Effect of Experimental Selective Logging on Tropical Butterflies

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Abstract: *I investigated the effects of an experimental selective logging regime on the assemblage of fruit-feeding butterflies in replicated experimental plots in the Chiquibul Forest, Belize. Over a 12-month period, I caught 1187 individuals of 49 species using fruit-baited traps. Selective logging at densities of six stems per ha 3 years before the study had little effect on butterfly species richness, the abundance of individual species, or the shape of species-abundance distributions. There was no tendency for taxa with restricted geographical ranges to be particularly sensitive to selective logging. Mark-release-recapture results suggest that most butterflies move relatively short distances, but that some dispersal occurs between plots separated by distances of ≥1 km. The apparent similarity of the fruit-feeding butterfly assemblage in selectively logged and unlogged forest contrasts with previous studies of butterfly assemblages but mirrors results for birds in the same plots. A possible explanation is the high frequency of natural disturbance—hurricanes and associated fires—in the Chiquibul Forest. The species present appear to be adapted to naturally disturbed habitats and may therefore be relatively unaffected by selective logging. Local studies of the effects of selective logging must take into account the history of natural and human disturbance in the study area. The results support the case for "ecological forestry," in which sustainable management regimes work within the limits imposed by natural disturbance.*

Efectos de una Tala Selectiva Experimental en Mariposas Tropicales

Resumen: *Investigué los efectos de un régimen de tala selectivo experimental sobre los ensamblajes de mariposas frugívoras en cuadrantes experimentales replicados del bosque Chiquibul, Belice. Por un período de 12 meses, 1187 individuos de 49 especies fueron capturados en trampas cebadas con fruta. La tala selectiva a densidades de seis troncos por hectárea, tres años antes del estudio tuvo poco efecto en la riqueza de especies de mariposas, la abundancia de especies o la estructura de las distribuciones de especie-abundancia. No hubo una tendencia de que los taxones con rangos de distribución geográfica restringidos fueran particularmente sensibles a la tala selectiva. Resultados de marcado-liberación-recaptura sugieren que la mayoría de las mariposas se mueven en distancias relativamente cortas, pero que alguna dispersión ocurre entre cuadrantes separados por distancias de ≥ 1km. La aparente similitud del ensamblaje de mariposas frugívoras en bosques talados selectivamente y en bosques sin talar contrasta con estudios previos de ensamblajes de mariposas, pero refleja los resultados para aves en los mismos cuadrantes. Una explicación posible es la alta frecuencia de perturbaciones naturales (huracanes e incendios asociados) en el bosque Chiquibul. Las especies presentes aparentemente están adaptadas a hábitats naturalmente perturbados y por lo tanto pueden ser relativamente poco afectadas por la perturbación que la tala selectiva ocasiona al hábitat. Los estudios locales de los efectos de la tala selectiva deben tomar en consideración la historia de las perturbaciones naturales del área de estudio. Los resultados apoyan el caso de la ecología forestal, donde los regímenes de manejo sostenido funcionan dentro de los límites impuestos por la perturbación natural.*

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Introduction

Tropical forests contain at least 50% of the Earth's biodiversity, but only 4% of all tropical forests occur within reserves or national parks (Stork 1988; Whitmore & Sayer 1992; World Conservation Monitoring Centre 1992). Current and future demands for both timber and agricultural land in tropical countries mean that this area is unlikely to increase greatly over the next few decades, while pressure on unprotected forests is likely to escalate. For these reasons, some conservationists argue that the most realistic way of ensuring the conservation of forest biodiversity outside reserves is to find a way for these areas to be used on a sustainable basis. Considerable disagreement remains, however, about whether economic activity and the maintenance of tropical biodiversity can be reconciled (Johns 1992; Dudley et al. 1995; Hartshorn 1995; Sandbukt 1995; R. E. Rice et al. 1997; Hunter 1999).

One potentially sustainable and economically viable use of tropical forests is selective logging. Historically, almost all logging in tropical forests has been selective, in the sense that only the most valuable timber trees have been removed (Wadsworth 1997; Kellman & Tackaberry 1999). But, even extraction of trees at low densities can result in considerable damage to the residual stand and severe declines in biodiversity (Johns 1992; Kellman & Tackaberry 1999). More recently, forest managers have focused on the development of sustainable forest management regimes, with the aim of providing a renewable timber resource through rotational selective logging while minimizing negative effects on forest biodiversity (Bruenig 1996; Dickinson et al. 1996; Hunter 1999). The gross structure of the forest may be relatively unaffected by careful selective logging regimes, particularly if efforts are made to minimize damage to the residual stand by, for example, carefully planning the routes of access tracks and the direction of felling (Pinard & Putz 1996). Subtle changes in species composition and local extinctions of some species may occur, however, with potential consequences for ecosystem function (Didham et al. 1996). As selective logging regimes are devised and implemented throughout the humid tropics, it is becoming increasingly important to understand their effects on rainforest plants and animals (Boyle & Sayer 1995; Hartshorn 1995). Insects may have an important role to play in such assessments because of their dominance in terrestrial ecosystems (Wilson 1987), their short generation times that can result in rapid population responses to disturbance, and their wide range of life styles that make them sensitive to changes in the biotic and abiotic environments (Kremen et al. 1993).

Among the insects, butterflies have become a popular group for study, largely because they are relatively easy to record and identify (New 1991, 1997; Kremen 1992, 1994). Although a number of investigators have examined the effects of different forms of disturbance on butterfly assemblages (Bowman et al. 1990, Raguso & Llorente-Bousquets 1990; Spitzer et al. 1993, 1997; Kremen 1994; Daily & Ehrlich 1995; DeVries et al. 1997; Lawton et al. 1998; Lewis et al. 1998), few studies have looked specifically at selective logging (e.g. Hill et al. 1995; DeVries et al. 1997; Wood & Gillman 1998). A number of these studies fail to distinguish between selective logging and other forms of habitat disturbance, such as historic forest clearance for agriculture, or do not provide information on logging intensities and the time elapsed since logging ended. Sparrow et al. (1994) have drawn attention to the need for well-designed local studies of tropical butterfly faunas and in particular for studies focusing on the effects of human disturbance on butterfly diversity and abundance. In carrying out such studies, they stress the need to take into account the marked seasonality of many tropical insects and the need to control for the effects of different light regimes at study sites. Similarly, DeVries et al. (1997) identify a number of problems with the scope and experimental design of many studies of tropical butterfly diversity. A further issue of concern is the extent to which species with different geographical ranges are affected by habitat disturbance. For conservation purposes, not all species are of equal interest, and there is gathering evidence that endemic or restricted-range butterfly species may be particularly vulnerable to habitat disturbance (Thomas & Mallorie 1985; Thomas 1991; Hill et al. 1995; Hamer et al. 1997; Lewis et al. 1998).

My investigation addresses many of these issues in an area of naturally disturbed moist tropical forest in Belize, Central America. As far as I am aware, this is the first study where paired, replicated logged and unlogged plots have been used to investigate the effects of selective logging on tropical butterflies. The results provide a robust assessment of the short-term effect of a selective logging experiment on the assemblage of fruit-feeding butterflies.

Methods

Study Area and Experimental Plots

Belize is situated on the Caribbean coast of Central America, bordered to the north by the Yucatan peninsula of Mexico and to the west and south by Guatemala. An estimated 77% to 82% of the country is still covered by natural vegetation, including large areas of moist tropical forest, particularly in the south and west (Harcourt 1996; Jacobs & Castañeda 1998). This study took place near the Las Cuevas Research Station close to the centre of the 170,000-ha Chiquibul National Park and Forest Reserve in southwest Belize, in forest classified by Wright et al. (1959), as deciduous seasonal forest and deciduous/semievergreen seasonal forest. Typical canopy heights in the study area are 20–30 m. The research station is the only permanent settlement in the forest, although much of the area was under cultivation during the Mayan period (up to approximately 1000 years ago), and the vegetation of the area may still reflect this impact (Johnson & Chaffey 1973).

The Chiquibul Forest has historically been subject to low-intensity selective logging, particularly of mahogany (*Swietenia macrophylla* King) and Spanish cedar (*Cedrella odorata* L.) (Johnson & Chaffey 1973; Bird 1994, 1998). Probably a more significant disturbance factor has been repeated hurricane damage and associated fires. In 1961 Hurricane Hattie passed directly over the Chiquibul Forest, and up to 90% of canopy trees were toppled (Wolffsohn 1967), although large patches of forest remained relatively undisturbed, particularly in the shelter of hills (Johnson & Chaffey 1973). Dramatic disturbance events are likely to have been a regular feature of the study area because it is estimated that hurricanes hit Belize on average every 7 years (Friesner 1993).

Experimental Design

Replicated experimental plots were set up in the Chiquibul Forest Reserve by the Belize Forest Department's Forest Planning and Management Project (FPMP) in April and May 1995 as part of a 40-year investigation into the effects of low-intensity timber extraction on tree mortality, growth rates, and species composition. I investigated the fruit-feeding butterfly assemblage in two pairs of plots at Las Cuevas and San Pastor (Fig. 1). Both plots were between 530 and 560 m elevation. Bird (1994, 1998) describes in detail the background and execution of the FPMP experiment. The FPMP plot locations were determined at random from within areas of forest set aside for future selective logging. At each site, timber trees with diameter at breast height (dbh) in the range of 40–99 cm were harvested at a density of six stems per ha from the selectively logged section (selected at random), whereas the adjacent control section was left unlogged. Although low-intensity selective logging had occurred historically throughout the study area, the "unlogged" plots are the appropriate control in this situation because they are representative of the majority of Belize's forests (Bird 1998). Including buffer zones, the total area of each plot was 40 ha, and the matrix between plots consisted of "unlogged" forest (Fig. 1). Compared with traditional selective logging in Belize, a larger volume of timber (two or three times the typical value for commercial operations in the Chiquibul: Bird 1998) of a wider range of species were harvested, and better care was taken to avoid residual damage from felling and skidding (Pinard & Putz 1996; Bird 1998). The basal area of timber removed from the central hectare of selectively logged sections was 1.45 m^2 at Las Cuevas and 2.21 m^2 at San Pastor, representing 5.8% and 9.8% of the basal area, respectively (Bird 1998). Following logging, damage to the residual stand (stems over 10 cm dbh with damaged crowns or stems) was estimated as 13% at Las Cuevas and 14% at San Pastor (Bird 1998). One year after logging, selectively logged plots showed statistically significant reductions in stand density (Bird 1998) and increases in canopy openness (Mallory & Brokaw 1997).

I sampled butterflies with Van Someren-Rydon traps baited with mashed, over-ripe bananas. This method samples a subset of the butterfly assemblage, composed largely of members of the Nymphalidae; species from this family are particularly sensitive to forest disturbance (Kremen 1992; Wood & Gillman 1998). Trapping took place on 87 days between 26 October 1997 and 6 October 1998 in all months except December, January, and May. From October 1997 to March 1998, one trap was placed in each of the four plots. From March 1998 to October 1998, more traps were available, and four traps were placed in each plot. Traps were suspended from marker posts located at 20-m intervals around the central hectare of the logged and unlogged sections, with individual traps always separated by at least 100 m. During trapping periods, traps were checked and rebaited daily. To minimize trap location effects, traps were moved 20 m clockwise around the central hectare on each sampling day.

After an initial period when all specimens were collected for identification, most butterflies could be identified in the field to species and then released. Butterflies were identified according to DeVries (1987, 1997) and D'Abrera (1984, 1987*a*, 1987*b*, 1988), and voucher

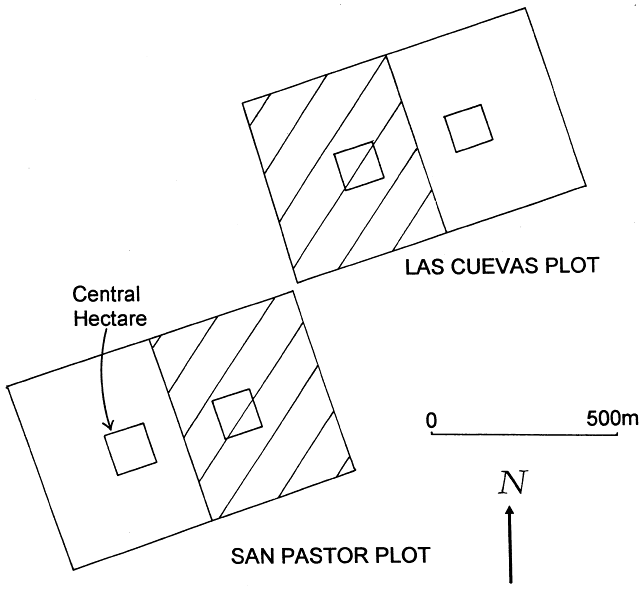

Figure 1. Location and layout of the experimental plots in Chiquibul Forest, Belize. Shaded sections were selectively logged in 1994.

specimens were checked against the collections of The Natural History Museum, London. Taxonomy follows Meerman (1999). To investigate the extent to which butterflies were dispersing between plots, I marked most released butterflies during the period 22 April 1998 to 3 October 1998 on the ventral wing surface with a unique code, using permanent marker pens.

Light Measurement

To investigate differences in forest openness between treatments and to assess the influence of light levels on butterfly abundance and diversity at particular trap locations, I measured light levels between 1100 hours and 1400 on 15 September 1998 at each trap location ($n = 80$) with a Skye quantum single-channel light meter placed on the forest floor. This device measures incident light levels (micromol/m^2/second). To assess the degree of shading, I placed a second light meter in an entirely unshaded location (at the center of the 4-ha clearing at the Las Cuevas Research Station within 1.5 km of all plots); readings from the plots and the clearing were taken simultaneously, co-ordinated by means of a hand-held radio. Light levels at each trap location were expressed as a fraction of the simultaneous unshaded reading. These values were log-transformed to achieve normality.

Analyses

Accumulation curves were plotted to show how the number of species recorded in each plot and treatment combination changed as sampling progressed. Because species richness (the number of species recorded) is strongly influenced by sample size (the number of individuals recorded), I used rarefaction or Coleman curves (Hurlbert 1971; Heck et al. 1975) to investigate the effects of selective logging on species richness. These curves show the expected species richness (with 95% confidence intervals) for samples of different sizes if these samples were drawn at random from the pooled samples for all plots.

I compared the abundance of individual species in logged and unlogged forest using chi-square tests, pooling data from the San Pastor and Las Cuevas plots. I adjusted for multiple comparisons using a sequential Bonferroni correction (W. R. Rice 1989; Sokal & Rohlf 1995).

Species-abundance distributions for pooled data from logged and unlogged forest were illustrated as rank abundance plots, with log-transformed abundance on the vertical axis and species sequence on the horizontal axis. Possible differences between the distributions were investigated with a Kolmogorov-Smirnov test. For fitting of species-abundance models (truncated lognormal and geometric series), species were grouped into $\log_3$ interval widths with interval edges at $3^n/3$. The alternative models were fitted by the methods described by Magurran (1988).

To investigate whether logged and unlogged forest were characterized by different species compositions, I used the Moritsa-Horn index to generate a matrix of similarity coefficients among the butterfly assemblages in the four sampling areas. This similarity coefficient takes into account the relative abundance of species as well as their identities and has been shown to be insensitive to variations in species richness among samples (Wolda 1981). I then used a clustering algorithm (unweighted arithmetic average, unweighted pair group method with arithmetic mean [UPGMA]) to draw a tree showing the degree of similarity among the plots.

I investigated whether the extent to which selective logging affected a species' abundance was correlated with the species' geographical range. I obtained information on the geographical range of each species, and, where relevant, the range of the particular subspecies present in the samples, from the literature (DeVries 1987, 1997; D'Abrera 1984, 1987*a*, 1987*b*, 1988; Meerman 1999). Precise distribution maps are unavailable, but these sources list the countries from which each taxon has been recorded or give the names of the countries at the limits of each taxon's range. I modified the classifications of Thomas (1991) to place taxa in one of four categories, listed in order of decreasing endemicity: 1) confined to Belize, Guatemala, and Mexico; 2) confined to Mexico and Central America, possibly extending into the southern United States; 3) present in both Central and northern South America, but range not reaching Brazil; and 4) widely distributed in Central and South America, extending at least as far south as Brazil. Modifying the methods of Hill et al. (1995) and Hamer et al. (1997), I assessed butterfly endemicity by ranking the species first in terms of the distribution of the species and second in terms of the distribution of the subspecies represented in the Chiquibul samples. This method gives the highest ranking to species found only in region 1 and the second-highest ranking to species with ranges included in region 2 but represented in the study area by a subspecies restricted to region 1.

The extent to which a species i was more common in control than in logged plots, R_{ic}, was measured as

$$R_{ic} = \frac{\log_{10}(N_{ic}+1) - \log_{10}(N_{il}+1)}{\log_{10}(N_{ic}+1) + \log_{10}(N_{il}+1)},$$

where N_{ic} and N_{il} are the total numbers of individuals of species i recorded in the two control plots and in the two logged plots, respectively. This index was chosen because the relationship between abundance in different species was approximately linear when plotted on logarithmic axes (see results section), so that R_c was uncorrelated with total abundance ($r = 0.047$, $n = 49$, $p > 0.5$) and $\log_{10}$ total abundance ($r = 0.126$, $n = 49$, $p > 0.2$).

Results

Species Richness and Abundance

Species accumulation curves (Fig. 2) were similar for each plot and treatment combination. Although individual accumulation curves did not reach an asymptote, there appears to be little difference in richness between plots in the two locations (San Pastor vs. Las Cuevas) and between selectively logged and unlogged forest. This impression was confirmed through rarefaction analysis (Fig. 3). Plotted on the same axes as the rarefaction curve for the pooled samples are the actual species richness values recorded in the four plots. In all cases, these were within the 95% confidence intervals: the number of species trapped in each plot was no lower or higher than would be expected through chance if species richness in all the plots was in fact identical.

At conventional levels of significance, 4 of the 18 species with sufficient sample sizes (total individuals trapped, ≥ 10) showed significant differences in abundance between logged and unlogged plots and had a consistent pattern in relative abundance at San Pastor and Las Cuevas (Table 1). *Hamadryas ipthime joannae* Jenkins, *Pareuptychia metaleuca* (Boisduval), *Chloreuptychia sericeella* (Bates), and *Consul electra* (West-wood) were significantly more abundant in logged forest. *Myscelia cyaniris cyaniris* (Doubleday) was significantly more abundant in unlogged forest (all $p < 0.05$). But following a sequential Bonferroni correction (Sokal & Rohlf 1995), only *H. i. joannae* and *M. c. cyaniris* showed significant differences in abundance between logged and unlogged forest (both $p < 0.05$).

The species-abundance distributions for logged and unlogged forest do not differ significantly from each other (Fig. 4; Kolmogorov-Smirnov two-sample test: maximum positive difference, 0.122; $p > 0.10$). Both the log series and lognormal distributions fit the data. The log series gave a marginally better fit in the unlogged forest and the truncated lognormal a marginally better fit in logged forest (Table 2).

Assemblage Similarity

Similarity measured by the Moritsa-Horn index was high, with values varying between 0.663 for the comparison between the Las Cuevas logged plot and the Las Cuevas control plot and 0.855 for the comparison between the San Pastor logged plot and the San Pastor control plot. The degree of similarity among plots (Fig. 5) shows no tendency for logged plots to cluster together, and neither the San Pastor samples nor the Las Cuevas samples clustered. This result is robust when a variety of alternative clustering algorithms (Krebs 1989) are used.

Butterfly Endemicity

There appears to be little tendency for species with relatively restricted geographic ranges to have lower than expected abundance in the logged plots (Fig. 6). This im-

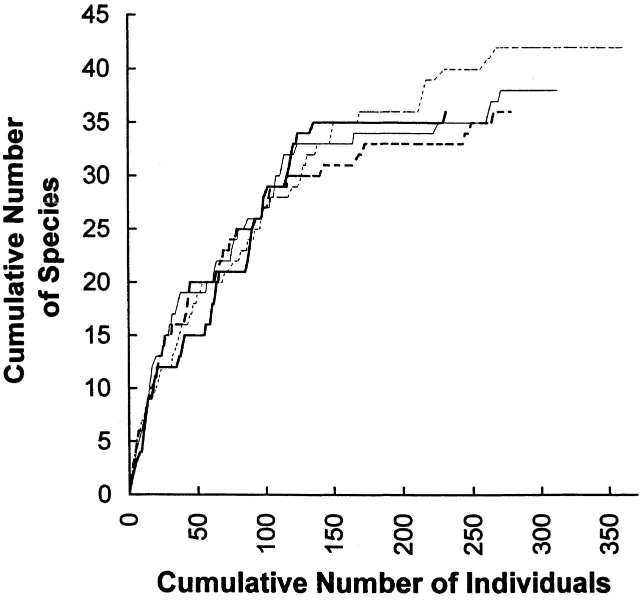

Figure 2. Butterfly species accumulation curves for the logged (broken lines) and control (solid lines) halves of the Las Cuevas (thick lines) and San Pastor (thin lines) plots.

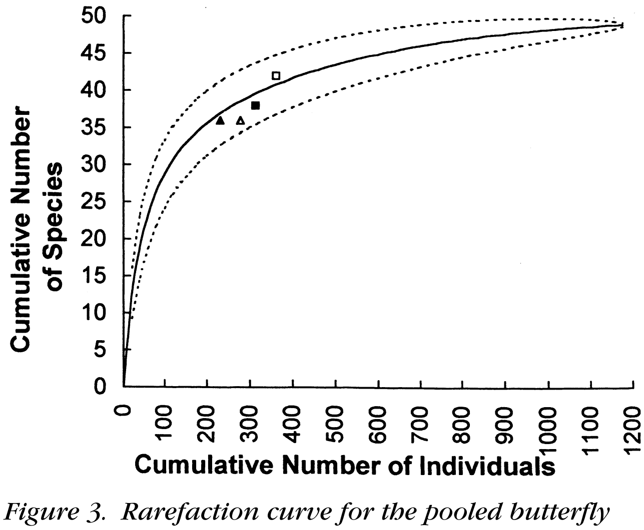

Figure 3. Rarefaction curve for the pooled butterfly data from all plots (solid line), with 95% confidence intervals (broken lines). Actual numbers of species recorded in each half of each plot are plotted on the same axes (solid square, San Pastor control plot; open square, San Pastor logged plot; solid triangle, Las Cuevas control plot; open triangle, Las Cuevas logged plot).

Table 1. Butterfly species recorded in study plots in Chiquibol Forest, Belize, with numbers of individuals recorded in each plot.*

Species	*SPL*	*SPC*	*LCL*	*LCC*	*Total*
Archaeoprepona demophon centralis Fruhstorfer	6	15	8	2	31
Archaeoprepona demophoon gulina Fruhstorfer	10	10	3	7	30
Archaeoprepona amphimachus amphimachus (Fabricius)	1	0	1	0	2
Zaretis ellops (Felder)	1	1	0	0	2
Consul electra (Westwood)	2	6	1	5	14
Memphis morvus boiduvali (Comstock)	8	0	1	1	10
Memphis oenomais (Boisduval)	2	0	1	0	3
Colobura dirce (Linnaeus)	6	2	1	8	17
Tigridia acesta (Linnaeus)	9	11	12	2	34
Historis odius odius (Fabricius)	0	1	0	2	3
Historis acheronta acheronta (Fabricius)	4	7	10	7	28
Smyrna blomfildia datis Fruhstorfer	16	17	8	25	66
Hamadryas guatemalena guatemalena (Bates)	0	0	0	2	2
Hamadryas ipthime joannae Jenkins	15	5	8	1	29
Hamadryas amphinome mexicana (Lucas)	2	2	11	6	21
Myscelia cyaniris cyaniris (Doubleday)	4	5	0	14	23
Marpesia chiron (Fabricius)	1	1	0	0	2
Eunica tatila caerulea Godman & Salvin	0	0	0	1	1
Nica flavilla canthara (Doubleday)	8	0	0	0	8
Catonephele mexicana Jenkins & de la Maza	11	1	7	16	35
Catonephele numilia esite (Felder)	7	0	7	14	28
Callicore guatemalina (Bates)	1	1	2	1	5
Callicore patelina patelina (Hewitson)	4	3	10	9	26
Adelpha felderi falcata Godman & Salvin	0	1	0	0	1
Napeogenes tolosa tolosa (Hewitson)	1	1	0	0	2
Hypothyris euclea valora (Haensch)	5	5	1	0	11
Pteronymia cotytto (Guërin)	40	5	5	3	53
Morpho polyphemus luna (Butler)	7	8	1	1	17
Morpho peleides montezuma Guenée	25	46	62	15	148
Opsiphanes quiteria quirinus Godman & Salvin	4	4	5	2	15
Opsiphanes cassina fabricii (Boisduval)	24	20	18	19	81
Eryphanis aesacus aesacus (Herrich-Schäffer)	2	1	2	0	5
Caligo memnon memnon (Felder & Felder)	1	0	0	0	1
Caligo eurilochus sulanus Fruhstorfer	1	2	0	0	3
Caligo uranus (Herrich-Schäffer)	3	2	1	4	10
Manataria maculata (Hopffer)	1	1	0	0	2
Taygetis rufomarginata Staudinger	4	5	4	2	15
Taygetis inconspicua Draudt	3	2	1	2	8
Taygetis leuctra Butler	2	6	7	3	18
Chloreuptychia sericeella (Bates)	5	0	2	1	8
Cissia confusa (Staudinger)	14	5	12	11	42
Cissia terrestris (Butler)	0	0	1	1	2
Magneuptychia libye (Linnaeus)	0	0	2	1	3
Ypthimoides remissa Weymer	7	8	2	3	20
Pareuptychia metaleuca (Boisduval)	53	45	44	17	159
Pareuptychia ocirrhoe (Fabricius)	2	3	1	1	7
Cepeuptychia glaucina (Bates)	38	54	16	22	130
Evenus telemus Cramer	0	1	0	1	2
Mesosemia lamachus Hewitson	2	1	1	0	4
Total	362	314	279	232	1187

**Abbreviations: SPL, San Pastor logged plot; SPC, San Pastor control plot; LCL, Las Cuevas logged plot; LCC, Las Cuevas control plot. Taxonomy follows Meerman (1999).*

pression is confirmed by statistical analysis: there was no significant correlation between levels of endemicity and R_{ic} (Spearman's $r_s = -0.123$, $n = 49$, $p > 0.2$). Similarly nonsignificant results were obtained if endemicity was measured by ranking species on the basis of the distribution of the species alone ($r_s = -0.065$, $n = 49$, $p > 0.5$) or the subspecies alone ($r_s = -0.145$, $n = 49$, $p > 0.2$).

Dispersal

A total of 578 individuals of 39 species were marked and released. Of these, just 47 individuals (8%) of 14 species were recaptured on one or more occasions, giving 64 recapture events. The maximum number of recaptures of any individual was 3. There were too few recaptures to

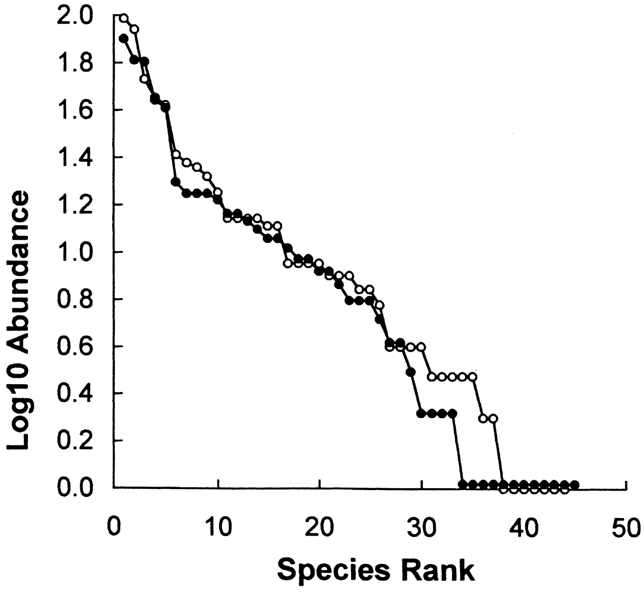

Figure 4. Butterfly rank-abundance plots for logged (open symbols) and unlogged (solid symbols) forest.

allow me to analyze mobility for species individually, so I pooled the movement data for all species to investigate dispersal of marked butterflies as a whole. Fifty-six (88%) of the recaptures involved movements within the plot half in which the individuals had been marked (movements of 20–141 m); six movements (9%) were detected between the logged and unlogged halves of the San Pastor or Las Cuevas plots (distances of 200–412 m), three by *P. metaleuca*, two by *Morpho peleides montezuma* Guenée, and one by *Colobura dirce* (L.). Two movements (3%), both by individuals of *P. metaleuca*, were detected between the Las Cuevas plots and the San Pastor plots (distance ≥ 1 km).

Effects of Light

Light intensity at trap locations was unaffected by selective logging and was similar at Las Cuevas and at San Pastor: there was no significant interaction between site and treatment ($F_{1,76} = 0.44, p = 0.522$), treatment effect ($F_{1,77} = 1.22, p = 0.273$), or site effect ($F_{1,77} = 2.15, p = 0.147$). Across all plots there was a weak but statistically significant positive correlation between light levels at trap locations and the mean number of individuals trapped ($r = 0.272$, $n = 80$, $p < 0.02$). Based on data from all plots for the 25% of trap locations with the highest illuminations and the 25% with lowest illuminations, species richness values did not differ significantly after differences in sample size were corrected for by rarefaction ($p > 0.05$).

Table 2. Fitted parameters and statistics of the log series and truncated lognormal distributions for butterflies sampled in Chiquibul Forest, Belize.

Forest type	*Log Series*				
	α	X	χ^2	*df*	*p*
logged	10. 709	0. 984	5. 463	5	0. 362
unlogged	11. 627	0. 979	4. 622	5	0. 464
	Log Normal				
	mean	*variance*	χ^2	*df*	*p*
logged	0. 838	0. 300	5. 238	5	0. 388
unlogged	0. 731	0. 334	6. 526	5	0. 258

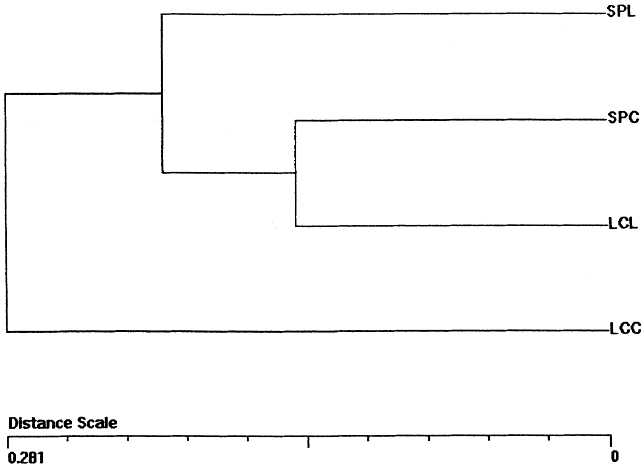

Figure 5. Degree of similarity among butterfly species assemblages in San Pastor control plot (SPC), San Pastor logged plot (SPL), Las Cuevas control plot (LCC), and Las Cuevas logged plot (LCL). Tree created using UPGMA clustering of Moritsa-Horn similarity values.

Discussion

Reaching accurate general conclusions about the effect of selective logging on biodiversity depends on drawing together information from many studies. Although recent work has highlighted the dangers of basing conservation decisions on one or a few "indicator" groups (Lawton et al. 1998), studies of taxonomically or ecologically restricted groups, particularly invertebrates, will still be of collective value (Kremen et al. 1993; Sparrow et al. 1994). A small but growing number of studies have investigated the effects of selective logging on the diversity and structure of tropical plant and animal assemblages (Nummelin & Hanski 1989; Holloway et al. 1992; Thiollay 1992; Belshaw & Bolton 1993; Hill et al. 1995; Nummelin 1996; Hamer et al. 1997; Intachat et al. 1997; Marsden 1998).

If such studies are to be used to plan or justify forest management regimes and to monitor their effect, we must be confident that their conclusions are robust. DeVries et al. (1997) list a number of problems with the

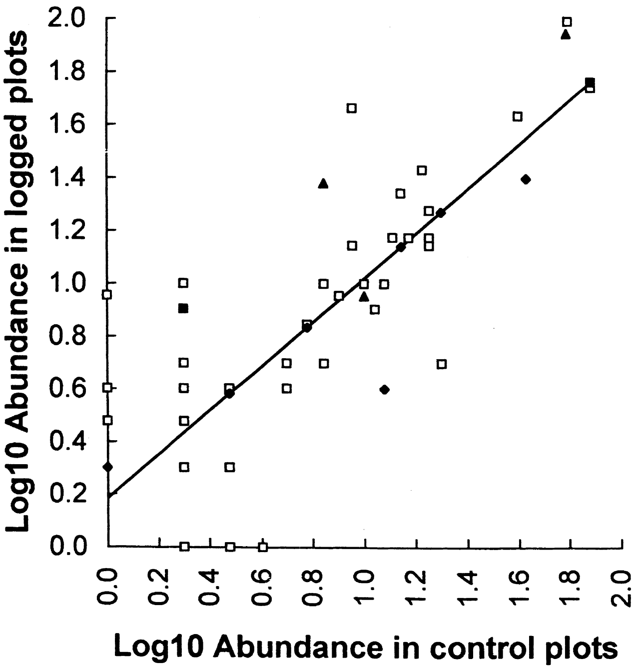

Figure 6. Relative abundance of butterfly species in the (pooled) logged and control plots. Line is the fitted model II regression line (Sokal & Rohlf 1995). Solid symbols indicate species with relatively restricted geographic ranges; solid squares, species restricted to region 1; triangles, subspecies restricted to region 1 but species occurring through region 2; diamonds, subspecies restricted to region 1 but species occurring through region 3.

scope and experimental design of many studies of tropical butterfly diversity, including short sampling periods, poor temporal resolution, nonstandardized sampling methods, use of presence-absence data only, extrapolations from small sample sizes, and lack of data on the vertical distribution of species within assemblages. Similar criticisms probably apply to studies of many other taxonomic groups. My study of fruit-feeding butterflies in a hurricane-disturbed tropical forest in Belize addresses many of these issues. In particular, the use of traps rather than sight records and the year-round sampling period (DeVries et al. 1997) give more reliable results. Compared with counts on transects, traps minimize problems with species identification in highly diverse tropical assemblages. A further advantage of my study is the use of paired, replicated experimental plots, where both locations and treatments have been allocated at random. In most studies of the effects of selective logging, investigators visit areas that have been subjected to recent selective logging and sample in logged and nearby unlogged habitats. But, if selective logging does not take place as part of a designed experiment, there are likely to be practical reasons why some areas are logged and some are left unlogged. For example, logged areas may have shallower slopes, fewer watercourses, or greater abundance of particular timber trees. This makes it difficult to determine whether any differences detected are a consequence of logging or simply reflect pre-existing differences between the study areas.

Furthermore, samples within large logged or unlogged areas of forest may give a false impression of replication, whereas in effect they may be repeatedly sampling the same fauna. This will be the case particularly in studies that use fixed trap locations. Both the richness and composition of trap samples can vary quite markedly over short distances, depending on trap location (as a consequence, for example, of variations in light levels; Sparrow et al. 1994). If a comparison of plots or sites is based on a limited number of trap locations, then the samples caught in these traps may be representative more of the trap location than of the plot or area as a whole. This problem may be alleviated by making trap locations as similar as possible (DeVries et al. 1997) or by pooling samples from arrays of traps placed at different heights and in different light conditions (Shuey 1997). I used a different solution: using 20 trap locations in each plot and moving traps systematically among these locations so that trap locations were effectively randomized rather than standardized.

One possible drawback of my methods was the restriction of trapping to the forest floor, leading to undersampling of the component of butterfly diversity present in the forest canopy (DeVries 1988; DeVries et al. 1997). Although it is possible to hoist traps into the forest canopy, the number of suitable sites for such traps within my study plots was limited, and lower catches in canopy traps (Wood & Gillman 1998) may also make sampling less efficient. Although it would have been interesting to sample the canopy butterfly fauna more fully, it is more important for comparative purposes to ensure consistency rather than to strive for a comprehensive species list from each habitat.

Selective logging 2–3 years before the study had little effect on the assemblage of fruit-feeding butterflies. Species richness, the abundance of individuals species, and the shape of the species-abundance distributions showed remarkably few differences between the selectively logged and control areas. The similarity of the species composition in each plot and treatment combination is emphasized by clustering diagrams based on Moritsa-Horn similarity indices. Not only did logged plots fail to cluster together, but there was also no tendency for plots at adjacent locations (San Pastor or Las Cuevas) to cluster. The results for butterflies are consistent with studies of the bird assemblages in the same experimental system. Mallory and Brokaw (1997) used mist netting and timed observations to compare logged and control plots at Las Cuevas, San Pastor, and two additional FPMP plots at Grano d'Oro and New Maria. Although there was some evidence of behavioral differences between birds foraging in logged and control plots and some evidence of a decline in insectivorous birds following selective logging, differences in species composition between treatments were smaller than year-to-year fluctuations within treatments (Mallory & Brokaw 1997).

Can we be sure that differences between the plots would have been detected had they been present? Examination of species accumulation curves for individual plots (Fig. 2) and for all plots pooled (the rarefaction curve in Fig. 3 is in effect a "smoothed" species accumulation curve) suggests that sampling was sufficient to have detected almost all species present in the study area. Further sampling in individual plots would no doubt add new species, but there is little reason to suspect that these rare species would change our conclusions about species richness, species-abundance differences, or the shape of species-abundance distributions.

Several of the butterflies recorded in small numbers during the study were species commonly observed during fieldwork around the study site but rarely caught in fruit-baited traps. These include the riodinid *Mesosemia lamachus* Hewitson, the ithomiid *Hypothyris euclea valora* (Haensch), the lycaenid *Evenus telemus* Cramer, and the nymphalid *Marpesia chiron* (Fabricius). If these species are not really part of the fruit-feeding butterfly guild, then including them in the analyses may introduce biases. In the Belize dataset, repeating the analyses without the data for these species did not change any of the conclusions. This may not always be the case, however, and the importance of ecological information for different butterfly species in the sensible interpretation of results must be stressed (Sparrow et al. 1994; DeVries et al. 1997). This is a particular advantage of using butterflies rather than other invertebrates for such assessments: autecological information is available, or can be gathered simply, for many species.

My results contrast with those of a number of other studies. Although the effects of selective logging and other disturbances on overall species richness have proved unpredictable, previous studies have revealed a tendency for marked changes in the abundance of particular species (e.g., Hill et al. 1995; DeVries et al. 1997). In particular, species typical of disturbed habitats are often more abundant in selectively logged forest, whereas the abundance of closed-canopy forest specialists is reduced (Hill et al. 1995; Hamer et al. 1997; Spitzer et al. 1997). Such changes in abundance may be reflected by changes in species-abundance distributions (Hill et al. 1995; Hamer et al. 1997), although evidence that fits to particular species-abundance models are indicative of disturbed or undisturbed habitats is lacking or controversial (Basset et al. 1998; Hill & Hamer 1998; Nummelin 1998; Watt 1998). Butterflies are highly sensitive to changes in light levels and consequent changes in the presence of food and nectar plants (Gilbert 1984; Brown 1991, 1997; Kremen 1992, 1994), and change in the light regime may be the main factor behind the changes in species richness, abundance of individual species, and species-abundance distributions observed in previous studies. In my study, the species of trees removed from selectively logged plots are known (Bird 1998), and none of these tree species correspond to known larval host plants of the butterfly species recorded (DeVries 1987). Thus, any changes in butterfly species composition would be mediated indirectly by changes in forest structure and light regime, rather than directly through removal of larval resources. Although the FPMP logging trials resulted in an increase in canopy openness 1 year after the experiment (Mallory & Brokaw 1997), I found similar light levels in logged and unlogged forest 2 years later, at the time of my investigation.

Previous studies of tropical butterflies have shown that species with small geographic ranges are adversely affected by forest disturbance (Thomas 1991; Spitzer et al. 1993; Hill et al. 1995; Spitzer et al. 1997; Lewis et al. 1998; but see Wood & Gillman 1998). In the Chiquibul Forest, there was no evidence that taxa with relatively small distributions tended to be lost from or to decline in selectively logged forest. Interestingly, my analyses revealed an absence of taxa with small geographical ranges: only two taxa were restricted to Belize, Guatemala, and Mexico at the specific level, and three were restricted at the subspecific level. Most of the species sampled had wide distributions in Central and South America.

If the lack of major differences in the butterfly assemblages in selectively logged and control plots is genuine, how can it be explained? One possibility is that butterfly dispersal between logged and unlogged forest is masking any differences in the composition and richness of the butterfly fauna actually using the two habitats as breeding areas. In other words, the scale of the logging experiment may be too small relative to typical butterfly dispersal distances. The mark-release-recapture data suggest that a small number of butterflies are indeed moving over distances greater than the plot dimensions, but that most dispersal is likely to be within plots. If differences between logged and unlogged plots are great, then dispersal is unlikely to entirely obscure these differences. But the possibility that more subtle differences in richness, abundance, and species composition are being masked by dispersal cannot be ruled out.

A history of natural and human disturbance is an alternative explanation for the similarity of the butterfly fauna of logged and unlogged forest. The Chiquibul Forest has been subject to selective logging over the past 100 years, albeit at intensities considerably lower than those of the 1995 experimental logging regime (Bird 1998). If this history of human disturbance has led to the extinction of closed-canopy specialist butterfly species in the study area, recent experimental selective logging may have little further effect on species composition. Natural disturbance from hurricanes is likely to have been a more significant factor. In 1961, Hattie, the most recent major hurricane, passed directly over the study site, creating a 50-km-wide band within which up to 90% of canopy trees were toppled (Wolffsohn 1967). This is one of the most severe cases of hurricane damage reported in the literature anywhere in the world (Everham & Brokaw 1996). It seems likely that the butterfly species present in the Chiquibul Forest are those able to survive high levels of disturbance of this sort; consequently, they may be well adapted to survive subsequent disturbance from selective logging. Some support for this explanation is provided by scrutiny of the list of species recorded during the study. Only species listed by DeVries (1987) as occurring in modified forest habitats in Costa Rica were recorded in the study. "Primary" or closed-canopy specialists appear to be absent from both selectively logged and unlogged forest. A few species recorded in this study are not present in Costa Rica, so data on habitat associations are unavailable, but there is little reason to suppose that these are not also disturbed-forest species.

It is increasingly recognized that the sensitivity of species to current threats may reflect "extinction filters" imposed by past events (reviewed by Balmford 1996). In the context of tropical forests, Danielsen (1997) suggests that bird assemblages in paleoecologically unstable areas might be less affected by human disturbance (for example, selective logging and fragmentation) than those in stable areas, although the existing data were insufficient for a rigorous test of his hypothesis. On a practical level, Seymour and Hunter (1999) argue that sustainability may be best achieved through "ecological forestry," in which "manipulation of a forest ecosystem should work within the limits established by natural disturbance patterns." My butterfly data, and the results of Mallory and Brokaw (1997), lend support to these suggestions. If correct, the implications for forest management and conservation are important. For example, selective logging may have a less permanent effect on biodiversity in areas that experience frequent natural disturbances.

It is worth stressing that my results are specific to the particular group of organisms investigated and the particular scale and location of the study. My results should not be taken as general evidence that selective logging in the study area had little effect on biodiversity as a whole or that butterflies in tropical forests elsewhere are unaffected by selective logging. Perhaps the most important message to come out of this study is that individual studies of the effects of selective logging and other human disturbance on tropical forests will inevitably be prone to the idiosyncrasies of the particular study area and study organisms. Generalizations should be made (and only then with great care) by looking at a range of studies of different organisms in different forest types and in different parts of the world. More field studies from a variety of regions, as well as literature-based reviews integrating data on the effect of natural disturbance and selective logging on plant and animal assemblages, would now be welcome.

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