

# Hawk Moth (Lepidoptera: Sphingidae) Richness in an Agricultural Ecosystem Associated with Tropical Deciduous Forest Fragments in Veracruz, Mexico<sup>1</sup>

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J. Entomol. Sci. 61(2): 000–000 (Month 2025)

DOI: 10.18474/JES25-28

**Abstract** Sphingidae (Latreille) is one of the largest families of tropical moths, with important roles in herbivory and pollination and great species richness. Although Veracruz has the largest number of hawkmoths recorded in Mexico, there are few studies and no research reported from the low deciduous forest or on mature stages in agricultural areas. This study aimed to evaluate the species richness of Sphingidae in an agricultural ecosystem associated with tropical deciduous forest fragments in Veracruz, Mexico. The study period for this work covers January 2023 to December 2024. Insects were collected using nocturnal capture methods with light traps from 18:00 to 06:00 h once each month. The results are equivalent to 288 effective hours of sampling, allowing the collection of 342 hawkmoths, representing 47 species from 22 genera, three subfamilies, and four tribes, with a 97.09% sample coverage. We report four new records for the state of Veracruz. Models indicated that temperature and precipitation explain 45.58% and 49.97% of the variability in abundance and species richness, respectively. This work includes the first records of hawkmoths associated with agricultural ecosystems and low deciduous forest in Veracruz and their relationship with environmental variables.

**Key Words** nocturnal pollinators, moth diversity, tropical ecosystems, taxonomy

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With over 123,000 species interacting with flowers worldwide, moths (Heterocera) make up one of the most diverse group of pollinators (Wardhaugh 2015, Ollerton 2017). Among moths, the family Sphingidae, known as sphinx, hawk,

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hummingbird, or bee moths, stands out for its relevance as ubiquitous pollinators (Wardhaugh 2015, Salem 2022). This cosmopolitan family consists of about 1,602 described species representing 205 genera (Kitching et al. 2018), and their largest diversity occurs in the tropical regions of the Americas, Africa, and Asia (Salem 2022).

Research on hawkmoths worldwide has focused on aspects associated with taxonomy, systematics, ecology, crop pollination, and even pest control in some important crops, producing an abundance of information (Forehand et al. 2006, Johnson et al. 2017, Stöckl and Kelber 2019, Buxton et al. 2022). Many of those studies have been conducted in the Americas, where hawkmoths are found from Nearctic to Neotropical regions, resulting in a wealth of scientific information that has enhanced our knowledge of the group (García 1978, Schreiber 1978, Haber 1983, Lamas 1985, Fernández Yépez and González 1994, Pescador Rubio 1994, Correa-Carmona et al. 2015, Valente and Teston 2024). Approximately 400 species have been identified from the Americas (Pescador Rubio 1994; Kitching and Cadiou 2000), which is the most diverse Neotropical region with 312 species recorded (Llorente-Bousquets et al. 2014, Lara-Pérez et al. 2020). Mexico is at the intersection of both regions (CONABIO 2020) with a record 201 species (León-Cortés 2000, Llorente-Bousquets et al. 2014, Lara-Pérez et al. 2020).

Within Mexico, Veracruz state appears to have the largest number of hawkmoths, with 131 species recorded (Beutelspacher 1989, León-Cortés and Pescador 1998, Hernández-Baz and Iglesias-Andrew 2001, Zaragoza-Villela et al. 2019, Lara-Pérez et al. 2020). However, taxonomic inventories have been recorded only in vegetation of high evergreen forests (Beutelspacher 1989), montane mesophyll forests (Beutelspacher 1978, Hernández-Baz, 1989, Cerón 2015), and midaltitude deciduous forests (Lara-Pérez et al. 2020). We have not been able to find investigations in the low deciduous forests in Veracruz. This type of vegetation is known for its high biodiversity and large percentage of endemic plant species. Unfortunately, it is also known that these ecosystems are facing problems due to the continuous fragmentation and diversity loss attributed mainly to the expansion of agricultural and livestock activities (Trejo and Dirzo 2000, Arias et al. 2002, Silva-Aparicio et al. 2018, CONABIO 2022).

The proximity and association of tropical forest remnants with agricultural ecosystems may increase some benefits of pollination services as reported by Ricketts (2004) and Ricketts et al. (2004). Therefore, agricultural ecosystems adjacent to deciduous forest fragments represent an opportunity to evaluate the interaction between biodiversity and agriculture. Climate change and continued fragmentation threaten low deciduous forests because of their marked climatic seasonality (CONABIO 2022). Previous studies have produced mixed results regarding the correlation of environmental variables with the richness and abundance of Sphingidae (Ríos-González et al. 2019, Lara-Pérez et al. 2020). Pollinator populations are experiencing a global decline (ENCUSP 2021). Because of this situation, analyses of how these variables interact in low deciduous forest environments are of interest (Siyum 2020). Our objective was to evaluate the species richness of the family Sphingidae in an agricultural ecosystem associated with fragments of a deciduous forest in Veracruz, Mexico. Because of the marked climatic seasonality of this ecosystem, unlike other ecosystems, we expected that the rainy seasons would support a greater richness and abundance of species.

## Materials and Methods

**Study site.** The study was conducted at La Bandera Experimental Center at the Agricultural Sciences School (FCA), Universidad Veracruzana at a site located in the Actopan municipality, Veracruz (19° 27' 27" N, 96° 34' 18" W) with an average altitude of 183 m above sea level. The area is about 21 ha, 14 ha of which are mostly used to grow *Manilkara zapota* (L.) P. Royen (sapodilla, chicozapote; Sapotaceae) and *Manguifera indica* L. (mango; Anacardiaceae), and 7 ha are a preserved area of low deciduous forest. The climate is tropical rainy with a dry season in winter and a mean annual temperature of 24°C and a mean annual rainfall of 1,026 mm (Domínguez and Ruíz 2013).

**Collection.** Specimens of Sphingidae were collected under SEMARNAT scientific collector license FAUT-0194 for 2 yr (January 2023 through December 2024). A light trap with a 250 W mercury vapor bulb on each side of the screen was used for indirect collection. The trap was located in the ecotone between the preserved area and the agricultural crops (19° 27' 37" N, 96° 34' 12" W). Entomological nets were used for direct collection. The overall collection was conducted once each month during nights with a new moon, from 18:00 to 06:00 h. The collected specimens were killed with ethyl acetate and stored in paper envelopes.

**Mounting and specimen identification.** Collected hawkmoths were identified to subfamily, genus, and species based on the information from D'Abrera (1986), Kitching and Cadiou (2000), Kitching (2023), and Haxaire and Melichar (2023). The obtained data are included in the "Moth" database at the Faculty of Biology, Universidad Veracruzana, Mexico, where the collected specimens are deposited.

**Statistical analysis.** Alpha diversity was evaluated with the Chao 1 estimator of the iNext package in the R programming language version 4.3.1 (R Core Team 2023) with a configuration of 40 iterations and bootstrap applied to 300 replications. Rarefaction and extrapolation curves were generated to assess the adequacy of the sampling effort and to project diversity. Sampling coverage curves were calculated to determine whether the current data obtained are representative of the actual diversity at the site (Chao et al. 2014, Hsieh et al. 2016).

Differences in species composition between rainy and dry seasons were evaluated with a multidimensional non-metric scaling analysis (NMDS) using the Bray-Curtis dissimilarity distance. The analysis was performed with the metaMDS function of the vegan package in R. The quality of the model fit was evaluated by the stress value, considering a value <0.2 as acceptable. A permutational analysis of variance (PERMANOVA) was applied using the adonis2 function to determine whether there were statistically significant differences in species composition between seasons, with 999 permutations. To identify indicator species associated with each season (rainy and dry), indicator value analysis (IndVal) was used.

The hypothesis that the richness and abundance of Sphingidae species are higher during the rainy season was tested. The data obtained were grouped into two climatic seasons: dry (November to May) and rainy (June to October). For this analysis the sampling unit was defined as each monthly sampling night. Because the data were not normally distributed, nonparametric Wilcoxon rank sum tests were used to compare richness and abundance between seasons. The tests were performed in the R programming language, using a one-way alternative hypothesis, which posits that values during the rainy season are significantly higher than those during the dry season.

A Spearman correlation analysis was performed to evaluate the relationships among the variables of richness, abundance, accumulated monthly precipitation, and mean monthly temperature, with a significance level of  $\alpha = 0.05$ . The climatic data were obtained from the meteorological station located in Los Idolos town, in the municipality of Actopan, Veracruz, 8.08 km from our study site. Multiple linear regression models were fitted to explore trends in greater detail. The analysis was conducted in the R program (version 4.3.1), using the packages “stats” for the calculation of Spearman correlations and “ggplot2” for the generation of scatter plots and visualization of trends.

## Results

Collections were conducted from January 2023 through December 2024, which was the equivalent of 288 effective hours of sampling. A total of 342 hawkmoths were collected, of which 47 species belonging to 22 genera, three subfamilies, and four tribes were identified, with a sex ratio of 85.09% males and 14.91% females. Macroglossinae was the most frequently represented subfamily with 269 individuals of 35 species, predominantly from the tribe Dilophonotini with 30 species and Macroglossini with five species. The second most abundant subfamily was Sphinginae with 66 individuals of 10 species, all in the tribe Sphingini. Smerinthinae was represented by seven individuals of two species within the tribe Ambulycini (Table 1).

The most abundant genera were *Erinnyis* (83 individuals), *Cautethia* (53 individuals), *Manduca* (38 individuals), *Eumorpha* (32 individuals), and *Callionima* (26 individuals). The most representative species were *Erinnyis yucatana* (H. Druce) (48 individuals), *Cautethia spuria* (Boisduval) (47 individuals), *Ceratomia igualana* (Schaus) (23 individuals), *Manduca florestan* (Stoll) (21 individuals), and *Erinnyis ello* (L.) (20 individuals). Species richness and abundance was temporally variable throughout the study period, and an increase was observed during June through September 2023 and July through September 2024, with the highest species richness and abundance in September 2024 (Fig. 1). The month of September in both 2023 and 2024 had the highest number of females recorded (Table 1).

The estimate of species richness ( $q = 0$ ) using Chao 1 was 47 species (95% confidence interval [CI]: 42.68–51.32) with a sampling coverage of 97.08% (Fig. 2a, b, c). If the sampling effort were doubled, the estimator indicated a total of 52.37 species (95% CI: 45.06–59.66) with a coverage of 99.28% and an asymptotic richness of 54.12 species. The observed Shannon index ( $q = 1$ ) was 25.51 (Fig. 1), and its asymptotic estimate was 27.78 (95% CI: 24.43–31.13). The observed Simpson index ( $q = 2$ ) was 16.15, with an asymptotic estimate of 16.90 (95% CI: 14.01–19.80) (Fig. 2).

The composition of the hawkmoth community did not differ significantly between seasons (PERMANOVA:  $P = 0.296$ ; NMDS: stress = 0.187) (Fig. 3a). However, *Callionima falcifera* (Gehlen) was moderately associated with the dry season (IndVal = 0.43,  $P = 0.04$ ), being 42.9% more frequent in this period. No other species had a significant seasonal preference. Species richness ( $W = 122$ ,  $P = 0.0012$ ) and abundance ( $W = 129$ ,  $P = 0.0003$ ) were significantly higher during the rainy season (Fig. 3b).

The Spearman correlation analysis indicated a significant positive correlation between temperature and the richness ( $\rho = 0.560$ ,  $P = 0.0045$ ) and abundance

Table 1. Richness and abundance of hawkmoths at the La Bandera Experimental Field, Actopan, Veracruz, Mexico.\*

Species	2023												2024												N
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Subfamily Macroglossinae																									
Tribe Dilothonotini																									
<i>Callionima falcifera</i> Gehlen	4 <sup>M</sup>								1 <sup>M</sup>			2 <sup>M</sup>	1 <sup>M</sup>	1 <sup>M</sup>							3 <sup>M</sup>				12
<i>Callionima parce</i> F.	1 <sup>M</sup>											2 <sup>M</sup>					1 <sup>M</sup>				8 <sup>M</sup> , 1 <sup>M</sup>	1 <sup>M</sup>			14
<i>Cautethia spuria</i> Boisduval	2 <sup>M</sup>			1 <sup>M</sup>	2 <sup>M</sup>		3 <sup>M</sup>	4 <sup>M</sup>	10 <sup>M</sup>		1 <sup>M</sup>			1 <sup>M</sup>	1 <sup>M</sup>	1 <sup>M</sup>			5 <sup>M</sup>	5 <sup>M</sup>	9 <sup>M</sup>	1 <sup>M</sup>		1 <sup>M</sup>	47
<i>Cautethia yucatana</i> Clark									3 <sup>M</sup>					1 <sup>M</sup>	1 <sup>M</sup>	1 <sup>M</sup>									6
<i>Enyo gorgon</i> Cramer	1 <sup>F</sup>	1 <sup>M</sup>														1 <sup>F</sup>	1 <sup>F</sup>								4
<i>Enyo lugubris</i> L.																1 <sup>F</sup>	1 <sup>M</sup>				1 <sup>M</sup>				3
<i>Enyo ocypete</i> L.				1 <sup>M</sup>																					1
<i>Enyo taedium</i> Schaas	2 <sup>M</sup>				1 <sup>M</sup>									1 <sup>M</sup>											4
<i>Erinnyis alope</i> Drury				1 <sup>M</sup>																					3
<i>Erinnyis crameri</i> Schaas						1 <sup>M</sup>			1 <sup>F</sup>	2 <sup>M</sup>															5
<i>Erinnyis ello</i> L.				1 <sup>M</sup>		3 <sup>F</sup>								1 <sup>M</sup>				1 <sup>M</sup>	1 <sup>M</sup>	1 <sup>M</sup> , 1 <sup>F</sup>	1 <sup>M</sup>	5 <sup>M</sup> , 6 <sup>F</sup>			20
<i>Erinnyis lessauxi</i> Boisduval													1 <sup>M</sup>			1 <sup>F</sup>									2
<i>Erinnyis obscura obscura</i> F.																			1 <sup>M</sup>			1 <sup>M</sup>			2
<i>Erinnyis oenotrus</i> Cramer																			1 <sup>M</sup>		1 <sup>M</sup>	1 <sup>M</sup>			3
<i>Erinnyis yucatana</i> Druce				1 <sup>F</sup>	1 <sup>M</sup>	1 <sup>M</sup>	3 <sup>M</sup> , 1 <sup>F</sup>	6 <sup>M</sup>	5 <sup>M</sup> , 1 <sup>F</sup>	2 <sup>M</sup>	1 <sup>M</sup> , 1 <sup>F</sup>	1 <sup>M</sup> , 1 <sup>F</sup>	1 <sup>M</sup>	1 <sup>M</sup>	1 <sup>M</sup>		2 <sup>F</sup>		2 <sup>M</sup>	6 <sup>M</sup>	11 <sup>M</sup> , 1 <sup>F</sup>			48	
<i>Eumorphia elisa</i> Smyth						3 <sup>M</sup>			1 <sup>M</sup>										2 <sup>M</sup>						6
<i>Eumorphia labruscae</i> L.																			1 <sup>M</sup>						1
<i>Eumorphia satellitia</i> L.						1 <sup>M</sup>		4 <sup>M</sup> , 1 <sup>F</sup>										2 <sup>M</sup>							8
<i>Eumorphia vitis</i> L.						2 <sup>M</sup> , 1 <sup>F</sup>		6 <sup>M</sup>										1 <sup>M</sup>	1 <sup>F</sup>	1 <sup>M</sup>	1 <sup>M</sup>	1 <sup>M</sup>			17
<i>Hemeroplanes triptolemus</i> Cramer			1 <sup>M</sup>																			1 <sup>M</sup>			2
<i>Isognathus rimosa inclitus</i> Edwards		1 <sup>M</sup>														1 <sup>F</sup>					3 <sup>M</sup> , 3 <sup>F</sup>				10
<i>Madoryx bubastus</i> Cramer			1 <sup>M</sup>																						1
<i>Madoryx oiclus</i> Cramer			1 <sup>M</sup>																						1

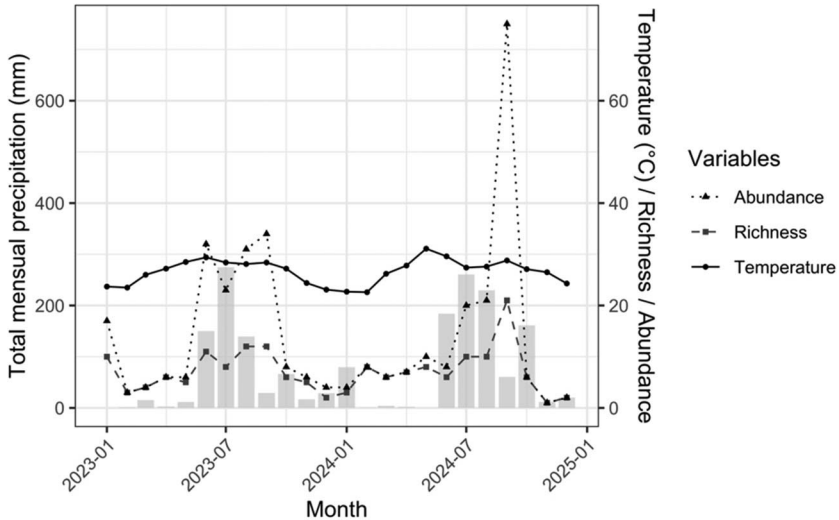
Table 1. Continued.

Species	2023												2024												N
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
<i>Nyceryx coffaeae</i> Walker														1 <sup>M</sup>											1
<i>Nyceryx riscus</i> Schaus	3 <sup>M</sup>																								3
<i>Pachylia ficus</i> L.						1 <sup>M</sup>			1 <sup>M</sup>								2 <sup>M</sup>	1 <sup>M</sup>							6
<i>Pachylioides resumens</i> Walker					1 <sup>F</sup>													1 <sup>M</sup>	1 <sup>M</sup>	1 <sup>M</sup>	3 <sup>M</sup>		1 <sup>M</sup>		7
<i>Perigonia ilus</i> Boisdual							1 <sup>F</sup>			1 <sup>M</sup>							1 <sup>M</sup>	2 <sup>M</sup>							5
<i>Perigonia lusca</i> F.	1 <sup>F</sup>																								1
<i>Pseudosphinx tetrio</i> L.																					1 <sup>F</sup>				1
Tribe Macroglossini																									1
<i>Darapsa myron mexicana</i> Gehlen				1 <sup>M</sup>			1 <sup>M</sup>		1 <sup>M</sup>	1 <sup>M</sup>						1 <sup>M</sup>					3 <sup>M</sup>				8
<i>Hyles lineata</i> F.						2 <sup>F</sup>	1 <sup>M</sup>										1 <sup>M</sup>				1 <sup>M</sup>				5
<i>Xylophanes ilbya</i> Druce	1 <sup>F</sup>	1 <sup>M</sup>					1 <sup>M</sup>														2 <sup>M</sup>	1 <sup>M</sup>			6
<i>Xylophanes pluto</i> F.	1 <sup>M</sup>		1 <sup>M</sup>						2 <sup>M</sup>								1 <sup>M</sup>								5
<i>Xylophanes turbata</i> Edwards										1 <sup>M</sup>															1
Subfamily Smerinthinae																									
Tribe Ambulicyni																									
<i>Adhemarius gammascus</i> Stoll																					1 <sup>F</sup>				1
<i>Protambulyx strigilis</i> L.									1 <sup>M</sup>	1 <sup>M</sup> , 1 <sup>F</sup>	1 <sup>M</sup>										2 <sup>F</sup>				6
Subfamily Sphinginae																									
Tribe Sphingini																									
<i>Agrius cingulata</i> F.	1 <sup>F</sup>																		1 <sup>M</sup>		1 <sup>F</sup>				3
<i>Ceratomia igualana</i> Schaus							11 <sup>M</sup>	2 <sup>M</sup> , 1 <sup>F</sup>	3 <sup>M</sup> , 1 <sup>F</sup>									2 <sup>M</sup> , 1 <sup>F</sup>	2 <sup>M</sup>						23
<i>Cocytus antaeus medor</i> Drury									1 <sup>M</sup>											1 <sup>H</sup>					2
<i>Manduca florestan</i> Stoll					1 <sup>M</sup>	14 <sup>M</sup>			2 <sup>M</sup>					1 <sup>M</sup>							3 <sup>M</sup>				21
<i>Manduca</i> sp. Clark							1 <sup>M</sup>												1 <sup>M</sup>						2

Table 1. Continued.

Species	2023												2024												N
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
<i>Manduca lichenaea</i> Buermeister								1 <sup>M</sup>																	1
<i>Manduca muscosa</i> Rothschild & Jordan					1 <sup>M</sup> , 1 <sup>F</sup>																				2
<i>Manduca ochus</i> Klug								1 <sup>M</sup>										2 <sup>M</sup>							3
<i>Manduca rustica</i> F.					1 <sup>M</sup>									1 <sup>M</sup>				1 <sup>M</sup>			4 <sup>M</sup>				7
<i>Manduca sexta</i> L.								1 <sup>M</sup>													1 <sup>M</sup>				2
Sexual proportion																									
Male	13	3	4	5	5	25	21	29	29	8	5	4	3	8	4	4	7	8	18	20	59	6	1	2	281
Female	4	0	0	1	1	7	2	2	5	0	1	0	1	0	2	3	3	0	2	1	16	0	0	0	51
Abundance	17	3	4	6	6	32	23	31	34	8	6	4	4	8	6	7	10	8	20	21	75	6	1	2	
Richness	10	3	4	6	5	11	8	12	12	6	5	2	3	8	6	7	8	6	10	10	20	6	1	2	
Total																									342

\* F = female; M = male; N = total number of individuals.



**Fig. 1. Monthly patterns of species richness, species abundance, and the climate variables of mean monthly temperature and total monthly precipitation throughout the study period (January 2023 through December 2024).**

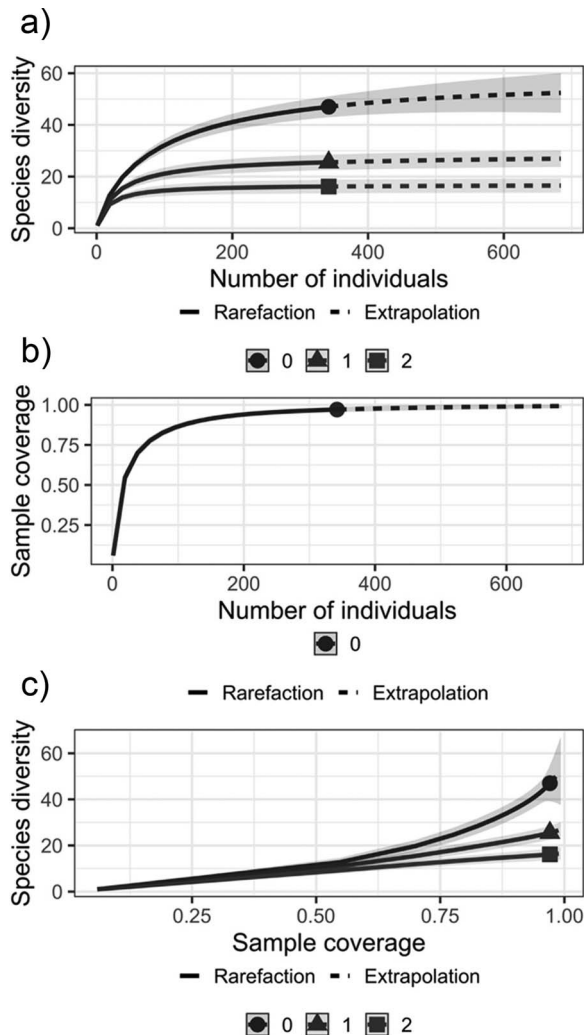
( $\rho = 0.642$ ,  $P = 0.0007$ ). In contrast, precipitation had positive correlations with only a lag of 1 mo (lag +1), both in richness ( $\rho = 0.476$ ,  $P = 0.0216$ ) and abundance ( $\rho = 0.473$ ,  $P = 0.0228$ ). Multiple linear regression analysis were used to evaluate the influence of monthly total rainfall with a 1-mo lag and monthly mean temperature on hawkmoth abundance and richness. For abundance, the model suggested that 45.58% of the variability could be explained by the climatic variables (multiple  $R^2$ : 0.5052; adjusted  $R^2$ : 0.4558). Lagged precipitation had a coefficient of 0.10208 ( $P = 0.00231$ ), indicating a significant positive relationship with abundance, as did temperature, which had a coefficient of 2.39388 ( $P = 0.04897$ ). The  $F$  test ( $F = 10.21$ ,  $P = 0.0008$ ) indicated that the model was statistically significant.

For species richness, the model suggested that 49.97% of the variability could be explained by climatic variables (multiple  $R^2$ : 0.5452; adjusted  $R^2$ : 0.4997). Precipitation had a coefficient of 0.024747 ( $P = 0.00313$ ), indicating a significant positive relationship with richness, as did temperature, with a coefficient of 0.805606 ( $P = 0.01104$ ). The  $F$  test ( $F = 11.99$ ,  $P = 0.0003$ ) indicated that the model was statistically significant.

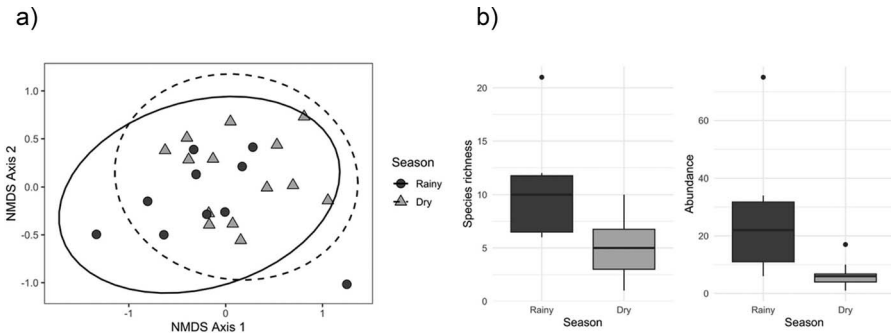
## Discussion

This study is the first in which the richness and abundance of hawkmoths was assessed in an agricultural environment associated with low deciduous forest fragments in the state of Veracruz. In total, 47 hawkmoth species were recorded, mainly from the subfamily Macroglossinae, tribe Dilophonotini, and both *E. yucatanana* and *C. spuria*. The only species identified as endemic was *Darapsa myron mexicana* Gehlen. The diversity analysis indicated effective sampling because a representative sample of the community was captured with a coverage of 97.08%





**Fig. 2.** Rarefaction and extrapolation curves of hawkmoth species richness based on sample size and coverage. (a) Rarefaction and extrapolation curves based on sample size for diversity orders  $q \geq 0$ . (b) Sample coverage curve relative to the number of individuals. (c) Rarefaction and extrapolation curves of species richness as a function of sample coverage. Solid lines represent observed data (rarefaction), dashed lines represent extrapolated estimates, shaded areas are 95% confidence intervals, and symbols indicate diversity orders.



**Fig. 3. Seasonal comparison of hawkmoth assemblages between rainy and dry seasons at the La Bandera Experimental Field, Actopan, Veracruz, Mexico. (a) NMDS (Bray-Curtis; stress = 0.187) of hawkmoth assemblage. Samples are represented by circles (rainy season) and triangles (dry season), with 95% confidence intervals depicted as solid lines (rainy season) and dashed lines (dry season). The overlap between groups confirms the similarity in species composition across seasons. (b) Comparison of species richness and abundance between the rainy and dry seasons.**

and an asymptotic estimate of up to 54.12 species. The high value of the Shannon index compared with the Simpson index suggests high species diversity with contributions from both common and rare species.

According to the species list of León-Cortés (2000), which includes 131 species for Veracruz, we documented four new records for the state: *Callionima falcifera* (Gehlen), *Eumorpha vitis* (L.), *Madoryx bubastus* (Cramer), and *Nyceryx coffaeae* (Walker), which increases the total to 135 species for the region. Of these, three species (*C. falcifera*, *E. vitis*, and *N. coffaeae*) with previous records in the Global Biodiversity Information Facility ([www.gbif.org](http://www.gbif.org)) are supported by preserved specimens. *Madoryx bubastus* represents a new record for Veracruz.

The results of this study indicate that species richness in our study site is higher than what has been previously documented in other studies conducted in the state of Veracruz. Lara-Pérez et al. (2020), who used a methodology similar to that of our study, recorded 41 species in the semideciduous forest of Veracruz with a sampling coverage of 96% and an asymptotic richness of 50 species. Cerón (2015) observed 35 species in the mesophytic forest of Zongolica, Veracruz. Hernández-Baz (1989) documented 39 species in the urban area and coffee plantations of the city of Xalapa. Beutelspacher (1978) recorded 42 species in the mountain mesophyll forest of Las Minas, Veracruz. The species richness found in the that study was lower than that reported by Beutelspacher (1989) in the high evergreen forest of Veracruz, where 71 species were recorded. The differences observed among these studies could be attributed to habitat heterogeneity, altitudinal gradient, climatic variations, or even differences in sampling effort.

Compared with other studies in low deciduous forests of Mexico and the Neotropical region, in general the species richness documented in the present work is lower. For example, Pescador Rubio (1994) reported 82 sphinx species on the Pacific slope in

Jalisco. Janzen (1986) recorded a similar richness with 83 species in the low deciduous forest of Santa Rosa National Park, Costa Rica. These differences can be attributed mainly to the difference in the extension and conservation status of the ecosystem. In Mexico, the low deciduous forest has a greater extension in the Pacific zone (CONA-BIO 2022), in contrast to the Atlantic region, where only three fragments are listed in the north, center, and south of the country (Rzedowski 1978). In a Costa Rican National Park, the richness could be associated with a greater extension and a better conservation status due to the protection efforts implemented in the Guanacaste Conservation Area (Janzen and Hallwachs 2020).

We found a high proportion of males (85.09%) than females (14.91%) throughout the study period. This finding is consistent with those of other studies because males tend to be more attracted to light traps. However, this difference may also be attributed to other factors, including the population or community structure itself; males could be more numerous or perhaps more active than females in the study area (Garris and Snyder 2010, Degen et al. 2016).

The results of the present study demonstrate the influence of rainfall and temperature on the population dynamics of Sphingidae in the study region. Although species composition did not differ significantly between the rainy and dry seasons, significant differences in species richness and abundance were observed, which were higher during the rainy season. This finding suggests that the same species are present throughout the year, but their numbers and representation fluctuate according to the season. This result supports the hypothesis that climatic seasonality (particularly wet conditions) positively influences the diversity of Sphingidae in agroecosystems associated with low deciduous forest fragments in Veracruz.

The models indicated that precipitation and temperature explain 49.97% and 45.58% (adjusted  $R^2$ ) of the variation in species richness and abundance, respectively. Precipitation, temperature, relative humidity, and photoperiods are among the main climatic factors that temporally influence noctuid moth species turnover (Montero-Muñoz et al. 2013, Ríos-González et al. 2019). Sphingids are ectothermal insects, so their behavior, physiology, phenotype, and reproductive success are closely linked to environmental variables such as temperature and precipitation, making these insects a good indicator of the impact of climate change (Hill et al. 2021). The positive correlation of precipitation with richness and abundance with a 1-mo lag indicates that precipitation has an indirect effect on species richness and abundance, suggesting that this correlation is due to the change in food resources or interactions between species in this area with such distinctive climatic seasonality based on the effect of rainfall (Deguines et al. 2017).

In the state of Veracruz, the study by Lara-Pérez et al. (2020) in the midaltitude semideciduous forest is the only one in which the relationship between temperature and precipitation and the richness and abundance of hawkmoths has been assessed. These authors did not find any correlation, contrary to the results of our work. This difference in results can be easily explained by the fact that most host plants in the midaltitude semideciduous forest have leaves all year round, which seems to be influencing the abundance of species (Lara-Pérez et al. 2020). Such findings are the reverse of what had been found in low deciduous forests, where the distribution and diversity of vegetation changes dramatically depending on climatic variations (Rzedowski 2006, Axmacher et al. 2009, Montero-Muñoz et al. 2013).

The state of Veracruz has no natural areas under protection, safeguarding fragments of low deciduous forest, and no taxonomic inventories of nocturnal butterflies have been done in protected areas in Mexico (ENCUSP 2021). Because inventories play an essential role in any conservation program or plan (Medina et al. 2022), the results of the present work contribute to a baseline for pollinator conservation, stressing the importance of implementing sustainable agricultural practices that favor coexistence with biodiversity.

### Acknowledgments

We thank CONAHCYT for grant 843339 and the School of Agricultural Sciences of Universidad Veracruzana for allowing us to use the La Bandera Experimental Center facilities. We are also indebted to Victor Zepeda for his assistance in most of the collections.

### References Cited

- Arias, D., O. Dorado and B. Maldonado. 2002.** Biodiversidad e importancia de la selva baja caducifolia: La Reserva de la Biosfera Sierra de Huautla. *Biodiversitas* 45: 7–12.
- Axmacher, J.C., G. Brehm, A. Hemp, H. Tunte, H.V.M. Lyaruu, K. Muller-Hohenstein and K. Fiedler. 2009.** Determinants of diversity in Afrotropical herbivorous insects (Lepidoptera: Geometridae): Plant diversity, vegetation structure or abiotic factors. *J. Biogeogr.* 36: 337–349.
- Beutelspacher, C.R. 1978.** Familias Sphingidae y Saturniidae (Lepidoptera) de Las Minas. *Anales Inst. Biol. Univ. Nac. Autón. Méx. Ser. Zool.* 49: 219–230.
- Beutelspacher, C.R. 1989.** Lepidópteros de Los Tuxtlas, Veracruz, México. La Familia Sphingidae. *Anales Inst. Biol. Univ. Nac. Autón. Méx. Ser. Zool.* 60: 359–382.
- Buxton, M.N., A.C. Gaskett, J.M. Lord and D.E. Pattemore. 2022.** A global review demonstrating the importance of nocturnal pollinators for crop plants. *J. Appl. Ecol.* 59: 2890–2901.
- Cerón, J.O.E. 2015.** Los Sphingidae (Insecta: Lepidoptera) del Municipio de Zongolica, Veracruz, México. Tesis Licenciatura. Facultad de Ciencias Biológico-Agropecuarias-Córdoba, Univ. Veracruzana, Veracruz, México. 49 pp.
- Chao, A., N.J. Gotelli, T.C. Hsieh, E.L. Sander, K.H. Ma, R.K. Colwell and A.M. Ellison. 2014.** Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecol. Monogr.* 84: 45–67.
- CONABIO (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad). 2020.** Regiones biogeográficas de México. 13 September 2023. (<https://www.biodiversidad.gob.mx/region/regiones-biogeograficas>).
- CONABIO (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad). 2022.** Ecosistemas de México—Selvas secas. 3 December 2024. (<https://www.biodiversidad.gob.mx/ecosistemas/selvaSeca>).
- Correa-Carmona, Y., A.H. Vélez-Bravo and M.I.W. Etcheverri. 2015.** Current status of knowledge of Sphingidae Latreille, 1802 (Lepidoptera: Bombycoidea) in Colombia. *Zootaxa*. 3987: 1–73.
- D'Abrera, B. 1986.** Sphingidae Mundi. Hawk Moths of the World. Classey, Faringdon, U.K.
- Degen, T., O. Mitesser, E.K. Perkin, N.S. Weiß, M. Oehlert, E. Mattig and F. Hölker. 2016.** Street lighting: Sex-independent impacts on moth movement. *J. Anim. Ecol.* 85: 1352–1360.
- Deguines, N., J.S. Brashares and L.R. Prugh. 2017.** Precipitation alters interactions in a grassland ecological community. *J. Anim. Ecol.* 86: 262–272.
- Domínguez, G.L.F. and L.M. Ruíz, Q. 2013.** Descripción de los árboles y arbustos nativos localizados en el rancho La Bandera, Actopan, Veracruz. Tesis de Licenciatura. Univ. Veracruzana, Veracruz, México.

- ENCUSP. 2021.** Estrategia Nacional para la Conservación y Uso Sustentable de los Polinizadores, 1st ed. Gobierno de México. 116 pp.
- Fernández Yépez, F. and J.M. González. 1994.** Fauna del Parque Nacional “Henri Pittier”, Aragua, Venezuela: Esfingidos (Lepidoptera: Sphingidae) de Rancho Grande. Bol. Mus. Ent. Univ. Valle. 2: 43–54.
- Forehand, L.M., D.B. Orr and H.M. Linker. 2006.** Insect communities associated with beneficial insect habitat plants in North Carolina. Environ. Entomol. 35: 1441–1549.
- García, J.L. 1978.** Influencia de los factores ambientales sobre la captura nocturna de Sphingidae (Lepidoptera) en Rancho Grande, Estado Aragua, Venezuela. Rev. Fac. Agron. (Maracay) 9: 63–107.
- Garris, H.W. and J.A. Snyder. 2010.** Sex-specific attraction of moth species to ultraviolet light traps. Southeast. Nat. 9: 427–434.
- Haber, W.A. 1983.** Checklist of Sphingidae, Pp. 645–650. In Janzen, D.H. (ed.), Costa Rican Natural History. Univ. Chicago Press, Chicago, IL.
- Haxaire, J. and T. Melichar. 2023.** A review of the *Xylophanes tyndarus* (Boisduval, 1875) species group, with the description of a new species (Lepidoptera, Sphingidae, Macroglossinae). Eur. Entomol. 15: 187–246.
- Hernández-Baz, F. 1989.** La familia Sphingidae (Lepidoptera: Heterocera) de Xalapa, Veracruz, México. Rev. Soc. Mex. Lepid. 13: 17–24.
- Hernández-Baz, F. and L. Iglesias-Andrew. 2001.** La diversidad del orden Lepidoptera en el estado de Veracruz, México: Una síntesis preliminar. Cuad. Biodivers. 7: 7–10.
- Hill, G.M., A.Y. Kawahara, J.C. Daniels, C.C. Bateman and B.R. Scheffers. 2021.** Climate change effects on animal ecology: Butterflies and moths as a case study. Biol. Rev. 96: 2113–2126.
- Hsieh, T.C., K.H. Ma and A. Chao. 2016.** iNEXT: An R package for interpolation and extrapolation of species diversity (Hill numbers). Methods Ecol. Evol. 7: 1451–1456.
- Janzen, D.H. 1986.** Biogeography of an unexceptional place: What determines the saturniid and sphingid moth fauna of Santa Rosa National Park, Costa Rica, and what does it mean to conservation biology. Brenesia 25: 51–87.
- Janzen, D.H. and W. Hallwachs. 2020.** Área de Conservación Guanacaste, northwestern Costa Rica: Converting a tropical national park to conservation via biodevelopment. Biotropica 52: 1017–1029.
- Johnson, S.D., M. Moré, F.W. Amorim, W.A. Haber, G.W. Frankie, D.A. Stanley, A.A. Cocucci and R.A. Raguso. 2017.** The long and the short of it: A global analysis of hawkmoth pollination niches and interaction networks. Funct. Ecol. 31: 101–115.
- Kitching, I.J. 2023.** Sphingidae Taxonomic Inventory. 10 August 2024. (<http://sphingidae.myspecies.info/>).
- Kitching, I.J. and J.M. Cadiou. 2000.** Hawkmoths of the World: An Annotated and Illustrated Revisionary Checklist (Lepidoptera: Sphingidae). The Natural History Museum, London and Cornell Univ. Press, Ithaca, NY.
- Kitching, I.J., R. Rougerie, A. Zwick, C.A. Hamilton, R.A. St. Laurent, S. Naumann and A.Y. Kawahara. 2018.** A global checklist of the Bombycoidea (Insecta: Lepidoptera). Biodivers. Data J. 6: e22236-13.
- Lamas, G. 1985.** The Castniidae and Sphingidae (Lepidoptera) of the Tambopata Reserved Zone, Madre de Dios, Perú: A preliminary list. Rev. Per. Entomol. 27: 55–58.
- Lara-Pérez, L.A., P.J. Ramírez-Barajas, J. Campos-Domínguez, I. Oros-Ortega, F. Hernández-Baz and F. Casanova-Lugo. 2020.** Species richness and seasonal abundance of hawk moth fauna in a fragment of tropical semi-deciduous forest of Veracruz, Mexico. Southwest. Entomol. 45: 147–160.
- León-Cortés, J.L. 2000.** Sphingoidea (Lepidoptera), Pp. 483–500. In Llorente, J.B., E.S. González and N. Papavero (eds.), Biodiversidad, Taxonomía y Biogeografía de Artrópodos en México: Hacia una Síntesis de su Conocimiento. UNAM, México City, México.
- León-Cortés, J.L. and A.R. Pescador. 1998.** The Sphingidae of Chajúl, Chiapas, México. J. Lepid. Soc. 52: 105–114.

- Llorente-Bousquets, J., I. Vargas-Fernández, A. Luis-Martínez, M. Trujano-Ortega, B.C. Hernández-Mejía and A.D. Warren. 2014.** Biodiversity of Lepidoptera in Mexico. *Rev. Mex. Biodivers.* 85: S353–S371.
- Medina, S.A., M.Y. Díaz and M.J.M. de la Cruz. 2022.** Propuesta de estrategia de conservación y monitoreo de lepidópteros en áreas protegidas administradas por ECOVIDA. *Rev. ECOVIDA* 12: 267–275.
- Montero-Muñoz, J.L., C. Pozo and M.F. Cepeda-González. 2013.** Recambio temporal de especies de lepidópteros nocturnos en función de la temperatura y la humedad en una zona de selva caducifolia en Yucatán, México. *Acta Zool. Mex.* 29: 614–628.
- Ollerton, J. 2017.** Pollinator diversity: Distribution, ecological function, and conservation. *Annu. Rev. Ecol. Evol. Syst.* 48: 353–376.
- Pescador Rubio, A. 1994.** Manual de identificación para las mariposas de la familia Sphingidae (Lepidoptera) de la estación de biología “Chamela”, Jalisco, México. UNAM Inst. Biol. Cuadernos 22: 1–103.
- R Core Team. 2023.** R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ricketts, T.H. 2004.** Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conserv. Biol.* 18: 1262–1271.
- Ricketts, T.H., G.C. Daily, P.R. Ehrlich and C.D. Michener. 2004.** Economic value of tropical forest to coffee production. *Proc. Natl. Acad. Sci. U.S.A.* 101: 12579–12582.
- Ríos-González, T.A., Y.T. Saldaña, G.A. Vargas and J.A. Bernal-Vega. 2019.** Sphingidae y Saturniidae (Insecta: Lepidoptera) de la Reserva Forestal Fortuna y el Parque Internacional La Amistad, Panamá. *Rev. Mex. Biodivers.* 90: 1–13.
- Rzedowski, J. 1978.** Vegetación de México. Limusa, México.
- Rzedowski, J. 2006.** Vegetación de México, 1st ed. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México.
- Salem, A.M.A. 2022.** Lepidoptera of Egypt part III: Revision of family Sphingidae (Bombycoidea). *Am. J. Entomol.* 6: 7–13.
- Schreiber, H. 1978.** Dispersal centres of Sphingidae (Lepidoptera) in the Neotropical Region. *Biogeographica*. Junk B.V., The Hague, Netherlands. 201 pp.
- Silva-Aparicio, M., A.E. Castro-Ramírez, G. Castillo-Campos and H. Perales-Rivera. 2018.** Estructura de la vegetación leñosa en tres áreas con Selva Baja Caducifolia en el Istmo-Costa de Oaxaca, México. *Rev. Biol. Trop.* 66: 863–879.
- Siyum, Z.G. 2020.** Tropical dry forest dynamics in the context of climate change: Syntheses of drivers, gaps, and management perspectives. *Ecol. Process.* 9: 1–16.
- Stöckl, A.L. and A. Kelber. 2019.** Felling on the wing: Sensory ecology of hawkmoth foraging. *J. Comp. Physiol. A* 205: 399–413.
- Trejo, I. and R. Dirzo. 2000.** Deforestation in seasonally dry tropical forests: A national and local analysis in Mexico. *Biol. Conserv.* 94: 133–142.
- Valente, D.M.P. and J.A. Teston. 2024.** Vertical stratification of Sphingidae moths (Lepidoptera: Bombycoidea: Sphingidae) in the Tapajós National Forest, Pará, Brazil. *Zoología* 41: 1–9.
- Wardhaugh, C.W. 2015.** How many species of arthropods visit flowers? *Arthropod-Plant Interact.* 9: 547–565.
- Zaragoza-Villela, E., R. Gámez-Pastrana and F. Hernández-Baz. 2019.** Distribución potencial del gusano cornudo del tabaco *Manduca sexta sexta* (Linnaeus, 1763) en México, Pp. 84–102. *In* Vinay, V.J.C., V.A. Esqueda E., O.H. Tosquy V. R., Zetina L., A. Ríos U., M.V. Vázquez H., A.L. Del Ángel P., and C. Perdomo M. (eds.), *Avances en Investigación Agrícola, Pecuaria, Forestal, Acuicola, Pesquería, Desarrollo Rural, Transferencia de Tecnología, Biotecnología, Ambiente, Recursos Naturales y Cambio Climático*. INI-FAP, CP, UACH, INAPESCA, UV, TecNM, Medellín, Veracruz, México.