

## Geographic and potential distribution of a poorly known South American bat, *Histiotus macrotus* (Chiroptera: Vespertilionidae)

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The vespertilionid bat *Histiotus macrotus* occurs in western Argentina, central regions of Chile and south of Argentina and Chile, and it may be also present in Bolivia and southern Peru. In this work, we analyzed the geographic and potential distribution of a poorly known species of South American bat. As a tool, environmental niche modeling has been used to study the distributional patterns of species and more recently, taxonomic boundaries of cryptic species. We used MaxEnt v 3.3.e, Worldclim database and a vegetation map, covering the entire area of species' occurrence. We registered 64 localities from Argentina (43), Chile (10), Peru (8) and Bolivia (5). We divided recording localities in different datasets according to several taxonomic schemes, and analyzed potential distribution models separately (i.e., all known records; Argentina-Chile; Peru) in five different models. Models including all known localities showed a disjoint distribution, with two basic core areas of high predictive values, one in NW Argentina and another in southern Chile and SW Argentina separated by the South American Arid Diagonal. A third area appeared in Atacama and Sechura deserts in the models that included Peruvian and Bolivian localities. Model including only Peruvian localities showed the opposite pattern, with high predictive values only in arid environments from southern Peru. We interpreted that localities correctly assigned to *H. macrotus* belong to a taxonomic complex distributed in two contrasting areas, each one inhabited by a different taxon: 1) Bolivia and NW Argentina and 2) S and central Chile and SW Argentina. Given the systematic uncertainty of *Histiotus*, these two forms might be sister species or may not share an immediate common ancestor within the genus. Further, we consider that the specimens from localities referred to *H. macrotus* from southern Peru should be revised. These alternatives await a comprehensive molecular phylogenetic analysis of *Histiotus*.

*Key words:* *Histiotus macrotus*, environmental niche modeling, MaxEnt, South American Arid Diagonal

### INTRODUCTION

Bats of the genus *Histiotus* Gervais, 1856 are endemic to South America (Handley and Gardner, 2007), with seven currently recognized species: *H. alienus*, *H. humboldti*, *H. laephotis*, *H. macrotus*, *H. magellanicus*, *H. montanus* and *H. velatus* (Simmons, 2005). Recent phylogenetic results recovered *Histiotus* nested within *Eptesicus* and so the former has often been treated as a subgenus of the latter (Hooper and Van Den Bussche, 2003; Lack and Van Den Bussche, 2010). As a group, *Histiotus* is distributed from cold areas in the Andes of Colombia and Venezuela, south to the Straits of Magellan (Handley and Gardner, 2007). Species of *Histiotus* are medium size, have long ears and corresponding

large tympanic bullae (Anderson, 1997; Handley and Gardner, 2007). The morphological and geographic limits among these species are not clearly understood (Anderson, 1997).

Particularly, *Histiotus macrotus* (Poeppig, 1835) has been known to occur in western Argentina, central regions of Chile and south of Argentina and Chile (Barquez *et al.*, 1999; Handley and Gardner, 2007). Some authors consider the species to be present also in Bolivia and southern Peru (Eisenberg and Redford, 1999; Zeballos *et al.*, 2000, 2001; Acosta and Venegas, 2006; Aragón and Aguirre, 2014). *Histiotus macrotus* presents a dark dorsal and a whitish ventral coloration, ears and wing membranes darker than the rest of the body (Barquez *et al.*, 1993, 1999; Handley and Gardner, 2007; Giménez, 2010). It can

be distinguished from its congeners by its longer (> 30 mm) ears (Barquez *et al.*, 1993; Giménez, 2010). The type locality of this species is Bío Bío, Antuco, Chile (Barquez *et al.*, 1999; Handley and Gardner, 2007).

*Histiotus macrotus* may be widely distributed in western and southern South America, but relatively few localities exist, and as a consequence the distribution of this species is poorly known. According to Barquez (2006), it occurs in several eco-regions at least in Argentina, including Dry Chaco, Espinal, Southern Andean Yungas, High Monte, Patagonian Forest, Patagonian Steppe, and Puna. In Chile the species has been recorded in Chilean Matorral and Valdivian Temperate Forest (*sensu* Olson *et al.*, 2001). Prima facie those records suggest that the species is a habitat generalist able to occupy quite extreme biomes from the desert to the montane rainforest, only avoiding lowland wet forest; whether this is the case requires proper evaluation.

Geographic distribution modeling is a relatively novel tool for predicting geographic ranges for species with poorly known distributions, using environmental data and recording localities (Godown and Peterson, 2000; Engler *et al.*, 2004; Guisan *et al.*, 2006; Phillips *et al.*, 2006). The analysis of the distribution pattern of a given species helps us understand its relationship with the environment, including biotic and abiotic factors (Franklin, 2009). In this respect environmental niche models (ENMs) have been recently used to explore ecological niches of cryptic species related to their taxonomic boundaries (Raxworthy *et al.*, 2007; Ahmadzadeh *et al.*, 2013; Chetan *et al.*, 2014). This is based on the idea that ENMs might allow identification of specific patterns of ecological niches between either independent lineages or related species (Ortiz-Martínez *et al.*, 2008).

The goals of this study were to assess: 1) the potential distribution of *H. macrotus* in its entire geographical range; 2) the main environmental and geographical variables that might affect the distribution of this species; and 3) the status of Peruvian and Bolivian records.

## MATERIALS AND METHODS

### *Samples and Taxonomy*

We studied the known geographic and modeled the potential distribution of *H. macrotus* along its entire known range of occurrence. To this end, we used recording localities for the species as currently understood, and applied techniques of ecological niche modeling as implemented in MaxEnt version 3.3.3e (Phillips *et al.*, 2006) using bioclimatic variables

(Hijmans *et al.*, 2005a) and vegetation cover data (Bontemps *et al.*, 2011).

We first performed the analysis for South America including record localities from Argentina, Bolivia, Chile and Peru (Appendix). We included all known localities of *H. macrotus* that were obtained from relevant literature sources and from mammalian collections of Argentina. We visited the following collections: Instituto Miguel Lillo (CML), San Miguel de Tucumán; Colección de Mamíferos del IADIZA (CMI), Mendoza; and Laboratorio de Investigaciones en Evolución y Biodiversidad (LIEB), Universidad Nacional de la Patagonia 'San Juan Bosco' Sede Esquel, Chubut. Localities without associated geographical coordinates were geo-referenced with Global Gazetteer (<http://www.fallingrain.com>) and reference maps (e.g., roads, towns, lakes), and plotted into a geographic information system (GIS). The analyses excluded localities referred with certainty to *H. macrotus laephotis* (Tuttle, 1970; Koopman, 1978; López-González *et al.*, 1998; López-González, 2005), given that we consider *H. laephotis* as a valid species, distinct from *H. macrotus* (following Barquez and Díaz, 2001, 2009; Simmons, 2005; Barquez, 2006; Díaz *et al.*, 2011). This is based on well-known differences in coloration of venter (whitish in *H. macrotus* versus yellowish in *H. laephotis*) and ears (very dark in *H. macrotus*), and external width across M3 (< 7 mm in *H. laephotis* and > 7 mm in *H. macrotus* — Barquez and Díaz, 2001, 2009; Díaz *et al.*, 2011). In addition, both species have been found in sympatry in some localities in NW Argentina (Barquez and Díaz, 2001).

On the other hand, the occurrence of *H. macrotus* in southern Peru and Bolivia is not entirely clear. Some authors consider that *H. macrotus* is distributed only in Chile and Argentina (Simmons, 2005; Handley and Gardner, 2007), while others also include Peru and Bolivia (Koopman, 1978, 1982; Eisenberg and Redford, 1999; Zeballos *et al.*, 2000, 2001; Acosta and Venegas, 2006; Aragón and Aguirre, 2014). This problem is mainly a result of the few characters that separate the species within this genus. Anderson (1997) mentions that this genus is in need of taxonomic revision and that its morphologic and geographical limits are uncertain, and for this reason the identifications must be regarded as tentative. Tuttle (1970) and Koopman (1978, 1982) included *H. macrotus* in the list of bats from Peru; however, they considered *H. macrotus* as a synonym of *H. laephotis*, or the latter as a subspecies of the former. These authors also indicated that the subspecies *H. m. laephotis* is the one that is present in southern Peru (Tuttle, 1970; Koopman, 1982). As previously stated, other authors consider *H. laephotis* as valid and a species distinct from typical *H. macrotus*, both species being sympatric in part of their distributions (i.e., northwest from Argentina — Barquez and Díaz, 2001; Simmons, 2005; Barquez, 2006). To these authors, only *H. laephotis* would be present in Peru and Bolivia (Simmons, 2005). According to Anderson (1997), *H. macrotus* is not included in the bat list of Bolivia, although its presence is likely, and Aguirre (2011) did not include *H. macrotus*, but did include *H. laephotis*.

### *Geographic Model Fitting*

The species potential distribution was modeled using MaxEnt (Phillips *et al.*, 2006), which was chosen because this program performs better than alternatives with small (<100 records) sample sizes and presence-only data (Elith *et al.*, 2006; Peterson *et al.*, 2007). This software provides response curves for each environmental variable, representing predictions on how each variable affects MaxEnt generated distributions

(Moratelli *et al.*, 2011). We used environmental variables with data from 1950 to 2000 and 30 arc-s of spatial resolution or ca. 1 km<sup>2</sup>. The variables included in the analyses were: altitude; average monthly minimum, medium, and maximum temperatures; monthly precipitation and the 19 bioclimatic variables available in the Worldclim database (<http://www.worldclim.org> — see Hijmans *et al.*, 2005a). We also used a map of vegetation cover available in GlobCover 2009 (Bontemps *et al.*, 2011), with a spatial resolution of 300 m. In this, each pixel represents a different vegetation type, ranging from bare areas and croplands to broadleaved forests or urban areas (Bontemps *et al.*, 2011).

In order to assess the potential distribution of *H. macrotus* we generated five models: A) including all registered localities from Argentina, Chile, Peru and Bolivia; B) same but including only localities after 1950; C) including only localities from Argentina and Chile; D) same but including only localities registered after 1950; and E) including only the registered localities of Peru. Ten replicates were performed for each model, with 25% of recorded localities used as test data, 500 iterations, random seed and 10,000 background points. We selected a cumulative output, and for visual mapping we assigned probability values of 100–51 (black, high prediction), 50–26 (dark gray, high-medium prediction), 25–11 (gray, medium prediction), 10–2 (light gray, low prediction), and 1–0 (white, null prediction). We used MaxEnt's jackknife tests to evaluate variable contributions. We also evaluated model predictions both with threshold-dependent and threshold-independent tests, using *P*-values at thresholds of 1, 5 and 10; area under curve (AUC), and receiver operating characteristics, respectively (Phillips *et al.*, 2004, 2006). As we used 25% of the data to test the models, MaxEnt delivers two AUC values (i.e., AUC<sub>training</sub> and AUC<sub>test</sub>). As the latter is thought not to suffer from the same overfitting problems as the first (Warren and Seifert, 2011), we presented only AUC<sub>test</sub> values. Likewise, to analyze possible overfitting in our models (which results in high AUC<sub>training</sub> but low AUC<sub>test</sub> values) we analyzed AUC<sub>diff</sub> as in Warren and Seifert (2011); a similar methodology has been recently used by Gutiérrez *et al.* (2014). We also analyzed the difference between the use of different regularization parameters (i.e.,  $\beta$ ) of 0.5, 1, 2, 3, 4 and 5 in Model A. We then evaluated the possible overfitting (between the different models) with AUC<sub>diff</sub> and performed *t*-tests for independent samples. We found no statistically significant difference ( $P < 0.01$ ) between the AUC<sub>diff</sub> of ENMs performed with  $\beta = 1$  and the rest of the ENMs using  $\beta$  values, as described above. Due to these results, we generated all the models with the default settings of MaxEnt ( $\beta = 1$ ). Similar studies in which the  $\beta = 1$  was chosen as the better regularization parameter include Cao *et al.* (2013) and Mason *et al.* (2014).

The use of ENMs is a highly useful tool to assess possible limits between related species (see Raxworthy *et al.*, 2007). For examples of the use of MaxEnt as a tool to study taxonomy between related species see Ahmadzadeh *et al.* (2013), Särkinen *et al.* (2013), and Chetan *et al.* (2014). Lastly, we integrated all the data in a GIS using DIVA-GIS version 7.5.0.0 (Hijmans *et al.*, 2005b), and analyzed the distribution of the species in a biogeographic context, using an eco-regional scheme taken from Olson *et al.* (2001), and assigning each locality to a different biogeographic category.

## RESULTS

A total of 64 localities were recorded for *H. macrotus*, from Argentina, Chile, Bolivia and Peru

(Fig. 1 and Appendix). Marginal occurrence records were located northward in Lomas de Atiquipa (15°47'S, 74°16'W), Arequipa department, Peru (Zeballos *et al.*, 2000); southward in Aysén region (45°23'59"S, 72°42'W — Reed, 1940); westward in Concepción (Concepción, 36°49'59"S, 73°02'59"W), Bío Bío region, Chile (Osgood, 1943); and eastward in Río Cuarto (33°08'S, 64°18'W), Córdoba province, Argentina (Barquez *et al.*, 1999). The westernmost and southernmost localities in Chile were all registered before 1950. The majority of records (67%;  $n = 43$ ) came from Argentina, 16% ( $n = 10$ ) from Chile, 12% ( $n = 8$ ) from Peru, and 5% ( $n = 3$ ) from Bolivia. Six localities from Chile, one from Argentina, and none from Peru and Bolivia were registered before 1950 (Appendix).

Models A to D (Figs. 2 and 3) exhibited a disjoint distribution for *H. macrotus*, with two large areas of mean (25–50%) and high (> 50%) predictive values. These two core areas (see circles 2 and 3 in Fig. 2A and 2B; and circles 1 and 2 in Fig. 3C and 3D) were separated by the South American Arid Diagonal sensu Bruniard (1982; dotted lines in Figs. 2 and 3), where predictive values drop below 10%. These areas differed in minor details across models (see Figs. 2 and 3). In addition, models A and B recovered a third region in the Atacama desert (Fig. 3) that was not predicted as suitable habitat when those records were removed (models C and D — Fig. 3 black arrow). Finally, model E (Fig. 4), which was based precisely upon those records from the desert, offered the reciprocal pattern of not predicting other known distributional areas, but instead suggesting distant potential areas associated with arid environments (Fig. 4). Following is a detailed interpretation of each model in terms of the environmental variables recovered as most influential.

Twenty variables (with values > 1%) contributed the most to Model A (90.7% of variance explained), seventeen variables to Model B (88.3%), 11 variables to Model C (90.5%), 16 variables to Model D (88.8%), and 11 variables to Model E (93.1% — Table 1). The variables with greatest influence in the distribution of *H. macrotus* were diverse for each model; specifically for Model A the main variables were: August mean temperature (19.3%), precipitation seasonality (12.9%), April precipitation (10%), vegetation cover (7.3%) and altitude (6.4%); for Model B: mean temperature of coldest quarter (16.7%), April precipitation (14.9%), temperature seasonality (10.4%), altitude (5.9%), and vegetation cover (5.6% — Table 1); for Model C: temperature seasonality (34.6%), precipitation seasonality (16%),

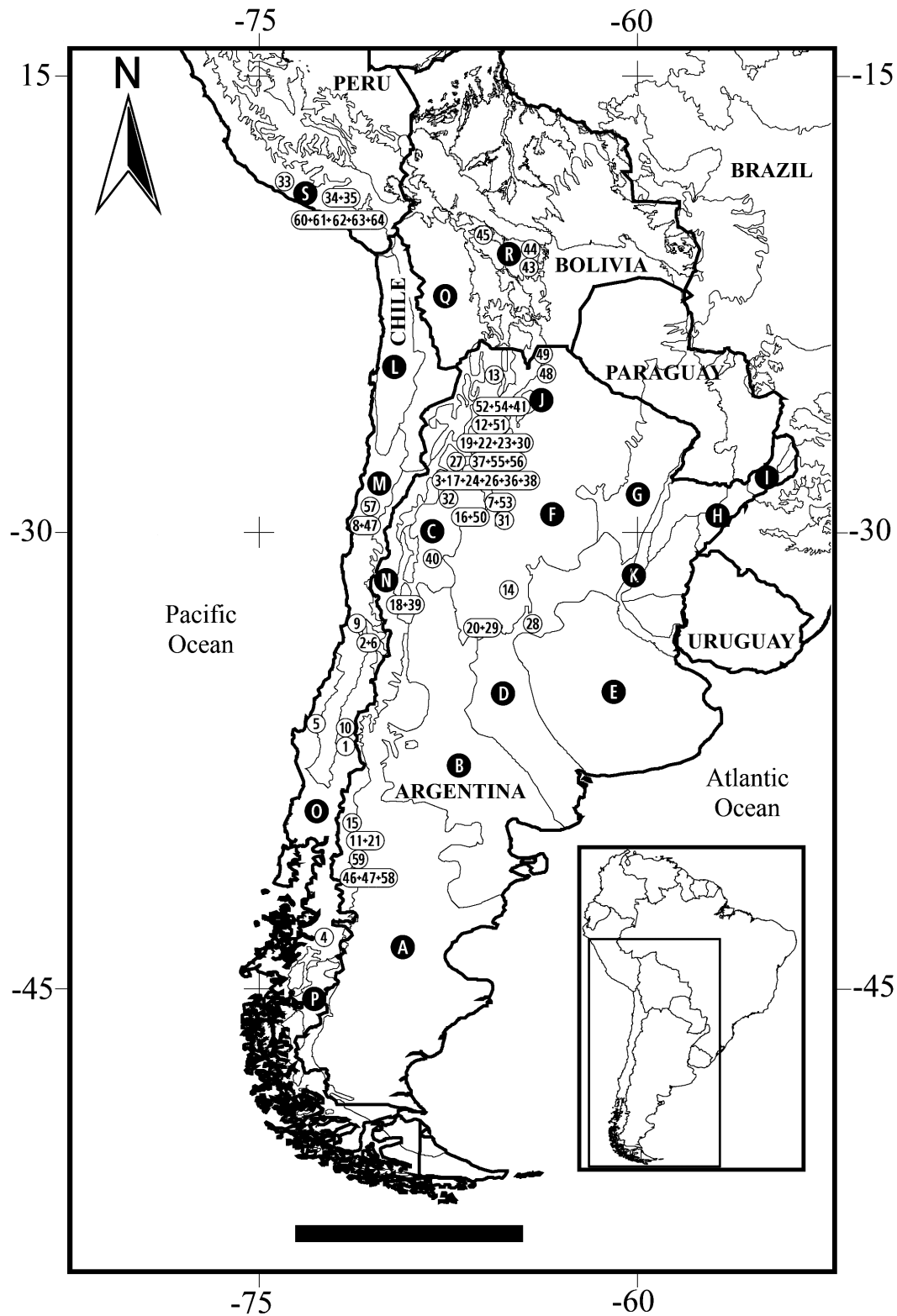


FIG. 1. Record localities for *H. macrotus* by date. Each number belongs to 'locality number' in the Appendix. Capital letters indicate the eco-regions following Olson *et al.* (2001): A — Patagonian Steppe, B — Low Monte, C — High Monte, D — Espinal, E — Humid Pampas, F — Dry Chaco, G — Humid Chaco, H — Southern Cone Mesopotamian, I — Alto Parana Atlantic Forests, J — Southern Andean Yungas, K — Parana Flooded Savanna, L — Atacama Desert, M — Chilean Matorral, N — Southern Andean Steppe, O — Valdivian Temperate Forest, P — Magellanic Subpolar Forest, Q — Central Andean Puna. Scale (black bar) = 1,000 km

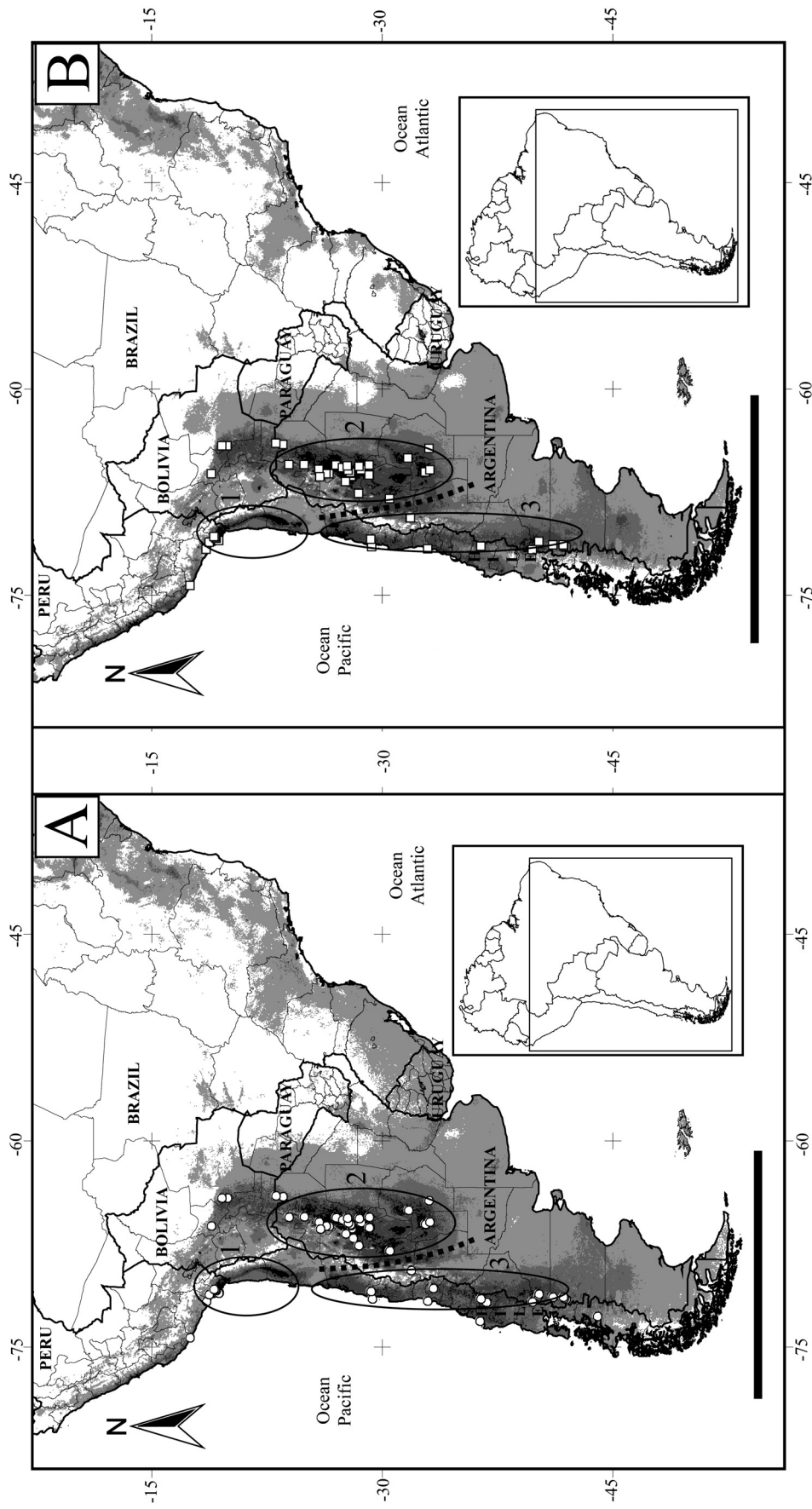


FIG. 2. Models A and B, potential distribution for *H. macrotus*. A — using all registered localities from Argentina, Chile, Peru and Bolivia; B — same but using only localities registered after 1950. Probability values are 100–51 (black, high prediction), 50–26 (dark gray, high-medium prediction), 25–11 (gray, medium prediction), 10–2 (light gray, low prediction), and 1–0 (white, null prediction). Changes are marked as selected areas (see Results). Scale (black bar) = 1,000 km

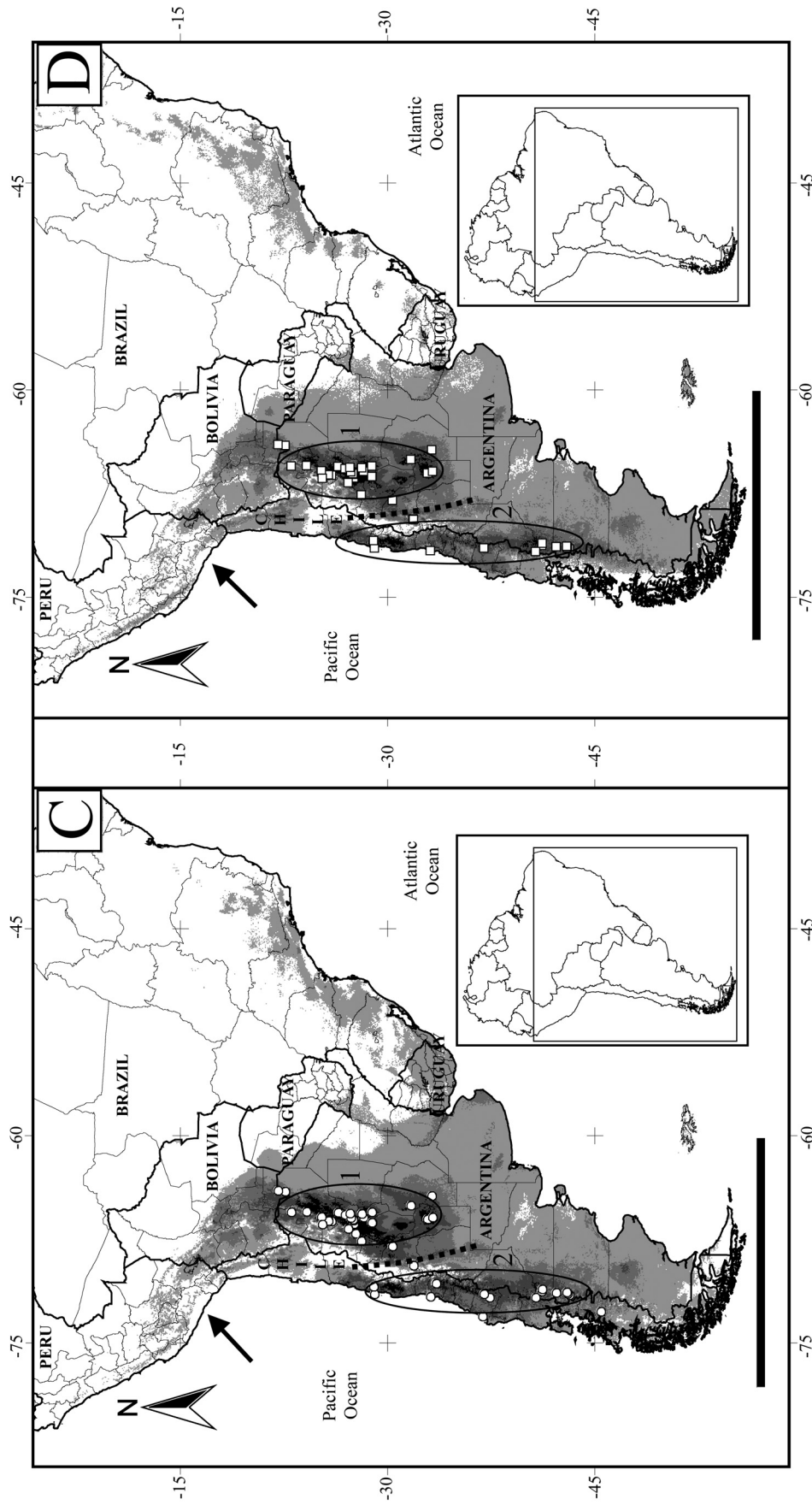


FIG. 3. Models C and D, potential distribution for *H. macrotus*. C — using only localities of Argentina and Chile, D — same but using only localities registered after 1950. Probability values are 100–51 (black, high prediction), 50–26 (dark gray, high-medium prediction), 25–11 (gray, medium prediction), 10–2 (light gray, low prediction), and 1–0 (white, null prediction). Changes are marked as selected areas and black arrows (see Results). Scale (black bar) = 1,000 km

altitude (10%), mean temperature of coldest quarter (9.3%) and vegetation cover (5.8); for Model D: temperature seasonality (33.6%), precipitation seasonality (13.6%), altitude (12%), vegetation cover (4.6%) and June minimum temperature (4.1%); finally, for Model E the variables with highest influence in the models were: March precipitation (53.8%), vegetation cover (9.6%), July precipitation (6.5%), precipitation of wettest month (5.2%) and June precipitation (4.2% — Table 1).

Jackknife tests showed that the environmental variables with the highest gain when used in isolation (i.e., that with the most useful information by itself), were: August mean temperature for Model A; April precipitation for Model B; minimum temperature of the coldest month for Model C; July

minimum temperature for Model D; and precipitation of the wettest quarter for Model E. The environmental variables that decreased the gain the most when omitted (i.e., those that contain information largely not present in the others variables), were vegetation cover for Models A, B, and C, altitude for Model D, and July precipitation for Model E (Table 2). Other jackknife tests (e.g., using test gain instead of training gain, and that using AUC) showed variable results. For Model A, August mean temperature, August precipitation, September mean temperature and precipitation seasonality; for Model B, annual precipitation, September precipitation, April precipitation and October precipitation; for Models C and D, June mean temperature and August precipitation, for model D, altitude and October precipitation; and

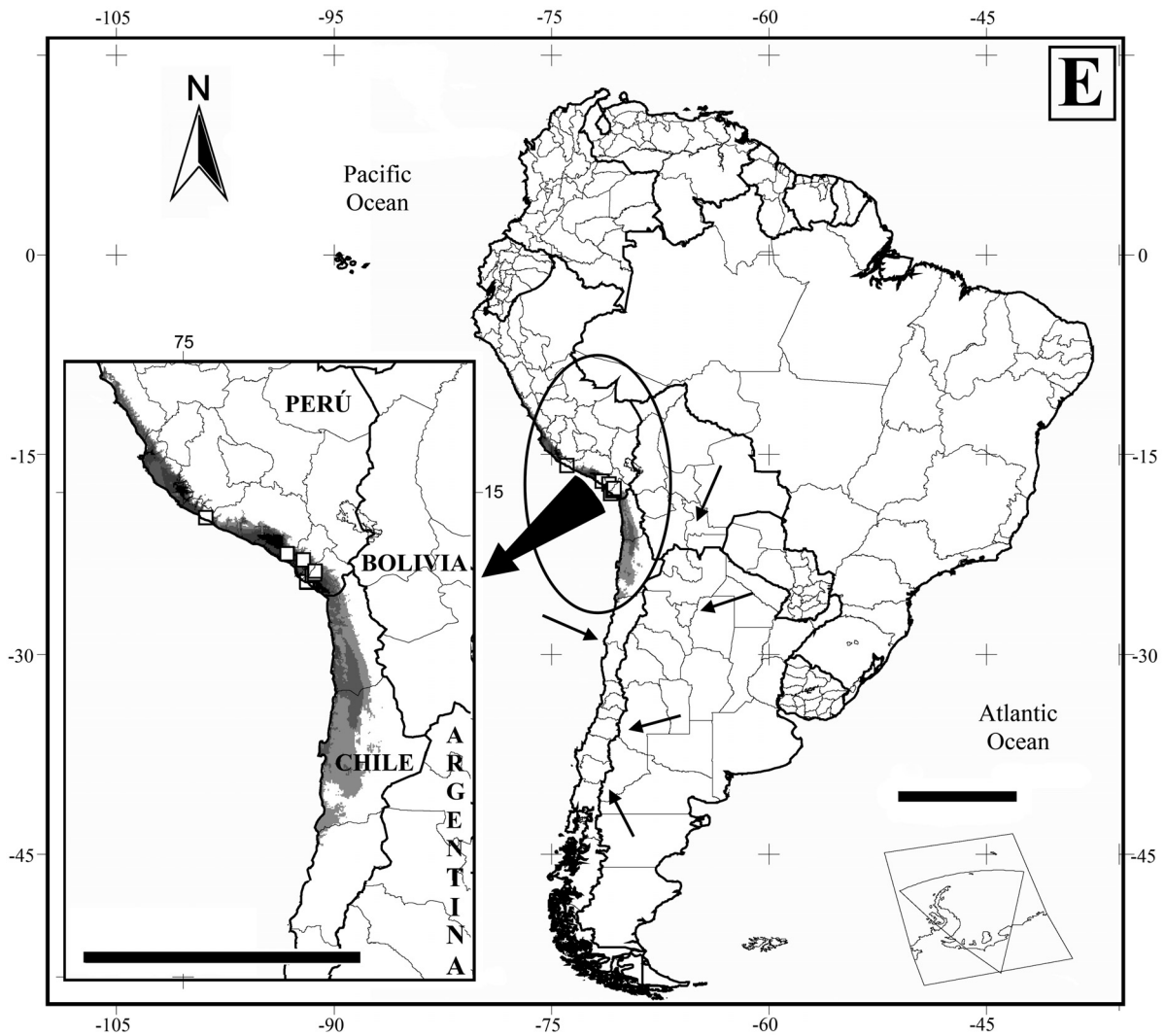


FIG. 4. Model E, potential distribution for *H. macrotus* using only the registered localities from Peru. Probability values are 100–51 (black, high prediction), 50–26 (dark gray, high-medium prediction), 25–11 (gray, medium prediction), 10–2 (light gray, low prediction), and 1–0 (white, null prediction). Changes with respect to previous, more complete models (Figs. 2 and 3), are marked as selected areas and black arrows (see Results). Scale (black bar) = 1,000 km

TABLE 1. Percent contribution (%C) and permutation importance (PI) of each variable for the four models (A-B-C-D-E) generated (see Results) for *H. macrotus*. Variables with major contributions are marked in bold

Variable	Model A		Model B		Model C		Model D		Model E	
	%C	PI	%C	PI	%C	PI	%C	PI	%C	PI
August mean temperature	<b>19.3</b>	<b>0.0</b>	0.4	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Precipitation seasonality	<b>12.9</b>	<b>8.2</b>	<b>10.4</b>	<b>3.6</b>	<b>16.0</b>	<b>14.0</b>	<b>13.6</b>	<b>8.3</b>	0.1	0.0
April precipitation	<b>10.0</b>	<b>4.2</b>	<b>14.9</b>	<b>2.6</b>	0.1	1.2	1.0	0.4	3.1	48.1
Vegetation cover	<b>7.3</b>	<b>2.6</b>	<b>5.6</b>	<b>0.9</b>	<b>5.8</b>	<b>2.0</b>	<b>4.6</b>	<b>0.9</b>	<b>9.6</b>	<b>0.0</b>
Altitude	<b>6.4</b>	<b>5.6</b>	<b>5.9</b>	<b>4.3</b>	<b>10.0</b>	<b>8.2</b>	<b>12.8</b>	<b>7.6</b>	1.6	0.0
Temperature seasonality	4.7	0.1	0.9	0.2	<b>34.6</b>	<b>0.6</b>	<b>33.6</b>	<b>0.3</b>	1.0	0.0
Isothermality	3.5	14.4	3.1	6.5	0.7	15.3	1.3	22.3	0.0	0.0
September precipitation	3.3	1.3	5.1	4.4	2.9	1.5	4.0	7.4	0.0	0.1
August precipitation	3.3	7.7	4.4	12.4	2.9	1.5	3.8	10.9	1.3	1.0
September mean temperature	2.8	0.4	0.2	0.2	0.1	0.0	0.0	0.0	0.0	0.0
Minimum temperature of coldest month	2.6	0.3	3.1	0.7	1.5	8.7	1.9	6.7	0.0	0.0
October precipitation	2.6	23.1	5.0	32.9	0.5	12.5	1.1	8.8	3.8	5.0
December precipitation	2.4	2.0	1.3	2.2	1.2	0.9	1.1	0.5	0.1	6.8
Mean temperature of coldest quarter	1.6	0.0	<b>16.7</b>	<b>1.3</b>	<b>9.3</b>	<b>0.0</b>	3.3	0.0	0.8	0.4
July minimum temperature	1.5	3.0	0.0	1.1	1.5	2.3	1.0	1.5	0.0	0.0
May precipitation	1.5	1.1	2.4	1.2	0.5	1.3	0.9	2.4	0.7	3.4
July maximum temperature	1.4	0.0	0.1	0.0	0.0	0.0	0.2	0.0	0.0	0.0
June maximum temperature	1.4	0.5	4.7	0.0	0.0	0.0	0.5	0.0	0.1	0.0
March precipitation	1.1	1.8	0.5	0.1	0.0	0.5	0.1	0.0	<b>53.8</b>	<b>5.9</b>
Precipitation of wettest month	1.1	0.5	1.2	0.0	0.4	1.7	0.9	1.5	<b>5.2</b>	<b>0.0</b>
Maximum temperature of warmest month	0.2	0.2	1.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0
June minimum temperature	0.5	0.0	0.2	0.0	2.9	13.5	<b>4.1</b>	<b>3.9</b>	1.3	0.0
June precipitation	0.0	0.1	1.0	7.9	0.8	1.1	0.4	1.5	<b>4.2</b>	<b>1.1</b>
Temperature annual range	0.4	0.1	0.6	0.1	0.5	0.1	0.8	0.2	2.7	0.0
July precipitation	0.5	0.3	0.8	1.8	0.0	0.1	0.2	0.2	<b>6.5</b>	<b>27.7</b>
Total	<b>90.7</b>		<b>88.3</b>		<b>88.6</b>		<b>88.4</b>		<b>93.1</b>	



TABLE 2. Results of the jackknife test of variable importance to the MaxEnt models generated for *H. macrotus*

Jackknife test	Model A	Model B	Model C	Model D	Model E
<i>Test of variable importance</i>					
Variable with highest explanatory power	August mean temperature	April precipitation	Minimum temperature of coldest month	July minimum temperature	Precipitation of wettest quarter
Variable with most 'unique' information	Vegetation cover	Vegetation cover	Vegetation cover	Altitude	July precipitation
<i>Test of variable importance using test gain</i>					
Variable with highest explanatory power	August mean temperature	September mean temperature	June mean temperature	June mean temperature	Precipitation of wettest month
Variable with most 'unique' information	August precipitation	Altitude	August precipitation	Altitude	July precipitation
<i>Test of variable importance using AUC</i>					
Variable with highest explanatory power	September mean temperature	September mean temperature	June mean temperature	June mean temperature	Precipitation of wettest month
Variable with most 'unique' information	Precipitation seasonality	Altitude	August precipitation	October precipitation	July precipitation

for model E, precipitation of wettest month and July precipitation (Table 2). All models showed better predictions than those generated at random, at cumulative values of 1, 5, and 10, with high AUC values ( $\pm$  SD): A =  $0.934 \pm 0.031$ , B =  $0.963 \pm 0.012$ , C =  $0.948 \pm 0.027$ , D =  $0.949 \pm 0.027$ , and E =  $0.998 \pm 0.002$  (Table 3).

From a biogeographical standpoint, the pooled records of *H. macrotus* are mostly concentrated in Southern Andean Yungas (21%,  $n = 14$ ), Valdivian Temperate Forest (14%,  $n = 9$ ), Dry Chaco (14%,  $n = 9$ ), Sechura Desert (12%,  $n = 8$ ), High Monte (11%,  $n = 7$ ), and Chilean Matorral (9%,  $n = 6$ ), sensu Olson *et al.* (2001). The remaining records are found in Espinal, Southern Andean Steppe, Patagonian Steppe, Central Andean Puna and Bolivian Montane Dry Forest, although none exceeding 5% of total records.

DISCUSSION

*Potential Distribution of H. macrotus*

As currently understood, *H. macrotus* is a broadly distributed species in the southern cone of South America. In spite of this, its distributional records remain scanty since its description in 1835, a time along which the species accumulated only 64 recording localities across four large South American countries. The pooled record set covered an unusually broad range of biomes, typical of a generalist occupying habitats from the desert to the montane cloud forest. However, the application of predictive distributional models based on environmental and topographical variables taken at localities of known occurrence yielded a disjoint distribution that invited revision. In addition, models with localities recorded after 1950 (B and D), showed a reduction in some areas of relatively high and medium predictive values as compared with the models generated with all records (i.e., A and C). This may indicate a recent reduction of suitable habitat for *H. macrotus*, which requires further inspection and validation in the field.

Models A to D recovered two principal areas of high predictive values: one centered in northwestern Argentina, and another one in central and southern Chile and southwestern Argentina. These core areas were disjoint, separated geographically by the South American Arid Diagonal (sensu Bruniard, 1982). Differences were also found between the models including or excluding localities from Peru. Thus, the models A and B showed two principal areas and an

area isolated in Sechura (south of Peru), and Atacama deserts (north of Chile), which is not recovered as part of a potential distribution area when the records from this area are excluded (Models C and D). Reciprocally, neither of the two core areas showed up in Model E, fitted with Sechura and Atacama data only, suggesting that these records did not belong in the same set as they are not mutually predicted. From these results, our interpretation is that specimens from southern Peru assigned to *H. macrotus* may correspond to another species. *H. laephotis* is one, perhaps obvious candidate. The areas of high prediction from southern Peru and northern Chile in Model E, coincide with distribution of *H. laephotis*. This species is distributed in Bolivia, Paraguay, Southern Brazil, northern Argentina, southern Peru and northern Chile (Anderson, 1997; López-González *et al.*, 1998; Acosta and Venegas, 2006; Miranda *et al.*, 2007). The remainder of specimens assigned to *H. macrotus* may correspond to a taxonomic complex distributed in two highly contrasting areas: 1) Bolivia and northwestern Argentina; and 2) south and Central Chile and southwestern Argentina. We hypothesize that each area may be populated by a distinct taxon, each adapted to specific environmental conditions, only one of them being the form that can be meaningfully associated with the type of *H. macrotus* (as *Nycticeus macrotus* Poepping, 1835, distributed in south and central Chile). Given the systematic uncertainty in *Histiotus*, these forms may either be successive sister species, or may not share an immediate common ancestor within *Histiotus*. These alternatives remain open to testing with the application of molecular phylogenetics to specimens samples from all three areas and relevant outgroups (other species of *Histiotus* and *Eptesicus*).

Different environmental variables had a distinct influence in the potential distribution models of *H. macrotus*. However, it is important to emphasize that model composition did agree on at least four variables, with varying different contribution percentages and importance: vegetation cover in Models A, B, C, D and E; precipitation seasonality, altitude in models A, B, C and D, and temperature

seasonality in models C and D. On this basis, we interpret that these are the four most important variables globally affecting the distribution of *H. macrotus* sensu lato. That is, seasonality of two key climatic variables (temperature and rainfall), one key biotic factor (vegetation), and one key geographic factor (altitude).

#### *Biogeographic Approximations and Climatic Determinants*

The disjunction apparent in all models, i.e., the area of very low predictive values between the two core areas, coincided largely with the South American Arid Diagonal. This region is oriented in a northwestern to southeastern direction, and extends from northern Peru in the Pacific coast, to the Patagonian coast of Argentina in the South Atlantic Ocean (Bruniard, 1982). This diagonal separates Neotropical forests from Austral (Subantarctic) forests, and represents a major component of the South American Transition Zone (Morrone, 2009), also separating the Neotropical Region from the Andean Region (Morrone, 2006). The Biogeographic Provinces of Central Andean Puna, Low Monte, Southern Andean Steppe and Patagonian Steppe, Atacama and Sechura deserts (sensu Olson *et al.*, 2001) are included within this Transition Zone. The models we generated suggest that *H. macrotus* is avoiding these environments, which have a dry climate, a great daily thermal amplitude, and low vegetation cover (Bruniard, 1982; Morello, 1985; Mancini *et al.*, 2005). In general, the diversity of small mammals including bats decreases in these environments (Ojeda *et al.*, 2000; Ojeda and Tabeni, 2009). It is important to emphasize that the localities of *H. macrotus* registered in the Sechura Desert are in fact located only in the coastal valleys and ‘Lomas’ of mist which are very peculiar environments in the desert matrix. These coastal valleys are located in fluvial plains of permanent rivers with native vegetation (principally ‘algarrobos’; *Prosopis* spp., Fabaceae) and crops (Ferreira, 1983; Morello, 1985). The ‘Lomas’ are environments of evergreen scrubs specialized in the capture and

TABLE 3. Results of predicted areas for cumulative threshold values of 1, 5, and 10 for the five models (A-B-C-D-E) generated

Cumulative threshold	Model A		Model B		Model C		Model D		Model E	
	Fractional predicted area	<i>P</i>	Fractional predicted area	<i>P</i>	Fractional predicted area	<i>P</i>	Fractional predicted area	<i>P</i>	Fractional predicted area	<i>P</i>
1	0.3286	0	0.2879	0	0.2248	0	0.2328	0.001	0.0065	0.131
5	0.1780	0	0.1631	0	0.1258	0	0.1242	0	0.0044	0.254
10	0.1132	0	0.1072	0	0.1242	0	0.0783	0	0.0033	0.253

retention of water from oceanic mist (Ferreira, 1983; Morello, 1985; Zeballos *et al.*, 2000; Aragón and Aguirre, 2014). In many areas, this mist is the only source of water (Ferreira, 1983; Morello, 1985; Zeballos *et al.*, 2000; Sotomayor Melo and Jiménez Milón, 2008). These particular environments allow the presence of a few bats species that live in otherwise extreme climatic conditions; *H. macrotus* has been cited among them (Zeballos *et al.*, 2000, 2001; Aragón and Aguirre, 2014). However, these specimens and localities need to be revised, since they can correspond to *H. laephotis* (see above).

Together with the South American Arid Diagonal, the Andes Mountains are one of the most prominent geomorphologic and climatic barriers of the Southern Cone (Ponce *et al.*, 2002). In this sense, the Peruvian Andes are an important barrier to faunal dispersal in general and bat dispersal in particular, between the eastern plains and the Pacific coast (Koopman, 1978). It is apparent that the high Andes act as a barrier separating the areas of potential distribution for *H. macrotus* in northern Argentina and Chile. In this region, the Andean montane environments, including the Central Andean Puna and Central Andean Dry Puna (*sensu* Olson *et al.*, 2001), exhibit extreme climatic conditions, with altitudes generally above 3,000 m a.s.l., cold weather and permanent snow in mountain tops (Morello, 1985; Burkart *et al.*, 1999). The mean annual temperature varies between 0° and 6°C with a high thermal amplitude, while precipitation ranges between 120 to 350 mm (Morello, 1985). The models showed null to very low predictive values of presence in these environments, which can represent an effective barrier for the species. Its absence from environments with great daily thermal amplitude and poor vegetation cover may reflect major ecological as well as physiological limitations for *H. macrotus* populations (see McNab, 1983). Moreover, *H. macrotus* possesses wings that are typical of bats capable of slow and highly maneuverable flight (Canals *et al.*, 2005; Giménez, 2010), which are also typical of poor dispersers and migrators (Norberg and Rayner, 1987; Jones *et al.*, 2003).

The potential distribution as estimated from our models A and B (with northern localities considered) versus models C and D (with northern localities removed), differ in details of predicted areas of occurrence (especially the occurrence in Bolivia), and also in the eco-regions of predicted occurrence. Models C and D showed that *H. macrotus* inhabit mainly forested areas (Southern Andean Yungas, Dry Chaco and Valdivian Temperate Forest), and

environments with intermediate vegetation coverage such as the High Monte and Chilean Matorral, with only marginal presence of the species in environments such as the Patagonian Steppe. Forested environments concentrated a greater number of localities. These environments are characterized by being highly heterogeneous (Laclau, 1997; Burkart *et al.*, 1999; Brown, 2009; Pacheco *et al.*, 2010; Malizia *et al.*, 2012), presenting high seasonality in temperature and precipitation (Laclau, 1997; Paruelo *et al.*, 1998; Burkart *et al.*, 1999; Naumann, 2006; Pacheco *et al.*, 2010; Malizia *et al.*, 2012). The vegetation of these eco-regions changes composition with both altitude and latitude and are highly heterogeneous across the geography (Laclau, 1997; Brown, 2009; Pacheco *et al.*, 2010; Malizia *et al.*, 2012). In addition, the forested eco-regions present stratified, dense vegetation cover (e.g., Southern Andean Yungas and Valdivian Temperate Forest). The wing morphology of *H. macrotus* allows its movements in these types of environments.

In conclusion, the potential distribution of *H. macrotus* *sensu lato*, as estimated with predictive models that use climatic and geographic variables from sites of known occurrence, may be consistent with the existence of three distinct taxa, each inhabiting a different set of neighboring eco-regions, rather than with a single taxon that is a habitat generalist able to occupy extremely different environments of the South American Southern Cone. The two major regions of predicted occurrence are separated by the South American Arid Diagonal, and also by the high Andes, generating a population in northwestern Argentina and southern Bolivia, and another population in southwestern Argentina and Central Chile. The South American Arid Diagonal could have acted as a barrier disjoining the *H. macrotus* distribution, perhaps leading to allopatric speciation. The Andean barrier lowers in Central Chile and permitted East-West population exchange. These hypotheses derived from the modeled potential distribution await testing applying techniques of molecular systematics with samples from all three regions and relevant outgroups, including other *Histiotus* species. In addition, the localities from southern Peru are also isolated and were not predicted as areas of occurrence for *H. macrotus* in models without these localities; for this reason we consider that the specimens from these localities should be revised.

According to this, morphological and molecular analyses would be necessary not only for *H. macrotus* (i.e., northern vs. southern populations), but for *Histiotus* as a whole. However this work aimed to

provide a framework for future studies that could increase the number of records for the species throughout its range, providing new information that may corroborate the results that we report; and for exploration of areas where the potential models suggest that the species might occur. It is very important to develop morphological and molecular studies to clarify the taxonomic boundaries of *Histiotus* species.

In general, predictive models of species geographic distributions are important for a variety of applications in ecology and conservation (Godown and Peterson, 2000; Papes and Gaubert, 2007; Thorn *et al.*, 2009; Urbina-Cardona and Flores-Villela, 2010; Moreno *et al.*, 2011). In this sense, *H. macrotus* has been classified in the Least Concern category of the Red List of Threatened Species (Barquez and Díaz, 2008) and Red Book of Argentine Mammals (Ojeda *et al.*, 2012); however our knowledge on distribution, natural history, ecology and populations status its highly incomplete. For this reason, although our results are exploratory, they should be very useful to establish future lines or research.

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#### LITERATURE CITED

- ACOSTA, L., and C. VENEGAS. 2006. Algunas consideraciones taxonómicas de *Histiotus laephotis* e *H. macrotus*, en Bolivia. *Kempffiana*, 2: 109–115.
- AGUIRRE, L. F. 2011. Lista oficial de los murciélagos de Bolivia (On line). Murciélagos de Bolivia. Available at <http://www.murcielagosdebolivia.com>.
- AHMADZADEH, F., M. FLECKS, M. A. CARRETERO, O. MOZAFFARI, W. BÖHME, D. HARRIS, S. FREITAS, and D. RÖDDER. 2013. Cryptic speciation patterns in Iranian rock lizards uncovered by integrative taxonomy. *PLoS ONE*, 8: e80563.
- ANDERSON, S. 1997. Mammals of Bolivia, taxonomy and distribution. *Bulletin of the American Museum of Natural History*, 231: 1–656.
- ARAGÓN, G., and M. AGUIRRE. 2014. Distribución de murciélagos (Chiroptera) de la Región Tacna, Perú. *Idesia*, 32: 119–127.
- BARQUEZ, R. M. 2006. Orden Chiroptera Blumenbach, 1779. Pp. 56–86, *in* Mamíferos de Argentina: sistemática y distribución (R. M. BARQUEZ, M. M. DÍAZ, and R. A. OJEDA, eds.). Sociedad Argentina para el Estudio de los Mamíferos (SAREM), Tucumán, 356 pp.
- BARQUEZ, R. M., and M. M. DÍAZ. 2001. Bats of the Argentine Yungas: a systematic and distributional analysis. *Acta Zoológica Mexicana (N.S.)*, 82: 29–81.
- BARQUEZ, R. M., and M. DÍAZ. 2008. *Histiotus macrotus*. The IUCN Red List of Threatened Species. Version 2015.2. Available at [www.iucnredlist.org](http://www.iucnredlist.org). Downloaded on 23 May 2015.
- BARQUEZ, R. M., and M. M. DÍAZ. 2009. Los murciélagos de Argentina. Clave de identificación. Programa de Conservación de Murciélagos de Argentina (PCMA), Tucumán, 84 pp.
- BARQUEZ, R. M., and S. C. LOUGHEED. 1990. New distributional records of some Argentine bat species. *Journal of Mammalogy*, 71: 261–263.
- BARQUEZ, R. M., and R. A. OJEDA. 1992. The bats (Mammalia: Chiroptera) of the Argentine Chaco, *Annals of Carnegie Museum*, 61: 239–261.
- BARQUEZ, R. M., N. P. GIANNINI, and M. A. MARES. 1993. Guide to the bats of Argentina. Oklahoma Museum of Natural History, Norman, viii + 119 pp.
- BARQUEZ, R. M., M. A. MARES, and J. K. BRAUN. 1999. The bats of Argentina. Special Publications of the Museum of Texas Tech University, Lubbock, 42: 1–275.
- BONTEMPS, S., P. DEFOURNEY, E. VAN BOGAERT, O. ARINO, V. KALOGIROU, and J. RAMOS PEREZ. 2011. GlobCover 2009 — products description and validation report. ESA and Université Catholique de Louvain, Frascati, Italy, 53 pp.
- BRACAMONTE, J. C. 2010. Murciélagos de bosque montano del Parque Provincial Potrero de Yala, Jujuy, Argentina. *Mastozoología Neotropical*, 17: 361–366.
- BROWN, A. D. 2009. Las selvas pedemontanas de las Yungas: manejo sustentable y conservación de la biodiversidad de un ecosistema prioritario del noroeste argentino. Pp. 13–36, *in* Selva pedemontana de las Yungas. Historia natural, ecología y manejo de los ecosistemas en peligro (A. D. BROWN, P. G. BLENGINGER, T. LOMÁSCOLO, and P. GARCÍA BES, eds.). Fundación ProYungas, Ediciones del Suptrópico, Tucumán, 487 pp.
- BRUNIARD, E. D. 1982. La diagonal árida argentina: un límite climático real. *Revista Geográfica*, 95: 5–20.
- BURKART, R., N. O. BÁRBARO, R. O. SÁNCHEZ, and D. A. GÓMEZ. 1999. Eco-regiones de la Argentina. Administración de Parques Nacionales, Programa Desarrollo Institucional Ambiental, Buenos Aires, 42 pp.
- CABRERA, A. 1930. Breve sinopsis de los murciélagos argentinos. *Revista del Centro de Estudiantes de Agronomía y Veterinaria, Universidad de Buenos Aires*, 23: 418–442.
- CANALS, M., B. GROSSI, J. IRIARTE-DÍAZ, and C. VELOSO. 2005. Biomechanical and ecological relationships of wing morphology of eight Chilean bats. *Revista Chilena de Historia Natural*, 78: 215–227.
- CAO, Y., R. E. DEWALT, J. L. ROBINSON, T. TWEDDALE, L. HINZ, and M. PESSINO. 2013. Using Maxent to model the historic distributions of stonefly species in Illinois streams: the effects of regularization and threshold selections. *Ecological Modelling*, 259: 30–39.
- CHETAN, N., K. K. PRAVEEN, and G. K. VASUDEVA. 2014. Delineating ecological boundaries of hanuman langur species complex in Peninsular India using MaxEnt modeling approach. *PLoS ONE*, 9: e91497.
- DÍAZ, M. M., L. F. AGUIRRE, and R. M. BARQUEZ. 2011. Clave de identificación de los murciélagos del cono sur de Sudamérica. Centro de Estudios en Biología Teórica y Aplicada, Cochabamba, Bolivia, 94 pp.
- EISENBERG, J. F., and K. H. REDFORD. 1999. Mammals of the Neotropics. Volume 3. The Central Neotropics: Ecuador, Perú, Bolivia, Brazil. University of Chicago Press, Chicago, x + 609 pp.
- ELITH, J., C. H. GRAHAM, R. P. ANDERSON, M. DUDÍK, S. FERRIER, A. GUISAN, R. J. HIJMANS, F. HUETTMANN, J. R.

- LEATHWICK, A. LEHMANN, *et al.* 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29: 129–151.
- ENGLER, R., A. GUISAN, and L. RECHSTEINER. 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology*, 41: 263–274.
- FERREYRA, R. 1983. Los tipos de vegetación de la costa peruana. *Anales Jardín Botánico de Madrid*, 40: 241–256.
- FRANKLIN, J. 2009. Mapping species distributions, spatial inference and prediction. Cambridge University Press, New York, 336 pp.
- GALAZ, J. L., and J. YAÑEZ. 2006. Los murciélagos de Chile: guía para su reconocimiento. Ediciones del Centro de Ecología Aplicada, Santiago, 80 pp.
- GIMÉNEZ, A. L. 2010. Primeros registros de *Histiotus macrotus* (Chiroptera: Vespertilionidae) en la Provincia del Chubut, Argentina. *Mastozoología Neotropical*, 17: 375–380.
- GIMÉNEZ, A. L., N. P. GIANNINI, M. I. SCHIAFFINI, and G. M. MARTIN. 2012. New records of the rare *Histiotus magellanicus* (Chiroptera, Vespertilionidae) and other bats from Central Patagonia, Argentina. *Mastozoología Neotropical*, 19: 213–224.
- GODOWN, M. E., and A. T. PETERSON. 2000. Preliminary distributional analysis of U.S. endangered bird species. *Biodiversity and Conservation*, 9: 1313–1322.
- GUISAN, A., O. BROENNIMANN, R. ENGLER, M. VUST, N. G. YOCOZ, A. LEHMANN, and N. E. ZIMMERMANN. 2006. Using niche based models to improve the sampling of rare species. *Conservation Biology*, 20: 501–511.
- GUTIÉRREZ, E. E., R. A. BORJA, and R. P. ANDERSON. 2014. Can biotic interactions cause allopatry? Niche models, competition, and distributions of South American mouse opossums. *Ecography*, 37: 741–753.
- HANDLEY, C. O., JR., and A. L. GARDNER. 2007. Genus *Histiotus* P. Gervais, 1856. Pp. 450–457, in *Mammals of South America*. Volume 1: marsupials, xenarthrans, shrews and bats (A. L. Gardner, ed.). University of Chicago Press, Chicago, 651 pp.
- HIJMANS, R. J., S. E. CAMERON, J. L. PARRA, P. G. JONES, and A. JARVIS. 2005a. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25: 1965–1978.
- HIJMANS, R. J., L. GUARINO, P. MATHUR, P. JARVIS, E. ROJAS, M. CRUZ, and I. BARRANTES. 2005b. DIVA-GIS version 7.5.0.0. Available at <http://www.diva-gis.org>.
- HOOFFER, S. R., and R. A. VAN DEN BUSSCHE. 2003. Molecular phylogenetic of the chiropteran family Vespertilionidae. *Acta Chiropterologica*, 5: 1–63.
- JAYAT, J. P., and P. E. ORTIZ. 2010. Mamíferos del pedemonte de Yungas de la alta cuenca del Río Bermejo en Argentina: una línea de base de diversidad. *Mastozoología Neotropical*, 17: 69–86.
- JONES, K. E., A. PURVIS, and J. L. GITTLEMAN. 2003. Biological correlates of extinction risk in bats. *The American Naturalist*, 161: 601–614.
- KOOPMAN, K. F. 1978. Zoogeography of Peruvian bats with emphasis on the role of the Andes. *American Museum Novitates*, 2651: 1–33.
- KOOPMAN, K. F. 1982. Biogeography of the bats of South America. Pp. 273–302, in *Mammalian biology in South America* (M. A. Mares and H. H. Genoways, eds.). University of Pittsburgh, Pittsburgh, Pennsylvania, 539 pp.
- LACK, J. B., and R. A. VAN DEN BUSSCHE. 2010. Identifying the confounding factors in resolving phylogenetic relationships in Vespertilionidae. *Journal of Mammalogy*, 91: 1435–1448.
- LACLAU, P. 1997. Los ecosistemas forestales y el hombre en el sur de Chile y Argentina. Fundación Vida Silvestre Buenos Aires, Argentina, Fondo Mundial para la Naturaleza. *Boletín Técnico*, 34: 1–147.
- LÓPEZ-GONZÁLEZ, C. 2005. Murciélagos del Paraguay. *Biosfera*, Publicaciones del Comité Español del Programa Hombre y Biosfera-Red IberoMaB, UNESCO, Madrid, iv + 300 pp.
- LÓPEZ-GONZÁLEZ, C., S. J. PRESLEY, R. D. OWEN, M. R. WILLIG, and I. GAMARRA DE FOX. 1998. Noteworthy records of bats (Chiroptera) from Paraguay. *Mastozoología Neotropical*, 5: 41–45.
- MALIZIA, L., S. PACHECO, C. BLUNDO, and A. D. BROWN. 2012. Caracterización altitudinal, uso y conservación de las Yungas Subtropicales de Argentina. *Ecosistemas*, 21: 53–73.
- MANCINI, M. V., M. M. PAEZ, A. R. PRIETO, S. STUTZ, M. TONELLO, and I. VILANOVA. 2005. Mid-Holocene climatic variability reconstruction from pollen records (32°–52°S, Argentina). *Quaternary International*, 132: 47–59.
- MANN FISCHER, G. 1978. Los pequeños mamíferos de Chile, marsupiales, quirópteros, edentados y roedores. *Gayana (Zoología)*, 40: 1–342.
- MARES, M. A., R. M. BARQUEZ, and J. K. BRAUN. 1995. Distribution and ecology of some Argentine bats. *Annals of Carnegie Museum*, 64: 219–237.
- MARES, M. A., R. M. BARQUEZ, J. K. BRAUN, and R. A. OJEDA. 1996. Observations of the mammals of Tucuman Province, Argentina. I. Systematics, distribution, and ecology of the Didelphimorphia, Xenarthra, Chiroptera, Primates, Carnivora, Peryssodactyla, Artiodactyla, and Lagomorpha. *Annals of Carnegie Museum*, 65: 8–152.
- MASON, N. A., P. O. TITLE, C. CICERO, K. J. BURNS, and R. C. K. BOWIE. 2014. Genetic variation among western populations of the horned lark (*Eremophila alpestris*) indicates recent colonization of the Channel Islands off southern California, mainland-bound dispersal, and postglacial range shifts. *Ornithological Advances*, 131: 162–174.
- MENABO, B. K. 1983. Energetics, body size, and the limits to endothermy. *Journal of Zoology (London)*, 199: 1–29.
- MIRANDA, J. M. D., M. F. M. AZEVEDO-BARROS, and F. C. PASSOS. 2007. First record of *Histiotus laeophotis* Thomas (Chiroptera, Vespertilionidae) from Brazil. *Revista Brasileira de Zoologia*, 24: 1188–1191.
- MORATELLI, R., C. S. DE ANDREAZZI, J. A. DE OLIVEIRA, and J. L. P. CORDEIRO. 2011. Current and potential distribution of *Myotis simus* (Chiroptera: Vespertilionidae). *Mammalia*, 75: 227–234.
- MORELLO, J. A. 1985. Grandes ecosistemas de Sudamérica. Textos para discusión. Fundación Bariloche/3, Bariloche, 116 pp.
- MORENO, R., R. ZAMORA, J. R. MOLINA, A. VASQUEZ, and M. A. HERRERA. 2011. Predictive modeling of microhabitats for endemic birds in South Chilean temperate forests using maximum entropy (Maxent). *Ecological Informatics*, 6: 364–370.
- MORRONE, J. J. 2006. Biogeographic areas and transition zones of Latin America and the Caribbean Islands based on Panbiogeographic and cladistic analyses of the entomofauna. *Annual Review of Entomology*, 51: 467–94.
- MORRONE, J. J. 2009. Evolutionary biogeography: an integrative approach with case studies. Columbia University Press, New York, 301 pp.

- NAUMANN, M. 2006. Atlas del Gran Chaco Sudamericano. Sociedad Alemana de Cooperación Técnica (GTZ), ErreGé & Asoc., Buenos Aires, 96 pp.
- NORBERG, U. M., and J. M. V. RAYNER. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London*, 316B: 335–427.
- OJEDA, R. A., and S. TABENI. 2009. The mammals of the Monte Desert revisited. *Journal of Arid Environments*, 73: 173–181.
- OJEDA, R. A., P. G. BLENDINGER, and R. BRANDL. 2000. Mammals in South American drylands: faunal similarity and trophic structure. *Global Ecology and Biogeography*, 9: 115–123.
- OJEDA, R. A., V. CHILLO, and G. B. DIAZ ISENRAH. 2012. Libro Rojo de Mamíferos Amenazados de Argentina. Sociedad Argentina para el Estudio de los Mamíferos (SAREM), Argentina, 257 pp.
- OLROG, C. C. 1959. Notas mastozoológicas. II. Sobre la colección del Instituto Miguel Lillo. *Acta Zoológica Lilloana*, 17: 403–419.
- OLSON, D. M., E. DINERSTEIN, E. D. WIKRAMANAYAKE, N. D. BURGESS, G. V. N. POWELL, E. C. UNDERWOOD, J. A. D'AMICO, I. ITOUA, H. E. STRAND, J. C. MORRISON, *et al.* 2001. Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience*, 51: 933–938.
- ORTIZ-MARTÍNEZ, T., V. RICO-GRAY, and E. MARTÍNEZ-MEYER. 2008. Predicted and verified distributions of *Ateles geoffroyi* and *Alouatta palliata* in Oaxaca, Mexico. *Primates*, 49: 186–194.
- OSGOOD, W. H. 1943. The mammals of Chile. *Field Museum of Natural History, Zoological Series*, 30: 1–268.
- PACHECO, S., L. R. MALIZIA, and A. D. BROWN. 2010. La provisión de agua como servicio ambiental de la Reserva de Biosfera de las Yungas, Argentina. Pp. 9–20, *in* Reservas de la Biosfera, su contribución a la provisión de servicios de los ecosistemas (P. ARAYA ROSAS and M. CLOSENEER-GODT, eds.). UNESCO, Chile, 224 pp.
- PAPES, M., and P. GAUBERT. 2007. Modeling ecological niches from low numbers of occurrences: assessment of the conservation status of poorly known viverrids (Mammalia, Carnivora) across two continents. *Diversity and Distributions*, 13: 890–902.
- PARUELO, J. M., A. BELTRÁN, E. JOBBÁGY, O. E. SALA, and R. A. GOLLUSCIO. 1998. The climate of Patagonia: general patterns and controls on biotic processes. *Ecología Austral*, 8: 85–101.
- PEARSON, O. P. 1995. Annotated keys for identifying small mammals living in or near Nahuel Huapi National Park or Lanin National Park, Southern Argentina. *Mastozoología Neotropical*, 2: 99–148.
- PEARSON, O. P., and A. K. PEARSON. 1989. Reproduction of bats in Southern Argentina. Pp. 549–566, *in* Advances in Neotropical Mammalogy (K. H. REDFORD and J. F. EISENBERG, eds.). University of Florida, Gainesville, Florida, 614 pp.
- PETERSON, A. T., M. PAGES, and M. EATON. 2007. Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography*, 30: 550–560.
- PHILLIPS, S. J., M. DUDÍK, and R. E. SCHAPIRE. 2004. A maximum entropy approach to species distribution modeling. *Proceedings of the 21st International Conference on Machine Learning*, Banff, Canada, 8 pp.
- PHILLIPS, S. J., R. P. ANDERSON, and R. E. SCHAPIRE. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190: 231–259.
- POEPPIG, E. 1835. Reise in Chile, Peru, und auf dem Amazonenstrom während der Jahre 1827–1832. F. Fleischer & J.C. Hinrichssche Buchhandlung, Leipzig, 1: xviii + 466 pp.
- PONCE, M., K. MEHLTRETER, and E. R. DE LA SOTA. 2002. Análisis biogeográfico de la diversidad pteridofítica en Argentina y Chile continental. *Revista Chilena de Historia Natural*, 75: 703–717.
- RAXWORTHY, C. J., C. M. INGRAM, N. RABIBISOA, and R. G. PEARSON. 2007. Applications of ecological niche modeling for species delimitation: a review and empirical evaluation using day geckos (*Phelsuma*) from Madagascar. *Systematic Biology*, 56: 907–923.
- SANABRIA, E., L. QUIROGA, J. VILLAVICENCIO, and G. CÁNOVAS. 2004. Lista comentada y estado de conservación de algunos quirópteros de la provincia de San Juan, Argentina. *Nótulas Faunísticas*, 17: 1–4.
- SANDOVAL, M. L., M. S. SÁNCHEZ, and R. M. BARQUEZ. 2010. Mammalia, Chiroptera Blumenbach, 1779. New locality records, filling gaps, and geographic distribution maps from Northern Argentina. *CheckList*, 6: 64–7.
- SÄRKINEN, T., P. GONZÁLES, S. KNAPP. 2013. Distribution models and species discovery: the story of a new *Solanum* species from the Peruvian Andes. *PhytoKeys*, 31: 1–20.
- SIMMONS, N. B. 2005. Order Chiroptera. Pp. 312–529, *in* Mammals species of the World: a taxonomic and geographic references, 3rd edition (D. E. WILSON and D. M. REEDER, eds.). Johns Hopkins University Press, Baltimore, Maryland, 2142 pp.
- SOTOMAYOR MELO, D. A., and P. JIMÉNEZ MILÓN. 2008. Condiciones meteorológicas y dinámica vegetal del ecosistema costero Lomas de Atiquipa (Caravelí-Arequipa) en el Sur del Chile. *Ecología Aplicada*, 7: 1–8.
- THOMAS, O. 1916. Notes on the bats of the genus *Histiotus*. *Annals and Magazine of Natural History*, 8 (17): 272–276.
- THORN, J. S., V. NIJMAN, D. SMITH, and A. I. NEKARIS. 2009. Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (Primates: *Nycticebus*). *Diversity and Distributions*, 15: 289–298.
- TUTTLE, M. D. 1970. Distribution and zoogeography of peruvian bats, with comments on natural history. *The University of Kansas, Science Bulletin*, 49: 46–86.
- VALLADARES FAÚNDEZ, P. 2012. Mamíferos terrestres de la Región de Atacama, Chile. *Comentarios sobre su distribución y estado de conservación*. *Gayana*, 76: 22–37.
- URBINA-CARDONA, J. N., and O. FLORES-VILLELA. 2010. Ecological-niche modeling and prioritization of conservation-area networks for Mexican herpetofauna. *Conservation Biology*, 24: 1031–1041.
- WARREN, D. L., and S. N. SEIFERT. 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*, 21: 335–342.
- ZEBALLOS, H., L. VILLEGAS, R. GUTIÉRREZ, K. CABALLERO, and P. JIMÉNEZ. 2000. Vertebrados de las Lomas de Atiquipa y Mejía, sur del Perú. *Revista de Ecología Latinoamericana*, 7: 11–18.
- ZEBALLOS, H., V. PACHECO, and L. BARAYBAR. 2001. Diversidad y conservación de los mamíferos de Arequipa, Perú. *Revista Peruana de Biología*, 8: 94–104.

## APPENDIX

Record localities for *H. macrotus*. Abbreviations and acronyms are as follows: Ar — Argentina; Ch — Chile; Bol — Bolivia; FMNH — Field Museum of Natural History; AMNH — American Museum of Natural History; collectors' names and years of collection are shown in brackets

N°	Localities	Latitude	Longitude	Model	Reference
1	Bío Bío, Antuco (Ch)	37°19'59"S	71°40'59"W	A-C	Poeppig (1835)
2	Metropolitana de Santiago, Santiago (Ch)	33°26'16"S	70°39'01"W	A-C	Thomas (1916)
3	Departamento Belén, Catamarca (Ar)	27°38'57"S	67°01'35"W	A-C	Cabrera (1930)
4	Aisen (Ch)	45°23'59"S	72°42'W	A-C	FMNH 49949 [Reed, 1940]
5	Bío Bío, Concepción (Ch)	36°49'59"S	73°02'59"W	A-C	Osgood (1943)
6	Santiago (Ch)	33°27'S	70°40'W	A-C	Osgood (1943)
7	El Rodeo 900 m, Catamarca (Ar)	28°13'S	65°52'W	A-B-C-D	Olrog (1959)
8	Atacama, Chañaral (Ch)	29°01'59"S	71°25'59"W	A-B-C-D	Mann Fischer (1978)
9	Valparaiso, near Valparaiso (Ch)	33°02'52"S	71°36'04"W	A-B-C-D	Mann Fischer (1978)
10	Bío Bío, Nuble, Termas de Chillan (Ch)	36°54'33"S	71°25'08"W	A-B-C-D	AMNH 238025 [Moreno, 1978]
11	Estancia El Cóndor 22 km SE de Bariloche, Río Negro (Ar)	41°7'S	71°13'W	A-B-C-D	Pearson and Pearson (1989)
12	Cafayate 20 km al NO, Salta (Ar)	25°54'S	66°09'W	A-B-C-D	Barquez and Loughheed (1990)
13	Tres Cruces 8 km al SO, Jujuy (Ar)	22°59'S	65°29'W	A-B-C-D	Barquez and Loughheed (1990)
14	Villa Cura Brochero, Córdoba (Ar)	31°40'S	65°00'W	A-B-C-D	Barquez and Ojeda (1992)
15	19 km al N de Villa La Angostura sobre ruta 234, Neuquén (Ar)	40°40'S	71°40'W	A-B-C-D	Mares <i>et al.</i> (1995)
16	Chumbicha 1 km al O del Balneario por ruta, Catamarca (Ar)	28°51'S	66°14'W	A-B-C-D	Mares <i>et al.</i> (1995)
17	Choya 13 km al NO de Andalgala, Catamarca (Ar)	27°32'S	66°24'W	A-B-C-D	Mares <i>et al.</i> (1995)
18	Complejo Astronómico El Leoncito, 7 km al O, San Juan (Ar)	31°48'S	69°20'W	A-B-C-D	Mares <i>et al.</i> (1995)
19	Las Juntas, 22 km al O de Choromoro, Tucumán (Ar)	26°24'S	65°31'W	A-B-C-D	Mares <i>et al.</i> (1995)
20	Paso del Rey 1 km N sobre A° de la Cañada Honda, San Luis (Ar)	32°57'S	66°00'W	A-B-C-D	Mares <i>et al.</i> (1995)
21	20 km al E de Bariloche, Río Negro (Ar)	41°08'09"S	71°04'18"W	A-B-C-D	Pearson (1995)
22	El Nohagar ruta 307, Tucumán (Ar)	27°01'S	65°40'W	A-B-C-D	Mares <i>et al.</i> (1996)
23	Ruta 307 km 43, Tucumán (Ar)	26°53'S	65°41'W	A-B-C-D	Mares <i>et al.</i> (1996)
24	Andalgala, Catamarca (Ar)	27°36'S	66°20'W	A-B-C-D	Barquez <i>et al.</i> (1999)
25	Balneario El Caolin 6 km al NO de Chumbicha, Catamarca (Ar)	28°52'S	66°14'W	A-B-C-D	Barquez <i>et al.</i> (1999)
26	Dique El Potrero 13 km al N de Andalgala, Catamarca (Ar)	27°32'S	66°20'W	A-B-C-D	Barquez <i>et al.</i> (1999)
27	Los Nacimientos ruta 40 km 869, Catamarca (Ar)	27°07'S	66°42'W	A-B-C-D	Barquez <i>et al.</i> (1999)
28	Río Cuarto, Córdoba (Ar)	33°08'S	64°18'W	A-B-C-D	Barquez <i>et al.</i> (1999)
29	Río Quinto, San Luis (Ar)	33°12'S	65°51'W	A-B-C-D	Barquez <i>et al.</i> (1999)
30	Ruta 307 km 46, Tucumán (Ar)	26°53'S	65°41'W	A-B-C-D	Barquez <i>et al.</i> (1999)
31	Sierra de Ancasti en ruta 2, 1700 msnm, Catamarca (Ar)	28°49'S	65°30'W	A-B-C-D	Barquez <i>et al.</i> (1999)
32	Tinogasta, Catamarca (Ar)	28°04'S	67°34'W	A-B-C-D	Barquez <i>et al.</i> (1999)
33	Lomas de Atequipa, Arequipa (Perú)	15°47'S	74°16'W	A-B-E	Zeballos <i>et al.</i> (2000)
34	Valle de Tambo, Arequipa (Perú)	16°58'S	71°38'W	A-B-E	Zeballos <i>et al.</i> (2001)
35	Lomas de Mejía, Arequipa (Perú)	17°10'S	71°07'W	A-B-E	Zeballos <i>et al.</i> (2001)
36	Cuesta del Clavillo 5 km al SO de la Banderita, Catamarca (Ar)	27°29'S	66°06'W	A-B-C-D	Barquez and Diaz (2001)
37	La Banderita, Catamarca (Ar)	27°19'S	65°58'W	A-B-C-D	Barquez and Diaz (2001)
38	La Banderita, Ruta 62, camino a Las Estancias, Catamarca (Ar)	27°28'S	66°01'59"W	A-B-C-D	Barquez and Diaz (2001)
39	Barreal (El Leoncito), San Juan (Ar)	31°51'S	69°22'W	A-B-C-D	Sanabria <i>et al.</i> (2004)

## APPENDIX. Continued

N°	Localities	Latitude	Longitude	Model	Reference
40	Baldes del Rosario, San Juan (Ar)	30°19'21"S	67°57'W	A-B-C-D	Sanabria <i>et al.</i> (2004)
41	Parque Provincial Potrero de Yala, Jujuy (Ar)	24°06'S	65°28'W	A-B-C-D	Bracamonte (2010)
42	Zona Costera de la provincia de Chañaral (Ch)	29°02'S	71°26'W	A-B-C-D	Galaz and Yañez (2006)
43	Vallegrande, Santa Cruz (Bol)	18°29'25"S	64°06'22"W	A-B	Acosta and Venegas (2006)
44	Pampa Grande, Santa Cruz (Bol)	18°05'10"S	64°05'56"W	A-B	Acosta and Venegas (2006)
45	Parque Nacional El Tunari, Cochabamba (Bol)	17°20'S	66°08'W	A-B	Acosta and Venegas (2006)
46	Escuela de Idioma Galés, Trevelin (Ar)	43°05'56"S	71°28'26"W	A-B-C-D	Giménez (2010)
47	Estancia El Principio, Chubut (Ar)	42°59'27"S	71°24'60"W	A-B-C-D	Giménez (2010)
48	App. 20 km al NO de Vespucio, sobre el Río Seco, Salta (Ar)	22°32'16"S	64°00'02"W	A-B-C-D	Jayat and Ortiz (2010)
49	Campo Largo km 74.5, ruta entre Acambuco y Campo Largo, Salta (Ar)	22°01'43"S	63°55'35"W	A-B-C-D	Jayat and Ortiz (2010)
50	5.2 km al NW de Chumbicha 626 m, Catamarca (Ar)	28°49'S	66°15'W	A-B-C-D	Sandoval <i>et al.</i> (2010)
51	3.5 km al S de Angastaco 1844 m, Salta (Ar)	25°41'S	66°07'W	A-B-C-D	Sandoval <i>et al.</i> (2010)
52	App. 15 km al O de Escoipe, sobre ruta provincial 33, Salta (Ar)	25°10'S	65°50'W	A-B-C-D	Sandoval <i>et al.</i> (2010)
53	El Durazno 8 km al S de La Viña por ruta 38 vieja, Catamarca (Ar)	28°06'S	65°36'W	A-B-C-D	Sandoval <i>et al.</i> (2010)
54	Laguna El Brealito, Salta (Ar)	25°17'S	66°22'W	A-B-C-D	Sandoval <i>et al.</i> (2010)
55	Parque Provincial El Cochuna (camping), Tucumán (Ar)	27°18'S	65°54'W	A-B-C-D	Sandoval <i>et al.</i> (2010)
56	Reserva Provincial La Florida Pueblo Viejo, Tucumán (Ar)	27°13'S	65°37'W	A-B-C-D	Sandoval <i>et al.</i> (2010)
57	Cordillera Domenyco, provincia de Charaña (Ch)	28°57'18"S	70°53'38"W	A-B-C-D	Valladares Faúndez (2012)
58	Esquel, Chubut (Ar)	42°54'49"S	71°18'39"W	A-B-C-D	Giménez <i>et al.</i> (2012)
59	Reserva El Colhue, Chubut (Ar)	42°09'44"S	71°18'35"W	A-B-C-D	Giménez <i>et al.</i> (2012)
60	Pampa Baja, Valle de Ite, Jorge Basadre (Peru)	17°52'58"S	70°58'54"W	A-B-E	Aragon and Aguirre (2014)
61	Humedales de Ite, Jorge Basadre (Peru)	17°52'29"S	71°00'25"W	A-B-E	Aragon and Aguirre (2014)
62	Anexo Aurora, Jorge Basadre (Peru)	17°40'38"S	70°49'32"W	A-B-E	Aragon and Aguirre (2014)
63	Anexo Cinto, Jorge Basadre (Peru)	17°31'19"S	70°43'33"W	A-B-E	Aragon and Aguirre (2014)
64	Anexo Conostoco, Jorge Basadre (Peru)	17°36'40"S	70°45'30"W	A-B-E	Aragon and Aguirre (2014)