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Estimating the potential distribution and conservation priorities of *Chironectes minimus* (Zimmermann, 1780) (Didelphimorphia: Didelphidae)

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The water opossum (*Chironectes minimus*) is an elusive and solitary Neotropical semi-aquatic species, whose population dynamics cannot be studied using traditional methods to capture small mammals. Therefore, some aspects of its distribution, habitat requirements, and abundance are mostly unknown; which makes a proper determination of its conservation status difficult. Considering that new techniques known as species distribution models (SDMs) allow us to estimate the suitable areas and the most important variables for the distribution of a species, we compiled water opossum occurrences and modeled its potential distribution on a continental scale. We performed a SDM for the water opossum using MaxEnt and assessed the extent of habitat loss (km^2) and the importance of Protected Areas (PAs). We compared the suitability values within and outside PAs using a Kolmogorov-Smirnov (KS) test to evaluate the efficiency of PAs. The results obtained were compared with the IUCN historical water opossum's map. Additionally, we identified gaps in the potential distribution where for future surveys should be focused. We obtained models that describe the distribution of this species based on 292 occurrences with new information for 16 countries. Deforestation reduced the area of suitable habitat by ~40 % and only ~18 % corresponds to natural forest within PAs. Areas inside PAs showed higher suitability values (0.351 ± 0.276; $P < 0.001$) than areas outside them. We identified gaps within the distribution that need attention during future surveys such as the frontier between Venezuela and Guyana, the Amazonian region, and central-eastern Brazil. Our results showed areas absent in the IUCN's distribution map, indicating that it needs to be updated. Thus, we proposed a new tentative extent of the water opossum distribution information here obtained. We demonstrated that PAs included areas with high habitat suitability values for *C. minimus,* which could protect the water opossum in the medium and long-term. Modifications to the physicochemical characteristics of the habitat due to forest loss and fragmentation can considerably affect water opossum populations and reduce local diversity. Thus, the preservation of river ecosystems and surrounding areas represents a necessary step for the conservation of *C. minimus*.

La zarigüeya de agua (*Chironectes minimus*) es una especie neotropical semi-acuática, de hábitos esquivos y solitarios, cuya dinámica poblacional no puede ser estudiada métodos tradicionales de captura de pequeños mamíferos. Es por ello que algunos aspectos de su distribución, sus requerimientos de hábitat y su abundancia siguen siendo desconocidos, dificultando su apropiada categorización. Considerando que modelos de distribución de especies (MDE) nos permiten estimar y las variables climáticas más importantes para la distribución; se recopilaron las ocurrencias de *C. minimus* y se modelo su distribución potencial a una escala continental. Utilizando el programa MaxEnt se definió un MDE para la zarigüeya de agua, evaluando el efecto de la pérdida de hábitat (km^2) y la importancia de las Áreas Protegidas (AP) en la extensión del mismo. La eficiencia de las APs fue evaluada con una prueba de Kolmogorov-Smirnov (KS) para comparar los valores de idoneidad del MDE obtenidos dentro y fuera de las APs. Los resultados obtenidos se compararon con el mapa de distribución histórica de la UICN. Adicionalmente, se identificaron vacíos de información en la distribución potencial donde enfocar esfuerzos de muestreo mediante el cálculo de un índice de prioridad. Se obtuvieron modelos a partir de 292 ocurrencias, con nueva información en 16 países. La deforestación redujo la distribución potencial en ~ 40 % y se observó que solo el ~ 18% corresponde a bosques naturales dentro de las AP. Las áreas de distribución potencial mostraron valores de idoneidad más altos dentro de las APs (0,351 ± 0,276, $p < 0{,}001$). Las áreas con vacíos de información fueron identificadas en la frontera entre Venezuela y Guyana, la región amazónica y el centro-este de Brasil. Los resultados indican áreas de distribución ausentes en el mapa de la UICN, sugiriendo que este necesita ser actualizado. Por lo tanto, se propone una nueva distribución de la zarigüeya de agua. Se demostró que las APs incluyeron áreas con altos valores de idoneidad de hábitat para *C. minimus*; lo que podría favorecer su protección a medio y largo plazo. Las modificaciones de las características fisicoquímicas del hábitat por la pérdida y fragmentación de los bosques pueden afectar considerablemente a las poblaciones de zarigüeyas de agua y reducir la diversidad local. La preservación de los ecosistemas fluviales y las áreas circundantes en su conjunto representa un paso esencial para la conservación de *C. minimus*.

Key words: conservation; ecological niche models; mammals; marsupials; species distribution models; water opossum.

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Introduction

The water opossum or Yapok, *Chironectes minimus* (Zimmerman 1780), is the only Neotropical semi-aquatic marsupial (Bressiani and Graipel 2008; Acosta and Azurduy 2009; Galliez *et al.* 2009). It belongs to a monotypic genus, which includes four subspecies (Stein and Patton 2007; Damasceno and Astúa 2016). The species is characterized by a silvery gray dorsal pelage with four black transverse patches connected by a narrow midline. Water opossums are adapted to semi-aquatic habitats, with several external morphological adaptations: 1) dense, short, and water-resistant pelage, 2) webbed hindfeet to swim, 3) impermeable pouch in females to keep the young dry, and 4) the ability to protect the male genitalia in the water with an incomplete pouch (Mondolfi and Medina 1957; Marshall 1978; Stein and Patton 2007; Voss and Jansa 2009).

Water opossums are widely distributed in the Neotropics (Figure 1), from southern Mexico to northeastern Argentina (Nowak 1999; Cuarón *et al.* 2008). This elusive and solitary species is mainly associated with river channels with stony substrates, clear and fast-running waters, and preserved riparian vegetation (Prieto-Torres *et al.* 2008; Galliez *et al.* 2009; Galliez and Fernandez 2012; Ardente *et al.* 2013). However, it is a species whose large-scale population dynamics (*e. g.*, distribution and abundance) cannot be studied using traditional methods, because they are not usually captured in common live traps for small mammals (Bressiani and Graipel 2008; Prieto-Torres *et al.* 2011). In fact, although there are some studies on the behavior, demographic patterns, habitat selection, morpho-physiological and genetic analyses of water opossums (*e. g.*, Nogueira *et al.* 2004; Galliez *et al.* 2009; Palmeirim *et al.* 2014; Fernandez *et al.* 2015), most of them are not-specific, faunistic surveys (*e. g.*, Handley 1976; Oliveira *et al.* 2007; Prieto-Torres *et al.* 2008; 2011; Ardente *et al.* 2013).

The water opossum is listed as Least Concern (Cuarón *et al.* 2008) on the International Union for Conservation of Nature (IUCN) red list due to its wide distribution, presumably large population, and its presence in several protected areas or "PAs" (Oliveira *et al.* 2007; Galliez *et al.* 2009; Ardente *et al.* 2013). However, recent work suggests a decreasing population trend in Brazil, where the species is considered threatened in at least five states due to habitat loss and degradation (Ardente *et al.* 2013; Palmeirim *et al.* 2014; Fernandez *et al.* 2015). Thus, there is an increasing need to define its actual distribution and ecological requirements (Cuarón *et al.* 2008).

The minimum convex polygon method is frequently used to estimate species' distribution (IUCN 2001, 2015), but ignores the species' ecological constraints (Brown *et al.* 1996; Mota-Vargas and Rojas-Soto 2012; Peterson *et al.* 2016). Thus, techniques like species distribution models (SDMs) have been developed to predict the potential distribution of a species, identifying the suitable areas and the most important variables for the persistence of the species (Peterson 2001; Soberón and Peterson 2005; Stohlgren *et al.* 2011). These models are widely used in ecology, evolution, conservation, and management (*e. g.*, Soberón and Peterson 2005; Stohlgren *et al.* 2011; Tôrres *et al.* 2012; Ortega-Andrade *et al.* 2013; 2015).

Due to the lack of information on the distribution of *C. minimus*, in this study we modeled its potential distribution on a continental scale, following part of the methodology of Rheingantz *et al.* (2014) employed for another semi-aquatic mammal. We determined the effect of habitat loss in the extents of habitat suitability for species and evaluated if the current PAs systems actually harbor the most suitable environmental conditions for its distribution. Finally, we identified gaps in the potential distribution where future survey efforts and ecological studies should be focused.

Material and Methods

Collection of historical records. We compiled a database of occurrences from three sources: 1) occurrences available in on-line databases (*i. e.*, Global Biodiversity Information Facility database [GBIF] and Mammal Networked Information System [MaNIS]); 2) specimens verified from biological collections (see Appendix 1); and 3) location records obtained from fieldwork and published literature (*e. g.*, Handley 1976; Mares *et al.* 1986; Oliveira *et al.* 2007; Bressiani and Graipel 2008; Prieto-Torres *et al.* 2008; 2011; Acosta and Azurduy 2009; Ardente *et al.* 2013; Brandão *et al.* 2014; Damasceno and Astúa 2016). We verified each locality using Google Earth and MapLink (www.maplink.com), correcting imprecise coordinates and/or eliminating duplicates when necessary. Geographic coordinates were provided in decimal degrees, based on the WGS 84 datum. We obtained data from sixteen countries between 1925 and 2015 describing the historical presence of the species (Figure 1, Appendix 1). In addition, we considered the largest water opossum home range (~3 km^2; Galliez *et al.* 2009) as a buffer area between records and cleared the points located close together, thereby reducing sampling bias (*e. g.*, Ortega-Andrade *et al.* 2015). We performed the SDM (see below) using 165 unique localities records (Appendix 1).

Species Distribution Model and validation. We modeled the potential water opossum distribution with MaxEnt version 3.3.3k (Peterson 2001; Elith *et al.* 2006; Phillips *et al.* 2006), which uses the principle of maximum entropy to calculate the most likely distribution of the focal species in function of occurrence localities and environmental variables. We used the 19 climatic variables of WorldClim 1.4 (Hijmans *et al.* 2005) and three topographic variables (*i. e.*, Digital Elevation Model [DEM], Slope and Aspect) from the Hydro 1K project (USGS 2001); with 30" of resolution (~1 km^2 cell size). Despite that topographic variables are not commonly used in SDM studies, they were included because numerous examples (*e. g.*, Mota-Vargas *et al.* 2013; Cauwer *et al.* 2014; Rheingantz *et al.* 2014; Kübler *et al.* 2016) show

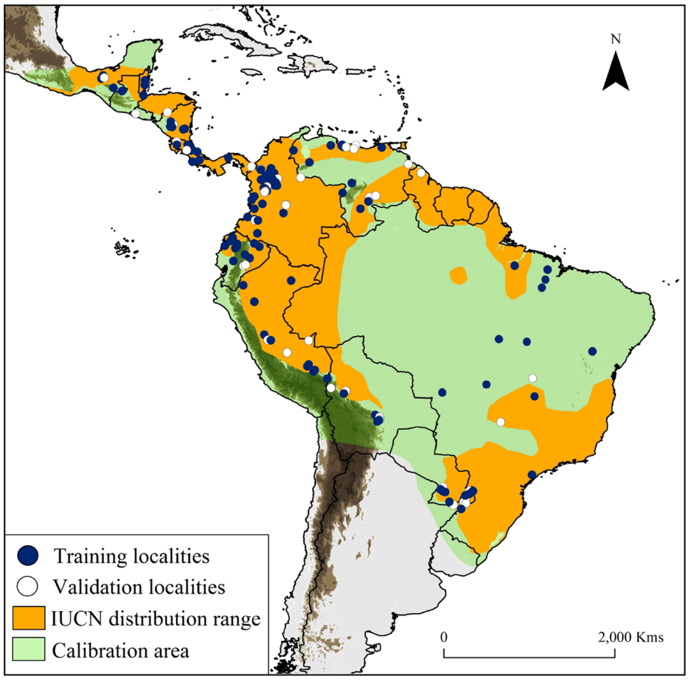

Figure 1. Map showing water opossum (*Chironectes minimus*) unique records ($n = 165$), overlaid with the IUCN distribution and model calibration area (light and dark green colors). Training localities (blue dots) and validation localities (white dots) were used to generate and validate the models. Dark brown color represents area with altitudes of up 1,200 m.

that these variables can be used as proxies for variables (*e. g.*, micro-climate or edaphic conditions) that are correlated with physiological requirements of species.

The potential distribution model was generated using the 75 % ($n = 124$) of the locality records and 25 % ($n = 41$) for internal evaluation. In this sense, the algorithm used localities of species records and environmental conditions to perform a certain number of iterations (1,000 in this case) before reaching a convergence limit. This algorithm for the logistic output produces a map of habitat suitability ranging from 0 (unsuitable) to 1 (perfectly adequate; Phillips *et al.* 2006; Phillips and Dubik 2008). We ran ten cross-validate replicates to calculate confidence intervals, and the best model was selected based on the performance of area under the curve or "AUC" (Elith *et al.* 2006; 2011). Then, we converted the obtained logistic values of suitability rating into a binary presence-absence map, based on two established threshold values: the "Fixed cumulative value 10" (FCV10) and the "5 percentile training presence" (5PTP; see Pearson *et al.* 2006; Liu *et al.* 2013).

It is important to note that there is no rule to set these thresholds because its selection depends on the data used or the objective of the map, and will vary from species to species. In our case, we used the FCV10 as we wanted a threshold that minimizes the commission errors in our final binary maps (Liu *et al.* 2013), and we used the 5PTP to identify pixels with the highest suitability values, rejecting the lowest (5 %) suitability values of training records. The 5PTP model is a sub-conjunct in the geographic and ecological space of FCV10 model.

Given that ENMs do not address the historical aspects relating to species distribution (*e. g.,* accessibility or "M" sensu BAM diagram [Soberón and Peterson 2005]), we used a geographical clip (Figure 1; Appendix 2) based on the intersection of Terrestrial Ecoregions (Olson *et al.* 2001) and the Biogeographical Provinces of the Neotropic (Morrone 2014) to create an area for model calibration (see Anderson and Raza 2010; Barve *et al.* 2011; Rodda *et al.* 2011). We selected the uncorrelated ($r < 0.8$) and most relevant variables using the Jackknife test of MaxEnt (Royle *et al.* 2012). These steps allowed us to reduce over-fitting of the generated suitability models (Peterson *et al.* 2011). Finally, we evaluated the performance of the selected MaxEnt model with the Partial-ROC (Receiver Operating Characteristic) curves test (Lobo *et al.* 2008). This criterion was used to solve problems associated with an inappropriate weighting of the omission and commission errors during the AUC analysis (see Lobo *et al.* 2008; Peterson *et al.* 2008).

Spatial analysis of the water opossum' distribution in the Neotropics. We performed three distinct spatial analyses to assess the conservation issues related to the species' potential distribution: 1) to evaluate the extent of habitat loss on the model; 2) to determine if the PAs system contains the highly suitable areas for the species; and 3) to identify the gaps where future survey efforts should be focused. The spatial analyses and map algebra were carried out with ArcMap 10.2.2 software (ESRI 2011), with a grid cell resolution of 30", corresponding to ~1 km^2 in each raster.

First, we used a vegetation land cover map (Hansen *et al.* 2013) considering only two categories "*natural forest*" and "*perturbed areas,*" to determine the effect of habitat loss in the obtained models. Perturbed areas included urban areas, deforested areas, farm lands, and pastures for cattle ranching (Hansen *et al.* 2013). The PAs extents were downloaded from ProtectedPlanet.net (IUCN and UNEP-WCMC 2012). To assess if the current PA system harbors the most suitable environmental conditions for the species we performed a Kolmogorov-Smirnov (KS) test in R (R-Core-Team 2012) comparing the suitability values within and outside PAs (Rheingantz *et al.* 2014). The results obtained from the deforestation and PAs analysis were compared with the IUCN species distribution.

Finally, to identify gaps in the potential distribution where future survey efforts and conservation initiatives should be focused, we followed the proposal by Rheingantz *et al.* (2014). In the analysis, we multiplied the suitability value of a pixel by its distance to the nearest occurrence and river, based on the assumption that ecological similarities decrease with distance among these factors. Then, we divided the index by its highest value to obtain a scale from 0 to 1. We therefore assumed that areas with high suitability values, located far from previous studies and near to rivers (the focal species is associated with water) were more likely to be in different ecosystems or to have dissimilar environmental characteristics (Rheingantz *et al.* 2014). Thus, studying water opossum in those areas could explain whether the species uses different habitats than previously reported.

Results

Historical records and SDM for water opossum. Our study includes new information on the distribution of water opossum, including a total of 292 occurrences in the 16 countries that encompass the recognized distribution ranges according to the IUCN (Figure 1; Marshall 1978; Cuarón *et al.* 2008). Including also new potential areas of distribution in Mexico, El Salvador, Nicaragua, Costa Rica, Colombia, Venezuela, Brazil, Bolivia, Peru and Ecuador.

The variables used and their percentage contribution to the model are shown in the Table 1 and are consistent with results found by previous studies on Neotropical mammals (*e. g.*, DeMatteo and Loiselle 2008; Tôrres *et al.* 2012; Rheingantz *et al.* 2014). We generated a model for water opossum distribution with a high Roc-Partial result (1.23 ± 0.09; $P < 0.05$). For the threshold FCV10 (0.160) and 5PTP (0.190), based on 41 test occurrences, we obtained 7 % ($n = 3$) and 5 % ($n = 2$) rates of omission, respectively. Performance assessment showed that models were statistically acceptable to describe the ecological niche and distribution of this species.

The water opossum potential distribution according to the FCV10 threshold totaled ~9,238,000 km^2, representing 45.9 % of the total areas used in the calibration of the model (Figure 2a). This FCV10 model is ~23 % wider than IUCN's historical distribution map (with ~72.29 % overlap). Considering the 5PTP threshold, we obtained ~7,787,700 km^2 of potential distribution for the species, representing 38.3 % of calibration areas and is ~4 % greater than the IUCN's distribution map (with ~65 % overlap). The 5PTP's potential species distribution was smaller in almost all countries compared to the IUCN map (Figure 2a). Comparing the IUCN map and FCV10 threshold, the only regions absent in the latter were predominantly areas in Mexico, savanna in Colombia and Venezuela, amazon in Peru, and the southeast of Brazil.

Table 1. Summary of the selected environmental variables with relative contributions (%) to the model of *Chironectes minimus* using MaxEnt 3.3.3k

Abbreviation	Environmental Variable	Percentage contribution
Bio 18	Precipitation of Warmest Quarter	24.7
Bio 11	Mean Temperature of Coldest Quarter	17.2
DEM	Digital Elevation Model	16.5
Bio 07	Temperature Annual Range (BIO5-BIO6)	13.1
Bio 14	Precipitation of Driest Month	12.9
Bio 04	Temperature Seasonality (standard deviation *100)	7.8
Bio 15	Precipitation Seasonality (Coefficient of Variation)	5.4
Bio 01	Annual Mean Temperature	1.4
Bio 03	Isothermality (BIO2/BIO7) (* 100)	0.9

Deforestation impact, protected areas and future areas of study. The predicted and remnant areas of the potential distribution model for the water opossum according the threshold values are detailed in Tables 2 and 3. Deforestation reduced the area of suitable water opossum habitat by ~40 % (38.07 – 43.39 %). Loss in area was most pronounced in the Mesoamerican region (from Mexico to Panama), the lowlands of the Andes region (from Peru to Colombia and northwest Venezuela), and the southeast region of South America (Paraguay, Argentina and Brazil; Figure 2b). Furthermore, only ~18 % of the potential water opossum distribution corresponds to natural forest within PAs (Figure 2b-c; Tables 2-3).

The current PAs system in the Neotropics represents ~20 % of species' potential distribution (Figure 2c). Areas inside PAs showed significantly higher suitability values (0.351 ± 0.276; KS, $P < 0.001$) than areas outside them (0.319 ± 0.238). The highest values were obtained in the Amazon areas (including Bolivia, Peru, Ecuador, Colombia, Venezuela, and Brazil; Figure 2), followed by the Guiana shield and the coast of the Atlantic forest. The index of suitable value multiplied by its distance to nearest occurrence and river identified gaps (index > 0.5) within the distribution that need attention during future surveys, such as the frontier between Venezuela and Guyana (mainly in the Guiana Highlands),

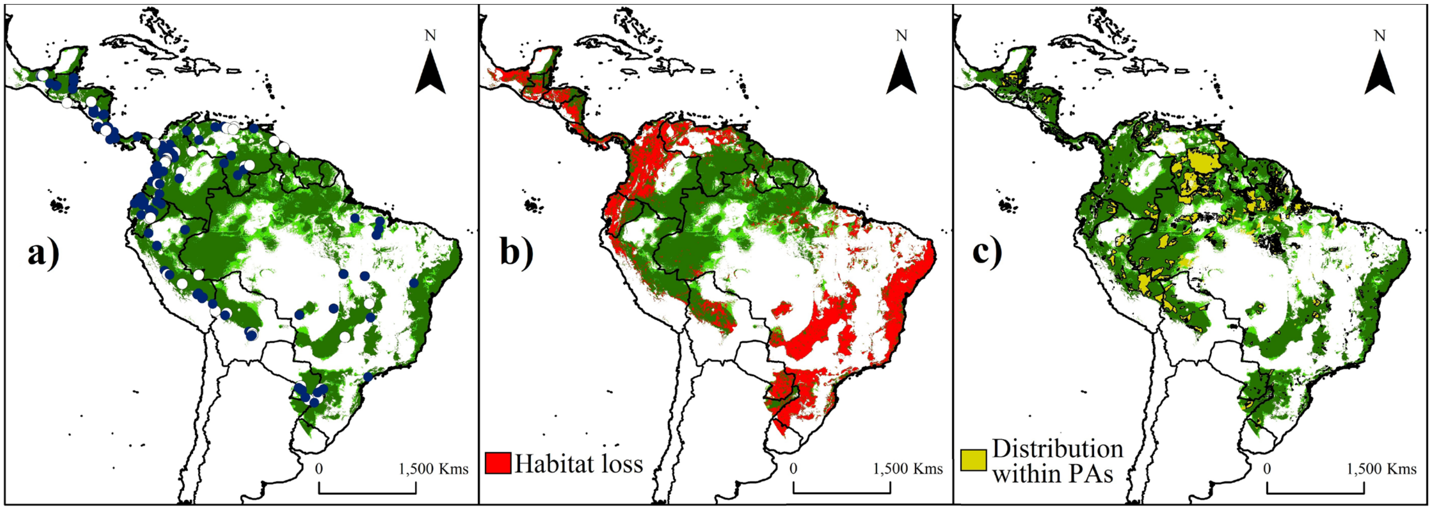

Figure 2. Potential suitability areas (a), remnant of natural forests (b) and predicted Protected Areas (c) throughout the distribution range of water opossum (*Chironectes minimus*). Training localities (blue dots) and validation localities (white dots) used to generate models are shown in (a). Potential distribution model (in a-c) is shown with the threshold value of Fixed cumulative value 10 (FCV10, light green) and 5 Percentile training presence (5PTP; dark green). Note an important reduction (~40 %, in greens [natural forests areas]) in the potential distribution model through the Mesoamerican region (from Mexico to Panama), the lowlands of the Andes region (from Peru to Colombia and northwest Venezuela), and the southeast of South America (Paraguay, Argentina and Brazil). The perturbed areas were calculated according the deforestation index map proposed by Hansen *et al.* (2013). Dark brown color represents area with altitudes of up 1,200 m.

the Amazonian region (including Colombia and the northwestern Brazil), and central-eastern Brazil (Figure 3a).

Discussion

Potential distribution range of water opossum and habitat loss effects. Our results confirm that the climate variables used in this study (Table 1) can be employed to model the potential distribution of terrestrial species associated with aquatic environments, as previously demonstrated for the otters *Lontra longicaudis* and *Pteronura brasiliensis* (Cianfrani *et al.* 2011; Rheingantz *et al.* 2014). Mean precipitation of the driest quarter and the warmest quarter were the most important variables for the water opossum's distribution in the Neotropics (Table 1), as was found for the Neotropical otter (Rheingantz *et al.* 2014). Altitude was another important variable which represents a gradient correlating directly with factors such as micro-climate or edaphic conditions (Mota-Vargas *et al.* 2013; Kübler *et al.* 2016). Although water opossum occurred between zero to ~3,000 m (including the Andes region), most of the occurrences were between zero to 500 m (n = 81) and zero to 2,000 m (n = 157; Appendix 1). This spatial distribution of species' occurrences suggests that the species has an altitudinal limit (due to climatic gradients by elevation) possibly associated with their physiological requirements. This last idea agrees with studies for the Neotropical otter, which is described as abundant at medium elevations (Lariviére 1999; Rheingantz *et al.* 2014).

It is important to observe that suitability model predicted for *C. minimus* was severely reduced due to habitat loss (~36 to 43 %); even inside of PAs (Tables 2 and 3). The habitat loss is associated with areas highly threatened by human activities (*e. g.*, expansion of cattle ranching and urban settlements), which remove vegetation cover thereby reducing water opossum's habitat (Prieto-Torres *et al.* 2008; 2011; Galliez *et al.* 2009). Similarly, previous studies report that the expansion of the agricultural frontier is a critical factor affecting biodiversity in the Neotropics (Shukla *et al.* 1990; Lees and Peres 2006; Bressiani and Graipel 2008; Ribeiro *et al.* 2009; Ortega-Andrade *et al.* 2015; Prieto-Torres *et al.* 2016). These conditions push the species to the edge of its distribution and increase fragmentation of predicted suitable areas, which could promote decreasing trends in populations (Ardente *et al.* 2013; Palmeirim *et al.* 2014; Fernandez *et al.* 2015). Thus, future conservation efforts should concentrate on reducing habitat loss and restoring identified natural habitats, especially considering

Table 2. Potential distribution models for *Chironectes minimus*, with percentage loss of potential distribution areas by effect of habitat loss and the percentage of potential distribution within Protected Areas (PAs) in the Neotropics

Model	**Area (~km²)**	**%**
Extent of occurrence (minimum convex polygon)	**13,878,685**	**-**
IUCN distribution map	**7,501,124**	**100.00**
Area of the model within natural forests	4,246,209	56.61
Area of the model within PAs	1,126,857	15.02
Remnant model within PAs and natural forests	978,935	13.05
Species Distribution Model (FCV10)	**9,238,072**	**100.00**
Area of the model within natural forests	5,721,975	61.93
Area of the model within PAs	1,840,152	19.91
Remnant model within PAs and natural forests	1,644,964	17.81
Species Distribution Model (5PTP)	**7,787,759**	**100.00**
Area of the model within natural forests	4,726,649	60.69
Area of the model within PAs	1,547,148	19.87
Remnant model within PAs and natural forests	1,381,237	17.74

Table 3. Potential distribution of water opossum (*Chironectes minimus*) estimated by country. Potential distributions are in km² and percentages for each country, considering the deforestation effects and PAs, based in the two threshold values used in this study.

Country	FCV10			5PTP		
	Modeled Area (%)	Intact Areas (%)	Intact areas in PAs (%)	Modeled Area (%)	Intact Areas (%)	Intact areas in PAs (%)
Brazil	4,555,022 (49.31)	2,642,873 (28.61)	774,870 (8.39)	3,604,227 (46.28)	1,980,563 (25.43)	569,951 (7.32)
Colombia	1,042,751 (11.28)	569,586 (6.16)	58,024 (0.63)	953,324 (12.24)	523,079 (6.72)	56,206 (0.72)
Venezuela	831,292 (8.99)	590,105 (6.38)	383,794 (4.15)	741,999 (9.53)	549,763 (7.06)	366,851 (4.71)
Peru	744,347 (8.06)	653,448 (7.07)	136,241 (1.47)	651,262 (8.36)	567,470 (7.28)	124,656 (1.60)
Bolivia	383,783 (4.15)	270,766 (2.93)	77,297 (0.84)	321,390 (4.12)	220,288 (2.83)	66,861 (0.86)
Ecuador	248,756 (2.69)	117,683 (1.27)	31,479 (0.34)	239,138 (3.07)	113,795 (1.46)	30,714 (0.39)
Guyana	211,967(2.29)	201,563 (2.18)	19,638 (0.21)	172,955 (2.22)	163,320 (2.09)	17,797 (0.23)
Mexico	206,711 (2.24)	91,310 (0.98)	20,817 (0.22)	183,380 (2.35)	83,238 (1.06)	17,907 (0.23)
Suriname	155,010 (1.68)	150,754 (1.63)	16,497 (0.18)	126,002 (1.62)	122,293 (1.57)	10,965 (0.14)
Paraguay	154,595 (1.67)	41,180 (0.44)	2,809 (0.03)	140,937 (1.81)	36,895 (0.47)	2,803 (0.04)
Nicaragua	114,767 (1.24)	64,038 (0.69)	12,556 (0.14)	112,145 (1.44)	63,173 (0.81)	12,546 (0.16)
Honduras	112,529 (1.22)	44,931 (0.48)	6,798 (0.07)	108,749 (1.39)	44,418 (0.57)	6,650 (0.08)
Guatemala	108,169 (1.17)	53,141 (0.57)	22,504 (0.24)	103,319 (1.33)	50,843 (0.65)	21,417 (0.27)
Argentina	102,436 (1.11)	65,902 (0.71)	17,084 (0.18)	90,662 (1.16)	58,660 (0.75)	16,630 (0.21)
French Guiana	79,829 (0.86)	79,018 (0.85)	38,863 (0.42)	67,426 (0.86)	66,917 (0.86)	33,904 (0.43)
Panama	73,839 (0.79)	38,500 (0.41)	8,544 (0.09)	67,499 (0.87)	36,004 (0.46)	8,284 (0.11)
Costa Rica	49,732 (0.54)	23,037 (0.25)	8,452 (0.09)	47,761 (0.61)	22,519 (0.29)	8,398 (0.11)
Uruguay	30,447 (0.33)	1,642 (0.017)	207 (0.002)	24,400 (0.31)	1,063 (0.013)	207 (0.002)
Belize	24,201 (0.26)	19,666 (0.21)	8,248 (0.09)	24,200 (0.31)	19,666 (0.25)	8,248 (0.11)
Trinidad and Tobago	4,909 (0.05)	2,402 (0.02)	228 (0.002)	4,785 (0.06)	2,385 (0.03)	228 (0.003)
El Salvador	2,980 (0.03)	430 (0.004)	14 (0.0001)	2,199 (0.03)	297 (0.003)	14 (0.0002)
Total	9,238,072 (100)	5,721,975 (61.93)	1,644,964 (17.81)	7,787,759 (100)	4,726,649 (60.69)	1,381,237 (17.74)

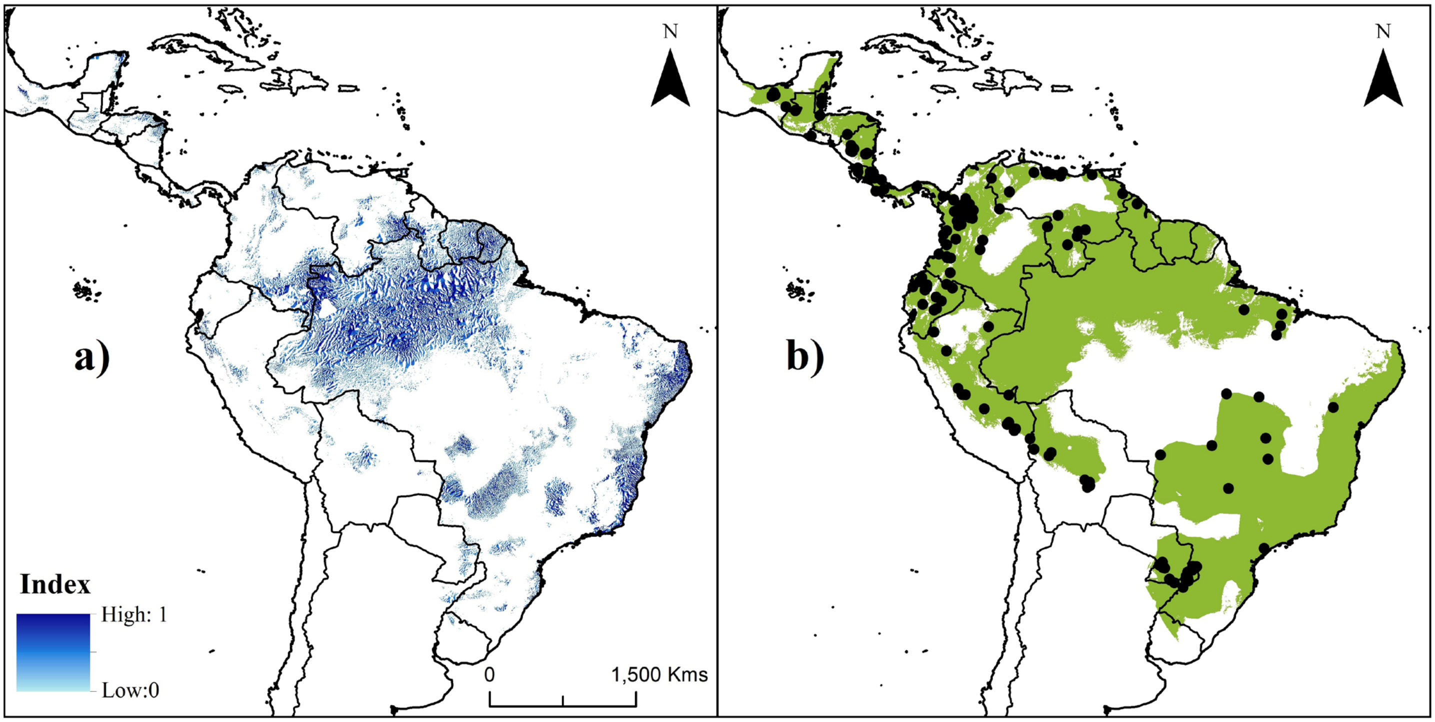

Figure 3. Maps showing priority areas for future studies (a) and the current proposed Neotropical distribution for water opossum, *Chironectes minimus* (b). Color palette in A corresponds to areas defined as priorities (from zero [light blue] to 1 [dark blue]) for future ecological studies and surveys for water opossum based on suitable value multiplied by its distance to nearest occurrence and water source (*i. e.*, rivers). Black points in B represent the unique historical records (*n* = 165) of species.

the restricted home range and unknown population size of the water opossum (Galliez *et al.* 2009; IUCN 2015).

Protected areas and gaps in areas for future studies. We demonstrated that PAs included areas with high habitat suitability values for *C. minimus*, which could protect it in the medium and long-term. Furthermore, our analysis supports the idea that SDMs can be used to evaluate whether PAs are really conserving species within them. Such studies allow us to identify potential areas of conservation priority for the species to achieve more realistic conservation goals in their present and future distributions (*e. g.*, Hannah *et al.* 2005, 2007; Dudley and Parish 2006; Lessmann *et al.* 2014).

The PAs system is especially important for the water opossum in the Amazon region, due to the low rate of deforestation of the remaining forest (Numata and Cochrane 2012). The persistence of PAs in this region will play a role in preventing environmental degradation in the central and south portion of the *C. minimus.* Meanwhile, populations along the Mesoamerican region (from Mexico to Panama), the western Andes (Ecuador, Colombia and Venezuela), and southeastern Brazil are more vulnerable to the effects of forest loss due to fewer PAs (Figure 2b-c). However, it is important to conserve not only PAs but also surrounding areas through forest restoration and sustainable development programs which include local people (Laurance *et al.* 2012; Rheingantz *et al.* 2014; Prieto-Torres *et al.* 2016). Additionally, studies under future climate change scenarios are needed to consider the role of the PAs system in protecting the species' habitat (*e. g.*, Hannah *et al.* 2005, 2007).

We suggest that future studies (*e. g.*, inventories, population monitoring, abundance patterns, and habitat evaluations) need to be focused on the Guiana Highlands, the Amazonian region (including Colombia and northwestern Brazil), and central-eastern Brazil (Figure 3a). Working in unexplored areas frequently provides new information on a species in the form of expansion of known distribution ranges and new records of unidentified specimens (Soberón and Peterson 2005; Mota-Vargas and Rojas-Soto 2012; Tôrres *et al.* 2012; Ortega-Andrade *et al.* 2013; Rheingantz *et al.* 2014). Thus, our results aid in identifying unexplored areas where future survey efforts should be focused in order to accelerate the discovery of new populations of water opossum.

Implications for C. minimus' conservation. Our results showed areas absent from the IUCN's distribution map, indicating that this needs to be updated. Thus, we proposed a new tentative extent of the water opossum distribution (Figure 3b) which integrated the information obtained in the SDMs, the IUCN historical range, and the newly reported localities. This proposal includes new distribution areas for Mexico, Venezuela, Suriname, Guyana, Ecuador, Peru, Bolivia, and Argentina-Brazil; and at the same time reduces or eliminates areas in northern Brazil and the savanna in Colombia and Venezuela.

Clearly, the limited knowledge about the habitat requirements, distribution range, and information obtained directly from field activities, could explain why the water opossum is currently listed as Least Concern. At the continental level, there are mammals which have been reassigned because threat categories have been based more on anecdotal criteria than on field surveys and population assessments (*e. g.*, Rheingantz and Trinca 2015). Apart from the problems associated with the lack of data for its categorization (Cuarón *et al*. 2008), our results in combination with the time elapsed since the first assignment justifies the need for a reassessment of the category, such as was done for *L. longicaudis,* whose threat category was up-listed from "Least Concern" to "Near Threatened" (Rheingantz and Trinca 2015).

On the other hand, it is important to note that our models showed that there is a disjunction in the distribution of water opossum, observed in the population of southeastern of Brazil (*C. m. paraguanensis* [Marshall 1978; Damasceno and Astúa 2016]). This disjunct distribution could represent ecological niche differences among subspecies, which could simultaneously affect the performance of our models (see Rojas-Soto et al. 2008; 2009; Mota-Vargas and Rojas-Soto 2016). It is reasonable to suggest that there are climatic and geographic factors acting (or that acted) as geographic barriers that contribute to the isolation of some populations (see Damasceno and Astúa 2016). Similar cases were documented for wide-ranging Didelphidae species: the genus *Didelphis,* the Black-eared opossums (*D. marsupialis*; Cerqueira 1985) and White-eared opossums (*D. albiventris;* Cerqueira and Lemos 2000), and the Lutrine Opossum, *Lutreolina crassicaudata* (Martínez-Lanfranco *et al*. 2014). From this perspective, our study suggests that the current taxonomic status of these populations needs to be adequately assessed using tools that could reveal their distinctiveness (Damasceno and Astúa 2016). Independently of the current taxonomic classification, a possible loss of one of these disjunct groups would be irreversible.

Although we only examined the environmental distribution of *C. minimus,* our results forecast a rapid decline in the potential distribution, principally attributed to a decrease in occupancy in areas affected by habitat loss and fragmentation (*e. g.* Prieto-Torres *et al*. 2011; Ardente *et al*. 2013; IUCN 2015; Palmeirim *et al.* 2014; Fernandez *et al.* 2015). Modifications to the physicochemical characteristics (*e. g.*, water conditions) of the habitat due to the aforementioned processes can considerably affect water opossum populations and reduce local diversity, as found for other aquatic mammals (*e.g.,* Bowyer *et al.* 1995; Rheingantz *et al*. 2014). Thus, considering physicochemical water conditions, the habitat structures to persist, and the habitat requirements to establish a viable population, will be crucial for the conservation of *C. minimus* and the preservation of river ecosystems as a whole.

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Appendix 1. Historical records of Chironectes minimus used to generate the Species Distribution Model. Geographic coordinates are provided in decimal degrees, based on the WGS 84 datum. Source: GBIF = Global Biodiversity Information Facility database; MaNIS = Mammal Networked Information System; MACN = Museo Argentino de Ciencias Naturales; USNM=Smithsonian Institution National Museum of Natural History; FMNH = Field Museum Natural History; AMNH = American Museum of Natural History; MHNB = Museo de Historia Natural de Bolivia; MSB = The University of New Mexico's Museum of Southwestern Biology; MHNG = Muséum d'histoire naturelle de la Ville de Genève; MVZ = Museum of Vertebrate Zoology; Corantioquia= Corporación Regional Autónoma del Centro de Antioquia; GMUA = Grupo de Mastozoología de la Universidad de Antioquia; ICN = Instituto de Ciencias Naturales de la Universidad Nacional, Colombia; LACM = Natural History Museum of Los Angeles County; MECN = Museo Ecuatoriano de Ciencias Naturales; ROM = Royal Ontario Museum; KU = Kansas University; UMMZ = Museum of Zoology at University of Michigan; LSUMZ = Louisiana Museum of Natural History; MSU = Michigan State University; QCAZ = Museo de Zoología de la Pontificia Universidad Católica del Ecuador; YPM =Yale Peabody Museum of Natural History; IBUNAM = Instituto de Biología de la Universidad Autónoma de México; MUSA = Museo de Historia Natural de la Universidad San Agustín de Arequipa; EBRG = Estación Biológica Rancho Grande, Venezuela; MHNLS = Museo de Historia Natural Fundación La Salle; ESNM = Earth Science Museum.

N°	Country	State/Province	Longitud	Latitud	Elevation (m)	Source
1	Argentina	Misiones	-54.2540	-25.9400	223	MACN 13547, 13548
2	Argentina	Misiones	-53.8957	-25.9817	545	MACN 13053
3	Argentina	Misiones	-54.2707	-26.2817	298	GBIF/MaNIS
4	Argentina	Misiones	-54.8540	-26.8233	203	MACN 13175, 13210
5	Argentina	Misiones	-54.6874	-27.0233	538	MACN 24435
6	Argentina	Misiones	-54.8707	-27.1400	419	GBIF/MaNIS
7	Argentina	Misiones	-54.6540	-27.2650	352	GBIF/MaNIS
8	Argentina	Misiones	-55.9540	-27.4483	130	GBIF/MaNIS
9	Argentina	Misiones	-55.1374	-27.8733	102	GBIF/MaNIS
10	Argentina	Misiones	-54.7124	-26.4650	140	GBIF/MaNIS
11	Belize	Stann Creek	-88.5289	16.7765	150	USNM 583002
12	Belize	Toledo	-88.5039	17.2515	42	FMNH 151051
13	Bolivia	La Paz	-67.3123	-15.4400	1,000	AMNH 264571, 264572, 264573
14	Bolivia	La Paz	-67.5207	-15.7317	985	MHNB 2294; MSB 68329, 68330, 235667, 235796, 235827, 235892, 235893
15	Bolivia	La Paz	-67.5123	-15.7317	1,161	MSB 141635
16	Bolivia	La Paz	-68.8873	-15.1317	2,995	AMNH 34121
17	Bolivia	Santa Cruz	-64.2123	-17.9817	1,831	Literature (Acosta & Azurday 2009)
18	Bolivia	Santa Cruz	-63.7623	-18.1900	1,451	Literature (Acosta & Azurday 2009)
19	Bolivia	Santa Cruz	-63.7290	-18.4817	1,285	Literature (Acosta & Azurday 2009)
20	Bolivia	Santa Cruz	-63.8123	-18.5234	2,119	Literature (Acosta & Azurday 2009)
21	Bolivia	Santa Cruz	-63.9790	-18.6567	1,760	Literature (Acosta & Azurday 2009)
22	Brazil	Bahia	-41.2874	-11.2817	904	MHNG 510.062, 713.027
23	Brazil	Goiás	-47.5167	-14.1167	1,149	Literature (Brandão et al. 2014)
24	Brazil	Goiás	-50.9333	-18.7500	572	Literature (Brandão et al. 2014)
25	Brazil	Maranhao	-46.0207	-2.6651	98	Literature (Oliveira et al. 2007)
26	Brazil	Maranhao	-46.1541	-3.7484	79	Literature (Oliveira et al. 2007)
27	Brazil	Maranhao	-46.5041	-4.5984	126	Literature (Oliveira et al. 2007)
28	Brazil	Mato Grosso	-51.1250	-10.0194	309	Literature (Brandão et al. 2014)
29	Brazil	Mato Grosso	-52.4736	-14.7925	367	Literature (Brandão et al. 2014)
30	Brazil	Mato Grosso	-57.2167	-15.6500	447	Literature (Brandão et al. 2014)
31	Brazil	Minas Gerais	-47.3041	-16.0484	883	MVZ 197759
32	Brazil	Para	-49.5041	-2.2484	1	FMNH 48933, 50908
33	Brazil	Sao Paulo	-47.6707	-24.2817	152	FMNH 94292
34	Brazil	Tocantins	-48.1283	-10.2972	426	Literature (Brandão et al. 2014)
35	Colombia	Antioquia	-75.2040	7.9932	71	Corantioquia
36	Colombia	Antioquia	-75.3540	7.5765	130	Corantioquia
37	Colombia	Antioquia	-74.8706	7.5015	87	Corantioquia
38	Colombia	Antioquia	-75.7706	7.1765	1,294	Corantioquia
39	Colombia	Antioquia	-75.1540	7.0682	1,544	Corantioquia
40	Colombia	Antioquia	-74.5040	6.9182	386	GMUA
41	Colombia	Antioquia	-75.0706	6.9099	1,667	Corantioquia
42	Colombia	Antioquia	-76.2540	6.8099	1,443	GMUA

43	Colombia	Antioquia	-75.0206	6.6015	1,448	Corantioquia
44	Colombia	Antioquia	-75.8290	6.5599	558	Corantioquia
45	Colombia	Antioquia	-74.7873	6.5599	925	Corantioquia
46	Colombia	Antioquia	-74.7123	6.5015	735	Corantioquia
47	Colombia	Antioquia	-75.3290	6.4432	1,466	Corantioquia
48	Colombia	Antioquia	-74.7706	6.4182	678	Corantioquia
49	Colombia	Antioquia	-74.8456	6.2265	854	GMUA
50	Colombia	Antioquia	-74.5790	6.1765	116	Corantioquia
51	Colombia	Antioquia	-75.6373	6.0932	1,921	Corantioquia
52	Colombia	Antioquia	-75.9790	5.9265	1,586	Corantioquia
53	Colombia	Antioquia	-75.8290	5.8682	1,534	Corantioquia
54	Colombia	Antioquia	-75.7873	5.8015	1,753	Corantioquia
55	Colombia	Antioquia	-75.7206	5.6682	1,910	Corantioquia
56	Colombia	Antioquia	-75.8790	5.6599	1,432	Corantioquia
57	Colombia	Antioquia	-75.6290	5.6182	1,341	Corantioquia
58	Colombia	Antioquia	-75.8206	5.6015	1,882	Corantioquia
59	Colombia	Antioquia	-75.8873	5.5099	2,276	GMUA
60	Colombia	Boyaca	-72.0873	7.0349	399	FMNH 92298
61	Colombia	Cauca	-77.6873	2.8682	1	FMNH 90066
62	Colombia	Cauca	-76.9623	2.6349	2,539	FMNH 90087, 900888, 90089
63	Colombia	Cauca	-76.8873	2.5349	1,908	FMNH 89360
64	Colombia	Cauca	-76.5873	2.5016	1,756	LACM 27309
65	Colombia	Choco	-76.9540	5.0515	90	FMNH 90094, 90352
66	Colombia	Choco	-77.2540	4.6682	12	FMNH 90090, 90091, 90092, 90093
67	Colombia	Cordoba	-76.3040	7.9015	113	FMNH 69328, 69329
68	Colombia	Cordoba	-76.2873	7.8515	113	FMNH 69224
69	Colombia	Meta	-73.6206	4.1516	488	FMNH 57248
70	Colombia	Meta	-73.6290	4.1432	505	ICN 2885, 2926
71	Colombia	Meta	-73.8873	3.2849	341	FMNH 87932
72	Colombia	Putumayo	-76.6456	1.1516	835	ROM 46429, 46429
73	Colombia	Valle del Cauca	-76.1123	4.2516	839	MHNG 1078.095
74	Colombia	Valle del Cauca	-76.9540	3.7349	95	FMNH 85800, 86757, 86758, 86759
75	Costa Rica	Alajuela	-85.1623	10.8182	467	KU 158456
76	Costa Rica	Cartago	-83.6539	9.8765	595	KU 26928
77	Costa Rica	Cartago	-83.9289	9.8515	1,420	KU 29302
78	Costa Rica	Guanacaste	-85.1373	10.4682	48	UMMZ 115399
79	Costa Rica	Heredia	-84.0206	10.4682	64	UMMZ 111995
80	Costa Rica	Limon	-83.7289	10.3849	49	LSUMZ 12629
81	Costa Rica	Limon	-83.7706	10.2182	289	LACM 25689
82	Costa Rica	Limon	-82.9706	9.7349	64	LACM 26027
83	Costa Rica	Puntarenas	-83.4873	8.7015	99	LACM 28701
84	Costa Rica	San Jose	-84.0873	9.9349	1,131	MHNG 849.059
85	Ecuador	Bolivar	-79.1789	-1.7651	710	QCAZ 2470
86	Ecuador	Cotopaxi	-78.9706	-0.4234	1,451	QCAZ 709
87	Ecuador	Esmeraldas	-79.2456	0.7016	297	MSU 9265
88	Ecuador	Manabi	-79.4706	0.3349	177	MSU 8476, 8477, 8478, 8479, 8480
89	Ecuador	Manabi	-80.0706	-0.1484	152	FMNH 53527
90	Ecuador	Morona Santiago	-78.1206	-2.2766	1,532	MECN 93
91	Ecuador	Morona Santiago	-77.8873	-2.1568	1,054	MECN 3097
92	Ecuador	Napo	-76.9873	0.0849	462	MSU 11754
93	Ecuador	Napo	-77.9539	-1.0818	641	YPM 3416, 10863
94	Ecuador	Pastaza	-77.4456	-1.4568	382	QCAZ 9597
95	Ecuador	Pichincha	-78.7873	0.0432	2,165	MECN 2621

96	Ecuador	Pichincha	-78.8039	-0.0318	1,482	UMMZ 155684, 155685, 155686
97	Ecuador	Santo Domingo de los Tsáchilas	-78.8206	-0.2318	1,938	QCAZ 2585
98	Ecuador	Santo Domingo de los Tsáchilas	-78.7956	-0.2318	1,894	QCAZ 2068
99	Ecuador	Sucumbios	-76.4373	-0.2568	268	MHNG 1706.007
100	El Salvador	La Libertad	-89.4706	13.7682	455	MVZ 43258, 130323, 130324, 130325, 130326, 1303237
101	Guatemala	Izabal	-88.6622	15.6765	278	KU 140279, 140280
102	Guyana	Barima-Waini	-59.3874	7.5182	50	ROM 98855
103	Mexico	Chiapas	-93.0789	17.5265	98	KU 102259
104	Mexico	Chiapas	-93.0872	17.4432	156	IBUNAM 24623
105	Mexico	Chiapas	-91.8122	16.4765	2,188	LACM 18911
106	Mexico	Chiapas	-90.8956	16.1515	154	IBUNAM 21005
107	Mexico	Chiapas	-90.9206	16.1348	174	IBUNAM 22980
108	Mexico	Chiapas	-90.9289	16.1265	185	IBUNAM 22189
109	Mexico	Tabasco	-92.9039	17.7765	24	LSUMZ 8102, 8665, 8666; UMMZ 119456
110	Mexico	Tabasco	-92.9539	17.5848	49	LSUMZ 8098, 8099, 8100, 8101, 8103
111	Mexico	Tabasco	-92.9706	17.5682	65	LSUMZ 8099, 8100, 8101, 8103
112	Mexico	Tabasco	-92.9289	17.5682	64	IBUNAM 26122
113	Mexico	Tabasco	-92.8039	17.5515	49	IBUNAM 6960, 6961, 6962
114	Nicaragua	Boaco	-85.5206	12.6099	354	KU 110653, 110654, 110655, 114474
115	Nicaragua	Boaco	-85.8372	12.4099	147	KU 114475, 114476, 114477, 114478, 114479
116	Nicaragua	Boaco	-85.6539	12.3432	263	KU 114480, 114481, 114482, 114483, 114484, 114485, 114486, 114487, 114488, 114489, 114490
117	Nicaragua	Matagalpa	-85.7872	12.9182	1,004	KU 70194
118	Nicaragua	Nueva Segovia	-86.1122	13.9265	652	KU 110651, 110652
119	Nicaragua	Zelaya	-84.3123	12.1682	36	KU 114491
120	Nicaragua	Zelaya	-84.4623	12.1099	99	KU 110656
121	Panama	Chiriqui	-82.7456	8.8599	1,226	USNM 516614
122	Panama	Colón	-79.7039	9.1182	51	MSU 33109
123	Panama	Darien	-77.2873	8.1849	1,278	UMMZ 165354
124	Paraguay	Cordilleras	-57.0540	-25.5483	307	MVZ 144314
125	Paraguay	Itapua	-56.3874	-27.1150	88	UMMZ 126289
126	Paraguay	Paraguari	-57.3207	-25.8067	74	UMMZ 124681
127	Paraguay	Paraguari	-57.0540	-26.0150	108	UMMZ 134022, 134023, 134024, 134025, 134559, 134560
128	Paraguay	Paraguari	-56.8374	-26.0983	92	MHNG 1624
129	Peru	Amazonas	-78.1289	-4.3151	724	MVZ 153307
130	Peru	Cuzco	-73.4956	-11.3901	931	MUSA 8620, 8621
131	Peru	Cuzco	-70.5873	-13.2484	493	FMNH 75092
132	Peru	Cuzco	-70.6373	-13.2650	569	FMNH 75090, 75091
133	Peru	Cuzco	-70.7206	-13.3984	2,846	FMNH 68335, 75093
134	Peru	Huanuco	-75.9206	-9.5234	979	MUSA 13444, 13457
135	Peru	Loreto	-73.0873	-3.8317	106	FMNH 106721
136	Peru	Loreto	-71.2206	-10.1317	265	LSUMZ 9263, 10003, 10004, 10005, 14842, 14843
137	Peru	Madre de Dios	-71.2206	-12.6650	769	FMNH 122188
138	Peru	Madre de Dios	-71.3873	-12.8484	1,002	MVZ 166507
139	Peru	Pasco	-75.5373	-10.0651	784	FMNH 24791
140	Peru	Pasco	-75.2206	-10.1067	299	MUSA 10222
141	Peru	Puno	-69.2540	-14.1567	2,959	FMNH 79921
142	Peru	San Martín	-76.9706	-6.0484	732	FMNH 19349
143	Peru	San Martín	-76.9706	-6.0567	732	FMNH 19350
144	Venezuela	Amazonas	-67.6540	5.4015	153	USNM 406972
145	Venezuela	Amazonas	-64.9207	4.5182	1,183	EBRG 17818
146	Venezuela	Amazonas	-65.7873	3.7349	348	MHNLS 7584

147	Venezuela	Aragua	-67.6957	10.4849	167	EBRG 1683, 1684, 1685, 1686, 1687, 1688, 2370, 2371, 16959
148	Venezuela	Aragua	-67.7707	10.4015	270	USNM 517235, 517237
149	Venezuela	Aragua	-67.6790	10.4015	1,167	EBRG 16899
150	Venezuela	Aragua	-67.6873	10.3515	972	UMMZ 110966
151	Venezuela	Aragua	-67.6290	10.3182	647	USNM 517241
152	Venezuela	Aragua	-67.6290	10.3015	611	EBRG 142
153	Venezuela	Aragua	-67.6040	10.2765	715	ESNM 517236, 517238, 517239, 517240
154	Venezuela	Aragua	-67.2707	10.2432	612	MHNLS 580, 581, 582
155	Venezuela	Bolivar	-66.6790	6.4432	852	EBRG 15944
156	Venezuela	Bolivar	-64.8207	4.9765	923	MHNLS 875
157	Venezuela	Bolivar	-64.1558	5.1150	378	MHNLS 12031
158	Venezuela	Delta Amacuro	-60.7290	8.4432	1	MHNLS 10596, 10807
159	Venezuela	Merida	-71.1540	8.6265	1,780	EBRG 4125, 4126
160	Venezuela	Merida	-71.1540	8.6182	1,780	USNM 385097
161	Venezuela	Miranda	-66.2790	10.4265	167	MHNLS 3685, 3686, 3687
162	Venezuela	Miranda	-66.4540	10.0599	550	MHNLS 1144
163	Venezuela	Monagas	-63.5290	10.2015	1197	USNM 406985
164	Venezuela	Yaracuy	-68.9040	10.4182	682	USNM 418562
165	Venezuela	Zulia	-72.8456	9.8849	616	Literature (Prieto-Torres et al., 2008, 2011)