# Estimating biodiversity: a case study on true bugs in argentinian wetlands 

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#### Abstract

The species richness and relative abundance of faunas in defined areas are the raw materials in biodiversity science. The research methodology to acquire these data is inventory, and inventory quality depends on a number of parameters, for example collecting methods, season, and collector experience. To assess the ability of rapid inventory techniques to estimate local richness seven collectors sampled the fauna of true bugs in the Iberá watershed (Corrientes, Argentina) with seven methods during early spring, summer, and late summer (December, May, September) of 1 year. Twenty-three families, 225 spp. and 4,678 adults were found. We also applied various statistical techniques to correct the observed data for undersampling bias, which suggested the lower bound of annual heteropteran species richness at Pellegrini was about 250-300 species. Among heteropteran families, the particular inventory methodology was especially efficient in sampling Miridae.


Keywords Biodiversity estimation • Collecting methods • Heteroptera • Iberá watershed

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## Introduction

Measures of biodiversity provide the base-line information on distribution, richness, and relative abundance of taxa required for conservation decisions, studies of ecosystems ecology, cladistic biogeography, and phylogenetic measures of conservation value (Blackmore 1996; Humphries et al. 1995; May 1988; Magurran 1988; Raven and Wilson 1992). Species richness in particular is an increasingly important statistic in conservation evaluation (Pearsall et al. 1986; Fuller and Langslow 1986; Usher 1986).

Considering their immense contributions to the world's biota, any general explanation of diversity should account for patterns in insects (MacArthur 1965). The advantage of working with megadiverse taxa is that they surely exhibit many repeated patterns, which can be clues to underlying processes. Insect species richness, however, is especially challenging to measure because it is nearly always underestimated. Undersampling bias may be detected and partly or wholly corrected, however, by application of appropriate sampling and statistical techniques (Southwood 1976; Heltshe and Forrester 1983; Coddington et al. 1991; Colwell and Coddington 1994; Butler and Chazdon 1998).

Efforts to detect and describe natural order in the organic world date back at least to Aristotle. The great natural scientist Carolus Linnaeus (1758) proposed a simple method to name and record species systematically, now known as taxonomy. He first recognized the higher group now called Hemiptera, which includes thrips, aphids, scale insects, cicadas and true bugs. The Hemiptera (Homoptera plus Heteroptera) currently ranks as the fifth most speciose order of insects, after beetles, flies, wasps, and moths (Wilson 1992). Heteroptera comprises 38,000 species (Schuh and Slater 1995) of predators, herbivores, and haematophages. Some are economically important, either negatively as vectors of Chagas' disease, one of the most important diseases in South America, or positively as biological control agents.

The knowledge of Heteroptera from Argentina is fragmentary and incomplete. Currently 1,244 species of terrestrial Heteroptera are known (Coscarón and Cuello 2000). Checklists for Miridae, Thaumastocoridae, Pachynomidae (Carpintero 1998a, b, c) and Reduviidae (Coscarón 1998) have been published. In Corrientes Province recent inventories focused on termites (Isoptera) (Torales 1998), kissing bugs (Reduviidae) (Bar et al. 1999), aquatic (Estevez et al. 2003) and terrestrial true bugs (Coscarón 2003). None of these quantified undersampling bias. Hodkinson and Casson (1991) did use figures for known and estimated global heteropteran richness to predict the global number of insect species.

Although much of the Earth's biological diversity resides in temperate areas (May 1990), south temperate diversity is much less well-known than north temperate diversity. The Ibera macrosystem (Fig. 1) comprises $20,000 \mathrm{~km}^{2}$ of land ( $90 \%$ wetlands) of which $60 \%$ is in one watershed. In Olson et al.'s (2001) classification of South American ecosystems, the Ibera macrosystem belongs to the "La Plata River Basin" system that includes the basins of the Paraná, Uruguay, and de La Plata rivers and their deltas. It also drains the great Mato Grosso Pantanal swamp via the Rio Paraguay. The system includes both subtropical and temperate regions. Biogeographically it includes three domains: the Chaquenian (northwest), Paranaense (northeast) and the Espinal pampeano (south) (Cabrera and Willink 1973). Although the aquatic insect fauna seems to be largely the same in all three areas, the differences in terrestrial vegetation impose correspondingly great differences in the terrestrial faunas. The Pellegrini study site is part of the Espinal pampeano and is dominated by Prosopis nandubay Lorentz ex Grisebach and Prosopis algarrobilla Grisebach (Leguminosae), and the terrestrial shrub Acacia caven Mol. (Mimosaceae), as well as Andropogon lateralis Nees, Paspalum notatum Flugge and Axonopus spp. (Poaceae) in the grasslands.


Fig. 1 Location of C. Pellegrini (Corrientes, Argentina) study site
The swamp community shows no zonal variation, and is repeated through the three domains. The dominant aquatic plant species are Cabomba australis, Utricularia foliosa, Egera nalas, and Schoenoplectus californicus; dominant amphibious species are Panicum grumosum, Typha spp., Talia multiflora and Zizaniopsis spp. At higher elevations ( $3-8 \mathrm{~m}$ ) small forest patches are dominated by Sapium haematospernum, Ocotea acitifolia and Croton urucurans, the typical Ibera ecosystem landscape (Carnevali 1994).

This paper aims to improve knowledge of the Ibera complex, one of the most important but least known South American wetlands, and of terrestrial heteropteran biodiversity. We use quantitative measures of inventory completion and statistical analyses to critique our results and to elucidate the effects of inventory design parameters, with a view towards increasing the efficiency and effectiveness of biological inventory.

## Methods

Study site
The study occurred during December 1-10, May 2-11, and September 21-27, (2001-2002) in Colonia Pellegrini, elevation approx. 65 m MSL $\left(28^{\circ} 32^{\prime} \mathrm{S} 57^{\circ} 09^{\prime} \mathrm{W}\right)$ in Corrientes,

118 km NE of Mercedes, Dto. of San Martín, Argentina ( 450 km . SE of the city of Corrientes). Colonia Pellegrini (Fig. 1) is located in the Espinal pampeano domain, Espinal Province, Nandubay District. All collecting occurred within a 50 ha area.

## Collectors

Four experienced and three inexperienced collectors sampled. Diurnal collecting varied according to the season, from 0900 to 1800 h (December and May), but 1030-1800 h in September to avoid wet vegetation.

We collected both night (light traps) and day to ensure sampling of diurnal and nocturnal species. Each sample was labeled with collector and method.

Collecting methods
The seven collecting methods were:
Sweeping: Sampling low vegetation with a 40 cm diametre sweep net. The net was emptied after a few sweeps to avoid damage to the specimens. Forty-five minutes constituted one sample. We used aspirators to transfer all heteropterans from sweeping (and beating) samples to vials.

Beating: Sharply tapping branches or comparable vegetation with a stout stick while holding a 90 cm beating net to catch falling insects. Forty-five minutes constituted one sample. Beating net size varied slightly among collectors, but because samples were defined by time, net area was probably unimportant.

Light trap: We used a mercury vapor light trap on December 2-9, May 4-10, and September 21-26 (18 days). Three hours per day (from 1830 to 2130 h ) constituted one sample.

Pitfall: Traps were arranged in three 100 m transects with 3 traps within $2 \mathrm{~m}^{2}$ every 10 m , for a total of 30 traps per transect. One transect sampled high vegetation, another low vegetation and the last sampled the edge of the swamp.

Malaise trap: One day's catch was one sample.
Searching: searching for adult true bugs under logs, rocks, and bark, and in rotten logs, leaf litter, holes, mushrooms, spider webs, and bird nests. One hour's collecting constituted a sample. Only implemented in the May sampling period.

Berlese: Twenty samples per field trip, each consisting of approximately $25 \mathrm{~cm} \times 25 \mathrm{~cm}$, depth 10 cm of soil and litter.

Fogging: A pyrethroid diluted in water was used to fog 2-7 m tall trees. Insects fell on a $4 \mathrm{~m}^{2}$ white sheet during a 2 h drop time.

Specimens and sorting procedures
Each sample in a $75 \%$ ethanol vial was labelled with the locality, date, collector, and method. Material was identified at the Museo de La Plata and Museo Argentino de Ciencias Naturales. In doubtful cases specialists were consulted. Voucher specimens of each species are deposited at the Museo de La Plata and Universidad Nacional del Nordeste, Argentina.

Statistical analysis
Statistical analyses and graphs were produced with Systat 10.0 (SPPS Inc. 2000). To analyze the effects of inventory design parameters on results, we used analyses of variance in
which method, collector identity and experience, and season were treated as independent factors, and numbers of adults and species per sample respectively were dependent variables. Post-hoc Tukey HSD tests were used to identify those treatments responsible for significant factor effects. Due to the large numbers of factors and treatments, some ANOVA cells were empty. For example, no inexperienced collectors participated in September, and collector identity and experience was inapplicable to Berlese, light trap, pitfall, and fogging techniques. Therefore, only beating and sweeping were analyzed by ANOVA. Additional analyses investigated the influence of individual collectors on the number of species per sample. Species accumulation curves and richness estimates were produced with EstimateS 7.5 (Colwell 2005) and Biodiversity-Pro (McAleece 1997). "Sampling intensity" is the ratio of specimens to species (Coddington et al. 1996; Sorensen et al. 2002). Given roughly comparable relative abundance distributions and richness, it crudely compares sampling effort to the size of the universe being sampled (but see Gotelli and Colwell 2001). Inventory completion (or completeness) is the extent to which an inventory, or inventory component, samples the faunal partition available to it (Sorensen et al. 2002). Equal sampling effort in microhabitats or diversity partitions that vary in richness can results in disproportionately rich microhabitats being disproportionately undersampled. We measure "inventory completion" in an inventory partition as the ratio of observed richness to the Chao 1 richness estimate for that partition (Sorensen et al. 2002). The Chao 1 estimator is especially appropriate for such a statistic because it performs well (Colwell and Coddington 1994; Walter and Martin 2001), is simply calculated from tabular data, and is the only nonparametric richness estimator that does not require replicate sampling. Because the value of Chao's estimated coefficient of variation (CV) for abundance distribution sometimes was CV $>0.5$, we re-compute Chao1 using the Classic instead of the Bias-Corrected option of the EstimateS program. Then, based on the results with the Classic option, we reported the larger Chao1 as the best estimate for abundance-based richness, as recommended by Chao (2004). It can therefore be applied to more kinds and qualities of inventory data, and will enable broader comparison of completion statistics across inventories. Retrospectively, we also used the statistical results to identify the heteropteran family that was easiest to sample and therefore a likely candidate for an indicator taxon.

## Results

The seven collectors produced 337 samples distributed over 6 days in May ( $n=105$ ), 5 days in September $(n=113)$ and 8 days in December $(n=119)$, which yielded 4,678 adults of 225 species (Table 1; Table S1 in Electronic supplementary material). Figure 2 shows the relation of the rank/abundance of the species of the studied community of Heteroptera at Carlos Pellegrini, Corrientes, Argentina during 2001-2002. Overall sample intensity (specimens: species) was 20.97, but it ranged from 1 to 19 depending on method (because different techniques can catch the same species, the overall sample intensity usually exceeds that of most data partitions). Sixty-eight species were singletons and 34 were doubletons. Despite the unusual size of the inventory, the percentage of singletons remained high at $30 \%$. Although CYD-01 at 640 individuals greatly exceeded the abundance of all other species, it accounted less than the $14 \%$ of the total inventory. No species particularly dominated, because CYD-01 was dominant in December (20.40\%) and May ( $18.12 \%$ ) but not in September where MIR-24 (17.46\%) was the dominant species. Samples averaged 13.9 individuals and 4.8 species overall. Pitfall sampling yielded the fewest average number of individuals per sample (1) and sweeping the most (17.7). Each
Table 1 Comparing the results obtained of the observed and estimates species richness, the sample intensity and the "inventory completion" by collecting methods and combinations of the most productive methods

|  | Beating | Berlese | Fogging | Light trap | Malaise | Pitfall | Sweep | Beat + sweep | Beat + sweep + light trap | Total |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| No. samples | 148 | 1 | 12 | 10 | 6 | 2 | 158 | 306 | 316 | 337 |
| No. individuals | 1,531 | 3 | 49 | 291 | 16 | 4 | 2,784 | 4,315 | 4,606 | 4,678 |
| Singletons | 55 | 3 | 9 | 17 | 10 | 0 | 49 | 61 | 64 | 68 |
| Doubletons | 20 | 0 | 6 | 4 | 1 | 2 | 21 | 33 | 29 | 34 |
| Singletons (\%) | 40 | 100 | 45 | 41 | 91 | 0 | 33 | 31 | 30 | 30 |
| No. unique spp. | 71 | 0 | 16 | 27 | 11 | 2 | 59 | 72 | 77 | 86 |
| No. duplicate spp. | 20 | 0 | 3 | 9 | 1 | 0 | 34 | 43 | 39 | 40 |
| No. spp. | 137 | 3 | 20 | 41 | 11 | 2 | 148 | 199 | 212 | 225 |
| Sample intensity | 11.18 | 1.00 | 2.45 | 7.10 | 1.45 | 2.00 | 18.81 | 21.68 | 21.73 | 20.79 |
| Chaol | 212.62 | 6.00 | 26.75 | 77.12 | 62.00 | 2.00 | 205.16 | 255.37 | 288.01 | 293.00 |
| Completion (\%) | 64 | 50 | 75 | 53 | 18 | 100 | 72 | 78 | 74 | 77 |



Fig. 2 Species rank/abundance curve from Heteroptera at Carlos Pellegrini, Corrientes, Argentina, during 2001-2002
light trap sample was 3 h , so the average number of adults per light trap hour was about 10 . Richness per sample ranged from 1 to 21 species, and abundance from 1 to 117 individuals.

Complementarity between methods and seasons
Figure 2 shows the relationship between the most productive collecting methods to Heteroptera in the studied area. It shows that in the same value of abundance beating method collected more species than sweeping, but the final result of the total sample time sweeping method collected more species and accumulative abundance of Heteroptera than beating. Considering only beating and sweeping, 111 species were unique to one or the other, and 87 occurred in both. No species were caught by all methods (maximum 4), and only 15 were taken by beating, sweeping and light-trapping, the three most productive methods. Of the 105 species theoretically abundant enough to appear in all seasons (abundance $\geq 3$ ), only 33 actually did; 31 of the remainder occurred in single seasons only, including 192 Derophthalma sp. (Miridae) individuals during September (Fig. 3).

Faunal depletion

Despite intense collecting, numbers of animals per sample did not decrease over the course of the study or within sampling periods. In fact the best fit least-squares line trends slightly, if insignificantly, upward (Fig. 4).

Inventory completion
The mean inventory completion by method was $62 \%$ (Table 1) and by season $71 \%$ (Table 2) and by most diverse families is showing on Table 3. Figure 5 compares observed


Fig. 3 Showing the relation of the most productive methods and the most productive combination of them to obtain more diversity of Heteroptera at Carlos Pellegrini, Corrientes, Argentina, in the studied period


Fig. 4 Sample abundances in chronological order and least squares fit
to estimated species richness for each method and the total inventory. Of the three most productive methods, sweep sampling was most complete at $72 \%$ and light-trapping least complete at $53 \%$. Beating was less complete than sweeping, despite essentially equal sampling effort (Fig. 5). Analysis of data by season (Fig. 6) shows that both the December and September inventories were substantially more complete than May (completion 74, 76

Table 2 Showing the results of the observed and estimated species richness by the most diverse Heteroptera families collected in Carlos Pellegrini, Corrientes, 2001-2002

| Familiy | ALY | COR | CYD | LYG | MIR | PENT | RED | RHOD | TIN |
| :--- | ---: | ---: | ---: | :--- | :--- | :--- | :--- | :--- | :--- |
| $N$ | 56 | 203 | 697 | 647 | 1,120 | 510 | 256 | 397 | 81 |
| $S$ | 5 | 18 | 12 | 34 | 39 | 420 | 22 | 9 | 9 |
| Singletons | 0 | 6 | 4 | 8 | 8 | 17 | 3 | 9 | 3 |
| Doubletons | 1 | 2 | 1 | 3 | 5 | 8 | 3 | 1 | 3 |
| Uniques | 0 | 6 | 6 | 14 | 10 | 21 | 6 | 1 | 5 |
| Duplicates | 3 | 5 | 1 | 1 | 11 | 5 | 3 | 2 | 3 |
| Chao 1 | 5 | 27 | 20 | 44.67 | 40.03 | 60.06 | 22.75 | 9 | 10.5 |
| Completion (\%) | 100 | 67 | 60 | 76 | 97 | 70 | 97 | 100 | 86 |

Table 3 Inventory data of Heteroptera at Carlos Pellegrini, Corrientes, Argentina by season

|  | December <br> 2001 | May <br> 2002 | September <br> 2002 |
| :--- | :--- | :--- | :--- |
| $N$ | 1.672 | 1.534 | 1.472 |
| $S$ | 117 | 128 | 112 |
| Singletons | 35 | 50 | 38 |
| Doubletons | 15 | 17 | 20 |
| No. de unique spp. | 51 | 65 | 48 |
| No. duplicate spp. | 17 | 24 | 34 |
| Sample intensity | 14.29 | 11.98 | 13.14 |
| Chao1 | 157.83 | 201.52 | 148.1 |
| Completion (\%) | 74 | 64 | 76 |

Completion by method


Fig. 5 Inventory completion by method
and $64 \%$, respectively (Table 2; Fig. 6). If December and September are combined completion remains at about $76 \%$, due to low overlap between seasons.

Richness estimation
Figure 7 represents the accumulative species curves of Heteroptera collected to the studied area by family and Fig. 8 represents the performance of the richness estimators in relation


Fig. 6 Total species observed for each month with Chao1 estimate


Fig. 7 Accumulative species curves by family, the sample value represent one collection day. The families considered are the most diverse collected, but Miridae is not included
to the observed species of Heteroptera collected at Carlos Pellegrini, Corrientes, Argentina. According with Fig. 8, all the richness estimators are very close between then except Bootstrap and Jackknife 2, despite of our effort, the nonparametric species richness estimators suggest that a good amount of species of Heteroptera (Table 4), are yet not collected (between 263 and 325 estimated species) at Pellegrini. Richness estimation curves for the beating and sweeping partitions combined show typical signs of an advanced


Fig. 8 Performance of the richness estimators in relations to the observed species of Heteroptera at Carlos Pellegrini, Corrientes, Argentina during 2001-2002. The samples represent the accumulative samples by days of collection

Table 4 Observed and estimated species richness using different richness estimators

| Observed species richness | 225 |
| :--- | :--- |
| Estimated species richness | $293 \pm 21.82$ |
| Chao1 | $317.45 \pm 26.53$ |
| Chao2 | $325.28 \pm 0.06$ |
| ICE | $301.23 \pm 3.29$ |
| ACE | 263.35 |
| Bootstrap | $310.35 \pm 16.92$ |
| Jacknife1 | 355.96 |
| Jacknife2 | 285.23 |
| Michaelis-Menten |  |

yet still incomplete inventory, too (Fig. 9). The observed accumulation curves is still rising and well below any estimator curves, the estimator curves are weakly asymptotic, if at all, but the unique's curve seems to have leveled off and the duplicate's curve is rising steadily. The richness estimators, on the whole, suggest a minimum annual richness at Pellegrini of at least $250-300$ heteropteran species (for the areas sampled by beating and sweeping during these seasons), of which less than 200 were actually observed.


Fig. 9 Observed and estimated species richness of Heteroptera collected by Beat and Sweep at Pellegrini, Corrientes, Argentina during 2001-2002

Indicator taxa
Inspection of the ratio of singletons to doubletons (or uniques to duplicates) by family revealed that Alydidae and Rhopalidae families were the most completely sampled (Fig. 7) of the families represented by less than 10 species, meanwhile Miridae (Fig. 10) was for the families at greater than 10 species. Estimator curves run only for Miridae confirm this: the estimators themselves are broadly asymptotic, the uniques curve is actually decreasing and almost crosses the duplicates curve, and the observed curve ends at about $87 \%$ of the estimate (Fig. 10).

## Discussion

The minimal realistic spatial scale that is biologically real is one large enough to include breeding populations of all resident species, species-area effects and undersampling issues aside (Scharff et al. 2003; Magurran 1988). This study site consisted of 50 ha, which one would think would encompass the lives of most heteropteran species. The population structure of heteropteran species is poorly understood, however, What is the average nearest neighbour distance between individuals in a population? In other words, one explanation for persistently rare species (singletons) is that their population structure is considerably larger than the scale of the inventory. Presumably, 50 ha should suffice for most species of Miridae, Lygaeidae, Coreidae, Cydnidae and Pyrrhocoridae, but possibly not for the predacious Reduviidae.

The terrestrial Heteroptera checklist of Corrientes province (Coscarón 2003) lists 146 spp.; the Pellegrini inventory found 225 spp . The latter is almost the double the former. Given the huge difference in areas $(9,250,000 \mathrm{vs} .50 \mathrm{ha})$, one can anticipate many more species in the province. At Pellegrini $87 \%$ of the fauna were herbivores and $13 \%$ predators.


Fig. 10 Showing the performance of the non-parametric species richness estimators for Miridae at Col. Carlos Pellegrini, Corrientes, Argentina, 2001-2002

The only other comparable quantitative work on heteropteran faunas seems to be that of Hodkinson and Casson (1991), who found 465 species of terrestrial Heteroptera in tropical rain forest in Sulawesi. They did not address the issue of undersampling. While the Sulawesi tropical rain forest indubitably supports more species than a south temperate wetland, the estimator curves for Pellegrini suggest that 300 species, or even more, for this small site is not unrealistic. The faunas also differ in relative species richness by family. The Pellegrini inventory found more coreid and pentatomid species but many fewer mirids, probably due to the mix of sampling methods.

At Pellegrini the May inventory found the most species (Fig. 8), probably because Heteroptera are more abundant in late summer (Southwood 1960). In fact the richness of the fauna during May increased so much that the resources available ( 103 samples) were insufficient even to obtain a stable estimate of the late summer heteropteran fauna.

Species apparently limited to only one or two seasons were probably present as eggs or hidden in retreats not accessible to the collecting methods during the off season.

Although reserve managers are often worried by the immense number of animals sampled during insect surveys, we saw no decrease in numbers of animals per sample throughout the study, suggesting that this intensity of sampling did not deplete the fauna.

In this survey, method had by far the strongest effect on abundance and richness of true bugs in samples. Collector experience and season moderately affected richness but not abundance.

The extreme ecological dominance of some species such as Galgupha sp. (Cydnidae) in all seasons and Derophthalma sp. (Miridae) in spring made this inventory less complete than it otherwise would have been. Insofar as none of the richness estimators require abundances in excess of 10 , most of the animals collected in this inventory were statistically superfluous. The obvious solution is to truncate collection of common species after some arbitrary number, say 20 (Colwell and Coddington 1994), but this requires species discrimination in the field. For heteropteran species accurate species discrimination in the field is not possible. Scharff et al. (2003) also make the point that extreme ecological dominance in temperate zones can make them harder in some ways to inventory than tropical sites.

Of the 23 heteropteran families encountered at Pellegrini, mirids were both diverse ( 39 species observed) and apparently easiest to sample ( $87 \%$ completion). Estimator curves suggest a fauna of perhaps 45 species (Fig. 10). However, lack of experience in collecting mirids may have substantially depressed the number of species observed. Still, all other things being equal, these data identify Miridae as the best candidate heteropteran taxon for long-term monitoring.

In this inventory, sweeping caught marginally more species in total and significantly more per sample than beating. Nevertheless, all methods seem to access different sampling universes (Table 1), which justifies as broad a spectrum of collecting methods as resources allow, if the inventory aims to be complete (Hammond 1990).

Sampling methods (Basset et al. 1997) access different components of the fauna, and these components may differ in numbers of species and how susceptible they are to a particular collecting method (Longino et al. 2002). Allocating equal effort to all methods implicitly assumes that methods are equally efficient and/or that the targeted faunal partitions contain roughly equal numbers of species with the same abundance distribution. This assumption is clearly unrealistic, and thus to minimize distorted results sampling effort should probably be allocated so as to compensate for such effects. At Pellegrini effort was allocated unevenly, but the resulting inventory completion ranged from 18 to $78 \%$ across all methods, not a particularly even result. At $64 \%$ beating, completion was roughly comparable to sweeping ( $72 \%$ ), but in the future more effort should go to lighttrapping (only $53 \%$ ). Although fogging in this inventory may seem fairly complete at $75 \%$, the method is complex and time-consuming to apply. Given the relatively low numbers of species obtained $(<20)$ by fogging, if resources are scarce they could arguably be invested elsewhere, although at some cost in coverage. Malaise sampling also yielded few species, but $90 \%$ of those captured were only caught in malaise traps. As expected, Berlese and pitfall sampling yielded very few species and individuals and should probably be dropped from future inventories.

Biström and Väisänen (1988) also found that beating and sweeping were the most efficient techniques. Holloway (1977) suggested that light traps produce low catches. Cold, wet, windy, or moonlight weather can all decrease the abundance and richness of insects in light traps. Dobbs (2002) collected 82 spp. in light traps in the Everglades. This inventory collected about half that ( 42 spp .), but the light trap designs were different and the Everglades is substantially more tropical. Hodkinson and Casson (1991) concluded that species known only from light traps must live in specialized or inaccessible habitats; the high proportion of species caught only in light traps in this inventory confirm this. Leston (1957) suggested that the heteropteran families most amenable to light-trapping were Miridae, Lygaeidae and Pentatomidae, which our results also confirm. Paula Silva and Ferreira (1998) found Miridae to be most abundant in light traps.

Heteroptera with specialized habits (the blood-feeding cimicids and triatomines) or habitats (aradids live under bark and decaying trees) are more difficult to sample. They require other methods than those used here.

In sum, this initial application of a semi-quantitative inventory protocol to Heteroptera shows that it yields comparable results to less-structured designs yet provides more insight into the effects of various factors on the results. In particular, the ability to detect and correct for undersampling bias provides a critical view of the inventory results. At almost 5,000 specimens and 225 species, this effort is certainly among the largest local inventories of Heteroptera anywhere in the world to date. Nevertheless, given the apparent diversity of heteropteran faunas, still more sampling effort will be necessary to obtain robust estimates of local species richness. Future heteropteran inventories should allocate more sampling effort to light-trapping. If an inventory design cannot command such resources and the goal is to estimate accurately faunal richness, the best strategy might be to restrict the inventory taxonomically. To that end, it appears that mirids are both diverse and relatively easy to sample. As such, they may be the best candidate indicator group for monitoring among heteropterans.

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