

<https://doi.org/10.15517/61cmxq06>

Distribution, richness, and abundance of Lycaenidae (Lepidoptera: Papilionoidea) in the Loxicha Region, Oaxaca, Mexico: A regional analysis on the Pacific slope

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Received 21-III-2025.

Corrected 23-VII-2025.

Accepted 12-VIII-2025.

ABSTRACT

Introduction: The Sierra Madre del Sur in Mexico, known for its geological complexity and elevational gradient, hosts diverse ecosystems. The Loxicha region in Oaxaca, with five vegetation types and a 2 500 m elevation range, has the richest documented butterfly fauna on the Pacific slope. This study focuses on Lycaenidae butterflies, exploring their distribution, richness, and abundance along vegetation and elevational transects.

Objective: To document geographic, elevational, and ecological patterns of Lycaenidae butterflies on the Pacific slope Loxicha region as part of a larger project on the distribution of diurnal butterflies in the state of Oaxaca, Mexico. Also, to compare Loxicha fauna with other regions to recognize biogeographical patterns at a larger scale.

Methods: Spatial and temporal patterns of Lycaenidae diversity are based on systematic sampling conducted between 2005 and 2014 along elevational (80 to 2 500 m) and vegetational transects. Exclusive and characteristic species for each elevation and vegetation type are recognized.

Results: A total of 123 species of Lycaenidae were recorded: nine species of Polyommata and 114 of Theclinae. The highest species richness occurs in May in tropical semi-deciduous forest. It decreases with increasing elevation. The results are compared with four other butterfly families. Lycaenid community similarity in the Sierra Madre del Sur and Pacific slope is correlated with elevation and vegetation type, though variability within each grouping is significant. Higher elevation faunal isolation also plays a role, as seen in other mountainous Papilionoidea taxa.

Conclusions: Lycaenidae is one of the most diverse and least known butterfly families in Mexico. This is the fourth study on the Loxicha Region's lepidopteran fauna, confirming its high diversity among five Papilionoidea families. Systematic studies aid in understanding speciation and endemism, particularly for stenotopic species. The distribution of Lycaenidae in the Loxicha region is the most comprehensive to date for any region in Mexico.

Key words: elevational gradient; Eumaeini; phenology; Sierra Madre del Sur.



RESUMEN

Distribución, riqueza y abundancia de Lycaenidae (Lepidoptera: Papilionoidea) en la Región Loxicha, Oaxaca, México: Un análisis regional en la vertiente del Pacífico

Introducción: La Sierra Madre del Sur en México, conocida por su complejidad geológica y gradiente de elevación, alberga ecosistemas diversos. La región de Loxicha en Oaxaca, con cinco tipos de vegetación y un rango de elevación de 2 500 m, tiene la fauna de mariposas documentada más rica en la vertiente del Pacífico. Este estudio se enfoca en las mariposas de la familia Lycaenidae, explorando su distribución, riqueza y abundancia a lo largo de transectos de vegetación y elevación.

Objetivo: Documentar los patrones geográficos, altitudinales y ecológicos de Lycaenidae en la región de Loxicha en la vertiente del Pacífico, como parte de un proyecto más amplio sobre la distribución de mariposas diurnas en el estado de Oaxaca, México. También, comparar la fauna de Loxicha con otras regiones para reconocer patrones biogeográficos a mayor escala.

Métodos: Los patrones espaciales y temporales de diversidad de Lycaenidae se basan en muestreos sistemáticos realizados entre 2005 y 2014 a lo largo de transectos de elevación (80 a 2 500 m) y vegetación. Se reconocen especies exclusivas y características de cada altitud y tipo de vegetación.

Resultados: Se registraron un total de 123 especies de Lycaenidae: nueve especies de Polyommata y 114 de Theclinae. La mayor riqueza de especies se observa en mayo en bosques tropicales semi-decíduos. Esta disminuye con el aumento de la elevación. Los resultados se comparan con otras cuatro familias de mariposas. La similitud de la comunidad de Lycaenidae en la Sierra Madre del Sur y la vertiente del Pacífico está correlacionada con la elevación y el tipo de vegetación, aunque la variabilidad dentro de cada agrupación es significativa. El aislamiento faunístico en elevaciones altas también juega un papel, como se observa en otros taxones de Papilionoidea de sistemas montañosos.

Conclusiones: Lycaenidae es una de las familias de mariposas más diversas y menos conocidas de México. Este es el cuarto estudio sobre la fauna lepidópteros de la región de Loxicha, confirmando su alta diversidad entre cinco familias de Papilionoidea. Los estudios sistemáticos ayudan a comprender la especiación y el endemismo, particularmente para las especies estenotópicas. La distribución de Lycaenidae en la región de Loxicha es la más completa hasta la fecha para cualquier región de México.

Palabras clave: gradiente altitudinal; Eumaeini; fenología; Sierra Madre del Sur.

INTRODUCTION

Mexico's Sierra Madre del Sur is recognized for its complex geological history and for an elevational gradient that generates ecosystem heterogeneity (Espinosa et al., 2016). This complexity is reflected in the Loxicha region (Oaxaca), which consists of five distinctive vegetation types and an elevation gradient of 2 500 m. It is an underlying reason why we have been investigating its butterfly richness along elevation and vegetation transects (Arellano-Covarrubias et al., 2018; Luis-Martínez et al., 2016; Luis-Martínez et al., 2020; Luis-Martínez et al., 2022). It has the richest documented butterfly fauna on Mexico's Pacific slope for the four families treated so far.

Lycaenidae present challenges for sampling. Adults tend to be more rarely encountered than

other butterflies, for example, at about half the rate as that of Riodinidae (Lamas et al., 2023). Bait traps with rotting carrion seem to be ineffective in Mesoamerican localities (Busby et al., 2019). These characteristics potentially bias the documentation of Lycaenidae spatial and temporal patterns compared to other butterflies.

New World Lycaenidae exhibit other ecological characteristics that distinguish the family. The caterpillars show significant variation in feeding habits, including extreme polyphagy (Chew & Robbins, 1984), florivory (Silva et al., 2014), detritivory (Duarte & Robbins, 2009; Robbins et al., 2010), and fungivory (Nishida & Robbins, 2020). Many species are facultatively myrmecophilous (DeVries, 1990; DeVries, 1991; Kaminski et al., 2012). More than 90 % of the species have adult males with secondary sexual organs (Valencia-Montoya et al., 2021).

The characteristics of Lycaenidae suggest that their spatial and temporal distributions might differ from those of other Papilionoidea. This study specifically examines the distribution, richness, and abundance of Lycaenidae along vegetation and elevational transects in the Loxicha region and is the first such investigation in any of Mexico's most diverse regions. The results are compared with those of other regions of the Pacific and Atlantic slopes in Mexico. An updated checklist with photographs of Lycaenidae from Loxicha is presented, serving as a reference for future identification within the family.

Documentation of the Mexican lycaenid butterfly fauna has progressed for more than a century. Godman and Salvin (1887-1901) monographed the diurnal butterfly fauna of Mesoamerica, recording 124 species of Mexican Lycaenidae. Hoffmann's (1933), Hoffmann's (1936), Hoffmann's (1940) and Hoffmann's (1941) checklist of Mexican Papilionoidea included distribution by state, physiographic unit, elevation, and climatic subtype. He included 221 Lycaenidae. Subsequently, Llorente-Bousquets et al. (2006) recorded 255 species and subspecies of Mexican Lycaenidae, which was later refined to 252 species and subspecies, representing 13 % of the Mexican Papilionoidea (Llorente-Bousquets et al., 2014).

Knowledge of the lycaenid fauna of Oaxaca has similarly steadily improved. Hoffmann (1940) and Hoffman (1941) recorded 164 lycaenid species in Oaxaca. More recently, Luis-Martínez et al. (2016) listed 180 lycaenid species, partitioned taxonomically into 169 Theclinae, 10 Polyommattinae, and 1 Lycaeninae.

MATERIAL AND METHODS

Previous data: The MARIPOSA database (Luis-Martínez et al., 2005) from the Zoology Museum of the Faculty of Science, UNAM has more than 65 000 records documenting the geographic distribution of Lycaenidae and other butterflies in Mexico. Some data are available on the CONABIO website (Gobierno de México, n. d.), and we are uploading more. The

data range from the late 19th century (Godman & Salvin, 1887-1901) to the present and include more than 2 300 sites. Using the database and publications on Lycaenidae from other Mexican regions (de la Maza & de la Maza, 1993, de la Maza & de la Maza, 2015; Luis-Martínez et al., 1991; Raguso & Llorente-Bousquets, 1991; Ross, 1966, Ross, 1976; Vargas-Fernández et al., 1994; Vargas-Fernández et al., 1999), the localities and regions (groups of localities) with the greatest recorded Lycaenidae richness in Mexico are listed (Table 1).

Faunistic inventory and localities: Since 2005, we conducted systematic butterfly sampling in the Loxicha region (Fig. 1), comprising 318 sampling days over seven years (2005, 2007, 2008, 2011–2014) at 21 localities (Table 2) (Arellano-Covarrubias et al., 2018; Luis-Martínez et al., 2016; Luis-Martínez et al., 2020; Luis-Martínez et al., 2021; Luis-Martínez et al., 2022). The surveys involved 16 participants, averaging five per locality per day, most of whom had extensive experience in sampling butterflies.

Localities were grouped by elevation and vegetation to analyze distribution patterns, which facilitates comparison with other localities. Vegetation type classification follows Rzedowski (1978) and Llorente-Bousquets (1984): tropical deciduous forest (TDF), tropical subdeciduous forest (TSDF), montane cloud forest (CF) with three subtypes, and oak-pine forest (OPF). Additionally, in some sites at elevations between 2 000 and 2 400 m, a vegetation type primarily comprising pine-oak forest with elements of high-altitude montane cloud forest was recognized, mostly located at the bottom of ravines. This high-altitude oak-pine and montane cloud forest (OPCF) is distinct from OPF and CF, although adjacent to them, and was considered a separate category (Arellano-Covarrubias et al., 2018; Luis-Martínez et al., 2020; Luis-Martínez et al., 2021; Luis-Martínez et al., 2022). Sampling focused on effective sites, such as sunny areas with small white inflorescences, where species of the subfamily Theclinae were primarily observed.



Table 1

Single sites and regions (Reg. is a group of sites with more than one elevation or vegetation zone) with highest species richness of Lycaenidae in Mexico.

Altitude (m)	Site / Region	spp. P / T / Total
Atlantic Slope		
0-1 700	Reg. Los Tuxtlas-Catemaco ^{3,4,5*} - Ver.	8 / 129 / 137
100-2 800	Reg. Sierra de Juárez ^{2*} - Oax.	8 / 117 / 125
500-1 500	Reg. Macizo Central ⁶ - Chis.	7 / 116 / 123+1 [^]
100-1 500	Reg. Selva Lacandona ⁶ - Chis.	4 / 115 / 119
0-2 500	Reg. Cuenca de Tulijá ⁶ - Chis.	4 / 109 / 113
250-1 000	Reg. Cuenca del Grijalva ⁶ - Chis.	4 / 108 / 112
140-200	Site. Río Lacantún ¹ - Chis.	5 / 103 / 108
200-350	Site. Cuetzalapan* - Ver.	2 / 101 / 103
350	Site. Catemaco* - Ver.	3 / 95 / 98
350-950	Reg. Barranca de Patla* - Pue.	5 / 86 / 91
650	Site. Tequezquitla* - Pue.	5 / 84 / 89
1 350	Site. San Antonio Buenavista (Sta Rosa)* - Chis.	4 / 81 / 85
350	Site. Presidio* - Ver.	4 / 77 / 81
1 200-1 600	Reg. Xalapa* - Ver.	7 / 71 / 78
900	Site. Carretera 175, Metates ^{2*} - Oax.	4 / 66 / 70
1 150-1 350	Site. Coatepec* - Ver.	4 / 64 / 68
300	Site. Tapalapan* - Ver.	3 / 64 / 67
860	Site. Cerro El Vigía, Santiago Tuxtla* - Ver.	2 / 64 / 66
1 200-1 500	Reg. Sierra Madre ⁶ - Chis.	5 / 59 / 64
500-1 500	Reg. Depresión Central ⁵ - Chis.	6 / 54 / 60
Pacific slope		
80-2 850	Reg. Loxicha - Oax.	9 / 114 / 123
400	Site. Rancho Hagia Sofía* - Oax.	7 / 84 / 91
300-2 500	Reg. Sierra de Atoyac ^{7*} - Gro.	7 / 81 / 88
750	Site. Rancho “El Zorrillo”, Cañada Húmeda* - Mich.	6 / 74 / 80
260	Site. Chiquihuitillo* - Mich.	6 / 65 / 70
250-1 800	Reg. Sierra de Manantlán ^{8*} - Jal. / Col.	8 / 59 / 67
2 250	Site. Santa Rosa, Comitán* - Chis.	6 / 60 / 66
900	Site. Planta Hidroeléctrica Cupatitzio* - Mich.	7 / 58 / 65
1 200-1 500	Reg. Soconusco ⁶ - Chis.	4 / 58 / 62+1 [^]
650	Site. Río Santiago, 4 km W* - Gro.	8 / 53 / 61
850	Site. Arteaga* - Mich.	6 / 55 / 61

P: Polyommatainae; T: Theclinae; Chis.: Chiapas; Col.: Colima; Gro.: Guerrero; Jal.: Jalisco; Mich.: Michoacán; Oax.: Oaxaca; Ver.: Veracruz; ^ Species recorded from the Lycaeninae subfamily. Source of data: *, MARIPOSA database (Luis-Martínez et al., 2005); 1, de la Maza & de la Maza (1993); 2, Luis-Martínez et al. (1991); 3, Ross (1966); 4, Ross (1976); 5, Raguso & Llorente-Bousquets (1991); 6, de la Maza & de la Maza (2015); 7, Vargas-Fernández et al. (1994); 8, Vargas-Fernández et al. (1999).

Taxonomy: Identification was carried out by comparison with the Lepidoptera Collection at the Museum of Zoology, Faculty of Sciences, UNAM (MZFC) and the National Museum of Natural History, Smithsonian Institution (USNM). The updated species list by subtribe follows Robbins et al. (2022).

Deposition and permits: Specimens were deposited in the Papilionoidea Collection (Lepidoptera) at the Museum of Zoology under registration number DFE.IN.071.0798 issued by the Secretariat of Environment, Natural Resources, and Fisheries (SEMARNAP). The specimens were collected under the scientific

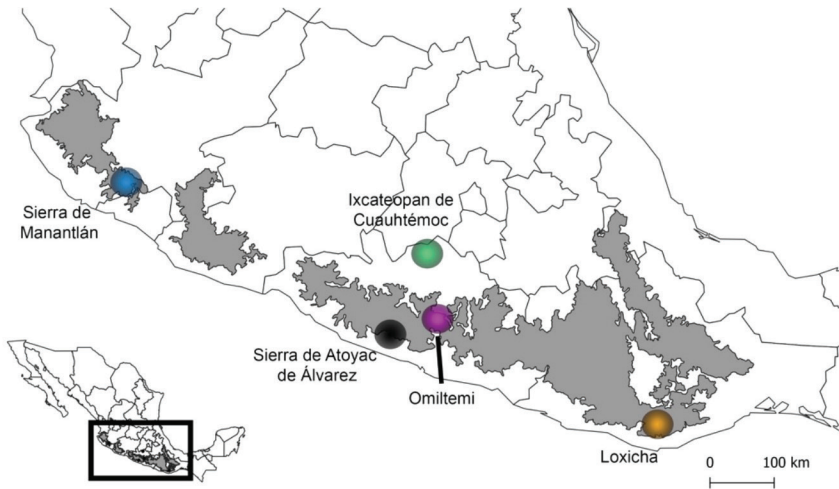


Fig 1. Location of the geographic units on the Pacific slope analyzed: Loxicha Region, Oaxaca; Sierra de Atoyac de Álvarez, Guerrero; Omiltemi Region, Guerrero; locality Ixcateopan de Cuauhtémoc, Guerrero; Sierra de Manantlán, Jalisco-Colima. The Sierra Madre del Sur province (grey) and state lines are outlined.

Table 2
Number of specimens and species by locality.

Altitude (m)		Vegetation / Site	P	T	Total
Tropical deciduous forest (TDF)					
0-500	80-100	Parque Nacional Huatulco, río Cacaluta	53 / 4	37 / 16	90 / 20
	100	Parque Nacional Huatulco	151 / 5	53 / 20	204 / 25
Tropical subdeciduous forest (TSDF)					
	380-500	Azulillo	298 / 8	212 / 37	510 / 45
	410	Rancho Hagia Sofía	303 / 7	1 738 / 84	2041 / 91
Cloud forest (CF)					
500-1 000	530-700	Río Molinos*	24 / 4	13 / 9	37 / 13
	600-1 200	Copalita, río Copalita*	3 / 2	19 / 15	22 / 17
	750-900	Magdalena, El Lirio	57 / 5	95 / 27	152 / 32
	900	Copalita, Los Plátanos*	0 / 0	1 / 1	1 / 1
	940	Copalita, Siete Veneros*	29 / 4	5 / 2	34 / 6
1 000-1 500	1 000	San Mateo Piñas*	0 / 0	3 / 3	3 / 3
	1 100-1 200	Pluma Hidalgo, 4 km NW “La Curva”	128 / 9	146 / 34	274 / 43
	1 100-1 250	Finca Aurora-Finca San Isidro	65 / 5	105 / 18	170 / 23
	1 200	Copalita, Llano de Ocote*	0 / 0	18 / 4	18 / 4
	1 200-1 530	Portillo del Rayo-Finca El Encanto	47 / 6	54 / 16	101 / 22
	1 470-1 550	La Soledad-Buenavista	54 / 6	63 / 21	117 / 27
	1 500-1 650	La Pasionaria	11 / 3	114 / 16	125 / 19
Oak-pine - cloud forest (OPCF)					
1 500-2 000	1 950-2 150	Puente Arroyo “El Guajolote”	53 / 5	26 / 12	79 / 17
>2 000	2 280-2 400	San José del Pacífico, 1 km S	281 / 6	264 / 32	545 / 38
	Oak-pine forest (OPF)				
	2 700-2 800	Manzanal-Doncella*	14 / 3	4 / 3	18 / 6
	2 700-2 800	Camino a San Agustín Loxicha*	0 / 0	2 / 2	2 / 2
	2 820-2 850	Nevería-La Ciénega*	1 / 1	2 / 2	3 / 3
Total			1 572 / 9	2 974 / 114	4 547 / 123

P: Polyommatae. T: Theclinae. specimens / number of species. * Localities considered without exhaustive sampling.



collecting permit issued to Jorge Enrique Llorente Bousquets by the Ministry of Environment and Natural Resources (SEMARNAT), with permit number FAUT-0148. Specimen data were incorporated into the MARIPOSA database (Luis-Martínez et al. 2005).

Species richness by vegetation and elevation: Species richness was estimated for each vegetation type and for five elevation zones: 0-500, 500-1 000, 1 000-1 500, 1 500-2 000, > 2 000 m. The non-parametric estimator Chao1 (Colwell & Coddington, 1994) was used with the SpadeR package (Chao et al., 2016). A confidence interval (95 %) with the standard error was calculated for each estimate using the Bootstrap technique. Significant differences in species richness among months, vegetation types, and elevation zones were evaluated by the overlap of confidence intervals for the estimates.

Additionally, for the elevation zones, ecological diversity was estimated as the exponential of the Shannon-Wiener index (H'), using the Chao & Shen (2003) method implemented in SpadeR (Chao et al., 2016). This diversity measure is also known as the Effective Number of Species (NES) (Jost, 2006). The index takes into account both species richness and their relative abundance.

Exclusive and characteristic species: Species recorded only in a single vegetation type or in a single elevation zone, were considered stenoecious *sensu* Udvardy (1969), occupying a narrow range of the habitats available, and referred as “exclusive”. Those with 80 to 99 % of their records in a particular vegetation type or elevation zone were considered amphieciuous and referred as “characteristic”, occupying two or more types of habitats with a broader ecological tolerance than stenoecious species, but still not as flexible as euryecious species. The rest of the species were considered euryecious, occupying a wide range of the habitats available.

Faunal similarity with other Mexican Pacific Slope localities: To determine how vegetation and elevation determine the occurrence

of lycaenid species on Mexico's Pacific slope, we calculated a distance matrix dendrogram from species abundance data using the Bray-Curtis index through the “vegan” package (Oksanen et al., 2022) in R 4.0.0 (R Core Team, 2023). The analysis included data from 31 localities (Fig. 1): 12 from the Loxicha region in Oaxaca (this study); 10 from Guerrero: El Faisanal, Las Parotas, Nueva Delhi, Puente de los Lugardo, and Río Santiago 4 km W in Sierra de Atoyac de Álvarez (Vargas-Fernández et al., 1994); Cañada W of La Gruta del Borrego, Potrerillo, Presa de la Perra, and Rancho Omiltemi in the Omiltemi region (Luis-Martínez & Llorente-Bousquets, 1993), and Ixcateopan de Cuauhtémoc. Also included were six localities from the Sierra de Manantlán in Jalisco-Colima: Agua Dulce, Ahuacapán, La Calera, Los Mazos 9 mi SW Autlán, Platanarillo, and Zenzontla (Vargas-Fernández et al., 1994). The localities were selected based on vegetation type, geographic location (region), elevation (100-2 600 m), and sampling coverage.

RESULTS

Mexican Lycaenidae richness by locality: The 17 individual localities and 14 regions (groups of localities) with the highest Lycaenidae species richness in Mexico are listed (Table 1). Two localities exceed 100 species: Río Lacantún in Chiapas with 108 (45 %) species (de la Maza & de la Maza, 1993) and Cuetzalapan in Veracruz with 103 (43 %) species (Luis-Martínez et al., 2005). The region (group of localities) with the highest number of species is Los Tuxtlas and the surroundings of Catemaco, Veracruz, with 137 species (57 % of the total recorded in the country); this is one of the regions with the most extensive sampling efforts primarily from 1960 to 1990 (Raguso & Llorente-Bousquets, 1991). More than 94 % of the 2 159 documented Mexican localities have 10 or fewer lycaenid species recorded. These data demonstrate the historic insufficiency of sampling effort in most of Mexico.

The Loxicha region: The MARIPOSA database (Luis-Martínez et al., 2005) had

200 specimen records from the Loxicha region between 1968 and 1992 from 100 to 2 280 m elevation. From these historic specimens, 41 genera were recorded, with five Polyommatae species and 53 Theclinae species. As a result of the faunistic work carried out for this study

from 2005 to 2014, an additional 4 547 specimens were sampled, belonging to 67 genera with nine species of Polyommatae and 114 of Theclinae (from 80 to 2 850 m elevation) (Fig. 2, Fig. 3, Fig. 4). A nomenclatural list of the species follows.

Family Lycaenidae [Leach], [1815])

Subfamily Theclinae Swainson, 1831

Tribe Eumaeini Doubleday, 1847

Subtribe Eumaeina Doubleday, 1847

Eumaeus Hübner, [1819]

1. *Eumaeus childrenae* (Gray, 1832)

2. *Eumaeus toxea* (Godart, [1824])

Micandra Staudinger, 1888

3. *Micandra cyda* (Godman & Salvin, 1887)

Subtribe Rhammina Prieto & Busby, 2021

Lathecla Robbins, 2004

4. *Lathecla latagus* (Godman & Salvin, 1887)

Subtribe Timaetina Prieto & Busby, 2021

Nesiostrymon Clench, [1964]

5. *Nesiostrymon dodava* (Hewitson, 1877)

Subtribe Atlidina Martins & Duarte, 2021

Brangas Hübner, [1819]

6. *Brangas neora* (Hewitson, 1867)

7. *Brangas getus* (Fabricius, 1787)

Atlides Hübner, [1819]

8. *Atlides halesus* (Cramer, 1777)

9. *Atlides gaumeri* (Godman, 1901)

10. *Atlides polybe* (Linnaeus, 1763)

11. *Atlides inachus* (Cramer, 1775)

12. *Atlides carpasia* (Hewitson, 1868)

Arcas Swainson, 1832

13. *Arcas cypria* (Geyer, 1837)

Pseudolycaena Wallengren, 1858

14. *Pseudolycaena damo* (H. Druce, 1875)

Denivia K. Johnson, 1992

15. *Denivia theocritus* (Fabricius, 1793)

16. *Denivia hisbon* (Godman & Salvin, 1887)

Subtribe Evenina Faynel & Grishin, 2021

Evenus Hübner, [1819]

17. *Evenus regalis* (Cramer, 1775)

Subtribe Jantheclina Robbins & Faynel, 2021

Contrafacia K. Johnson, 1989

18. *Contrafacia bassania* (Hewitson, 1868)

19. *Contrafacia ahola* (Hewitson, 1867)

Allosmaitia Clench, [1964]

20. *Allosmaitia strophius* (Godart, [1824])



- Laothus* K. Johnson, Kruse & Kroenlein, 1997
21. *Laothus erybathis* (Hewitson, 1867)
- Subtribe Paiwarriina Lamas & Robbins, 2021
- Kolana* Robbins, 2004
22. *Kolana ligurina* (Hewitson, 1874)
- Subtribe Cupatheclina Lamas & Grishin, 2021
- Cupathecla* Robbins, 2002
23. *Cupathecla cupentus* (Stoll, 1781)
- Subtribe Parrhasiina Busby & Robbins, 2021
- Parrhasius* Hübner, [1819]
24. *Parrhasius polibetes* (Stoll, 1781)
 25. *Parrhasius orgia* (Hewitson, 1867)
 26. *Parrhasius moctezuma* (Clench, 1971)
- Ignata* K. Johnson, 1992
27. *Ignata gadira* (Hewitson, 1867)
- Michaelus* Nicolay, 1979
28. *Michaelus jebus* (Godart, [1824])
 29. *Michaelus hecate* (Godman & Salvin, 1887)
 30. *Michaelus ira* (Hewitson, 1867)
- Apuecla* Robbins, 2004
31. *Apuecla maeonis* (Godman & Salvin, 1887)
- Dicya* K. Johnson, 1991
32. *Dicya carnica* (Hewitson, 1873)
- Symbiopsis* Nicolay, 1971
33. *Symbiopsis* sp.
- Subtribe Ipideclina Martins & Grishin, 2021
- Ipidecla* Dyar, 1916
34. *Ipidecla miadora* Dyar, 1916
- Subtribe Calycopidina Duarte & Robbins, 2010
- Gigantorubra* Johnson, 1993
35. *Gigantorubra collucia* (Hewitson, 1877)
- Ziegleria* K. Johnson, 1993
36. *Ziegleria hesperitis* (Butler & H. Druce, 1872)
 37. *Ziegleria hoffmani* K. Johnson, 1993
- Arzecla* Duarte & Robbins, 2010
38. *Arzecla ceromia* (Hewitson, 1877)
- Kisutam* K. Johnson & Kroenlein, 1993
39. *Kisutam syllis* (Godman & Salvin, 1887)
- Rubroserrata* K. Johnson & Kroenlein, 1993
40. *Rubroserrata mathewi* (Hewitson, 1874)
- Electrostrymon* Clench, 1961
41. *Electrostrymon hugon* (Godart, [1824])
 42. *Electrostrymon joya* (Dognin, 1895)
- Pendantus* K. Johnson & Kroenlein, 1993
43. *Pendantus denarius* (Butler & H. Druce, 1872)
 44. *Pendantus guzanta* (Schaus, 1902)
- Mercedes* K. Johnson, 1992
45. *Mercedes clarina* (Hewitson, 1874)

46. *Mercedes atnius* (Herrich-Schäffer, [1853])
 47. *Mercedes demonassa* (Hewitson, 1868)
 48. *Mercedes calus* (Godart, [1824])
- Calycopis* Scudder, 1876
49. *Calycopis isobea* (Butler & H. Druce, 1872)
- Subtribe Strymonina Tutt, 1907
- Thereus* Hübner, [1819]
50. *Thereus orasus* (Godman & Salvin, 1887)
 51. *Thereus oppia* (Godman & Salvin, 1887)
 52. *Thereus ortalus* (Godman & Salvin, 1887)
- Rekoa* Kaye, 1904
53. *Rekoa meton* (Cramer, 1779)
- Heterosmaitia* Clench, [1964]
54. *Heterosmaitia palegon* (Cramer, 1780)
 55. *Heterosmaitia zebina* (Hewitson, 1869)
 56. *Heterosmaitia marius* (Lucas, 1857)
 57. *Heterosmaitia stagira* (Hewitson, 1867)
- Arawacus* Kaye, 1904
58. *Arawacus togarna* (Hewitson, 1867)
 59. *Arawacus sito* (Boisduval, 1836)
 60. *Arawacus jada* (Hewitson, 1867)
- Strymon* Hübner, 1818
61. *Strymon melinus* (Hübner, 1818)
 62. *Strymon albata* (C. Felder & R. Felder, 1865)
 63. *Strymon bebrycia* (Hewitson, 1868)
 64. *Strymon yojoa* (Reakirt, [1867])
 65. *Strymon cestri* (Reakirt, [1867])
 66. *Strymon bazochii* (Godart, [1824])
 67. *Strymon istapa* (Reakirt, [1867])
 68. *Strymon serapio* (Godman & Salvin, 1887)
 69. *Strymon megarus* (Godart, [1824])
 70. *Strymon ziba* (Hewitson, 1868)
- Panthiades* Hübner, [1819]
71. *Panthiades bathildis* (C. Felder & R. Felder, 1865)
 72. *Panthiades sierrae* (Dyar, 1916)
 73. *Panthiades ochus* (Godman & Salvin, 1887)
- Subtribe Strephonotina K. Johnson, Austin, Le Crom & Salazar, 1997
- Tmolus* Hübner, [1819]
74. *Tmolus echion* (Linnaeus, 1767)
 75. *Tmolus crolinus* Butler & Druce, 1872
- Nicolaea* K. Johnson, 1993
76. *Nicolaea dolium* (H.H. Druce, 1907)
- Crimsinota* K. Johnson, 1993
76. *Crimsinota velina* (Hewitson, 1868)
- Ministrymon* Clench, 1961
77. *Ministrymon clytie* (W.H. Edwards, 1877)
 78. *Ministrymon arola* (Hewitson, 1868)
 79. *Ministrymon zilda* (Hewitson, 1873)



80. *Ministrymon inoa* (Godman & Salvin, 1887)
81. *Ministrymon phrutus* (Geyer, 1832)
82. *Ministrymon azia* (Hewitson, 1873)
83. *Ministrymon una* (Hewitson, 1873)
- Gargina Robbins, 2004
84. *Gargina gargophia* (Hewitson, 1877)
85. *Gargina caninius* (H.H. Druce, 1907)
86. *Gargina thoria* (Hewitson, 1869)
- Siderus Kaye, 1904
87. *Siderus philinna* (Hewitson, 1868)
- Theclopsis Godman & Salvin, 1887
88. *Theclopsis mycon* (Godman & Salvin, 1887)
- Ostrinotes K. Johnson, Austin, Le Crom & Salazar, 1997
89. *Ostrinotes keila* (Hewitson, 1869)
- Strephonota K. Johnson, Austin, Le Crom & Salazar, 1997
90. *Strephonota tephraeus* (Geyer, 1837)
91. *Strephonota syedra* (Hewitson, 1867)
- Celmia K. Johnson, 1991
92. *Celmia celmus* (Cramer, 1775)
- Subtribe Callophryidina Tutt, 1907
- Radissima Johnson, 1992
94. *Radissima umbratus* (Geyer, 1837)
- Thaides K. Johnson, Kruse & Kroenlein, 1997
95. *Thaides theia* (Hewitson, 1870)
- Ocaria Clench, 1970
96. *Ocaria petelina* (Hewitson, 1877)
97. *Ocaria ocrisia* (Hewitson, 1868)
- Chlorostrymon Clench, 1961
98. *Chlorostrymon simaethis* (Drury, 1773)
99. *Chlorostrymon telea* (Hewitson, 1868)
- Magnastigma Nicolay, 1977
100. *Magnastigma elsa* (Hewitson, 1877)
- Cyanophrys Clench, 1961
101. *Cyanophrys fusius* (Godman & Salvin, 1887)
102. *Cyanophrys herodotus* (Fabricius, 1793)
103. *Cyanophrys miserabilis* (Clench, 1946)
104. *Cyanophrys longula* (Hewitson, 1868)
105. *Cyanophrys agricolor* (Butler & H. Druce, 1872)
- Callophrys Billberg, 1820
106. *Callophrys guatemalena* Clench, 1981
- Erora Scudder, 1872
107. *Erora quaderna* (Hewitson, 1868)
108. *Erora nitetis* (Godman & Salvin, 1887)
109. *Erora carla* (Schaus, 1902)
110. *Erora gabina* (Godman & Salvin, 1887)
111. *Erora opisena* (H.H. Druce, 1912)
112. *Erora muridosca* (Dyar, 1918)
- Semonina Robbins, 2004

113. *Semonina semones* (Godman & Salvin, 1887)
Chalybs Hübner, [1819]
 114. *Chalybs hassan* (Stoll, 1790)
 Subfamily Polyommatainae Swainson, 1827
Leptotes Scudder, 1876
 115. *Leptotes cassius cassidula* (Boisduval, 1870)
 116. *Leptotes marina* (Reakirt, 1868)
Zizula Chapman, 1910
 117. *Zizula cyna* (W.H. Edwards, 1881)
Brephidium Scudder, 1876
 118. *Brephidium exilis exilis* (Boisduval, 1852)
Cupido Schrank, 1801
 119. *Cupido comyntas* (Godart, [1824])
Celastrina Tutt, 1906
 120. *Celastrina echo gozora* (Boisduval, 1870)
Hemiargus Hübner, 1818
 121. *Hemiargus ceraunus astenidas* (Lucas, 1857)
Echinargus Nabokov, 1945
 122. *Echinargus isola* (Reakirt, [1867])
Icaricia Nabokov, 1945
 123. *Icaricia acmon* (Westwood, [1851])



Fig. 2. Lycaenidae from the Loxicha Region. The numbers correspond to the species list (Line: scale 1 cm). Only species not shown in Fig. 8 and Fig. 9 are included.



Fig. 3. Lycaenidae from the Loxicha Region (continued). The numbers correspond to the species list (Line: scale 1 cm).



Fig. 4. Lycaenidae from the Loxicha Region (continued). The numbers correspond to the species list (Line: scale 1 cm).

Encounter rates: Most species sampled were rarely encountered, which is a widely observed pattern among animals and plants (Kunin & Gaston, 1993). Thirty-five species (28 %) were sampled once or twice, representing an

encounter rate of less than 0.03 %. Alternatively, the ten most commonly encountered species made up 51 % of the individuals, namely *Cupido comyntas* (413 specimens), *Leptotes cassius cassidula* (378), *Celastrina echo gozora*

(323), *Calycopis isobea* (262), *Pseudolycaena damo* (242), *Hemiargus ceraunus astenidas* (222), *Theclopsis mycon* (169), *Ministrymon arola* (157), *Arawacus sito* (148), and *Zizula cyna* (122). Half the species are Polyommatainae and half are Theclinae.

Patterns of species richness: The Lycaenidae richness of the Loxicha region represents 53 % of the Mexican fauna (Llorente-Bousquets et al., 2014) and 71 % at the state level (Luis-Martínez et al., 2016). The richness of the Loxicha region is equivalent to that of the Central Chiapas Massif (de la Maza & de la Maza, 2015) and is slightly less than the Los Tuxtlas-Catemaco region, Veracruz (with the highest richness: 137 species) and the Sierra de Juárez, Oaxaca (125 species) (Luis-Martínez et al., 1991). Llorente-Bousquets et al. (2014) reported 106 Lycaenidae species for the Sierra Madre del Sur, with 17 species fewer than the Loxicha region. Loxicha hosts four of the eight Mexican endemic Theclinae species: *Ipidecla miadora* (7 specimens), *Laothus erybathis* (43), *Semonina semones* (4), and *Symbiopsis* sp. (2) (Trujano-Ortega et al., 2024).

The Loxicha locality with the highest richness was Rancho Hagia Sofía, with 84 Theclinae and seven Polyommatainae (Table 2). The sample included 80 % of the species and 45 % of the specimens in the Loxicha region. It ranks fourth among the 18 most species-rich localities in Mexico, and is the richest on the Pacific slope, surpassing Rancho “El Zorrillo” and Cañada Húmeda in Michoacán by 11 species (Table 1). The locality also had the greatest sampling effort with 47 fieldwork days.

A contrast to Rancho Hagia Sofía is Azulillo, with an equivalent number of vegetation and elevational zones. During 43 days of sampling for Theclinae, we recorded about half as many species and 12 % of the specimens compared to Rancho Hagia Sofía (Table 2). In contrast, for Polyommatainae, Azulillo had one more species than Rancho Hagia Sofía and nearly the same number of specimens.

The remaining 20 localities complete the richness of the Loxicha region with 33 species

and 55 % of the specimens. Notably, Azulillo and Pluma Hidalgo (4 km NW “La Curva”) show similar richness with 45 and 43 species, respectively, even though Azulillo is located at lower elevation (Table 2). The locality of San José del Pacífico stands out for its richness with 38 species; it had the second-highest number of specimens after Rancho Hagia Sofía and is the richest among the localities above 2 000 m in Mexico (e.g., Luis-Martínez & Llorente-Bousquets, 1990, Luis-Martínez & Llorente-Bousquets, 1993; Luis-Martínez et al. 1991; Vargas-Fernández et al., 1994; Vargas-Fernández et al., 1999).

Phenology: Both abundance and estimated richness show the same annual variation (Fig. 5, SMT 1). According to the estimates, richness is highest at the beginning of the rainy season (May-June), remaining consistent with no significant differences until October (Fig. 5, SMT 1). At the start of the dry season (November), there is a significant decrease in both richness and abundance, with minimum values in February. The estimates indicate sufficient sampling for most months, although the confidence intervals are wide, particularly for December, due to lower abundance and a higher proportion of rarely encountered species.

Vegetation type: The greatest number of Loxicha Lycaenidae inhabit tropical subdeciduous forest (124 estimated species) and montane cloud forest (106 estimated species) (Fig. 6, SMT 1). High-elevation oak-pine and montane cloud forest are less rich (62 estimated species). The wide confidence intervals for richness estimates in tropical deciduous forest, tropical subdeciduous forest, and high-altitude oak-pine and montane cloud forest are due to the high frequency of rarely encountered species. In contrast, no species were rarely encountered in oak-pine forest, and the confidence interval was low.

Elevation: Lower elevations (0-500 m) with 103 estimated species and the 1 000-1 500 m zone with 123 species had the highest estimated

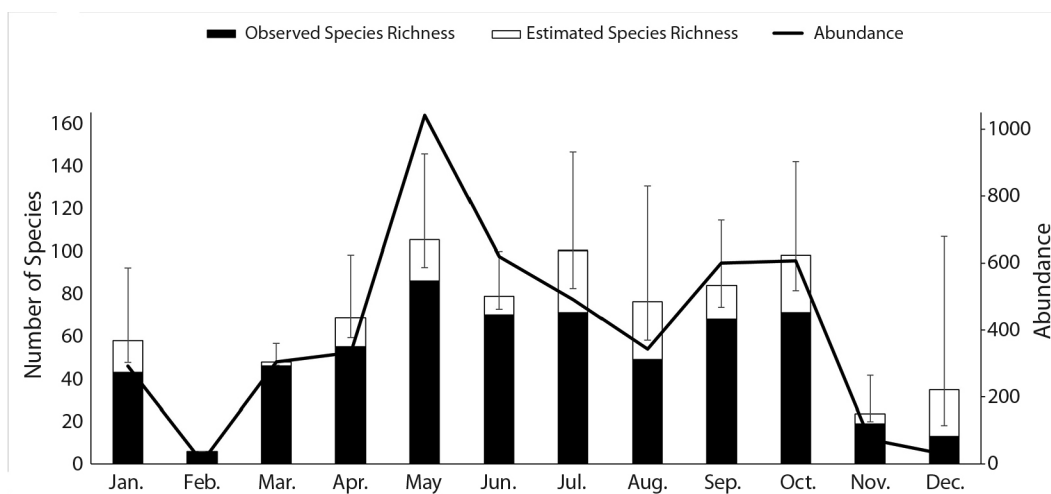


Fig. 5. Observed species richness, estimated richness, and abundance of Lycaenidae by month. Both parameters show a peak at the beginning of the rainy season in May and a decrease at the start of the dry season in November. The estimated richness indicates good sampling levels for each month, except December.

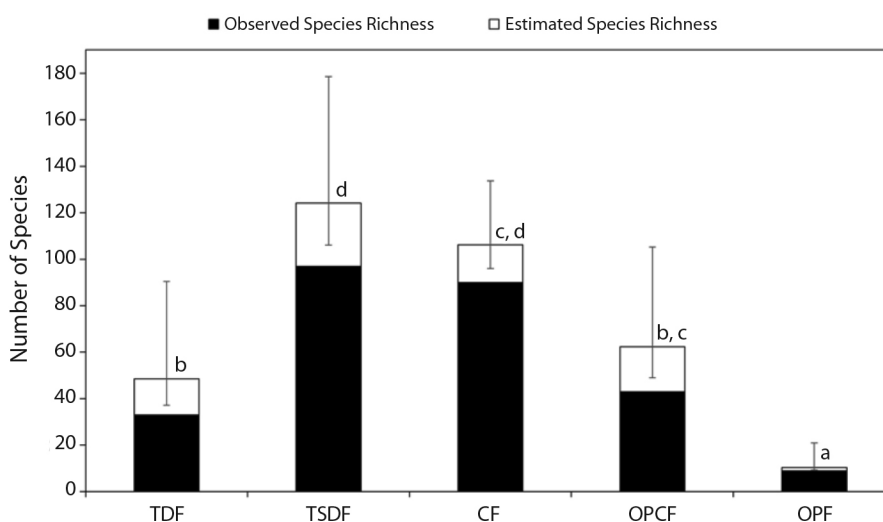


Fig. 6. Estimation of species richness by vegetation type. CF shows high richness considering it covers a smaller area. The letters indicate significant differences ($p < 0.05$) in the estimation of species richness based on the overlap of confidence intervals. TDF: tropical deciduous forest; TSDF: tropical subdeciduous forest; CF: cloud forest; OPCF: oak-pine – cloud forest; OPF: oak-pine forest.

richness (Fig. 7). The 0-500 m range is the best sampled, with 91 % of the species sampled, according to the estimation. In contrast, for the 1000-1500 m range, only 56 % of the species were sampled. Additionally, the wide confidence interval at this elevation (a high frequency of rarely encountered species) may be

due to the montane cloud forest. On the other hand, ecological diversity (Effective Number of Species) is high at the lowest elevations and decreases with elevation (Fig. 7). This ecological diversity is affected by the proportion of rare and dominant species present in each elevation zone. In general, encounter rates are low, with

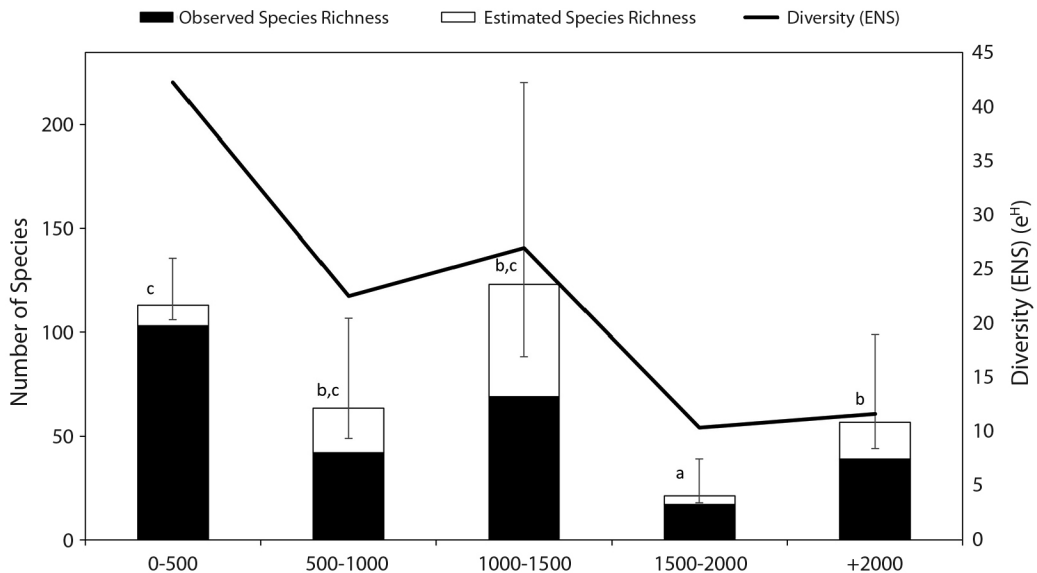


Fig. 7. Species richness and diversity by elevation. Observed species richness is higher in the lowest elevational range, although the estimation shows no differences with intermediate altitudes, which had lower sampling effort. Both richness and ecological diversity decrease with elevation. Letters indicate significant differences ($p < 0.05$) in species richness estimation, based on the overlap of confidence intervals.

33 % of the 123 sampled species represented by five or fewer specimens. We note that the elevation range with the fewest “unseen” species is 1 500-2 000 m, which may be a sampling artifact because only one locality occurs at this elevation (Table 2).

Exclusive and characteristic species by vegetation type: Forty-four species (Table 3, Fig. 8) were sampled in only one vegetation type, but 25 were represented by only one or two specimens (Table 3). The exclusive species are all Theclinae species, with a majority (29 species, 65 %) limited to tropical subdeciduous forest. The most abundant exclusive species in tropical subdeciduous forest are *Rekoa meton* (37 specimens), *Gargina thoria* (24), and *G. caninius* (17). In montane cloud forest, 12 exclusive species were recorded, with the most abundant being *Arawacus togarna* (5). In Oak-Pine cloud forest, only three exclusive species were present: *Erora quaderna*, *E. nitetis*, and *Thereus ortalus*.

For characteristic species (80 to 99 % of specimens in a specific vegetation type),

tropical subdeciduous forest has the highest number, with 26 species, followed by montane cloud forest with six species and oak-pine cloud forest with five (Table 3, Fig. 9). Three Polymmatinae species were each characteristic of one vegetation type: *Icaricia acmon* (tropical subdeciduous forest), *Zizula cyna* (montane cloud forest), and *Celastrina echo gozora* (high-altitude oak-pine and montane cloud forest). Despite its small extent, the montane cloud forest had 12 exclusive and six characteristic species, with the most frequently encountered being *Zizula cyna*, *Pendantus denarius*, *Eumaeus toxea*, and *E. childrenae*. The other two vegetation types (tropical deciduous forest and oak-pine forest) did not have exclusive or characteristic species.

Community composition: The distance matrix dendrogram based on species abundance data results in three groupings of faunal similarity characterized by elevation and vegetation type (Fig. 10). The first group consists of seven localities above 1 800 m elevation, including the two highest localities in the

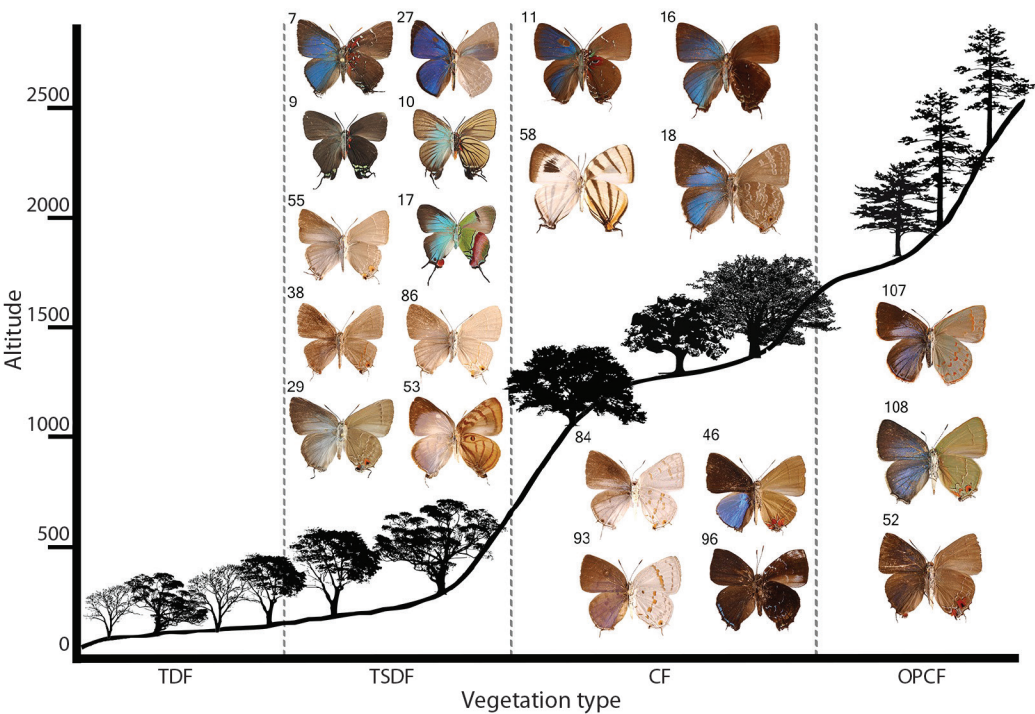


Fig. 8. Distribution of ‘exclusive’ species recorded only in one type of vegetation. The numbers correspond to the species list.

Table 3
‘Exclusive’ and ‘characteristic’ species by vegetation type.

Tropical Subdeciduous Forest 55	<u>Atlides carpasia</u> , <u>Allosmaitia strophius</u> , <u>Arzecla ceromia</u> (13), <u>Atlides gaumeri</u> (9), <u>Atlides polybe</u> (11), <u>Brangas getus</u> (7), <u>Brangas neora</u> (1), <u>Cyanophrys fusius</u> , <u>Chalybs hassan</u> , <u>Cyanophrys herodotus</u> , <u>Cyanophrys miserabilis</u> , <u>Chlorostrymon telea</u> , <u>Cupathea cupentus</u> (1), <u>Denivia theocritus</u> , <u>Erora carla</u> , <u>Electrostrymon hugon</u> , <u>Electrostrymon joya</u> (2), <u>Erora gabina</u> (2), <u>Erora muridosca</u> (2), <u>Erora opisena</u> (6), <u>Evenus regalis</u> (12), <u>Gigantorubra collucia</u> , <u>Gargina caninius</u> (17), <u>Gargina thoria</u> (24), <u>Heterosmaitia marius</u> , <u>Heterosmaitia stagira</u> , <u>Rekoa meton</u> (37), <u>Heterosmaitia zebina</u> (14), <u>Icaricia acmon</u> , <u>Ipidecla miadora</u> , <u>Ignata gadira</u> (7), <u>Kisutam syllis</u> (1), <u>Lathecla latagus</u> (1), <u>Ministrymon arola</u> , <u>Mercedes clarina</u> , <u>Mercedes demonassa</u> , <u>Michaelus jebus</u> , <u>Ministrymon phrutus</u> , <u>Magnastigma elsa</u> (2), <u>Mercedes calus</u> (2), <u>Michaelus hecate</u> (14), <u>Ministrymon inoa</u> (1), <u>Ministrymon zilda</u> (2), <u>Nicolaea dolium</u> (11), <u>Pseudolycaena damo</u> , <u>Panthiades sierrae</u> , <u>Parrhasius orgia</u> (6), <u>Radissima umbratus</u> , <u>Siderus philinna</u> , <u>Strephonota tephraeus</u> , <u>Semonina semones</u> (4), <u>Strymon melinus</u> (2), <u>Symbiopsis</u> sp. (2), <u>Tmolus echion</u> , <u>Ziegleria hesperitis</u> (1)
Cloud forest 18	<u>Arawacus togarna</u> (5), <u>Atlides inachus</u> (1), <u>Celmia celmus</u> (1), <u>Contrafacia bassania</u> (2), <u>Denivia hisbon</u> (3), <u>Eumaeus childrenae</u> , <u>Eumaeus toxea</u> , <u>Mercedes atnius</u> (1), <u>Ministrymon una</u> (1), <u>Nesiostrymon dodava</u> (1), <u>Ocaria petelina</u> (1), <u>Panthiades ochus</u> , <u>Pendantus denarius</u> , <u>Strephonota syedra</u> (1), <u>Thaides theia</u> (1), <u>Theorema eumenia</u> (1), <u>Thereus orasus</u> , <u>Zizula cyna</u>
Oak-Pine cloud forest 8	<u>Arawacus jada</u> , <u>Atlides halesus</u> , <u>C. guatemalena</u> , <u>Celastrina echo gozora</u> , <u>Erora nitetis</u> (2), <u>Erora quaderna</u> (8), <u>Parrhasius moctezuma</u> , <u>Thereus ortalus</u> (1)

‘Characteristic’ species (underlined) have 80 to 99 % of their records in one type of vegetation. The number of records for the ‘exclusive’ species is indicated in parentheses.

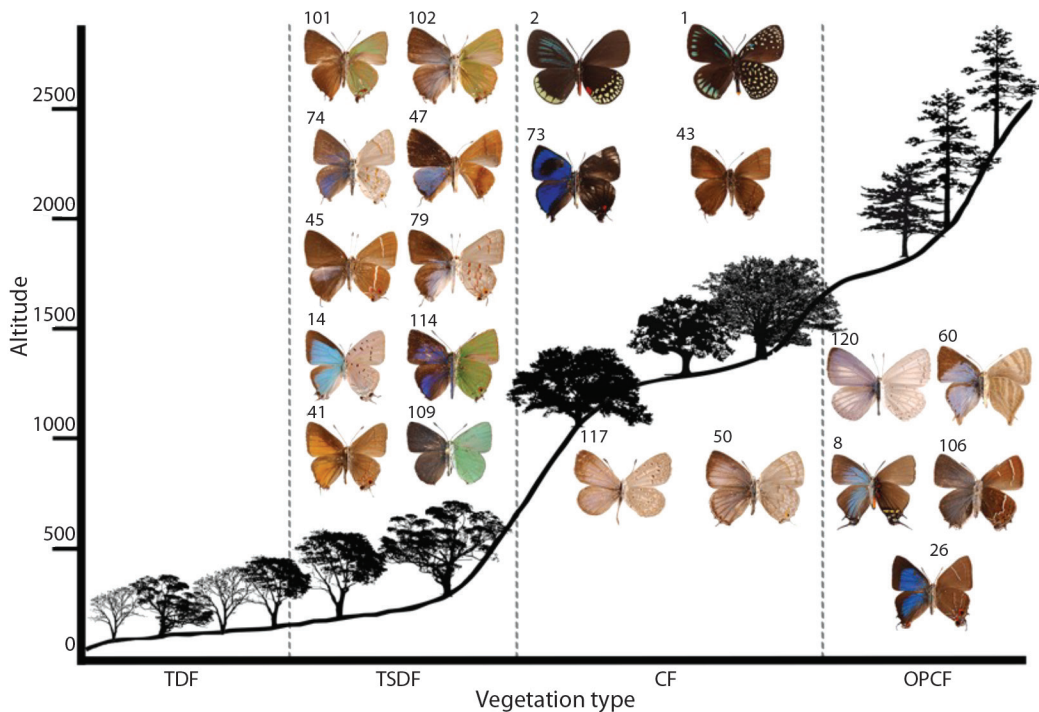


Fig. 9. Distribution of ‘characteristic’ species, which account for 80 to 99 % of their records in one type of vegetation. The numbers correspond to the species list.

Loxicha region and four localities in Omiltemi. In addition to elevation, this group is also characterized by the predominance of oak forests and high-altitude oak-pine, which are environments exclusive to this group.

The second group is characterized by the presence of tropical subdeciduous forest and tropical deciduous forest. Eight localities occur under 1 000 m elevation, but there are also nine localities at this elevation in the third group. In other words, vegetation type explains more than elevation explains similarity between localities in the second group.

The third group includes the five localities from the Sierra de Atoyac, nine from the Loxicha region, and Los Mazos from the Sierra de Manantlán region. This group contains localities between 1 000 and 1 500 m mixed with lower-altitude localities. The common characteristic of 12 of the 16 localities is the presence of montane cloud forest. Thus, similar to

group 2, the similarity among these localities, which belong to three different regions, are mainly determined by vegetation type.

DISCUSSION

Species richness: The Loxicha region fauna represents about 11 % of the Neotropical Eumaeini fauna (Robbins, 2004). It is the highest documented Lycaenidae species richness on Mexico’s Pacific slope, as was the case for other butterfly families (Arellano-Covarrubias et al., 2018; Luis-Martínez et al., 2016, Luis-Martínez et al., 2020; Luis-Martínez et al., 2022). The only Mexican regions with a greater Lycaenidae species richness are Los Tuxtlas-Catemaco in Veracruz and the Sierra de Juárez in Oaxaca on the Atlantic slope, both regions with well-documented sampling during the 1960s to 1980s (Luis-Martínez et al., 1991; Raguso & Llorente-Bousquets, 1991; Ross, 1966; Ross, 1976).

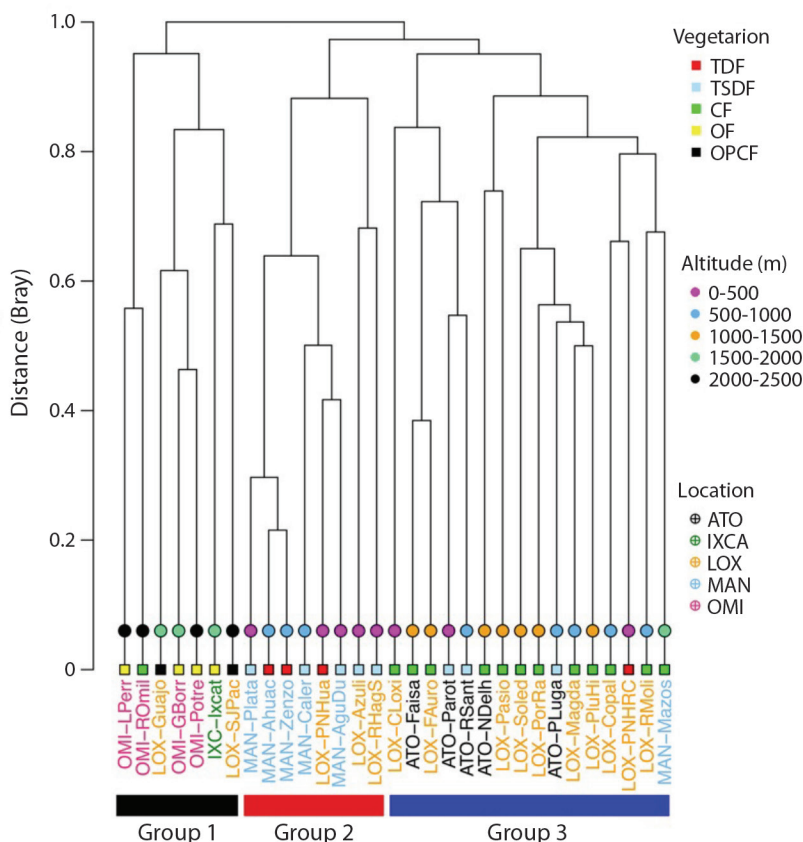


Fig. 10. Similarity in the composition of Lycaenidae species from the Pacific slope. Three groups of localities are recognized, characterized by the altitude and the type of vegetation they present. Vegetation types: TDF, tropical deciduous forest; TSDF, tropical subdeciduous forest; CF, cloud forest; OF, oak forest; OPCF, oak-pine – cloud forest. Regions: ATO, Atoyac; IXCA, Ixcateopan; LOX, Loxicha; MAN, Manantlán; OMI, Omiltemi. Localities: Azuli, Azulillo; CLoxi, Candelaria Loxicha; Copal, Copalita Siete Veneros; FAuro, Finca Aurora-Finca San Isidro; Pasio, La Pasionaria; Soled, La Soledad-Buenavista; Magda, Magdalena El Lirio; PNHua, Parque Nacional Huatulco; PNHRC, Parque Nacional Huatulco Río Cacaluta; PluHi, Pluma Hidalgo 4 km NW “La Curva”; PorRa, Portillo del Rayo-Finca El Encanto; Guajo, Puente Arroyo “El_Guajolote”; RhagS, Rancho Hagia Sofia; RMoli, Río Molinos; SJPac, San José del Pacífico 1 km S; Faisa, El Faisanal; Parot, Las Parotas; NDelh, Nueva Delhi; PLuga, Puente de los Lugardo; RSant, Río Santiago 4 km W; GBorr, Cañada W de la Gruta del Borrego; Potre, Potrerillo; LPerr, Presa de la Perra; ROMil, Rancho Omiltemi; Ixcac, Ixcateopan de Cuauhtémoc; AGuDu, Agua Dulce; Ahuac, Ahuacapan; Caler, La Calera; Mazos, Los Mazos 9 mi SW Autlán; Plata, Platanarillo; Zenzo, Zenzontla.

Among the Loxicha region localities, Hagia Sofia stands out for its richness, accounting for 73 % of the species. It has a diversity similar to less-studied entire regions. The high richness at Hagia Sofia may be due to the prevalence of areas suitable for adult foraging, as previously noted by Arellano-Covarrubias et al. (2018) for Riodinidae. At this site, inflorescences of the introduced rambutan (*Nephelium lappaceum* L.) and Indian almond trees (*Terminalia*

catappa L.) were major nectar sources. We suspect that the differences in Theclinae diversity between Hagia Sofia and Azulillo – similar environments and sampling effort – are due to the presence of these trees at the former locality.

The high species richness of the Loxicha region on its Pacific slope is the result of its biogeographic history, altitudinal-vegetational heterogeneity, and its location within the Sierra Madre del Sur. The Sierra Madre del Sur is

recognized as a region of high diversity due to its complex geological history and altitudinal gradient that generates ecosystem heterogeneity (Espinosa et al., 2016). This is reflected in the Loxicha region, which includes five types of vegetation. Therefore, the altitudinal gradient and environmental heterogeneity of the Loxicha region explain the high butterfly species richness, particularly that of Lycaenidae.

Encounter rates: For the Loxicha region, 54 species (44 % of the fauna) were represented by 10 or fewer individuals. This result is frequent in faunistic studies of hyperdiverse groups and is pronounced in Theclinae (Arellano-Covarrubias et al., 2018; Lamas et al., 2021; Luis-Martínez & Llorente-Bousquets, 1990; Luis-Martínez et al., 1991; Vargas-Fernández et al., 1994; Vargas-Fernández et al., 1999). The significance of this low encounter rate for many species is that it indicates a large number of “unseen” species. Statistically, this significance is reflected in large species richness estimate intervals. In sharp contrast to the Theclinae, most species of Polyommata were frequently encountered, perhaps because they tend to inhabit highly disturbed habitats.

Of the species previously recorded for the Loxicha region but not sampled during fieldwork, four were recorded from a single specimen in La Soledad – Buenavista during the 1970s and 1980s (*Atlides inachus*, *Ministrymon una*, *Nesiostrymon dodava*, and *Strephonota syedra*). Low encounter rates are a probable explanation for the result, but we note the possibility that this locality was confused with La Soledad in the Sierra de Juárez region on the Gulf slope.

Phenology: The seasonal distribution of Lycaenidae in the Loxicha region is similar to that for Papilionidae, Pieridae, and Riodinidae (Arellano-Covarrubias et al., 2018; Luis-Martínez et al., 2020; Luis-Martínez et al., 2022). In all families, a marked decrease in richness and abundance occurs at the transition from the wet to the dry season (November). Alternatively, greatest richness and abundance occur

at the transition from the dry to the wet season in May and June except in Nymphalidae, with greatest richness in September and October (Luis-Martínez et al., 2022).

At other Neotropical sites, Lycaenidae richness is also lowest at the transition from wet to dry seasons. It may be greatest during the dry season (Bates, 1864; Robbins & Small, 1981), during the wet season (Prieto & Dahners, 2009), or at the transition from dry to wet seasons (Lamas et al., 2021; Robbins et al., 1996).

Vegetation types: Lycaenidae distribution by vegetation type shows similarities with butterfly families Papilionidae, Pieridae, and Nymphalidae (Luis-Martínez et al., 2020; Luis-Martínez et al., 2022). All are most diverse in tropical subdeciduous forest and montane cloud forest and are least diverse in oak-pine forest. Tropical subdeciduous forest and montane cloud forest have the most exclusive and characteristic Lycaenidae species, as is the case with Papilionidae and Nymphalidae (Luis-Martínez et al., 2020; Luis-Martínez et al., 2022).

In contrast to these patterns of butterfly diversity in the Sierra Madre del Sur, ferns (Tejero-Díez et al., 2016), gymnosperms (Contreras-Medina, 2016), *Quercus* (Valencia-Ávalos & Morales-Saldaña, 2016), and *Salvia* (Martínez-Gordillo et al., 2016) have greatest richness in oak-pine forest and montane cloud forest but lower richness in tropical subdeciduous forest. In other words, in the Sierra Madre del Sur, it would appear that plant diversity, albeit a small sample of plants, need not beget butterfly diversity.

Elevation: Species richness of Lycaenidae in the Loxicha region is greatest at lower elevations, similar to Riodinidae, Papilionidae, Pieridae, and Nymphalidae (Arellano-Covarrubias et al., 2018; Luis-Martínez et al., 2020; Luis-Martínez et al., 2022). More generally, butterfly richness decreases as elevation increases (Álvarez-García et al., 2016; Lamas et al., 2021; Luis-Martínez & Llorente-Bousquets, 1990; Luis-Martínez & Llorente-Bousquets, 1993; Luis-Martínez et al., 1991; Vargas-Fernández



et al., 1994; Vargas-Fernández et al., 1999). In contrast, butterflies from Serra do Cipó, Brazil (Pires et al., 2020) and Geometridae from Costa Rica (Brehm et al., 2007) show greater diversity at intermediate elevations. McCoy (1990) found that short-term studies find higher diversity at intermediate elevations, while longer studies, like this one for Lycaenidae, find greater diversity at lower elevations. Given the broad estimates of species richness (Fig. 7), definitive conclusions would require more sampling.

Species composition similarity: The three main community similarity groupings for lycaenids in the Sierra Madre del Sur and the Pacific slope are, as expected, correlated with elevation and vegetation type (Fig. 10). However, the substantial variability of elevation and vegetation type within each similarity grouping is perhaps unexpected. In other words, elevation and vegetation type do not definitively predict the lycaenid community that will occur in a habitat. Rather, groupings appear to also be explained by isolation of faunas at higher elevations, as found in other Papilionoidea (*s.l.*), of mountainous systems (Llorente-Bousquets, 1984; Llorente-Bousquets & Escalante, 1994; Llorente-Bousquets & Luis-Martínez, 1998).

This is the fourth publication on the lepidopteran fauna of the Loxicha Region (Arellano-Covarrubias et al., 2018; Luis-Martínez et al., 2020; Luis-Martínez et al., 2022), confirming that for the five Papilionoidea families analyzed, it is one of the most diverse regions in the country. Systematic faunistic studies with adequate sampling provide a foundation for investigating biological processes. They allow for the recognition of disjunct distributions in mountainous systems, and with that, processes of speciation and endemism. They can also serve as the basis for measuring changes in species distribution due to climate change, especially for stenotopic species that could lead to local extinctions (*e.g.* Molina-Martínez et al., 2016).

Lycaenidae has historically received less attention than other butterfly families in Mexico. The geographic, seasonal, elevational, and vegetational distribution of Lycaenidae in the

Loxicha region is the most comprehensive to date for Mexican Lycaenidae. The high proportion of rarely encountered species is a notable characteristic of Lycaenidae, but many seasonal, elevational, and vegetation-associated patterns that we document are similar to those of other butterfly families.

Ethical statement: The authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

See supplementary material
a48v73n1-suppl. 1

ACKNOWLEDGMENTS

Authors thank CONABIO, which in its three decades of existence have supported the Lepidoptera collection, granting resources for infrastructure, fieldwork, and data repatriation from specimens in USA collections (1991-2000) and now included in the MARIPOSA database. Also, we thank the research project PAPIIT-IN212925, for financial support. MTO thanks the support from CONAHCYT (Estancias Posdoctorales por México para la Formación y Consolidación de las y los Investigadores por México; CVU131802). To the curators of the collections who granted access to specimens, data and specialized literature during the development of the MARIPOSA database: Frederick Rindge † (American Museum of Natural History, Nueva York), Jerry Powell and John Chemsak ("Essig" Collection Department of Entomological Sciences, University of California, Berkeley campus, California), John E. Rawlins † (Carnegie Museum of Natural History, Pittsburgh, Pennsylvania), David K. Faulkner and John W. Brown (San Diego Natural History Museum, California), Paul Arnaud Jr. and Norman Penny (California Academy of

Sciences, San Francisco, California), Brian V. Brown and Brian Harris (Los Angeles County Museum, California), Lee D. Miller † (Allyn de Entomology Museum, Sarasota, Florida), George T. Austin † (Nevada State Museum), Philip Ackery and Dick Vane-Wright (British Museum of Natural History), Harry Brailovsky (Colección Entomológica del Instituto de Biología, UNAM, Cd. de México), Thomas Emmel † and Jacqueline Miller † (Collection of the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida), Carmen Pozo de la Tijera (Colección de Lepidoptera del Colegio de la Frontera Sur (Chetumal)) and Mercedes Luna (Colección de Lepidoptera del Museo de Zoología de la Facultad de Estudios Superiores Zaragoza, UNAM). Our great gratitude to the residents of Oaxaca and owners of the lands, like Armando Canavati (Rancho Hagia Sofía, Santa María Huatulco), who supported us in the fieldwork. To the managers of the natural protected area Parque Nacional Huatulco for their support for the fieldwork during five years. To Isabel Vargas Fernández, Jimena Castro, and Uri García for their help in the laboratory tasks, as well as Alejandra Sánchez García, Andrew D. Warren, Blanca Claudia Hernández Mejía, Ela Stephanie Esquivel Ruíz, Jessica Hernández Jerónimo, John Kemner, José Luis Salinas Gutiérrez, Marisol Esther Almaraz Almaraz, and Sandra Nieves Uribe, who participated in the sampling. Finally, Atzinameyali Sánchez Castañeda, who prepared and labeled the collected specimens for their incorporation into the museum collection.

REFERENCES

- Álvarez-García, H., Ibarra, A., & Escalante, P. (2016). Riqueza y distribución altitudinal de las mariposas de la Sierra Mazateca, Oaxaca (Lepidoptera: Papilionoidea). *Acta Zoológica Mexicana (Nueva Serie)*, 32(3), 323–347. <https://doi.org/10.21829/azm.2016.323967>
- Arellano-Covarrubias, A., Llorente-Bousquets, J., & Luis-Martínez, A. (2018). Distribución y fenología de la familia Riodinidae (Lepidoptera: Papilionoidea) en el bosque tropical subcaducifolio de la porción media del Pacífico de Oaxaca, México. *Revista de Biología Tropical*, 66(2), 503–558. <http://dx.doi.org/10.15517/rbt.v66i2.33378>
- Bates, H. W. (1864). VI. Contributions to an insect fauna of the Amazon Valley. Coleoptera: Longicornes. *Annals and Magazine of Natural History*, 13(73), 43–56. <https://doi.org/10.5962/bhl.title.110205>
- Brehm, G., Colwell, R. K., & Kluge, J. (2007). The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. *Global Ecology and Biogeography*, 16, 205–219. <http://dx.doi.org/10.1111/j.1466-822x.2006.00281.x>
- Busby, R. C., Faynel, C., Moser, A., & Robbins, R. K. (2019). *Sympatric diversification in the upper Amazon: A revision of the Eumaeine genus Paraspiculatus (Lepidoptera: Lycaenidae)*. Smithsonian Institution Scholarly Press.
- Chao A., Ma, K. H., Hsieh, T. C., & Chiu, C. (2016). *SpadeR: Species-richness prediction and diversity estimation with R. R package*. (Version 0.1.1.) [Software]. <https://CRAN.R-project.org/package=SpadeR>
- Chao, A., & Shen, T. J. (2003). Nonparametric estimation of Shannon's index of diversity when there are unseen species in sample. *Environmental and Ecological Statistics*, 10(4), 429–443. <https://doi.org/10.1023/A:1026096204727>
- Chew, F. S., & Robbins, R. K. (1984). Egg-laying in butterflies. In R. I. Vane-Wright, & P. R. Ackery (Eds.), *The biology of butterflies* (pp. 65–79). Academic press.
- Colwell, R. K., & Coddington, J. A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 345(1311), 101–118. <https://doi.org/10.1098/rstb.1994.0091>
- Contreras-Medina, R. (2016). Las gimnospermas de la Sierra Madre del Sur. In I. Luna-Vega, D. Espinosa, & R. Contreras-Medina (Eds.), *Biodiversidad de la Sierra Madre del Sur* (pp. 157–165). Universidad Nacional Autónoma de México.
- de la Maza, R. E., & de la Maza, J. E. (1993). *Mariposas de Chiapas*. Espejo de Obsidiana.
- de la Maza, R. E., & de la Maza, J. E. (2015). La fauna de mariposas (Lepidoptera: Rhopalocera) del río Lacantun. In R. de la Maza, J. Carabias, J. de la Maza, & R. Cadena (Eds.), *Conservación y desarrollo sustentable en la Selva Lacandona. 25 años de actividades y experiencias* (pp. 187–192). Natura y Ecosistemas Mexicanos A. C.
- DeVries, P. J. (1990). Enhancement of symbioses between butterfly caterpillars and ants by vibrational communication. *Science*, 248(4959), 1104–1106. <https://doi.org/10.1126/science.248.4959.1104>



- DeVries, P. J. (1991). Call production by myrmecophilous riordinid and lycaenid butterfly caterpillars (Lepidoptera): Morphological, acoustical, functional, and evolutionary patterns. *American Museum Novitates*, 3025, 21–23. <http://hdl.handle.net/2246/5054>
- Duarte, M., & Robbins, R. K. (2009). Immature stages of *Calycopis bellera* (Hewitson) and *C. janeirica* (Felder) (Lepidoptera, Lycaenidae, Theclinae, Eumaeini): Taxonomic significance and new evidence for detritivory. *Zootaxa*, 2325, 39–61. <https://doi.org/10.11646/zootaxa.2325.1.4>
- Espinosa, D., Ocegueda-Cruz, S., & Luna-Vega, I. (2016). Introducción al estudio de la biodiversidad de la Sierra Madre del Sur: Una visión general. In I. Luna-Vega, D. Espinosa, & R. Contreras-Medina (Eds.), *Biodiversidad de la Sierra Madre del Sur* (pp. 23–36). Universidad Nacional Autónoma de México.
- Gobierno de México. (n. d.). CONABIO. <http://www.conabio.gob.mx>
- Godman, F. D., & Salvin, O. (1887–1901). *Biologia Centrali Americana. Zoología, Insecta, Lepidoptera, Rhopalocera* (Vol. 2). Taylor and Francis.
- Hoffmann, C. C. (1933). La fauna de lepidópteros del distrito del Soconusco (Chiapas). Un estudio zoogeográfico. *Anales del Instituto de Biología Universidad Nacional de México*, 4(3-4), 207–307.
- Hoffmann, C. C. (1936). Relaciones zoogeográficas de los lepidópteros mexicanos. *Anales del Instituto de Biología Universidad Nacional de México*, 7(1), 47–58.
- Hoffmann, C. C. (1940). Catálogo sistemático y zoogeográfico de los lepidópteros mexicanos. Primera parte. Papilionoidea. *Anales del Instituto de Biología Universidad Nacional de México*, 11(2), 639–739.
- Hoffmann, C. C. (1941). Catálogo sistemático y zoogeográfico de los lepidópteros mexicanos. Segunda parte. Hesperioidea. *Anales del Instituto de Biología Universidad Nacional de México*, 12(1), 237–294.
- Jost, L. (2006). Entropy and diversity. *Oikos*, 113(2), 363–375. <https://doi.org/10.1111/j.2006.0030-1299.14714.x>
- Kaminski, L. A., Rodrigues, D., & Freitas, A. V. L. (2012). Immature stages of *Parrhasius polibetes* (Lepidoptera: Lycaenidae): Host plants, tending ants, natural enemies, and morphology. *Journal of Natural History*, 46, 645–667. <https://doi.org/10.1080/00222933.2011.651630>
- Kunin, W. E., & Gaston, K. J. (1993). The biology of rarity: Patterns, causes and consequences. *Trends in Ecology & Evolution*, 8(8), 298–301. [https://doi.org/10.1016/0169-5347\(93\)90259-R](https://doi.org/10.1016/0169-5347(93)90259-R)
- Lamas, G., Turner, J. D., McInnis, M. L., & Robbins, R. K. (2023). Riordinid butterfly fauna (Lepidoptera) of the Cosñipata Region, Peru: Annotated checklist, community structure, and contrast with Lycaenidae. *Insecta Mundi*, 0988, 1–35.
- Lamas, G., McInnis, M. L., Busby, R. C., & Robbins, K. R. (2021). The lycaenid butterfly fauna (Lepidoptera) of Cosñipata, Peru: Annotated checklist, elevational patterns, and rarity. *Insecta Mundi*, 0861, 1–34.
- Llorente-Bousquets, J. (1984). Sinopsis sistemática y biogeográfica de los Dismorphiinae de México con especial referencia al género *Enantia* Hübner (Lepidoptera: Pieridae). *Folia Entomológica Mexicana*, 58, 3–206.
- Llorente-Bousquets, J., & Escalante, P. (1994). Insular biogeography of submontane humid forests in México. In S. P. Darwin, & A. L. Welden (Eds.), *Biogeography of Mesoamerica* (pp. 139–146). University of Louisiana.
- Llorente-Bousquets, J., & Luis-Martínez, A. (1998). Análisis conservacionista de las mariposas mexicanas: Papilionidae (Lepidoptera: Papilionoidea). In T. Ramammorthy, R. Bye, A. Lot, & J. Fa (Eds.), *Diversidad biológica de México: Orígenes y distribución* (pp. 149–178). Instituto de Biología UNAM.
- Llorente-Bousquets, J., Luis-Martínez, A., & Vargas-Fernández, I. (2006). Apéndice general de Papilionoidea: Lista sistemática, distribución estatal y provincias biogeográficas. In J. J. Morrone, & J. Llorente-Bousquets (Eds.), *Componentes bióticos principales de la entomofauna mexicana* (Vol. 2, pp. 945–1009). Las Prensas de Ciencias, Universidad Nacional Autónoma de México.
- Llorente-Bousquets, J., Vargas-Fernández, I., Luis-Martínez, A., Trujano-Ortega, M., Hernández-Mejía, B. C., & Warren, A. D. (2014). Biodiversidad de Lepidoptera en México. *Revista Mexicana de Biodiversidad, Suplemento Biodiversidad de México*, 85, 353–371. <https://doi.org/10.7550/rmb.31830>
- Luis-Martínez, A., Vargas-Fernández, I., & Llorente-Bousquets, J. (1991). Lepidoptero-fauna de Oaxaca I. Distribución y fenología de los Papilionoidea de la Sierra de Juárez. *Publicaciones Especiales del Museo de Zoología UNAM*, 3, 1–121.
- Luis-Martínez, A., & Llorente-Bousquets, J. (1990). Mariposas en el Valle de México: Introducción e Historia. 1. Distribución local y estacional de los Papilionoidea de la Cañada de los Dínamos, Magdalena Contreras, D. F., México. *Folia Entomológica Mexicana*, 78, 95–198.
- Luis-Martínez, A., & Llorente-Bousquets, J. (1993). Mariposas. In J. Llorente-Bousquets, & I. Luna-Vega (Eds.), *Historia Natural del Parque Ecológico Estatal Omiltemi, Chilpancingo, Guerrero, México* (pp. 307–385). Facultad de Ciencias Universidad Nacional Autónoma de México.
- Luis-Martínez, A., Ávalos-Hernández, O., Trujano-Ortega, M., Arellano-Covarrubias, A., Vargas-Fernández, I.,

- & Llorente-Bousquets, J. (2021). Riqueza y endemismo de Papilionoidea (Lepidoptera) de la región Loxicha en el estado de Oaxaca, México. *Dugesiana*, 28(2), 233–246. <https://doi.org/10.32870/dugesiana.v28i2.7165>
- Luis-Martínez, A., Ávalos-Hernández, O., Trujano-Ortega, M., Arellano-Covarrubias, A., Vargas-Fernández, I., & Llorente-Bousquets, J. (2022). Distribution, diversity, endemism, and ecology of Nymphalid butterflies (Lepidoptera: Nymphalidae) in the Loxicha Region, Oaxaca, Mexico. *Revista de Biología Tropical*, 70, 363–407. <https://doi.org/10.15517/rev.biol.trop.v70i1.48821>
- Luis-Martínez, A., Hernández-Mejía, B., Trujano-Ortega, M., Warren, A. D., Salinas-Gutiérrez, J. L., Ávalos-Hernández, O., Vargas-Fernández, I., & Llorente-Bousquets, J. (2016). Avances faunísticos en los Papilionoidea (Lepidoptera) *sensu lato* de Oaxaca, México. *Southwestern Entomologist*, 41(1), 171–224. <https://doi.org/10.3958/059.041.0119>
- Luis-Martínez, A., Llorente-Bousquets, J., & Vargas-Fernández, I. (2005). MARIPOSA database. Una megabase de datos de mariposas y la regionalización biogeográfica de México. In J. Llorente-Bousquets, & J. J. Morrone (Eds.), *Regionalización geográfica en Iberoamérica y tópicos afines: Primeras jornadas biogeográficas de la Red Iberoamericana de Biogeografía y Entomología Sistemática (RIBES XII.X-CYTED)* (pp. 269–294). Las prensas de Ciencias Universidad Nacional Autónoma de México.
- Luis-Martínez, A., Sánchez-García, A., Ávalos-Hernández, O., Salinas-Gutiérrez, J. L., Trujano-Ortega, M., Arellano-Covarrubias, A., & Llorente-Bousquets, J. (2020). Distribution and diversity of Papilionidae and Pieridae (Lepidoptera: Papilionoidea) in Loxicha Region, Oaxaca, Mexico. *Revista de Biología Tropical*, 68(1), 139–155. <https://doi.org/10.15517/rbt.v68i1.37587>
- Martínez-Gordillo, M., Fragoso-Martínez, I., Leautaud-Valenzuela, P., Ginez-Vázquez, L., Martínez-Ambriz, E., & Méndez-Solís, V. (2016). Diversidad y endemismo del género *Salvia* (Lamiaceae) en la Sierra Madre del Sur de Guerrero, México. In I. Luna-Vega, D. Espinosa, & R. Contreras-Medina (Eds.), *Biodiversidad de la Sierra Madre del Sur* (pp. 177–191). Universidad Nacional Autónoma de México.
- McCoy, E. D. (1990). The distribution of insects along elevational gradients. *Oikos*, 58, 313–322. <https://doi.org/10.2307/3545222>
- Molina-Martínez, A., León-Cortés, J. L., Regan, H. M., Lewis, O. T., Navarrete, D., Caballero, U., & Luis-Martínez, A. (2016). Changes in butterfly distributions and species assemblages on a Neotropical mountain range in response to global warming and anthropogenic land use. *Diversity and Distributions*, 22, 1085–1098. <https://doi.org/10.1111/ddi.12473>
- Nishida, K., & Robbins, R. K. (2020). One side makes you taller: A mushroom-eating butterfly caterpillar (Lycaenidae) in Costa Rica. *Neotropical Biology and Conservation*, 15(4), 463–470. <https://doi.org/10.3897/neotropical.15.e57998>
- Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M. G., Bedward, M., Bolker, B. M., Borcard, D., Carvalho, G., Chirico, M., De Cáceres, M., Durand, S., ... Weedon, J. (2022). *vegan: Community Ecology Package. R package* (Version 2.6-4) [Software]. <https://CRAN.R-project.org/package=vegan>
- Pires, A. C., Barbosa, M., Beiroz, W., Beirao, M. V., Marini-Filho, O. J., Duarte, M., Mielke, O. H. H., Ladeira, F. A., Nunes, Y. R. F., Negreiros, D., & Fernandes, G. W. (2020). Altitudinal variation in butterfly community associated with climate and vegetation. *Anais da Academia Brasileira de Ciências*, 92(2), e20190058. <https://doi.org/10.1590/0001-3765202020190058>
- Prieto, C., & Dahners, H. W. (2009) Resource utilization and environmental and spatio-temporal overlap of a hilltopping Lycaenid butterfly community in the Colombian Andes. *Journal of Insect Science*, 9(1), 16. <https://doi.org/10.1673/031.009.1601>
- R Core Team. (2023). *R: A language and environment for statistical computing* [Software]. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Raguso, R. A., & Llorente-Bousquets, J. (1991). The butterflies (Lepidoptera) of the Tuxtla Mts., Veracruz, Mexico. Revisited: Species-richness and habitat disturbance. *Journal of Research on the Lepidoptera*, 29(1-2), 105–133. <https://doi.org/10.5962/p.266622>
- Robbins, R. K. (2004). Introduction to the checklist of Eumaeini (Lycaenidae). In J. B. Heppner (Ed.), *Atlas of Neotropical Lepidoptera* (Vol. 5A, pp. 24–30). Association for Tropical Lepidoptera Scientific Publishers.
- Robbins, R. K., & Small, G. B. (1981). Wind dispersal of Panamanian hairstreak butterflies (Lepidoptera: Lycaenidae) and its evolutionary significance. *Biotropica*, 13(4), 308–315. <https://doi.org/10.2307/2387810>
- Robbins, R. K., Aiello, A., Feinstein, J., Berkov, A., Caldas, A., Busby, R. C., & Duarte, M. (2010). A tale of two species: Detritivory, parapatry, and sexual dimorphism in *Lamprospilus collucia* and *L. orcidia* (Lycaenidae: Theclinae: Eumaeini). *Journal of Research on the Lepidoptera*, 42, 64–73. <https://doi.org/10.5962/p.266516>
- Robbins, R. K., Cong, Q., Zhang, J., Shen, J., Busby, R. C., Faynel, C., Duarte, M., Martins, A. R. P., Prieto, C., Lamas, G., & Grishin, N. V. (2022). Genomics-based higher classification of the species-rich hairstreaks (Lepidoptera: Lycaenidae: Eumaeini). *Systematic*



- Entomology*, 47(3), 445–469. <https://doi.org/10.1111/syen.12541>
- Robbins, R. K., Lamas, G., Mielke, O. H. H., Harvey, D. J., & Casagrande, M. M. (1996). Taxonomic composition and ecological structure of the species-rich butterfly community at Pakitza, Parque Nacional del Manu, Perú. In D. E. Wilson, & A. Sandoval (Eds.), *Manu: The biodiversity of southeastern Peru* (pp. 217–252). Smithsonian Institution.
- Ross, G. N. (1966). Life history studies on Mexican butterflies IV. *Annals of the Entomological Society of America*, 59, 985–1003. <https://doi.org/10.1093/aesa/59.5.985>
- Ross, G. N. (1976). An ecological study of the butterflies of the Sierra de Tuxtla in Veracruz, Mexico (Continued). *The Journal of Research on the Lepidoptera*, 15(3), 185–200. <https://doi.org/10.5962/p.333730>
- Rzedowski, J. (1978). *Vegetación de México*. Limusa.
- Silva, N. A. P., Duarte, M., Araújo, E. B., & Morais, H. C. (2014). Larval biology of anthophagous Eumaeini (Lepidoptera: Lycaenidae, Theclinae) in the Cerrado of Central Brazil. *Journal of Insect Science*, 14(1), 184. <https://doi.org/10.1093/jisesa/ieu046>
- Tejero-Díez, J. D., Torres-Díaz, A. N., & Sánchez-González, A. (2016). Helechos de la Sierra Madre del Sur. In I. Luna-Vega, D. Espinosa, & R. Contreras-Medina (Eds.), *Biodiversidad de la Sierra Madre del Sur* (pp. 121–155). Universidad Nacional Autónoma de México.
- Trujano-Ortega, M., Luis-Martínez, A., Vargas-Fernández, I., Ávalos-Hernández, O., & Llorente-Bousquets, J. (2024). Introduction to the analysis, synthesis, and comparisons of endemic butterflies in Mexico. *Zootaxa*, 5479(1), 1–73. <https://doi.org/10.11646/ZOOTAXA.5479.1.1>
- Udvardy, M. D. F. (1969). *Dynamic Zoogeography: With special reference to land animals*. Van Nostrand Reinhold Company.
- Valencia-Ávalos, S., & Morales-Saldaña, S. (2016). El género *Quercus* en la Sierra Madre del Sur. In I. Luna-Vega, D. Espinosa, & R. Contreras-Medina (Eds.), *Biodiversidad de la Sierra Madre del Sur* (pp. 167–175). Universidad Nacional Autónoma de México.
- Valencia-Montoya, W. A., Quental, T. B., Tonini, J. F. R., Talavera, G., Crall, J. D., Lamas, G., Busby, R. C., Carvalho, A. P. S., Morais, A. B., Oliveira, M. N., Romanowski, H. P., Liénard, M. A., Salzman, S., Whitaker, M. R. L., Kawahara, A. Y., Lohman, D. J., Robbins, R. K., & Pierce, N. E. (2021). Evolutionary trade-offs between male secondary sexual traits revealed by a phylogeny of the hyperdiverse tribe Eumaeini (Lepidoptera: Lycaenidae). *Proceedings of the Royal Society B: Biological Sciences*, 288, 20202512. <https://doi.org/10.1098/rspb.2020.2512>
- Vargas-Fernández, I., Llorente-Bousquets, J., & Luis-Martínez, A. (1994). Listado Lepidopterofaunístico de la Sierra de Atoyac de Álvarez en el estado de Guerrero: Notas acerca de su distribución local y estacional (Rhopalocera: Papilionoidea). *Folia Entomológica Mexicana*, 86, 41–178.
- Vargas-Fernández, I., Llorente-Bousquets, J., & Luis-Martínez, A. (1999). Distribución de los Papilionoidea (Lepidoptera: Rhopalocera) de la Sierra de Manantlán (250-1 650 m) en los estados de Jalisco y Colima. *Publicaciones Especiales del Museo de Zoología*, 11, 11–53.