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RESEARCH ARTICLE

Species richness and community composition of sphingid moths (Lepidoptera: Sphingidae) along an elevational gradient in southeast Peru

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ABSTRACT. A clear low-elevation skewed unimodal richness pattern is presented for hawkmoths in Southeast Peru. Several hypotheses offer plausible explanations for such a distribution. The effects of water-energy dynamics are partially supported by a strong correlation between temperature and species richness at higher elevations. Further, hypotheses of plant diversity influences on hawkmoth ranges are supported by species richness peaking in transitional habitats. Sphingid subfamilies do not appear to be influenced by habitat type or elevational factors, such as temperature. This may make subfamily analysis a poor means of characterizing sphingid community composition unless study sites vary in the level of disturbance. This study documents 134 species in 23 genera of Sphingidae from five Southeastern Peru sites from the 7,545 specimens collected for the study.

KEY WORDS. Biodiversity, community structure, elevation, Neotropical region.

INTRODUCTION

One major challenge to studying patterns and mechanisms of biodiversity is finding gradients sufficiently large enough to observe any patterns while limiting confounding factors, such as biogeographical differences, between sites (Beck and Chey 2008). It becomes harder to study local-scale influences on diversity without accounting for the role of historical differences as the size of the study area increases (Ricklefs 2004). Mountains offer one potential solution by providing environmental gradients, such as temperature, area, and habitat, within a limited area, allowing for studies of local biodiversity processes while minimizing confounding factors. Additionally, the abundance of elevational gradients allows for high reproducibility and comparison of patterns from a variety of habitats and latitudes (McCain 2007, Beck and Kitching 2009).

One common type of elevational diversity pattern is a mid-elevation diversity peak. Historically, such a pattern was attributed to sampling artifacts (McCoy 1990), but the description of a unimodal pattern in many recent studies (Brehm et al. 2007, McCain 2007, Beck and Chey 2008, Beck and Kitching 2009) has led to its acceptance as a legitimate altitudinal diversity pattern. Several hypotheses attempting to explain mid-elevational diversity peaks are based on water-energy (Hawkins et al. 2003, McCain 2007).

Beck and Chey (2008) suggested that diversity is limited by ambient energy (for which temperature can act as a proxy) at high elevations and water availability at lower elevations. This hypothesis is adapted from findings showing a shift from temperature to water as a limiting factor to diversity as latitude decreases, and is based on an indirect, trophic cascade effect (Hawkins et al. 2003). Beck and Chey (2008) found support for energy limitation at high elevations, but not for water limitation at lower elevations, for geometrid moths in Borneo. Beck and Kitching (2009) found support for temperature, and weak support for water, as predictive factors of peak species richness for sphingid moths. McCain (2007), for bats, and Hawkins et al. (2003), for plants, vertebrates, and invertebrates, however, found that both water and energy had strong predictive capabilities for diversity patterns.

The Sphingidae are probably one of the most well-known moth families, with the fauna of Borneo (Barlow and Woiwod 1989, Schulze et al. 2001, Schulze and Fiedler 2003, Beck et al. 2006a, Beck and Kitching 2009) and Central America (Haber and Frankie 1989, Powell and Brown 1990) being particularly well studied, which allows them to be confidently used in diversity studies (Schulze et al. 2001, Amorim et al. 2009). Compared to the amount of information on sphingids from Southeast Asia, relatively little work has been done on the communities of the South American Neotropics, and the species rich altitudinal gradient between the Andes mountains and Amazonian lowlands is an ideal location for diversity studies (Myers et al. 2000, Malhi et al. 2010). Studies in a variety of taxa show this to be a particularly diverse area (e.g., Myers et al. 2000 for plants and vertebrates, Spector 2002 for beetles, Orme et al. 2005 for birds, Jackson and Flowers 2006 for aquatic insects, Ignatov et al. 2011 for moths). Southeastern Peru is an example of an area in this Andes-Amazon transitional zone, and the site of the current study. Since little work has been done on hawkmoths in Peru, the present study will both add to our understanding of Peruvian sphingid diversity and the pool of knowledge available for studies of global diversity patterns.

This study aims to 1) describe the species richness and community composition of hawkmoths along an elevational gradient in Southeastern Peru, 2) describe whether species or genera are characteristic of a particular elevational range, and 3) investigate the predictive power of temperature in explaining any observed patterns. Although not specifically testing the "water-energy hypothesis" of McCain (2007) and Beck and Chey (2008), this study addresses the correlation of temperature and species richness.

MATERIAL AND METHODS

Detailed descriptions are given for the two sites not previously reported in the literature, Vitobabma and Culebrayoc. Short descriptions of the remaining three sites, Los Amigos, Atalaya, and Wayquecha, are included, but for more detailed information see Ignatov et al. (2011). Site descriptions are given in order of elevation (Fig. 1).

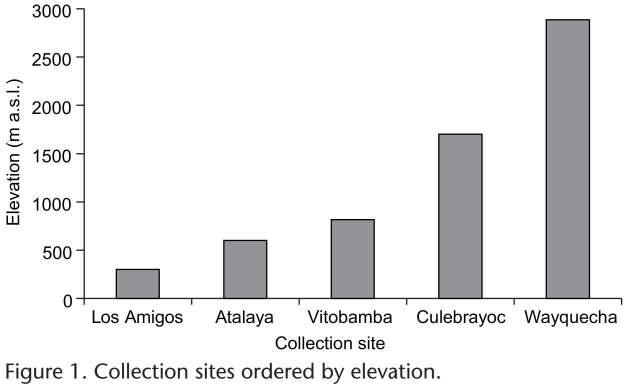


Figure 1. Collection sites ordered by elevation.

Los Amigos Biological Station is located in lowland rainforest at 300 m a.s.l. Atalaya is in tropical moist/pluvial forest at 600 m a.s.l. Wayquecha Cloud Forest Research Station is in a montane cloud forest at ~2,900 m a.s.l.

Vitobamba (13°18.596'S; 70°48.984'W; 818m a.s.l.) is a transitional forest between lowland tropical rainforest and montane rainforest. The collection site was in an area of low mountains on a former plantation that has transitioned secondary forest. The site was approximately 75 m from a paved road, which was recently under construction, and 400 m from a small river. Vegetation within the forest consisted of trees, shrubs, herbs, and lianas. The understory had patches of bamboo and semi-thick undergrowth; it was not thick enough to impede travel or obscure vision. About 50 m from the trap site, inside the forest, was a newly established vanilla plantation, about 50x30 m in size. Vegetation at the forest's edge immediately surrounding the light trap consisted of an invasive species of ginger. Collections at this site were made in 2010 from June 8th to June 15th, August 7th to August 15th, and October 3rd to October 11th. Average nightly temperatures ranged from 20.3 °C (June) to 19.0 °C (August). October is the start of the rainy season, so there was more precipitation, during the day and evening, than in June or August.

Culebrayoc (13°29.979'S; 70°53.977'W; 1,701 m a.s.l.) is a montane rainforest. The collection site was located within a low valley in the Andes Mountains. The site was approximately 50 m from a river and 100 m from the edge of primary forest. To one side of the trap was a flat, open, graveled area, which was under construction in September. Nearby was a patch of secondary forest consisting of bamboo, trees, and herbs; a small garden with coffee, corn, tomato, and a yuca relative was also near the light trap. Understory vegetation in both the secondary and primary forests tended to be thick, making it difficult to travel off trails. Collections at Culebrayoc were made in 2010 from July 7th to July 16th (except for July 13th), September 4th to September 14th (except for September 10th and 11th), and November 1st to November 9th. It was common for a strong breeze to pick up during the night, and occasionally a heavy fog was present for the first one to two hours of collecting. Average nightly temperatures ranged from 15.1 °C (July) to 16.3 °C (November), and there were no noticeable differences in precipitation among the three months.

Moths were collected nine nights each month, alternating between sites, from June to November of 2010, making three collections at each site. Collecting was conducted around the new moon, generally beginning four nights before the new moon and continuing four nights after the new moon. A 175-watt mercury-vapor bulb (Bioquip), powered by a Honda EU-1000 generator, was suspended in front of a 2 x 2 m white sheet to attract moths. Traps that emit light in the ultra violet spectra, such as those using mercury-vapor or black lights, have been shown to be more efficient at attracting sphingids than white lights (Nabli et al. 1999). Black lights are a weaker light source, and are preferable to MV bulbs when sampling needs to be restricted to a small spatial scale, such as a particular vegetation layer (Schulze et al. 2001, Axmacher and Fiedler 2004). A clear, plastic roof structure was installed at each site to protect the mercury-vapor bulb and allow collecting during precipitation. Schulze et al. (2001) found that at the Mount Kinabalu National Park (Sabah, East Malaysia) most sphingid diversity was concentrated in the canopy, with only one understory specialist. Since the goal of this study was to describe total sphingid diversity, and not just that from a single forest layer, collections were made 5m to 100m outside the tree line. In the understory, light is not able to penetrate the canopy. Collecting at the tree line allows the light to penetrate the understory and canopy, attracting moths from both vegetation layers.

Each night the light was turned on between 5:45 and 6:00 pm, and collections were made hourly from 7:00 pm to 3:00 am. Each hour all sphingids present on the sheet were collected and killed by injecting a 3:1 mixture of alcohol:ethyl acetate into the thorax. Specimens were stored in individual glassine envelopes labeled with the location, date, and time of capture. In addition, temperature was recorded every three hours from 6:00 pm till 3:00 am using a digital thermometer (RadioShak).

In the field, moths were stored in plastic containers containing silica gel and paradiclorobenzene (PDB). Upon returning to the field station, moths were dried, sorted into morphospecies, and stored in plastic bags with PDB. All species were identified to species, with the exception of a small number that consisted of distinct morphospecies in a given genus, but whose species identification could not be accurately assured. Identifications were aided by the reference collection at the San Marcos Museo de Historia Natural in Lima, Peru. Nomenclature follows Kitching and Cadiou (2000). Representatives of each morphospecies were deposited in the San Marco Museo de Historia Natural.

For all data analyses hawkmoth abundance data and temperature readings from previous collections made at the Los Amigos Biological Station, Atalaya, and Wayquecha Cloud Forest Research Station during 2004–2006 were used. Temperature data for Los Amigos was obtained from Atrium Biodiversity Information System (AABP Atrium, http://atrium.andesamazon.org), while data for Atalaya and Wayquecha was obtained from John P. Janovec (unpublished data). The procedure described in Ignatov et al. (2011) was used in order to facilitate the incorporation of their data into these analyses. Wei et al. (2010) and Walther and Morand (1998) determined that the performance of species richness estimators varies with sampling intensity, so standardized sampling intensity was used by only using June, August, and October data from Los Amigos and Atalaya and July, September, and November data from Wayquecha. This allowed comparisons to the three alternating months of sampling at each site during the same June-November sampling window.

It is well known that obtaining a complete inventory of any species rich taxonomic group is exceedingly difficult (Price et al. 1995), so observed species richness is a poor estimator of actual species richness (Wei et al. 2010). Non-parametric estimators and extrapolating species accumulation curves provide more reliable alternatives to estimating species richness than the observed number of species (Walther and Morand 1998, Wei et al. 2010). Three non-parametric, abundance-based estimators, Chao1, Jackknife1 (Jack1), and abundance-based coverage estimator (ACE), were used to estimate total species richness. Since each estimator gives a slightly different estimation of species richness, the average of the three estimates was used for all analyses. Chao1 and Jack1 use the number of singletons and doubletons (species with an abundance of one and two respectively) to estimate the total number of observed and unobserved species (Palmer 1991, Chao et al. 2005). ACE functions in a similar manner; it uses the frequency of rare species (those with ten or fewer individuals) to estimate species richness (Chao et al. 2005). To evaluate differences in alpha diversity between the sites, Fisher's alpha was calculated. EstimateS 8.2.0 (R.K. Colwell, http://viceroy.eeb.uconn.edu/estimates) was used for all calculations of species richness and diversity. A linear regression was used to test for any relationship between temperature and estimated species richness or temperature and Fisher's alpha. For data that shows a break in the trend, as is seen in unimodal humps, a single linear regression will not give any significant results. Breakpoint regression allows for the regression before and after the breakpoint to be calculated separately (Beck and Chey 2008). Therefore, breakpoint regression was used to analyze the relationship between (log)elevation and estimated species richness following Beck and Chey (2008). For all regression analyses, r^2 and p-values were calculated using Minitab.

The percent contribution of each subfamily to species richness and total abundance at each site was calculated and used to analyze community composition and structure. Species were classified using the method of Beck and Kitching (2009), who determined species' ranges by assuming they occupied all areas between their highest and lowest altitudinal record. Species were classified as 1) cosmopolitan (those collected at least at Los Amigos and Wayquecha, and so assumed to occupy the entire gradient), 2) lowland (those only collected at the three lowest sites), 3) montane (those where at least 80% of the specimens were collected at the two highest sites), or 4) endemic (those only collected at a single site). Endemics were further divided into 1) regular endemics (those with more than three individuals), and 2) rare endemics (those with fewer than three individuals). These classifications, from Ignatov et al. (2011), were used to make comparisons between the two data sets easier.

RESULTS

Species richness

Among the five sites, 134 species in 23 genera were collected (data not corrected for sampling intensity). Table 1 provides a full list of species and their abundances at each site and Table 2 gives a list of observed richness, estimated richness, and Fisher's alpha for each site. The most speciose site was Vitobamba, followed by Atalaya, Los Amigos, and Culebrayoc; Wayquecha was the least speciose. A clear unimodal pattern is present, though it is skewed toward the lower elevations (Fig. 2). Species richness decreases faster at the lower elevations than higher elevations. This is evidenced by the fact that Los Amigos and Culebrayoc have nearly equal estimated species richness values, but Culebrayoc is 900 m up slope from Vitobamba

Table 1. Species abundances at each site. Data for Los Amigos, Atalaya, and Wayquecha is not corrected for sampling intensity.

No	Species	Los Amigos	Atalaya	Vitobamba	Culebrayoc	Wayquecha
1	*Adhemarius dentoni* (Clark, 1916)	0	2	0	0	0
2	*Adhemarius gagarini* (Zikan, 1935)	1	0	0	0	0
3	*Adhemarius palmeri* (Boisduval, 1870)	43	15	17	0	0
4	*Adhemarius sexoculata* (Grote, 1865)	0	0	0	25	108
5	*Adhemarius tigrina* (Felder, 1874)	0	0	16	34	0
6	*Adhemarius ypsilon* (Rothschild & Jordon, 1903)	0	1	8	0	0
7	*Adhemarius* sp. 1 (likely *A. gannascus* or *A. daphne*)	21	26	30	42	0
8	*Agrius cingulate* (Fabricius, 1775)	3	8	2	6	54
9	*Amphimoea walker* (Boisduval, 1875)	18	1	1	0	0
10	*Callionima acuta* (Rothschild & Jordon, 1910)	44	24	6	0	1
11	*Callionima denticulate* (Schaus, 1895)	0	6	5	0	0
12	*Callionima falcifera* (Gehlen, 1943)	30	4	0	0	1
13	*Callionima inuus* (Rothschild & Jordon, 1903)	27	18	1	4	0
14	*Callionima nomius* (Walker, 1856)	8	4	1	1	0
15	*Callionima pan* (Cramer, 1779)	21	6	0	0	0
16	*Callionima parce* (Fabricius, 1775)	12	28	13	7	0
17	*Cocytius antaeus* (Drury, 1773)	0	3	1	0	1
18	*Cocytius belzebuth* (Boisduval, 1875)	9	0	0	0	0
19	*Cocytius duponchel* (Poey, 1832)	121	27	36	31	11
20	*Cocytius lucifer* (Rothschild & Jordon, 1903)	7	2	19	1	0
21	*Enyo bathus* (Rothschild, 1904)	7	5	0	1	0
22	*Enyo cavifer* (Rothschild & Jordon, 1903)	0	1	0	3	0
23	*Enyo gorgon* (Cramer, 1777)	1	0	0	0	0
24	*Enyo lugubris* (Linnaeus, 1771)	14	8	3	16	40
25	*Enyo ocypete* (Linnaeus, 1758)	62	29	17	3	1
26	*Erinnyis alope* (Drury, 1773)	12	56	23	2	23
27	*Erinnyis crameri* (Schaus, 1898)	0	0	0	2	2
28	*Erinnyis ello* (Linnaeus, 1758)	43	93	8	4	217
29	*Erinnyis impunctata* Rothschild & Jordon, 1903	0	0	3	0	0
30	*Erinnyis lassauxii* (Boisduval, 1859)	3	25	0	0	0
31	*Erinnyis obscura* (Fabricius, 1775)	3	13	2	3	15
32	*Erinnyis oenotrus* (Cramer, 1780)	13	51	27	4	8
33	*Eumorpha anchemolus* (Cramer, 1779)	13	11	6	2	1
34	*Eumorpha capronnieri* (Boisduval, 1875)	8	11	16	0	0
35	*Eumorpha cissi* (Schaufuss, 1870)	0	1	2	39	0
36	*Eumorpha fasciatus* (Sulzer, 1776)	1	1	0	0	4
37	*Eumorpha labruscae* (Linnaeus, 1758)	3	0	1	1	2
38	*Eumorpha megaeacus* (Hübner, 1816)	0	1	0	0	0
39	*Eumorpha obliquus* (Rothschild & Jordon, 1903)	0	0	2	0	0
40	*Eumorpha phorbas* (Cramer, 1775)	17	33	12	0	1
41	*Eumorpha satellitia* (Linnaeus, 1771)	4	17	3	0	0
42	*Eumorpha triangulum* (Rothschild & Jordon, 1903)	2	13	81	37	0
43	*Eumorpha vitis* (Linnaeus, 1758)	5	8	0	7	0
44	*Euryglottis aper* (Walker, 1856)	0	0	0	1	18
45	*Euryglottis dognini* Rothschild, 1869	0	0	0	88	29
46	*Euryglottis guttiventris* (Rothschild & Jordon, 1903)	0	0	0	128	8
47	*Hemeroplanes ornatus* Rothschild, 1894	1	2	1	0	0
48	*Hemeroplanes triptolemus* (Cramer, 1779)	1	4	0	0	0
49	*Isognathus caricae* (Linnaeus, 1785)	0	1	0	0	0
50	*Isognathus excelsior* (Boisduval, 1875)	0	1	1	0	0
51	*Isognathus leachii* (Swainson, 1823)	59	31	0	0	2
52	*Lintneria aurigutta* (Rothschild & Jordon, 1903)	0	0	0	11	0
53	*Madoryx bubastus* (Cramer, 1777)	5	1	0	0	0
54	*Madoryx plutonius* (Hübner, 1819)	5	3	4	0	0
55	*Madoryx* sp. 1	2	0	0	0	0
56	*Madoryx* sp. 2	1	0	0	0	0
57	*Manduca albiplaga* (Walker, 1856)	19	16	13	0	0
58	*Manduca andicola* (Rothschild & Jordon, 1916)	5	1	13	1	0
59	*Manduca clarki* (Rothschild & Jordon, 1916)	2	1	0	0	0
60	*Manduca dalica* (Kirby, 1877)	5	0	7	0	0
61	*Manduca diffissa* (Butler, 1871)	15	22	14	0	0
62	*Manduca extrema* (Gehlen, 1926)	0	27	52	0	0
63	*Manduca florestan* (Stoll, 1782)	0	9	3	0	0
64	*Manduca hannibal* (Cramer, 1779)	10	3	1	0	1
65	*Manduca lamasi* Eitschberger & Haxaire, 2007	47	9	4	0	0
66	*Manduca lefeburii* (Guérin-Méneville, 1844)	0	3	8	0	0

Continues

No	Species	Los Amigos	Atalaya	Vitobamba	Culebrayoc	Wayquecha
67	*Manduca rustica* (Fabricius, 1775)	9	34	4	0	0
68	*Manduca schausi* (Clark, 1919)	0	0	11	0	1
69	*Manduca scutata* (Rothschild & Jordon, 1903)	0	3	0	0	0
70	*Manduca sexta* (Linnaeus, 1763)	12	4	0	0	0
71	*Manduca trimacula* (Rothschild & Jordon, 1903)	0	0	12	1	0
72	*Manduca* sp. 1	2	0	0	0	0
73	*Manduca* sp. 2	0	2	0	0	0
74	*Manduca* sp. 3	0	2	0	0	0
75	*Manduca* sp. 4	22	2	51	32	1
76	*Manduca* sp. 5	3	0	0	0	0
77	*Neococytius cluentius* (Cramer, 1776)	45	6	9	3	18
78	*Nyceryx coffaeae* (Walker, 1856)	8	9	1	0	0
79	*Nyceryx hyposticta* (Felder, 1874)	0	1	1	20	45
80	*Nyceryx maxwelli* (Rothschild, 1896)	0	1	1	0	0
81	*Nyceryx nictitans* (Boisduval, 1875)	0	0	4	0	0
82	*Nyceryx stuarti* (Rothschild, 1894)	15	18	0	0	0
83	*Nyceryx tacita* (Druce, 1888)	0	0	2	0	0
84	*Oryba achemenides* (Cramer, 1779)	3	3	1	0	0
85	*Oryba kadeni* (Schaufuss, 1870)	2	2	4	0	0
86	*Pachylia darceta* Druce, 1881	338	54	37	0	0
87	*Pachylia ficus* (Linnaeus, 1758)	84	28	24	9	11
88	*Pachylia syces* (Hübner, 1819)	1	2	0	0	1
89	*Pachylioides resumens* (Walker, 1856)	31	19	15	20	2
90	*Perigonia grisea* Rothschild & Jordon, 1903	0	2	1	12	0
91	*Perigonia lusca* (Fabricius, 1777)	18	6	1	3	0
92	*Perigonia stulta* Herrich-Schaffer, 1854	0	3	18	9	9
93	*Perigonia* sp. 1	0	0	0	0	1
94	*Perigonia* sp. 2	0	0	0	0	2
95	*Protambulyx astygonus* (Boisduval, 1875)	0	1	0	0	0
96	*Protambulyx eurycles* Rothschild & Jordon, 1903	22	2	5	0	0
97	*Protambulyx goeldii* Rothschild & Jordon, 1903	27	9	0	0	0
98	*Protambulyx ockendeni* Rothschild & Jordon, 1903	5	0	0	1	0
99	*Protambulyx strigilis* (Linnaeus, 1771)	99	17	33	5	0
100	*Pseudosphinx tetrio* Rothschild & Jordon, 1903	38	215	2	0	37
101	*Xylophanes amadis* (Stoll, 1872)	7	1	0	0	0
102	*Xylophanes anubus* (Crammer, 1777)	23	4	29	1	1
103	*Xylophanes chiron* (Drury, 1773)	100	61	15	2	39
104	*Xylophanes cyrene* (Druce, 1881)	0	3	0	0	0
105	*Xylophanes cosmius* Rothschild & Jordon, 1903	41	22	10	0	0
106	*Xylophanes docilis* (Butler, 1875)	0	0	19	259	4
107	*Xylophanes dolius* (Rothschild & Jordon, 1906)	18	40	28	0	0
108	*Xylophanes elara* (Druce, 1878)	6	0	1	0	0
109	*Xylophanes fassli* Gehlen, 1928	0	0	8	1	0
110	*Xylophanes fusimacula* (Felder, 1874)	0	15	30	0	0
111	*Xylophanes guianensis* (Rothschild, 1894)	5	3	0	0	1
112	*Xylophanes germen* (Schaus, 1890)	0	0	8	3	0
113	*Xylophanes hannemanni* Closs, 1917	0	17	13	0	0
114	*Xylophanes lamontagnei* Vagilia & Haxaire, 2003	0	7	32	51	0
115	*Xylophanes libya* (Druce, 1878)	45	89	61	1	0
116	*Xylophanes loelia* (Druce, 1878)	0	2	0	0	1
117	*Xylophanes mariae* Haxaire, 2013	0	0	0	39	123
118	*Xylophanes media* Rothschild & Jordon, 1903	0	14	30	0	0
119	*Xylophanes ockendeni* Rothschild, 1904	0	0	0	4	0
120	*Xylophanes pluto* (Fabricius, 1777)	4	27	2	1	0
121	*Xylophanes porcus* (Hübner, 1823)	0	2	30	0	0
122	*Xylophanes* Pyrrhus Rothschild & Jordon, 1906	0	0	1	79	9
123	*Xylophanes resta* Rothschild & Jordon, 1903	0	0	0	198	7
124	*Xylophanes rhodotus* Rothschild, 1904	0	0	0	1	0
125	*Xylophanes schausi* (Rothschild, 1894)	3	0	0	1	0
126	*Xylophanes tersa* ((Linnaeus, 1771)	2	13	31	71	17
127	*Xylophanes thyelia* (Linnaeus, 1758)	8	43	66	0	0
128	*Xylophanes titana* (Druce, 1787)	16	40	25	7	0
129	*Xylophanes undata* Rothschild & Jordon, 1903	2	43	82	0	0
130	*Xylophanes* sp. 1	0	0	1	0	0
131	*Xylophanes* sp. 2	0	0	23	0	0
132	*Xylophanes* sp. 3	0	0	99	507	36
133	*Xylophanes* sp. 4	3	1	0	0	0
134	*Xylophanes* sp. 5	0	3	21	0	0
	Total: 7,545	1,820	1,581	1,385	1,845	914

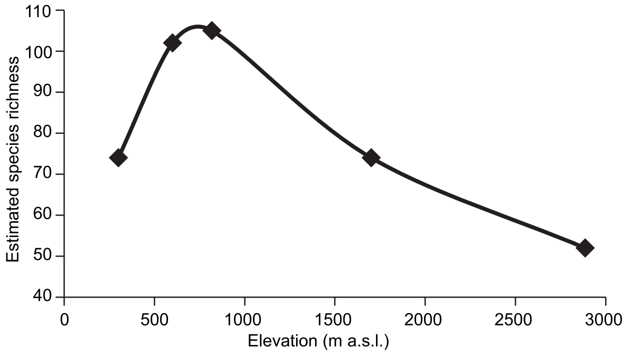
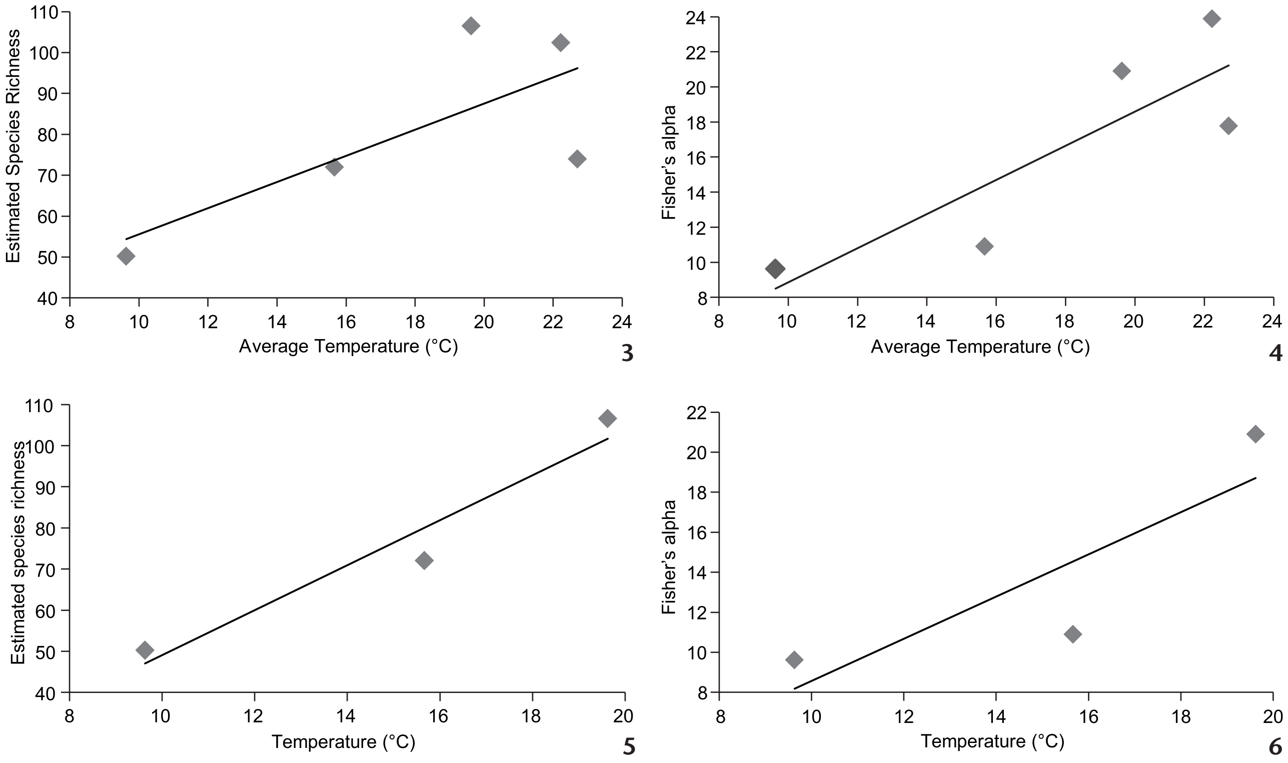


Figure 2. The relationship between elevation and species richness. There is a clear low-elevation skewed unimodal pattern, which peaks around 800 m.

while Los Amigos is only 500 m down slope. Both species richness estimations and Fisher's alpha positively correlated with temperature. The relationship was weak and not significant when considered for the whole elevational range for estimated species richness ($r^2 = 0.552$, $p = 0.150$) but the relationship had a higher correlation for Fisher's alpha ($r^2 = 0.726$, $p = 0.067$) (Figs 3–6). When the relationship was only considered for the three highest elevations it was relatively highly correlated, but still non-significant, for species richness ($r^2 = 0.939$, $p = 0.159$), and not significant for Fisher's alpha ($r^2 = 0.736$, $p = 0.343$) (Fig. 7). Species richness was positively, but not significantly, correlated with (log)elevation below the breakpoint (300–818 m a.s.l.; $r^2 = 0.953$, $p = 0.139$) and was negatively, significantly correlated with elevation above the breakpoint (818–2,886 m a.s.l.; $r^2 = 0.999$, $p = 0.003$); Fisher's alpha did not significantly correlate with (log)elevation above or below the breakpoint, and was only strongly correlated with (log)elevation above the breakpoint (300–818 m a.s.l.; $r^2 = 0.357$, $p = 0.593$; 818–2,886 m a.s.l.; $r^2 = 0.901$, $p = 0.203$).

Table 2. Observed and estimated species richness, observed number of genera, and Fisher's alpha for Los Amigos, Atalaya, Vitobamba, Culebrayoc, and Wayquecha. S_{obs} = observed number of species; S_{est} = estimated number of species; completeness = percentage of S_{est} collected at each site; $Genera_{obs}$ = observed number of genera.

Site	S_{obs}	S_{est}	Completeness (%)	$Genera_{obs}$	Fisher's alpha
Los Amigos	65	74	87.84	19	17.77
Atalaya	85	103	82.52	20	23.88
Vitobamba	86	105	81.90	21	20.29
Culebrayoc	56	74	75.68	17	10.90
Wayquecha	39	52	75.00	17	9.61



Figures 3–6. Regression analysis across the entire gradient for average temperature with (3) estimated species richness, (4) Fisher's alpha, and regression analysis at the three highest elevations for average temperature with (5) estimated species richness, and (6) Fisher's alpha. (3) $r^2 = 0.5518$, $p = 0.150$; (4) $r^2 = 0.7264$, $p = 0.067$; (5) $r^2 = 0.9391$, $p = 0.159$; (6) $r^2 = 0.7364$, $p = 0.343$.

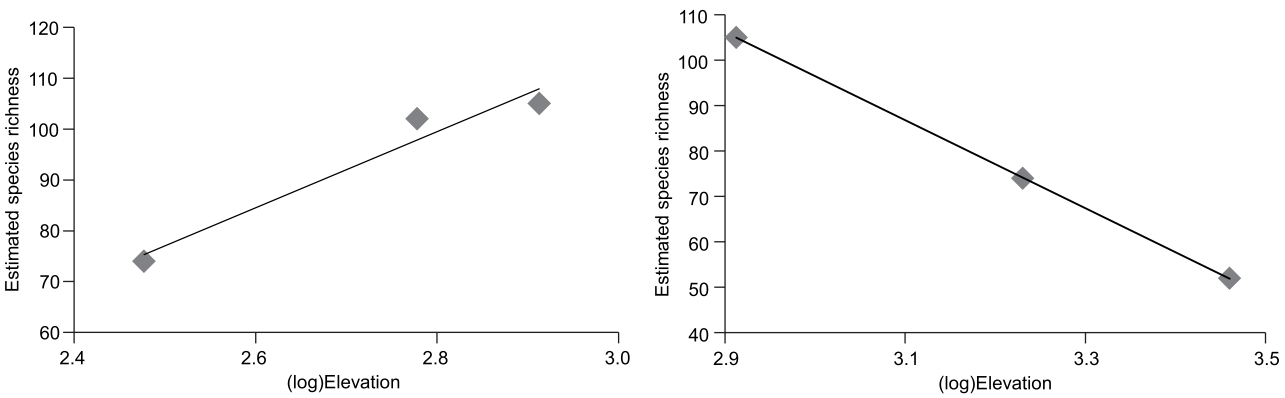


Figure 7. Breakpoint regression analysis for (log)elevation with estimated species richness. Vitobamba (800 m), which was the break point, is included in both graphs. The characteristic mid-elevation unimodal richness pattern can be seen with the increase in species richness with elevation up to Vitobamba ($r^2 = 0.953$, $p = 0.139$), and the decrease in species richness with elevation above Vitobamba ($r^2 = 0.999$, $p = 0.003$).

There were only 26 cosmopolitan species, which accounted for 21.0% of the total species richness and 34.2% of the total abundance (Table 3). Lowland species comprised 34.7% of total species richness and 23.2% of total abundance. Low land species had similar contributions to total species richness and total abundance at Los Amigos and Vitobamba. At Culebrayoc, montane species only accounted for 17.9% of the species richness but 71.9% of the total abundance, which is far greater than at either Vitobamba or Wayquecha (Table 3). This is primarily due to three species: *Xylophanes docilis* (Butler, 1875), *X. resta* Rothschild & Jordan, 1903, and *X.* sp. 3, whose combined abundances accounted for 964 of the 1,845 moths collected at Culebrayoc (Table 1). Endemic species contributed 21.0% to total species richness, but much less to total abundance (1.2%), and very little to the species richness or abundance at any one site (Table 3). Only four endemic species: *Cocytius belzebuht* (Boisduval, 1875), *Lintneria aurigutta* (Roghschild & Jordan, 1903), *Nyceryx nictitans saturate* Rothschild & Jordan, 1903, and *Xylophanes* sp. 2 were represented by more than three specimens (Table 1).

Table 3. Percent contribution of cosmopolitan, montane, lowland, and endemic species to species richness and total abundance at individual sites and all sites combined. Cosmo = cosmopolitan species; LL = lowland species; MO = montane species; endemic = endemic species; total = total species richness or total abundance.

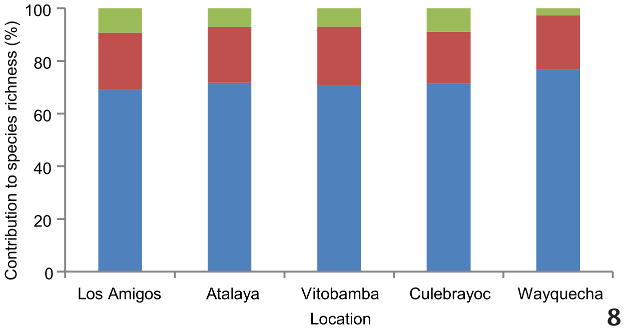
Site	Contribution to species richness (%)				Contribution to total abundance (%)			
	Cosmo	LL	MO	Endemic	Cosmo	LL	MO	Endemic
Los Amigos	32.5	38.8	0	8.8	43.9	39.5	0	1.0
Atalaya	26.0	42.7	0	8.3	47.1	32.7	0	0.9
Vitobamba	24.4	38.4	3.5	7.0	23.1	37.6	8.6	2.5
Culebrayoc	30.4	0	17.9	5.4	11.4	0	71.9	0.9
Wayquecha	60.5	0	23.3	4.7	55.8	0	37.6	0.3
Total	21.0	34.7	8.1	21.0	34.2	23.3	23.7	1.2

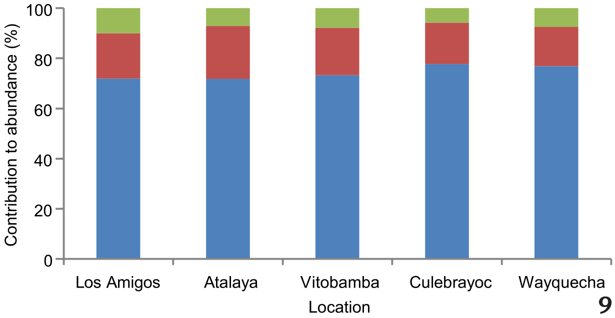
Community composition

On a species level, there appears to be a division between lowland species, those collected at Los Amigos, Atalaya, and Vitobamba, and montane species, those with populations centered at Culebrayoc and Wayquecha (Table 1). Even cosmopolitan species and species found at both lowland and montane sites can be divided into two groups: those with Los Amigos-Atalaya-Vitobamba centered populations or those with Vitobamba-Culebrayoc-Wayquecha centered populations. These species had individuals extending beyond their population centers, but only in small numbers. *Protambulyx strigilis* (Linnaeus, 1771), for example, had 73 individuals collected at lowland sites but only five individuals from Culebrayoc. Few species showed uniform distributions among high and low elevations.

Most genera were cosmopolitan, with species along the entire altitudinal gradient. Some genera, however, appeared to be more restricted in range, and most of these were lowland centered. The genera *Callionima*, *Eumorpha*, *Hemeroplanes*, *Madoryx*, *Manduca*, *Nyceryx*, *Oriba*, and *Protambulyx* all contain predominantly lowland species, with high elevation representatives being rare. Three genera, *Hemeroplanes*, *Madoryx*, and *Oriba*, appear to be lowland endemics, with all individuals coming from Los Amigos, Atalaya or Vitobamba. Only one genus, *Euryglottis*, was completely restricted to montane forests. Individuals of all three species, *Euryglottis aper* (Walker, 1856), *E. dognini* Rothschild, 1896, and *E. guttiventris* (Rothschild & Jordan, 1903), were only collected in Culebrayoc and Wayquecha, with the majority of individuals collected in Culebrayoc.

The contributions of the three sphingid subfamilies, Macroglossinae, Sphinginae, and Smerinthinae, to species richness and total abundance were similar at all five sites (Figs 8–9). Moreover, at each site the contribution of each subfamily to species richness was similar to its contribution to abundance. There were no sites in which a subfamily made up a large proportion





Figures 8–9. Contribution of sphingid subfamilies to (8) species richness and (9) total abundance. Blue bars = Macroglossinae; orange bars = Sphinginae; grey bars = Smerinthinae. Contributions of each subfamily are similar among sites, and contributions of any particular subfamily to richness and abundance are similar within a site.

of species richness but a small proportion of the abundance, or vice versa. For example, at Los Amigos Macroglossinae made up 69.2% of the species richness and 71.9% of the abundance.

DISCUSSION

Factors affecting species richness

Hawkmoth diversity did not correlate well with temperature across the entire elevational range. However, Hawkins et al. (2003) and McCain (2007) noted that with water-energy dynamics the importance of energy depended on the latitude or altitude, and Beck and Chey (2008) stated that temperature could be expected *a priori* to only be correlated with richness at higher elevations. When the temperature-species richness relationship is only considered for the three highest elevations the predictive power of temperature increases dramatically, which is consistent with other studies. Temperature should, then, only be part of what drives species richness. Longino and Colwell (2011) found that although temperature was the best predictor of elevational species richness, no single environmental variable matched the unimodal, low-elevation skewed richness pattern they observed for litter ants in Costa Rica.

Species richness peaked at ~800 m. This is consistent with the findings of other studies on altitudinal insect diversity patterns (e.g., Samson et al. 1997 for ants, Beck and Chey 2008 for geometrids, Beck and Kitching 2009 for sphingids, Longino and Colwell 2011 for litter ants). Transitional plant communities at the sites of peak richness can potentially explain a unimodal pattern. The two sites with the highest species richness (Atalaya and Vitobabma) both contain multiple plant communities. The vegetation at Atalaya is characterized by a combination of moist lowland tropical forest and pluvial submontane tropical forest, while Vitobamba is characterized by a transition from lowland to montane forest. These transitional plant communities likely contain food plants for montane and lowland forest hawkmoths. Beck et al. (2002) and Beck and Chey (2008) reported positive correlations between moth and plant species richness, though Beck and Chey only found this at higher elevations; Schulze et al. (2001) found evidence that, for some butterflies, distribution was influenced by host plant distribution. Atalaya and Vitobamba may represent the lower boundary limit for the range of some montane plants and the upper boundary limit for lowland plant species, and therefore the range limit for the moths that depend on those plants. Overlap between lowland and montane faunas could explain the mid-elevational peak in species richness (Holloway et al. 1990 referenced in Beck et al. 2006b, but see Beck and Chey 2008). To test this specifically, plant species richness and sphingid host plant data are needed for these sites.

The question remains as to what factors drive species richness. As mentioned previously, hypotheses of indirect, trophic cascade effects (host plant diversity) (Beck and Chey 2008) and a combination of direct and indirect effects (McCain 2007) have been proposed as means by which water-energy dynamics limit species richness. Addressing the determinants of species' ranges may also prove insightful to understanding diversity patterns. Longino and Colwell (2011) raise the question as to why mobile species are not constantly expanding their range. They consider a hypothesis in which the upper limits of a species' range is constrained by its thermoregulatory adaptations while lower range limits are determined by competitive interactions (references within Longino and Colwell (2011) provide more information and support for this hypothesis). Gaston and Chown (1999) showed that the thermal minimum temperature of beetles decreased strongly with elevation while the thermal maximum only decreased slightly. This suggests that high elevation species are physiologically able to inhabit lower elevations, but some other factor, such as competition, is restricting their range, further supporting the hypothesis in Longino and Colwell (2011). The extent to which this can explain sphingid ranges depends on the intensity of interspecific competition. Kitching and Cadiou (2000) describe hawkmoth larvae in the Guanacaste Conservation Area, Costa Rica as being host specific, only feeding on a specific genus or several genera within a single family. Depending on the amount of host plant overlap, this would suggest interspecific competition to be either relatively strong or weak. If there is competition between lowland and montane communities, the larger number of lowland centered species with ranges extending into montane habitats would suggest that lowland sphingids are competitively dominant. Unfortunately, this data set is unable to answer these questions. Even with detailed data on plant and moth richness, larval host plants, rainfall, and temperature, the complex nature of these interactions will likely make it difficult to identify the mechanisms driving moth species richness.

Community composition

Community composition changed between the five sites on a species but not on a subfamily level. Other researchers (Kemp et al. 1990 for grasshoppers, Boggs and Murphy 1997 for butterflies, Kumar et al. 2009 for paper wasps, Longino and Colwell 2011 for ants) have also observed similar species level community composition changes. Boggs and Murphy (1997) noted that weather conditions, such as temperature and precipitation, affect the availability of food resources and therefore the distribution of species. Kemp et al. (1990) found that habitat type largely influenced species presence, and habitat type, precipitation, and elevation were important in structuring community composition. This explanation fits with the hypothesis that vegetation type and water-energy dynamics are important determinants of species richness.

The analysis of community composition at the subfamily level shows this to be too broad a taxonomic level for describing sphingid communities at a small scale. Even at the generic level it is likely that many of the community composition changes would have been missed, since most genera are found throughout the altitudinal gradient. Analyzing data at the species level seems to be the most accurate means of describing community composition dynamics. Analysis of sphingids at the subfamily level does reveal, however, that although species, and even some genera, are restricted to particular habitats, none of the subfamilies appear to specialize in any one habitat or elevational range. Beck et al. (2006a) investigated the relative contributions of sphingid subfamilies to faunas of Southeast Asia and Malesia, and found that forest cover was a strong, though not significant, predictor of Smerinthinae and Macroglossinae. This rainforest effect was strongest for Smerinthinae, which they attributed to life history characteristics. Beck et al. (2006b) showed disturbance had a significant effect on subfamily frequency (negative for Smerinthinae and positive for Macroglossinae) while there was only a trend between elevation and subfamily frequency. These studies suggest that disturbance is the main driving force behind proportional abundances of sphingid subfamilies. The small proportion of Smerinthinae, large proportion of Macroglossinae, and similar subfamily frequencies between all five sites in this study suggests that the five sampling locations have faced comparable levels of disturbance in the past.

There appear to be two distinct moth communities: a lowland community which extends up to Vitobamba, and a montane community which extends down to Vitobamba. Differences in these communities were due solely to changes in species presence rather than a combination of changes in the proportional abundance or richness of subfamilies. Ignatov et al. (2011) also described a distinct split between lowland and montane sphingid communities. Although cosmopolitan species, by definition, were found throughout the gradient, they too followed a pattern similar to the community divisions. For example, *Callionima acuta* (Rothschild & Jordan, 1910), *Enyo ocypete* (Linnaeus, 1758), and *Eumorpha phorbas* (Cramer, 1775), all had low elevation centered populations with only a few individuals collected in the montane region, while *Enyo lugubris* (Linnaeus, 1771) showed a montane-centered population with few individuals from the lowlands. A difference in plant communities is the most intuitive explanation for this pattern. Below Vitobamba the dominant vegetation type is lowland forest, while areas above Vitobamba are dominated by montane forest. Ignatov et al. (2011) reported that many of the lowland genera feed on plants that are most abundant and diverse at lower elevations; species of *Eumorpha*, for example, specialize on "Vitaceae, represented by the genus *Cissus* in the study region, which is largely absent or less diverse at the cloud forest site [Wayquecha]." Since hawkmoths tend to be host plant specialists (Kitching and Cadiou 2000), it should be expected that these two forest types support different moth communities.

Endemic species contributed little to single site species richness, or single site abundance (Table 3). This seems contradictory to the findings of Ignatov et al. (2011), who reported a high number of endemic species (up to 23.4% at one site). This decrease is mainly a result of many of the endemics being reclassified after they were collected at a second site. For example, *Adhemarius sexoculata* (Grote, 1865), *Erinnyis crameri* (Schaus, 1898), *Euryglottis aper*, *Euryglottis dognini* Rothschild, 1896, and *Xylophanes mariae* Haxaire, 2013 were classified as endemics from Wayquecha by Ignatov et al. (2011), but were collected at Culebrayoc in this study, placing them in the montane classification. If montane ecosystems are thought to be hotspots for endemism (Meyers et al. 2000, Orme et al. 2005), why is the number of endemic species so low? Endemic as used in this paper, to describe species that were only collected at a single site, is somewhat misleading. This terminology was adopted to allow more accurate comparisons with the results from Ignatov et al. (2011). In their study on overall species richness, threatened species, and endemic species, Orme et al. (2005) defined endemic as the "25% of species with the smallest geographical breeding ranges." The narrow definition of "endemic" as used in this paper likely underestimates the true number of endemic hawkmoth species. In future papers it may be more constructive to use a more traditional definition of the term.

Sources of potential errors

Estimated species richness at Los Amigos, calculated from the corrected data, was lower than observed species richness from all 11 months of sampling. Reexamination of the raw data revealed that all the species which were lost in the correction process were only collected between November and May, the rainy season. Data used for analysis only came from the dry season. This raises the potential concern that, when data from only one season is used, non-parametric richness estimators cannot account for species turnover between seasons. Gotelli et al. (2010), using different methods from this paper, commented that few existing models account for imperfect detection, such as only sampling during the wet or dry season. This suggests that species richness was underestimated at all five sites. If it is the case that non-parametric estimators do not account for temporal turnover, researchers may face problems when trying to estimate species richness from single season samples.

One other potential problem is the small number of sample sites and the lack of replicates. Such a coarse-grained view makes it difficult to determine the exact elevation of peak species richness. Longino and Colwell (2011) faced a similar problem when studying litter ants in Costa Rica. A true mid-elevation peak (~1,400 m) seems unlikely, and in fact may not be expected (Beck and Chey 2008). A finer altitudinal resolution with replicates at some elevations will give a clearer picture of the elevation-species richness relationship, and allow for more rigorous hypothesis testing of determinants of species richness.

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