

Temporal and Spatial Diversity and Distribution of Arboreal Carabidae (Coleoptera) in a Western Amazonian Rain Forest¹

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ABSTRACT

Diversity of arboreal carabid beetles was sampled by fumigation in 100 3 × 3 m stations within a 100 × 1000 m terra firme forest plot in Ecuadorian Amazonia. Nine sampling dates from January 1994 to October 1996 yielded 2329 individuals belonging to 318 species of which more than 50 percent were undescribed species. A high percentage of the species sampled were rare; the proportion that occurred once per sampling date (singletons) ranged from 50.0 to 62.5 percent. Estimates of species richness were from 82 to 282 species of arboreal carabids in the study plot on a given sampling date. Most richness values were greater than 173 species. Species accumulation curves attained asymptotes for all but one sampling date, indicating that an adequate level of sampling effort was used to characterize the diversity of carabid fauna. Total accumulation curves based on pooled data failed to reach asymptotes. There was a high turnover in species composition between sampling dates; less than 50 percent of the species between the majority of sampling dates were shared, suggesting that the total species pool may be extremely large. Although species composition changed seasonally, species richness varied little. Spatial autocorrelation analysis revealed that the structure of this species assemblage was significantly patterned at distances below 280 m. Taken together, the large percentage of undescribed species, the failure of the overall species accumulation curves to level off, and the high turnover in species composition indicate that the species diversity of carabid beetles is far higher than previously thought.

RESUMEN

La diversidad de carábidos arbóreos en la Amazonía del Ecuador se muestreó mediante fumigación en 100 sitios de 3 × 3 m dentro de un área de 100 × 1000 m de bosque terra firme. En nueve fechas de muestreo, desde enero de 1994 hasta octubre de 1996, se observaron 2329 individuos de 318 especies. Más del 50 por ciento del número total de especies no estaba descrito. Muchas de las especies encontradas son raras. Las proporciones de las especies que estuvieron representadas por un solo individuo por fecha (singletons) tuvieron un rango de 50.0 a 62.5 por ciento. La estimación estadística de la riqueza de especies indicó la presencia de 82 a 282 especies en las fechas de muestreo. Las curvas de acumulación de especies se estabilizaron en todas las fechas con excepción de una. Estos resultados confirmaron que el nivel de esfuerzo de muestreo fue adecuado para caracterizar la diversidad de los carábidos. Las curvas de acumulación total no se estabilizaron a lo largo de todo el estudio. Se observaron diferencias en la composición de especies entre las fechas de muestreo, con menos de un 50 por ciento de especies compartidas entre la mayoría de las fechas. Sin embargo, entre las estaciones se registró poca variación en la riqueza de especies. El análisis de autocorrelación espacial reveló que la estructura de este grupo taxonómico tiene patrones significativos a distancias menores de 280 m. En total, el alto porcentaje de especies no descritas, la falta de nivelación de las curvas de acumulación y la baja proporción de especies compartidas entre fechas, indican que la diversidad de carábidos es mucho más alta de lo pensado.

Key words: Amazon; canopy; Carabidae; distribution; diversity; Ecuador; lowland tropical rain forest; species richness.

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INSECTS ARE A VITALLY IMPORTANT COMPONENT OF GLOBAL BIODIVERSITY as they contribute ca 80 percent of described species (Hammond 1992) and may comprise as much as 97 percent of global spe-

cies richness (Erwin 1997). Yet the mechanisms that structure and regulate the diversity of insect assemblages in the tropics, where most of the species occur, are poorly understood despite recent studies that have focused on determining the richness, species distributions, and the regulatory mechanisms influencing tropical insect communities (Janzen 1973, Basset & Kitching 1991, Stork 1991, Price *et al.* 1995, Basset & Novotny 1999). Estimates of total insect diversity are wide-ranging and controversial. Erwin's (1982) estimate placed insect diversity at *ca* 30 million species and sparked a lively debate over the accuracy of the number as well as the mechanisms that could allow such great numbers of insects to exist (Gaston 1991, Hodkinson & Casson 1991, Basset *et al.* 1996). Despite recent studies that are long-term, sampling intensive, and focused at the species level on isolated assemblages (Novotny & Basset 2000), satisfactory assessments of insect species diversity and distributions continue to elude researchers.

Although precise estimates of total species numbers remain uncertain, beetles are clearly the most species-rich group of insects (Hammond 1992, Erwin 1997). New beetles have been described on the order of 2300 species yearly since 1979, primarily from tropical rain forests. These discoveries have placed this order as the group of arthropods with the fastest rate of growth; however, as this study demonstrates, even a family of beetles, many of which live in the canopy and have been extensively studied, are still poorly known, and very little is known about the biology of most described species.

Studies of tropical insect diversity and distribution in relation to local habitat characteristics have been conducted mainly on non-predaceous insect assemblages (Janzen 1973, Farrell & Erwin 1988, Estrada *et al.* 1993, Price *et al.* 1995, Basset 1996, DeVries *et al.* 1997, Wolda *et al.* 1998, Basset & Novotny 1999, DeVries *et al.* 1999, Novotny & Basset 2000). Carabid beetles are, in contrast, almost exclusively predaceous. Most species are not limited to a single host and appear to be broadly distributed across the prey spectrum.

Commonly known as ground beetles, the Carabidae is a large and widespread family of almost exclusively predaceous (two tribes prey upon seeds), small (1.0–3.0 cm), nonsocial beetles that is particularly abundant in Neotropical forest canopies (Erwin 1994). Although primarily known to be denizens of the forest floor in most of the world, recent sampling techniques, notably canopy fogging (Erwin 1989), have brought attention to

many new species of canopy-dwelling Carabidae in Amazonia. In the present study, greater than half and likely 70 percent of the species sampled were previously undescribed. Part of the difficulty in determining community distribution of arboreal Carabidae is their small size, a complicating factor in assessing the habits of these insects that reside 15–35 m above the forest floor.

Assessment of species richness in assemblages of predaceous insects presents an opportunity to examine the distribution of species having an organization that is not linked specifically to host plants. We thus seek to fill a gap in the understanding of species diversity and distribution patterns within complex communities by exploring the parameters of this family of predaceous beetles at a single study site.

Although little is known about the life histories of many of the newly found canopy species, the available information about their morphology and habits (Erwin 1994) suggests that microhabitat specialization may be an important factor contributing to the high diversity of tropical insects. If small-scale edaphic factors are relevant variables in determining insect species density and composition (Erwin 1993), then habitat architecture within the canopy, a result of tree distribution across an edaphic matrix, may aid our understanding of insect occurrence patterns.

MATERIALS AND METHODS

FIELD SITE.—Data on carabid beetles and site vegetation came from a canopy arthropod diversity study conducted by TLE at Onkone Gare Station, Ecuador (00°39'10"S, 076°26'00"W), between January 1994 and October 1996. Onkone Gare is an area of primary tropical rain forest near Yasuni National Park in Ecuadorian Amazonia, located in the Napo province. The site is a terra firme (non-floodplain) forest containing extremely diverse moist lowland forest vegetation, which is characteristic of the forests of the Western Amazon basin (N. Pitman, pers. obs.). Precipitation is seasonal, with the dry and wet seasons running from approximately November to April and May to October, respectively.

The study area included 100 3 × 3 m stations within a 100 × 1000 m plot (Fig. 1) that consisted of ten 100 m transect lines spaced 100 m from one another, ascending toward 52° ENE. At each transect line the ten collection sites were randomly placed within the 10 × 100 m zone. Together, the ten 10 × 100 m zones equaled 1.0 ha spread across

Map of Species Richness

- 5 - 11
- 12 - 15
- 16 - 20
- 21 - 24
- 25 - 31

Transect 10

Transect 9

Transect 8

Transect 7

Transect 6

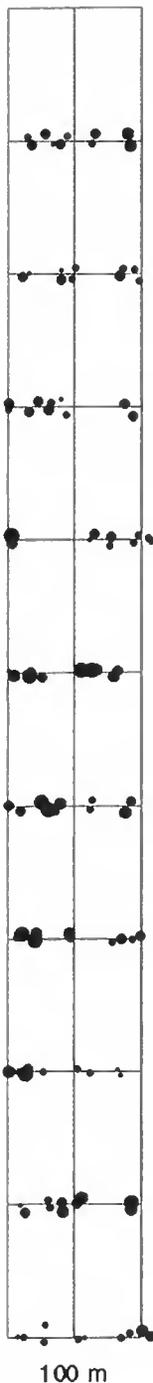
Transect 5

Transect 4

Transect 3

Transect 2

Transect 1



Map of Carabid Beetle Abundance

- 6 - 16
- 17 - 23
- 24 - 33
- 34 - 50
- 51 - 86

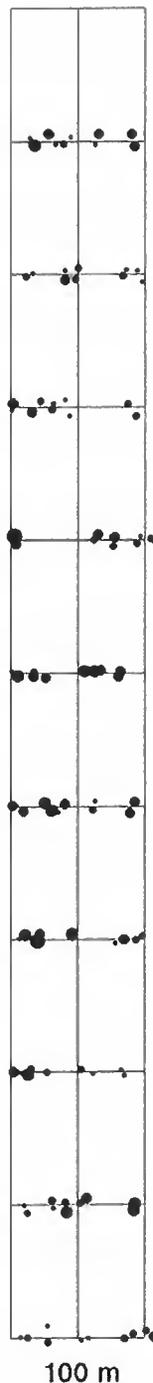


FIGURE 1. Cumulative number of species and abundance of beetles encountered at each station, represented by the relative size of the station symbol. The 100 sampling stations were distributed along ten transects within a 100 × 1000 m rain forest plot.

1.0 km of forest. Stations were numbered 1–100 at the beginning of the study and remained as permanent sampling locations for all nine collecting seasons.

To characterize the forest composition, trees within the plot's ten transect lines with diameter at breast height (DBH) greater than 10 cm were tagged and identified as thoroughly as possible. Within the ten transects of the study plot, 669 trees with DBH >10 cm represented 250 species and 53 families (TLE, pers. obs.). Forty trees (6%) remain unidentified, and so the true plot richness may be 10 or 15 species higher. The most common tree families, represented by more than 20 trees, include (in order of abundance) Arecaceae (36), Fabaceae (33), Moraceae (26), Lecythidaceae (25), Cecropiaceae (21), Bombacaceae (21), and Burseraceae (20). The basic architectural features of each station were assessed and assigned numerical values for presence/absence or degree. These factors included the number of strata, large trees, small trees, palms, large branches, woody vines, epiphytes, arroids, mosses and lichens, suspended dry leaves, and vine tangles.

COLLECTION.—Collection spanned three years, from January 1994 through October 1996. To account for seasonal variation, sampling took place in January/February, the dry season, and June/July, the wet season, as well as in October, to represent a transition period between the two distinct seasons.

Carabid samples were obtained using the canopy arthropod fogging technique described in Erwin (1989). Two transects (20 stations) were sampled each day for five days in the following manner. Three meter by 3 m nylon collecting sheets were suspended 1 m above the ground at sampling sites by attaching cords from the corners to stakes or nearby trees. From the center of each sheet hung a central collecting jar, which was partially filled with 80 percent alcohol just before fogging. Fogging took place between 0345 and 0500 h, when insects are least mobile and convection currents are minimal. The insecticide used was the synthetic pyrethroid chemical Resmethrin, used in a Dynafogger, which expels a thick plume of insecticidal fog. The motor in the fogging machine heats the kerosene, which rises and expands in the cool night forest, carrying the suspended insecticide particles into the canopy above the collection sheet. The fog was directed upward over each collection sheet for 60 seconds. Resmethrin affects arthropods by entering through membranes and blocking neurotransmit-

ters, causing the affected animals to convulse in spasms and thereby propel themselves out of the tree canopies and onto the collection sheet below. Two hours were allotted between fogging the stations and collecting the samples to ensure that the Resmethrin had taken full effect on the insects in the fog column. All of the arthropods at each sample site were swept into the alcohol-filled collecting jar attached at the center of each sheet and stored in 80 percent alcohol. This collection technique represents most, but not all, of the canopy arthropod community, as it fails to sample insects that have burrowed into substrates or are firmly attached (e.g., Coccidae [scale insects]). Previous experiments have demonstrated that faunal repopulation occurs within ten days after fogging (TLE, pers. obs.). Thus, the sampling setup and methodology permitted resampling of the same stations at four-month seasonal intervals throughout the three-year study without affecting species abundance. Specimens were sorted at the Onkone Gare field site, and carabids were extracted from Coleoptera sets at the Smithsonian Institution in Washington, DC by TLE, who also sorted them to the species level.

STATISTICAL ANALYSIS.—We investigated the numbers of carabid beetle species and their distribution patterns on different spatial and temporal scales. We first assessed the accumulated richness of species over the entire study and examined how this cumulative richness was spatially structured. We then explored how the distribution of species richness was influenced by the architecture of the forest canopy. We also examined temporal variation in species richness.

We used species richness to describe the number of different species encountered within the plot, both overall and on individual sampling dates. To isolate important components of richness, we examined the occurrence of rare species, including singletons (species represented by a single specimen per sampling date) and doubletons (species represented by only two specimens per sampling date). "Unique" species were species encountered in only one sample and represented by only a single specimen.

We calculated true species richness within the plot from the observed numbers of species using the Chao 2 incidence-based estimator in the program EstimateS (Version 5.0.1; R. K. Colwell, pers. comm.), using station as the sampling unit (100 samples). The Chao 2 formula is $S_{\text{chao2}} = S_{\text{obs}} + (Q_1^2/2Q_2)$, where S_{obs} is the number of species

observed in samples, Q_1 is the number of species that occurred in only one sample, and Q_2 the number of species that occurred in two samples. To prevent bias in calculations due to sample order, the number of observed species in each sample was randomized 50 times. Curves of observed species accumulation were also randomized for clarity in graphical representation. Chao 2 was used (rather than Chao 1) to facilitate comparison with previous studies. Although the data are not presented here, the per-date species richness of carabids calculated using Chao 1 differed little from the reported Chao 2 values, and the shape of accumulation curves mirrored those shown here.

Repeated measures MANOVA was run to determine if number of species per station varied significantly between sampling dates, with values $\log_{10}(x + 1.1)$ transformed. Species turnover in the plot over time was calculated by considering the percent of species shared between any pair of sampling dates. We used the formula $\%SS = (S)/((N_1 + N_2)/2)$, where the number of species common to any two dates (S) is divided by the average of the total number of species (N) encountered on date one and date two. To verify if species richness occurred in significant spatial patterns within the plot, we performed a Mantel test with the spatial autocorrelation program in R (Legendre & Vaudoir 1991), using the cumulative number of species across all sample dates. The same program calculated a correlogram with 13 distance classes to demonstrate the scale at which diversity was distributed. Regression analysis was used to assess the influence of 11 canopy architectural habitat characteristics on the species density of individual stations: number of strata, large trees, small trees, palms, large branches, woody vines, epiphytes, aroids, mosses and lichens, suspended dry leaves, and vine tangles. Variables were $\log_{10}(x + 1.1)$ transformed because they did not present normal distributions. Statistical analyses were conducted using JMP software version 4.0.4 (SAS institute, 1989–2001, Cary, North Carolina), and spatial autocorrelations using the program R. Maps of the study plot were constructed using the GIS program ArcView™ version 3.1 (ESRI, Redlands, California).

RESULTS

OBSERVED AND ESTIMATED DIVERSITY.—The 900 canopy fogging samples collected at the 100 sampling stations over three years yielded 2329 carabid beetles belonging to 318 species. As shown in Fig-

TABLE 1. Abundance (number of individuals) of the ten most common carabid beetle species represented by more than 50 individuals over the entire study.

Genus	Morphospecies	Abundance
<i>Lebia</i>	<i>Cara008</i>	119
<i>Hyboptera</i>	<i>Cara029</i>	85
<i>Inna</i>	<i>Cara013</i>	84
<i>Agra</i>	<i>Cara019</i>	77
<i>Batesiana</i>	<i>Cara011</i>	76
<i>Colliuris</i>	<i>Cara002</i>	62
<i>Batesiana</i>	<i>Cara021</i>	62
<i>Onota</i>	<i>Cara006</i>	61
<i>Euprocinius</i>	<i>Cara025</i>	60
<i>Lebia</i>	<i>Cara023</i>	58

ure 1, both the species richness and the abundance of carabid beetles when pooled across all sampling dates were unevenly distributed throughout the study plot.

The richness of this community was composed largely of rare species. There were 91 “unique” species, which composed 28.6 percent of all species sampled. Few species were found in abundance. Only 10 species occurred in abundances greater than 50 individuals over the entire study (Table 1). These common species comprised 31.9 percent of the individuals, but made up a relatively small proportion of species richness (3.1%).

Figure 2 presents species accumulation curves for observed and Chao 2 estimated species richness on the nine sampling dates, with stations as the sampling unit. In the figures, the differences in slopes reflect the number of rare species in each sample, with a steep, positive slope indicating a high proportion of singletons to doubletons in the sample (Colwell & Coddington 1994). Therefore, a sample in which the rarest species are found more commonly presents a slope close to zero; the leveling off indicates that the sample more reliably represents the breadth of diversity in the species pool. The accumulation curves for observed richness on all dates display steep slopes that never level off; however, all of the curves of estimated species richness but one (January 94) level off. The noticeably low curve in both figures represents samples from July 1996, apparently an El Niño affected season. The mean number of observed species per sample date was 102.6, while the average projected species richness per sampling date was 206.9 species.

Although 318 species were observed in total, using Chao 2 the true total species richness was estimated to be 399.4 species (Fig. 3). The total

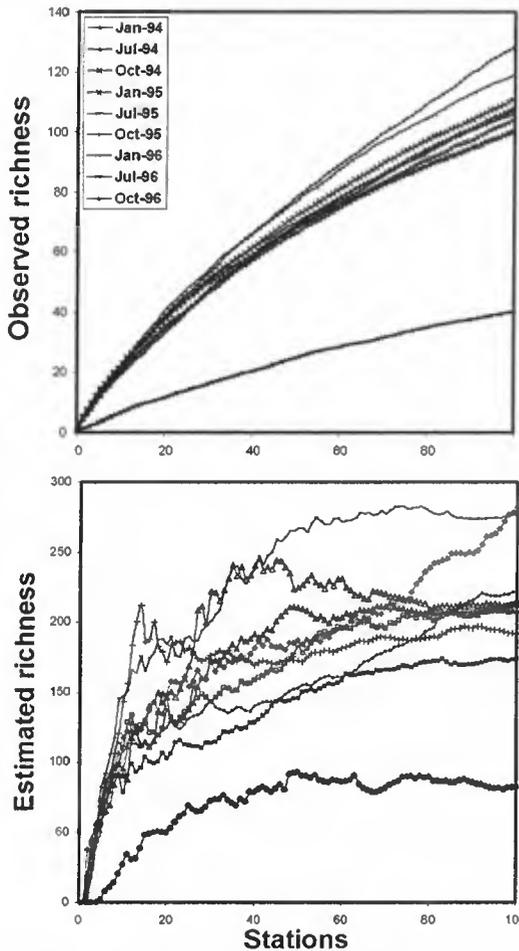


FIGURE 2. Species accumulation curves for observed richness and estimated richness of canopy carabids on all nine sampling dates. Estimated values were calculated by Chao 2.

number of species observed and the estimated total were much greater than the species richness of any individual sampling date. Neither the species accumulation curve for total observed nor that for total estimated species richness reached an asymptote, indicating that the entire community had not been fully sampled and that the true carabid richness in this community may extend well beyond the values predicted here.

SPATIAL VARIATION.—Cumulative totals of the number of species encountered at each station ranged from 5 to 31, with a total mean of 17 species per station. Stations differed not only in the number of species but in abundance and species composition as well. Both common and rare species were

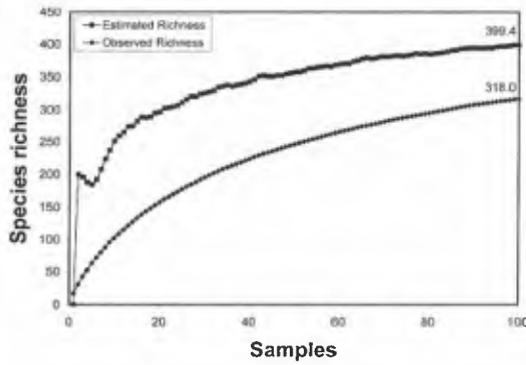


FIGURE 3. Species accumulation curves for total richness of canopy carabids within the study plot. Richness is pooled across all sampling dates and presented as the total number of observed species (diamonds) and the total number of species estimated by Chao 2 (squares).

distributed across all stations, and of the 10 common species, none exhibited site fidelity. A Mantel test was used to test the hypothesis that there were significant spatial patterns of species richness within the entire plot. The test found a significant correlation between a matrix of distances among stations and species density (Mantel's $r = 0.142$, $P = 0.001$). Subsequent Moran's I spatial autocorrelation tests revealed that species richness was significantly and positively correlated at distances of 70.0, 140.1, and 280.2 m (Fig. 4).

HABITAT STRUCTURE.—Regression analysis showed that the only factor that significantly influenced the richness of carabid beetles in the plot was the number of palms ($F = 12.556$, $P = 0.0006$), which was inversely correlated with species richness.

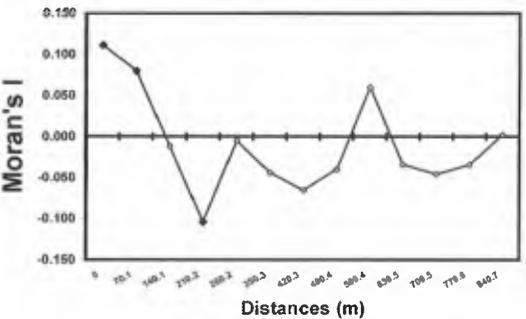


FIGURE 4. Correlogram of the spatial distribution of species richness within the study plot. The x-axis represents distance classes and the y-axis standardized Mantel's r statistic. Solid data points indicate the scales at which species richness was significantly (positively or negatively) correlated (70.1, 140.1, and 280.2 m).

TABLE 2. Results of repeated measures MANOVA, indicating the presence of significant variance among the richness of all dates and the lack of effect of time when analyzed with the values for July 1996 omitted. Note also the significant interaction between time and station, both with and without July 1996 values, suggesting that richness is influenced by both spatial and temporal factors.

Source	df	F	P
All Dates			
Between stations	1, 98	0.586	0.4457
Within time	8, 91	6.211	<0.0001
Time * station	8, 91	2.610	<0.0128
July 1996 Removed			
Between stations	1, 98	0.599	0.4410
Within time	7, 92	1.948	0.0708
Time * station	7, 92	3.016	0.0067

TEMPORAL VARIATION.—Repeated measures MANOVA indicated significant temporal variation in species richness over the nine sampling periods (Table 2). This variation appears to be due largely to the low species richness in July 1996. This effect was substantiated by omitting the July 1996 period

and rerunning repeated measures MANOVA, which then indicated a nonsignificant effect of time. In both sets of analyses there was significant interaction between time and station, indicating that the combined effects of spatial and temporal variation influence species richness.

The sphericity condition (Huynh & Feldt 1970) was met for each of the repeated measures MANOVA tests (both with July 1996 and without) as indicated by using chi-square tests of the Mauchly criterion, which were nonsignificant ($\chi^2 = 43.9$; $df = 1, 35$; $P < 0.14$ with July 1996; $\chi^2 = 33.4$; $df = 1, 27$; $P < 0.18$ without July 1996). This enabled use of the unadjusted univariate *F*-ratios reported in Table 2.

The paucity of species in July 1996 was likely due to the effects of El Niño Southern Oscillation (ENSO), which caused unusual weather patterns just prior to that date. Figure 5 displays the SOI (Southern Oscillation Index) values during the fieldwork for this study (NOAA Climate Prediction Center, Camp Springs, Maryland). The July 1996 sample contained low numbers of individuals; however, its composition of species and singletons remained similar to all other dates.

Although the number of species remained rel-

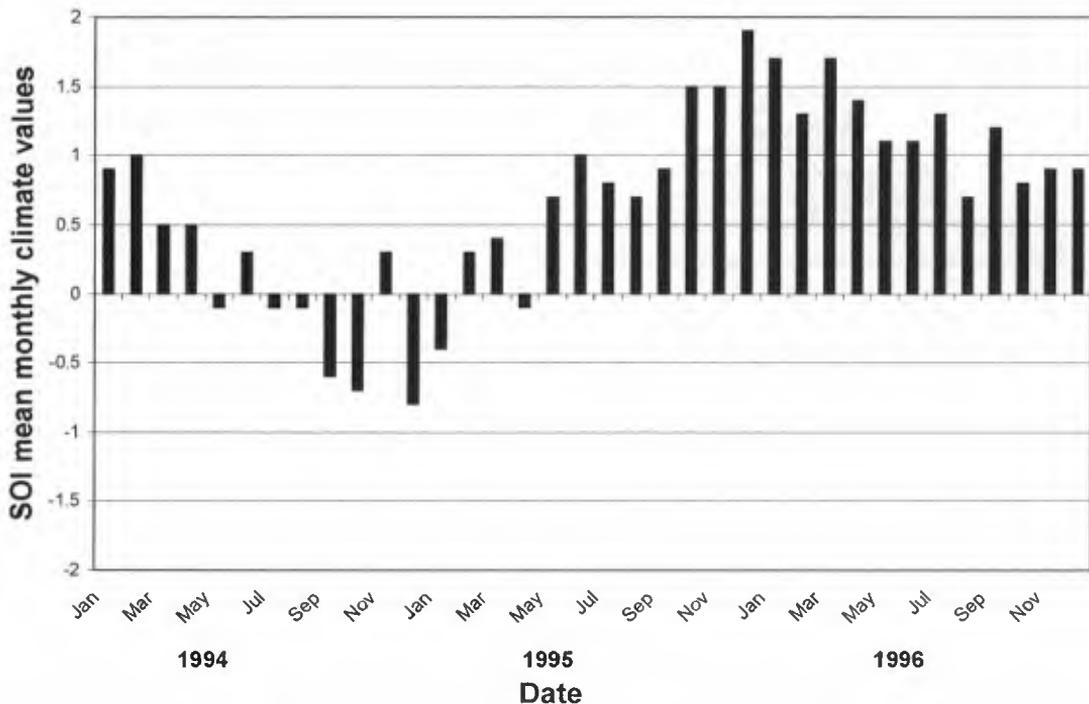


FIGURE 5. Histogram of Southern Oscillation Index (SOI) mean monthly climate values for 1994 through 1996. Note the rise in values just prior to July 1996.

TABLE 3. Percent shared species between all pairs of sampling dates. In the lower half of the matrix, the data are grouped into fewer than 40 percent (*italic*), 40–50 percent (**bold**), and greater than 50 percent (**bold italic**) shared species.

	Jan-94	Jul-94	Oct-94	Jan-95	Jul-95	Oct-95	Jan-96	Jul-96	Oct-96
Jan-94		47.2	40.9	41.2	42.9	46.4	51.1	30.6	42.2
Jul-94	40–50%		48.4	42.3	49.5	44.7	45.8	32.4	44.1
Oct-94	40–50%	40–50%		55.0	53.5	41.3	51.7	35.8	42.7
Jan-95	40–50%	40–50%	<i>>50%</i>		51.5	40.6	35.6	30	39.5
Jul-95	40–50%	40–50%	<i>>50%</i>	<i>>50%</i>		44.1	48	38.4	45.3
Oct-95	40–50%	40–50%	40–50%	40–50%	40–50%		54.0	34	47.7
Jan-96	<i>>50%</i>	40–50%	40–50%	<i><40%</i>	40–50%	<i>>50%</i>		37.7	50.2
Jul-96	<i><40%</i>		28.6						
Oct-96	40–50%	40–50%	40–50%	<i><40%</i>	40–50%	40–50%	<i>>50%</i>	<i><40%</i>	

actively consistent from one sampling date to the next, the average standard deviation highlights the heterogeneity of these values ($\bar{x} = 102.6 \pm 36$, $N = 9$). The proportion of singletons in samples remained similar among all dates, invariably comprising slightly more than half of the total number of species. The mean number of rare species per sampling date was 58.2 (± 14.4) singletons (56.8% of species).

Species composition displayed high turnover between all samples. Overall, the percent average of species shared between any two sampling seasons was 42.9 percent (44.8 species), which can also be read as an average turnover of 57.1 percent between any two sampling dates (Table 3). The high species turnover was evident among common as well as rare species. Even the ten most commonly occurring species were not present in all seasons. These ten common species were not found to exhibit high fidelity to specific stations at all, neither from season to season nor within a season from year to year.

DISCUSSION

OBSERVED AND ESTIMATED DIVERSITY.—Results show that the carabid community in Ecuadorian Amazonia is very diverse, and like other megadiverse communities in the tropics (Estrada *et al.* 1993, DeVries *et al.* 1997, Wolda *et al.* 1998, DeVries *et al.* 1999), remains yet to be fully sampled. The high degree of species turnover from one sampling date to the next indicates that the total species pool is much larger than can be ascertained by sampling at one time. We expected high richness and anticipated that species accumulation curves might not reach asymptotes even though the sampling regime was long term, as has been seen in samples of other tropical insects (Erwin & Scott 1980, Stork 1991,

Price *et al.* 1995, Basset 1996, Willott 1999, Novotny & Basset 2000). It was therefore interesting to find that, while species richness overall did not level off, estimated richness accumulated across sampling stations on all but one date did achieve asymptotes, indicating that sampling effort was sufficient to reliably reflect species richness within the plot.

A pattern of high number of species, composed largely of rare species, permeated the data. Nearly one-third of all observed species were encountered only once throughout the study, and more than half of the species on any sampling date were singletons. While the majority of species were found in low abundances, several species did occur in high numbers. Ten species were represented by more than 50 individuals over the three-year study. The individuals of these species comprised almost one-third of the total number of specimens collected, reiterating the simultaneous patterns of rarity in many species and high abundance in few that has repeatedly been observed in other assemblages (reviewed in Erwin 1995, DeVries *et al.* 1997, Wolda *et al.* 1998, DeVries *et al.* 1999, Novotny & Basset 2000).

The estimated numbers of species for each sampling date suggest that the true richness per date is *ca* 200 species, nearly double the observed richness; however, the observed and estimated richness on individual sample dates did not approach the total number of species observed (318) and estimated (400) over the duration of the study. Although most dates presented similar species richness values, the total richness accumulated over the duration of the study (both observed and estimated) was roughly three times greater than the mean richness of sampling dates. The disparity between the richness of single dates and the overall number of species relates to turnover, likely stemming from an

extremely rich regional species pool. The accumulation curves for species observed and estimated over the entire study, unlike those for individual sample dates, did not level off, suggesting that the richness of the species pool in this area is likely to surpass 400 species, the maximum estimates here. Further sampling, now underway in a nearby field site, will indicate whether Chao 2 estimates of carabid richness have in fact underestimated richness, as has been the case with richness estimates of Ecuadorian butterfly populations (DeVries *et al.* 1999) and tropical tree diversity (Condit *et al.* 1996).

Although rare species in this study clearly drive the maximum species richness, their paucity complicates our understanding of why they are rare. The "causes" of rarity have been widely discussed (Hubbell & Foster 1986, Price *et al.* 1995, Novotny & Basset 2000), and among Neotropical flora and fauna rarity is considered to be linked to sampling effects, which include the scope and the duration of study. Many carabids may be locally scarce but abundantly distributed on a larger scale; however, causes of rarity in this family are not yet clear.

SPATIAL VARIATION.—Cumulative and per-date species richnesses of stations within the plot were notably heterogeneous. The most species-rich station contained more than six times the number of species as the poorest station overall, but these stations were not the richest and the poorest on all dates. Species richness among the stations was not uniform, and the Mantel test demonstrated that the heterogeneity of species richness across the plot was distributed in significant patterns. Moran's *I* indicated that richness occurred in patterns on scales of 70.0, 140.1, and 280.2 m, the first, second, and fourth smallest scales of examination. These results suggest that influences on community organization do occur on scales examined in this study and that the influential factors exist on smaller, rather than larger scales. Because the finest detail distinguished was on a scale of 70 m, it is possible and likely that patterning exists on even finer scales. Studies on the diversity of tropical flora, such as that of Hubbell and Foster (1983, 1986), Pitman *et al.* (1999), and Tuomisto *et al.* (1995), have demonstrated that tree distributions are subject to influences on large regional scales. It is likely that with insects, however, the factors that structure community distribution may exist on much smaller, insect-sized scales.

HABITAT STRUCTURE.—Of the 11 architectural variables measured in each sampling location, the only factor that significantly influenced richness of carabid beetles was the number of palms. Although populations are undoubtedly influenced by other components of habitat structure, it appears that the factors measured here were not examined on a scale pertinent to the study organisms. Palms may impact the number of species while other factors likely affect the composition of species. This influence is probably due to the fact that palms are monocots and offer a distinct habitat to insects from that of dicot trees. They generally offer less leaf-surface area and provide a more uniform, less complex substrate than other trees that hold epiphytes in their branches, and therefore offer more varied microhabitats.

Variance in station richness over time, particularly sporadically high richnesses, may be due to punctuated local events such as fruiting, flowering, leaf flush, or other short-term changes in canopy structure (as suggested by Basset & Novotny 1999). Events such as these affect the architecture of the tree canopy and also attract different guilds of animals to the tree (*e.g.*, potential carabid prey or predators), which may influence richness of carabid beetles.

TEMPORAL VARIATION.—Richness, in terms of species observed and estimated in the plot, and number of singletons varied little from one season to the next, with the exception of one date. The July 1996 richness diverged from the trend of high species richness in presenting less than half of the mean number of species found per date. The dramatic difference in the number of species in this sample appears to have been caused by short-term climatic variation from the El Niño Southern Oscillation. Precipitation records show that the mean Southern Oscillation Index of the months in late 1995 and early 1996 were notably higher than in preceding years. Studies of the El Niño effect on system productivity have demonstrated that increased precipitation alters primary productivity as well as consumer abundance and composition (Polis *et al.* 1997). Our results suggest that this is an important influence on populations in this system as well.

The relative homogeneity in richness from one season to the next appears to negate Wolda's (1983) assertion that seasonal variation is the rule rather than the exception in tropical animals; however, when examining the carabid beetle fauna on the level of individual species, there is little consistency

in abundance from one season to the next. It is possible that species abundances vary according to specific temporal factors that this study did not take into account. It appears that species specific patterns of seasonal variation, in addition to spatial variation, are important elements of the dynamics of diversity in this system.

The distinct difference in overall richness and per-date richness can be explained by species turnover. Although richness remained relatively consistent among sampling dates, species composition varied dramatically over time. With high turnover, as each sample presented a steady influx of new species, richness accrued over time. On average, more than 50 percent of the species were different between any two sampling dates. July 1996 presented the lowest percentage of shared species with other dates, but this is likely to be an effect of the low number of individuals collected in that season's samples.

To our knowledge, this study is the largest and most rigorous species-based assessment of carabid beetle diversity to date. As the Carabidae is a fairly well studied family, the discovery of so many unknown species indicates that our understanding of tropical insect diversity in this assemblage is far from complete. Following the results of this study, it is clear that efforts to measure species diversity in this system must necessarily consider both the extent of the total species pool and the many fac-

tors that influence species distribution and abundance, locally, regionally, and temporally. Establishing dependable baseline measures is an essential first step toward effective conservation planning and one sorely needed to preserve community integrity and protect biodiversity.

With increasing concern about the conservation of biodiversity under human threat, there is a pressing need to gain a better understanding of diverse communities as well as the processes structuring and regulating their diversity. To accurately make such assessments, continued long-term, large-scale, and species-specific studies are a necessity, one which will hopefully be met before the very biodiversity we attempt to measure is gone.

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