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Mapping Patterns of β — Diversity for Beetles Across the Western Amazon Basin: A Preliminary Case for Improving Inventory Methods and Conservation Strategies

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Beetles sampled by insecticidal fogging were investigated to test for temporal and spatial β-diversity between two western Amazon rain forest sites located less than one-degree latitude from the equator and 21 kilometers distant from each other. A rigorously controlled sampling regime of terrestrial arthropods in the canopy and understory resulted in a dataset containing trans-seasonal and trans-annual information. This paper focuses on the Carabidae and Curculionidae (Otidocephalini) from a larger dataset because the species accumulation curves for them nearly reaches an asymptote, that is, enough samples have been sorted to account for nearly all the canopy species in the general area. Canopy trees in the two sites are very different at the species level (Complementarity Index = 0.73), moderately different at the generic level (CI = 0.53), but similar at the family level (CI = 0.26). The beetle fauna was predicted to be different at the two sites depending upon feeding guilds because the tree species composition is so different. The assumption is made that plant feeding species have some degree of host specialization, whereas predators and scavengers do not. For otidocephaline Curculionidae and Carabidae, this analysis suggests the opposite of that prediction: a larger percentage of herbivore species are shared between sites than predator species. These results suggest variable degrees of species turnover across short distances in both forest composition and their insect dependents in the western Amazon Basin and this may impact inventory methods and the conservation strategies derived from them.

Se estudiaron coleópteros muestreados con la técnica de fumigación para determinar la tasa de recambio temporal y espacial de especies (diversidad-β) entre dos sitios que corresponden a Bosque Húmedo Tropical, localizados a menos de un grado de latitud de la línea Ecuatorial y 21 kilómetros de distancia entre ellos. Un riguroso muestreo de artrópodos terrestres habitantes del dosel y sotobosque, resultó en un amplio registro de datos conteniendo información inter-estacional e inter-anual. Esta investigación se centra principalmente en las familias Carabidae y Curculionidae (Otidocephalini) debido a que sus curvas de acumulación de especies casi alcanzan una asíntota, esto significa, que se han tomado suficientes muestras para registrar todas las especies presentes en el área general. Entre los dos sitios, los árboles son muy diferentes a nivel especie (Indice de Complementariedad = 0.73), moderadamente diferentes a nivel de género (IC= 0.53), pero similares a nivel de familia (IC =

0.26). Predecimos que los escarabajos difieren dependiendo de sus gremios tróficos ya que la composición de árboles es diferente. Se asume que las especies herbívoras tienen algún nivel de especialización hacia las plantas huéspedes, mientras que los predadores y carróñenos no. Para los Otidocephalini y Carabidae, nuestro análisis sugiere lo opuesto a nuestra predicción: encontramos que el porcentaje de especies herbívoras compartidas entre sitios es mayor que el porcentaje de las especies predadoras compartidas. Estos resultados sugieren grados variables en la tasa de recambio de especies a través de distancias cortas tanto a nivel de composición vegetal del bosque como en los insectos asociados en la cuenca Amazónica Occidental, lo cual puede tener un impacto en los métodos de inventario y en las estrategias de conservación derivadas de estos.

Crucial to strategic planning for conservation areas is knowledge of species diversity and their distributions, at both local and regional scales across a multitude of fractal universes. If the goal of conservation strategies is to provide reserved areas for *most* of biodiversity, and that *should* be the goal, knowledge is needed from the fractal universe of mites and tardigrades to that of large trees and their vertebrate inhabitants. Eventually, as technology catches up with inventory, this means that the minute organisms (internal and external parasites, bacteria, viruses, etc.) inside and on the mites and tardigrades will need documentation, as well. However, at present we have no reasonably complete biodiversity map (Wilson 2000) that is valid for more than a miniscule percentage of life on the planet, nor do we have practical technology to access the smallest of species — the prokaryotes. Not even all vertebrates, butterflies, nor tree species are well mapped at scales to be significantly meaningful at a global scale. As pointed out by Lowman and Wittman (1996) and Basset (2001), we know little thus far about patterns in tropical forest canopies, the very heart of biodiversity (Erwin 1988). Thus, the question arises, how does one plan areas for conserving most of the species occurring locally or regionally? Areas now receiving attention may or may not contain the same species, whereas those not attended to may have a substantially different fauna and flora. Assumptions derived from larger and supposedly well-known organisms may not serve at all for minute insects living in the rain forest canopy (*cf.* Carroll and Pearson 1998).

Our investigation was undertaken to determine spatial and temporal turnover (β-diversity) across 21 kilometers distance in tropical lowland rain forest at the equator in the western Amazon Basin (on the margin of Yasuni National Park) with a very large dataset containing trans-seasonal and trans-annual information. By definition, the two sites studied are representatives of the local fauna and flora in a continuous lowland rain forest, but the question remains, how much of the regional forest biodiversity do they actually represent? Such Neotropical forests are complex not only in species composition, but also in forest architecture. Because these equatorial forested sites are complex, it was thought that a study of their canopy and understory arthropod fauna might provide crucial insights regarding the distribution of most of biodiversity in time and space. They were, thus, chosen for intensive long-term biodiversity and taxonomic studies. Several studies have suggested that the western Amazon Basin is the richest biome on Earth (Erwin 1982, 1983a, 1983b, 1988; Lamas et al. 1991; Gentry 1993; Kress et al. 1998; Heyer et al. 1999; and Pitman et al. 2001). Preliminary observations across the western Amazon Basin of one family of a dominant tropical canopy beetle family (Carabidae) indicated that nearly complete species turnover might be occurring every 250 kilometers (*cf.* Lucky et al. 2002). Unfortunately, methods of collecting and sample size were not sufficient to give solid evidence for this pattern. For the most part, carabid beetles are predators. What might be the turnover across distance/seasons for other guilds of beetles? One might predict that scavengers, like predators, would be more widespread, whereas herbivores and other types of feeding specialists would be more restricted. In addition, one might predict that host restricted herbivores and fungivores would have a similar pattern to their hosts locally, but what about co-occurring regional patterns? Do local patterns hold regionally? This investigation opens exploration of some of these questions and predictions with canopy and understory fogging events (Erwin 1989; Lucky et al. 2002) on the equator in the western Amazon Basin.

Here, we initiate our reports stemming from fogging events at each of two localities resulting in more than 500,000 beetle specimens. This initial paper focuses on our methods, sites, suite of study taxa, particularly beetles of two families, and observations from preliminary data of another 14 family-group taxa. We regard our 16 family-group taxa as a first cut into the massive amount of data collected over eight years of field work at four month intervals over an eight year period. Processing 1800 samples containing one half million specimens and taking them to an identification level of morphospecies are not easy chores. However, we believe that by reporting on our studies periodically we will provoke debate and interest in the project. Our subsequent investigations will include as many feeding guilds and phylogenetic lineages as possible.

Field Sites and Methods

Data for the beetles and site vegetation reported in out investigation came from a canopy arthropod biodiversity study, conducted at Onkone Gare Station (cited as “Piraña” in Pitman et al. 2001), (0°39′25.685″S, 76°27′10.813″W; 216 m), and Tiputini Biodiversity Station (cited as “Tiputini” in Pitman et al. 2001) (0°37′55.397″S, 76°08′39.204″W; 216 m) Ecuador, between January 1994 and July 2002. These two sites are connected by continuous primary tropical rain forest at the margin of Yasuní National Park in the Ecuadorian part of the Amazon Basin located in Orellana Province. Both sites are at first sight very similar *terra firma* forest (non-floodplain) containing extremely diverse lowland forest vegetation and characteristic of the forests of the western Amazon Basin (Condit et al. 2002; Pitman et al. 2001; Erwin and Aschero [in preparation]). Precipitation is somewhat seasonal, 2.7 m of rainfall per year, with the dry and wet seasons running from approximately November to April, and May to October, respectively.

Samples

Sampling by insecticidal fogging was employed to gather the specimens we analyzed to determine species turnover of a component of species living in the canopy/understory fractal universes, a measure of at least ⅔ of the biodiversity at this site (*cf*. Erwin 1982). In order to determine the insect biodiversity of the forested sites, we established two study plots (Lucky et al. 2002), one in 1994 (Piraña) and the other in 1997 (Tiputini). Each was a 100 m × 1000 m area that consisted of ten 10 m × 100 m transects spaced at 100 m from each other along the plot. Ten collection stations, each 3 m × 3 m, were randomly located within each 10 m × 100 m zone arrayed on both sides of a centerline. Fogging stations at each site were numbered 1–100 at the beginning of the study and were then, each one, used repeatedly for 9 sampling events across three years, “three seasons” per year (dry, wet, and wet to dry transitional). Canopy/understory sampling spanned eight years from January 1994 through July 2002 (intermittent funding as well as sporadic political unrest in Ecuador extended the field work at Tiputini), three at the Piraña site and parts of five years at the Tiputini site to account for trans-annual variation. In order to account for seasonal variation, sampling took place in January/February the dry season, June/July the wet season, as well as October, which represented a transition period between the wet and dry seasons. The fogging techniques have been described previously (Erwin 1983a, 1983b). The only modification made for this study as opposed to those previously undertaken was the use of 3 m×3 m sampling sheets suspended by

FIGURE 1. Diagrammatic depiction of fogging event station with column of effective fog and tree architecture.

nylon string tied to trees or stakes and arranged one meter off the ground at each station (Fig. 1). Foggings were made from just above each sheet as a column (1 m to ‘n’ m high) into the canopy at 0345–0500 hours. Height of fog ascendancy was measured for all fogging events. Hence, the target was a column of forest including the understory above one meter and the canopy strata at each station. In this area, canopy strata vary from one to three levels, with some super-emergent trees rising above 40 m. None of the widely dispersed super-emergents was located over any of the fogging stations.

Specimens collected from each fogging event at Piraña were sorted and 14 target taxa were extracted, including the Coleoptera, for another purpose (monitoring Maxus Oil Company road building activities and their impact on forest arthropods). In order to test for β-Diversity, a plot at Tiputini was established in 1997. Subsequently, a portion of the beetles from both sites was resorted to acquire the 16 family-group taxa for the present project. We then sorted at least 600 samples, 300 or more from Piraña and 300 from Tiputini from like seasons, of many of the 16 family-group taxa to the level of morphospecies (Table 1). Two of these family-group taxa had been previously removed from all samples for other studies (Carabidae, *cf.* Lucky et al. 2002 and Cleridae for taxonomy). We focus here on two of the family-group taxa because only they reached nearly an asymptote on the species accumulation curve when samples from both plots were combined. No family-group taxon at this point in our investigation has reached an asymptote at one site. We discuss some other family-group taxa here to illustrate certain points.

In total, the area sampled within each of the two plots (Piraña and Tiputini) was 9250 m^2, a mere 1.11% of the entire plot area. Previous experiments have demonstrated that faunal re-population occurs within 10 days after fogging (Erwin unpublished data) and rapid re-population was again demonstrated with data from the present study at a time interval of four months. Thus, the sampling setup and methodology permitted re-sampling of the same stations at four-month seasonal intervals throughout the three-year study at Piraña without affecting species abundance and diversity (Lucky et al. 2002).

In order to provide a characterization of forest composition, trees within the two plots’ ten transect zones with diameter at breast height (dbh measured at 1.33 m from tree base) greater than 10 cm were tagged by the senior author’s team and subsequently identified by Nigel Pitman and colleagues (Pitman et al. 2001).

Analysis

We wanted to know if our sampling procedures of selecting 600 samples, one third of our total of 1800 samples, would be sufficient for comparisons between the two study sites. These comparisons would have validity only if the Complementarity Index (see below) demonstrates that most of the targeted fauna at each site is included. In no family-group taxa sorted thus far did we achieve an absolute asymptote on the accumulation curves with 600 samples. We believe, however, that we are close enough using 600 samples to analyze the data from one family-group taxon (Curculionidae–Otidocephalini), and we were close enough using the 1200 samples of Carabidae for initial insights in the local distribution of beetle taxa in our area. Thus, these preliminary results are based on far fewer than our total 1800 available samples we took in the field over a period of 8 years. We recognize that each family-group taxon will respond differently to the Complementarity analysis depending upon its real diversity, i.e., the larger the taxon's diversity the greater is the overestimation bias (Colwell and Coddington 1994).

Analysis Tools

We used the EstimateS Version 6.01b program (Colwell 2000) to obtain the species accumulation curves and we used the Complementarity Index (CI) of Colwell and Coddington (1994) to determine the difference (or turnover) in faunas between the two sites. Sigma Plot 8.0 was used to graph the data from EstimateS. For explanations of the estimators we use here, such as ICE, ACE, Chao 1, Chao 2, and Jack 2, see Colwell and Coddington (1994) and documentation of the program EstimateS at <*http://viceroy.eeb.uconn.edu/estimates*>.

Results

Characterization of Forest Composition

Within the ten transect zones of the study plot at Piraña, 669 trees with dbh >10cm were found to represent 250 species and 51 families (data from Pitman, pers. commun.). Forty trees (5.98%) remain unidentified, so the true plot richness may be 9 to 15 species higher. The most common tree families, i.e., represented by more than 19 trees each, include (in order of abundance): Fabaceae (87 individuals), Arecaceae (60), Bombacaceae (57), Moraceae (46), Lecythidaceae (43), Burseraceae (36), Cecropiaceae (24) Myristacaceae (22), and Euphorbiaceae (19). The commonest tree is *Matisia malacocalyx s. lat.* (Bombacaceae) and is represented by 42 individuals.

The trees at Tiputini were similarly tagged by Erwin's team and subsequently identified, again by Pitman's team. Within the ten transect zones of the study plot at Tiputini, 623 trees with dbh >10 cm were found to represent 252 species, and 48 families (data from N. Pitman pers. comm.). Twenty-nine trees (4.65%) remain unidentified, so the true plot richness may be 5 to 10 species higher. The most common tree families, represented by 19 or more trees, include (in order of abundance) Fabaceae (82), Moraceae (57), Arecaceae (41), Bombacaceae (27), Cecropiaceae (34), and Myristacaceae (34), Lecythidaceae (30), Euphorbiaceae (27), Sapotaceae (27), Lauraceae (26), Meliaceae (20), and Burseraceae (19). The commonest species is the palm *Iriartea deltoidea* Ruiz & Pav. and it is represented by 40 individuals.

Although the most common tree species of western *terra firma* forests are represented in our plots, only part of the total regional tree species is represented. In addition to our plots, Pitman's team studied 22 other plots, each one square hectare, across the Yasuni region. He listed 1176 tree species (Pitman. pers. commun.). The two plots studied here have about 250 species each, thus each plot represents 21.42% (Tiputini) and 21.26% (Piraña) of regional tree species richness. However, because each plot has a different composition, together they represent about 34% of tree species richness in the Yasuni region.

As demonstrated above, tree composition at the two sites is very similar at the family level (CI

= 0.26), Fabaceae, Arecaceae, Moraceae, Bombacaceae, Moraceae, Lecythidaceae, Burseraceae, Cecropiaceae, Myristacaceae, and Ephorbiaceae are the commonest families at both sites. However, at the generic level, the difference is more pronounced (CI = 0.52) and at the species level, dramatically so (CI = 0.73) (Erwin and Aschero, in prep.).

Beetle Diversity

The canopy sampling regime from forest columns at Piraña, as described above, resulted in capture of some 1.7 million counted specimens belonging to 16 target taxa. The total sampling regime acquired, based on estimates of other taxa, indicate that we have 3.8 million specimens, 49% of which are ants. Beetles in the 900 Piraña samples accounted for 214,747 individuals, 13% of the total of fogging captures. This count was second in abundance at 22% to Diptera (although this dipteran abundance is because of one family whose populations burst out incredibly in the rainy season when fungus are available, i.e., Mycetophilidae). We detected no significant seasonal difference for abundance in the 16 target taxa (see below) across the nine seasonal fogging events at Piraña (ANOVA: F = 0.39, P >0.05). From 300 of the samples at Piraña, plus another 300 like samples at the second site, Tiputini, specimens of 16 family-group beetle taxa were extracted for our study.

From these Piraña and Tiputini samples, a total of 15,126 adults representing 2010 morphospecies of the target taxa have been sorted to date (Table 1). For one family-group taxon, Curculionidae (Otidocephalini), combining 300 samples from both sites proved adequate to nearly reach a species accumulation curve asymptote for the area (Fig. 2), whereas in Buprestidae (Fig. 3), Artematopodiae (Fig. 4), Cleridae (Fig. 5), and the rest of the families, at least 300 or more samples will need to be added to the database to reach a species accumulation curve asymptote. One other family, Carabidae, required analysis of 1200 fogging events to close in on an asymptote (Fig. 6). The Carabidae at Piraña were not adequately sampled with 900 samples, however the 300 samples of carabids that have been processed thus far from Tiputini provided enough additional species for a species accumulation curve to reach an asymptote for the local area. When these two family-group taxa were analyzed for Complementarity between the two sites, values were CI= 0.29 for otidocephaline Curculionidae and CI=0.69 for Carabidae (Table 1).

The Taxa

Artematopodidae ATRM (Fig. 7). The artematopodid beetles are known to be associated with mosses as larvae and adults are found on foliage. There are 60 described species worldwide, and they are relatively common in tropical forest canopies in the Amazon Basin. The study plots combined have 287 individuals representing seven morphospecies (Table 1) in the 600 samples studied. Occurrence was observed in 24.5% of those samples. The three most common species accounted for 94% of the abundance.

Buprestidae BUPR (Fig. 8). The "Jewel Beetles" visit flowers as adults and bore in plant tissue as larvae. There are 15,000 described species worldwide and these beetles are very common in the Amazon Basin. The study plots combined have 544 individuals representing 194 morphospecies (Table 1) in the 600 samples studied. Occurrence was observed in 47% of those samples. The three most common species accounted for 6.13% of the abundance.

Carabidae CARA (Fig. 9). The "Ground Beetles" (appropriately named in temperate region, however, in the tropics more than 50% of the species live on shrubs and trees) are for the most part predatory on other arthropods or their eggs, as both adults and larvae. Members of the dominant canopy genus, *Agra*, have been observed drinking plant exudates (Arndt et al. 2001). Two large

TABLE 1. Data for sixteen family-group beetle taxa. ACE, ICE and Chao 1 are estimators in the program EstimateS (see Methods); S Obs = Species observed; CI = Complementarity Index. Coleoptera Family-group codons are as follows: ARTM, Artematopodidae; ATTL, Attelabidae; BUPR, Buprestidae; CARA, Carabidae; CCAN, Ceratocanthidae; C-CRPC, Cryptocephalinae; Chrysomelidae, C-HISP, Hispinae; CLER, Cleridae; C-OTID, Curculionidae, Otidocephalini; C-ENTI, Curculionidae, Entiminae; CNTH, Cantheridae; ELAT, Elateridae; EROT, Erotylidae; MORD, Mordellidae; SCAR, Scarabaeidae; T-STRG, Tenebrionidae, Strongyliini.

Taxon	*# Samples*	*Occurrence*	*% Occurrence*	*S Obs*	*Individuals*	*Singletons*	*Doubletons*	*ACE*	*ICE*	*Chao 1*	*CI*	*Feeding Guild*
ARTM	600	84	7	7	287	2	0	10	7.9	6.4		Herbivore
ATTL	not yet processed											Herbivore
BUPR	600	282	47	194	544	41	49	323	234	315		Herbivore
CARA	1200	911	76	462	3536	37	58	475	477	473	0.7	Predator/ Nectivore
CCAN	600	132	22	31	208	4	3	52	36	38		Fungivore
C-CRPC	600	288	48	138	695	62	68	217	227	209		Herbivore
C-HISP	1000	423	42	196	835	89	32	314	316	318		Herbivore
C-ENTI	600	236	39	39	640	3	4	61	45	41		Herbivore
C-OTID	600	291	49	35	572	4	2	43	37	39	0.3	Herbivore
CLER	1200	600	50	122	1083	18	18	180	139	137		Predator
CNTH	not yet processed											Herbivore/ Pollinator
ELAT	600	447	75	120	1774	25	24	174	138	130		Herbivore/ Nectaries
EROT	600	362	60	145	967	34	33	210	168	175		Fungivore
MORD	1000	833	83	322	3000	45	54	428	361	347		—
SCAR	1000	444	44	115	821	16	19	174	133	136		Herbivore/ Fungivore
T-STRG	600	168	28	75	219	17	16	127	90	113		Fungivore
Totals				2001	15181	397	380					
						19.84%	18.99%					

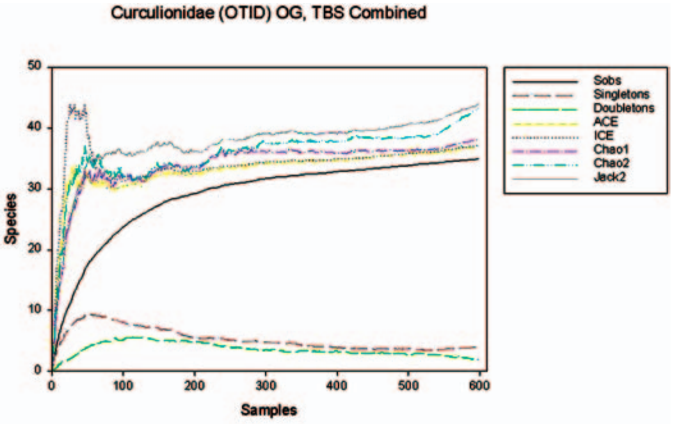
Curculionidae (OTID) OG, TBS Combined

FIGURE 2. Observed species accumulation curve and five estimation curves (ACE, ICE, CHAO 1, CHAO 2, JACK 2) for Curculionidae (Otidocephalini) with data combined from both sites.

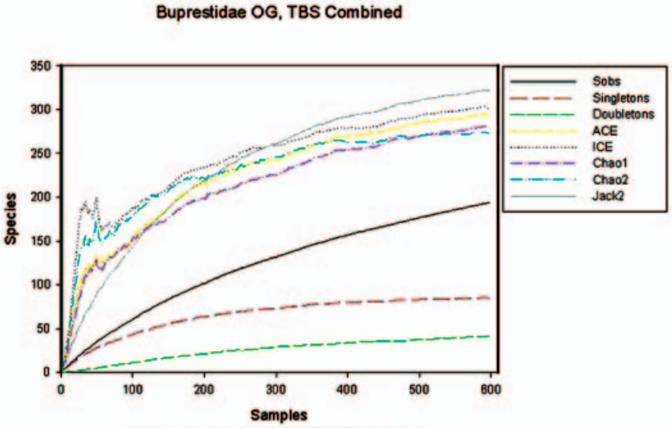
Buprestidae OG, TBS Combined

FIGURE 3. Observed species accumulation curve and five estimation curves (ACE, ICE, CHAO 1, CHAO 2, JACK 2) for Buprestidae with data combined from both sites.

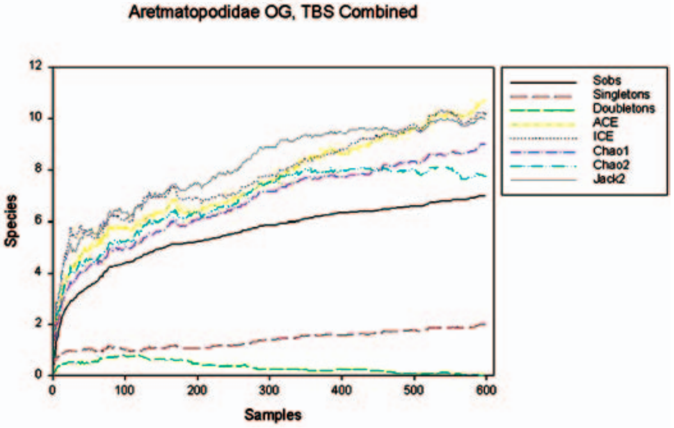
Aretmatopodidae OG, TBS Combined

FIGURE 4. Observed species accumulation curve and five estimation curves (ACE, ICE, CHAO 1, CHAO 2, JACK 2) for Artematopodiae with data combined from both sites.

tribes have specialized as seed predators (Erwin 1981); however, these are not arboricolous species. There are 39,000 described species worldwide and these beetles are very common in the Amazon Basin. The study plots combined have 3536 individuals representing 462 morphospecies (Table 1) in the 1200 samples studied. Occurrence was observed in 76% of those samples. The three most common species accounted for 5.15% of the abundance.

Cleridae CLER (Fig. 10). The "Checkered Beetles" are mostly predators as adults and as lar-

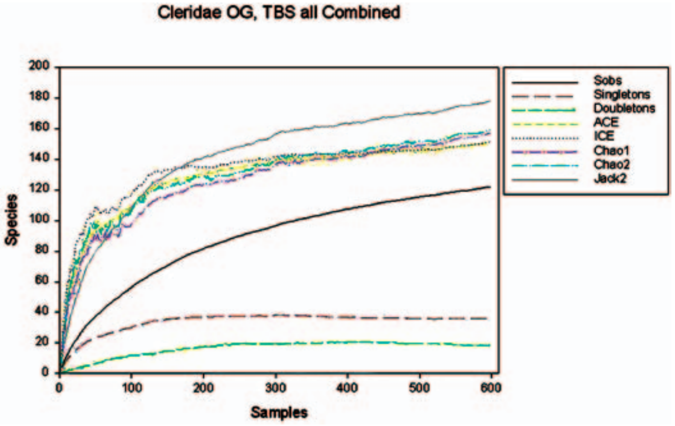

FIGURE 5. Observed species accumulation curve and five estimation curves (ACE, ICE, CHAO 1, CHAO 2, JACK 2) for Cleridae with data combined from both sites.

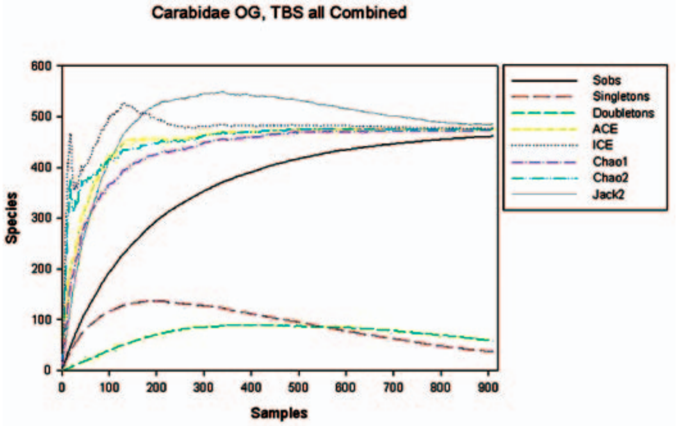

FIGURE 6. Observed species accumulation curve and five estimation curves (ACE, ICE, CHAO 1, CHAO 2, JACK 2) for Carabidae with data combined from both sites.

vae. There are 3400 described species worldwide; they are very common in the Amazon Basin. The study plots combined have 1083 individuals representing 122 morphospecies (Table 1) in the 1200 samples studied. Occurrence was observed in the 50% of those samples. The three most common species accounted for 35.94% of the abundance.

Curculionidae (Otidocephalini) OTID (Fig. 11). The otidocephaline beetles are known to be associated with several families of plants in which they mine stems. There are 35 described species in the New World; they are relatively common in tropical forest canopies in the Amazon Basin. The study plots combined have 572 individuals representing 35 morphospecies (Table 1) in the 600 samples studied. Occurrence was observed in 49% of those samples. The three most common species accounted for 44.9% of the abundance.

DISCUSSION

Patterns Observed

A consistent set of patterns emerged in the data for 14 of the 16 family-group taxa thus far investigated. In these taxa, even with the rigorous sampling regime, more samples than 600 are needed to know the universe of canopy/understory species in the local area (Figs. 3–5), and certainly more than 300 samples at one site, even for the smallest of families (Fig. 4). The only exceptions amongst the 16 family-group taxa were the otidocephaline Curculionidae (Fig. 2) that nearly


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FIGURE 7 (upper left). Image of one species of Artematopodidae (Genus *Artematopus*), length 5.0mm.
FIGURE 8 (upper right). Image of one species of Buprestidae (Genus *Leiopleura*), length 4.0mm.
FIGURE 9 (lower left). Image of one species of Carabidae (Genus *Otoglossa*), length 6.5mm.
FIGURE 10 (lower right). Image of one species of Cleridae (Genus *Axina*), length 7.0mm.
FIGURE 11. Image of one species of oditocephaline Curculionidae (Genus *Hammatostylus*), length 22.0mm.

reach an asymptote with 600 samples and the Carabidae (Fig. 6) that required 1200 samples, but only when samples were combined from both sites.

The difference in number of individual trees at Piraña (669) and Tiputini (623) is accounted for by a blow-down along two transects between the time of setting up the plot and its inventory by Pitman's team. Some 30 trees were felled in this blow-down and were not included on the identification list. Even so, both of our study sites represent accurately the expected tree composition of the *terra firma* forests in the equatorial Amazon Basin. The Piraña site accounts for 80.5% and Tiputini for 82.9% of the total 41 common species identified that dominate this type of vegetation in the Yasuni area (Pitman et al. 2001). For a more detail explanation of how similar western Amazonian forests are in terms of tree oligarchies, and particularly the Ecuadorian forests, see Pitman et al. (2001).

Analyses Compared

Even though we did not have all possible species at either of the two sites, we had indications that we had close to all the species of the "regional" fauna in two family-group taxa. So, we decided to do an analysis of complementarity for those. We predicted that we would get an overestimation of distinctness for the sites and this would be more exaggerated for the highly diverse Carabidae (*cf*. Colwell and Coddington 1994). Even so, based on the disparity between the CIs, the relationship between the two CIs was of interest, even if overestimated. This analysis hinted at a high degree of turnover for the carabids between the sites (CI = 0.69), and much less so for the otidocephaline Curculionidae (CI = 0.29). This is the opposite of what we predicted. The former are predators and would not be expected to be dependent on the vegetation in some way as food. Lucky et al. (2002) showed that only palms significantly affected carabids negatively at Piraña, that is, the more palms the less carabid species richness. The weevils are herbivores and should reflect the marked degree of complementarity of tree species between the sites, but they do not. We do not know enough about the host plants for the weevils; perhaps they use only the commonest tree species as hosts which make up the majority of the tree flora at both sites (see above); therefore they could occur everywhere in this type of forest.

Even though members of both Carabidae and Cleridae are comparable predator taxa, the clerids (Fig. 5) were not sampled with the same efficiency as the carabids. The carabids form two distinct components of the fauna: ground dwellers and canopy dwellers. Almost no ground dwellers were sampled by fogging. Thus, the results are based on species that live in the canopy habitat. Whereas adult clerids concentrate on fallen trees and limbs in the understory, perhaps moving to the canopy occasionally where there is dead wood and their prey, there are many more chance captures with the fogging technique for clerids, and hence more singletons or doubletons turn up which affect the EstimateS algorithms.

A careful look at the larger dataset for Carabidae reveals that after inadequately reaching the accumulation curve asymptote at the Piraña site, more than 100 additional species were found at Tiputini in a mere ⅓ of the available samples. Then, with both sites combined using various estimators, an asymptote was nearly reached. This was due to lowering the number of singletons and doubletons with additional samples. Are the other family patterns the same? Or, will the smaller families behave as did the Cleridae that were not adequately sampled at Piraña, nor fully sampled regionally even with 1200 samples. It is likely that some definitive conclusions might be reached when all 1800 samples of several families are analyzed. Until these are all processed, what does this preliminary step in the study tell us?

Results Applied

A faunistic and floristic inventory can be an important and necessary tool for planning and creating protected areas. Also, such inventories establish the basic information for monitoring community dynamics in space and time. Our study provides methodological information that could assist in the design and creation of protocols for entomofauna inventories in the Amazonian *terra firma* forests and elsewhere. We have demonstrated that it is likely possible to adequately sample insect family-group taxa for a local area in a relatively short time, inexpensively, even in an area of incredible diversity.

A series of fogging plots across a region at various floristically determined locals rigorously sampled, as were Piraña and Tiputini, may better describe the apparent mosaic distribution of canopy and understory arthropods (e.g., in plants, see Tuomisto et al. 2003). For all terrestrial arthropod species and other organisms, larger and more diversely sampled plots will be necessary (Erwin, in prep.) and undertaken on the scale accomplished by Tuomisto et al. (2003). This should lead to better understanding of species diversity and distributions, in turn leading to better strategic planning for conservation areas.

Equatorial forests are incredibly rich in beetle species dwelling in the canopy and understory vegetation, even at a local scale. The pattern of distribution of species is likely arrayed in a mosaic or discontinuous pattern rather than evenly distributed across the local landscape (Tuomisto et al. 2003). With our present knowledge, we cannot predict whether it is very subtle forest, soil, or climatic differences, or perhaps something historical that accounts for the pattern; likely, it is a combination of many things and probably a different suite of things for different taxa. Our results hint at a variable degree of species turnover across feeding guilds and across a forest mosaic within short distances even in similar forests in the western Amazon Basin, which in turn suggests that a conservation strategy of a few large conservation areas widely separated may not preserve a large share of existing biodiversity, namely insect species. Perhaps a new conservation paradigm may be necessary if we are to protect much of Earth's precious natural heritage in the fractal universe humans normally ignore, that of very small terrestrial arthropods.

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