Species diversity in spatial and temporal dimensions of fruit-feeding butterflies from two Ecuadorian rainforests

PHILIP J. DeVRIES* AND THOMAS R. WALLA

Department of Biology, University of Oregon, Eugene, Oregon 97403-1210, U.S.A.

HAROLD F. GREENEY

Department of Entomology, University of Arizona, Tucson, Arizona 85721, U.S.A.

To test the hypotheses that butterflies in an intact lowland rainforest are randomly distributed in space and time, a guild of nymphalid butterflies was sampled at monthly intervals for one year by trapping 883 individuals of 91 species in the canopy and understory of four contiguous, intact forest plots and one naturally occurring lake edge. The overall species abundance distribution was well described by a log-normal 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-β-diversity/γ-diversity), significant β-diversity existed in each dimension. Individual abundance and observed species richness were lower in the canopy than in the understory, but rarefaction analysis suggested that the underlying species richness was similar in both canopy and understory. Observed species richness varied among four contiguous forest plots, and was lowest in the lake edge plot. Rarefaction and species accumulation curves showed that one forest plot and the lake edge had significantly lower species richness than other forest plots. Within any given month, only a small fraction of total sample species richness was represented by a single plot and height (canopy or understory). Comparison of this study to a similar one done in disturbed forest showed that butterfly diversity at a naturally occurring lake edge differed strongly from a pasture-forest edge. Further comparison showed that species abundance distributions from intact and disturbed forest areas had variances that differed significantly, suggesting that in addition to extrapolation, rarefaction and species accumulation techniques, the shapes of species abundance distributions are fundamental to assessing diversity among sites. This study shows the necessity for long-term sampling of diverse communities in space and time to assess tropical insect diversity among different areas, and the need of such studies is discussed in relation to tropical ecology and quick surveys in conservation biology.

© 1999 The Linnean Society of London

ADDITIONAL KEY WORDS:—Nymphalidae – species abundance distributions – species diversity – rarefaction – vertical stratification – habitat disturbance – edges – conservation.

* Corresponding author. Email: pdevries@darkwing.uoregon.edu. Address from April 2000: Center for Tropical Diversity, Milwaukee Public Museum, 800 Wells Street, Milwaukee, WI 53233, U.S.A.

CONTENTS

INTRODUCTION

Once upon a time lowland tropical forests were extensive wilderness areas teeming with unknown life forms and buffered from the ravages of human civilization. In the span of two generations, however, human commercial activities have largely reduced these forests to degraded habitat remnants. Since tropical forests are being destroyed faster than ever (Bowles *et al.*, 1998), and the organisms within them remain largely unknown, modern studies of species diversity are crucial for understanding remaining tropical communities and their conservation (Heywood, 1995; Gaston, 1996; Wilson & Sandoval, 1996). Although documenting variation in species abundance distributions of organisms through space and time can help identify general ecological properties of tropical diversity, relatively few studies have done so (e.g. Wolda, 1978, 1992; Hubbell & Foster, 1986; Morse, Stork & Lawton, 1988; Terborgh *et al.*, 1990; Gill, 1991; Kato *et al.*, 1995; Condit *et al.*, 1996; DeVries, Murray & Lande, 1997; Novotny & Basset, 1998). Rather, the urgency of habitat destruction has forced most biologists to perform rapid inventories (e.g. Roberts, 1991; Anon, 1993), or develop extrapolation techniques to estimate species richness in a variety of habitat types (Noss, 1990; Ryti, 1992; Colwell & Coddington, 1994; Hammond, 1994; Pearson, 1994; Keister *et al.*, 1996; Longino & Colwell, 1997). For example, although recent books are devoted to measurement of diversity and its application to community ecology and conservation biology (Magurran, 1988; Groombridge, 1992; Ricklefs & Schluter, 1993; Edwards, May & Web, 1994; Forey, Humphries & Vane-Wright, 1994; Huston, 1994; Heywood, 1995; Gaston, 1996; Hayek & Buzas, 1996), much focus in conservation biology is on inventories rather than detailed studies of factors contributing to biological diversity. Regardless of their widespread use, the validity of quick assessments or strict inventories must ultimately be tested against long-term studies documenting variation of many species through space and time.

Many plant and animal species in tropical forests exhibit stratified distributions between canopy and understory (Allee, 1926; Bates, 1944; Richards, 1952; Pearson, 1977; Sutton & Hudson, 1980; DeVries, 1988; Stork, 1988; Longino & Nadkarni, 1990; Gill, 1991; Wolda, 1992; Malcolm, 1994; Erwin, 1995; Mallet & Gilbert, 1995; DeVries *et al.*, 1997), and such vertical stratification is of obvious importance to estimating diversity. Although vertical stratification is a significant component of diversity, it is seldom addressed or measured directly. Given the recent surge of interest in documenting canopy biotas (reviewed in Lowman & Nadkarni, 1995),

surprisingly few investigations have measured species diversity simultaneously in both canopy and understory environments through time (e.g. DeVries, 1988; Basset, Aberlenc & Delvare, 1992; Wolda, 1992; Malcolm, 1994; Kato *et al.*, 1995; DeVries *et al.*, 1997).

As the majority of all described species on earth are insects (Groombridge, 1992) this group has great promise for illuminating patterns and processes of biological diversity. Due to their relatively large size, colourful appearance and ease of sampling, butterflies have broad appeal as models for understanding tropical insect diversity and conservation biology (see Gilbert, 1984; DeVries, 1987, 1997; Brown, 1991; Kremen, 1992, 1994; Beccaloni & Gaston, 1995; Daily & Ehrlich, 1995; Robbins *et al.*, 1996; Brown & Hutchings, 1997; DeVries *et al.*, 1997 and references therein). Although spatial and temporal factors are important components of ecological diversity (e.g. MacArthur, 1972; Cody & Diamond, 1975; Ricklefs & Schluter, 1993; Rosenzweig, 1995), their effects on diversity in tropical butterfly communities have seldom been addressed directly. As a result many studies concerned with butterflies and other insects are frequently limited by short sampling periods, use of non-comparable sampling methods, presence-absence data only, small sample sizes, and lack of data on spatial and temporal distributions within communities (e.g. Basset *et al.*, 1992; Daily & Ehrlich, 1995; Robbins *et al.*, 1996). It is therefore often difficult or impossible to compare diversity studies from different areas.

A recent Ecuadorian field study measured the diversity of fruit-feeding nymphalids in spatial and temporal dimensions, and provided an assessment of habitat disturbance on these butterflies (DeVries *et al.*, 1997). Recognizing that, like most studies of tropical diversity, their investigation was conducted in a forest with considerable human disturbance, DeVries *et al.* (1997) concluded that the generality of their findings required testing them against data sets gathered from forests with less disturbance.

Accordingly this study was designed to characterize the diversity of an Ecuadorian fruit-feeding nymphalid community from an intact forest and compare it to the community studied by DeVries *et al.* (1997). To achieve our goals we first test the hypothesis that fruit-feeding nymphalid butterflies are randomly distributed in space and time among areas within continuous forest. After describing the species abundance distribution of our total sample, we partition the measures of diversity among subsets of the community in multiple dimensions, and analyse these partitions statistically. Secondly, we compare our samples to those of DeVries *et al.* (1997) and ask how the butterfly diversity of an intact forest compares to that from a similar forest that has experienced greater disturbance. By gathering and analysing standardized samples in different dimensions this study provides a unique comparison that accents differences between two tropical butterfly communities, and points to patterns that warrant comparative investigations from other areas.

MATERIAL AND METHODS

Study site

This research was conducted from 6 August 1993 to 19 July 1994 at the La Selva Lodge (hereafter abbreviated LSL), Sucumbios Province, eastern Ecuador in the
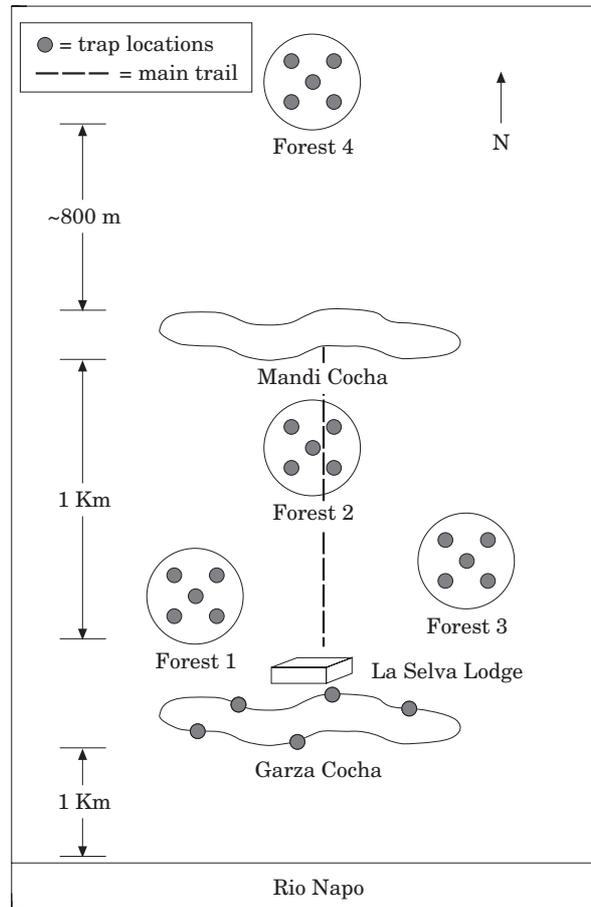
Figure 1. Schematic map of the La Selva Lodge study area showing approximate locations of the five plots (Lake Edge, Forest 1 through 4) and five replicate sampling sites nested within each plot.

upper Amazon Basin 75 km E.S.E. of Coca in an area 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. Sampling sites were located within an approximately 1000 hectare section of forest around and between two oxbow lakes (Garza Cocha and Mandi Cocha) with a further sample site situated about 800 m north of Mandi Cocha. Rainfall data from 1995–1997 indicates that this area receives between 3.5 and 4.0 m of precipitation per year, with a dry season from January to March. The forest surrounding the LSL study site includes at least 30 000 hectares of floodplain forest that harbors an intact vertebrate fauna and flora, including some of the most species rich forest known from Ecuador. All available evidence suggests that the LSL study site represents continuous old growth forest that has escaped severe disturbance of modern human civilization; although it is noteworthy that much of the surrounding area is currently under threat of destruction by the petroleum industry (Olson *et al.*, 1996). Here we provide a schematic map of the LSL area and trapping design in Figure 1 that is pertinent to this study. A detailed map and analysis of the LSL trap study will appear elsewhere (DeVries & Walla, in prep.).

Study community

Neotropical butterfly communities divide quite readily into two general adult trophic guilds (see DeVries, 1987, 1988; DeVries *et al.*, 1997): (1) flower feeders—those species obtaining most nutritional requirements from flower nectar (most Papilionidae, Pieridae, Lycaenidae, Riodinidae, and some Nymphalidae), and (2) fruit-feeding nymphalids—whose adults gain their nutritional requirements by feeding on juices of rotting fruits or plant sap. The fruit-feeding guild is generally understood to include the nymphalid subfamilies Charaxinae, Morphinae (Morphinae + Brassolinae of some authors, e.g. De Jong *et al.*, 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; DeVries *et al.*, 1997), and may comprise between 40–55% of the total nymphalid richness in tropical forests (DeVries, 1987, and unpublished). For completeness we note that at some neotropical sites a small proportion of species in the subfamily Ithomiinae are found occasionally in fruit-traps (DeVries, Lande & Murray, in press). Ithomiines, however, typically feed on flower nectar, and are not strictly part of the fruit-feeding guild as defined here. The few individual ithomiines trapped during this study were excluded from our analyses.

Field methods

At LSL we established five sampling plots within intact, contiguous forest, each containing five replicate sampling sites (Fig. 1). The five plots include: (1) Lake Edge: along the oxbow lake, Garza Cocha, where traps were located at the interface of forest edge and open water. This plot represented a naturally occurring forest edge distinct from the other four plots that were all located within closed canopy forest; (2) Forest 1: located approximately 400 m WNW off the main trail between the two lakes; (3) Forest 2: located along the northernmost 500 m of the central trail to within 50 m S of Mandi Cocha; (4) Forest 3: located approximately 1 km due east of the central trail and ranging from 500–700 m north of Garza Cocha; and (5) Forest 4: located approximately 800 m north of Mandi Cocha.

In all plots each replicate sampling site was fitted with one understory trap and one canopy trap for a total of ten traps in each area—five canopy, and five understory (see DeVries, 1987; DeVries *et al.*, 1997 for trap design and methods). Excluding rare emergent trees, the average height of the forest canopy at La Selva ranged between 18 and 29 m above the ground. In all cases our traps were positioned to sample from within the canopy; that is, 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. Understory traps were suspended from low branches such that the bases hung between 1 and 1.5 m above ground and could be serviced directly. In the case of the Lake Edge plot all traps (canopy and understory) were serviced from a dugout canoe.

Baited traps were maintained continuously for a 5-day sampling period within the first week of every month. As in a similar study (DeVries *et al.*, 1997) traps were baited with locally-obtained bananas which were mashed, mixed well, and fermented

for 48 h in one large container prior to use, and on the day prior to the sampling interval, bait was placed in a small plastic cup fixed inside each trap, and a small amount of new bait from the common reservoir was added to each trap on the third sampling day. During trap months all 50 baited traps were sampled daily for 5 days. On the last day of the sampling period baits were removed from all traps, and traps remained unbaited for 3 weeks. New bait was made prior to the subsequent sampling interval, and the protocol repeated throughout the study. As shown previously (DeVries, 1988; DeVries *et al.*, 1997) butterflies were not attracted to unbaited traps.

All butterflies were identified to species, and depending on the species, individual butterflies were treated in one of two ways. In most cases each individual was collected and placed in a glassine envelope with all pertinent data written on the envelope, and used for subsequent identification and ecological measurements. For a few abundant species, individuals were marked with a unique number, released, and the information recorded in a notebook. Only data for the first date of capture of any individual were included in the analyses reported here. Results of the mark-recapture study will be reported elsewhere (DeVries & Walla, in prep.).

Excepting a few refinements of Ehrlich's (1958) higher classification of butterflies, all subsequent systematic studies indicate that the phylogeny of nymphalid subfamily relationships are unresolved (see summary in De Jong *et al.*, 1996). In the absence of a well resolved phylogeny it therefore seems almost arbitrary as to which higher level classification is used, provided that the one chosen is unambiguous and well known. As in a previous study (DeVries *et al.*, 1997) we follow the conservative synthesis of Ackery (1984) which is based upon Ehrlich (1958), and represents a widely known, functional classification of nymphalid subfamilies.

Statistical analyses

Species abundance distributions were graphed following Williams (1964) who noted that, in contrast to log base 2 (or any even number) interval widths, log base 3 interval widths with interval edges at $3^n/2$ do not overestimate rare species, or violate the independence of data points. The species abundance distribution in Figure 3 was plotted using log base 3 interval widths, and the goodness-of-fit to the observed distribution was assessed for log series and log-normal distributions (Fisher, Corbet & Williams, 1943; Williams, 1964; May, 1975). The position of the lowest observed relative abundance (the 'veil line' of Preston (1948)) provided an estimate of how completely the community had been sampled (Fig. 3).

We measure β-diversity as the component of total diversity among subdivisions of the community in the dimensions of height (canopy and understory), area (Lake Edge, Forest plots 1–4), or time (month). Specifically, the total, or γ-diversity is estimated by the diversity of the pooled data set for the entire sample; α-diversity is the weighted average diversity within subdivisions (weighted by sample size); and β-diversity equals γ-diversity minus α-diversity. Thus, 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 areas was evaluated using Chi-squared tests.

Chi-squared tests for homogeneity of observed species abundance distributions at taxonomic levels of the total community and subfamilies were used to assess the significance of β-diversity among sample subsets in dimensions of height, area, and time. A sequential Bonferoni 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), and community similarity indices corresponding to each of these measures were calculated as 1-β-diversity/γ-diversity (Lande, 1996).

Species accumulation curves for horizontal subdivisions of the LSL sample were compared to assess the influence of sample size on species richness estimates (Colwell & Coddington, 1994; Longino & Colwell, 1997). However, as estimates of species richness in diverse communities are highly sensitive to sample size, direct comparisons between subdivisions require a method that corrects for differences in sample sizes. We calibrated species richness in vertical and horizontal subsets against the rarefaction curve for the total sample (Sanders, 1968; Hurlbert, 1971; Gotelli & Graves, 1996) which gives the expected species richness in a random subset of any particular size. The statistical significance of such comparisons was 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 compare fruit-feeding nymphalid diversity from an intact forest (LSL) to that of a disturbed forest (Jatun Sacha) the larger sample size of the Jatun Sacha data set (see DeVries *et al.*, 1997) was rarefied to that of the present study and plotted with 95% confidence intervals onto the rarefaction curve of the total LSL sample.

To test the hypothesis that the difference between variances of the log-normal species abundance distributions fitted to the LSL and Jatun Sacha samples was an artifact of the difference in the two sample sizes, the following random sampling test was written using *Mathematica*™ version 3.0 (Wolfram, 1996). Individuals were sampled at random, without replacement, from the larger Jatun Sacha sample to form 10 000 simulated communities, each with the same number of individuals as the smaller LSL data set. A log-normal distribution was fitted to the observed species abundance distribution for each simulated community, and the variance of each fitted distribution was calculated following Pielou (1975). The variance of the fitted log-normal distribution for the LSL sample was compared to the distribution of variances obtained for the fitted distributions from our 10 000 simulated communities, and the proportion of the simulated variances greater than or equal to the observed LSL variance was determined.

RESULTS

A total of 883 individual butterflies belonging to 91 species in five subfamilies were captured during the 12 sampling periods (Table 1). The rank abundance distribution of the entire sample showed that a large proportion of trapped butterflies were accounted for by relatively uncommon species (Fig. 2): over 75% of species were represented by 10 or fewer individuals. The species abundance distribution ranged from 22 species represented by single individuals to one species, *Nessaea hewitsoni*, represented by 104 individuals (Figs 2 & 3).

Table 1. A, species richness of the La Selva Lodge sample 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 La Selva Lodge sample partitioned by vertical position

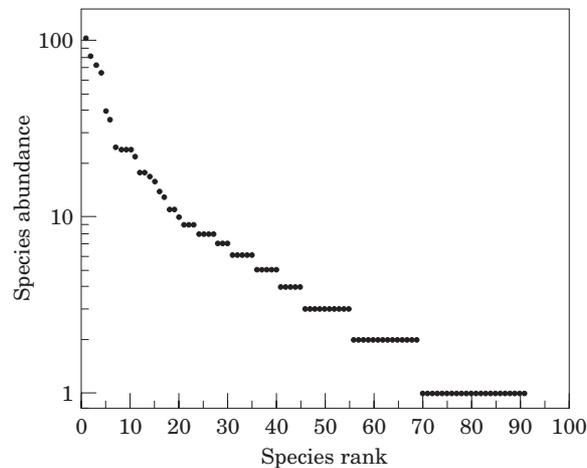|	Canopy	Understory	Both	Total
(A) Species richness				
Rare species	22	26	3	51
Common species	6	18	16	40
Total species	28	44	19	91
(B) Individual abundance				
Total individuals	303	580		883

Figure 2. Rank-abundance distribution for total sample of fruit-feeding nymphalids.

Summary data showed that species richness and abundance were distributed unequally between canopy and understory. Thirty-one per cent of the species were found in canopy only, 48% were found in understory only, and the remaining 21% of species were found in both strata (Table 1). When only the 51 rare species (represented by ≤ 4 individuals) were considered, the frequency of rare species was distributed evenly with respect to vertical dimension; 22 species were found in canopy only, 26 in understory only, and 3 were found in both. In contrast, a larger proportion of common species (represented by ≥ 5 individuals) were found in the understory in comparison to the canopy, and 66% of the total individual abundance was found in the understory (Table 1).

Partitioning the entire sample into five sample areas (Lake Edge, Forest 1, Forest 2, Forest 3 and Forest 4) showed that observed species richness was unequal among areas. Forest 3 had highest species richness and most unique species, the Lake Edge had lowest species richness, and other areas had approximately equivalent species richness and numbers of unique species (Table 2). The hypothesis of equal numbers of species among areas, however, is not subject to standard statistical tests since
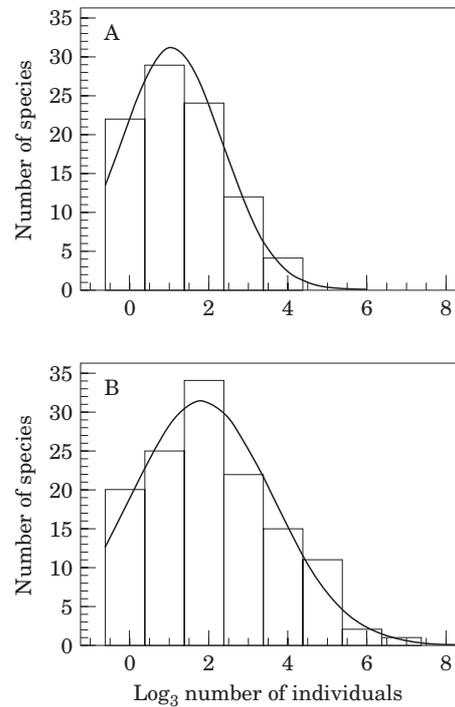
Figure 3. A, Species abundance distribution for total sample of fruit-feeding nymphalids (histogram) from intact forest at the La Selva Lodge (91 species and 883 individuals). Parameters of the fitted log-normal distribution (solid curve) using the method of Pielou (1975) on a log base 3 scale are: mean 1.053, variance 1.674, and estimated total number of species 100.73. The log-normal distribution ($\chi^2 = 0.429$, $P = 0.934$) gives a better fit than the log-series distribution ($\chi^2 = 1.293$, $P = 0.862$). The parameters of the log-series distribution (not illustrated) are $\alpha = 25.456$ and $x = 0.972$. B, species abundance distribution from disturbed forest (130 species and 6690 individuals) at Jatun Sacha (after DeVries *et al.*, 1997). Parameters of the fitted log-normal distribution (solid curve) are: mean 1.824 and variance 3.279. Note that variances of species abundance distributions of Jatun Sacha and La Selva Lodge differ significantly ($P<0.01$) in a random sampling.

TABLE 2. Distribution of total species richness (91 species), unique species, and total abundance among sampling areas

Area	Unique species	Total species	Abundance
Lake Edge	2	25	94
Forest 1	3	47	145
Forest 2	4	42	125
Forest 3	16	70	295
Forest 4	5	42	224

species are not independent (due to phylogenetic relationships), nor could they be identically distributed (due to differences in abundance).

Species richness provided a measure of how rare and common species were

TABLE 3. Overlap of 91 species among areas. Area abbreviations: LE = Lake Edge, F = Forest. Numbers in bold face are species unique to particular areas. A, overlap of rare species ($n \leq 4$ individuals) occurring in area pairs. B, overlap of common species ($n \geq 5$ individuals) occurring in area pairs. C, overlap of rare and common species occurring in 3–5 areas. Note that most shared species are among the forest plots

(A)			Rare species		
	LE	F1	F3	F2	F4
F4	0	4	5	0	**5**
F2	2	3	7	**4**	
F3	5	8	**16**		
F1	2	**3**			
LE	**1**				

(B)			Common species		
	LE	F1	F3	F2	F4
F4	10	29	30	23	**0**
F2	13	26	27	**0**	
F3	13	30	**0**		
F1	13	**0**			
LE	**1**				

(C)	Overlap of 3–5 areas	
Area combinations	Rare species	Common species
LE-F1-F3	1	10
LE-F1-F2	0	12
LE-F1-F4	0	10
LE-F3-F2	1	11
LE-F3-F4	0	9
LE-F2-F4	0	9
LE-F1-F2-F3	0	10
LE-F1-F2-F4	0	9
LE-F1-F3-F4	0	9
LE-F2-F3-F4	0	9
F1-F3-F2	2	24
F1-F3-F4	3	28
F1-F2-F4	0	22
F3-F2-F4	0	23
F1-F3-F2-F4	0	22
All 5 areas	0	9

shared among sites (Table 3). A comparison using the 51 rare species ($n \leq 4$ individuals) showed that the Forest 3 sample contained over three times as many unique species as other sites, samples representing area triads of Forest 1, 3, 4 and Forest 1, 2, 3 shared three and two species respectively, but no rare species were shared by combinations of four areas (Table 3). For the remaining 40 common species only the Lake Edge sample contained one unique species (*Cissia erigone*), but no other areas contained unique common species. The greatest overlap of common species (from 55 to 70%) occurred between those three and four way area combinations that did not include the Lake Edge sample, and 22% of the common species were shared by all five areas (Table 3). In summary, the greatest number of
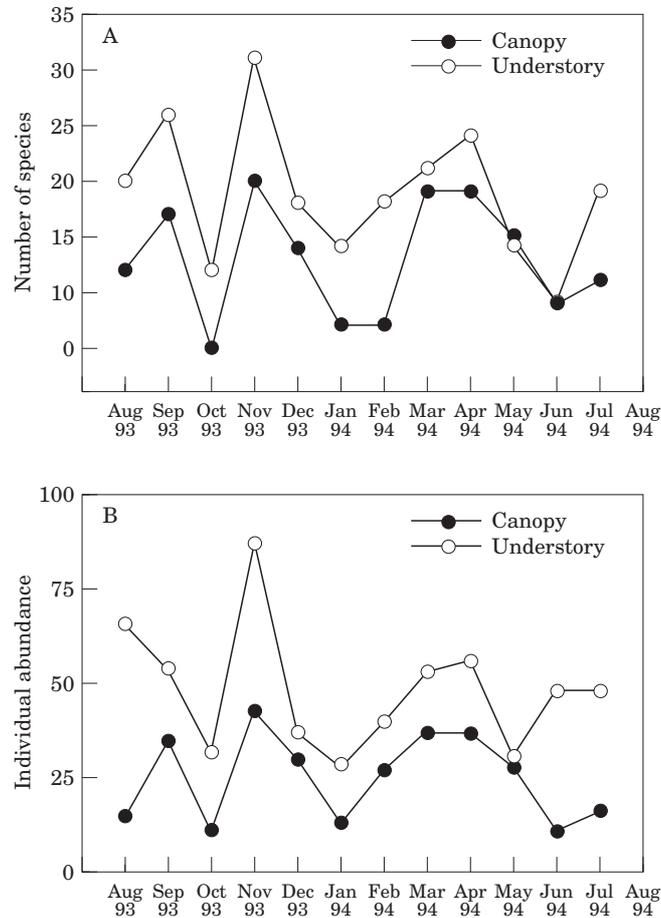
Figure 4. Temporal variation of the total La Selva Lodge sample by vertical position. A, species richness. B, individual abundance.

species were shared among combinations of plots that did not include the Lake Edge.

Total abundances among the five areas differed significantly ($\chi^2 = 25.21$, df $= 4$, $P<0.0001$), where the greatest abundance was found in the Forest 3 sample, and the least in the Lake Edge sample (Table 2).

Temporal variation was evident in species richness and abundance in both canopy and understory. Both species richness and abundance showed regular increases and decreases through time (Fig. 4). Even these simple plots show the important role temporal variation plays in the measurement of tropical species diversity.

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 4. The Shannon–Wiener and Simpson indices showed a relatively high similarity among subdivisions in vertical, horizontal and temporal dimensions in our sample, whereas species richness showed less similarity among these dimensions.

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

Measure		Community similarity among		
		heights	areas	months
Species richness	91	0.631	0.553	0.354
Shannon–Wiener	3.645	0.861	0.891	0.840
Simpson	0.954	0.961	0.980	0.974

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

TABLE 5. Chi-squared tests for homogeneity of species abundance distributions among heights, areas, and months for the total sample and subfamilies. Significance levels are: ns = not significant, ** = $P<0.01$, *** = $P<0.001$. Application of the sequential Bonferroni test (Rice, 1989) did not affect the significance of our results. Note: as all Morphinae were found in understory no statistical test was performed for heights

Taxon	Species richness	Abundance	Heights	Areas	Months
Total sample	91	883	***	***	***
Subfamily					
Charaxinae	17	75	***	ns	***
Nymphalinae	26	398	***	***	***
Morphinae	4	95	—	ns	ns
Brassolinae	12	96	***	***	**
Satyrinae	32	219	***	***	ns

Chi-squared tests for homogeneity of species abundance distributions demonstrated that our sample was distributed non-randomly in all dimensions. The total sample showed significant differences in species composition among subdivisions of vertical position (canopy or understory), area, and sampling period (Table 5). Relative frequencies of species in each subfamily differed significantly between canopy and understory, among five areas (excepting Charaxinae and Morphinae), and with the exception of Morphinae and Satyrinae, among sampling periods (Table 5).

Species accumulation curves showed that, among the plots, Forest 3 had the most species, and Lake Edge and Forest 4 had the least species (Fig. 5). Whether Forest 1 and Forest 2 would continue to accumulate species more slowly than Forest 3 could only be determined by additional sampling.

Rarefaction of the entire LSL sample (Fig. 6) indicates that, in contrast to raw data uncorrected for sample size (e.g. Table 2), Forest 1, 2 and 3 contained similar numbers of species, while the Lake Edge and Forest 4 areas had significantly fewer species than expected from a random sample of the entire community. Both canopy and understory samples fell below the rarefaction curve for the total sample (Fig. 6) indicating strong heterogeneity in the vertical dimension. The individual rarefaction curves for canopy and understory showed no indication of crossing, and rarefaction of the understory to the sample size of the canopy (with 95% confidence intervals) suggests that the understory is expected to have approximately the same number of species as the canopy (Fig. 6).
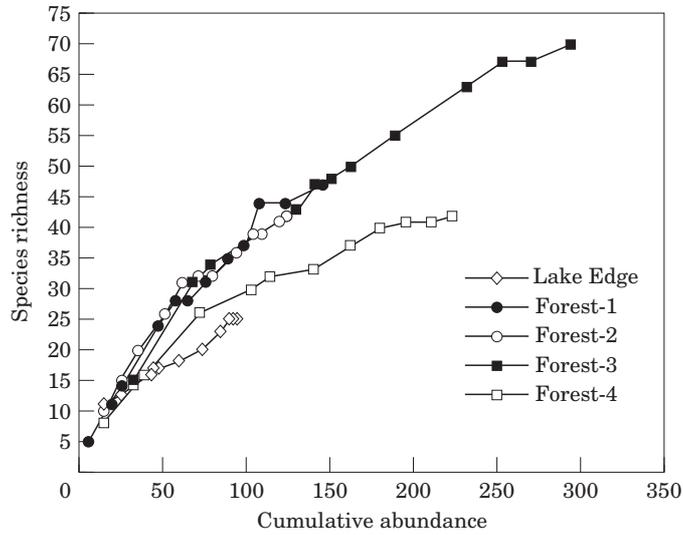
Figure 5. Species accumulation curves showing total species versus cumulative individual abundance through time in five sampling areas.
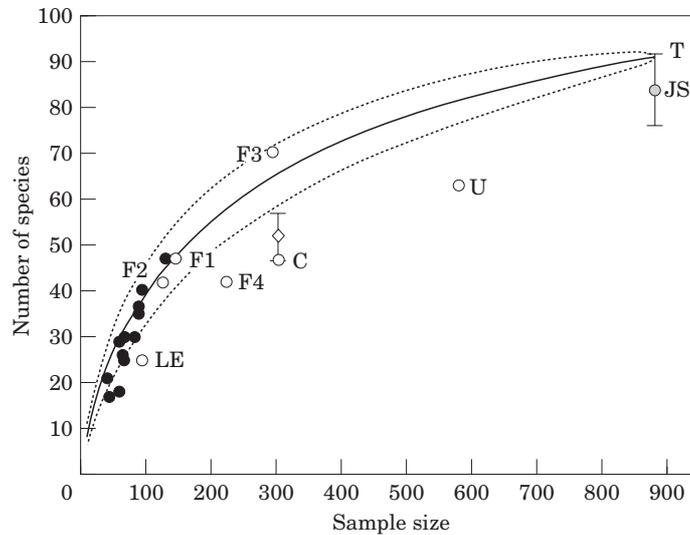

Figure 6. Rarefaction curve (solid curve) and approximate 95% confidence interval (dashed curves) for the total La Selva Lodge sample of fruit-feeding nymphalids compared to observed species richness in subdivisions of the sample along dimensions of height and area. Abbreviations: T = total community; C = canopy; U = understory; LE = Lake Edge, F1 = Forest 1, F2 = Forest 2, F3 = Forest 3, F4 = Forest 4 (individual points = ○); (●) months; (◇) understory rarefied to sample size of canopy (with 95% confidence intervals); (●) total Jatun Sacha sample rarefied to sample size of La Selva Lodge (with 95% confidence intervals).

When the total sample of Jatun Sacha (6690 individuals) was rarefied to that of LSL (883 individuals) it fell below the LSL rarefaction curve, but within the 95% confidence intervals (Fig. 6). Thus, rarefaction suggests that, despite the disparity between species richness at these sites (130 species at Jatun Sacha and 91 species at LSL), when standardized to the sample size of LSL species richness in these two communities does not differ significantly.

Our random sampling test suggested that the difference between variances of fitted species abundance distributions from LSL and Jatun Sacha was not an artifact of sample size (Fig. 3). Ninety-nine per cent of the communities simulated from the Jatun Sacha sample had variances greater than the observed variance of the LSL sample, indicating that the shapes of the species abundance distributions of LSL and Jatun Sacha samples differed significantly ($P<0.01$).

DISCUSSION

The scale and momentum of habitat destruction requires ecologists to accept the practical need for quick surveys of biodiversity in ecological monitoring and conservation planning (e.g. see Heywood, 1995; Laurence & Bierregaard, 1997). Ultimately, however, the accuracy of quick surveys in tropical areas can be justified only by testing their accuracy against long-term studies with intensive sampling that partition diversity into spatial and temporal components. We show that fruit-feeding nymphalid butterflies provide a model system for testing the accuracy of quick biodiversity surveys, and performing detailed comparisons among sites. In contrast to inventory or estimation techniques that rely on sampling with hand nets, sight records or sampling at irregular intervals by different collectors (e.g. Daily & Ehrlich, 1995; Robbins *et al.*, 1996; Brown & Hutchings, 1997), the system described here allows more rigorous comparisons of butterfly diversity among samples in space and time.

Trap studies have clearly advanced our understanding of tropical insect ecology and diversity (e.g. Wolda, 1978, 1992; Hanski & Cambefort, 1991; Muirhead-Thomson, 1991). However, it is well known that sampling bias might arise from variance among trap positions, and variance among species in attraction to baits (Williams, 1964; Muirhead-Thomson, 1991). Pooling replicate traps within plots (as done here) can reduce individual trap variance, but species attraction to baits can only be addressed by intensive mark-recapture studies (Seber, 1982) and/or detailed observations on diet preference. As noted elsewhere (DeVries, 1988; DeVries *et al.*, 1997; DeVries, Lande & Murray, 1999) our methods estimate species abundance of where adult butterflies were trapped, but not the distribution of host plants, courtship sites, or other life history components. Nevertheless, our methods can reduce or avoid the sampling biases in all hand net techniques that pool the efforts of multiple persons, and trapping is clearly superior to sight records. Although susceptibility of fruit-feeding nymphalids to traps has not been established for all species, our methods are important for assessing tropical species diversity because they permit more accurate comparisons and statistical analysis to be made among samples in space and time than has been done previously.

This study provided unique estimates of spatial and temporal components of species diversity and individual abundance for fruit-feeding nymphalid butterflies

TABLE 6. Comparison of species diversity between a natural lake edge at La Selva Lodge (this study) and forest-pasture edge at Jatun Sacha (data from DeVries *et al.*, 1997)

	Species richness	Total edge abundance	*Cissia penelope* total abundance	*Cissia penelope* edge abundance
La Selva Lodge	25	94	2	0
Jatun Sacha	86	3686	1618	1556

within an intact tropical forest. Despite the fact that 78% of the species were represented by fewer than 10 individuals, and 56% of the species were represented by ≤ 4 individuals (Fig. 2), the species abundance patterns in our sample fit the log-normal distribution (Fig. 3). The position of the veil line (Preston, 1948) provided an estimate of total species richness of 100.7 species using Pielou's (1975) method, and the method of Chao (1984) provided an estimate of 108.3 ± 9.6 species. Subsequent sampling has shown these to be underestimates of the fruit-feeding nymphalid species richness occurring at LSL (DeVries & Walla, unpublished), and this issue will be addressed elsewhere.

Chi-square tests for homogeneity of species abundance distributions in the total community showed significant β-diversity in vertical, horizontal and temporal dimensions. Significant β-diversity existed among heights for all subfamilies, and most subfamilies showed significant β-diversity among areas and months (Table 5, Fig. 4). Significant temporal and spatial variation in abundance and species richness as seen in this and other studies (Kato *et al.*, 1995; DeVries *et al.*, 1997) suggests that such heterogeneity is a fundamental feature of tropical forest insect communities. Continuous observations over 5 years indicate that many species comprising Table 5 (in addition to others not sampled in this study) manifest consistent vertical distributions at LSL (DeVries & Walla, unpublished), emphasizing the importance of accounting for vertical dimension in tropical insect diversity estimates.

In many communities vegetation structure may have profound effects on species richness (e.g. MacArthur, Recher & Cody, 1966; Southwood, Brown & Reader, 1979), and responses to edge effects may depend upon the focal group of organisms (Murcia, 1995). Comparing LSL and Jatun Sacha serves to illustrate how Amazonian butterfly species diversity may differ between forest edges. The edge at LSL comprised a natural interface between a body of water and forest where butterfly diversity showed a low individual abundance and species richness (Tables 2 & 6, Fig. 6). In contrast, the edge at Jatun Sacha represents the interface between cattle pasture and forest where butterfly diversity showed a relatively high individual abundance and species richness (DeVries *et al.*, 1997). Further, in a spectacular case of ecological release (Table 6), over 1600 individuals of *Cissia penelope* were sampled at the Jatun Sacha edge (DeVries *et al.*, 1997), yet this species was represented by only two specimens in the total LSL sample (neither from the Lake Edge). This simple comparison highlights how different types of edges (one natural, the other due to human disturbance) can affect two butterfly communities that share a large number of species.

Although accumulation curves suggest a ranking of the five areas with respect to species richness, ultimately the differences implied between them could only be verified through continued sampling (Fig. 5). Given that intermediate levels of

disturbance may increase species richness (e.g. Connell, 1978; Huston, 1979, 1994; Denslow, 1987), the greater richness of Forest 3 could suggest that plot has experienced greater disturbance in the recent past than the other plots. This may, in fact, be the case as indigenous residents report that a localized storm blew down a significant number of large trees near this plot in August 1975, but left other areas unaffected (L. Chowamongo, J. Hualinga and S. Machoa, pers. comms.).

Rarefaction analysis verified spatial heterogeneity in both vertical and horizontal dimensions. The canopy and understory both fell below the 95% confidence intervals of the rarefaction curve (Fig. 6) showing that each sample had a distinct species composition, and only when combined did they reflect the species richness of the total sample. Rarefaction of the understory sample to that of the canopy suggests that both strata have similar species richness, a contrast to the disturbed Jatun Sacha site where the canopy was shown to have a higher species richness (DeVries *et al.*, 1997). Rarefaction of the total community (Fig. 6) also showed that Lake Edge and Forest 4 both fell below the rarefaction curve, confirming significant differences in species richness among sampling plots.

The most suitable measures of species diversity for quick surveys 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-λ, and to a lesser extent Shannon–Wiener information, H, satisfy this criterion (Lande, 1996). Although it is the least reliable statistic, species richness is often employed in conservation applications because it is the only commonly used measure that is sensitive to rare species (Peet, 1974). However, since species richness is highly sensitive to the small sample sizes that are typical of quick surveys, comparison of species richness among samples requires correction for differences in sample size using rarefaction, species accumulation curves, and extrapolation techniques which are best performed on large samples.

Comparisons of species richness are often used to discriminate among natural areas to be conserved. For example, during a 12 month period we sampled 91 species of fruit-feeding nymphalids from an intact forest (Tables 1 & 2), but a previous 12 month study (DeVries *et al.*, 1997) sampled 130 species from a markedly disturbed forest (Jatun Sacha). In other words, using the same sampling regime 43% more species were found at Jatun Sacha than in the present study. Extrapolation techniques also indicate that Jatun Sacha has a higher species richness than LSL (see DeVries *et al.*, 1997, and below), and under conservation practices favouring species richness one might argue that LSL is less worthy of protection than Jatun Sacha. Rarefaction, however, suggests that the apparent difference may be due to disparity in the sizes of the two samples (Fig. 6).

Although rarefaction is a robust statistical tool for comparing samples of different size, the shapes of the species abundance distributions are important for interpreting comparisons among different communities. Estimates of total species richness using the methods of Pielou (1975) and Chao (1984) suggest that Jatun Sacha has a higher species richness than LSL. Alternatively, rarefaction suggests that at the sample size of LSL the species richness of these communities do not differ significantly (Fig. 6). Although the rarefaction curves for the two communities do not cross, the shapes of the species abundance distributions (Fig. 3) indicate that further sampling from LSL would yield rarefaction curves that intersect, and at large sample sizes the LSL curve would fall below that of Jatun Sacha. This is because, at the LSL sample size, rarefaction of the Jatun Sacha community considers a smaller proportion of the

area beneath the log-normal species abundance distribution, and accounts for only a small proportion of the total Jatun Sacha community (Fig. 3). This emphasizes the importance of estimating the shape of the species abundance distribution when comparing diversity of two sites.

Even though species abundance distributions are frequently used to describe communities (Williams, 1964; Engen, 1978; Preston, 1980; Gray, 1987; Tokeshi, 1993), few field investigations consider the effect of disturbance on the shape of the species abundance distribution. Both LSL and Jatun Sacha species abundance distributions are well described by the log-normal distribution, but the LSL sample has a significantly smaller variance than the more disturbed Jatun Sacha habitats (Fig. 3). Results of our random sampling tests support the hypothesis that differences in variance are not an artifact of sampling error, but reflect real differences in the underlying distributions of our samples. We note that compared to LSL the higher extrapolated total species richness at Jatun Sacha likely reflects a greater diversity of habitats that have been created by recent disturbance at this site.

Species abundance patterns are known to vary depending on the community sampled (Williams, 1964; May, 1981). For example, the classic study by Patrick, Hohn & Wallace (1954) noted explicitly that diatom communities in polluted streams had fewer species with greater abundances than communities in unpolluted streams, resulting in differences in shapes of species abundance distributions. Studies of other communities have also suggested that pollution causes similar changes in the shape of species abundance distributions (Gray & Mirza, 1979; Ugland & Gray, 1982; but see Lambshead, Platt & Shaw, 1983). These studies, in combination with our findings based on two butterfly communities (Fig. 3), suggest that the generality of differences in variances of species abundance distributions between disturbed and undisturbed tropical forests deserves further critical investigation.

The vertical and horizontal distribution of organisms within tropical forests, including insectivores, is well established (see Munn, 1985; Lowman & Nadkarni, 1995). Vertical and horizontal habitat partitioning by neotropical avian communities (Munn, 1985; Cannaday, 1997), and their high degree of prey specialization (Snow, 1976; Rosenberg, 1990) reinforces the view that bird community structure plays a significant role in the evolution and spatial association of tropical insects, and particularly butterflies (Papageorgis, 1975; Ackery & Vane-Wright, 1984; DeVries, 1988; Turner & Mallet, 1996; Beccaloni, 1997; DeVries et al., 1999). Although the strength of selection by predators on the structure of forest butterfly communities remains obscure, given that small selective effects maintained over long periods of time can produce major evolutionary changes (Wright, 1931; Haldane, 1932; Fisher, 1958; Lande, 1976), documenting diverse insect communities in space and time (as done here) can reveal ecological patterns relevant to elucidating the evolution of community structure in complex tropical habitats.

In concert with a previous investigation (DeVries et al., 1997) this study confirms both the utility of long-term, standardized sampling in diverse tropical butterfly communities and application of statistical techniques that allow comparisons among spatial and temporal components of diversity. Our results reinforce the prevalence of variation in diversity along vertical, horizontal and temporal dimensions, accentuating the significance of considering tropical butterfly diversity in space and time. The variation of species diversity observed here in fruit-feeding nymphalid butterflies is likely due to underlying ecological and evolutionary factors, and implies that such variation is inherent in other tropical insect communities. Our comparison

of two butterfly communities revealed intriguing differences in the shapes of species abundance distributions from intact and disturbed forest that, when considered in combination with previous work on diatom communities, invites further investigation. Finally, studies of tropical butterfly communities have rarely, if ever, employed standardized methods to compare diversity among different sites as reported here. This study therefore encourages comparisons of fruit-feeding nymphalid butterfly communities among other intact and disturbed tropical sites, and points to a means of advancing our understanding of how spatial and temporal factors may influence tropical insect diversity and community structure.

REFERENCES

Ackery PR. 1984. Systematic and faunistic studies on butterflies. *Symposium of the Royal Entomological Society of London* **11:** 9–21.

Ackery PR, Vane-Wright RI. 1984. *Milkweed butterflies: their cladistics and biology.* London: British Museum (Nat. Hist.), Entomology.

Allee WC. 1926. Measurement of environmental factors in the tropical rainforest of Panama. *Ecology* **7:** 273–302.

Anon. 1993. Rapid biodiversity assessment. *Proceedings of the Biodiversity Assessment Workshop, Macquarie University 1993.* Sydney: Research Unit for Biodiversity and Bioresources, Macquarie University.

Basset Y, Aberlenc H, Delvare G. 1992. Abundance and stratification of foliage arthropods in a lowland rain forest of Cameroon. *Ecological Entomology* **17:** 310–318.

Bates M. 1944. Observations on the distribution of mosquitoes in a tropical forest. *Ecology* **25:** 159–170.

Beccaloni GW. 1997. Vertical stratification of ithomiine butterfly (Nymphalidae: Ithomiinae) mimicry complexes: the relationship between adult flight height and larval host-plant height. *Biological Journal of the Linnean Society* **62:** 313–341.

Beccaloni GW, Gaston KJ. 1995. Predicting the species richness of neotropical forest butterflies: Ithomiinae (Lepidoptera: Nymphalidae) as indicators. *Biological Conservation* **71:** 77–86.

Bowles IA, Rice RE, Mittermeir RA, daFonseca GAB. 1998. Logging and tropical forest conservation. *Science* **280:** 1899–1900.

Brakefield PM, Reitsma F. 1991. Phenotypic plasticity, seasonal climate and population biology for *Bicyclus* butterflies (Satyridae) in Malawi. *Ecological Entomology* **16:** 291–303.

Brown KS Jr. 1991. Conservation of neotropical environments: insects as indicators. In: Collins NM, Thomas JA, eds. *The conservation of insects and their habitats*. London: Academic Press, 449–504.

Brown KS Jr, Hutchings RW. 1997. Disturbance, fragmentation, and the dynamics of diversity in Amazonian butterflies. In: Laurence WF, Bierregaard Jr, eds. *Tropical forest remnants*. Chicago: University of Chicago Press, 91–110.

Cannaday C. 1997. Loss of insectivorous birds along a gradient of human impact in Amazonia. *Biological Conservation* **77:** 63–77.

Chao A. 1984. Non-parametric estimation of the number of classes in a population. *Scandanavian Journal of Statistics* **11:** 265–270.

Colwell RK, Coddington JA. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London* **B345:** 101–118.

Cody ML, Diamond J, eds. 1975. *Ecology and evolution of communities*. Cambridge: Harvard University Press.

Condit R, Hubbell SP, Lafrankie JV, Sukumar R, Manokaran N, Foster RB, Ashton PS. 1996. Species-area and species-individual relationships for tropical trees: a comparison of three 50-ha plots. *Journal of Ecology* **84:** 549–562.

Connell JH. 1978. Diversity in rain forests and coral reefs. *Science* **199:** 1302–1310.

Daily GC, Ehrlich PR. 1995. Preservation of biodiversity in small rainforest patches: rapid evaluations using butterfly trapping. *Biodiversity and Conservation* **4:** 35–55.

De Jong R, Vane-Wright RI, Ackery PR. 1996. The higher classification of butterflies (Lepidoptera): problems and prospects. *Entomologica Scandanavica* **27:** 65–101.

Denslow JS. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* **18:** 431–451.

DeVries PJ. 1987. *The Butterflies of Costa Rica and their Natural History. I: Papilionidae, Pieridae and Nymphalidae*. Princeton, NJ: Princeton University Press.

DeVries PJ. 1988. Stratification of fruit-feeding nymphalid butterflies in a Costa Rican rainforest. *Journal of Research on the Lepidoptera* **26:** 98–108.

DeVries PJ. 1997. *The Butterflies of Costa Rica and their Natural History. II: Riodinidae*. Princeton, NJ: Princeton University Press.

DeVries PJ, Murray D, Lande R. 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society* **62:** 343–364.

DeVries PJ, Lande R, Murray D. 1999. Associations of co-mimetic ithomiine butterflies on small spatial and temporal scales in a neotropical rainforest. *Biological Journal of the Linnean Society* **67:** 73–85.

Edwards PJ, May RM, Web NR, eds. 1994. *Large scale ecology and conservation biology*. London: Blackwell Scientific.

Ehrlich PR. 1958. The comparative morphology, phylogeny, and higher classification of the butterflies. *University of Kansas Science Bulletin* **39:** 305–370.

Engen S. 1978. *Stochastic abundance models with emphasis on biological communities and species*. London: Chapman & Hall.

Erwin TL. 1995. Measuring arthropod biodiversity in the tropical forest canopy. In: Lowman MD, Nadkarni N, eds. *Forest Canopies*. San Diego: Academic Press, 109–127.

Fisher RA. 1958. *The Genetical Theory of Natural Selection*. 2nd edition. New York: Dover.

Fisher RA, Corbet AS, Williams CB. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* **12:** 42–58.

Forey PL, Humphries CJ, Vane-Wright RI, eds. 1994. *Systematics and Conservation Evaluation*. Systematics Assoc. Special, Vol. 50. Oxford: Clarendon Press.

Gaston KJ. 1996. *Biodiversity*. Oxford: Blackwell Science.

Gilbert LE. 1984. The biology of butterfly communities. *Symposium of the Royal Entomological Society of London* **11:** 41–54.

Gill BD. 1991. Dung beetles in tropical American forests. In: Hanski I, Cambefort Y, eds. *Dung beetle ecology*. Princeton, NJ: Princeton University Press, 211–229.

Gotelli NJ, Graves GR. 1996. *Null models in ecology*. Washington, D.C.: Smithsonian Institution Press.

Gray JS. 1987. Species-abundance patterns. In: Gee JHR, Giller PS, eds. *Organization of communities past and present*. Oxford: Blackwell Scientific, 53–67.

Gray JS, Mirza FB. 1979. A possible method for detecting pollution-induced disturbance on marine benthic communities. *Marine Pollution Bulletin* **10:** 142–146.

Groombridge B, ed. 1992. *Global biodiversity*. London: Chapman & Hall.

Haldane JBS. 1932. *The causes of evolution.* London: Longmans, Green & Co.

Hammond PM. 1994. Practical approaches to the estimation of the extent of biodiversity in speciose groups. *Philosophical Transactions of the Royal Society of London* **B345:** 119–136.

Hanski I, Cambefort Y. 1991. Spatial processes. In: Hanski I, Cambefort Y, eds. *Dung beetle ecology.* Princeton, NJ: Princeton University Press, 283–304.

Hayek LC, Buzas MA. 1996. *Surveying natural populations.* New York: Columbia University Press.

Heck KL, van Belle G, Simberloff D. 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. *Ecology* **56:** 1459–1461.

Heywood VH, ed. 1995. *Global biodiversity assessment.* Cambridge: Cambridge University Press.

Hubbell SP, Foster RB. 1986. Commonness and rarity in a neotropical forest: implications for tropical tree conservation. In: Soulé ME, ed. *Conservation biology. The science of scarcity and diversity.* Sunderland: Mass.: Sinauer Associates, 205–231.

Hurlbert SH. 1971. The non-concept of species diversity: a critique and alternative parameters. *Ecology* **52:** 577–586.

Huston M. 1979. A general hypothesis of species diversity. *American Naturalist* **113:** 81–101.

Huston MA. 1994. *Biological diversity, the coexistence of species on changing landscapes.* Cambridge: Cambridge University Press.

Kato M, Inoue T, Hamid AA, Nagamitsu T, Merdek MB, Nona AR, Itino T, Yamane S, Yumoto T. 1995. Seasonality and vertical structure of light-attracted insect communities in a dipterocarp forest in Sarawak. *Researches on Population Ecology* **37:** 59–79.

Keister AR, Scott JM, Csuti B, Noss RF, Butterfield B, Sahr K, White D. 1996. Conservation prioritization using GAP data. *Conservation Biology* **10:** 1332–1324.

Kremen C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* **2:** 203–217.

Kremen C. 1994. Biological inventory using target taxa: a case study of butterflies of Madagascar. *Ecological Applications* **4:** 407–422.

Lambshead PJD, Platt HM, Shaw KM. 1983. Detection of differences among assemblages of benthic species based on an assessment of dominance and diversity. *Journal of Natural History, London* **17:** 859–974.

Lande R. 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* **30:** 314–334.

Lande R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* **76:** 5–13.

Laurence WF, Bierregaard RO, eds. 1997. *Tropical forest remnants.* Chicago: University of Chicago Press.

Longino JT, Nadkarni N. 1990. A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a tropical montane forest. *Psyche* **97:** 81–94.

Longino JT, Colwell RK. 1997. Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. *Ecological Applications* **7:** 1263–1277.

Lowman MD, Nadkarni N, eds. 1995. *Forest canopies.* San Diego, CA: Academic Press.

MacArthur RH. 1972. *Geographical ecology.* Princeton, NJ: Princeton University Press.

MacArthur RH, Recher H, Cody ML. 1966. On the relation between habitat-selection and species diversity. *American Naturalist* **100:** 319–325.

Magurran AE. 1988. *Ecological diversity and its measurement.* Princeton, NJ: Princeton University Press.

Malcolm JR. 1994. Edge effects in central Amazonian forest fragments. *Ecology* **75:** 2438–2445.

Mallet J, Gilbert LE. 1995. Why are there so many mimicry rings? Correlations between habitat, behavior and mimicry in *Heliconius* butterflies. *Biological Journal of the Linnean Society* **55:** 159–180.

May RM. 1975. Patterns of species diversity and abundance. In: Cody ML, Diamond JM, eds. *Ecology and evolution of communities.* Cambridge, MA: Harvard University Press, 81–120.

May RM. 1981. Patterns in multi-species communities. In: May RM, ed. *Theoretical ecology: principles and applications.* Oxford: Blackwell, 197–227.

Morse DR, Stork NE, Lawton JH. 1988. Species number, species abundance and body length relationships of arboreal beetles in Bornean lowland rain forest trees. *Ecological Entomology* **13:** 25–37.

Munn CA. 1985. Permanent canopy and understory flocks in Amazonian species composition and population density. *Ornithological Monographs* **36:** 683–712.

Murcia C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution* **10:** 58–62.

Muirhead-Thomson RC. 1991. *Trap responses of flying insects.* London: Academic Press.

Noss RF. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* **4:** 355–364.

Novotny V, Basset Y. 1998. Seasonality of sap-sucking insects (Auchenorrhyncha, Hemiptera) feeding on Ficus (Moraceae) in a lowland rain forest in New Guinea. *Oecologia* **115:** 514–522.

Olson D, Dinnerstein E, Castro G, Maravi E, eds. 1996. Identifying gaps in botanical information for biodiversity conservation in Latin America and the Caribbean. Washington, D.C.: World Wildlife Fund.

Papageorgis CA. 1975. Mimicry in Neotropical butterflies. *American Scientist* **63:** 522–532.

Patrick R, Hohn M, Wallace J. 1954. A new method for determining the pattern of the diatom flora. *Noctulae Natura Academy of Natural Sciences, Philadelphia* **259:** 1–12.

Pearson DL. 1977. A pantropical comparison of bird community structure on six lowland forest sites. *Condor* **79:** 232–244.

Pearson DL. 1994. Selecting indicator taxa for the quantitative assessment of biodiversity. *Philosophical Transactions of the Royal Society of London* **B345:** 75–79.

Peet RK. 1974. The measurement of species diversity. *Annual Review of Ecology and Systematics* 5: 285–307.

Pinheiro CEG, Ortiz JVC. 1992. Communities of fruit-feeding butterflies along a vegetation gradient in central Brazil. *Journal of Biogeography* **19:** 505–511.

Pielou FC. 1975. *Ecological diversity.* New York: Wiley.

Preston FW. 1948. The commonness and rarity of species. *Ecology* **29:** 254–283.

Preston FW. 1980. Noncannonical distribution of commonness and rarity. *Ecology* **61:** 88–97.

Richards PW. 1952. *The tropical rain forest, an ecological study.* Cambridge: Cambridge University Press.

Rice WR. 1989. Analyzing tables of statistical tests. *Evolution* **43:** 223–225.

Ricklefs R, Schluter D, eds. 1993. *Species diversity in ecological communities.* Chicago: University of Chicago Press.

Robbins RK, Lamas G, Mielke OH, Harvey DJ, Casagrande MM. 1996. Taxonomic composition and ecological structure of the species-rich butterfly community at Pakitza, Parque Nacional del Manu, Peru. In: Wilson DE, Sandoval A, eds. *La Biodiversidad del Sureste del Peru.* Lima, Peru: Editorial Horizonte, 201–236.

Roberts L. 1991. Ranking the rain forests. *Science* **251:** 1559–1560.

Rosenberg KV. 1990. Dead-leaf foraging specialization in tropical forest birds: measuring resource availability and use. In: Morrison ML, Ralph CJ, Jehl JR Jr, eds. *Avian foraging: theory, methodology, and applications. Studies in Avian Biology* **13:** 360–368.

Rosenzweig ML. 1995. *Species Diversity in Space and Time.* Cambridge: Cambridge University Press.

Ryti RT. 1992. Effect of the focal taxon on the selection of nature reserves. *Ecological Application* **2:** 404–410.

Sanders HL. 1968. Marine benthic diversity: a comparative study. *American Naturalist* **102:** 243–282.

Seber GAF. 1982. *The estimation of animal abundance and related parameters.* 2nd ed. London: Charles Griffin.

Snow DW. 1976. *The web of adaptation: bird studies in the American tropics.* New York: Quadrangle.

Southwood TRE, Brown VK, Reader PM. 1979. The relationship of plant and insect diversities in succession. *Biological Journal of the Linnean Society* **12:** 327–348.

Stork NE. 1988. Insect diversity: facts, fiction and speculation. *Biological Journal of the Linnean Society* **35:** 321–337.

Sutton SL, Hudson PJ. 1980. The vertical distribution of small flying insects in the lowland rainforest of Zaire. *Zoological Journal of the Linnean Society* **68:** 111–123.

Terborgh J, Robinson SK, Parker TA, Munn CA, Pierpont N. 1990. Structure and organization of an Amazonian forest bird community. *Ecological Monographs* **60:** 213–238.

Tokeshi M. 1993. Species abundance patterns and community structure. *Advances in Ecological Research* **24:** 111–186.

Turner JRG, Mallet JB. 1996. Did forest islands drive the diversity of warningly coloured butterflies? Biotic drift and the shifting balance. *Philosophical Transactions of the Royal Society* **B351:** 835–845.

Ugland KI, Gray JS. 1982. Lognormal distributions and the concept of community equilibrium. *Oikos* **39:** 171–178.

Williams CB. 1964. *Patterns in the balance of nature and related problems in quantitative ecology.* London: Academic Press.

Wilson DE, Sandoval A, eds. 1996. *La Biodiversidad del Sureste del Peru.* Lima, Peru: Editorial Horizonte.

Wolda H. 1978. Fluctuations in abundance of tropical insects. *American Naturalist* **112:** 1017–1045.

Wolda H. 1992. Trends in abundance of tropical forest insects. *Oecologia* **89:** 47–52.

Wolfram S. 1996. *Mathematica* 3.0. Wolfram Industries.

Wright S. 1931. Evolution in Mendelian populations. *Genetics* **16:** 97–159.