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A Potential Distribution Model and Conservation Plan for the Critically Endangered Ecuadorian Capuchin, *Cebus albifrons aequatorialis*

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Abstract Conservation actions that effectively and efficiently target single, highly threatened species require current data on the species' geographic distribution and environmental associations. The Ecuadorian capuchin (*Cebus albifrons aequatorialis*) is a critically endangered primate found only in the fragmented forests of western Ecuador and northern Peru, which are among the world's most severely threatened ecosystems. We use the MAXENT species distribution modeling method to model the potential distribution and environmental associations of *Cebus albifrons aequatorialis*, using all known presence localities recorded within the last 2 decades as well as 13 climate, topography, vegetation, and land-use data sets covering the entire geographic range of the subspecies. The environmental conditions that our model predicted to be ideal for supporting *Cebus albifrons aequatorialis* included ≥20% tree cover, mild temperature seasonality, annual precipitation <2000 mm, and low human population density. Our model identified 5028 km^2 of suitable habitat remaining, although many of these forest fragments are unprotected and are unlikely to support extant populations. Using the median population density across all sites for which data are available, we estimate the total carrying capacity of the remaining habitat to be 12,500 total individuals. The true number of remaining individuals is likely to be considerably lower due to anthropogenic factors. We highlight four critical regions of high predicted suitability in western Ecuador and northern Peru on which immediate conservation actions should focus, and we lay out clear priorities to guide

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conservation actions for ensuring the long-term survival of this gravely threatened and little known primate.

Keywords *Cebus albifrons aequatorialis* · Conservation plan · Distribution model · Ecuadorian capuchin · MAXENT · Northern Peru · Western Ecuador

Introduction

As the funds and resources available for conservation are scarce, decisions that focus on conserving single, highly threatened species must have a sound basis, including knowledge of the species' current geographic distribution and environmental associations. Although such "focal-species" approaches to conservation have been criticized (Lindenmayer *et al*. 2002), certain species make logical conservation targets because they may be successful at raising public awareness and increasing available conservation funds (Lambeck 1997; Wilson *et al*. 2009). The tropical forests of western Ecuador and northern Peru are among the most imperiled ecosystems on earth (Dodson and Gentry 1991), yet they constitute the only refuge of the critically endangered Ecuadorian capuchin, *Cebus albifrons aequatorialis* (Allen 1914; Cornejo and de la Torre 2008). Dodson and Gentry (1991) suggest that only 4.4% of the original forest remains in western Ecuador, and many of the remaining forest tracts in this region have been severely degraded by human disturbance that is largely attributable to exponential human population growth in the region since 1960. This rapid habitat loss has had devastating consequences on the region's unique biodiversity (Brooks *et al*. 2002; Dodson and Gentry 1991; Parker and Carr 1992), leading to Conservation International's designation of the region as one of the world's leading biodiversity hotspots (Myers *et al*. 2000). This rampant deforestation also played a key role in the recent decision by the International Union for Conservation of Nature (IUCN) to revise the conservation status of *Cebus albifrons aequatorialis* from near threatened to critically endangered (Cornejo and de la Torre 2008; Tirira 2011). Capuchins in western Ecuador and northern Peru are likely to be good indicators of overall ecosystem health because they are conspicuous, require relatively large areas of forest (Jack and Campos 2012), and tend to disappear from small, isolated forest fragments and heavily disturbed areas (Bierregaard 2001; Peres 2001). Thus, *Cebus albifrons aequatorialis* can serve as umbrella species for identifying and delineating areas of high-quality forest that may support more cryptic species that are also in danger of extinction (Caro and O'Doherty 1999). Moreover, primates in the Neotropics have been successfully used as flagship species to attract public attention and support for conservation initiatives (Caro and O'Doherty 1999; Kleiman and Mallinson 1998).

Extant populations of *Cebus albifrons aequatorialis* have been recorded in the last 2 decades at a total of 20 localities in western Ecuador and northern Peru (Albuja and Arcos 2007; Charlat *et al*. 2000; Cornejo and de la Torre 2008; Encarnacion and Cook 1998; Hores 2006; Jack and Campos 2012; Parker and Carr 1992). Here, we model the suitability of habitat for *Cebus albifrons aequatorialis* across its geographic range by combining published locality data on the species' occurrence with remotely sensed environmental data. We provide estimates of the total carrying capacity of remaining suitable habitat as well as the current total population size. We use the habitat suitability model to determine which environmental variables most strongly predict the species' occurrence. We also provide a predictive map of the species' potential distribution that can be used to identify additional areas where *Cebus albifrons aequatorialis* might occur, and to guide conservation actions for *C. a. aequatorialis* and other threatened organisms in this ecosystem. Finally, we identify four critical areas on which immediate conservation actions should focus, and we suggest specific conservation priorities that will help to ensure the continued survival of this gravely threatened and little known primate.

Methods

Locality Data

The presence/absence data include 42 sites in western Ecuador and extreme northern Peru. We carried out surveys for the presence of *Cebus albifrons aequatorialis* at 11 of these sites between 2002 and 2005 (Jack and Campos 2012). The other 31 localities are drawn from published sources, including a rapid assessment survey undertaken by a team from Conservation International (Parker and Carr 1992) and the published reports of Albuja (2002), Albuja and Arcos (2007), Charlat *et al*. (2000), Encarnacion and Cook (1998), Gavilanez-Endara (2006), and Hores (2006) (Table I; Fig. 1). We used the online databases provided by DarwinNet (www.darwinnet.org) and BirdLife International (www.birdlife.org) and the Google Earth application to verify that the coordinates provided for each site corresponded to the areas described. It was evident that a small number of the published coordinates corresponded to populated areas or administrative areas at the periphery of the surveyed sites, which might poorly reflect the actual areas used by *Cebus albifrons aequatorialis* at the scale of our habitat suitability model. Therefore, we used satellite imagery in Google Earth to adjust the coordinates for these sites to a forested point at the approximate geographic center of the protected area. Although this introduces a bias in the model toward forested areas, we feel that it is an appropriate adjustment based on knowledge of this arboreal primate's behavioral ecology. We excluded the presence locality Cerros de Amotape National Park, Peru, which is reported to have *Cebus albifrons aequatorialis* (Cornejo and de la Torre 2008), from our model because we were unable to find geographic coordinates for a confirmed sighting locality. As this national park encompasses 913 km^2 of variable habitat, designating a single pixel as the presence locality would have been arbitrary.

Modeling Habitat Suitability

We modeled the habitat suitability of *Cebus albifrons aequatorialis* with MAXENT version 3.3.3k (Phillips *et al*. 2006). Although many methods are available for modeling species' distributions, comparative studies have found that MAXENT exhibits high predictive accuracy for a wide range of species in diverse regions, even with small sample sizes (Elith *et al*. 2006; Hernandez *et al*. 2006; Pearson *et al*. 2007; Vidal-García and Serio-Silva 2011). Moreover, our absence data do not fully

Table I Locality data used to develop the habitat suitability model for *Cebus albifrons aequatorialis*

Site	Latitude	Longitude	*C. a. aequatorialis* present?	Map number	Source
Bilsa Biological Reserve	0.37656	–79.71080	Present	9	1
Cerro Azul	–3.46842	–79.73256	Present	34	2
Cerro Blanco Protected Forest	–2.15775	–80.04076	Present	23	3, 4
Chirije	–0.70270	–80.47306	Present	12	4
Cooperativa 31 de Agosto	–3.15884	–79.71623	Present	30	2
Cerro de Hayas-Naranjal Reserve	–2.79960	–79.65842	Present	27	2
Cordillera La Tapada	–2.00811	–80.39858	Present	22	2
El Palmar	–0.02684	–80.11596	Present	4	2
Hacienda el Paraíso	–0.26006	–80.35264	Present	7	4
Jauneche	–1.24866	–79.65691	Present	17	3, 4
La Hesperia Biological Reserve	–0.36652	–78.86958	Present	10	4
Machalilla N.P. / La Mocora	–1.61419	–80.71027	Present	19	2, 3, 5
La Planada	–1.33370	–80.65165	Present	18	2
Lalo Loor Dry Forest Reserve	–0.09510	–80.14211	Present	5	4
Loma Alta Ecological Reserve	–1.85520	–80.61131	Present	12	2, 4
Manglares-Churute Ecological Reserve	–2.41250	–79.63384	Present	15	2, 4
Cerro Pata de Pájaro Protected Forest	0.02055	–79.97897	Present	3	3
Tito Santos Biological Reserve	–0.14481	–80.20775	Present	6	2, 4
Tumbes Reserved Zone	–3.82205	–80.25665	Present	39	6
Bosque Petr. de Puyango	–3.85200	–80.02724	Absent	40	2
Cabo Pasado	–0.39605	–80.47390	Absent	8	4
Casacay (Río Jubones)	–3.32606	–79.71869	Absent	33	2
Destacament Cap. Díaz	–3.49592	–80.15229	Absent	35	2
El Guayacán (La Maná)	–0.85950	–79.12073	Absent	13	2
Jaramijó	–0.99589	–80.58914	Absent	14	2
La Comuna (Soledad)	–3.22123	–79.65188	Absent	31	2
La Cotona	0.55232	–79.97143	Absent	1	2
La Liga de Oro	–3.09167	–79.70900	Absent	29	2
Las Planchas	–1.77011	–79.23085	Absent	20	2
Las Vegas	–4.07994	–80.40121	Absent	42	2
Mangaurquillo	–4.00820	–80.19261	Absent	41	2
Manta Real	–2.56697	–79.34944	Absent	25	3
Montecristi	–1.05894	–80.66233	Absent	15	2
Palo Marcado	–3.25865	–79.68515	Absent	32	2
Ramón Campaña	–1.13297	–79.07910	Absent	16	2
Cerro Seco Biological Reserve	–0.61103	–80.43605	Absent	11	4
Buenaventura Reserve	–3.65181	–79.74549	Absent	37	2
Arenillas Ecological Reserve	–3.51681	–80.13337	Absent	36	3
San Isidro	–0.36667	–80.18334	Absent	9	4
San Pedro (Eloy Alfaro)	–2.86388	–79.61401	Absent	28	2
Vía Balsas Marcabelí	–3.76392	–79.86790	Absent	38	2

Table I (continued)

Site	Latitude	Longitude	*C. a. aequatorialis* present?	Map number	Source
Vía Jesús Maria	–2.65888	–79.44700	Absent	26	2

Sources: 1, Charlat *et al*. (2000); 2, Albuja and Arcos (2007); 3, Parker and Carr (1992); 4, Jack and Campos (2012); 5, Hores (2006); 6, Encarnacion and Cook (1998).

represent the range of habitats from which *Cebus albifrons aequatorialis* is absent; we therefore chose a modeling method that uses presence data only. We constructed the model using all 19 known presence localities for *Cebus albifrons aequatorialis* (Table I). MAXENT uses occurrence localities to model environmental suitability based on a set of environmental variables that are likely to influence the species'

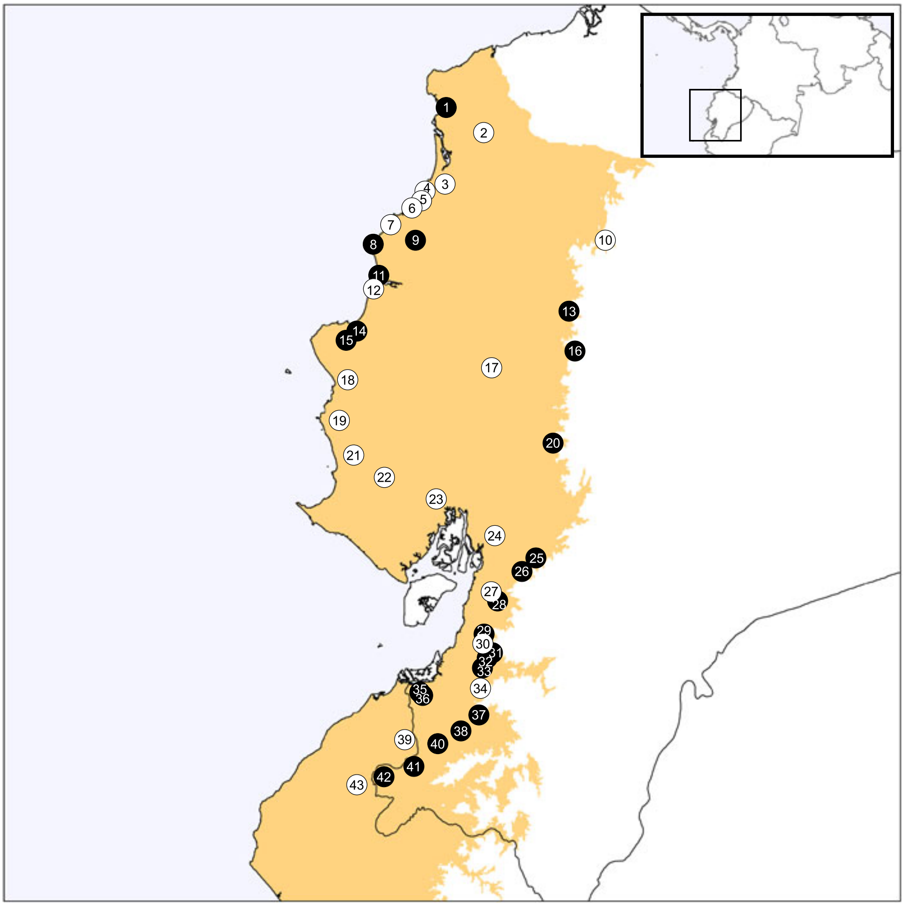

Fig. 1 Presence localities (white circles) used to construct the potential distribution model for *Cebus albifrons aequatorialis*, and absence localities (black circles) used to evaluate the model. Locality names and references are listed in Table I. The shaded region represents the maximum geographic extent of *C. a. aequatorialis*. We excluded all areas outside this region for constructing the potential distribution model.

occurrence. MAXENT calculates a value of relative suitability for each cell in the study area based on the relationship between the presence localities and the environmental variables measured at each cell. We used default values for convergence threshold (10^{-5}), maximum number of iterations (500), regularization multiplier (1), and maximum number of background points (10^4). We present the model's output in logistic format, which assigns to each cell a probability of presence between 0 and 1. Although MAXENT output is often interpreted as the probability of a species' occurrence, additional factors not included in our model, such as hunting, geographic barriers, history, and biotic interactions, are likely to influence the occupancy of suitable environments (Robinson *et al*. 2010). Therefore, we refer the model's output as a map of potential distribution, with values indicating habitat suitability rather than probability of occurrence.

Environmental Variables

We compiled 13 climate, topography, vegetation, and land-cover data sets (Table II) in ESRI ArcGIS 9.3.1 as input variables in the habitat suitability model. Each environmental data set was a grid with identical geographic limits and cell size covering the known geographic range of *Cebus albifrons aequatorialis* in western Ecuador and northern Peru (Fig. 2). All data sets were converted to the WGS 1984 geographic coordinate system. We attempted to select data sets that were collected as close as possible to the 2002–2005 time period, during which most of the presence/absence survey localities were recorded. The 13 environmental variables are numbered and described in the text that follows.

We assessed 19 "bioclimatic variables" from WorldClim 1.4 (Hijmans *et al*. 2005; http://www.worldclim.org/) for strength of pairwise correlations and discarded one variable at random from highly correlated pairs (|r| > 0.85). This selection process resulted in six bioclimatic variables used for the model: 1) mean diurnal temperature range (°C), 2) temperature seasonality (°C), 3) minimum temperature of the coldest month (°C), 4) temperature annual range (°C), 5) annual precipitation (mm), and 6) precipitation seasonality (coefficient of variation). These data sets are derived from interpolated mean monthly temperature and rainfall data collected at weather stations

Table II Summary of contributions by the 13 environmental variables to the habitat suitability model

	Name	Description	Percent contribution	Training gain without	Training gain with only	Permutation importance
1	MeanDiTempRange	Mean diurnal temperature range (°C)	7.20	1.57	0.120	0.00
2	TempSeasonality	Temperature seasonality (°C)	0.011	1.57	0.133	0.126
3	MinTempColdestM	Minimum temperature in coldest month (°C)	1.48	1.53	0.0448	5.56
4	TempAnnualRange	Temperature annual range (°C)	2.52	1.52	0.254	$\boxed{28.8}$
5	AnnualPrecip	Annual precipitation (mm)	11.2	$\boxed{1.36}$	0.125	$\boxed{20.9}$
6	PrecipSeasonality	Precipitation seasonality (coefficient of variation)	0.00	1.57	0.0291	0.00
7	Elevation	Elevation (m)	3.54	1.55	0.218	4.79
8	Slope	Slope (degrees to the horizontal)	6.41	1.54	0.309	2.87
9	TreeCover	Percent tree cover	$\boxed{36.9}$	$\boxed{1.43}$	$\boxed{0.651}$	$\boxed{18.0}$
10	NDVIMean	Mean of normalized difference vegetation index (NDVI)	0.113	1.57	0.165	0.00
11	NDVIStdDev	Standard deviation of NDVI	1.54	1.55	0.0752	0.600
12	HumanPopDensity	Square root of human population density (per km^2)	12.8	1.51	0.405	0.0067
13	LandCover	Land cover category	16.3	$\boxed{1.35}$	$\boxed{0.467}$	$\boxed{18.3}$

Boxed cells indicate values that are at least one standard deviation from the mean across all variables for the given measure of variable importance.

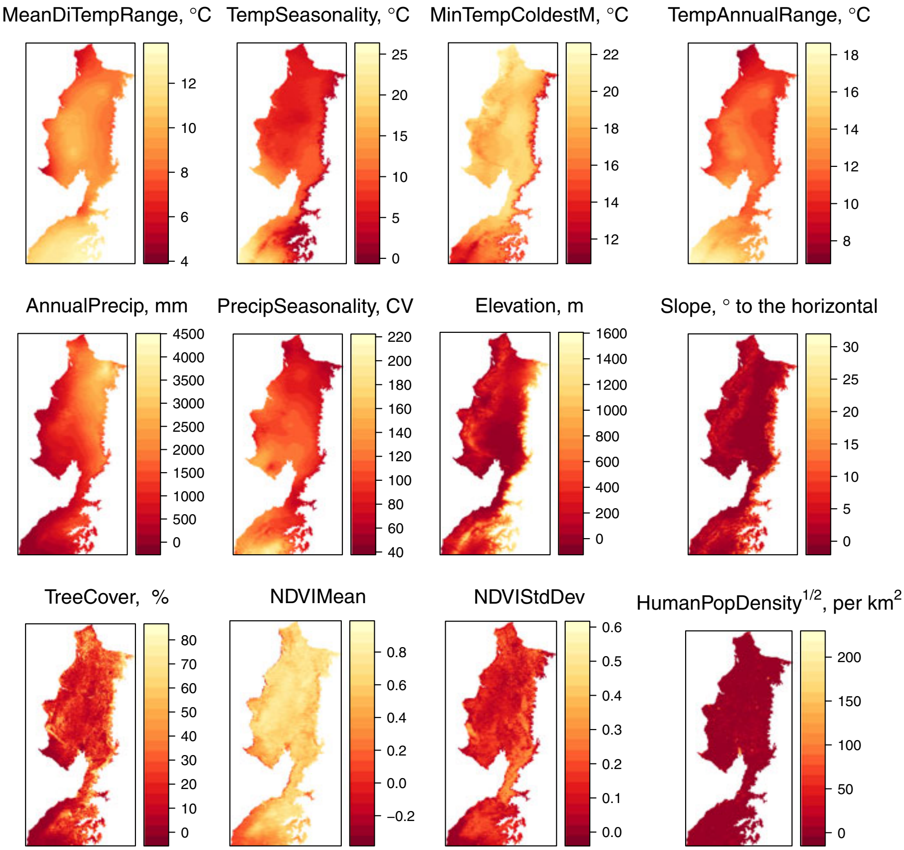

Fig. 2 Maps of the 12 continuous environmental data sets used to construct the potential distribution model for *Cebus albifrons aequatorialis*. An additional categorical data set used to construct the model, land cover, is shown in Online Resource 1. Variable names are described in Table II.

from *ca*. 1950 to 2000. We also acquired from WorldClim 1.4 a digital elevation model (DEM) to represent 7) elevation (m) and 8) slope (degrees to the horizontal). We derived slope from the DEM using the ArcInfo Spatial Analyst extension. We used 9) the Vegetation Continuous Fields Tree Cover product (M. Hansen *et al*. 2007; Global Land Cover Facility, www.landcover.org), which depicts proportion of tree canopy cover for each pixel based on light penetration to the ground. This data set is provided at a spatial resolution of 500 × 500 m (15.1632' ') at the equator. To cover the extent of the study area, we mosaicked two coverages from 2005. We used MODIS Terra Vegetation Indices (Global MOD13A3 data) to derive two variables: 10) annual mean Normalized Difference Vegetation Index (NDVI) and 11) standard deviation of annual NDVI for the year 2004. NDVI is a widely used measure of green vegetation based on the wavelengths of radiation characteristically reflected and absorbed by chlorophyll; therefore, NDVI values correlate strongly with the photosynthetic capacity of vegetation (Myneni *et al*. 1995). Global MOD13A3 data are provided monthly at 1-km spatial resolution and are distributed by the Land Processes Distributed Active Archive Center (LP DAAC), located at the U.S. Geological Survey (USGS) Earth Resources Observation and Science (EROS) Center (lpdaac.usgs.gov). We used the Raster Calculator in the ArcInfo Spatial Analyst extension to calculate mean NDVI and standard deviation of NDVI based on four monthly NDVI layers from 2004 corresponding to February (peak wet season), May (wet–dry transition), August (peak dry season), and November (dry-wet transition). We used calculated 12) human population density from population count and area grid data from the LandScan 2008 High Resolution global Population Data Set. Because the raw population density values exhibited extremely high variance, we applied a square root transform. Finally, we used 13) the Vegetation Map of Latin America (Eva *et al.* 2002), a thematically detailed land-cover map of South America produced for the Global Land Cover 2000 database coordinated by the European Commission's Joint Research Centre (Bartholome and Belward 2005; GLC 2003). This data set features 73 regionally optimized land-cover classes based on differences in vegetation, geology, elevation, rainfall, and anthropogenic disturbance. We reclassified the 73 regional classes into 15 global classes using the global legend transformation in Fritz *et al.* (2003).

We clipped all rasters to exclude areas outside the known range of *Cebus albifrons aequatorialis*, with boundaries as follows: to the west the Pacific Ocean; to the north the Esmeraldas-Guayllabamba River (Jack and Campos 2012); to the east a contour line along the Andes mountains at 1500 m, the maximum recorded elevation for the subspecies (Allen 1914; Harris *et al.* 2008); and to the south the latitude –4.66, which is *ca.* 100 km south of the southernmost presence locality and south of which the landscape appears too arid to support *Cebus* populations (Fig. 1). For all data sets, we adjusted grid cell resolution and alignment to match the Worldclim 1.4 data, which have a resolution of 30' ' (0.93 × 0.93 km at the equator).

Model Evaluation

Presence-only species distribution models are typically validated with an independent set of presence points by assessing how accurately the model predicts occurrence at these points. However, Pearson *et al.* (2007) note that when the models are based on a small number of localities, the output can be strongly influenced by exactly which localities are included. Therefore, we used all available presence points as inputs in the model and used two alternative methods to assess the model's performance.

First, we assessed the area under the receiver operating characteristic curve (Manel *et al.* 2001), which measures the model's ability to correctly distinguish presence localities from randomly chosen background pixels (Manel *et al.* 2001; Phillips *et al.* 2006). AUC values of >0.9 indicate high accuracy. Second, we used the threshold-based jackknife validation procedure described by Pearson *et al.* (2007). Many practical applications of a species distribution model require that the model's continuous, probabilistic output be converted to a binary map (suitable/unsuitable). This conversion involves specifying a threshold of occurrence, with suitable conditions predicted above the threshold and unsuitable conditions predicted in the text that follows. There are a variety of methods for selecting threshold values (Liu *et al.* 2005), and the best strategy may vary with different research and management objectives (Jimenez-Valverde and Lobo 2007; Loiselle *et al.* 2003; Robinson *et al.* 2010). In particular, the potential costs of omission errors (predicting absence at a true presence site) must be weighed against the potential costs of commission errors (predicting presence at a true absence site) for the system under study. For conservation applications with rare and highly endangered species, there is a delicate balance to be struck: too-conservative a threshold (underestimation) may cause failure to correctly identify new populations in need of protection (Robinson *et al.* 2010), whereas too-lenient a threshold (overestimation) may cause misdirection of critical conservation actions (Loiselle *et al.* 2003). In such cases, particularly with small sample sizes and incomplete absence data, Pearson *et al.* (2007) recommend using the "lowest presence threshold": the lowest predicted value for habitat suitability at any observed presence locality. However, the locality with the lowest presence locality for our data set was a clear outlier (see Results), suggesting that the lowest presence threshold might overestimate considerably the potential distribution of *Cebus albifrons aequatorialis*. Therefore, we examined several other commonly used candidate threshold values. Two recent studies that evaluated the performance of a variety of threshold-selection methods agree that the method introduced by Manel *et al.* (2001) performs well (Jimenez-Valverde and Lobo 2007; Liu *et al.* 2005). This threshold corresponds to the value at which discrimination accuracy is maximized between true presences and pseudo-absences (random background points). Specifically, it uses the point on the receiver operating characteristic curve at which the sum of sensitivity and specificity for the training data is maximized (Manel *et al.* 2001). Two additional lines of evidence suggest that this threshold value is appropriate for our data set. First, it happens to be equal to the next lowest presence threshold if we were to exclude the one extreme outlier, as well as the commonly used 10-percentile presence threshold. Second, this value nearly minimized the number of omission and commission errors among the survey locality data (presence localities below the threshold and absence localities above the threshold).

Suitable Habitat Assessment and Population Estimates

Using the maximum training sensitivity plus specificity threshold (Manel *et al.* 2001), we calculated the total area of habitat predicted to be suitable for *Cebus albifrons aequatorialis* across its entire geographic range. This resulted in many small, isolated pixels (area 0.93 km^2) that are unlikely to be capable of supporting viable populations of this primate. To remove these pixels, we applied a majority filter to the suitable habitat map (Fig. 3). This process replaced suitable/unsuitable cells if at least half of the four neighboring orthogonal cells were predicted to be of the other suitability category. We also

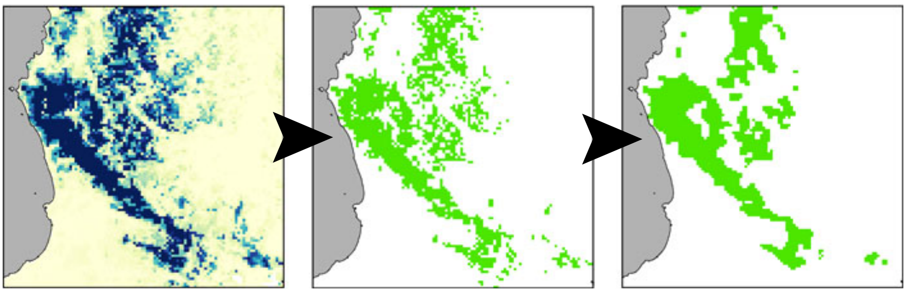

Fig. 3 Illustration of applying the habitat suitability threshold and majority filter method used to discriminate suitable from unsuitable habitat, remove isolated pixels, and clean the boundaries of the areas predicted to be suitable for *Cebus albifrons aequatorialis*. The left panel shows raw output from the Maxent algorithm, with darker shading representing more suitable habitat. The middle panel shows the resulting habitat estimate after applying the suitability threshold; all areas with predicted suitability below the threshold are excluded. The right panel shows the final habitat estimate after applying the majority filter.

calculated a coarse estimate of the remaining total population size by multiplying the median population density across all sites for which data were available (2.4 individuals/km^2; Jack and Campos 2012) by the area of remaining suitable habitat. The median population density reported by Jack and Campos (2012) excludes the presence locality Jauneche, which was a clear outlier, with very low estimated suitability in this study (see Results) but extraordinarily high population density, perhaps owing to the abundant crops on which the monkeys feed (Jack and Campos 2012).

Results

Model Predictions and Performance

The area under the receiver operating characteristic curve for the habitat suitability model was 0.971, which indicates that the model was highly effective at discriminating presence localities from random background pixels. The predicted suitability values for all 42 survey localities are plotted in Fig. 4. The model was reasonably successful at discriminating the 19 presence localities from the 23 absence localities, which were not used to generate the model (18/19 presence localities and 19/23 absence localities categorized correctly), despite the fact that the absence localities represent forested areas, some of which are under protection. The potential

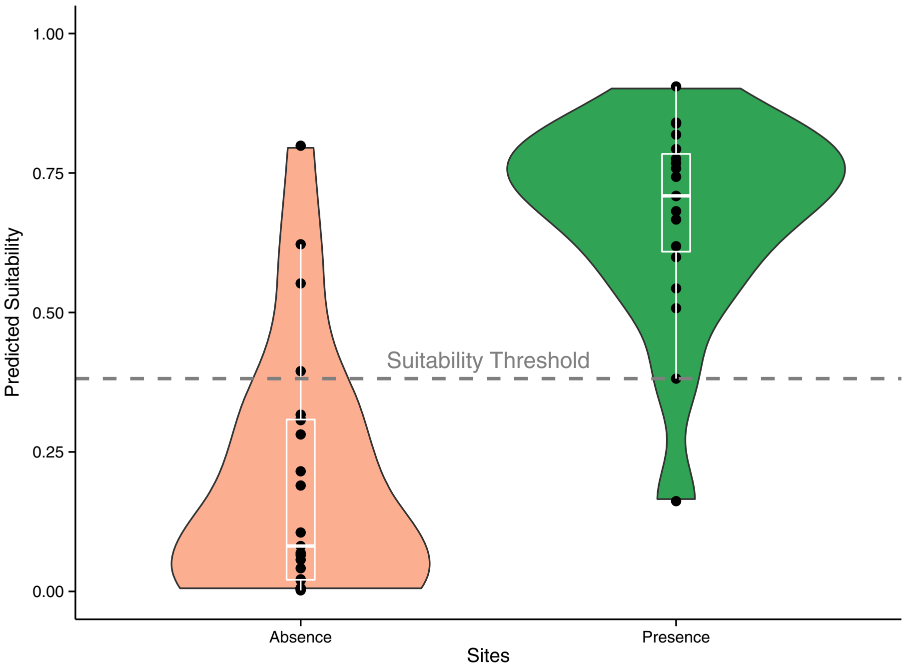

Fig. 4 Violin plots of predicted habitat suitability for *Cebus albifrons aequatorialis* at presence and absence localities. Violin plots combine elements of standard box plots with kernel density plots, and are useful for visualizing dispersion and skew in the data. Black circles represent the 42 localities, and the white boxplots show median values as well as first and third quartiles. The dashed horizontal line represents the threshold value used to discriminate suitable from unsuitable habitat.

distribution map identified four general regions containing substantial patches of high predicted suitability: the Chongon-Colonche hills near the coast of south-central Ecuador and west of Guayaquil, the northern coast of the Manabí province in Ecuador, the foothills of the Andes Mountains in southern Ecuador, and the Tumbes and Piura regions of northern Peru (Fig. 5).

Environmental Factors and Habitat Suitability

Of the 13 environmental variables investigated, 4 provided important contributions to the habitat suitability model (Table II). The MAXENT jackknife analysis revealed that the most important variable for determining habitat suitability was percent tree cover. Inspection of the individual variables' response curves —which show how predicted suitability changes as each environmental variable changed while keeping the other variables at their mean values— indicated that habitat suitability is maximized when percent tree cover is ≥25%, above which suitability appears to plateau (Fig. 6). The

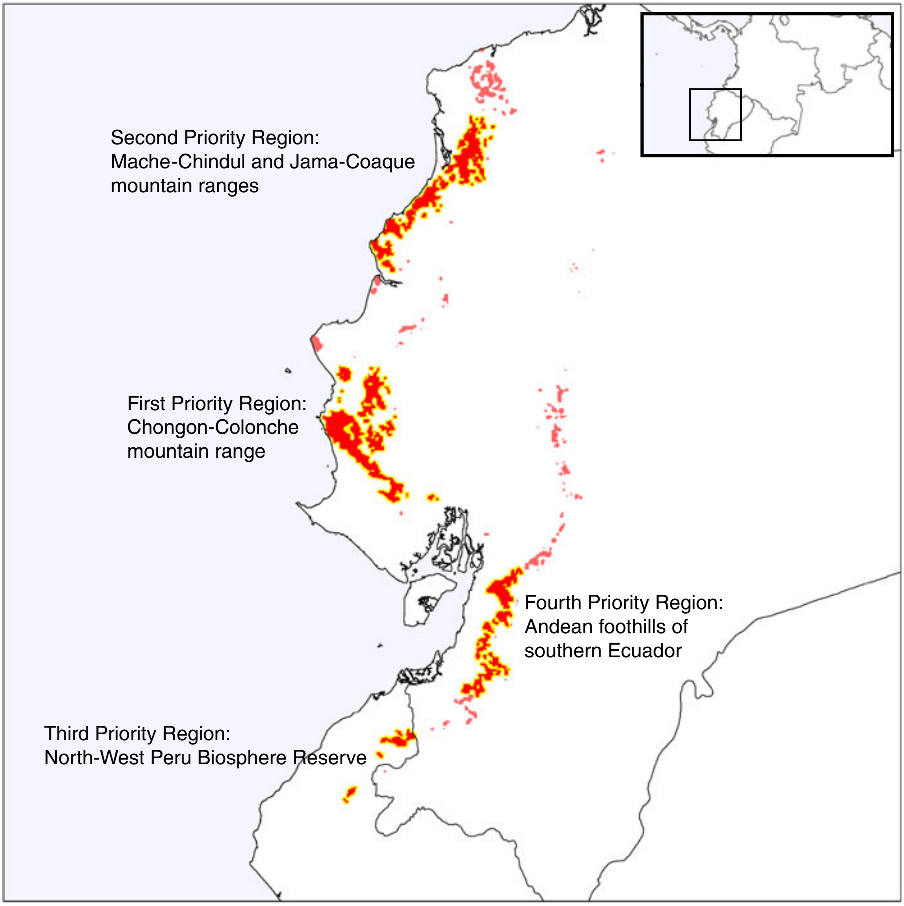

Fig. 5 Map of suitable habitat (red shaded areas) for *Cebus albifrons aequatorialis* across its entire geographic range. Suitable areas contained within the four indicated priority regions (bright red with a yellow outline) are of particular conservation concern.

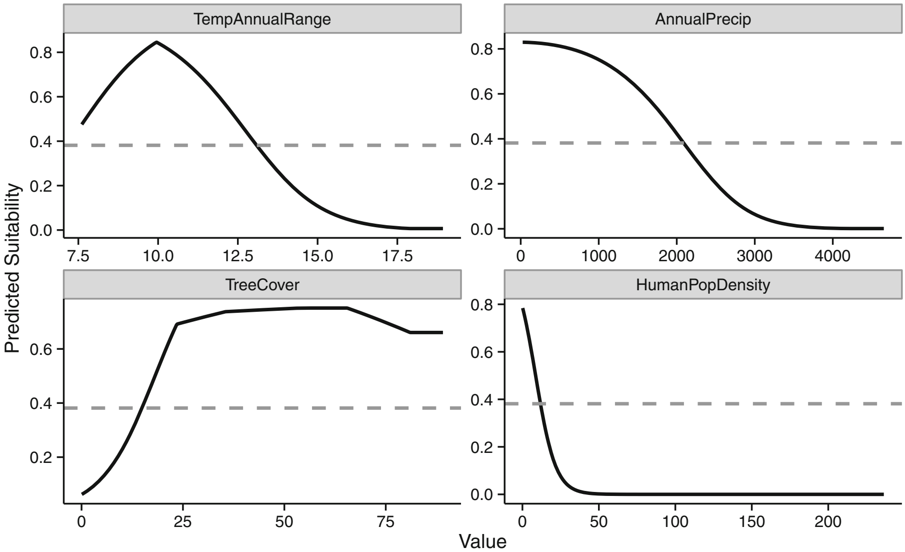

Fig. 6 Response curves for four variables found to be important for determining habitat suitability for *Cebus albifrons aequatorialis*: temperature annual range (°C), annual precipitation (mm), percent tree cover (%), and square root transformed human population density.

importance attributed to percent tree cover was evident in all four measures of variable importance (Table II). In accordance with this finding, land-cover category was identified as important in three of the measures of variable importance (Table II), with the most suitable habitat occurring in deciduous or evergreen broadleaved forest, or to a lesser degree, forested cropland mosaic. Annual precipitation, temperature annual range, and human population density appeared to be relatively important in some tests but not others. These discrepancies commonly occur with the MAXENT algorithm owing to correlations among the predictor variables, but nonetheless suitable habitat tended to exhibit relatively low annual precipitation, low annual temperature range, and low human population density (Fig. 6). Percent tree cover and land cover exhibited the highest gain when used in isolation to build the model (Table II), which indicates that these two variables contained the most relevant information for predicting habitat suitability. The removal of percent tree cover, annual precipitation, and land cover caused the greatest reduction in gain during the jackknife procedure (Table II), which indicates that these three variables contained the most information that was absent from the other variables.

Habitat Suitability and Maximum Population Size

The habitat suitability threshold that maximized discrimination accuracy was 0.381. Applying this threshold to the model results produced an estimate of 5208 km^2 of suitable habitat (shaded area in Fig. 5) and a total carrying capacity of 12,500 individuals if all habitats were occupied at the median population density. The jackknife validation procedure indicated that this threshold-based scenario was significantly better than random at predicting the presence of *Cebus albifrons* *aequatorialis* in the study region (prediction success 12/19, $P \approx 0$). The apparently modest success among jackknife iterations at correctly predicting the excluded locality as a presence point indicates that the specific localities included in each model influenced the resulting habitat estimates considerably. This is likely due to our small sample size, which further justifies our decision to use all presence points for the final model. The very small *P*-value despite this modest success rate is due to the fact that only a small proportion of the study area was considered suitable (mean 0.0753, range 0.0400–0.0964).

Discussion

Habitat Associations of the Ecuadorian Capuchin

Although extant populations of *Cebus albifrons aequatorialis* occur in a range of habitats including dry forest, mature moist forest, and premontane forest (Albuja and Arcos 2007; Jack and Campos 2012; Parker and Carr 1992), our results suggest that their continued survival may well depend on conservation of the acutely threatened Ecuadorian and Tumbes-Piura tropical dry forests with which the species appears most closely associated. The environmental conditions that our model predicted to be ideal for supporting *Cebus albifrons aequatorialis* —including ≥25% tree cover, mild temperature seasonality, annual precipitation below 2000 mm, and low human population density— more accurately describe tropical dry forest than other forest biomes in this region. A threshold value of 25% tree cover has been used previously with MODIS VCF data to discriminate forest from nonforest pixels (Liknes *et al.* 2010). Our finding that habitat suitability reaches a plateau between 25% and 100% tree cover is consistent with our previous observations that *Cebus albifrons aequatorialis* readily exploits a variety of habitat types ranging from disturbed areas and secondary forest to mature forest. Pixels with tree cover values at the lower end of the suitable range (25–60%) are likely to represent relatively open woodlands and secondary forest (M. C. Hansen *et al.* 2000). As in a recent study that identified areas in Mexico likely to be inhabited by primates (Vidal-García and Serio-Silva 2011), the results of our modeling approach facilitate the difficult task of establishing clear conservation priorities by revealing unsurveyed areas that may harbor undetected populations and identifying the areas that may be most capable of supporting viable *Cebus albifrons aequatorialis* populations in the long term.

The total current extent of Ecuadorian and Tumbes-Piura dry forest in western Ecuador and northern Peru was estimated recently to be 7940 km^2 (Portillo-Quintero and Sánchez-Azofeifa 2010), which is comparable to, but somewhat larger than, the 5028 km^2 of suitable habitat estimated by our potential distribution map. A visual comparison between our habitat estimate and the tropical dry forest map in Portillo-Quintero and Sánchez-Azofeifa (2010) indicates that our habitat estimate excludes sizable areas of relatively sparse dry forest that were included in Portillo-Quintero and Sánchez-Azofeifa's estimate, especially in central Manabí and northern Guayas provinces western Ecuador. However, our estimate includes additional regions humid premontane and lower montane cloud forest in the Andean foothills of central and southern Ecuador.

A Realistic Population Size Assessment

Although we have estimated the total carrying capacity of the remaining suitable habitat to be 12,500 total individuals, we make the case below that the true total population size of *Cebus albifrons aequatorialis* is likely to be considerably smaller. First, the carrying capacity figure assumes that all suitable habitats are occupied. This assumption is certainly false, as extant populations of *Cebus albifrons aequatorialis* are known to be absent from some highly suitable areas that have been extensively surveyed (Fig. 4), and they have no doubt been extirpated from other unsurveyed areas that may still appear to be suitable (one example is described in Jack and Campos 2012). It is possible that some extant *Cebus albifrons aequatorialis* populations occur in areas predicted to be unsuitable in our model; Jauneche (Fig. 1, locality 17) is one such locality. However, we believe that these omission errors are probably rare and are unlikely to offset the more common commission errors described above. Second, the carrying capacity figure assumes that all occupied habitats have a population density equal to the median value from sites with available data (Albuja and Arcos 2007; Jack and Campos 2012). However, four of the five sites from which population density was calculated have some form of protected status, whereas the vast majority of suitable habitat identified in our model is under no official protection. We believe it is likely that population densities of *Cebus albifrons aequatorialis* will be higher in protected forests than in unprotected forests owing to the combined effects of hunting pressure, tree felling, uncontrolled fires associated with land clearing, and other anthropogenic factors. Third, the highly fragmented configuration of suitable habitat remaining suggests that occupied patches will have suffered increased probability of local extinctions, with little chance of recolonization after a local extinction (Brooks *et al*. 2002). We currently lack sufficient data to state with confidence how much the carrying capacity figure that we calculated overestimates true population size. However, given the issues discussed in the preceding text, we believe it is not unreasonable to speculate that the true total population size may be less than half of the carrying capacity, which suggests a total population size of fewer than 6250 individuals.

Focal Regions and Conservation Priorities

We highlight four key regions, in descending order of importance, that we deem critical for the long-term survival of *Cebus albifrons aequatorialis* in western Ecuador and northern Peru (Fig. 5). These priority regions were not ranked based on a quantitative scheme for optimal resource allocation. Such an analysis —which would require a comprehensive understanding of monetary costs, the likelihood of success, and the social and political feasibility for each proposed action— is beyond the scope of this study (Game *et al*. 2013; Wilson *et al*. 2006, 2009). Given the recent history of catastrophic forest loss across western Ecuador (Dodson and Gentry 1991), all of the remaining areas containing suitable habitat for *Cebus albifrons aequatorialis* should be considered highly threatened and irreplaceable. Our ultimate goal for setting conservation priorities here is to maximize the number of *Cebus albifrons aequatorialis* individuals remaining across the region. Thus, we give greater priority to areas with 1) greater extent of continuous and/or undisturbed forest and 2) greater likelihood of conservation success due to existing (though possibly inadequate) protection.

The area of highest priority is located along the Chongón-Colonche range of coastal mountains in the Guayas and Manabí provinces of Ecuador (Fig. 5, First Priority Region). We believe that conservation efforts aimed at improving protection in the Chongon-Colonche range, including Machalilla National Park (Fig. 1, locality 19), could have the most significant impact on this primate's long-term survival prospects. There are three main reasons for this: 1) the Chongon-Colonche range represents the largest and most continuous region of high predicted suitability across the entire geographic range of *Cebus albifrons aequatorialis*; 2) although officially protected, Machalilla National Park suffers from intense human pressures that have led to habitat degradation in many areas of the park (Best and Kessler 1995; Parker and Carr 1992); and 3) between Machalilla National Park and Cerro Blanco (Fig. 1, locality 23), there is a large area that currently has no official protection aimed at preserving biodiversity. South of Machalilla National Park, the tropical dry forest covering the upper parts of the Chongon-Colonche range has been managed since 1994 to maintain its important function as a rain catchment area, but the wildlife is not protected (Best and Kessler 1995). Improving the protection of biodiversity in the Chongon-Colonche range could have long-term ancillary benefits for human inhabitants in the region, as the preservation of pollinating and seed-dispersing animals may be necessary for the forested hills to retain their economic value as a rain catchment. Finally, the Chongon-Colonche range has great potential as an ecotourism destination, given its unique flora and avifauna, which includes many charismatic range-restricted or endemic species (Best and Kessler 1995; Parker and Carr 1992). The largest continuous block of suitable habitat in this region extends *ca*. 80 km from Machalilla National Park in the northwest to the town of Simón Bolívar in the southeast. About 20 km north of this area, near Cerro Achi (La Planada, locality 18 in Fig. 1), there is another small area of high predicted suitability that is separated from the former area by gaps of low suitability within and just outside of Machalilla National Park. There are at least four localities in this region inhabited by *Cebus albifrons aequatorialis* (Albuja and Arcos 2007; Hores 2006; Jack and Campos 2012; Parker and Carr 1992). A fifth inhabited site, the Cerro Blanco Protected Forest (Fig. 1, locality 23), is separated from the main block of suitable habitat in the Chongon-Colonche range by *ca*. 20 km of unsuitable habitat.

The second area of high priority is a chain of small suitable areas in the Mache-Chindul and Jama-Coaque mountain ranges, which extend north from Bahía de Caráquez to Mache-Chindul National Park (Fig. 1, locality 2) along the northern coast of Ecuador's Manabí Province and southern Esmeraldas Province (Fig. 5, Second Priority Region). The suitable areas in Manabí appear highly discontinuous, with many relatively small and isolated forest fragments separated by gaps of unsuitable habitat. Surveys revealed the presence of *Cebus albifrons aequatorialis* in at least six of these fragments, two of which are privately owned, protected areas: the Lalo Loor Dry Forest Reserve (Fig. 1, locality 5) and the Tito Santos Biological Reserve (Fig. 1, locality 6) (Albuja and Arcos 2007; Jack and Campos 2012). Forest fragments in this region are gravely threatened by logging, cattle, and human settlement. A recent local extinction of *Cebus albifrons aequatorialis* has been recorded in at least one such forest fragment (Jack and Campos 2012). The largest tract of suitable habitat in this region lies within and around the southern portion of Mache-Chindul National Park. An extant population of *Cebus albifrons aequatorialis* is known to occur here, and although the park remains poorly surveyed, it may harbor biodiversity of potentially great conservation importance (Best and Kessler 1995). An effective conservation plan for this region should focus on shoring up existing protection by supporting the efforts of private reserve owners, promoting connectivity among remaining forest fragments via reforestation along biological corridors, and determining the conservation value of Mache-Chindul National Park.

The third priority area includes two sites located in the Tumbes and Piura regions of northern Peru with high predicted suitability for *Cebus albifrons aequatorialis*, the Tumbes Reserved Zone (Fig. 1, locality 43) and the Cerros de Amotape National Park, both of which are nationally protected areas within the North-West Peru Biosphere Reserve (Fig. 5, Third Priority Region). Both sites are reportedly inhabited by *Cebus albifrons aequatorialis* (Cornejo and de la Torre 2008; Encarnacion and Cook 1998). The North-West Peru Biosphere contains the largest and most continuous tract of relatively undisturbed forest in the Tumbesian Region, and it should therefore be considered of high conservation importance. Owing to its size, this region could potentially harbor relatively large primate populations. At present, the North-West Peru Biosphere apparently experiences lower levels of human disturbance than the other regions discussed here owing to its remoteness and the low human population density in surrounding areas (Best and Kessler 1995), making it a promising area for targeted conservation initiatives.

The fourth priority region is located in southern Ecuador, where there are numerous small areas of humid forest along the foothills of the Andes in the provinces of Azuay, El Oro, and Guayas (Fig. 5, Fourth Priority Region). The largest of these patches encompasses the 2500-ha private reserve Cerro de Hayas-Naranjal (Fig. 1, locality 27), which is the only protected site in this region known to be inhabited by *Cebus albifrons aequatorialis* (Albuja and Arcos 2007). The two other inhabited sites in this region —Cerro Azul (Fig. 1, locality 34) and Cooperativa 31 de Agosto (Fig. 1, locality 30)— do not currently have protected status. There are a number of small, mostly unprotected forest fragments and private reserves in this region (Best and Kessler 1995), although *Cebus albifrons aequatorialis* is apparently absent from several that our model predicted as suitable (Albuja and Arcos 2007). We emphasize that in addition to protecting inhabited core areas, an effective conservation plan for *Cebus albifrons aequatorialis* should promote connectivity among the remaining forest patches in these regions. Therefore, it is important not to ignore areas of lower predicted suitability that may function as corridors between or buffer zones around the core areas.

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