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ORIGINAL ARTICLE

Range prediction for the Giant Fruit-Eating Bat, *Artibeus amplus* (Phyllostomidae: Stenodermatinae) in South America

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Suitable habitat range for *Artibeus amplus* in the Neotropics was predicted using maximum entropy niche modeling, environmental covariates, and museum records from 61 locations across Colombia, Venezuela, Guyana, and Suriname. Environmental covariates included (a) bioclimatic data; (b) elevation; (c) geology; and (d) soil. Model selection was based on graphic analyses of omission/commission, and Akaike information criterion (AIC), small sample size corrected AIC (AIC_c) and Bayesian information criterion (BIC). Models incorporating all of the above covariates performed best. The predicted suitable habitat range adjusted well to the known range of *A. amplus*. However, our analysis identifies northern Brazil as a spot requiring further research to determine the presence of *A. amplus*.

Keywords: *Artibeus amplus*; suitable habitat; model; distribution; South America

Introduction

Artibeus amplus is one of the most poorly known bat species in the northern Neotropics (Lim et al. 2003). Among the large *Artibeus* species, *A. amplus* is distinguished by its enigmatic distributional pattern: it is both the most restricted and fragmented among the bat species ranges mapped by Koopman (1976, 1982). Although the population trend of this species is unknown, it is considered of least concern by the IUCN Red List of Threatened Species (IUCN 2010). However, Rodríguez (1998) and Rodríguez & Rojas-Suárez (2008) more realistically included it in the “data deficient” category.

Species range size is one of the best predictors of the likelihood of extinction (Jones et al. 2003; Gaston & Fuller 2009). *Artibeus amplus* is probably the only species of *Artibeus* that could be facing conservation threats based on its relatively small range. More generally, there is a deficit of basic knowledge for *A. amplus*. For example, whether the distributional range proposed by Koopman (1976, 1982) corresponds to the boundaries that would be expected based on environmental factors is unknown. Lim et al. (2002) explored the geographic distribution of this bat species, but the study was limited to Guyana and the authors provided no further information beyond a statement that the

predicted geographic distribution of *A. amplus* is reasonable given the current knowledge. Thus, detailed analysis of habitat suitability for *A. amplus* is needed to better assess its population viability. A full knowledge of the habitat range of this species will improve monitoring of population trends and eventually implementation of conservation strategies. Because field surveys are expensive and time consuming, several approaches to spatial modeling of species distributions have been proposed (Elith et al. 2006). These models have played a fundamental role in assessing potential distributions of species under current (Pearson et al. 2007; Tittensor et al. 2009), past and future climatic conditions (Rodríguez-Sánchez & Arroyo 2008; Stralberg et al. 2009), conservation planning (Kremen et al. 2008), and research on evolutionary and ecological processes (Wiens & Graham 2005; Gaston & Fuller 2009; Buckley et al. 2010).

Species distribution models are based on the concept of the ecological niche, whereby the location of a given species in a landscape is determined by environmental factors that underpin the successful ecological performance of such species (Hutchinson 1957). Thus, the presence of similar environmental conditions can be used to predict additional regions where a given species could be present.

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The goal of the present study was to predict the suitable habitat range of *A. amplus* under current environmental conditions using maximum entropy models constrained by the limited data available on the distribution of this poorly known Neotropical bat species.

Material and methods

Datasets and sources of information

We compiled information from specimens of *A. amplus* deposited in 10 museum collections in Canada, Colombia, USA and Venezuela (Appendix 1): Royal Ontario Museum (ROM), Instituto Alexander von Humboldt (IND), Instituto de Ciencias Naturales of Universidad Nacional de Colombia (INC), American Museum of Natural History (AMNH), Carnegie Museum (CMNH), Smithsonian National Museum of Natural History (NMNH), Colección de Vertebrados de la Universidad de Los Andes (CVULA), Estación Biológica Rancho Grande (EBRG), Museo de Biología de la Universidad Central de Venezuela (MBUCV), and Museo de Historia Natural La Salle (MHNLS).

The dataset for analysis included 196 specimens from 61 localities in Colombia, Venezuela, Guyana, and Suriname, collected between 1960 and 2005.

We are confident that these specimens from international or national collections are correctly identified to species because most have been revised by experts such as Handley (1976, 1987; specimens deposited at NMNH and EBRG), or Lim et al. (2003; specimens deposited at ROM and CMNH). Specimen information was provided directly by the curators (B Lim, ROM; D Perico, IND; S McLaren, CMNH; P Soriano, CVULA; A Lander, EBRG; R Pérez and M Salazar, MBUCV; H Rojas and JC Señaris, MHNLS), or obtained online: INC (<http://www.biovirtual.unal.edu.co/ICN/>), AMNH (<http://entheros.amnh.org/db/emuwebamnh/Query.php>), and NMNH (<http://collections.mnh.si.edu/search/mammals/>). We corroborated the presence of the species in the field at two localities (55 and 56, Appendix 1).

The georeferencing of these localities varied from GPS recordings to names of nearest towns listed on specimen labels. We used a variety of gazetteers, scientific publications, and resources available from local governments to infer coordinates from the available locality information, unless this information was provided by the collection itself. Geographic coordinates were transformed to the decimal degree system, the format required by the software used in our analyses.

Modeling habitat suitability range

Climate conditions correspond to the 19 bioclimatic variables, representing combinations of temperature and precipitation from Worldclim, version 1.4 (Hijmans, Cameron, et al. 2005), obtained from Worldclim website (<http://www.worldclim.com/current.htm>). Physical data on elevation came from the same source. WorldClim is a set of grid layers, in a latitude/longitude coordinate reference system (datum WGS84), and for the present study the grids of 5 minute pixels were used.

After eliminating duplicate localities, each presence locality was assigned to its corresponding pixel according to its geographical position following the Worldclim grid format, and combining points that fell within a given pixel. Following this procedure, 56 unique pixels remained (Figure 1). These pixels were examined to identify outliers with respect to bioclimatic and elevation variables and to detect possible errors using DIVA-GIS, version 5.4 (Hijmans, Guarino, et al. 2005).

To remove the effects of colinearity, Pearson's correlation among the 20 continuous variables was tested for the 56 pixels in which *A. amplus* was present, excluding the highly correlated ones ($r \geq 0.75$) and retaining the ecologically most important ones for further analyses.

Spatial autocorrelation was evaluated for each variable through Moran's I coefficients calculated using "ape" package in R (Paradis et al. 2004) and a matrix of spatial weights (W_{ij}) calculated as a distance-based weight which was the inverse distance between locations i and j ($1/d_{ij}$). Distances between locations were calculated using Geofunc.xla, an Excel[®] add-in available from <http://nmml.afsc.noaa.gov/Software/ExcelGeoFunctions/excelgeofunc.htm>, and then transformed to kilometers. Correlograms were plotted to evaluate autocorrelation trends, using package "ncf" in R (Bjørnstad 2008).

The contribution of two additional categorical variables was evaluated in the modeling process. First, we coded geological provinces in South America using a generalized base map based on geological data from Schenk et al. (1999). Second, we coded soil types based on data from the Soil and Terrain Database for Latin America and the Caribbean (SOTERLAC version 2.0; downloaded from <http://www.isric.org>) (Dijkshoorn et al. 2005), which combines geographical information on soil unit distribution and attribute data of representative soils. We included these two layers of information to explore whether habitat suitability was shaped by the effect of either the geologic history, i.e. the way in which rock deposits have evolved until recent times, or the product of interactions between the

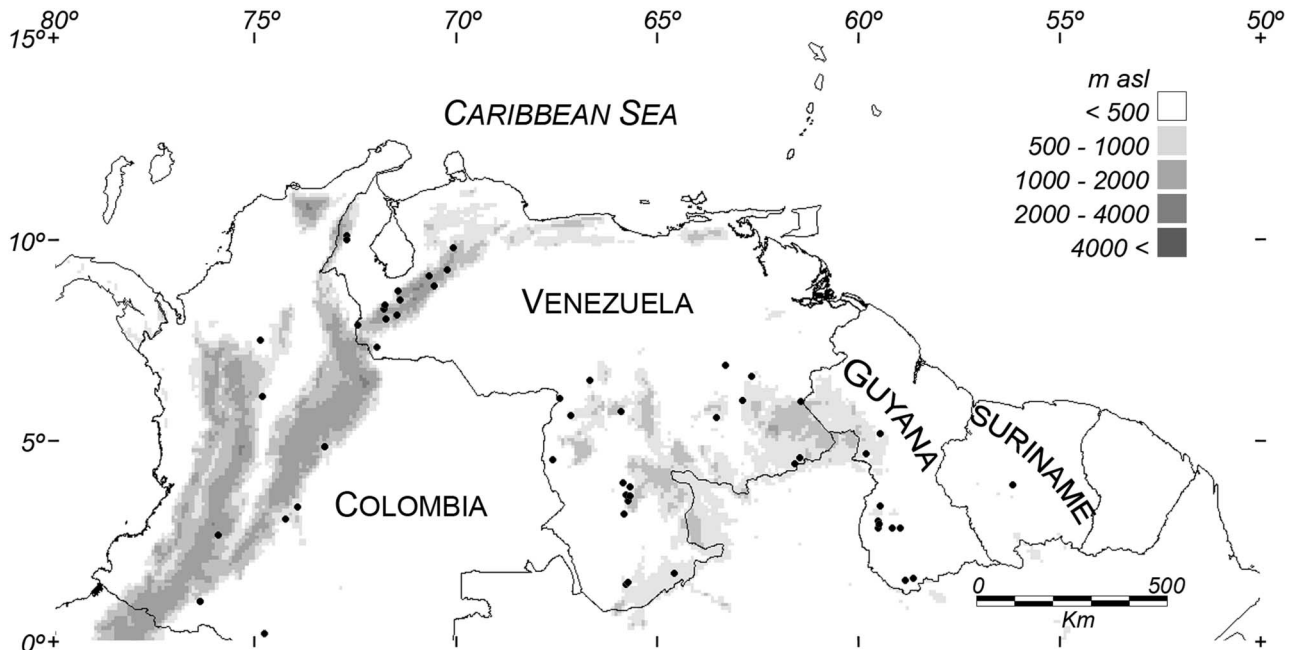


Figure 1. Northern South America, showing the countries where *Artibeus amplus* has been collected. Black dots correspond to the 56 pixels obtained after data reduction (see text for details).

lithosphere, hydrosphere, atmosphere and biosphere, which is reflected in different soil types.

We explored the performance of four groups of models based on four possible combinations of variables: (a) models based uniquely on continuous variables (bioclimatic and elevation, hereafter CON); (b) models combining continuous and geologic variables (C+G); (c) models combining continuous and soil variables (C+S); and (d) models combining all variables (C+G+S).

Land-cover data have been used to obtain more accurate spatial predictions (Tingley & Herman 2009). However, this variable was not included in the analyses because the presence dataset for bats included specimens collected over 40 years. During this time period South America has had heterogeneous but mostly high deforestation rates (FAO 2010). Since tolerance to habitat degradation has not been studied for this bat species, we did not include this information in our analysis. We also consider that any possible insights from this information would be correlated with the soil type, given that land use changes tend to be constrained by soil type (Christian 1958).

The model was developed using MaxEnt, version 3.3.3e (Phillips et al. 2004, 2006), available from <http://www.cs.princeton.edu/~schapire/maxent/>, a machine-learning method that uses the principle of maximum entropy on presence-only data to estimate a set of functions to best identify the link between environmental variables and habitat suitability, to

approximate the species' niche and potential geographic distribution. We opted for MaxEnt because of its better performance compared to other commonly used methods (Elith et al. 2006; Phillips et al. 2006; Pearson et al. 2007).

To remove the uncertainty that arises due to different use of pseudo-absence points, we cross-validated model predictions. Briefly, we evaluated how good the models were at predicting data ("test data") not used to fit the model ("training data"). For cross-validation, 10 runs were conducted, splitting training and test data on a ratio of 90:10. Thus, each point was used for both training and testing. Projections were made for each run, and the average projection (and the corresponding standard deviation) were also created. The significance of each variable was tested through jackknifing.

The study area was limited to the tropical portion of the South American sub-continent: A rectangle within 12°35' N, 81°25' W (northwestern corner), and 12°35' S, 34°40' W (southeastern corner). We constrained the area in order to avoid artifacts in the results (Lobo et al. 2008).

Akaike information criterion (AIC) (Akaike 1974), small sample size corrected AIC (AIC_c) (Hurvich & Tsai 1989), and Bayesian information criterion (BIC) (Schwarz 1978) scores were calculated for model selection using the testing version of ENMTools 1.2 (www.enmtools.com) (Warren et al. 2010; Warren & Seifert 2011).

Finally, a binary map of presence/absence was created to facilitate the visualization of model predictions based on the lowest presence threshold (LPT) proposed by Pearson et al. (2007).

Results

Datasets

Several localities were outliers with respect to current bioclimatic conditions. However, no locality was excluded from the analyses for this reason. The observed outliers might reflect the character of the species more than errors from other sources. The wide elevation range of the species reinforces this perspective. Indeed, data indicate that *A. amplus* occurs from 9 m asl. (at Arrecifes, Tayrona National Park, Colombia) to 2630 m asl. (at Finca El Triunfo, Cauca, Colombia), with a median of 500 m asl. However, these localities are not evenly distributed, being skewed toward the lower elevations (Figure 2). A correlation matrix (Table 1) indicates three groups of highly correlated variables. The first one was integrated by temperature-based variables including Bio 1, Bio 2, Bio 3, Bio 4, Bio 9, Bio 10, Bio 11, and Bio 15 (precipitation seasonality) as exception.

The second group is a set of the precipitation-based variables Bio 12, Bio 13, Bio 16 and Bio 19. The third group also included precipitation-based variables Bio 14 and Bio 17. We kept variables Bio 1 (annual mean temperature), Bio 12 (annual precipitation) and Bio 14 (precipitation of driest month) for further analyses. Correlations of variables Bio 5, Bio 6, Bio 7, Bio 8, Bio 18 and Elevation were below 0.75 in all cases and thus were considered in the models. Table 2 summarizes statistics for these nine variables used for habitat modeling.

All variables showed some degree of spatial autocorrelation. Moran's I coefficients ranged from 0.249 for Bio 18, to 0.345 for Bio 12, averaging 0.294 (Figure 3).

However, in all cases the omission rate on test samples was higher than the predicted omission rate, indicating independence between the test and training data. The latter result also implies the lack of spatial autocorrelation influence on the models (Figure 4). Moreover, the receiver operating curves (ROC) for both training and test data were clearly different, reinforcing the notion of independence between both datasets, with higher AUC_{Train} than AUC_{Test} (Table 3).

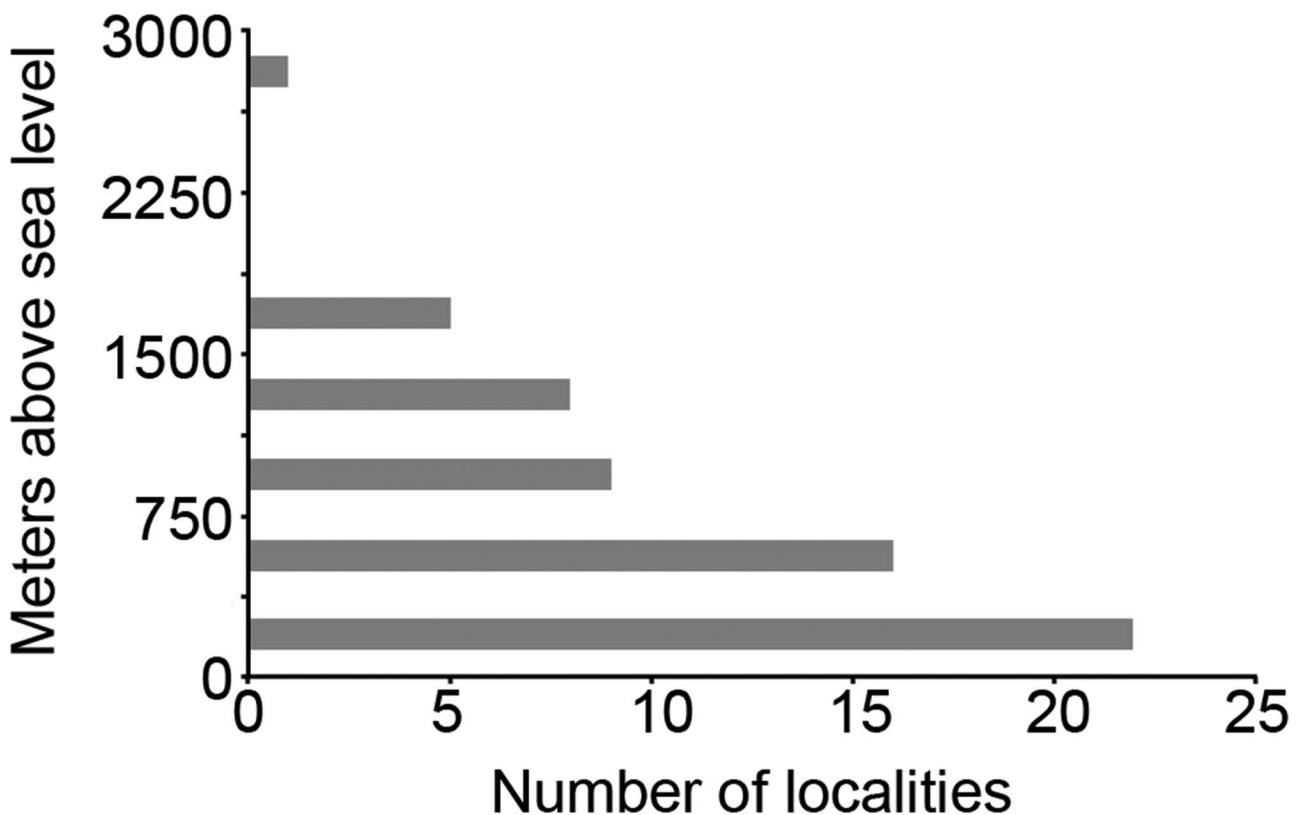


Figure 2. Distribution of the 61 localities where *Artibeus amplus* has been collected with respect to elevation. Specific coordinates for the locations are presented in Appendix 1.

Table 1. Pearson correlation coefficients between pairs of variables considered in the modeling process.

	Bio 1	Bio 2	Bio 3	Bio 4	Bio 5	Bio 6	Bio 7	Bio 8	Bio 9	Bio 10	Bio 11	Bio 12	Bio 13	Bio 14	Bio 15	Bio 16	Bio 17	Bio 18	Bio 19	Elev
Bio 1	1.00																			
Bio 2	0.78	1.00																		
Bio 3	0.98	0.87	1.00																	
Bio 4	1.00	0.78	0.98	1.00																
Bio 5	0.20	0.13	0.19	0.20	1.00															
Bio 6	0.35	0.23	0.33	0.35	0.20	1.00														
Bio 7	0.08	0.07	0.07	0.08	0.37	0.44	1.00													
Bio 8	0.67	0.49	0.65	0.67	0.30	0.17	-0.03	1.00												
Bio 9	0.97	0.75	0.95	0.97	0.17	0.31	0.08	0.63	1.00											
Bio 10	0.92	0.74	0.90	0.92	0.14	0.30	0.06	0.60	0.94	1.00										
Bio 11	0.76	0.57	0.73	0.76	0.36	0.21	0.08	0.47	0.73	0.70	1.00									
Bio 12	-0.06	-0.12	-0.06	-0.06	0.20	0.13	0.09	-0.09	-0.10	-0.13	0.01	1.00								
Bio 13	-0.02	-0.06	-0.01	-0.02	0.19	0.06	0.07	-0.08	-0.07	-0.07	0.08	0.91	1.00							
Bio 14	0.08	-0.08	0.06	0.08	0.14	0.26	0.07	0.00	0.02	-0.05	-0.06	0.67	0.43	1.00						
Bio 15	1.00	0.78	0.98	1.00	0.20	0.35	0.08	0.67	0.97	0.92	0.76	-0.06	-0.02	0.08	1.00					
Bio 16	-0.03	-0.07	-0.02	-0.03	0.19	0.05	0.07	-0.08	-0.08	-0.07	0.07	0.92	0.99	0.43	-0.03	1.00				
Bio 17	0.07	-0.07	0.05	0.07	0.16	0.26	0.08	-0.01	0.02	-0.05	-0.05	0.75	0.50	0.98	0.07	0.50	1.00			
Bio 18	-0.14	-0.20	-0.15	-0.14	0.13	0.11	-0.02	-0.04	-0.15	-0.21	-0.11	0.63	0.39	0.60	-0.14	0.40	0.63	1.00		
Bio 19	0.05	-0.02	0.05	0.05	0.12	0.14	0.10	-0.07	0.01	0.00	0.09	0.77	0.82	0.42	0.05	0.82	0.49	0.22	1.00	
Elev	-0.21	-0.26	-0.24	-0.21	-0.09	-0.04	0.12	-0.13	-0.16	-0.16	-0.18	-0.37	-0.53	-0.18	-0.21	-0.50	-0.19	0.08	-0.41	1.00

Bio 1: Annual mean temperature [1]. Bio 2: Mean monthly temperature range [2]. Bio 3: Isothermality $(2/[7] \times 100)$ [3]. Bio 4: Temperature seasonality $(STD \times 100)$ [4]. Bio 5: Max temperature of warmest month [5]. Bio 6: Min temperature of coldest month [6]. Bio 7: Temperature annual range $([5]-[6])$ [7]. Bio 8: Mean temperature of wettest quarter [8]. Bio 9: Mean temperature of driest quarter [9]. Bio 10: Mean temperature of warmest quarter [10]. Bio 11: Mean temperature of coldest quarter [11]. Bio 12: Annual precipitation [12]. Bio 13: Precipitation of wettest month [13]. Bio 14: Precipitation of driest month [14]. Bio 15: Precipitation seasonality (CV) [15]. Bio 16: Precipitation of wettest quarter [16]. Bio 17: Precipitation of driest quarter [17]. Bio 18: Precipitation of warmest quarter [18]. Bio 19: Precipitation of coldest quarter [19]. Elev: Elevation.

Table 2. Summary statistics for explanatory variables used to model *Artibeus amplus* habitat in intra-tropical America obtained from Worldclim (Hijmans, Cameron, et al. 2005).

Variable	<i>A. amplus</i> locations			Study area		
	Mean	SD	Range	Mean	SD	Range
Bio 1	23.8	3.6	15.2–28.3	25.1	3.2	0.2–29.1
Bio 5	30.1	3.8	22.1–36.0	32.0	3.3	6.2–36.3
Bio 6	17.8	4.0	7.7–22.8	18.6	3.9	–10.4–23.9
Bio 7	12.3	1.0	10.8–15.4	13.4	2.7	5.7–22.8
Bio 8	23.4	3.3	15.6–28.1	25.0	3.1	1.0–29.1
Bio 12	2196.8	916.1	827–4274	2032.3	814.2	2–9967
Bio 14	57.6	43.8	5–239	54.1	58.1	0–666
Bio 18	383.5	179.6	29–771	365.0	218.5	0–2442
Elev	720.4	618.0	28–2316	358.5	605.8	–19–5111

Discrete variables

Artibeus amplus has been mainly recorded in two main areas in northern South America with different geological histories: the more recent (Miocene–Pliocene) mountain ranges in the west and northwest (including portions of the Colombian and Venezuelan Andes, Santa Marta and Perijá) and the antique Guiana Shield of southern Venezuela, Guyana and Suriname. In the first case, occurrence points fall in seven of the geologic provinces defined by Schenk et al. (1999): (1) west-central Cordillera, (2) eastern Cordillera, (3) Putumayo-Orient Marañon Basin, (4) Sierra Nevada de Santa Marta, (5) Llanos Basin in Colombia, (6) Perijá–Venezuelan coastal ranges, and (7) Maracaibo Basin in Venezuela. Particularly, 33.3% of occurrence points fall in Paleogene areas, 29.2% in Precambrian, 20.8% in Mesozoic, and 16.7% in Paleozoic. On the other hand, 93.8% of occurrence points in the Guiana Shield correspond to Precambrian, 3.1% to Paleozoic and 3.1% to Quaternary.

Occurrence points fell in 31 different SOTERLAC units, most of them including different kinds of Cambisols (30.4%) and Leptosols (30.4%), but also Ferralsols (12.5%), Regosols (8.9%), Acrisols (7.1%), Arenosols (7.1%) and Alisols (3.6%).

The lowest and the highest AIC_c scores corresponded respectively to CON and C+G+S models (Table 3). By contrast, the other model selection criteria showed the opposite pattern, with the lowest scores for the C+G+S model and the highest for CON. ROCs of the different models tested indicated a better performance in terms of sensitivity/specificity for those models combining continuous and categorical information instead of just the CON model (Figure 4).

The relative contribution of each environmental variable to the different models is shown in Table 4. Elevation had the highest contribution in the CON model, and the corresponding

permutation importance (i.e. the jackknife significance test) indicates heavy dependence of the model on that variable. Geological information had the highest contribution value in the case of the C+G model, but the corresponding permutation importance indicates little dependence of the model on that variable. Finally, soil data had the highest contribution value in the case of the C+S model and the permutation importance indicated a heavy dependence of the model on that variable. A similar result was observed for the C+G+S model.

Modeling habitat suitability range

The CON model predicted suitable habitat in a range wider than the currently known distribution for *A. amplus* (Figure 5). New areas included the northern portion of the Mata Atlántica as well as parts of northern Brazil, areas in central French Guiana, low and mid-elevation parts of the Ecuadorian Andes and the northeastern Peruvian Andes.

In Colombia, the model correctly predicted suitable habitat in the mountainous regions of the country, where the species has been reported, but also in parts of the Pacific basin (Chocó), and in most of the Colombian Llanos, although the model failed by excluding a locality (Putumayo). In Venezuela, the range of suitable habitat correctly included the low-to-mid elevations of the Andes, Perijá and the Guiana shield, but also the northern mountain ranges (San Luis, La Costa and Turimiquire). In Guyana and Suriname, the model fits the known distribution of the species.

In comparison, the C+G model (Figure 5) excluded most of the Mata Atlántica in Brazil, as well as Peru, western Ecuador, and most of French Guiana. Conversely, it predicted wider areas in northern Brazil. In Colombia, the model included parts of northwestern Amazonia and the Central Andes,

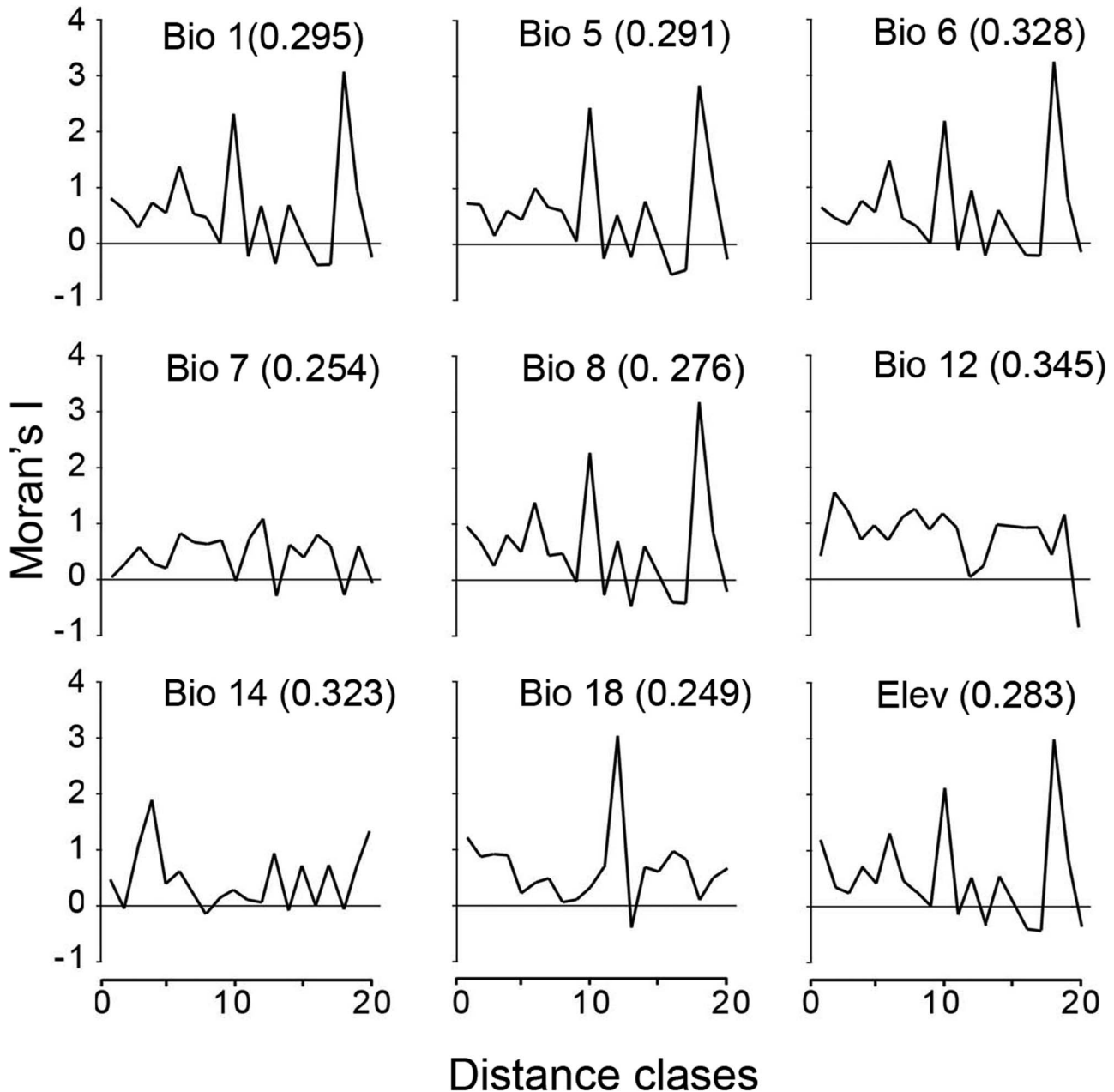


Figure 3. Correlograms of the bioclimatic and elevation variables considering the first 20 distance classes. Numbers in parentheses indicate Moran's I coefficients observed for the bioclimatic variables and elevation, considering all 56 localities. Standard deviation was 0.05 for all cases.

and excluded parts of the western range of the Andes. Again, the model failed by excluding the same locality (Putumayo). In Venezuela, the model correctly excluded the northern mountain range. It also included wide areas of Guyana and Suriname.

The range of suitable habitat predicted by the C+S model (Figure 5) excluded the Mata Atlântica in Brazil and most of Ecuador. In Colombia, it included central and western Amazonia, the eastern Llanos, Chocó and Guajira lowlands. In Venezuela, the predicted area

included the northern Cordilleras. The range predicted in the Guianas is similar to that predicted by the C+S model.

Finally, the C+G+S (Figure 5) excluded most of the Mata Atlântica in Brazil, Peru, most of Ecuador and most of French Guiana, and included wide areas in northern Brazil. In Colombia, the model included the Andes, Santa Marta, western Amazonia at Putumayo and Caquetá Departments, eastern Llanos and Guajira lowlands, excluding most

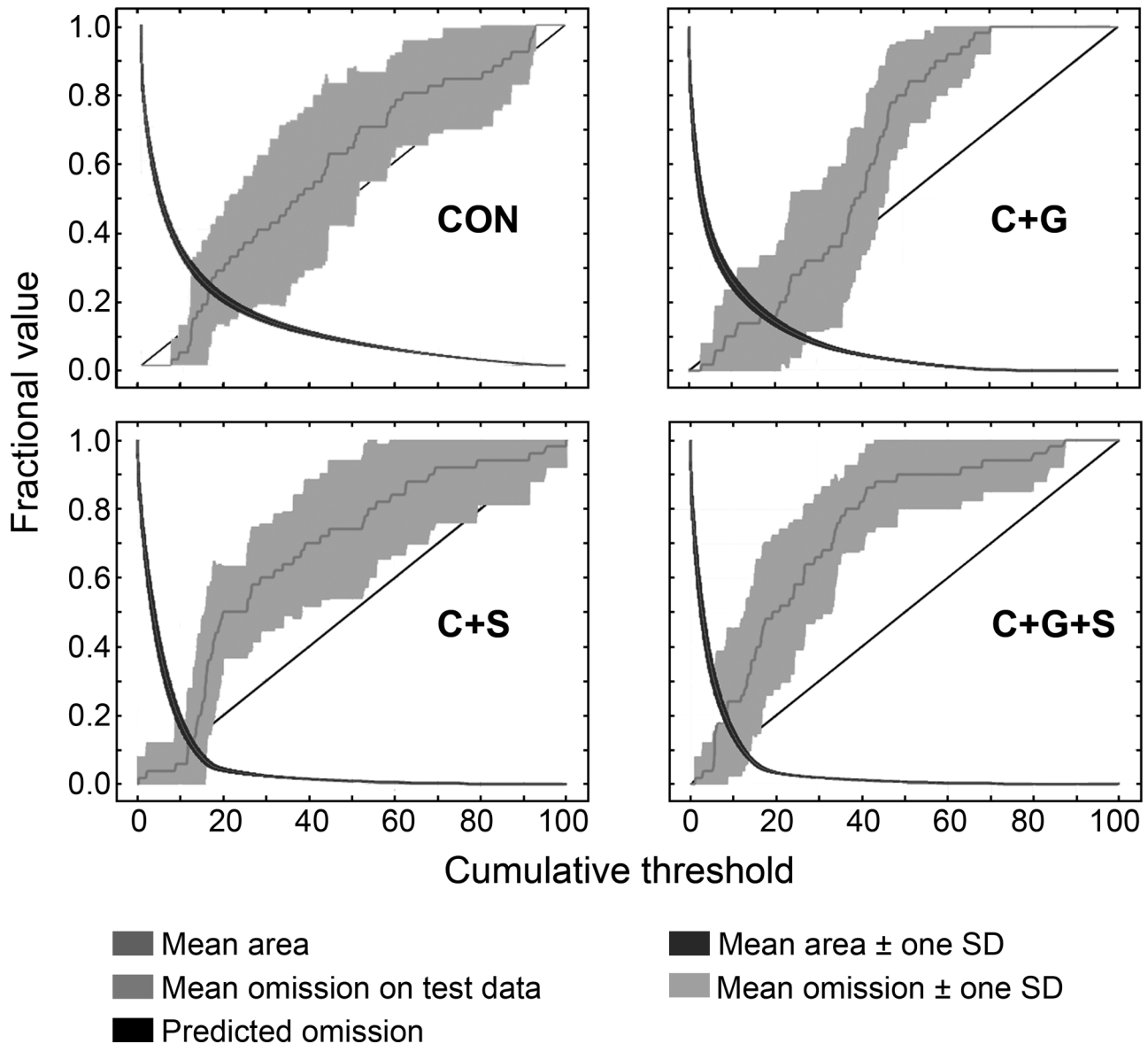


Figure 4. Analyses of omission/commission showing omission rates and predicted areas as a function of the cumulative thresholds averaged over the replicates runs. CON: models based on continuous variables. C+G: models based on continuous variables and geological information. C+S: models based on continuous variables and soil information. C+G+S: models based on continuous variables, as well as geological and soil information.

Table 3. Model selection for the four possible combinations of continuous and categorical variables.

Model	AIC	AIC _c	BIC	AUC _{Train}	AUC _{Test}
CON	1211.1 ± 7.3	1404.1 ± 97.3	1287.4 ± 17.0	0.927 ± 0.005	0.869 ± 0.044
C+G	1117.0 ± 11.6	2100.6 ± 1010.9	1212.6 ± 16.8	0.974 ± 0.003	0.883 ± 0.050
C+S	1029.4 ± 6.8	1721.0 ± 797.6	1121.4 ± 10.2	0.990 ± 0.001	0.937 ± 0.044
C+G+S	1015.7 ± 18.4	3366.1 ± 1520.2	1121.3 ± 17.4	0.994 ± 0.000	0.903 ± 0.083

AIC = Akaike's information criterion scores. AIC_c = sample size corrected AIC scores. BIC = Bayesian information criterion scores. AUC_{Train} = area under the curve on training data. AUC_{Test} = area under the curve on test data. CON = models based uniquely on continuous variables (bioclimatic and elevation). C+G = models combining continuous and geologic variables. C+S = models combining continuous and soil variables. C+G+S = model combining all variables.

Table 4. Average relative contribution of each environmental variable.

Variable	CON		C+G		C+S		C+G+S	
	C %	P.I.	C %	P.I.	C %	P.I.	C %	P.I.
Bio 1	4.3	6.5	4	8.4	2.3	1.2	1.9	1
Bio 5	2.3	0.9	1.4	0.6	0.1	0.1	0	0
Bio 6	2.9	3.9	0.6	0.2	0.7	0.6	0.5	0.3
Bio 7	18.5	27.1	2.7	4.1	0.3	1.8	1.1	5.7
Bio 8	0.3	0.2	0.3	0	0.1	0	0.1	0
Bio 12	1.8	3.6	0.8	2.2	0.2	0.8	0.1	0.3
Bio 14	18.4	4.1	12.7	6.2	8.1	2.4	7.8	0.5
Bio 18	0.9	1.5	0.2	2.3	0.1	0.6	0.1	0.3
Elev	50.7	52.3	23.2	42	16.8	10.7	13.9	4.4
Geol			54.1	34	7.6	0.5	21.2	17.4
Soil					63.8	81.3	53.3	70

C%: percent contribution values. P.I.: permutation importance. CON = models based uniquely on continuous variables (bioclimatic and elevation). C+G = models combining continuous and geologic variables. C+S = models combining continuous and soil variables. C+G+S = model combining all variables. Bold highlights the greatest percent contribution value.

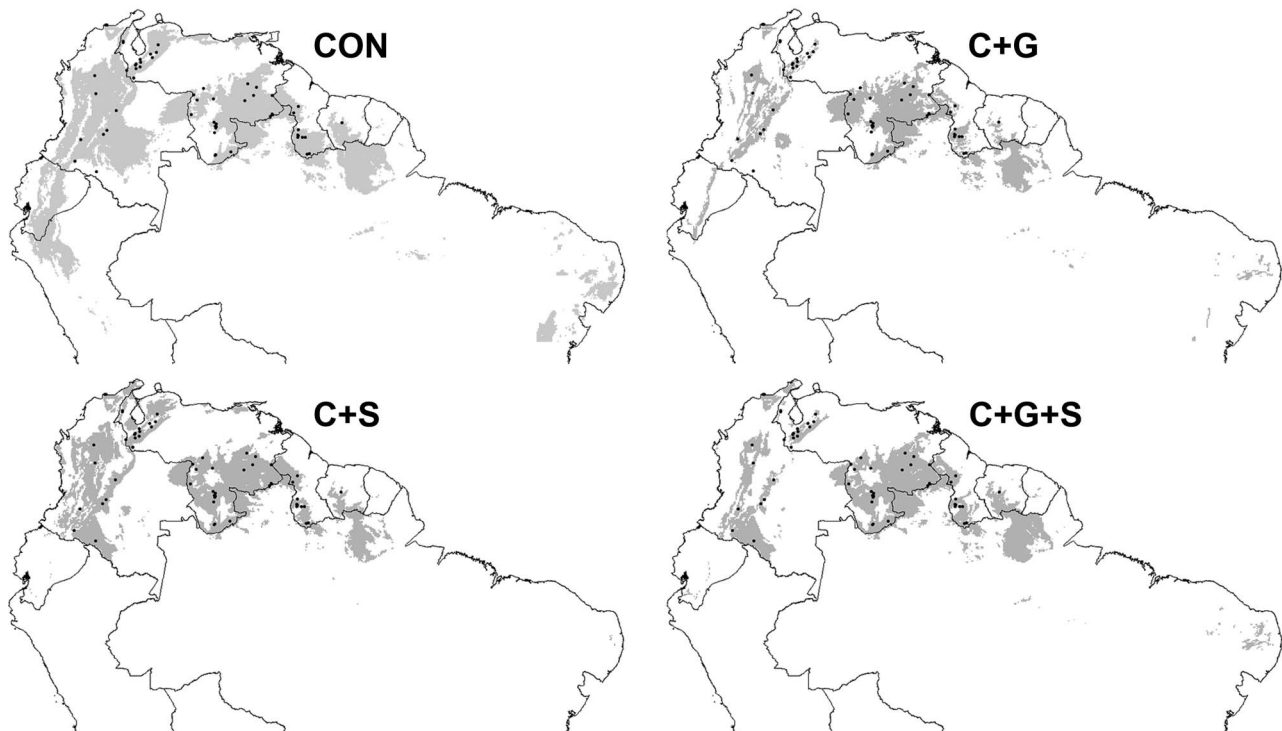


Figure 5. Average predicted habitat suitability ranges of *A. amplus*. CON: models based on continuous variables. C+G: models based on continuous variables and geological information. C+S: models based on continuous variables and soil information. C+G+S: models based on continuous variables, as well as geological and soil information.

of Chocó. In Venezuela, the range of suitable habitat included Perijá, Andes and the Guiana shield, excluding northern mountain ranges. In Guyana and Suriname the range of suitable habitat included the middle to southern portions of those countries.

Discussion

Model selection

We predicted habitat suitability for *A. amplus* under current conditions using bioclimatic variables, elevation, information on geology and soil, as well as data

available on *A. amplus* distribution. The best models, all of which relied on the hypothesis that environmental factors can predict the niche of a species, also showed some differences regarding the extension of suitable habitat for this bat species. Several authors have suggested that AIC_c should be preferred over other model selection criteria, provided it penalizes parameter number in relation to the amount of inputted data (Warren et al. 2010). AIC_c scores suggest the selection of CON as the best model. However, the best model according to this model selection criterion did not perform as well as the model selected with BIC and AIC – the C+G+S model – when model performance was cross validated, i.e. tested with data not used to construct the model, revealed by the high ratio of fractional predicted area to average omission. The C+S model, which had AIC and BIC scores similar to C+G+S, predicted suitable habitat in regions where *A. amplus* has not been recorded. This point is illustrated by the prediction of northern Venezuelan mountain chains (San Luis, Costa and Turimiquire) as suitable habitats, despite the fact that intensive research at caves in the area over the past 30 years has yielded no capture records of *A. amplus*. Thus, the absence of this species records could simply reflect the fact that this area is not actually part of its geographic distribution. Perhaps similar considerations could be made for Chocó in Colombia: a widely recognized area of endemism (Gentry 1982; Morrone 2001), where collecting efforts have been conducted (Alberico 1987; Cadena et al. 1998; Asprilla-Aguilar et al. 2007), and records of *A. amplus* have not been reported but where the C+S model predicted suitable habitat. Thus, the C+G+S model seems to offer a better picture of reality.

Effect of soil

Soil was far more important to *A. amplus* than any other variable in both C+S and C+G+S models. Soil quality is related to tree diversity (Coronado et al. 2009), influencing the net primary productivity (Aragão et al. 2009), which in turn impacts the availability and quality of food resources, shaping the abundance and diversity of vertebrate assemblages (Peres 2008; Beja et al. 2010) including those of bats (Pereira et al. 2009).

Evidence from plants (Kreft et al. 2004), arthropods (Sigrist & Carvalho 2009), amphibians (Symula et al. 2003), reptiles (Vanzolini 1988; Sigrist & Carvalho 2009), birds (Haffer 1987; Prum 1988; Bates et al. 1998), and mammals (da Silva & Oren 1996; Patton & da Silva 1998) indicate that biodiversity is unevenly distributed across the South American lowlands. Some areas have a high endemism

holding unique biotas, whose origins, history and ecological mechanisms are themes of continuous debate (Tuomisto & Ruokolainen 1997; Bush 2005; Haffer 2008).

The CON model predicted areas in eastern Ecuador and Peru as suitable habitats for *A. amplus*, despite the absence of records for this species in such regions. In contrast, models including soil information set the Putumayo river as the southernmost border, agreeing with most of the articles cited in the previous paragraph and, partially, with the currently accepted ecoregional division of South America (Olson et al. 2001). Thus, our results suggest the presence of edaphic differences acting as geographic barriers for *A. amplus*. This pattern is consistent with the hypothesis that current patterns of biotic distribution in the Amazon basin are based on edaphic differences (Salo 1987). Thus, our study suggests a bottom-up effect of soil properties on animal distributions, a topic that has been primarily studied outside the tropics, mainly on plants (Sormunen et al. 2011) and invertebrates (Titeux et al. 2009).

Effect of geology

Geologic information was the second most important factor explaining the distribution of *A. amplus* in the C+G+S model. While C+S predicted suitable habitats in areas where this bat species has not been recorded (Chocó in Colombia, and San Luis, Costa and Turimiquire mountain ranges in Venezuela), the inclusion of geologic information yielded models that correctly exclude those areas.

Except for *A. amplus*, the remnant species in the “*jamaicensis*” subclade (Lim et al. 2004) use more widely available roosts such as hollow trees and modified or unmodified leaves (Goodwin & Greenhall 1961; Foster & Timm 1976; Evelyn & Stiles 2003; Muñoz-Romo & Herrera 2003; Haynes & Lee 2004; Kunz & McCracken 2006; Muñoz-Romo et al. 2008) and show wider and continuous distributional ranges. Conversely, caves are the only known roosts used by *A. amplus* (Handley 1987), which apparently prefer the highest parts (Muñoz-Romo & Ramoni-Perazzi, pers. obs.). This leads us to suggest the range of *A. amplus* is restricted by its roosting biology, which requires caves that are patchily distributed because of the geologic history of South America.

We suggest that the complex process of cave formation (Gillieson 1996) influences the absence of *A. amplus* from caves where this species has not been recorded despite the suitable habitat prediction by models CON and C+S. For example, mountain ranges in west/northwest and northern

South America where *A. amplus* has been recorded (Santa Marta, Colombian and Venezuelan Andes, and Perijá) are seismically (USGS 1990–2006, 1990–2009) and geologically (Schenk et al. 1999) more complex than mountain ranges where suitable habitats were predicted but *A. amplus* has never been found.

Habitat suitability distributions for vertebrates, as illustrated by this study of *A. amplus*, provide important information for establishing study sites for assessing the actual distribution of rare and endangered species. Areas robustly predicted as suitable habitats for poorly studied species support the need for spatially targeted capture efforts and the verification of museum specimens. For *A. amplus*, our results show that northern Brazil is an area requiring additional capture efforts to test our model predictions, especially in forested locations with potential roosts (i.e. caves) near Boa Vista, Marabá, Humaitá, and Cruzeiro do Sul. Similarly, reliable identification of museum specimens collected in these locations will be critical for meeting these goals. Future field surveys focused on rare species will also need to collect fresh tissue for the extraction of molecular information that can be used for taxonomic and phylogenetic studies of poorly known species.

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Appendix 1. Localities for specimens of *Artibeus amplus* used in this study

Coordinates are presented in the decimal degree system.

COUNTRY	First Administrative Division	Locality	Museum and catalog number(s)	Latitude	Longitude
COLOMBIA					
Antioquia					
1	San Luis, Corregimiento El Prodigio, via El Prodigio – El Tigre, finca Cobidal	[San Luis, township El Prodigio, El Prodigio – El Tigre road, Cobidal farm]	UNC 13344	6.1000000	-74.8000000
2	25 km S, 22 km W, de Zaragoza. (La Tirana)		IND 3603	7.5000000	-74.8666667
	Boyacá				
3	Santa María, Vereda La Calichana, sitio La Almenara	[Santa María, La Calichana rural settlement, La Almenara place]	UNC 16325	4.8930560	-73.2805560
4	Santa María, Quebrada Las Moyas, sendero ecológico	[Santa María, Las Moyas brook, ecologic path]	UNC 15065	4.8930560	-73.2805560
5	Santa María, Barrio La Libertad, junto a cancha de fútbol,	[Santa María, La Libertad neighborhood, close to the football court]	UNC 16311	4.8500000	-73.2666667
	Cauca				
6	Santa Rosa, Vda. El Carmen o El pozo Mira Flor No. 1, Fca El Triunfo	[Santa Rosa, El Carmen rural settlement or Mira Flor No. 1 well, El Triunfo farm]	IND 5815	2.6427778	-75.9147222
7	Santa Rosa, Vda. Nabueno, Fca. El Diamante	[Santa Rosa, Nabueno rural settlement, El Diamante farm]	IND 5802	?	?
	Magdalena				
8	Santa Marta, Parque Nacional Natural Tayrona, Cañaveral	[Santa Marta, Tayrona National Park, Cañaveral]	UNC 7922	11.3077780	-73.9258330
9	Santa Marta, Parque Nacional Natural Tayrona, Arrecifes	[Santa Marta, Tayrona National Park, Arrecifes]	UNC 7921	11.3000000	-73.9525000
10	Santa Marta, Parque Nacional Natural Tayrona, El Cedro	[Santa Marta, Tayrona National Park, El Cedro]	UNC 8989	11.3094440	-73.9933330
11	Santa Marta, Parque Nacional Natural Tayrona, Pueblito	[Santa Marta, Tayrona National Park, Pueblito]	UNC 7924, 7925	11.3336110	-74.0336110
	Meta				
12	San Juan de Arama, Parte norte Serranía La Macarena, caño Guamalito	[San Juan de Arama, North portion of La Macarena mount, Guamalito stream]	UNC 10630, 10639, 10642, 10643, 10650, 10652, 10656, 10658, 10664, 10672, 10673, 10682, 10684, 10687, 10688	3.3500000	-73.9333333
13	Mesetas, Vereda San Isidro, cuenca media del río Duda, margen izquierda Putumayo	[Mesetas, San Isidro rural settlement, Duda river middle basin, left margin]	UNC 11596, 11598, 11599, 11600	3.0402778	-74.2213889

14	Puerto Leguizamo GUYANA	[Leguizamo port]	NMNH 596428	0.2000000	-74.7666667
15	Potaro-Siparuni Kaieteur Falls		NMNH 565531	5.1666667	-59.4666670
16	Kato, Chiung River Upper Demerara-Berbice		NMNH 565620, 565621, 565622	4.6666667	-59.8166667
17	Kuitaro river, 48 km E Dadanawa		Lim & Wilson (1993)	2.8333333	-58.9500000
18	Upper Takutu/Upper Essequibo		Lim & Wilson (1993)	2.8166667	-59.1500000
19	Shea Village, Kumakowri river Nappi Kreek, Kanuku Mountains, 40 km E Lethem		Lim & Wilson (1993)	3.3833333	-59.4666667
20	Danawa		ROM 70125 ¹	2.8333333	-59.5166667
21	Sand Creek Village, 32 to 48 km down river		ROM 106748, 106761	3.0000000	-59.5166667
22	Essequibo river, 7 km S Gunn's Strip		ROM 106679, 106697, 106722	1.5833333	-58.6333333
23	Kamoa River, 50 km SWW Gunn's Strip		ROM 67311 ¹	1.5333333	-58.8333333
24	Weri More, Quash Wau area, 19 km NE Dadanawa		ROM 67311 ¹	2.9333333	-59.4833333
25	SURINAME Saramacca Center of Arrowhead Basin, Augustus Creek, Tafelberg VENEZUELA Amazonas		CMNH 76795	3.9000000	-56.1666667
26	rio Siapa, campamento 2	[Siapa river, camp number 2]	MBUCV 5115	1.7166667	-64.5833333
27	Alto Cunucunuma, raudal Wamujatado; Departamento Atabapo	[Upper Cunucunuma, Wamujatado torrent, Atabapo Department]	MHNL 9205	3.8500000	-65.6666670
28	Cerro Duida, Caño Culebra, 50 km NNW Esmeralda	[Duida mount, Culebra stream]	NMNH 405301, 405302	3.6166667	-65.6833333
29	Cerro Duida, cabecera del Caño Culebra, 40 km NNW Esmeralda. (Includes: "Cerro Duida", "Cerro Duida Cabecera Caño Culebra", "Cerro Duida Cabecera caño Culebra 40 km NNO La Esmeralda")	[Duida mount, Culebra stream head]	NMNH 405303-405309, 405316, 405342-405349, 405362, 405363, 494169-494171; EBRG 12151, 14344, 14345, 14347-14352	3.5000000	-65.7166667
30	Talud Este, cerro Aracamuni	[East slope, Aracamuni mount]	MBUCV 5239	1.4833333	-65.7333333
31	Belén, 56 km NNW Esmeralda, rio Cunucunuma. (Includes: "rio Cunucunuma, Belén")	[Belén, 56 km NNW Esmeralda, Cunucunuma river]	NMNH 405297, 405298, 405300, 405313, 405322, 405335, 405336, 405339, 405341; EBRG 14343, 14346	3.6500000	-65.7666667
32	Aracamuni, Campamento Popa	[Aracamuni, Popa camp]	EBRG 21929	1.4333333	-65.7833333
33	Tamatama, rio Orinoco, 2 km above Boca del Casiquiare	[Tamatama, Orinoco river, 2 km above Casiquiare mouth]	NMNH 494208	3.1666667	-65.8166667

(Continued)

Appendix 1. (Continued).

	COUNTRY	First Administrative Division	Locality	Museum and catalog number(s)	Latitude	Longitude
34	rio Cunucunuma, raudal Mapaco; Departamento de Atabapo		[Cunucunuma, river, Mapaco torrent; Atabapo Department]	MHNLS 9238	3.9500000	-65.8500000
35	Cerro Yaví, Campamento 1		[Yaví mount, camp number 1]	EBRG 20339	5.7166667	-65.9000000
36	3 km aguas abajo del Salto Nieves, río Cataniapo, Departamento Atures		[3 km downstream from Nieves fall, Cataniapo river, Atures Department]	EBRG 5886	5.6166667	-67.1500000
37	Pozon, 50 km NE Puerto Ayacucho			ROM 107847, 107904	6.0500000	-67.4166667
38	San Felipe Raudalito, río Sipapo. (Includes: "1 km antes San Felipe Raudalito, río Sipapo")		[San Felipe Raudalito, Sipapo river; includes: "1 km before San Felipe Raudalito, Sipapo river"]	EBRG 8079, 8086	4.5333333	-67.5833333
39	Apure Nulita, 29 km SSW Santo Domingo, Selvas de San Camilo		[Nulita, 29 km SSW Santo Domingo, San Camilo forests]	NMNH 418364, 441362, 494145	7.3166667	-71.9500000
40	Barinas Cerro Alto, 2 km NW de la Soledad			CVULA 5915-5917, 6087	8.8333330	-70.5333330
41	Bolívar 85 km SSE El Dorado km 125. (Includes: "km. 125. 85 km SSE El Dorado")			EBRG 14341, 14342; NMNH 387390-387395	5.9833330	-61.4333330
42	El Polaco, S Paraytepu, Distrito Roscio		[El Polaco, S Paraytepu, Roscio District]	EBRG 18111-18117	4.5833333	-61.4500000
43	Icabaru, 28 km NE Icabaru			NMNH 441171	4.4666667	-61.5500000
44	Icabaru, 21 km NE Icabaru, El Pauji. (Includes: "21 km NE Icabaru, El Pauji", "22.5 km NE Icabaru Independencia", "20.8 km SE Icabaru El Pauji").			NMNH 441174-441176, 494217, 494218; EBRG 12216, 14354, 14355	4.4166670	-61.5833330
45	rio Parapay		[Parapay river]	EBRG 18109, 18110	6.5933333	-62.6500000
46	Cerro Taute, aproximadamente 3,6 km SW de la laguna Canaima, Parque Nacional Canaima		[Taute mount, approximatedly 3.6 km SW from Canaima lagoon, Canaima National Park]	MHNLS 11607	6.2333333	-62.8833333
47	Las Piñas, La Paragua			CVULA 2238, 2278	6.8663889	-63.3113889
48	Municipio Raul Leoni, Mount Guaiquinima, Carapo River, Camp #7			AMNH 265347, 265348	5.5833333	-63.5333333
49	Serranía Pijiguao 140 km SO Caicara del Orinoco, Distrito Cedeño		[Pijiguao mountains, 140 km SO Caicara del Orinoco, Cedeño District]	EBRG 11920-11927, 15805-15807, 15809, 15831, 15832	6.5000000	-66.6666667
	Lara					

50	Parque Nacional Dimira, Fundo Santa Teresa, Sector Paramito, Municipio Moran Mérida	[Dimira National Park, Santa Teresa farm, Paramito area, Moran Municipality]	EBRG 24488, 24701, 24702	9.797778	-70.0666667
51	Lagunillas, Parque Yohama 25 km SW de Mérida	[Lagunillas, Yohama Park 25 km SW from Merida]	CVULA 7409	8.5047222	-71.3950000
52	Cueva del Pirata, La Azulita	[El Pirata cave, La Azulita]	CVULA 6818	8.7105556	-71.4291667
53	Cueva 10 min en carro de Canaguá (vía a Mucuchachi)	[cave located 10 min driving from Canaguá (on the road to Mucuchachi)]	CVULA 2068	8.1286111	-71.4586111
54	km 3 carretera Zea-Tovar, 1.5 km SE Zea	[km 3 on the road Zea -Tovar, 1.5 km SE Zea]	CVULA 3048	8.3630556	-71.7722222
55	Cueva de El Salado 4 km de Bailadores	[El Salado cave, 4 km from Bailadores]	CVULA 3017-3019	8.2555556	-71.7955556
56	Táchira Cueva de Las Escaleras 2 km ESE	[Las Escaleras cave, 2 km ESE from Pregonero]	CVULA 2999-3006, 3766-3768	8.0205556	-71.7419444
57	Pregonero El Palotal, 6 km SSE de Ureña Trujillo		CVULA 6932	7.8700000	-72.4377778
58	Finca La Nona, 5 km E Boconó, Guaramacal	[La Nona farm, 5 km E Boconó, Guaramacal]	CVULA 3078-3080, 3111-3113, 3117, 3122-3124, 3304-3306	9.2422222	-70.2230556
59	Quebrada Comboco, 5 km SE de La Puerta Zulia	[Comboco brook, 5 km SE from La Puerta]	CVULA 3307, 3308	9.0999510	-70.6748690
60	Kasmera, 21 km SW Machiques		NMNH 440931-440933	9.9833333	-72.7166667
61	Novito, 19 km WSW Machiques		NMNH 441228	10.0333333	-72.7166667
62	15 km west of Machiques		AMNH 185366	10.0833333	-72.7166667

¹Lim et al. (2003).