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RESEARCH ARTICLE

Modelling habitat suitability for a potential flagship species, the hooded capuchin, of the Paraguayan Upper Paraná Atlantic Forest

Rebecca L. Smith[1,2] | David Lusseau[2,3]

[1]Centro IDEAL, Fundación Para La Tierra, Pilar, Paraguay

[2]School of Biological Sciences, University of Aberdeen, Aberdeen, UK

[3]National Institute for Aquatic Resources, Technical University of Denmark, Kgs. Lyngby, Denmark

Correspondence
Rebecca L. Smith, Centro IDEAL, Fundación Para La Tierra, Mariscal José Félix Estigarribia 321, Pilar, Ñeembucú, Paraguay.
Email: rebecca@paralatierra.org

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Abstract

1. The hooded capuchin (*Sapajus cay*) is an adaptable, generalist primate species found throughout eastern Paraguay with preferences for the Paraguayan Upper Paraná Atlantic Forest (BAAPA). BAAPA is one of the world's most critically endangered terrestrial habitats with more than 90% of its original cover lost to industrial agriculture. Given its charismatic characteristics, the capuchin species is a candidate flagship species for this ecoregion; however, its habitat preferences in BAAPA degraded fragments are unknown.
2. We develop a species distribution model using MAXENT to determine the remotely sensed microhabitat features associated with habitat suitability in forests that had experienced different levels of degradation. The model was fitted to presence-only observations at two sites, Rancho Laguna Blanca and Nueva Gambach, to determine how hooded capuchin distribution is associated with remotely sensed habitat features in BAAPA fragments.
3. Wetness (mean and standard deviation), a measure of soil moisture and canopy closure, was found to be the most important driver at both sites. The capuchins showed a preference for more mature forest, bamboo dominated forest and flooded forest (that has experienced little selective logging in the past).
4. The capuchin was a forest obligate species and avoided crop fields. The monkeys were less likely to be found in degraded areas, even though they were still forested. As Paraguayan deforestation involves the creation of large crop fields separating BAAPA fragments, the probability that the hooded capuchin can move between those fragments is low.
5. The hooded capuchin is a candidate flagship species for an agroforestry reforestation programme to reconnect BAAPA fragments. We propose that combining native tree corridors with shade grown yerba mate and slash pine plantations would create habitat for the capuchin and other wildlife while helping to alleviate poverty in the area and the pressure that this causes on the forests' natural resources.

KEYWORDS
capuchin, ecological requirements, flagship, MAXENT, remote sensing, SDG 8, SDG 15

1 INTRODUCTION

We have now exceeded safe operating levels for biodiversity loss and forested area loss (Steffen et al., 2015). Tropical and subtropical forests are amongst the most biodiverse habitats on the planet yet are also the most threatened. These threats include anthropogenic activities such as illegal logging, expansion of industrial agriculture and fires (Laurance, 2013; Peres et al., 2006). In some regions, deforestation can be uniform, eroding the edges of larger tracts of intact forest, but in other areas forests are lost or degraded through more complex habitat fragmentation. Fragmentation causes large blocks of forests to be divided into ever-smaller areas, increasingly isolated by roads, farmland or human habitation (Wilcove et al., 1986; Zuidema et al., 1996). While at a superficial level this process may appear less damaging to the environment than 'slash and burn' clearing, fragmentation can result in the decline, and even regional extinction, of native tree species through reduced seedling recruitment (Tabare, 2004) and increased edge effects (Harper et al., 2005). It increases access to forest interiors for hunters and loggers (Kosydar et al., 2014) and creates barriers to gene flow, reducing within-species genetic diversity (Wang et al., 2017).

One of the world's most endangered forested habitats is the Atlantic Forest of South America. This forest once extended through Brazil, eastern Paraguay, northern Argentina and into Uruguay but it has been decimated with most of what remains existing in fragments of less than 100 ha (Zanella et al., 2012). In Paraguay, the Upper Paraná Atlantic Forest (BAAPA) is a highly diverse ecosystem (Catterson & Fragano, 2004), characterized by deciduous, mesophytic, broadleaf plants (Lowen et al., 1996), that covered around 86,000 km^2 until around the 1940s (Da Ponte, Kuenzer, et al., 2017). By 2000, Paraguay suffered one of the highest deforestation rates in the world (~2000 km^2/year: Da Ponte, Roch, et al., 2017) mainly to cater to expanding industrial agriculture, especially soybean monocultures, and only around 25% of the forest remained intact (Huang et al., 2006). Deforestation rate in eastern Paraguay drastically slowed after the declaration of the Zero-Deforestation law (2542/04) enacted in 2004. However, clearing did not halt with a further 7500 km^2 being destroyed by 2016, or about 35% of what remained in 2000 being lost (Da Ponte, Kuenzer, et al., 2017; Da Ponte, Roch, et al., 2017).

Within the BAAPA, there are around 19 publicly and privately owned areas with varying degrees of protection. In total, protected areas within the BAAPA region only account for around 3.4% of the land (Catterson & Fragano, 2004). The largest and most famous are Área para Parque San Rafael (Tekoha Gusau) and Reserva Natural del Bosque Mbaracayú (a private reserve managed by Fundación Moises Bertoni)—these sites are the only two areas of BAAPA in Paraguay of more than 50,000 ha. San Rafael/Tekoha Guasu is an 'area designated to become a National Park' and consists of more than 40 different properties that are privately owned. Though its official area is 73,000 ha, it has suffered heavily from logging and forest fires in the last decade. Outside of these areas, most of the remaining BAAPA exists in small, isolated fragments that have experienced significant degrees of degradation.

Conservation of tropical forests such as the BAAPA is of global importance for human health and well-being. Intact BAAPA can store an average of 223.5 tons of carbon/ha (Gasparri et al., 2008) and even secondary BAAPA can sequester 13 tons of carbon per hectare per year (Calmon et al., 2011). However, BAAPA conservation for its own sake is hard to prioritize in Paraguay, where the economy is dominated by agriculture (particularly soybean production and cattle ranching).

A single charismatic species (a flagship) can increase support for conservation initiatives more than the promotion of programmes focused on saving ecosystems (Caro et al., 2004; Dietz et al., 1994; McGowan et al., 2020; Senzaki et al., 2017; Thomas-Walters & Rihani, 2017). Flagship species that are properly selected can improve both the ability to raise funds and direct where the funds should be invested for maximum conservation impact (McGowan et al., 2020). Primates are particularly good flagship species. Their obvious similarities with humans make them easy to connect with emotionally and their long life histories and rich social lives qualify them as the ideal face of a long-term project such as the conservation and regeneration of a forest habitat. Paraguay does not have the primate diversity of some of its neighbours (with only five species recorded in the country). The hooded capuchin (*Sapajus cay*) is mainly found in the highly populated Oriental region (east of the Paraguay River) in what remains of the Upper Paraná Atlantic Forest (as well as marginally into the gallery forests of the Cerrado [Smith et al., 2021]). The species is the most widely recognized of Paraguay's primates by the general public (Smith et al., 2016) and is a well-liked animal (Smith, Ayala Santacruz, et al., 2018). It has the potential to be a flagship species for BAAPA conservation.

Previous studies have shown that hooded capuchins in Paraguay can alter their diets in forests of differing 'quality' or levels of disturbance (Smith, 2021). These monkeys appear to require less space than other capuchin species (genera *Cebus* and *Sapajus*) with small home ranges of 50–80 ha (*Sapajus nigritus*: 5–465.3 ha [Di Bitetti, 2001; Izar et al., 2007; Rímoli, 2001]; *Sapajus flavius*: 270 ha [de Souza Lins & Ferreira, 2019]; *Sapajus libidinosus*: 345 ha [Presotto et al., 2018]; *Sapajus apella*: 320 ha [Gómez-Posada et al., 2019]). In degraded Paraguayan BAAPA, hooded capuchins were found to preferentially select sleeping sites displaying characteristics of more mature forests such as taller trees with higher diameter at breast height, greater canopy connectivity and more main branches (Smith, Hayes, et al., 2018). Even when these monkeys have access to more 'undisturbed' habitat, they have been observed to use arboreal crop plants, such as Slash pine plantations, for both feeding and sleeping sites (Smith, Hayes, et al., 2018; Smith, 2021).

Identifying what environmental factors are associated with habitat selection is an important factor in planning effective conservation and habitat protection measures (Fitzgerald et al., 2018). Species distribution models (SDMs) have been used widely to estimate habitat suitability based on species occurrence and environmental conditions when data for habitat models are lacking (Booth et al., 2014). SDMs can help make inferences about environmental variables associated with species presence (Fourcade et al., 2014; Liu et al., 2020) and are useful for estimating the likelihood of a species to occur in an area that has not been sampled but of which environmental characteristics fall within the range of characteristics sampled in the fitted SDM (Hernandez et al., 2008). SDMs based on a maximum entropy (Maxent) fitting algorithm are able to produce useful models in data-poor conditions (Hernandez et al., 2008; Gouveia et al., 2016). Remote sensing data, including data from LANDSAT satellites, have been used to assess species distribution, often in relation to land usage and habitat loss (Legaard et al., 2015), and provide a rapid and cost-effective way to inform SDM in data-poor conditions (Cavada et al., 2017).

The aim of this study was to estimate the remotely sensed habitat features associated with the occurrence of a potential flagship species for the endangered BAAPA. We compared the species occupancy patterns in both a small and disturbed fragment and a more mature and intact forest. To be an effective flagship species, hooded capuchins need to depend on BAAPA, yet be flexible enough for degraded BAAPA to be a suitable habitat and for coping with a wide range of potential conservation interventions.

2 | MATERIALS AND METHODS

2.1 | Permissions

Fundación Para La Tierra is a registered Paraguayan NGO (80086144) and RL Smith is registered with the RNVS programme of the Ministry of the Environment. Oral permission to carry out the work was provided by all landowners.

2.2 | Study area and sites

We surveyed two sites in two departments in the BAAPA region from January 2013 to March 2020. From January 2013 to May 2017, observations were collected in Rancho Laguna Blanca (RLB) in San Pedro department (23°49′52.0″S, 56°17′42.2″W). RLB is typical of much of the remaining BAAPA outside of protected areas with a 243-ha fragment of secondary forest completely isolated from nearby fragments by soy fields, cattle ranches and human settlements. The forest fragment had a history of human exploitation, including logging and fires, until 2010 when it was classified as a private reserve. Reserve status formally ended in February 2015 when the property was put up for sale.

From May 2017 to March 2020, observations were collected at Nueva Gambach (NG), a property at the southern tip of Área para Parque Nacional San Rafael/Tekoha Guasu in Itapúa, San Rafael (26°62′62.5″S, 55°66′52.2″W). The NG property contains 150 ha of near-undisturbed forest surrounded on three sides by organic soy fields and connected at its northern border to the rest of San Rafael/Tekoha Guasu. With little to no primary or undisturbed (old growth forest that has not experienced a history of selective logging or anthropogenic alteration) BAAPA left in Paraguay (Da Ponte, Roch, et al., 2017), the forest of San Rafael/Tekoha Guasu is as close to undisturbed as remains in the country and for the purpose of this study will be classed as 'near-undisturbed'. We are defining disturbance as contemporary logging, fire damage or other extractive activity and are not including the historical use of forest by indigenous people. This forest is of extremely high conservation importance, being categorized by WWF as one of the top 200 most important areas of biodiversity globally (Esquivel et al., 2019).

2.3 | Occurrence data

At RLB, two groups of semi-habituated hooded capuchins were followed from dawn until dusk 6 days a week. At NG, a semi-habituated focal group of hooded capuchins was followed from dawn until dusk (and three other non-habituated groups opportunistically whenever they were encountered) 15 days per month. All data were collected by the first author. The locations of focal groups were recorded every 30 min using a Garmin 62S handheld GPS unit. Capuchin monkeys can travel at speeds from 0.01 m/min to more than 25 m/min (Crofoot, 2013; Janson & Di Bitteti, 1997) and to avoid pseudoreplication, if the monkeys did not move more than 100 m during the 30-min period, a second GPS point was not recorded at the same location. If it was not possible to enter the area where the monkeys were, then the GPS location was taken as close as possible to them and the distance in metres and direction in degrees from observer recorded. The point was then manually moved using the programme Garmin Basecamp. At both sites, location was recorded at the centre of the largest subgroup, and if subgroups were more than 100 m apart then a location was recorded for each. As well as direct observations, GPS locations of indirect evidence such as faecal samples or appearance on camera traps were also recorded. At both sites, the full area was searched comprehensively. A total of 1200 occurrence points were recorded throughout the study period: 679 at RLB and 521 at NG.

2.4 | Remotely sensed predictor variables

Raster layers at a 30×30 m^2 spatial resolution (the resolution of the LANDSAT satellite sensors for visible, NIR and SWIR spectrums as well as the smallest resolution to give the maximum detail within the monkey's small home range [Smith, unpublished data]) were acquired and prepared in R (version 4.0.3) using LANDSAT 8 imagery. For RLB, 102 passes were obtained between January 2013 and December 2017 and at NG 24 passes were obtained between May 2017 and July 2018. The data for LANDSAT 8 passes has not yet been made available for 2019–2020. Images with more than 10% cloud cover were removed. The images were stacked and used to derive mean and standard deviation for the Normalized Difference Vegetation Index (NDVI). NDVI is widely used in ecological research as a measure of the healthy, photosynthetically active vegetation within each raster cell (Fitzgerald et al., 2018; Petorelli et al., 2011). NDVI is calculated from the red and near-infrared bands (NIR) of the satellite image that are created by reflectance from red light wavelengths absorbed by photosynthetic pigments like chlorophyll and NIR wavelengths scattered by the mesophyll cells of leaves (Baig et al., 2014; Campbell & Wynne, 2011; Fitzgerald et al., 2018; Petorelli et al., 2011).

NDVI values range from −1, which indicates water or bare ground, to +1 which indicates thick and healthy vegetation. We also determined microhabitat characteristics using Tasselled Cap Transformation (TCT) of the original LANDSAT 8 image stack. TCT compresses the bands of the original spectral data without loss of data and transforms them orthogonally into a new set of axes that are aligned with physical features, traditionally known as Brightness, Greenness and Wetness (Baig et al., 2014; Fitzgerald et al., 2018). Brightness accounts for the most variability in the image and is associated with bare soil and man-made features. Greenness is an indication of photosynthetically active vegetation (Baig et al., 2014; Fitzgerald et al., 2018) and Wetness is an indication of soil moisture (Crist et al., 1986; Fitzgerald et al., 2018) and has been found to be related to forest structure (Cohen, 1991; Cohen & Spies, 1992). Landsat 8 images were stacked and mean and standard deviation for Brightness, Greenness and Wetness were derived from the stacks (January 2013 to December 2017 for RLB and May 2017 to January 2018 for NG).

We tested for seasonal variability in the effect of the environmental variables on monkey occurrence (Hot and Cold seasons). The Hot season included data collected between October and March and the Cold season between April and September. Mean and standard deviation for NDVI, Brightness, Wetness and Greenness were calculated for each site for the entire study period as well as for each season.

2.5 | Modelling approach

We determined the contribution of the environmental variables to capuchin habitat suitability, using a maximum entropy SDM based on presence-only data implemented in MaxEnt version 3.3.3 (using package Dismo [Hijmans et al., 2020], R version 4.0.3) (Philips et al., 2006). The Maxent algorithm has been consistently shown to perform well with presence-only data (Fitzgerald et al., 2018; Hernandez et al., 2008; Philips et al., 2006; Widyastuti et al., 2020) and estimates the probability of a species being present in a given location based on occurrence data and user-selected variables (Fitzgerald et al., 2018; Franklin, 2009; Philips et al., 2006). We determined habitat suitability (the predicted occurrence rate of monkeys in a given area) using model selection and generated response curves showing the importance of each of the environmental variables to the predicted occurrence rate of capuchin monkeys for the best model. We observed the environmental variable value under each occurrence observations and we generated 10,000 pseudo-absence observations within each study area.

Eight models were run per site where the response variable was subsetted in different ways: (1) all the site occurrence data; (2) all occurrence data for both sites; (3) seasonal occurrence data, where occurrence data at a given site were separated by hot and cold season; and (4) seasonal occurrence data for both sites together, where all the occurrence data (RLB and NG) were considered for each season separately. Model fit and predictive performance were evaluated using AUC (area under [ROC] curve) and PCC (percentage correctly classified) estimates. The AUC measures the probability that the monkeys will be present at a known location (i.e. the habitat is suitable), will be ranked higher than a randomly chosen background location and is a value ranging from 0 to 1 (with 0.5 indicating the probability of random prediction and 1 indicating perfect prediction [Jie et al., 2020]). Values over 0.7 are considered to be ecologically relevant, meaning that there is a greater-than-random chance that a presence site selected at random will have a higher value than a background site selected at random (Elith et al., 2008; Fitzgerald et al., 2018). The PCC (implemented using *PresenceAbsence*; Freeman & Moisen, 2008) describes how many of the test sightings were correctly predicted by the model. The threshold was set to 0.5 and the mean AUC and PCC for each model were obtained by using a 10 k-fold cross validation (Wich et al., 2012) using the R package *cvTools* (Alfons, 2015).

2.6 | Habitat classification

While remotely sensed observations provide microscale features of the areas occupied by monkeys, as well as how it varies intra-annually, we also need to know whether the monkey's habitat is representative of BAAPA. Habitat surveys were conducted at both sites using the quarter-point method (Ganzhorn et al., 2011). Plots (20 × 20 m at RLB and 100 × 100 m at NG) were used and the results extrapolated to give results per hectare (Smith, Hayes, et al., 2018). Tree diameter at breast height (DBH) was calculated using a measuring tape to give the circumference and dividing by pi to give the diameter. Tree heights were measured using a clinometer. We used these data and other physical characteristics to classify areas of the study sites into 14 broad categories (Table 1). Habitat polygons were created for both sites using Quantum GIS 3.18.3-Zürich (QGIS, 2021). Broad-scale land cover maps alone can miss key habitat features and combining this coarse, temporally fixed habitat categorization with remotely sensed features provides a more complete understanding of habitat requirements (Oeser et al., 2020; Ryan et al., 2006).

2.7 | Association between predicted occurrence rate and habitat types

Once we could predict the capuchin monkey's occurrence rate at both sites using the SDM, we could then assess whether they were, on

TABLE 1 Habitat types and descriptions at RLB and NG sites

Habitat type	Description	Present at
High Canopy "Undisturbed" Forest	High, closed canopy (18–33 m), old growth forest, little undergrowth and no history of selective logging. Hard wood species abundant.	NG only
Older Growth Forest	Mid-height (10–16 m), more open canopy. Dense undergrowth and few hard wood species.	RLB only
Degraded Forest	Secondary forest with a history of heavy selective logging (until 2010)	RLB only
Flooded Forest	Mid-height canopy forest (history of selective logging). Forest floor completely flooded.	RLB only
Swamp	Open canopy with swampy (but not flooded) understory. Dominated by Pindo Palms and shorter trees.	Both sites
Chachi Forest	High canopy forest with several streams and small rivers and undergrowth dominated by the tree ferns (*Alophilia* sp. and *Cyathea* sp.)	Both sites
Bamboo Dominated Forest	Taller canopy forest with understory and mid-canopy layer dominated by two native bamboo species: *Chusquea ramosissima* (Pocaece) and *Guadua chacoensis* (Poaece).	Both sites
Burned area	Cleared area with no large trees, recovering from a large forest fire in August 2013.	RLB only
Cattle Field	Cleared cattle field, invasive grass species, few large trees with no connected canopy.	Both sites
Soy Field	Monoculture crop fields—mainly planted with soy beans but occasionally with maize or wheat.	Both sites
Grassland	Mesopotamian Flooded Grasslands	NG only
Beach/Human Habitation	Beach with houses and tourist centre.	RLB only
Pine Plantation	Plantation of slash pines (*Pinus elliottii*)	NG only
Lake	RLB—spring-fed lake. NG—stream-fed (man-made) lake.	Both sites
Transitional forest	Drier forest where BAAPA meets the Cerrado ecosystem.	RLB only

average, more likely to occur in a particular habitat. To do so, we fitted a generalized linear model with beta-distributed errors to assess the association between the SDM-predicted occurrence rate for the spatial points used to fit the SDM and the habitat type estimated at each point. To account for spatial autocorrelation, we included as explanatory variables Moran eigenvectors defined from the coordinates of the point assuming a spherical correlation structure. We only retained the Moran eigenvectors providing significant information about the coordinate's spatial autocorrelation, estimated using Moran's *I*. The beta-GLMs were fitted using glmmTMB (Brooks et al., 2017) and the Moran eigenvector mapping performed using spmoran (Murakami, 2021). Residual diagnostics to ensure the distribution assumptions were met were performed using DHARMa (Hartig, 2016).

3 | RESULTS

3.1 | Model performance and validation

All of the models were ecologically relevant with AUCs ranging from 0.785 to 0.949 and standard deviations ranging from 0.007 to 0.025 (Table 1). The PCC values did not vary greatly across the models, ranging from 0.849 to 0.983. The final models selected were site specific and did not vary by season for RLB (AUC: 0.943/PCC: 0.928) or NG (AUC: 0.838/PCC: 0.890) (Table 2). At both sites, the final models showed that the most important variable in predicting occurrence was Mean Wetness (Figures 1 and 2). For RLB, mean Wetness (~70%), mean NDVI (~20%) and the standard deviation of the NDVI (~10%) were the more influential variables in the final SDM (Figure 1a). For NG, mean Wetness was also the most important variable (~30%) and Mean Brightness and standard deviation of Brightness were the second and third most important variables (both between 20–25%) (Figure 2).

3.2 | Association with habitat types

At RLB predicted occurrence rates were associated with habitat types that included more mature forest, older growth forest, bamboo dominated forest and swamps, or flooded forest. At NG, the Pine plantation had the highest predicted occurrence rate of capuchin but there was no equivalent habitat type at RLB. In the natural forest at NG, the habitat types most likely to have capuchins were the swamps, chachi forest, bamboo dominated forest and high canopy forest (Figures 3a,b, 4, 5a, and 6).

TABLE 2 Model validation statistics. Final models in bold

Site	Model	Threshold	PCC	Sensitivity	Specificity	Kappa	AUC	PCC.sd	Sensitivity.sd	Specificity.sd	Kappa.sd	AUC.sd
RLB unseasonal	**Site specific**	**0.5**	**0.928**	**0.729**	**0.932**	**0.262**	**0.943**	**0.003**	**0.031**	**0.003**	**0.018**	**0.007**
RLB unseasonal	Sites combined	0.5	0.892	0.823	0.892	0.205	0.933	0.003	0.027	0.003	0.014	0.007
RLB unseasonal	Site specific seasonal	0.5	0.928	0.734	0.932	0.265	0.943	0.003	0.031	0.003	0.018	0.007
RLB unseasonal	Sites combined seasonal	0.5	0.981	0.823	0.893	0.933	0.933	0.003	0.027	0.003	0.014	0.007
RLB cold	Site specific	0.5	0.931	0.820	0.932	0.326	0.949	0.004	0.036	0.004	0.257	0.011
RLB cold	Sites combined	0.5	0.894	0.891	0.894	0.251	0.943	0.004	0.029	0.004	0.020	0.010
RLB hot	Site specific	0.5	0.930	0.655	0.933	0.210	0.936	0.004	0.052	0.004	0.025	0.009
RLB hot	Sites combined	0.5	0.895	0.786	0.897	0.175	0.934	0.004	0.045	0.004	0.021	0.008
NG unseasonal	**Site specific**	**0.5**	**0.890**	**0.481**	**0.896**	**0.939**	**0.838**	**0.003**	**0.040**	**0.003**	**0.012**	**0.013**
NG unseasonal	Sites combined seasonal	0.5	0.959	0.179	0.971	0.101	0.799	0.002	0.031	0.002	0.021	0.014
NG unseasonal	Site specific seasonal	0.5	0.891	0.487	0.893	0.092	0.837	0.003	0.040	0.003	0.011	0.013
NG unseasonal	Sites combined	0.5	0.959	0.185	0.971	0.105	0.801	0.002	0.031	0.002	0.014	0.014
NG cold	Site specific	0.5	0.849	0.573	0.855	0.095	0.843	0.005	0.051	0.005	0.014	0.015
NG cold	Sites combined	0.5	0.952	0.156	0.967	0.086	0.785	0.003	0.040	0.003	0.026	0.017
NG hot	Site specific	0.5	0.945	0.283	0.953	0.092	0.795	0.003	0.059	0.003	0.024	0.022
NG hot	Sites combined	0.5	0.983	0.217	0.993	0.228	0.803	0.002	0.054	0.001	0.054	0.025

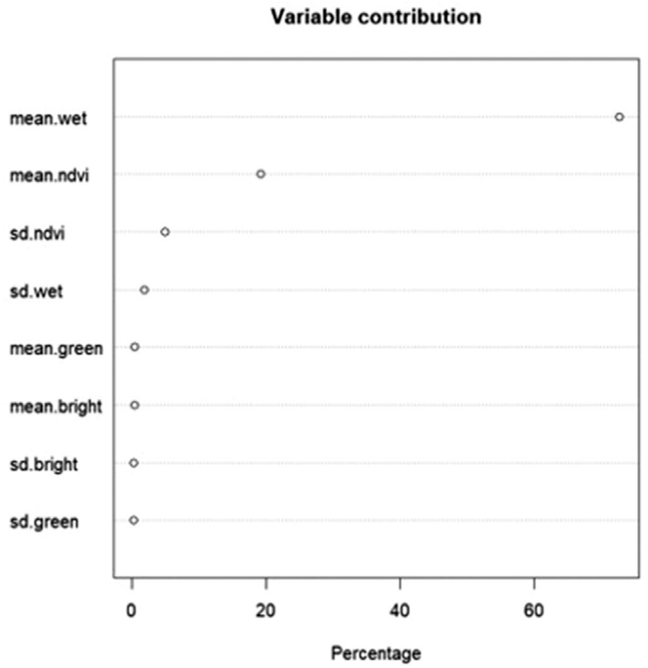

FIGURE 1 Contribution of variables of the final model for RLB site (AUC: 0.943, PCC: 0.928)

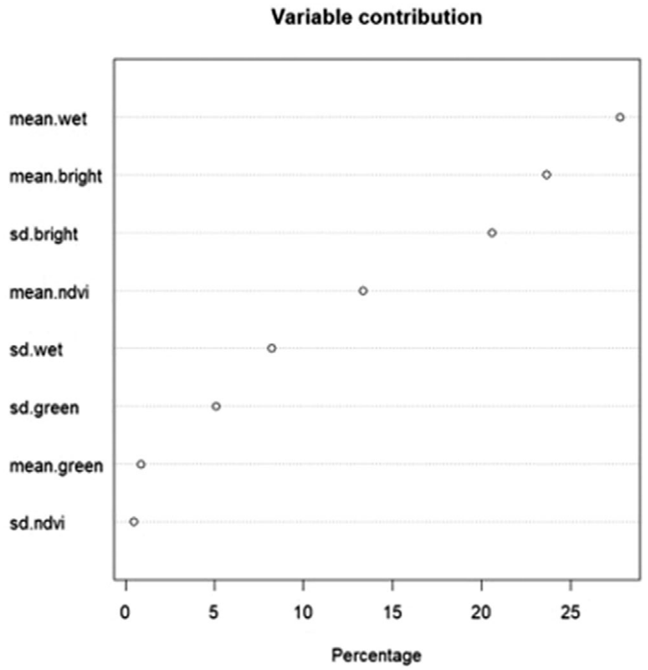

FIGURE 2 Contribution of variables of the final model for NG site (AUC: 0.838/PCC: 0.890)

4 | DISCUSSION

The aim of this study was to understand BAAPA habitat features associated with habitat suitability for hooded capuchins. This information is important to understand whether the species can exist throughout the range of ecological conditions in which we can find BAAPA now. Although the hooded capuchin is adaptable, as would be expected from members of their genus (Smith, Hayes, et al., 2018; Smith, 2021), it is a forest obligate species, requiring at least some forest cover to persist in an area and with virtually no probability of being found in crop fields. In Paraguay, the drastic forest loss over the last 60 years has not occurred through gradual degradation and fragmentation of intact forests but rather by widescale clear cutting and complete transformation to crop fields. While the hooded capuchin is an adaptable species, the extreme level of complete forest loss in Paraguay (Da Ponte, Kuenzer, et al., 2017; Da Ponte, Roch, et al., 2017; Huang et al., 2006) may pose a threat to their long-term survival as forest fragments are likely disconnected for the species.

Within the forest, habitat suitability was mainly influenced by remotely sensed Wetness (mean and standard deviation) in both the anthropogenically altered and geographically isolated secondary forest and in the near-undisturbed, 'higher quality' forest of one of Paraguay's two remaining large tracts of BAAPA. Though the forest at NG is surrounded by soy fields, the forest itself has not been subjected to selective logging (Hans Hostettler, personal communication) and is an older, more mature forest than RLB which experienced intensive logging and fire damage until 2010 (Ayala Santacruz, personal communication). The predicted occurrence rate of capuchins across most of the NG forest is more even than at RLB where high predicted occurrence rates coincide with older growth areas, bamboo forest and swamps. The forest at NG is more uniform than the regenerating RLB forest, indicating that forest maturity becomes a more important driver of habitat quality when older forest becomes a limited resource. Degraded areas of the forest fragment at RLB showed reduced probability of capuchin presence, though there were still trees in these areas. Wetness can be considered a measure of forest maturity through level of canopy moisture (Cohen & Spies, 1992; Samarawickrama et al., 2017). The SDM outcomes therefore indicate that capuchins preferred mature forest, as suggested before (Smith, Hayes, et al., 2018). The increasing pressure on Paraguay's little remaining forest from illegal logging, marijuana plantations, charcoal production and illegal settlements may result in an increase in degraded fragments where there is little forest in a mature enough condition to support viable populations of capuchins.

At both sites, NDVI and Greenness were other important features associated with habitat quality, and at RLB there is a strong positive relationship between these drivers (Samarawickrama et al., 2017). Both are measures of the amount of healthy, photosynthetically active vegetation and it would be expected to be higher in areas with denser, more mature forest (Baig et al., 2014; Fitzgerald et al., 2018). NDVI was found to be a slightly more important predictor at RLB than at NG which again may be a result of the history of habitat alteration making the vegetation quality at RLB far more heterogenous than the forest at NG. Greenness was not one of the top four associated features influencing habitat quality at NG and, in fact, Brightness, a measurement related to bare soil, was more influential than NDVI or Greenness at this site. This may also be related to the more homogenous level of forest quality at the far less disturbed site of NG. If the quality of the forest at NG, reflected in the Greenness and NDVI, is more uniform

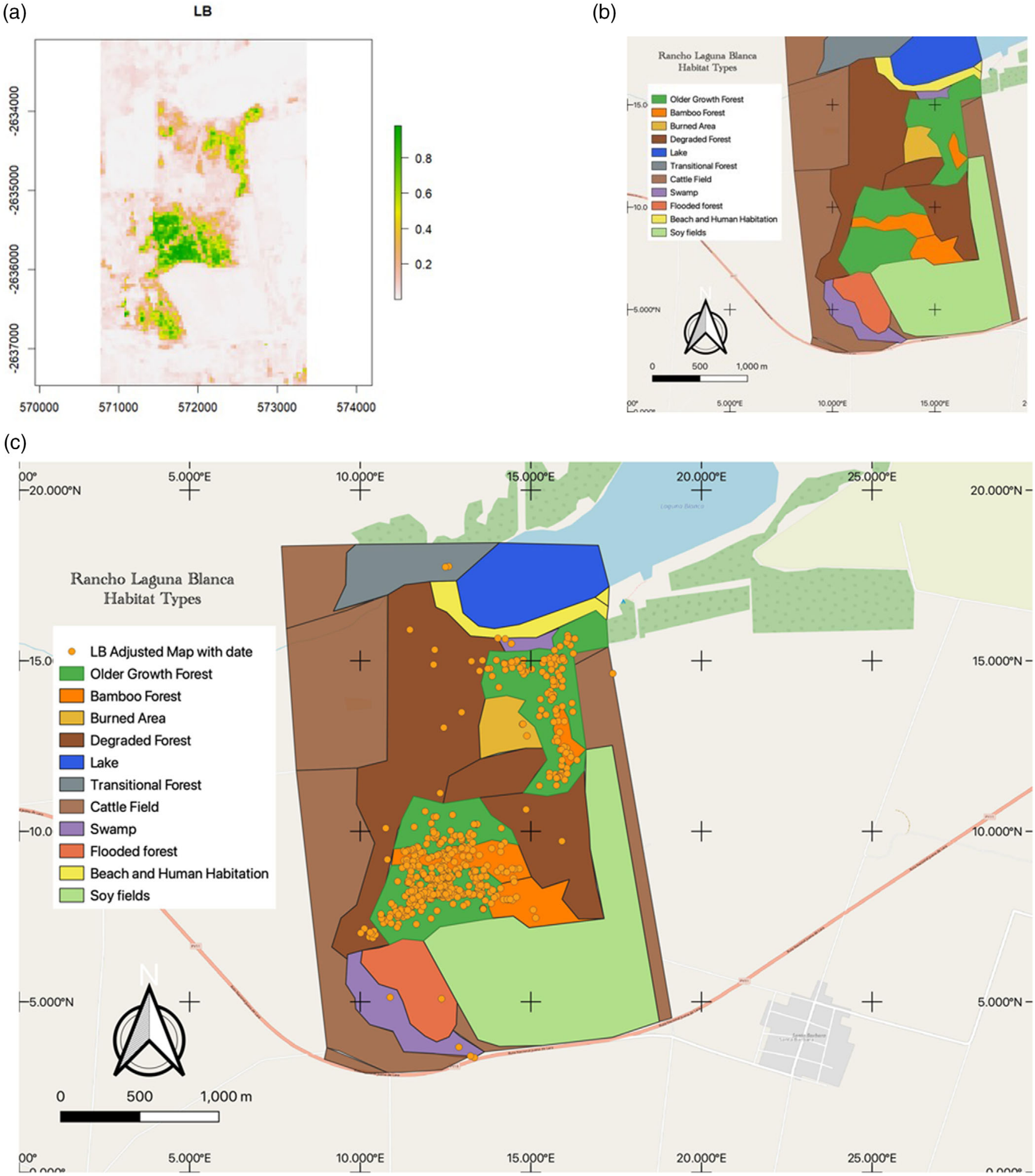

FIGURE 3 (a) Map of suitable habitat according to final model (AUC: 0.943, PCC: 0.928). (b) Broad scale habitat type map of Rancho Laguna Blanca. (c) Broad scale habitat type map of Rancho Laguna Blanca with capuchin monkey sightings

than in the highly disturbed fragment of RLB, then this could explain why areas with higher Brightness, a factor associated with bare ground, have a stronger association with capuchin presence, with the capuchins less likely to be in areas with higher Brightness because of the lack of trees.

While the capuchins used all non-plantation forested space more or less equally at NG, they did not use degraded forest homogenously. At RLB, the areas with the highest rate of occurrence of capuchins were the older growth forest, bamboo dominated forest and flooded forest (that has experienced little selective logging in the past). While the

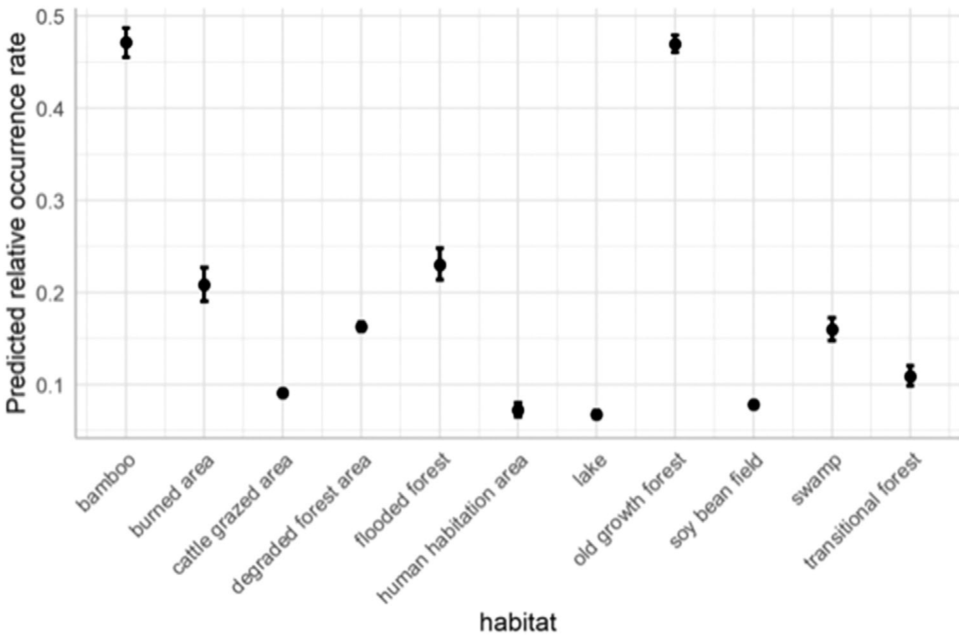

FIGURE 4 Predicted occurrence rate at RLB depending on habitat type using a beta-GLM with six Moran eigenvectors to account for spatial autocorrelation. Overdispersion parameter for the beta family estimated to be 3.8. Error bars are 95% confidence intervals

bamboo-dominated forest often has fewer large trees and therefore is possibly unlikely to be able to support the capuchins without the surrounding matrix of other forest types, the bamboo itself is an important resource for the capuchin groups at both site with the bamboo shoot making up ~10%–30% of the capuchins diet at RLB and ~5%–40% of the capuchins diet at NG (depending on the season) (Smith et al., 2022). In addition to feeding directly on the bamboo, the monkeys also use the large stems as a source of drinking water (Smith, personal observation) The monkeys occurred less in the degraded areas, even though these areas were still forested. This information is crucial to understand the suitability of typical BAAPA fragments left which are mostly degraded (Akers et al., 2013; Howard et al., 2012).

4.1 | Management implications for BAAPA conservation in Paraguay

With so little of the BAAPA remaining, it is not only important to consider conservation of the remaining larger fragments but also to begin to implement programmes to reconnect smaller fragments (Naidoo et al., 2018). The capuchin's habitat quality is associated with similar features in near-undisturbed and degraded BAAPA fragments. Those correlate with not only native mature forest, but also arboreal crop species. We can use this insight to make inferences about habitat suitability for hooded capuchins across the BAAPA region in Paraguay and identify areas suitable for reforestation projects, using the capuchin monkey as the flagship species to garner public support for the project. That the monkey is a charismatic, popular, well-known species in the country and the results indicate that it cannot survive in clear-cut crop fields makes it a highly suitable flagship for such a project. In addition, recent studies show that though this species is currently classified as Least Concern at a national and global level, its dependence on forest in an area where forests are clear cut to make way for soy fields means that this status must be re-evaluated (Smith, 2021). This status change would have a significant impact on its effectiveness as a flagship species, highlighting the urgency of the situation.

The SDM for NG showed that even though the capuchins had access to some of the nearest-to-undisturbed forest left in the country, they were most likely to be found in the 1.5 ha Slash pine tree (*Pinus elliottii*) that bordered the forest. The monkeys spent significant amounts of time feeding on pinecone seeds (42%–69% of feeding observations: Smith, 2021; Smith et al., 2022) but also used the pine trees as an important sleeping site, with over half of their nights spent in the plantation (Smith, 2021). As this species is a timber crop, this behaviour does not generate conflicts with economic activities. That the monkeys are willing and able to adjust their microhabitat preferences to available, yet non-native, forest provides an opportunity to implement a programme combining reforestation with financial benefits for local communities. We propose that a reforestation programme incorporating pines in corridors to connect BAAPA fragments would be beneficial to both capuchins and local people. Monkeys slept and ate in the pine plantation, but during the day the monkeys spent most of their time in the natural forest (Smith, unpublished data). This indicates that though the monkeys used the plantation, they still required the natural forest as well and does not provide evidence that the plantation alone is enough for the survival of the monkeys.

The Zero-Deforestation Law (Law 2524/2004) that was introduced in 2004 and recently extended until 2030 (ABC Color, 2020) includes several provisions to prevent further deforestation including the provision that landowners with over 20 ha must keep 25% of their

FIGURE 5 (a) Map of suitable habitat according to final model (AUC: 0.838/PCC: 0.890). (b) Broad scale habitat type map of Nueva Gambach. (c) Broad scale habitat type map of Nueva Gambach with capuchin monkey sightings

land forested. This agroforestry approach to reforestation could therefore be underpinned by the Zero-Deforestation Law with its associated financial incentives. The Zero-Deforestation law promotes reforestation efforts such as the Payments for Environmental Service (PES) programme. The Zero-Deforestation law Payments for Environmental Services (PES) instruments include 75% of site preparation costs, 75% of maintenance costs during the first 3 years (Gonzalez-Gimenez, 2002) and a 50% reduction in property tax for forestry plantations (Frey, 2007). The results of this study can be incorporated within this existing policy and management framework

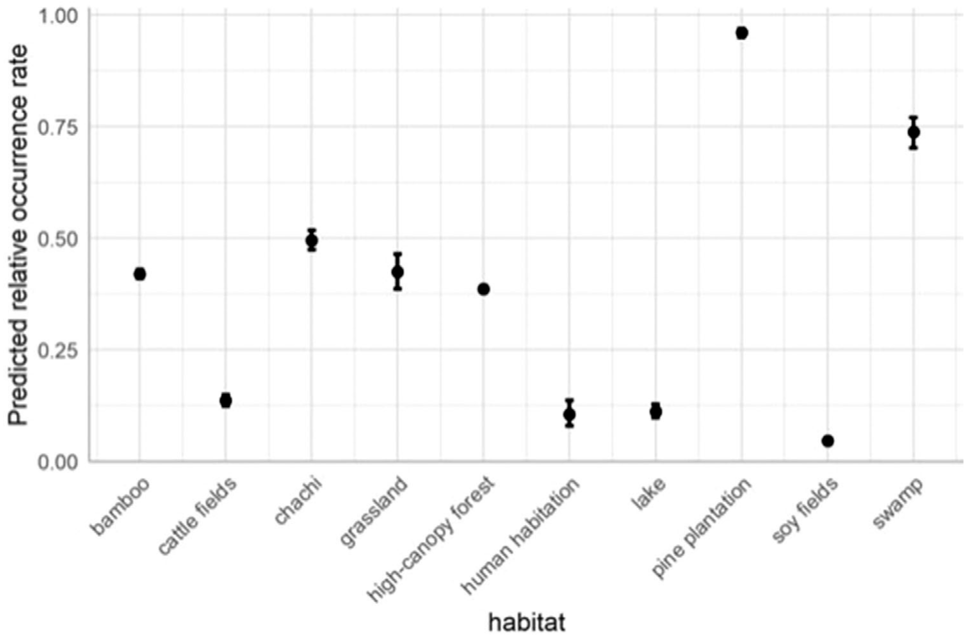

FIGURE 6 Predicted occurrence rate at NG depending on habitat type using a beta-GLM with four Moran eigenvectors to account for spatial autocorrelation. Overdispersion parameter for the beta family estimated to be 5.1. Error bars are 95% confidence intervals

to incentivize landowners to create corridors between forest fragments on their land using native trees, mixed with cash-crops including shade-grown yerba mate (*Ilex paraguariensis*) and Slash Pine tree plantations.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

RS designed the study, collected the data and performed data analysis. DL performed data analysis. Both authors contributed to the drafts and gave final approval for publication.

STATEMENT OF INCLUSION

This study was conducted by authors born in European countries and who, like many ecologists, have been living in other countries through their professional career. The first author has been a resident of Paraguay for close to a decade. The second author has difficulties categorizing his cultural identity using national geographical boundaries alone. The outreach programme led by the first author ensures regular uptake of community position and considerations of community knowledge. Interactions have been noted in the manuscript including personal communication from named individuals when doing so would not put individuals at risk. All relevant work from the region and in the native languages were considered. Results of this work have been presented at local conferences in the local languages, as well as in workshops throughout Paraguay.

DATA AVAILABILITY STATEMENT

Data for this project is available from the GitHub Repository at https://zenodo.org/badge/latestdoi/484409302.

PEER REVIEW

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ORCID

Rebecca L. Smith https://orcid.org/0000-0002-0278-9071
David Lusseau https://orcid.org/0000-0003-1245-3747

REFERENCES

ABC Color. (2020). *Abdo promulga Ley de Deforestación Cero y dinero para subisidios*. https://www.abc.com.py/nacionales/2020/12/10/abdo-promulga-ley-de-deforestacion-cero-y-dinero-para-subisidios/

Akers, A. A., Islan, M. A., & Nijman, V. (2013). Habitat characterization of western hoolock gibbons *Hoolock hoolock* by examining home range microhabitat use. *Primates; Journal of Primatology*, *54*, 341–348.

Alfons, A. (2015). *Package "cvTools."* https://cran.r-project.org/web/packages/cvTools/cvTools.pdf

Baig, M. H. A., Zhang, L., Shuai, T., & Tong, O. (2014). Derivation of a tasselled cap transformation based on Landsat 8 at-satellite reflectance. *Remote Sensing Letters*, *5*(5), 423–431.

Booth, T. H., Nix, H. A., Busby, J. R., & Hutchinson, M. F. (2014). bioclim: The first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. *Diversity Distribution*, *20*, 1–9.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Martin Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modelling. *The R Journal*, *9*(2), 378–400.

Calmon, M., Brancalion, P. H. S., Paese, A., Aronson, J., Castro, P., da Silva, S. C., & Rodrigues, R. R. (2011). Emerging threats and opportunities for large-scale ecological restoration in the Atlantic Forest of Brazil. *Restoration Ecology*, *19*(2), 154–158.

Campbell, J. B., & Wynne, R. H. (2011). *Introduction to remote sensing* (5th ed.). The Guilford Press.

Caro, T., Engilis, A., Jr., Fitzherbert, E., & Gardner, T. (2004). Preliminary assessment of the flagship species concept at a small scale. *Animal Conservation*, *7*, 63–70.

Catterson, T. M., & Fragano, F. V. (2004). *Tropical forestry and biodiversity conservation in Paraguay: A report to USAID/Paraguay*. https://rmportal.net/library/content/1/118_paraguay/at_download/file

Cavada, N., Ciolli, M., Rocchini, D., Barelli, C., Marshall, A. R., & Rovero, F. (2017). Integrating field and satellite data for spatially explicit inference on the density of threatened arboreal primates. *Ecological Applications*, *27*, 235–243.

Cohen, W. B. (1991). Response of vegetation indices to changes in three measures of leaf water stress. *Photogrammetric Engineering & Remote Sensing*, *57*, 195–202.

Cohen, W. B., & Spies, T. A. (1992). Estimating structural attributes of Douglas Firs/Western Hemlock forest stands from LANDSAT and SPOT imagery. *Remote Sensing of the Environment*, *41*, 1–17.

Crist, E. P., Laurin, R., & Cicone, R. C. (1986). *Vegetation and soils information contained in transformed Thematic Mapper data*. Proceedings, IGARSS "86 Symposium, Zurich, Switzerland, 8–11 September 1986, ESA Publ. Division, SP-254, pp. 1465–1470.

Crofoot, M. C. (2013). The cost of defeat: Capuchin groups travel further, faster and later after losing conflicts with neighbors. *American Journal of Physical Anthropology*, *152*, 79–85.

Da Ponte, E., Kuenzer, C., Parker, A., Rodas, O., Oppelt, N., & Fleckenstein, M. (2017). Forest cover loss in Paraguay and perception of ecosystem services: A case study of the Upper Parana Forest. *Ecosystem Services*, *24*, 200–212.

Da Ponte, E., Roch, M., Leinenkugel, P., Dech, S., & Kuenzer, C. (2017). Paraguay's Atlantic Forest cover loss – Satellite-based change detection and fragmentation analysis between 2003 and 2013. *Applied Geography*, *79*, 37–49.

De Souza Lins, P. G. A., & Ferreira, R. G. (2019). Competition during sugarcane crop raiding by blond capuchin monkeys (*Sapajus flavius*). *Primates; Journal of Primatology*, *60*, 81–91.

Di Bitetti, M. S. (2001). Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. *Journal of Zoology*, *253*, 33–45.

Dietz, J. M., Dietz, L. A., & Nagagata, E. Y. (1994). The effective use of flagship species for conservation of biodiversity, the example of lion tamarins in Brazil. In P. J. S. Olney, G. M. Mace, & A. T. C. Feistner (Eds.), *Creative conservation* (pp. 32–49). Chapman and Hall.

Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, *77*, 802–813.

Esquivel, A., Zarza, R., Tiffer-Sotomayor, R., Díaz, A., Pérez, D., & Veláquez, M. (2019). Conservation status and challenges of Atlantic Forest birds in Paraguay. *Diversity*, *11*, 247.

Fitzgerald, M., Coulson, R., Lawing, A. M., Matsuzawa, T., & Koops, K. (2018). Modelling habitat suitability for chimpanzees (*Pan troglodytes verus*) in the Greater Nimba Landscape, Guinea, West Africa. *Primates; Journal of Primatology*, *59*, 361–375.

Fourcade, Y., Engler, J. O., Rödder, D., & Secondi, J. (2014). Mapping species distributions with MAXENT using a geographically biased sample of presence data: A performance assessment of methods for correcting sampling bias. *PLoS ONE*, *9*(5), e97122.

Franklin, J. (2009). *Mapping species distributions: Spatial inference and prediction*. Cambridge University Press.

Freeman, E. A., & Moisen, G. (2008). PresenceAbsence: An R package for presence absence analysis. *Journal of Statistical Software*, *23*(11), 1548–7660.

Frey, G. E. (2007). *Timber investment returns in Paraguay*. World Bank.

Ganzhorn, J. U., Rakotondranary, S. J., & Ratovonamana, Y. R. (2011). Habitat description and phenology. In J. M. Setchell & J. D. Curtis (Eds.), *Field and laboratory methods in primatology: A practical guide* (2nd ed., pp. 51–68). Cambridge University Press.

Gasparri, N. I., Grau, H. R., & Manghi, E. (2008). Carbon pools and emissions from deforestation in extra-tropical forests of northern Argentina between 1900 and 2005. *Ecosystems*, *11*(8), 1247–1261.

Gómez-Posada, C., Rey-Goyeneche, J., & Tenorio, E. A. (2019). Ranging responses to fruit and arthropod availability by a tufted capuchin group (*Sapajus apella*) in the Colombian Amazon. In R. Reyna-Hurtado & C. Chapman (Eds.), *Movement ecology of neotropical forest mammals* (pp. 195–215). Springer.

Gonzalez-Gimenez, R. (2002). *Diagnóstico de la situación legal e institucional y plan de acción para implementación de proyectos de sumideros de carbono*. Oficina Nacional de Cambio Climático, Secretaría del Ambiente, GTZ.

Gouveia, S. F., Souza-Alves, J. P., Rattis, L., Dobrovolski, R., Jerusalinsky, L., Beltrão-Mendes, R., & Ferrari, S. F. (2016). Climate and land use changes will degrade the configuration of the landscape for titi monkeys in eastern Brazil. *Global Change Biology*, *22*, 2003–2012.

Harper, K. A., MacDonald, S. E., Burton, P., Chen, J., Brosofsky, K. D., Saunders, S., Euskirchen, E. S., Roberts, D., Jaieth, M., & Esseen, P. A. (2005). Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology*, *19*, 768–782.

Hartig, F. (2016). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. R package version 0.1.0. CRAN /GitHub.

Huang, C., Kimb, S., Altstatt, A., Townshend, J. R. G., Davis, P., Song, K., Tucker, C. J., Rodas, O., Yanosky, A., Clay, R., & Musinsky, J. (2006). Rapid loss of Paraguay's Atlantic forest and the status of protected areas—A Landsat assessment. *Remote Sensing of Environment*, *106*, 460–466.

Hernandez, P. A., Franke, I., Herzog, S. K., Pacheco, V., Paniagua, L., Quintana, H. L., Soto, A., Swenson, J. J., Tovar, C., Valqui, T. H., Vargas, J., & Young, B. E. (2008). Predicting species distributions in poorly-studied landscapes. *Biodiversity and Conservation*, *17*, 1353–1366.

Hijmans, R. J., Philips, S., Leathwick, J., & Eldith, J. (2020). *Package "Dismo."* https://rspatial.org/raster/sdm/

Howard, A. M., Bernardes, S., Nibbelink, N., Biondi, L., Presotto, A., Fragaszy, D. M., & Madden, M. (2012). A maximum entropy model of the bearded capuchin monkey habitat incorporating topography and spectral unmixing analysis. *ISPRS Annals of the Photogrammetry, Remote Sensing and Spatial Information Sciences*, *1*(2), 1–5.

Izar, P., Ramos-da-Silva, E. D., de-Resende, B. D., & Ottoni, E. B. (2007). A case of infanticide in tufted capuchin monkeys (*Cebus nigritus*). *Mastozoologia Neotropical*, *14*(1), 73–76.

Janson, C. H., & Di Bitteti, D. S. (1997). Experimental analysis of food detection in capuchin monkeys: Effects of distance, travel speed, and resource size. *Behavioral Ecology and Sociobiology*, *41*(1), 17–24.

Jie, L., Fitzgerald, M., Haohong, L., Yongmei, L., Tong, J., Xuaolan, L., Xuerong, Y., Satoshi, H., & Matsuzawa, T. (2020). Modelling habitat suitability for Yunnan Snub-Nosed monkeys in Laojun Mountain National Park. *Primates; Journal of Primatology*, *61*, 277–287.

Kosydar, A. J., Rumiz, D. I., Conquest, L. L., & Tewksbury, J. J. (2014). Effects of hunting and fragmentation on terrestrial mammals in the Chiquitano forests of Bolivia. *Tropical Conservation Science*, *7*(2), 288–307.

Laurance, W. F. (2013). Emerging threats to tropical forests. In M. Lowman, S. Devy, & T. Ganesh (Eds.), *Treetops at risk* (pp. 71–79). Springer.

Legaard, K. R., Sader, S. A., & Simons-Legaard, E. M. (2015). Evaluating the impact of abrupt changes in forest policy and management practices on landscape dynamics: Analysis of a Landsat image time series in the Atlantic Northern Forest. *PLoS ONE*, *10*(6), e0130428.

Lowen, J. C., Bartina, L., Clay, R. P., & Tobias, J. A. (1996). *Biological surveys and conservation priorities in eastern Paraguay*. CBS Conservation Publications.

Liu, C., Wolter, C., Xian, W., & Jeschke, J. M. (2020). Species distribution models have limited spatial transferability for invasive species. *Ecology Letters*, *23*, 1682–1692.

McGowan, J., Beaumont, L. J., Smith, R. J., Chauvenet, A. L. M., Harcourt, R., Atkinson, S. C., Mittermeier, J. C., Esperon-Rodriguez, M., Baumgartner, J. B., Beattie, A., Dudaniec, R. Y., Grenyer, R., Nipperess, D. A., Stow, A., & Possingham, H. P. (2020). Conservation prioritization can resolve the flagship species conundrum. *Nature Communications*, *11*, 994.

Murakami, D. (2021). *Package "spmoran."* https://cran.r-project.org/web/packages/spmoran/spmoran.pdf

Naidoo, R., Kilian, J. W., Du Preez, O., Beytell, P., Aschenborn, O., Taylor, R. D., & Stuart-Hill, G. (2018). Evaluating the effectiveness of local- and regional-scale wildlife corridors using quantitative metrics of functional connectivity. *Biological Conservation*, *217*, 96–103.

Oeser, J., Heurich, M., Senf, C., Pflugmacher, D., Belotti, E., & Kuemmerle, T. (2020). Habitat metrics based on multi-temporal Landsat imagery for mapping large mammal habitat. *Remote Sensing in Ecology and Conservation*, *6*, 52–69.

Peres, C. A., Barlow, J., & Laurance, W. F. (2006). Detecting anthropogenic disturbance in tropical forests. *Trends in Ecology and Evolution*, *21*, 227–229.

Petorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M., & Kausrud, K. (2011). The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in animal ecology. *Climate. Research*, *46*, 15–27.

Philips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modelling of species geographic distributions. *Ecological Modelling*, *190*, 231–259.

Presotto, A., Verderane, M. P., Biondi, L., Mendonça-Furtado, O., Spagnoletti Madden, N. M., & Izar, P. (2018). Intersection as key locations for bearded capuchin monkeys (*Sapajus libidinosus*) traveling within a route network. *Animal Cognition*, *21*, 393–405.

QGIS.org. (2021). *QGIS geographic information system*. QGIS Association. http://www.qgis.org

Rímoli, J. (2001). *Ecologia de macacos-prego (*Cebus apella nigritus, *Goldfuss, 1809) na Estação Biológica de Caratinga (MG): Implicações para a conservação de fragmentos de Mata Atlântica*. Universidade Federal do Pará, Museu Paraense Emílio Goeldi, Embrapa.

Ryan, S. J., Knechtel, C. U., & Getz, W. M. (2006). Range and habitat selection of African buffalo in South Africa. *The Journal of Wildlife Management*, *70*, 764–776.

Samarawickrama, U., Piyaratne, D., & Ranagalage, M. (2017). Relationship between NDVI with Tasseled cap indices: A remote sensing based analysis. *International Journal of Innovative Research in Technology*, *3*(12), 13–19.

Senzaki, M., Yamaura, Y., Shoji, Y., Kubo, T., & Nakamura, F. (2017). Citizens promote the conservation of flagship species more than ecosystem services in wetland restoration. *Biological Conservation*, *214*, 1–5.

Smith, R. L., Sarvary, J. G., & Ayala Santacruz, J. D. (2016). *La Evaluación de las Actitudes de la Población Local hacia Reserva Natural Laguna Blanca, la ONG Fundación Para La Tierra y la Conservación de los Primates Silvestres como base para un Programa de Educación Ambiental*. Seminario de Educación y Gestión Socio-Ambiental en la Reforma Universitaria.

Smith, R. L., Hayes, S. E., Smith, P., & Dickens, J. K. (2018). Sleeping site preferences in *Sapajus cay* Illiger 1815 (Primates: Cebidae) in a disturbed fragment of Upper Paraná Atlantic Forest Fragment, Rancho Laguna Blanca, Eastern Paraguay. *Primates; Journal of Primatology*, *59*(1), 79–88.

Smith, R. L., Ayala Santacruz, J. D., & Sarvary, J. G. (2018). *Paraguay's little monkeys: Inspiring Paraguayan primate conservation heroes and tackling the primate pet trade*. International Primatological Society Conference.

Smith, P., Rios, S., & Smith, R. L. (2021). Paraguayan primatology: Past, present and future. *Primate Conservation*, *35*, 1–22.

Smith, R. L. (2021). *The ecology and conservation of the hooded capuchin (*Sapajus cay*) in the Upper Paraná Atlantic Forest* (PhD thesis). University of Aberdeen.

Smith, R. L., Rebergen, K., Payne, C., Megaponas, E., & Lusseau, D. (2022). Dietary plasticity of an umbrella species (*Sapajus cay*) in a biodiversity hotspot: Applying ecological traits to habitat conservation in the Upper Paraná Atlantic Forest. *Folia Primatologica*, https://doi.org/10.1163/14219980-20210407

Steffen, W., Richardson, K., Rockström, J., Cornell, S. E., Fetzer, I., Bennett, E. M., Biggs, R., Carpenter, S. R., De Vries, W., De Wit, C. A., Folke, C., Gerten, D., Heinke, J., Mace, G. M., Persson, L. M., Ramanathan, V., Reyers, B., & Sörlin, S. (2015). Developments in the planetary boundaries concept provide a framework to support global sustainability. *Science*, *347*(6223), 1259855.

Tarabelli, M., Da Silva, M. J. C., & Gascon, C. (2004). Forest fragmentation, synergisms and the impoverishment of neotropical forests. *Biodiversity and Conservation*, *13*, 1419–1425.

Thomas-Walters, L., & Raihani, N. J. (2017). Supporting conservation: The roles of flagship species and identifiable victims. *Conservation Letters*, *10*, 581–587.

Wang, W., Qiao, Y., Li, S., & Yao, M. (2017). Low genetic diversity and strong population structure shaped by anthropogenic habitat fragmentation in a critically endangered primate, *Trachypithecus leucocephalus*. *Heredity*, *118*, 542–553.

Wich, S. A., Gaveau, D., Abram, N., Ancrenaz, M., Baccini, A., Brend, S., Curran, L., Delgado, R. A., Erman, A., Fredriksson, G. M., Goossens, B., Husson, S. J., Lackman, I., Marshall, A. J., Naomi, A., Molidena, E., Nardiyono, N. A., Odom, K., Panda, A., … Meijaard, E. (2012). Understanding the impacts of land-use policies on a threatened species: Is there a future for the Bornean orang-utan? *PLoS ONE*, *7*(11), e49142.

Widyastuti, S., Perwitasari-Farajallah, D., Prasetyo, L. B., Iskander, E., & Setiawan, A. (2020). Maxent modelling of habitat suitability for the endangered Javan gibbon (*Hylobates moloch*) in less-protected Dieng Mountains, Central Java. *IOP Conf. Series: Earth and Environmental Science*, *457*, 1–10.

Wilcove, D. S., McClellan, C. H., & Dobson, A. P. (1986). Habitat fragmentation in the temperate zone. In M. E. Soule (Ed.), *Conservation biology: The science of scarcity and diversity* (pp. 237–256). Sinauer Associates.

Zanella, L., Borém, R. A. T., Souza, C. G., Alves, H. M. R., & Borém, F. M. (2012). Atlantic forest fragmentation analysis and landscape restoration management scenarios. *Natureza and Conservação*, *10*(1), 57–63.

Zuidema, P., Sayer, J., & Dijkman, W. (1996). Forest fragmentation and biodiversity: The case for intermediate-sized conservation areas. *Environmental Conservation*, *23*(4), 290–297.

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