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The Butterflies (Lepidoptera) of the Tuxtlas Mts., Veracruz, Mexico, Revisited: Species-Richness and Habitat Disturbance.

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Abstract. Checklists of the butterflies (Lepidoptera) collected in two rainforest study sites in the Tuxtlas Mts., Veracruz, Mexico are presented. A total of 182 species of butterflies were recorded at Laguna Encantada, near San Andres Tuxtla, and 212 species were recorded from the nearby Estacion de Biologia Tropical "Los Tuxtlas" (EBITROLOTU). We collected 33 species not included in G. Ross' (1975–77) faunistic treatment of the region, 12 of which are new species records for the Tuxtlas. We present a list of the skipper butterflies (Hesperioidea) of the Tuxtlas, including a state record for the giant skipper, *Agathymus rethon*.

At both study sites, we observed seasonal patterns in species abundance during periods of reduced precipitation. Our data indicate an apparent increase in butterfly species-richness in the Tuxtlas over the last 25 years. This increase reflects more efficient sampling due to advances in lepidopteran ecology and improved collecting methods, as well as the effects of habitat disturbance. A comparison between the butterfly faunas of the two rainforest sites revealed that a higher percentage of weedy, cosmopolitan species were present at Laguna Encantada, the smaller, more disturbed site. We anticipate further changes in butterfly species-richness and faunal composition as the mosaic of habitats in the Tuxtlas continue to be modified.

Introduction

Historically, the rainforests of the Sierra de Los Tuxtlas, Veracruz, Mexico have been the focus of varied and extensive ecological research (Ross 1966, 1975–77, Soto 1976, Horvitz and Beattie 1980, Horvitz and Schemske 1988, de la Cruz and Dirzo 1987, Popma, *et al.* 1988, etc.). Following Ross'(1975–77) comprehensive three year survey of the Tuxtlas butterfly fauna, studies have generated additional records and range extensions for many butterfly taxa (Welling 1982, 1983, G. Busby, unpub. data, R. Robbins and C. Beutelspacher, pers. comms.). These records provide a comparative base from which to examine changes in the profile of a Neotropical lepidopteran fauna in a region of high human impact.

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Recent expansion of cattle ranches, agricultural development and logging have reduced much of the formerly extensive rainforest of the Tuxtlas to scattered enclaves on steep slopes, in secluded volcanic craters or in local parks, resulting in a mosaic of heterogeneous rainforest patches. A lowland Neotropical wet forest may suffer local extinction of highly specialized plant species as a result of clear cutting and land conversion (Gomez-Pompa 1973). How has the Tuxtlas butterfly fauna responded to such human disturbance?

Checklists of the butterfly species collected in two separate rainforest study sites in the Tuxtlas are given here. Laguna Encantada and the "Los Tuxtlas" biological field station of the Universidad Nacional Autonoma de Mexico (EBITROLOTU, by Mexican convention) are similar in elevation (ca. 350 m) and vegetation, but differ greatly in both forest area (Laguna Encantada = 56 ha, EBITROLOTU >> 700 ha) and the extent of disturbance. We report new species records for the region and compare our findings to those of earlier studies in the Tuxtlas. Preliminary evidence is presented indicating seasonal peaks in adult flight activity among the butterfly faunas of Laguna Encantada and EBITROLOTU, corresponding to periods of reduced precipitation. Finally, we calculate the percentages of weedy, cosmopolitan species associated with disturbed habitats that presently comprise the butterfly faunas of each site as an index of disturbance.

Materials and Methods

Study Sites

The Tuxtlas Mountains are an isolated volcanic range 88.5 km long and 53.1 km wide stretching northwest to southeast along the Isthmus of Tehuantepec (Ross 1975–77, see Figure 1). The region is characterized by a warm-humid climate and represents the northernmost extension of evergreen tropical rainforest in the Americas (Gomez-Pompa 1973). Most annual precipitation occurs from June to October and varies greatly across the Sierra, ranging from 1996 mm at San Andres Tuxtla to 4700 mm at EBITROLOTU (Soto 1976, Alvarez 1982).

Our objectives were to collect and identify all butterfly species occuring at two study sites within the Tuxtlas. Ross' study generated lists of butterflies characteristic of vegetational formations such as montane rainforest, swamp forest, savanna, etc. Both Laguna Encantada and EBITROLOTU are examples of lower montane rainforests (*selva alta perenifolia*, Gomez-Pompa 1973, Ross 1975–77). Laguna Encantada (el. 350 m.) is located 2 km northeast of San Andres Tuxtla and features a small freshwater caldera flanked by steep volcanic slopes and dense rainforest dominated by *Ceiba pentandra* and *Ficus* sp. trees. Cattle grazing and logging have created numerous disturbed areas on the slopes, where successional trees such as *Cecropia mexicana*, *Cassia* sp., *Piper* sp., and *Annona* sp. grade into open grassy pastures and clusters of *Agave* sp. dot the high lip of Laguna Encantada's crater. Plants such as *Crotalaria vitellina*, *Bidens pilosa* var. *bimucronata*, *Cordia alliodora*, *C. spinescens* and *Lantana* sp. provide nectar resources not usually found within primary rainforests. Due to selective logging, human disturbance occurs within the forest as well as on its periphery. Numerous paths traverse treefall gaps, deep forest, stream beds and grassy meadows over an area of 54 ha (C. Horvitz, pers. comm.).

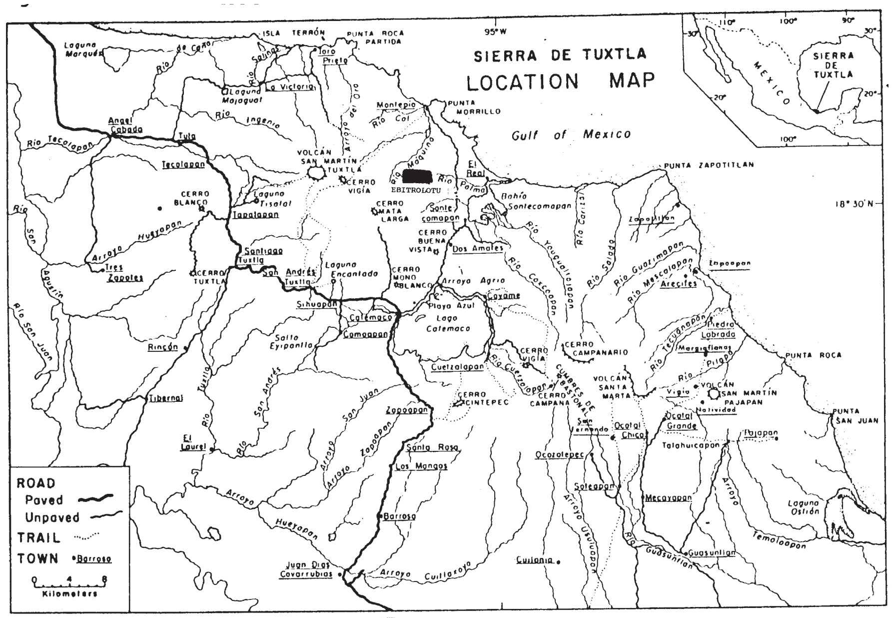

Figure 1. Maps of the Sierra de Tuxtlas, Veracruz, Mexico, after Ross (1975 above) and Lot-Helgueras (1979 below).

The second study was conducted ca. 15 km northeast of the Laguna Encantada site at EBITROLOTU. This 700 ha reserve is located ca. 34 km north of Lago Catemaco and towards the Gulf of Mexico and ranges from 150 to 530 m in elevation (Lot-Helgueras 1976, Alvarez 1982). Its steep slopes are cloaked in lower montane rainforest, with an understory of *Astrocarium mexicanum* palms (Ross 1975–77). Although primary rainforest extends well beyond EBITROLOTU's western and southern boundaries, butterflies were only collected within the confines of the reserve. Disturbed areas are found to the north of the station and secondary forest flanks the road to Montepio at the reserve's eastern end (S. Guevara-Sada and A. Gomez-Pompa 1976). The EBITROLOTU site features greater topodiversity and more primary forest than the smaller Laguna Encantada site (see Lot-Helgueras 1976, de la Cruz and Dirzo 1987).

Cursory surveys were performed from 0900 to 1500 hrs on 25.vii and 4.viii.1985 at nearby Playa Azul, situated on the northeast shore of Lago Catemaco (see Figure 1). Volcanic craters, swamps, coffee and banana plantations and rainforest remnants can all be found within a three km radius of this site (Ross 1975–77). The Playa Azul surveys were performed with the sole intention of identifying regional species records. We will include these surveys in our discussion of butterfly species-richness in the Tuxtlas but exclude them from our comparisons of the Laguna Encantada and EBITROLOTU study sites.

Collection of Specimens

Butterflies were collected from 20.vii to 31.viii.1985 at Laguna Encantada, and during most of 1985, 1986 and parts of 1987 at EBITROLOTU. Skippers (Hesperioidea) were not collected at EBITROLOTU. We employed similar collecting methods at both study sites. Prominent nectar sources, oozing sap, puddles, treefall gaps and creek beds were inspected during three half-hour intervals: 0730–0800, 1200–1230, and 1500–1530 hrs. Van Someren-Rydon traps of vertical cylindrical netting were hung above rotting bananas, mangos, animal waste and carrion, and placed near lightgaps, forest margins and moist trails (cf. Beutelspacher 1982, J. de la Maza and R. de la Maza 1985a, DeVries 1987). Traps were inspected three times daily for captured specimens at both Laguna Encantada and EBITROLOTU.

Identification of Specimens

Butterflies from Laguna Encantada were curated and deposited at the Yale Peabody Museum, New Haven, CT with representative specimens retained by the Museo de Zoologia, Facultad de Ciencias, U.N.A.M., Mexico City. Specimens collected at EBITROLOTU are currently housed in the systematic insect collection at that field station.

Specimens were identified using a variety of sources including Evans (1951–1955), Singer, DeVries and Ehrlich (1983), Lamas (1987), DeVries (1987), Godman and Salvin (1879...), Hoffmann (1940), Jenkins (1983, 1984, 1985a) and Scott (1986). We used reference collections housed at the Yale Peabody Museum of Natural History, American Museum of Natural History, Los Angeles County Museum of Natural History, Museo de Zoologia U.N.A.M., California Academy of Sciences, and the Essig Museum of Entomology, University of California, Berkeley. Individual experts were consulted in order to identify difficult taxa (see Acknowledgements).

Faunal Surveys and Comparisons

Butterfly species data from Laguna Encantada and EBITROLOTU were examined in three different contexts. First, our findings were compared to those of previous studies performed within the Tuxtlas (Ross 1975–77, etc.) and throughout tropical Mexico in an effort to identify new regional records.

Second, we suspected that the brevity of our study at Laguna Encantada may have produced unrepresentative samples due to seasonality effects. Beutelspacher (pers. comm.) warns that a six week survey may not account for highly seasonal or reclusive butterfly species. Clench (1979) described a method by which sampling effort is used to calculate the species total for a given locality:

$$S = Se\ (N)/(N + K)$$

where S = cumulative total of species observed
Se = total species theoretically present
N = cumulative total of collector/observer hours
K = constant of "collectability"

This equation describes saturation curves such as a substrate-limited enzymatic reaction (e.g. Michaelis-Menten equation) or, in this case, the observation and collection of butterfly species in a finite area over time. Given local species introductions, extinctions and chance events, a plot of species collected (S) versus time spent collecting (N) shows a sharply rising curve which tapers asymptotically at the limit of total species (Se) theoretically present at that site. This limit is calculated by solving simultaneous equations for (Se) and (K) with data from two well-spaced points on the fitted curve (Clench 1979). Deviations may accrue if the collecting protocol is changed or if butterfly abundance is seasonal. A double reciprocal transformation linearizes these data and facilitates the calculation of Se (cf. Lineweaver-Burke [case II] equation in the enzymatic analogy; W. Watt, pers. comm.).

Finally, we sought to assess the effects of habitat disturbance upon the butterfly faunas of the two rainforest sites. Recent studies have focused upon the presence or absence of bird species restricted to primary forests as indicators of human disturbance in temperate rainforests (e. g. *Strix occidentalis*; Franklin, 1988). While certain butterfly species such as *Nessaea aglaura* and *Heliconius sapho leuce* are thought to be quite habitat-restricted and intolerant of disturbance, other forest species (e. g. *Parides iphidamas*, *Cissia libye*, *Battus* sp., ithomiines, sphingid moths) are known to occur in numerous habitat types or to migrate between wet and dry forests or along altitudinal gradients (DeVries 1987, Janzen 1984). Ross' listings of the butterfly species indicative of human disturbance were more useful for our purposes. We compiled a list of species characteristic of human disturbance by pooling Ross' (1975–77) species listings from two such conditions present near our study sites: abandoned maize fields (*milpas*) and pastures (see Appendix 1). From this list, we calculated the percentage of such species among the respective faunas of each site and compared them using a 2 x 2 G-test of independence (Sokal and Rohlf, 1981: pp. 737–738). We used the ratio of collector hours/hectare calculated for each site to standardize these data for sampling effort and then repeated the 2 x 2 G-test comparison.

Results

Checklists, Species-Richness and New Records:

We collected a total of 1293 specimens representing 254 species of butterflies and skippers. Of this number, 33 species were not listed in Ross' survey of the Tuxtlas butterfly fauna, and 13 are new regional records (see Appendix 2).

During a six week study period we collected 146 species of butterflies and 36 species of skippers at Laguna Encantada. Although skipper species records for Veracruz (especially the Catemaco area) can be found throughout the literature (Evans 1951–1955, Hoffmann 1940, Freeman 1966, 1969b), our list of Hesperioidea is the first published for the Tuxtlas, and includes the first recorded observation of *Agathymus rethon* (Megathymidae) in this area. The surveys at Playa Azul produced one regional butterfly species record, *Calydna sturnula hegias* (Riodinidae), and four additional skipper species.

A total of 684 specimens representing 212 species of butterflies (Papilionoidea) were collected from February 1985 to June 1987 at EBITROLOTU (see checklist, Appendix 2). This total includes 11 new species records for the Tuxtlas region: *Parides lycimenes septentrionalis*, *Eurytides marchandi* (Papilionidae), *Sarota chrysus*, *Cremna thasus subrutila*, *Napaea eucharila picina*, *Emesis vulpina* (Riodinidae), *Zizula tulliola* (Lycaenidae), *Memphis neidhoeferi*, *Memphis xenocles*, *Cissia renata disafecta*, and *Megisto rubricata anabelae* (Nymphalidae).

Compared with Ross' data for the entire region, the number of butterfly species at Laguna Encantada, Playa Azul and EBITROLOTU combined (254) was low. This was expected, as Ross' study had encompassed a diversity of habitats from sea level to the highest elevations of the Tuxtlas, over a much larger area. It now appears that Ross' findings, particularly among the Lycaenidae, were conservative. After a five year survey of butterflies and skippers conducted in the vicinity of Lago Catemaco, G. Busby and his colleagues found that Ross' estimates of butterfly species-richness in the Tuxtlas may represent less than 77% of the actual butterfly fauna (Welling 1982, 1983, G. Busby, unpub. data). The 13 regional records included among our 254 butterfly species further indicate that Ross' totals underestimate the present species-richness of the Tuxtlas butterfly fauna.

Seasonality

A cumulative plot of the butterfly species collected at Laguna Encantada is given in Figure 2a. Upon closer inspection, the species tally levels off slightly after the first ten days, then rises sharply again during the first week in August, 1985 (see arrow). A double reciprocal plot of S and N (Figure 2b) reveals what appear to be two separate functions intrinsic to this plot, visualized more clearly when plotted independently (Figures 2c and 2d). These functions may represent the temporal overlap of two distinct seasonal faunas. A similar pattern appears in a cumulative plot

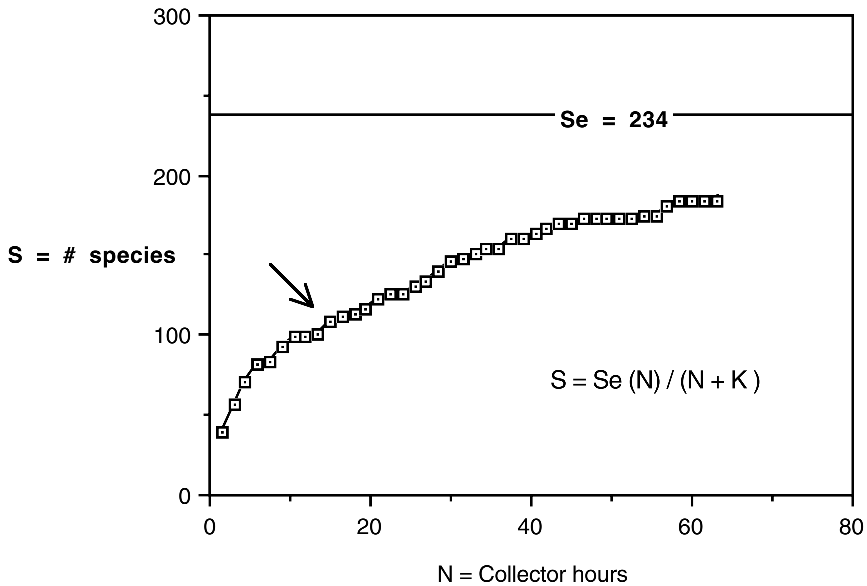

Figure 2a. Cumulative species collected, Laguna Encantada, Veracruz, 1985.

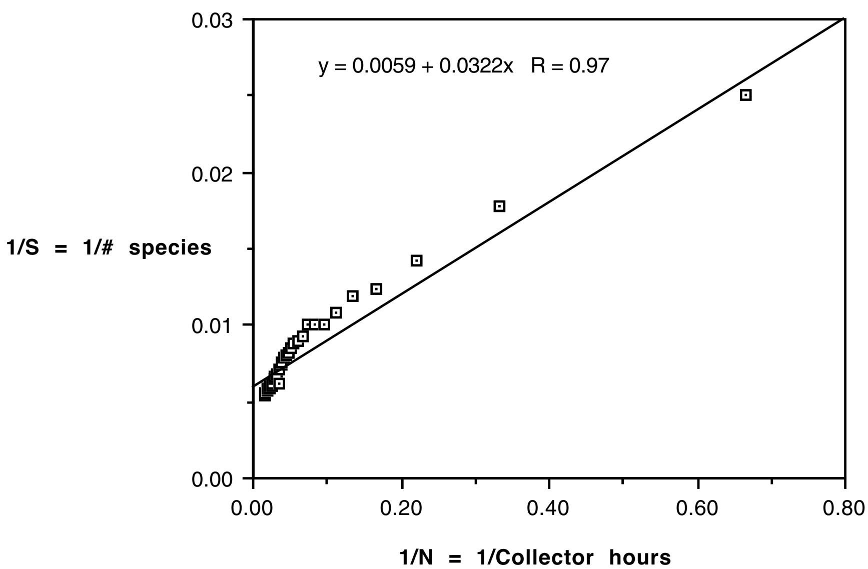

Figure 2b. Reciprocal Plots of species vs. collector-hours, Laguna Encantada, 1985.

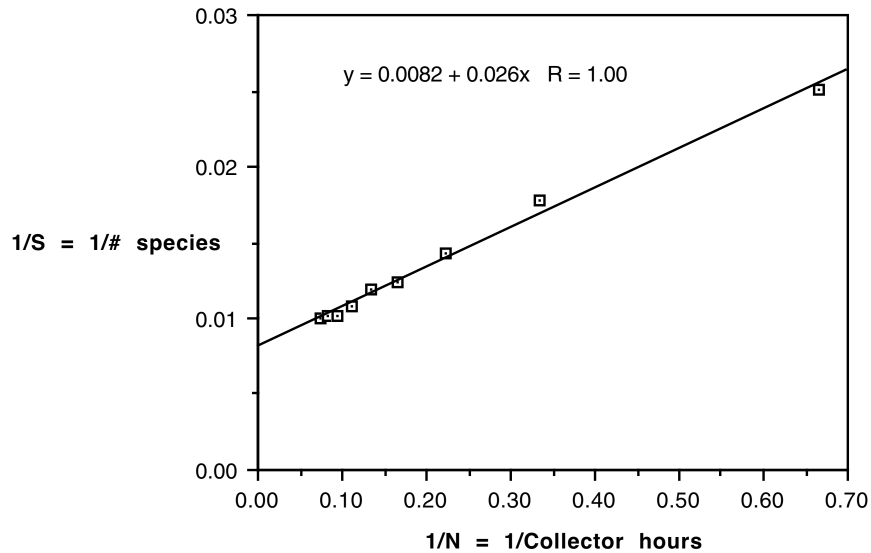

Figure 2c. Reciprocal Plot 21 - 29 July 1985, Laguna Encantada.

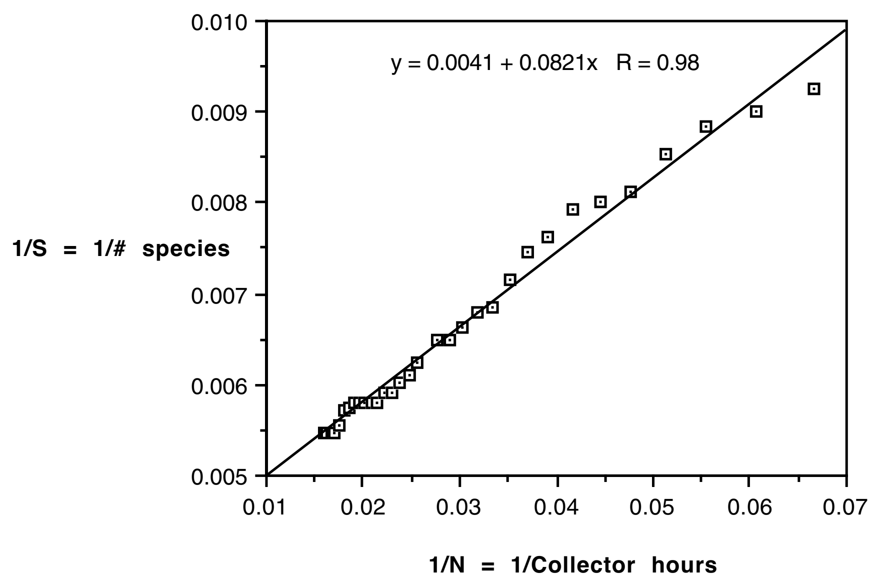

Figure 2d. Reciprocal Plot 30 July - 31 Aug. 1985, Lag. Encantada.

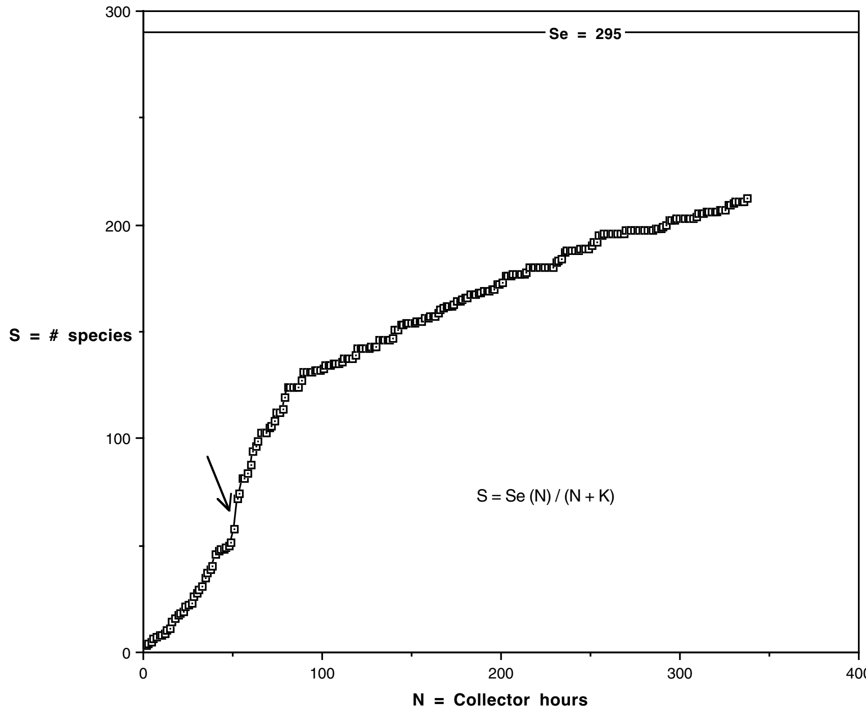

Figure 3. Cumulative species collected, EBITROLOTU, Veracruz, 1985-1987.

of butterflies collected at EBITROLOTU (see Figure 3), where the sharpest increase in number of species collected occurred between 15 and 22.iv.1985 (see arrow).

Comparison of Study Sites

According to the theoretical species total (Se = 234) calculated for Laguna Encantada, we sampled 78% of its butterfly fauna during a six week period. Similarly, our species total at EBITROLOTU (212) represents about 72% of the theoretical species-richness calculated for that site (Se = 295). The ratios of collector hours to hectares (Laguna Encantada = 1.125, EBITROLOTU = 0.484), which we use as a rough index of sampling efficiency, emphasize the great size disparity between our two study sites.

The butterfly species that presently constitute the faunas of our respective study sites are markedly dissimilar. Only about 70% of the butterfly species collected at Laguna Encantada were also a subset of the 212 species sample collected at EBITROLOTU (see Appendix 3). The number of species associated with disturbed habitats at both Laguna Encantada and EBITROLOTU is given as a percentage of the total number of species collected at each respective study site. The outcome of

Table 1. Comparison of butterfly species composition between two rainforest study sites, Veracruz, Mexico.

Study site	Laguna Encantada	EBITROLOTU
Collector-hours (N)	63 hrs	337.5 hrs
Area	56 ha	700 ha
Sampling effort (hrs/ha)	1.125	0.484
Total species Papilionoidea collected and observed (S)	146	212
Number of species characteristic of disturbed habitats* (pasture and milpa)	31	27
Percentage of total for each study site	21.23%	12.74%

I. 2 x 2 G-test of Independence G = 4.52 P < 0.05
II. Data transformed to standardize sampling effort
2 x 2 G-test of Independence G = 2.76 P < 0.10

* sensu Ross 1975-77

a 2 x 2 G-test of independence illustrates that the butterfly fauna of Laguna Encantada includes a significantly higher percentage of weedy, cosmopolitan species (21.23%) than that of the more extensive forest at EBITROLOTU (12.74%, G = 4.52, see Table 1). When we repeat this comparison after standardizing the weedy species data by multiplication with the collector hours/hectare ratios, the differences between the butterfly faunas of these two rainforest sites are still significant to the > 90% level (G = 2.76, see Table 1).

Discussion

Species Richness and New Records

Some patterns in butterfly species-richness emerge from a comparison of recent faunal surveys conducted in tropical Mexico (see Table 2). An increase in species-richness accompanies the transition from a Nearctic to a Neotropical butterfly fauna as elevation decreases from Jalapa, Veracruz southeast to the Gulf Coast lowlands (Beutelspacher 1975a, Llorente, *et al.* 1986). All authors attribute high species-richness in the Tuxtlas to the combination of habitats, vegetational types, geographic isolation and climatic stability that characterize the region (Beutelspacher 1975a, Ross 1975–77, J. de la Maza and R. de la Maza 1985a, 1985b, Llorente, *et al.* 1986). Our findings, when combined with those of Ross (1975–77) and Busby (unpublished data) indicate a total of roughly 719 butterfly and skipper species for the Tuxtlas Region. In southern Mexico, this total dwarfs that of neighboring Tabasco (C. Routledge 1977) and is

Table 2. Comparison of Lepidoptera surveys, Mexico and Costa Rica.

Author Year, Locality, elev., duration, area	Number of species by family[1]						
	Total	Hes.	Pap.	Pie.	Lyc.	Rio.	Nym.
Ross 1975-77, Tuxtlas, Veracruz, 0-1700 m, 15 mon., NA	359	—	21	36	88	48	166
C. Routledge 1977, Tabasco, 0-900 m, 14 mon., 532,656 ha	141	—	15	23	7	8	88
Raguso and Llorente 1990, a. Laguna Encantada,Veracruz, 350 m, 1.5 mon., 56 ha	182	36	9	16	20	17	84
b. EBITROLOTU, Veracruz, 170-350 m, 27 mon., 700 ha	212	—	14	19	39	27	113
Llorente, et al. 1986, Teocelo/Jalapa, Veracruz, 600-1350 m, < 6 yrs., NA	333[2]	—	20	36	66	49	162
Beutelspacher 1975, Las Minas, Veracruz, 1500 m, 16 mon., NA	127	33	9	24	12	4	45
Beutelspacher 1981, Chamela, Jalisco, 0-500 m, 12 mon., 4.44 ha	150	45	14	22	8	10	52
Beutelspacher 1982, El Chorreadero, Chiapas, 650 m, > 24 mon., NA	174	36	11	25	13	14	78
J. & R. de la Maza 1985, Boca del Chajul, Chiapas, 150 m, 4 yrs., 800 ha	544	148	26	31	64	76	199
DeVries 1983, Costa Rica, 0-3500m, NA, NA.	1467	353	40	71	275[3]	300[4]	428

[1] Key to abbreviations: Hes. = Hesperioidea, Pap. = Papilionidae, Pie. = Pieridae, Lyc. = Lycaenidae, Rio. = Riodinidae, Nym. = Nymphalidae., NA= not available
[2] plus 20 unidentified species
[3] R. Robbins pers. comm.
[4] P. DeVries pers. comm.

exceeded only by the butterfly fauna of Chiapas (see J. de la Maza and R. de la Maza 1985a, 1985b, Beutelspacher 1982).

In the 25 years since Ross' study took place, four new butterfly species, *Adelpha leucerioides*, *A. diazi* (Beutelspacher 1975b), *A. milleri* (Beutelspacher 1976) and *Mesosemia gemina* (J. de la Maza and R. de la Maza 1980), and two new subspecies, *Prepona brooksiana escalantiana* (Descimon, Mast de Maeght and Stoffel 1974) and *Dismorphia eunoe popoluca* (Llorente and Luis 1988) have been described from the Tuxtlas. Numerous species records have appeared in the works of Freeman (1966, 1969b), Welling (1982, 1983), Busby (unpub. data) and this paper. Recent censuses of hairstreak butterflies (Lycaenidae) in the Tuxtlas have accounted for nearly twice as many species as Ross had collected (R. Robbins, G. Busby, pers. comm.). If butterfly species-richness in the Tuxtlas has increased, what are the causes?

Let us examine the traits of the 13 species newly observed in the Tuxtlas. Five of these species are members of the Riodinidae; a family of butterflies whose life histories are poorly understood. Many adult riodinids perch on the undersides of leaves and are crepuscular in nature (Ross 1975–77). These habits may have allowed riodinids to remain undetected during previous butterfly censuses.

Butterfly species that fly high above the forest floor, avoid flowers, or are difficult to identify may also escape notice. *Memphis neidhoeferi* and *M. xenocles* are elusive charaxines that fly in primary and secondary rainforest canopies, descending to feed on rotting fruit, feces and carrion (DeVries 1987). The use of Van Someren-Rydon traps, the most reliable method for capturing *Memphis* butterflies, was not widespread during the years of Ross' study (1962–65). Many of the metallic blue-colored *Memphis* species are also variable and difficult to identify (Comstock 1961, DeVries 1987). Similarly, females of the swallowtail butterfly *Parides lycimenes* are easily confused with those of *Parides iphidamas*, *P. erithalion* and *P. sesostris*. The satyrine *Cissia renata* flies in bright sunlight in all forest habitats and also visits animal dung and rotting fruit (DeVries 1987). Llorente and Luis (1989) have collected increased numbers of riodinid, charaxine and satyrine species by using Van Someren-Rydon traps and by collecting in early morning and late evening. The butterfly species discussed above were probably omitted from previous surveys due to incomplete sampling or misidentification.

The observed increase in lycaenid species-richness may reflect a combination of habitat disturbance and sampling efficiency. Ross collected most of his 83 species of hairstreak butterflies near Catemaco at flowers of *Cordia spinescens*, *C. alliodora*, *Crotalaria vitellina* and *Bidens pilosa*; plant species indicative of forest margins and pastures. Most of Busby's 150 hairstreak species were collected at blossoms of *Cordia* (unpublished data). The availability of *Bidens*, *Cordia* and *Crotalaria* nectar resources, which appear to increase in direct proportion to the development of forest land, may lure lycaenids from the forest canopy down to ground level, and thus facilitate their capture. This phenomenon may account for our record of *Zizula tulliola* at EBITROLOTU.

A similar combination of disturbance and increased sampling efficiency could explain the current abundance of *Opsiphanes cassina fabricii* and *O. tamarindi sikyon*; two brassolines not observed during Ross' study. These species utilize plants of the Musaceae, Arecaceae and Heliconiaceae as hosts and exploit the coconut palms and banana plantations which accompany urban development and agriculture. Coconut and banana are not new to the Tuxtlas, and *Opsiphanes cassina* and *O. tamarindi* have probably inhabited local secondary forests with native *Heliconia* and palms for centuries. However, these butterflies are now regularly seen flying at dusk through the streets of Catemaco and San Andres Tuxtla, and it is likely that agriculture and urbanization have contributed to their abundance and detection.

Our three remaining species records for the Tuxtlas are butterflies that were probably overlooked because they are rare. *Eurytides marchandi* is a distinctively golden-colored swallowtail that flies near rivers and forest edges. It may be a recent introduction from the southeast, where it is known from lowland Chiapas (J. de la Maza and R. de la Maza 1985a), or it may simply be scarce in the Tuxtlas.

Megisto rubricata is a grass-feeding satyrine which is generally found in shady oak-pine forests and arid canyons from Texas to Guatemala (Scott 1986). We collected *M. rubricata* at EBITROLOTU from February to October in 1985 and 1986. Since the only substantial oak-pine forests in the Tuxtlas lie roughly 40 km southeast of EBITROLOTU on the southern slopes of the Santa Marta volcano (Ross 1975–77), the habitat requirements for *M. rubricata* may not be as strict as was previously thought.

The presence of *Agathymus rethon* at Laguna Encantada is an enigma. *A. rethon* has been collected at 1200 m in Puebla, Morelos, Guerrero and the Oaxaca/Chiapas border. Like other megathymids, it is closely wed to its foodplant, *Agave sisalana* (Stallings and Turner 1957, Freeman 1969a). In early August 1985, we observed two adults perched on a small, dark green-leaved *Agave* on the northern lip of Laguna Encantada's crater. Gomez-Pompa (1973) identified *Agave* species from three localities in Veracruz - the high pine forests of Jalapa, the arid hills of Perote, near Puebla, and the desert bordering Hidalgo - but made no mention of *Agave* in the Tuxtlas. Likewise, *Agave* seeds were not discussed in studies of seed dispersal by birds (Trejo-Perez 1976, Van Dorp 1985) or bats (Orozco-Segovia, *et al.* 1985) conducted at EBITROLOTU. Nevertheless, Ross (1975–77) found *Agave* sp. to be locally abundant in elfin woodland on the exposed upper ridges of the San Martin and Santa Marta volcanoes in the Tuxtlas. We think that the *Agave*/*Agathymus rethon* association at Laguna Encantada is probably one of a few scattered relicts of a drier period in the Tuxtlas' history.

In summary, we attribute the apparent increase in butterfly species-richness in the Tuxtlas to the following factors:

1. improved collecting methods
2. increased knowledge of species' life histories
3. the effects of human disturbance on local habitats and vegetation
4. the gradual detection of rare species as a function of cumulative sampling effort.

Seasonality

Mid to long-term faunal surveys such as Ross'work in the Tuxtlas (15 months) and our study at EBITROLOTU (27 months) bear the important feature of having sampled the butterflies of those sites during at least one entire year. Shorter-term censuses, on the scale of our study at Laguna Encantada (6 weeks), may highlight seasonal fluctuations in butterfly species abundance. Shapiro (1975) and Hill (1988) have discussed the importance of temporal distribution and seasonality to the measurement of butterfly species-richness. Studies of the butterfly faunas of tropical rainforests in Panama (Emmel and Leck 1970) and Queensland, Australia (Hill 1988) indicate that butterfly seasonal abundance is a complex phenomenon linked to environmental factors such as precipitation. Fox, *et al.* (1965) observed peak butterfly abundance in Liberia during the dry season, while Owen (1971) found butterflies in adjacent rainforests in Sierra Leone to be most abundant during the rainy season.

In their analysis of the butterfly fauna of southern Chiapas, J. de la Maza and R. de la Maza (1985b) described two peaks of adult butterfly flight activity during the Mexican summer; the first occurring toward the end of the dry season in April and the second during the sunniest segment of the wet season in August and September. These authors predicted that such patterns would be consistent throughout the rainforests of the Mexican Gulf Coast.

We observed an increase in butterfly species at Laguna Encantada in early August 1985 that corresponded to reduced precipitation during this period (personal observation). While it is important not to extrapolate meteorological data overzealously across the Tuxtlas, a record of precipitation collected at EBITROLOTU (C. Field, unpublished data, see Figure 4) illustrates reduced rainfall during August 1985. By the end of August, the number of new butterfly species encountered at Laguna Encantada had diminished to nearly zero.

Seasonal patterns were also evident at EBITROLOTU. The sharp increase in butterfly species encountered in mid-April 1985 also corresponded to reduced precipitation (see Figure 4). We did not, however, observe an additional species increase at EBITROLOTU during the first week of August 1985. The species that first appeared during this time at Laguna Encantada (eg. *Parides erithalion polyzelus*, *Colobura dirce*, *Epiphile adrasta*) are multiple-brooded and had already been collected at EBITROLOTU during the spring months. Using Clench's method,

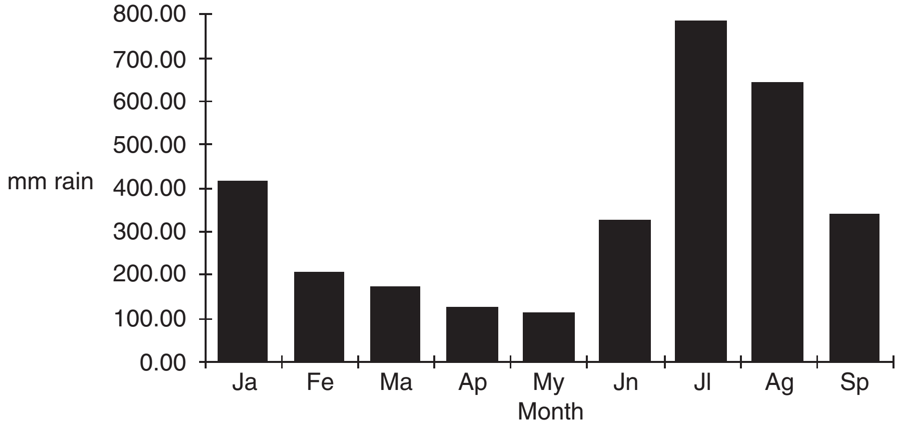

Figure 4. Rainfall Data, EBITROLOTU, Veracruz, 1985 (C. Field, unpublished data).

seasonal effects are visible only during the early stages of a cumulative species census. The use of mark-release-recapture studies (Ehrlich and Davidson 1960), malaise traps (Covell and Freytag 1979), and the observational methods of Pollard (1977) and Hill (1988) are better suited to the specific study of butterfly seasonality.

Comparison of Study Sites

At Laguna Encantada and EBITROLOTU, we have sampled what appear to be distinctly different butterfly faunas. At Laguna Encantada we encountered a significantly higher percentage of generalist butterfly species than that found at the larger, less disturbed EBITROLOTU site. In addition, at least 13 species putatively associated with lower montane rainforest were present at EBITROLOTU but absent at Laguna Encantada (see Appendix 3). Do our results highlight the effects of habitat disturbance, the artifacts of imperfect experimental design or simply an unforseen dissimilarity between rainforest microhabitats in the Tuxtlas?

Many workers have addressed the effects of habitat disturbance on local resource availability and biological diversity (May 1973, 1981; Connell 1978; see Denslow 1985 for review). Although our discussion has stressed disturbance brought about by human activities, natural events such as hurricanes, fires and treefalls may cause ecological disturbance of comparable magnitude. Depending on its historical scale and frequency, habitat disturbance may elicit a variety of responses from the members of a given Neotropical butterfly community.

According to Blau (1980), who studied populations of *Papilio polyxenes* in Costa Rica, there is a large assemblage of Neotropical insect species adapted for exploiting habitats produced by localized disturbances. In his ecological analysis of the moth fauna of Costa Rica's Santa Rosa region, Janzen (1988a) extends this discussion to the spatial and tempo ral variation in land use and ecological disturbance near Guanacaste National Park. Janzen (1988b) notes that the resulting mosaic of habitats and successional stages of vegetation presently accomodates more species of Lepidoptera than a pristine dry tropical forest, past or future, could realistically support.

There are important differences between cosmopolitan species that can exploit disturbed forest habitats and organisms that are adapted to undisturbed primary forests. We have discussed the prevalence of weedy, cosmopolitan species at the disturbed Laguna Encantada site and note that a similar pattern was observed by Welling (1966) for *Papilio*, *Euptoieta*, *Zerene* and *Phoebis* species in patches cut into dense thorn forests of the Yucatan Peninsula. Many of these butterflies are migratory habitat generalists with catholic hostplant requirements and broad distributions throughout the tropical Americas, and could rapidly invade disturbed rainforest patches in the Tuxtlas. For example, at Laguna Encantada we frequently observed *Phoebis philea* and *Anteos clorinde nivifera* flying at the forest's borders and over its canopy and ovipositing on *Cassia* trees in light gaps within the forest. If the disturbances that promote the recruitment of *Cassia* trees in rainforest gaps are frequent, we believe that these pierid species, which range from Texas to Argentina, will persist at Laguna Encantada.

Have we censused the butterfly faunas of Laguna Encantada and EBITROLOTU thoroughly enough to legitimize the comparisons presented in this paper? As discussed by R. Routledge (1980) and Pielou (1960, see Peet 1974 for review), it is difficult to remove sampling bias from experimental measurements of diversity in large communities. Despite the limitations discussed by Clench (1979, especially regarding K, the collectability constant.), we chose the enzymatic model to analyze the results of our surveys because of its applicability to our collecting methods and its emphasis on sampling effort.

Although we sampled roughly 78% of the butterfly fauna of Laguna Encantada in six weeks, we calculate from our model that an additional 4000 collector-hours would have been required to account for its complete fauna. By this reasoning, many more collector hours would have been necessary to fully sample the butterfly fauna of the larger EBITROLOTU site. Sampling effort on this scale is only practical for long-term studies conducted by numerous researchers. Although we spent five times as many collecting hours at EBITROLOTU than at Laguna Encantada, our sampling at the former site was slightly less thorough. This result and the ratios of collector hours/hectare illustrate the great size disparity between the two study sites and the difficulties inherent to biotic surveys of different-sized habitats.

It is not clear whether the distinctive differences between the butterfly faunas of EBITROLOTU and Laguna Encantada are a consequence of human disturbance or simply a reflection of intrinsic differences between these two sites. Were primary forest specialists present at

EBITROLOTU (e.g. *Nessaea aglaura*) driven to local extinction by disturbance at Laguna Encantada, or were they never there in the first place? It will be important to return to Laguna Encantada and look for these potential indicator species. The presence of older *Cecropia*, *Ceiba* and *Ficus* trees at Laguna Encantada suggests that disturbance has played a historical role in the ecology of that site. On the other hand, differences in altitude, precipitation and topography may render the rainforests at Laguna Encantada and EBITROLOTU more dissimilar than they appear. An experiment such as Brazil's "Minimum Critical Area" project, in which forest patches of different sizes were cut from continuous lowland rainforest, would be better suited to address these questions.

Rainforests throughout the Tuxtlas Mountains of Veracruz, Mexico are becoming highly fragmented, and our study sites, particularly Laguna Encantada, are likely to become even more disturbed and isolated. Which members of a fragmented forest's butterfly fauna will be sustained if external sources of immigrants have been eliminated? In Costa Rica, the protected dry forests of Guanacaste National Park will become more homogeneous and pristine with succession. Janzen (1988b, also see Gilbert 1980) predicts the disappearance of many species of Lepidoptera in these forests, because potential sources of species immigration external to the park were destroyed long ago and thus will be unable to counter local extinction. In time, the extensive faunistic data bases from Guanacaste should facilitate the testing of that hypothesis. Unlike Guanacaste, the Tuxtlas region of Veracruz, Mexico will continue to suffer human disturbance and cannot presently be said to have reached its zenith in butterfly species-richness. We simply don't understand the history of human occupation and disturbance in the Tuxtlas well enough to predict the fates of its forests and their faunas. It will be important to update surveys such as ours periodically, paying particular attention to species introductions and disappearances and the state of proximal forests as potential sources of immigrants.

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Appendix 1. Butterfly species characteristic of disturbed habitats, after Ross (1977) and Robbins (pers. comm.).

Papilionidae	* Papilio thoas
Pieridae	* Ascia monuste
	Eurema daira
	Eurema mexicana
	* Eurema nicippe
	Gluthophrissa drusilla
	* Phoebis sennae
	* Phoebis philea
	* Phoebis argante
	Pyrisitia boisduvaliana
	Pyrisitia proterpia
	* Pyrisitia lisa
	Pyrisitia dina
	Pyrisitia nise
	* Zerene cesonia
Nymphalidae	Anaea aidea
	Anartia fatima
	Anartia jatrophae
	Anthanassa ardys
	Castilia myia
	Castilia griseobasalis
	Chlosyne janais
	Chlosyne lacinia
	* Danaus gilippus
	Dryas iulia
	* Euptoieta hegesia
	Hermeuptychia hermes
	* Marpesia chiron
	Phyciodes vesta
	Thessalia theona
Lycaenidae	Calycopis isobeon
	Everes comyntas
	Hemiargus ceraunus
	Hemiargus huntingtoni
	Leptotes cassius striata
	Rekoa palegon
	Rekoa marius
	† Strymon columella
	† Tmolus azia
	† Tmolus echion
Riodinidae	Juditha molpe

* cited by Ross (1975-1977) or DeVries (1987) as being migratory.

† Robbins pers. comm.

Appendix 2. A Checklist of the Butterflies of Laguna Encantada and La Estacion de Biologia Tropical "Los Tuxtlas" (EBITROLOTU), U.N.A.M., Veracruz, Mexico.

Totals: 254 species, 1293 specimens.
R denotes taxon not found in Ross' checklist 1975-77.
N denotes taxon not previously reported from Tuxtlas.
S denotes definitive sight record; all others are collected specimens.
PA denotes specimen collected at Playa Azul, near Catemaco.

Taxon	Study Sites: Laguna Encantada 20 vii - 31 viii 1985	EBITROLOTU i 1985 - vi 1987
HESPERIOIDEA		
HESPERIIDAE		
Pyrginae		
Epargyreus exadeus (Cramer 1779)	**2**	-
Urbanus proteus (Linnaeus 1758)	**2**	-
Urbanus dorantes (Stoll 1790	**2**	-
Urbanus procne (Plotz 1880)	**1**	-
Astraptes anaphus (Cramer 1777)	**1**	-
Astraptes fulgerator (Welch 1775)	**4**	-
Autochton neis (Geyer 1832)	**3**	-
Aethilla lavocrea Butler 1872	**1 PA**	-
Achalarus toxeus (Plotz 1882)	**1 PA**	-
Cogia calchas (Herrich-Schaeffer 1869)	**2**	-
Nisoniades rubescens(Moschler 1876)	**3**	-
Nisoniades ephora (Herrich-Schaeffer 1870)	**1**	-
Carrhenes canescens (R. Felder 1869)	**1**	-
Xenophanes trixus (Stoll 1780)	**2**	-
Achlyodes thraso (Hubner 1807)	**1**	-
Achlyodes busirus (Stoll 1782)	**2**	-
Timochares trifasciata (Hewitson 1868)	**2**	-
Gesta gesta invisus (Butler & H. Druce 1892)	**1**	-
Ephyriades brunneus floridalis (Bell & W. Comstock 1948)	**2**	-
Pyrgus communis (Grote 1872)	**2**	-
Pyrgus oileus (Linnaeus 1767)	**3**	-
Heliopetes macaira (Reakirt 1866)	**1 PA**	-
Heliopetes arsalte (Linnaeus 1758)	**1 PA**	-
Quadrus cerealis (Stoll 1782)	**3**	-
Quadrus lugubris (R. Felder 1869)	**1**	-
Nascus phocus (Cramer 1777)	**1**	-
Theogenes lactifera (Butler & Druce 1872)	**1**	-
Antigonus nearchus (Latreille 1824)	**1**	-
Hesperiinae		
Calpodes ethlius (Stoll 1782)	**1**	-
Cymaenes odilia (Burmeister 1878)	**3**	-
Ancylocypha arene (Edwards 1871)	**1**	-
Pompeius pompeius (Latreille 1824)	**3**	-
Talides sergestus (Cramer 1775)	**1**	-
Vettius fantasos anaca (Evans 1955)	**2**	-
Cynea cynea (Hewitson 1876)	**1**	-
Parphorus decorum (Herrich-Schaeffer 1869)	**1**	-
Moerus striga stroma (Evans 1955)	**1**	-
Anthoptes epictelus (Fabricius 1793)	**1**	-
Papias subcostulata integra (Mabille 1891)	**1**	-

Megathyminae		
Agathymus rethon (Dyar 1913)	**1 (+1S) N**	-
PAPILIONOIDEA		
PAPILIONIDAE		
Papilioninae		
Parides photinus (Doubleday 1844)	**6**	-
Parides erithalion polyzelus (R. Felder 1865)	**3**	**5**
Parides lycimenes septentrionalis (J. de la Maza and Diaz 1978)	-	**8 R, N**
Parides iphidamas (Fabricius 1793)	-	**7**
Parides eurimedes mylotes (Bates 1856)	-	**8**
Parides sesostris zestos (Gray 1852)	-	**2**
Battus belus varus (Kollar 1850)	-	**5**
Papilio polyxenes asterias (Stoll 1782)	**1 S, PA**	-
Papilio cresphontes (Cramer 1777)	-	**1 R**
Papilio thoas autocles (Rothschild & Jordan 1906)	**6**	**1**
Papilio androgeus epidaurus (Godman & Salvin 1890)	**1 S**	**2**
Pyrrhosticta victorinus (Doubleday 1844)	-	**2**
Priamides anchisiades idaeus (Fabricius 1793)	**2**	**7**
Eurytides marchandi (Boisduval 1836)	-	**3 R, N**
Eurytides phaon (Boisduval 1836)	**1 PA**	**3**
Eurytides belesis (Bates 1834)	**1**	**7**
Eurytides branchus (Doubleday 1846)	**1**	-
Eurytides philolaus (Boisduval 1846)	**1**	-
Eurytides epidaus (Doubleday 1846)	**2**	-
PIERIDAE		
Dismorphiinae		
Dismorphia amphiona praxinoe (Doubleday 1844)	**2**	**2**
Dismorphia theucarilla fortunata (Lucas 1854)	-	**3**
Pierinae		
Ascia monuste (Linnaeus 1764)	**9**	**1**
Melete isandra (Linnaeus 1764)	**2**	-
Itaballia pisonis kicaha (Reakirt 1863)	-	**5**
Catasticta nimbice ochracea (Boisduval 1836)	-	**1**
Pieriballia viardi (Boisduval 1836)	-	**5**
Gluthophrissa drusilla poeyi (Butler 1872)	-	**5**
Coliadinae		
Zerene cesonia (Stoll 1791)	**2**	**1**
Anteos clorinde nivifera (Fruhstorfer 1907)	**5**	-
Phoebis sennae marcellina (Cramer 1777)	**10**	**3**
Phoebis philea (Linnaeus 1763)	**8**	**2**
Phoebis argante (Fabricius 1775)	**4**	**2**
Phoebis agarithe (Boisduval 1836)	**2**	**1**
Rhabdodryas trite (Linnaeus 1758)	-	**3**
Pyrisitia proterpia (Fabricius 1775)	**5**	**2**
Pyrisitia lisa (Boisduval & LeConte 1833)	-	**3**
Pyrisitia nise nelphe (R. Felder 1864)	**8**	**4**
Pyrisitia dina westwoodi (Boisduval 1836)	**6**	-
Eurema albula celata (R. Felder 1869)	**7**	**6**
Eurema daira eugenia (Wallengren 1860)	**6**	**4**
Eurema xanthochlora (Kollar 1850)	**1**	**6**
Eurema nicippe (Cramer 1780)	**1**	-

LYCAENIDAE		
Theclinae		
Pseudolycaena damo (Druce 1875)	**2**	**5**
"Thecla" theocritus (Fabricius 1793)	**1 PA, R**	**1**
"Thecla" hesperitis (Butler and Druce 1872)	**1**	**0**
"Thecla" sp. aff. plusios Godman and Salvin 1887	-	**2**
"Thecla" barajo (Reakirt 1866)	**1**	**3**
"Thecla" tephraeus (Geyer 1837)	**1**	-
"Thecla" halciones (Butler and Druce 1872)	**1**	-
"Thecla" 7 unidentified species	-	**total 8**
Rekoa marius (Lucas 1857)	**6**	-
Rekoa meton (Cramer 1782)	**1 S**	**1**
Eumaeus toxea (Hubner 1806)	**2 PA**	**4**
Brangas coccineifrons (Godman & Salvin 1887)	-	**1**
Atlides polybe (Linnaeus 1758)	**1**	-
Ministrymon arola Hewitson 1868	**2**	-
Tmolus echion (Linnaeus 1758)	**2**	-
Tmolus azia (Hewitson 1873)	**1 PA**	-
Tmolus 3 unident. species.	-	**total 3**
Oenomaus ortygnus (Cramer 1782)	**1**	-
Calycopis isobeon (Butler & Druce 1872)	**8**	**6**
Calycopis 3 unident. species.	-	**total 7**
Cyanophrys 5 unident. species.	-	**total 5**
Cyanophrys miserabilis Clench 1946	**3**	-
Cyanophrys herodotus (Fabricius 1793)	**1**	-
Arawacus sito (Boisduval 1836)	**3**	**3**
Arawacus togarna (Hewitson 1863)	-	**8**
Panthiades bathis (Fabricius 1781)	**1**	**1**
Panthiades bitias (Cramer 1777)	-	**1**
Strymon sp.	-	**1**
Strymon columella Reakirt 1866	**1 PA**	-
Strymon rufofusca (Hewitson 1877)	**2 PA**	-
Electrostrymon sp. aff. cyphara (Hewitson 1874)	**3**	-
Arcas cypria (Geyer 1837)	-	**1**
Theritas sp.	-	**1**
Chalybs sp.	-	**3**
Polyommatinae		
Hemiargus isola (Reakirt 1866)	-	**1**
Hemiargus ceraunus zachaeina (Butler and Druce 1872)	**2**	-
Leptotes cassius striata (Edwards 1887)	**2**	**3**
Everes comyntas texanus (R. Chermock 1944)	**3**	**6**
Celastrina ladon gozora (R. Chermock 1944)	-	**1**
Zizula tulliola (Godman & Salvin 1887)	-	**1 R, N**
RIODINIDAE		
Euselasiinae		
Euselasia sergia (Godman & Salvin 1885)	-	**6**
Hades noctula (Westwood 1851)	**1**	**8**
Riodininae		
Perophthalma tullius lasus Westwood 1851	-	**6**
Leucochimona vestalis (Bates 1865)	-	**4**
Leucochimona lepida nivalis (Godman & Salvin 1885)	-	**5**
Mesosemia gemina J. de la Maza and R. de la Maza 1980	-	**2**
Mesosemia telegone (Boisduval 1836)	**5 R**	-
Eurybia elvina (Stichel 1910)	**3 R**	**1**

Calospila sudias (Hewitson 1856)	**5**	-
Napaea umbra (Boisduval 1870)	-	**1**
Napaea eucharila picina Stichel 1910	-	**3 R, N**
Cremna thasus subrutila Stichel 1910	-	**3 R, N**
Charis velutina (Godman & Salvin 1878)	-	**6**
Calephelis sp. 1	**2**	**4**
Calephelis sp. 2	**2**	-
Melanis pixe (Boisduval 1836)	**4**	**5**
Charmona gynaea zama (Bates 1868)	**7**	-
Lasaia agesilas callaina Clench 1972	**1 S, R**	-
Lasaia unident. sp.	-	**2**
Mesene croceela Bates 1865	-	**2**
Symmachia tricolor hedemanni (R. Felder 1869)	-	**1**
Sarota myrtea (Godman & Salvin 1886)	-	**4**
Sarota chrysus (Cramer 1782)	-	**6 R, N**
Calydna lusca venusta (Godman and Salvin 1886)	**1**	-
Calydna sturnula hegias (R. Felder 1869)	**1 PA, R, N**	-
Emesis mandana (Cramer 1780)	-	**2**
Emesis vulpina (Godman & Salvin 1886)	-	**2 R, N**
Emesis lucinda saturata Godman and Salvin 1886	**9 R**	-
Emesis lupina (Godman and Salvin 1886)	**4**	-
Thisbe lycorias (Hewitson 1853)	**5**	**1 R**
Lemonias agave (Godman & Salvin 1886)	-	**2**
Juditha molpe (Hubner 1808)	**8**	**6**
Theope 2 unident. sp.	-	**total 3**
Theope virgilius Fabricius 1793	**3 R**	-
Theope eupolis Schaus 1890	**1 R**	-
Theope bacenis Schaus 1890	**1 R**	-
Pandemos godmanii DeWitz 1877	-	**1 R**
Menander menander purpurata Godman & Salvin 1878	-	**5**
NYMPHALIDAE		
Heliconiinae		
Agraulis vanillae incarnata (Riley 1926)	**3**	**3**
Dione juno huascuma (Reakirt 1866)	**1**	**4**
Dryas iulia moderata (Stichel 1926)	**5**	**6**
Eueides isabella eva (Cramer 1775)	**16**	**4**
Eueides lineata (Salvin 1868)	**5**	**2**
Eueides aliphera gracilis Stichel 1903	-	**1**
Heliconius ismenius telchina (Doubleday 1847)	**5**	**1**
Heliconius erato petiverana (Doubleday 1847)	**11**	**4**
Heliconius hortense (Guerin-Meneville 1829)	**1**	**1**
Heliconius charitonius vazquezae (Comstock & Brown 1950)	**5**	**3**
Heliconius doris transiens (Staudinger 1896)	-	**1**
Philaethria dido diatonica (Fruhstorfer 1912)	-	**1**
Dryadula phaetusa (Linnaeus 1758)	-	**2**
Nymphalinae		
Hypanartia lethe (Fabricius 1793)	**4**	-
Siproeta epaphus (Latreille 1882)	**2**	**1**
Siproeta stelenes biplagiata (Fruhstorfer 1907)	**4**	**2**
Anartia fatima (Godart 1793)	**4**	**5**
Anartia jatrophae (Godart 1820)	**4**	**1**
Junonia evarete (Cramer 1782)	**4**	**1**

Argynninae		
Euptoieta hegesia hoffmanni (Comstock 1944)	**2**	**4**
Melitaeinae		
Chlosyne janais (Drury 1782)	**1 PA**	**3**
Chlosyne erodyle (Bates 1864)	-	**1**
Chlosyne lacinia (Geyer 1837)	**5**	**1**
Chlosyne hippodrome (Geyer 1837)	**1 (3 PA)**	-
Thessalia theona (Menetries 1855)	**4**	-
Phyciodes vesta (W. H. Edwards 1869)	**2**	-
Anthanassa tulcis (Bates 1864)	**1 PA**	-
Anthanassa ptolyca (Bates 1864)	**2 R**	-
Eresia phillyra (Hewitson 1852)	**2**	**2**
Castilia myia (Hewitson 1864)	**2**	**7**
Tegosa guatemalena (Bates 1864)	**3**	-
Limenitidinae		
Adelpha melanthe (Bates 1866)	**4**	**3**
Adelpha leuceria Druce 1879	-	**9**
Adelpha celerio diademata (Fruhstorfer 1915)	**4 R**	**5**
Adelpha phylaca (Bates 1860)	-	**2**
Adelpha ixia leucas (Fruhstorfer 1915)	-	**1 R**
Adelpha felderi (Boisduval 1870)	-	**1 R**
Adelpha milleri Beutelspacher 1975	-	**1 R**
Adelpha diazi Beutelspacher 1975	-	**1 R**
Adelpha leucerioides Beutelspacher 1975	-	**1**
Adelpha iphiclus (Linnaeus 1758)	**5**	-
Adelpha sp**.**	-	**1**
Myscelia ethusa (Doyere 1840)	**4**	-
Myscelia cyaniris (Doubleday 1848)	**1**	**2**
Dynamine postverta mexicana (d'Almeida 1952)	**9**	**1**
Dynamine dyonis (Geyer 1837)	**3**	-
Eunica alcmena Doubleday & Hewitson 1850	-	**1**
Eunica monima (Cramer 1782)	**1**	-
Diaethria anna (Guerin-Meneville 1844)	**1**	**4**
Diaethria astala (Guerin-Meneville 1844)	**2**	-
Callicore lyca (Doubleday & Hewitson 1847)	-	**1**
Callicore texa titania (Salvin 1869)	-	**1**
Nessaea aglaura (Doubleday 1848)	-	**5**
Biblis hyperia aganisa (Boisduval 1836)	**5**	-
Mestra amymone (Menetries 1857)	**3 PA**	-
Hamadryas februa ferentina (Godart 1824)	**7**	**2**
Hamadryas feronia farinulenta (Fruhstorfer 1916)	**8**	-
Hamadryas guatemalena marmarice (Fruhstorfer 1916)	-	**5**
Hamadryas amphinome mexicana (Lucas 1853)	**7**	**4**
Hamadryas iphthime (Bates 1864)	-	**1**
Colobura dirce (Linnaeus 1758)	**5**	**3**
Historis odius (Fabricius 1775)	**1 S**	**1**
Smyrna blomfildia datis (Fruhstorfer 1908)	**8**	**2**
Coea acheronta (Fabricius 1775)	-	**4**
Marpesia chiron marius (Cramer 1780)	**3**	**3**
Marpesia petreus tethys (Fabricius 1777)	**1 S**	**1**
Marpesia harmonia (Doubleday & Hewitson 1847)	-	**8**
Temenis laothoe hondurensis (Fruhstorfer 1907)	**1**	**4**
Epiphile adrasta (Hewitson 1861)	**4**	**2**
Nica flavilla canthara (Doubleday 1849)	**3**	**1**
Pyrrhogyra neaerea hypsenor (Godman & Salvin 1884)	**1**	**1**

Pyrrhogyra otolais (Bates 1864)	**1**	**5**
Catonephele mexicana (Jenkins & De la Maza 1985)	**5**	**9**
Catonephele numilia esite (R. Felder 1869)	-	**4**
Apaturinae		
Doxocopa laure (Drury 1773)	-	**1**
Charaxinae		
Prepona omphale octavia Fruhstorfer 1904	-	**3**
Archaeoprepona demophon centralis (Fruhstorfer 1905)	**2**	**2**
Archaeoprepona demophoon ssp. nov.	**1**	**6**
Archaeoprepona amphimachus amphiktion (Fruhstorfer 1916)	**3**	**2**
Zaretis callidryas (Felder 1869)	**2**	**1**
Zaretis itys (Cramer 1777)	-	**1**
Anaea aidea (Guerin-Meneville 1844)	**9**	-
Consul fabius cecrops (Doubleday 1849)	**4**	**2**
Consul electra (Westwood 1850)	**5**	**2**
Memphis pithyusa (R. Felder 1869)	-	**15**
Memphis morvus boisduvali (W. Comstock 1961)	**1**	**5**
Memphis oenomaus (Boisduval 1870)	**1**	**6 R**
Memphis neidhoeferi (Rotger 1965)	-	**4 R, N**
Memphis forreri (Godman and Salvin 1884)	-	**3 R**
Memphis xenica (Bates 1864)	-	**5 R**
Memphis proserpina (Salvin 1869)	-	**4**
Memphis xenocles (Westwood 1850)	-	**1 R, N**
Fountainea eurypile confusa (Hall 1929)	-	**5**
Fountainea ryphea (Cramer 1775)	-	**1 R**
Siderone marthesia (Cramer 1777)	-	**1**
Satyrinae		
Pierella luna heracles (Boisduval 1870)	**6**	**5**
Taygetis andromeda inconspicua (Draudt 1931)	**5**	**2**
Taygetis virgilia rufomarginata (Staudinger 1888)	**1**	-
Pareuptychia ocirrhoe (Sulzer 1779)	**1**	**5**
Pareuptychia metaleuca (Boisduval 1870)	**3**	**4**
Cissia usitata pieria (Butler 1866)	**11**	**12**
Cissia labe (Butler 1869)	-	**2**
Cissia renata disaffecta (Butler 1874)	-	**3 R, N**
Cissia libye (Linnaeus 1797)	**2**	**6**
Hermeuptychia hermes sosybius (Fabricius 1793)	**6**	**7**
Euptychia westwoodi (Butler 1866)	**4**	-
Euptychia jesia (Cramer 1869)	**1**	-
Megisto rubricata anabelae Miller 1976	-	**7 R, N**
Brassolinae		
Opsiphanes tamarindi sikyon Fruhstorfer 1912	**2 PA, R**	**1**
Opsiphanes cassina fabricii (Boisduval 1870)	**2 PA**	**6**
Opsiphanes quiteria quirinus Godman and Salvin 1881	-	**2 R**
Caligo memnon (C. Felder & R. Felder 1865)	**4**	**3**
Caligo uranus (Herrich-Schaffer 1853)	-	**5**
Morphinae		
Morpho polyphemus luna (Butler 1872)	**1 S**	**3**
Morpho peleides montezuma (Guenee 1859)	**6**	**12**
Acraeinae		
Altinote ozomene nox (Bates 1864)	**1**	**4**

Danainae		
Danaus plexippus (Linnaeus 1758)	**1 S**	**1**
Danaus gilippus thersippus (Bates 1863)	**5**	**6**
Danaus erisimus montezuma (Talbot 1943)	**1 PA**	-
Lycorea cleobaea atergatis (Doubleday & Hewitson 1847)	**3**	**4**
Ithomiinae		
Tithorea harmonia hippothous (Godman and Salvin 1879)	**1 PA**	**4**
Melinaea lilis imitata (Bates 1864)	**3**	**4**
Mechanitis polymnia lycidice (Bates 1864)	**6**	**10**
Mechanitis menapis (Bates 1864)	**3**	**6**
Oleria paula (Weymer 1883)	**1**	**3**
Aeria pacifica (Godman & Salvin 1879)	**3**	**3**
Dircenna klugii (Geyer 1837)	**1**	**6**
Pteronymia cotytto (Guerin-Meneville 1844)	**3**	**14**
Greta oto (Hewitson 1855)	**5**	**1**
Greta nero (Hewitson 1855)	-	**5**
Hyposcada virginiana (Hewitson 1855)	-	**5**
Napeogenes tolosa (Hewitson 1855)	-	**4**
Ithomia patilla (Hewitson 1852)	-	**1**
Hypoleria cassotis (Bates 1864)	**1**	-

Appendix 3. Butterfly species associated with lower montane rainforest, found at EBITROLOTU but absent at Laguna Encantada.

Papilionidae		Parides iphidimas
		Parides eurimedes
Pieridae	*	Dismorphia theucarila
	*	Itaballia pisonis
		Pieriballia viardi
Nymphalidae:		Caligo uranus
		Cissia labe
		Greta nero
		Heliconius doris
		Ithomia patilla
		Mechanitis lysimnia
		Napeogenes tolosa
	*	Nessaea aglaura

* Habitat specialist sensu DeVries 1987