FOREST MANAGEMENT AND BIODIVERSITY: A STUDY OF AN INDICATOR INSECT GROUP IN SOUTHERN MEXICO

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SUMMARY

Previous studies on succesional dynamics of insect communities have revealed important changes along succesional stages among community structures and insect life histories. This work evaluates the changes and diversity of a butterfly fauna in a forest-managed landscape in Southern Mexico. One-hundred and forty three species were collected belonging to 102 genera in five families. Nymphalidae was the most diverse family with 54 species (38%). Rarefaction and rank abundance curves recorded in each forest stand suggested important differences for species richness values at comparable levels of sampling effort. Species abundances were positively correlated with their landscape distribution sizes. Based on field observations and on literature review, a designation of habitat preferences for a set of species was given. A significant association between habitat use and geographic range for 63 butterfly species was detected (χ^2= 13.26, df= 1, p<0.005). Species with narrow geographic ranges were usually grouped in unmodified habitats, whereas widespread species were much more likely to make some use of human-modified habitats. A declining proportion of species restricted to unmodified, or primary, habitats with increasing geographic range was quantified. Forest-management practices on local habitats as well as differences among species' habitat preferences and geographical distributions can account for an increasing proportion of widespread species in the study landscape and comparable sites. Monitoring of insect indicator groups in extractive landscapes is needed to establish guidelines for ecologically, economically, and socially sustainable forest zoning and use regimes.

Introduction

Succesional stages represent an ecologically important case of change in diversity through time. Former studies on succesional dynamics of insect communities reveal important changes along succesional stages among community structures and insect life histories, namely host plant specificity, migrations, and body size, among others. For example, excessive extraction of native tree species from forests can affect the structure of communities, impacting the pattern of colonization and diversity of insects in fragmented systems (Wood and Gillman, 1998; Shahabuddin and Ponte, 2004; Waltz and Covington, 2004; Ohwaki *et al*., 2007). It is thought that an optimal strategy to safeguard adequate levels of species richness under some semi-intense forest management could be achieved through the maintenance of a patchwork that ideally includes areas of primary forest, and a network of forest patches with a given management regime (Wood and Gillman, 1998). In addition, in order to be considered a genuinely sustainable method of forest management, selective logging needs to be economically viable, provides a sustainable yield of timber, and preserves biodiversity (Bawa and Seidler, 1998). However, in tropical systems the costs of forest disturbance, mostly caused by selective logging, upon biodiversity have been poorly measured. Can significant effects of forest management upon biodiversity elements be expected?

Insects are considered to be adequate responders to habitat change (Brown and Freitas, 2000; Caballero *et al*., 2009). Their sensitivity to disturbance and change allow them to be good models for the study in environmental gradients, as is the case for dragonflies, beetles, moths, butterflies and ants (Tyler *et al*., 1994; Brown and Freitas, 2000; Arellano *et al*., 2008). Butterflies in particular are useful responders in environmental studies because they could decrease in abundance or even disappear due to (even subtle) changes in habitat quality, namely, forest cover and vegetation composition and structure (León Cortés *et al*., 2004). Additionally, butterflies have been proposed as useful responders in restoration schemes due to their quick reaction to changes as regards to habitat quality and quantity (Thomas, 1984; Tyler *et al*., 1994; Wood and Gillman, 1998). However, the response of some butterfly species to habitat disturbance depends upon the characteristics of particular organisms, such as body size, dispersal ability, life history, population size or rarity, because in some cases, narrowly-distributed species seem to experience no adverse effects of forest disturbance. Increasing habitat fragmentation could even benefit generalists, which have recorded important population increases as habitat becomes more heterogeneous (Brandle *et al*., 2002; León-Cortés *et al*., 2004; Waltz and Covington, 2004).

KEYWORDS / Butterfly / Chiapas / Forestry Development / Forest Management / Indicator Species /

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MANEJO FORESTAL Y BIODIVERSIDAD: ESTUDIO DE UN GRUPO INDICADOR DE INSECTOS EN EL SUR DE MÉXICO

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RESUMEN

Estudios previos sobre dinámica sucesional de comunidades de insectos revelan cambios importantes a lo largo de los estadios sucesionales en la estructura de las comunidades y la historia de vida de los insectos. Se evaluaron cambios y diversidad de las mariposas en un paisaje con manejo forestal del sur de México, recolectándose 143 especies pertenecientes a 102 géneros de cinco familias, siendo Nymphalidae la más diversa (54 especies; 38%). Las curvas de rarefacción y los niveles de abundancia registradas en cada rodal sugirieron diferencias importantes en riqueza de especies para niveles de esfuerzo de captura comparables. La abundancia de especies estuvo correlacionada positivamente con el tamaño de su distribución. Con base en observaciones de campo y revisión de la literatura, se designaron preferencias de hábitat para las especies. Se detectó una asociación significativa entre uso de hábitat y extensión geográfica para 63 especies de mariposas (χ^2= 13,26, dl= 1, p<0,005). Las especies con extensiones geográficas reducidas se agruparon usualmente en hábitat no modificados, mientras que las de distribución amplia tendían a hacer uso de hábitat intervenidos. Se registró una baja proporción de especies restringidas a hábitat no modificados en relación con el incremento de su distribución geográfica. Las prácticas locales de manejo forestal así como las diferencias en la preferencia de hábitats y distribución geográfica de las especies conllevan una creciente proporción de especies de distribución amplia en la zona de estudio y sitios comparables. Se requiere del monitoreo de grupos indicadores de insectos en zonas de extracción para establecer pautas para la subdivisión y régimen de uso ecológico, económica y socialmente sostenibles.

MANEJO DE SELVAS E BIODIVERSIDADE: ESTUDO DE UM GRUPO INDICADOR DE INSETOS NO SUL DO MÉXICO

Yariely del Rocío Balam-Ballote e Jorge L. León-Cortés

RESUMO

Estudos prévios sobre dinâmica sucesional de comunidades de insetos têm revelado mudanças importantes ao longo dos estadios sucessionais na estrutura das comunidades e a história de vida dos insetos. Foram avaliadas mudanças e diversidad e das borboletas em uma selva protegida do sul do México,se recolhendo 143 espécies pertencentes a 102 gêneros de cinco familias, sendo Nymphalidae a mais diversa (54 espécies; 38%). A rarefação e curvas de níveis de abundância registradas em cada stand sugerem diferenças importantes em riqueza de espécies para níveis de esforço de captura comparáveis. A abundância de espécies se correlacionou positivamente com a extensão de sua distribuição. Com base em observações de campo e revisão da literatura, se designaram preferências de hábitat para as espécies. Houve associação significativa entre uso de hábitat e extensão geográfica para 63 espécies de borboletas (χ^2= 13,26, dl= 1, p<0,005). As espécies com extensões geográficas reduzidas agruparam-se usualmente em hábitats não modificados, enquanto que as dispersas tendiam a fazer uso de hábitats interditados. Foi achada uma proporção em descenso de espécies restringidas a hábitats não modificados (primários) que aumentavam sua extensão geográfica. As práticas de manejo florestal local e as diferenças na preferência de distribuição das espécies levam a uma crescente proporção de espécies de ampla distribuição na área do estudo e locais comparáveis. Requere-se de monitoramento de insetos indicadores em zonas de extração para estabelecer pautas para a subdivisão e regime de uso ecológico, económica e socialmente sustentáveis.

The objectives of this paper are 1) to assess the local (forest stand) and landscape diversity of butterflies in a forest-managed landscape, 2) to examine changes in species composition as regards to species habitat preferences and geographical distributions, and 3) to compare the overall butterfly diversity and species composition patterns of the study landscape as regards to other sites for which butterfly diversity assessments have been carried out. Ultimately, it is discussed whether the type of forest management implemented in the landscape considered in the present study is as ecologically sustainable as it claims to be.

Methods

Study site

The ejido Coapilla (hereafter "Coapilla", 17º05'10", 17º11'02"N; 93º05'45", 93º12'25"W; Figure 1) is located in northern Chiapas, México, and entitles a total area of 13571ha. The area receives an average annual rainfall of 1800mm. The climate is warm and humid with heavy summer rains between June and October. Roughly 75% of the total area of Coapilla is characterized by steep slopes where forest stands are imbibed; the remaining 25% of land consists of flat areas located around the Coapilla's urban settlement (Gerez-Fernández *et al*., 2003).

The original Coapilla landscape included mostly cloud forest habitats, but an important proportion (16%, ~1000ha) of this landscape has now been converted into forest stands that include different successional stages, which mostly result from logging and in lesser proportion from farming and livestock activities. In particular, logged areas through the Coapilla landscape include a one-year intensive rotation scheme in which four selective cuttings (with different intensity) are expected to allow regeneration of forest stands over a 10-year period. Very few biodiversity assessments have been carried out in this area, but recent insect surveys suggest the area of Coapilla to be a site holding unusual numbers of endemic and narrowly-distributed species for beetles and ants (Robert S. Anderson and John T. Longino, personal communication). No previous butterfly assessments had been carried out in Coapilla.

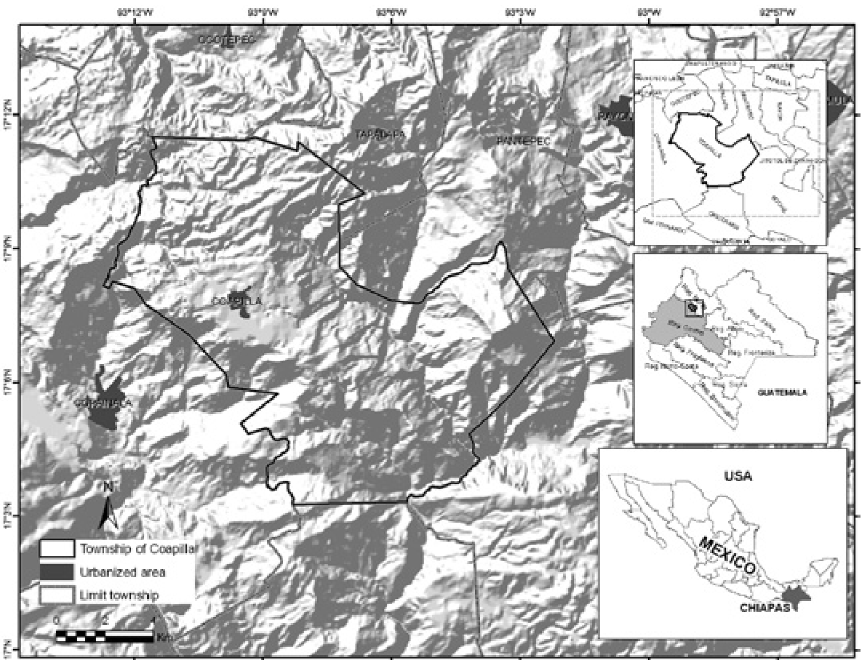

Figure 1. The location of the Coapilla landscape in Chiapas, Mexico

Butterfly sampling

Before carrying out butterfly transects, a six-month pilot study was set up for identifying butterflies at sight. Previous experience in this and other sites in Chiapas allowed us to identify specimens at sight (León-Cortés *et al.*, 2004; Molina-Martínez and León-Cortés 2006; Marín *et al.*, 2009). Nonetheless, certain species complexes were caught using aerial nets; e.g., the representatives of tribes Achlyodidini, Pyrrhopygini, Erynnini, Eumaeini, and Polyommatinae. Caught specimens were prepared and identified in the Entomological Collection of ECOSUR (voucher specimens have been deposited therein).

In April 2007, fixed transects of ~500m in length (Table I) were established along each of the forest stands. From May to November 2007, transect routes were walked between 9:00 and 15:00, under ideal conditions to record butterflies (Pollard and Yates, 1993; Tyler *et al.*, 1994). We followed DeVries (1987, 1997), Tyler et *al*, (1994), and Garwood and Lehman (2005), as well as the entomological collections of El Colegio de la Frontera Sur, the Zoology Museum at Faculty of Science, UNAM, and their curators, for butterfly identifications.

Accumulation and dominance curves

To examine local diversity (the recorded diversity at each forest stand), rarefaction curves of butterfly species were built up for each forest stand in Coapilla, using the program EstimateS (Colwell, 1997). Since one or more accumulation curves failed to reach an asymptote, sample-based rarefaction curves scaled to individuals and samples were standardized and truncated to the value of the lesser entry of the total sample, and hence allowing for a comparison of relative richness values among forest stands. In doing so it was attempted to differentiate under-sampling effects from real differences among forest stand values.

In addition, for each forest stand, rank-abundance curves were constructed with the values grouped in descending order, and abundance values were compared among each other (Magurran, 1988). In addition, the slopes of the equations of the linear regressions for each rank-abundance distribution were calculated and compared among forest stands. When the slope is zero, distribution of abundance values of the species is approximately equivalent (Tokeshi, 1993).

Butterfly abundance-distribution relationship

The abundance-distribution relationship for Coapilla's butterflies was examined at the landscape scale. Butterfly distributions were proportions of forest stands occupied, whereas butterfly abundances were recorded from transect counts at forest stands. Linear regressions between abundance and distribution were calculated using the ordinary least squares method (model 1; Gaston *et al.*, 2000). Abundance was used as the dependent variable. Before statistical analyses were conducted, both abundance values and distributions were transformed so as to homogenize variance. Abundance values were $\log_{10}$ transformed, whilst distributions were Arcsine transformed (distributional data are proportions of all forest stands occupied).

Habitat use and geographic range categories

Habitat preferences and geographic range data were analyzed for Papilionidae, Pieridae and Nymphalidae, based on the information provided by DeVries (1987), Llorente-Bousquets *et al.* (2006), Warren *et al.* (2010) and Tyler *et al.* (1994). Only 63 of the 143 species recorded in Coapilla were included in the analysis. Following Thomas (1991) and Léon-Cortés *et al.* (2003) butterflies were classified as occupying unmodified habitat (when no mention was made

TABLE I
THE NUMBER OF TRANSECTS AND HABITAT FEATURES FOR EACH FOREST STAND IN COAPILLA, DURING 2007

Forest stand	Fixed number of transects	Transect length (m)	Total number of transects	Butterfly diversity	Number of flowering plants	Vegetation height (cm)	Number of tree species recorded
1	2	500	13	59 (391)	33	59	12
2	1	800	7	44 (213)	15	61	4
3	1	800	9	55 (310)	30	91	12
4	2	500	11	42 (219)	45	126	10
5	1	800	9	52 (248)	29	119	9
6	1	1500	11	79 (1070)	35	83	6
7	1	800	11	57 (6134)	39	107	2
8	1	1500	9	58 (312)	40	124	13
9	1	800	11	55 (427)	29	65	3
Forest	1	500	11	28 (108)	22	74	14
Total	12		102				

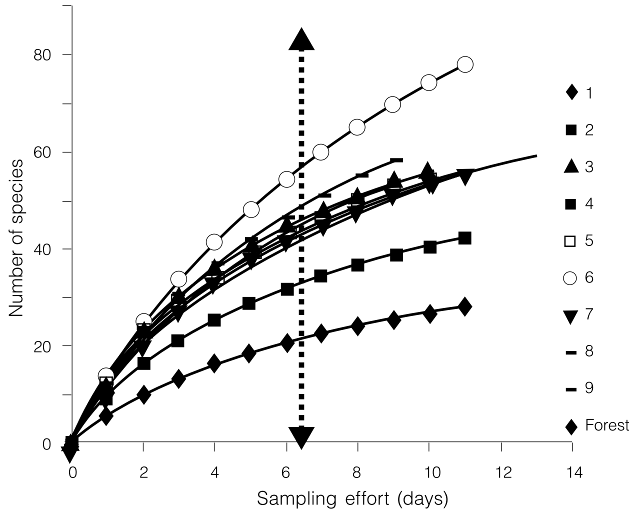

Figure 2. Rarefaction curves per forest stand (numbers on the right). The discontinuous vertical arrow indicates standardized sample values at which forest stands were compared.

that they occupy secondary or agricultural habitats), or as occupying secondary, agricultural, or other human-modified habitats. In addition, each species was assigned to a given geographical range category. Geographic range categories were grouped as:

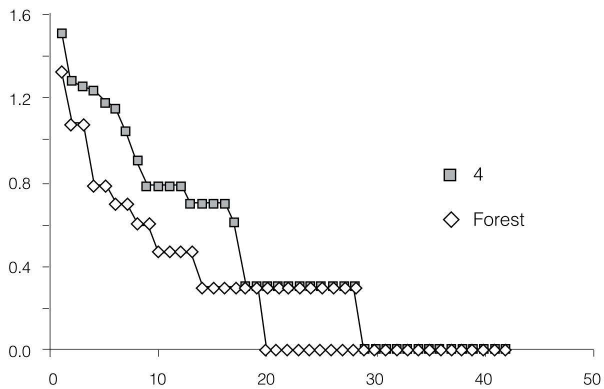

Figure 3. Rank-abundance curves (log scale in Y axis) for two representative forest stands in Coapilla, during 2007.

1- Restricted to southeast Mexico and Central America but not further south than Panama.

2- North America to Central America and/or southern Mexico to northern South America.

3- Widespread in the Neotropics (at least reaching Brazil or Bolivia).

Because the sample size for each family was rather small, family samples were collated to examine a possible overall association between habitat use and geographical range using χ^2 tests.

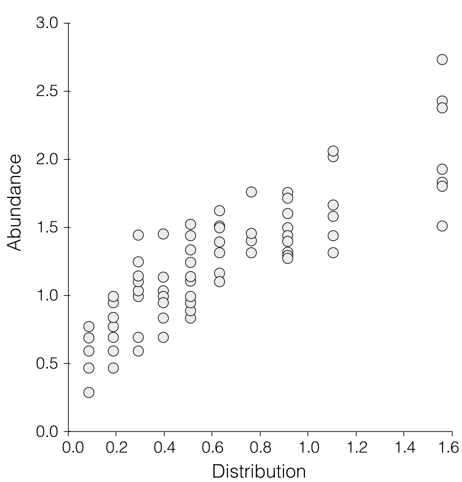

Figure 4. Abundance distribution- relationship for butterflies in Coapilla, Chiapas.

Species composition in Coapilla and comparable sites

The proportion of species grouped for each geographic range categories for Coapilla and other sites for which butterfly diversity assessments have been carried out were compared using ANOVA tests (Sokal and Rohlf, 1997). Comparisons were restricted to sites that exhibited similar vegetation patterns, mostly associated to mountainous habitats in southern Mexico, and for which adequate inventories are known to have been carried out (Armando Luis-Martínez, personal communication).

Results

Butterfly diversity

A total of 9432 butterfly individuals was recorded and grouped in 143 species and five families. Fifty four species were recorded in the Nymphalidae family (38%), 32 in Hesperiidae (22%), 27 in Pieridae (19%), 20 in Lycaenidae (14%), seven in Papilionidae (5%) and three in Riodinidae (2%). The most abundant species recorded were *Eunica monima* (6522 records; 69%), *Hermeuptychia hermes* (554 records; 6%), and *Eurema mexicana mexicana* (271 records; 3%). Table I shows butterfly total richness recorded per forest stand. Stand 6 and "Forest" recorded the highest and poorest butterfly richness, respectively.

In addition, rarefaction curves per forest stand suggested important differences for species richness values at comparable levels of sampling effort (Figure 2). Levels of species richness remained comparable when changing sample units. Forest stand 6 recorded the highest diversity of butterflies, whereas the most pristine forest stand remained as the relatively poorest condition in Coapilla.

Abundance ranks distributions

Abundance ranks distributions differed among forest stands studied (Figure 3). Less disturbed forest stands showed abundance curves with gentler slopes in comparison to most disturbed habitats.

Abundance distribution relationship

A positive relationship between abundance and distribution was identified at the landscape scale. Species' abundances were positively correlated with their landscape distribution sizes ($F_{1,146}$= 603.7, P<0.001, r=0.89; Figure 4).

Habitat use categories and geographical distribution

A significant association between habitat use and geo-

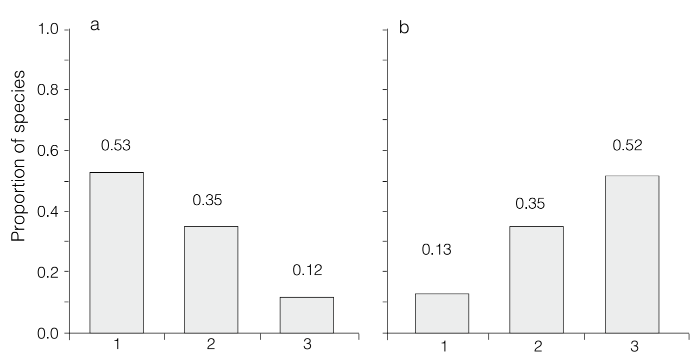

Figure 5. The proportion of butterfly species using unmodified (a) and modified (b) habitats, when increasing geographic range; geographic distribution categories, 1: restricted to southeast Mexico and Central America but not further south than Panama, 2: North America to Central America, and/or southern Mexico to northern South America, and 3: widespread in the Neotropics. (Geographic categories modified from Thomas, 1991).

graphic range for 63 species ($\chi^2 = 13.26$, df= 1, $p<0.005$; Figure 5) was detected in Coapilla. Seventeen species were classified as using unmodified habitats, and 46 species were placed as mostly occupying modified habitats. Species with narrow geographic ranges were commonly grouped in unmodified habitats; whilst widespread distributed species were associated to human-modified habitats.

Species composition between Coapilla and other sites

The proportion of species grouped in distinct geographical distribution categories was significantly different among a sample of sites for which butterfly diversity had been thoroughly assessed ($F_4 = 11.615$, $p<0.001$; Figure 6). Less disturbed sites, such as Santiago Comaltepec and Los Mazos (sites 4 and 5, respectively; in Figure 6) showed a relatively even proportion of species distributed among distinct geographical categories. In contrast, heavily disturbed sites, such as Los Altos de Chiapas, exhibited a poor representation of narrowly-distributed species.

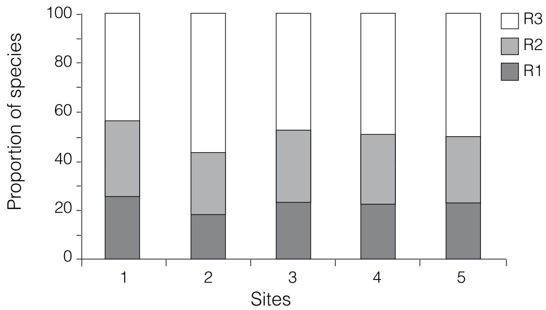

Figure 6. The proportion of species recorded in five different sites in Mexico as regards to their geographical distribution category. Geographic range is R1: restricted to southeast Mexico and Central America but not further south than Panama, R2: North America to Central America, and/or southern Mexico to northern South America; and R3: widespread in the Neotropics. Sites are 1: Coapilla (this work), 2: Los Altos Chiapas (Miss-Barrera *et al*., 2010), 3: Sierra de Atoyac, Guerrero (Vargas-Fernández *et al*., 1991), 4: Santiago Comaltepec, Oaxaca (Luis-Martínez *et al*., 1991), 5: Los Mazos, Jalisco (Vargas-Fernández *et al*., 1999).

Discussion

The 143 species of butterflies registered in forest stands of Coapilla represent ~12% of the total number of species recorded for Chiapas (Luis-Martínez *et al*., 2003). Even considering these important levels of butterfly diversity for a single landscape, butterfly distribution and structure have experienced important shifts at the local (forest stand) and landscape scales. There was almost a three-fold increase in butterfly diversity between the most evenly-forested site (what we recognized as the "pristine condition") and forest stand 6 (the most heterogeneous condition). Previous results have suggested that diversity often increases with disturbance near or below natural levels (perhaps the condition of forest stand 6), although some sensitive species might be eliminated at even low levels of interference. For example, some spatially-restricted species, namely *Satyrotaygetis satyrina*, *Enantia jethys*, *Dismorphia crisia virgo* and *Jonaspyge jonas* were almost exclusively found in forest stands with important levels of forest cover as is the case for "Forest", and forest stands 4, 1 and 2. In contrast, widely and common species such as *Eunica monima*, *Phoebis sennae* and *Danaus gilippus* were recorded in open heavily-used forest stands, as is the case for forest stands 6, 8 and 9. These species have been able to locate scattered resources throughout the landscape, and although moderate levels of disturbance generate a patchy structure of habitats, this could be beneficial for an important set of species. In line with this idea, species such as *Adelpha iphicleola iphicleola*, *Altinote ozomene nox*, *Catasticta nimbice nimbice*, *Dircenna klugii klugii* and *Parides photinus* exhibited a mix of preferences (i.e. occurring in a variety of habitats, from open to relatively preserved conditions). These butterflies might seek for several pieces of habitat to complete what it has been called "functional habitat" (Dennis *et al*., 2003).

In addition, species abundance and identity showed important responses to increased disturbance and different forest-use regimes. Typically, forest-affiliated species were associated to forest habitats (Table II). Sedentary species that persist within relatively small forest areas were found rarely and in low densities. In contrast, some common species that occur in the surrounding region were extremely abundant, such as *E. monima*, resulting in numerous and widespread distribution records. At a landscape scale, sedentary species have greater potential to be localized within the study area (Cowley *et al*., 1999) and, in contrast, mobile species sometimes have a higher probability of being recorded away from their main breeding habitats, resulting in widespread distributions. In general, the densities and distributions of Coapilla butterflies were positively related at the landscape scale (Figure 4). These results are broadly consistent with previous studies on other taxonomic groups that have demonstrated positive relationships between density and distribution regardless of the spatial scale considered (Niemelä and Spence, 1994; Cowley *et al*., 2001).

What changes in species composition can be perceived as a result of forest management? Depending on its scale and frequency, habitat modification may provoke a variety of responses from the members of a given Neotropical butterfly community (Raguso and Llorente-Bousquets, 1991). Previous assessments have suggested that agricultural and silvicultural mosaics with >30% conversion, including selective logging, show shifts in species composition with irreversible loss of many components of butterfly communities, and otherwise indicating non-sustainable land and resource use (Brown, 1997). On the other hand, Janzen (1988) has suggested that a resulting mosaic of habitats and successional stages of vegetation can support more species of Lepidoptera than a pristine tropical forest could realistically support. The analysis of habitat preferences and geographic distributions for a set of species from Coapilla showed that few forest species that possess relatively narrow geographic ranges were classified as making use of modified habitats. Geographically restricted or endemic butterfly species are often regarded as biotope specialists, although they can be among the most abundant species at sites where they occur (León-Cortés *et al*., 2000). Some biotope specialists might occupy disturbed habitats, but in most cases the latter are used very rarely by these species, and usually only when modified and unmodified habitats are adjacent (Thomas, 1991). For instance, many savannah and tropical dry forest butterflies appear to congregate in mesic habitats, such as gallery forests, or migrate to higher elevations in dry seasons (DeVries, 1987). Furthermore, many species may be specialists on naturally-occurring successional habitats, and so be able to occupy human-modified areas that provide the same successional conditions. At this point, and for the species whose habitat preferences and geographic distributions could be determined, there seems to be an increasing proportion of rather "weedy" species (>25% Coapilla butterflies have been regarded as widespread and common species) in this forested landscape. Furthermore, comparisons for species composition of Coapilla butterflies and other sites in Mexico yielded significant differences.

TABLE II
CHECK-LIST OF BUTTERFLIES FROM COAPILLA, CHIAPAS, MEXICO [a, b]

Taxon	Abundance	Range	Habitat
Abaeis nicippe (Cramer)	4	2	2
Achlyodes pallida (Felder)	8	NA	NA
Adelpha iphicleola iphicleola (Bates)	12	1	2
Adelpha leuceria leuceria (Druce)	9	1	1
Adelpha pithys (Bates)	13	1	1
Agraulis vallinae incarnata (Riley)	1	3	2
Altinote ozomene nox (Bates)	3	1	2
Anartia fatima fatima (Fabricius)	1	NA	NA
Ancyloxypha numitor (Fabricius)	3	NA	NA
Anteos clorinde (Godart)	2	3	2
Anteos maerula (Fabricius)	2	3	2
Anthanassa ardys ardys (Hewitson)	2	2	2
Anthanassa drusilla leeles (Bates)	5	3	2
Anthanassa otanes otanes (Hewitson)	2	NA	NA
Anthanassa aff. ptolyca ptolyca (Bates)	2	NA	NA
Anthanassa texana texana (Edwards)	2	NA	NA
Aphrissa statira statira (Cramer)	1	3	2
Apuecla maeonis (Godman & Salvin)	1	NA	NA
Astraptes fulgerator (Walch)	4	NA	NA
Autochton cellus (Boisduval & Leconte)	24	NA	NA
Autochton vectilucis (Butler)	69	NA	NA
Autochton sp.	52	NA	NA
Biblis hyperia aganisa (Boisduval)	2	3	2
Calephelis sp.	31	NA	NA
Caligo uranus Herrich-Schäffer	2	1	2
Calycopis clarina (Hewitson)	1	NA	NA
Calycopis isobeon (Butler & Druce)	21	NA	NA
Catasticta flisa flisa (Herrich-Schäffer)	12	2	1
Catasticta nimbice nimbice (Boisduval)	28	1	2
Catasticta nimbice ochracea (Bates)	1	NA	NA
Catasticta teutila flavifaciata Beutelspacher	1	2	1
Celastrina argiolus gozora (Boisduval)	20	NA	NA
Chlosyne erodyle erodyle (Bates)	17	1	2
Chlosyne janais janais (Drury)	14	2	2
Chlosyne aff. marina (Geyer)	2	NA	NA
Cissia pompilia (Felder & Felder)	2	NA	NA
Consul excellens genini (Le Cerf)	2	NA	NA
Cupido comyntas (Godart)	58	NA	NA
Cyllopsis hedemanni hedemanni Felder	27	1	2
Cyllopsis hilaria (Godman)	3	NA	NA
Danaus gilippus thersippus (Bates)	13	2	2
Danaus plexippus plexippus (Linnaeus)	6	3	2
Denivia augustinula (Goodson)	2	NA	NA
Diaethria anna anna (Guérin-Ménéville)	28	NA	NA
Diaethria pandama (Doubleday)	1	NA	NA
Dione juno huascuma (Reakirt)	18	3	2
Dione moneta poeyii Butler	86	3	2
Dircenna klugii klugii (Geyer)	38	1	2
Dismorphia crisia virgo (Bates)	27	1	1
Doberes anticus (Plötz)	1	NA	NA
Dryas iulia moderata (Riley)	10	3	2
Echinargus isola (Reakirt)	2	NA	NA
Electrostrymon sangala (Hewitson)	1	NA	NA
Enantia jethys (Boisduval)	10	NA	NA
Epargyreus aspina Evans	6	NA	NA
Erynnis tristis tatius (Edwards)	3	NA	NA
Eunica monima (Stoll)	6522	3	2
Euptoieta claudia daunius (Herbst)	3	NA	NA
Euptoieta hegesia meridiania Stichel	32	2	2
Eurema albula celata (Felder)	2	3	2
Eurema daira eugenia (Wallengren)	42	3	2
Eurema mexicana mexicana (Boisduval)	271	3	2
Eurema salome jamapa (Reakirt)	244	2	1
Fountainea glycerium glycerium (Doubleday)	1	NA	NA
Ganyra josephina josepha (Salvin & Godman)	1	NA	NA
Greta annette annette (Guérin-Ménéville)	28	1	1
Hamadryas februa ferentina (Godart)	8	3	1
Heliconius charithonia vazquezae (Comstock & Brown)	25	3	2
Heliconius hortense (Guérin-Ménéville)	20	NA	NA
Hemiargus hanno antibubastus Hübner	2	NA	NA
Heraclides thoas autocles (Rothschild & Jordan)	4	2	2
Hermeuptychia hermes (Fabricius)	554	NA	NA
Hypanartia godmani (Bates)	6	2	1
Hypoleria lavinia cassotis (Bates)	31	1	1
Jonaspyge jonas (Felder & Felder)	17	NA	NA
Laothus barajo (Reakirt)	1	NA	NA
Leptophobia aripa elodia (Boisduval)	20	2	1
Leptotes marina (Reakirt)	2	NA	NA
Lerema accius accius (Smith)	3	NA	NA
Lerema lumina (Herrich-Schäffer)	20	NA	NA
Librita librita (Plötz)	1	NA	NA
Lieinix nemesis atthis (Doubleday)	1	NA	NA
Marpesia chiron marius (Cramer)	6	3	2
Marpesia petreus (Cramer)	13	3	2
Marpesia zerynthia dentigera (Fruhstorfer)	1	NA	NA
Mechanitis polymnia lycidice Bates	3	3	2
Melanis pixe pixe (Boisduval)	1	NA	NA
Mestra dorcas amymone (Ménétriés)	17	2	2
Methion aff. *melas* Godman	27	NA	NA
Morpho helenor montezuma Guenée	2	2	2
Nathalis iole Boisduval	9	NA	NA
Niconiades sp.	2	NA	NA
Noctuana lactifera bipuncta (Plötz)	1	NA	NA
Noctuana stator (Godman)	1	NA	NA
Oxeoschistus tauropolis tauropolis (Westwood)	1	NA	NA
Panthiades bathildis (Felder)	1	NA	NA
Papias aff. *dictys* (Godman)	9	NA	NA
Papilio polyxenes asterius Stoll	1	2	2
Parides photinus (Doubleday)	114	1	1
Parrhasius moctezuma (Clench)	1	NA	NA
Pereute charops nigricans Joicey & Talbot	13	NA	NA
Phocides urania urania Godman & Salvin	1	NA	NA
Phoebis agarithe agarithe (Boisduval)	64	3	1
Phoebis neocypris virgo (Butler)	9	NA	NA
Phoebis philea phílea (Linnaeus)	19	3	2
Phoebis sennae marcellina (Cramer)	9	3	2
Poanes inimica (Butler & Druce)	12	NA	NA
Poanes melane (Edwards)	32	NA	NA
Poanes zabulon (Boisduval & Leconte)	40	NA	NA
Pompeius pompeius (Latreille)	4	NA	NA
Protographium epidaus epidaus (Doubleday)	4	NA	NA
Pterourus garamas electryon (Bates)	4	1	1
Pterourus menatius victorinus (Doubleday)	1	NA	NA
Pyrgus communis (Grote)	4	NA	NA
Pyrgus oileus (Linnaeus)	25	NA	NA
Pyrisitia dina westwoodi (Boisduval)	3	2	2
Pyrisitia nise nelphe (Felder)	107	3	3
Pyrisitia proterpia (Fabricius)	31	3	2
Quasimellana sp.	2	NA	NA
Quinta cannae (Herrich-Schäffer)	1	NA	NA
Rekoa menton (Cramer)	1	NA	NA
Remella sp.	8	NA	NA
Satyrotaygetis satyrina (Bates)	57	1	1
Siproeta epaphus epaphus (Latreille)	33	2	2
Siproeta stelenes biplagiata (Fruhstorfer)	1	3	2
Smyrna blomfildia datis Fruhstorfer	5	2	1
Strymon cestri (Reakirt)	1	NA	NA
Strymon melinus (Hübner)	1	NA	NA
Synapte salenus (Mabille)	1	NA	NA
Tegosa anieta cluvia (Godman & Salvin)	10	NA	NA
Theagenes aegides (Herrich-Schäffer)	1	NA	NA
Thecla maeonis (Godman & Salvin)	1	NA	NA
Tmolus crolinus Butler & Druce	1	NA	NA
Urbanus prodicus Bell	46	NA	NA
Urbanus simplicius (Stoll)	6	NA	NA
Urbanus teleus (Hübner)	7	NA	NA
Vanessa annabella (Field)	4	NA	NA
Vanessa virginiensis (Drury)	20	2	2
Vehilius inca (Scudder)	2	NA	NA
Yphthimoides renata (Stoll)	3	NA	NA
Zerene cesonia cesonia (Stoll)	2	NA	NA
Ziegleria ceromia (Hewitson)	2	NA	NA
Zizula cyna (Edwards)	27	NA	NA

[a] The author of each taxon is given. The order is alphabetic, first by genus, then by species, subspecies (taxonomic authorities after Llorente-Bousquets *et al*., 2006, and Warren *et al*., 2010).
[b] Abundance denotes the total number of individuals recorded for a given species. Range indicates the geographic range categories assigned for a given species: 1) restricted to southeast Mexico and Central America but not further south than Panama; 2) North America to Central America, and/or southern Mexico to northern South America; and 3) widespread in the Neotropics. Habitat indicates the habitat use recorded for a given species: 1) species making use of unmodified habitat; 2) species making use of modified habitat. NA: habitat use or geographic range information not available.

Within the bounds of geographical or historical factors that might produce inherent differences among butterfly faunas, it is concluded that current differences in species composition might be a result of landscape conditions; and hence, changes in the proportions of widespread or spatially-restricted species might potentially differ due to fundamental changes in the landscape conditions. The immediate effect that expansions of secondary vegetation are producing in previously pristine landscapes, includes a decreasing difference between the faunas of different locations or regions (i.e., endemic species will be removed with the loss of primary forest, and the same widespread species will be left inhabiting secondary vegetation in each region). If unmodified habitats continue to be lost, local (alpha) diversity may not noticeably decrease, and may sometimes increase (e.g. Raguso and Llorente-Bousquets, 1991) but regional (beta) diversity will decline (Thomas, 1991).

Overall, the measures of abundance and diversity are considered to be useful tools in the offer and recognition of priority areas for species' conservation and management. Nevertheless, these measures are not always adapted to determine the status of quality or the condition of conservation of a forest. However, because most forest products are just as tightly tied into the overall system function as are insect populations or soil organisms, the ecological and economic aspects of sustainability run together, with the changes in indicator groups serving as an early warning for later changes in the economic potential of the system (Brown, 1997). Indeed, the usefulness of forest systems to humans is just one aspect of their overall complex functioning, just as likely to be modified by a change in forest structure (such as removal of large trees) as are the composition and richness of understory vegetation, soil biota, and indicator insect communities.

Mexico is a megadiverse country, but it has high rates of deforestation and many ecological-impoverished areas resulting from supposed sustainable forest-managing practices. Mapping α and β diversity can contribute to the conservation of natural resources by helping to identify species-rich hotspots and areas that include as many species (Gentry, 1992). However, one important addition to this agenda is the research directed towards identifying patterns of species composition and rarity (Williams *et al*., 1996) such as the present study, which in turn adds the identification and measure of important ecological components of biodiversity, largely independent of patterns of α diversity. At present, the Coapilla landscape seems to hold important levels of diversity for butterflies. The resulting affiliations of the organisms that persist or colonize these forest-managed areas should be a matter of concern when weighting how much of the biodiversity components are being modified in natural insect communities when encouraging forestry practices. A continuing-monitoring of several insect indicator groups (mostly the ecological specialists) in this extractive landscape will help suggest guidelines for ecologically, economically, and socially sustainable zoning and use regimes in the long run.

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