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Species diversity and community structure in neotropical fruit-feeding butterflies

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To test the veracity of previous studies and illuminate major community patterns from an intact community, a guild of nymphalid butterflies was sampled at monthly intervals for five consecutive years by trapping in the canopy and understorey of five contiguous forest plots in the same rainforest. Significant numbers of species belonged to either the canopy or understorey fauna, confirming fundamental vertical stratification, and showing that sampling in one vertical position is a poor estimator of diversity. Significant monthly variation showed that intermittent or short-term sampling would underestimate diversity, and significant variation among years and areas showed that diversity was strongly influenced by sampling year. Even when the underlying communities were the same, temporal interactions strongly affected species diversity in both horizontal and vertical dimensions. An unprecedented seasonal inversion of species richness and abundance was detected between the canopy and understorey that occurred at the onset of all rainy seasons. This investigation suggests that long-term studies evaluating spatial and temporal patterns of species diversity among many sites may be required for a better understanding of tropical communities and how best to conserve them. © 2001 The Linnean Society of London

ADDITIONAL KEY WORDS: long-term sampling – species abundance distribution – tropical butterfly communities – spatial effects – vertical distribution – temporal effects – conservation.

INTRODUCTION

Tropical forest communities that are characterized by their high species richness and low abundance have played a fundamental role in the development of evolutionary biology (Darwin, 1859; Bates, 1862; Wallace, 1878). Furthermore, considerable theoretical interest has focused on why there are so many tropical species and how they are maintained in the communities they occupy (Preston, 1948, 1980; Dobzhansky, 1950; Hutchinson, 1959, 1975; Connell & Orias, 1964; MacArthur, 1965, 1972; Janzen, 1970; Hubbell, 1997; May, 1975). Thus, consideration of tropical forest systems has made important contributions to understanding patterns of species diversity and community structure (e.g. Elton, 1958, 1973; Fischer, 1960; Paine, 1966; Pianka, 1966; Cody & Diamond, 1975; Connell, 1978; Wolda, 1978, 1983a,b, 1992; Orians, 1969; Hubbell, 1979; Wiens, 1984; Terborgh *et al.*, 1990; Ricklefs & Schluter, 1993; Condit *et al.*, 1996; Patton *et al.*, 2000) and, more recently, the conservation of biodiversity (e.g. Hubbell & Foster, 1986, 1992; Ehrlich & Wilson, 1991; Lande, 1993; Heywood, 1995; Caughly & Gunn, 1996; Laurence & Bierregaard, 1997; Lande, DeVries & Walla, 2000).

Due to increasing global habitat destruction, modern studies of species diversity are of vital importance for understanding biological communities and their conservation (Purvis & Hector, 2000). Perhaps because of the difficulties associated with the richness and complexity of tropical systems compared to temperate systems, relatively few empirical studies have documented species abundance distributions in space and time from tropical communities – despite their importance as ecological measures (MacArthur, 1955, 1972; Elton, 1958; Williams, 1964; Rosenzweig, 1995). Instead, much recent work concerned with community and conservation biology has concentrated on developing extrapolation techniques to estimate species richness, performing quick assessments of species richness among areas, or modelling community dynamics (Ryti, 1992; Pearson, 1994; Coddington *et al.*, 1991;

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Colwell & Coddington, 1994; Forey, Humphries & Vane-Wright, 1994; Keister *et al.*, 1996; Keating & Quinn, 1998; Kunin, 1998; Ziv, 1998). Nevertheless, if biological communities are to be understood and conserved, the validity of quick assessments, extrapolation techniques and theoretical models ultimately requires testing against long-term studies documenting species diversity through space and time.

The importance and diversity of insects in tropical systems suggests that they hold great promise for illuminating patterns and processes of biological diversification (Wilson, 1992). Insects occupy a central position in studies focusing on tropical biology, community diversity and habitat conservation (e.g. Janzen, 1970; Elton, 1973; Hölldobler & Wilson, 1990; Gaston, 1991; Wolda, 1992; Groombridge, 1992; Edwards, May & Web, 1994; Kato *et al.*, 1995; Longino & Colwell, 1997). The appeal and ease of sampling butterflies has made them a focal group for characterizing tropical insect diversity, community structure, disturbance effects and as tools in conservation biology (e.g. Gilbert, 1984; DeVries, 1987, 1997; Brown, 1991; Brakefield & Reitsma, 1991; Beccaloni & Gaston, 1995; Beccaloni, 1997; Robbins *et al.*, 1996; Brown & Hutchings, 1997; DeVries, Murray & Lande, 1997; DeVries, Walla & Greeney, 1999; DeVries, Lande & Murray, 1999; Willott *et al.*, 1998; Lees, Kremen & Andriamampianina, 1999; Walpole & Sheldon, 1999; Shahabuddin & Terborgh, 2000). However, as is the case with other insect groups, studies concerned with butterfly diversity often do not address the effects of time and space on community diversity directly. Rather, many are limited by short sampling periods, use of non-comparable sampling methods, small sample sizes and contain little information on spatial and temporal distributions within communities. It is, therefore, often difficult or impossible to assess community patterns accurately or compare diversity studies from different areas.

Some of our recent work has used a standardized sampling design to show how species diversity of fruit-feeding nymphalid butterflies in Ecuadorian rainforests varies in spatial and temporal dimensions (DeVries *et al.*, 1997, 1999a). Both of these one-year studies pointed to how space, time, sample size and sampling techniques affect measures of butterfly diversity, and thus the interpretation of community structure. However, to be useful for understanding tropical insect community structure and conservation, the generality of our findings required testing against long-term data sets taken from the same community. Accordingly this study forms a natural progression by extending our sampling design over a 5-year period to explore the effects long-term sampling has on characterizing species diversity within the same butterfly community. Specifically this report analyses major community patterns observed in fruit-feeding nymphalids over the course of five years to elucidate how species diversity varies in space and time within an intact community. After demonstrating the efficacy of this system for probing diversity in space and time, we then discuss the contributions this study makes toward understanding butterfly diversity and conservation in tropical forests. Elsewhere we use the findings here as a foundation to explore models of community spatial autocorrelation (Engen, Walla & DeVries, in prep.), behaviour of diversity measures under different temporal and spatial sampling designs (Walla & DeVries, in prep.), and the seasonal dynamics of population structure (DeVries & Walla, in prep.).

MATERIAL AND METHODS

STUDY SITE

This research was conducted from 5 August 1994 to 9 July 1999 at the La Selva Lodge, Sucumbios Province, eastern Ecuador in the upper Amazon Basin 75 km E.S.E. of Coca (hereafter abbreviated as LSL). The study area consisted of approximately 2 km^2 of undisturbed forest bounded by the Rio Napo, and the oxbow lakes Garza Cocha and Mandi Cocha (0°29′50.3″S; 76°22′28.9″W) near the settlement of Anyañgu (see DeVries, *et al.*, 1999a). The study site is situated within approximately 30 000 hectares of intact floodplain forest that has escaped the severe disturbance of modern logging and human settlement common to this area. Daily rainfall records taken between 1995 and 1999 indicate that, on average, the area receives between 3.5 and 4.0 m of precipitation per year, with a dry season from December to March.

STUDY COMMUNITY

Adult butterflies in the family Nymphalidae that are attracted to, and feed on, the juices of rotting fruit comprise a feeding guild commonly referred to as fruit-feeding nymphalids (see DeVries *et al.*, 1997, 1999a). This feeding guild is generally understood to include the nymphalid subfamilies Charaxinae, Morphinae (Morphinae + Brassolinae of some authors, e.g. DeJong, Vane-Wright & Ackery, 1996), Brassolinae, Amathusiinae, Satyrinae and particular genera of Nymphalinae (Limenitinae of some authors). Fruit-feeding nymphalids are easily sampled in spatial and temporal dimensions using traps baited with rotting fruits (e.g. DeVries, 1988; Brakefield & Reitsma, 1991; Pinheiro & Ortiz, 1992; Daily & Ehrlich, 1995; DeVries *et al.*, 1997, 1999a; Shahabuddin & Terborgh, 2000; Willott *et al.*, 1998), and may comprise between 40 and 55% of the total nymphalid richness in tropical forests (DeVries, 1987, and unpublished).

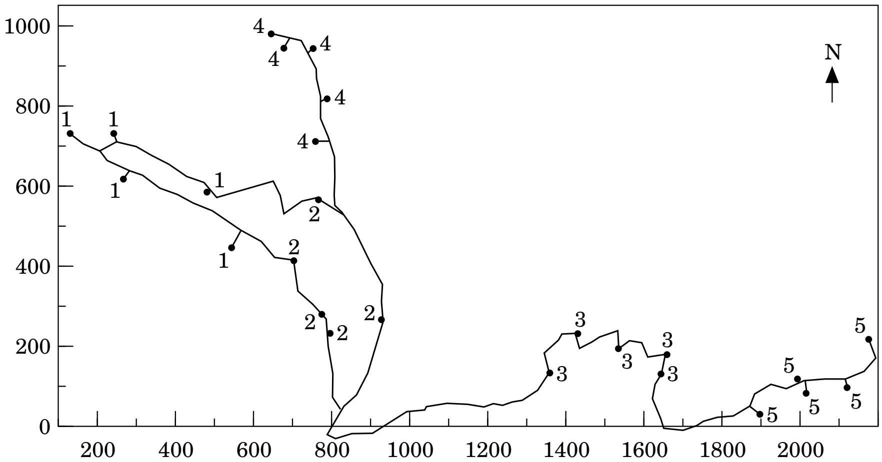

Figure 1. Map of study site. Numbers designate individual replicate trap sites in the sampling areas (1–5). Each replicate site represents one canopy and one understorey trap. Solid lines represent trails. Scale bars are in metres.

FIELD METHODS

We established five sampling plots within intact forest at LSL containing five replicate sampling sites (Fig. 1), and the positions of only two plots differ from the study of DeVries *et al.* (1999a). Each replicate sampling site was fitted with one understorey trap and one canopy trap for a total of ten traps in each plot, five canopy and five understorey (see DeVries, 1987, 1988 for trap design and methods). Excepting rare emergent trees, the forest canopy in our study area ranged between about 18 and 29 m above the ground. In all cases traps were positioned to sample from within the canopy; that is to say, within the crown of the trap tree. Canopy traps were suspended from thin ropes run over branches of an emergent tree, such that all traps could be raised and lowered from the ground. Understorey traps were suspended from low branches such that the bases hung between 1 and 1.5 m above ground and could be serviced directly.

We used the same sampling design established in a previous study at LSL (DeVries *et al.*, 1999a). Traps were baited with bananas obtained locally, mashed, mixed and fermented for 48 h in a large container prior to use each month. Sampling was done for five consecutive days during the first week of each month. Traps were baited on the day prior to the first day of sampling and new bait was added on the third day of sampling. On sampling days all trapped butterflies were either collected for positive identification or, if easily identified, marked with a unique number and released. Released butterflies were recorded in a notebook and subsequent recaptures were excluded from this analysis. All butterflies were identified to species and, as in previous work (DeVries *et al.*, 1997, 1999a), we used Ackery's (1984) widely known, functional classification of nymphalid subfamilies.

STATISTICAL ANALYSES

Species abundance distributions were graphed following Williams (1964) using interval widths of logarithm base 3 with interval edges at $3^N/2$ to avoid overestimating rare species or violating the independence of data points. Log-normal and log-series distributions were assessed for goodness-of-fit to the observed species abundance distribution (Fisher, Corbet & Williams, 1943; Preston, 1948; Williams, 1964; May, 1975), and the position of Preston's veil line (Preston, 1948) provided an estimate of how completely the entire community had been sampled. We believe that a carefully gathered, long-term, empirical sample is likely to give a more realistic estimate of total species richness than many current methods used to extrapolate species richness from short-term samples. Therefore we provide only one estimate of true community species richness using the method of Pielou (1975).

The change in species composition among habitat partitions is commonly referred to as β-diversity, and here we consider β-diversity as the difference in diversity among vertical, horizontal or temporal subdivisions of the total community. While a useful ecological concept, β-diversity is a somewhat impractical quantitative measure because it depends strongly upon the diversity measure employed to measure it (May, 1975; Magurran, 1988). This problem stems from a similar difficulty associated with the general concept of diversity, a topic that has received considerable discussion (Hurlbert, 1971; May, 1975; Wilson & Mohler, 1983; Magurran, 1988) and as yet fails to be satisfactorily quantified by any single statistic or descriptor. The slipperiness of diversity measures is exacerbated by the fact that diversity, almost without exception, is measured by sampling, and this invokes the associated difficulties of accounting for sample size dependencies, sampling error and the heterogeneity of sampling probabilities among species (see May, 1975; Magurran, 1988; Lande, 1996). Given these caveats, one effective analytical method is to choose a suite of measures that emphasize different aspects of a data set in terms of diversity and β-diversity and to assess the quantitative measures of each jointly. This is the approach we follow here.

As done previously (DeVries *et al.*, 1997, 1999a) we measure β-diversity as the component of total diversity among subdivisions of the community in the dimensions of height (canopy and understorey), area (forest 1–5), or time (month or year). In other words, it provides a description of the relative difference in diversity among vertical, horizontal or temporal subdivisions of the total community. Specifically, the total or γ-diversity is estimated by the diversity of the pooled data set for the entire sample; α-diversity is the average diversity within subdivisions (weighted by sample size); and β-diversity equals γ-diversity minus α-diversity (Lande, 1996). Thus, we use an additive partition of diversity such that α-diversity plus β-diversity equals γ-diversity. As noted by Lande (1996), the proportion of total diversity within subdivisions in a given dimension therefore provides a natural measure of similarity among the subdivisions that accounts for sample size differences. Intuitively then, high measures of similarity indicate a large proportion of shared species and consequently low β-diversity.

We evaluated the null hypothesis that the 74 commonest species (≥ 8 individuals) representing all five subfamilies had identical abundance in the canopy and understorey using separate binomial tests for each species.

Significance of β-diversity among community subsets in spatial and temporal dimensions was analysed using chi-squared tests for homogeneity of observed species abundance distributions. A sequential Bonferroni test (Rice, 1989) was then used to assess potential table-wide type I errors at the $\alpha = 0.05$ level.

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

Species accumulation curves represent unique, ordered samples that allow inspection of trends in particular community subsets as sample size increases over time. Here species accumulation curves for vertical and horizontal dimensions were used to assess the effect of sample size on species richness (Colwell & Coddington, 1994). However, direct comparison of species richness among community subsets required correction for differences in sample size. Thus we calibrated species richness in spatial and temporal subsets against the rarefaction curve for the total sample (see Gotelli & Graves, 1996; Hayek & Buzas, 1996), which gave the expected species richness in a random subset of any particular size. The statistical significance of these comparisons was evaluated using 95% confidence limits for the rarefaction curve, calculated as ± 2 standard deviations around expected values (Heck, van Bell & Simberloff, 1975).

We plotted five-year monthly means for species richness, individual abundance and rainfall to estimate the contribution of seasonal patterns to community diversity.

To test the hypothesis that total individual abundance was evenly distributed in space and time we employed a factorial ANOVA with the number of individuals in each trap per month as the dependent variable. Month (12 levels), year (5 levels), and vertical (2 levels) were treated as fixed factors, and forest area (5 levels) was treated as a random factor. This analysis also provides a statistical assessment of interactions between factors affecting total abundance.

RESULTS

We trapped 11 861 individual fruit-feeding nymphalids in 128 species and five subfamilies. Over 30% of the species were represented by less than 5 individuals (Fig. 2). The species abundance distribution (Fig. 2) ranged from 18 species representing single individuals to five species each with over 600 individuals (*Historis acheronta*, *Panacea prola*, *Nessaea hewitsoni*, *Morpho achilles* and *Taygetis* sp-1) comprising 49% of the total abundance. The species abundance distribution was best fitted by the log-normal distribution (Fig. 2), and the position of Preston's veil line indicated the community was well sampled.

Raw summary data for the five-year sample period provided a rough estimation of how species richness and abundance varied in space and time. Twenty-five per cent of the species were found only in canopy, 32% were found in the understorey only, and 42% were found in both strata, but total abundance was nearly equal in the canopy and understorey (Table 1).

When partitioned among yearly intervals species richness varied from 87 to 101 species, and individual abundance varied from 1350 to 3302 total individuals (Table 2). The proportion of singletons (species represented by one individual) differed significantly among years ($\chi^2 = 25.212$, $df = 4$, $P < 0.0001$), and despite ranking fourth in overall abundance, year 3 had the most unique species and substantially more singletons than other years.

Among the 74 most common species in the total sample, all but eight showed significant vertical stratification (Table 3). This study (see below) and our

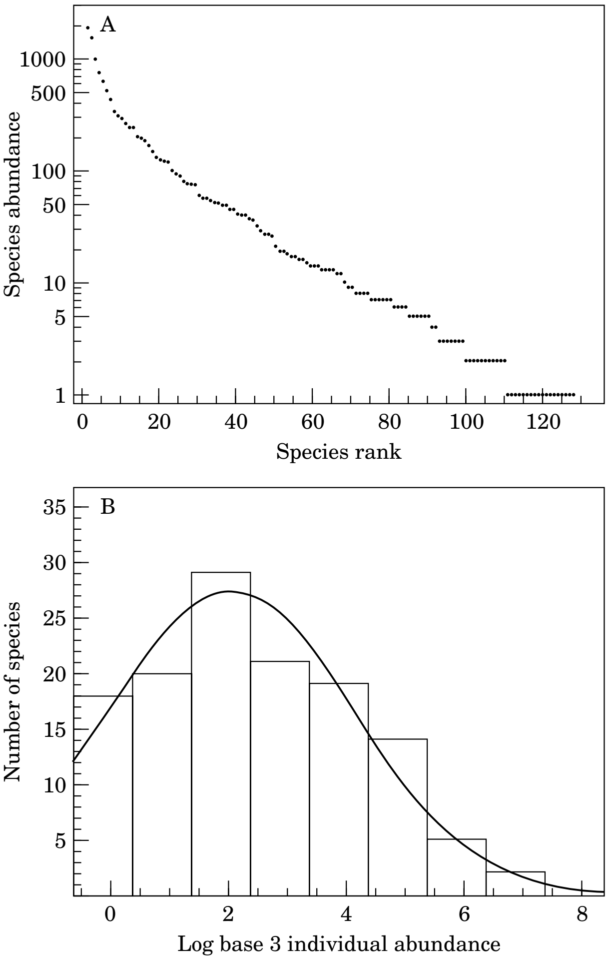

Figure 2. Abundance distributions. (A) Rank-abundance distribution for the total sample. (B) Species abundance distribution for the total sample (histogram). The log-normal distribution (solid line) was fitted using the method of Pielou (1975) with parameters mean 2.028, variance 4.312, and estimated total number of species 142.25. The log-normal distribution ($\chi^2 = 2.6021$, $P = 0.919$) provided a better fit than the log-series distribution ($\chi^2 = 4.319$, $P = 0.742$). The parameters of the log-series distribution (not illustrated) are $\alpha = 20.043$ and $\chi = 0.9983$.

Table 1. Species richness and abundance partitioned by vertical position. Species richness determined by presence or absence at each vertical position

	Canopy	Understory	Both	Total
Species richness	32	41	55	128
Total individuals	5840	6021	—	11 861

Table 2. Species richness and abundance partitioned by year. Singletons are species represented by one individual, and unique species were not captured in any other year

Subset	Abundance	Species richness	Singletons	Unique species
Year 1	1350	87	20	2
Year 2	2885	94	18	2
Year 3	1697	98	30	10
Year 4	3302	101	19	7
Year 5	2627	87	21	0
Total	11 861	128	18	

previous ones found that vertical position was strongly associated with subfamily–most species of Nymphalinae and Charaxinae were trapped in the canopy, and most Brassolinae, Satyrinae, and Morphinae species were trapped in the understorey (Table 3).

Common diversity indices and measures of similarity among community subsets are presented in Table 4. Shannon–Wiener and Simpson measures both indicated greater shared diversity among forest areas and less shared diversity among vertical and temporal subdivisions. In contrast species richness showed the greatest shared diversity among years. All three diversity measures indicated months had the least shared diversity.

Chi-square tests for homogeneity of species abundance distributions demonstrated significant β-diversity in all temporal and spatial dimensions (Table 5). The relative frequency of species among subsets differed significantly in all subfamilies except Charaxinae and Morphinae. Although Charaxinae showed significant β-diversity in the vertical dimension, compared to the total community neither Charaxinae nor Morphinae indicated strong differences in the relative abundance of species in time or among forest areas (Table 5).

Species accumulation curves showed that the canopy accumulated species faster than the understorey in the first year, but subsequently more species were captured in the understorey (Fig. 3). Individual abundance and species richness in the five forest areas were similar, but the intersecting curves showed that the rate of species accumulation in each area depended upon the sample year (Fig. 3). However, the differences among these curves could not be evaluated statistically.

Rarefaction of the total sample provided a standard for comparing various subsets of our data. Both canopy and understorey samples were significantly less species-rich than the total community, and their positions below the total rarefaction curve indicated strong heterogeneity in the vertical dimension (Fig. 4). Despite the significant differences shown by chi-square tests (Table 5), none of the five areas (each pooled across vertical strata) differed in species richness from the total rarefaction curve (Fig. 4). Finally, rarefaction showed that species richness in years 1, 2, and 4 did

Table 3. Vertical distribution of individuals for 74 abundant species ($N \geq 8$). Abundance of individual species pooled across areas and months tested against a null hypothesis of equal abundance between canopy and understorey. Significance levels are: *** = $P<0.001$, ** = $P<0.01$, ns = not significant. Abbreviations: (SF) = subfamily, (U) understorey, (C) = canopy. Application of sequential Bonferroni tests (Rice, 1989) did not affect significance levels

	Abundance				
Taxon	SF	C	U	Total	*P*
Agrias sardanapalis (Bates, 1860)	C	10	0	10	***
Archaeoprepona amphimachus (Fabricius, 1775)	C	5	44	49	***
Archaeoprepona demophon (Linnaeus, 1758)	C	63	63	126	ns
Archaeoprepona demophoon (Hübner, 1814)	C	14	0	14	***
Archaeoprepona licomedes (Cramer, 1777)	C	1	39	40	***
Memphis arachne (Cramer, 1776)	C	36	1	37	***
Memphis florita (Druce, 1877)	C	136	33	169	***
Memphis polycarmes (Fabricius, 1775)	C	15	1	16	***
Prepona laertes (Hübner, 1814)	C	74	2	76	***
Prepona pylene Hewitson, 1854	C	8	0	8	**
Zaretis itys (Cramer, 1777)	C	50	4	54	***
Baeotus amazonicus (Riley, 1919)	N	9	0	9	***
Baeotus deucalion (Felder & Felder, 1860)	N	40	1	41	***
Batesia hypochlora (Felder & Felder, 1862)	N	36	113	149	***
Callicore cyllene (Doubleday, 1847)	N	81	0	81	***
Callicore hesperis (Guerin, 1844)	N	44	1	45	***
Callicore hystaspes (Fabricius, 1782)	N	201	1	202	***
Catonephele acontius (Linnaeus, 1758)	N	176	67	243	***
Catonephele numilia (Cramer, 1776)	N	25	1	26	***
Colobura dirce (Linnaeus, 1758)	N	273	250	523	ns
Diaethria clymena (Cramer, 1776)	N	29	0	29	***
Hamadryas amphinome (Linnaeus, 1767)	N	72	3	75	***
Hamadryas arinome (Lucas, 1853)	N	108	14	122	***
Hamadryas chloe (Stoll, 1791)	N	2	12	14	**
Hamadryas feronia (Linnaeus, 1758)	N	15	0	15	***
Hamadryas laodamia (Cramer, 1777)	N	60	0	60	***
Historis acheronta (Fabricius, 1775)	N	1882	26	1908	***
Historis odius (Fabricius, 1775)	N	299	11	310	***
Mycelia capenas (Hewitson, 1857)	N	31	5	36	***
Nessaea hewitsoni (Felder & Felder, 1859)	N	19	984	1003	***
Panacea divalis (Bates, 1868)	N	244	21	265	***
Panacea prola (Doubleday, 1848)	N	1028	535	1563	***
Panacea regina (Bates, 1864)	N	182	14	196	***
Paulogramma pyracmon (Godart, 1823)	N	32	0	32	***
Smyrna blomfildia (Fabricius, 1782)	N	100	1	101	***
Temenis laothe (Cramer, 1777)	N	49	3	52	***
Tigridia acesta (Linnaeus, 1758)	N	29	65	94	***
Caligo eurilochus (Cramer, 1776)	B	2	184	186	***
Caligo idomenius (Linnaeus, 1758)	B	2	242	244	***
Caligo placidianus (Staudinger, 1887)	B	0	57	57	***
Caligo teucer (Linnaeus, 1758)	B	0	17	17	***
Catoblepia berecynthia (Cramer, 1777)	B	3	336	339	***
Catoblepia soranus (Westwood, 1851)	B	0	27	27	***
Catoblepia xanthus (Linnaeus, 1758)	B	4	289	293	***
Opsiphanes cassina (Felder, 1862)	B	72	18	90	***
Opsiphanes invirae (Hübner, 1808)	B	40	5	45	***
Opsiphanes quiteria (Cramer, 1782)	B	8	49	57	***

continued

Table 3 – *continued*

	Abundance				
Taxon	SF	C	U	Total	*P*
Antirrhea avernus (Hopffer, 1874)	M	0	8	8	**
Morpho achilles (Linnaeus, 1758)	M	5	751	756	***
Morpho menelaus (Linnaeus, 1758)	M	1	131	132	***
Bia actorion (Linnaeus, 1763)	S	8	426	434	***
Chloreuptychia arnaea (Fabricius, 1776)	S	0	19	19	***
Chloreuptychia herseis (Godart, 1824)	S	0	27	27	***
Chloreuptychia hewitsonii (Butler, 1867)	S	0	17	17	***
Chloreuptychia tolumnia (Cramer, 1777)	S	1	7	8	**
Cissia erigone (Butler, 1867)	S	0	19	19	***
Cissia myncea (Cramer, 1782)	S	5	8	13	ns
Cissia proba (Weymer, 1911)	S	0	12	12	***
Cissia terrestris (Butler, 1867)	S	3	6	9	ns
Cithaerias aurorina (Wymer, 1910)	S	0	21	21	***
Haetera piera (Linnaeus, 1758)	S	0	77	77	***
Mageuptychia analis (Godman, 1905)	S	6	7	13	ns
Mageuptychia antonoe (Cramer, 1776)	S	117	3	120	***
Mageuptychia nr. helle-1	S	9	7	16	ns
Pareuptychia binocula (Butler, 1867)	S	1	17	18	***
Pareuptychia ocirrhoe (Fabricius, 1776)	S	1	11	12	***
Pierella astyoche (Erichson, 1848)	S	0	13	13	***
Pierella lena (Linnaeus, 1767)	S	0	14	14	***
Taygetis mermeria (Cramer, 1776)	S	0	40	40	***
Taygetis sp-1	S	8	621	629	***
Taygetis sp-2	S	0	49	49	***
Taygetis sp-3	S	0	51	51	***
Taygetis valentina (Cramer, 1780)	S	0	8	8	***
Taygetis virgilia (Cramer, 1776)	S	0	13	13	**
Total		5774	5922	11 696	

not differ statistically, but year 3 had significantly more species than expected, and year 5 had significantly fewer species than expected (Fig. 4).

Table 4. Measures of community diversity and similarity for the total community of fruit-feeding nymphalid butterflies at La Selva Lodge

		Community similarity* among			
Measure	Total	Vertical	Area	Month	Year
Species richness	128	0.72	0.72	0.34	0.76
Shannon–Wiener	3.36	0.86	0.98	0.86	0.97
Simpson	0.93	0.95	0.99	0.94	0.99

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

Species richness and individual abundance varied among years and months (Fig. 5). On average we sampled 37 species (range: 6–59) and 198 individuals (range: 6–504) each month. Canopy samples averaged 20 species (range 4–39) and 97 individuals (range: 4–289) per month, and understorey samples averaged 23 species (range: 2–42) and 100 individuals (range: 2–242) per month. Both richness and abundance were consistently low from November to January (the dry season), and higher in other months (Fig. 5). Although variation in total species richness was relatively small among years (mean 93.4, range 87–101), variation in total abundance among years was considerable (mean 2372, range 1350–3302). Finally, we found that during the seasonal transition from dry season to rainy season (February to May) the vertical subdivisions underwent a marked inversion. Unlike most months, the canopy samples showed greater species richness and abundance relative to understorey samples throughout this period (Fig. 5).

Table 5. Chi-square tests for homogeneity of species abundance distributions among community subsets: A, vertical, B, horizontal, and C, temporal dimension including individual year (Y) and all months combined. Significance levels are: ns = not significant, * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$. Application of the sequential Bonferroni test (Rice, 1989) did not affect the significance of our results. Note: as canopy sample size for Morphinae was zero in most years no test was performed for heights

	Y1	Y2	Y3	Y4	Y5	Total	Months	Annual
A. VERTICAL								
Total community	***	***	***	***	***	***		
Subfamily								
Brassolinae	***	***	***	***	***	***		
Charaxinae	***	***	**	***	***	***		
Morphinae	—	—	—	—	—	—		
Nymphalinae	***	***	***	***	***	***		
Satyrinae	***	***	***	***	***	***		
B. FOREST AREAS								
Total community	***	***	***	***	***	***		
Subfamily								
Brassolinae	ns	ns	*	*	*	***		
Charaxinae	ns	ns	ns	ns	ns	*		
Morphinae	ns	ns	ns	ns	ns	ns		
Nymphalinae	***	***	***	***	***	***		
Satyrinae	***	***	*	***	**	***		
C. TEMPORAL								
Total community	***	***	***	***	***		***	***
Subfamily								
Brassolinae	***	***	***	*	ns		***	***
Charaxinae	ns	ns	ns	ns	***		***	ns
Morphinae	***	ns	ns	ns	ns		***	*
Nymphalinae	***	***	***	***	***		***	***
Satyrinae	ns	***	ns	***	**		***	***

[a] As canopy sample size for Morphinae was zero in most years no test was performed for heights.

Community abundance varied significantly through time. Temporal factors accounted for more variance in total abundance among community subsets than did spatial factors (Table 6). The main effects of month and year were both highly significant, but the main effects of area and vertical position were not. All significant interaction terms contained at least one temporal factor, including the interaction effect of month and vertical position, something not assessed by other analyses. In this instance understorey samples generally had greater monthly abundance than canopy, but during the early rainy season (March to May) canopy abundance was consistently greater than understorey abundance (Fig. 5). These results not only emphasize temporal variation as a critical measure of insect diversity, but also suggest that temporal community patterns may not be spatially uniform in the vertical dimension.

DISCUSSION

Any empirical study of tropical forest insect diversity must confront the typically high species richness and low individual abundance of the focal community and the spatial complexity inherent to these systems. The burgeoning number of studies devoted to estimating tropical species richness attest to the widespread recognition of habitat loss, species extinction, and the emergent discipline of conservation biology (see Groombridge, 1992; Heywood, 1995; Laurence & Bierregaard, 1997; Pimm & Raven, 2000; Purvis & Hector, 2000). Although rapid surveys and extrapolation methods help provide a general framework for assessing biodiversity, understanding the dynamics of species diversity in communities requires long-term data sets that partition diversity into its natural components of space and time. By extending standardized sampling beyond our previous work (DeVries *et al.*, 1997, 1999a), here we firmly establish the significance of multiple spatial and temporal factors affecting a diverse tropical butterfly community. Taking its strength from long-term, exceptionally rich samples of a closely related guild of butterflies, the present study represents one of the most detailed descriptions of tropical insect community structure in multiple ecological dimensions. Therefore, we believe this study

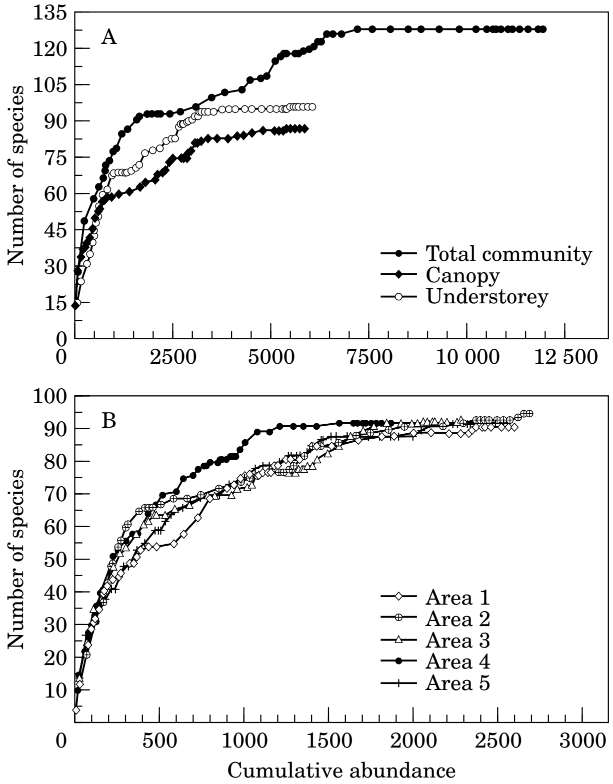

Figure 3. Species accumulation curves showing total species versus cumulative individual abundance in order of collection. On all graphs each point represents a single month (A) Canopy, understorey and total community. (B) Five forest areas.

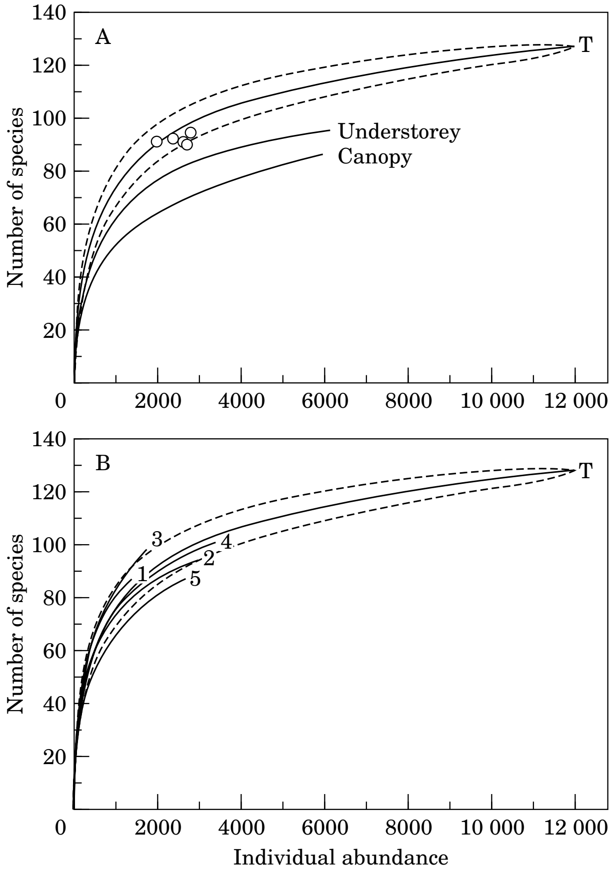

Figure 4. Rarefaction curves for the total community compared to observed species richness in community subdivisions. Dashed lines are 95% confidence intervals for the total community. (A) Species richness among five forest areas (○) and vertical dimensions. (B) Species richness among the five sampled years (1–5).

offers a standard means for comparing species diversity among sites, and exploring general spatial and temporal patterns in tropical forest communities.

As discussed elsewhere, our methods estimate species abundance of where adult butterflies were trapped, not the distribution of host plants, courtship sites, or other life history components (DeVries *et al.*, 1997). Sampling bias might arise from variance among trap positions, and variance among species in attraction to bait (Muirhead-Thomson, 1991), but pooling replicate traps within plots (as done here) can reduce individual trap variance. However, species attraction to bait can only be addressed by intensive mark-recapture studies (Seber, 1982) and/or detailed observations on diet preference. Although susceptibility for all species of fruit-feeding nymphalids to traps has not been established, our standardized methods allowed us to compare the relative abundance among species, thus avoiding the sampling biases in all hand net or sight record techniques that pool the efforts of multiple persons.

Abundance distributions showed that our fruit-feeding nymphalid community was vertically structured. Sixty months of sampling established that a significant number of species were members of either canopy or understorey faunas (Tables 3, 5, Figs 3, 4), thereby confirming that canopy or understorey samples alone are poor estimators of total community richness (DeVries *et al.*, 1997, 1999a). As vertical distribution is well documented in many insect groups (e.g. Allee, 1926; Bates, 1944; Basset, Aberlene & Delvare, 1992; Kato *et al.*, 1995; Intachat & Holloway, 2000), we conclude that even long-term studies of tropical forest insects that sample only from the canopy or understorey cannot estimate species diversity accurately, even those using particular focal taxa or feeding guilds. Consequently we urge future studies to address the vertical component of species diversity in tropical forest insects, and thereby assess an essential concept in community ecology (i.e. MacArthur, 1958, 1972).

As in previous investigations (DeVries, 1988; DeVries *et al.*, 1997, 1999a; Willott *et al.*, 1998; Shahabuddin & Terborgh, 2000), we found significant vertical

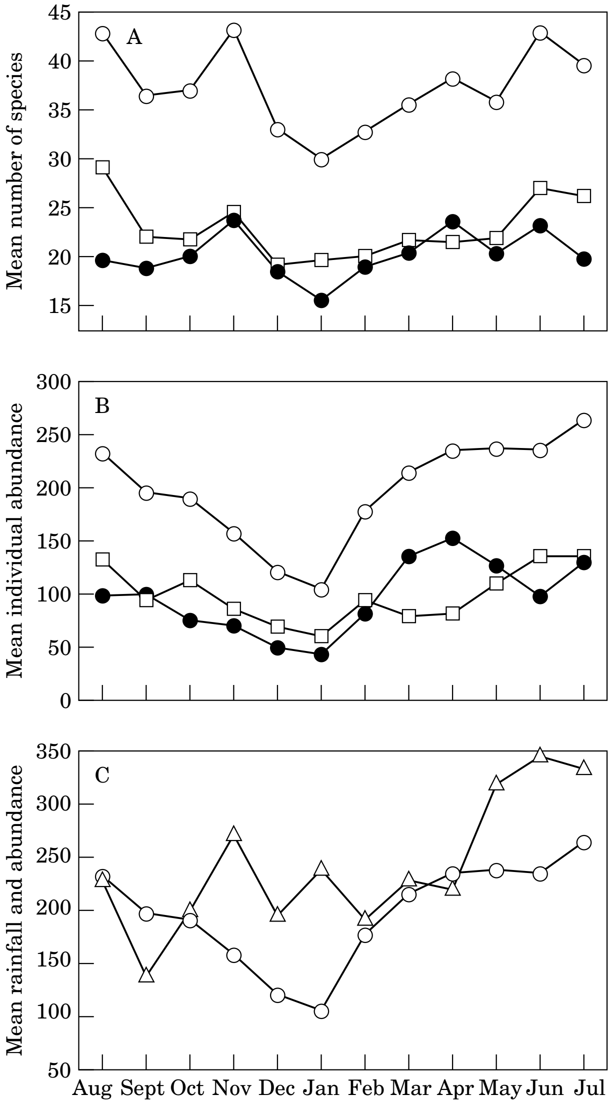

Figure 5. Temporal variation in the total community of fruit-feeding nymphalids. Each monthly point represents a five-year mean. (A) Species richness. (B) Individual abundance. (C) Individual abundance and mm rainfall. (●) canopy; (□) understorey; (■) total; (△) rainfall; (○) abundance.

Table 6. Factorial ANOVA tests for homogeneity of total individual abundance in space and time. Monthly number of individuals per trap was used as the dependent variable, and forest areas were treated as random factors

Source	MS	DF	F	*P*
Area	175.54	4	2.70	ns
Vertical	10.92	1	0.38	ns
Month	239.42	11	12.70	***
Year	1122.17	4	20.86	***
Year • Vertical	50.99	4	2.38	ns
Year • Area	53.80	16	1.99	ns
Month • Area	18.85	44	1.28	ns
Month • Vertical	119.69	11	13.01	***
Month • Year	276.4	44	17.02	***
Vertical • Area	28.53	4	1.43	ns
Year • Vertical • Area	21.44	16	2.01	*
Month • Year • Vertical	49.06	44	4.59	***
Month • Year • Area	16.24	176	1.5	**
Month • Vertical • Area	9.20	44	0.86	ns
Month • Year • Vertical • Area	10.69	176	0.96	ns

stratification in fruit-feeding nymphalids by subfamily (Table 3). In concert these studies indicate that members of Charaxinae and Nymphalinae occur mostly in the canopy, and members of Brassolinae, Satyrinae and Morphinae occur mostly in the understorey. This suggests phylogeny may prove important for understanding vertical stratification in butterflies specifically, and the structure of tropical forest insect communities in general.

When pooled across the vertical dimension species richness among forest areas did not differ from the total rarefaction curve (Fig. 4, Table 4). This suggested that, after accounting for sample size, the areas represented random subsamples of the total community, and differences among them could largely be explained by sampling error (Fig. 4). However, significant differences were noted among the five areas (Table 5), and we know that some species were concentrated in particular areas. For example, at LSL 75% of all of *Myscelia capenas* individuals were found in one area, and 93% of all *Hamadryas amphinome* individuals were found in three areas (Table 7). In these examples, *M. capenas* represents a rare species with a geographical range restricted to the upper Amazon basin (Jenkins, 1984), whereas *H. amphinome* is widespread and common throughout the Neotropics (Jenkins, 1983). More broadly, we also know that many other butterfly species show locally restricted abundance patterns within our study site (DeVries & Walla, unpublished.).

A potential consequence of overlooking intrinsic distribution patterns on small scales may be the extinction of species in preserved areas because they are insufficient to foster viable population densities (Pimm & Raven, 2000). Even within noticeably large tracts of rainforest, fruit-feeding butterflies may have population structures restricted to a small scale. At LSL *Hamadryas*, *Panacea*, and *Batesia* species (among others) tend to be concentrated in small spatial areas where their larval host plants are found (DeVries & Walla, per. obs.), an ecological pattern also noted by Shahabuddin & Terborgh (2000). Therefore elucidating population structure of many species from within communities occurring in large, intact habitats may be

Table 7. Exemplar species unevenly distributed among horizontal areas. Sums represent total number of individuals sampled in each area over the entire study

Species	Area 1	Area 2	Area 3	Area 4	Area 5	Total
Mycelia capenas	27	4	2	0	3	36
Hamadryas amphinome	2	18	22	3	30	75
Catoblepia xanthus	60	40	100	19	74	293
Colobura dirce	130	56	105	68	164	523
Panacea prola	433	523	132	181	294	1563

required for understanding habitat fragmentation effects on the demographic and genetic structure of tropical butterfly populations.

One task of community ecology is to detect patterns of diversity in natural systems and describe their variation in space and time. A natural question might be, how much sampling effort was required to understand the LSL community? The answer depends on what aspects of the community are of interest. Species accumulation curves showed notable differences among forest areas during the first two years, but any differences disappeared by the fourth year of sampling (Fig. 3). Species accumulation curves also appeared to be saturated after two years, yet 17 more species were added in the third year. Thus, if the goal were to estimate true species richness, our samples indicate that few new species accrued after the third year, a sample size of about 7500 individuals (Figs 3, 4). However, since the degree to which populations are observed to fluctuate may increase with the length of study (Pimm & Redfearn, 1988; Cyr, 1997), it is likely that many more years of sampling would be required to understand the magnitude of temporal variability in population densities or community stability (Tables 5, 6).

Species richness and abundance were lowest during the drier months, and highest during the wetter months (Fig. 5), consonant with the idea that a seasonal correlation with rainfall is typical of tropical insect communities (Wolda, 1978, 1992; Kato *et al.*, 1995; Novotny & Basset, 1998). Other measures, however, illuminated the temporal dynamics of tropical forest insect diversity more dramatically.

At LSL, monthly variation in species abundances showed that intermittent or short-term sampling would have underestimated diversity, including, for example, monthly sampling for two years (Figs 3, 5; Tables 5, 6). Moreover, variation in total species richness and abundance among years and across areas highlighted that significant changes in community diversity depended on sampling year (Tables 2, 5, 6; Fig. 4). Even with a smaller sample size, year 3 had significantly more species than year 5, in part due to the large number of singletons and unique species captured during year 3 (Fig. 4, Table 2). This exposes the dynamic nature of tropical butterfly communities by showing that in particular areas some species could be common one year, but rare or impossible to locate in others.

We exposed a seasonal inversion in canopy and understorey faunas that has not been reported previously. Canopy abundance and richness increased during the onset of the rainy season while understorey abundance decreased simultaneously (Fig. 5). Several factors may help to explain this seasonal inversion and its contribution to variation in spatial and temporal diversity (Table 6). First, various butterflies typically undergo seasonal, multi-species migrations at this time of year (DeVries 1987; Oliveira *et al.*, 1998), and some (e.g. *Historis acheronta, Smyrna blomfildia*) contributed to the increase in canopy abundance. Second, the small windows of sunshine between showers that are typical of this period may have been sufficient to trigger butterfly activity in the canopy, but not in the shaded understorey. Third, availability of natural fruit sources may have caused differential attraction of canopy and understorey butterflies to our banana-baited traps. Of these potential factors the first two are consistent with our natural history observations. Whatever the ultimate causes may be, establishing a seasonal inversion at LSL sets a precedent for testing its occurrence in other forest types and among other insect groups.

Some of the most comprehensive empirical studies of tropical communities derive from monitoring tree diversity (e.g. Hubbell & Foster, 1986; Condit *et al.*, 1996; Terborgh *et al.*, 1990; Hubbell *et al.*, 1999). However, as long generation times of trees often make it difficult to interpret the dynamics of species-rich forest communities, there is continued interest in developing theoretical models, or using experimental laboratory microcosms to understand the dynamics of community diversity (e.g. Ziv, 1998; McGrady-Steed & Morin, 2000). In this context, the present study is important because it captured at least five, and very likely ten or more generations for at least 50% of the species in the community. Therefore, this study may serve as a calibration point against which the community structure and seasonal dynamics of other tropical forest butterfly and/or insect communities can be compared.

It appears that accounting for seasonal trends is vital for accurately comparing diversity among sites and conservation planning. Seasonal variation alone was sufficient to account for significant differences in LSL community composition, even when the underlying communities were the same (Tables 5, 6; Fig. 5), indicating that temporal interactions fundamentally affected diversity in both horizontal and vertical dimensions. Essentially this shows that comparisons of diversity among sites require sampling designs that can detect temporal effects on spatial dimensions within and among years. These observations also have an impact on interpreting studies that compare samples taken at different times of the year from the same site, or among different sites.

Long-term studies with intensive sampling such as this one help reveal the nature of tropical communities and emphasize the challenges of measuring their species diversity. Here we confirmed that both temporal and spatial parameters determine the population dynamics of fruit-feeding nymphalids in a diverse community. In particular vertical stratification was fundamental to community structure, and species richness and abundance of canopy and understorey faunas varied in time. After five years of sampling the species richness among our five forest areas did not differ, but the abundance of particular species remained concentrated in only one or a few areas. Although there was significant variation in the magnitude of richness and abundance among years, the inversion of canopy and understorey faunas at the onset of the rainy season pointed to an underlying pattern of seasonal population fluctuations. Therefore, this study is relevant to general ecology and its practical application in conservation because the major spatial and temporal patterns illustrated here may serve as a baseline for comparing species diversity and community structure among other tropical forests and focal organisms. Given the stark reality of global habitat destruction we believe that conducting other such long-term empirical studies at many sites can provide a better understanding of tropical communities and how best to conserve them.

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