

Using Species Distribution Modeling to Assess Factors that Determine the Distribution of Two Parapatric Howlers (*Alouatta* spp.) in South America

Ingrid Holzmans · Iliaria Agostini ·
Karen DeMatteo · Juan Ignacio Areta ·
Mariano L. Merino · Mario S. Di Bitetti

Received: 4 April 2014 / Accepted: 12 August 2014 / Published online: 6 November 2014
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Abstract Through presence-only data, ecological niche modeling can use environmental variables to generate maps of areas that are potentially suitable for the presence of a species, improving our knowledge of its niche requirements and extending our understanding of its geographic distribution. We used the ecological niche model MaxEnt to predict the potential distribution of black-and-gold howlers (*Alouatta caraya*) and brown howlers (*Alouatta guariba clamitans*) in

Electronic supplementary material The online version of this article (doi:10.1007/s10764-014-9805-1) contains supplementary material, which is available to authorized users.

I. Holzmans (✉) · I. Agostini · M. S. Di Bitetti
Instituto de Biología Subtropical (IBS), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Misiones (UNaM), 3370 Puerto Iguazú, Misiones, Argentina
e-mail: holzmanningrid@yahoo.com.ar

K. DeMatteo
Division of Biological Sciences, University of Missouri, Columbia, Missouri 65211, USA

K. DeMatteo
WildCare Institute, Saint Louis Zoo, St. Louis, Missouri 63110, USA

J. I. Areta
Instituto de Bio y Geociencias del Noroeste Argentino (IBIGEO), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Salta, Mendoza 2, Salta 4400, Argentina

M. L. Merino
Centro de BioInvestigaciones. Comisión de Investigaciones Científicas de la Provincia de Buenos Aires, Universidad Nacional del Noroeste de la Provincia de Buenos Aires (UNNOBA), Pergamino 2700 Buenos Aires, Argentina

M. S. Di Bitetti
Facultad de Ciencias Forestales, Universidad Nacional de Misiones, Bertoni 124, 3380 Eldorado, Misiones, Argentina

South America, as well as the potential sympatry area between both species. We modeled distributions of *Alouatta caraya* (196 presence localities, 8 bioclimatic variables) and *A. guariba clamitans* (74 presence localities, 13 bioclimatic variables) using bioclimatic variables from WorldClim with habitat suitability categorized as low, moderate, or high. *Alouatta caraya* showed a broader potential distribution, occupying a wide variety of habitats in a broad range of temperatures. Temperature annual range (Bio 7) was the bioclimatic variable with most influence in modeling the potential distribution of this species. *Alouatta guariba clamitans* was more restricted to rainy areas of mature forests at higher altitudes with low minimum temperatures. Mean temperature of coldest quarter (Bio 11) was the bioclimatic variable with the highest influence in this model. The predicted area of potential sympatry of both species was a relatively small area in the interior Atlantic Forest ecoregion, and a new syntopy locality occurred within the predicted area of sympatry. This narrow zone of overlap could be maintained, among other causes, by the role of the Paraná River as a natural barrier for dispersion, differences in niche requirements, potential inter-specific competition, and hybridization.

Keywords *Alouatta caraya* · *Alouatta guariba clamitans* · MaxEnt · Potential geographic distribution

Introduction

The geographic distribution of an organism is the result of a complex series of historical and ecological events related to the species' natural history. Theoretically, four conditions or factors should be present and interact with each other in the area where a species is present: 1) suitable abiotic (environmental) conditions, 2) suitable biotic factors (interactions with other species), 3) connectivity between source and sink populations (dispersal ability), and 4) evolutionary capacity of the species to adapt to new conditions (Soberón 2007; Soberón and Peterson 2005). In the last few years, new approaches helped to develop an understanding of species' distributions and identify factors, typically environmental, that influence current distribution patterns. Ecological niche modeling (or habitat modeling; Kearney 2006) is a technique that can use abiotic and biotic factors to generate maps of areas that are potentially suitable for the presence of a species. The ability to develop these models using presence-only data provides a useful tool to deal with problems associated with information gaps (Boublil and Lima 2009; Brito *et al.* 2009; Martínez-Freiria *et al.* 2008; Phillips and Dudík 2008; Vidal-García and Serio-Silva 2011). Although it is typically possible to know where a species is present, it is more difficult to confirm a species' absence and to understand why the species is absent when ecological and environmental conditions are adequate. The key to presence-only models is that they deal with the consequences of a lack of absence data, specifically sample bias (when some locations are more intensively sampled than others) and the inability to determine species' prevalence (proportion of occupied sites), to minimize omission errors (false absences) and maximize accuracy in the predicted species distribution (Elith *et al.* 2011).

MaxEnt (Maximum Entropy; Phillips *et al.* 2006) is an algorithm that has been demonstrated to deal successfully with the lack of absence data (Elith *et al.* 2006, 2011) and that generates predictive models of species' potential distribution using presence-only data. When compared with other algorithms such as the Genetic Algorithm for Rule-set Prediction (GARP), Bioclim, or DOMAIN, MaxEnt has been found to be consistently better in its prediction performance (Phillips *et al.* 2006; Tognelli *et al.* 2009). Because these predictions are likely to include areas where no presence records currently exist (Scott *et al.* 2002), they provide a powerful tool that allows researchers, conservationists, and land managers to direct attention or effort at areas where species' presences are likely to be but not actually documented. However, correctly interpreting the results of these models requires an understanding of classical niche concepts. A species' *ecological niche* is the range of ecological conditions (abiotic and biotic) that define what is required for the species to survive and reproduce (Hutchinson 1978). A species' *fundamental niche* represents the maximum range of ecological conditions that allow for long-term survival of the species (Jiménez-Valverde *et al.* 2011; Soberón and Peterson 2005), whereas the species' *realized niche* is the actual range of ecological conditions that the species occupies (Hutchinson 1957; Jiménez-Valverde *et al.* 2011; Soberón and Peterson 2005). A species' realized niche may be more restricted or narrow than its fundamental niche because of a variety of factors including direct or indirect interspecific interactions, e.g., competition and predation, human influence, and geographic barriers that restrict movement.

Models derived from environmental data and presence-only localities have been questioned on the basis of uncertainties about what is actually being modeled and specifically whether models represent the species' fundamental or realized niche (Kearney 2006). Because presence data points are considered to have the ecological conditions suitable for species occurrence, models generated from these data approximate the species' realized niche (Kearney and Porter 2004; Phillips *et al.* 2006). Although it is likely difficult to model a species' fundamental niche, fully increasing the geographical area covered by the occurrence localities will increase the fraction of the fundamental niche that is represented in the model (Kearney and Porter 2004; Phillips *et al.* 2006) and consequently the model quality (Soberón and Peterson 2005).

Howlers (*Alouatta* spp.) are Neotropical primates with a broad geographical distribution from Mexico to southern Brazil and northeastern Argentina (Crockett 1986). The 9 or 10 howler species (Groves 2001) have essentially parapatric distributions, with only a few contact zones among pairs of species (Agostini *et al.* 2008). Black-and-gold howlers (*Alouatta caraya*) are distributed in Brazil, Argentina, Paraguay, and Bolivia and associated with a variety of habitats including the Humid Chaco, Pantanal, Cerrado, Caatinga, and the Atlantic Forest (Fernández-Duque *et al.* 2008; Hirsh *et al.* 1991; Fig. 1). In contrast, brown howlers (*Alouatta guariba*, with two subspecies, *guariba* and *clamitans*; Groves 2001) are endemic to the Atlantic Forest ecoregion in Brazil and Argentina (Hirsh *et al.* 1991; Mendes *et al.* 2008; Fig. 1). In Argentina, only the subspecies *Alouatta guariba clamitans* occurs and solely in the northeastern portion of the country, in the province of Misiones (Mudry *et al.* 2006). The known distributional range of these two species overlaps along a narrow band of Atlantic Forest (Fig. 1). Within this small area of sympatry, hybrids between *Alouatta caraya* and



Fig. 1 Geographic distribution of *Alouatta caraya* (stippled grid) and *A. guariba* (hatched grid) according to IUCN 2014, and known sympatry areas of both species (black dots).

A. guariba clamitans have been described in three different areas: one in Misiones, Argentina (Agostini *et al.* 2008) and two in Brazil, one in the state of Parana (Aguiar *et al.* 2007, 2008) and the other in the state of Rio Grande do Sul (Bicca-Marques *et al.* 2008; Fig. 1).

The main objectives of this article are to: 1) map the current and potential distributions of *Alouatta caraya* and *A. guariba clamitans* using point data from published sources and new presence localities for both species; 2) use presence-only distribution models to compare the niche requirements of these species; and 3) analyze the geographic overlap of both species with special emphasis on a comparison between actual and potential sympatry zones.

Methods

Howler Occurrence Data

We obtained locality records for both howler species from three sources: 1) museum specimens obtained through Global Biodiversity Information facility (GBIF, www.gbif.org/), which provides access to museum collections worldwide; 2) publications

compiled through a bibliographic and online search in relevant journals including those of primatology, natural history, mammalogy, and gray literature that could contain distributional data; 3) unpublished records from colleagues and local people in Argentina, Paraguay, Brazil, and Bolivia; and 4) a field survey from March 2008 through November 2009 that collected new presence localities in the province of Misiones, Argentina.

Surveys Within Misiones (Argentina)

Surveys began after two yellow fever outbreaks (2008 and 2009), which seriously affected the populations of both species in Misiones (Holzmann *et al.* 2010). I. Holzmann (with I. Agostini, J. I. Areta, or C. Acosta) conducted 12 field surveys from March 2008 to November 2009, visiting 35 localities ($N=30$ protected areas, $N=5$ nonprotected areas; Electronic Supplementary Material [ESM] Fig. S1). We surveyed each locality for at least 2 full days by walking preexisting trails in the area, noting direct observations on howlers and indirect signs of presence, such as roars. In addition, during our field surveys we gathered presence localities through interviews with park rangers, colleagues, and local people familiar with both study species.

Potential Distribution Models

We modeled howler distributions with MaxEnt 3.3.3k using default settings (500 iterations, 0,00001 convergence threshold, 10,000 maximum background points, and all 5 auto feature classes). The program randomly withholds 25% of the presence locations to test the model performance (Phillips *et al.* 2006). To not skew the model's results, we rasterized locations to a 1 km² area, so that even if numerous howler locations were reported for an area, presence data were reduced to a single record per 1-km² grid cell (DeMatteo and Loiselle 2008). We chose a 1-km² grid size taking into account that howlers occupy home ranges between 0.017 and 1.25 km² (Bravo and Sallenne 2003; Shlichte 1978).

Because predictive models are directly dependent on the accuracy of the locations used, we were conservative and used only localities for which geographic coordinates were available for the collected/observed/published specimen (DeMatteo and Loiselle 2008). For both species, we ran a first model in MaxEnt using 19 WorldClim bioclimatic variables (a set of global climate layers with about 1 km² resolution; Table 1) of data collected between 1950–2000 at a resolution of 30 arc-seconds (*ca.* 1 km²; www.worldclim.org/; Hijmans *et al.* 2005). We evaluated the predictive efficacy of these 19 variables using the jackknife test of variable importance (training and test data) and variable response curves (Baldwin 2009). The jackknife test is useful in identifying which variables contribute the most individually because it allows comparison of the training gain of each variable run independently vs. with all the variables together (Phillips *et al.* 2006). We do not use the percent contribution of each variable in the model or whether there was a decrease in gain when the variable is left out as criteria to select model variables because both of these measurements can be inadequate and/or subjective (Phillips *et al.* 2006). We eliminated variables that showed low (close to 0) or negative gain values for the training data. Low gains indicate that the variables did not have useful information by themselves for estimating distribution,

Table 1 WorldClim Bioclimatic variables that were used (crosses) and not used (dashes) in the final model of *Alouatta caraya* and *A. guariba clamitans*

Variables	<i>A. caraya</i>	<i>A. guariba clamitans</i>
BIO1 (Annual mean temperature)	X	X
BIO2 (Mean diurnal temperature range)	—	—
BIO3 (Isothermality (P2/P7) ($\times 100$))	X	—
BIO4 (Temperature seasonality)	—	X
BIO5 (Max temperature of warmest month)	—	X
BIO6 (Min temperature of coldest month)	—	X
BIO7 (Temperature annual range (Bio5–Bio6))	X	X
BIO8 (Mean temperature of wettest quarter)	—	X
BIO9 (Mean temperature of driest quarter)	—	—
BIO10 (Mean temperature of warmest quarter)	—	X
BIO11 (Mean temperature of coldest quarter)	—	X
BIO12 (Annual precipitation)	X	X
BIO13 (Precipitation of wettest month)	—	—
BIO14 (Precipitation of driest month)	X	—
BIO15 (Precipitation seasonality)	—	X
BIO16 (Precipitation of wettest quarter)	—	X
BIO17 (Precipitation of driest quarter)	X	X
BIO18 (Precipitation of warmest quarter)	X	—
BIO19 (Precipitation of coldest quarter)	X	X

while negative gains indicate that the variables make the model less transferable to other conditions, such as future climatic conditions. With these variables removed, we ran a final model for both species using only the informative variables (Table 1). We recognize that correlation between informative variables can lead to spurious results, and therefore eliminating correlated variables from the model might be desirable. To explore the correlation between these informative variables and confirm the accuracy of our final models, we extracted bioclimatic information from distributional data points of both howler species and ran pairwise correlation analyses among them (one correlation matrix for each set of informative variables per species). We then ran an additional model eliminating those variables with r values >0.75 (using only Bio 1, 7, 12, 18, and 19 in *Alouatta caraya* and Bio 4, 5, 7, 8, 11, 12, and 16 in *A. guariba clamitans*); however, these additional models had higher commission errors with an over prediction of potential distribution in areas with low presence probability for the species. In building predictive models, determining the optimal combination of variables does not follow a single line of logic but instead involves balancing the need to optimize the predictive power of the variables and correlations that may have a negative effect on the model with the species' ecology, something we believe our final model achieves.

We evaluated the final model performance using area under the curve (AUC) values, which are automatically generated in MaxEnt using random pseudoabsence background points and provide a threshold-independent measure of overall model accuracy

(Fielding and Bell 1997). Whereas an AUC =1 indicates that the model accurately discriminates between areas with presence and nonpresence, an AUC =0.5 indicates the model predicts as well as a random model and an AUC <0.5 indicates that the model's predictive capability is worse than random (Elith *et al.* 2006).

The logistic output represents the potential habitat suitability of the species on a scale of 0–1, with higher values representing more favorable conditions for the presence of the species (Phillips *et al.* 2006). We applied the minimum training presence (MTP) as a threshold or “cutoff” value for each model because it is the most conservative threshold, as it identifies the minimum predicted area possible while still maintaining a zero omission rate for both training and test data (Liu *et al.* 2005). Ecologically, the MTP can be interpreted to contain those cells that are predicted to be at least as suitable as those where the species was identified as present. In contrast, other thresholds (such as 10 percentile training presence (10PT) or maximum test sensitivity plus specificity (MTSS)) had unacceptable omission rates and their predicted areas were believed to be ecologically inaccurate (Liu *et al.* 2005; Phillips *et al.* 2006). We divided habitat suitability in our final model into three classes: low suitability (MTP value-0.3), moderate suitability (0.3–0.6), and high suitability (0.6–highest limit of the prediction set by the model).

To gain insight into the usefulness of modeling to understand geographic distribution of both howler species, we compared the final predictive model to the species' IUCN 2014 historical distribution map (www.iucnredlist.org/). We modeled the potential sympatry zone of both species by overlapping the two species-specific final modeled maps using only those areas where both species showed moderate to high presence probability (i.e., >0.3).

All research reported in this article complied with the protocols approved by the appropriate institutional Animal Care and Use Committee, and adhered to the legal requirements of Argentina. All research protocols were reviewed and approved by the Ministry of Ecology and Natural Resources of the province of Misiones, where most of the fieldwork took place.

Results

Howler Occurrence Data

We compiled 271 presence localities for *Alouatta caraya* and 127 for *A. guariba clamitans* (ESM Tables SI and SII). After removing duplicates from each grid cell (converting to raster) and leaving only exact presence localities, we used a total of 196 presence points to model the potential distribution of *Alouatta caraya* and 74 to model that of *A. guariba clamitans*. Using the three data sources, we compiled a total of 24 localities for *Alouatta caraya* and 12 for *A. guariba clamitans* for Misiones (ESM Tables SI and SII). We collected important new data during our 2-day survey of the 35 areas in Misiones including 9 new localities for *Alouatta caraya* and 7 localities for *A. guariba clamitans* (indicated with an asterisk in ESM Tables SI and SII). In addition, our survey confirmed a new area of syntopy between the two species of howlers (double asterisk in ESM Tables SI and SII).

Potential Distribution of *Alouatta caraya*

The distributional model was able to discriminate areas of species presence and absence in *Alouatta caraya* (Fig. 2), as both the training (AUC = 0.94) and test (AUC = 0.92) data had a good performance. The MTP threshold, or the level at which no omission errors were detected, was 0.011. When the MTP threshold was applied, the area predicted for the species (824,871,600 ha) was 62% larger than the IUCN historical distribution (Fernández-Duque *et al.* 2008) of this species (313,591,147,887 ha). Most of the area predicted as suitable for this species had low suitability (638,827,900 ha) in comparison to areas of moderate (133,315,300 ha) and high (52,728,400 ha) suitability (Fig. 2).

Jackknife test results for the original model with all 19 bioclimatic variables resulted in 11 variables being eliminated from the final model (ESM Table SI and Fig. S3). In the final model ran with the 8 remaining variables, Bio 7 (temperature annual range [Bio5–Bio6]) was the bioclimatic variable that had the highest gain for the training and test data when used in isolation, and Bio 1 (annual mean temperature) the one that reduced the gain the most when excluded from the model, i.e., the variable that appeared to have the most information not present in the other variables.

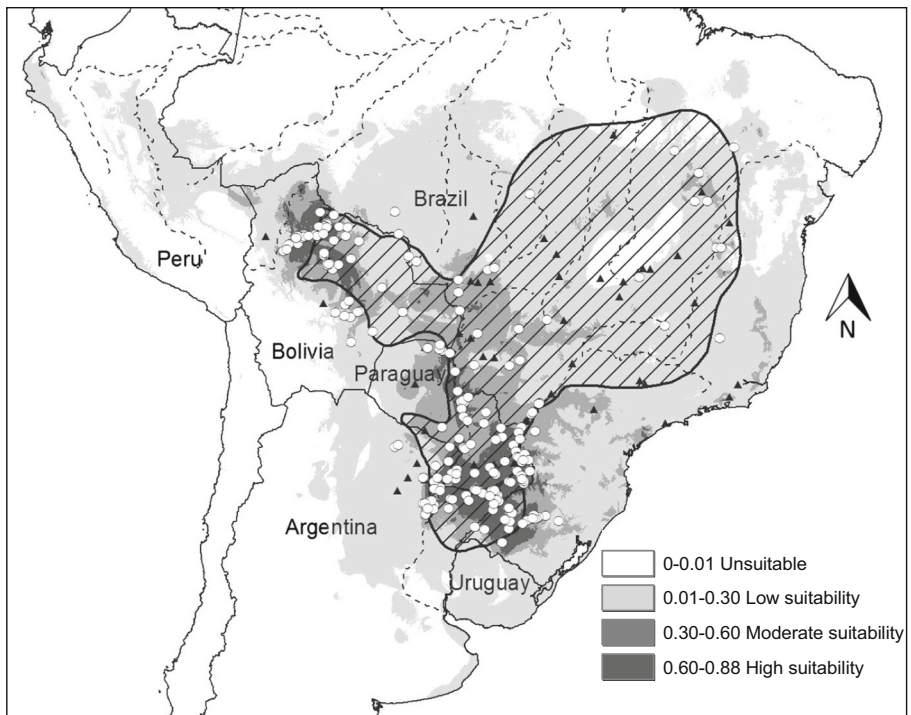


Fig. 2 Presence localities and potential distribution of *Alouatta caraya* as predicted by MaxEnt. The minimum training presence (MTP: cutoff between unsuitable and suitable areas) is 0.01. Exact presence localities used to build the model (white circles; $N=196$), imprecise presence localities not used in the model (black triangles; $N=75$), and geographic boundaries of the species according to IUCN 2014 (black grid; Fernández-Duque *et al.* 2008, www.iucnredlist.org/). Principal rivers are shown on the map (dashed lines).

Potential Distribution of *Alouatta guariba clamitans*

The distributional model successfully discriminated areas of species presence and absence in *Alouatta guariba clamitans* (Fig. 3) with strong model performance (AUC =0.97) for both training and test data sets. The MTP threshold was 0.16. When the MTP threshold was applied, the area predicted for the species (183,133,000 ha) was 45% larger than the IUCN historical distribution (Mendes *et al.* 2008) of this species (101,595,174, 518 ha). Most of the area predicted as suitable for this species had moderate suitability (80,480,100 ha) in comparison to areas of low (65,197,100 ha) and high (37,455,800 ha) suitability (Fig. 3).

Jackknife test results for the original model with all 19 bioclimatic variables resulted in 6 variables being eliminated from the final model (ESM Table SI and Fig. S3). In the final model we ran with the 13 remaining variables Bio 11 (mean temperature of coldest quarter) had the highest training and test gain when used in isolation, and Bio 4 (Temperature seasonality) was the one that reduced the gain the most when excluded from the model, i.e., the variable that appeared to have the most information not present in the other variables.

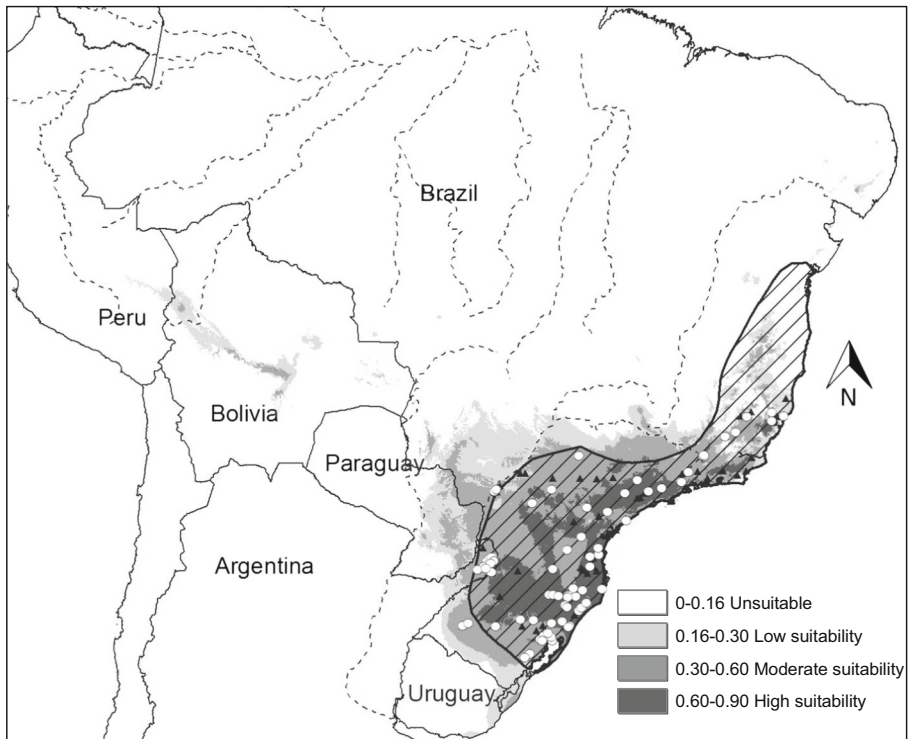


Fig. 3 Presence localities and potential distribution of *Alouatta guariba clamitans* in South America as predicted by MaxEnt. The minimum training presence (MTP: cutoff between unsuitable and suitable areas) is 0.16. Exact presence localities used to build the model (white circles; $N=74$), imprecise presence localities not use for modeling (black triangles; $N=53$), and geographic boundaries of the species according to IUCN 2014 (black grid, Mendes *et al.* 2008, www.iucnredlist.org/). Principal rivers are shown on the map (dashed lines).

Potential Areas of Overlap Between Both Howler Species

MaxEnt predicted a relatively narrow potential area of overlap (40,402,200 ha) falling mostly in the interior Atlantic Forest and representing only the 4% of the sum of suitable areas for both species (1,008,004,600 ha) (Fig. 4). All four syntopy localities occurred well within the limits of the largest and more continuous block of potential sympatry in our model (Fig. 4).

Dicussion

Temperature annual range (Bio 7) and mean temperature of the coldest quarter (Bio 11) were the two bioclimatic variables with the most influence in modeling potential distributions of *Alouatta caraya* and *A. guariba clamitans*, respectively. MaxEnt also predicted a relatively narrow potential area of overlap between both species falling mostly in the interior Atlantic Forest. We also contributed new distributional records of both species, including a new syntopy locality in Argentina.

According to our extensive locality compilation, the present distribution of *Alouatta caraya* is wider than that considered by IUCN 2014 (Fernández-Duque *et al.* 2008; Fig. 2), especially in northern Bolivia, west-central and southern Brazil, northern

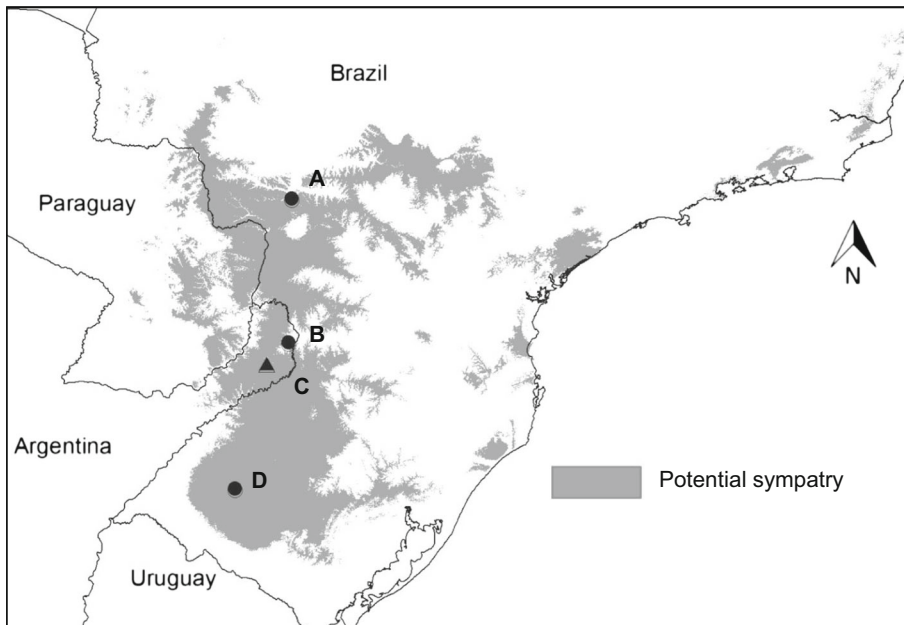


Fig. 4 Map of syntopy localities and potential sympatry of *Alouatta caraya* and *A. guariba clamitans*. Potential sympatry zone between *Alouatta caraya* and *A. guariba clamitans* resulting from overlap of modeled areas where both species had moderate to high presence probability (>0.3 , dark gray). Known syntopy localities (black dots): **(a)** Mata do Bugio in Paraná State (Brazil, Aguiar *et al.* 2007); **(b)** El Piñalito Provincial Park in Misiones (Argentina, Agostini *et al.* 2008); **(c)** the new syntopy locality (black triangle): Caá Yari Provincial Park also in Misiones; and **(d)** Cerro dos Negros in Rio Grande do Sul (Brazil, Bicca-Marques *et al.* 2008).

Paraguay, and northeastern Argentina, where many compiled localities are outside the distributional borders of this species. Thus, new data indicates the need to update and reevaluate the geographic boundaries even for a well-known species like *Alouatta caraya*.

In our final model, the entire Atlantic Forest ecoregion was indicated as a suitable area for *Alouatta caraya*; however, presence probabilities decreased drastically from high presence probabilities in the interior toward low probabilities in the Atlantic Coast. The Humid (eastern) Chaco and vast areas of the Pantanal also showed high presence probabilities of this species. Drier ecoregions such as the Dry (western) Chaco (Argentina and Paraguay), the Cerrado, and the Caatinga (Brazil) showed low presence probabilities. However, many of the localities from our database placed in the Cerrado were not used for modeling because exact geographic coordinates were not available (black triangles in Fig. 2). Higher predicted probabilities could be obtained for the Cerrado if all these localities (if with precise geographic coordinates) were included in a model. The southern Amazon region also showed low presence probabilities in Brazil compared to higher values in the Beni region of Bolivia. Areas identified by the model as suitable in Peru (although with low probability of presence), but with no actual historical records of this species, can be considered as a model overprediction. The only specimen (an embryo in alcohol) originally identified as *Alouatta caraya*, with collection label indicating an origin from Peru (LSUMZ 22320) but whose geographic coordinates place it in Bolivia, is probably a misidentified specimen of *A. seniculus* (M. Hafner *in litt.* 2012). Although areas with overpredictions can be true commission errors (false positives; DeMatteo and Loiselle 2008; Jimenéz-Valverde *et al.* 2011), they can in fact represent areas where the species is absent despite its potential suitability, especially if they have been thoroughly surveyed. These areas are very useful in helping interpret the complexity of geographic distributions by indicating that environmental conditions are not the only necessary conditions that determine a species' presence.

Our model indicated very low presence probabilities of *Alouatta caraya* in Uruguay. The single record of *Alouatta caraya* in Uruguay may relate to escapees from captive facilities or private households (Villalba *et al.* 1995).

Presence data for *Alouatta guariba clamitans* are in agreement with the present distribution proposed by IUCN 2014 (Mendes *et al.* 2008; Fig. 3). All records confirm that this species is restricted to the Atlantic Forest in Brazil and Argentina, where modeling showed the highest probabilities of occurrence. Unlike *Alouatta caraya*, *A. guariba clamitans* showed the highest presence probabilities within the rainy portion of the Atlantic Forest, and probabilities decreased toward the interior (drier) portion of this ecoregion. The model and the present distribution of the species suggest that *Alouatta guariba clamitans* is particularly associated with montane forests (Harris *et al.* 2005) in areas with elevated and fractured profiles corresponding to the Brazilian Shield. Two potential areas call for an explanation. First, the model predicted a moderate probability presence of *Alouatta guariba clamitans* in the Andes of central Bolivia, very far from its known distributional limits. Bioclimatic and orographic similarities with the Atlantic Forest may account for this overprediction, indicating that historical factors, and not niche limitations, explain this pattern. Second, eastern Paraguay is dominated by interior Atlantic Forest with a few elevated areas of up to 760 m (Galindo-Leão and Gusmão Câmara 2003) with conditions of moderate

suitability for *Alouatta guariba clamitans* (Fig. 3). However, there are no records of this species in Paraguay. The absence of historical records of the species in Paraguay suggests that deforestation and hunting are unlikely explanations for the observed pattern. The role of the Paraná River as a barrier, coupled with habitat preferences, seems the most likely explanation for this distributional pattern. Indeed, all presence localities (Fig. 3) are placed to the east of the Paraná River. The role of rivers in the speciation of *Alouatta* is thought to differ among species. For some species such as *Alouatta caraya* riverine barriers do not accurately explain present geographic distribution, but for other species such as *A. maconelli*, *A. belzebul*, and *A. seniculus*, Amazonian rivers appear to set important distributional limits (Ascunce *et al.* 2007; Ayres and Clutton-Brock 1992; Cortés-Ortiz *et al.* 2003). The Paraná River is the second longest south American river (after the Amazonas). Although in its upper and middle sections this river is not very wide, *ca.* 300 m, it is a turbulent river with cliffs. The role of rivers as barriers for primate dispersal is still debated, although a river can be considered as a barrier when a species distribution stops at the river (Harcourt and Wood 2012). Moreover, it may be hard to disentangle the effects of two potential factors: the role of the river as a physical barrier or the lack of adequate environmental conditions for the species settlement on the other side of the river margin (Oates 1988).

The zone of potential overlap between both species is a relatively small area restricted almost exclusively to the interior Atlantic Forest, but with a few isolated areas in the coastal portion of this ecoregion. This relatively small area of potential overlap suggests that the two species occupy different habitat types and differ in their fundamental niches. Whereas *Alouatta caraya* is more plastic and lives in areas with marked seasonal changes in temperature within its ample range (Thorington *et al.* 1979), such as open areas, riverine forests, semi-arid areas (Caatinga), and/or dense forests (Atlantic Forest), *A. guariba clamitans* is restricted to rainy areas of mature forests that are generally at higher altitudes with low minimum temperatures ($<0^{\circ}\text{C}$) within the Atlantic Forest. These niche descriptions are in accordance with the bioclimatic variables indicated by the models as the most relevant to predict the distribution of each species: Bio 7 (annual temperature range) for *Alouatta caraya* and Bio 11 (mean temperature of coldest quarter) for *A. guariba clamitans*. Given that most howler species have essentially parapatric distributions, it is likely that several ecological and historical factors have combined to produce the parapatric distribution of these two species. First, differences in the structural features of their most common habitats have influenced their distributions; *Alouatta caraya* inhabits semi-open woodlands and forest patches in natural grassland matrices in nonmontane terrain, whereas *A. guariba clamitans* is a denizen of mature forests, mostly in mountainous terrain. Second, the Paraná River may have acted as a barrier to the dispersal of *Alouatta guariba clamitans* to the west across forested areas while the grasslands and Chaco forests may have limited its dispersal to the south. However, the wider geographic distribution of *Alouatta caraya* and the ability to exploit semi-open habitats may have allowed it to cross either the Paraná River at some point or to overcome this barrier above its head water and to use its riverine forests as corridors (Ascunce *et al.* 2007), later spreading to meet *A. guariba clamitans* in the interior Atlantic Forest. Third, high levels of niche overlap among these two howler species in sympatry may also play an ecological role, maintaining narrow contact zones and parapatric distributions through potential competition (Agostini *et al.* 2010a, b). Fourth, hybridization between the two

species could also limit their overlap. Evidence shows that hybridization between two different howler species (*Alouatta palliata* and *A. pigra*) follows Haldane's rule, in which the heterogametic sex is sterile or not viable (Cortés-Ortiz *et al.* 2007). In this case individuals living in sympatry zones may show reduced fitness in comparison to individuals living in areas with conspecifics only, resulting in narrow sympatry areas.

MaxEnt models can be updated with new presence localities. Future models of howler distribution may increase their explanatory power by including categorical variables such as the presence of another howler species, geographic barriers, or impact of yellow fever (a powerful disease that decimates howler populations and is known to have acted in the sympatry zone of howlers in Argentina; Holzmann *et al.* 2010). Other important variables to include in future models could be land use, fragmentation, and habitat loss. Habitat loss can skew presence distribution points by making a species absent where environmental conditions are given for the species to be present, so the possibility of local extinctions due to this factor must be evaluated in future modeling attempts. These models are distributional hypotheses that must be tested in the field. Our survey in Misiones added a new syntopy locality within the predicted area of sympatry, corroborating the distributional models of both *Alouatta caraya* and *A. guariba clamitans*. Future surveys will likely increase their number, allowing for a better characterization of the narrow area of overlap between *Alouatta caraya* and *A. guariba clamitans* and a better understanding of the factors that shape the distributions of howlers.

Acknowledgments We thank the Ministry of Ecology of Misiones for the research permit and all the people who contributed to this article with presence localities of both howler species: M. Repenning, H. del Castillo, R. Clay, J. Escobar, A. Bodrati, K. Roesler, J. Segovia, C. Madders, C. and V. Maciel, E. Lestani, P. Tujague, L. Oklander, V. Sandoval, R. Wallace, G. Pugnalli, E. Pizzio, R. Abrahamson C. Chaves, Tomo's family, De Barba's family, D. Tatarin, M. Higa, and R. Invernon. We also thank Charlie Sandoval from Yacutinga Lodge. We thank Carolina Acosta for field assistance and express special thanks to Daphne Colcombet for her support during the study period. I. Holzmann thanks M. Ferrari and K. Holzmann for unconditional support during the entire field study. Valuable suggestions from two anonymous reviewers and Joanna Setchell greatly improve the manuscript. This research was supported by fellowships from the National Research Council of Argentina (CONICET), the Comité Ejecutivo de Desarrollo e Innovación Tecnológica (CEDIT), and The Rufford Small Grant.

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