Diversity of Two Beetle Taxa at a Western Amazonian Locality (Coleoptera: Histeridae; Staphylinidae, Pselaphinae)

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Abstract

We analyzed data from two beetle taxa, Pselaphinae (Staphylinidae) and Histeridae, collected during a seven-week expedition to Yasuni National Park (Napo Province, Ecuador) during June–August 1999. Smoothed species accumulation curves and richness estimators were used to assess the effectiveness of Berlese extraction, flight intercept traps, light traps, and a combination of other techniques in sampling these two focal taxa. From a total of 3,465 specimens, including 871 pselaphines and 2,574 histerids, we sorted 385 species, 178 pselaphine species and 207 histerid species representing 62 pselaphine genera and 63 histerid genera. We offer regional comparisons to assess the scale of diversity documented at Yasuni. Finally, we used these empirical data, richness estimates, and simple percentages to predict that beetle diversity at this site in Yasuni National Park ranges from 9,871 to 14,102 species, and total insect diversity ranges from 24,665 to 35,255 species.

Estimating global and regional patterns of diversity has taken on increasing importance in recent years as the extinction crisis has become more acute and our basic ignorance of species richness has become more obvious. Knowing the number and taxonomic distribution of species within a habitat is a necessary starting point for understanding complex ecosystem processes such as energy flow and productivity, competition, predator/prey interactions, and symbiotic relationships. Species richness estimates also serve the needs of conservationists making difficult decisions about preserving areas in an increasingly degraded and exploited global landscape (*e.g.,* Anderson and Ashe 2000). Global insect diversity has proven to be a particularly controversial topic. Although its importance in assessing overall terrestrial species diversity is well recognized, reliable estimates among localities and regions for use as comparative baselines have proven difficult to obtain. Estimates of global insect diversity ranging from five to 30 million (Solis 1999) are mostly based on extrapolations of limited empirical data from single-site or limited regional inventories, and usually of only a few focal taxa (Hammond 1994). Such taxa must be within the investigators' areas of expertise, must be easily sampled with the resources at hand, and should be taxonomically tractable, or at least easy to sort to species.

Here we provide an example of a site analysis following seven weeks of intensive collecting at Yasuni National Park, Ecuador. Focal taxa chosen for detailed study included the beetle family Histeridae, and the staphylinid beetle subfamily Pselaphinae. In addition to compiling a basic inventory of species of these two taxa represented at Yasuni, we documented the relative contributions of various collecting methods to the total species accumulation curves. We used these data and richness estimates derived from them to predict total beetle and insect species diversity at the study site.

The Pselaphinae is a monophyletic subfamily of staphylinid beetles containing about 8,500 described species worldwide (Newton and Chandler 1989; Newton and Thayer

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1995). Most pselaphines are predators of other small organisms as both larvae and adults, but some highly integrated inquilines (supertribe Clavigeritae) may subsist wholly or partially on trophallaxis from social insect hosts. The family Histeridae comprises about 4,000 described species (Mazur 1997). As with pselaphines, histerids are predatory beetles with a substantial number (mainly in the subfamilies Hetaeriinae and Chlamydopsinae) of inquilinous species that are integrated into the colonies of social insects.

Materials and Methods

Research was conducted at the Yasuni Research Station, Napo Province, Ecuador, which is operated by Pontificia Universidad Catolica del Ecuador (Quito). It is located in western Amazonia, on the middle Rio Tiputini (tributary of the Rio Napo) (0°40.5′S, 76°24′W) at *ca*. 250 m elevation. Forests around the Station are within Yasuni National Park and Biosphere Reserve. Together with the Huaorani Indian Reserve, these lands represent *ca*. 15,500 km^2 of nearly undisturbed Western Amazon rainforest.

Forests at the study sites are growing on rough terrain cut by numerous creeks into more or less narrow ridges with steep slopes and deep (up to 50 m) ravines. The only apparent human impact in the area is a loose network of well-managed gravel roads along some dominant ridges, oil pipelines, and small clearings for crude oil extraction and processing. Most collecting was done in the *terra firme* forests, although seasonally flooded forests and transition zones were also sampled. The majority of work was conducted within a 3 km radius of the field station. For additional descriptive and comparative information about forests at the study area, see Pitman *et al*. (2001) and references cited therein.

Beetle taxa analyzed for the current study were collected by AKT, CEC, and Victoria Bayless using the following collecting methods (total effort in parentheses) during 52 days of fieldwork: flight intercept traps (FIT's) (nine traps; 335 trap days); forest litter sifting and Berlese extraction (32 samples, approximately 5 kg/sample); light traps (mercury vapor and UV) (29 trap nights); hand collecting techniques (bark peeling, direct sampling from ant and termite nests and columns, sweeping and beating vegetation) (37 samples); and baiting with dead fish (two samples). One trap day or night represents a single trap run during one 24-h period.

Each FIT consisted of a 1×3 m fine mesh nylon ("no-see-um" netting) screen tied between two trees and covered by a clear plastic rain canopy. Shallow plastic trays containing a 1:1 mixture of propylene glycol and water, with a small amount of liquid soap were used to kill and preserve specimens during service intervals (three–five days).

Berlese samples were obtained by sifting moist forest litter through 1 cm wire mesh screens. Samples typically weighed 3–5 kg. Extraction of organisms was accomplished using four hanging vinyl Berlese funnels (1440 cm^2 surface area/funnel) under 100 watt lights.

Mercury vapor lights were operated on a hill overlooking the field station. Ultraviolet lights were operated opportunistically at various points in the forest.

We used the species richness estimator program EstimateS (version 5.0.1, R. K. Colwell, unpubl.) for data analysis. This program generates species and specimen accumulation curves based on empirical data and uses these data to extrapolate potential diversity based on eight different statistical algorithms (Colwell and Coddington 1994). Only estimators giving maximum and minimum values are included in the figures.

We calculated pairwise complementarity between methods using Sorenson's Similarity Indices (Sorensen 1948). This index was calculated using the formula S =
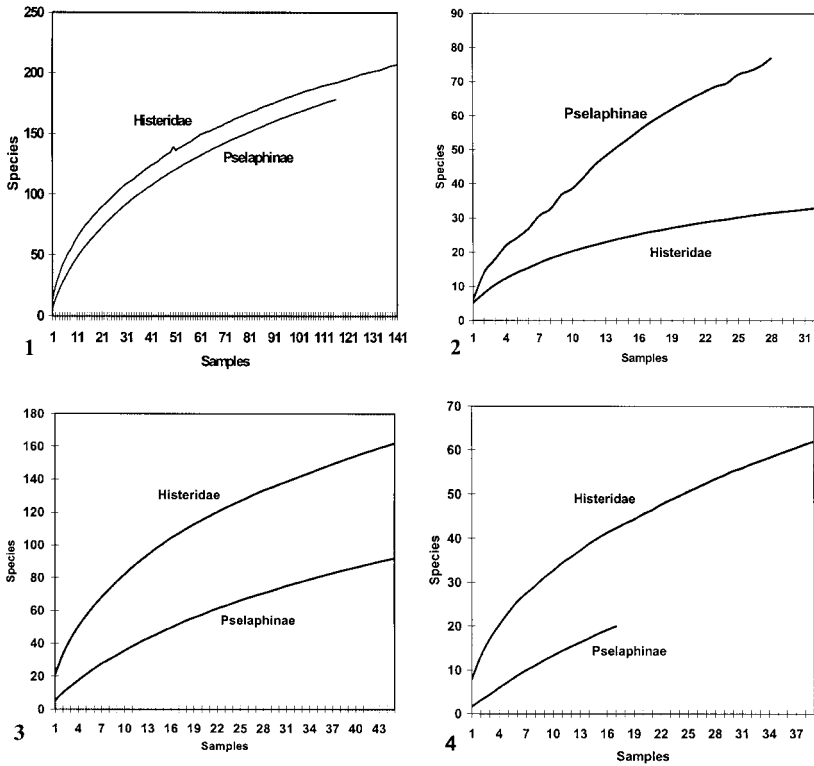
Figs. 1–4. Species Accumulation Curves. **1)** All methods combined; **2)** Berlese samples; **3)** light intercept trap samples; **4)** hand collecting and other methods.

2 c/(A + B) where c = number of species common to both samples and A + B = total number of species in both samples.

Collector days, trap days, or individual samples were the basic units for generating species accumulation and richness estimator curves, using 100 runs and 10 incidence classes. For analysis our methods were categorized as (1) flight intercept, (2) Berlese sampling, (3) light trapping, and (4) other. The "other" category was dominated by hand collecting techniques, but also included the dead fish trap.

Voucher specimens are deposited at the Louisiana State Arthropod Museum and at the Pontificia Universidad del Ecuador, Quito. A checklist of species sorted and identified for this project may be viewed at the following website: http://www.agctr.lsu.edu/arthropodmuseum/.

Results

A total of 3,465 specimens were used for the analysis. Pselaphines were represented by 891 specimens, 178 species, and 62 genera. Histerids were represented by 2,574 specimens, 207 species, and 63 genera. The number of genera is a conservative estimate. Generic identities within some genus-group taxa are problematic (*e.g.,* pselaptine and trimiine pselaphines; hetaeriine and exosternine histerids). Species
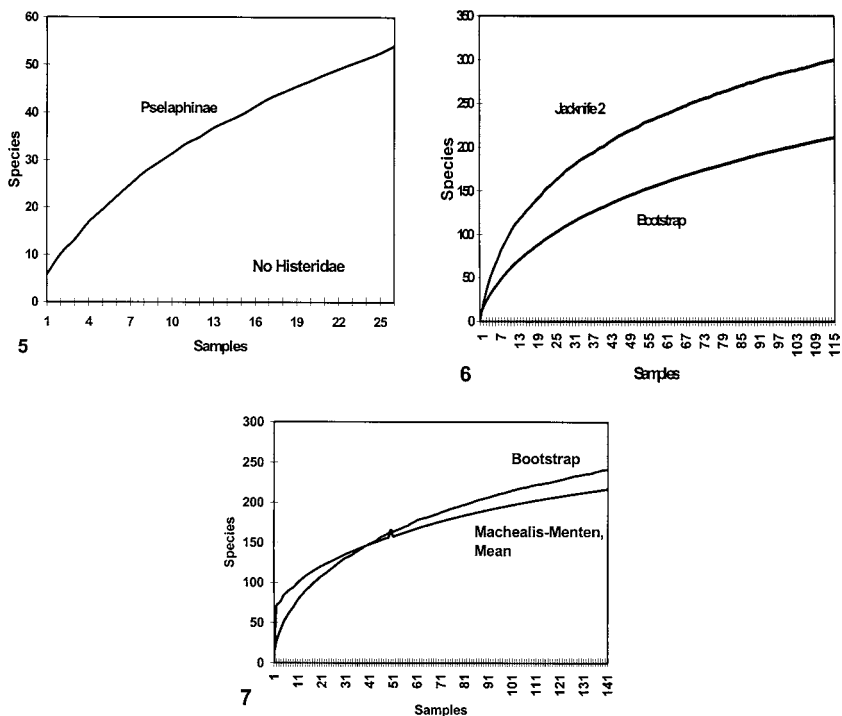
Fig. 5. Light trap species accumulation curves.
Figs. 6–7. Maximum and minimum species richness estimates. **6)** Pselaphinae; **7)** Histeridae.

accumulation curves across all methods (Fig. 1) for both taxa were approximately parallel. The shorter line for pselaphines was a result of fewer samples containing specimens of that taxon. Neither line is asymptotic.

Seventy-six (42.7%) of 178 pselaphine species were represented by single individuals (singletons) and 35 (19.7%) were represented by two individuals (doubletons). Singleton and doubleton figures for histerids were 79 species (38.2%) and 27 (13.0%), respectively, out of 207 total species.

When the species accumulation curves were broken down by methods, differential effectiveness for collecting the two taxa was revealed, with Berlese sampling (Fig. 2) the most effective method for pselaphines but performing poorly for histerids. Flight intercept trapping (Fig. 3) was highly successful for histerids, but much less effective for pselaphines. Hand collecting and other methods (Fig. 4) were moderately effective for histerids, but were the least effective methods for pselaphines, with only 20 species taken by hand. The "other methods" included the fish bait trap, but this contributed only a small number of histerid specimens and no pselaphines. Light trapping (Fig. 5) produced moderate numbers of pselaphines, but not a single histerid.

The highest and lowest species richness estimators (Figs. 6–7) indicate disparate results for pselaphines, with the lowest estimate roughly corresponding to the empirical number of observed species and the maximum estimate exceeding 300 species. By contrast, the histerid estimates are clustered between 200 and 240 species.

Sorenson's Indices (Table 1) were low. Maximum values for any two methods for

Table 1. Sorensen's similarity matrices.

	Pselaphines				Histerids		
	Light trap	FIT	Other	Berlese	FIT	Other	Berlese
Light trap	x	—	—	—	(not applicable)[1]		
FIT	.163	x	—	—	x	—	—
Other	.081	.106	x	—	.163	x	—
Berlese	.183	.376	.144	x	.151	.048	x

[1] No histerids were captured in light traps.

pselaphines was .376 in FIT and Berlese samples. Minimum values for pselaphines was .081 in light traps and "other" samples. Complementarity among methods for histerids was less, with maximum values of .163 in FIT and "other" samples and only .048 shared by Berlese and "other" samples.

Discussion

The important message of this analysis to surveyors of insect diversity is that different methods produce dramatically different results for different taxa, and these differences may not be apparent until the contribution of each method is critically examined. Although histerids and pselaphines presumably share many of the same niches, and we specifically targeted those niches, clearly there was no single "most effective" technique for maximizing recovery of both taxa. We expect that examinations of other taxa will reveal similar heterogeneity with regard to sampling success.

The clustering of the richness estimates for histerids around the empirical results suggests that we are approaching a complete sample of histerid species present in the area, though the empirical species accumulation curve did not flatten out (the assumption being that it would have soon if we had kept collecting). The effectiveness of microhabitat-focused hand collecting for histers probably served an important function in filling gaps left by the various mass-collecting methods.

The estimators of pselaphine diversity differed substantially. This disparity is caused by the differential effects that sensitive variables (singletons, doubletons, uniques, duplicates, and others) have on the various algorithms (Colwell and Coddington 1994). The large number of these variables suggests that actual species richness of pselaphines is considerably higher than the 178 observed, perhaps in the vicinity of 250, the middle range of the estimates. Our percentages of singletons (42.7% of pselaphines; 38.2% of histerids) are similar to those reported in several diversity studies of arthropods at other Neotropical localities. Silva and Coddington (1996) reported 41.6% singletons for spiders collected in Madre de Dios, Peru. Didham *et al*. (1998) reported 45% for beetles at a site near Manaus, Brazil. The lowest figure we could find was 23.6% for Odonata at Parque Nacional Manu, Madre de Dios, Peru (Louton *et al*. 1996).

Comparisons of our results with other single site beetle diversity estimates are fragmentary at best due to the lack of such studies, at least within the neotropics. For pselaphines, the observed species richness at Yasuni is almost one-third of the total observed species richness (508) for the entire country of Panama given by Chandler (1992). The only other Amazonian locality where pselaphine diversity as been analyzed is a site near Manaus, Brazil. Didham *et al*. (1998) reported that 109 species were sorted by D. S. Chandler from 9201 m^2 Berlese samples collected between January and August 1994. Collections made during several expeditions to a moist semideciduous forest at Rio Bravo Conservation and Management area in Belize have yielded 57

pselaphine species from approximately 800 specimens (C. Carlton, unpubl. data), about one-third the diversity at Yasuni.

The Yasuni single locality histerid species count equals about 30% of all described South American histerids (Mazur 1997). For the inquilinous histerid subfamily Hetaeriinae, the richest local lists for neotropical lowland rainforest sites yielded only about two-thirds of our Yasuni count (37–38 vs. 56 morphospecies). These data are extracted from multi-month efforts by various investigators using taxon-specific methods at Barro Colorado Island, Panama and Hamburg Farm, Costa Rica (A. Tishechkin, unpubl. data).

For both taxa pairwise similarity for methods that contributed substantially to total species richness lies within the .13–.18 range with one exception (pselaphine FIT/ Berlese, .376) (Table 1). This magnitude of similarity is similar to that reported for site to site similarity at regional scales (sites separated by tens of hundreds of kilometers) (Louton *et al*. 1996; Pogue 1999). These data reinforce the need to follow the suggestion of Coddington *et al.* (1996) for maximizing success of arthropod sampling efforts: "The idea is to use an array of collecting techniques that complement each other, rather than trying to design one technique with minimal bias."

We can use the empirical data and estimates to predict total beetle and insect species diversity at Yasuni. Based on the current global diversity figure of 320,000 species of Coleoptera, the midpoint between Lawrence's (1991) liberal estimate of 350,000 and Arnett's (2000) more conservative 290,000, pselaphines account for about 2.7% of total species diversity and histeridae for another 1.2%, or about 3.9% for both groups (8,500 pselaphines + 4,000 histerids/320,000). Checking this against continental faunas, we find that the combined percentages vary somewhat, but still suggest they may be useful in estimating diversity at higher taxonomic levels within a reasonable margin of error. These two taxa represent approximately 4.6% of North American beetle diversity (710 + 435/25,000) (Newton *et al*. 2001; Kovarik and Caterino 2001; Lawrence 1991; Marske and Ivie 2003) and 3.8% of Australian beetle diversity (900 + 185/28,300) (Lawrence and Britton 1991). Thus, if we accept the global percentage, 3.9%, as a conservative baseline, the possible range of total Coleoptera species diversity at our study site in Yasuni National Park may be calculated using a multiplication factor of 25.64 (100/3.8). Using the observed species of our two focal taxa (385) to extrapolate, a minimum of 9,871 beetle species is predicted. Using the combined total for the two highest richness estimates for these two taxa (approximately 550 species), a high estimate of 14,102 is predicted. If we further extrapolate to total insect diversity using the widely circulated assertion that beetles represent 40% of total insect diversity, then the number of insects at this single site in Ecuador may range from 24,665 to 35,255, or between 30% and 40% of the number of species described for all of North America, 87,000 according to Arnett (2000). Erwin (1982) estimated 41,389 *arthropod* species per hectare in Panamanian seasonal forest. Though somewhat more conservative, our estimates for insect diversity are within the same order of magnitude. Regardless of whether the low or high estimates are favored, these figures must be viewed as conservative starting points for understanding actual diversity within the study area. They are based on fieldwork conducted over a limited timeframe and not all habitats were sampled (*e.g.,* tree canopies). Thus, Erwin's figures may well come close to the mark with more complete sampling.

Based on these estimates derived from our empirical data, the Western Amazon again emerges as an amazing center of diversity for beetles and insects as a whole. Analyses of local diversity, and the identified specimens on which they are based, are essential for addressing questions such as site complementarity, regional and global patterns of diversity, and changes in species diversity through time. By intensively analyzing the proceeds of collecting expeditions, systematists can contribute valuable

information to the ongoing effort to document species diversity in remaining undisturbed habitats worldwide.

Acknowledgments

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BOOK REVIEW

A. Viñolas and M. C. Cartagena. 2003. **Revisión del Genero *Phylan* Stephens, 1857 (Coleoptera: *Tenebrionidae*: Dendarini).** Entomological Monographs of Agrania, Barcelona, 93 pp. Price: 36 Euros (about $45 US). Available from http://entomopraxis.com/argania.

The darkling beetle genus *Phylan* is revised in this monograph. The work is a naked alpha-taxonomic treatment, no more and no less. The only ecological notes in the 93 printed pages are two sentences in the introduction (my translation), "Of crepuscular habits, they are encountered hidden beneath stones or at the base of plants, from sea level to 3,000 meters. They feed basically on plant detritus."

Even under the heading "Distribución" following each descripción, there is only a listing of (presumably) collection localities devoid of information concerning dates, elevations, habitat, method of collection, or names of collectors. For each of the 46 species there is a brief one paragraph morphological description, a photograph of the dorsal habitus, and a line drawing of the aedeagus. The photographs are redundant in that there are no discernible differences among the species. Inspecting the keys one finds that the separations are based on such characters as the relative size of the tarsomeres and subtle variations in the sculpturing of the integument. I was delighted to see distinct specific differences in the form of the aedeagi and equally delighted to find that these character-states are not included in the keys (one to subgenera and separate keys for each subgenus). There are 18 satellite photographs, one depicting Europe and the distribution of the type species, *Phylan gibbus* (F.), while 17 are of the Iberian peninsula with circles and ovals indicating the distributions of the less ubiquitous species. The circles are more schematic than informative, because for example, the area within the line depicting the boundaries in the range of *P. gibbus* from Norway to North Africa is about equal parts water and land, including all of the British Isles, when in fact, this species is restricted to the littoral dunes of the Atlantic coast.

Usefully the authors provide a table of synonyms, and an index, at the end of the text. There is a brief review of the nomenclatural history of the genus, but, no new taxa are proposed and none are sunk. Aside from the lack of ecological data, there is also no cladogram, no biogeographic analysis, and no phylogenetic hypothesis. In short, there is only knowledge. This minimalist approach appropriately reflects the stark realities of darkling beetle bionomics: they all look alike and, insofar as we know, the only thing they do is eat dead plants and make more darkling beetles. I wish such a monograph were available for every genus of tenebrionid.

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