

GEOGRAPHIC AND ECOLOGICAL AMPLITUDE IN THE NECTARIVOROUS BAT *ANOURA FISTULATA* (PYHLLOSTOMIDAE: GLOSSOPHAGINAE)

Amplitud geográfica y ecológica en el murciélago nectarívoro *Anoura fistulata* (Pyhllostomidae: Glossophaginae)

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ABSTRACT

The wide range of feeding habits among phyllostomid bats has resulted in the selection of unique and contrasting morphological attributes. It has been suggested that nectarivorous bat species co-evolve with the plants they use as primary source of food, and changes in morphology and behavior in the bat, are in some way directed by changes in morphology and phenological cycles of the plants. The nectarivorous bat *Anoura fistulata* (Pyhllostomidae: Glossophaginae) has the longest tongue in proportion to body size among mammals; feature that apparently allows the species to take nectar from flowers with long corollas, some of them typical of highland ecosystems. In spite of this unique morphological adaptation, little is known on the ecological requirements of the species. Herein, Geographic Information System-based analyses and niche modeling techniques were applied to investigate the geographic and ecological niche breadth of *A. fistulata*. We also introduce the first Bolivian record of the species collected at Hernando Siles, Department of Chuquisaca (20°10'0.0" S, 64°15'0.00" W, at 1,524 m), which represents a remarkable extension in the distribution of the species of more than 7°. Our analyses revealed that *A. fistulata* occurs in contrasting ecosystems, from Andean montane and pre-montane moist forest in Western Ecuador and Central Colombia, up to arid and semiarid environments in southern Colombia and Bolivia. *Anoura fistulata* occurs across a wide elevational range between 1,175 and 2,510 m, which is well represented along the geologic unit of the Batholith of Ecuador. A constriction of this elevational belt along the Peruvian Punas and Yungas was suggested as a natural barrier for the establishment of *A. fistulata*. The Peruvian Punas and Yungas isolate *A. fistulata* of Bolivia from records in the northern range of the distribution of the species.

Key words. *Anoura fistulata*, Bolivia, distribution extension, morphology, new record.

RESUMEN

El amplio espectro de hábitos alimentarios entre los murciélagos filostómidos ha resultado en la selección de atributos morfológicos únicos y contrastantes. Se ha sugerido que las especies de murciélagos nectarívoros han co-evolucionado con las plantas que usan como fuente principal de alimento y que cambios en la morfología y el comportamiento de los murciélagos son, de alguna manera, dirigidos por cambios en la morfología y los ciclos fenológicos de las plantas. El murciélago nectarívoro *Anoura fistulata* (Pyllostomidae: Glossophaginae) posee la lengua más larga en comparación a su tamaño corporal entre los mamíferos, característica que aparentemente le permite utilizar flores de corolas largas, algunas de ellas típicas de ecosistemas de alta montaña. A pesar de esta adaptación morfológica única, poco se sabe de los limitantes ecológicos de la especie. En este estudio se aplicaron Sistemas de Información Geográfica en combinación con técnicas de modelamiento de nicho para investigar la amplitud de nicho de *A. fistulata* a escala geográfica y ecológica. También presentamos el primer registro de la especie para Bolivia, recolectado en Hernando Siles, Departamento de Chuquisaca (20°10'0.00" S, 64°15'0.00" W, at 1,524 m), el cual representa una extensión considerable de la distribución de la especie en 7° de latitud. Nuestros análisis revelan que *A. fistulata* existe en ecosistemas contrastantes que incluyen desde bosques andinos premontanos y montanos en el occidente de Ecuador y centro de Colombia, hasta ambientes áridos y semiáridos en el sur de Colombia y Bolivia. *Anoura fistulata* existe en un amplio intervalo de elevaciones entre 1,175 y 2,510 m, intervalo bien representado en la unidad geológica del batolito de Ecuador. Una constricción de este cinturón de elevaciones a lo largo de las Punas peruanas y las Yungas se identifica como una barrera natural para el establecimiento de *A. fistulata*. Las Punas y las Yungas peruanas aíslan *A. fistulata* de Bolivia de registros en la parte norte del área de distribución de la especie.

Palabras clave. *Anoura fistulata*, Bolivia, extensión de distribución, morfología, nuevo registro.

INTRODUCTION

The charismatic nectar feeding bat *Anoura fistula* Muchhala *et al.* (2005) (Pyllostomidae: Glossophaginae) is characterized by some of the most extreme morphological adaptations for nectar consumption, including the longest tongue in proportion to body size among mammals. Such a remarkable adaptation has been interpreted as a specialization for the consumption of resources difficult to exploit by other sympatric nectar feeders (Muchhala, 2006). Dietary studies conducted by Muchhala (2006) suggested that the overextended tongue of *A. fistulata* is an evolutionary adaptation that enables this species to take nectar from flowers characterized by extremely elongated

corollas (9–12 cm) such as *Centropogon nigricans* (Campanulaceae), which apparently is not visited by the sympatric congeneric species *Anoura caudifer* (Geoffroy) and *A. geoffroyi* Gray. The implied co-evolutionary relationship between *C. nigricans* and *A. fistula* suggests that morphological variation in this nectar-feeding species is the result of a process of adaptive specialization (*sensu* Gould and Vbra, 1982). It has been accepted that highly specialized feeding strategies are usually accompanied by a reduction of species niche breadth (Page and Swofford, 1984).

Anoura fistulata is only known from less than 20 localities in northern South America, the majority of them within adjacent bioregions

in Colombia, Ecuador, and Peru (Muchhala, 2005; Muchhala *et al.* 2005; Lee *et al.*, 2008, 2010; Mantilla-Meluk and Baker, 2008; Mantilla-Meluk *et al.*, 2009; Pacheco *et al.*, 2009). However, new records extended the distribution of the species into the southern portion of Peru in the region of Puno (Chacaneque, Ollachea district, Carabaya province), close to the border with Bolivia (Garate-Bernardo and Carrasco-Rueda, 2011).

During an appraisal of museum specimens of *Anoura* deposited at the Field Museum of Natural History (FMNH), we found a female specimen of *A. fistulata* (FMNH 106088) collected in the Bolivian Department of Chuquisaca, which represents the first documented record of this species for the country. We present a comparative morphometric analysis of this specimen to evaluate and describe its morphometric variation and phenetic similarities with other species of the genus.

In this work we investigate the environmental variability associated with *A. fistulata* recorded localities. We proposed two competing hypotheses regarding niche breadth of *A. fistulata*: 1) if extreme morphological adaptations in *A. fistulata* increase the opportunity of the species to exploit a wider variety of plant resources, then we expect a high environmental variability across its distributional range, and 2) if extreme morphological adaptations in *A. fistulata* are an evolutionary response to the use of specific plant resources, then we expect a greater environmental homogeneity across its distributional range. To test these hypotheses, we evaluate the niche breadth of *A. fistulata* across its distributional range using niche modeling and Geographic Information Systems (GIS)-based analyses.

MATERIALS AND METHODS

Morphological and morphometric characterization.- Skull morphology of specimen FMNH 106088 was contrasted against 374 adult specimens including the following taxa: 46 *A. aequatoris* (Bolivia 2; Colombia 33, Ecuador 10, and Peru 1); 2 *A. cadenai* (Colombia); 31 *A. caudifer* (Bolivia 1; Brazil 29; Colombia 1), 29 *A. cultrata* Handley (Colombia 18; Costa Rica 10; Peru 1); 4 *A. fistulata* (Colombia); 34 *A. geoffroyi* (Brazil 3, Trinidad 31), 5 *A. latidens* Handley (Venezuela); 11 *A. luismanueli* Molinari (Colombia 9; Venezuela 2); and 212 *A. peruana* (Bolivia 10, Colombia 172, Ecuador 6, Peru 24) deposited in the following institutions: Instituto de Ciencias Naturales of the Universidad Nacional de Colombia (ICN); Field Museum of Natural History (FMNH); Museo de Historia Natural de la Universidad de Caldas (MHNUC), Southwestern Biology Collection of the University of New Mexico (MSB); and the Museum of Texas Tech University (TTU). To evaluate and describe the morphometric variation and phenetic similarities of the newly introduced record of *A. fistulata* from Bolivia, a principal component analysis (PCA) was performed on 11 craniodental variables recorded from a selected group of female specimens (N=179), including all recognized species of *Anoura*, except *A. cadenai* (only represented by male specimens), in the statistical package PAST (ver. 2.17) available at (<http://folk.uio.no/ohammer/past/index.html>).

Ecological and geographic analyses.- To assess the environmental affinities among *A. fistulata* collecting localities, a PCA and a Cluster Analysis (CA) were performed based on four environmental variables including: Elevation, Maximum Temperature of the Warmest Month of the Year, Minimum

Temperature of the Coldest Month of the Year, and Precipitation. Environmental data were derived from raster layers available at (<http://www.worldclim.org/bioclim>) by applying the extract values to point tool of the Spatial Analyst extension in ArcGIS 9.3.1. Variables were log-transformed and statistical analyses were performed in the statistical package PAST (ver. 2.17), available at (<http://folk.uio.no/ohammer/past/index.html>).

Ecological niche modeling.- An ecological-niche model was produced to evaluate the suitable habitat for *A. fistulata* using the maximum entropy machine learning algorithm in the software MaxEnt (Phillips *et al.*, 2006, 2008). MaxEnt estimates a target probability distribution based on environmental information in the study area associated to presence-only data. The model generates a probability distribution that respects a set of constraints (expressed in terms of environmental variables) derived from the occurrence data (Phillips *et al.*, 2006, 2008).

Nineteen sampling localities including records reported by Muchhala *et al.* (2005) (N=10); Lee *et al.* (2008) (N=1), Lee *et al.* (2010) (N=1), Mantilla-Meluk and Baker (2008) (N=1), Mantilla-Meluk *et al.* (2009) (N=3), Garate-Bernardo and Carrasco-Rueda (2011) (N=1); Pacheco *et al.* (2009) (N=1), and the new record from Bolivia introduced in this work were used as input. Sampling localities were tested for duplicated occurrence data within the same 1 km² grid cell using ENM tools (Warren *et al.*, 2008). This procedure allowed us to have only one point per grid cell, and each remaining point was moved to the center of its grid cell. Collecting localities used to develop the MaxEnt model are contained in Appendix II. A total of 19 bioclimatic parameters of the current climate conditions were used in the model (WorldClim data set, from Hijmans *et al.*, 2005). The data layers used were generated through interpolation of

average monthly climate data from weather stations on a 30 arc-second resolution grid (~1 km² resolution). General accuracy of model was evaluated by the Area Under the Curve (AUC) of Receiver Operating Characteristic (ROC plots) as a measure of prediction success (Fielding and Bell, 1997). Models providing AUC values in the range > 0.9 are considered highly accurate, between 0.7–0.9 useful, and lower than 0.7 poorly accurate (according to Sweets, 1988).

RESULTS

First record of A. fistulata for Bolivia.- Adult Female (FMNH 106088) collected by R. S. Crossin, (collectors number: 7275) on November, 26, 1972 at the Department of Chuquisaca, Azero, Hernando Siles (Misspelled “Hernando Silez” on tag), 16 Km N Monteagudo, Bolivia, 20°10'0.00” S, 64°15'0.00”W, at 1,524 m, preserved as skull extracted, in good condition (Fig. 1a), and body in fluid (Fig. 1b). We were not able to determine if the name Azero on the tag of specimen FMNH 106088 refers to the older name of Hernando Siles, or to the River Azero.

Diagnostic characters.- Specimen FMNH 106088 corresponds to a medium-sized *Anoura* (forearm 39.0 mm), characterized by an elongated, tubelike lower lip (Fig. 1b) extending beyond the upper lip; interfemoral membrane relatively wide (3.5 mm) with an inverted V-shaped margin as described for *A. fistulata* (Muchhala *et al.*, 2005). Muchhala *et al.* (2005) identified the length of the tongue among the most important diagnostic characters of *A. fistulata*; unfortunately, the tongue of specimen FMNH 106088 was partially removed as part of the procedure of skull extraction (previously performed) preventing us from determining its actual length. However, the remaining portion of the basal part of the tongue in our specimen follows the anatomical description of *A.*

fistulata's tongue in Muchhala (2006). In specimen FMNH 106088, the basal part of the tongue passes back through the throat into the thoracic cavity and it is inserted at the base of the sternum (Fig. 1b). At its base, the tongue is distinctively surrounded by a sleeve of connective tissue, described as a glossal tube by Muchhala (2006), which follows the ventral position of the trachea (Fig. 1b). The placement of the tongue in a deeper position between the sternum and the heart, as well as the presence of a glossal tube are claimed as autopomorphies of *A. fistulata* (Muchhala *et al.*, 2006), contrasting the typical placement of the tongue at the base of the oral cavity of other nectarivorous bats (Griffiths, 1982), or at the upper part of the sternum as in other choeronycterines, such as *Choeronycteris mexicana*, as confirmed based on the dissections of specimens of this taxon (N=3).

Skull comparisons.- Skull of *A. fistulata* FMNH 106088 is greater than that in *A. aequatoris* and *A. lusimanueli*, and falls within the morphometric ranges reported for *A. caudifer* and *A. fistulata* (Mantilla-Meluk and Baker, 2006; Muchhala *et al.*, 2005) (Table 1). The first upper molar has the typical enlarged anteroexternal cusp and a reduced associated cristid, characters identified as synapomorphies of the *A. caudifer* complex (Griffiths and Gardner, 2008; Mantilla-Meluk and Baker, 2010 Fig. 8 Pg. 15). This character differentiates *A. fistulata* from *A. carishina*, *A. geoffroyi*, and *A. peruana* (Mantilla-Meluk and Baker, 2010). Additionally, *A. fistulata* has complete zygomata, differentiating it from *A. peruana* and *A. latidens*. In *A. fistulata*, the upper canines have a smooth anterior face with no sulci; first lower premolar not enlarged and bladeliike shape as in *A. cultrata* (Handley, 1960). The dentary in *A. fistulata* is straight

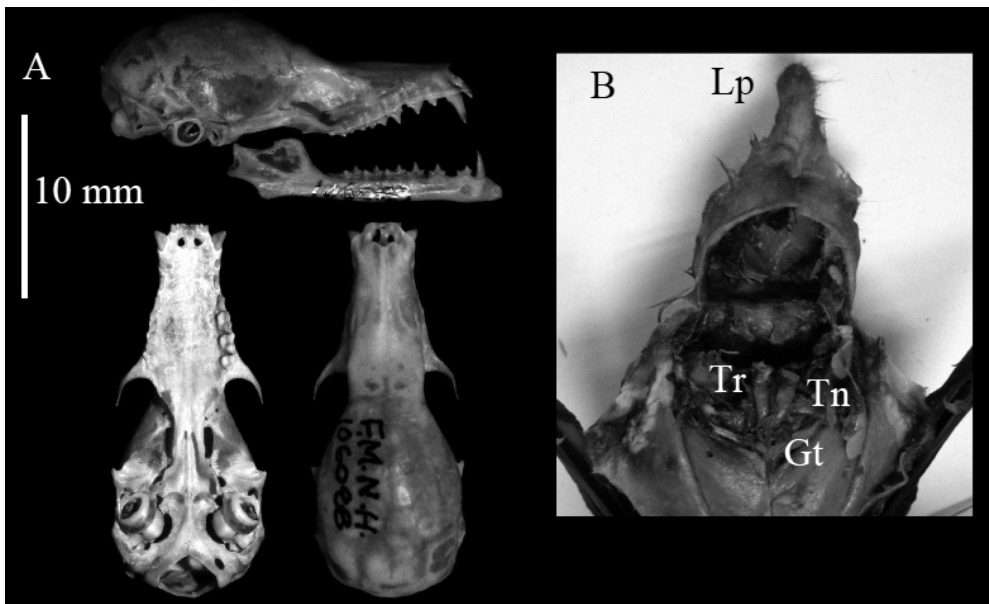


Figure 1. A) Skull views of *Anoura fistulata* FMNH 106088, from Chuquisaca, Bolivia, showing characters included in *A. fistulata* description (Muchhala *et al.* 2005): protruded mandibular symphysis, elongated, straight and slender dentary, gap between the lower 1st and 2nd premolars; and the short postpalatal spine; B) insertion of the tongue (Tn) at the base of the sternum, glossal tube (Gt) that follows the trachea (Tr), as well as the elongated lower lip tubelike structure (Lp).

and slender resembling that of *A. caudifer* from Brazil and contrasting the most robust and curved dentary of *A. aequatoris* from Bolivia, Colombia, and Peru. Although the dentary in *A. cadenai* is also straight, it is more robust than that of *A. fistulata*. In *A. fistulata* the lower tooth row is characterized by a noticeable gap between the 1st and 2nd lower premolars (0.61 mm), a character present in six specimens analyzed by Muchhala *et al.* (2005) (0.54 mm), which is absent in *A. cadenai*. Although a gap between the 1st and 2nd lower premolars was also present in *A. caudifer* specimens from Brazil (N=8), it was less noticeable (< 0.6 mm) than in *A. fistulata*. The mandible of *A. fistulata* is also characterized by a protrusion at the mandibular suture (mandibular keel) that is absent in *A. cadenai*, and less developed in other species of the genus such as *A.*

aequatoris, *A. caudifer* from Brazil and *A. luismanueli* (Mantilla-Meluk and Baker, 2006, Fig. 6, Pg. 12).

Principal components analysis of morphometric data.- Most of the skull variation in our dataset was explained by the first two components (PC1 = 83.84% and PC2 = 5.30%) with greater loadings associated with GSL and CBL. Although specimens with GSL greater than 23.0 mm largely overlap in the morphospace of our PCA (Fig. 2), *A. fistula* proved to be morphometrically independent from other members of the *A. caudifer* complex (*A. aequatoris*, *A. caudifer*, and *A. luismanueli*) and closely related in skull morphology to *A. carishina* and small *A. peruana* in the northern range of the distribution of this species in Colombia.

Table 1. Skull measurements of a selected group of specimens of *Anoura* in all recognized species in the genus. All specimens correspond to females except those of *A. cadenai* (*), represented by only males. Measurements of specimen *A. fistulata* FMNH 10688 from Chuquisaca, Bolivia are also included. Description of the measurements are included in Appendix I.

		GSL	CB	PAL	PO	MB	BCW	BCH	TR	M-M	C-C	Mand	ManTR
<i>A. aequatoris</i>		22.00	21.32	11.65	4.53	8.34	8.83	6.85	8.11	5.46	3.95	15.54	8.49
N= 17	StDv	0.55	0.67	0.67	0.19	0.34	0.39	0.33	0.34	0.20	0.18	0.49	0.25
<i>A. cadenai</i> *		23.47	22.51	12.46	4.92	8.43	9.23	8.34	8.75	5.68	4.31	16.67	9.16
N= 4	StDv	0.33	0.31	0.30	0.36	0.15	0.25	0.17	0.15	0.16	0.10	0.34	0.10
<i>A. carishina</i>		24.04	23.31	11.98	4.86	8.88	9.55	7.22	8.98	5.99	4.11	16.58	9.47
N= 4	StDv	0.00	0.04	0.29	0.19	0.27	0.35	0.37	0.07	0.15	0.06	0.12	0.03
<i>A. caudifer</i>		22.7	22.1	12.5	4.7	8.4	8.9	6.9	8.3	5.4	4.3	16.2	8.6
N= 13	StDv	0.6	0.6	0.5	0.2	0.2	0.2	0.3	0.2	0.2	1.2	0.5	0.4
<i>A. cultrata</i>		24.26	22.45	12.17	5.02	9.05	9.65	7.64	8.38	5.78	4.77	16.91	8.87
N= 11	StDv	0.58	3.08	0.44	0.16	0.17	0.22	0.22	0.23	0.32	0.14	0.36	0.32
<i>A. fistulata</i>		24.14	23.50	12.86	4.61	8.58	9.21	8.02	8.83	5.75	4.20	16.08	9.15
N=4	StDv	0.66	0.66	0.80	0.15	0.45	0.32	0.41	0.55	0.19	0.19	1.52	0.50
FMNH 106088		23.75	23.09	12.72	4.56	8.1	8.74	8.0	8.5	5.78	3.96	16.31	8.76
<i>A. geoffroyi</i>		24.90	24.05	13.25	5.17	9.20	9.76	7.54	9.46	6.23	4.46	17.39	9.77
N= 11	StDv	0.358	0.34	0.48	0.21	0.27	0.25	0.36	0.18	0.19	0.14	0.29	0.28
<i>A. latidens</i>		24.23	23.50	12.18	22.30	9.09	9.61	6.87	9.23	6.10	4.25	77.76	9.34
N= 29	StDv	0.57	0.74	0.48	93.61	0.23	0.23	0.29	0.19	0.18	0.17	315.81	1.12
<i>A. lasyopiga</i>		24.74	24.22	13.49	4.97	9.14	9.69	7.26	9.56	6.00	4.28	17.52	9.80
N= 4	StDv	0.38	0.42	0.28	0.19	0.12	0.12	0.08	0.42	0.20	0.14	0.32	0.36
<i>A. luismanueli</i>		21.51	20.77	11.16	4.53	8.27	9.01	6.62	7.58	4.75	4.01	15.29	8.48
N= 3	StDv	0.42	0.26	0.28	0.21	0.07	0.16	0.26	0.41	0.29	0.29	0.33	0.28
<i>A. peruana</i>		25.16	24.22	13.10	4.89	9.13	9.68	7.31	9.39	5.97	4.33	17.44	9.76
N= 87	StDv	1.18	1.16	1.46	0.19	0.22	0.22	0.51	0.30	0.20	0.16	0.67	0.59

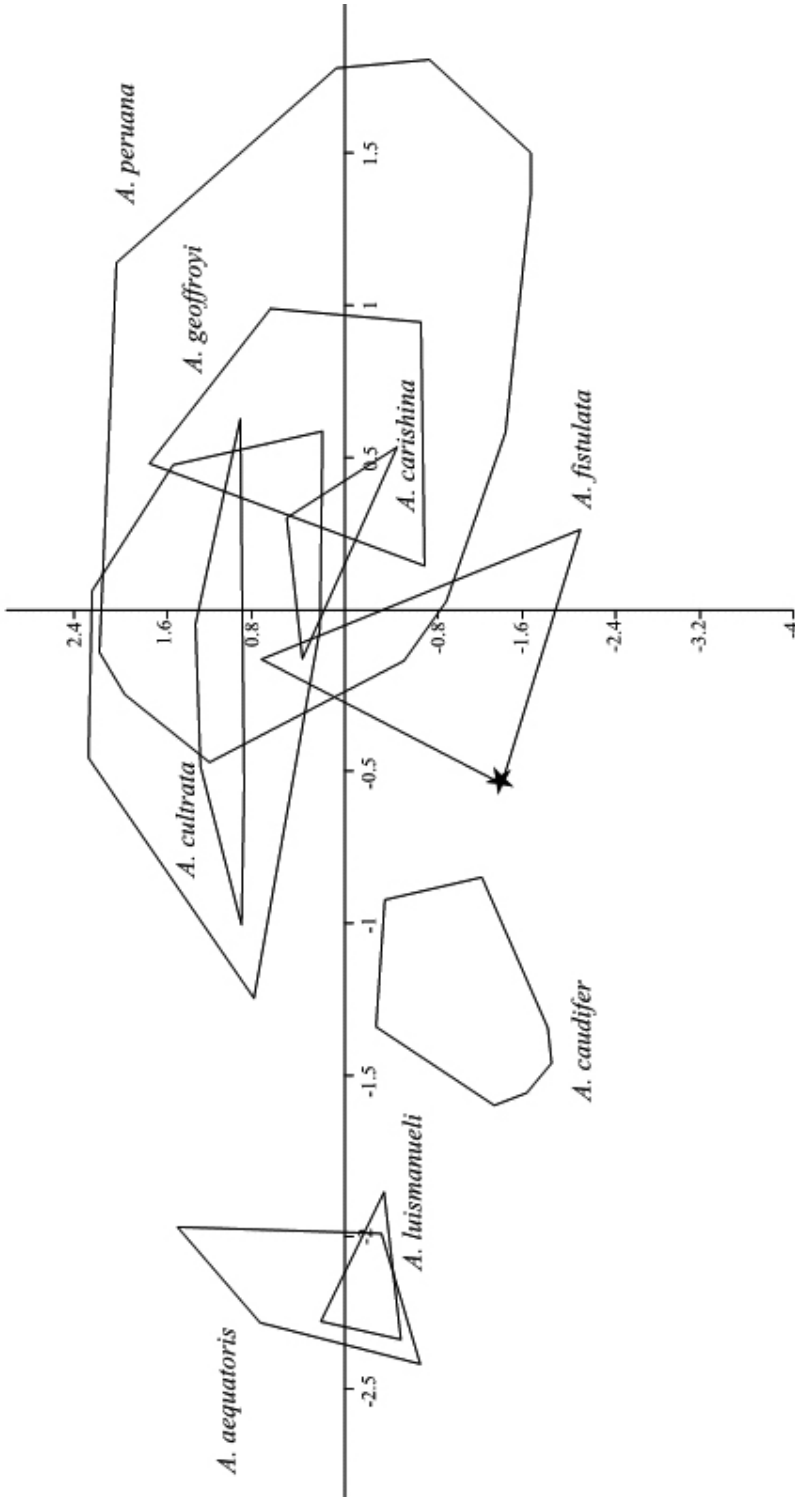


Figure 2. Principal Component Analysis of 11 craniodental variables of 179 female specimens: *A. aequatoris* (8); *A. carishina* (4); *A. caudifer* (26); *A. cultrata* (9); *A. fistulata* (6); *A. geoffroyi geoffroyi* (5); *A. g. lasiopyga* (4); *A. latidens* (26); *A. luismanuelli* (3); *A. peruana* (88). *Anoura fistulata* specimen FMNH 106088, from Bolivia is marked by a black star.

Range extension of A. fistulata.- *Anoura fistulata* was described from Condor Mirador, near the Destacamento Militar (3°38'08" S, 78°23'22" W) on the Cordillera del Condor, 1,750 m, Zamora Chichipe Province, Ecuador (Muchhala *et al.*, 2005). Besides the type locality, the authors recorded the species in eleven other localities in Ecuador, two of them on the western versant of the Andes. Lee *et al.* (2010) reported an additional record from western Ecuador from Imbabura (0°19'51" N, 78°55'55" W), which represents the lowest elevation reported for the species (702 m). Mantilla-Meluk and Baker (2008) extended the distribution of *A. fistulata* into the Colombian territory based on a specimen from Llorente, Nariño (0°49'0.00" N, 77°15'0.00" W), with a posterior extension of the range of the species into the northern portion of the Colombian Andes by Mantilla-Meluk *et al.* (2009) based on a specimen collected in Pueblo Rico, Department of Risaralda, on the road to La Bocatoma (5°14'18" N, 76°2'11" W) at 2,460 m. In the southern part of its range, the distribution of the species was extended by Jiménez *et al.* (2008) into the Peruvian territory based upon a specimen collected at Playa Colorada, District Huicungo, Department of San Martín (7°16'60" S, 76°47'60" W) at 1,704 m. Pacheco *et al.* (2009) also reported *A. fistulata* for the Abiseo River, San Martín (not specific locality provided by the authors), deposited at the Museo de la Universidad de San Marcos (MUSM 7213, 7215) and proposed that the species is likely to be present in southern localities along the Andes. Later Gárate-Bernardo and Carrasco-Rueda (2011) reported the species for Puno, southern Peru (13°39'42" S, 70°28'56" W). Herein, we present the morphological evidence associated with the first record of *A. fistulata* from Bolivia, which also constitutes the southernmost known locality of the species. The locality is part of the Bolivian montane dry forest (Olson *et al.*, 2001), which encloses the Bolivian Inter-Andean dry forest (Ibish *et al.*, 2003).

Analysis of environmental variation.- In our PCA the first component accounted for most of the variation among *A. fistulata* collecting localities (PC1 65.86 %, PC2 20.67), with Minimum Temperature (-0.834), Mean Annual Precipitation (-0.427), and Maximum Temperature (-0.290) having a negative loadings and Elevation (0.191) having positive loading.

In our PCA and CA, Puno, Peru and Llorente, Serranía de los Churumbelos in Colombia, represented the most divergent localities in terms of the environmental variables analyzed. Puno, Peru had the lowest minimum temperature; while Llorente had the highest precipitation among analyzed localities (Mean Annual Precipitation > 2,490 mm). The rest of the environmental variation was grouped into a single cluster, subdivided into four clusters without geographic structure (Fig. 5).

MaxEnt algorithm niche model.- Areas of high suitability for the species represented by probability values greater than 75% were located in the northern portion of the Andean Region of southern Colombia and Ecuador (Figure 3). In our niche model, the northernmost known locality for the species in Pueblo Rico, Risaralda, Colombia, the westernmost locality at Imbabura, Ecuador; while the southernmost record in that reported for Puno, Peru. In our MaxEnt model, the locality of Puno was associated with predictive values greater than 45%; while the newly reported record from Hernando Siles, Chuquisaca, Bolivia fell within an area characterized by probability values lower than 5%. Additionally, the area of Chuquisaca, Bolivia, is isolated from suitable environments in the northern range of the *A. fistulata* distribution by the Bolivian Yungas which were represented by probability values lower than 5% (Fig. 3).

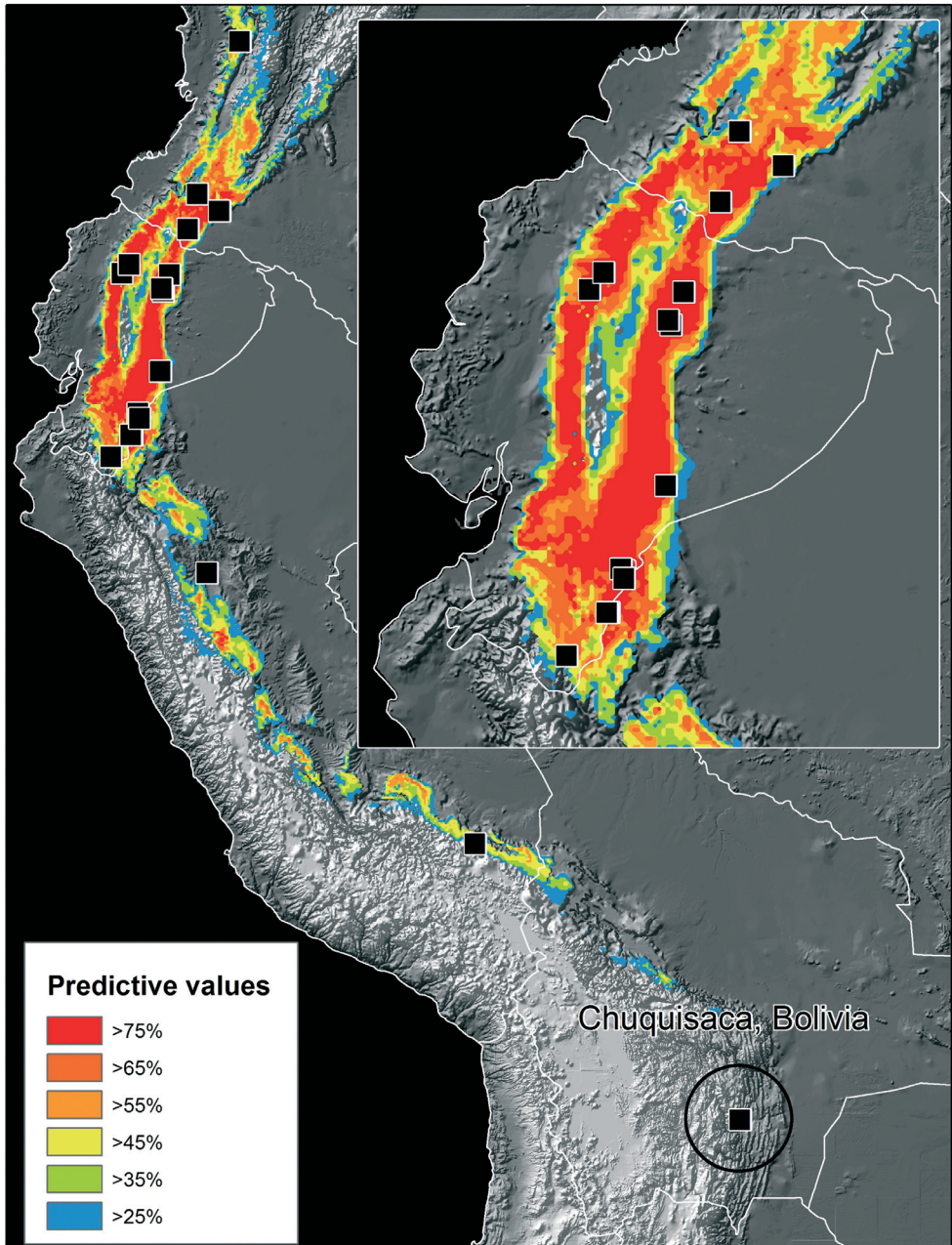


Figure 3. MaxEnt niche model constructed for *A. fistulata* based on the 19 known localities for the species. Areas with high probability of species occurrence in warm colors, areas enclosing low probability values in cool colors. Locality enclosed by the circle represents the new record of *A. fistulata* from Chuquisaca, Hernando Siles, Bolivia.

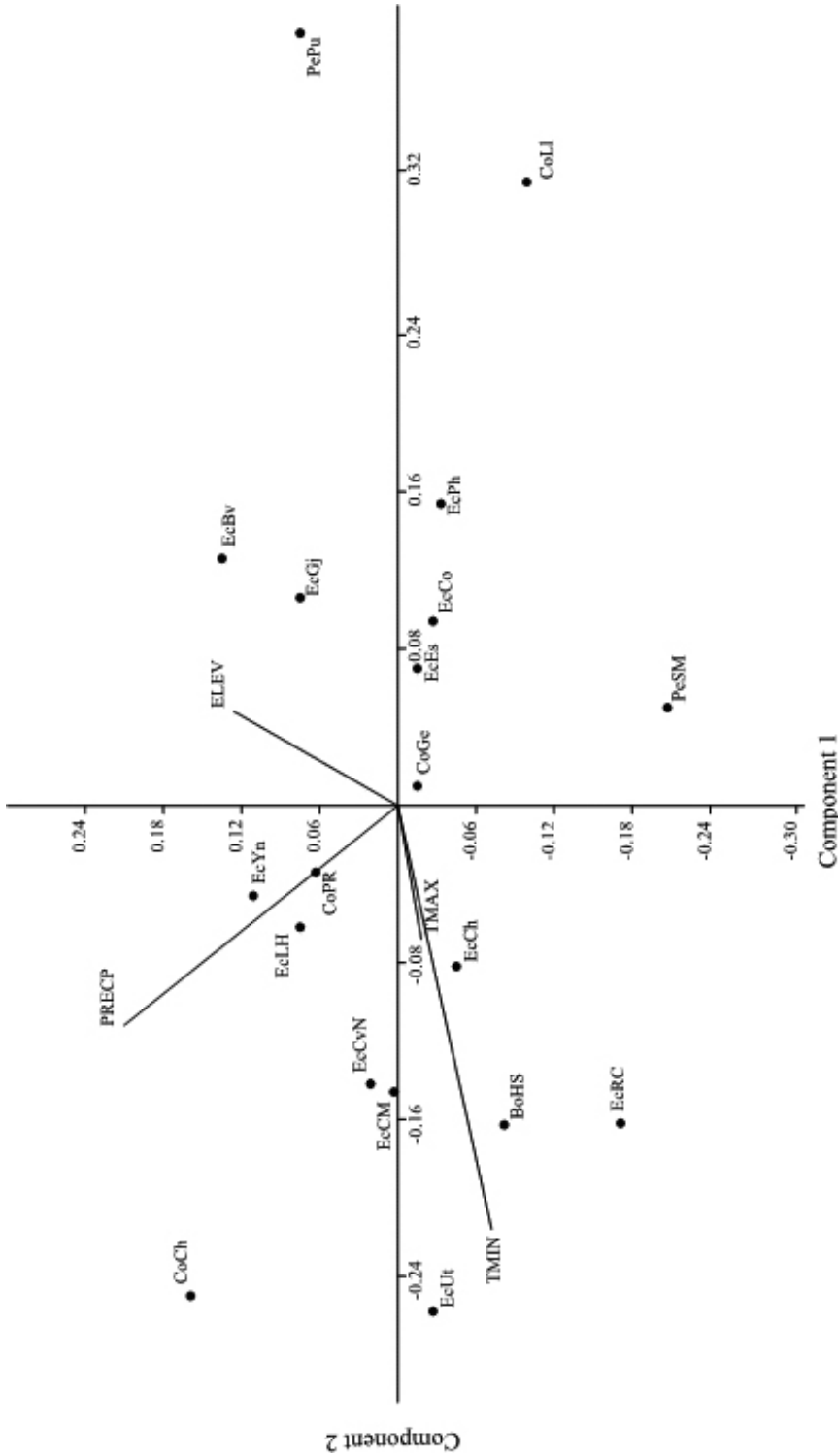


Figure 4. Scatter plot of the PCA and minimum spam tree of four environmental variables (Elevation, Mean Annual Maximum Temperature, Mean Annual Minimum Temperature, and Mean Annual Precipitation) analyzed among known collecting localities of *A. fistulata*. Abbreviations used to designate the localities: BOLIVIA: Hernando Siles (BoHS); COLOMBIA: Génova (CoGe); Lorente (CoLI); Pueblo Rico (CoPR); Serranía de Los Churumbelos (CoCh); ECUADOR: Bellavista (EcBv); Condor Mirador (EcCM); Cotundo (EcCo); Chimapinza (EcCh), 1,700 m; Cuevas de Numbala (EcCvN); Imbabura (EcImb); El Salado (EcES); Guajalito (EcGj); La Herradura (EcLH); Pahuma (EcPh); Río Cristalino (EcRC); Uunsuants (EcUt); Volcán Sumaco (EcVS); Yanayacu (EcYn); PERU: Playa Colorada (PePC); Puno (PePu).

DISCUSSION

Elevation explained most of the variation among *A. fistulata* collection localities. *Anoura fistulata* occurs between 702 and 2,517 m (mean = 1,846 m, standard deviation 335 m), altitudinal belt which is well represented along the Andean unit constituted by the Batholith of Ecuador and associated areas in Colombia and Peru. This area is part of three adjacent but ecologically contrasting bioregions: the Eastern Cordillera real montane forest, the Northwestern Andean montane forest, and the Ucayali moist forest (Olson *et al.*, 2001). The elevational belt delimited by maximum and minimum elevations reported for *A. fistulata*, experiences a substantial reduction in area at central and southern Peru where the Andes are steeper (Fig. 3). Although we agree with Pacheco *et al.* (2009) and believe that the absence of *A. fistulata* in central Peru may be an artifact of sampling, and lack of detailed analyses of specimens, the reduction in area of suitable elevations for *A. fistulata* at this portion of the country may constitute an ecological limiting factor for the establishment of the species, and may be an alternative explanation for the gap of records between San Martin and Puno.

The northern range of the distribution of *A. fistulata* enclosed the most divergent environments for the analyzed variables. In this portion of its distribution *A. fistulata* inhabits three adjacent but ecologically contrasting bioregions: the Eastern Cordillera real montane forest, the Northwestern Andean montane forest, and the Ucayali moist forest as defined by Olson *et al.* (2001). In both our PCA and CA the Andean montane moist forests of Western Ecuador and Central Colombia, represented by the localities of Imbabura and Serranía de los Churumbelos, respectively, as well as the premontane forests of Southern Colombia in Llorente were classified in independent groups in our cluster analysis (Fig. 5). This result reflects

the great variety of environments inhabited by *A. fistulata*.

One of the most significant results of this study is the latitudinal extension of the distribution of *A. fistulata* by more than 7° into Hernando Siles in Bolivia. In both our PCA and CA, the geographically isolated *A. fistulata* Bolivian locality clustered with those in the northern portion of the distribution of the species (Figs. 4 and 5). The *A. fistulata* Bolivian locality at the *Bolivian Inter-Andean dry forests* biome (Ibish *et al.* 2003) is characterized by a marked seasonality with a dry period of 8 to 10 months, and the area is dominated by xerophytic dwarf forests (*chaparral*), columnar, and terrestrial cacti (Ibish *et al.* 2003). Although not representing arid enclaves, Ecuadorian collecting localities of: Chinapinza, Cuevas de Numbala and Condor Mirador shared low Precipitation values and high Minimum and Maximum Temperature and cluster with *A. fistulata* Bolivian locality (Figs. 4 and 5).

Areas identified as arid enclaves in southern Colombia and Ecuador were also included in our *A. fistulata* MaxEnt model. With a disjunctive distribution, arid enclaves are relatively common along the Andean System from Venezuela south to Chile and glossophagine bats and particularly representatives of the genus *Anoura* are a typical component of their faunas (Soriano and Ruiz 2002, Sanchez *et al.* 2006). Pollen of the cacti *Opuntia dillenii*, *Pilosocereus* sp., and *Stenocereus griseus* has been found in the guts of the congeneric *A. carishina* (Mantilla-Meluk and Baker 2010) from arid enclaves in the southern Andes of Colombia, enclosed within areas associated with *A. fistulata* intermediate presence probabilities (>35%) in our MaxEnt model (Fig. 3). Several studies have pointed on the co-evolutionary relationship that exists between glossophagine bats and columnar cacti characterizing chiropterophylic

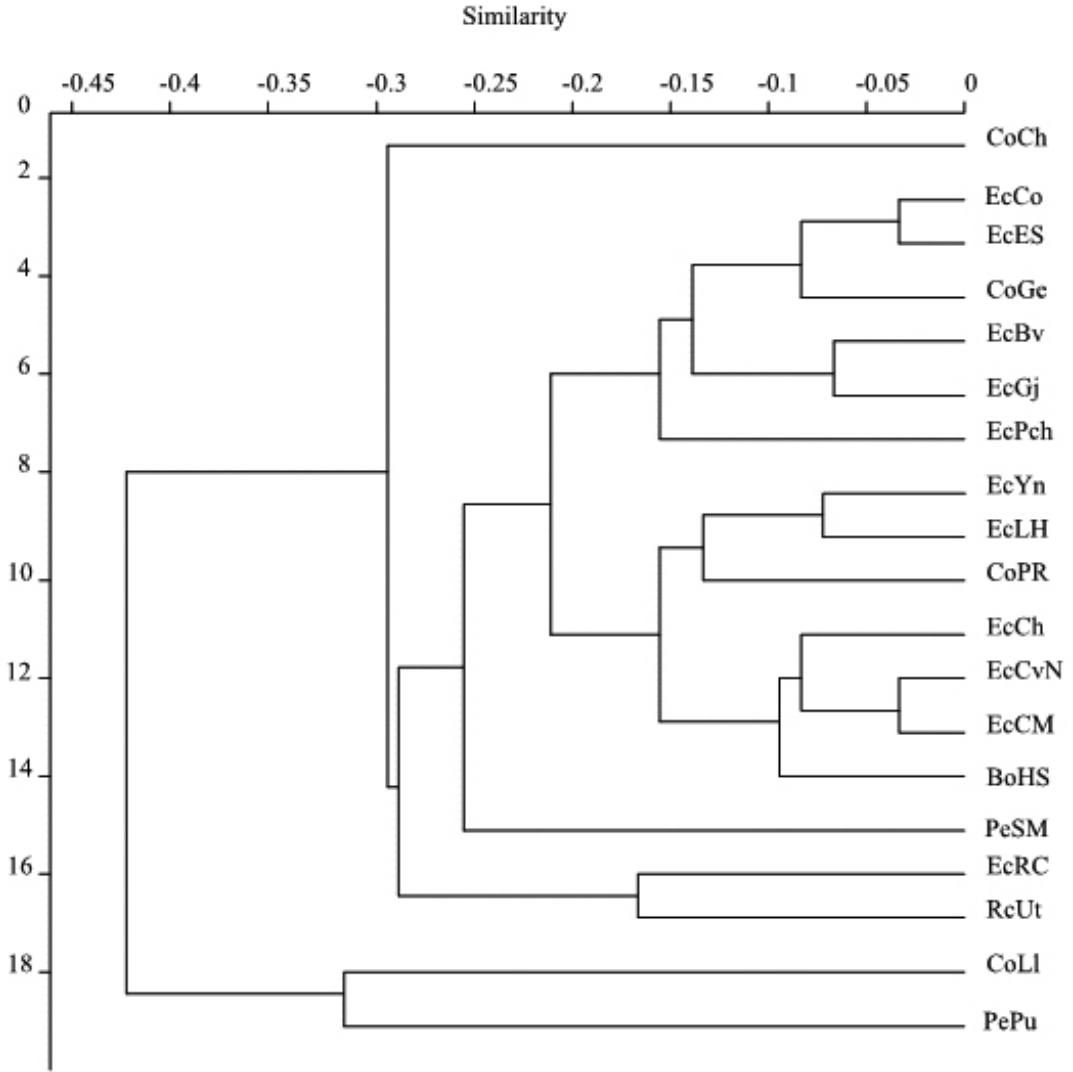


Figure 5. Cluster analysis of *A. fistulata* collecting localities based on euclidian distances of four environmental variables (Elevation, Mean Annual Maximum Temperature, Mean Annual Minimum Temperature, and Mean Annual Precipitation). Abbreviations used to designate *A. fistulata* localities: BOLIVIA: Hernando Siles (BoHS); COLOMBIA: Génova (CoGe); Llorente (CoLI); Pueblo Rico (CoPR); Serranía de Los Churumbelos (CoCh); ECUADOR: Bellavista (EcBv); Condor Mirador (EcCM); Cotundo (EcCo); Chinapinza (EcCh), 1,700 m; Cuevas de Numbala (EcCvN); Imbabura (EcImb); El Salado (EcES); Guajalito (EcGj); La Herradura (EcLH); Pahuma (EcPh); Río Cristalino (EcRC); Uunsuants (EcUt); Volcán Sumaco (EcVS); Yanayacu (EcYn); PERU: Playa Colorada (PePC); Puno (PePu).

syndromes that consist of anatomical and behavioral adaptations of both cacti and bats to promote and facilitate bat pollination (Baker *et al.* 2012, Fleming *et al.* 2009, Nassar *et al.* 1997, Rivera-Marchand and Ackerman 2006, Ruiz *et al.* 1997, Soriano and Ruiz 2006, Valiente-Banuet *et al.* 1997). The co-evolutionary history between Neotropical nectar feeders and cacti supports their existence in relatively wide latitudinal gradients across divergent bioregions enclosing arid enclaves.

Anoura fistulata proved to exist in a wide altitudinal range in divergent bioregions enclosing ecologically contrasting localities. Most of the ecological variation among known localities is associated with the northern portion of the species distribution. The prevalence of *A. fistulata* along the geologic unit of the Batholith of Ecuador as well as the absence of the species across Central and Southern Peru is apparently explained by differences in steepness and its effect on the area of the elevational belt between 1,175 m and 2517 m. A reduction of this elevational belt in Central and Southern Peru may constitute an ecological barrier for the establishment of *A. fistulata* in that region, isolating the arid environments inhabited by the species in the southern portion of its distribution in Bolivia.

Although there is not a unified definition that makes specialization comparable across study systems (Lara *et al.*, 2002), the term “specialized” is used to describe species that possess unique attributes (Hintzpeter and Bauer 1986) or a restricted ability to respond to varying environmental parameters (Klopfer and MacArthur, 1960; Endler, 1986), or both (Westoby, 1978; Leisler, 1980; Benkman, 1988; Futuyma and Moreno, 1988). Although other species of nectarivorous bats have long tongues, the size of the tongue in *A. fistulata* is remarkably longer when compared with other sympatric congeneric species. To date,

there is no a detailed analysis on *A. fistulata* diet, but the data presented herein revealed that the species can occur in contrasting ecosystems presumably having differences in plant compositions, and thus suggesting that unique attributes of *A. fistulata* do not necessitate stereotypy. Altogether our results support our first hypothesis that interprets extreme adaptations of *A. fistulata* as features that allow the species to survive in contrasting ecosystems across its distributional range.

Table 2. Loadings of collecting localities in the four axes of our PCA for the four environmental variables analyzed.

Locality	Axis 1	Axis 2	Axis 3	Axis 4
EcUt	0,25038	0,029171	0,095396	-0,01022
EcRC	0,15734	0,17249	0,13645	-0,015108
EcCo	-0,09162	0,02774	-0,013053	0,0018196
EcES	-0,068289	0,014477	0,0085036	-0,0030054
EcBv	-0,12227	-0,13693	0,0027879	-0,019774
EcGj	-0,10363	-0,073067	0,012319	-0,010255
EcPh	-0,15274	0,02953	-0,098027	0,024233
EcYn	0,044443	-0,10837	-0,019381	-0,0071039
EcLH	0,058591	-0,071609	0,041699	-0,020912
EcCh	0,078192	0,04323	-0,0067959	0,022955
EcCvN	0,13687	-0,022277	-0,037474	0,019495
CoLI	-0,31288	0,10048	-0,073593	-0,042427
PeSM	-0,048248	0,2043	-0,074622	0,027683
BoHS	0,15572	0,077378	0,013545	0,0075025
CoGe	-0,012502	0,015025	-0,0029493	-0,048665
CoCh	0,24473	-0,15828	-0,038114	0,010245
CoPR	0,030977	-0,063196	-0,11623	0,008585
EcCM	0,14327	-0,0056678	-0,0098785	0,013256
PePu	-0,38833	-0,07443	0,17942	0,041696

Abbreviations used to designate collecting localities: BOLIVIA: Hernando Siles (BoHS); COLOMBIA: Génova (CoGe); Llorente (CoLI); Pueblo Rico (CoPR); Serranía de Los Churumbelos (CoCh); ECUADOR: Imbabura (EcImb); Unuants (EcUt); Río Cristalino (EcRC); Cotundo (EcCo); El Salado (EcES); Bellavista (EcBv); Guajalito (EcGj); Pahuma (EcPh); Yanayacu (EcYn); La Herradura (EcLH); Chinapinza (EcCh), 1,700 m; Cuevas de Numbala (EcCvN); Condor Mirador (EcCM); PERU: Playa Colorada (PePC); Puno (PePu).

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Appendix II. *Collecting localities of A. fistulata analyzed*

BOLIVIA: **Chuquisaca:** Azero, Hernando Siles, 16 Km; N Monteagudo, 1,524 m, 20°10'0.00" S, 64°15'0.00" W. COLOMBIA: **Nariño:** Génova, Municipio de Colón, Vereda Bordo Alto, 1,979 m, 1° 38'47" N, 77° 1'27" W; Llorente, 2,088 m, 0°49'0.00" N, 77°15'0.00" W; **Risaralda:** Pueblo Rico, on the road to La Bocatoma, 2,460 m, 5°14'18" N, 76°2'11" W; **Cauca:** Serranía de Los Churumbelos, Municipio de Santa Rosa, Vereda La Petrolera, Tataui, 2,100 m, 1°14'32.32" N, 76°30'28.34" W; ECUADOR: **Imbabura:** 10 km east of Santa Rosa, 702 m 0°19'51" N, 78°55'55" W; **Morona Santiago:** Unsuants, 1,300 m, 2°33'09" S, 77°53'48" W; Río Cristalino, 1,061 m, 3°31'12" S, 78°25'48" W; **Napo:** Cotundo, 1,870 m, 0°38'30" S, 77°50'15" W; El Salado; Alto Coca, 1,800 m, 0°15'0.00" S, 77°41'0.00" W; **Pichincha:** Bellavista, 2,200 m, 0°00'08" S, 78°41'02" W; Guajalito, 2,000 m, 0°13'09" S, 78°48'00" W; Pahuma, 2,275, 0°01'04" S, 78°38'00" W; Yanayacu, 2,075 m, 0°35'03" S, 77°52'08" W; **Zamora Chichipe:** La Herradura, 1,750 m, 4°02'02" S, 78°34'12" W; Chinapinza, 1,700 m, 4°02'19" S, 78°35'40" W; Cuevas de Numbala, 1,890 m, 4°32'48" S, 79°04'05" W; Destacamento Militar, Condor Mirador, 1,750 m, 3°38'08" S, 78°23'22" W; Volcán Sumaco, 0°34'19" S, 77°35'64" W; PERU: **Puno:** the village of Chacaneque, Ollachea district, Carabaya province, 13°39'42" S, 70°28'56" W; **San Martín:** District of Huicungo; Playa Colorada, 1,704 m, 7°16'60" S, 76°47'60" W.