Patterns of Richness, Composition, and Distribution of Sphingid Moths Along an Elevational Gradient in the Andes-Amazon Region of Southeastern Peru

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ABSTRACT The adult sphingid communities of three sites in southeastern Peru representative of the moist tropical forest of the lowland Amazon, the pluvial tropical forest of the upper Amazon and Andean foothills, and the montane cloud forest of the eastern slopes of the Andes were sampled during 2004–2006 by using mercury vapor light traps. In total, 119 species of Sphingidae were documented. Species diversity was highest in the upper Amazon and Andean foothills, with 94 species (21 genera), followed by 80 species (21 genera) in the Amazonian lowlands, and 43 species (17 genera) in the montane cloud forest. The greatest number of endemics (22) was registered at the upper Amazon-Andean foothills site. The montane cloud forest site was characterized by the highest relative percentage of endemic species. The species assemblages of the lowland Amazon and the Andean foothills were more similar in composition to each other than to the montane assemblage. All three assemblages proved to be more distinctive than expected based on the proximity of the sampled sites and seemingly good flight capabilities of sphingid moths. This was reflected by the endemics accounting for nearly 40% of the total species pool. By contrast, cosmopolitans numbered only 26 species, or 22% of the total assemblage. We hypothesize that the composition and distribution of sphingid species along this elevational gradient may reflect floristic similarities and differences between the study sites and the extent to which different species are adapted to cope with certain environmental conditions, such as temperature and air humidity.

KEY WORDS Amazon, Andes Mountains, Peru, Sphingidae

Although occasional sampling of selected sites by entomologists in the Andes Mountains and the Amazon is not uncommon, rarely has there been a long-term systematic monitoring of several sites representative of distinctively different phytogeographic zones. Our present knowledge of the diversity and distributional patterns of many macrolepidopteran families in the Amazon Basin is relatively patchy. Even more rudimentary is our understanding of the patterns of macrolepidopteran species distributions among the different environmental and phytogeographic zones of this immense region, especially the adult night-flying moths, such as the sphingids.

Three types of moth surveys are widely used. The most common and perhaps technically feasible are the surveys that deal with a certain single ecosystem or vegetation type (Fleming 1947, Janzen 1981, Lamas 1985, Haber and Frankie 1989, Alvarez and Alvarez 1994, Motta 1998, Devries and Walla 2001, Darrault and Schlindwein 2002, Duarte Júnior and Schlindwein 2005, Summerville and Christ 2005). Regional inventories are a more classic and labor-consuming method due to the typically larger areas covered by such research efforts. Inventories of this kind focus not so much on the ecosystems as on certain geographic areas and regions, which can harbor few or a large number of ecosystems and vegetation types. Some of the classical regional inventories of adult nocturnal Lepidoptera and specifically sphingid faunas are those of Laroca and Mielke (1975) and Holloway (1976, 1984, 1987, 1993). General patterns of sphingid distributions in the Neotropics are discussed in Schreiber (1978).

Today, many studies place a major focus on the effects of disturbance (especially anthropogenic) on adult moth (and other insect) communities. Those of Holloway et al. (1992), Chey (1994, 2002), Chey et al. (1997), Willott (1999), Beck et al. (2002), Schulze and Fiedler (2003), Fiedler and Schulze (2004) and Beck et al. (2006) involved comparisons between relatively intact or little disturbed ecosystems and highly dis-

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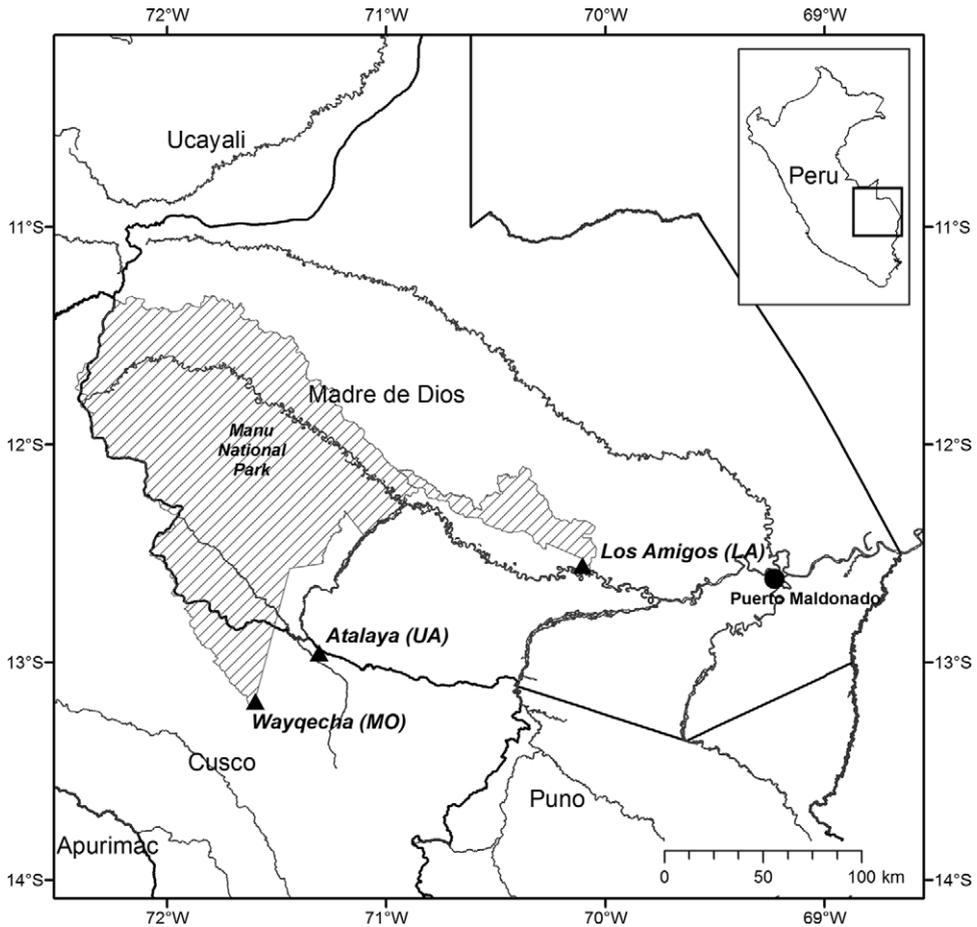
Fig. 1. Map showing the location of the three sites where this study was carried out: Los Amigos Biological Station in the Amazonian lowlands (LA), Atalaya in the upper Amazon at the base of the Andean foothills (UA), and Wayqecha Biological Station in the montane cloud forest of the Andes Mountains (MO).

turbed or artificial habitats. Others, such as those of Intachat et al. (2001), Slik (2004), and Itioka and Yamauti (2004), focused on disturbance caused by extreme weather conditions and seasonal phenological variations. Yet another study carried out by Garcia (1978) dealt with the influence of several general environmental factors upon nighttime sampling.

Against this background our study is something of a novelty. First, we are not aware of any other equally intensive long-term systematic survey that would involve the Western Amazon. The study conducted in southeastern Peru (the Tambopata Reserved Zone) by Lamas (1985) was a relatively low-intensity investigation that resulted in the capture of only 43 species of adult Sphingidae over a 4-yr period. Second, and most importantly, our study involves a basic comparative survey of several intact ecosystems.

This is the first in a series of articles analyzing the results of our studies of sphingid diversity, composition, and distribution patterns over a 2-yr period in the Andes-Amazon region of southeastern Peru. Here, we present results from basic inventory and monitoring of

sphingid communities of three major phytogeographic zones in the Andes-Amazon region of southeastern Peru: (1) lowland tropical rainforest of the Amazon, (2) pluvial tropical forest of the upper Amazon and Andean foothills, and (3) montane cloud forest of the eastern slopes of the Andes. Our primary goal in this paper is to describe the sphingid species richness, composition, and distribution patterns encountered in the region. We also provide recommendations toward the improvement of sphingid sampling along elevational gradients in biological hot spots such as the Andes-Amazon region of southeastern Peru.

Materials and Methods

Study Sites. The study was conducted during 2004–2006 at the following three sites located along one major elevational gradient in the Andes-Amazon region of southeastern Peru (Fig. 1).

Lowland Amazon (LA). Los Amigos Biological Station in the Department of Madre de Dios is located at 300 m above sea level (masl) in the Amazonian low-

lands (12° 33′36.3″ S and 70° 06′17.3″ W). The climate is tropical with a marked dry season from June to September and a rainy season from November to April. Mean annual rainfall is between 2,500 and 3,500 mm, and the mean annual temperature is 24°C, with a range from 10 to 38°C. The area is covered by continuous moist lowland tropical forest of the Amazonian type, and three major vegetation formations can be distinguished in the study area: 1) terra firme forests, which are a predominant forest type; 2) floodplain forests; and 3) wetlands.

Upper Amazon (UA). Atalaya in the Department of Cusco is located in the upper Madre de Dios River watershed at 600 masl in tropical moist to pluvial forest of the upper Amazon and the Andean foothills (12° 53′29.8″ S and 71° 21′38.8″ W). The area is characterized by the hilly relief dissected by relatively narrow river valleys, gorges, and ravines. The upland vegetation is marked by a transition from the moist lowland tropical forest to the pluvial submontane tropical forest. River valleys harbor narrow tongues of bottomland alluvial forest on high and low terraces similar to that of the Amazon Lowland. The climate is very humid; the annual precipitation is 3,000 mm, and the mean annual temperature is 27°C.

Montane Cloud Forest (MO). Wayqecha Cloud Forest Research Station in the Department of Cusco is located at 2,886 masl on the eastern slopes of the Andes (MO), in the area of Sunchubamba, which forms part of the Kcosñipata Valley (13° 10′58.5″ S and 71° 35′07.9″ W). The surrounding area is characterized by a mountainous relief dissected by narrow valleys and steep-sloped gorges. The dominant vegetation is a relatively low-stature montane cloud forest characterized by a high abundance of epiphytes. Some portions of the area are covered by grassland vegetation, which is mostly the result of anthropogenic burning and cattle grazing. The mean annual temperature is 15°C, although during the dry season (July–August) the temperature may drop below 0°C. The climate is extremely humid with an annual precipitation of 1,000–1,300 mm and nighttime relative humidity near 100%.

Inventory Technique. Sampling of sphingid moths was achieved using standard light trap techniques consisting of a 175-W mercury vapor lamp suspended in front of a white sheet hanging from ≈2 m in height and draping to the ground. A Honda EU-1000 generator was used to power the light trap. Because of frequent precipitation in the region, a small plastic roof structure was installed at the permanent trap point at each field site.

During the initial phase of the project in 2004–2005, sampling was carried out for 11 consecutive months at LA. The second phase of the project lasted for 12 mo during 2005–2006 and involved alternative months of sampling, with 6 mo at each of the UA and MO study sites. Due to budgetary, personnel, and logistical limitations, only one site could be sampled per month.

One month of sampling consisted of 15 d of light trapping at the same, permanent trap point at each of the three study sites. Each day the light trap was turned on before nightfall (0530–1800 hours), and collections were made between 1900 and 0300 hours. Moth collections and data were accompanied by the collection of temperature and relative humidity readings four times per night of sampling (1800, 2100, 2400, and 0300 hours).

All Sphingidae encountered at the light trap each night were collected and preserved by injecting a mixture of 90% absolute alcohol and 10% formol into the abdomens. Preserved moths were stored in the field temporarily in an environment of ethyl acetate vapor in waterproof, plastic boxes.

All moth specimens were processed the morning after each night of sampling. Individual moths were grouped by morphospecies and counted, and observations regarding their morphology and taxonomy were recorded. Each moth was placed individually into a protective, glassine envelope for storage and transport from field sites in waterproof plastic containers equipped with silica gel packets to keep the specimens dry.

All moth specimens were permanently deposited at the Entomology Laboratory of the San Marcos Natural History Museum in Lima, Peru. A selection of duplicate specimens of each species was exported to the Botanical Research Institute of Texas for permanent deposition. During 2006–2007, ≈12 mo of museum work were required to process, mount, accession, and identify all of the specimens from the project. Nearly all species have been identified, with the exception of two morphospecies that require further study.

For our analysis we divided the species assemblage into three groups: 1) Cosmopolitan species are those species that were collected at all three sites; 2) Paired species are the species collected in any two neighboring environmental zones (either the montane zone and the foothills of the Andes or the foothills and the lowland Amazon); 3) Endemics are those species that were collected only at one site. For a greater precision, the latter group can be subdivided into two subgroups: 1) regular endemics, represented by abundant, common, and infrequent species; and 2) rare potential endemics, including those species that were collected only in very small numbers (three individuals or less). There is a possibility that these rare species were sampled only at a single locality because they are rare, rather than because they only occur at a single locality. Species accumulation curves (Fig. 2) and Sørensen similarity indices (Sørensen, 1948) were generated for each site.

Results

Species Richness. In total, 119 species belonging to 22 genera of Sphingidae were collected at three sites. The species diversity was highest at the UA site, where 94 species belonging to 21 genera were registered, and the lowest species diversity was within the cloud forest zone (MO), where 43 species belonging to 17 genera were collected. The LA site, with 80 species belonging to 21 genera, was characterized by the intermediate
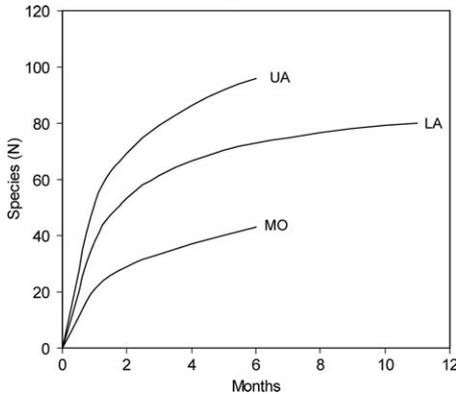
Fig. 2. Species accumulation curves for sites LA, UA, and MO.

level of species richness that was much higher than at MO but somewhat lower than at UA (Table 1).

The species accumulation curves (Fig. 2) seem to be regular enough to make comparisons in species richness and composition among the three sites valid. Curves show relatively similar patterns after every single month of sampling, with the number of collected species being always highest at UA and lowest at MO, and with LA falling in between. It seems that 11 mo of sampling at LA resulted in a nearly complete species list. The relevant curve suggests that 6 mo of sampling at LA would result in ≈72 species, or only eight species (or 10%) less than sampled during 11 mo. The potential for more species to be collected at UA and MO cannot be denied. Yet given the dynamics demonstrated by the curves, it is unlikely that their relatively similar pattern would considerably change if UA and MO were sampled for 11 mo instead of 6 mo. Most remarkably, even after 11 mo of collecting, the total number of species sampled at LA was essentially lower than after 6 mo of collecting at UA. This fact is clearly indicative of the considerably higher species richness of the sphingid moths in the Andean foothills than in the Amazonian lowlands.

Only 26 cosmopolitan species were registered in this study. These make up <22% of the total assemblage (Table 2). However, in terms of the total numbers of individuals, widespread species account for disproportionately large proportions of the site-specific catch population pools: 43.7% at LA, 44.7% at UA, and 55.5% at MO. Endemics form the largest group with 47 species, accounting for nearly 40% of the total species assemblage pool (Table 2). However, only a few of them are of common or frequent occurrence—and only so in the MO assemblage. The majority of endemics (31.1% of the total species assemblage pool) are represented by relatively scarce or very scarce catch populations and their overall shares in the catch population pools at LA (1.6%) and UA (8.2%) are insignificant. By contrast, the share of endemics in the catch population pool at MO is 38.1%. Here, some endemic species are represented by relatively large and even very large (≥100 individuals) catch populations.

The shorter period of sampling may have marginally affected few species groups at UA and MO. For example, the shorter the period of sampling, the higher is the possibility that some rare Sphingidae will be missing from the collection pool. There also may be species missing from this study because some genera are well known not to come to light (i.e., in genera *Aleuron* and *Unzela*), and *Aellopos* and possibly *Eupyrrhoglossum* are diurnal. All these need to be captured at flowers.

Species Composition. The compositional similarity between LA and UA is greater than between either one of these two assemblages and that of MO (Sørensen similarity: MO-UA, 0.4234; MO-LA, 0.4228; UA-LA, 0.7816). In total, at least 68 species of Sphingidae show shared occurrence between LA and UA. These species make up 85% of the LA and 72.3% of the UA assemblages. Of these species, 42 are paired species, which make up 52.5% of the LA and 47.9% of the UA assemblages. By contrast, there are only four paired species shared by UA and MO.

At the generic level, the major compositional partition seems to exist between the two low-elevation sites and Wayqecha. Certain genera present at LA and UA, such as *Hemeroplanes*, *Madoryx*, *Oryba*, and *Protambulyx*, are absent from the MO assemblage. Some other genera common or abundantly represented at LA and UA only marginally extend into the montane cloud forest environment of Wayqecha (MO). The species of those genera that do extend upslope into the montane cloud forest can be typically related to two groups: either they represent the upper termination points of certain cosmopolitan (but de facto foothills/lowland-centered) populations or they are montane narrow specialists. For example, the second most species rich foothills-lowland (UA-LA) genus, *Manduca*, which is represented by 13 species at UA and 12 species at LA, has only three species at MO. All of those three species are represented by single individuals and one, *Manduca schausi*, is a rare potential endemic. The same trend is shown by another important foothills-lowland genus, *Callionima*. This genus is represented by seven species at UA, six species at LA, and only two at MO. The latter two species are again represented by single individuals. The important foothills-lowland genus *Eumorpha* has nine species at UA, eight species at LA, and only four species at MO, of which two are likewise represented by single individuals. Yet another foothills/lowland-centered genus, *Adhemarius*, has a single representative at MO. This species, *A. sexoculata*, is an abundantly represented montane forest endemic.

There is a single, relatively small genus, *Euryglottis*, which is endemic to the montane assemblage of MO. Another genus, *Perigonia*, is centered at MO and UA; it is the only genus that shows a montane/foothills-centered pattern of distribution. Thus, most species endemic to the cloud forest zone belong to the cosmopolitan genera, frequently with low elevation-centered distributions.

Most genera present in the total catch pool can be characterized as foothills/lowland-centered (LA-

Table 1. Distribution of Sphingidae species among three sites: Wayqecha (MO, cloud forest at 2,500 masl at the eastern slope of the Andes), Atalaya (UA, upper Amazon at 600 masl), and Los Amigos (LA, lowland Amazon at 300 masl)

No	Species	Tentative status	MO (individuals)	UA (individuals)	LA (individuals)
1	*Adhemarius dentoni* (Clark)	UA-rare		2	
2	*Adhemarius gagarini* (Zikán)	LA-rare			1
3	*Adhemarius gannascus* (Stoll)	UA/LA		26	21
4	*Adhemarius palmeri* (Boisduval)	LA/UA		15	43
5	*Adhemarius ypsilon* (Rothschild & Jordan)	UA-rare		1	
6	*Adhemarius sexoculata* (Grote)	MO-ns	108		
7	*Agrius cingulata* (F.)	Cosmopolitan	54	8	3
8	*Amphimoea walkeri* (Boisduval)	LA-ns		1	18
9	*Callionima acuta* (Rothschild & Jordan)	Cosmopolitan	1	24	44
10	*Callionima denticulata* (Schaus)	UA-ns		6	
11	*Callionima falcifera* (Gehlen)	Cosmopolitan	1	4	30
12	*Callionima inuus* (Rothschild & Jordan)	LA/UA		18	27
13	*Callionima nomius* (Walker)	LA/UA		4	8
14	*Callionima pan* (Cramer)	LA/UA		6	21
15	*Callionima parce* (F.)	UA/LA		28	12
16	*Cocytius antaeus* (Drury)	UA/MO	1	3	
17	*Cocytius beelzebuth* (Boisduval)	LA-ns			9
18	*Cocytius duponchel* (Poey)	Cosmopolitan	11	27	121
19	*Cocytius lucifer* Rothschild & Jordan	LA/UA		2	7
20	*Enyo bathus* Rothschild	LA/UA		5	7
21	*Enyo cavifer* Rothschild & Jordan	UA-rare		1	
22	*Enyo gorgon* (Cramer)	LA-rare			1
23	*Enyo lugubris* (L.)	Cosmopolitan	40	8	14
24	*Enyo ocypete* (L.)	Cosmopolitan	1	29	62
25	*Erinnyis alope* (Drury)	Cosmopolitan	23	46	12
26	*Erinnyis crameri* (Schaus)	MO-rare	2		
27	*Erinnyis ello* (L.)	Cosmopolitan	217	58	43
28	*Erinnyis lassauxii* (Boisduval)	UA/LA		5	3
29	*Erinnyis obscura* (F.)	Cosmopolitan	15	8	3
30	*Erinnyis oenotrus* (Cramer)	Cosmopolitan	8	14	13
31	*Eumorpha anchemolus* (Cramer)	Cosmopolitan	1	11	13
32	*Eumorpha capronnieri* (Boisduval)	UA/LA		11	8
33	*Eumorpha cissi* (Schaufuss)	UA-rare		1	
34	*Eumorpha fasciatus* (Sulzer)	Cosmopolitan	4	1	1
35	*Eumorpha labruscae* (L.)	Cosmopolitan	2		3
36	*Eumorpha megaeacus* (Hübner)	UA-rare		1	
37	*Eumorpha phorbas* (Cramer)	Cosmopolitan	1	33	17
38	*Eumorpha satellitia* (L.)	UA/LA		17	4
39	*Eumorpha triangulum* (Rothschild & Jordan)	UA/LA		13	2
40	*Eumorpha vitis* (L.)	UA/LA		8	5
41	*Euryglottis aper* (Walker)	MO-ns	18		
42	*Euryglottis dognini* Rothschild	MO-ns	29		
43	*Euryglottis oliver* Eitschberger	MO-ns	8		
44	*Hemeroplanes ornatus* Rothschild	UA/LA		2	1
45	*Hemeroplanes triptolemus* (Cramer)	UA/LA		4	1
46	*Isognathus caricae* (L.)	UA-rare		1	
47	*Isognathus leachii* (Swainson)	Cosmopolitan	2	30	59
48	*Isognathus occidentalis* Clark	UA-rare		1	
49	*Madoryx bubastus* (Cramer)	LA/UA		1	5
50	*Madoryx plutonius* (Hübner)	LA/UA		3	5
51	*Madoryx oiclus* (Cramer)	LA-rare			2
52	*Madoryx* sp. 2	LA-rare			1
53	*Manduca albiplaga* (Walker)	LA/UA		16	19
54	*Manduca andicola* (Rothschild & Jordan)	LA/UA		1	5
55	*Manduca clarki* (Rothschild & Jordan)	LA/UA		1	2
56	*Manduca dalica* (Kirby)	LA-ns			5
57	*Manduca diffissa* (Rothschild & Jordan)	UA/LA		22	15
58	*Manduca extrema* (Gehlen)	UA-ns		27	
59	*Manduca florestan* (Stoll)	UA-ns		9	
60	*Manduca hannibal* (Cramer)	Cosmopolitan	1	3	10
61	*Manduca lanuginosa* (Edwards)	LA-rare			3
62	*Manduca lefeburii* (Guérin-Méneville)	UA-rare		3	
63	*Manduca pellenia* (Herrich-Schäffer)	Cosmopolitan	1	2	22
64	*Manduca rustica* (F.)	UA/LA		34	9
65	*Manduca schausi* (Clark)	MO-rare	1		
66	*Manduca scutata* (Rothschild & Jordan)	UA-rare		3	
67	*Manduca sexta* (L.)	LA/UA		4	12
68	*Manduca* sp. 1	LA-rare			2

Table 1. Continued

No	Species	Tentative status	MO (individuals)	UA (individuals)	LA (individuals)
69	*Manduca vestalis* (Jordan)	LA/UA		9	47
70	*Neococytius cluentius* (Cramer)	Cosmopolitan	18	6	45
71	*Nyceryx coffaeae* (Walker)	UA/LA		9	8
72	*Nyceryx hyposticta* (C. & R. Felder)	MO/UA	45	1	
73	*Nyceryx maxwelli* (Rothschild)	UA-rare		1	
74	*Nyceryx stuarti* (Rothschild)	UA/LA		18	15
75	*Oryba achemenides* (Cramer)	UA/LA		3	3
76	*Oryba kadeni* (Schaufuss)	UA/LA		2	2
77	*Pachylia darceta* (Druce)	LA/UA		54	338
78	*Pachylia ficus* (L.)	Cosmopolitan	11	28	84
79	*Pachylia syces* (Hübner)	Cosmopolitan	1	2	1
80	*Pachylioides resumens* (Walker)	Cosmopolitan	2	19	31
81	*Perigonia grisea* Rothschild & Jordan	UA-rare		2	
82	*Perigonia ilus* Boisduval	LA/UA		6	18
83	*Perigonia lusca* (F.)	MO-rare	1		
84	*Perigonia* sp. 2	MO-rare	2		
85	*Perigonia stulta* Herrich-Schäffer	MO/UA	9	3	
86	*Protambulyx astygonus* (Boisduval)	UA-rare		1	
87	*Protambulyx eurycles* (Herrich-Schäffer)	LA/UA		2	22
88	*Protambulyx goeldii* Rothschild & Jordan	LA/UA		9	27
89	*Protambulyx ockendeni* Rothschild & Jordan	LA-ns			5
90	*Protambulyx strigilis* (L.)	LA/UA		17	99
91	*Pseudosphinx tetrio* (L.)	Cosmopolitan	37	215	38
92	*Xylophanes acrus* Rothschild & Jordan	UA-rare		3	
93	*Xylophanes amadis* (Stoll)	LA/UA		1	7
94	*Xylophanes anubus* (Cramer)	Cosmopolitan	1	4	23
95	*Xylophanes crotonis* (Walker)	MO-ns	36		
96	*Xylophanes ceratomioides* (Grote & Robinson)	UA-ns		7	
97	*Xylophanes chiron* (Cramer)	Cosmopolitan	39	61	100
98	*Xylophanes cosmius* Rothschild & Jordan	LA/UA		22	41
99	*Xylophanes docilis* (Butler)	MO-ns	4		
100	*Xylophanes dolius* Rothschild & Jordan	UA/LA		40	18
101	*Xylophanes elara* (Druce)	LA-ns			6
102	*Xylophanes fusimacula* (C. & R. Felder)	UA-ns		15	
103	*Xylophanes guianensis* (Rothschild)	Cosmopolitan	1	3	5
104	*Xylophanes hannemanni* Closs	UA-ns		17	
105	*Xylophanes hydrata* Rothschild & Jordan	LA/UA		1	3
106	*Xylophanes libya* (Druce)	UA/LA		89	45
107	*Xylophanes loelia* (Druce)	UA/MO	1	2	
108	*Xylophanes media* Rothschild & Jordan	UA-ns		14	
109	*Xylophanes nabuchodonosor* Oberthür	MO-ns	123		
110	*Xylophanes neoptolemus* (Cramer)	UA-rare		3	
111	*Xylophanes pluto* (F.)	UA/LA		27	4
112	*Xylophanes porcus* (Hübner)	UA-rare		2	
113	*Xylophanes pyrrhus* Rothschild & Jordan	MO-ns	9		
114	*Xylophanes resta* Rothschild & Jordan	MO-ns	7		
115	*Xylophanes schausi* (Rothschild)	LA-rare			3
116	*Xylophanes tersa* (L.)	Cosmopolitan	17	13	2
117	*Xylophanes thyelia* (L.)	UA/LA		43	8
118	*Xylophanes titana* (Druce)	UA/LA		40	16
119	*Xylophanes undata* Rothschild & Jordan	UA/LA		43	2
Total individuals = 4,203			914	1,469	1,820

Terms and abbreviations used: LA, lowland Amazonian; UA, upper Amazonian; MO, montane; Cosmopolian, species found at all three sites; ns, narrow specialist; rare, rare narrow specialist.

UA). The most representative of these are (in decreasing order) *Xylophanes, Manduca, Eumorpha, Callionima,* and *Adhemarius.* These five genera are together responsible for 57.1% of the total species pool. *Xylophanes* is the most species rich genus at all three sites, but it is also the largest genus overall . Of the foothills/lowland-centered genera, many peak in species richness at UA. Most representative of this type of distribution are the genera *Xylophanes, Nyceryx,* and *Isognathus.* By contrast, only one genus, *Madoryx,* peaks in species richness at LA.

Patterns of species dominance are shown in Table 3. The dominant association of MO is represented by the shortest species list, whereas that of LA by the longest list. The dominant associations of LA and UA consist exclusively of cosmopolitan and paired species. Thus, all the dominant species from the LA association are also present (albeit not necessarily as dominant) at UA, and vice versa. Cosmopolitan species form the majority in the dominant association at LA, whereas paired species are more important in the dominant association at UA. Of the most abundantly represented species, two, *Erinnyis ello* and *Pseudosphinx tetrio,* are cosmopolitan in distribution and one species, *Pachylia darceta,* is a paired species peaking at LA but also frequent at UA.

Table 2. Distribution of four major groups of species among three sites along an elevational gradient: montane cloud forest (MO), upper Amazon (UA), and lowlands Amazon (LA)

Species status (species groups)	All sites	MO	UA	LA
Narrow endemic (registered at 1 site)	21 (17.7)	9 (20.9)	7 (7.4)	5 (6.3)
Rare narrow endemic	26 (21.8)	4 (9.3)	15 (16.0)	7 (8.7)
Paired (species registered at 2 sites)	46 (38.7)	4 (9.3)	46 (48.9)	42 (52.5)
Cosmopolitan[a] (registered at 3 sites)	26 (21.8)	26 (60.5)	26 (27.7)	26 (32.5)

Number of species (*N*) is shown for each species group, with the total percentage of all species at each given site (%).

[a] One of the species included in this group, *E. labruscae*, was registered in two opposite environmental zones—MO and LA but not in UA. This disjunct distribution is suggestive of the possibility that the species also occurs in UA and thus can be qualified as cosmopolitan.

By contrast, a relatively large proportion of the MO dominant species are endemics. Two species of this group, *Xylophanes nabuchodonosor* and *Adhemarius sexoculata*, are the second and the third most abundant components of the MO assemblage. Yet another species, *Nyceryx hyposticta*, is "nearly" endemic, because, apart from MO, it is represented by only a single individual at UA.

Discussion

There are ≈150 sphingid species currently known in all of Peru (Kitching et al. 2010) and in approximately 2 yr of sampling at just three sites in the Andes-Amazon region of southeastern Peru, a total of 119 species (or 79% of all species in Peru) were documented. The most diverse sphingid communities have been documented in Malesia, with 311 species (Beck et al. 2006). A few available studies allow comparison of sphingid communities between different regions of the Neotropics. Lamas (1985) documented 43 species at one site in Madre de Dios, Peru. Haber and Frankie (1989) documented 65 species in a Costa Rican dry forest. Duarte Júnior and Schlindwein (2005) collected 23 species in the Atlantic forest of northeastern

Brazil. Hawes et al. (2009) documented 65 species in the Amazonian lowlands of northern Brazil. In tropical Mexico Leon-Cortes et al. (1998) documented 68 and 81 species at two separate sites. With 119 species collected in this study, the Andes-Amazon region of Peru, as a recognized biological hotspot (Myers et al. 2000) seems to be an important area of sphingid diversity in the Neotropics. J.G. recently found similarly high diversity in the central jungle of Junin, Peru, with ≈130 species (J.G., unpublished data).

The study region corresponds at least in part with the Yungas center of sphingid distribution described by Schreiber (1978), extending over the eastern slopes of the Andes Mountains and into the upper Amazon from Bolivia to northern Peru. The diverse Sphingidae community documented in this study is characterized by a relatively high level of differentiation between the assemblages found at the three surveyed sites. The LA and UA foothills sites are compositionally more similar to each other than either is to the Andean montane cloud forests (MO), which is characterized by the relatively high level of species endemism. This pattern is not surprising, because the elevational difference between MO and UA is more than seven times that between UA and LA. Yet, the Andean foothills (UA) assemblage is characterized by the highest species richness and the largest number of endemic species. Beck and Kitching (2009) showed a midelevation peak of sphingid diversity between 1,000 and 1,400 masl in southeastern Asia. It was not possible in this study to sample between the UA foothills and the montane cloud forest (MO) sites in that elevational range. It is likely that future sampling ≈1,500 masl along this elevational gradient in the Andes-Amazon region will result in greater numbers of species and perhaps more species overlap between lowland and upland sites.

Holloway (1987), working in southeastern Asia, found that lowland species are sometimes taken in high numbers at high elevation sites but are probably not resident there; they may migrate upwards "hill-topping." Thus large catches of common lowland species were also taken above 2000 masl. With that in mind, however, we

Table 3. Associations of dominant species at three sites montane cloud forest (MO), upper Amazon (UA), and lowland Amazon (LA)

MO	UA	LA
Erinnyis ello, 217	*Pseudosphinx tetrio*, 215	*Pachylia darceta*, 338
Xylophanes nabuchodonosor, 123	*Xylophanes libya*, 89	*Cocytius duponchel*, 121
Adhemarius sexoculata, 108	*Xylophanes chiron*, 61	*Xylophanes chiron*, 100
Agrius cingulata, 54	*Erinnyis ello*, 58	*Protambulyx strigilis*, 99
Nycerix hyposticta, 45	*Pachylia darceta*, 54	*Pachylia ficus*, 84
Enyo lugubris, 40	*Erinnyis alope*, 46	*Enyo ocypete*, 62
	Xylophanes thyelia, 43	*Isognathus leachii*, 59
	Xylophanes undata, 43	*Manduca vestalis*, 47
	Xylophanes dolius, 40	*Xylophanes libya*, 45
	Xylophanes titana, 40	*Neococytius cluentius*, 45
		Callionima acuta, 44
		Adhemarius palmeri, 43
		Erinnyis ello, 43
		Xylophanes cosmius, 41

Included here are the abundant (≥100 individuals), very frequent (≥70 individuals), and frequent (≥40 individuals) species. Cosmopolitan species are bolded and underlined, paired species are underlined, and narrow specialists are unmarked.

found the three sampled assemblages to be composition-ally more distinctive than had been expected based on the relative proximity of the studied sites and seemingly good flying capacities of sphingid moths. Increase in elevation seems to produce a rather conspicuous compositional transformation of the sphingid communities along the transect. However, future sampling at 1,500 masl in the study region will provide more insight into this observed pattern.

From the Amazonian lowlands to the Andean foothills, a seemingly insignificant change in elevation (only 300 m) from LA to UA results in the replacement of 12 lowland endemic species by 22 foothills zone endemics. The differentiation between the UA and LA assemblages is further emphasized by more than half (52.3%) of the shared species being strongly centered either at UA or LA. Instead of being just a transitional zone between the lowland forest (LA) and the montane cloud forest (MO), UA with its 22 species of narrow specialists seems to be a focal point of environmental endemism. Endemics make up 23.4% of the UA assemblage.

Compared with UA, the LA seems to be a somewhat more impoverished environment although it is definitely much richer than the MO. Despite the longer period of sampling, there are fewer species, fewer narrow specialists, and fewer rare species in the LA than in the Andean foothills (UA). Given the longer period of collection in the lowland Amazon, UA and MO are not equal with LA in terms of collection intensity and duration.

Standing apart from the low-elevation assemblages of LA and UA is the MO. This assemblage consists of two main components: cosmopolitans (60.5%) and endemics which make up close to one third of the site's species pool (Table 3). Despite a far smaller total number of species compared with LA and UA, the peak of richness of regular endemics was found at the montane site (MO, Table 3). What makes the composition of the MO assemblage essentially different from those of LA and UA is a very marginal role of the species with paired distributions. The lack of the paired species shared with the lowland Amazon site (LA) was expected due to the location of MO in the Andes at the high-elevation extreme of the sampling transect. But the negligible role of the species shared in the Andean foothills (UA) was somewhat surprising (Table 3).

Although we are in the early stages of correlating the known natural history of sphingid species to better explain the diversity and distribution patterns documented in this study, some preliminary comments can be made. For example, as mentioned above, genera present at LA and UA, such as *Hemeroplanes*, *Madoryx*, *Oryba*, and *Protambulyx*, are absent from the MO assemblage. These genera are among the more oligophagous sphingids when it comes to larval hosts and so may be excluded from high elevation for this reason, as well as climatic and other reasons. The genus *Callionima* is represented by seven species at UA, six species at LA, and only two at MO where they are represented by only two individuals. This could be explained by the fact that most larval records of this genus are from lowland plant genera of the Apoc-

ynaceae (i.e., *Aspidosperma*, *Rauvolfia*, and *Stemmadenia*). Similarly, the important foothills-lowland (UA-LA) genus *Eumorpha* has nine species at UA, eight species at LA, and only four species at MO, of which two are represented by single individuals. One species, *E. fasciatus*, was found at all three sites and is known to specialize on the Onagraceae, which occurs in the Andes and the Amazon regions. However, most of the species of this genus specialize on plants in the Vitaceae, represented by the genus *Cissus* in the study region, which is largely absent or less diverse at the cloud forest site (MO). Yet another foothills/lowland-centered genus, *Adhemarius*, has a single representative at MO. This species, *A. sexoculata*, is an abundantly represented montane forest endemic. With this in mind, it is interesting that *Adhemarius* species are restricted to Lauraceae, which is abundant at all three sites, but much more diverse in the lowlands. Lastly, there is a single, relatively small genus, *Euryglottis*, which is endemic to the montane cloud forest assemblage (MO). Interestingly, this genus is largely confined to high elevations; their furry bodies would seem to be an adaptation to colder climates. Also, because we stopped the light at 0300 hours, we may have missed a few rare species that are known to fly at dawn (e.g., rare species in the genus *Protaleuron*). Future integration of information about the natural history of all species will shed more light on the documented patterns of Sphingid moth richness, composition, and distribution in the Andes-Amazon region.

Acknowledgments

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