

<https://doi.org/10.15517/rev.biol.trop..v70i1.48821>

Distribution, diversity, endemism, and ecology of Nymphalid butterflies (Lepidoptera: Nymphalidae) in the Loxicha Region, Oaxaca, Mexico

Armando Luis-Martínez¹;  <https://orcid.org/0000-0002-1044-3986>
Omar Ávalos-Hernández¹;  <https://orcid.org/0000-0002-5476-9400>
Marysol Trujano-Ortega^{1, 2};  <https://orcid.org/0000-0001-8911-8504>
Arturo Arellano-Covarrubias¹;  <https://orcid.org/0000-0001-9515-5782>
Isabel Vargas-Fernández¹;  <https://orcid.org/0000-0001-6524-7184>
Jorge Llorente-Bousquets¹;  <https://orcid.org/0000-0003-0876-0533>

1. Museo de Zoología (Entomología), Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, Av. Universidad 3000, Circuito Exterior S/N, C.P. 04510, Ciudad de México, México; alm@ciencias.unam.mx, omaravalosh@ciencias.unam.mx, marysol_trujano@yahoo.com.mx, arellano.covarrubias@gmail.com, ivf@ciencias.unam.mx, llorentebousquets@gmail.com (* Correspondence).
2. Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México (UNAM), Batalla 5 de Mayo s/n, Ejercito de Oriente, Iztapalapa, 09230, Ciudad de México, México.

Received 26-X-2021. Corrected 14-III-2022. Accepted 27-V-2022.

ABSTRACT

Introduction: The Loxicha Region of Oaxaca, Mexico, has been historically important for the study of Nymphalidae, second in the Papilionoidea for species richness. Describing the diversity patterns of this butterfly clade in Loxicha can improve our understanding of the evolutionary history of the Sierra Madre del Sur, the Mexican Pacific slope, and Mexico in general.

Objective: To describe the temporal and spatial patterns of Nymphalidae diversity along an elevational gradient (80-2 600 m), and to compare Loxicha's fauna with other regions in Mexico.

Methods: We obtained 28 756 records from 21 sites in the Loxicha Region, representing seven years of sampling. We estimate and analyze the diversity, endemism, and distributional patterns for three elevational levels and five vegetation types. We estimated species composition and similarity with other regions of the Pacific and Atlantic slopes.

Results: We identified 189 taxa, including species and subspecies, from 85 genera and ten subfamilies of Nymphalidae. Loxicha contains 46 % of the species in the family recognized for Mexico, including ten endemic species and 56 endemic subspecies. Cloud forest and low elevations were the most diverse habitats for this family. There is a clear divergence between the Atlantic and Pacific faunas, and the Sierra Madre del Sur has two faunal components. High-elevation sites in Oaxaca, and in the neighboring state of Guerrero, have a distinctive fauna, apparently isolated from low-elevation sites, revealing an archipelagic distribution for cloud forest Nymphalidae.

Conclusions: The Loxicha Region is one of the richest areas for Nymphalidae in Mexico. Distribution on the Pacific slope is determined by geographical history and ecological conditions, including elevation. Nymphalidae can be used to test hypotheses of biogeographic regionalization in Mexico.

Key words: Brush-footed butterflies; elevational gradient; sampling efficiency; phenology; biogeographic provinces; Van Someren-Rydon traps.



Brush-footed butterflies (Nymphalidae) represent the second most diverse family of Papilionoidea worldwide, behind the skip-pers (Hesperiidae). Because of the remarkable diversity and local endemism featured within Nymphalidae, the description and analysis of spatio-temporal patterns of this group are a priority for advancing conservation and systematics. This is particularly true for Mexico, which is a megadiverse country and biodiversity hotspot where Nymphalidae constitute 25 % (413 species) of the country's Papilionoidea fauna *sensu lato* (Llorente-Bousquets et al., 2014).

Oaxaca is one of the most biodiverse states in Mexico (Flores-Villela & García-Vázquez, 2014; García-Mendoza & Meave del Castillo, 2011; Navarro-Sigüenza et al., 2014), and this pattern is reflected in Nymphalidae. Some 339 species or 82 % of the country's nymphalids are documented from Oaxaca, ranking it second only to the state of Chiapas in nymphalid species richness (Luis-Martínez et al., 2016). This outstanding biodiversity in Oaxaca is attributable to the convergence of five different biogeographic provinces in the state, with the most well-represented of these being the Sierra Madre del Sur, Costa del Pacífico, and Golfo de México (Morrone, 2005; Morrone et al., 2002). The Loxicha Region of Oaxaca lies within the Sierra Madre del Sur, and it is of special faunal interest. Loxicha experienced two main collecting periods in the 20th century, during which numerous species of Nymphalidae were described and named (Luis-Martínez et al., 2020). The MARIPOSA database (Luis-Martínez et al., 2005), contains 1 248 records from the Loxicha Region during that century, with 139 species of Nymphalidae being documented by more than 30 collectors. Particularly notable among those collectors were Eduardo Cecilio Welling with 66 species (265 records), and John Kemner with 78 species (402 records).

Modern description and analysis of the Papilionoidea from the Pacific slope of the Loxicha Region has been the core focus of an ongoing project, begun in 2005, to analyze the butterfly fauna of Oaxaca (Luis-Martínez et al., 2016). To date, the families Papilionidae,

Pieridae, and Riodinidae of the Loxicha Region have been analyzed (Arellano-Covarrubias et al., 2018; Luis-Martínez et al., 2020). The present study aims to describe the temporal and spatial patterns of Nymphalidae diversity in the Loxicha Region. Based on a review of the literature and historical records, coupled with sampling from 2005-2014 along an elevational gradient from 80–2 600 m, we document this diversity and make a preliminary comparison of nymphalids in Loxicha to other comparatively well-sampled regions to describe broad-scale patterns.

Historical outline of the collection of Papilionoidea from the Pacific slope and the Loxicha Region: The historical collection and classification of Mexican species of Papilionoidea began at the end of the 19th century and continued through the early 1980's. Collectors generally focused on the Southeastern states, the Atlantic slope, and the states of Guerrero and Morelos due to the high diversity of these areas and to the presence of associated highways (*v. gr.* Llorente-Bousquets et al., 1986; Llorente-Bousquets & Luis-Martínez, 1993; Llorente-Bousquets et al., 1998; Luis-Martínez et al., 2000; Luis-Martínez et al., 2003; Michán et al., 2004). During this period, sporadic collections were also made in Northern Mexico, mostly carried out by academic institutions of the USA (*v. gr.* Comstock, 1953; Holland, 1995; Spade et al., 1988; Stanford, 1998). The Pacific slope of Mexico was often ignored by collectors, resulting in relatively few publications except for a butterfly checklist for the Chamela Biological Research Station in the state of Jalisco (Beutelspacher, 1982), notes on the butterflies of some Pacific islands (Vázquez, 1958; Vázquez, 1959; Vázquez, 1960), and a contribution on the fauna of the Pacific slope of Jalisco (*v. gr.* Comstock & Vázquez, 1961). Additionally, Members of the Mexican Society of Lepidopterology published the results of periodic collections along this slope (*v. gr.* Maza & Maza, 1981; Maza & Maza, 1983; Maza et al., 1982; Velázquez, 1976; Velázquez

& Velázquez, 1975), with the main goal of describing new taxa from unexplored areas.

The first systematic sampling of the Pacific slope extended from the coast (Puerto San Blas) to the mountains (Sierra San Juan) in the state of Nayarit during 1978-1980, spanning an elevational gradient from sea level to 1 300 m. This effort documented 135 species of Nymphalidae, marking the beginning of dedicated research on the distribution of Papilionoidea from the Pacific slope. A decade later, faunistic studies were carried out in the Sierra de Atoyac (Vargas-Fernández et al., 1994) and the Omiltemi region (Luis-Martínez & Llorente-Bousquets, 1993) of the Sierra Madre del Sur (SMS) in the state of Guerrero. The former spanned an elevational range of 300-3 100 m, and the latter a range of 2 300-3 000 m (*v. gr.* Llorente-Bousquets, 1984; Llorente-Bousquets et al., 2004; Warren & Llorente-Bousquets, 1999).

Further studies on the faunistic composition of Papilionoidea from the Pacific slope were completed during the last three decades in Pedernales, state of Michoacán (Balcázar, 1993); Mismaloya, Jalisco and Bahía de Banderas, Nayarit (Warren & Llorente-Bousquets, 1999); the Sierra de Manantlán, Jalisco-Colima (Vargas-Fernández et al., 1999); and Western Michoacán (Luis-Martínez, 1997; Luis-Martínez, 1999; MARIPOSA database 2001). Additional analyses of the alpha and beta diversity of the Nymphalidae (Tapia-Sedeño, 2013) and the lepidopterofauna of the Loxicha Region, Oaxaca (Arellano-Covarrubias et al., 2018; Luis-Martínez et al., 2020) were also released. Most of these studies focused on the local, regional, or elevational distribution and the phenology of Papilionoidea species, under distinct ecological conditions and across a wide environmental gradient. Some faunal comparisons between different areas have also been made (*v. gr.* Monteagudo-Sabaté & Luis-Martínez, 2013; Monteagudo-Sabaté et al., 2001; Monteagudo-Sabaté et al., 2014).

When analyzing the fauna of the Pacific region and the Sierra Madre del Sur, the diversity of the state of Morelos must be considered. This state is located mainly in the

Eje Neovolcánico and Cuenca del Balsas biogeographic provinces (Morrone et al., 2002). Michoacán and Guerrero also include portions of these two provinces. More than half of Guerrero lies in the Cuenca del Balsas, and the state also encompasses a large portion of the Sierra Madre del Sur, particularly its Pacific slopes (Luna-Reyes et al., 2012). There are 450 species or subspecies of Papilionoidea *sensu lato* recorded from Morelos, classified in 214 genera. The Nymphalidae is represented in Morelos by 147 species or subspecies, of which 42 are endemic to Mexico (Luna-Reyes, 2020).

Besides these faunistic studies over the past three decades, species lists have been published for 10 of the 11 states in the Pacific slope. Table 1 presents current data for the number of species and endemics in these Mexican states according to Llorente-Bousquets et al. (2014) and Luis-Martínez et al. (2016).

MATERIALS AND METHODS

Faunistic inventory and sites: To update the Papilionoidea species list for Oaxaca published by Luis-Martínez et al. (2004), systematic sampling was begun in 2005 (Luis-Martínez et al., 2016) which increased scientific knowledge of the geographical and vegetational distribution of the group. This sampling effort focused on areas with the greatest diversity and endemism. The Loxicha Region is one such area, and thus was subject to 267 sampling days over seven years (2005, 2007, 2008, 2011-2014), including 21 sampling sites that span eight municipalities within the Pacific slopes of the Sierra Madre del Sur (Table 2). In 12 of these sites, sampling was systematic. A total of 16 collectors participated in the sampling effort, with 13 to 65 sampling days per site. Sites were grouped by elevational levels and vegetation type for comparison and analysis purposes. Vegetation classification followed Rzedowski (1978) and Llorente-Bousquets (1984), with four types recognized in the Loxicha Region: tropical deciduous forest (TDF), tropical sub-deciduous forest (TSDF), cloud forest (low- and mid-elevation)



TABLE 1
Species richness and endemism of Nymphalidae in Mexico and its Pacific-slope states

State	spp.	E	%	Reference
Baja California	41	0	0	Brown et al., 1992
Baja California Sur	43	2	5	Brown et al., 1992
Sonora	101	6	6	Bailowitz et al., 2017
Sinaloa	106	8	8	
Nayarit	144	12	8	Llorente-Bousquets et al., 2004
Jalisco	176	18	10	Llorente-Bousquets, Luis-Martínez et al., 1996; Vargas-Fernández et al., 1996; Vargas-Fernández et al., 1999; Warren et al., 1996
Colima	139	15	11	Llorente-Bousquets, Warren et al., 1996
Michoacán	168	15	9	
Guerrero	216	22	10	Vargas-Fernández et al., 1994
Oaxaca	339	31	9	Luis-Martínez et al., 2016
Chiapas	351	26	7	Maza & Maza, 1993; Luis-Martínez et al., 2011
Mexico (country)	413	123	12	

spp.: species, E: taxa endemic to the state/country, %: percentage of endemics relative to the total species richness of the state/country.

Note. Chiapas endemism is reduced because species' ranges extend towards Central America as a biogeographical and ecological unit; the same occurs in Baja California.

(CF), and oak-pine forest (OPF). Besides these, a fifth vegetation type was recognized in some sites at 2 000-2 400 m elevation, denominated as oak-pine and high-elevation cloud forest (OPCF). OPCF is similar to OPF but has intermixed elements of CF. Because the OPCF can be easily distinguished from both the OPF and the CF, and is located at different elevations in the region, this vegetation type was considered a distinct category (Arellano-Covarrubias et al., 2018; Luis-Martínez et al., 2020).

Taxonomic determination: Taxa were identified by comparison with specimens in the Lepidoptera Collection of the Zoology Museum, Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC), together with the taxonomic expertise of the authors and reference to specialized literature. The list of species follows the taxonomic order proposed by Vargas-Fernández et al. (2016), and Llorente-Bousquets, Luis-Martínez et al. (2006), for the Satyrinae subfamily. All specimens were deposited in the Lepidoptera Collection of the MZFC, which is registered at the Secretaría de Medio Ambiente, Recursos Naturales

y Pesca (SEMARNAP) (DFE.IN.071.0798). Specimens were collected under scientific collecting permit FAUT-0148 issued by the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT). Collecting data were entered into the MARIPOSA database (Luis-Martínez et al., 2005).

Nets and Van Someren-Rydon traps: Sampling techniques included 4-6 aerial nets set for eight hours and 10-20 Van Someren-Rydon traps (Rydon, 1964) placed daily 1-2.5 m high along transects, with 50 m between each trap. Traps used a mixture of water, brown sugar, pineapple, and banana as bait. Transects covered distinct microhabitats (open and closed vegetation) to obtain a more representative sample. The number of specimens captured with traps in each locality is presented in Table 2.

Species richness estimation and diversity analysis by vegetation type and elevational level: A species accumulation curve was estimated using data from all specimens collected. Data were randomized (500 runs) with

TABLE 2
Sampling sites in the Loxicha Region, Oaxaca, Mexico

Site	Elevation (m)	Geographic location		Vegetation type	SE/ R /T
		Lat North	Long West		
a. Parque Nacional Huatulco, Río Cacaluta	80-100	15°47'07"	96°10'34"	TDF	16/ 1 627 /781
b. Parque Nacional Huatulco	100	15°45'20"	96°09'19"	TDF	24/ 1 869 /977
c. Azulillo	380-500	15°53'25"	96°29'27"	TSDF	65/ 4 929 /1 755
d. Rancho Hagia Sofía	410	15°52'01"	96°21'55"	TSDF	49/ 6 672 /3 430
e. Río Molinos*	530-700	15°56'10.8"	96°30'41.8"	CF	4/ 71 /30
f. Copalita, Río Copalita*	600-1 200	15°56'48"	96°20'23.43"	CF	21/ 1 200 /450
g. Magdalena, El Lirio	750-900	15°55'11"	96°23'34"	CF	13/ 1 934 /789
h. Copalita, Los Plátanos*	900			CF	1/ 31 /6
i. Copalita, Siete Veneros*	940			CF	24/ 1 066 /457
j. San Mateo Piñas*	1 000	15°59'57.50"	96°20'4.47"	CF	27/ 426 /132
k. Pluma Hidalgo, 4 km NW "La Curva"	1 100-1 200	15°56'23"	96°25'59"	CF	41/ 2 243 /528
l. Finca Aurora-Finca San Isidro	1 100-1 250	15°56'30"	96°24'13"	CF	25/ 1 013 /390
m. Copalita, Llano de Ocote*	1 200			CF	17/ 434 /229
n. Portillo del Rayo-Finca El Encanto	1 200-1 530	15°58'38"	96°31'11"	CF	24/ 1 218 /622
o. La Soledad-Buenavista	1 470-1 550	15°58'18"	96°31'54"	CF	31/ 1 690 /574
p. La Pasionaria	1 500-1 650	15°66'09"	96°25'08"	CF	15/ 1 153 /420
q. Puente Arroyo "El Guajolote"	2 020-2 150	16°03'28"	96°30'18"	OPF-OPCF	17/ 274 /53
r. San José del Pacífico, 1 km S	2 280-2 400	16°09'28"	96°29'21"	OPF-OPCF	33/ 771 /126
s. Manzanal-Doncella*	2 700-2 800	16°07'47.9"	96°30'12"	OPF	1/ 1 /-
t. Camino a San Agustín Loxicha*	2 700-2 800	16°07'41.57"	96°29'54.2"	OPF	2/ 5 /-
u. Nevería-La Ciénega*	2 820-2 850	16°12'01"	96°20'56"	OPF	2/ 19 /-

* Sites without systematic sampling; SE: sampling effort (days); R: records (specimens); T: specimens collected with Van Someren-Rydon traps; Vegetation types: tropical deciduous forest (TDF), tropical sub-deciduous forest (TSDF), cloud forest (low- and mid-elevation) (CF), oak-pine forest (OPF), and oak-pine and high-elevation cloud forest (OPCF). (Arellano-Covarrubias et al., 2018; Llorente-Bousquets, 1984, Luis-Martínez et al., 2020; Rzedowski, 1978). Note Van Someren-Rydon traps were not used at sites s, t, and u.

EstimateS 9.1 (Colwell, 2013) and fitted to the Clench model (Soberón & Llorente-Bousquets, 1993) to estimate species richness. Species richness was also estimated for each vegetation type (Table 2) and three elevational levels: 0-750 m, 750-1 800 m, and 1 800-2 850 m (Luis-Martínez et al., 2020). For the elevational analysis, the non-parametric estimation method Chao1 (Colwell & Coddington, 1994) was implemented in SPADE (Chao & Shen, 2010). For each estimation, the 95 % confidence interval (CI) was estimated using the bootstrap technique. Significant differences between the species richness of distinct vegetation types or elevational levels were evaluated by comparison and overlap of the confidence intervals.

Additionally, the real diversity defined as the exponential of the Shannon-Wiener index (H') was estimated for each elevational level along with the 95 % CI, using the method proposed by Chao and Shen (2003) implemented in SPADE (Chao & Shen, 2010). The scale of the real diversity (effective number of species) is linear; therefore, the values of each elevational level can be compared directly using the CI overlap (Jost, 2006).

Species composition similarity analysis: Similarities were estimated in species composition between the Loxicha Region and other regions with roughly equivalent sampling effort on the Pacific and Atlantic slopes of



Oaxaca and other states. Besides Loxicha, our analysis included the Sierra de Juárez, Oaxaca (Luis-Martínez et al., 1991), the Sierra Mazateca, Oaxaca (Álvarez-García et al., 2016), the Sierra de Atoyac de Álvarez, Guerrero (Vargas-Fernández et al., 1994), the Sierra de Manantlán, Jalisco-Colima (Vargas-Fernández et al., 1999) and the Sierra de San Juan, Nayarit (MARIPOSA database). A distance matrix was estimated with presence/absence data of the species in each region using the Jaccard index with the “vegan” package (Oksanen et al., 2019) in R 4.0.0 (R Core Team, 2020). Using the same method, the similarity among 77 sites distributed across Mexico was estimated, including multiple biogeographic provinces and both Pacific and Atlantic slopes.

Natural history: Some biological observations made during fieldwork are presented, which include elevational migrations and species aggregations among other data. These observations are valuable for describing the fine-scale spatial and temporal distribution of some rare or hard-to-find species and could aid future efforts to collect these species.

RESULTS

Species list: Based on a review of published records (1950-2004) and a query of the MARIPOSA database up to the year 2000, 139 taxa of Nymphalidae were historically recorded from the Loxicha Region. Our subsequent field sampling from 2005-2014 across 21 sites in the region (Table 2) increased that list to 189 taxa, including 10 subfamilies, 23 tribes, 15 subtribes, and 85 genera. Our sampling effort resulted in 28 756 records plus 1 248 records from historical collections archived in the MARIPOSA database, for a total of 30 004 records of Nymphalidae for the Loxicha Region. Data from publications and scientific collections are mostly from the 400-1 400 m elevational range, while records from our field work are distributed from 80-2 850 m. All species and subspecies historically recorded for

the region were collected during our fieldwork except for *Adelpha donysa* ssp., *Pedaliodes dejecta* ssp., and *Actinote guatemalena guerrensis* J. Maza, 1982.

The Nymphalidae species documented in the Loxicha Region constitute 46 % of Mexican nymphalid species and 56 % of those recorded from Oaxaca (Luis-Martínez et al., 2016). A total of 10 species and 56 subspecies endemic to Mexico are represented in the Loxicha Region. These endemic taxa were binned into four groups according to their degree of endemism (Fig. 1): group 1, endemic to the Loxicha Region (5 spp.); group 2, endemic to the Sierra Madre del Sur (13 spp.); group 3, endemic to the Pacific slope (23 spp.); and group 4, endemic to Mexico (15 spp.). The taxa exclusive to the Loxicha Region are *Memphis wellingi* (L. Miller & J. Miller, 1976); *Cylopsis jacquelineae* (L. Miller, 1974); *Callicore texa loxicha* (R. G. Maza & J. Maza, 1983); *Chlosyne gaudialis wellingi* (L. Miller & Rotger, 1979), and *Altinote stratonice oaxaca* (J. Miller & L. Miller, 1979).

Species list of Nymphalidae for the Loxicha Region, Oaxaca. Taxa in bold text are endemics, and superscript numbers correspond to their degree of endemism: 1, endemic to the Loxicha Region; 2, endemic to the Sierra Madre del Sur; 3, endemic to the Pacific slope; 4, endemic to Mexico.

Family NYMPHALIDAE

Rafinesque, 1815

Subfamily Libytheinae Boisduval, 1833

1. *Libytheana carinenta mexicana*
Michener, 1943

Subfamily Danainae Boisduval, 1833

Tribe Euploeini Herrich-Schäffer, 1849

Subtribe Itunina Reuter, 1896

2. *Anetia thirza thirza* Geyer, [1833]
3. *Lycorea halia atergatis* Doubleday, [1847]
4. *Lycorea ilione albescens* (Distant, 1876)

Tribe Danaini Boisduval, 1833

Subtribe Danaína Boisduval, 1833

5. *Danaus eresimus montezuma* Talbot, 1943
6. *Danaus gilippus thersippus* (Bates, 1863)
7. *Danaus plexippus plexippus* (Linnaeus, 1758)

Subfamily Ithomiinae Godman & Salvin, 1879

Tribe Tithoreini Fox, 1940

8. *Aeria eurimedia pacifica* Godman & Salvin, 1879
9. *Tithorea harmonia hippothous* Godman & Salvin, 1879
10. *Tithorea tarricina duenna* Bates, 1864

Tribe Melinaeini Clark, 1947

11. *Melinaea lilis flavicans* Hoffmann, 1924³

Tribe Mechanitini Bar, 1878

12. *Mechanitis lysimnia utemaia* Reakirt, 1866
13. *Mechanitis menapis doryssus* Bates, 1864
14. *Mechanitis polymnia lycidice* Bates, 1864

Tribe Oleriini Fox, 1940

15. *Oleria paula* (Weymer, 1883)

Tribe Dircennini D'Almeida, 1941

16. *Dircenna klugii klugii* (Geyer, 1837)
17. *Episcada salvinia portilla* J. Maza & Lamas, 1978³
18. *Pteronymia artena praedicta* J. Maza & Lamas, 1982²
19. *Pteronymia cotytto cotytto* (Guérin-Méneville, [1844])
2. *Pteronymia rufocincta* (Salvin, 1869)³

Tribe Godyridini D'Almeida, 1941

21. *Greta annette moschion* (Godman, 1901)³

22. *Greta morgane morgane* (Geyer, 1837)³

Subfamily Charaxinae Guenée, 1865

Tribe Anaeni Reuter, 1896

23. *Hypna clytemnestra mexicana* Hall, 1917
24. *Consul electra electra* (Westwood, 1850)
25. *Consul excellens genini* (Le Cerf, 1922)
26. *Consul fabius cecrops* (Doubleday, [1849])
27. *Phantos callidryas* (R. Felder, 1869)
28. *Siderone galanthis* ssp.
29. *Zaretis ellops* (Ménétriés, 1855)
30. *Anaea troglodyta aidea* (Guérin-Méneville, [1844])
31. *Fountainea euryppyle glanzi* (Rotger, Escalante & Coronado, 1965)³
32. *Fountainea glycerium glycerium* (Doubleday, [1849])
33. *Fountainea nobilis rayoensis* (J. Maza & Díaz, 1978)³
34. *Memphis forreri* (Godman & Salvin, 1884)
35. *Memphis perenna perenna* (Godman & Salvin, [1884])
36. *Memphis pithyusa pithyusa* (R. Felder, 1869)
37. *Memphis wellingi* L. Miller & J. Miller, 1976¹

Tribe Preponini Rydon, 1971

38. *Archaeoprepona amphimachus baroni* J. Maza, 1982²
39. *Archaeoprepona demophon occidentalis* Stoffel & Descimon, 1974³
40. *Archaeoprepona demophoon mexicana* Llorente, Descimon & K. Johnson, 1993³
41. *Archaeoprepona phaedra* ssp.²
42. *Prepona laertes octavia* Fruhstorfer, 1905
43. *Prepona brooksiana ibarra* Beutelspacher, 1982³



Subfamily Morphinae Newman, 1834

Tribe Morphini Newman, 1834

Subtribe Morphina Newman, 1834

44. *Morpho polyphemus* Westwood, [1850]
 45. *Morpho helenor guerrerensis* Le Moulton & Réal, 1962³

Tribe Brassolini Boisduval, 1836

Subtribe Brassolina Boisduval, 1836

46. *Caligo telamonius memnon* (C. Felder & R. Felder, 1867)
 47. *Caligo uranus* Herrich-Schäffer, 1850
 48. *Opsiphanes boisduvallii* Doubleday, [1849]
 49. *Opsiphanes cassina fabricii* (Boisduval, 1870)
 50. *Opsiphanes quiteria quirinus* Godman & Salvin, 1881
 51. *Opsiphanes tamarindi tamarindi* C. Felder & R. Felder, 1861

Subfamily Satyrinae Boisduval, 1833

52. *Manataria hercyna maculata* (Hopffer, 1874)
 53. *Oxeoschistus hilara* ssp.²
 54. *Oxeoschistus tauropolis* ssp.³
 55. *Pedaliodes dejecta* ssp.²
 56. *Cissia similis* (Butler, 1867)
 57. *Cissia terrestris* (Butler, 1867)
 58. *Cissia* sp.
 59. *Cissia themis* (Butler, 1867)
 60. *Cyllopsis clinas* (Godman & Salvin, 1889)²
 61. *Cyllopsis diazi* L. Miller, 1974⁴
 62. *Cyllopsis hedemanni hedemanni* R. Felder, 1869
 63. *Cyllopsis jacquelineae* L. Miller, 1974¹
 64. *Cyllopsis nayarit* (R. L. Chermock, 1947)⁴
 65. *Cyllopsis pyracmon pyracmon* (Butler, 1867)
 66. *Cyllopsis suivalenoides* L. Miller, 1974
 67. *Euptychia fetna* Butler, 1870
 68. *Hermeuptychia hermes* (Fabricius, 1775)
 69. *Megisto rubricata pseudocleophes* L. Miller, 1976⁴
 70. *Paramacera xicaque rubrosuffusa* L. Miller, 1972²

71. *Pindis squamistriga* R. Felder, 1869

72. *Taygetis kerea* Butler, 1869

73. *Taygetis mermeria griseomarginata* L. Miller, 1978³

74. *Taygetis uncinata* Weymer, 1907⁴

75. *Taygetis virgilia* (Cramer, 1776)

76. *Taygetis weymeri* Draudt, 1912

77. *Gyrocheilus patrobas patrobas* (Hewitson, 1862)⁴

Subfamily Apaturinae Boisduval, 1840

78. *Asterocampa idyja argus* (Bates, 1864)

79. *Doxocopa laure laure* (Drury, 1773)

80. *Doxocopa pavon theodora* (Lucas, 1857)

Subfamily Biblidinae Boisduval, 1833

Tribe Cyrestini Guenée, 1865

81. *Marpesia chiron marius* (Cramer, 1779)

82. *Marpesia petreus* ssp. nov.

83. *Marpesia zerynthia dentigera* (Fruhstorfer, 1907)

Tribe Biblidini Boisduval, 1833

Subtribe Biblidina Boisduval, 1833

84. *Biblis hyperia aganisa* Boisduval, 1836

85. *Mestra dorcas amymone* (Ménétriés, 1857)

Subtribe Ageroniina Doubleday, [1847]

86. *Hamadryas amphinome mazai* Jenkins, 1983³

87. *Hamadryas atlantis lelaps* (Godman & Salvin, 1883)³

88. *Hamadryas februa ferentina* (Godart, [1824])

89. *Hamadryas glauconome glauconome* (Bates, 1864)

90. *Hamadryas guatemalena marmarice* (Fruhstorfer, 1916)⁴

Subtribe Epicaliina Guenée, 1865

91. *Eunica alcmena alcmena* (Doubleday, [1847])

92. *Eunica monima* (Stoll, 1782)

93. *Eunica tatila tatila* (Herrich-Schäffer, [1855])

94. *Catonephele cortesi* R. G. Maza, 1982³
95. *Catonephele numilia immaculata* Jenkins, 1985²
96. *Myscelia cyananthe cyananthe* C. Felder & R. Felder, 1867⁴
97. *Myscelia cyaniris alvaradia* R. G. Maza & Díaz, 1982³
98. *Myscelia ethusa ethusa* (Doyère, [1840])
- Subtribe Epiphilina Jenkins, 1987
99. *Nica flavilla bachiana* (R. G. Maza & J. Maza, 1985)²
100. *Temenis laothoe quilapayunia* R. G. Maza & Turrent, 1985³
101. *Bolboneura sylphis beatrix* R. G. Maza, 1985³
102. *Epiphile adраста escalantei* Descimon & Mast, 1979⁴
103. *Pyrrhogyra edocla paradisea* R. G. Maza & J. Maza, 1985³
104. *Pyrrhogyra neaerea hypsenor* Godman & Salvin, 1884
- Subtribe Callicorina Orfila, 1952
105. *Diaethria anna mixteca* J. Maza, 1977²
106. *Diaethria astala asteroide* R. G. Maza & R. F. Maza, 1985²
107. *Callicore texa loxicha* R. G. Maza & J. Maza, 1983¹
108. *Cyclogramma pandama* (Doubleday, [1848])
- Subtribe Eubagina Burmeister, 1878
109. *Dynamine dyonis* Geyer, 1837
110. *Dynamine postverta mexicana* D'Almeida, 1952
111. *Dynamine theseus* (C. Felder & R. Felder, 1861)
- Subfamily Limenitidinae Behr, 1864
- Tribe Limenitidini Behr, 1864
- Subtribe Limenitidina Behr, 1864
112. *Adelpha barnesia leucas* Fruhstorfer, 1915
113. *Adelpha basiloides* (Bates, 1865)
114. *Adelpha bredowii* Geyer, 1837
115. *Adelpha diocles* ssp.³
116. *Adelpha donysa* ssp.²
117. *Adelpha fessonia fessonia* (Hewitson, 1847)
118. *Adelpha iphicleola iphicleola* (Bates, 1864)
119. *Adelpha iphichus iphichus* (Linnaeus, 1758)
120. *Adelpha leuceria leuceria* (Druce, 1874)
121. *Adelpha leucerioides* ssp.³
122. *Adelpha lycorias melanthe* (Bates, 1864)
123. *Adelpha naxia naxia* (C. Felder & R. Felder, 1867)
124. *Adelpha paraena massilia* (C. Felder & R. Felder, 1867)
125. *Adelpha phylaca phylaca* (Bates, 1866)
126. *Adelpha pithys* (Bates, 1864)
127. *Adelpha serpa celerio* (Bates, 1864)
- Subfamily Nymphalinae Rafinesque, 1815
- Tribe Coeini Scudder, 1893
128. *Historis acheronta acheronta* (Fabricius, 1775)
129. *Historis odius dious* Lamas, 1995
130. *Pycina zamba zelys* Godman & Salvin, 1884
- Tribe Nymphalini Rafinesque, 1815
131. *Colobura dirce dirce* (Linnaeus, 1758)
132. *Smyrna blomfieldia datis* Fruhstorfer, 1908
133. *Smyrna karwinskii* Geyer, [1833]
134. *Hypanartia dione disjuncta* Willmott, J. Hall & Lamas, 2001
135. *Hypanartia godmanii* (Bates, 1864)
136. *Hypanartia lethe* (Fabricius, 1793)
137. *Hypanartia trimaculata autumnna* Willmott, J. Hall & Lamas, 2001
138. *Nymphalis antiopa antiopa* (Linnaeus, 1758)
139. *Vanessa atalanta rubria* (Fruhstorfer, 1909)
140. *Vanessa cardui* (Linnaeus, 1758)
141. *Vanessa virginiensis* (Drury, 1773)
- Tribe Victorinini Scudder, 1893
142. *Siproeta epaphus epaphus* (Latreille, [1813])



143. *Siproeta stelenes biplagiata* (Fruhstorfer, 1907)
144. *Anartia fatima fatima* (Fabricius, 1793)
145. *Anartia jatrophae luteipicta* Fruhstorfer, 1907
- Tribe Junoniini Reuter, 1896
146. *Junonia coenia* Hübner, [1822]
147. *Junonia evarete nigrosuffusa* Barnes & McDunnough, 1916
148. *Junonia genoveva* ssp. nov.
- Tribe Melitaeini Herrich-Schäffer, 1843
- Subtribe Nova
149. *Chlosyne cynisca* (Godman & Salvin, 1882)⁴
150. *Chlosyne erodyle* ssp.
151. *Chlosyne gaudialis wellingi* L. Miller & Rotger, 1979¹
152. *Chlosyne hippodrome hippodrome* (Geyer, 1837)
153. *Chlosyne janais janais* (Drury, 1782)
154. *Chlosyne lacinia lacinia* (Geyer, 1837)
155. *Chlosyne marina marina* (Geyer, 1837)
156. *Chlosyne melanarge* (Bates, 1864)
157. *Chlosyne theona theona* (Ménétriés, 1855)
158. *Microtia elva elva* Bates, 1864
- Subtribe Phyciodina Higgins, 1981
159. *Phyciodes graphica graphica* (R. Felder, 1869)
160. *Phyciodes mylitta thebais* Godman & Salvin, 1878
161. *Phyciodes palleescens* (R. Felder, 1869)⁴
162. *Phyciodes phaon phaon* (Edwards, 1864)
163. *Phyciodes tharos tharos* (Drury, 1773)
164. *Tegosa guatemalena* (Bates, 1864)
165. *Anthanassa ardys ardys* (Hewitson, 1864)⁴
166. *Anthanassa argentea* (Godman & Salvin, 1882)
167. *Anthanassa atronia* (Bates, 1866)
168. *Anthanassa frisia tulcis* (Bates, 1864)
169. *Anthanassa nebulosa alexon* (Godman & Salvin, 1889)⁴
170. *Anthanassa otones oaxaca* Beutelspacher, 1990⁴
171. *Anthanassa polyca amator* (Hall, 1929)⁴
172. *Anthanassa sitalces cortes* (Hall, 1917)⁴
173. *Anthanassa texana texana* (Edwards, 1863)
174. *Eresia phillyra phillyra* Hewitson, 1852
- Subfamilia Heliconiinae Swainson, 1822
- Tribe Acraeini Boisduval, 1833
175. *Altinote stratonice oaxaca* (J. Miller & L. Miller, 1979)¹
176. *Actinote guatemalena guerrerensis* J. Maza, 1982²
- Tribe Heliconiini Swainson, 1822
- Subtribe Heliconiina Swainson, 1822
177. *Agraulis vanillae incarnata* (Riley, 1926)
178. *Dione junio huascuma* (Reakirt, 1866)
179. *Dione moneta poeyii* Butler, 1873
180. *Dryas iulia moderata* (Riley, 1926)
181. *Dryadula phaetusa* (Linnaeus, 1758)
182. *Eueides aliphera gracilis* Stichel, 1903
183. *Eueides isabella eva* (Fabricius, 1793)
184. *Heliconius charithonia vazquezae* W. P. Comstock & F. M. Brown, 1950
185. *Heliconius erato cruentus* Lamas, 1998³
186. *Heliconius hortense* Guérin-Ménéville, [1844]
187. *Heliconius ismenius telchinia* Doubleday, 1847
- Tribe Argynnini Swainson, 1833
- Subtribe Euptoietina Simonsen, 2006
188. *Euptoieta claudia daunius* (Herbst, 1798)
189. *Euptoieta hegesia meridiania* Stichel, 1938

Alpha diversity: Considering only the data obtained during our fieldwork, 186 Nymphalidae species were collected. When species from the literature review and historically collected specimens were added, the list reached

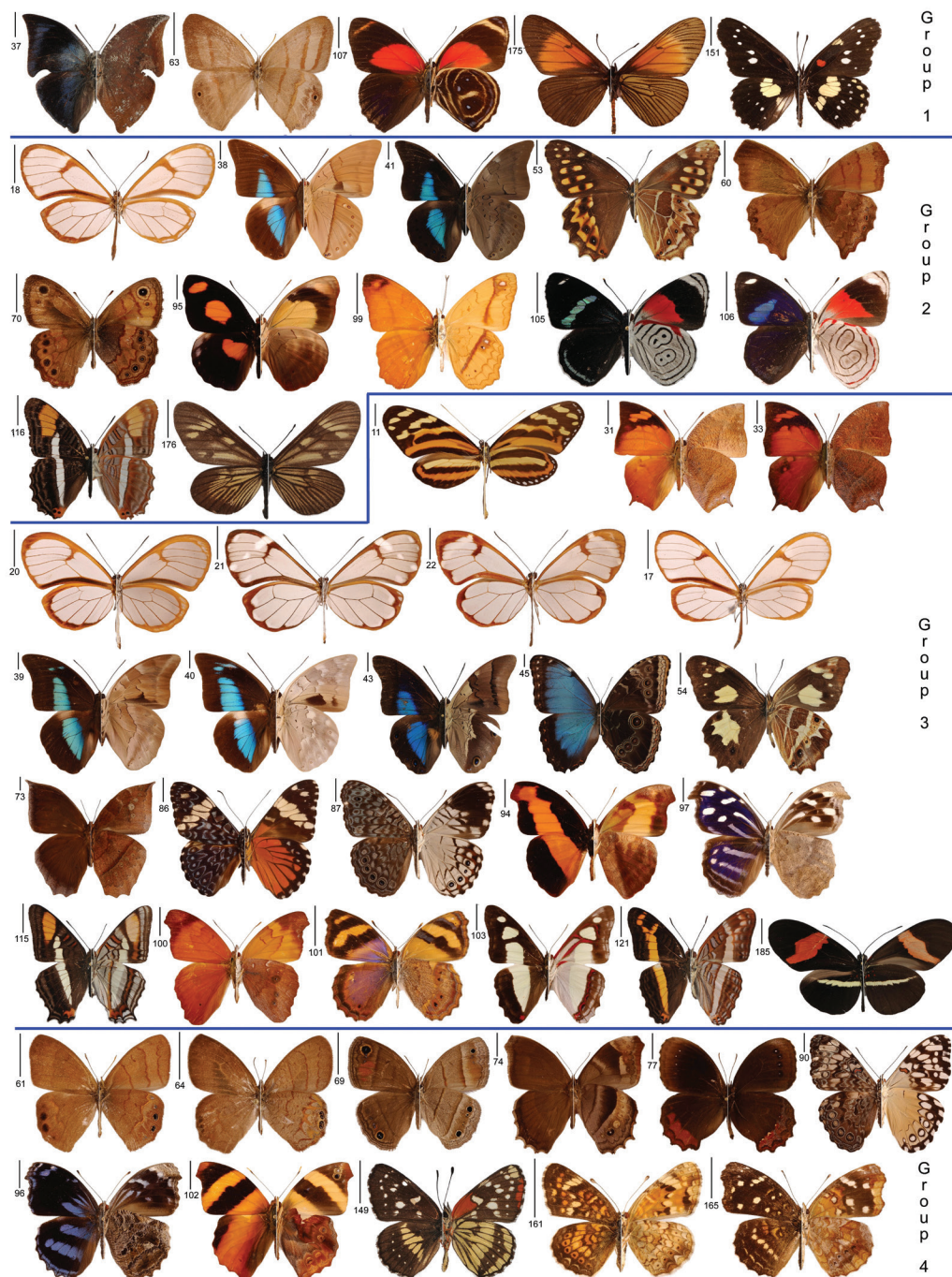


Fig. 1. Nymphalidae taxa endemic to Mexico that occur in the Loxicha Region, Oaxaca. Numbers correspond to names available in our species list. Dorsal view: left side of the specimen; Ventral view: right side.



189 species. The Clench model estimated 188 species (Fig. 2) while Chao1 estimated 193 species. Therefore, the Clench model underestimated the region's species richness, while the Chao1 estimator was potentially more reliable. According to Chao1, our list is 98 % complete.

Across the 11 states of Mexico's Pacific slope from Baja California to Chiapas (Table 1), the nymphalid species richness of the Loxicha Region alone (189 spp.) surpasses all states except for Guerrero (216 spp.) and Chiapas (351 spp.). The high species richness in Guerrero is attributable to the biogeographic provinces Planicie Costera del Pacífico and Sierra Madre del Sur occupying most of the state, with the SMS having substantial faunal endemism. In Chiapas, the high species richness can be explained by the convergence of Atlantic and Pacific slopes in the state, as well as the presence of tropical evergreen forest, a vegetation type that supports more than 50 % of Mexican species of Papilionoidea (Salinas-Gutiérrez et al., 2004).

Species composition similarity across regions: We compared nymphalid faunal richness across eight regions with differing elevational gradients, comprising six from the Pacific slope and two from the Atlantic slope (Table 3). All regions have roughly similar

sampling effort, and species estimation methods indicate that more than 90 % of the species have been recorded from each, thus validating the comparison. The Loxicha Region is the most diverse for Nymphalidae on the Pacific slope, and the second most diverse in Oaxaca, behind only the Sierra de Juárez (259 spp.) of the Atlantic slope. Identical patterns exist for Papilionidae and Pieridae (Luis-Martínez et al., 2020).

Similarity analysis shows two main groups (Fig. 3), corresponding to the arrangement of mountain ranges in Mexico and the consequent isolation of the lepidoptero fauna. The first group comprises the Sierra Mazateca and the Sierra de Juárez, on the Atlantic slope of Oaxaca. The second group is composed of six regions on the Pacific slope or in the Amacuzac-Cuenca del Balsas, which are divided into two subgroups with a similarity value of more than 50 %. The first subgroup contains the regions of the Southern Sierra Madre del Sur: Atoyac and Loxicha, which share 66 % of their species (142 spp.). The second subgroup corresponds to the regions located North of the Costa del Pacífico, in the Western Eje Neovolcánico (San Juan-Manantlán), the Northern Sierra Madre del Sur (SMS-Michoacán), and Morelos which includes parts of two biogeographic provinces: Cuenca del Balsas and Eje Neovolcánico.

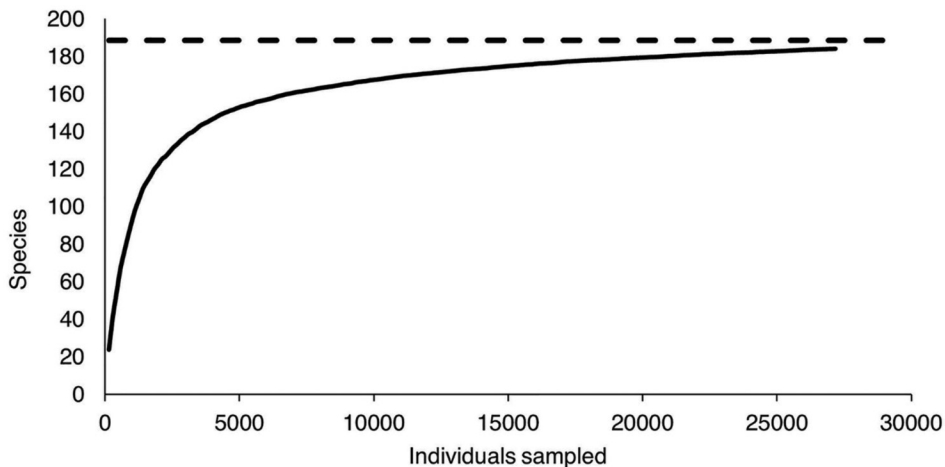


Fig. 2. Species accumulation curve of Nymphalidae in the Loxicha Region, Oaxaca, Mexico fitted to the Clench model. The asymptote (dashed line) corresponds to 188 estimated species.

TABLE 3
Species richness of Nymphalidae across eight regions in Mexico

Region	spp.	Elevation (m)	Slope
1. Sierra de Juárez, Oaxaca	259	100-3 100	Atlantic
2. Sierra Mazateca, Oaxaca	185	100-2 200	Atlantic
3. Loxicha Region, Oaxaca	189	80-2 600	Pacific
4. Sierra de Atoyac, Guerrero	170	300-3 100	Pacific
5. Morelos (state)	147	1 000-3 000	Pacific -CB
6. Michoacán, SMS portion	134	800-1 800	Pacific
7. Sierra de Manantlán, Jalisco-Colima	144	250-1 750	Pacific
8. Sierra de San Juan, Nayarit	135	0-1 350	Pacific

1: Luis-Martínez et al., 1991; 2: Álvarez-García et al., 2016; 3: this article; 4: Vargas-Fernández et al., 1994; 5: Luna-Reyes et al., 2012 and Luna-Reyes, 2020; 6 and 8: MARIPOSA database; 7: Vargas-Fernández et al., 1999. CB: Cuenca del Balsas.

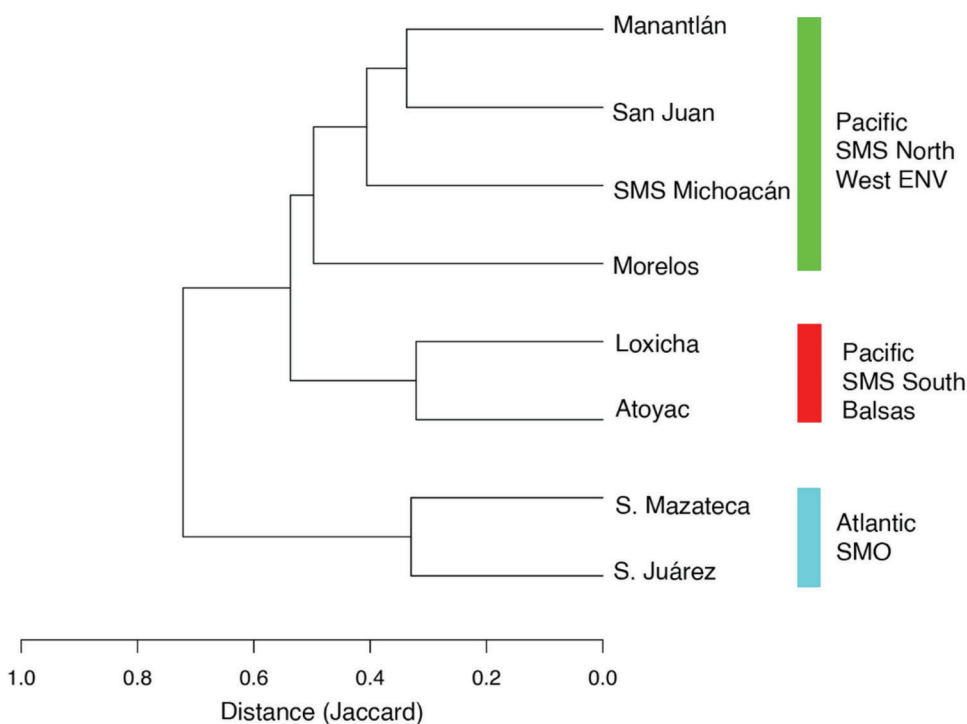


Fig. 3. Similarity of Nymphalidae species composition across eight regions in Mexico. The distance matrix was estimated with the Jaccard index. For full names of the regions see Table 3.

Species composition distances between Loxicha and other regions are correlated with geographic distances, but also with biogeographic regionalization (Fig. 3). The two regions with the greatest faunistic distance are those from the Atlantic slope (the Sierra de Juárez and Sierra Mazateca), even though

they are the closest geographically. The same pattern was observed with Morelos, which belongs to the Cuenca del Balsas: although Morelos is closer to Loxicha than regions like San Juan and Manantlán, these two have lower faunistic distances. Considering only the four regions in the SMS, faunistic distances



are correlated with geographic distances, with Atoyac being the closest and most similar to Loxicha while also being the farthest and most distinct relative to San Juan.

Species richness by site: The MARIPOSA database contains records of Nymphalidae species from more than 5 000 sites across Mexico. However, only 40 of those sites have over 100 species recorded, eight of which are on the Pacific slope while the other 32 are distributed elsewhere in Mexico (Table 4). From the Loxicha Region, only Azulillo and Rancho Hagia Sofía exceed 100 species, placing them in sixth and fourth place at a national scale, respectively. Areas like Acahuzotla, Guerrero (158 spp.) and Candelaria Loxicha, Oaxaca (138 spp.) also have high species richness but are not specific sites, instead being extended

areas that include several sites with wide variation in elevation and vegetation type. These extended or historical “sites” served as geographic references for decades prior to this study, where collected specimens from other sites were gathered and labeled. Additional such historical “sites” across Mexico include Xalapa, Catemaco, and Presidio in the state of Veracruz (Luis-Martínez et al., 1996), Chiltepec, Oaxaca (Luis-Martínez et al., 1991), and some others on the Atlantic slope.

Of the 40 sites with more than 100 species of Nymphalidae (Table 4), 16 have been sampled by members of the MZFC, and 30 are located in 11 of the regions with highest diversity of Papilionoidea in Mexico. Of these high-diversity regions, nine were recognized by Luis-Martínez et al. (2003): 1, Orizaba-Córdoba-Fortín de las Flores corridor;

TABLE 4
Sites with more than 100 species of Nymphalidae along the Atlantic and Pacific slopes of Mexico

State	R	Site	spp.	State	R	Site	spp.
Atlantic slope							
Veracruz	3	Xalapa*	193	San Luis Potosí		Tamazunchale	109
Veracruz	1	Córdoba	180	Chiapas		Santa Rosa	108
Veracruz	1	Presidio	170	Veracruz	3	Parque Francisco Javier Clavijero ¹	107
Chiapas		San Antonio Buena Vista	162	Oaxaca	4	Cerro Armadillo ¹	106
Oaxaca	4	San José Chiltepec	156	Veracruz		Cuetzalapan	104
Oaxaca	4	Metates ¹	152	Veracruz	2	Popoctépetl	104
Veracruz	3	Barranca de Cayoapa* ¹	149	Oaxaca	4	Soyolapan El Bajo ¹	103
Puebla	10	Tequezuitla	145	Oaxaca		Matías Romero	102
Veracruz	1	Fortín de las Flores* ¹	146	Oaxaca		La Gringa, Sta. María Chimalapa ¹	102
Veracruz	2	Catemaco	142	Veracruz	1	Orizaba	102
Veracruz	2	Dos Amates	138	Veracruz	2	Tapalapan	102
Veracruz	1	Presidio, Ixhuatlán del Café*	134	Pacific slope			
Veracruz	3	Teocelo ¹	132	Guerrero	8	Acahuzotla*	158
Puebla	10	Barranca de Patla*	132	Oaxaca	11	Candelaria Loxicha*	138
Oaxaca	4	La Esperanza ¹	131	Oaxaca	11	Rancho Hagia Sofía ¹	121
Chiapas		Santa Rosa, Comitán	130	Chiapas		San Jerónimo, Tacaná	117
Chiapas		Zona Arqueológica Yaxchilán ¹	129	Jalisco	6	La Calera ¹	115
Oaxaca	4	Puerto Eligio ¹	110	Oaxaca	11	Azulillo ¹	109
Veracruz	2	Laguna de Catemaco	117	Guerrero	5	Río Santiago ¹	106
Tabasco		Cerro del Coconá ¹	115	Guerrero	5	El Faisanal ¹	105
Oaxaca	4	Naranjal Chiltepec	115				

*: extended or historical “sites” that combine records from multiple distinct sites under a single name (see text); ¹: sites collected by MZFC members; **R**: sites that lie in the most diverse regions of Mexico (see text).

2, Tuxtlas; 3, Xalapa-Coatepec-Teocelo corridor; 4, Sierra de Juárez; 5, Sierra de Atoyac; 6, Sierra de Manantlán; 7, Mismaloya-Bahía de Banderas corridor; 8, Acahuizotla; and 9, Sierra de San Juan. Recently, two more high-diversity regions were recognized: 10, La Sierra Norte de Puebla (MARIPOSA database), and 11, Loxicha (Arellano-Covarrubias et al., 2018; Luis-Martínez et al., 2016; Luis-Martínez et al., 2021; data presented here).

Species composition similarity across sites: Of the 77 sites included in the species composition similarity analysis (Table 5), 62 are on the Pacific slope and 15 on the Atlantic slope, 44 have been sampled by

members of the MZFC, 32 are located between 0-750 m, 27 between 800-1 750 m, and six above 1 800 m elevation. Five vegetation types are included: TDF, TSDF, OPF, OF, and CF. The latter includes three elevation-delimited subtypes: low-CF (750-1 199 m), medium-CF (1 200-1 800 m), and high-CF (> 2 000 m). Additionally, we recognize six ecotones: OF-CF, OPF-CF, TDF-TSDF, TDF-TSDF-CF, TSDF-CF and TSDF-OPF. Twenty-four sites are in the CF, and seven more exist in an ecotone that includes CF. Therefore, CF is the most well-represented vegetation type across the sites (48 % of the sites).

The similarity analysis showed two groups corresponding to the sites of the Atlantic and

TABLE 5
Sites included in the species composition similarity analysis for Mexican Nymphalidae

State	Site	Spp.	Abbreviated name	Elevation	Vegetation type
Atlantic slope					
San Luis Potosí	Tamazunchale	109	SLP_Tam_350	350	TEGF
Puebla	Tequezquitla	145	PUE_Teq_650	650	TSDF-CF
Puebla	Barranca de Patla	132	PUE_Bpa_600	600	TSDF-CF
Veracruz	Barranca de Cayoapa ¹	149	VER_Bca_600	600	CF
Veracruz	Catemaco	142	VER_Cat_250	250	TEGF
Veracruz	Córdoba	180	VER_Cor_900	900	CF
Veracruz	Fortín de las Flores ¹	146	VER_FF1_900	900	CF
Veracruz	Xalapa	193	VER_Jal_1350	1 350	CF
Veracruz	Teocelo ¹	132	VER_Teo_1200	1 200	CF
Oaxaca	San José Chiltepec	156	OAX_Chi_100	100	TEGF
Oaxaca	La Esperanza ¹	131	OAX_Esp_1750	1 750	CF
Oaxaca	Metates ¹	152	OAX_Met_900	900	CF
Oaxaca	Puerto Eligio ¹	110	OAX_Pel_650	650	TEGF
Chiapas	San Antonio Buena Vista	162	CHIS_SAB_1350	1 350	CF
Chiapas	Santa Rosa, Comitán	130	CHI_SRC_1800	1 800	CF
Pacific slope					
Nayarit	Compostela ¹	41	NAY_Com_800	800	TDF
Nayarit	Jumatán ¹	78	NAY_Jum_300	300	TDF
Nayarit	La Bajada ¹	61	N_Baj_250	250	TSDF
Nayarit	La Yerba, Tepeltite ¹	72	NAY_Yer_900	900	CF
Nayarit	Mecatán ¹	47	NAY_Mec_300	300	TSDF
Nayarit	Palapita ¹	66	NAY_Pal_650	650	TSDF
Nayarit	Pintadeño ¹	23	NAY_Pin_750	750	OF
Nayarit	San Blas ¹	45	NAY_SBI_50	50	MAN
Nayarit	Singayta ¹	59	NAY_Sin_50	50	OP
Nayarit	Venustiano Carranza ¹	69	NAY_Vca_1250	1 250	CF



State	Site	Spp.	Abbreviated name	Elevation	Vegetation type
Jalisco	Ahuacapán ¹	85	JAL_Ahu_900	900	TDF
Jalisco	Estación de Biología, UNAM, Chamela	50	JAL_Cha_100	100	TDF
Jalisco	La Calera ¹	115	JAL_Cal_650	650	TDF
Jalisco	Los Mazos ¹	76	JAL_Maz_1600	1 600	CF
Jalisco	Puerto Vallarta	49	JAL_Pva_50	50	TDF
Jalisco	Zenzontla ¹	77	JAL_Zen_800	800	TDF
Colima	Agua Dulce ¹	86	COL_Agu_250	250	TSDF
Colima	Platanarillo ¹	88	COL_Pla_350	350	TSDF
Michoacán	Arteaga	70	MICH_Art_900	900	TDF
Michoacán	Chiquihuitillo	75	MICH_Chi_260	260	TDF
Michoacán	Los Chorros del Varal ¹	72	MICH_Cho_900	900	TSDF
Michoacán	P.H. Cupatitzio	83	MICH_CUP_1000	1 000	TSDF-PF
Michoacán	Rancho “El Zorrillo”	92	MICH_Rzo_750	750	TDF
Michoacán	Rancho “El Zorrillo”, Cañada Húmeda	70	MICH_RzC_750	750	TDF-TSDF
Morelos	3 km al NE de Chiautla	41	MOR_Shia_1000	1 000	TDF
Morelos	Km 1.5 Carretera Tetecala-Coatlalco	56	MOR_TC_1100	1 100	TDF
Morelos	Cañón de Lobos	51	MOR_CL_1200	1 200	TDF
Morelos	1.5 Km al E de Palo Grande	57	MOR_PG_1200	1 200	TDF
Morelos	Sierra de Huautla	58	MOR_SH_1000	1 000	TDF-TSDF
Guerrero	Agua Salada		MOR_AS_760	760	TDF
Guerrero	Coapango	74	GRO_Coa_1330	1 330	TDF
Guerrero	Las Vías	72	GRO_LV_1200	1 200	TDF
Guerrero	Cascada de las Granadas	81	GRO_CdeG_1370	1 370	TDF
Guerrero	Los Amates	65	GRO_Ama_980	980	TDF
Guerrero	Quetzalapa	66	GRO_Que_850	850	TDF
Guerrero	Piedras Negras	54	GRO_PN_1300	1 300	TDF
Guerrero	Palmillas	57	MOR_Pal_1050	1 050	TDF
Guerrero	Acahuizotla	158	GRO_Aca_900	900	TDF-TSDF-CF
Guerrero	El Faisanal ¹	94	GRO_Fai_1250	1 250	TSDF-CF
Guerrero	El Iris ¹	24	GRO_Iris_2000	2 000	OF-CF
Guerrero	La Golondrina ¹	45	GRO_LGo_1800	1 800	CF
Guerrero	Las Parotas ¹	78	GRO_Par_350	350	TSDF
Guerrero	Los Retrocesos	71	GRO_Ret_1600	1 600	CF
Guerrero	Nueva Delhi ¹	82	GRO_Nde_1350	1 350	CF
Guerrero	Puente de Los Lugardo ¹	94	GRO_PLL_800	800	TSDF
Guerrero	Puerto del Gallo ¹	38	GRO_Pga_2350	2 350	BPE-CF
Guerrero	Río Santiago, 4 km W ¹	106	GRO_Rsa_680	680	TSDF
Oaxaca	Azulillo ¹	109	OAX_Azu_380	380	TSDF
Oaxaca	Copalita, Río Copalita	58	OAX_Cop_600	600	CF
Oaxaca	Copalita, Siete Veneros	54	OAX_Ven_940	940	CF
Oaxaca	Finca Aurora-Finca San Isidro ¹	63	OAX_FAS_1100	1 100	CF
Oaxaca	La Pasionaria ¹	72	OAX_Pas_1500	1 500	CF
Oaxaca	La Soledad-Buenavista ¹	70	OAX_Sbu_1470	1 470	CF
Oaxaca	Magdalena, El Lirio ¹	95	OAX_Mag_750	750	CF
Oaxaca	Parque Nacional Huatulco ¹	68	OAX_PNH_100	100	TDF
Oaxaca	Parque Nacional Huatulco, Río Cacaluta ¹	74	OAX_PNHC_80	80	TDF
Oaxaca	Pluma Hidalgo, 4 km NW “La Curva” ¹	95	OAX_Phi_1100	1 100	CF

State	Site	Spp.	Abbreviated name	Elevation	Vegetation type
Oaxaca	Portillo del Rayo-Finca El Encanto ¹	88	OAX_PRa_1200	1 200	CF
Oaxaca	Puente Arroyo “El Guajolote” ¹	74	OAX_Gua_2020	2 020	OPF
Oaxaca	Rancho Hagia Sofía ¹	121	OAX_Rha_410	410	TSDF
Oaxaca	San José del Pacífico, 1 km S ¹	61	OAX_Pac_2280	2 280	OPF-CF
Chiapas	San Jerónimo, Tacaná	117	CHIS_Sje_750	750	CF

¹: sites collected by MZFC members; CF, cloud forest; MAN, mangrove; OF, oak forest; OP, *Orbygnia* palmar; OPF, oak-pine forest; TDF, tropical deciduous forest; TEGF, tropical evergreen forest; TSDF, tropical sub-deciduous forest.

Pacific slopes, respectively (Fig. 4). Sites of the Atlantic slope, in the low part of the phenogram (1), are associated with the vegetation and environmental conditions of the Gulf of Mexico (East of Chiapas). This group has 163

exclusive taxa, six of which are distributed in 85 % of the sites of the group: *Archaeoprepona demophon centralis* (Fruhstorfer, 1905), *Catonephele mexicana* Jenkins & R. G. Maza, 1985, *Fountaininea euryphle confusa* (A. Hall, 1929),

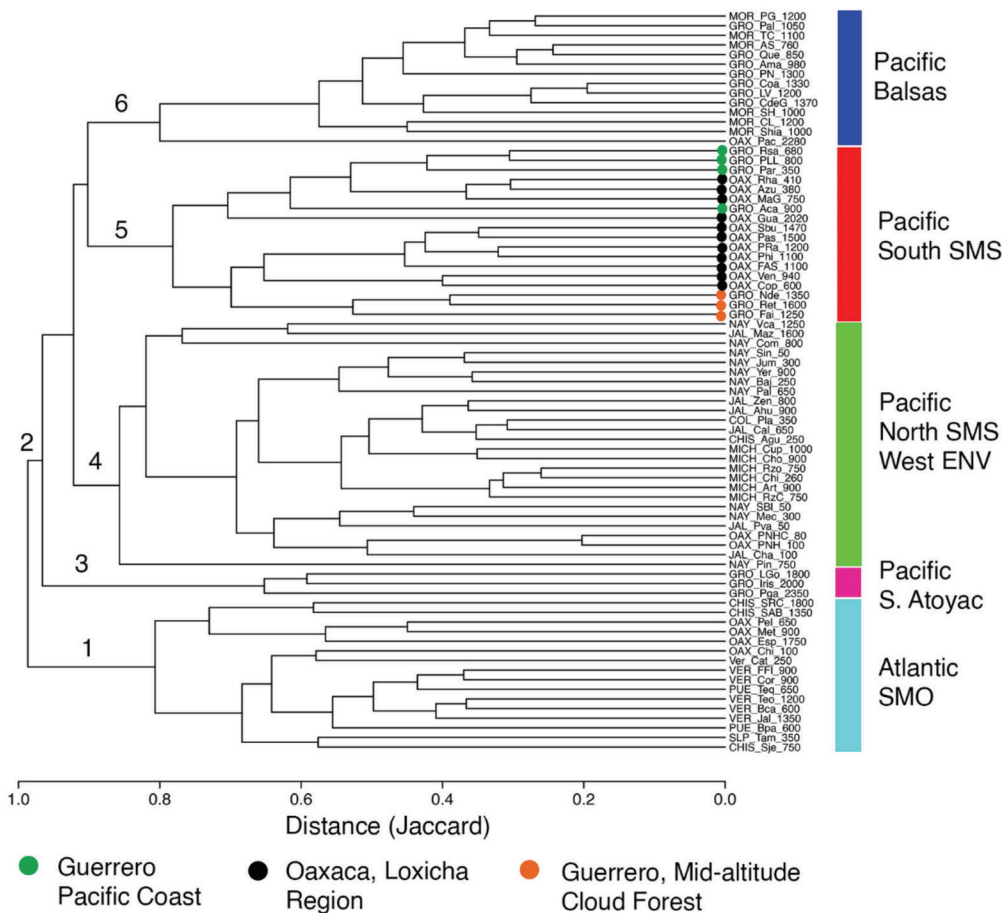


Fig. 4. Nymphalidae species composition similarity across 77 sites in Mexico (15 in the Atlantic and 62 in the Pacific slopes). The distance matrix was estimated with the Jaccard index. Groups: 1. Atlantic slope; 2. Pacific slope; 3. Sierra de Atoyac high-lands; 4. Costa del Pacífico, Northern Sierra Madre del Sur, and Western Eje Neovolcánico; 5. Sierra Madre del Sur (Guerrero-Oaxaca); 6. Cuenca del Balsas (Guerrero-Morelos).



Hamadryas amphinome mexicana (Lucas, 1853), *Morpho helenor montezuma* Guenée, 1859, and *Taygetis thamyra* (Cramer, 1779). The second group comprises the sites in the Pacific slope (2), divided into four subgroups. In the first subgroup are the sites of the highlands of the Sierra de Atoyac de Álvarez (La Golondrina, El Iris, and Puerto del Gallo) (3). No exclusive species were recorded for these three sites. Interestingly, although these sites are geographically close to the sites of Balsas and SMS, they segregate from other sites of the Pacific because of their high-elevation species assemblage (1 800-2 350 m). In the second subgroup are the sites of the biogeographic provinces Costa del Pacífico, Northern Sierra Madre del Sur, and Western Eje Neovolcánico (4). Six species are exclusive to this subgroup: *Bolboneura sylphis sylphis* (Guérin-Méneville, 1844), *Chlosyne rosita montana* A. Hall, 1924, *Cyllopsis pallens* L. Miller, 1974, *Fountainea halice tehuana* (A. Hall, 1917), *Polygonia interrogationis* (Fabricius, 1798), and *Texola elada hepburni* (Godman, 1901), but all are restricted to just 4-12 % of the sites in the subgroup. A third subgroup is formed by the sites in the Balsas province of Guerrero and Morelos (6). These sites support mostly TDF and lie at elevations from 760-2 280 m. Of the three exclusive species to Balsas, *Zischkaia lupita* (Reakirt, [1867]) is in 79 % of the sites of this subgroup, while *Chlosyne cyneas cynisca* (Godman & Salvin, 1882) and *Cyllopsis pertepida pertepida* (Dyar, 1912) are documented only in 7 % of the sites. The fourth subgroup includes the Loxicha Region and is composed of the sites of Oaxaca and Guerrero in the SMS (5). Exclusive species recorded in at least 80 % of the sites of this subgroup are *Archaeoprepona amphimachus baroni*, *Catonephele numilia immaculata*, *Diaethria astala asteroide*, and *D. anna mixteca*. This subgroup is divided into two sets of sites: those with low-elevation CF, and those with TSDf between 350-900 m. However, the high-elevation site El Guajolote (2 202 m) is similar to these sites, possibly because of its geographical proximity. The other set of sites are those within the SMS

with mid-elevation CF, between 600-1 600 m. A clear distinction exists between the sites of Oaxaca and those of Guerrero. These results show that the position of the sites in the phenogram corresponds to their geographic location but also to their respective elevations (Fig. 4).

Diversity of the Loxicha Region relative to other regions of the Sierra Madre del Sur and Costa del Pacífico:

The Mexican Pacific slope, particularly in Guerrero and Oaxaca, stands out for its remarkable diversity and endemism at both the species and genus level. In this area, only two faunistic studies exist that cover a complete elevational gradient, and that have an inventory completeness level higher than 95 % according to the species richness estimators. The first study was carried out in the Sierra de Atoyac, Guerrero, from 300-3 100 m (Vargas-Fernández et al., 1994) and the second one is the present study from 80-2 850 m (Table 6). Including both inventories, the diversity of Nymphalidae in the area is 214 species including 11 subfamilies and 84 genera. Of these 214 species, 88 % occur in the Loxicha Region and 78 % in the Sierra de Atoyac. Species richness is higher in Loxicha for nine of the 11 subfamilies, with the greatest difference being in Nymphalinae (11 spp.); only Satyrinae has a higher species richness in the Sierra de Atoyac, with nine subspecies.

Considering both transects, 13 species endemic to Mexico were recorded: *Pteronymia rufocincta*, *Cyllopsis caballeroi* Beutelspacher, 1982, *C. clinas*, *C. diazi*, *C. jacquelineae*, *C. nayarit*, *C. perplexa* L. Miller, 1974, *Paramacera copiosa* L. Miller, 1972, *Taygetis uncinata*, *Catonephele cortesi*, *Chlosyne cynisca*, *Chlosyne eumeda* (Godman & Salvin, 1894), and *Phyciodes pallescens*. At the subspecies level there are 66 endemics, constituting 31 % of the Nymphalidae recorded in these areas. At a national scale, Loxicha and the Sierra de Atoyac contain 43 % of the species or subspecies of Nymphalidae endemic to Mexico. Of these endemics, 56 are present in the Loxicha Region and 55 in the Sierra de Atoyac, with 64 % of the endemics shared

TABLE 6
Species richness and endemism of Nymphalidae subfamilies for two regions of the Pacific slope of the Sierra Madre del Sur, Mexico (modified from Luis-Martínez et al., 2021)

Subfamily	Loxicha Region, Oaxaca			Sierra de Atoyac, Guerrero		
	Genera	Species	Subspecies	Genera	Species	Subspecies
Libytheinae	1	1/0	1/0	1	1/0	1/0
Danainae	3	6/0	6/0	3	5/0	5/0
Ithomiinae	9	2/1	15/6	7	2/1	12/8
Charaxinae	10	4/1	21/8	9	3/0	16/6
Morphinae	3	3/0	8/1	3	2/0	7/1
Satyrinae	12	16/5	26/12	12	20/8	35/16
Apaturinae	2	3/0	3/0	1	1/0	1/0
Biblidinae	16	5/1	31/15	14	6/1	29/14
Limnithidinae	1	3/0	16/3	1	2/0	13/2
Nymphalinae	16	12/2	47/8	15	12/1	36/5
Heliconiinae	9	2/0	15/3	7	19/0	12/3
TOTAL						
Richness/Endemism	82	57/10	189/56	73	73/11	167/55

between the two (Llorente-Bousquets, Trujano-Ortega et al., 2006; Luis-Martínez et al., 2003; Luis-Martínez et al., 2016; Luis-Martínez et al., 2021). As with the endemics of the Loxicha Region, endemics of the Sierra de Atoyac were grouped into four categories: 1, endemic to the Sierra de Atoyac (3 spp: *Drucina championi* ssp., *Eunica malvina almae* Vargas, Llorente & Luis, 1996, and *Eueides isabella nigricornis* R. G. Maza, 1982); 2, endemic to the Sierra Madre del Sur (17 spp.); 3, endemic to the Pacific slope (23 spp.); and 4, endemic to Mexico (12 spp.). These numbers are very similar to those of the Loxicha Region, with differences of at most three species. In both regions, Nymphalinae has the highest species richness and Biblidinae has most of the endemic taxa. Libytheinae, Danainae, and Apaturinae have the lowest richness, a common pattern in America (Lamas, 2004; Pelham, 2008). Additionally, in Loxicha these three subfamilies have no endemic taxa.

Phenology, elevational patterns, and exclusivity of species in the transect

Phenology: Temporal distribution of the species richness and abundance of Nymphalidae is influenced by season (Fig. 5). Richness and abundance both reach their maximum

values in October (the end of the rainy season), after which both parameters suddenly drop to their lowpoints in December. The increase in species richness is more or less steady, with just a few more species in the rainy season compared with the dry season; in contrast, abundance has a steep increase from the dry to the rainy season. April shows a slight increase in species richness but a decrease in abundance, suggesting an increase of rare species during this month, compared with other months.

Elevational diversity patterns: Species richness and diversity (e^H) of Nymphalidae decrease abruptly at elevations above 1 800 m, with just 33 % of the total species assemblage compared with 79 % at low elevations and 82 % at mid elevations (Fig. 6). Although observed species richness is higher at the 750-1 800 m level (151 spp.) than at the 0-750 m level (146 spp.), diversity estimates show no significant difference between these two levels. However, diversity is higher at low elevations, which may be because of a higher dominance of *Hermeuptychia hermes* and *Cissia similis* at mid elevations which reduces overall diversity.

Elevational abundance patterns: Abundance is highest at low elevations with 58 %

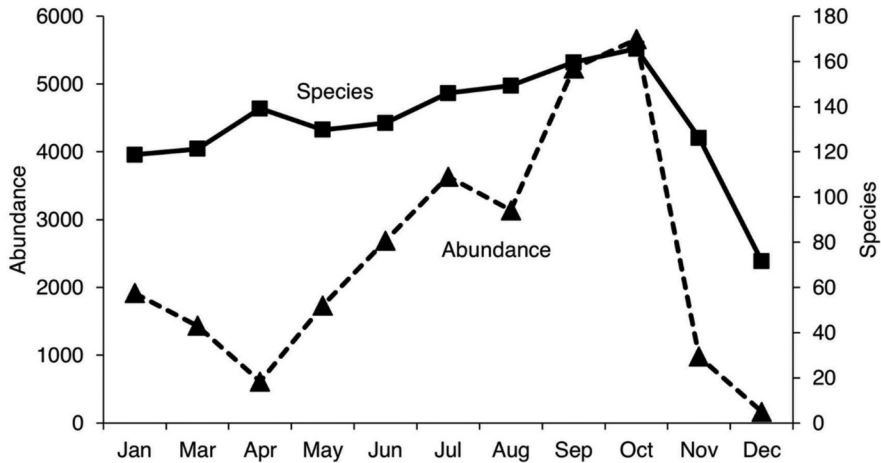


Fig. 5. Phenology of Nymphalidae abundance and species richness in the Loxicha Region, Oaxaca, Mexico based on seven years of sampling data. February was not sampled during this study.

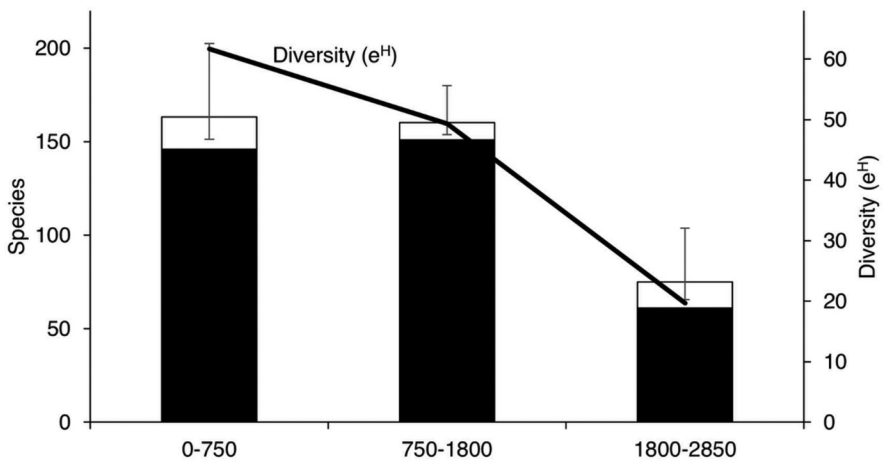


Fig. 6. Observed (black) and estimated (white) Nymphalidae species richness and diversity (exponential of Shannon-Wiener index) across three elevational levels in the Loxicha Region, Oaxaca, Mexico.

of the total (15 861 records), decreases at mid elevations with 39 % (10 520 records), and is just 3 % (796 records) at high elevations. Each level has dominant or characteristic species, but the overall proportions of those dominant species are highest in the mid and high elevations. The most abundant species in each level belong to the Satyrinae subfamily. At low elevations, *Cissia similis* (607 records) and *Hermeuptychia hermes* (869 records) account for 5.1 and 5.4 % of the specimens, respectively;

at mid elevations, *H. hermes* is also the most abundant species with 1 273 records (12 %); at high elevations, 22 % of the specimens (177 records) are *Paramacera xicaque rubrosuffusa* (Satyrinae) and 15 % (122 records) are *Anthanassa a. ardys* (Nymphalinae).

A total of 35 species were collected from all three elevational levels (Appendix 1), but these species showed the following three distinct distribution patterns. Pattern A: *Dione moneta poeyii*, *Paramacera xicaque*

rubrosuffusa, and *Vanessa virginiensis* mainly occur at high elevations with just one to three records from low elevations. Pattern B: 19 spp. (v. gr. *Anartia f. fatima*, *Cissia similis*, *Smyrna blomfieldia datis*) with the opposite pattern, being abundant at low elevations and decreasing at mid elevations, with just a few specimens at high elevations. Pattern C: 13 species (v. gr. *Anthanassa a. ardys*, *Chlosyne h. hippodrome*, *Hermeuptychia hermes*) that are abundant at mid elevations with fewer records at both low and high elevations. Most of the taxa (104, 56 %) are present in two elevational levels, mainly in the low and mid elevations with just 10 species in both the mid and high elevations (v. gr. *Anthanassa atronia*, *A. otanes oaxaca*) (see Appendix 1). Remarkably, eight species *Adelpha f. fessonia*, *Anartia jatrophae luteipicta*, *Chlosyne m. marina*, *Danaus eresimus montezuma*, *Doxocopa l. laure*, *Phyciodes*

g. graphica, *P. mylitta thebais*, and *Pteronymia artena praedicta* were collected only in the low and high elevations, implying that they are also present in the mid elevations. Finally, 45 species are restricted to a single elevational level (Table 7). Of these, 17 species are exclusive to 0-750 m elevation, with the most abundant being *Bolboneura sylphis beatrix*, *Hamadryas g. glauconome*, and *Hypna clytemnestra mexicana*; 20 species are exclusive to mid elevations where *Anthanassa argentea* and *Cyllopsis diazi* comprised most of the records; and eight species are distributed only in the highest elevations where *Adelpha bredowii*, *Nymphalis a. antiopa*, and *Phyciodes t. tharos* were the most abundant.

Diversity patterns by vegetation type:

The vegetation type with the most observed Nymphalidae species is the CF (147 species);

TABLE 7
Exclusive species of each elevational level (m)

Taxa	0-750	750-1 800	1 800-2 850
Danainae			
<i>Lycorea ilione albescens</i>		9	
<i>Danaus p. plexippus</i>		1	
Ithomiinae			
<i>Episcada salvinia portilla</i>		22	
<i>Pteronymia c. cotyto</i>	9		
Charaxinae			
<i>Hypna clytemnestra mexicana</i>	159		
<i>Memphis p. perenna</i>		33	
<i>Memphis wellingi</i>	1		
<i>Archaeoprepona phaedra</i> ssp.	2		
<i>Prepona brooksiana ibarra</i>		2	
Morphinae			
<i>Caligo uranus</i>		1	
<i>Opsiphanes quiteria quirinus</i>	1		
<i>Opsiphanes t. tamarindi</i>	6		
Satyrinae			
<i>Oxeoschistus hilara</i> ssp.		5	
<i>Oxeoschistus tauropolis</i> ssp.		2	
<i>Cyllopsis clinas</i>		1	
<i>Cyllopsis diazi</i>		124	
<i>Cyllopsis h. hedemanni</i>		87	
<i>Cyllopsis nayarit</i>		5	
<i>Megisto rubricata pseudocleophes</i>			2

however, according to estimations the species richness in the TSDF, the CF, and the OPCF are not significantly different (Fig. 7). Interestingly, the OPCF has just 9 % of the abundance of both the TSDF and the CF. Below these three types, the TDF supports 47 % of the species in the region with 90 estimated taxa. The species richness in the OPF is much lower than the other vegetation types, with no rare species, so the total richness estimate is also low (six spp.). Estimations indicate that all vegetation types were adequately sampled. The difference between estimated and observed species is higher in the OPCF, suggesting either lower sampling effort or greater numbers of rare species in this vegetation type.

Abundance patterns by vegetation type:

The TSDF and the CF present the highest and most similar abundance of Nymphalidae, with 11 703 (43 %) and 10 903 (40 %) records, respectively. Abundance in other vegetation types is distinctly different, with just 3 496 records (13 %) in the TDF and 1 028 (4 %) in the OPCF. This family is even scarcer in the OPF, with less than 1 % of the overall abundance (47 records) in the Loxicha Region.

Dominant species in most vegetation types mainly belong to the Satyrinae. Dominance

is low in most vegetation types, except in the OPF where *Nymphalis a. antiopa* (24 specimens) and *Paramacera xicaque rubrosuffusa* (17 specimens) comprise 87 % of the records. *Paramacera xicaque rubrosuffusa* is also the most abundant species in the OPCF with 15 % of the recorded specimens, followed closely by *Anthanassa a. ardis* with 14 % of the abundance in this vegetation. The most abundant species in the CF and the TSDF is also a member of the Satyrinae: *Hermeuptychia hermes*, with 12 and 7 % of the records, respectively. The TDF is the only vegetation type where Satyrinae are not dominant, but is also the vegetation where dominance is lowest, with *Microtia e. elva* and *Hamadryas g. glauconome* comprising only 9 % and 8 % of the records, respectively.

Most species (80 %) were collected in multiple vegetation types, although some have just one or two records in the vegetation at the highest or lowest elevations. The only species found in all five vegetation types was *Smyrna blomfieldia datis*, with one record in the OPF. Thirty-seven species are exclusive to a vegetation type (Table 8), half of which are rare species with one or two records. Fig. 8, Fig. 9, Fig. 10, Fig. 11, and Fig. 12 show the elevational distribution by vegetation type of these

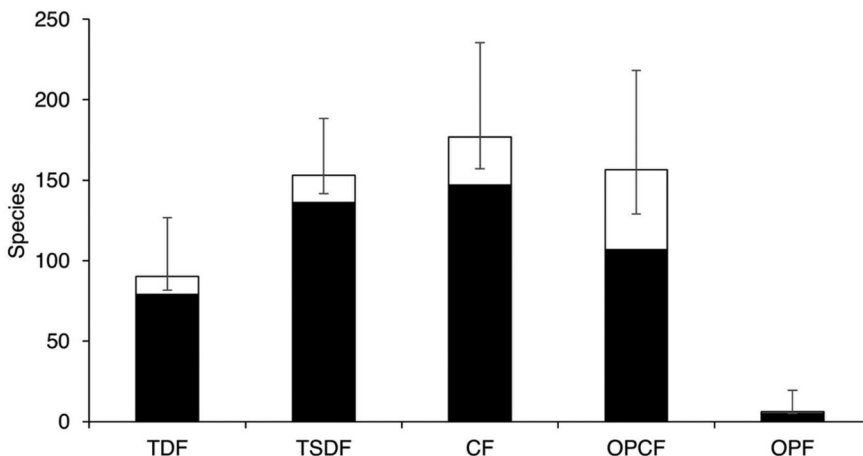


Fig. 7. Observed (black) and estimated (white) species richness by vegetation types of Nymphalidae in the Loxicha Region, Oaxaca, Mexico. TDF = tropical deciduous forest, TSDF = tropical sub-deciduous forest, CF = cloud forest (low- and mid-elevation), OPCF = oak-pine and high-elevation cloud forest, OPF = oak-pine forest.

TABLE 8
Nymphalidae species exclusive to each vegetation type in the Loxicha Region, Oaxaca, Mexico

Taxa	TDF	TSDF	CF	OPCF	OPF
Danainae					
<i>Lycorea ilione albescens</i>			9		
<i>Danaus p. plexippus</i>			1		
Ithomiinae					
<i>Dircenna k. klugii</i>			134		
<i>Episcada salvinia portilla</i>			22		
<i>Pteronymia c. cotytto</i>		9			
Charaxinae					
<i>Memphis perenna perenna</i>			33		
<i>Memphis wellingi</i>		1			
<i>Archaeoprepona phaedra</i> ssp.		2			
<i>Prepona brooksiana ibarra</i>			2		
Morphinae					
<i>Caligo uranus</i>			1		
<i>Opsiphanes quiteria quirinus</i>		1			
<i>Opsiphanes t. tamarindi</i>		6			
Satyrinae					
<i>Oxeoschistus tauropolis</i> ssp.			2		
<i>Cyllopsis clinas</i>				1	
<i>Cyllopsis h. hedemanni</i>			87		
<i>Megisto rubricata pseudocleophes</i>				2	
<i>Taygetis virgilia</i>		1			
<i>Gyrocheilus p. patrobas</i>				4	
Apaturinae					
<i>Asterocampa idyja argus</i>			18		
Biblidinae					
<i>Marpesia zerynthia dentigera</i>			18		
<i>Myscelia c. cyananthe</i>	11				
<i>Bolboneura sylphis beatrix</i>	211				
<i>Pyrrhogyra edocla paradisea</i>			1		
Limnitiidae					
<i>Adelpha barnesia leucas</i>		3			
<i>Adelpha bredowii</i>				15	
<i>Adelpha diocles</i> ssp.				1	
Nymphalinae					
<i>Pycina zamba zelys</i>			4		
<i>Smyrna karwinskii</i>			2		
<i>Hypanartia trimaculata autumnna</i>			42		
<i>Nymphalis a. antiopa</i>					24
<i>Vanessa cardui</i>			1		
<i>Junonia genoveva</i> ssp. nov.		5			
<i>Chlosyne cyneas cynisca</i>				1	
<i>Phyciodes pallescens</i>			1		
<i>Phyciodes p. phaon</i>				24	
<i>Phyciodes t. tharos</i>				19	
<i>Anthanassa texana texana</i>				8	
Heliconiinae					
<i>Dryadula phaetusa</i>		4			
<i>Heliconius ismenius telchinia</i>			1		

Vegetation types: TDF = tropical deciduous forest, TSDF = tropical sub-deciduous forest, CF = cloud forest (low- and mid-elevation), OPCF = oak-pine and high-elevation cloud forest, OPF = oak-pine forest. For each species listed, the habitat preference value is 90-100 %.

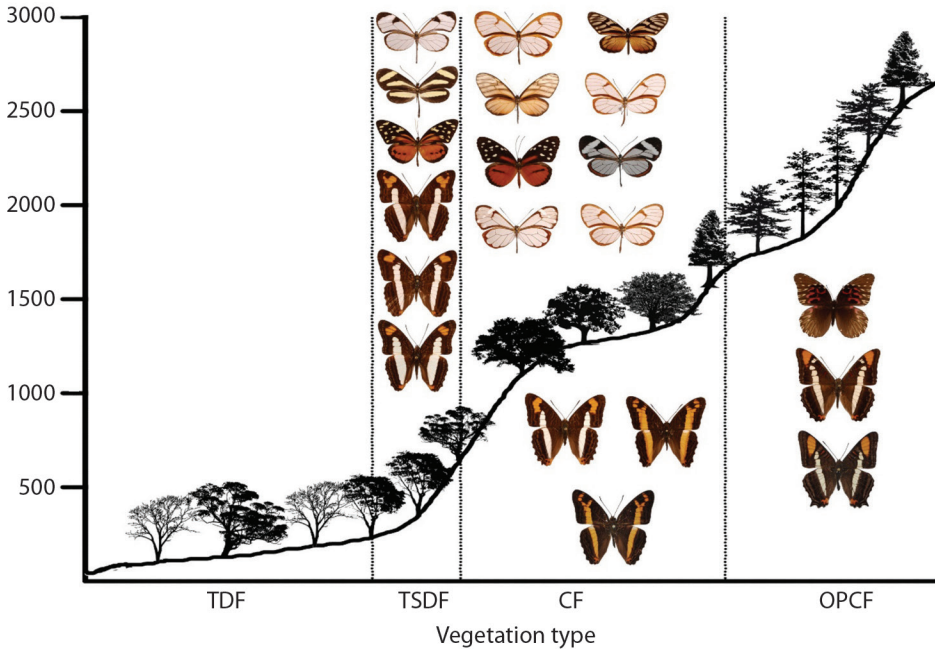


Fig. 8. Elevational profiles and characteristic species of Limenitidinae, Danainae, and Ithomiinae for each vegetation type in the Loxicha Region, Oaxaca, Mexico. TDF = tropical deciduous forest, TSDF = tropical sub-deciduous forest, CF = cloud forest (low- and mid-elevation), OPCF = oak-pine and high-elevation cloud forest.

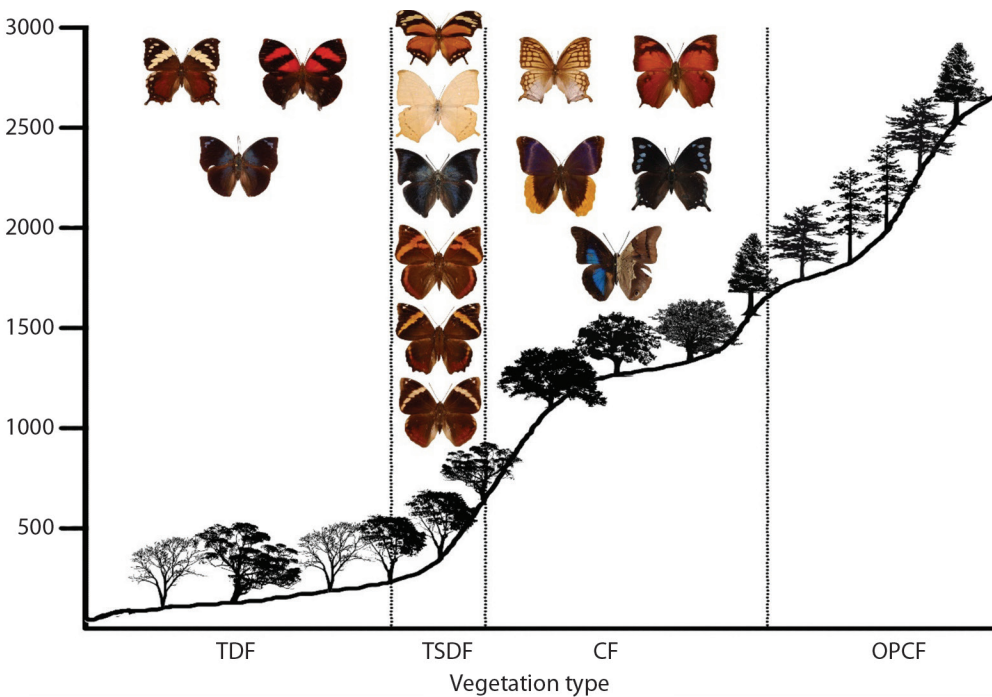


Fig. 9. Elevational profiles and characteristic species of Charaxinae and Morphinae for each vegetation type in the Loxicha Region, Oaxaca, Mexico. TDF = tropical deciduous forest, TSDF = tropical sub-deciduous forest, CF = cloud forest (low- and mid-elevation), OPCF = oak-pine and high-elevation cloud forest.

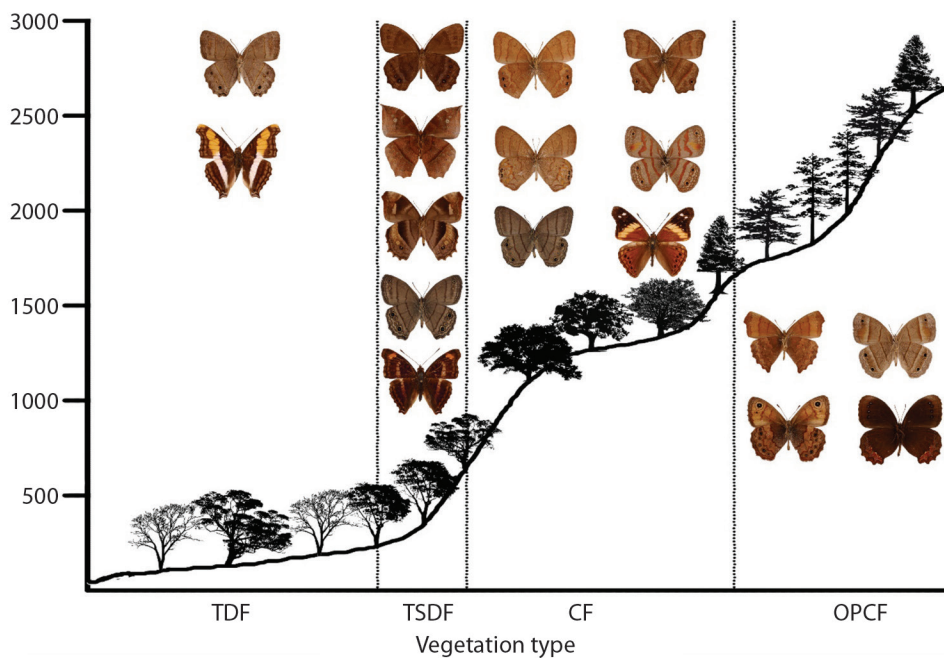


Fig. 10. Elevational profiles and characteristic species of Satyriinae and Apaturinae for each vegetation type in the Loxicha Region, Oaxaca, Mexico. TDF = tropical deciduous forest, TSDF = tropical sub-deciduous forest, CF = cloud forest (low- and mid-elevation), OPCF = oak-pine and high-elevation cloud forest.

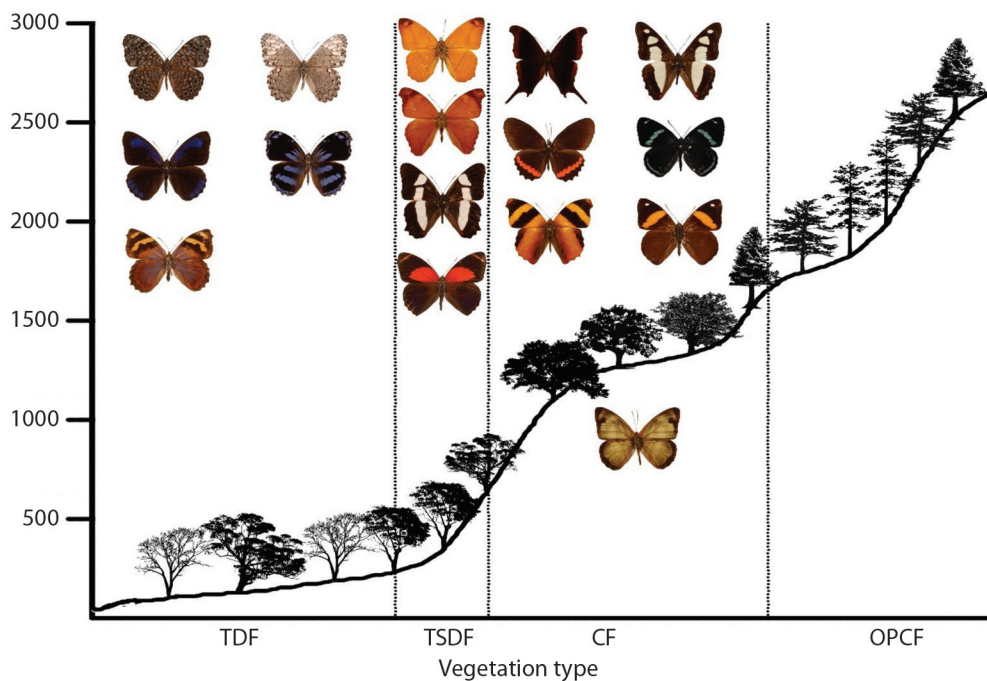


Fig. 11. Elevational profiles and characteristic species of Biblidinae for each vegetation type in the Loxicha Region, Oaxaca, Mexico. TDF = tropical deciduous forest, TSDF = tropical sub-deciduous forest, CF = cloud forest (low- and mid-elevation), OPCF = oak-pine and high-elevation cloud forest.

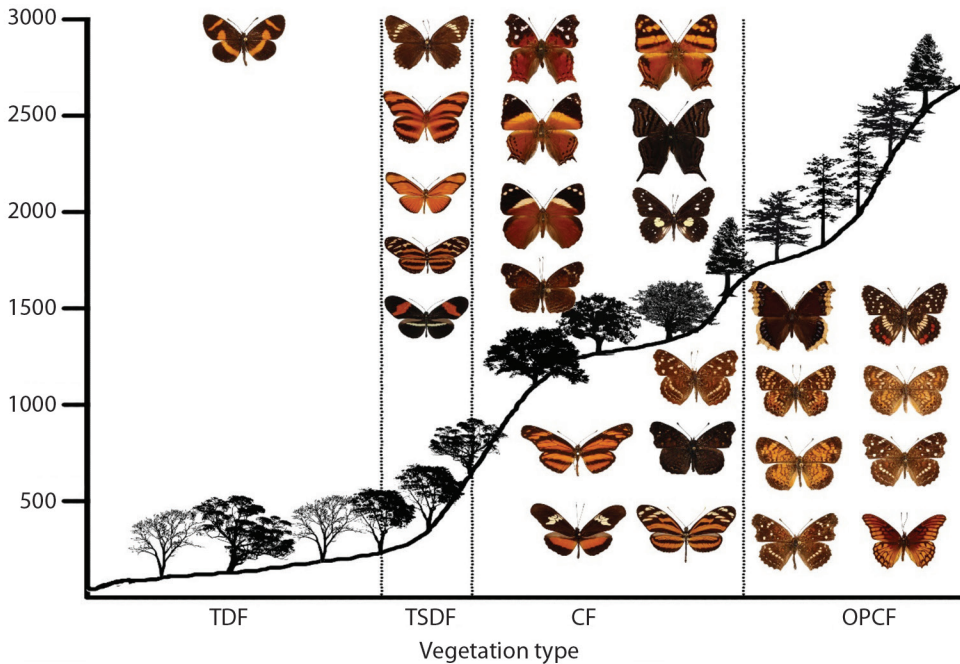


Fig. 12. Elevational profiles and characteristic species of Nymphalinae and Heliconiinae for each vegetation type in the Loxicha Region, Oaxaca, Mexico. TDF = tropical deciduous forest, TSDF = tropical sub-deciduous forest, CF = cloud forest (low- and mid-elevation), OPCF = oak-pine and high-elevation cloud forest.

37 species (Table 8); all species with 95 % or more of their records in a single vegetation type were also included.

Efficiency and efficacy of Van Someren-Rydon traps: During our fieldwork, 94 species of seven subfamilies of Nymphalidae were collected with Van Someren-Rydon traps (Appendix 2). These taxa represent 50 % of the species recorded and 41 % of the specimens. Some species were captured with both traps and aerial nets, but abundance was higher in traps (11 543; 73 %). Only 18 species (173 specimens) were collected exclusively in traps. Biblidinae was the subfamily with most species recorded in traps with 24 spp., followed by Satyrinae and Charaxinae with 23 and 21 species, respectively; these three subfamilies account for 74 % of the specimens collected in traps (Fig. 13). In terms of abundance, Satyrinae was the subfamily with the most records (40 % of the specimens), followed by Nymphalinae (21 %). Comparing the relative abundance and species

richness solely of trapped specimens for each subfamily, two patterns can be recognized: A. Satyrinae and Nymphalinae had greater abundance than richness; B. Charaxinae, Biblidinae, and Morphinae presented a relatively higher richness than specimens, but still lower abundance than subfamilies in pattern A (Fig. 13).

The efficiency and efficacy of the traps at each elevational level (0-750 m, 750-1 800 m, and 1 800-2 850 m) were evaluated based on the species and specimens captured relative to the totals. The percentage of specimens collected with traps decreased at higher elevations (Appendix 2; Fig. 14), and this was more evident for Apaturinae and Nymphalinae. However, traps reduce to almost 40 % of their efficiency at the higher elevations. On the other hand, efficacy measured as the % of recorded species of each subfamily, remained constant along the elevational gradient. Traps captured 100 % of the species of Charaxinae and Morphinae at all levels (Fig. 15). Efficacy was lower at higher elevations for Apaturinae

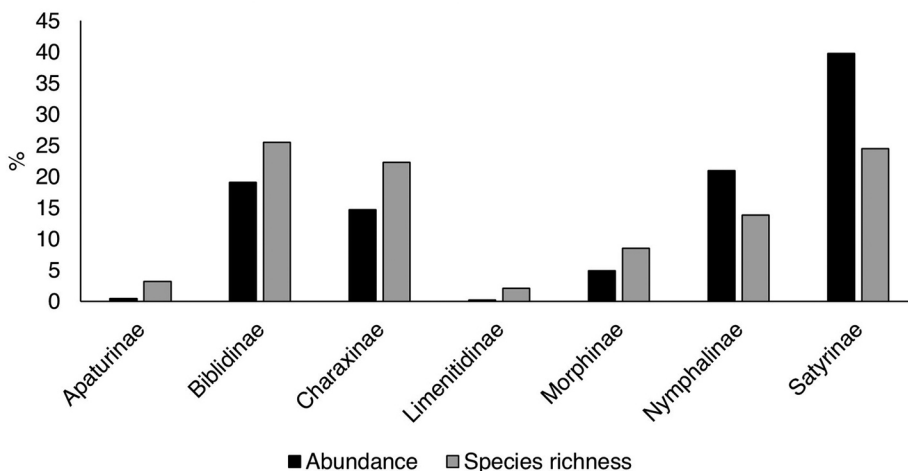


Fig. 13. Relative abundance (black) and species richness (grey) of seven subfamilies of Nymphalidae collected in Van Someren-Rydon traps in the Loxicha Region, Oaxaca, Mexico.

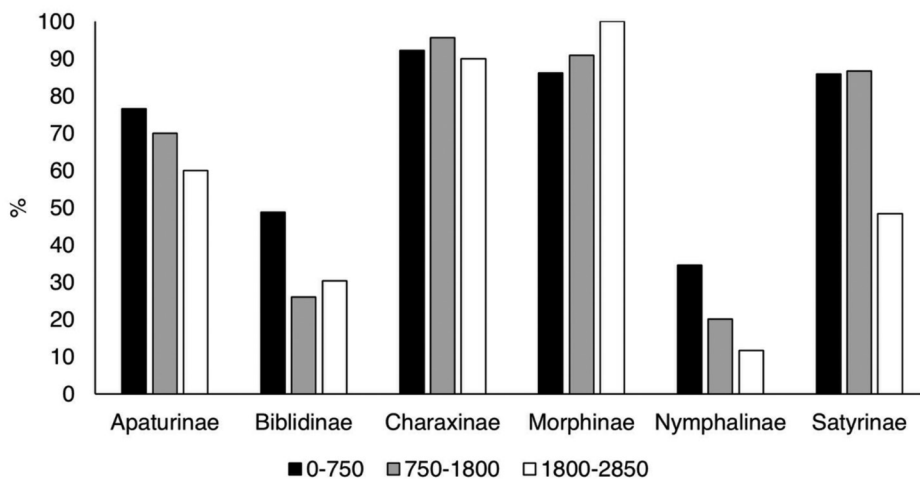


Fig. 14. Percentage of specimens of each Nymphalidae subfamily captured in Van Someren-Rydon traps by elevational level, relative to all specimens captured in that level, in the Loxicha Region, Oaxaca, Mexico.

and Biblidinae, and slightly lower for Satyrinae. Finally, Van Someren-Rydon traps are less effective in capturing species of Nymphalinae, since percentages are lower than 40 % in all elevational levels, although this efficacy stays constant along the gradient. Of note, 16 species of Limenitidinae were recorded in the Loxicha Region but only two were collected in traps, with an efficiency of 19 specimens out of the 298 collected of those species: *Adelpha basioides* (5/227) and *Adelpha i. iphicus* (14/71).

Natural history remarks on selected taxa of the Loxicha Region: During our fieldwork, some nymphalid species were particularly abundant or showed special behaviors. We summarize that natural history data for each relevant species below.

Hypna clytemnestra mexicana. Found in the understory of the TDF, mainly in humid and dark microhabitats. Easily collected with traps in two sites: Parque Nacional Huatulco, and Río Cacaluta within Parque Nacional

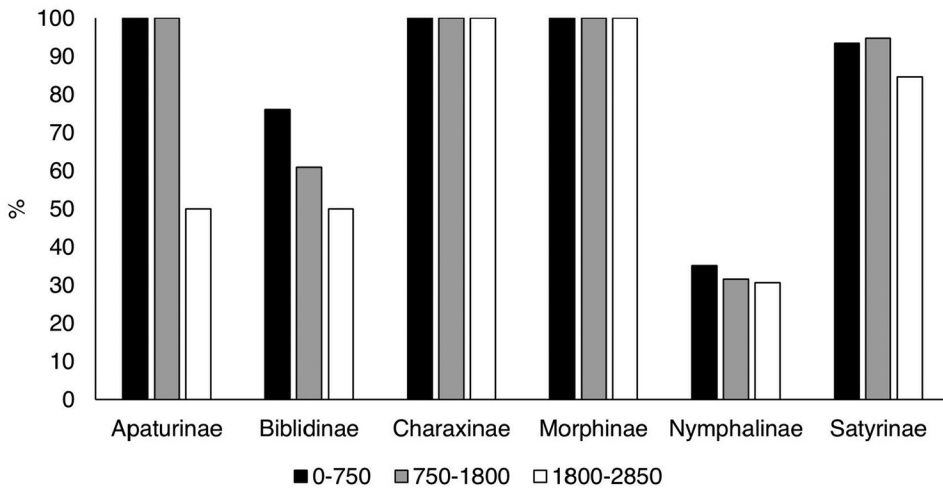


Fig. 15. Percentage of species of each Nymphalidae subfamily recorded in Van Someren-Rydon traps by elevational level, relative to all species recorded in that level, in the Loxicha Region, Oaxaca, Mexico.

Huatulco. More abundant in the rainy season (July–November).

Consul excellens genini. Recorded and collected in OPF, mostly on humid cliffs where elements of CF are present. Attracted to fermented fruit. Recorded mainly in San José del Pacífico.

Chlosyne gaudialis wellingi. Flight faster than other species of this genus, and flies unusually high in search of flowers three to four meters above ground level, in sunny open places. Unusually low abundance relative to other species of *Chlosyne*, which tend to be very abundant.

Pycina zamba zelys. In Mexico, this taxon has been recorded at just a few sites and with low abundance. Only four specimens were collected, the first records for the Pacific slope. All specimens were collected on a wet wall along a road where a stream formed puddles. Many other species were also collected in this microhabitat: *Pycina zamba zelys* specimens were licking the wet wall five or six meters above ground level, as were specimens of *Hypanartia dione disjuncta*, *H. godmanii*, *H. lethe*, *H. trimaculata autumnna*, *Historis a. acheronta*, *Epiphile adrasta escalantei*, *Diaethria anna mixteca*, *D. astala asteroide*, *Marpesia chiron marius*, *Siproeta e. epaphus*, and *S. stelenes*

biplagiata, among other common taxa that exploit this special microhabitat.

Altinote stratonice oaxaca. This species is associated with low elevation CF from 1 000-2 500 m, making large elevational migrations at the end of the summer. Present in open spaces, with a slow flight, visiting bushes with white composite flowers.

Archaeoprepona demophoon mexicana. An elusive species, mainly occurring in the forest canopy but sometimes in the understory associated with open spaces like roads or riverbanks. Along rivers it can be found feeding on minerals dissolved in wet sand and shows similar behavior along roads with some humidity on the ground. Feeds mostly on decomposing fruit and exudates of certain trees. Rapid fliers that quickly flee when disturbed, often into the forest canopy. Males are territorial and chase away other males.

Bolboneura sylphis beatrix. Mostly alongside roads or streams. If near rivers, it is likely to be found on moist sand feeding on dissolved minerals; if along roads, likely feeding on small flowers. Flight is slow and halting, generally about 50 cm above ground level. Groups of more than 10 specimens can be found alongside streams. When resting usually perches on leaves. Recorded only in TDF.

Heliconius erato cruentus. Found mainly in open spaces and along roads and small paths. Flight slow and halting, always less than one meter above ground level. Often feeds at roadside flowers, but sometimes also attracted to decomposing fruit. Gregarious, forming groups to overnight in protected places.

Microtia elva elva. Frequently found along open roads with some shade. Flight low and halting, at most 50 cm above ground level. Feeds mostly on small composite flowers along roadsides. When disturbed, usually flies just a few meters away.

DISCUSSION

More than 60 % of Mexico's surface is covered by mountains, but faunal surveys of Lepidoptera across elevational gradients are scarce, except for those done by members of the MZFC (Arellano-Covarrubias et al., 2018; Luis-Martínez & Llorente-Bousquets, 1990; Luis-Martínez et al., 1991; Luis-Martínez et al., 2020; Vargas-Fernández et al., 1994; Vargas-Fernández et al., 1999). This type of analysis provides important insight into various biological processes. Such insights include the recognition of disjunct distributions across mountain archipelagos due to speciation and endemism processes, and the ability to detect changes of species distribution due to climate change, especially in stenotopic species vulnerable to extinction.

Of all elevational gradients in Mexico, the Loxicha Region is the most systematically sampled area for Papilionoidea *sensu lato*, particularly for the Nymphalidae (Table 2). Many experienced collectors have sampled this region for decades (Álvarez-García et al., 2016; Arellano-Covarrubias et al., 2018; Luis-Martínez et al., 2000; Luis-Martínez et al., 2003; Luis-Martínez et al., 2020; Michán et al., 2004; Pozo et al., 2008). Estimates of Nymphalidae species richness in the Loxicha Region show that it has the highest percentage of inventory completeness for any region in Mexico (Vargas-Fernández et al., 1994; Vargas-Fernández et al., 1999). Furthermore, it has the highest

species richness of any region on the Pacific slope (Table 1 and Table 3) and the second richest in the country, behind only the Sierra de Juárez (Table 3).

Sampling in the Loxicha Region began in 1960, based on historical specimens that we checked and on publications that described a dozen taxa from those specimens. However, even with Loxicha's great species richness and endemism, the present work is the first systematic study that provides a detailed regional description of the diversity and distributional patterns of Nymphalidae, mirroring similar works published previously for Riodinidae (Arellano-Covarrubias et al., 2018), Papilionidae, and Pieridae (Luis-Martínez et al., 2020).

Species richness of Nymphalidae by site:

Comparison of the diversity on both the Pacific and Atlantic slopes confirms that the latter has higher species richness (*v. gr.* Andresen, 2008; Ceballos, 1995; Flores-Contreras & Luna-Reyes, 2017; González-Ramírez et al., 2017; Luis-Martínez et al. 2003; Salinas-Gutiérrez et al. 2004). Of sites with 100 or more species of Nymphalidae, only 20 % are on the Pacific slope. Moreover, among these Pacific slope "sites" are Acahuizotla, Guerrero and Candelaria Loxicha, Oaxaca, which are larger areas that historically encompassed a group of sites with distinct elevations and vegetation types but labeled under a single site name. These areas were used as reference points for collectors for three decades (1950-1980) of the 20th century. Therefore, actual species richness of these reference sites is lower than cited, further reducing to 15 % the Pacific slope sites with over 100 species. In the last 40 years, more than 10 faunistic studies on Papilionoidea were done on the Pacific slope by members of the MZFC (Llorente-Bousquets et al., 1996; Llorente-Bousquets et al., 2004; Luis-Martínez & Llorente-Bousquets, 1993; Luis-Martínez, 1997; Luis-Martínez, 1999; Luis-Martínez, 2001; Vargas-Fernández et al., 1994; Vargas-Fernández et al., 1996; Vargas-Fernández et al., 1999; Warren & Llorente-Bousquets, 1999; Warren et al., 1996; Warren et al., 1998), but only



six sites exceed 100 species. Of these, only four are in Sierra Madre del Sur (two in the Sierra de Atoyac and two in the Loxicha Region), which is the mountain range with the greatest diversity on the Pacific slope despite lacking tropical evergreen forest vegetation. San Jerónimo, Tacaná, Chiapas is the only Mexican site with more than 100 species that lacks a systematic faunistic study; data from this site were obtained from national and international specimen collections (MARIPOSA database).

Species composition similarity across regions: The similarity analysis reflects how Lepidoptera are associated with mountain archipelagos, as described by Llorente-Bousquets (1984) and Halffter (1987). In Mexico, the states of Guerrero and Oaxaca support the most faunistically similar mountain habitat “islands” (Llorente-Bousquets, 1984). These two isolated regions each have exclusive or endemic species, yet they share at least 50 % of their species, forming geographic and genealogic relations between them. Other areas are disjunct, each with its own biogeographic history based on patterns of biotic provinces defined by Morrone et al. (2002) and Morrone (2005). The distinction between the diurnal Lepidoptera on the Atlantic and Pacific slopes had been further revealed using panbiogeographic methods (Llorente-Bousquets, Trujano-Ortega et al., 2006; Luis-Martínez et al., 2006; Oñate-Ocaña et al., 2006; Vargas-Fernández et al., 2006).

The faunistic similarity of Nymphalidae shows a division in the Pacific slope and SMS in two parts, a Northwest section (Nayarit, Jalisco, Michoacán) and a Southeast section (Guerrero, Oaxaca), with the latter including the Loxicha Region. This division of the SMS in two subprovinces was proposed by Santiago-Alvarado et al. (2016) based on data from 32 species endemic to the SMS. No distribution was consistent with the SMS as a whole. Later, Morrone (2017) named and described three subprovinces in the SMS: the West subprovince with the Jalisciense and Jalisciense-Manantlán districts, the Central subprovince with the Michoacán district, and the Oriental

subprovince comprising the Guerrerense and Tierras Altas de Oaxaca districts. Although Nymphalidae data do not reflect the separation of these three subprovinces, when analyzing the data at a site-level scale, Nymphalidae of the Southwest SMS are shown to be more similar to the Balsas province fauna than to the fauna of the Northeast SMS.

Species composition similarity of sites:

Diurnal Lepidoptera associated with the CF at all elevational levels are an excellent model for the study of complex dispersion, vicariance, and speciation patterns, due to the disjunct distribution and isolation of this vegetation community (Rzedowski, 1978). Generally, CF fauna distribution patterns are consistent with the geographic barriers that delimit each of the mountain ranges of Mexico. An integrated phylogeographic analysis that included birds, mammals, and plants concluded that the evolution of the biota of the CF in Mesoamerica resulted from a complex combination of distinct histories of range expansion, isolation, and biotic differentiation (Ornelas et al., 2013). A similar process seems to have occurred with the Papilionoidea *sensu lato* and particularly with Nymphalidae, based on distribution patterns resolved by multiple studies (Llorente-Bousquets, 1984; Llorente-Bousquets & Escalante, 1994; Llorente-Bousquets & Luis-Martínez, 1998).

Nymphalidae assemblages are closely related to vegetation type and elevation but are also influenced by geographic history and distance. Sites are grouped in six sets according to their similarity (Fig. 4). The first one corresponds to the Atlantic slope, while the other subgroups represent the diverse faunas of the Pacific slope distributed in distinct physiographic units and biotic provinces. These results concur with the data published in faunistic studies and generic reviews, describing the distribution of fauna in three elevational levels of the CF based on the proposal of Llorente-Bousquets (1984). Sites on the Pacific slopes (Fig. 4, subgroups 3 to 6) are grouped similarly to the elevational gradients (Fig. 3).

The Sierra Madre del Sur (Guerrero and Oaxaca portion) (Fig. 4, subgroup 5) is more similar to the Cuenca del Balsas (Fig. 4, subgroup 6), than to the sites in the Costa del Pacífico, Northern Sierra Madre del Sur, and Western Eje Neovolcánico provinces (Fig. 4, subgroup 4). Notably, the sites above 1 800 m in the Sierra de Atoyac de Álvarez (Fig. 4, subgroup 3, La Golondrina, El Iris, and Puerto del Gallo) are separated from subgroups 4 and 6, and from the sites above 1 800 m in the Loxicha Region (Puente Arroyo “El Guajolote” and San José del Pacífico, 1 km S), even though these two regions are geographically close. Puente Arroyo “El Guajolote” is part of the subgroup of low elevation Guerrero-Oaxaca sites below 900 m, while San José del Pacífico is separated from other sites of the Sierra Madre del Sur, placed near the sites of the Cuenca del Balsas, as the most distinct site of this group. These similarity patterns of the high-elevation sites of Atoyac and Loxicha suggest that these are isolated communities, with a distinctive fauna, different from nearby low-elevation sites as well as from other high-elevation sites.

In general, the faunistic composition of Nymphalidae agrees with the biogeographic history of Mexico and its proposed provinces (Morrone, 2005; Morrone et al., 2002). First, there is a clear distinction between the faunas of the Atlantic and the Pacific. At a finer scale, a division of the Sierra Madre del Sur into a Northern and Southern portion was recognized. Within the Southern portion of SMS, sites are grouped by elevation and vegetation type, with high elevation sites separated from the rest. Therefore, distribution patterns of Nymphalidae in Mexico are produced at large scales by historical elements and at smaller scales by ecological elements.

Phenology: In the Loxicha Region, the temporal distribution of Nymphalidae species richness and abundance is correlated directly with the summer-associated rainy season (Fig. 5), which is common in most of the regions in Mexico (Álvarez-García et al., 2016; 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 the Loxicha Region, nymphalid species richness and abundance are higher from July to October. This pattern is echoed in the Sierra de Juárez (Oaxaca), the Sierra de Atoyac (Guerrero), the Sierra de Manantlán (Jalisco-Colima), and the Sierra de San Juan (Nayarit), although the month with the highest species richness differs among the regions. In Loxicha, October had the highest richness. In comparison, September is the month with most species recorded in the Sierras de Juárez, Manantlán, and San Juan, while in the Sierra de Atoyac most species were recorded in July. As rainfall decreases so too does species richness, with April and May being both the driest months and having among the lowest species richness in all regions.

Diversity and abundance by vegetation type: Stenoic species of Nymphalidae have a wider distribution across different vegetation types (Table 8) than the stenoic species of Papilionidae, Pieridae, and Riodinidae, which mostly occur in the TSDF and CF (Arellano-Covarrubias et al., 2018; Luis-Martínez et al., 2020). The elevational profiles (Fig. 8, Fig. 9, Fig. 10, Fig. 11, and Fig. 12) show that the stenoic species of both Satyrinae and Nymphalinae are characteristic of each vegetation type. In contrast, Charaxinae and Biblidinae lack stenoic species in the OPCF but are represented in the lower-elevation vegetation types. The TDF is the vegetation type with the fewest stenoic species, with only 11 characteristic species of four subfamilies: Charaxinae, 3 spp.; Satyrinae, 1 sp.; Apaturinae, 1 sp.; Biblidinae, 5 spp.; and Nymphalinae, 1 sp. Comparing with other families, Riodinidae has a single characteristic species of the TDF (Arellano-Covarrubias et al., 2018). In Papilionidae only the TSDF has a significant number of stenoic species with five of the 10 species recorded, while the number of stenoic species of Pieridae does not differ among vegetation types (Luis-Martínez et al., 2020).



The observed species richness and abundance of Nymphalidae show that the OPCF is the most diverse vegetation type. Although the estimated species richness for the OPCF is not significantly different from that of the CF and the TSDF, the OPCF abundance is lower, with nine exclusive species. Despite being originally considered a combination of two vegetation types (Luis-Martínez et al., 2020), these nymphalid results support the recognition of the OPCF as a distinct ecological unit. We suggest the analysis of other taxonomic groups to further characterize this vegetation type. In comparison, the CF presented the highest number of exclusive species with 16 taxa, although the strong dominance of some species decreases its diversity to a value lower than that of the OPCF. Considering the diversity and exclusive species of Nymphalidae that they support, we recommend that the OPCF, CF, and the TSDF be considered conservation priorities.

Van Someren-Rydon traps: Fruit-feeding butterflies constitute approximately 50 % of all Nymphalidae species (Santos et al., 2011). Similarly, other authors have reported 40-55 % of fruit-feeding Nymphalidae species from tropical forests, with some variation in the composition among the subfamilies (Daily & Ehrlich, 1995; DeVries & Walla, 2001; DeVries et al., 1999; Freire-Jr. et al., 2021a; Pinheiro & Ortiz, 1992; Uehara-Prado et al., 2004; Vargas et al., 1994; Vargas et al., 1999). In the last two decades, this guild has been used in analyses of forest fragmentation, conservation, monitoring, community structure, and ecology, because these species are more easily sampled (Freire Jr., Oliveira, et al., 2021; Freitas et al., 2003; González-Valdivia et al., 2016; Pozo, 2006; Pozo et al., 2005; Pozo et al., 2009). The growing importance of this guild underscores the relevance of the Van Someren-Rydon trap efficiency and efficacy data presented here.

During our fieldwork, all species of Charaxinae, Morphinae, and Apaturinae were collected in traps, along with most species of Satyrinae (92 %) and Biblidinae (77 %). In contrast, only two species of Limenitidinae

were collected in traps (13 %). Apparently, Limenitidinae are only occasional visitors to traps, probably looking for water as some Ithomiinae also do, since neither of these two subfamilies belong to the fruit-feeding guild (Meave del Castillo & Luis-Martínez, 2000). Traps are especially useful for collecting Charaxinae because these species frequent open spaces above the forest canopy, while Satyrinae frequent the understory less than one meter above ground (Freire Jr., Ribeiro, et al., 2021). Across all Nymphalidae, 19 % of the taxa were collected exclusively with this technique, and for 69 % of the species documented, 75 % of the specimens were trapped. We thus emphasize that Van Someren-Rydon traps are critical for accurately documenting the species richness, abundance, and elevational and vegetational distributions of Nymphalidae.

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 acknowledgements section. A signed document has been filed in the journal archives.

ACKNOWLEDGMENTS

JLB and ALM thank the projects DGAPA PAPIIT IN220521, PAPIME PE202820, CONACyT 284966, and CONABIO JF018 for financial support. MTO thanks the Postdoctoral Research Fellowship CONACyT 284966. AAC thanks the Posgrado en Ciencias Biológicas de la Universidad Nacional Autónoma de México. We thank the Departamento de Biología Evolutiva of the Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), México; Armando Canavati, owner of Rancho Hagia Sofía; and the authorities of the Parque Nacional Huatulco for their support during this project. Thanks to Sandra Nieves, Blanca Claudia Hernández and other colleagues and students who participated in the field work, and to

Adriana Atzinameyali Sánchez Castañeda for processing the collected material. The authors thank Adam G. Clause for English language review, and the peer reviewers for their comments on the manuscript.

RESUMEN

Distribución, diversidad, endemismo y ecología de las mariposas Nymphalidae (Lepidoptera: Nymphalidae) en la Región Loxicha, Oaxaca, México

Introducción: La Región Loxicha de Oaxaca, México, ha sido históricamente importante para el estudio de Nymphalidae, segunda en riqueza de especies en Papilionoidea. Describir los patrones de diversidad de este taxón de mariposas en Loxicha puede mejorar nuestra comprensión de la historia evolutiva de la Sierra Madre del Sur, la vertiente del Pacífico mexicano y México en general. **Objetivo:** Describir los patrones temporales y espaciales de la diversidad de Nymphalidae a lo largo de un gradiente altitudinal (80-2 600 m), y comparar la fauna de Loxicha con otras regiones de México.

Métodos: Obtuvimos 28 756 registros de 21 sitios de la Región Loxicha, que representan siete años de muestreo. Estimamos y analizamos la diversidad, el endemismo y los patrones de distribución para tres niveles altitudinales y cinco tipos de vegetación. Estimamos la composición de especies y la similitud con otras regiones de las vertientes del Pacífico y Atlántico de México.

Resultados: Identificamos 189 taxones, incluyendo especies y subespecies, de 85 géneros y diez subfamilias de Nymphalidae. Loxicha contiene 46 % de las especies de la familia reconocidas para México, incluidas diez especies endémicas y 56 subespecies endémicas. El bosque mesófilo y las elevaciones bajas fueron los hábitats más diversos para esta familia. Existe una clara divergencia entre las faunas del Atlántico y del Pacífico, y la Sierra Madre del Sur tiene dos componentes faunísticos. Los sitios de elevaciones altas en Oaxaca, y en el estado vecino de Guerrero, tienen una fauna distintiva, aparentemente aislada de los sitios de elevaciones bajas, lo que revela una distribución archipelágica para los Nymphalidae del bosque mesófilo.

Conclusiones: La Región Loxicha es una de las zonas más diversas para Nymphalidae en México. La distribución en la vertiente del Pacífico está determinada por la historia geográfica y las condiciones ecológicas, incluida la elevación. Nymphalidae puede usarse para probar hipótesis de regionalización biogeográfica en México.

Palabras clave: mariposas ninfálicas; gradiente de elevación; eficiencia de muestreo; fenología; provincias biogeográficas; trampas Van Someren-Rydon.

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APPENDIX 1

Nymphalidae of the Loxicha Region across a vegetational-elevational gradient

Monthly vegetational and elevational distribution of 189 species of Nymphalidae in the Loxicha Region, Oaxaca, Mexico. Records were obtained from 267 sampling days over seven years (2005, 2007, 2008, 2011–2014) in 21 sites from eight municipalities. The first column (Sp.) is the species identifier number corresponding to the list of species in the Results section. The next 11 columns are the months of the year excluding February from which no records are available. Column 13 (Total) is the total number of records for each species. The next five columns are the specimens recorded in each vegetation type: TDF, tropical deciduous forest; TSDF, tropical subdeciduous forest; CF, cloud forest; OPCF, oak-pine forest with elements of high-elevation cloud forest; OPF, oak-pine forest. The next two columns (100 and >70 %) present the elevational range where 100 % and more than 70% of the specimens of each species were recorded, respectively. These two columns show the elevational range with the highest probability for finding the species, although some taxa undergo seasonal elevational migrations. The last column (%) refers to the percentage of specimens collected in the >70 % elevational range. The last two rows correspond to the total number of specimens (TAb) and species (TSp) of each column. Species **55**. *Pedaliodes dejecta* ssp., **116**. *Adelpha donysa* ssp., and **176**. *Actinote guatemalena guerrerensis* were not recorded during fieldwork and hence are not included in this table.

Sp.	J	M	A	M	J	J	A	S	O	N	D	Total	TDF	TSDF	CF	OPCF	OPF	100	>70%	%
1					10	6	8	3	2			29	10	18	1			80-900	80-500	97
2								1	9			10			3	7		500-2400	1200-2400	92
3	3	8	1	5	1	3		3	8	1		33	5	21	7			290-1650	100-500	81
4						1	1		7			9			9			290-1650	1100-1650	92
5	20	1	1	6	13	29	4	2	36			112	65	40	6	1		80-2400	80-410	93
6		2	2	3	7	9	4	3	11	2		43	17	21	5			80-900	80-500	88
7						1						1			1			1500-2400	1500-2400	100
8	1				2	3	9	25	11	1	2	54		53		1		100-2150	350-500	99
9	10	3	1	4	10	32	48	76	57	13	4	258		243	12	3		290-2150	350-500	93
10	2	2	2	1	3	3	31	6	8			58		1	57			350-1650	750-1250	69
11				4	1	3	4	12	9			33		14	19			350-1530	410-1250	97
12	10	3	1	3	2	12	9	43	30	6	5	124		51	73			350-1530	350-900	79
13		2					2	20	18	1		43		22	21			290-1650	350-1300	89
14	3			14	3	13	10	40	113	5		201	3	150	47	1		80-2150	350-900	94
15	63	15	7	6	11	18	58	115	119	12	3	427		86	341			350-1650	350-1300	98
16	2					7		21	91	21		142			142			290-1650	1100-1650	89
17	1								17	4		22			22			1200-1650	1200-1650	100
18									1	2		3			2	1		600-2400	600-850	67
19					1	8						9		9				350-500	350-500	100
20	3	4	2	8	3	18	76	35	14	4		167		1	165	1		410-1650	1100-1650	69
21	1			9			8	1	28			47			43	4		1200-2400	1200-1650	92
22	3	8		8	9	22	69	86	80	8		293		74	215	4		350-2150	350-940	74
23		5	3	33	8	75		17	18			159	157	2				80-410	80-100	99
24	1				1	2	3	3	3	1		14		4	10			410-1650	410-1650	100
25		1	1				1		8			11			10	1		1200-2400	1500-1650	82
26	10	6	1	9		16	9	53	30		2	136	1	117	15	3		410-2150	350-500	87
27	3	1	4	2			1	15	5			31	7	22	1	1		80-2150	350-500	72
28		8	1	2			1	3	4			19	13	3	3			80-900	80-900	100
29	31	48	10	42	14	21	7	145	51		1	370	104	244	22			80-900	80-500	95
30		8	4	26	52	80	9	13	4			196	116	14	59	7		100-2400	80-940	88
31	1	6		4	1	4	4	4	28	2		54	11	8	35			80-1650	80-1650	100
32				6	11	87	37	13	75	29		258	100	1	157			80-1650	80-1650	100
33		6	1		2	16	19	38	9	5	1	97		2	95			80-1550	940-1550	88



Sp.	J	M	A	M	J	J	A	S	O	N	D	Total	TDF	TSDF	CF	OPCF	OPF	100	>70%	%	
34	4	12	12	3	7	33		12	19		1	103	87	15	1			80-900	100-500	99	
35	4	1			1	2	1	5	18	1		33			33			1200-1650	1200-1550	95	
36	3	1	1		11	4	6	17	8			51	19	18	13	1		80-2400	100-500	73	
37									1			1		1				410-500	410-500	100	
38	7	11	5	4	5	19	25	31	26	7	1	141		86	52	3		410-2150	350-940	93	
39	7	6	10	4	8	7	5	7	2	5	1	62	6	26	28	2		100-2150	350-940	77	
40	3	7	1	4	10	31	5	20	20	1	1	103	12	82	8	1		80-2150	350-500	80	
41								2				2		2				410-1530	410-1530	100	
42		2		3	1	5	3	4	1			19	3	14	1	1		80-2150	350-500	77	
43					1	1						2			2			1470-1550	1470-1550	100	
44			8	19	17	5	15	38	57	2	1	162	55	75	32			80-1550	80-500	81	
45	2	4	3	6	1	39	118	138	72	4		387	1	214	171	1		80-2150	350-900	86	
46	1		1	1		11	6	6	8			34		26	8			290-1300	350-900	95	
47		1										1			1			500-900	500-900	100	
48				3	8	9	4	1	2			27	10	11	6			80-1530	80-500	80	
49	3	1	1	3	8	5	6	11	4		1	43	3	38		2		80-2150	350-500	90	
50				1								1		1				350-500	350-500	100	
51					3	1	1	1	1			6		6				350-500	350-500	100	
52					2							2		1	1			350-1300	350-1300	100	
53				2				1		2		5			3	2		1470-2150	1470-2150	100	
54								1	1			2			2			500-1550	1200-1550	75	
55																					
56	66	85	56	155	34	50		435	63	1	2	947	148	645	151	3		80-2400	350-700	70	
57	53			1	12	17	44	5	17	1		150		54	96			410-1650	350-1300	86	
58	6	42	6	13	58	55	66	103	87	41	4	481	4	153	324			80-1650	350-1530	98	
59		1	3		32	215	89	5	9			354	18	308	28			80-1650	350-500	86	
60							1					1				1		2020-2150	2020-2150	100	
61	8	4		3	2		8	35	52	11	1	124			121	3		1100-2150	1100-2150	100	
63	20	1					4	2	7	2		36		5	31			350-1650	350-1650	100	
64	1				1			2		1		5			4	1		1100-1530	1100-1530	100	
62	4	1	1		5	12	30	10	30	2		95			95			444-1650	1100-1550	77	
65	1			6	1		1		3			12			3	9		1200-2400	2280-2400	75	
66																		1200-1530	1200-1530	100	
67	2		4	51	18	62	34	62	61			294		22	270	2		410-2400	750-1550	73	
68	194	100	46	91	346	269	292	339	496	81	13	2267	43	791	1430	3		80-2400	350-1650	98	
69				2								2				2		2280-2400	2280-2400	100	
70		4	30	58	13		3	4	68			180		1	1	161	17	2020-2800	2280-2400	88	
71	3			2		1	1		4	1		12		4	8			290-1650	290-1650	100	
72	3			2	4	12	2	6	6	1		36		35		1		240-2150	350-500	95	
73		1	1		1	4	5	6	2			20		18	1	1		350-2150	350-500	93	
74	35	21	12	13	28	102	62	98	66			437	16	399	20	2		80-2150	350-500	91	
75							1					1		1				410-500	410-500	100	
76	3		2	1	12	3	37	9	16	2	1	86		71	15			350-1530	350-1530	100	
77									4			4					4		2280-2400	2280-2400	100
78				1			9	3	5			18			18			1100-1650	1100-1650	100	
79	5	2	1		3			1				12	8	1		3		80-2400	80-2400	100	
80	3	3		1	2	1	4	12	14	1	1	42	3	35	2	2		80-2150	350-500	86	

Sp.	J	M	A	M	J	J	A	S	O	N	D	Total	TDF	TSDF	CF	OPCF	OPF	100	>70%	%	
81	6	3	1	25	71	54	24	21	39		1	245	24	206	11	4		80-2150	350-500	84	
82	12	5		6	40	17	5	7	10	1		103	47	40	15	1		2280-2400	100-500	85	
83	2	1			5	2	5	2	1			18			18			500-1650	1100-1650	76	
84	4	8		3	7	45	41	23	56	26		213	6	9	198			100-1550	80-900	86	
85							1			2		3			1	2		410-850	410-850	100	
86	5	5	3	19	7	63	20	107	20			249	14	208	26	1		80-2150	350-500	85	
87		6	3	5	13					1		28	26	2				80-410	80-410	100	
88	21	196	41	68	53	91	16	56	28			570	158	305	107			80-1650	80-500	83	
89	11	90	26	32	105	18	1	4	5			292	276	16				80-500	80-100	94	
90	4	6	2	38	40	38	10	91	46	6		281	86	175	19	1		80-2150	80-500	95	
91		6	2	3	100	29	5		1			146	119	22	5			80-1530	80-100	77	
92	6	4	1	3	35	46	16	12	8	2	1	134	30	71	30	3		80-2150	350-500	54	
93						1	2	1	4			8			3	5		350-900	750-900	63	
94	7	6			1	11	14	9	11	2		61	2	26	31	2		100-2150	80-940	91	
95	2	4				2	28	55	53	13		157			71	86		290-1650	350-1300	93	
96		2	3	5	1							11	11					80-500	80-100	92	
97	2	8	15	23	2			1	4			55			41	14		350-1650	350-900	98	
98				3	3			1	3			10	3	7				80-410	80-410	100	
99	16	4		2	11	59	48	99	84	2	2	327	17	295	14	1		80-2150	350-500	94	
100	7	5	4	17	11	22	24	56	50			196	11	179	4	2		80-2150	350-500	92	
101		3	2	2	174	24		3	3			211	211					80-100	80-100	100	
102	9	6	1	1	1	6	7	6	34	12		83			10	72	1	350-2150	1000-1650	75	
103									1			1				1		500-900	500-900	100	
104	6	12	5	27	55	60	22	23	37	1	1	249	30	217	1	1		80-2150	80-500	98	
105	71	17	4	11	21	109	171	179	338	108		1029			55	972	2	410-2150	1100-1650	80	
106	8	7	1		2	24	20	17	59	8		146			11	135		410-1650	1100-1650	73	
107				2	2	10	14	29	20			77	4	58			15	80-2150	350-500	80	
108	1	3		1		3	8	3	20	8		47				46	1	940-2400	1470-1650	75	
109					3	22	25	22	34	16		122	1	2	119			410-1250	600-940	95	
110	11		2	4	27	51	45	70	116	2		328	73	232	22	1		80-2150	350-500	71	
111				1	3			2	16			22	1	9	12			80-940	410-940	96	
112								3				3			3			410-500	410-500	100	
113	6	3	4	2	7	17	14	117	49	8		227			201	5	21	350-2150	350-500	90	
114		5	4	1				2	3			15					15	2280-2400	2280-2400	100	
115		1										1					1	2280-2400	2280-2400	100	
116																					
117		5	1					1	1			8	5	2			1	100-2400	100-500	89	
118	5	4	1	4	15	6	23	52	40	7		157	14	84	44	15		100-2400	80-900	70	
119		1		1		5	3	16	45			71			26	44	1	410-2150	410-940	99	
120	1						4		2			7				6	1	500-2150	500-1530	95	
121	12				3		4	14	11	10		54				53	1	600-2150	1100-1650	95	
122								2	3			5			2	3		410-1300	410-900	94	
123					2	1		5	4			12	2	8			2	80-2150	80-500	91	
124		5	1	3	2	5	4	3	6			29	4	17	3	5		100-2150	100-900	86	
125		2	3			6	4	4	8			27			16	6	5	290-2150	400-900	88	
126	3			2			8	2	6	11		32			1	30	1	350-2150	1100-1650	82	
127	4		2					5		4	5	20			18	2		290-1530	290-500	87	



Sp.	J	M	A	M	J	J	A	S	O	N	D	Total	TDF	TSDF	CF	OPCF	OPF	100	>70%	%
128		3	1	8	3	6	2	2	1			26	8	13	4	1		80-2150	80-2150	100
129	1	1	2	36	7	17	11	25	7	2		109	28	57	24			80-1300	350-940	73
130									4			4						1470-1550	1470-1550	100
131	33	15	3	19	18	20	34	180	41	10	6	379	6	317	55	1		80-2150	350-500	83
132	77	41	9	134	113	157	148	173	185	182	10	1229	191	340	693	4	1	80-2400	80-940	72
133					4							4						1200	1200	100
134	14	8	3	16	2		11	11	25	10		100		1	79	20		350-2400	1100-1650	83
135	3	3		1	1	3	6	8	24	11	1	61		3	57	1		350-2400	1100-1650	77
136	23	12	4	6	9	12	32	57	99	21	1	276		8	242	26		350-2400	1100-1650	80
137	5						2	13	14	9		43			43			444-1650	1100-1650	88
138		10	3	2		1			8			24					24	1500-2400	2280-2400	75
139				3	1							4				1	3	1500-2400	2280-2400	75
140										2		2			2			940	940	100
141	1	5	4	22	8		1		21	1		63	1		12	49	1	80-2400	2280-2400	75
142	11	1			2	22	11	17	24	5		93		22	70	1		350-2150	350-980	65
143	71	54	6	12	85	100	30	123	114	4		599	188	283	124	4		80-2400	350-500	72
144	88	29	7	13	37	171	104	203	165	88	9	914	34	548	328	4		100-2400	350-940	88
145	2				2	5	2	7	24			42	16	24		2		100-2400	80-500	95
146	2		1	1			1	1	2	1		9		4	1	4		350-2400	350-2400	100
147	3						1	6	1			11		9	2			350-1530	350-500	82
148								5				5		5				410-500	410-500	100
149									1			1					1	2280-2400	2280-2400	100
150	1	3	1	4	12	10	3	33	22			89		21	65	3		350-2400	350-940	65
151	6	2	1			5	17	3	34			68		1	66	1		350-1650	1100-1650	84
152	29	7	26	48	81	185	124	176	195	35	10	916	1	343	562	10		80-2400	350-1300	88
153	53	30	11	14	49	44	48	62	78	38		427	6	41	380			80-1650	1000-1650	69
154		1	1	8	15	20	59	40	42	14		200	11	89	100			80-1650	410-1650	95
155				14				1	4			19		1		18		410-2400	2280-2400	90
156			2	15	9	15	17	76	61	1		196	22	167	4	3		80-2400	350-500	85
157	3			5	6	51	104	47	47	12		275	2	162	109	2		80-2400	350-500	66
158	5			1	87	130	23	106	31		1	384	317	66	1			80-1300	80-100	82
159					1		1	4				6	1			5		80-2400	2280-2400	83
160		1	9	7		1		9				27		1		26		350-2400	2280-2400	87
161					1							1			1			1100-1300	1100-1300	100
162			1		1	20		2				24				24		500-2400	2280-2400	88
163			1	9	2		1	1	5			19				19		2280-2400	2280-2400	100
164	167	91	17	8	32	24	63	100	74	51	2	629		109	519	1		290-2150	750-1650	78
165	42	21	25	110	104	62	99	30	122	24		639		3	493	143		410-2400	1100-2400	98
166	9	20	10	10	58	1	41	87	26	6		268			267	1		444-2150	1100-1300	92
167	7				60	29	1	6				103			100	3		1100-2400	1100-1650	98
168	85	3	7	29	44	35	14	96	146	13	8	480	239	187	41	13		80-2400	80-500	88
169	25	22	11	12	30	14	32	44	23	7		220		1	213	6		235-2400	1000-1650	95
170	7	29	1	50	49	17	15	42	46	13		269			237	32		940-2400	1000-1650	87
171	31	14	6	12	3			1	2	15		84		2	79	3		290-2400	1000-1650	91
172				14	3		3		19			39				1	38	1200-2450	2280-2400	88
173			1	1					6			8					8	2280-2400	2280-2400	89
174	4	9	1		10	4	31	33	49	13	1	155		15	140			290-1650	530-1650	86

Sp.	J	M	A	M	J	J	A	S	O	N	D	Total	TDF	TSDF	CF	OPCF	OPF	100	>70%	%
175	1	2	1	3			3	7	98	1		116			1	67	48	350-2400	1100-2400	96
176																				
177	5	1	2	6	18	24	5	6	3			70	47	14	4	5		100-2400	80-500	87
178	2	16	2	3			31	18	5	13	1	92	1	51	23	17		80-2400	350-500	57
179	2	4	10	14	1	1	4	5	64	4		109	3		15	87	4	80-2400	1470-2400	89
180	59	21	8	25	44	111	93	159	135	36	18	709	30	503	172	4		80-2400	350-940	86
181				3			1					4			4			410-500	410-500	100
182	6				3	3	14	12	74	9	11	132			124	4	4	290-2150	350-500	92
183	3			2	1	3		7	28			44	1	40	3			410-1550	410	81
184	54	35	15	23	11	54	81	64	142	35	7	521	48	259	193	21		80-2400	80-940	81
185	97	22	19	33	61	113	68	112	123	23	20	691	32	643	15	1		80-2150	80-500	98
186	13	7		5	6	17	18	8	28	25		127			125	2		600-2400	1100-1650	93
187							1					1				1		1200-1530	1200-1530	100
188				1	1							2	1	1				80-410	80-410	100
189	12	9	9	20	24	61	44	18	41		1	239	42	187	3	7		80-2400	350-500	79
TAb	1914	1432	610	1746	2688	3938	3443	5570	6002	1256	163	28756	3496	11699	12487	1051	23			
TSp	109	106	96	120	120	126	135	146	159	91	40	189	79	36	147	108	4			

APPENDIX 2

Nymphalidae of the Loxicha Region captured in Van Someren-Rydon traps

Monthly and elevational distribution of Nymphalidae species captured with Van Someren-Rydon traps in the Loxicha Region, Oaxaca, Mexico. The list includes 94 species of seven of the 11 subfamilies of Nymphalidae, representing 50 % of all species recorded and 41 % of all specimens collected. The first column (Sp.) is the species identifier number corresponding to the list of species in the Results section. The next 11 columns are the months of the year excluding February from which no records are available. Column 13 (VSRT) is the number of records of each species obtained in Van Someren-Rydon traps. Column 14 (Total) is the total number of specimens captured during our study. The next column (%) shows the percentage of specimens captured with traps out of the total number of specimens. The last three columns represent the number of specimens collected in traps at each elevational level (m): **1**, 0–750; **2**, 750–1 800, and **3**, 1 800–2 850. The last two rows correspond to the total number of specimens (TAb) and species (TSp) of each column.

Sp.	J	M	A	M	J	J	A	S	O	N	D	VSRT	Total	%	1	2	3	
23			5	3	33	4	69		17	18		149	159	93.71	149			
24	1					1	2	2	3	1		10	14	71.43	4	6		
25			1	1						8		11	11	100		10	1	
26	10		6		6		13	8	39	25		2	109	136	80.15	94	14	1
27	3		1	4	2			1	15	3			29	31	93.55	27	1	1
28			8	1	2			1	3	4			19	19	100	16	3	
29	30		47	9	38	13	20	7	135	48		1	348	370	94.05	327	21	
30			8	4	26	48	68	9	13	4			180	196	91.84	114	59	7
31	1		5		2	1	3	4	3	27	2		48	54	88.89	14	34	
32					6	11	82	34	12	72	25		242	258	93.80	96	146	
33			6	1		2	14	17	36	9	5	1	91	97	93.81	2	89	
34	4		11	12	3	7	31		11	15		1	95	103	92.23	94	1	
35	4		1			1	2	1	5	18	1		33	33	100		33	
36	3		1	1		11	4	6	17	8			51	51	100	37	13	1
37										1			1	1	100	1		
38	7		11	5	4	4	17	25	30	26	7	1	137	141	97.16	84	50	3



Sp.	J	M	A	M	J	J	A	S	O	N	D	VSRT	Total	%	1	2	3
39	7	5	10	4	8	7	5	7	2	4	1	60	62	96.77	31	27	2
40	3	6	1	4	10	28	5	19	20	1	1	98	103	95.15	90	7	1
41								2				2	2	100	2		
42		2		3	1	5	3	4	1			19	19	100	17	1	1
43							1	1				2	2	100		2	
44			8	13	15	5	14	31	41	2	1	130	162	80.25	100		30
45	2	4	2	6	1	36	106	122	66	4		349	387	90.18	192	156	1
46	1		1	1		10	3	6	8			30	34	88.24	24		6
47		1										1	1	100			1
48				2	7	7	4		1			21	27	77.78	17		4
49	3	1	1	3	7	5	5	10	4		1	40	43	93.02	38		2
50				1								1	1	100	1		
51						3	1	1	1			6	6	100	6		
52						2						2	2	100	1	1	
53				2				1		2		5	5	100		3	2
54								1	1			2	2	100		2	
56	60	71	44	138	28	42		356	50	1	1	791	947	83.53	672	117	2
57	53			1	10	17	44	3	15	1		144	150	96	53	91	
58	6	41	6	9	48	49	60	84	65	37	4	409	481	85.03	132	277	
59		1	3		27	182	81	4	9			307	354	86.72	283	24	
60							1					1	1	100			1
61	7			2	2		8	27	52	11	1	110	124	88.71		108	2
62	4	1	1		5	7	20	10	30	2		80	95	84.21		80	
63	13						4		2	2		21	36	58.33	1	20	
64	1				1			1		1		4	5	80		4	
65				6			1		2			9	12	75		2	7
67	2		3	43	13	54	24	51	52			242	294	82.31	18	222	2
68	171	84	41	86	305	228	267	303	443	76	12	2016	2267	88.93	770	1245	1
70			10	48			1	1	18			78	180	43.33			78
71	3			2		1	1		4	1		12	12	100	4	8	
72	3			2	1	5	2	3	6	1		23	36	63.89	22		1
73		1	1		1	3	4	5	2			17	20	85	16	1	
74	34	12	11	8	19	89	57	71	53			354	437	81.01	336	16	2
75							1					1	1	100	1		
76	3		2	1	10	3	33	9	15	1	1	78	86	90.70	66	12	
77									4			4	4	100			4
78				1			7	2	3			13	18	72.22		13	
79	1	2	1		3			1				8	12	66.67	5		3
80	1	3				1	3	11	11	1	1	32	42	76.19	31	1	
81						15	10					25	245	10.20	24	1	
84	3	3		2	7	33	31	15	46	21		161	231	69.70	12	149	
86	5	5	3	13	3	47	19	87	15			197	249	79.12	173	23	1
87		3	3	3	9							18	28	64.29	18		
88	19	154	30	50	39	71	14	47	22			446	570	78.25	359	87	
89	11	66	19	27	84	16	1	4	4			232	292	79.45	232		
90	4	6	2	38	35	28	8	66	38	2		227	281	80.78	216	11	
91						14	5		1			20	145	13.79	20		

Sp.	J	M	A	M	J	J	A	S	O	N	D	VSRT	Total	%	1	2	3
92		4		2	35	32	10	4	8		1	96	134	71.64	86	9	1
93						1	2					3	8	37.50	3		
94	7	4			1	11	14	8	11	1		57	61	93.44	28	27	2
95	2	4				2	22	45	46	13		134	157	85.35	57	77	
96		1		5	1							7	11	63.64	7		
97	2	4	14	20	2			1	4			47	55	85.45	39	8	
98				2	2			1	1			6	10	60	6		
99	12	2		1	11	43	33	78	66	2	1	249	327	76.15	236	13	
100	7	5	4	13	10	20	18	39	34			150	196	76.53	144	4	2
101			1		9							10	211	4.74	10		
102	4	6	1	1	1	1	4	2	10	8		38	83	45.78	1	36	1
104		3		1		1	6	3	4			18	249	7.23	18		
105	13					1	22		69			105	1029	10.20	6	99	
106									2			2	146	1.37		2	
107						1		3	1			5	77	6.49	3		2
108							3		2	4		9	47	19.15		8	1
113						1	4					5	227	2.20	5		
119						3	3	8				14	71	19.72	13		1
128		3	1	7	3	5	1	2	1			23	26	88.46	18	4	1
129	1	1	2	33	7	15	10	24	7	2		102	109	93.58	78	24	
131	30	12	3	17	11	20	34	146	34	8	6	321	379	84.70	277	43	1
132	76	41	9	133	113	148	148	173	185	182	10	1218	1229	99.10	525	688	5
134	10	6	3	13	2		5	6	8	9		62	100	62	1	49	12
135	3	2		1	1	2	4	7	18	6	1	45	61	73.77	3	41	1
136	21	6		5	6	10	20	56	45			169	276	61.23	2	155	12
137	4						1	8	12	8		33	43	76.74		33	
138		10	3			1			5			19	24	79.17			19
139				1								1	4	25			1
141				6	1				1	1		9	63	14.29		5	4
142		1			2	3		3	10	4		23	93	24.73	8	14	1
143	56	48	5	10	60	77	24	88	83	4		455	599	75.96	357	96	2
TAb	731	746	290	912	1080	1736	1357	2409	2061	463	49	11543	15824	72.95	6609	4709	191
TSp	49	53	43	57	57	63	69	68	76	38	20	94	94		74	69	42