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Survey and Quantitative Assessment of Flea Beetle Diversity in a Costa Rican Rainforest (Coleoptera: Chrysomelidae: Alticinae)

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ABSTRACT

Only 113 species in 43 genera of Alticinae are recorded in the literature from Costa Rica. The Arthropods of La Selva project (ALAS) carried out a quantitative inventory of the Alticinae at the La Selva Biological Station, a rainforest site in the Atlantic lowlands of Costa Rica. In addition, collections were examined for additional alticine material for Costa Rica as a whole. The quantitative inventory yielded 3221 specimens from Malaise traps, 2260 from canopy fogging, and 203 from miscellaneous other methods. A total of 247 species in 68 genera was obtained. The abundance distribution was bimodal, deviating from a lognormal by an overabundance of rare species. Canopy fogging was more efficient than Malaise trapping when compared on a per sample basis, but Malaise traps were far more efficient than canopy fogging on a per individual basis. Thus, over a long time Malaise trapping is more efficient. There was broad overlap in the species composition of the two sampling methods, and combining methods did not improve efficiency over single methods. Fogging multiple species of trees captured species at a higher rate than fogging single species when species accumulation curves were compared on a per individual basis, but not when compared on a per sample basis. Richness estimates did not stabilize as sample size increased, and the species accumulation curve was logarithmic, with no evidence of approaching a plateau. However, final richness estimates were only 10-15% higher than observed species richness, and the singletons curve was beginning to decline. Adding additional records from elsewhere in Costa Rica, there are about 350 species in 89 genera known from the country as a whole. This study recorded 10 genera new to Central America and 47 new to Costa Rica. Based on this study we predict there may be 1000 species of Alticinae in Costa Rica. All Central American countries certainly have a much higher actual diversity than is recorded in the literature.

RESUMEN

En la literatura de Costa Rica unicamente se han registrado 112 especies de 43 géneros de Alticinae. El proyecto Artrópodos de La Selva (ALAS), realizó un inventario cuantitativo de los Alticinae en la

Estación Biológica La Selva, localizada en el bosque tropical lluvioso, en las tierras bajas del atlántico de Costa Rica. Además, se examinaron colecciones para incluir material adicional de los Alticinae. El inventario cuantitativo dió un resultado de 3,221 especimenes en trampas de Malaise, 2260 especimenes de la fumigación del dosel, y 203 obtenidos por otros métodos. Un total de 247 especies en 68 géneros fueron obtenidos. La distribución de abundancia fue bi-modal, desviándose del logaritmo normal por la sobre abundancia de especies raras. La fumigación del dosel fue más eficiente que las trampas de Malaise cuando comparamos por muestra, pero las trampas de Malaise fueron mucho más eficientes que la fumigación del dosel cuando comparamos a nivel de individuos. De este modo a largo plazo las trampas de Malaise son más efectivas. Obtuvimos un amplio traslape en la composición de las especies de los dos métodos de muestreo, y si los combinamos esto no ayuda a la eficacia sobre métodos individuales. La fumigación de multiples especies de árboles registró una alta proporción de especies comparada con la fumigación de árboles de la misma especie, cuando las curvas de acumulación fueron comparadas a nivel individual, pero no cuando las comparamos a nivel de muestra . Las estimaciones de riqueza no se estabilizaron cuando incrementamos el tamaño de muestra, y la curva de acumulación de especies fue logarítmica, sin ninguna evidencia de que alcance la estabilidad. Sin embargo, las estimaciones finales de riqueza fueron de 10-15% más altas que la observada en la riqueza de las especies, y la curva de "singletons" empezó a declinar. Añadiendo registros adicionales de otros lados de Costa Rica, encontramos que hay cerca de 350 especies en 89 géneros conocidos para todo el país. Basado en éste estudio predecimos que hay cerca de 1000 especies de Alticinae en Costa Rica. Todos los paises Centroamericanos poseen una diversidad más alta de la que se indica en la literatura.

INTRODUCTION

The Chrysomelidae are a major component of tropical arthropod biodiversity (Wagner, 2000), and the flea beetles (Alticinae) comprise the largest subfamily. These highly diverse, phytophagous insects have important ecological roles as abundant herbivores, and many species have become important agricultural pests that affect human welfare. Detailed knowledge of species-level diversity patterns is important for conservation biology, natural product development, biodiversity monitoring, community ecology, and systematics research. Costa Rica is attempting to develop such knowledge through a nation-wide biodiversity inventory carried out by the Instituto Nacional de Biodiversidad (INBio). An important contribution to INBio's national inventory effort is the Arthropods of La Selva project (ALAS, Longino, 1994), which provides inventories for many arthropod taxa at one lowland rainforest site, La Selva Biological Station. This long-term, large-scale inventory is a collaboration of locally-trained people (parataxonomists) and taxonomic specialists from many institutions. We contribute to this effort by reporting here a detailed assessment of alticine diversity.

Inventory and monitoring using arthropods can often be more informative than using vertebrates, because invertebrates are often more sensitive indicators of environmental change and usually consist of more diverse species assemblages. Too often diversity studies and resulting planning for conservation or sustainable use concentrates on well-known groups (e.g., mammals, birds, and plants) and have ignored the most diverse ("hyperdiverse") organisms (e.g., arthropods, nematodes, and fungi) (Colwell and Coddington, 1994). More knowledge of the correlation between the well-known and hyperdiverse groups is needed before the "indicator group" strategy can be reliably applied to biodiversity surveys and estimates (Colwell and Coddington, 1994). Good inventory information about invertebrates can be very useful for management and planning in conservation efforts and

areas, assessing the sustainable use of natural resources, and measuring changes in an ecosystem in response to natural processes or human activities (Kremen *et al.*, 1993). Some invertebrate groups can be more effective indicators than others and Alticinae offer great potential, not only because of their high diversity, but also because of the relatively close association with their food plants. However, a requirement for an effective indicator group is that they can be readily and accurately identified to the species level. This is still a steep challenge for Neotropical Alticinae because of few specialists, few reliably determined collections, few monographs and keys, and lack of easy accessibility to good collections.

There are many implications of diversity studies in tropical rainforests. It is well known that much of the world's biological diversity resides in tropical rainforests, especially in the canopies of such forests, and that much of this diversity consists of species and even genera previously unknown to science. Therefore, purely from the perspective of discovery such surveys are fascinating and exciting. Many models, predictions and attempts at application of the results of diversity surveys and inventories have been made with the goal of conservation. Some studies have applied the results of diversity studies to statistical modeling and others have used them to demonstrate optimum and effective sampling methods for estimating biological diversity (Longino and Colwell, 1997).

For hyperdiverse taxa, intensive local inventories are a valuable starting point for understanding diversity at larger spatial scales. There are a variety of reasons why it is important to know local species richness or diversity, including the study of geographical patterns of species richness, chronological changes in species richness, causes of tropical diversity, altitudinal changes in diversity, and application to conservation issues and sustainable use (Longino, *et al.* 2002). Ecologists have devised methods for estimating species richness based on quantitative sampling (Soberón and Llorente, 1993, Colwell and Coddington, 1994), but traditional methodologies of collecting species information in the field have been inconsistent and non-quantitative (Colwell and Coddington, 1994, Longino *et al.* 2002). Many studies of species diversity have relied on observed species richness, which is always an underestimate of true community richness. Most diversity studies use limited sampling techniques carried out over a limited amount of time, which results in observed richness being far lower than true community richness.

Since the early 1980s there have been many attempts to estimate the global species richness of insects. For many of the studies on which the estimates have been based in tropical rainforests the main sampling method has been canopy fogging (Erwin, 1982). Subsequently there has also been significant debate as to whether the global estimates of species richness are accurate (Gaston, 1991, Erwin, 1991). These global estimates usually rely on assumptions of host specificity of insect herbivores, assumptions that are rarely tested. Novotny and Basset (2000) have made significant progress in revealing patterns of host specificity in chrysomelid communities. They conducted a three-year study in Papua New Guinea, in which they sampled from thousands of trees and carried out extensive feeding tests on live material. More recently Novotny *et al.* (2002) indicates that most herbivores in tropical forests have lower host specificity than assumed in many previous species richness/abundance studies. Our study does not address host plant relationships, but relies almost entirely on various mass-sampling techniques.

In a quantitative survey of the ants of La Selva, Longino *et al.* (2002) emphasized that it is difficult to estimate species richness for diverse faunas without a major sampling effort. They found that when single methods were examined, a high proportion of species were rare, species accumulation curves did not appear asymptotic, various richness estimates failed to stabilize, and the richness estimates were usually much higher than the observed richness. In contrast, when multiple sampling

methods were employed, the proportion of rare species declined, and the species accumulation curve showed signs of approaching an asymptote. Richness estimates still did not stabilize, but they did closely converge with observed richness (i.e., no more than 6% above observed). Longino *et al.* (2002) proposed that convergence of estimated and observed species richness was a good indicator of inventory completeness. Specialized collecting by an ant expert (Longino) was an important method. Longino found 293 of 437 species, a higher proportion than any other single method. Quantitatively structured sampling was good for estimating relative abundance of common species, but under-represented many species due to the limited scope and number of methods. Specialized collecting, actually the non-quantitative application of many methods, made it unlikely that there was a large pool of rare, unseen species at La Selva. Thus, a combination of non-quantitative specialist (taxonomist) collecting and quantitatively structured sampling resulted in a relatively complete inventory.

In surveys, inventories and other biological diversity studies the subject of species rarity is often discussed, but its cause is still somewhat enigmatic. Rarity is often quantified in terms of singletons (species known from one specimen), doubletons (species known from two specimens), uniques (species known from one sample, regardless of how many individuals occur in each sample), and duplicates (species known from two samples). Richness estimates are highly influenced by rare species, and often an attempt is made to partition rare species into low density elements of local communities and those that somehow do not belong ("tourists").

Longino *et al.* (2002) used natural history and distribution data to classify a number of the unique ant species as geographic or methodological "edge" species, the former being common outside of La Selva but rare on the property itself, and the latter possibly common at La Selva but not easily captured with any of the methods used. They also pointed out that species rare in ecological samples are often not rare to museum taxonomists. For taxonomists, rare species are often methodological edge species. It was striking how many of the La Selva uniques were known from additional collections outside of La Selva. Only 7 of 437 ant species were known from only one collection in the world.

Our current knowledge of alticine diversity is based on a history of collecting by taxonomists rather than quantitative inventories. There are over 500 genera of Alticinae and probably 8,000 species worldwide. Of these, over 230 genera have been described from the Neotropical Region (Seeno and Wilcox, 1982). The only key to Neotropical genera was done by Scherer (1962). However, since then about 50 new genera have been described, making even genus-level determinations extremely difficult. Faunal records for Costa Rican Alticinae have gradually accumulated over time. In the Biologia Centrali Americana, Jacoby (1884-1892) recorded 16 genera and 38 species. In the Coleopterorum Catalogus, Heikertinger and Csiki (1939-1940) recorded 16 genera and 39 species. Wilcox (1975) recorded 29 genera and 51+ species. Based on all the previous literature Furth and Savini (1996, 1998) listed 41 genera and 107 species. Furth (1998) added 3 *Blepharida* Chevrolat species records, Savini (1999) added *Heikertingerella marini* Bechyné and Bechyné, Duckett and Moya (1999) described *Ptocadica tica*, and Savini and Furth (2001) added *Neosphaeroderma coerulea* (Jacoby), raising the total number of recorded species to 113. Furth and Savini (1996, 1998) listed the following Alticinae diversity from some other Central American countries: Panama with 70 genera and 270 species; Mexico with 75 genera and 391 species; and a total from all Central America of 113 genera and 884 species. These totals were taken from previous catalogues, checklists, monographs, revisions and other taxonomic publications.

As for most arthropod groups, relatively little comprehensive new fieldwork had been attempted in order to more accurately or realistically understand the Alticinae diversity of Costa Rica. Nor

have there been many attempts to survey museum collections in order to determine this diversity based on various collecting events of many entomologists over time. Large numbers of undetermined Alticinae reside in many institutional collections and in private collections. Part of this is because this largest subfamily of the Leaf Beetles (Chrysomelidae) is very confused nomenclaturally and taxonomically and very few specialists can even reliably determine correct generic names much less specific ones. So the quantity of undetermined Alticinae continues to grow in collections and few specialists have tried to do significant sorting. Point surveys of alticine diversity are few. Farrell and Erwin (1988) found 126 common species of chrysomelids at a single site in Peru, but 64 (mostly Alticinae) could not even be identified to genus.

We present here an analysis of the alticine fauna of La Selva, based on an intensive program of structured sampling, and we review the knowledge of the fauna for Costa Rica as a whole. The results reveal how little we know of the Neotropical alticine fauna in general, and suggest efficient sampling methods for future surveys.

METHODS

Study Site

The study site is La Selva Biological Station (Heredia, Costa Rica) [84° 01'W, 10° 26'N]. It consists of a lowland tropical rainforest of about 1500 hectares with elevations from 50-150 meters and a mean annual rainfall of 4 meters. The habitat is a mosaic of lowland rainforest, second growth forest of various ages and abandoned pastures (McDade *et al.*, 1993).

Project ALAS

The Alticinae inventory was conducted as part of Project ALAS (http://viceroy.eeb.uconn.edu.ALAS/ALAS.html). Project ALAS is a large collaborative effort to survey the arthropods of La Selva Biological Station. A generalized set of sampling methods has been applied to a wide range of arthropod taxa, from spiders and mites to many groups of Coleoptera, Diptera, Lepidoptera and Hymenoptera. Field sampling and sample processing has been carried out largely by a resident staff of four persons (including the third author) recruited from communities surrounding La Selva and trained in entomological techniques (parataxonomists, *sensu* Janzen, 1991). A relational database of collection, specimen, and identification data is managed using the biodiversity database application *Biota* (Colwell, 1996). This on-going project is a collaboration with the Instituto Nacional de Biodiversidad in Costa Rica (INBio, Gamez, 1991). All specimens resulting from this project are labeled with INBio barcodes (in addition to standard locality labels). Specimens are deposited in the INBio collections facility in Santa Domingo de Heredia, Costa Rica, with the exception of those distributed to taxonomic specialists or collaborators, following INBio and Costa Rican regulations.

Sampling Methods in this Study

Malaise traps. A program of quantitative sampling was initiated in March 1993. Sixteen areas were selected on a La Selva station map, stratified by soil type (alluvial vs. residual) and forest type (primary vs. secondary). This design yielded four replicates for each soil and forest type combination. Sites were easily accessible from a trail system, but widely dispersed. A Malaise trap (Marris House,

with black vertical panel and white roof) was erected in each area. Malaise traps are open-sided tents with a collecting head in which flying or crawling arthropods are trapped and accumulate. The collecting head was a plastic bottle containing 75% ethanol. Malaise traps were placed in light gaps and potential flyways and maintained from March 1993 to March 1994, for a total of 13 months. At the beginning and the middle of each month, the collecting bottle with accumulated arthropods was removed and replaced with a fresh bottle of ethanol. After the first two months four distant traps were changed to a monthly sampling regime, resulting in a few one-month samples, but these are less than 5% of the processed samples. New traps were installed and a second series of Malaise samples was taken from June 1995 until June 1996. The traps were installed at the same sites as previously, excluding the 4 most distant sites. This sampling program yielded a total of 664 samples. Finally, a single Malaise trap was installed in a recent treefall gap near the laboratory in 1999, from which 6 samples were processed.

Fogging. Canopy fogging was done using the general procedures of Erwin (1983), Adis *et al.* (1984), and Stork (1988). During the 1993-1994 sampling period, eighteen trees were selected for canopy fogging: six individual trees of the most common tree species at La Selva (*Pentaclethra macroloba* (Willd.) O. Ktze., Fabaceae), six individual trees of a species of intermediate abundance (*Virola koschnyi* Warb., Myristicaceae), and one individual each of trees from six additional families. Six areas were chosen on a La Selva station map, such that the areas were dispersed across the available primary forest, and at the same time accessible from the trail system. In each area three trees were selected: a *Pentaclethra*, a *Virola*, and one of the six unique species. Trees were chosen that had large crowns, little overlap with adjacent crowns, and good access for climbing. The three trees in a group were usually fogged on consecutive days, and the 6 groups were fogged at approximately two-month intervals over one calendar year. A second set of fogging samples was obtained in October and November of 1994. Seven sets of three trees were fogged, all compressed into this two-month period instead of spread over a year. Again each group of three contained a *Pentaclethra macroloba*, a *Virola koschnyi*, and a distinct species in the "other" category. Finally, a set of six samples was taken in late December 1999 and early January 2000. These were from diverse species in a variety of families, all from one area in primary forest.

Arthropods were captured in funnels slung beneath tree crowns. Ropes were strung from trunk to trunk between the focal tree and neighboring trees to form an irregular network 2-3m high above ground level. Forty funnels, each intercepting an area of 1 square meter, were suspended from these ropes, distributed as evenly as possible in the area beneath the crown of the focal tree. The funnels were composed of ripstop nylon mounted on a metal hoop, with a threaded ring at the bottom for the attachment of a plastic sample bottle. Palm leaves and other vegetation immediately above the funnels were clipped or bent back, but otherwise the understory vegetation was left intact. Funnels were left upside down on the ground overnight to avoid accumulation of debris before fogging. Before dawn the next morning the funnels were re-suspended and the bottles filled with 75% ethanol. An operator climbed to the first branches at the base of the crown, 15 to 20m above ground level, and commenced fogging at about 0600hrs. We used a Golden Eagle DynaFogger, on setting 6, to fog 3.8 l of Pyrethrins 123 insecticide (Summit Chemical Co.). This is a 3% solution of a natural pyrethrin insecticide with synergists, in a petroleum distillate carrier. The operator gradually fogged in a 360 degree circle, attempting to cover the crown evenly. Following fogging, a two-hour drop time was allowed, after which the sides of the funnels were washed down with ethanol and the bottles were collected. Fogging events were classified into three "treatments" related to tree species: *Pentaclethra macroloba*, *Virola koschnyi*, and "diverse" (comprising many species of trees from many

families). At the time of this analysis 29 fogging events had been processed: 7 *Pentaclethra macroloba*, 9 *Virola koschnyi*, and 13 diverse.

Other. A few specimens were hand collected or netted by the ALAS staff and visiting scientists. A few specimens were collected at lights and one in a Berlese sample. The first author collected at La Selva by selective sweeping of the vegetation for several days in August of 1989 and for 2 days in January 1995.

Species Identification

The first author identified the ALAS samples first to genus using published literature on the Neotropical Alticinae fauna as well as an unpublished key to genera. In addition specimens were determined to genus or species by comparison to types or reliably identified specimens from a variety of institutional collections. Many identifications were possible because of the indefinite loan to the first author of M. Jacoby specimens in the F. C. Bowditch Collection (Museum of Comparative Zoology, Harvard University). Specimens were identified to actual species name or to genus name with a morphospecies name (e..g., *Acallepitrix* DF-002). Such morphospecies names were used consistently throughout the study and vouchers are deposited both at INBio and the U. S. National Museum of Natural History (USNMNH). Unique vouchers are temporarily maintained by the first author for further identifications and until either more specimens are discovered or the project is concluded, in which case uniques will be deposited at INBio. Generic author names can be found in Furth and Savini (1996, 1998).

In addition to the ALAS project specimens, the first author has examined and determined specimens from additional collections at INBio and USNMNH, both from La Selva and from elsewhere in Costa Rica. These additional collections add notable genus and species records to the knowledge of the Alticinae diversity of Costa Rica.

Inventory Efficiency and Richness Estimation

Data were analyzed using the program EstimateS (Version 5, R. K. Colwell, http://viceroy.eeb.uconn.edu/estimates). This program calculates species accumulation curves and associated values for a variety of richness estimators, presenting the mean of a user-designated number of random re-orderings of the samples. Species accumulation curves were "sample-based rarefaction curves" (*sensu* Gotelli and Colwell, 2001) and were examined based on number of samples (a measure of species density) and number of individuals (a measure of species richness) (Gotelli and Colwell, 2001). Inventory efficiency was investigated using the combined curve method of Longino and Colwell (1997). Species accumulation curves for Malaise samples, fogging samples, and the two methods combined were examined. In like manner, the three fogging treatments were compared with the combined curve method. The fogging treatments were also compared with respect to within-sample measures of diversity, using 1-way ANOVA. Two variables were examined: number of species, and number of species following rarefaction. Rarefaction was calculated using the Coleman equation, with each fogging sample rarefied to the sample size (number of individuals) of the smallest fogging sample.

Species richness was estimated with two estimators: fitting of the Michaelis-Menten equation to the smoothed species accumulation curve and the Abundance-based Coverage Estimator (ACE) (Colwell and Coddington 1994, Chazdon *et al.* 1998, and see the EstimateS website for references

and calculation methods). Richness estimates were evaluated by plotting them as a function of sample size, with presence of a plateau being indicative of a reliable richness estimate, and convergence with observed species richness being a measure of inventory completeness (e.g., Longino *et al.*, 2002).

RESULTS

This survey more than doubled the known diversity of Costa Rican Alticinae, at both the generic and species level (Tables 1 and 2). Generic diversity rose from 43 previously known genera to 89 reported here (Table 1). Of these 46 new genera, 3 are new to science, 10 new to Central America (8 from La Selva) and 33 are new to Costa Rica (26 from La Selva). From Table 1, of the 10 genera new to Central America are: *Andiroba* Bechyné and Bechyné; *Calipeges* Clark; *Chaparena* Bechyné (not recorded from La Selva); *Coroicona* Bechyné; *Egleraltica* Bechyné and Bechyné; *Loxoprosopus* Guerin; *Palmaraltica* Bechyné; *Paralacticoides* Bechyné and Bechyné (not recorded from La Selva); *Roicus* Clark; and *Stenophyma* Baly. And of the 33 genera new to Costa Rica, 7 are not recorded from La Selva: *Acrocyum* Jacoby; *Calliphron* Jacoby; *Euphenges* Clark; *Hydmosyne* Clark; *Lacpatica* Bechyné and Bechyné; and *Megasus* Jacoby; *Octogonotes* Drapiez. In addition, the following 12 genera have been previously recorded from Costa Rica (Furth and Savini, 1996, 1998, Furth, 1998), but were not found at La Selva during the current ALAS Project sampling: *Ayalaia* Bechyné and Bechyné; *Blepharida* Chevrolat; *Cacoscelis* Chevrolat; *Chalatenanganya* Bechyné and Bechyné; *Diphaulaca* Chevrolat; *Distigmoptera* Blake; *Hylodromus* Clark; *Macrohaltica* Bechyné; *Megistops* Boheman; *Pedilia* Clark; *Pseudogona* Jacoby; and *Resistenciana* Bechyné. Specimens of all the above genera are represented in the collections of INBio and/or USNMNH.

Species richness rose from 113 species recorded for the country as a whole to 247 species and morphospecies known from La Selva alone (Table 2). Only 11 of the La Selva species were previously recorded from Costa Rica. Even though most of the species from La Selva have only a morphospecies name, the first author believes that almost all of these are not conspecific with any of the species in the same genera previously recorded from Costa Rica. Adding records of additional species examined in collections but not known to occur at La Selva, the total for Costa Rica is about 350 species.

The Total column of Table 2 indicates species abundance with a typical pattern for rich tropical faunas with a few common species and many "rare" species, represented by either a single (singleton) specimen or by 2 (doubleton) specimens.

There were relatively few "abundant" species (more than 200 specimens captured): *"Aphthona" robusta*; *Genaphthona transversicollis*; *Glenidion jacobyi* (Bechyné); *Heikertingerella* DF-001; *Hypolampsis* DF-001; and *Neothona* DF-001. It is perhaps not surprising that two of these belong to the two most diverse Neotropical genera of Alticinae *Heikertingerella* and *Hypolampsis* (Furth, unpublished), and many species were represented by relatively few specimens.

Of the 74 species that can be considered as "rare": 26 species were represented by singletons (uniques) and 48 species by doubletons. Fig. 4 demonstrates the situation of the rare and very rare species (doubletons and uniques, respectively). The doubletons continue to increase slightly and the uniques decline slightly with increased sampling. It is also interesting that the total of singletons is continually higher than that for doubletons. Until the host plant relationships of the Alticinae of La Selva are better understood or until host plant testing of the species is conducted along with the sampling, especially for canopy fogging, it will be difficult to discern the cause or reasons for the rare and very rare species there. As demonstrated by this and other surveys, rare species are a

Table 1. Genera of Alticinae currently known from Costa Rica. This list was compiled from previous literature records (Furth and Savini, 1996, 1998 and included references), the ALAS quantitative sampling program, additional hand collecting by the senior author and others, and additional examination of museum collections at INBio and USNMNH. An "x" in the La Selva column indicates genera known from La Selva. An "x" in the Costa Rica column indicates genera known from Central America but newly reported for Costa Rica. An "x" in the Central America column indicates genera known from the Americas but newly reported for Central America. An "x" in the New Genus column indicates genera new to science. A number of genera (e.g., *Ayalaia*, *Chalatenanganya*, etc.) have no "x" indication in any of the columns, this is because these genera have been recorded in the literature as being from Costa Rica, but were not found in this study of La Selva.
* "*Aphthona*" is not considered as a separate genus because it actually belongs to another genus of the Aphthonini (*sensu* Bechyné) included here.

Genus	La Selva	Costa Rica	Central America	New Genus
Acallepitrix	x	x		
Acanthonycha	x			
Acrocyum		x		
Alagoasa	x			
Allochroma	x			
Andiroba	x		x	
*"Aphthona"**	x			
Asphaera	x			
Ayalaia				
Bellacincta	x	x		
Blepharida				
Brasilaphthona	x	x		
Cacoscelis				
Calipeges	x		x	
Calliphron		x		
Centralaphthona	x	x		
Cerichrestus	x	x		
Chaetocnema	x			
Chalatenanganya				
Chaparena			x	
Coroicona	x		x	
Cyrsylus	x			
Dinaltica	x	x		
Diphaltica	x			
Diphaulaca				
Disonycha	x			
Distigmoptera				
Egleraltica	x		x	
Epitrix	x			
Epitrix A	x			x
Euphenges		x		
Exartematopus	x	x		
Exoceras	x			
Genaphthona	x			
Gioia	x			
Glenidion	x			

Table 1. Continued.

Genus	La Selva	Costa Rica	Central America	New Genus
Heikertingerella	x			
Heikertingeria	x	x		
Homotyphus	x	x		
Hydmosyne		x		
Hylodromus				
Hypolampsis	x	x		
Lacpatica		x		
Leptophysa	x	x		
Longitarsus	x	x		
Loxoprosopus	x		x	
Lupraea	x			
Macrohaltica				
Margaridisa	x			
Megasus		x		
Megistops				
Mesodera	x	x		
Monomacra	x			
Monoplatini	x			x
Monotalla-like	x			x
Nasigona	x			
Neodiphaulaca	x	x		
Neosphaeroderma	x			
Neothona	x	x		
Notozona	x			
Octogonotes		x		
Omophoita	x			
Palmaraltica	x		x	
Panchrestus	x			
Paralacticoides			x	
Parasyphraea	x	x		
Parchicola	x	x		
Pedilia				
Phenrica	x			
Phylacticus	x	x		
Physimerus	x			
Platiprosopus	x			
Plectotetra	x	x		
Pseudogona				
Ptocadica	x			
Resistenciana				
Rhinotmetus	x	x		
Roicus	x		x	
Sparnus	x	x		
Sphaeronychus	x	x		
Stegnea	x	x		
Stenophyma	x		x	
Strabala	x			

Table 1. Continued.

Genus	La Selva	Costa Rica	Central America	New Genus
Styrepitrix	x	x		
Syphrea	x			
Systena	x			
Tetragonotes	x			
Trichaltica	x	x		
Varicoxa	x			
Walterianella	x			
Total Genera	**68**	**33**	**10**	**3**
Grand Total: 89				

Table 2. Alticine species known from La Selva Biological Station. Trap bias ("M" for Malaise traps, "F" for canopy fogging) was examined with a binomial test for each species, with the binomial probability equal to the proportion of all individuals across all species in canopy fogging samples (0.41). * = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$. "Other" indicates species captured by methods other than Malaise traps and fogging, including hand collecting by the senior author.

Species	Fogging	Malaise	Total	Trap Bias	Other
Acallepitrix DF-001	1	5	6		+
Acallepitrix DF-002	0	2	2		+
Acanthonycha DF-001	2	3	5		
Acanthonycha DF-002	0	1	1		
Acanthonycha DF-003	0	0	0		+
Alagoasa DF-001	0	0	0		+
Alagoasa DF-002	0	5	5		+
Alagoasa DF-003	2	0	2		+
Alagoasa DF-004	0	0	0		+
Alagoasa gemmata (Jac.)	0	0	0		+
Alagoasa montana (Jac.)	44	101	145	M**	+
Allochroma basalis (Jac.)	1	12	13	M**	
Allochroma DF-001	19	1	20	F***	
Allochroma DF-002	0	11	11	M**	+
Allochroma DF-004	8	0	8	F***	+
Allochroma DF-005	0	1	1		+
Allochroma DF-006	7	0	7	F**	
Allochroma DF-007	0	1	1		
Allochroma DF-008	1	0	1		
Allochroma guatemalensis Jac. near	7	0	7	F**	
Andiroba DF-001	0	141	141	M***	+
Andiroba DF-001A	0	10	10	M**	+
Andiroba DF-002	0	14	14	M***	
Andiroba DF-003	0	9	9	M**	
Andiroba DF-004	0	50	50	M***	+
"Aphthona robusta " (Jac.)	36	165	201	M***	+
Asphaera DF-001	8	3	11	F*	+
Asphaera DF-002	0	0	0		+

Table 2. Continued.

Species	Fogging	Malaise	Total	Trap Bias	Other
Asphaera DF-003	0	4	4		
Asphaera DF-004	0	1	1		
Asphaera DF-005	1	0	1		
Asphaera nobilitata (Fab.)	14	147	161	M***	+
Asphaera reichei (Har.)	0	3	3		+
Bellacincta clarki (Jac.)	17	21	38		+
Brasilaphthona DF-001	0	17	17	M***	
Brasilaphthona DF-002	0	17	17	M***	+
Brasilaphthona DF-003	0	0	0		+
Brasilaphthona DF-004	3	0	3		
Brasilaphthona DF-005	0	4	4		+
Brasilaphthona DF-006	3	3	6		
Brasilaphthona DF-007	3	17	20	M*	
Brasilaphthona palpalis (Jac.) (?)	0	1	1		+
Calipeges DF-001	3	1	4		+
Centralaphthona DF-001	0	1	1		
Centralaphthona DF-002	1	2	3		
Centralaphthona DF-003	0	1	1		
Cerichrestus clarki Jac.	0	14	14	M***	+
Cerichrestus DF-001	0	14	14	M***	+
Cerichrestus DF-002	0	1	1		
Cerichrestus DF-003	0	7	7	M*	
Cerichrestus DF-004	0	2	2		+
Chaetocnema DF-001	0	6	6	M*	+
Chaetocnema DF-002	1	1	2		+
Chaetocnema DF-003	0	1	1		
Chaetocnema DF-004	0	1	1		+
Chaetocnema DF-005	0	1	1		
Chaetocnema DF-006	0	0	0		+
Chaetocnema DF-007	0	0	0		+
Coroicona DF-001	92	15	107	F***	
Cyrsylus DF-002	0	9	9	M**	+
Cyrsylus DF-003	0	11	11	M**	+
Cyrsylus recticollis Jac. (?)	0	25	25	M***	+
Dinaltica DF-001	93	36	129	F***	
Dinaltica DF-002	0	62	62	M***	
Diphaltica DF-001	0	17	17	M***	+
Disonycha DF-001	0	0	0		+
Disonycha trifasciata Clark	0	0	0		+
Egleraltica DF-001	14	7	21	F*	
Epitrix DF-001	1	4	5		+
Epitrix DF-002	0	1	1		+
Epitrix DF-003	0	0	0		+
Epitrix DF-004	0	2	2		
Epitrix DF-005	0	0	0		+
Epitrix DF-006	0	1	1		+
Epitrix DF-007	0	0	0		+

Table 2. Continued.

Species	Fogging	Malaise	Total	Trap Bias	Other
EpitrixA DF-001	15	15	30		
EpitrixA DF-002	0	17	17	M***	+
EpitrixA DF-003	0	3	3		
EpitrixA DF-004	0	14	14	M***	
Exartematopus DF-002	0	2	2		
Exoceras DF-001	2	73	75	M***	
Exoceras DF-002	0	45	45	M***	+
Exoceras DF-003	0	15	15	M***	
Exoceras DF-004	3	5	8		
Exoceras DF-005	0	1	1		
Genaphthona DF-001	14	92	106	M***	
Genaphthona transversicollis (Jac.) near	0	213	213	M***	
Gioia DF-001	3	10	13		+
Glenidion jacobyi (Bech.)	216	116	332	F***	+
Heikertingerella DF-001	203	233	436	F*	
Heikertingerella DF-002	3	7	10		
Heikertingerella DF-003	9	3	12	F*	
Heikertingerella DF-004	0	1	1		
Heikertingerella DF-005	2	0	2		
Heikertingerella DF-006	0	1	1		
Heikertingerella DF-007	15	78	93	M***	+
Heikertingerella DF-008	2	15	17	M**	
Heikertingerella DF-009 (?)	0	0	0		+
Heikertingerella DF-010	109	35	144	F***	
Heikertingerella DF-011	44	26	70	F***	+
Heikertingerella DF-012	57	16	73	F***	
Heikertingerella DF-013	0	4	4		
Heikertingerella DF-014	1	9	10	M*	
Heikertingerella DF-015	7	14	21		
Heikertingerella DF-016	13	1	14	F***	
Heikertingerella DF-017	1	0	1		
Heikertingerella DF-018	0	2	2		
Heikertingerella DF-019	4	1	5		
Heikertingerella DF-020	0	0	0		+
Heikertingerella DF-021	0	1	1		
Heikertingerella DF-022	1	0	1		
Heikertingerella marini Bech.& Bech.	0	6	6	M*	+
Heikertingeria DF-001	0	8	8	M*	
Heikertingeria DF-002	1	7	8		
Heikertingeria DF-003	2	1	3		+
Homotyphus DF-001	0	0	0		+
Homotyphus DF-002	12	0	12	F***	
Homotyphus DF-003	0	4	4		
Homotyphus DF-004	0	2	2		
Homotyphus DF-005	0	2	2		
Homotyphus DF-006	1	0	1		
Homotyphus DF-007	0	2	2		+

Table 2. Continued.

Species	Fogging	Malaise	Total	Trap Bias	Other
Homotyphus DF-008	0	1	1		
Hypolampsis DF-001	289	16	305	F***	
Hypolampsis DF-002	0	11	11	M*	+
Hypolampsis DF-003	1	3	4		
Hypolampsis DF-004	0	4	4		+
Hypolampsis DF-005	7	1	8	F**	+
Hypolampsis DF-006	12	6	18	F*	
Hypolampsis DF-007	0	6	6	M*	
Hypolampsis DF-007A	0	0	0		+
Hypolampsis DF-008	0	2	2		+
Hypolampsis DF-009	2	2	4		
Hypolampsis DF-010	1	4	5		
Hypolampsis DF-011	5	1	6		
Hypolampsis DF-012	1	0	1		
Hypolampsis DF-013	0	0	0		+
Hypolampsis DF-014	0	1	1		+
Hypolampsis DF-015	0	12	12	M**	
Hypolampsis DF-016	1	0	1		
Hypolampsis DF-017	6	0	6	F**	
Leptophysa DF-001	1	2	3		
Leptophysa DF-002	0	1	1		
Longitarsus DF-001	2	3	5		+
Longitarsus DF-002	0	2	2		+
Longitarsus DF-003	0	1	1		
Longitarsus DF-004	0	0	0		+
Loxoprosopus DF-001	8	2	10	F*	
Loxoprosopus DF-002	0	5	5		
Lupraea DF-001	0	2	2		+
Lupraea DF-002	42	1	43	F***	
Lupraea DF-003	79	2	81	F***	
Lupraea DF-004	6	36	42	M***	
Lupraea DF-005	19	10	29	F**	
Lupraea DF-006	5	9	14		
Lupraea DF-007	18	2	20	F***	
Lupraea DF-008	3	2	5		
Lupraea DF-009	0	1	1		+
Lupraea DF-010	0	2	2		
Lupraea DF-011	0	0	0		+
Lupraea subrugosa (Jac.) near	46	1	47	F***	+
Margaridisa DF-001	0	0	0		+
Margaridisa managua (Bech.) (?)	5	28	33	M***	+
Mesodera fulvicollis Jac. near	0	36	36	M***	+
Monomacra chontalensis (Jac.)	0	6	6	M*	+
Monomacra DF-001	8	5	13		+
Monomacra DF-002	0	1	1		
Monomacra violacea (Jac.)	0	13	13	M***	+
Monoplatini new genus	82	1	83	F***	

Table 2. Continued.

Species	Fogging	Malaise	Total	Trap Bias	Other
Monotalla-like (near) DF-001	23	5	28	F***	+
Monotalla-like (near) DF-002	2	1	3		
Monotalla-like (near) DF-003	0	2	2		
Nasigona DF-001	0	2	2		+
Neodiphanlaca zenda Bech.&Bech. (?)	0	47	47	M***	
Neosphaeroderma coerulea (Jac.)	0	2	2		+
Neothona DF-001	185	67	252	F***	
Notozona DF-001	4	0	4	F*	
Omophoita aequinoctialis (Linn.)	3	83	86	M***	+
Omophoita clerica (Erichs.)	5	1	6		
Palmoraltica DF-001	0	0	0		+
Panchrestus denticollis Blake	4	4	8		
Parasyphraea DF-001 (near *minuta*)	7	66	73	M***	
Parasyphraea DF-002	17	86	103	M***	+
Parasyphraea DF-003	4	71	75	M***	+
Parasyphraea DF-004	14	3	17	F***	
Parasyphraea minuta (Jac.)	3	30	33	M***	+
Parchicola DF-001	1	5	6		+
Parchicola DF-002	0	2	2		+
Parchicola DF-003	0	0	0		+
Phenrica DF-001	0	1	1		+
Phenrica DF-002	0	1	1		+
Phenrica DF-003	0	2	2		
Phylacticus major Jac.	1	0	1		
Phylacticus ustulatus Clark	2	16	18	M**	+
Physimerus DF-001	6	4	10		
Platiprosopus DF-001	7	0	7	F**	
Platiprosopus DF-002	0	1	1		
Plectotetra DF-001	0	2	2		
Ptocadica bifasciata Jac.	0	9	9	M**	+
Ptocadica straminea Har. near	0	9	9	M**	+
Rhinotmetus DF-001	0	0	0		+
Rhinotmetus DF-002	0	1	1		
Rhinotmetus DF-003	0	6	6	M*	
Rhinotmetus DF-004	1	12	13	M**	
Rhinotmetus DF-005	6	4	10		
Roicus DF-001 (n.sp.)	0	2	2		+
Roicus DF-002 (n.sp.)	0	0	0		+
Sparnus apicalis Jac. (n.sp.) near	0	1	1		+
Sparnus chiriquiensis Jac. (?)	0	1	1		
Sparnus DF-001	1	0	1		
Sparnus DF-002	1	0	1		
Sparnus DF-003	10	0	10	F***	
Sparnus DF-004	1	0	1		
Sparnus flavicollis Jac.	2	0	2		
Sphaeronychus DF-001	9	3	12	F*	
Sphaeronychus DF-002	1	7	8		

Table 2. Continued.

Species	Fogging	Malaise	Total	Trap Bias	Other
Sphaeronychus puncticollis (Jac.) near	25	7	32	F***	
Stegnea DF-001	0	13	13	M***	
Stenophyma modesta Weise (?)	78	4	82	F***	
Strabala subcostata (Jac.)	0	0	0		+
Styrepitrix boqueronica Bech.&Bech.	0	62	62	M***	
Syphrea DF-001	6	14	20		+
Syphrea DF-002	0	15	15	M***	+
Syphrea DF-003	0	0	0		+
Syphrea DF-004	0	11	11	M**	
Syphrea DF-005	4	5	9		
Syphrea DF-006	0	1	1		
Syphrea DF-007	0	2	2		+
Syphrea DF-008	0	2	2		
Syphrea DF-009	0	3	3		+
Systena DF-001	0	5	5		+
Systena DF-002	0	2	2		+
Tetragonotes DF-001	16	3	19	F***	
Trichaltica DF-001	2	2	4		
Trichaltica variabilis (Jac.)	1	36	37	M***	+
Varicoxa clarki (Jac.) (?)	0	0	0		+
Varicoxa minuta (Jac.)	24	67	91	M**	
Varicoxa ustulata centralis Bech.	0	36	36	M***	+
Walterianella DF-001	0	0	0		+
Walterianella DF-002	0	0	0		+
Walterianella DF-003	0	0	0		+
Walterianella DF-004	2	1	3		+
Walterianella DF-005	0	2	2		+
Walterianella DF-006	0	2	2		
Walterianella DF-007	2	0	2		
Walterianella oculata (Fabr.)	6	10	16		
Walterianella tenuicincta (Jac.)	3	0	3		
Total Individuals	**2260**	**3221**	**5481**		
Total Species	**112**	**191**	**216**		**114**
Grand Total Species: 247					

significant part of rainforest ecology, albeit often difficult to study, and should be viewed as a potentially separate and informative aspect of the rainforest community for more targeted study (Novotny and Basset, 2000).

The first author collected over 63 species in 1989 and 1995, ten of these were only collected then, they are represented in Table 2 by a +: *Chaetocnema* DF-006; *Chaetocnema* DF-007; *Disonycha trifasciata* Clark; *Epitrix* DF-007; *Hypolampsis* DF-007A; *Longitarsus* DF-004; *Lupraea* DF-011; *Margaridisa* DF-001; *Parchicola* DF-003; and *Strabala subcostata* (Jacoby).

The abundance distribution for alticines at La Selva clearly reveals a mode at the fourth octave (Fig. 1). However it does not appear symmetrically lognormal. There is an overabundance of rare species in the lowest octave, resulting in a secondary peak.

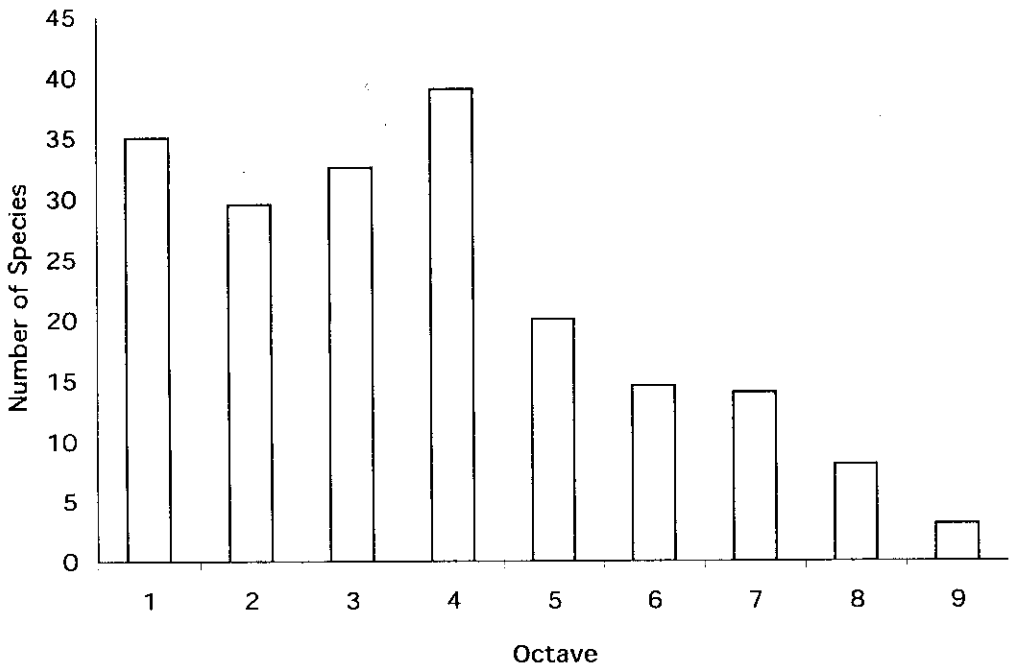

Figure 1. Abundance distribution for quantitative sampling of alticine diversity at La Selva Biological Station. Abundances are based on total number of individuals summed across fogging and Malaise samples. Octave assignment follows Preston (1948, see also Longino *et al.*, 2002), in which abundance classes or "octaves" have boundaries 0.5, 1, 2, 4, 8, etc. If a species falls on a boundary, then its abundance is evenly split between the two adjacent octaves, adding 0.5 to each one. The first visible octave is 1–2, which contains one half the singletons plus one half the doubletons (the other half of the singletons necessarily ignored).

The 670 Malaise samples yielded 3221 specimens and the 29 canopy fogging samples yielded 2260 specimens (Table 2). Based on binomial tests, of the 216 species collected in the Malaise trapping and canopy fogging program, 60 show a bias toward Malaise traps and 37 show a bias toward canopy fogging (Table 2). Canopy fogging is far more productive than Malaise traps on a per sample basis, but the reverse is true on a per individual basis (Fig. 2). Combining the two methods does not improve inventory efficiency in either case (Fig. 2).

The average number of species captured per canopy fogging event was 17.7 (range 8 to 33). There was no significant difference in number of species among fogging treatments (*Pentaclethra macroloba*, *Virola koschnyi*, "other"). The smallest number of individuals in any canopy fogging event was 21. When all fogging events were rarified to 21 individuals, the average number of species was 9.4 (range 4.0 to 13.8) and there continued to be no significant treatment effect. The three fogging treatments did not differ in species accumulation rate based on number of samples (Fig. 3). However, the diverse treatment was more efficient than the two monospecific treatments when based on number of individuals (Fig. 3).

The overall species accumulation curve for the combined Malaise and fogging samples shows no sign of approaching a plateau (Fig. 4). It appears more logarithmic than asymptotic. Richness estimates based on Michaelis Menton and ACE also are not asymptotic. For the full dataset, the two estimators

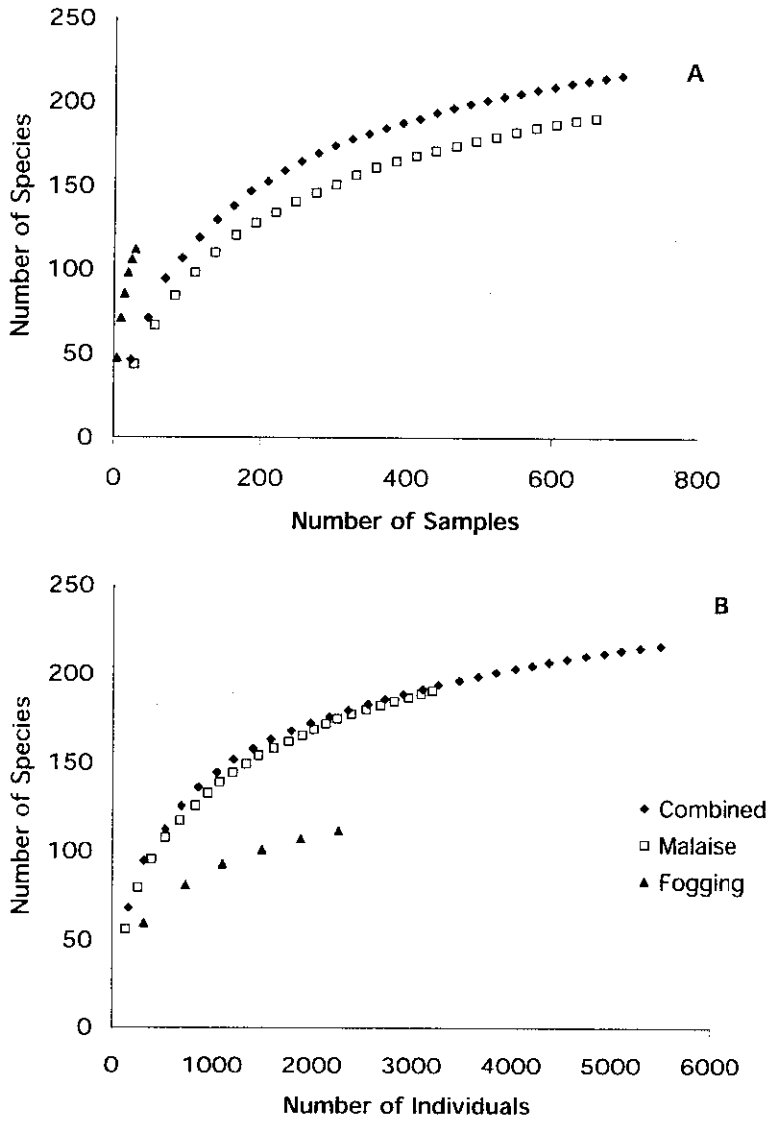

Figure 2. Sample-based rarefaction curves for the Alticinae of La Selva, based on (A) number of samples and (B) number of individuals. On a per sample basis there is relatively little difference in efficiency of Malaise traps versus canopy fogging, and the combination of methods is not more productive than single methods. Malaise trapping is far more productive than canopy fogging when based on number of individuals.

are 10 and 15% above the observed richness, respectively. When the final richness estimates are compared to the total known fauna of 247 species, which includes some species collected by other methods and not collected by Malaise or fogging, Michaelis Menten underestimates richness and ACE hits it almost exactly. The singleton curve was beginning to decline.

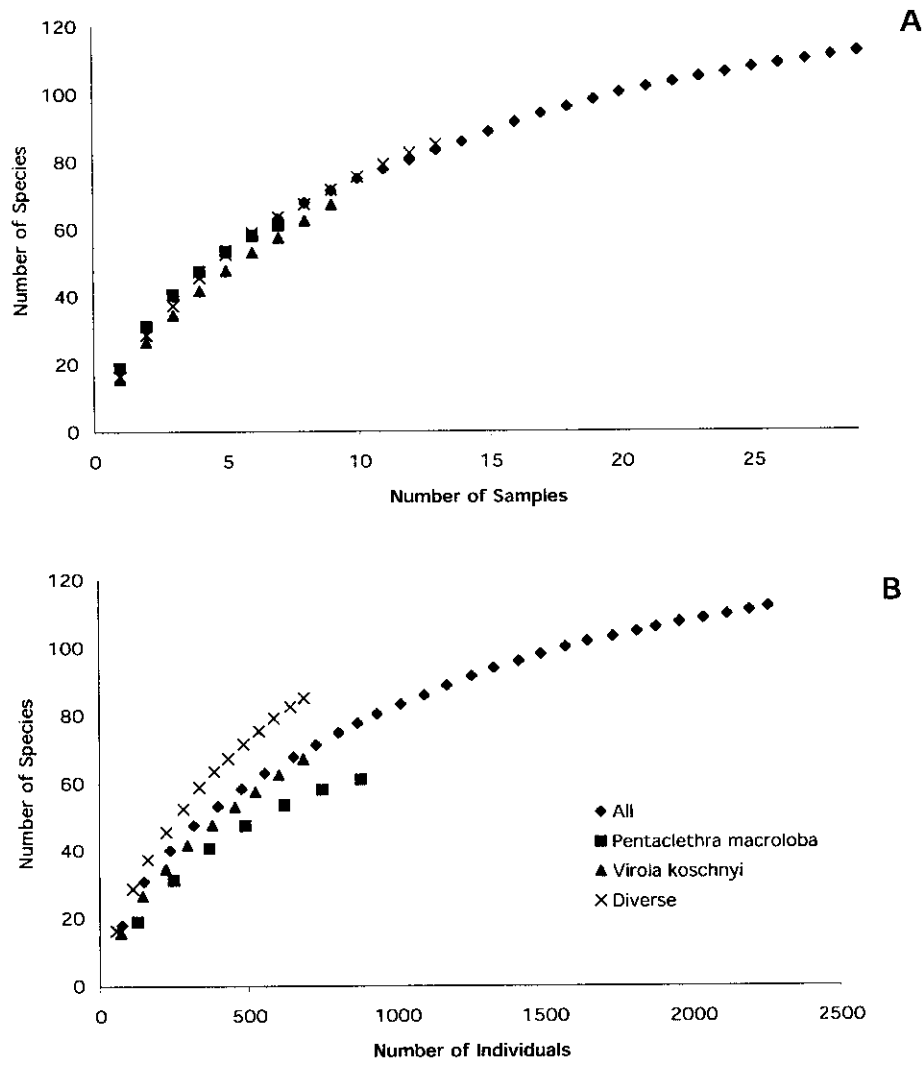

Figure 3. Sample-based rarefaction curves for alticinae in canopy fogging samples, broken down by three fogging treatments, based on (A) number of samples and (B) number of individuals.

DISCUSSION

This study dramatically increased the known diversity of Costa Rican Alticinae. The number of genera increased from 43 to 89, and the number of species from 112 to about 350. Given that most of this increase was due to an intensive survey at a single site, it is evident that there will be many more genera and species discovered when similar or even less intensive inventory projects are conducted elsewhere in Costa Rica. This will be especially true if fieldwork, including various collecting methods, is conducted in other ecological zones (e.g. Pacific lowland rain forests, montaine cloud

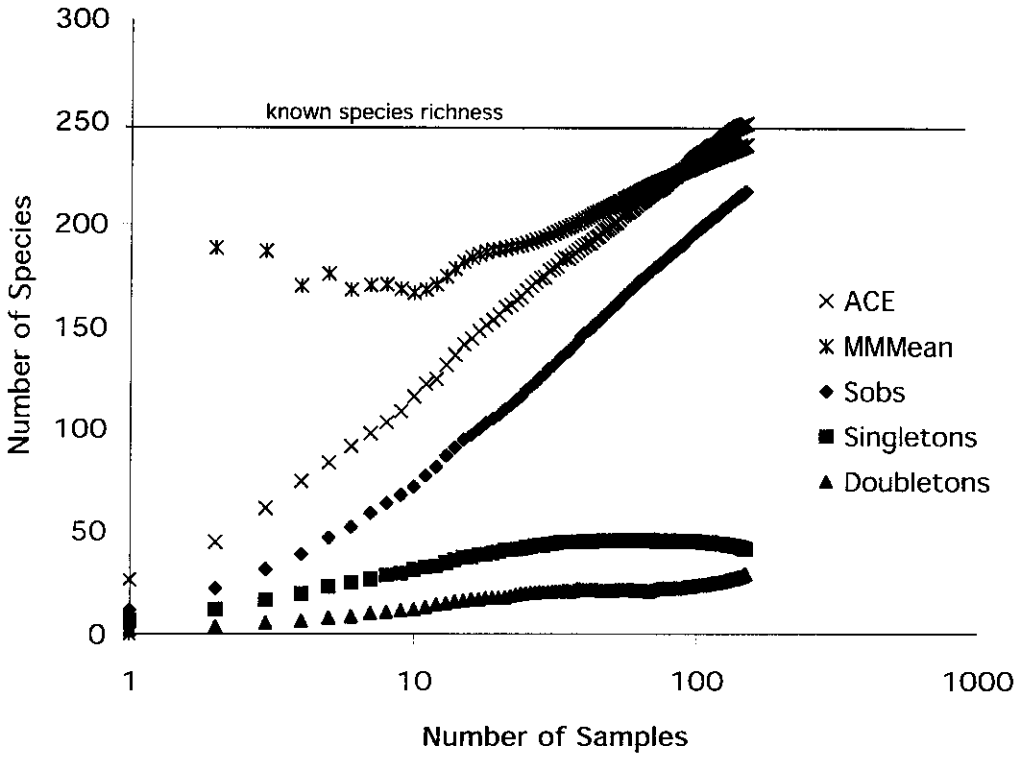

Figure 4. Species richness estimates of Alticinae at La Selva, based on combined Malaise and canopy fogging samples. Known species richness includes species collected by other methods.

forests, dry forests, etc.). Additional new records for Costa Rica will also certainly be generated from more comprehensive examination of various institutional historical collections. Therefore, although there is no completely accurate way to predict or estimate the actual number of Alticinae in Costa Rica, the first author predicts that there are approximately 1000 species of Alticinae present in Costa Rica. This also means that the estimate by Flowers (1995, *in litt.*) of 2000 species of Chrysomelidae is probably too low. The fact that this survey for one site so dramatically increased the known diversity of Costa Rica, combined with the fact that we know nothing about faunal turnover with distance, reveals that we are still largely ignorant of the magnitude of tropical alticine diversity, and that we have just scratched the surface in our attempts to know it.

The quantitative results for the intensive La Selva survey revealed a diverse community. The abundance distribution was similar to a lognormal, with a well-revealed mode, but with an overabundance of rare species generating a secondary mode in the lowest abundance class. This distribution was reminiscent of the heuristic model proposed in Longino and Colwell (1997), in which observed distributions are a result of two overlapping distributions, one a roughly lognormal distribution comprised of the local or resident community, and one a unimodal distribution with the mode at the lowest abundance class, comprised of a large pool of vagrant or "tourist" species. The distribution also matches the new zero sum multinomial distribution of Hubbell (2001), a neutral model of community composition that relies on explicit demographic and speciation

mechanisms, but not on competitive interactions among species or niche partitioning. As demonstrated by this and other surveys, rare species are a significant part of rainforest ecology, albeit often difficult to study, and should be viewed as a potentially separate and informative aspect of the rainforest community for more targeted study (Novotny and Basset, 2000, Wagner, 2000).

The survey revealed that Malaise trapping and canopy fogging differed in efficiency, with Malaise traps being more efficient on a per individual basis and fogging being more efficient on a per sample basis. About 140 2-week Malaise samples were required to yield the same number of species as the 29 canopy fogging samples. Canopy fogging often generated large numbers of a few common species, which resulted in a lower efficiency on a per individual basis. Also, although individual species often showed a greater abundance in one method versus the other, it was usually a matter of relative abundance differences rather than presence/absence differences. There was little evidence for a unique high canopy fauna only obtained by fogging. If anything, more species showed a greater abundance near ground level than in the canopy. Thus, combining methods did not improve the rate of species capture relative to single methods. Longino *et al.* (2002) found a similar redundancy of Malaise traps and fogging when examining the same samples for ants. This suggests that alticine sampling does not require both methods, and that one method can be selected. Individual projects can weigh the relative cost of field sampling, comparing the cost of obtain a set of fogging samples to the cost of Malaise samples. An advantage of canopy fogging is that it can be done rapidly, whereas Malaise trapping requires either time or a large number of traps. An advantage of Malaise trapping is that it is logistically easier and can be more easily carried out at remote sites.

This result is contradictory to the popular notion that the rainforest canopy is a reservoir of abundant and largely unexplored biodiversity, and that canopy fogging is the best way to sample it. We may find that for hyperdiverse herbivorous groups such as alticines, only a small proportion of the community is comprised of high canopy specialists, and a larger fraction of the community is found in low herbaceous vegetation, early successional stages, forest edges, river margins, treefall gaps, and landslides.

The ALAS fogging program was structured to investigate the effect of tree species on fogging efficiency. The expectation was that if there were some degree of host specificity among arthropods, then fogging multiple species of trees would produce more species than fogging single species of trees. The results for ants revealed no or little effect of tree species (Longino and Colwell, 1997, Longino *et al.*, 2002), but since most ants are not phytophagous such a result was expected. This survey of Alticinae is the first to examine a phytophagous group. Thus it was somewhat of a surprise to find relatively little tree species effect. It is obvious from the biology of alticines that there are all degrees of host specificity, and this has been quantified recently in studies that include feeding trials (Novotny and Basset, 2000), even if within large or related plant genera as for other tropical chrysomelids (Novotny *et al.*, 2002). It may be that the complexity of individual tree crowns masks any tree species effect. Fairly large-scale canopy fogging as carried out here captures arthropods from a column of fogged vegetation. Although that column contains primarily the crown of the focal tree, it also contains the edges of adjacent crowns, lianas in the focal tree, and countless species of epiphytes.

What has not been thoroughly investigated in this study, is whether additional methods such as sweep-net sampling and beating would improve inventory efficiency and to what degree collecting by taxonomic specialists would improve the rate of species capture. It was clear from the studies of ant diversity (Longino and Colwell, 1997, Longino *et al.*, 2002) that specialist collecting is very efficient and contributes greatly to inventory work, and similar results are to be expected for any

taxonomic group, including alticines. The process of specialist collecting as well as expert identification of specimens from institutional collections and field surveys could be accomplished much faster and more effectively if there were resources available to train and employ additional specialists, especially in the countries with high biological diversity.

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