera	Australia (Queensland)	10 000	1514	612	7	40	Monteith & Davies 1984 (approx. values)
Coleoptera: Curculionidae	Panama (BCI)	28 521	703	131	41	19	Wolda 1987 (Fisher's α)
Coleoptera: Pselaphidae, Anthicidae	Panama (BCI)	6482	114	19·7	57	17	' '
Coleoptera	Panama (BCI)	34 705	597	102·5	58	17	' '
Coleoptera	New Guinea	4840	633	321	8	51	Allison *et al.* 1993
Coleoptera	New Guinea	3977	418	199	10	48	Allison *et al.* 1997
Coleoptera	Peru (Tambopata)	15 869	3429	1728	5	50	Erwin 1997
Coleoptera	Sulawesi	18 000	1355	623	13	46	Hammond *et al.* 1997 (approx. values)
Coleoptera	Brazil	8454	993	446·9	9	45	Didham *et al.* 1998 (singletons calculated)
Coleoptera: Curculionidae	Honduras	26 891	293	38	9	13	Anderson & Ashe 2000
Coleoptera: Staphylinidae	Honduras	7349	224	53	33	24	' '
Coleoptera	Malaysia	8028	1711	823	5	48	Chung *et al.* 2000
Coleoptera	Uganda	29 736	1433	596	21	42	Wagner 2000
Coleoptera	Ecuador	2329	318	91	7	29	Lucky *et al.* 2002
Coleoptera: Scarabaeinae	Bolivia	4050	73	7	55	10	Spector & Ayzama 2003
Coleoptera: Pselaphinae, Histeridae	Ecuador	3465	385	155	9	40	Carlton *et al.* 2004
Coleoptera: Phytophagous	Panama	3009	364	139	8	38	Ødegaard 2004
Coleoptera	Ecuador	15 181	2001	397	8	20	Erwin *et al.* 2005
Coleoptera: Scarabaeinae	Colombia	7894	101	20	78	20	Escobar *et al.* 2005
Coleoptera	Brazil (Parana)	1883	518	266	4	51	Ganho & Marinoni 2005
Coleoptera: Aticini	Brazil (Parana)	1891	106	32	18	30	Linzmeier *et al.* 2006
Coleoptera	Australia	29 986	1473	526	20	36	Stork & Grimbacher 2006
Diptera: Muscidae	Brazil (Parana)	7014	91	10	77	11	Costacurta *et al.* 2003
Diptera: Phoridae	Costa Rica	3341	115	20	29	17	Brown 2004
Diptera: Syrphidae	Brazil (Parana)	392	76	12	5	16	Marinoni *et al.* 2004
Ephemoptera	Panama (Corriente Grande)	7178	27	4	266	15	Wolda & Flowers 1985 (Fisher's α)
Ephemoptera	Panama (Miramar)	29 120	33	4	882	12	' '
Ephemoptera	Zaire	29 892	21	2	1423	10	' '
Hemiptera	Australia	6004	98	35	61	36	Andrew & Hughes 2005
Homoptera	Panama (BCI)	22 046	458	82·1	48	18	Wolda 1987 (Fisher's α)

Table 1. *Continued*

Taxon	Study site	Abun.	Spp.	Singletons	Intensity	Percentage of Singletons	Source
Homoptera	Panama (Pipeline Rd.)	1324	332	126	4	38	Wolda 1979
Hymenoptera: Parasitica	Sulawesi	700	293	179	2	61	Noyes 1989
Hymenoptera: Formicidae	Costa Rica (Monteverde)	3998	53	6	75	11	Longino & Nadkarni 1990
Hymenoptera: Formicidae	Costa Rica	7904	437	51	18	12	Longino *et al.* 2002
Hymenoptera: Apidae	Brazil (Minas Gerais)	1183	20	6	59	30	Nemesio & Silveira 2006
Lepidoptera: butterflies	Malaysia	9031	620	118	15	19	Corbet 1942
Lepidoptera: moths	Malaysia	9461	1048	538	9	51	Barlow & Woiwod 1989
Lepidoptera: butterflies	Ecuador	6690	130	20	5	15	DeVries *et al.* 1997
Lepidoptera: butterflies	Ecuador	883	91	22	10	24	DeVries *et al.* 1999
Lepidoptera: butterflies	Ecuador	11 861	128	18	93	14	DeVries & Walla 2001
Lepidoptera	Borneo	485	53	16	9	30	Schulze *et al.* 2001
Lepidoptera: butterflies	Thailand	1936	53	4	37	8	Ghazoul 2002
Lepidoptera: Geometridae	Ecuador	23 720	868	161	27	19	Hilt *et al.* 2006
Odonata	Peru	1537	136	31	11	23	Louton *et al.* 1996
Orthoptera	Panama (BCI)	1566	73	15·9	21	22	Wolda 1987 (Fisher's α)
Psocoptera	Panama (BCI)	10 092	148	20	68	14	Broadhead & Wolda 1985 (Fisher's α)
Psocoptera	Panama (Fortuna)	4301	84	10	15	12	＇ ＇
Araneae	Bolivia (50 m)	875	191	89	5	47	Coddington *et al.* 1991, 1996
Araneae	Bolivia (1200 m)	1109	329	147	3	45	＇ ＇
Araneae	Bolivia (2200 m)	654	158	70	4	44	＇ ＇
Araneae	Brazil (Manaus)	75	62	32	1	52	Höfer *et al.* 1994
Araneae	Tobago	1777	98	27	18	28	Hormiga & Coddington 1994
Araneae	Peru (Samiria)	5895	1140	520	5	46	Silva 1996
Araneae	Peru (Pakitza)	2616	498	207	5	42	Silva & Coddington 1996
Araneae	Costa Rica	7144	86	11	83	13	Bodner 2002
Araneae	Tanzania (understorey)	9096	170	32	54	19	Sørensen *et al.* 2002
Araneae	Tanzania (canopy)	5233	149	35	35	23	Sørensen 2003
Araneae	Malaysia	6999	578	145	12	25	Floren & Deeleman-Reinhold 2005, personal communication
Araneae	Mt. Cameroon (500 m)	573	231	93	2	40	Coddington *et al.*, unpublished
Araneae	Mt. Cameroon (3000 m)	1555	55	14	28	25	＇ ＇
Araneae	Peru (Tambopata)	1821	635	341	3	54	Coddington & Silva, unpublished
Araneae	Peru (Manu)	222	123	78	2	63	Erwin & Coddington, unpublished
Araneae	Guyana	5964	351	101	17	29	This study
Averages		9372	464	176	61·6	31·6	

Singleton tropical arthropod species are anomalous for several reasons. First, minimum viable population sizes are conventionally at least 500 individuals (Gilpin & Soulé 1986). Second, many arthropods begin life clumped because eggs are clumped when laid – in spiders eggs are clustered within an egg sac. Most nonvolant arthropods are small and probably rarely travel hundreds or even dozens of metres to mate. Third, clumped distributions in nature are far more common than random or dispersed (Krebs 1999). While clumping certainly depends on scale, at hectare scales randomness is typical of canopy trees and jaguars, not small, nonflying, sedentary arthropods such as spiders.

Ad hoc explanations for singletons often invoke aspects of the biology of particular groups, such as host or food plant specificity (Price *et al.* 1995). In spiders, males of sedentary web-spinning species must wander to find females (potentially passing through atypical habitat patches, i.e., tourists), and are likely to be small and rare (Vollrath & Parker 1992). General explanations include source-sink phenomena or mass-effects (e.g. 'ecological drift,' Hubbell 2001) at both local ('tourist') and regional ('waif' or 'vagrant') scales (Schmida & Wilson 1985; Pulliam 1988; Southwood 1996; Stork & Hammond 1997; Novotný & Basset 2000; Magurran & Henderson 2003; Basset *et al.* 2004; Ødegaard 2004). Time, space, or method 'edge effects' are also frequent explanations. Adults outside their breeding seasons are scarce, and if only adults are identifiable (true for spiders), will be artefactually rare (Ulrich 2001; Longino, Coddington, & Colwell 2002; Scharff *et al.* 2003; Basset *et al.* 2004). Nocturnality or seasonal migration could produce similar effects. Space edge effects are usually microhabitat preferences. Species patches just trespassing on plot boundaries might produce many 'false' singletons. Method edge effects are the accidental sampling of a species by an inappropriate method, such as a canopy species in a pitfall trap (Longino *et al.* 2002; Scharff *et al.* 2003). Finally, singletons may be absolutely rare, i.e. sparse with large nearest-neighbour distances throughout their range. Perhaps, as is now recognized for tropical trees (Pitman *et al.* 1999; Kenfack *et al.* 2006), we drastically underestimate the scale at which many tropical arthropod species live and ought to be sampled.

Undersampling bias and biological explanations are not mutually exclusive. However, if repeated random sampling of communities modelled on statistical parameters estimated from the sample mimic the observed results, undersampling should serve as the initial null explanation for high singleton frequencies (McGill 2003), analogous to the use of null models in other fields (Harte *et al.* 2001; Hubbell 2001). Variation not explained by undersampling may then be attributed to more complex causes.

Statistical methods to assess undersampling bias are relatively recent; quantitative estimates of its magnitude have been historically difficult, if not impossible, to obtain. Observed richness values are traditionally used for descriptive or comparative purposes (Groombridge 1992; Heywood & Watson 1995; Levin 2001). If high singleton frequencies indicate undersampling, however, then tropical arthropod
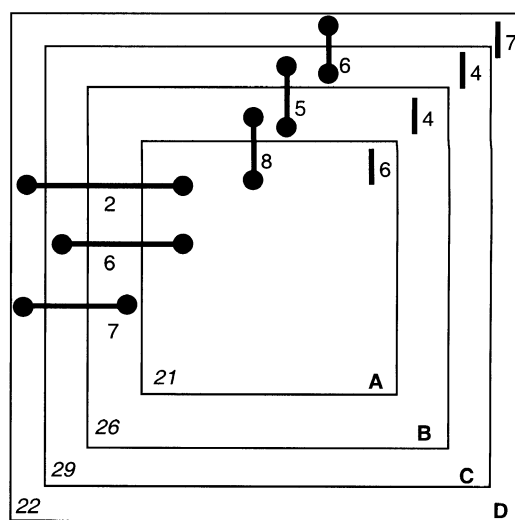

Fig. 1. Plot design of four nested 0·25-ha subplots A-D with counts of singletons (italics) per subplot and doubletons per subplot pairs (lines with adjacent numbers).

communities are substantially larger than measured, and comparisons based on observed numbers are misleading. This has important implications for conservation biology, and also implies that typical inventories are under-resourced and/or poorly designed.

Here we use the results of an intensive 1-ha survey of spiders to test various explanations for high singleton frequency. Although spiders are typical sedentary arthropod predators and these results may apply only to that guild, high singleton frequencies also characterize inventories of other tropical arthropods (Table 1). Specifically, we test four process hypotheses and the null hypothesis of undersampling bias: singletons tend to be small and therefore missed; singletons tend to be males because as adults they travel further than females; nearest conspecific distances exceed 0·25–1 ha spatial scales (population structure is much larger than anticipated); singletons are 'cryptic' and hard to detect; and singletons are simply an artefact of undersampling because the scope of the survey exceeded sampling resources.

Methods

STUDY SITE

The study was carried out during 10 days, 5–14 July, 1999, in a primary lowland blackwater rainforest (1°36′46″N, 58°38′15″W) on the bank of Essequibo River, 240 m elevation, 4·42 km south of Gunn's landing, Upper Takutu-Upper Essequibo, Guyana. Four nested, concentric 0·25-ha subplots (total 1 ha) were established in uniform closed canopy forest (Fig. 1). Five experienced collectors worked simultaneously in the field during both day and night using a battery of collecting methods that broadly access most of the spider fauna (see Coddington *et al.* 1991; Sørensen, Coddington, & Scharff 2002; Scharff *et al.* 2003 for details).

CONSPECIFIC DISTANCES

The nested subplot design provided a range of spatial scales. If singletons are spatial edge effects – multi-individual clumps or patches with only one individual in the subplot or plot – the outermost subplot with the largest perimeter should contain the most singletons (Fig. 1). Likewise, doubletons of spatially clumped species should occur in the same subplot. More generally, we tested for clumping by comparing the observed distribution of singletons and doubletons among subplots against the null hypothesis of equal frequency in all possible subplot combinations (e.g. A, B, C, or D for singletons, and AA, AB, AC, AD, BB, etc. for doubletons).

BODY SIZE

We measured total body length to the nearest 0·1 mm of one individual of each sex (when available) of each species. The 'average' tropical spider is then the mean of these lengths (assuming equal sex ratios) weighted by the relative abundance of each species. A *t*-test then compared mean size of singletons to nonsingletons.

SEX RATIO

Using the observed sex ratio in the total sample as the null, we compared the singleton sex ratio to it with a chi-squared test, both for singletons as a whole and for singletons of web-spinning species only, where males must wander to encounter the sedentary females.

CRYPTIC HABITS

Generally speaking, spider species within families are more alike in their biology than between (Coddington and Levi 1991). Araneids mostly spin orb-webs, mostly above the forest floor, but anapids and symphytognathids spin theirs mostly in the leaf litter. Philodromids run on leaves, and salticids jump between them (but only during the day). Because tropical 1-ha inventories usually find at least 30 families, testing the relative frequency of singletons among families against a null of the relative abundance of families in the total sample should detect whether singletons tend to have one lifestyle more frequently than another.

UNDERSAMPLING BIAS

We assessed inventory completeness by visually inspecting the average of 50 resamples of the observed species accumulation curve, as well as the singleton and doubleton curves, and four commonly used species richness estimators (Chao1, Chao2, ICE and ACE; Peterson & Slade 1998; Walther & Martin 2001; Colwell 2005). In a complete inventory, the observed curve should asymptote and singletons should tend to zero, with doubletons lagging singletons. If incomplete but sufficient to estimate richness accurately, estimator curves should asymptote (Colwell & Coddington 1994). Constantly rising curves of all sorts imply incomplete inventories.

We also fit the data to a lognormal distribution using the method described in Scharff *et al.* (2003) and Longino *et al.* (2002). We use the lognormal as a reasonable null hypothesis (McGill 2003). Other models, such as the parameter-rich zero-sum multinomial, have been proposed as better fits to empirical data than the lognormal (e.g. Hubble 2001), however, a recent detailed test fails to support that claim, and indeed showed the opposite (McGill 2003). Given the high number of parameters in the zero-sum model, the cumbersome procedure of fitting the model, and lack of evidence for its superior fit to empirical data, McGill advised the preferential use of the lognormal as the simpler (more parsimonious) null model. Using the best-fit lognormal parameters, we generated and randomly sampled 6000 individuals from 1000 replicate communities of each of four sizes: 500, 600, 700, or 800 species, which parameters were chosen to mimic the empirical sample. We then compared the observed sample to these 4000 simulated samples on numbers of singletons, doubletons, and species. If the observed sample clearly deviated, undersampling bias alone does not explain high singleton frequency.

Statistical tests, curve fitting, modelling, resampling procedures, and species richness estimation used a combination of SYSTAT 11 (Systat Software, Inc., Richmond, CA, USA), EstimateS 7·50 (Colwell 2005), and Microsoft Excel 2007 (Microsoft Corp., Redmond, WA, USA).

Finally, a few measures of leaf litter, shrub/subcanopy, and canopy tropical moist forest spider densities per m² have been published (Table 2). Extrapolated to 1 ha, these statistics provide crude estimates of spider abundance that can be compared to the total abundances predicted by the lognormal model.

SPECIMENS AND SORTING PROCEDURES

Each sample was labelled with plot, date, collector, method, and replicate number if two samples were otherwise identical. Team members (all arachnological taxonomists) or other experts on particular families sorted the specimens to morphospecies. All identifications of singletons and doubletons were checked and verified by at least two of the team members. Voucher specimens of each species identified in this study are deposited at the National Museum of Natural History (NMNH), Smithsonian Institution, Washington DC.

Results

The five collectors accumulated 300 samples over 10 days from the 1-ha plot (Table 3) containing a total of 5965 adults (and 6953 juveniles) of 352 species, of which 101 were singletons (29%) and 56 were doubletons. The most abundant species numbered 412. Inventory completion (observed richness/ Chao1 estimate) ranged from 15% to 71% among methods, and overall was 79%. Sampling intensity (no. of ind./no. of spp.) ranged from 1·4 to 10·5 among methods and overall was 17. The survey compares favourably to other large published efforts in intensity and numbers of species encountered, considering that most spider species cannot be trapped (Table 1). However, the continually rising accumulation curves and richness estimators indicate that the inventory was still incomplete by the end of sampling (Fig. 2). The 95% upper confidence limit of the Chao2 estimator (itself only a lower-bound estimate), for example, was 520 species, but clearly had not reached a limit. True species richness in the hectare almost certainly exceeded 500 species, and probably much more.

The mean and standard deviation of the body lengths of adults collected was 2·89 ± 2·85 mm (thus an estimate of the average size of an adult lowland tropical moist forest spider). The mean singleton body length was 5·30 ± 4·67 mm. Singletons are significantly larger, not smaller, than the average species.

Table 2. Spider density in tropical forests. Estimated number of total and adult spiders in a hectare of primary tropical rainforest. Min, computed from minimum values; max, from maximum values. References for this table are listed in the Appendix

Layer	Place	Method	Density (n/m²)		Source
			Total	Adults	
Ground					
	Brazil	Berlese	221	71·8	Höfer & Brescovit 2001
	Brazil	Berlese	330	125·2	Höfer & Brescovit 2001
	Brazil	Berlese	129	41·9	Morais 1985
	Brazil	Berlese	108	35·1	Adis & Schubart 1984
	Mean		197·0	68·5	
Shrub					
	Brazil	Beating	0·5	0·2	Höfer & Brescovit 2001
	Brazil	Beating	3·5	1·1	Höfer & Brescovit 2001
	Guyana	Beating Day	2·7	0·9	This study
	Guyana	Beating Night	1·9	0·6	This study
	Mean		2·2	0·7	
Canopy					
	Brunei	Fog	4·7	1·5	Russell-Smith & Stork 1994
	Sulawesi	Fog	4·6	1·5	Russell-Smith & Stork 1995
	Australia	Fog	8·6	2·8	Basset 1990, 1991
	Tanzania	Fog	4·8	1·5	Sørensen 2003
	Brazil	Fog	4·8		Adis 1984
	Brazil	Fog	2·0	0·7	Höfer et al 2001
	Brazil	Fog	5·5	1·8	Höfer et al. 1994
	Mean		5·0	1·6	
	Total spiders (1 m² column)		204	71	
	Min spiders (1 m² column)		111	36	
	Max spiders (1 m² column)		342	129	
	Total spiders (ha)		2 041 500	708 333	
	Min spiders (ha)		1 105 000	360 000	
	Max spiders (ha)		3 421 000	1 291 000	

Table 3. Collecting methods and results. AE, BE, CR, GR, PF, SW, D and N stand for aerial, beating, cryptic, ground, pitfall, sweeping, day, and night collecting methods, respectively (see text). Sample intensity is total individuals/total species. Inventory completion is total species/Chao1 estimate

	AED	AEN	BED	BEN	CRD	CRN	GRD	GRN	PF	SWD	SWN	Total
No. of samples	12	76	36	19	28	20	28	32	46	2	1	300
Total individuals	102	2210	644	272	528	399	621	703	439	23	24	5965
Total species	45	210	138	95	69	72	69	115	57	15	17	352
Singletons	32	73	57	53	29	34	30	54	25	11	14	101
Doubletons	2	29	29	15	9	13	9	17	4	2	1	54
Sample intensity	2·3	10·5	4·7	2·9	7·7	5·5	9·0	6·2	7·7	1·5	1·4	17·0
Percentage of Singletons	71%	35%	41%	56%	42%	47%	43%	47%	44%	73%	82%	29%
Chao1 estimate	301	302	194	189	112	120	115	200	135	45	n/a	443
Inv. completion	15%	70%	71%	50%	62%	60%	60%	57%	42%	33%		79%

The overall male : female sex ratio in the sample was significantly female biased (1:1·3, $P < 0·01$). The overall singleton sex ratio was as biased as the total sample (1:1·7, $P = 0·18$). Sedentary web-spinner singletons were equally biased (1:2·8, $P = 0·12$). Singletons, therefore, are not disproportionately males of sedentary web-spinning species.

The distribution of doubletons across subplots (Fig. 1) was random ($P = 0·82$) as was the incidence of singletons from the centre to the outermost subplot ($P = 0·80$). Tripletons also showed no tendency to clump within subplots. Conspecific nearest neighbour distances, therefore, are not clumped at the coarse 0·25- to 1-ha scales tested here.

Singletons showed no taxonomic pattern, occurring in families in proportion to the latter's relative abundance ($P > 0·99$). If undersampling bias varied according to lifestyle defined as family identity, the effect was not detectable at this level of sampling intensity.

The observed data fit the lognormal distribution well (Fig. 3, $0·9 > P > 0·5$). The predicted number of species in the modal octave S_0 was $76·4 \pm 13$ ($\mu = 6·2562$), the variance term
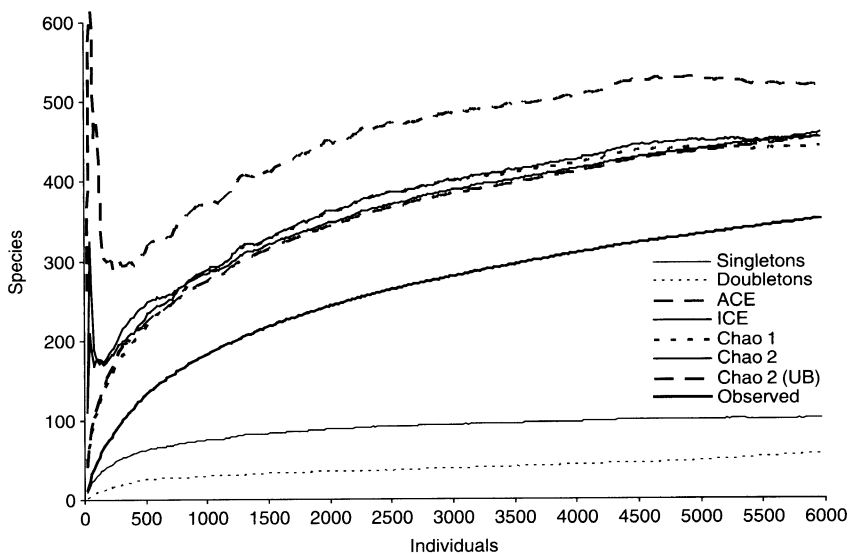
Fig. 2. Four species richness estimators (ACE, ICE, Chao 1, Chao 2), the 95% upper confidence limit of the Chao2 estimator, observed, singleton, and doubleton curves for data of Table 3.
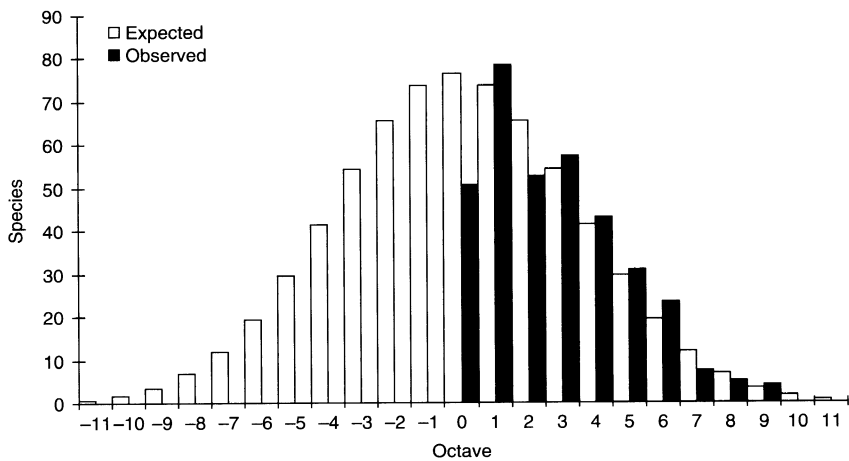

Fig. 3. Lognormal fit $(0.9 > P > 0.5)$ to data of Table 3. Predicted community size is 694 species. Note the over-estimation of abundant species at the right-hand tail.

('a') was 0.195 ± 0.210 ($\sigma = 3.6262$) and estimated community size 694 species.

Figure 4 shows the results of 1000 random draws of constant sampling effort (6000 individuals) from simulated lognormal distributions with the above parameter values for 500, 600, 700, and 800 total species, compared to the observed data (arrow). For clarity, only 25 randomly chosen samples from each community size are plotted, as otherwise the observed data point would have been completely obscured. Observed richness rises with total richness, and numbers and percentages of singletons and doubletons rise because, as richness increases, sampling intensity decreases. On these three statistics, the empirical sample falls between the 700 and 800 species model communities, roughly agreeing with the lognormal richness estimate in Fig. 3. Overall, it falls well within the stochastic variation seen in these random draws from 'null' lognormal distributions (Fig. 4). True singletons in the model lognormal communities averaged only 4% of the total.

To assess how many more specimens would be required to enable richness estimators to cover true community richness under these circumstances, we sampled 60 000 (intensity 170)
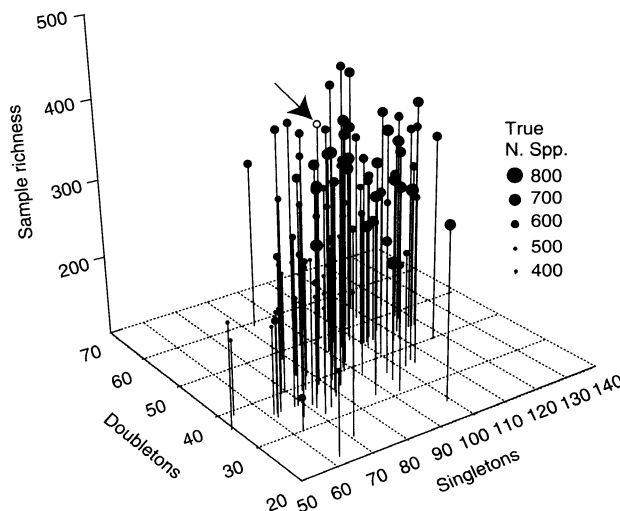

Fig. 4. Singleton, doubleton, and observed species totals from the Guyana study (open circle, arrow) and 25 random samples of 6000 individuals from model lognormal communities of 500, 600, 700, and 800 species.
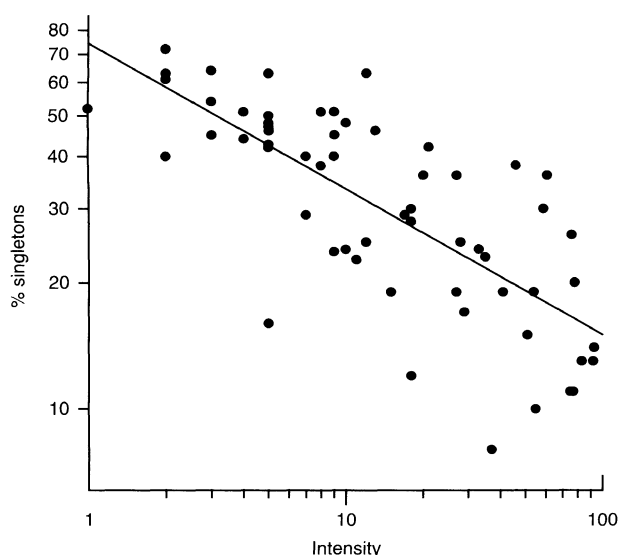
Fig. 5. Log-log plot of sampling intensity vs. percentage of singletons for data of Table 1 ($r^2 = 0.58$; $P = 0.001$).

and 120 000 individuals (intensity 340) from the 700 species lognormal community, thus 10 and 20 times the actual sampling effort. At an intensity of 170, percentage of singletons was 14%, and the Chao and coverage estimators were 595–600 species with Chao upper confidence intervals of 636 species – still short of the true 700 species richness. At an intensity of 340, the Chao and coverage estimators were 650–663 species, with a Chao upper confidence interval of 702 species – thus just covering the true richness value – and percentage of singletons fell to 9%.

Figure 5 depicts the logarithmic decline in singletons with sampling intensity for the data of Table 1, and predicts zero singletons at sampling intensities of roughly 1100. Sampling the model community at that intensity yielded on average 4% singletons and 658 species observed.

We present what few data exist on tropical spider densities in Table 2. Ignoring differences due to locality and construed as a ground to canopy vertical 1 m² column, the leaf litter contains most individuals, the canopy/subcanopy less, and the shrub/understorey layer least. Given the decrease in leaf area or other substrate with height above the ground, the decline is plausible. It predicts, extremely roughly, about 2 million total spiders per hectare of tropical forest (range 1·1–3·4 M). The modelled lognormal populations ranged between 1·2 and 3·3 million individuals, which agrees with Table 2.

Discussion

Rare species and estimating total species richness in particular are difficult statistical problems (Bunge & Fitzpatrick 1993; Ulrich 2001; Brose, Martinez, & Williams 2003; Magurran 2004; Ellison & Agrawal 2005; Cunningham & Lindenmayer 2005; Mao & Colwell 2005; Walther & Moore 2005). Estimating how many data are required to obtain robust and reliable species richness estimates is also difficult (Keating *et al.* 1998;

McArdle 1990). This complicates inventory design. Modelling studies have suggested that nonparametric richness estimators do not begin to cover the true value until about two-thirds to four-fifths of the species have been observed (Walther & Morand 1998; Mao & Colwell 2005). On the other hand, intensely sampled communities usually are lognormal at local scales, even if the full distribution is truncated by failure to detect rare species (Sugihara 1980; Longino *et al.* 2002; Connolly *et al.* 2005, but see Williamson & Gaston 2005).

In this study, the empirical sample of 6000 individuals may have included only half the species present, with singletons comprising 29% of species observed. Nonparametric richness estimators suggested only 443–460 species, a shortfall of 35% compared to the lognormal estimate. While any singleton may have been due to any of the process explanations discussed above, the simplest explanation for the high frequency is undersampling. As sampling continues and singleton frequencies drop, biological explanations become more plausible.

Two 'biological' explanations were statistically significant, but neither in the direction hypothesized. Singletons were significantly larger (not smaller) than the average spider. Twenty-three singletons over 7 cm caused that difference. These were mostly large cursorial species (including ctenids, sparassids, and miturgids) for which absolute densities of one, or very few individuals per hectare are plausible. Singletons are also disproportionately females, not males, but the sample in general was female-biased, and singletons no more so, even among sedentary web-spinning species where the presumed bias towards singleton wandering males should have been most pronounced. Adult male spiders are relatively short lived and wandering males experience exceptionally high mortality (Vollrath & Parker 1992); both of these factors likely contribute to a female-biased sex ratio in the inventory data, even if the sex ratio at birth were even (as they are for most spiders examined to date, see Avilés & Maddison 1991, Avilés, McCormack, Cutter & Bukowski 2000).

The other explanations tested, lifestyle, spatial edge effects, and clumping of individuals at 1-ha scales and below, were insignificant. Novotný & Basset (2000) and Ulrich (2001) also found that few biological explanations of singletons were supported. Magurran & Henderson (2003) use a 21-year data set on a temperate fish community of 80 species to show that about a third to a half of the species accumulated over that time-span were tourists or waifs. In any given short-term sampling event, however, presumably few of the rare species would have been tourists or waifs. In a spider inventory of a 'known' fauna, Scharff *et al.* (2003) hypothesized 58% of singletons as phenological, methodological, or spatial edge effects, but they did not test the null hypothesis of undersampling bias. For relatively instantaneous events such as this inventory, singleton frequencies are about what one would expect from random samples of a lognormally distributed community – in this case, of about 700 species. The null hypothesis of undersampling bias cannot be rejected.

This was an intense, short-term inventory (300 person-hours), designed to yield an 'instantaneous' richness estimate that avoided the confounding effect of phenological change.

Especially in relatively aseasonal tropical habitats, sampling year round or for multiple years might yield a more complete inventory over and above the effect of greater sampling intensity (DeVries, Walla, & Greeney 1999; Scharff *et al.* 2003). Increasing the sampling area might also improve efficiency, especially if, as perhaps suggested by the significantly larger singleton size and the possibility that some true singletons occur in any given hectare, we underestimated the scale at which sedentary tropical arthropods should be sampled. Their lifetime ranges may encompass much larger areas. On the other hand, species richness increases logarithmically with area (Rozenzweig 1995), burdening species richness estimates. Regardless, the key point is that the scope of the inventory must be carefully matched to available resources.

What little we know of tropical spider communities broadly agrees with the predictions of the lognormal fit (Table 2). Our empirical sample included only nine of 23 predicted octaves, yet the implied community, when randomly sampled at the same intensity, compared well to empirical observations of total species, numbers of singletons and doubletons, maximum abundance, and total numbers of individuals (Fig. 4). None of the collecting methods used in Table 2 are completely efficient, therefore, the actual hectare abundance of spiders is probably higher.

When the modelled 700 species community was sampled at an intensity of 1100, on average 658 species and 4% singletons resulted. Lognormal distributions always predict some singletons (here on average 28 or 4%), and stochastic replicates never contain all 700 species (here on average 685). Practically speaking, sampling intensities of 1100 detects just about as many species as stochastic models provide.

For these data, a sampling intensity of 340 (10 times the actual sampling effort) was just sufficient to include the known richness within the upper bound of the Chao2 estimator. This implies that inventories, as a rule of thumb, should aim for intensities between that and 1100 to obtain realistic nonparametric estimates of species richness.

Richness estimators are relatively more efficient if they can report the true richness based on relatively few data. The efficiency of available nonparametric richness estimators is poor in the sense that roughly three quarters of the community must be observed before the estimator confidence interval actually covers the true value (Walther & Morand 1998). Chao estimators, moreover, have a maximum upper bound of about half the square of the observed richness (if the sample of n species contains n-1 singletons or uniques and one doubleton or duplicate), but in practice such efficiencies are never achieved because of the improbability of so biased a sample.

The lognormal distribution can potentially result in higher richness estimates than nonparametric approaches (given the same data) because it assumes the relative abundance distribution is symmetric around the modal octave (Sugihara 1980; Longino *et al.* 2002), and therefore tends to at least double the observed richness. A number of authors argue that empirical communities show an asymmetric excess of rare species (Nee, Harvey, & May 1991; Nekola & Brown 2007), and Hubbell and co-workers argue from first principles that such is expected (Hubbell 2001; Volkov *et al.* 2003). However, McGill (2003) suggests that this observed skew in species abundance distributions may also be a sampling artefact. One might also point out that the lognormal even less realistically overestimates the abundant tail of the distribution (Fig. 3, Longino *et al.* 2002; Magurran & Henderson 2003). However, even if the lognormal slightly underestimates rare species, that error is small compared to the gross negative bias of nonparametric estimators at small sample sizes.

The stochastic variation in small samples drawn from the same lognormal population is impressive (Fig. 4). For the 700 species case, 1000 draws of 6000 individuals produced singleton counts of 62–134 and observed richnesses from 121–414, which comfortably cover the observed statistics of 101 and 351. The lognormal distribution therefore may still be a useful method to estimate species richness under circumstances where many data are available, yet not enough for nonparametric estimators to function well. Unlike the relative abundance distribution-based estimators of Ulrich (1999, 2005), it does not require an explicit ratio of sampled to total habitat area, and thus is more practical in the field.

If general, this result implies that even large survey efforts (Table 1, Fig. 5) continue to undersample tropical arthropod biodiversity by perhaps a factor of 2 if singletons average 32% of the total. In many surveys, the figure is much higher (Table 1). Undersampling is a serious issue even for large mammal and bird surveys, where singletons average 16% (Bernard & Fenton 2002; Shankar and Sukamar 2002; McCain 2004). Consequently, typical surveys will underestimate species richness, with obvious implications for our understanding of biodiversity, and for any conservation decisions based on such data.

In summary, it appears that most tropical arthropod biodiversity surveys have been severely under-resourced if their goal was to census or estimate species richness of a defined taxonomic community at a particular place and time. Reliable methods do exist to estimate how many data are required to estimate many ecological statistics (Krebs 1999; Magurran 2004), but species richness historically is an exception. One may hope that future statistical research will improve estimator efficiency, but in the meantime the use of existing estimators dramatically exposes the gap between inventory design as implemented and the minimum necessary to obtain reliable richness estimates. Here the lognormal was more efficient than nonparametric estimators, and perhaps should be used more frequently. Species richness estimators are increasingly used in basic research to detect undersampling bias; results thus far suggest that it is ubiquitous and severe. Rather than scaling back inventory goals, we suggest that inventory analyses continue to assess undersampling bias in order to justify the budgets required to obtain adequate data. Funding sources and consumers of these essential data can scarcely argue that inadequate results are acceptable. If results continue to demonstrate that much greater sampling intensities are required, such will eventually become the norm, rather than the exception.

Acknowledgements

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Appendix 1. References for Tables 1 and 2

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