

## Small sample, substantial contribution: additions to the Honduran hawkmoth (Lepidoptera: Sphingidae) fauna based on collections from a mountainous protected area (Cusuco National Park)

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**Abstract** With the largest part of diversity in the world absorbed by invertebrates, ignoring invertebrates in biodiversity surveys and monitoring of areas under conservation would give a strongly incomplete image. The poor knowledge of most invertebrate taxa and their enormous diversity limits most surveys to the better-studied groups. Hawkmoths (Lepidoptera: Sphingidae) are one of the more charismatic and well-known groups among the Lepidoptera and hence a valuable group commonly used in biodiversity research. In this small-scale study, 42 museum specimens of sphingids from Cusuco National Park (Cortés, Honduras) were identified and compared to recent published accounts. This yielded three new country records and, in addition, four new regional records for the park. Some of the additions to the Honduran fauna probably result from recent taxonomic changes. However, the several contributions using a small collection of this well-studied group in

an area which has attracted previous research interest, demonstrate the incomplete data availability and the necessity for more rigorous surveying. Several new records concern high altitude species, indicating the data gap in mountains. As elevation is an important determinant of sphingid community structure, sampling across an altitudinal range is recommended. This study also underpins the usefulness of a reference collection-based approach in particular, as many hawkmoth species are identified using subtle diagnostic characters.

**Keywords** *Adhemarius* · Biodiversity · *Eumorpha* · *Manduca* · Meso-America · *Xylophanes*

The size and attractiveness of its representatives have made the hawkmoths (Lepidoptera: Sphingidae) one of the better studied groups of lepidopterans, with monographs dating

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back to the 19th century (e.g. Druce 1881–1900; Smith 1888; Weidemeyer et al. 1903; Moss 1920) and approximately 1450 recognised species (Kitching et al. 2011). Their charismatic and conspicuous habitus, the substantial amount of information available and their importance as pollinators of many plants (see Young 1972; Haber and Frankie 1989; Darrault and Schlindwein 2002) make sphingids prime focal species in biodiversity surveys and monitoring efforts (e.g. Owen 1972; Motta et al. 1998; Darrault and Schlindwein 2002; Duarte and Schlindwein 2008; Duarte et al. 2008; Amorim et al. 2009). They have featured as target organisms in ecological research (e.g. Seifert 1974; León-Cortés et al. 1998; Marinoni et al. 1999).

Lepidoptera depend on a range of crucial habitat features for their survival, including nectar sources for adults, host plants for the larva and suitable pupation sites. Any change in the ecosystem that alters the availability of these requirements will affect a population's viability (Moss 1920; Pittaway 1993). Therefore, habitat loss and disturbance pose substantial threats to hawkmoth diversity. This sensitivity to habitat alterations together with their contribution to ecological services and high species numbers means many moth species are of particular conservation concern (Birkinshaw and Thomas 1999; Fox et al. 2011). Although hawkmoths are a relatively well-studied group, there are still major shortfalls in their taxonomy (Kitching and Cadiou 2000), geographic distribution and population density estimates, all of which are needed to evaluate rarity and hence their conservation status. There is a geographical bias on the amount of information available for this group with especially some parts of Central America largely understudied.

The recent checklist of Honduran Sphingidae listed 107 species, 33 of which were new country records (Samayoa and Cave 2008). It was composed based on museum specimens and material collected from four national parks, including Cusuco National Park (CNP) (Departamento de Cortés, Honduras). In the latter, Samayoa and Cave (2008) reported 25 sphingid species. The core zone of CNP consists of lower montane tropical rain forest, gradually transitioning to upper montane rain forest with patches of primary cloud forest at the highest point (Cerro Jilincó—2 245 m masl). We studied a small collection of 42 sphingid moths at the Oxford University Museum of Natural History (accession number OUMNH-2006-082). The insects were collected as part of the Operation Wallacea yearly biodiversity survey from May to August 2006. In contrast to “classic” mercury vapour lights, actinic light traps were used (though higher wattage, e.g. 250 or 400 W, mercury vapour lights have also been proven effective) (see Sinclair 2004; van Langevelde et al. 2011). Species were identified using D’Abrera (1986), Cadiou and Haxaire (1997), Cadiou and Hodges (1998), Kitching and Cadiou (2000), Vaglia and Haxaire (2005) and Martin et al. (2011).

*Xylophanes* and *Adhemarius* were the dominant genera in terms of diversity and abundance, confirming the study of Sinclair (2004) in CNP. The present batch contained 13 species, three of which were hitherto unknown from Honduras. Another four species, previously recorded from the country, were new to the department (Cortés) and thus to CNP (Table 1). This collection also contains the second formal country record for *Adhemarius dariensis* (Rothschild and Jordan, 1916), *A. ypsilon* (Rothschild and Jordan, 1903) and *Xylophanes belti* (Druce, 1878). The other sphingids collected—*Eumorpha vitis vitis* (Linnaeus, 1758), *X. ceratomioides* Grote and Robinson 1866 and *X. germen germen* (Schaus, 1890)—have been previously reported and are widespread in Honduras.

Cusuco National Park is one of the four study sites for the extensive and year-round survey of Samayoa and Cave (2008). It is therefore surprising that the present small-scale sampling effort has yielded four additional regional records and nearly as many new country records. Some of these additions to the Honduran fauna are likely to have arisen from recent taxonomic changes, dividing up species along their geographical range (e.g. *X. cthulhu* is likely to have been identified as *X. neoptolemus*, though this species was not recorded from Cortés by Samayoa and Cave (2008)). While such cases do not represent a true increase in the sphingid diversity, it is difficult to ascertain which of the (sub)species listed by Samayoa and Cave (2008) could have accommodated the other new species first recorded here. Moreover, we would like to note that some of the specimens depicted in Samayoa and Cave (2008) represent, in our view, misidentifications (Table 2), which could have led to errors in the national and regional species lists as well (e.g. *X. hannemanni hannemanni*).

Mountain reaches and cloud forests in Meso-America are characterized by a particular fauna and flora, often with a high rate of endemism, in particular for invertebrates (Anderson and Ashe 2000). These substantial contributions to the Honduran sphingid fauna emphasize the limited knowledge we have, even of the better-studied large-bodied invertebrate groups in this region, something which has previously been highlighted for relatively well-studied beetle taxa such as Scarabaeoidea (Schuster and Cano 2006) as well as Curculionidae and Staphylinidae (Anderson and Ashe 2000). It is hard to extrapolate from the studied sphingid material a total species richness (León-Cortés et al. 1998). Nevertheless, substantial contributions from small collections illustrate the need for more intensive (standardized) surveys over all habitat and elevation ranges, in order to reliably predict species distributions and adequately assess other parameters needed for conservation purposes, e.g. Red List assignment (see Lewis and Senior 2011). This situation is far from unique. Recent surveys continue to provide new records and

**Table 1** New species records for the state of Cortés and for Honduras

	Species	Classification	Geographical distribution	Known altitudinal range in Honduras (m)	Collection altitude (m)
New to Cortés	<i>Eumorpha phorbis</i> (Cramer, 1775)	Macroglossinae, Philampelini	MEX, GTM, BLZ, NIC, CRC, VEN, COL, SUR, FG, PER, ECU, BOL, BRA	35–185	534
	<i>Manduca pellenia</i> (Herrich-Schäffer, 1854)	Sphinginae, Sphingini	MEX, BLZ, GTM, NIC, CRC, PAN, COL, ECU	175–1,450	1,572
	<i>Xylophanes anubus</i> (Cramer, 1777)	Macroglossinae, Macroglossini	MEX to ARG	35–1,450	ca. 1,200
	<i>X. hannemanni hannemanni</i> Closs, 1917	Macroglossinae, Macroglossini	MEX to BOL	/	1,174–1,379
New to Honduras	<i>Adhemarius fulvescens</i> (Closs, 1915)	Smerinthinae, Ambulycini	MEX, GTM, BLZ, CRC, NIC	/	1,174–1,546
	<i>X. staudingeri</i> (Rothschild, 1894)	Macroglossinae, Macroglossini	MEX, SLV, GTM, NIC, CRC, PAN	/	1,656
	<i>X. thulhu</i> Haxaire and Vaglia, 2008	Macroglossinae, Macroglossini	MEX, GTM, CRC	/	534

ARG Argentina, BLZ Belize, BOL Bolivia, BRA Brazil, COL Colombia, CRC Costa Rica, ECU Ecuador, FG French Guiana, GTM Guatemala, GUY Guyana, MEX Mexico, NIC Nicaragua, PAN Panama, PER Peru, SLV El Salvador, SUR Suriname, VEN Venezuela

Classification follows Kitching and Cadiou (2000); distributional data are taken from Maes (1998), Samayoa and Cave (2008), Martin et al. (2011), Kitching et al. (2011), Oehlke (2011) and references therein. Note that for *X. hannemanni*, albeit tentatively mentioned for Honduras by Oehlke (2011), no detailed observations are provided by this author nor by Samayoa and Cave (2008), leading us to believe we are dealing with the first formal record of this species in the region. While *X. staudingeri* is hard to distinguish from *X. cyrene* (Druce, 1881) and species status has been under discussion (Kitching and Cadiou 2000), the pronounced green color of the specimen and the sampling altitude (see Oehlke 2011) led us to identify it as *X. staudingeri*. As neither of them has been previously recorded from Honduras, even regarding them as a species complex would mean an addition to the country’s fauna

**Table 2** Probable misidentifications (middle column) and our species assignments (right) based on hawkmoth pictures in Samayoa and Cave (2008)

Lámina/plate	Probable misidentification	Our assignment
Fig. II	<i>Madoryx plutonius</i> (Hübner, 1819)	<i>M. plutonius dentatus</i> Gehlen, 1931
Fig. III	<i>Perigonia lusca</i> (Fabricius, 1777)	<i>P.ilus</i> Boisduval, 1870
Fig. IV	<i>Xylophanes acrus</i> Rothschild and Jordan, 1910	<i>X. cyrene</i> (Druce, 1881)
	<i>X. damocrita</i> (Druce, 1894)	<i>X. josephinae</i> Clark, 1920
Fig. V	<i>X. neoptolemus</i> (Cramer, 1780)	<i>X. thulhu</i> Haxaire and Vaglia, 2008
	<i>X. porcus continentalis</i> Rothschild and Jordan, 1903	<i>X. hannemanni hannemanni</i> Closs, 1917
Fig. VI	<i>Eumorpha anchemolus</i> (Cramer, 1779)	<i>E. triangulum</i> (Rothschild and Jordan, 1903) (female)
	<i>E. triangulum</i>	<i>E. anchemolus</i>
Fig. VII	<i>Adhemarius donysa</i> (Druce, 1889)	<i>A. dariensis</i> (Rothschild and Jordan, 1916) (male)
	<i>A. gannascus</i> (Stoll, 1790)	<i>A. fulvescens</i> (Closs, 1915) (female)
Fig. VIII	<i>Manduca hannibal</i> (Cramer, 1779)	<i>M. hannibal mayeri</i> (Mooser, 1940)

Note that *Lintneria merops* (Boisduval, 1870) (assigned to *Lintneria* Butler, 1876 by Tuttle (2007)) was treated by Samayoa and Cave (2008) as *Sphinx merops*

species discoveries, even for well-studied insect and other invertebrate groups that have been proposed as useful models in biodiversity research or as of conservation importance in terms of their ecosystem function. Examples from the Neotropics include Scarabaeoidea (Schuster and Cano 2006), Drosophilidae (Medeiros and Klazcko 2004; Mata et al. 2008, 2010), Odonata (Kalkman et al. 2008) and corals (Reaka-Kudla 1997), in addition to countless smaller and less conspicuous organisms no less functionally

important, e.g. endophagous mites and insects and soil-dwelling nematodes (Lewinsohn et al. 2005).

*Adhemarius fulvescens* and *X. staudingeri*, two of the three species reported in this study as new to Honduras, were recorded from sites at relatively high altitude, particularly *X. staudingeri*. Likewise, some of the new records for Cortés constitute confirmed altitude extensions for two species (Table 1). Despite a decline of species richness with increasing elevation (Samayoa and Cave 2008), this

demonstrates the need to include high altitude surveying in biodiversity studies, especially for sphingids since Ignatov et al. (2011) previously showed the importance of altitude as factor in sphingid community composition.

Raising entities previously considered to be geographical forms to species status might not increase local biodiversity. It does however point to the fact that populations concerned should be managed as entities that are less widely distributed than previously assumed, possibly deserving additional conservation effort. Genetic analysis would be beneficial both in terms of clarifying the species status and in order to establish the degree of genetic distinctiveness of the population particularly in light of the high proportion of endemic insects already known from CNP (Anderson and Ashe 2000; Schuster and Cano 2006). Evolutionary Significant Units (Moritz 1994) can be defined through detailed molecular analysis and used for management purposes to ensure conservation of maximal genetic diversity in a given species. Several sphingids in this study have recently undergone taxonomic reevaluation based on characters that are nearly impossible to use in the field (see e.g. Cadiou and Hodges 1998; Vaglia and Haxaire 2005), sometimes in combination with genetic data (e.g. Vaglia et al. 2008). Genital features can be useful in view of the many documented cases of intraspecific morphological variation in size or colour pattern (e.g. Brou 1994; Hundsdoerfer and Wink 2006; Schmidt 2009), in some lepidopterans possibly influenced by altitude and other environmental factors (Sullivan 2007). Hence, in order to clarify possible misidentifications, especially for “cryptic” species, further revision supported by voucher specimens deposited in accessible museum collections which can be made available for study by specialist taxonomists is strongly recommended.

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## References

- Amorim FW, de Ávila RS Jr, de Camargo AJA, Vieira AL, Oliveira PE (2009) A hawkmoth crossroads? Species richness, seasonality and biogeographical affinities of Sphingidae in a Brazilian Cerrado. *J Biogeogr* 36:662–674
- Anderson RS, Ashe JS (2000) Leaf litter inhabiting beetles as surrogates for establishing priorities for conservation of selected tropical montane cloud forests in Honduras, Central America (Coleoptera; Staphylinidae, Curculionidae). *Biodivers Conserv* 9(5):617–653
- Birkinshaw N, Thomas CD (1999) Torch-light transect surveys for moths. *J Insect Conserv* 3:15–24
- Brou VA (1994) A new species of *Lapara* (Sphingidae) from southeastern United States. *J Lepid Soc* 48(1):51–57
- Cadiou J-M, Haxaire J (1997) Description of new taxa in the genera *Paonias*, *Nyceryx* and *Xylophanes* with a revision of associated species (Lepidoptera, Sphingidae). *Lambillionea* 97:569–584
- Cadiou J-M, Hodges RW (1998) *Adhemarius donysa* (Druce): identification and notes on closely related species (Lepidoptera: Sphingidae). *Proc Entomol Soc Wash* 100(2):202–208
- D’Abreu B (1986) Sphingidae Mundi—hawk moths of the world. E.W. Classey Ltd., Faringdon
- Darrault RO, Schlindwein C (2002) Esfingídeos (Lepidoptera, Sphingidae) no Tabuleiro Paraibano, nordeste do Brasil: abundância, riqueza e relação com plantas esfingófilas. *Rev Bras Zool* 19(2):429–443 [Hawkmoths (Lepidoptera, Sphingidae) in the Tabuleiro Paraibano, northeastern Brazil: abundance, richness and relations to sphingophilous plants.]
- Druce H (1881–1900) *Insecta. Lepidoptera-Heterocera* vol III. R.H. Porter, London
- Duarte JA Jr, Schlindwein C (2008) Hawkmoth fauna of a northern Atlantic rain forest remnant (Sphingidae). *J Lepid Soc* 62(2):71–79
- Duarte M, Carlin LF, Marconato G (2008) Light-attracted hawkmoths (Lepidoptera: Sphingidae) of Boracéia, municipality of Salesópolis, state of São Paulo, Brazil. *CheckList* 4(2):123–136
- Fox R, Randle Z, Hill L, Anders S, Wiffen L, Parsons MS (2011) Moths count: recording moths for conservation in the UK. *J Insect Conserv* 15:55–68
- Haber WA, Frankie GW (1989) A tropical hawkmoth community: Costa Rican dry forest Sphingidae. *Biotropica* 21(2):155–172
- Hundsdoerfer AK, Wink M (2006) Incongruence of morphology and genetic markers in *Hyles tithymali* (Lepidoptera: Sphingidae) from the Canary Islands. *J Zool Syst Evol Res* 44(4):316–322
- Ignatov II, Janovec JP, Centeno P, Tobler MW, Grados J, Lamas G, Kitching IJ (2011) Patterns of richness, composition, and distribution of sphingid moths along an elevational gradient in the Andes-Amazon region of Southeastern Peru. *Ann Entomol Soc Am* 104(1):68–76
- Kalkman VJ, Clausnitzer V, Dijkstra K-DB, Orr AG, Paulson DR, van Tol J (2008) Global diversity of dragonflies (Odonata) in freshwater. *Hydrobiologia* 595:351–363
- Kitching IJ, Cadiou J-M (2000) Hawkmoths of the world—an annotated and illustrated checklist (Lepidoptera: Sphingidae). The Natural History Museum, London and Cornell University Press, Ithaca and London
- Kitching IJ, Scoble MJ, Smith CR, James S, Young R, Blagoderov V (2011) CATE sphingidae. <http://www.cate-sphingidae.org>. Accessed 21 Nov 2011
- León-Cortés JL, Soberón-Mainero J, Llorente-Bousquets J (1998) Assessing completeness of Mexican sphinx moth inventories through species accumulation functions. *Divers Distrib* 4:37–44
- Lewinsohn TM, Freitas AVL, Prado PI (2005) Conservation of terrestrial invertebrates and their habitats in Brazil. *Conserv Biol* 19(3):640–645
- Lewis OT, Senior MJM (2011) Assessing conservation status and trends for the world’s butterflies: the sampled red list index approach. *J Insect Conserv* 15:121–128
- Maes JM (1998) Insectos de Nicaragua. SETAB BOSAWAS, MARZOENA, Managua
- Marinoni RC, Dutra RRC, Mielke OHH (1999) Levantamento da fauna entomológica no Estado do Paraná. IV. Sphingidae

- (Lepidoptera). Diversidade alfa e estrutura de comunidade. Rev Bras Zool 16(2):223–240 [Survey of the entomological fauna in Paraná State. IV. Sphingidae (Lepidoptera). Alpha diversity and community structure.]
- Martin A, Soares A, Bizarro J (2011) A guide to the hawkmoths of the Serra dos Orgaos. Regua Publications, South-eastern Brazil
- Mata RA, Roque F, Tidon R (2008) Drosophilids (Insecta, Diptera) of the Paranã valley: eight new records for the Cerrado biome. Biota Neotrop 8(1):55–60
- Mata RA, McGeoch M, Tidon R (2010) Drosophilids (Insecta, Diptera) as tools for conservation biology. Nat Conserv 8(1):60–65
- Medeiros HF, Klaczko LB (2004) How many species of *Drosophila* (Diptera, Drosophilidae) remain to be described in the forests of São Paulo, Brazil? Species lists of three forest remnants. Biota Neotrop 4(1):1–12
- Moritz C (1994) Defining ‘Evolutionarily Significant Units’ for conservation. Trends Ecol Evol 9(10):373–375
- Moss AM (1920) Sphingid of Para. Brasil. Early stages, food plants, habits, etc. Novit Zool 27:333–415
- Motta CS, Aguilera-Peralta FJ, Andreazze R (1998) Aspectos da Esfingofauna (Lepidoptera: Sphingidae), em área de terra firme, no Estado do Amazonas, Brasil. Acta Amaz 28(1):75–92
- Oehlke B (2011) Sphingidae of the Americas. <http://www.silkmoths.bizland.com/danjansphinx.htm>. Accessed 3 Nov 2011
- Owen DF (1972) Species diversity in tropical Sphingidae and a systematic list of species collected in Sierra Leone. J Nat Hist 6(2):177–194
- Pittaway AR (1993) The hawkmoths of the western Palearctic. Harley Books, Colchester
- Reaka-Kudla ML (1997) The global biodiversity of coral reefs: a comparison with rain forests. In: Reaka-Kudla ML, Wilson DE, Wilson EO (eds) Biodiversity II: understanding and protecting our biological resources. Joseph Henry Press, Washington, DC, pp 83–108
- Samayoa AC, Cave RD (2008) Catálogo de las especies de Sphingidae (Lepidoptera) en Honduras. Ceiba 49(1):103–117
- Schmidt BC (2009) *Hemaris thetis* (Boisduval, 1855) (Sphingidae) is a distinct species. J Lepid Soc 63(2):100–109
- Schuster JC, Cano EB (2006) What can Scarabaeoidea contribute to the knowledge of the biogeography of Guatemala? Coleopt Bull 60(5):57–70
- Seifert JL (1974) The Sphingidae of Turrialba, Costa Rica. J New York Entomol Soc 82(1):45–56
- Sinclair F (2004) Tropical forest conservation and the importance of national parks: study of the ecology of several *Chrysina* species (Coleoptera: Scarabidae: Rutelinae), and the species richness of the lepidopteran family Sphingidae in Cusuco National Park, Honduras. MSc thesis, University of London and Imperial College, London
- Smith JB (1888) A monograph of the Sphingidae of America north of Mexico. American Entomological Society, Philadelphia
- Sullivan JB (2007) Intraspecific body size variation in Macrolepidoptera as related to altitude of capture site and seasonal generation. J Lepid Soc 61(2):72–77
- Tuttle J (2007) The hawk moths of North America, a natural history study of the Sphingidae of the United States and Canada. Wedge Entomological Research Foundation, Washington, D.C
- Vaglia T, Haxaire J (2005) Revision des *Adhemarius* du complexe *gannascus* (Stoll, 1790) (Lepidoptera Sphingidae). Lambillionea 105(1):3–39
- Vaglia T, Haxaire J, Kitching IJ, Meusnier I, Rougerie R (2008) Morphology and DNA barcoding reveal three cryptic species within the *Xylophanes neoptolemus* and *loelia* species-groups (Lepidoptera: Sphingidae). Zootaxa 1923:18–36
- van Langevelde F, Ettema JA, Donners M, WallisDeVries MF, Groenendijk D (2011) Effect of spectral composition of artificial light on the attraction of moths. Biol Conserv 144:2274–2281
- Weidemeyer JW, Calverley S, Edwards WH (1903) Illustrations of North American Lepidoptera Sphingidae. American Entomological Society, Philadelphia
- Young AM (1972) Notes on a community ecology of adult sphinx moths in Costa Rican lowland tropical rain forest. Carib J Sci 12(3–4):151–163