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The Hooded Capuchin Monkey (*Sapajus cay*) is Vulnerable in Paraguay and at Least Near Threatened Globally According to Red List Criteria

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Abstract

Habitat loss and fragmentation, particularly because of agrarian and urban expansions, are threatening biodiversity worldwide. Paraguay is predicted to lose all its primary moist forests by 2028. The most endangered habitat in Paraguay is the Upper Paraná Atlantic Forest (BAAPA), which has been decimated by industrial agriculture in the past 60 years. The hooded capuchin (*Sapajus cay*) is the best-known Paraguayan primate and the only species mostly restricted to the remaining BAAPA. We used local (defined as people living in Paraguay) knowledge about the known presence of the species in a habitat fragment to assess whether species' presence was associated with forest cover in fragments by using a binomial general linear model (GLM). Using the results of the GLM, we then assessed how forest cover changed through the hooded capuchin range and its predicted range in Paraguay using Global ForestWatch forest cover prediction for 2000 to 2019. The GLM showed that the presence of hooded capuchins required predominance of forest cover with the monkey being 80% likely to be present for 56% cover and 90% for 70% cover. The capuchin has lost 23% of highly suitable habitat across its whole range and 58% in Paraguay. Suitable habitat for hooded capuchin monkeys is, therefore, decreasing across the full extent of the species. In Paraguay, the remaining habitat is being fragmented and degraded and distance between fragments is increasing. Because the situation in Paraguay is critical, we recommend that the capuchin is classified as Vulnerable by the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List at a national level under criterion B1, b(i), b(ii), and b(iii). Predictions across the species range warrant at least a classification of Near Threatened for the species. These results demonstrate that the

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conservation situation faced by a primate species can differ greatly depending on local, national, and range wide political and social situations. Therefore, we recommend that national assessments are performed for species that are found in multiple countries in order to gain a true picture of threats a species faces.

Keywords Conservation · Forest loss · IUCN · Latin America · Primate · Red List · *Sapajus cay*

Resumen La pérdida y fragmentación del hábitat, particularmente debido a las expansiones agrarias y urbanas, están amenazando la biodiversidad en todo el mundo. Se predice que Paraguay perderá todos sus bosques húmedos primarios para el 2028. El hábitat más amenazado en Paraguay es el Bosque Atlántico del Alto Paraná (BAAPA), que ha sido suprimido por la agricultura industrial en los últimos 60 años. El mono capuchino encapuchado (Sapajus cay) es el primate paraguayo más conocido y la única especie restringida principalmente al BAAPA remanente. Aquí utilizamos el conocimiento local (por las personas que viven en Paraguay) sobre la presencia de la especie en el fragmento de hábitat para evaluar si la presencia de la especie estaba asociada con la cobertura forestal en los fragmentos utilizando un modelo lineal general binomial (GLM). Usando los resultados del GLM, evaluamos cómo cambiaba la cubierta forestal a través del área de distribución de los capuchinos y su distribución predicada en Paraguay utilizando la predicción de cobertura forestal de Global ForestWatch para 2000 hasta 2019. El GLM demostró que la presencia de capuchinos requiere un predominio de cubierta forestal con una probabilidad del 80% para encontrar el mono en una cobertura del 56% y un 90% para una cobertura del 70%. El capuchino ha perdido el 23% de su hábitat altamente adecuado a través de toda su área de distribución y el 58% en Paraguay. Por lo tanto, el hábitat adecuado para los monos capuchinos encapuchados está disminuyendo en toda su extensión. En Paraguay, el hábitat restante se está fragmentando y degradando, y la distancia entre los fragmentos está aumentando. Debido a que la situación en Paraguay es crítica, recomendamos que el capuchino sea clasificado como Vulnerable por parte de la Lista Roja de la Unión Internacional para la Conservación de la Naturaleza y Recursos Naturales (UICN) a nivel nacional bajo el criterio B1, b(i), b(ii) y b(iii). Las predicciones a lo largo del rango de la especie justifican que asuma al menos una clasificación de Casi Amenazada. Estos resultados demuestran que la situación de conservación a la que se enfrenta una especie de primate puede diferir mucho según las situaciones políticas y sociales a niveles locales, nacionales y de rango amplio y, por lo tanto, recomendamos que se lleven a cabo evaluaciones nacionales para las especies que se encuentran en varios países con el fin de obtener una imagen verdadera de las amenazas a las que se enfrentan esas especies. ***The translated abstract was not copy-edited by Springer Nature.**

Palabras Claves Conservación · Deforestación · UICN · América Latina · Primates · Lista Roja · *Sapajus cay*

Ñemombyky

Tekoha opa ha eñemomichĩmba rupi, ara ha ara okakuaveva umi kokue kuera o ñemity rehegua ha upeicha avei umi tava kuera. Pea omoi opataha umi biodiversida opárupi. Oje'e opataha ka'aguy yvate Parguaipe amo 2028 gotyo. Paraguaipe pe tekoha ojekyhyje añetava oparo guara ha'e pe ka'aguay yvate, ejehepyme'e porã rupi umi kokuepe guare rehe ha mba'apoguasu kuera avei 60 ary pukukue. Pe ka'i ha'e pe ka'i ojekuaaveva Paraguaipe ha ha'e ha'eñominte la ahasa asyva pe ka'aguy eñemomichimba rupi. Ape roipuru pe arandu tavaygua mba'eva roikuaa hagua oĩpa añete umi ka'i pe ka'aguy michime ikatu haguaicha roikuaa añete moo moopa ka'i kuera ikatu oiko o terã ojejuhu. Ha rotopa umi ka'i oikotevẽha 56% ka'aguyrehe ikatu haguaicha ejotopa pepe 80% ka'i rehe, ha katu 90% ojetopa hugua ka'i rehe oikotevẽ 70% Ka'aguy rehe. Ha uperire katu rohecha mbe'eichapa okambia pe ka'aguy kuera pe ka'i rekoha pokukue *Sapajus cay*. Paguaipe, roipuru pe ñemoarandú Global ForestWatch 2000 a 2019 rehegua. Pe ka'i capuchino operde 58% pe oikoha ka'aguy pokukue javeve Paraguaipe. Ha avei, michimba oparupiete ka'aguy ka'i rekoha Paaraguai ryepyrehe. Paraguaipe, umi ka'i rekoha ara ha arande ojeytyva ha peicha oñemombyrypa ka'aguy kuera ojuehegui ha katu Paraguaipe ivaima. Rojerure pe ka'i eñemoi hagua Vulnerable Paraguaipe oihaicha pe criteriope B1, b(i), b(ii) y b(iii) He'i haicha pe ñemo'arandupe, ha pe ka'i rekoha pukukue katu ohechauka ojeclasifica hagua haimetema oi amenazado.

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Ñe'e okendavoka

Mbyteamérika ha Ñembyamérikagua; Ñangareko; Ka'aguykuéra ñehundi; UICN; Ka'ikuera; Lista Pytã; *Sapajus cay*

Introduction

The process of classifying species on the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List is a quantitative ranking system with set categories and criteria based on extinction probability (Mace & Lande, 1991). The criteria include both time-scales and flexibility in the data required and in the species and population units to which it applies, ensuring repeatability and objectivity (Ginsburg, 2002; Mace & Lande, 1991).

The Red List assessment classifies species into one of nine categories with three "Threatened" categories: Critically Endangered, Endangered and Vulnerable, and two "Lower Risk" categories: Near Threatened and Least Concern. The classification process has five main criteria, A–E, which evaluate extinction risk (Collen *et al*., 2016). For many terrestrial species Criterion B, which focuses on the geographical range in addition to evidence of habitat fragmentation, population decline or extreme fluctuations, is the most frequently used Red List requirement (Brooks *et al*., 2019; Collen *et al*., 2016). The two measures of geographical range are B1: Extent of Occurrence (EOO) and B2: the Area of Occupancy (AOO) (IUCN, 2021). The AOO represents the area of habitat that is occupied by the species. This metric must be calculated at a scale of 2 km × 2 km to maintain consistency across assessments (IUCN Standards & Petitions Committee, 2019). The AOO is thought of as an "insurance effect" against spatially explicit threats with less risk that a threat will impact all individuals in all habitat patches (IUCN Standards & Petitions Committee, 2019). The availability of remote sensing data and spatial datasets has enabled the development of another metric: Area of Habitat (AOH) (Brooks *et al*., 2019; Hansen *et al*., 2013). This measure is not equivalent to either EOO or AOO but should be used as a compliment to these measures, providing an estimate for the upper limit of both (Brooks *et al*., 2019).

Calculations of EOO and AOO have been used in several primate species to assist in the determination of current range and to estimate historical and/or potential future habitat loss (Boubli *et al*., 2019; Rabelo *et al*., 2020).

Habitat loss and fragmentation are two of the biggest threats to global biodiversity, particularly in tropical forests that are home to half of the world's known species (Dirzo & Raven, 2003; Laurance, 1999; Myers, 1984; Wright, 2005). Habitat fragmentation is a landscape scale process, including both the loss of habitat and the breaking up of large areas of habitat into smaller pieces (Fahrig, 2003; Wilcove *et al*., 1986). The effects of fragmentation can be very varied. Not only is habitat removed completely during the process of fragmentation, but the remaining patches will have different properties to the continuous habitat (van den Berg *et al*., 2001). Fragmentation can impact species' composition and richness through habitat loss (Echeverría *et al*., 2007; Püttker *et al*., 2020) and increased edge effects (Laurance & Yensen, 1991; Laurance *et al*., 2007). Animals that are found within forests may be especially vulnerable to these potential negative effects (Arroyo-Rodríguez & Dias, 2009; Chapman & Peres, 2001). Whereas fragmentation can be measured at the patch or landscape scale (Hesselbarth *et al*., 2019), the impact of fragmentation is best understood by using varied landscape feature indicators (Arroyo-Rodríguez *et al*., 2013a).

Paraguay represents an extreme case of deforestation and habitat fragmentation. It is predicted to become the first country in the world to lose all its moist forests, by as soon

as 2028 (European Commission, 2019). The Upper Paraná Atlantic Forest (BAAPA) once covered around 86,000 km^2 of eastern Paraguay. Despite the Zero-Deforestation Law (2542/04) covering Paraguay's eastern (Oriental) region implemented in 2004, 91% of the forest had been cleared by 2016 (7,500 km^2 between 1999–2016 alone) (Da Ponte *et al*., 2015, 2017a, b), mainly for industrial agriculture, in particular soybean monocultures. Protected areas within the BAAPA region only account for approximately 3.4% of the territory (Catterson & Fragano, 2004), and the degree of fragmentation of forests occurring outside of these areas is high. Only two areas of BAAPA of more than 50,000 ha remain: Área para Parque Nacional San Rafael (or Tekoha Guasu) and Reserva Natural del Bosque Mbaracayú (managed by Fundación Moises Bertoni). All of Paraguay's National Parks, private reserves, and Área para Parque Nacional San Rafael/Tekoha Guasu are under extreme pressure from illegal logging and settlements, marijuana plantations, and fires (ABC Color, 2020, 2021; Ultima Hora, 2022). Little scientific research has been performed to understand the impact of this extreme level of deforestation and fragmentation on the wildlife of Paraguay's BAAPA.

The hooded capuchin (*Sapajus cay*) is the only member of its genus in Paraguay, and it is mostly restricted to the remnants of the Upper Paraná Atlantic Forest and the gallery forests of the Cerrado (Smith *et al*., 2021; Stallings, 1985). The hooded capuchin was classified as Least Concern at a global scale from 2008 (when it was listed as *Cebus cay*) (Wallace, 2008). Historically, this capuchin has been understood to be a widespread, generalist species (Rímoli *et al*., 2018). The official estimate of extent of occurrence (EOO) of the species covers an area of 123,615.35 km^2 (full range map can be found in Rímoli *et al*., 2018, 2021), well above the 20,000 km^2 EOO required to qualify for the first Red List Threatened category (Vulnerable). However, much of the data used in the 2021 assessment of this species were more than three decades old, and information on its behavior and ecology have been severely lacking (Rímoli *et al*., 2021; Smith *et al*., 2021).

The most recent regional assessment of the hooded capuchin in Paraguay occurred in 2017 (Cartes *et al*., 2017). The species was estimated to still be Least Concern and facing no major threats in this national assessment similarly to the global estimate. This assessment used data from the early 1980s (Stallings, 1985) at a time when the Paraguayan landscape was drastically different to the current conditions. Furthermore, the entire Ñeembucú Wetland Complex (Ñeembucú department in the southwest corner of Paraguay) was included as part of the EOO of the species, despite there being no confirmed record of the species' presence then and since (Smith, 2021; Smith *et al*., 2021).

Given both the reduction in total forest cover associated with deforestation in the country, as well as deterioration of remaining forest patches, it is crucial to understand not only the current EOO for the species but also habitat quality in the range. This study was designed to determine the area of forest at different levels of habitat suitability remaining, both in Paraguay and across the recognized IUCN range map, as well as the amount of forest lost between 2000 and 2019 and how fragmented is what remains. Using this information, we evaluated the IUCN Red List status of the capuchin at a national and range level under criterion B and made recommendations for its conservation in Paraguay.

Methods

Ethical Statement Fundación Para La Tierra is a registered Paraguayan NGO (80,086,144–2). R. L. Smith is a Paraguayan permanent resident registered with the RNVS program of the Ministry of the Environment and Sustainable Development (MADEs). The research complied with all local laws. All our data was collected in a noninvasive manner and complied with the American Society of Primatologists Code of Best Practices for Field Primatology 2014. All participants in the Forest Guard Training Course and data collection WhatsApp group consented to the use of the sightings that they submitted.

Data Availability All data for this project are available from the corresponding author on reasonable request.

Conflict of Interest The authors declare that they have no conflict of interest.

Habitat Suitability for the Hooded Capuchin Based on Forest Cover

Between January 2013 and March 2021, the Para La Tierra Primate Team and the Fauna Paraguay team opportunistically collected capuchin presence data from throughout Paraguay (total of 71 locations). In December 2018, the Fundación Para La Tierra team held a week-long training course for 42 forest guards representing 15 protected areas (all Paraguay's habitats except the Ñeembucú Wetland Complex and the Pantanal). Five Paraguayan NGOs (PRO COSARA, OPADEs, Guardaparques Voluntarios, Fundación Moises Bertoni, and Guyra Paraguay) and the Ministerio de Ambiente y Desarrollo Sostenible (MADEs—the Ministry of the Environment and Sustainable Development) participated. We trained the guards in recognizing the five Paraguayan primate species and recording GPS locations with their smart phones. We formed a WhatsApp group. Every time a member sighted a primate, the data, including the date and time of sighting, the species, the number of individuals observed, and the GPS coordinates, were shared with the group between December 2018 and March 2021. Researchers from Fundación Para La Tierra and Fauna Paraguay represented the Ñeembucú Wetland Complex and the Pantanal habitats. We included in the model areas that had been extensively explored by the research teams from Fundación Para La Tierra and Fauna Paraguay (e.g., in Ñeembucú and Misiones departments) where capuchin absence could be confirmed (283 confirmed absence locations).

Each point (presence and absence) was assumed to correspond to a square shaped (to smooth the intersections) area of 700 m×700 m—a conservative estimate of a capuchin group's home range in Paraguay (Smith unpublished data). Spatial autocorrelation was not an issue as only one GPS point location was used per area. We created polygons at 1 km from the centroid to give a resolution of 2 km×2 km. We chose this resolution to meet the IUCN Red List requirements for calculating Area of Occupancy (IUCN, 2019). We assessed whether monkey presence (a proxy for habitat suitability) depended on forest cover by fitting a generalised linear model to the observations. Residual distribution

Table I Descriptions of habitat fragmentation indices calculated by the landscapemetrics package (Patch – the isolated areas of forest remaining after visible human alteration of the landscape) used to assess the fragmentation dynamics of the hooded capuchin monkey (*Sapajus cay*) habitat between 2000 and 2019 across the entire IUCN recognized range of the species and the recognized range within Paraguay

Measure	Definition
Mean patch area (and standard deviation of area)	Describes the composition of the landscape in terms of the size of forest patches. Provides an idea of patch structure (number of small vs. large patches)
Cohesion	Characterises the connectedness of patches and can be used to assess if patches of the same class are aggregated or isolated. Gives information about the landscape configuration
Mean of Contiguity index	Method of measuring patch shape based on connectedness. Larger and more connections between patches results in larger contiguity index values
Mean of euclidean nearest-neighbour distance (and standard deviation of ENN)	ENN measures the distance to the nearest neighboring patch of the same class; i.e., the distance is measured from edge-to-edge
Number of patches	Number of isolated areas of forest
Contagion	An aggregation metric that measures the degree of clumping of forest patches

and variance were graphically inspected to ensure assumptions were met. The response variable was the presence/absence of monkeys at an assessed patch (354 samples), and the explanatory variable was the percentage of forest cover in the 4-km^2 sample

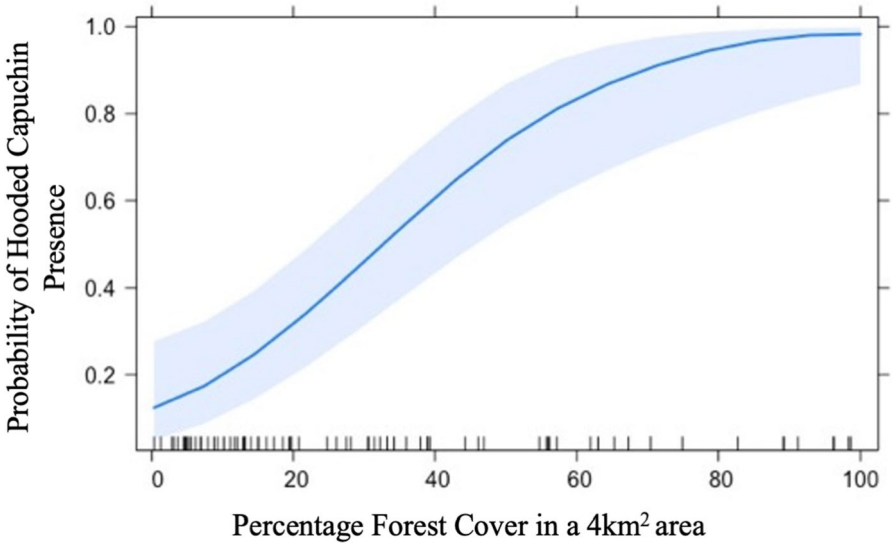

Fig. 1 Results of the generalized linear model giving predicted association between percentage of forest cover and probability of capuchin (*Sapajus cay)* presence in a given area (at a scale of 2 km × 2 km) ($X^2_1 = 28.8$, n presence = 71, n absence = 283 (January 2013-March 2021), $p < 0.00001$). Black ticks on the x-axis are absences. The shaded band represents the 95% confidence interval.

Table II Forest cover (proxy for probability of capuchin presence), area of remaining forest in 2000 and 2019 and percentage lost across the hooded capuchins full range

Forest cover	Probability of capuchin presence	Forest cover in 2000 (km^2)	Forest cover in 2019 (km^2)	% Loss
70%	90%	161,580	124,048	23.23
56%	80%	237,372	183,704	22.61
47%	70%	303,036	239,896	20.84
40%	60%	355,512	289,276	18.63
33%	50%	402,872	337,884	16.13

(estimated as described above), assuming a binomial distribution of residuals. We calculated forest cover in each grid cell from the 2019 Global Forest Watch forest cover data (Hansen *et al*., 2013; Hansen/UMD/Google/USGS/NASA; GFW, 2021). There is no procedural consensus on the probability of species presence required to be assured that the measured habitat is suitable for the species. We therefore estimated the forest cover required for monkey presence to be 50%, 60%, 70%, 80%, and 90% probable.

Forest Loss and Remaining Suitable Habitat

We created rasters using the *Sapajus cay* IUCN range map (Rímoli *et al*., 2021) and for the hooded capuchin's range in Paraguay by masking the IUCN map with the map of Paraguay from the rnaturalearth R package (South, 2017). We obtained data on

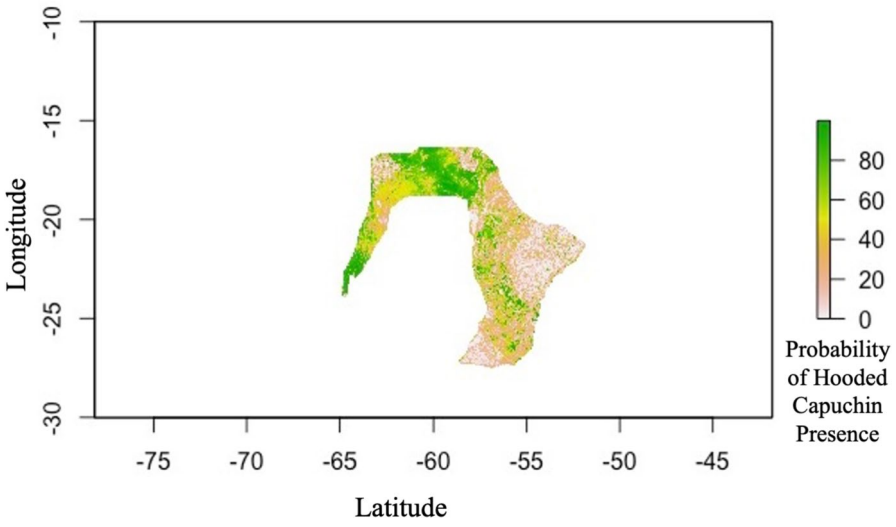

Fig. 2 Predicted probability of hooded capuchin monkey (*Sapajus cay*) presence given the proportion of forest cover in a 2-×2-km grid cell across official IUCN range in 2000 calculated from forest percent cover for each cell. That calculation is provided from the data from Global Forest Watch. Forest cover source: Hansen *et al*., 2013. We recorded presence and absence data opportunistically between January 2013 and March 2021.

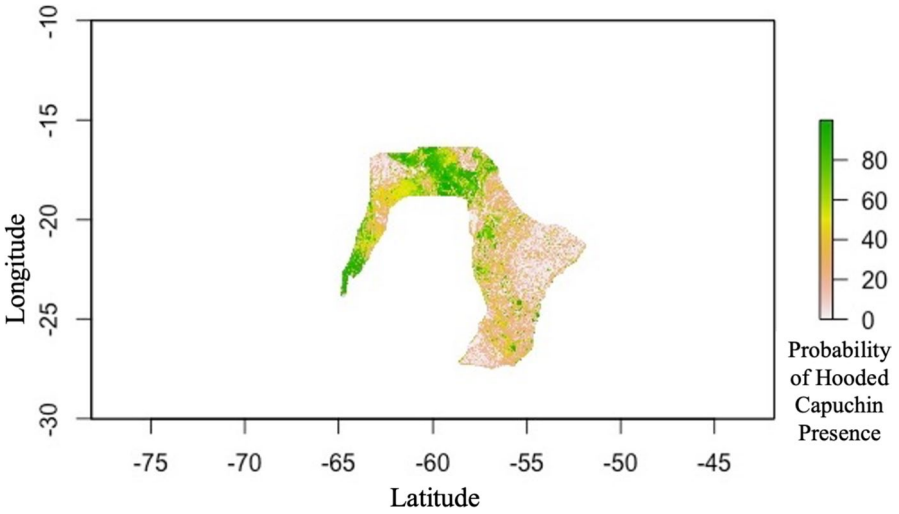

Fig. 3 Predicted probability of hooded capuchin monkey (*Sapajus cay*) presence given the proportion of forest cover in a 2-×2-km grid cell across official IUCN range in 2019 calculated from forest percent cover for each cell. That calculation is provided from the data from Global Forest Watch. Forest cover source: Hansen *et al*., 2013. We recorded presence and absence data opportunistically between January 2013 and March 2021.

forest cover change from 2000–2019 from Global Forest Watch (Hansen *et al*., 2013; Hansen/UMD/Google/USGS/NASA; GFW, 2021) and created raster files at a resolution of 2 km×2 km of annual forest cover (existing forest in 2000 minus cumulative forest loss to a given year plus cumulative forest gain to a given year) for the period 2000–2019. The resolution of 2 km×2 km is the required resolution for an IUCN evaluation (IUCN, 2019). We performed all analyses at the full range level and at a national level. We calculated area of forest (km^2) for 2000 and 2019 at each of the five identified forest cover levels of monkey presence probability (50% to 90% thresholds).

Habitat Fragmentation

We estimated suitable habitat fragments and associated fragmentation indices at both the global range and national scale using the R package "landscapemetrics"

Table III Forest cover (proxy for probability of capuchin presence), area of remaining forest in 2000 and 2019 and percentage lost in Paraguay's Oriental region

Forest cover	Probability of capuchin presence	Forest cover in 2000 (km^2)	Forest cover in 2019 (km^2)	% Loss
70%	90%	22,516	9368	58.39
56%	80%	39,349	19,880	42.56
47%	70%	54,740	31,444	42.56
40%	60%	69,516	44,128	36.52
33%	50%	87,156	61,588	29.34

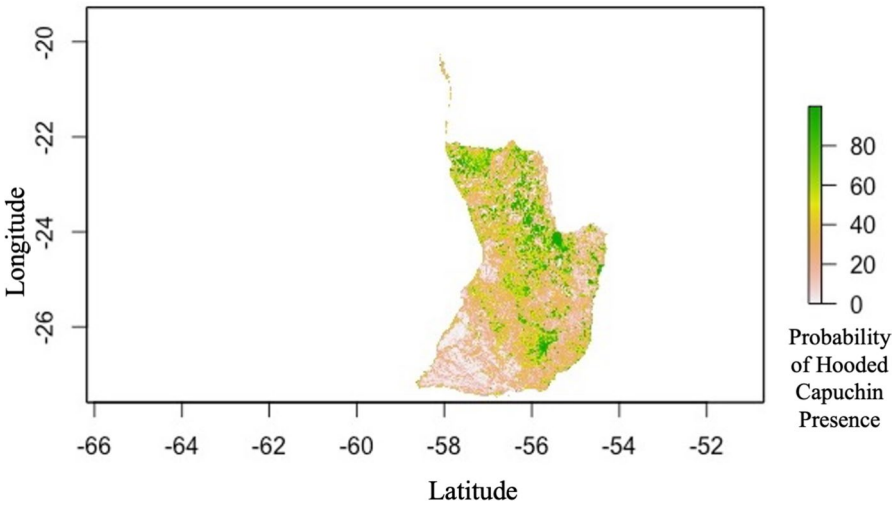

Fig. 4 Predicted probability of hooded capuchin monkey (*Sapajus cay*) presence given the proportion of forest cover in a 2-×2-km grid cell in Paraguay in 2000 calculated from forest percent cover for each cell. That calculation is provided from the data from Global Forest Watch. Forest cover source: Hansen *et al*., 2013. We recorded presence and absence data opportunistically between January 2013 and March 2021.

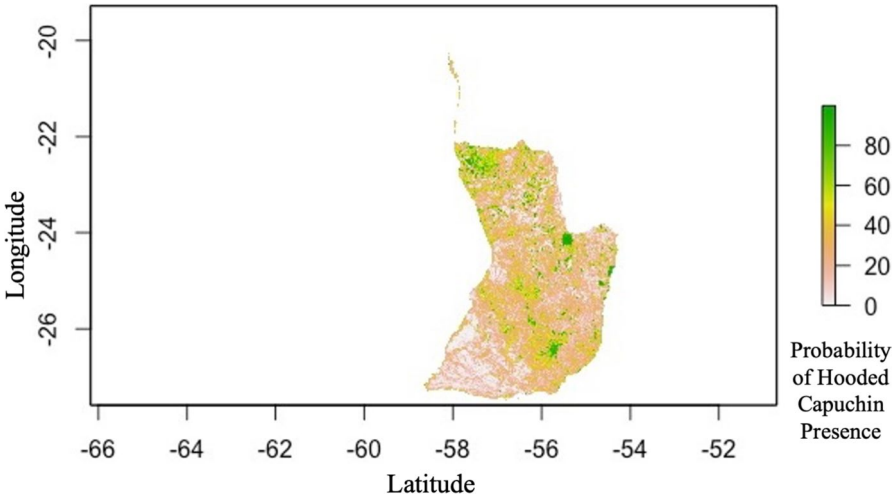

Fig. 5 Predicted probability of hooded capuchin monkey (*Sapajus cay*) presence given the proportion of forest cover in a 2-×2-km grid cell in Paraguay in 2019 calculated from forest percent cover for each cell. That calculation is provided from the data from Global Forest Watch. Forest cover source: Hansen *et al*., 2013. We recorded presence and absence data opportunistically between January 2013 and March 2021.

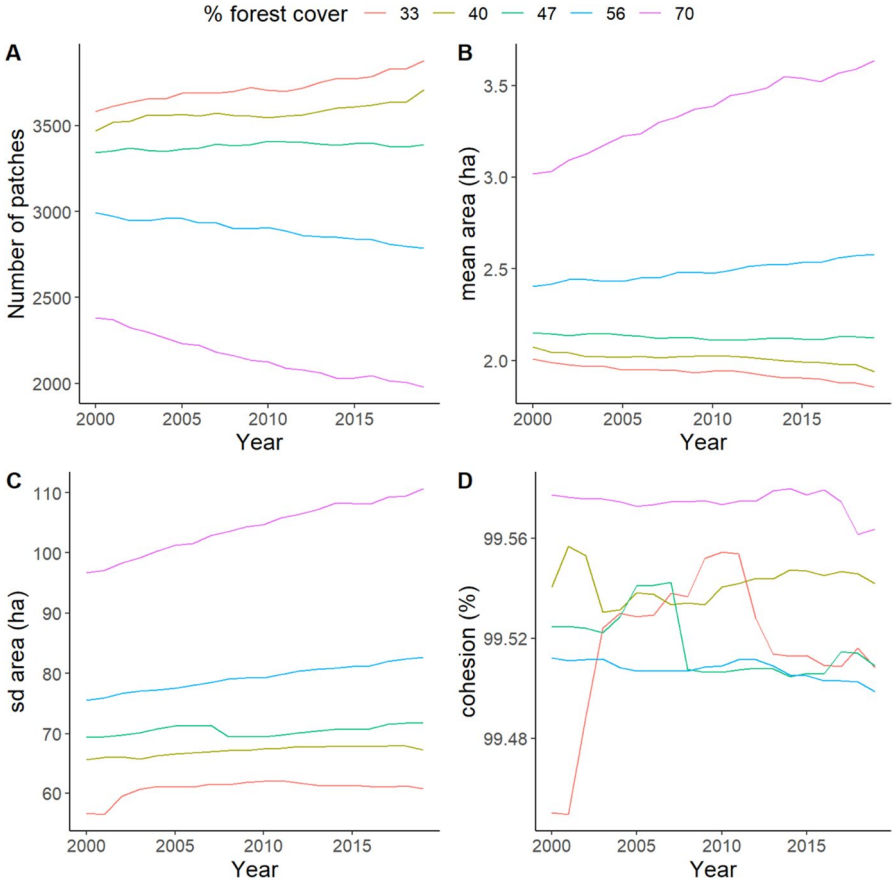

Fig. 6 **A)** Change in number of patches; **B)** Change in mean area of patches (in hectares); **C)** Change in standard deviation of patch area (hectares); **D)** Change in the degree (%) of clumping of patches in the landscape. All measured at different levels of habitat suitability across the IUCN hooded capuchin polygon between 2000 and 2019. (Patch – the isolated areas of forest remaining after visible human alteration of the landscape).

(Hesselbarth *et al*., 2019). We calculated eight measures of fragmentation level each year (cumulatively) from 2000 to 2019 at the five levels of habitat suitability (Table I; Riiters *et al*., 1996; Hesselbarth *et al*., 2019).

Results

Habitat Suitability Based on Forest Cover

The presence of capuchins was significantly associated with forest cover ($X^2_1 = 28.8$, n presence = 71, n absence = 283, $p < 0.00001$) (Fig. 1). Capuchins are 50% likely

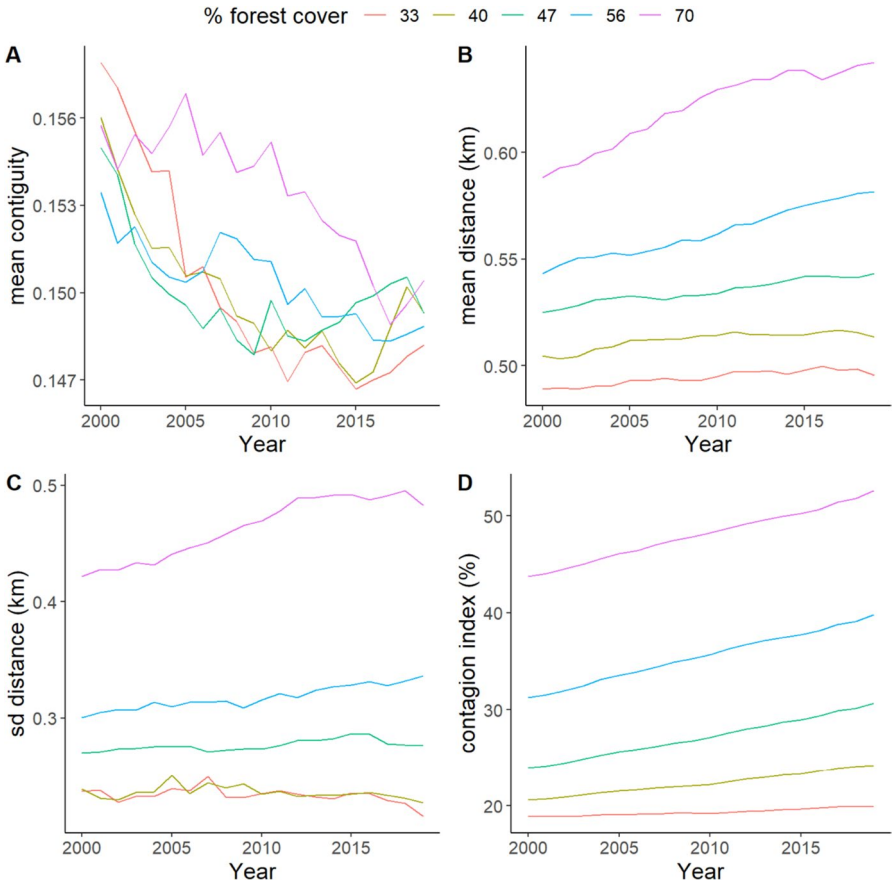

Fig. 7 **A)** Change in number and size of connections between patches; **B)** Change in distance (m) between patches; **C)** Change in standard deviation of distance between patches; **D)** Change in the degree (%) of clumping of patches in the landscape. All measured at different levels of habitat suitability across the IUCN hooded capuchin polygon between 2000 and 2019. (Patch – the isolated areas of forest remaining after visible human alteration of the landscape).

to be present when the area has 33% forest cover, 60% for 40% cover, 70% for 47% cover, 80% for 56% cover, and 90% for 70% cover.

Forest Loss and Remaining Suitable Habitat across Species Range

Between 2000 and 2019, forest cover declined at all levels of hooded capuchin habitat suitability across the official IUCN range map (Table II; Figs. 2 and 3). We used these thresholds in the calculations of forest cover loss.

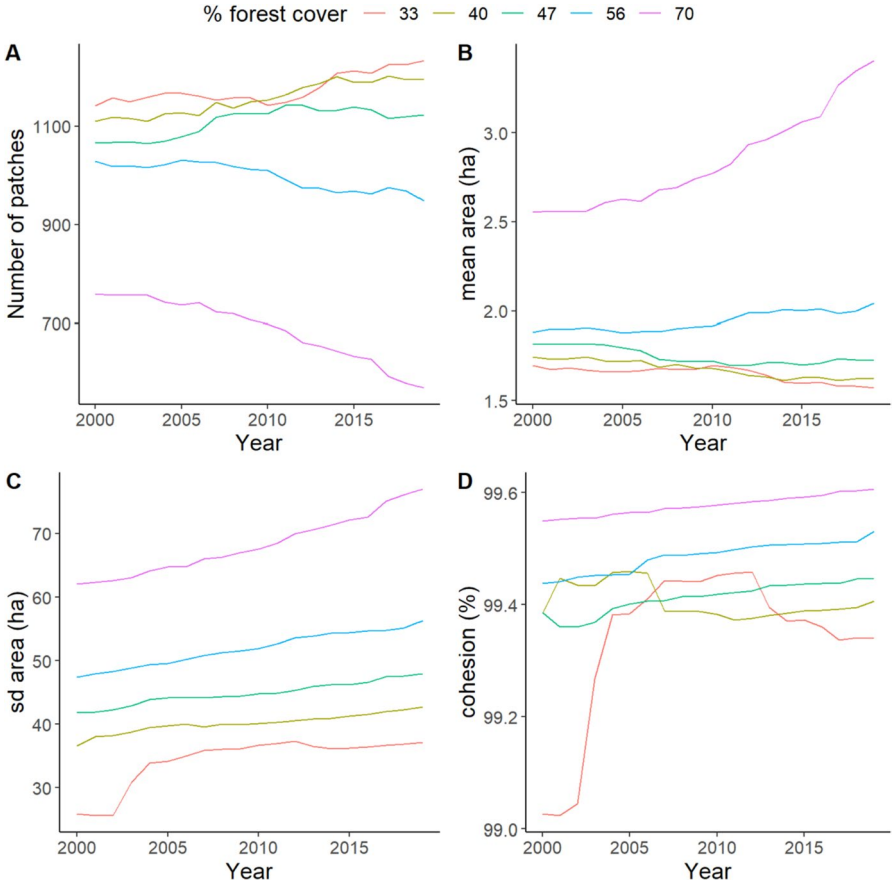

Fig. 8 **A)** Change in number of patches; **B)** Change in mean patch area (ha); **C)** Change in standard deviation of patch area (ha); **D)** Change in the degree (%) of clumping of patches in the landscape. All measured at different levels of habitat suitability across the hooded capuchin range in Paraguay between 2000 and 2019. (Patch – the isolated areas of forest remaining after visible human alteration of the landscape).

Forest Loss and Remaining Suitable Habitat in Paraguay

Across the Paraguayan section of the capuchins' range, overall forest cover declined at all levels of habitat suitability between 2000 and 2019 (Table III; Figs. 4 and 5). Over this period, a greater percentage of forest cover was lost at all levels of suitability in Paraguay than across the entire range.

Habitat Fragmentation across Species Range

During 2000–2019, around 17% of high suitability fragments (> 90% monkey presence probable) were lost (Fig. 6A). The number of patches where monkey presence probability is better than by chance (> 50%) has remained relatively

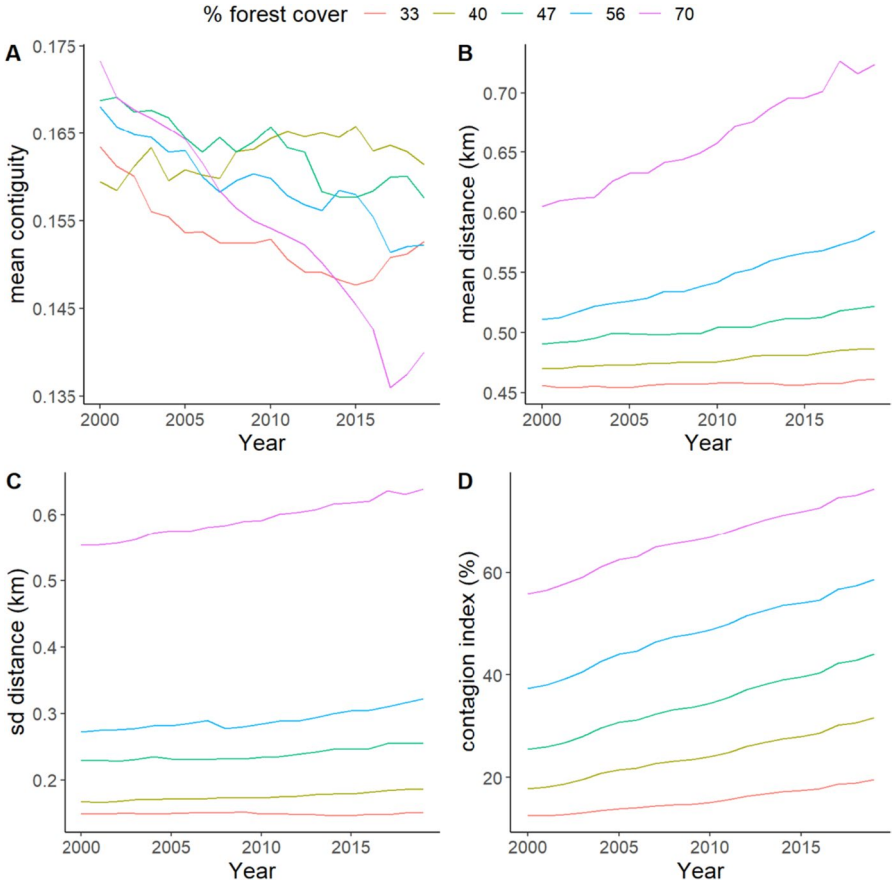

Fig. 9 **A)** Change in in the number and size of connections between similar patches; **B)** Change in mean distance (km) between patches; **C)** Change in standard deviation of distance (km) between similar patches; **D)** Change in the degree (%) of clumping of patches in the landscape. All measured at different levels of habitat suitability across the hooded capuchin range in Paraguay between 2000 and 2019. (Patch – the isolated areas of forest remaining after visible human alteration of the landscape).

stable but the number of low suitability patches (50% presence probability) has increased. The mean area of patches was found to increase from 2000 to 2019 (Fig. 6B), but the standard deviation also was found to increase (Fig. 6C). The Cohesion index, which demonstrates the level of dispersion of similar patch types in the environment, was variable at all levels of habitat suitability throughout the period. The lowest suitability (33%) and mid-suitability (47%) forest were the most variable with large increases, followed by decreases in cohesion between 2004 and 2008 (Fig. 6D).

The contiguity index showed a decreasing trend in the size and number of connections between fragments (Fig. 7A). The mean distance and standard deviation of distance between fragments of the same suitability increased between

high and medium suitability patches and decreased between lower suitability fragments (Fig. 7B and C). The Contagion index for all but the lowest level of forest cover increased over the study period (Fig. 7D).

Habitat Fragmentation in Paraguay

In Paraguay from 2000 to 2019, approximately 20% of high suitability forest fragments were lost (Fig. 8A). The number of high suitability patches decreased over the period, but the mean area of high suitability patches almost doubled. The mean patch area remained relatively consistent for the four lower levels of habitat suitability. The standard deviation of patch area followed a similar pattern with SD increasing for all habitat suitability levels (Fig. 8B and C). The Cohesion index remained relatively stable, with a slight increasing trend, for the mid and high suitability habitat but for the low suitability habitat was much more variable with greater increases until 2010 when a downward trend began to be observed (Fig. 8D).

Similar to the pattern observed across the whole range of the species, the contiguity index showed a decreasing trend in the size and number of connections between fragments at all levels of habitat suitability. However, for mid and high suitability forest patches the trend reversed drastically around 2018 and the contiguity values increased. For the lowest suitability habitat levels, the contiguity values also increased in 2018 (Fig. 9A). Both the mean distance and standard deviation of distance between patches of similar suitability remained constant at lowest levels of habitat suitability throughout the period. The mean distance between high suitability patches increased until 2018 when a decrease was observed, followed by a slight increase the following year (Fig. 9B and C). The Contagion index showed that an increasing trend for all habitat suitability levels (similar to that observed across the whole range) (Fig. 9D).

Discussion

Habitat Suitability

The habitat suitability GLM showed model predictions were consistent with an independent fine-scale species distribution model which relied on richer data available at a smaller scale associated with environmental features (Smith & Lusseau, 2022). Cells (area of 4 km^2) with below 33% forest cover had probability of capuchin presence no better than by chance. Few data are available for other species of capuchin, but this shows that this species, despite being a forest obligate (Smith & Lusseau, 2022), can probably adapt to the loss of significant forest cover (~63%). However, capuchin presence becomes most probable between 70 and 100% forest cover, indicating that ideal habitat for this species is a more intact, less degraded forest (Fig. 1). Habitat suitability for the Ecuadorian capuchin (*Cebus albifrons aequatorialis*) plateaus between 25 and 100% forest cover (Campos & Jack, 2013). For the bearded capuchin (*Sapajus libidinosus*), the most important driver of presence is green vegetation cover, and the monkeys were most likely to occur in areas

with vegetation coverage of approximately 50% (Howard *et al*., 2012). These data from closely related species contradict the 2021 IUCN hooded capuchin assessment that concluded that the hooded capuchin is more adaptable than closely related species (Rímoli *et al*., 2021). While the capuchin can be found in areas with marginal habitat (< 33% forest cover), further studies will be required to determine population viability in these areas.

The IUCN range polygon has historically overestimated EOO of the capuchin in Paraguay as the distribution map extends to the southwest corner of the country. However, there are no confirmed records of the capuchin in Ñeembucú department (Smith *et al*., 2021), and the results indicated that habitat in this part of the country (humid Chaco, Ñeembucú Wetland Complex and Mesopotamian grasslands) is highly unsuitable for the capuchins (Figs. 2, 3, 4, 5). We recommend that this area (at least the Ñeembucú department, 12,147 km^2) be removed from the official range map.

Whole Range

Expanding these data to examine the whole, currently accepted range of the hooded capuchin must be taken with one main caveat. The habitat requirements calculated for this species are based solely on the information available from Paraguay. This species is found throughout several different habitat types through its range, including pampas forest in Bolivia, Yungas in Argentina, and Cerrado, Atlantic Forest, and Pantanal in Brazil. Therefore, extrapolating from the data collected in Paraguay may not provide the best insight into the requirements of this species in different habitat types.

While taking this caveat into account, the data available for this species are so limited and out of date that it is worth considering this new information. Between 2000 and 2019, 23.23% (37,532 km^2) of highly suitable forest was lost across the full range of the species. While the area of remaining forest remains above the 20,000 km^2 threshold for the lowest threatened category of Vulnerable, the area still lost highly suitable forest at a rate of 1975.4 km^2 per year.

The loss of the high suitability forest is not the only issue. The fragmentation indices show that the habitat has been increasingly fragmenting. During the 19-year period, approximately 17% of high suitability habitat patches were lost; however, the mean area and standard deviation of the area of the patches was found to increase. This is an indication that smaller fragments were being completely cleared while larger areas were becoming more fragmented, increasing the mean area. The distance between fragments (at all levels of suitability) increased every year, and the connectedness of fragments decreased, potentially showing patches shrinking away from each other as they are degraded. How clumped the fragments were in the landscape increased over all levels of suitability, potentially indicating that larger areas were being split into multiple fragments, hence increasing the number of fragments yet also increasing the clumped spread of fragments in the landscape. The downward trend in forest continuity at all suitability levels is another indication of increasing fragmentation.

Paraguay

The scale of the forest loss and fragmentation in Paraguay is drastic, especially when it is taken into consideration that, for 15 of the 19 years being examined in this study, it was illegal to transform or clear BAAPA in Paraguay under the Zero-Deforestation Law (*Ley 2524/04*) (Da Ponte *et al*., 2017a, b). The loss of forest at all levels of habitat suitability was higher in Paraguay than across the whole range, with 58.4% (13,148 km^2) of highly suitable fragments being lost.

During the 19-year period, approximately 20% of high suitability forest patches were lost, higher than across the total range and coinciding with increases in the number of all classes of lower suitability patches. The mean area also increased following the pattern observed for the total range, indicating that larger fragments were being broken into small ones while small fragments were being cleared completely. This is an indication that the amount of forest remaining was so low, with so many smaller fragments having been totally cleared that large areas of high suitability patches were being degraded and cleared, rather than just fragmented. One of the biggest threats to the BAAPA in Paraguay are illegal settlements. Those often are created by people entering deep into a forest patch and clearing from the inside out, rather than degrading the forest edges, to evade detection. This leads to larger patches being broken into smaller areas.

The mean distance between high suitability patches increased until 2018, demonstrating that until this point larger patches may have been being degraded from the edges, increasing the distance between them. After 2018, these patches were being broken into smaller fragments, causing a decrease in the mean distance between these patches. For all habitat suitability levels, the contiguity showed a decreasing trend. For the other fragmentation indices, this may indicate that larger patches are being broken into smaller ones but that they have not yet been degraded enough to remove the connections between them. The degree of clumping of similar patches in the landscape also showed the same pattern of increasing slowly across all suitability levels. This, when taken in context with the increasing mean area of patches, may indicate that smaller forest patches are being completely cleared, leaving only larger areas, with more continuity, intact. Together the fragmentation indices demonstrate that the landscape is becoming more characterized by fewer, but larger, fragments of lower-quality forest.

Implications for Conservation

The results unequivocally show that suitable habitat for hooded capuchin monkeys is decreasing both across the full extent of the species range and particularly rapidly within Paraguay. The remaining habitat is being fragmented and degraded, and the distance between fragments increasing, raising questions about the ability for the species to colonize fragments, which could increase the risk of local extinction (Arroyo-Rodríguez *et al*., 2008; Estrada & Coates-Estrada, 1996; Hanski, 1999). Increasing isolation of fragments can inhibit dispersal and increase the risk of inbreeding (Camara and Mittermeier, 1984; Mota *et al*., 2018). Decreasing area of fragments may affect the ability of the area to support a population of primates due

to decreases in resources causing groups to vanish from smaller fragments (Mota *et al*., 2018; Rylands & Keuroghlian, 1988).

At a national level in Paraguay, we recommend that the capuchin be classified as Vulnerable under criterion B1, B(bi), B(ii), and B(iii). If the AOH of a species should act as the upper limit of the EOO (Brooks *et al*., 2019), then even with areas of 56% forest cover, the EOO falls below the < 20,000 km^2 threshold. In addition, the extreme levels of habitat loss and fragmentation indicates ongoing threats to the survival of the species in the country, particularly due to the worsening of the situation after the data we used in this study were collected. From 2019–2021, San Rafael/Tekoha Guasu, the largest and most important patch of BAAPA in Paraguay, was annually ravaged by fires. In October 2020 alone, approximately 33,000 ha of the patch was destroyed by fire. In May 2021, 12 separate, illegal settlements were recorded encroaching into the interior of the park. One of these settlements cleared 1,300 ha of forest in 3 weeks (Hostettler, personal communication, 2021).

At the species range level, our results would support a reclassification of the species as Near Threatened under criterion B1, B(bi), B(ii), and B(iii). Data available in other parts of the range showed that our predictions were conservative. The analyses that we present in this study were used along with this additional data, and the capuchin was classified as Vulnerable at a global level in 2022 (Rímoli *et al*., 2022). This was the first time that the species had been included in one of the IUCN Threatened categories and an important example of how understudied species can "fly under the radar" if they have a large geographic range in which more regional conservation dynamics are not fully understood or taken into account.

Practical Application for Hooded Capuchin Conservation

The threats to the Paraguayan BAAPA, and, therefore, to the hooded capuchin in the country, are grave and need to be urgently addressed before it is too late. It is essential that conservation of the remaining forest be combined with reforestation efforts focused on reconnecting smaller fragments to secure the long-term future of the capuchin. Paraguayans support the conservation of the hooded capuchin and believe that it is important for Paraguay (Smith *et al*., 2016, 2018b). The hooded capuchin is both a suitable flagship species and umbrella species for BAAPA conservation and restoration in Paraguay and raising its national Red List category to match the new global status of Vulnerable is crucial to push for more local conservation measures. The behavioural flexibility of the species (Smith, 2021; Smith & Lusseau, 2022; Smith *et al*., 2018a, 2022) provides an opportunity to implement reforestation of native tree species combined with cash crop species, such as slash pines (*Pinus elliotii*) and yerba mate *(Ilex paraguayensis*). Other species of capuchin respond favorably to a habitat matrix that includes forestry and crop, because it can facilitate movement between fragments while providing an alternate food source (Arroyo-Rodríguez *et al*., 2013b; Dunning *et al*., 1992; Hendges *et al*., 2017) Because the monkeys can survive in anthropogenically altered habitats, provided that a minimum amount of forest cover remains, and have been shown to use pine plantations for foraging and sleeping (Smith, 2021; Smith *et al*., 2018a, 2022), this approach would

have benefits for the monkeys while providing financial benefits for the communities whose livelihoods are tied to the use of the land required for the species, helping to reduce the pressure on the native forest.

Importance of Regional Data in IUCN Assessments of Primates

The results demonstrate the importance of smaller scale assessments when dealing with a wide-ranging species. When a species crosses political boundaries, it is unlikely that the threats it faces in one area will be the same across the range due to differences in history, cultures, laws, and social issues in different countries. The situation in terms of habitat loss, degradation, and fragmentation is very different at the whole range scale than it is within Paraguay. Because habitat loss is impacted by political and economic factors (Estrada, 2015; Fearnside, 1987), it is important to understand the drivers at a national level. Every country has different laws regarding implementations of international environmental commitments as well as different degrees of effectiveness of enforcement. Although the Red List assessments themselves are robust, the way in which the threats facing a species are considered, and often ranked in terms of importance during the assessments, lacks the rigour of the rest of the assessment, often being solely dependent on the opinion of an expert or workshop attendees (Cassini, 2011; Hayward, 2009). For example, the 2021 assessment of the hooded capuchin states "*In Paraguay, there are no major threats*" (Rímoli *et al*., 2021), despite the well-documented deforestation (Da Ponte *et al*., 2017a, b), and the only evidence to support this statement is from work that was performed in 1982 (Stallings, 1985) when pressures to deforest were significantly different. With more than 75% of primate species thought to be experiencing population declines (Estrada *et al*., 2017), primatologists must consider trends from throughout the region when evaluating extinction risks.

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Authors Contribution RLS and DL designed the methodology; RLS collected the data; RLS and DL analysed the data; RLS and DL wrote of the manuscript. Both authors gave final approval for publication.

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