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Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest

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To test the hypotheses that fruit-feeding nymphalid butterflies are randomly distributed in space and time, a community of fruit-feeding nymphalid butterflies was sampled at monthly intervals for one year by trapping 6690 individuals of 130 species in the canopy and understory of four forest habitats: primary, higraded, secondary, and edge. The overall species abundance distribution was well described by a lognormal distribution. Total species diversity (γ-diversity) was partitioned into additive components within and among community subdivisions (α-diversity and β-diversity) in vertical, horizontal and temporal dimensions. Although community subdivisions showed high similarity ($1-\beta$-diversity/γ-diversity), significant β-diversity existed in each dimension. Individual abundance and observed species richness was lower in the canopy than in the understory. However, rarefaction analysis and species accumulation curves revealed that canopy had higher species richness than understory. Observed species richness was roughly equal in all habitats, but individual abundance was much greater in edge, largely due to a single, specialist species. Rarefaction analysis and species accumulation curves showed that edge had significantly lower species richness than all other habitats. Samples from a single habitat, height and time contained only a small fraction of the total community species richness. This study demonstrates the feasibility, and necessity, of large-scale, long-term sampling in multiple dimensions for accurately measuring species richness and diversity in tropical forest communities. We discuss the importance of such studies in conservation biology.

ADDITIONAL KEY WORDS:—Nymphalidae – species abundance distribution – species richness – rarefaction – species accumulation surve – vertical stratification – environmental monitoring – habitat disturbance – conservation.

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INTRODUCTION

In view of global destruction of tropical forests, the measurement of species diversity has become critically important to understanding tropical communities and their conservation. However, due to the extraordinary species richness in tropical forests, relatively few studies have documented variation in species abundance distributions of tropical organisms through space and time (e.g. Hubbell & Foster, 1986; Morse, Stork & Lawton, 1988; Wolda, 1978, 1992; Terborgh *et al.*, 1990; Gill, 1991; Hanski & Cambefort, 1991b). Instead, most recent efforts to estimate tropical diversity for conservation have concentrated on performing rapid inventories (e.g. Roberts, 1991; Anon, 1993), utilizing focal taxa (e.g. Noss, 1990; Pearson, 1994; Pearson & Cassola, 1992; Ryti, 1992), or developing extrapolation techniques to estimate diversity in a variety of habitat types (Colwell & Coddington, 1994; Vane-Wright, Humphries & Williams, 1991; Hammond, 1994; Kiester *et al.*, 1996).

The stratification of biota between forest canopy and understory is a significant factor contributing to tropical diversity. Although vertical stratification has been documented in tropical mammals (Allee, 1926), birds (Pearson, 1977), plants (Richards, 1952), and various insect groups (Bates, 1944; Sutton & Hudson, 1980; DeVries, 1988; Stork, 1988; Longino & Nadkarni, 1990; Gill, 1991; Erwin, 1995; Mallet & Gilbert, 1995; Beccaloni, in press), the importance of stratification as a component of diversity is seldom addressed or measured directly. Despite the increasing interest in canopy biotas (Erwin, 1982, 1990; Morse *et al.*, 1988; Basset & Kitching, 1991; Lowman & Nadkarni, 1995), few studies have simultaneously measured species diversity in both canopy and understory environments through time (e.g. DeVries, 1988; Longino & Nadkarni, 1990; Malcolm, 1994; Wolda, 1992).

Considering that over half of all described species are insects (Groombridge, 1992), this group is of central importance to understanding patterns and processes of biological diversification. Due to their relatively large size, colourful appearance, ease of sampling, and broad appeal, butterflies are the best known group of insects and offer great potential for understanding insect diversity and conservation. Butterfly studies have been used as models of tropical insect diversity (see Vane-Wright & Ackery, 1984; Brown, 1991; DeVries, 1987, 1997; Lamas, Robbins & Harvey, 1991; Malcolm & Zalucki, 1993; Robbins *et al.*, 1996, and references therein), and particular butterfly taxa have been used to predict patterns of diversity in conservation studies (e.g. Kremen, 1992, 1994; Kremen *et al.* 1993; Beccaloni & Gaston, 1995; Scriber, Tsubaki & Lederhouse, 1995). However, as is the case for studies on other insect groups, those concerned with butterflies are often restricted in scope and experimental design. Typical problems include short sampling periods and poor temporal resolution, sampling methods that are non-comparable to other areas, the use of presence-absence data only, extrapolation from small sample sizes, and a lack of data on vertical distributions within communities.

A deeper understanding of tropical insect diversity can be achieved through

studies that partition diversity along different habitat dimensions, with sample sizes large enough to allow measurement of diversity among several subsets of a community. Such studies will encourage the acquisition of comparative data important for testing hypotheses that address ecological dynamics and the conservation of tropical insects. Accordingly, we report here a study of a diverse community of fruit-feeding nymphalid butterflies that was designed to test the hypotheses that these butterflies are randomly distributed in space and time. We provide estimates of species richness, abundance, seasonal changes, and vertical stratification among adjacent habitats in a neotropical rainforest. After describing the species abundance distribution of our sample from the community, we partition the measures of diversity among subsets of the community in multiple dimensions and analyse them statistically. This study demonstrates the feasibility of gathering large standardized samples in multiple dimensions for a diverse community of tropical forest insects, and illustrates statistical methods for analysing diversity in different dimensions. To our knowledge this study represents the most extensive data set gathered on a species-rich guild of tropical butterflies at one site, and thus provides a model for developing a more profound understanding of tropical insect diversity by pointing to testable ecological patterns that are important to conservation biology.

MATERIAL AND METHODS

Study site

This research was conducted at the Jatun Sacha Biological Station and Reserve, Napo Province, eastern Ecuador (01°4′ S; 77°36′ W). The 1700 hectare reserve lies at the base of the eastern Andes in the upper Amazon Basin and is bounded by the Rio Napo and the Rio Arahuno. A brief description of Jatun Sacha that is pertinent to this study is provided below; a broader description of the entire reserve can be found in Pearman, Velasco & Lopez (1995). The Jatun Sacha Reserve comprises a patchwork of habitats that include substantial areas of primary forest (where most edible mammals and birds have been hunted out), smaller areas where select timber species were extracted by local people about 15–20 years ago (hereafter referred to as higraded), a section consisting of secondary forest that was clear cut about 15–20 years ago and left to regenerate (A. Suarez & D. Neill, pers. comms.), and land currently under subsistence agriculture. Our study was conducted within a contiguous 200 hectare patch of the Jatun Sacha reserve that formed a disturbance gradient composed of four contiguous habitat types: primary forest, secondary forest, higraded forest, and an edge located at the abrupt interface of primary forest and pasture.

Study community

With the exception of males (and rarely females) of some species that visit wet soil or plant material to obtain non-nutritional resources (Norris, 1936; Adler & Pearson, 1982; Boppré, 1984), tropical butterfly communities divide quite naturally into two adult feeding guilds (DeVries, 1987, 1988). One guild is composed of species that obtain the majority of their nutritional requirements from flower nectar,

and includes most species of the Papilionidae, Pieridae, Lycaenidae, Riodinidae, and some groups within the Nymphalidae. The second guild is composed of certain subfamilies of the Nymphalidae whose adults gain virtually all of their nutritional requirements by feeding on the juices of rotting fruits or plant sap. In the neotropics this guild includes species of the subfamilies Charaxinae, Morphinae (Morphinae + Brassolinae of some authors, e.g. De Jong *et al.*, 1996), Brassolinae, Satyrinae, and some genera of the Nymphalinae. This second guild (hereafter known as fruit-feeding nymphalids) can be attracted to rotting fruits and conveniently trapped. By exploiting their feeding habits, investigators have used these butterflies to document vertical stratification in neotropical forests (DeVries, 1988; Pinheiro & Ortiz, 1992; DeVries & Walla, manuscripts in preparation) and as focal organisms for forest insect dynamics and conservation studies (DeVries, 1988, 1994; Kremen, 1994). For completeness we note that some species in the subfamily Ithomiinae are found occasionally in fruit-traps. The ithomiines, however, typically feed on flower nectar, and are not strictly part of the fruit-feeding guild as defined here. The ithomiines trapped during the study are therefore excluded from the data analysed here. However, we will present an analysis of this group elsewhere (DeVries, Lande & Murray, manuscript in preparation).

Field methods

Within the 200 hectare study area, five replicate sampling sites were established in each of the four habitat types. Each sampling site was fitted with one understory trap, and one canopy trap (see DeVries, 1987, 1988 for trap design and methods) providing a total of ten traps in each habitat—five canopy, and five understory. The height of canopy traps varied between *c.* 16 and 27 m above the ground, but in all cases traps were positioned to sample from within the canopy. Canopy traps were suspended from thin ropes run over branches of an emergent tree, such that the traps could be raised and lowered from the ground. Understory traps were suspended from low branches such that the bases hung between 1 and 1.5 m above the ground and could be serviced directly.

Traps were baited with locally-obtained bananas which were mashed, mixed well, and fermented for 48 hours in one large container prior to use. On the day prior to the sampling interval, bait was placed in a small plastic cup fixed inside each trap, and replenished with fresh bait each subsequent trapping day. On the last day of the seven day sampling period, baits were removed from all traps, and the reservoir of bait was discarded. New bait was made prior to the subsequent sampling interval, and the protocol repeated throughout the study.

The trap study extended from 16 August 1992 to 26 August 1993, with baited traps being maintained for a 7 day sampling period every month except October 1992. During trap months all 40 baited traps were sampled daily for 7 days, and then left unbaited for 3 weeks. Traps were then re-baited and the procedure repeated. No butterflies were attracted to traps without bait in this study, or in similar studies performed elsewhere (DeVries, pers. obs.).

Trapped butterflies were treated in one of two ways depending on the species. In most cases, each individual was collected and placed in a glassine envelope with all pertinent data written on the envelope. These voucher specimens were used for subsequent identification and ecological analysis. In the case of a few abundant

species, individuals were marked with a unique number, released back into the population, and the information recorded in a notebook. Recaptures were not included in the analysis reported in this study. Rather, each individual was recorded only upon the first date of capture. The results of the mark-recapture study will be reported elsewhere.

All butterflies were identified to species by comparison with museum specimens and pertinent literature, or aided by taxonomists working on particular groups. Despite numerous taxonomic studies on the butterflies, the higher level systematics of the family Nymphalidae has never been resolved. Except for a few refinements of Ehrlich (1958), all modern systematic analyses indicate that nymphalid subfamilial relationships are unclear (e.g. Scott, 1985; Harvey, 1991; De Jong *et al.* 1996). In the absence of a definitive phylogeny it therefore seems almost arbitrary as to which higher level classification is used, provided that the one chosen is unambiguous and well known. The higher level classification used here follows the conservative synthesis of Ackery (1984) which is based upon the work of Ehrlich (1958), and represents a widely used, functional classification of nymphalid subfamilies. A complete species inventory of the butterflies collected within the Jatun Sacha Reserve, including those in this study, will be presented elsewhere (D. Murray, in prep.).

Statistical analyses

Our graph of the species abundance distribution in the community differs from other recent studies by following Williams (1964) who noted that the commonly used log base 2 (or any even number) interval widths or 'octaves' (*sensu* Preston, 1948) does not provide a consistent representation of rare versus common species; log base 2 species abundance distributions overestimate frequencies of rare species (e.g. Hubbell & Foster, 1986; Magurran, 1988; Gaston, 1994), unless species with abundance equal to 2^n (for integer n) are split between adjacent octaves as in Preston (1948). However, such splitting violates independence of the data points in adjacent 'octaves'. In contrast, log base 3 interval widths with interval edges at $3^n/2$ do not exhibit these problems of overestimating rare species when shown graphically, or violate the independence of data points. The species abundance distribution in Figure 2 is thus plotted using log base 3 interval widths and compared to log series and lognormal distributions (Fisher, Corbet & Williams, 1943; Williams, 1964; May, 1975). The position of Preston's 'veil line' at the lowest observed relative abundance provides an estimate of how completely a community has been sampled (Fig. 2).

We measure β-diversity as the component of total diversity among subdivisions of the community in the dimensions of height (canopy and understory), habitat (primary, higrade, secondary, edge); or time (month). More specifically, total, or γ-diversity is estimated by the diversity of the pooled data set for the entire community; α-diversity is the weighted average diversity within subdivisions (weighted by sample size); and β-diversity equals γ-diversity minus α-diversity. In other words, we use an additive partition of diversity such that α-diversity plus β-diversity equals γ-diversity. The proportion of total diversity within subdivisions in a given dimension therefore provides a natural measure of similarity among the subdivisions (Lande, 1996).

The hypothesis that total individual abundance for the entire community was

identical among all habitats was evaluated using Chi-squared tests. Vertical stratification of the most common species in each subfamily was assessed using binomial tests for each species.

Significance of beta diversity among community subsets in dimensions of height, habitat, or time was assessed using Chi-squared tests for homogeneity of species abundance distributions at different taxonomic levels ranging from the total community to subfamilies, and genera with sufficient diversity and sample size.

Species diversity was calculated using three standard measures: species richness, Shannon-Wiener information, and the Simpson diversity (Magurran, 1988). Community similarity indices corresponding to each of these measures were also calculated as $1-\beta$-diversity/γ-diversity (Lande, 1996).

Estimates of species richness in diverse communities are highly sensitive to sample size because rare species are likely to be absent from small samples. This makes it necessary to correct for sample size when comparing diversity between samples of different size. For simplicity we calibrate species richness in a particular subset against the rarefaction curve for the total community (Sanders, 1968; Hurlbert, 1971; Gotelli & Graves, 1996), which gives the average species richness in a random subset of any particular size. Our use of a single rarefaction curve as a standard of comparison is further justified by the high similarity among subsets of the community in spatial and temporal dimensions (Table 3). The statistical significance of such comparisons are evaluated using the approximate 95% confidence limits for the rarefaction curve, calculated as ± 2 standard deviations around expected values (Heck, van Bell & Simberloff, 1975).

To further assess the influence of sample size on species richness estimates, we compared species accumulation curves for subdivisions of the entire community (Colwell & Coddington, 1994). A species accumulation curve represents the cumulative number of species as a function of the cumulative abundance of individuals in the particular order of collection through time. In contrast, a rarefaction curve plots the expected number of species against the size of random subsets of the total sample from the community. An important difference between these two representations is that a confidence interval can be constructed around the rarefaction curve, whereas the species accumulation curve results from a unique temporal ordering of individuals, and is not subject to the same kind of statistical analysis.

RESULTS

During twelve sampling periods we captured a total of 6690 individual butterflies belonging to 130 species in five subfamilies (excluding the Ithomiinae). The rank abundance distribution of our sample from the community showed that a large proportion of the trapped butterflies were accounted for by rare species (Fig. 1): more than half of the species in the study were represented by 10 or fewer individuals. Abundances ranged over several orders of magnitude, from 20 species represented by single individuals, to the edge specialist, *Cissia penelope*, represented by 1618 individuals (Fig. 2).

Species richness and abundance were distributed unequally between canopy and understory (Table 1). Nineteen per cent of the species were found in the canopy only, 34% were found in the understory only, and the remaining 47% of the species

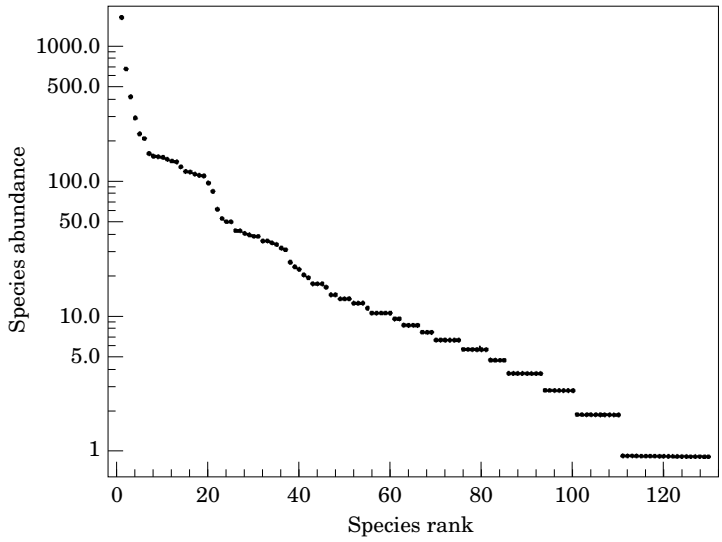

Figure 1. Rank-abundance distribution for total community of fruit-feeding nymphalids.

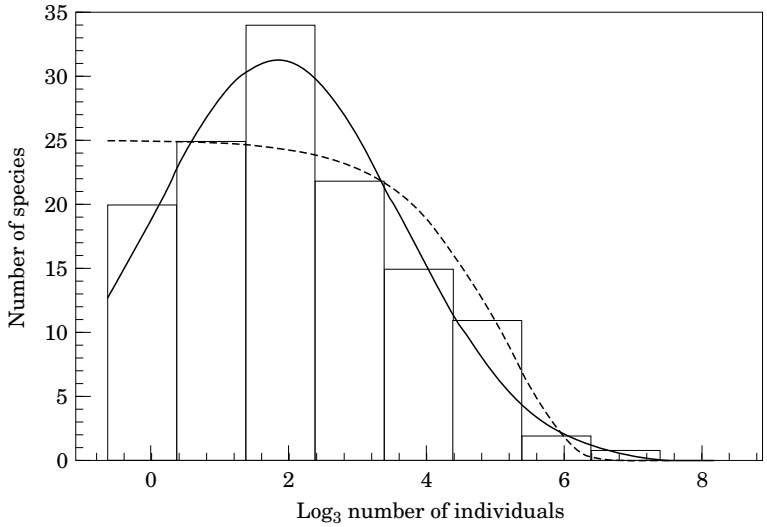

Figure 2. Species abundance distribution for total community of fruit-feeding nymphalids (histogram). Parameters for the fitted log-series distribution (dashed curve) are $\alpha = 22.8842$ and $x = 0.996591$. Parameters of the fitted log-normal distribution (solid curve) using the method of Pielou (1975) on the log base 3 scale are mean 1.82382, variance 3.27872, and estimated number of actual species 142.5. The log-normal distribution ($\chi^2 = 3.069$, $P = 0.80$) fits better than the log-series distribution ($\chi^2 = 5.409$, $P = 0.49$).

were found in both strata (Table 1). When only the 45 rarest species (represented by ≤ 4 individuals) were considered, 17 species were found in canopy only, 16 in understory only, and 12 were found in both. Thus, frequency of rare species was distributed evenly with respect to vertical dimension. In contrast, a large proportion

TABLE 1. (A) Species richness of total community partitioned by vertical position. Rare species are those represented by ≤ 4 individuals, and common species are those represented by ≥ 5 individuals. (B) Individual abundance of the community partitioned by vertical position

	Canopy	Understory	Both	Total
(A)				
Rare species	17	16	12	45
Common species	8	28	49	85
Total species	25	44	61	130
(B)				
Total individuals	1173	5517	—	6690

TABLE 2. Distribution of total species richness (130 species) among habitats, and those species unique to particular habitats

Habitat	Unique	Total
Primary	6	82
Higrade	6	85
Secondary	10	97
Edge	11	86

of common species (represented by ≥ 5 individuals) were found in both canopy and understory, while fewer were found in canopy than in understory (Table 1).

Based on observed species richness, the least disturbed habitat (primary) had lowest species richness and fewest unique species, whereas the most disturbed habitats (secondary and edge) had the highest species richness and most unique species (Table 2). Although no large differences were apparent among habitats, the distribution of species numbers suggests that disturbance had a positive effect on species richness and number of unique species among habitats (Table 2).

Species richness also provided a measure of species distribution among habitats, and of how species were shared among habitats. For clarity, the higrade habitat was omitted in the following comparisons, thus reducing the total species in the community considered elsewhere (e.g. Table 2) to 124, and to keep the proportion of rare species approximately the same as in the previous comparison (i.e. Table 1), rare species are here defined as being represented by ≤ 3 individuals. This comparison using 43 rare species showed that the secondary habitat contained more unique species than the primary and edge habitats; primary and secondary habitats shared the highest proportion of rare species; and only 5% of the rare species were shared

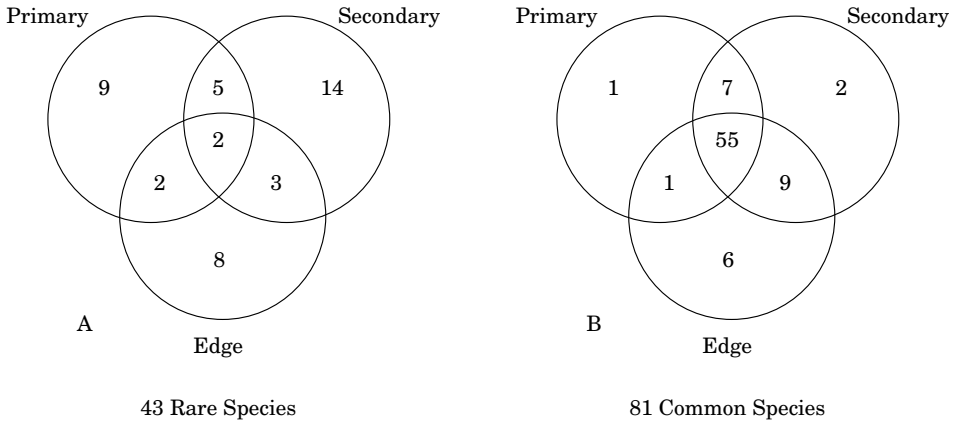

Figure 3. Species overlap among three habitats. For graphic clarity the higrade habitat was omitted in this analysis, giving 124 total species. A, rare species represented by $n \leq 3$ individuals. B, common species represented by $n \geq 4$ individuals.

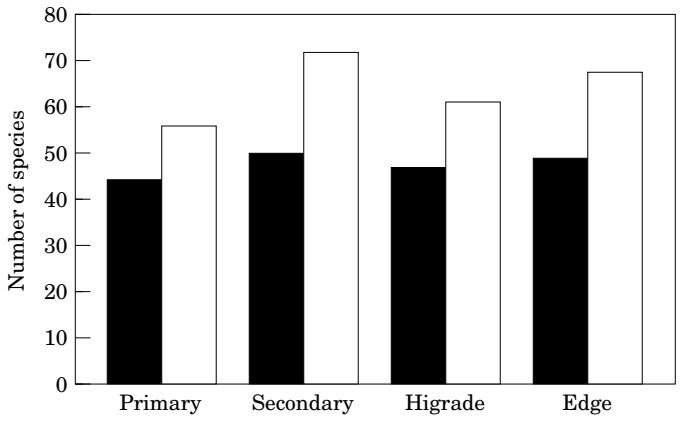

Figure 4. Species richness partitioned by habitat and height in forest. Canopy counts (■), understory counts (□). Note apparent eveness of species richness among habitats.

by all three habitats (Fig. 3). For the remaining 81 common species, the edge habitat contained the most unique species, primary the least, and primary and edge habitats shared the fewest species. Finally, 68% of the common species were shared by all three habitats. Again, on the basis of species richness, the most disturbed habitats contain the highest diversity.

When the entire sample was partitioned into four habitats (primary, secondary, higrade, edge), and then each habitat further partitioned into canopy and understory, the proportion of species among the habitats was found to be evenly distributed (Fig. 4). That is to say that observed species richness did not differ from an hypothesis predicting equal species richness among habitats. Although this pattern is obvious by inspection of Figure 4, the hypothesis of equal numbers of species among habitats is not subject to standard statistical tests since the species are not independent (due

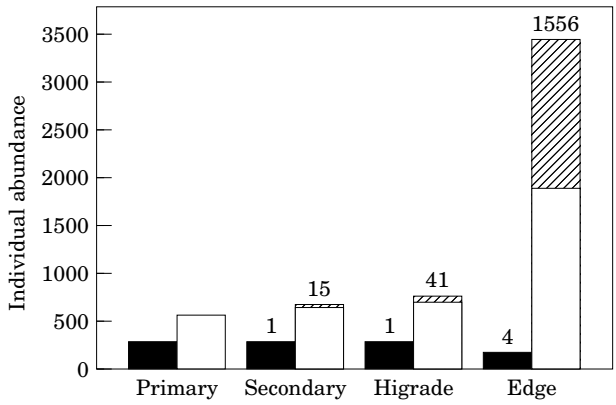

Figure 5. Individual abundance of total community partitioned by habitat and height in forest. Canopy counts (■), understory counts (□), single edge species *Cissia penelope* (▨). Numbers on top of each histogram represent total number of *C. penelope* found in each habitat. Note apparent evenness of individual abundance among all habitats, excepting for edge.

to phylogenetic relationships), nor could they be identically distributed (due to differences in abundance).

Total abundances among four habitats differed significantly ($\chi^2 = 793.4$, df = 3, $P < 0.001$), and inspection of Figure 5 reveals that the greatest abundance was found in the understory of edge habitat. The edge specialist species, *Cissia penelope* (Fabricius, 1775), accounts for 45% of the total abundance in this habitat. The difference in abundance among habitats remained significant ($\chi^2 = 364.0$, df = 3, $P < 0.001$) even when this species is omitted from analysis. (Abundances in edge habitat with, and without *C. penelope* differed significantly; $\chi^2 = 32.67$, df = 1, $P < 0.001$). However, when edge habitat was excluded from analysis, thus comparing forested areas only, abundances among primary, secondary, and higrade habitats did not differ significantly ($\chi^2 = 3.055$, df = 2, $P = 0.22$).

Seasonal variation in both species richness and abundance was readily apparent for our sample from the community as a whole, and when canopy and understory were considered individually (Fig. 6). There was a cyclical regularity where both measures showed periods of decline followed by periods of increase. Consequently seasonal variation is seen to be a dynamic component in this system that directly influenced other measures of diversity.

Three commonly used measures of community diversity (Magurran, 1988), and corresponding measures of similarity among subdivisions of the community in space and time (Lande, 1996) are provided in Table 3. These measures suggest that Jatun Sacha fruit-feeding nymphalids show a high similarity among subdivisions in vertical, horizontal and temporal dimensions.

In contrast to measures of community diversity, Chi-squared tests for homogeneity of species abundance distributions revealed that our sample from the community was distributed non-randomly in all dimensions. The total sample showed significant differences in species composition among vertical position (canopy or understory), habitat, and sampling period (Table 4). Relative frequencies of species in each subfamily differed significantly between canopy and understory, among four habitats, and (with the exception of Brassolinae), among sampling periods (Table 4). Within

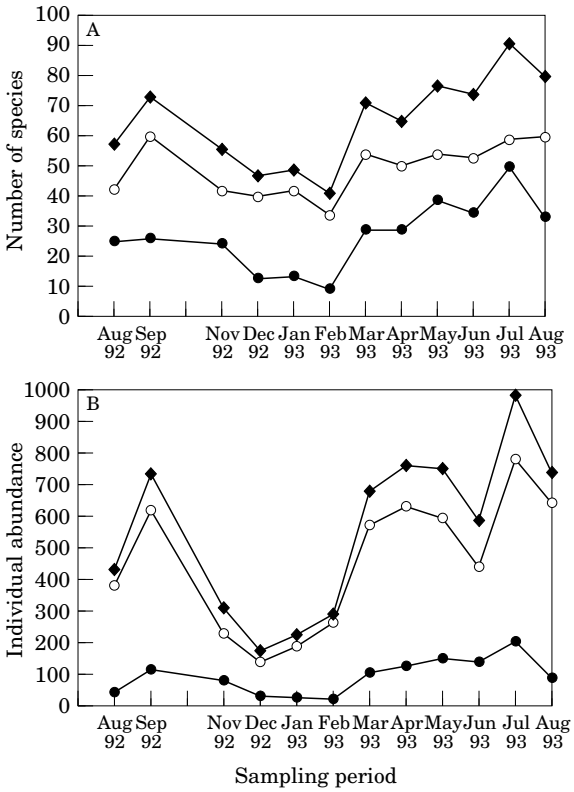

Figure 6. Seasonal variation of total community, and by vertical position. A, species richness. B, individual abundance. Total (◆); canopy (●); understory (○).

particular genera, species abundance distributions showed significant differences between canopy and understory in all cases, sometimes with respect to habitat, but never with respect to sampling period (Table 4).

Pooled comparisons of the six most abundant species in each subfamily suggested that, independent of habitat, vertical distribution by individual species was non-random (Table 5). Other observations on fruit-feeding nymphalids further support the suggestion of vertical distribution by particular species. A comparative study that has run continuously for over 3 years at Garza Cocha, Ecuador (DeVries & Walla, manuscript in preparation) indicates that the species listed in Table 5 (in addition to others) show consistent, non-random vertical distributions (see also DeVries, 1988). Therefore, even in the absence of ecological and behavioral details for most neotropical butterflies, the species abundance distributions presented here point to the necessity of accounting for vertical distributions in studies aimed at estimating butterfly diversity.

Rarefaction of the entire community, with approximate 95% confidence intervals, was used as a standard of comparison for various subsets of our data in different dimensions (Fig. 7). This shows that, at any given sample size, the canopy sample is expected to be more diverse than the understory. Edge is expected to be least diverse among four habitats, while primary and higrade habitats are expected to be

TABLE 3. Measures of community diversity and similarity for fruit-feeding nymphalid butterflies at Jatun Sacha

	Measure	Community similarity among		
A.	Species richness	heights	habitats	months
Total community	130	0.782	0.669	0.547
Subfamilies				
Nymphalinae	35	0.715	0.667	0.510
Charaxinae	25	0.807	0.769	0.510
Morphinae	7	0.851	0.466	0.349
Brassolinae	13	0.886	0.872	0.772
Satyrinae	50	0.967	0.618	0.597
(B)	Shannon–Wiener	heights	habitats	months
Total community	3.376	0.913	0.862	0.935
Subfamilies				
Nymphalinae	2.117	0.868	0.927	0.906
Charaxinae	2.523	0.926	0.946	0.859
Morphinae	0.637	0.922	0.770	0.599
Brassolinae	2.313	0.869	0.911	0.882
Satyrinae	2.455	0.968	0.848	0.930
(C)	Simpson	heights	habitats	months
Total community	0.917	0.975	0.935	0.978
Subfamilies				
Nymphalinae	0.806	0.953	0.968	0.943
Charaxinae	0.873	0.974	0.984	0.963
Morphinae	0.268	0.944	0.911	0.754
Brassolinae	0.891	0.926	0.960	0.950
Satyrinae	0.818	0.989	0.932	0.960

* Community similarity $= 1 - \beta/\gamma$, where β is beta-diversity among subdivisions in a given dimension and γ is total community diversity (Lande, 1996).

TABLE 4. Chi-squared tests for homogeneity of species abundance distributions among heights, habitats, and months for the total community, subfamilies and genera. Significance levels are: ns = not significant, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$

Taxon	Abundance	Heights	Habitats	Months
Total community	6690	***	***	***
Subfamily				
Nymphalinae	1769	***	***	***
Charaxinae	396	***	*	**
Morphinae	115	***	*	***
Brassolinae	302	***	***	ns
Satyrinae	4108	***	***	***
Genus				
Catonephele (2 spp)	120	***	ns	ns
Hamadryas (4 spp)	90	***	***	ns
Archaeoprepona (4 spp)	80	***	ns	ns
Opsiphanes (3 spp)	81	*	ns	ns
Mageuptychia (8 spp)	47	**	***	ns

TABLE 5. Vertical stratification of individuals in the 6 most abundant species in each subfamily. Data pooled across habitats and months were tested against the null hypothesis of equal abundance between canopy and understory. Significance levels are: ns = not significant, * = $P<0.05$, *** = $P<0.001$. Abbreviations: (C)= Charaxinae, (N) = Nymphalinae, (M) = Morphinae, (B) = Brassolinae, and (S) = Satyrinae. Note: because of the low relative abundance of Morphinae only one species of this subfamily is included

Taxon		Individual abundance			
		Canopy	Understory	Total	*P*
Prepona laertes (Hübner, 1814)	(C)	15	0	15	***
Archaeoprepona demophon (Linnaeus, 1758)	(C)	14	37	51	***
Zaretis itys (Cramer, 1777)	(C)	25	11	36	*
Memphis arachne (Cramer, 1776)	(C)	89	23	112	***
Memphis offa (Druce, 1877)	(C)	21	3	24	***
Memphis xenocles (Westwood, 1850)	(C)	32	8	40	***
Catonephele acontius (Linnaeus, 1758)	(N)	22	89	111	***
Nessaea obrina (Linnaeus, 1758)	(N)	0	209	209	***
Nessaea hewitsoni (Felder & Felder, 1859)	(N)	1	153	154	***
Smyrna blomfildia (Fabricius, 1782)	(N)	197	28	225	***
Historis odius (Fabricius, 1775)	(N)	106	8	114	***
Colobura dirce (Linnaeus, 1758)	(N)	238	438	676	***
Morpho achilles (Linnaeus, 1758)	(M)	0	98	98	***
Caligo illioneus (Cramer, 1776)	(B)	0	33	30	***
Caligo idiomenius (Linnaeus, 1758)	(B)	0	40	40	***
Catoblepia xanthus (Linnaeus, 1758)	(B)	0	42	42	***
Catoblepia berecynthia (Cramer, 1777)	(B)	0	44	44	***
Opsiphanes cassina (Felder, 1862)	(B)	21	14	35	ns
Opsiphanes invirae (Hübner, 1808)	(B)	27	5	32	***
Hermeuptychia hermes (Fabricius, 1775)	(S)	12	141	153	***
Cissia proba (Weymer, 1911)	(S)	0	161	161	***
Cissa myncea (Cramer, 1782)	(S)	0	151	151	***
Cissia penelope (Fabricius, 1775)	(S)	8	1612	1620	***
Pareuptychia occirhoe (Fabricius, 1776)	(S)	1	419	420	***
Ypthimoides erigone (Butler, 1867)	(S)	0	295	295	***

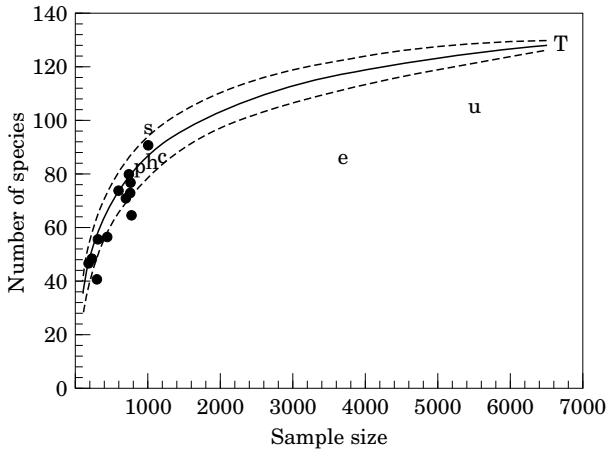

Figure 7. Rarefaction curve (solid curve) and approximate 95% confidence interval (dashed curves) for the total community of fruit-feeding nymphalids compared to observed species richness in subdivisions of the community along dimensions of height, habitat, and time. T = total community; c = canopy, u = understory; p = primary, s = secondary, h = higrade, e = edge; (●) = months.

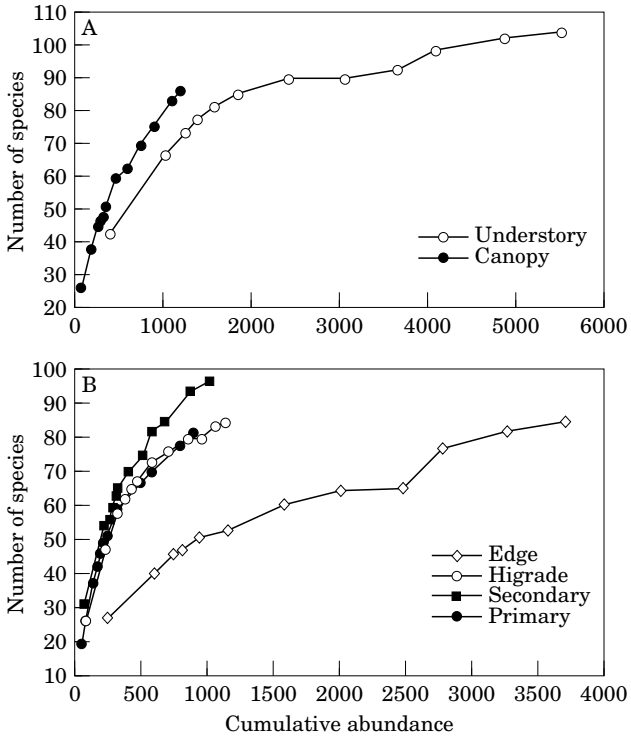

Figure 8. Species accumulation curves showing total species versus cumulative individual abundance through time in. A, canopy and understory. B, four habitats.

more diverse than suggested by the raw data (uncorrected for sample size), and second growth is expected to be the most species rich. Rarefaction analysis shows that edge habitat has much lower diversity, and second growth habitat has slightly higher diversity than expected from a random sample of the entire community. Finally, the relatively low diversity within months and low similarity among months, compared to those for habitats or vertical position (Table 3), are seen by comparison with the rarefaction curve to be largely a function of sample size. The existence of significant β-diversity in each dimension (Table 4) accounts for the observation that a significant number of the data points in each dimension lie below the lower 95% confidence limit of the rarefaction curve for the entire community (Fig. 7).

Species accumulation curves confirm patterns revealed by rarefaction. For vertical dimension (Fig. 8A), the canopy accumulation curve is clearly steeper, and at comparable sample sizes the canopy is more diverse than the understory. Species accumulation curves for the four habitats also corroborate the conclusions that second growth is the most diverse, and edge is the least diverse (Fig. 8B). Whether the second growth accumulation curve would remain above the primary and higrade curves if all of them were projected to their asymptotes (Fig. 8B) can only be determined by additional sampling. Therefore, the patterns shown by rarefaction, and by species accumulation, emphasize that both vertical and horizontal dimensions are important for accurate estimates of tropical forest butterfly diversity.

DISCUSSION

The global scale and rapidity of biodiversity destruction (Wilson, 1988) forces most ecologists to accept the practical need for quick surveys of biodiversity in conservation planning and monitoring (Roberts, 1991; Anon, 1993). However, these can ultimately be justified only by testing their accuracy against large-sample, long-term studies that partition diversity into its spatial and temporal dimensions. Fruit-feeding nymphalid butterflies constitute a model system ideal for large-sample long-term studies to test quick biodiversity surveys, for several reasons. This diverse group is mostly confined to tropical forest, and is taxonomically among the best known of all butterflies; they are well represented in museum collections, therefore facilitating identification. The trap design and methods are simple, inexpensive, and in contrast to traditional surveys that rely on hand net and/or visual sampling by different collectors, standardized replicated traps can be employed for comparisons among forest sites with different levels of disturbance, or between different geographical areas.

In any trapping study sampling bias might arise from microenvironmental variance among traps, and variance among species in attraction to baits (Williams, 1964). Pooling replicate traps within habitats (as done in this study) can reduce individual trap variance, but species attraction to baits can only be addressed by intensive mark-recapture studies (Seber, 1982) and/or natural history observations. As discussed by DeVries (1988) trap methods used here provide estimates of species abundance where the adult butterflies were trapped, but no information on the distribution of hostplants, roosting areas (e.g. Mallet & Gilbert, 1995; Beccaloni, 1997), courtship sites, or other life history components. Observations over a 3-year period from Garza Cocha using traps and other inventory methods show that most of the rare species reported here are also rare elsewhere in forested Amazonian Ecuador, regardless of whether trapped or caught with a hand-net (DeVries & Walla, unpublished). Compared to other commonly used techniques, our methods can reduce, or avoid the sampling biases in all net techniques that rely on pooling efforts of multiple persons, and trapping is clearly superior to sight records. Even though susceptibility of fruit-feeding nymphalids to traps has not been established for all species, the trap data can easily be compared to those collected at other sites, and among various habitats. Trap studies have made important contributions to our understanding of tropical insect ecology and diversity (e.g. Hanski & Cambefort, 1991b; Wolda 1978, 1983). By allowing more accurate comparisons and statistical analysis to be made among samples in space and time, the methods outlined here are important to butterfly diversity studies and conservation biology.

Several observations suggest that our sample of 130 species in a distinct guild captured a large fraction of the total species diversity in this community. Despite the large proportion of rare species in the overall sample (Fig. 1), the species abundance patterns for the Jatun Sacha fruit-feeding nymphalid community fit the log-normal distribution (Fig. 2). In Figure 2 the position of the veil line (Preston, 1948) indicates a total of 142.5 species estimated from the fitted log-normal distribution by the method of Pielou (1975), or a total of 150 ± 10 species estimated by the method of Chao (1984). Furthermore, we accounted for 69% of the total fruit-feeding nymphalids reported from the entire Jatun Sacha reserve during an intensive 3-year inventory (D. Murray, unpublished) which included areas not sampled in the present study. Thus, we are confident that our study provides a

realistic estimate of the fruit-feeding nymphalid diversity from our 200 hectare plot.

The most appropriate measures of species diversity for use in quick surveys for purposes of conservation planning have the desirable statistical property of small bias when sample size is small. Of the three most commonly used measures of species diversity, only Simpson diversity, $1-\lambda$, and to a lesser extent Shannon-Wiener information, H, satisfy this criterion (Lande, 1996). Although species richness is the least reliable statistic to use in quick surveys, it nevertheless is often employed in conservation applications because most diverse tropical ecosystems typically have a large number of rare species, and because rare species are often at greatest risk of extinction they are targets for conservation. Furthermore, species richness is the only commonly used measure that is sensitive to rare species (Peet,1974). Since rare species are likely to be absent in small or moderate samples, species richness is highly sensitive to sample size. Therefore, comparison of species richness among samples requires correction for differences in sample size using the techniques of rarefaction and species accumulation curves, which can best be performed on large samples.

Based on simple measures of species richness and abundance, the fruit-feeding nymphalids in our sample showed a non-random distribution with respect to vertical position (Table 1), corroborating other work on the stratification of these butterflies (DeVries, 1988; DeVries & Walla, manuscript in preparation). These estimates showed that richness and abundance of common species (≥ 5 individuals) was highest in the understory, that rare species showed an even vertical distribution, and that 19% of all species were found only in canopy samples (Table 1). The most abundant species in each subfamily also showed non-random vertical distributions (Table 5). Therefore, even these simple statistics point to the need to account for stratification in diversity studies.

It is well known that low or intermediate habitat disturbance generally has a positive effect on species richness (Connell, 1978; Huston, 1979; Denslow, 1987). As measured by species richness, the least disturbed habitat (primary) had the lowest species richness and fewest unique species, whereas the most disturbed habitats (secondary and edge) had the highest species richness and most unique species (Table 2; Fig. 3). Although these differences are slight, under conservation practices favoring habitats based on species richness (e.g. Oliver & Beattie, 1996), one could argue for preservation of neotropical secondary and edge habitats over primary forest. However, as noted below, such a view would be inaccurate.

Vegetation structure and taxonomic composition are well known to have a major influence on community diversity (e.g. MacArthur, Recher & Cody, 1966; Southwood, Brown & Reader, 1979). Among the four contiguous habitats we studied, there were substantial differences in plant species composition and overall structural diversity of the vegetation (D. Neill, pers. comm; Pearman *et al.*, 1995), both of which can be attributed to human disturbance. This study was designed to estimate effects of disturbance along a habitat gradient, and we expected to find differences in cumulative species richness in the community that were reflected among habitats. In contrast to our expectations, habitat disturbance had little effect on the distribution of species richness, which overall, showed similar species richness among habitats (Fig. 4).

Among habitats, the greatest individual abundance occurred in the understory edge habitat, and a large proportion of this was contributed by a single species, *Cissia penelope* (Fig. 5). This species is generally rare in lowland Ecuadorian forests

with low or moderate levels of disturbance (DeVries, pers. obs.). The strong edge effect shown by *Cissia penelope* demonstrates how a species can be released by drastic habitat alteration. Other satyrine species in our samples: *Cissia myncea* (Cramer, 1782), *Hermeuptychia hermes* (Fabricius, 1775), *Pareuptychia ocirrhoe* (Fabricius, 1776), and *Ypthimoides erigone* (Butler, 1867) also showed this pattern. Excluding the abrupt edge as unnatural habitat for most fruit-feeding nymphalids, there was a nearly even distribution of both individual abundance and species richness among the primary, secondary, and higrade habitats, and nearly constant ratios between canopy and understory within each of these habitats (Figs 4 and 5). These cumulative patterns among heights and habitats were evident even though richness and abundance changed seasonally (Fig. 6). Much of the apparent similarity among habitats is likely an area effect due to their close proximity and recent human disturbance in the greater Jatun Sacha area that created a patchwork of successional habitats. In essence, many of the fruit-feeding nymphalids appear to have treated the four habitats as a single, fine-grained, patchy habitat.

The slight increase in species richness with level of disturbance in our total sample (Fig. 4) could, in the absence of abundance estimates, be taken to mean that secondary forest and edge habitat are more deserving of conservation than undisturbed primary forest. This is incorrect for two reasons: First, species specialized to primary forest disperse into other habitats only because of the local proximity of these habitats; such species probably could not persist in a large area converted completely to secondary forest and edge (Janzen, 1973; Lovejoy *et al.*, 1986; Halpern & Spies, 1995; Didham *et al.*, 1996). Second, rarefaction analysis indicates that edge habitat has significantly fewer species than any other habitat, and that increased species richness in second growth barely reaches statistical significance (Fig. 7).

Lovejoy *et al.* (1986); showed that edge significantly reduced plant, bird, and mammal species richness, but increased species richness of butterflies in the subfamilies Ithomiinae and Satyrinae (no other groups were measured). Our results appear to reflect patterns of species richness at the edge for plants and vertebrates in Lovejoy *et al.* (1986), but not butterflies (Figs 7 and 8). This disparity is interesting and merits further investigation, but without rarefaction analysis and/or species accumulation curves it is difficult to determine whether the patterns they observed might have been attributable to sample size differences among habitats. If these patterns are real, a natural history observation may help explain some of the disparity of edge effects found by Lovejoy *et al.* (1986) between plants and vertebrates on one hand, and butterflies on the other. To obtain alkaloids needed in mating and defense, male ithomiine butterflies travel through a variety of habitats to visit plants that typically grow at edges and open areas (DeVries, 1987; DeVries & Stiles, 1990; Beccaloni & Gaston, 1995). An increase in edge species richness could result if ithomiine samples were predominantly male as they could represent migratory individuals from within the forest. Note that *Heliconius* butterflies also move from the forest interior to second growth to feed at flowers (Mallet & Gilbert, 1995).

Seasonal fluctuations in abundance and species richness have been documented in a number of neotropical insect groups (Wolda, 1978; Wolda & Wong, 1988; Smythe, 1982). The seasonal variation during our study (Fig. 6) resembles that observed at another lowland Ecuadorian site along the Rio Napo (Garza Cocha) that has a similar climate. For example, both species richness and abundance of nymphalid butterflies at Garza Cocha are depressed during the dry season (approximately December through mid-March), and increase into the rainy season

(DeVries & Walla, unpublished). This general seasonal pattern has been noted for a number of tropical insect groups (e.g. Wolda, 1983, 1992; Janzen, 1984; Brown, 1991). However, in contrast to studies conducted at temperate zone sites that have monitored insect diversity over long periods of time (e.g. Cook & Graham, 1996), the magnitude of annual variation in species richness and abundance for Jatun Sacha or other Ecuadorian sites is unknown. Nevertheless, these observations point to one obvious flaw in sporadic or quick assessment techniques frequently used to estimate tropical diversity—because seasonality influences measures of diversity, seasonal fluctuations in the magnitude of diversity over time emphasize the need for regular and comparable sampling designs.

Partitioning of diversity for species richness showed that a substantial proportion of the total species richness in the community occurred as beta diversity among the subdivisions in different dimensions: 22% for heights, 33% for habitats, and 45% for months (Table 3). This indicates that quick, small-sample surveys of a single understory habitat in one month would only capture a small fraction of the total species richness in the community. Increasing proportions of beta diversity found in these three dimensions largely reflect different sample sizes among their subdivisions, since the total sample from the community was divided into two heights, four habitats and twelve months (Fig. 7). Due to the high sensitivity of species richness to sample size, community similarity in species richness should not be used to test for the existence of significant beta diversity. For this purpose, tests of homogeneity of species abundance distributions among subdivisions of a community (using contingency table analysis with Chi-squared or likelihood tests) are much more powerful.

Beta diversity in species richness in vertical, horizontal, and temporal dimensions of the total community was highly significant (Table 4). The subfamilies all showed highly significant beta diversity among heights, and most subfamilies showed significant or highly significant beta diversity among habitats and months. Selected genera showed significant or highly significant beta diversity among heights, but some showed no significant beta diversity among habitats, and no genus showed significant beta diversity among months. Within each taxonomic level, the differences in overall significance of beta diversity among subdivisions of the community in space and time were again largely a function of differing sample sizes.

When sample sizes were standardized by rarefaction, several patterns emerged which are important to understanding the Jatun Sacha community (Fig. 7). Recall that the strength of rarefaction is that it gives the expected number of species as a function of the sample size of random subsets of the total community, and the results are subject to statistical analysis (Heck *et al.*, 1975). In marked contrast to the raw numbers, rarefaction showed that the canopy community is expected to be more diverse than the understory, and the highly disturbed edge is expected to have many fewer species than primary and higrade habitats, while second growth is expected to be slightly more species rich (Fig. 7).

Species accumulation curves recently have become important in assessing diversity of tropical arthropod communities (Colwell & Coddington, 1994). Curves generated explicitly for the Jatun Sacha community reflected conclusions from rarefaction in both vertical and horizontal dimensions (Fig. 8). Accumulation curves (Fig. 8A) indicate that the Jatun Sacha canopy community is more diverse than simple species counts might suggest (Table 1), and reinforces the importance of accounting for the canopy community when measuring tropical forest insect diversity. Accumulation

curves for habitats provided further support for patterns obtained by rarefaction and showed the important effect that sample sizes have on comparative diversity estimates (Fig. 8B). Although these curves suggest how the habitats rank with respect to species richness, differences implied between primary, secondary, and higrade habitat accumulation curves could only be verified through additional sampling.

In conclusion, this study establishes the feasibility of long-term, intensive sampling of diverse tropical butterfly communities and illustrates statistical methods of analysing species diversity in different dimensions. By standardizing and extending spatial and temporal sampling regimes beyond previous work, this study shows the importance of partitioning forest insect diversity into different dimensions, and allows us to perceive tropical diversity in a more dynamic light. Future studies from other tropical forests are now needed to test the generality of the patterns reported here. Finally, we emphasize that only through such detailed studies of diversity patterns, combined with inquiry into the natural history and ecology of particular species, will we gain a better understanding of tropical rainforest diversity, and what we are trying to conserve.

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